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THE CONDITIONS REQUIRED FOR THE MAINTENANCE OF BINOCULARITY IN THE KITTEN'S VISUAL CORTEX

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SUMMARY

1. In young kittens, cortical neurones, which are usually binocularly driven, have their binocularity reduced if one eye is covered, or if the eyes are made strabismic or alternately occluded. Some of the factors causing these changes were analysed.

2. If the contrast of one retinal image is abolished with no difference in mean illumination, the input from that eye is virtually lost.

3. If one eye merely has its mean retinal illumination attenuated, that eye does not specifically lose its influence in the cortex, although there is a reduction in the proportion of binocular units. This change might partly be due to a difference in the *timing* of signals from the two eyes but is more likely to be caused by a difference in the *strength* of the discharges.

4. There is little change in binocularity if one image is dimmed but contrast is absent from both.

5. If contours of very different orientation fall simultaneously on corresponding retinal regions, binocularity breaks down, as in the case of strabismus or when different patterns are presented to the two eyes. But as long as the patterns on corresponding retinal points have similar orientation, even if the visual axes are misaligned, binocularity can be maintained.

6. If the eyes are not stimulated simultaneously, binocularity is reduced, even if the contours falling on the two retinae (at different times) are identical.

7. Roughly simultaneous stimulation, with roughly congruent patterns on the two receptive fields, are needed for the upkeep of binocular connexions on to cortical cells.

INTRODUCTION

It is now well established that at the time when a kitten first opens its eyes, the majority of excitable neurones in the visual cortex already have convergent excitatory input from both retinae: moreover this binocularity survives even if both eyes are deprived of patterned visual experience by suturing the lids or keeping the kitten in total darkness (Hubel & Wiesel, 1963; Wiesel & Hubel, 1965; Pettigrew, 1974; Blakemore & Van Sluyters, 1975). The pattern of neurones dominated sequentially by one eye and then the other, recorded during oblique penetrations in the cortex of adult cats, which is taken to represent a system of 'ocular dominance columns', is also present in very young kittens with no previous visual experience (Blakemore & Van Sluyters, 1975; Blakemore, Van Sluyters & Movshon, 1976).

However, this situation is a fragile one during the first few weeks of a kitten's life. A number of manipulations that interfere with normal binocular vision cause a rapid break-down of cortical binocularity. Covering one eye, by suturing together the lids, results in a virtual loss of functional input from that eye at the visual cortex: neurones can almost always be excited only from the experienced eye (Wiesel & Hubel, 1963). This profound change can occur after just a few hours of monocular deprivation (Pettigrew & Garey, 1974; Olson & Freeman, 1975; Peck & Blakemore, 1975) and seems to be accompanied by rapid shrinkage of the physiologically-identified 'columns' dominated by the deprived eye (Movshon, 1975). There is anatomical evidence that the shift in ocular dominance is associated with a partial loss of afferent axons originating in the deprived laminae of the lateral geniculate nucleus (Thorpe & Blakemore, 1975).

Binocularity can also be degraded by treatment less severe than the deprivation of one eye. Alternate occlusion of the two eyes (so that they both see but at different times), or the induction of an artificial strabismus or rotation of one eye (so that they each see different things at the same time), leads to a reduction in the number of binocularly driven neurones and an exaggerated pattern of physiological ocular dominance columns (Hubel & Wiesel, 1965; Blakemore, Van Sluyters, Peck & Hein, 1975). Results like these led Hubel & Wiesel (1970) to suggest that there is 'binocular competition' between the geniculostriate axons from the right-eye and left-eye laminae of the lateral geniculate nucleus at their synaptic input to cortical cells. Synchronous and correlated signals in the two pathways might be necessary for the maintenance of binocular input on to individual neurones. The concept of binocular competition is strongly supported by Sherman, Guillery, Kaas & Sanderson's (1974) finding that if a retinal lesion is made in the open eye of a monocularly deprived kitten, cells can still be excited through the deprived eye in the region of the cortex corresponding to the retinal lesion, where the competitive interaction is thus removed.

The present study is concerned with defining the precise factors that lead to a break-down in binocularity in the visual cortex and hence with specifying more exactly just what conditions must be fulfilled in order for binocular input to be preserved in the normal kitten.

METHODS

All the techniques for recording from the visual cortex, correcting the optics of the eyes, plotting receptive fields and reconstructing penetrations histologically have been described in detail before, together with the methods for housing kittens in a darkroom except for occasional exposure to a normal visual environment or to special patterns displayed inside large cylindrical chambers (Blakemore & Van Sluyters, 1975). The strategy for sampling cells (Blakemore & Van Sluyters, 1975) involved making a single long penetration starting on the medial side of the crest of the post-lateral gyrus and extending far down its medial bank (Pl. 1). This ensured that the track mainly ran obliquely through the palisades of cortical cell bodies, and that rather few cells were recorded from the deep layers of the very central representation where simple cells tend to be predominantly monocularly driven, even in normal adult cats (Albus, 1975*a*). All receptive fields were centred within 10 deg of the area centralis.

Goggles

Some animals received their only visual experience wearing goggles that permitted separate control of the input to each eye. The lightweight goggles were made of black Perspex and were held securely to the head by an elasticated fabric surround: they seemed to cause no discomfort, since kittens wearing them actively explored their surroundings and played with their colleagues quite naturally, and did not attempt to remove the goggles after the first one or two sessions. In some goggles, various inserts could be fitted into the apertures in front of the eyes. These inserts were:

(1) a totally opaque disk for complete occlusion;

(2) a disk of translucent opal Perspex giving a reduction in flux of 0·25 log units, when trans-illuminated with omnidirectional light, and virtually total abolition of contrast;

(3) various transparent neutral density filters sandwiched between thin transparent Perspex.

With these goggles the field of view of each eye was restricted to about 90 deg in diameter and it included the entire normal binocular field except for a narrow crescent corresponding to the extreme temporal retina of each eye.

Other goggles contained powerful bi-convex lenses (focal length 25 mm) in front of both eyes. A short tube cemented in front of each lens held a transparency of a pattern of stripes at such a position that its optical distance from the kitten, viewing through the lens, was about 50 cm. The total field covered by the stripes was about 55 deg in diameter and the widths of the individual bars of the grating ranged from about 0·25 to about 4 deg. A thin diffusing screen beyond the transparency ensured even trans-illumination of the grating when the kitten wore these goggles in a normal lighted room.

RESULTS

The experiments deal with two main questions. Firstly, are the effects of monocular deprivation by lid suture due to the reduction in mean retinal illumination in the deprived eye, or to the virtual abolition of contrast in its retinal image? Secondly, is the loss of binocularity seen after alternating monocular occlusion and strabismus simply caused by a failure of the two receptive fields of each binocularly driven cell to receive exactly simultaneous stimulation, whatever the nature of the stimulus, or by the fact that the patterns received on the two receptive fields at the same or different times are very unlikely to be similar in shape? The results are based on a qualitative study of the properties of 687 cortical cells from twenty kittens. In every case, recordings were taken from the right hemisphere.

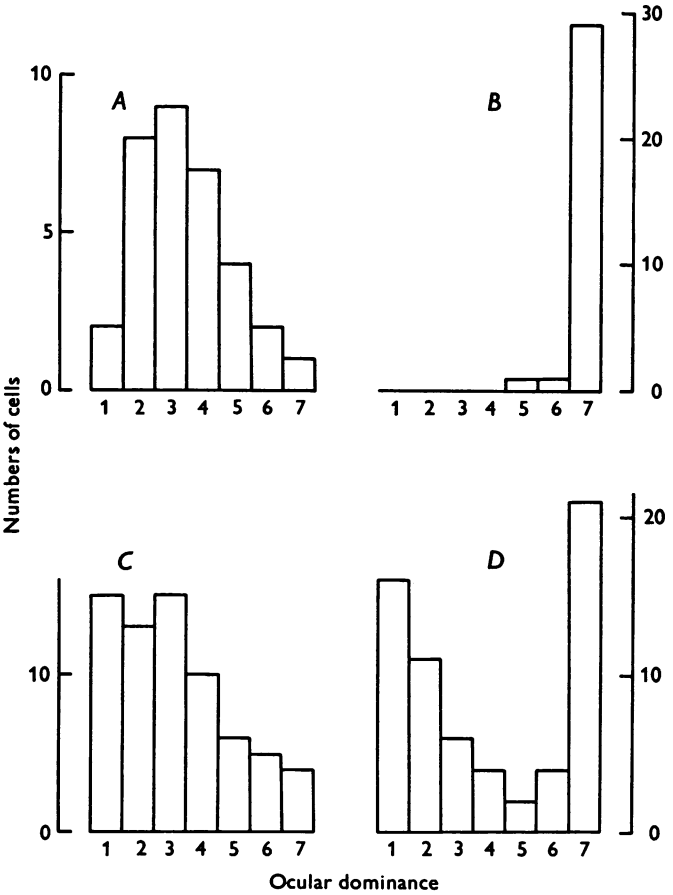
A control experiment

Since the goggles themselves slightly restricted the visual field, it seemed possible that they alone might have caused some reduction in the binocularity of cortical cells, particularly since the pupillary axes appear very divergent when the eyes first open (Sherman, 1972) and they only gradually adopt their normal straight-ahead position. One kitten (K336) was therefore reared in the dark-room from before the time of natural eye-opening, like all the other animals in this series, and received exposure for an hour or two each day, in the normally illuminated colony room, wearing the goggles alone with no insert in front of either eye. It had a total exposure of 46 h between the ages of 3 and 8 weeks, a regime similar to that used for all the experimental animals, listed in Table 1. This animal therefore also served as a control for any possible deleterious consequences of this rather limited total period of visual experience.

The recordings, taken at 9 weeks, in fact showed the cortex to be completely normal with respect to both binocularity and the general properties of the receptive fields, all of which were orientation selective, except for one pure direction selective unit (Blakemore & Van Sluyters, 1975). The results are shown in Text-fig. 1*A* in the form of an ocular dominance histogram, of the type introduced by Hubel & Wiesel (1962). The seven classes describe the relative influence of the two eyes on cortical cells, ranging from units that are monocularly driven only from the contralateral eye (group 1) through cells that are equally driven from each eye (group 4), to neurones that are only excitable through the ipsilateral eye (group 7). In this case, as for all other animals in this series,

TABLE 1. Each heading gives a brief description of the experimental procedure. All animals exposed wearing goggles or in striped environments were housed in the dark-room. The columns show, in order, the kitten code number, the age during the experimental exposure, the total duration of visual experience, the age at recording and the Figures that illustrate the results

Control: occasional normal visual experience wearing empty goggles				
K336	3–8 weeks	46 h	9 weeks	Text-fig. 1*A*
Goggles: opal diffuser over left eye, matched neutral density filter over right				
K296	3–7 weeks	37 h	8½ weeks	Text-fig. 1*B*
Goggles: neutral density filter over left eye				
1 *log unit filter*				
K294	3–7 weeks	39 h	9 weeks	Text-fig. 1*C*
K315	3–7 weeks	49 h	9 weeks	
2 *log unit filter*				
K329	3–8 weeks	50 h	10 weeks	Text-fig. 1*D*
K368	3–5 weeks	33 h	7 weeks	Text-fig. 2
Goggles: opal diffuser over both eyes, plus neutral density filter over left				
1 *log unit filter*				
K301	4–7½ weeks	30 h	8 weeks	Text-fig. 3*A*
2 *log unit filter*				
K308	3–7 weeks	40 h	7½ weeks	Text-fig. 3*B*
Control: surgical divergent strabismus; normal environment				
K91	2–8 weeks	Continuous	8 weeks	Text-fig. 4*A*
Control: alternating occlusion; normal environment				
K292	3–9 weeks	34 h each eye	10 weeks	Text-fig. 4*B*
Stripe-reared; no surgical strabismus				
K8	3½–5½ weeks	33 h	15 weeks	Text-fig. 5*A*
K189	4–6 weeks	27 h	7½ weeks	
Stripe-reared with surgical divergent strabismus				
K52	3–8½ weeks	51 h	9 weeks	Text-fig. 5*B*
K65	3½–8 weeks	58 h	9 weeks	
Goggles: vertical contours to left eye, horizontal to right				
K309	4½–12 weeks	99 h	13 weeks	Text-figs. 5*C* and 6
Goggles: alternate occlusion; vertical contours to left eye, horizontal to right				
K307	3–10½ weeks	45 h	18½ weeks	Text-fig. 7*A*
Both eyes open; alternating exposure to horizontal and vertical				
K52	3–8½ weeks	51 h each orientation	9 weeks	Text-fig. 7*B*
K20	3–8½ weeks	50 h each orientation	9 weeks	
Goggles: alternate occlusion viewing stripes of one orientation				
K291	3–9 weeks	34 h each eye	10 weeks	Text-fig. 8*A*
K293	3–9 weeks	34 h each eye	10 weeks	Text-fig. 8*B*



Text-fig. 1. Four ocular dominance histograms in which the relative influence of the two eyes in exciting cortical neurones is classified into the seven groups of Hubel & Wiesel (1962). Cells in group 1 are monocularly driven by the contralateral eye, those in group 7 by the ipsilateral eye. Cells in all other groups are binocularly driven, with a spectrum of dominance from those excited much more strongly by contralateral than ipsilateral (group 2) to those driven much more powerfully by ipsilateral than contralateral (group 6). *A*, results for one kitten (K336) that had 46 h of visual experience wearing empty goggles that merely slightly restricted the field of view of each eye. *B*, K296: exposed to a normal environment wearing goggles with a translucent diffuser in front of the contralateral eye and a matched, transparent neutral density filter over the ipsilateral eye. *C*, K294 and K315: pooled results from two animals reared with a 1 log unit neutral density filter over the contralateral eye. *D*, K329 and K368: two animals that wore goggles containing a 2 log unit neutral density filter in front of the contralateral eye.

the recordings were taken from the right hemisphere. The histogram is indistinguishable from that for normal cats (Hubel & Wiesel, 1962; Blakemore & Pettigrew, 1970), with only three out of thirty-three cells (9 %) monocularly driven, and a tendency towards over-all dominance by the contralateral eye.

Monocular deprivation

Unilateral attenuation of contrast with matched retinal illumination

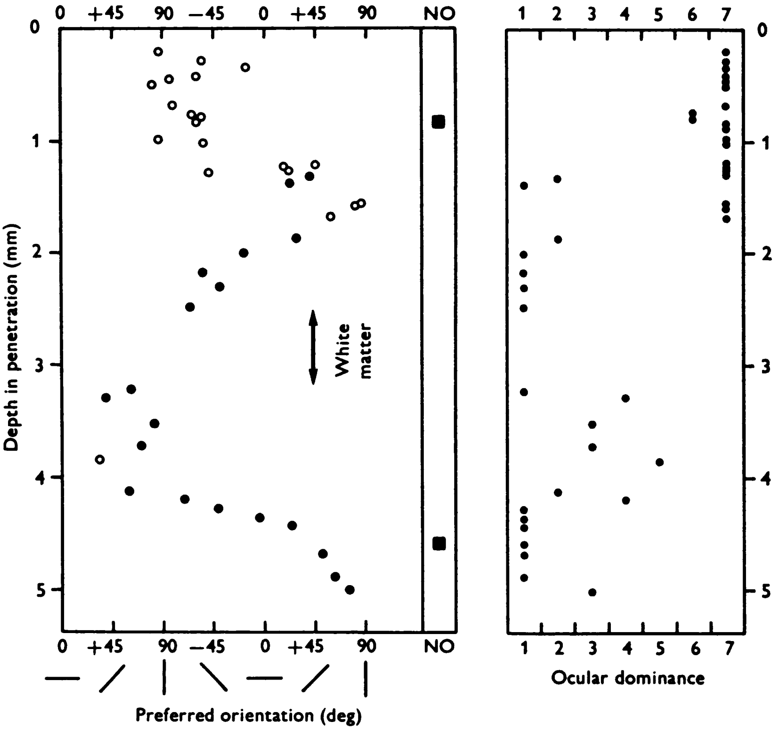
One kitten (K296) was housed in the dark from before natural lid opening, and, between the ages of 3 and 7 weeks, it was occasionally brought out into the cat colony room wearing goggles containing a translucent opal diffuser over the left eye and a transparent 0·25 log unit neutral density filter over the right eye (giving a reduction in mean retinal illumination the same as that produced by the diffuser when trans-illuminated with omni-directional light). The kitten received a total of 37 h of visual experience in the normally illuminated room wearing these goggles, and recordings were taken from the cortex at 8½ weeks (Table 1).

The ocular dominance histogram is shown in Text-fig. 1*B*: all cells were completely or strongly dominated by the ipsilateral (right) eye, which had seen through the neutral density filter. The left eye, which received similar mean retinal illumination but little or no pattern, lost its influence just as completely as if it had been simply deprived by lid suture in the normal manner.

Unilateral reduction in retinal illumination with contrast preserved

Four kittens were reared in the darkroom with occasional exposure to a normal environment wearing goggles containing only a transparent neutral density filter over the left eye with no insert in the right eye's aperture.

The results are shown in Text-fig. 1*C*, for K294 and K315, whose filter had a density of 1 log unit, and Text-fig. 1*D*, for K329 and K368, who saw through a 2 log unit filter. There was no obvious difference between the ocular dominance histograms for the two members of each pair, so they have been pooled. The first, and most immediately relevant conclusion, is that there is certainly no tendency for the filtered left eye (contralateral) to lose its influence in the cortex. The histogram for the animals that wore a 1 log unit filter over the left eye is probably, within the limitations of the sampling method, not clearly distinguishable from that of normal cats. There are, however, nineteen monocularly driven cells out of sixty-eight (28 %), and this is rather higher than would be expected in a normal animal when using the same angle of penetration and sampling procedure. The suspicion that binocularity has been reduced in



Text-fig. 2. Two schematic reconstructions of the electrode penetration in K368, an animal that wore a 2 log unit neutral density filter over the contralateral eye (see Text-fig. 1*D*), causing a break-down in binocularity in the visual cortex. (The photomicrograph in Pl. 1*A* shows the course of the penetration, down the medial bank of the post-lateral gyrus.) In these two reconstructions, the ordinates plot the depth of each isolated unit below the surface of the cortex. On the left the abscissa shows the preferred orientation: for each cell the preferred angle in the dominant eye is plotted as a circle, unfilled for the right eye, filled for the left. Over the first 1 mm of the penetration, angled approximately parallel to the radial palisades of cortical cell bodies, the preferred orientations do not change dramatically, but in the rest of the penetration, passing more nearly parallel to the surface, down the medial bank, there is a more continuous shift in angle from one cell to the next, with occasional reversals in the sequence. In the narrow column labelled 'NO', filled squares are used to plot the depths of two cells with non-oriented receptive fields. A region of the penetration during which no cellular action potentials were isolated, because the electrode was passing through the fibre layer under the cortex (see Pl. 1*A*), is marked 'White matter'. The second reconstruction, on the right, shows the ocular dominance groups for the same neurones. Note the emphasized pattern of ocular dominance columns with sudden shifts from groups of cells dominated by the ipsilateral (right) eye to groups driven mainly by the contralateral (left) eye.

this case is further substantiated by the result (Text-fig. 1*D*) from the animals that wore a unilateral 2 log unit filter: here, fully thirty-seven out of sixty-four cells (54%) are monocularly driven and the resulting histogram is very similar to that from a strabismic or alternately occluded kitten (Hubel & Wiesel, 1965). Still there is no evidence that the filtered eye has specifically lost its influence. Cells dominated by the filtered left (contralateral) eye are as common as those dominated by the right eye, within the error of the sampling procedure.

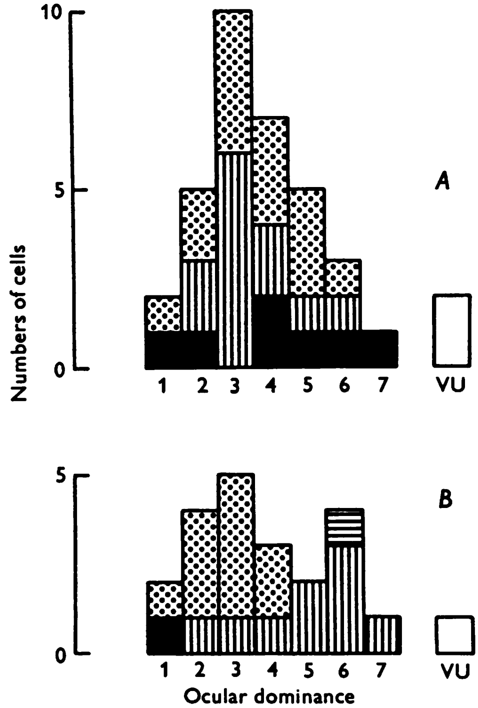
The columnar grouping of cells according to ocular dominance is emphasized in these animals, as it is in squinting kittens. The photomicrograph in Pl. 1*A* shows a coronal section through the post-lateral gyrus of the right hemisphere in K368, which was exposed with a 2 log unit filter over the left eye. An electrolytic lesion placed at the end of the penetration is marked 'L' and the course of the micro-electrode track (reconstructed from two other lesions, visible in neighbouring sections) is indicated by a continuous line.

This penetration is illustrated schematically in Text-fig. 2. In the first reconstruction, on the left, each point, plotted at the depth of a unit, shows its preferred orientation in the dominant eye (open symbols for the right, ipsilateral eye, filled for the left). The squares in the extra column headed 'NO' show the depths of two cells with non-oriented receptive fields. This schematic reconstruction of the penetration shows some regions in which orientation preference is quite similar for a number of neighbouring cells, with sudden shifts in preferred orientation from one group to the next, as originally described by Hubel & Wiesel (1962). In other places the sequential shifts in preferred orientation are much more rapid and continuous, like those often found in the striate cortex of monkey (Hubel & Wiesel, 1974) and cat (Albus, 1975*b*).

In the second reconstruction of the same penetration, the units are now plotted in columns that show the ocular dominance groups. There is very distinct regional aggregation of cells according to ocular dominance. This extreme exaggeration of ocular dominance columns is apparently invariably found in animals in which over-all binocularity is reduced, by strabismus, alternating monocular occlusion or some other experimental manipulation (Hubel &Wiesel, 1965; Blakemore & Van Sluyters, 1974*a*; Movshon & Blakemore, 1974; Movshon, 1976).

Unilateral reduction in retinal illumination with bilateral attenuation of contrast

Since alternating occlusion of the eyes is known to cause a break-down in binocularity it seems parsimonious to propose that the similar result seen in the animals reared with a neutral density filter over one eye is due to a difference in the *timing* of bursts of impulses reaching cortical neurones from the two eyes as patterns move across the retinae (Enroth-Cugell & Lennie, 1975). However, changes in background illumination also affect the *mean maintained discharge* of retinal ganglion cells (Barlow & Levick, 1969*a*) and alter the *evoked firing rate* produced by patterned stimulation (Barlow & Levick, 1969*b*). It is conceivable that these differences in the maintained or evoked *rates* of discharge from the two eyes cause the change in binocular interaction.



Text-fig. 3. Ocular dominance histograms for two animals only exposed to light when wearing goggles that contained translucent diffusers in front of *both* eyes but with an additional neutral density filter over the contralateral eye (*A*, 1 log unit; K301, *B*, 2 log units, K308). The blocks show the receptive field types for these cells, as plotted through the dominant eye: filled = orientation selective; vertically hatched = orientational bias; horizontally hatched = pure direction selective; stippled = non-oriented; the additional column labelled 'VU', with open blocks, represents visually unresponsive cells.

To test whether it is simply the difference in *maintained* discharge in the two retinae that causes the reduction in binocularity, two animals were reared with occasional exposure wearing goggles with opal Perspex diffusers in front of *both* eyes and, in addition, a neutral density filter in front of the left eye: 1 log unit for K301 and 2 log units for K308. Thus these animals received virtually no patterned retinal illumination but the mean illumination differed in the two eyes. They wore wide conical ruffs around their necks, which protruded in front of the goggles, preventing the animals from approaching objects very closely; this precluded the possibility of the animals experiencing large transient changes in retinal illumination by putting the apertures of the goggles in close contact with objects that might occlude or partly occlude one eye or the other.

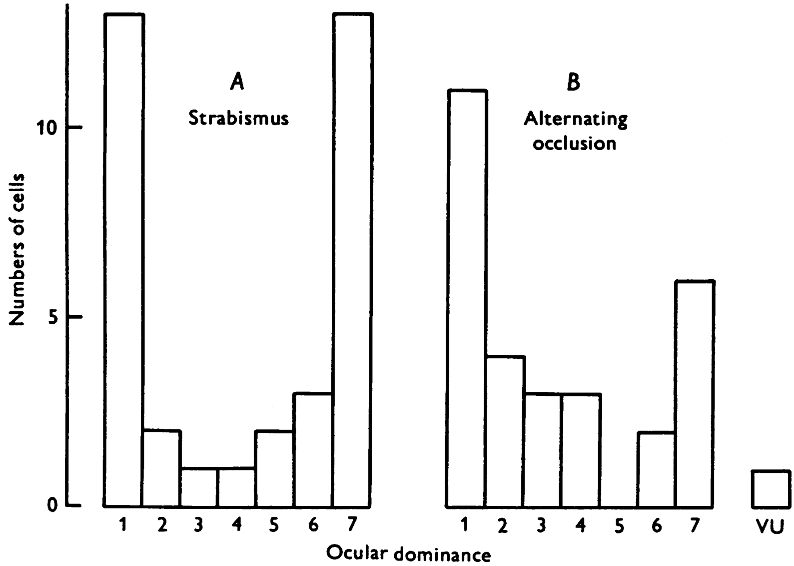
Text-fig. 3*A* shows the ocular dominance histogram for K301, Text-fig. 3*B* for K308. The most relevant observation is that binocularity is not obviously reduced in either animal. The percentage of monocularly driven cells was only 9% (three out of thirty-three) in K301 and 14% (three out of twenty-one) in K308. The blocks of the histogram also represent the receptive field types (as plotted through the dominant eye) for these cells, using the classification of Blakemore & Van Sluyters (1975). The few neurones (20%, seven out of thirty-five, in K301; 5%, one out of twenty-two, in K308) that were genuinely orientation selective, by the strict criteria of Pettigrew (1974), had the characteristics of simple cells (Hubel & Wiesel, 1962). More than one third of all cells had receptive fields with an orientational bias, often dependent simply on a preference for one axis of movement. A few neurones were pure direction selective or visually unresponsive, and the remainder, about 40% of the total, were non-oriented. All this confirms very closely Blakemore & Van Sluyters' (1975) previous description of receptive field properties in animals completely deprived of patterned visual experience.

The principal conclusion from this experiment is that unilateral reduction of retinal illumination does not cause an obvious break-down in cortical binocularity unless both eyes receive patterned retinal images (compare Text-figs. 1*C* and *D* with 2*A* and *B*). Therefore the main cause of the effect seen after simple monocular dimming is probably not the difference in maintained discharge in the two eyes. The question of whether it is more likely to be due to difference in the timing or the discharge frequency of evoked bursts will be taken up in the Discussion.

Strabismus and alternating occlusion

Control experiments

Two animals were used to confirm the effects of strabismus and alternating monocular occlusion first described by Hubel & Wiesel (1965). In one of the animals (K91), the right eye was made to deviate laterally by section of the medial rectus muscle at 2 weeks of age. The kitten was housed in the normal colony room until recording at 8 weeks, by which time, as shown in Text-fig. 4*A*, the majority of cortical neurones had become monocularly driven: fully 74% (twenty-six out of thirty-five) were in groups 1 and 7, with equal numbers in the two. Not surprisingly, there was very pronounced ocular dominance clustering during the penetration.

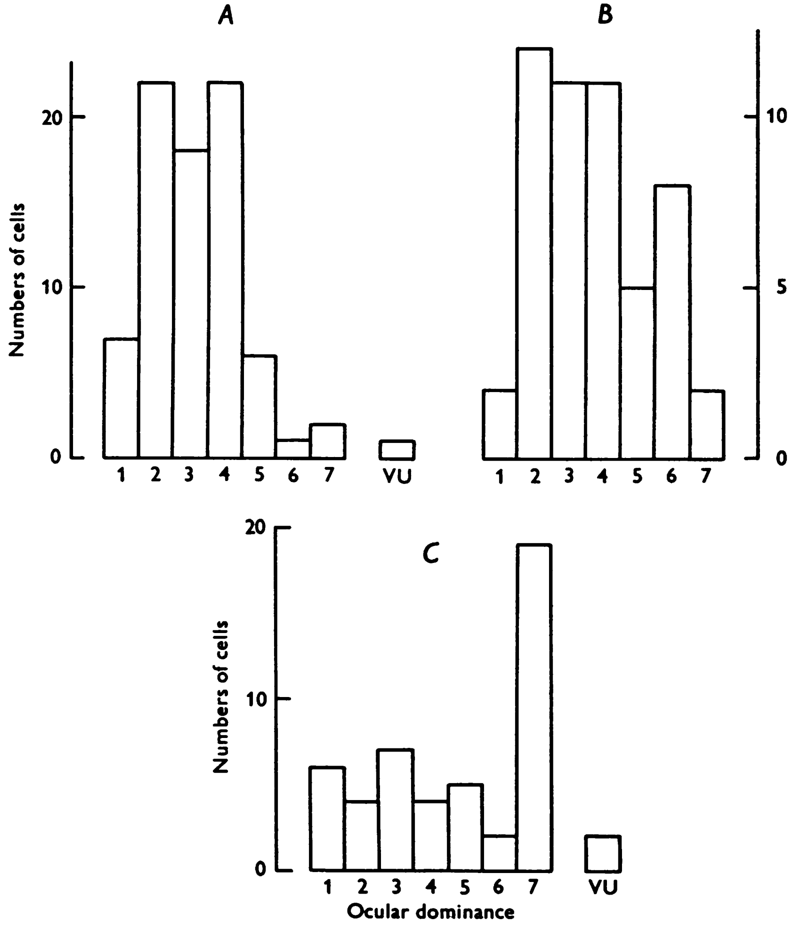


Text-fig. 4. Ocular dominance histograms for *A*, K91, an 8-week-old animal made artificially exotropic at 2 weeks; *B*, K292, an animal that was reared with alternate occlusion of the two eyes, each one seeing a normal environment for an hour at a time.

Equally orthodox was the result for the other control animal (K292), which was kept in the dark and brought out into the colony room wearing goggles with an opaque occluder over one eye. The occluder was shifted from one eye to the other between trials, so each eye was exposed alone, for an hour at a time, with a minimum gap of 2 h between exposures. This was continued between the ages of 3 and 9 weeks, until each eye separately had had 34 h of visual experience. The result, shown in Text-fig. 4*B*, illustrates the consequences of alternating monocular occlusion. The ocular dominance histogram was strongly biased in favour of monocular cells, just as after strabismus: 55% (eighteen out of thirty-three) of the visually responsive units were monocularly driven. (One was visually unresponsive.) This all confirms Hubel & Wiesel's (1965) earlier description.

The cause of monocularity after strabismus

The most obvious explanation for the loss of binocularity after strabismus is the failure of the eyes to view similar patterns on corresponding parts of the two retinae. Hence cortical neurones are deprived of *congruent* signals from the two eyes – signals concerning the same orientations of



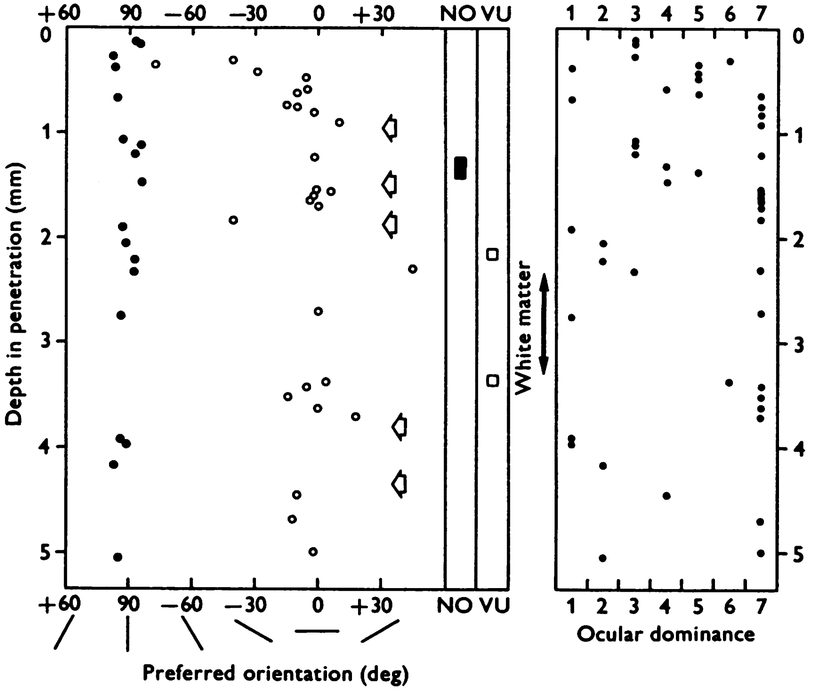
Text-fig. 5. *A*, pooled results for two animals reared in the dark but with occasional binocular exposure to striped environments, vertical for K8, horizontal for K189. *B*, results for two stripe-reared animals (vertical for K52, horizontal for K65) that were also made artificially exotropic before the exposure began (data of R. C. Van Sluyters and C. Blakemore). *C*, results for one kitten (K309) reared in the manner of Hirsch & Spinelli (1970) with visual experience restricted to vertical stripes in the left eye and horizontal in the right, viewed simultaneously as transparencies fixed in goggles.

contour. Conceivably, however, the mere deviation of one eye itself might somehow cause a change in the organization of the cortex, regardless of the images received by the two eyes.

Text-fig. 5 presents evidence that the former hypothesis is correct. Firstly, Text-fig. 5*A* and *B* show ocular dominance histograms for four kittens reared in environments of stripes, using the exposure apparatus described by Blakemore & Van Sluyters (1975). The two normal animals for Text-fig. 5*A* were exposed to a single orientation, vertical for K8, horizontal for K189, for a total of about 30 h, between about 4 and 6 weeks of age. These animals, which were members of a lengthy series of such experiments, were chosen because their period of exposure was similar to all the other animals discussed in this paper (Table 1). Their ocular dominance histograms were also quite typical of those for stripe reared animals: only 12% of all visually responsive units (nine out of seventy-eight) were monocularly driven. It should be said that we have, in this laboratory, occasionally seen clearly reduced binocularity in stripe-reared kittens, especially when the periodicity of the stripes was very regular (C. Blakemore, R. C. Van Sluyters and J. A. Movshon, in preparation), and also in animals exposed to patterns of sparsely scattered spots (Blakemore & Van Sluyters, 1975). But in the majority of stripe-reared animals, binocularity was quite normal. However, R. C. Van Sluyters and C. Blakemore (in preparation) noticed that such animals very often have considerably misaligned visual axes: thus, binocularity can survive in the presence of a 'natural' strabismus.

The two kittens whose results are shown in Text-fig. 5*B* were also reared in the dark room and occasionally exposed to vertical (K52) or horizontal (K65) stripes, for a total of about 55 h, but in addition they had an *artificial* divergent strabismus surgically induced before the exposure began. As already reported by Blakemore & Van Sluyters (1974*b*; and R. C. Van Sluyters & C. Blakemore, in preparation), these animals did not have dramatically reduced binocularity (12% monocular units; nine out of seventy-eight visually responsive cells). Apparently the spatial redundancy of a striped pattern may be adequate to ensure that, on average, roughly similar contours are present on the receptive fields of each binocularly driven cell, despite the misalignment of the visual axes: and this is sufficient to sustain binocularity.

In a normal visual environment the initially binocular neurones of a squinting kitten will usually find quite different contours on their receptive fields in the two eyes. This condition was mimicked in a reduced form in one animal (K309), whose results are shown in Text-fig. 5*C*. It was kept in the dark and periodically exposed in the manner of Hirsch & Spinelli (1970), wearing goggles that presented vertical contours to the left eye and horizontal to the right. The stripes, on photographic transparencies, were irregular in width and filled the whole of the 55° field of each eye when viewed through the high-power positive lenses mounted in the goggles. The distance between lenses and stripes was arranged so that an emmetropic eye would require about 2 D of accommodation to bring the pattern to focus. The high-contrast transparencies were transilluminated through diffusers in the ends of the goggles. Binocularity was much reduced in this animal, just as described by Hirsch & Spinelli (1970, 1971) and Stryker & Sherk (1975). 53 % of the visually responsive units were monocularly driven (twenty-five out of forty-seven) and there was a strong



Text-fig. 6. Schematic reconstructions of the penetration in K309 (see Text-fig. 5*C*) which was exposed simultaneously to vertical lines in the left eye, horizontal in the right. The conventions and arrangement are exactly as Text-fig. 2, except that the additional column headed 'VU' shows the positions of visually unresponsive cells, and the unfilled arrows indicate positions at which sudden shifts from dominance by the ipsilateral (right) to the contralateral (left) eye are accompanied by equally abrupt changes in receptive field orientation from horizontal to vertical, or vice versa. The actual penetration is shown in the micrograph of Pl. 1*B*. The cortical units recorded within the white matter had action potential wave forms typical of axon recordings.

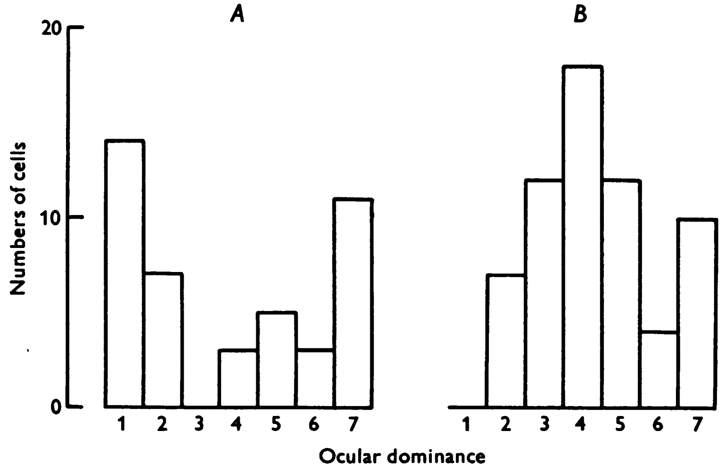
tendency for those units dominated by the left eye to have near-vertical preferred orientations while those dominated by the right eye usually had preferences close to horizontal. The result for this animal is illustrated in more detail in Text-fig. 6, in the form of a schematic reconstruction, like that in Text-fig. 2. The micrograph in Pl. 1*B* shows the penetration itself; again, one of the electrolytic lesions, at the end of the track is visible in the section. Separate plots in Text-fig. 6 show the sequences of receptive field orientation, as plotted through the dominant eye, and the exaggerated ocular dominance pattern. The columns labelled 'NO' and 'VU' show cells that were non-oriented or visually unresponsive, respectively. In general, sudden shifts in ocular dominance coincided with equally abrupt changes in orientation from near vertical to near horizontal or vice versa. Particularly clear instances of large changes in preferred orientation, coincident with shifts in ocular dominance, are indicated by unfilled arrows.

The cause of monocularity after alternating monocular occlusion

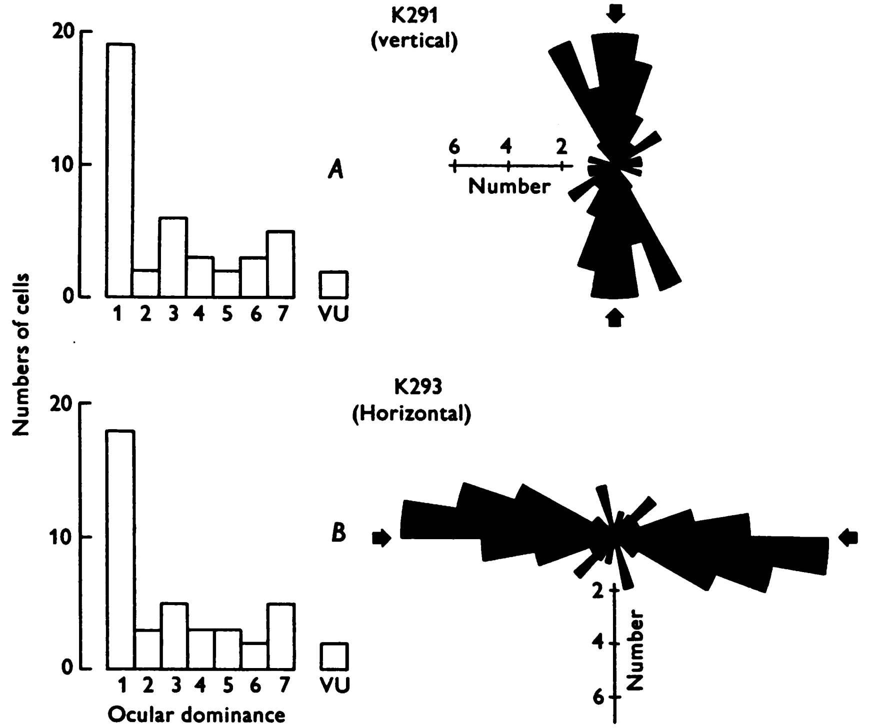
During alternating monocular occlusion in a normal environment, not only are the two receptive fields of each binocular cell not stimulated simultaneously but also the images that fall on them will differ in orientation. This situation was mimicked, in a reduced form in the animal (K307) whose results appear in Text-fig. 7*A*. This animal was dark-reared and exposed alternately, for an hour at a time, with at least a 2 h gap between exposures, to a vertically and then a horizontally striped environment. It wore goggles with an occluder which was moved from one eye to the other between exposures. So the left eye only saw vertical edges and the right only saw horizontal, for a total of 45 h each. The reduction in binocularity in this cat (58 % of units were monocularly driven) was not obviously greater than the animal that saw different orientations in the two eyes but at least saw them simultaneously (Text-fig. 5*C*).

For comparison, two animals were, in the same way, exposed alternately to horizontal and vertical (K52 for 0·5 h at a time, K20 for 2 h at a time, up to a total of about 50 h) but they had both eyes uncovered all the time. Their ocular dominance (Text-fig. 7*B*) was fairly normal (16 % monocular units; ten out of sixty-three). So the mere alternation of orientation does not disrupt binocularity, as long as both eyes are open.

Finally one can ask whether the effects of alternating monocular occlusion are solely due to the fact that the two eyes are never simultaneously stimulated, or whether it is the dissimilarity of pattern from one exposure to the next that is the crucial factor. Would cortical cells retain binocular connexions if they always saw the same orientation through the two eyes but at different times? Text-fig. 8 shows that they do not. Two animals were exposed with alternate monocular occlusion in a striped environment, vertical for K291 (Text-fig. 8*A*) and horizontal for K293 (Text-fig. 8*B*), until each eye had had 34 h of experience. For each animal, both eyes had always seen the same kind of pattern but never at the same time. Binocularity was just as much reduced (59% of visually responsive cells were monocular) as in their litter-mate, K292, whose eyes were alternately occluded in a normal environment (Text-fig. 4*A*). The over-all dominance by the contralateral eye in both of these animals is rather surprising, but is probably within the limits of variability in samples from kittens with alternately occluded eyes, and could not reasonably be attributed to the additional procedure of stripe-rearing. Incidentally, the distributions of preferred orientation, shown in Text-fig. 8 as polar histograms, were quite strongly biased toward the experienced orientation, just as has been previously described for stripe-reared animals (e.g. Blakemore & Cooper, 1970; Pettigrew & Garey, 1974; Tretter, Cynader & Singer, 1975; but see a contradictory report by Stryker & Sherk, 1975). (The orientation of exposure for each animal was not known by the experimenter in the present case, until both recording experiments had been completed.)



Text-fig. 7. *A*, results for K307, which received alternate monocular occlusion, each eye in turn viewing stripes for an hour at a time; vertical for the left eye, horizontal for the right. *B*, results for K20 and K52, which were exposed successively to vertical stripes, then horizontal, and so on, but with *both* eyes open each time.



Text-fig. 8. Results for two animals exposed to stripes of a single orientation but with the two eyes alternately occluded so that they never saw simultaneously. *A*, K291, exposed to vertical. B, K293, exposed to horizontal. The histograms on the left show the ocular dominance of cortical cells, while the polar histograms on the right plot the distributions of preferred orientation for all the orientation selective neurones. Each segment of these histograms indicates by its total diameter, as shown in the inset scale, the number of preferred orientations falling within that particular range of angle. The filled arrows show the orientation to which each animal was exposed.

DISCUSSION

The main findings of this report can be summarized as follows:

(1) A gross reduction of contrast, but not of mean illumination, in one retinal image will cause that eye to lose its influence on cortical cells (Text-fig. 1*B*).

(2) If the two eyes simultaneously view patterns of equal mean contrast but totally lacking congruence in orientation, binocularity is specifically reduced (Text-figs. 4*A* and 5*C*).

(3) Even if the visual axes are misaligned, as long as the images falling on corresponding points are similar in orientation, binocularity can be preserved (Text-fig. 5*A* and *B*).

(4) If the two eyes are stimulated alternately, with a long delay between exposures, binocularity is reduced (Text-figs. 4*B* and 7*A*) even if the images are congruent in orientation (Text-fig. 8).

(5) A neutral density filter over one eye causes a similar reduction in binocularity with no tendency for the filtered eye differentially to lose influence (Text-fig. 1*C* and *D*). This effect is unlikely to result solely from the slight difference in maintained discharge of retinal ganglion cells caused by the interocular difference in mean illumination *per se* (Barlow & Levick, 1969*a*), since it does not occur if contrast is also abolished in both eyes (Text-fig. 3). However, reduction of background illumination also causes both an increase in the *latency* of cat ganglion cells (by approximately 6 msec per log unit; Enroth-Cugell & Lennie, 1975) and a reduction in the *rate of discharge* elicited by any particular incremental stimulus (Barlow & Levick, 1969*b*). Since binocularity is certainly disrupted by a 2 log unit filter over one eye (Text-fig. 1*D*) the difference in latency is unlikely to be the sole disturbing factor, since the bursts of activity elicited by stimulation of the receptive fields would enormously outlast the 12 ms or so difference in their arrival times at the cortex. Therefore the loss of binocularity under these conditions may be caused by the disparity in evoded activity, perhaps with synergistic effects due to differences in maintained discharge, latency and evoked responses.

(6) Under the most favourable, normal conditions, some 10–15% of cortical neurones remain directly excitable through one eye alone, although such apparently monocularly driven cells probably always have subtle inhibitory and excitatory influences from the 'silent' eye (Henry, Bishop & Coombs, 1969).

(7) Under the most unfavourable conditions, when the spatial and/or the temporal congruence of the retinal images is absent (Text-figs. 4, 5*C* and 7*A*), some 25–50% of cells still retain excitatory influence from both eyes.

(8) A reduction in binocularity, whatever its cause, is apparently always accompanied by an exaggeration of the ocular dominance columnar sequence of neurones during each penetration (Text-figs. 2 and 6).

A number of the experimental procedures described here are similar to those used in an independent study by M. Cynader and G. Chernenko (personal communication in 1975), and in general my results are very similar to theirs. They too describe a decline in binocularity after unilateral reduction of retinal illumination. They used a powerful lens (rather than a diffuser) in front of one eye to reduce the contrast of the retinal image (also introducing anisometropia and aniseikonia) and likewise observed a reduction in cortical input from that eye.

The marked loss of binocularity in an animal that simultaneously saw horizontal contours in one eye and vertical in the other (Text-fig. 5*C*) confirms the reports of Hirsch & Spinelli (1970, 1971). While it seems likely that cortical cells are capable, to some extent of adopting different preferred orientations on the two retinae (Blakemore & Van Sluyters, 1974*a*; Blakemore, Van Sluyters & Movshon, 1976; Movshon, 1976), a 90° difference is, apparently, too much for most of them. This might, in part, be due to the fact that conjugate horizontal or vertical eye movements across contours of orthogonal orientation in the two eyes would necessarily move one eye across the contours but the other eye along them (effectively generating no image motion). This would result in signals elicited by the movement in one eye not being accompanied by activity in the other.

The necessary condition, then, for the maintenance of binocularity is that cortical neurones should be stimulated by patterned retinal images with contours of approximately the same orientation falling, roughly simultaneously, on the receptive fields in the two eyes. It remains to define exactly how much dissimilarity in timing and shape can be tolerated.

Note added in proof. Very recent results by R. C. Van Sluyters and C. Blakemore suggest that there is some variability in the effectiveness of exposure to repetitive patterns in maintaining cortical binocularity in artificially strabismic kittens. The early results, illustrated in Text-fig. 5*B*, are representative of some of our most successful experiments: in a few strabismic kittens there has been a definite decrease in the proportion of binocularly driven neurones, despite exposure to a striped environment. The variability in these results, together with the recent report that strabismic kittens reared in total darkness can have reduced cortical binocularity (Maffei & Bisti, 1976), suggest that further factors, perhaps the simple decreased mobility of one eye, may be involved in the changes in cortical organization caused by artificial strabismus.

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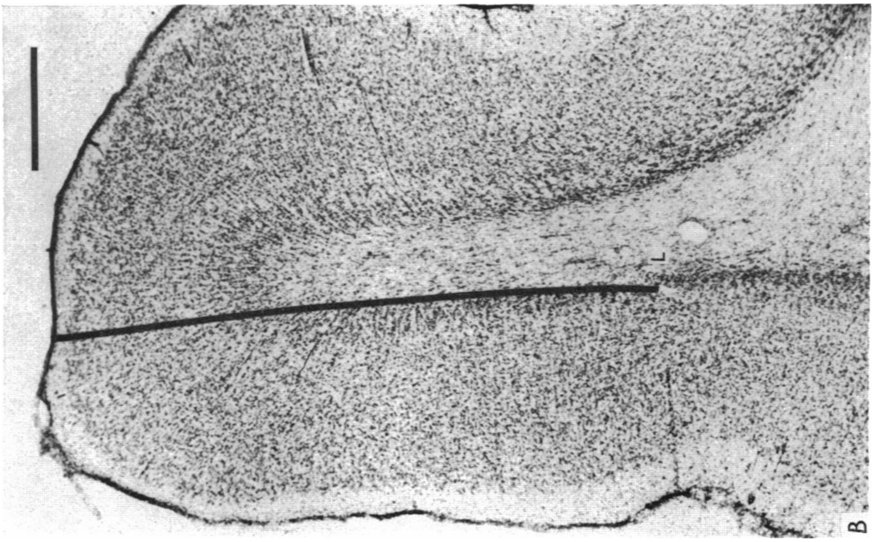
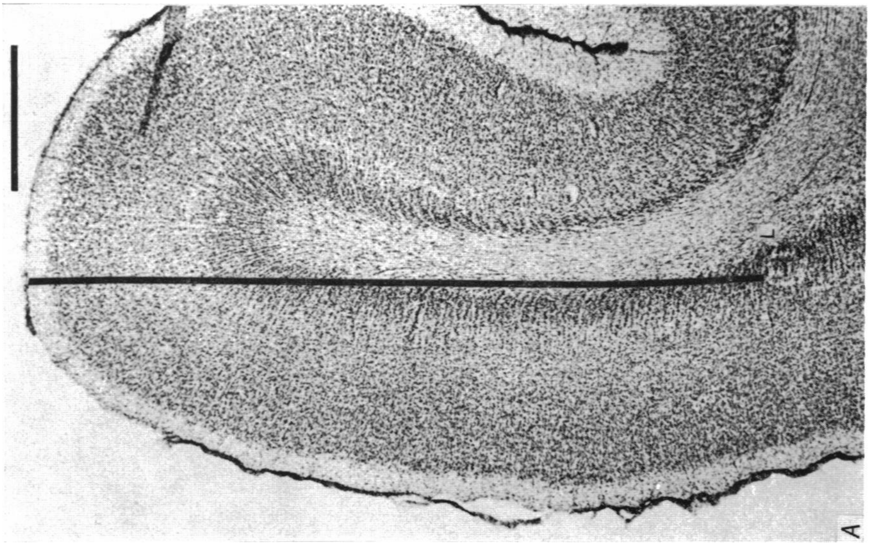
EXPLANATION OF PLATE

Photomicrographs of coronal sections, stained with cresyl violet, through the post-lateral gyrus of the right hemisphere. In each case the course of the penetration, reconstructed from electrolytic lesions placed at intervals along the track, is marked with a continnous line, running from the apex of the gyrus, down the medial bank, passing into the fibre layer under the cortex and terminating in the grey matter at the final lesion, marked L. The horizontal scale marker = 1 mm, corrected for shrinkage.

A, K368, this penetration is schematically illustrated in Text-fig. 2.

B, K309, this penetration is schematically illustrated in Text-fig. 6.


L
B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