

Effects of Monocular Exposure to Oriented Lines on Monkey Striate Cortex*

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This study examines the extent to which the restriction of visual experience to lines of a single orientation influences the organization of the striate cortex in infant monkeys (*Macaca mulatta*). Previous studies of kittens raised with monocular exposure to a single line orientation have consistently shown the response preference of cells driven by that eye to be biased towards the experienced orientation. Studies of binocular exposure to restricted orientations have been equivocal. In the infant monkey cortex responses to oriented lines have virtually all the specificity of responses seen in the adult animal. In an effort to clarify the phenomenon and the mechanism by which orientation bias might be obtained, we examined the effects of monocular exposure to a restricted orientation in infant macaques. Three monkeys were used. Each monkey was raised with one open eye exposed to lines of a single orientation and one eye occluded by lid suture. As in other cases of monocular deprivation in either cat or monkey, few binocularly driven cells were recorded and the majority of cells were dominated by the open eye. Cells driven by the open eye had normal representation of all orientation preferences and there was no overall increase in the number of cells preferring the orientation to which the eye had been exposed. The cells dominated by the occluded eye, however, showed a lack of cells responding to orientations to which the open eye had been exposed. These findings suggest that a competitive mechanism operates between the two eyes to provide an orientation-selective advantage to the open eye.

INTRODUCTION

The original experiments examining the effects of early monocular lid suture on the anatomy and physiology of the cat visual pathway^{19,20} have since been extended to include a number of species and different kinds of deprivations. One of the most interesting variations had its origin with experiments by Hirsch and Spinelli⁷ and Blakemore and Cooper¹, in which kittens had vision restricted to stripes of a single orientation. Since then, these experiments have been repeated with a wide range of modifications and widely diverging results, from failure to replicate the original (and very dramatic) findings to confirmation and extension of them (for reviews see refs. 5 and 13). Today there seems to be little doubt that by restricting early vision to stripes of a single orientation one can change the relative numbers of cortical cells that respond to that orientation. It is less clear wheth-

er the changes reflect shifts in orientation allegiance of individual cells, or represent a mere reduction in the selectivity or responsiveness of some cells, or a biasing of the fate of cells that at birth were uncommitted. Behind most of these experiments has lurked the old controversy over the degree to which cortical neuronal connections are determined as a result of experience, as opposed to genetics.

Compared with the cat, the rhesus monkey at birth has a far more mature visual system. Cells in the striate cortex show a degree of response specificity that in many respects (including line orientation preference) approaches that of the adult and the system of orientation columns is already established²². Because of these differences it seemed worthwhile to repeat some of the stripe-rearing experiments in monkeys. We were also motivated by studies that show that in man early astigmatism gives rise to a lowered visual acuity restricted to the orientations that were

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out of focus¹². In the present experiments we occluded one eye by lid suture and exposed the other eye to stripes of a single orientation. Monocular closure was used because it is known to produce, in infant monkeys, dramatic physiological and anatomical changes in eye dominance, even after brief periods of deprivation^{2,11,18}. We assumed that combining lid closure with orientation deprivation would provide us with two measures of the effects of the rearing procedures.

MATERIALS AND METHODS

Subjects

Three infant macaques were raised with the left eye exposed only to lines of a single orientation and the right eye sutured for the duration of the exposure. Table I presents the age, species, and the duration and orientation of exposure.

Rearing apparatus and procedures

The newborn monkeys, all of normal gestational age and birth weight, were removed from the mother the day after birth. Prior to surgery for right eye closure they were housed in ordinary incubators in the Primate Center nursery unit which was lighted about 12 h/day. After right-eye suture the animals were transferred to a completely darkened, light-tight room which contained the rearing apparatus.

The animal was housed in a plastic cage (30.5 × 30.5 × 30.5 cm) with a thermostatically controlled electric heating pad on the floor. A molded plastic face mask with eye holes was mounted over a 7.6-cm opening in the front of the cage. When the monkey's head was properly positioned inside the mask the entire visual field was filled by a 33.0-cm translucent, mushroom-shaped glass globe. Two electrodes were mounted in the brow area of the mask which, when contacted simultaneously, activated a Kodak carousel projector. The projector, in turn, illuminated the

globe and displayed stripe patterns of a single orientation for the duration of contact. When the animal remained in contact with the electrodes for a specified duration, it received a drop of milk (SMA human formula) from a nipple mounted in the mouth area of the mask. Since the animal was in total darkness except when in contact with the face mask and electrodes, this arrangement assured a fixed orientation of the monkey's head relative to the stripe pattern stimulus.

On the first day in the apparatus the animal's head was placed in the mask and held against the nipple and electrodes to assure that it learned the correct procedure to obtain reinforcement. After repeated placement in the mask on the first day, the animal learned the location of the mask and spent increasing lengths of time with its head in the mask. Over the next few days it spent increasing lengths of time with its head in the mask without assistance. During the first week it received a single drop of milk for each accumulated 2-s electrode contact and exposure to the stripe pattern. Over the next few weeks a variable duration schedule was introduced into the programming system, which required different durations of contact to obtain a single milk delivery (variable durations of 2 s–2 min, for an average 30-s duration). The hours of exposure obtained in the apparatus for the 3 animals are shown in Fig. 1. Regular observations of the animal during exposure confirmed that the head was upright during the projection of the stripe patterns. Through a fiber optic viewer mounted in the eye area of the mask, it was possible to verify that the left eye was open during exposure periods. The animals were taken directly from the rearing apparatus in a light-tight box to the laboratory for physiological recordings.

The projector contained 80 slides of 4 different patterns of 6–8 lines which changed automatically each minute. The lines were composed of strips of stippled transparencies which diminished in density

TABLE I

Age and condition of rearing and physiological procedures

<i>Macaque</i>	<i>Age at right eye suture</i>	<i>Orientation exposure</i>	<i>Age at onset of exposure</i>	<i>Duration of exposure</i>	<i>Age and date at physiological recordings</i>
<i>No. 1 M. Arctoides</i>	23 days	vertical	41 days	15 h (37 days)	78 days (April 23, 1975)
<i>No. 2 M. Mulatta</i>	12 days	vertical	13 days	57 h (42 days)	55 days (June 24, 1975)
<i>No. 3 M. Arctoides</i>	6 days	horizontal	7 days	107 h (57 days)	64 days (November 13, 1975)

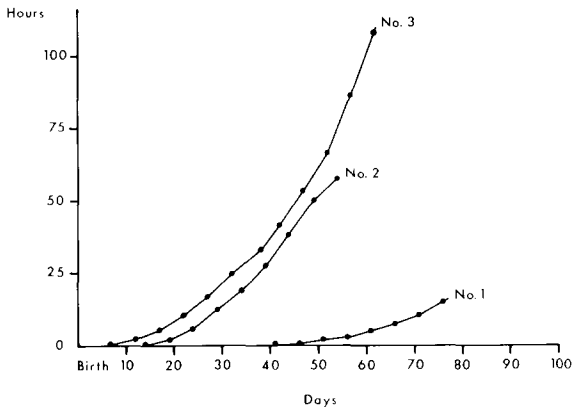


Fig. 1. The graph shows accumulated monocular exposure (in hours) to stripe patterns plotted relative to age (in days) for the 3 infant monkeys. The initial point of each curve indicates that day the animal was placed under the fully restricted routine in the rearing apparatus.

and width at the ends to eliminate an obvious edge. At their widest dimension the lines were 5–20° in width and spaced at 1–16° intervals, representing a variety of spatial frequencies. Half the slides consisted of light lines on a dark background and half of dark lines on a light background. The illumination levels were in the photopic range, dark areas measured 8 cd/m² and bright areas 300 cd/m².

Physiological and anatomical methods

The recording methods used in these studies have been described previously^{9,10}. Animals were kept continuously anesthetized with sodium pentobarbital, paralyzed with a mixture of Flaxedil and D-tubocurarine and artificially ventilated during the course of the recording session. Body temperature and expired CO₂ were monitored and kept within normal physiological range. The sutured lids were opened and the eyes refracted by means of contact lenses upon a tangent screen 1.45 m away.

Unit activity was recorded through tungsten electrodes moved in steps of 25–50 μm in extensive tangential penetrations in area^{10,17}. The size, orientation specificity and binocular interactions of receptive fields of cells were mapped on the tangent screen with a hand-held projector. The location of the receptive fields was determined relative to the projected locations of the optic discs and foveas for each eye. Two of the authors (Hubel and Wiesel) did not know the rearing orientation for the 3 animals until

the end of the recording sessions. Two or 3 penetrations were made in each animal and small electrolytic lesions (2 μA for 2 s) were made at transitional points through the penetration (e.g. right eye to left eye transition, layer IVc–V border). At the termination of the recording sessions animals were perfused with saline followed by formol saline. The brains were blocked and cut in the parasagittal plane, and the 25-μm frozen sections were stained with cresyl violet. Finally, histological reconstructions were made of electrode tracks, all of which were well within area 17.

RESULTS

The 3 experimental animals were raised under the same conditions of monocular exposure to lines of a single orientation, but the age of lid suture, onset and duration of exposure differed as summarized in Table I. The rate and total accumulation of restricted visual stimulation in the rearing apparatus are illustrated in Fig. 1.

Monkey No. 1 had normal visual experience until 23 days of age, when the right eye was closed. Over the next two weeks the animal was put into the rearing apparatus and exposed to the vertical stripe patterns for several hours a day but was otherwise kept in a normal light–dark environment. The fully restricted rearing routines were not begun until 41 days of age. During the next 37 days the monkey exposed its left eye to a total of 15 h of vertical stripe stimulation; the rest of the time it spent in complete darkness.

Some effects of both monocular deprivation and of restricted viewing of vertical orientations can be seen in this animal although it has a history of 23 days of binocular and 18 days of monocular visual exposure in the nursery before the orientation restriction procedure was begun. All the cells recorded (excluding non-oriented cells recorded in layer IVc) responded normally to oriented lines. There was, however, a decline in the number of binocular cells and the ocular dominance distribution was skewed in favor of the exposed eye (Fig. 2A). The histogram is not unlike that found in animals raised with artificial strabismus^{8,23} or after binocular closure²¹. Table II shows that of the 64 oriented cells recorded, the left (exposed) eye was dominant for 59% (groups 1–3), whereas the right (closed) eye dominated in only

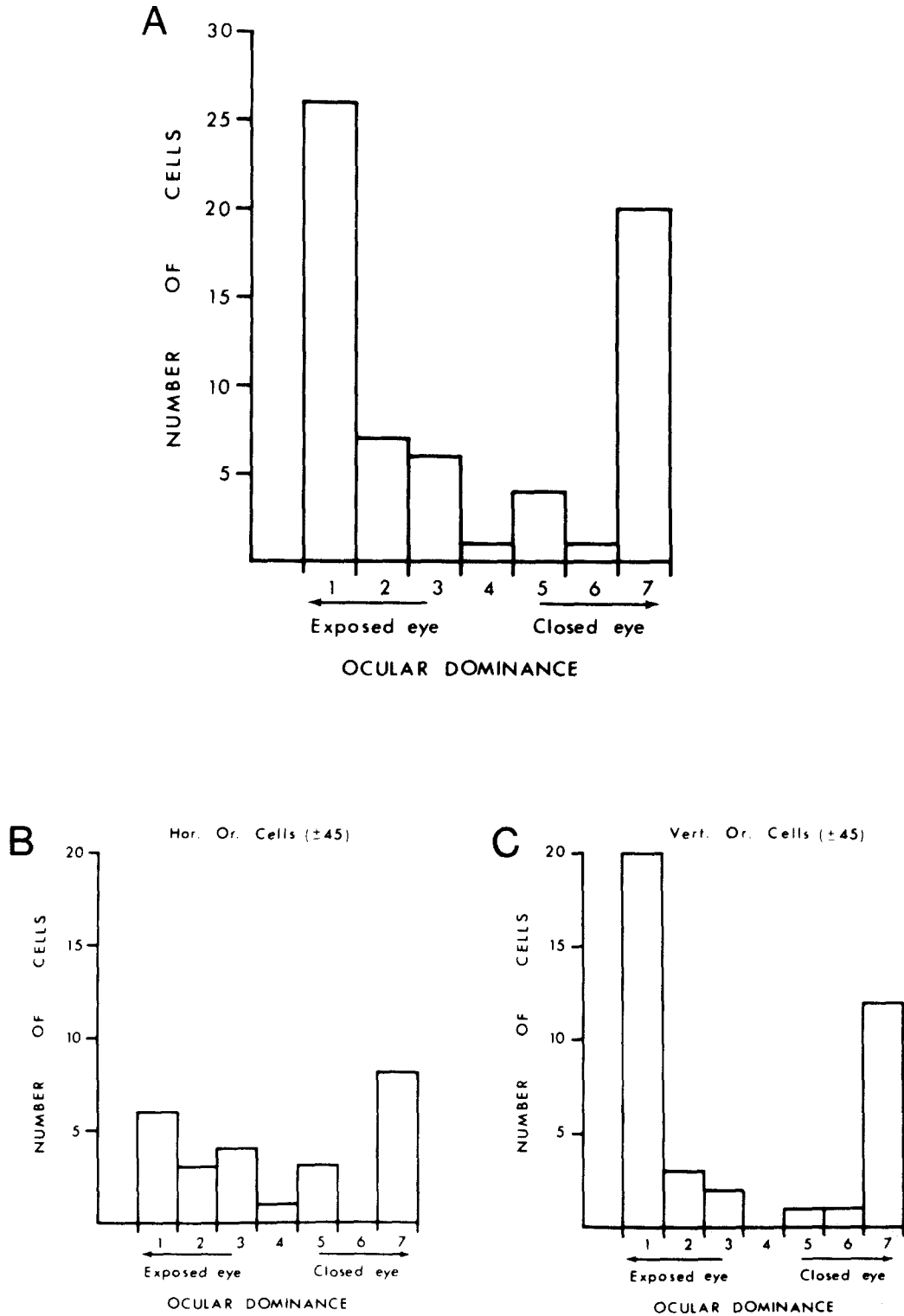


Fig. 2. Monkey No. 1 experienced a normal visual environment for the first 23 days at which time its right eye was sutured. It received 15 h of restricted orientation exposure over the next 37 days. Recordings were begun at 78 days of age. A: ocular dominance histogram for all oriented cells recorded. B: ocular dominance histogram for cells with $\pm 45^\circ$ horizontal orientation preference. C: ocular dominance histogram for cells with $\pm 45^\circ$ to vertical orientation preference. (Definition of ocular dominance groups: cells of group 1 were driven only by the contralateral eye; for cells of group 2 there was marked dominance of the contralateral eye; for group 3, slight dominance. For cells in group 4 there was no obvious difference between the two eyes. In group 5 the ipsilateral eye dominated slightly; in group 6, markedly, and in group 7 the cells were driven only by the ipsilateral eye.)

TABLE II

Orientation preference and ocular dominance

RE, right eye; LE, left eye; H-OR, cells with $\pm 45^\circ$ horizontal orientation preference; V-OR, cells with \pm vertical orientation preference; LE-DOM, cells in groups 1–3 bins in ocular dominance histograms; RE-DOM, cells in groups 5–7 bins in ocular dominance histograms; GRP 4, cells in group 4 bin, equally dominated by RE and LE; T, total.

<i>Macaque</i>	<i>Oriented cells</i>	<i>H-OR cells</i>	<i>V-OR cells</i>	<i>LE-DOM cells</i>	<i>RE-DOM cells</i>	<i>Group 4 cells</i>	<i>H-OR Cells</i>			<i>V-OR Cells</i>	
		<i>(% of T)</i>	<i>(% of T)</i>	<i>(% of T)</i>	<i>(% of T)</i>		<i>LE (% of H)</i>	<i>RE (% of H)</i>	<i>Group 4 (% of H)</i>	<i>LE (% of V)</i>	<i>RE (% of V)</i>
No. 1	64	25 (39)	39 (61)*	38 (59)*	25 (39)	1 (2)	13 (52)*	11 (44)	1 (4)	25 (64)*.**	14 (36)
No. 2	76	48 (63)*	28 (37)	49 (64)*	27 (36)	–	28 (58)*	20 (42)	–	21 (75)*.**	7 (25)
No. 3	96	42 (44)	54 (56)*	66 (69)*	30 (31)	–	31 (74)*.**	11 (26)	–	35 (65)*	19 (35)

* Highest percent for single orientation.

** Highest percent of LE dominance for either orientation.

39% (groups 5–7). When the cells were divided into two groups according to orientation preference (cells favoring horizontal $\pm 45^\circ$ and those favoring vertical $\pm 45^\circ$), the horizontal group showed no preference of one eye over the other, while in the vertical group, cells dominated by the exposed eye exceeded those dominated by the closed eye by nearly 2:1 (Fig. 2C; see also Table II).

The second monkey was raised under similar conditions having the right eye occluded by lid suture and the left exposed to vertical stripes. The main differences in this animal were that the deprivation (the monocular occlusion and stripe exposure) began at 12 and 13 days of age and that the total accumulation of visual stimulation was 57 h compared to 15 h in the first instance.

The activity of cells in the striate cortex appeared normal also in this animal, as in the first one, with the usual distribution of cells responding selectively to different orientations. The cells recorded in a single, 4-mm long, tangential penetration through the superficial layers is shown in Fig. 3. Throughout the penetration the orientation preference shifted in small regular steps first counterclockwise, then clockwise, just as seen in normal monkeys¹⁰ and in newborn monkeys with little or no visual experience²². In particular there was no suggestion of any compression or expansion of areas preferring horizontal or vertical orientations, as might be expected if the rearing procedure had led to a distortion of orientation columns. There was, however, a clear decrease in the repre-

sentation of the occluded eye and an increase in the areas dominated by the exposed eye, especially in regions of vertical orientation preference.

This differential distribution of orientation preferences for individual cells is shown in Fig. 4. Fig. 4A consists of cells dominated by the occluded eye and Fig. 4B consists of the cells preferring the exposed eye. There was a striking paucity of cells which prefer vertical orientation in the occluded eye and a rather uniform distribution of orientation preferences in the eye exposed to vertical stripes. The few binocular cells recorded had the same orientation preference in the two eyes and those with orientations around the vertical (marked by numbers 186, 188 and 190 in Fig. 4B) were dominated by the exposed eye.

An examination of the ocular dominance histogram of the cells recorded in the second monkey also revealed this asymmetry. As in the first monkey there was a decline in the number of binocular cells and an overall dominance of the exposed eye (Fig. 5A and Table II). This dominance was slight for cells preferring horizontal orientations (Fig. 5B), but more marked for cells with orientation preference around the vertical (Fig. 5C).

In the third case the animal was lid-sutured at 6 days of age and entered the rearing apparatus on the following day. The monkey was exposed to horizontal stripes over a period of 57 days and accumulated a total of 107 h of exposure. Thus this monkey had more stimulation to a single orientation than the others and the exposures were confined to the period of

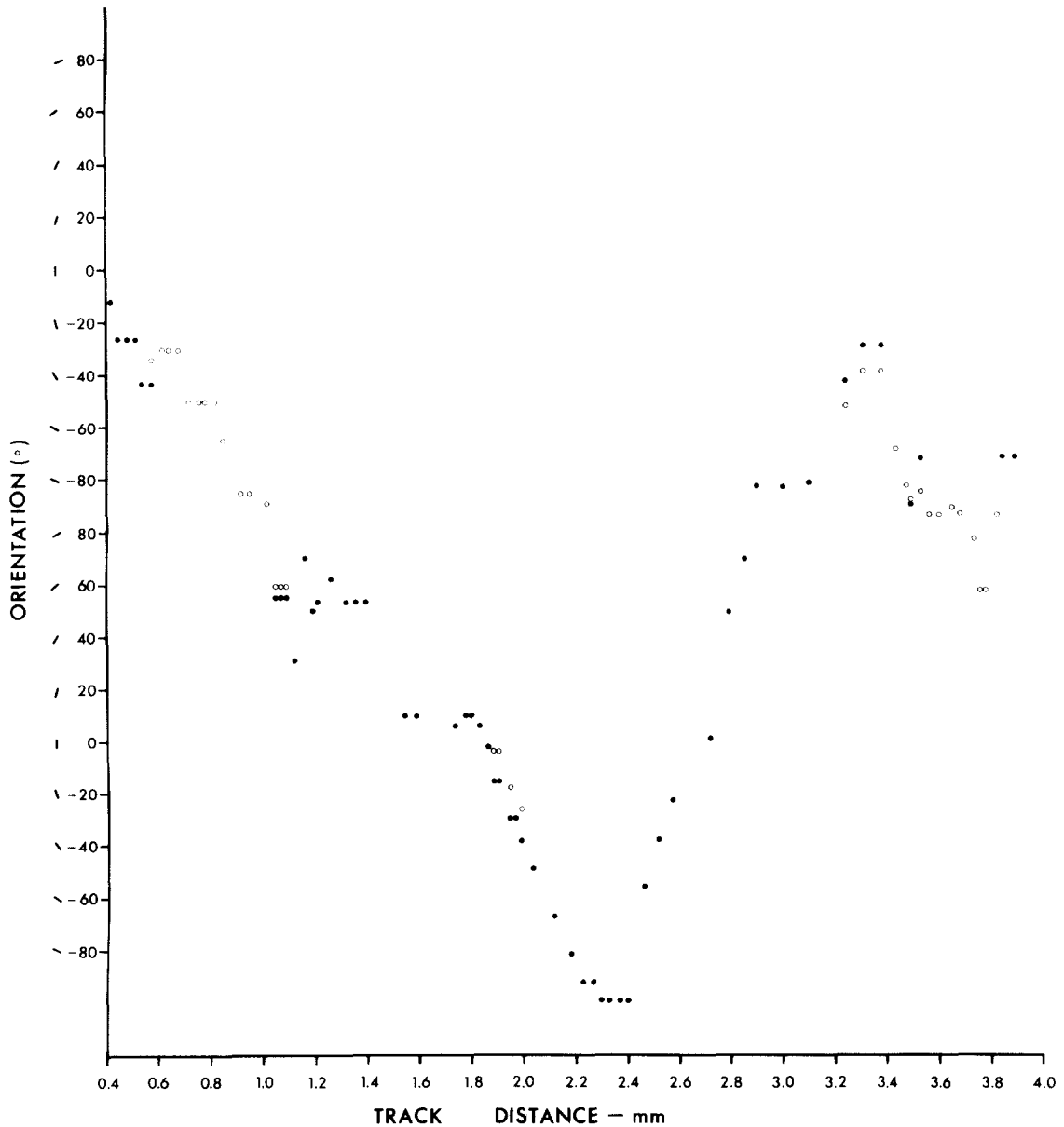


Fig. 3. Monkey No. 2 had normal visual experience until 12 days of age at which time its right eye was sutured. On the following day it was placed continuously in the rearing apparatus where it received a total of 57 h of exposure to vertical lines over the next 42 days. Recordings were begun at 55 days of age. Graph of orientation vs tract distance for cells driven by the open eye (closed circles) and for cells driven by the closed eye (open circles) recorded in a 4-mm oblique penetration in Monkey No. 2.

high susceptibility to visual deprivation¹¹. Of the 3 monkeys, this one showed the most marked decline in the number of binocular cells and the most striking asymmetry, again in favor of the open eye (Fig. 6A). To our surprise, however, there was little difference in this asymmetry between cells favoring orientations around the horizontal axis and those favoring the vertical axis (Fig. 6B, C). The asymmetry was slightly

greater for horizontal, but not so great that one was able to guess what orientation had been used for the rearing (Table II).

To summarize, the monocular stripe-rearing procedure in these 3 monkeys resulted in a decline in the number of binocular cells and a decline in the influence of the closed eye. The decline in the effectiveness of the closed eye, seen mainly for cells respond-

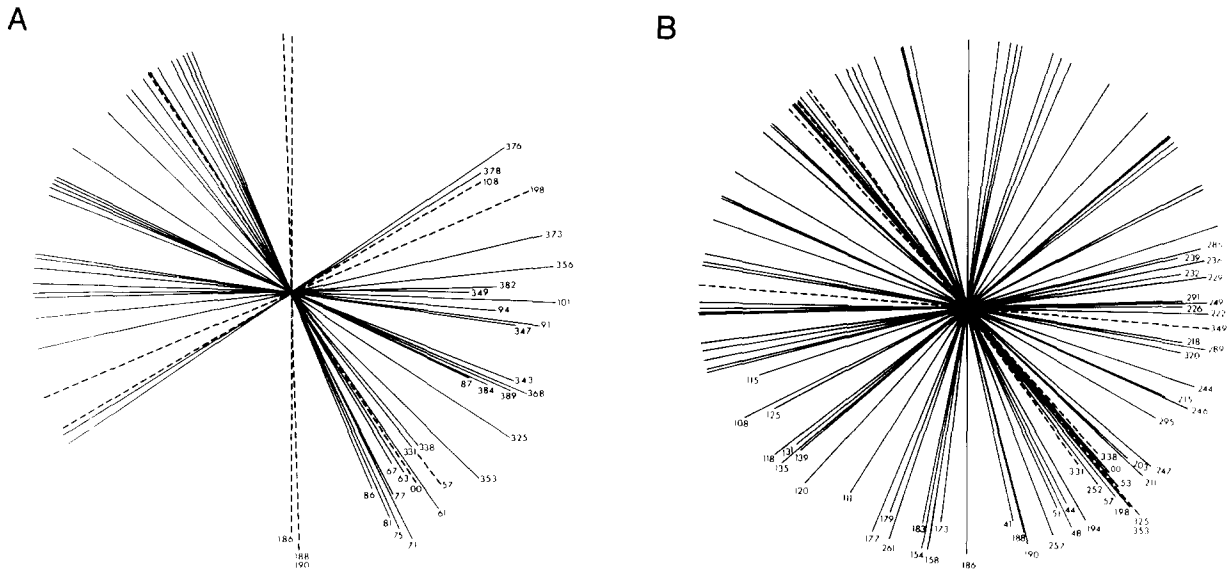


Fig. 4. Monkey No. 2. Orientation of cells recorded in the oblique penetration through striate cortex illustrated in Fig. 3. Continuous lines indicate monocular cells or cells preferring the designated eye. Interrupted lines indicate binocular cells or cells preferring the other eye. Numbers refer to micrometer depth readings (in $\text{mm} \times 100$). A: orientation of cells driven by the closed eye. B: orientation of cells driven by the exposed eye.

ing to orientations close to the one used in the rearing procedure, was statistically significant ($P = 0.02$, two-sample t -tests on 3 animals combined). The difference in the effectiveness of the two eyes for cells responding to orthogonal orientations was not significant (see Table II).

DISCUSSION

The results from these monkeys make it clear that preferential exposure of one eye early in life to stripes of a single orientation can change the ocular dominance distribution of cortical cells. In all 3 animals, the population of cells as a whole came to favor the open eye, and the earlier the deprivation and the longer its duration, the greater was the shift in eye preference (Figs. 2, 3, 6, parts A). Not unexpectedly, the shift was greatest for the cells having orientations at and around the orientation of the stripes used in the exposure. That this difference was least striking — and perhaps not even significant — in the third monkey, which had the earliest and longest deprivation, was a surprise to us and we have no ready explanation.

In the case of the first two monkeys, it might at first glance seem strange that after exposure of one eye to

stripes of one orientation the distribution of cells according to optimal orientation through that eye should remain unchanged (e.g. Fig. 4B) and that meanwhile the other eye should be robbed of its control over cells having the orientation used in rearing (Fig. 4C). This result, however, is just what is predicted from the earlier simpler procedures, in both cats and monkeys, of rearing in a normal visual environment with one eye closed, as opposed to having both eyes closed. The monocular closure is by far the more drastic procedure, and there is now an abundance of evidence that the difference is due to competitive effects between the two eyes^{6,11,21}. In the present experiments where, say, only vertical stripes were presented to one eye, the procedure amounted to a binocular deprivation for horizontal and monocular deprivation for vertical. In cats very similar results have been obtained in kittens in which the rearing procedures took advantage of this competition in a similar way, with selective exposure of one eye to a single orientation, the other eye being either open or closed¹⁵. Similar results were likewise obtained when the selective deprivation was achieved by means of artificial astigmatism produced by a cylindrical lens over one eye⁴. In fact, studies in which competition has played a part have consistently produced striking

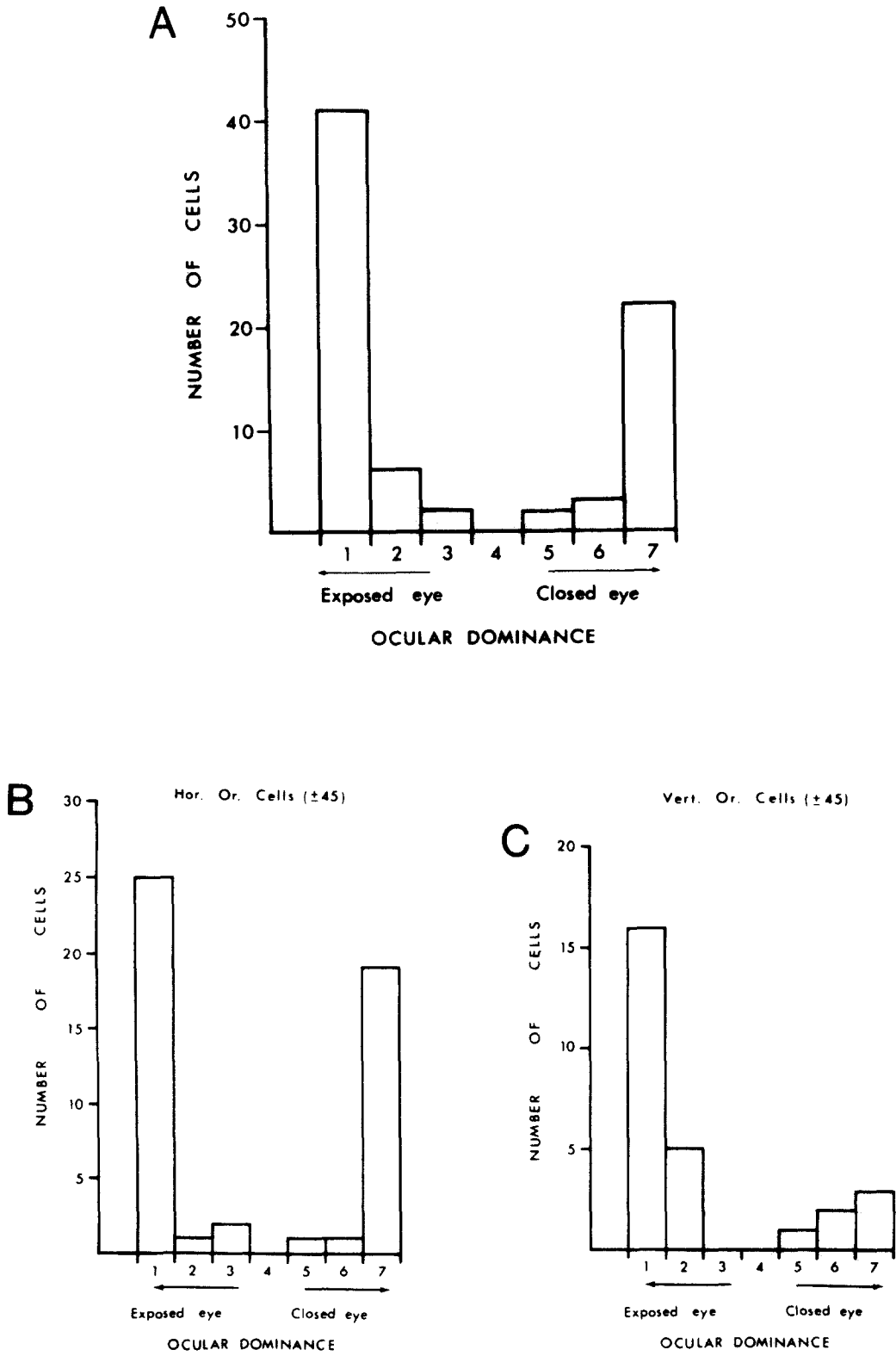


Fig. 5. Monkey No. 2. A: ocular dominance histogram for all oriented cells recorded. B: ocular dominance histogram for cells with $\pm 45^\circ$ horizontal preference. C: ocular dominance histogram for cells with $\pm 45^\circ$ vertical preference.

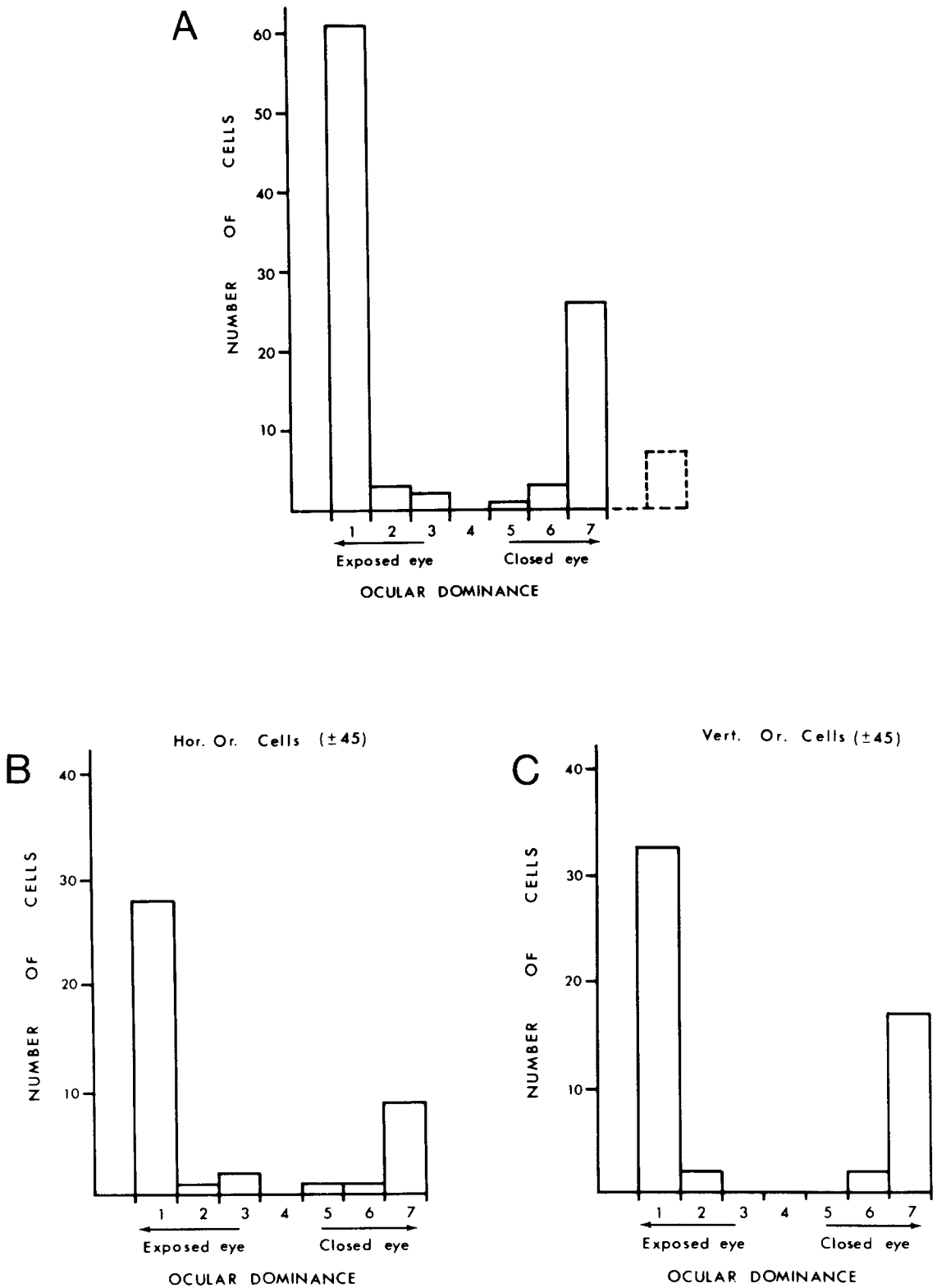


Fig. 6. Monkey No. 3 was given normal visual experience until 6 days of age when its right eye was sutured. It was placed in the rearing apparatus on the following day. Over the next 57 days a total of 107 h of restricted exposure to horizontal lines was obtained. Recordings were begun at 64 days of age. A: ocular dominance histograms for all oriented cells recorded. B: ocular dominance histogram for cells with $\pm 45^\circ$ horizontal preference. C: ocular dominance histogram for cells with $\pm 45^\circ$ vertical preference.

abnormalities in the cortical physiology, beginning with the original work of Hirsch and Spinelli⁷, in which goggles produced stimuli of one orientation to one eye and the orthogonal to the other, up to recent confirmation in a more strictly controlled study by Stryker et al.¹⁷. The results of kitten experiments in which both eyes were exposed to a single orientation have been much more varied, from the profound effects seen originally by Blakemore and Cooper¹ to the lack of any effects seen by Stryker and Sherk¹⁶. Rauschecker and Singer¹⁴ raised kittens with cylindrical lenses and concluded from their study that both 'selective and instructive processes' may be operating in the development of orientation preference. The wide discrepancies between all these studies remain unexplained but are perhaps not surprising in view of the variations in results that can be seen in a single set of experiments — for example Figs. 2 and 5 vs. Fig. 6 of the present paper!

Despite the changes reported here, the present experiments in macaque monkeys provided no support for the notion that it is possible to modify innately determined orientation preference of striate cortex cells by rearing animals viewing only horizontal or vertical lines. Cells of all orientations were recorded in the exposed eye of these monkeys and there was no obvious preponderance of cells preferring the orientation to which the eye has been exposed. In fact, in monkeys No. 2 and No. 3 the majority of cells (63% and 56% respectively) showed preferences for

the orientation orthogonal to the rearing orientation. Furthermore, in sequences of cells recorded in long tangential penetrations we saw regular shifts in orientation, similar to those seen in newborn or normally reared monkeys^{10,22}. This indicates that the orientation columns present at birth remained intact despite orientation deprivation in one eye and pattern deprivation in the sutured eye during the first two months of life. Thus these results give no support to the suggestion that orientation preferences are induced by visual experience.

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