Ordered Arrangement of Orientation Columns in Monkeys Lacking Visual Experience

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ABSTRACT The main object of this study was to see whether ordered sequences of orientation columns are present in very young visually naive monkeys. Recordings were made from area 17 in two macaque monkeys three and four weeks of age, whose eyes had been closed near the time of birth. The first monkey was born normally, but one day elapsed before eye closure could be done. The second was delivered by Cesarean section and the lids sutured shut immediately. The results in these two animals were very similar; in both, highly ordered sequences of orientation shifts were present, and were in no obvious way different from those seen in the adult. For example, average values for the size of orientation shifts, for the horizontal component of the distance between shifts, and for the slopes of orientation vs. track distance curves, were all similar to adult values. This indicates that the ordered column system is innately determined and not the result of early visual experience. In these two monkeys and a third one, sutured at two days and examined at 38 days, most of the cells seemed normal by adult standards, with simple, complex or hypercomplex receptive fields, showing about the same range in orientation specificity as is found in adults. About 10–15% of cells showed abnormalities similar to those seen in monkeys binocularly deprived of vision for longer periods. Furthermore, all three deprived monkeys showed a decided lack of cells that could be influenced from both eyes, whereas a normal three-week-old control animal seemed similar to the adult, with binocular cells comprising over half of the total population. A monkey deprived by binocular closure from the third to the seventh week also showed a diminution in number of binocularly influenced cells, suggesting that the deprivation from birth resulted in a deterioration of innate connections subserving binocular convergence. To be sure that the abnormalities in the deprived animals represented a deterioration of connections, we recorded from 23 cells in a normal two-day-old monkey: here the ocular dominance distribution of cells was about the same as in the adult, and the response characteristics of the cells were normal by adult standards.

In the past few decades evidence has steadily mounted for an astonishing degree of specificity of connections in the mature central nervous system. Not surprisingly, more and more attention has been given to the origin of this specificity and, in particular, to the relative importance of genetic as opposed to postnatal environmental factors. In the striate cortex of newborn and visually inexperienced kittens, we recorded several years ago from cells responding to specifically oriented stimuli, and found evidence suggesting that the orientation columns are already formed (Hubel and Wiesel, '63;

Wiesel and Hubel, '65). Monkeys brought up for several months with both eyes sutured closed likewise have cells with orientation specificity in area 17 (Wiesel and Hubel, unpublished). In the first paper of the present series (Hubel and Wiesel, '74) we found in adult and juvenile monkeys a remarkable degree of orderliness in the arrangement of orientation columns: it was thus natural to push the question of innate specificity a step further by asking whether the entire system of columns is present at birth and hence probably genetically programmed. This is the purpose of the present study.

METHODS

Six monkeys were used. Of these, two were normal and four had both eyes sutured at various ages and for varying periods (table 1). Techniques for stimulating and recording were generally the same as in previous papers (Hubel and Wiesel, '68, '74). For the experiment of figure 4B, in the 2-day-old normal monkey, the moving-slit stimuli were generated on a television screen using a specially designed electronic stimulator, and the average responses for each orientation from 0° to 360° were plotted on-line using a PDP12 computer.

RESULTS

Because experiments designed to examine orientation-shift sequences tend to be protracted, we decided against attempting them in newborn monkeys. In two monkeys we sutured both eyes closed and waited a few weeks before doing the acute experiments. One of these animals (table 1, no. 1) had the eyes sutured two days after birth and was recorded from at 17 days. The second (table 1, no. 2) was delivered by Cesarian section and the eyes sutured immediately; this monkey was born with the eyes closed, and the lids had to be pried open in order to trim the margins so that they could be sutured. Careful examination of the lids in the ensuing

weeks showed the suturing to be completely successful (as was so for all animals in this series). Since no sign of the pupils or sclerae could be seen through the lids, it seemed unlikely that any images fell on the retinae. A third monkey was sutured at two days of age and studied at 38 days; in this animal our object was to examine receptive fields and ocular dominance.

Graphs of receptive-field orientation versus electrode-track position are shown for the first monkey in figure 1 and for the second in figure 2. These graphs are generally similar to those we obtained in normal adult (or juvenile) monkeys and indicate that the orientation-column system is present in the newborn monkey, with the same high degree of order.

Table 2 gives the results of measurements made from these graphs. This table is to be compared with a similar one for the normal adult (Hubel and Wiesel, '74, table 1). As before, each straight-line sequence is listed separately. A comparison of the four averages (uncorrected and corrected slopes, angle/shift, horizontal distance/shift) in adult and visually naive baby monkeys shows very little difference between the two, and in particular there is nothing to suggest that the system of orientation columns is any coarser in the visually naive monkeys. For example, the average shift in the baby monkey was

TABLE 1

Monkey	Type	Type of study	Figure
1	binoc closure 2–17 days	orientation shifts ocular dominance distribution	1, 3A
2	binoc closure (Cesarian) 0–30 days	orientation shifts ocular dominance distribution	2, 3B
3	binoc closure 2–38 days	receptive fields ocular dominance distribution	3C
4	21 day normal	ocular dominance distribution orientation specificity	3D
5	binoc closure 21–49 days	ocular dominance distribution orientation specificity	3F
6	2 day normal	ocular dominance distribution orientation specificity	4

TABLE 2

Experiment	Penetration no.	Sequence no.	Field distance from fovea	Span of sequence	Track length	Angle (θ)	Horizontal track length	Slope uncorrected	Slope corrected	Number of shifts	Angle/shift	Horizontal distance/shift	Figure no.
			deg	deg	mm	deg	mm	°/mm	°/mm		deg	μ	
1. binoc. closure 2–17 days	1	1	4	87	0.395	36	0.319	+219	+271	9	9.7	35	1
		2	4	174	0.776	36	0.628	+273	+337	16	10.8	39	
	2	1	4	179	1.016	41	0.767	+183	+243	19	9.4	40	
		2	4	74	0.226	41	0.170	−284	−376	4	18.5	43	
2. Cesarian bin. closure 0–30 days	1	1	8	107	0.339	48	0.225	−320	−478	7	15.0	32	2
		2	8	51	0.225	48	0.150	+219	+327	6	8.5	25	
	2	1	8	72	0.339	48	0.227	+219	+327	7	10.3	32	
		2	8	99	0.185	48	0.124	−134	−200	6	13.0	21	
Averages								231 ±59	320 ±86		11.90 ±3.4	33.38 ±7.5	
Averages, adult normals (Hubel and Wiesel, '74, table 1)								222 ±83	281 ±93		11.91 ±3.4	43.26 ±11.5	

11.90°, compared with 11.91° for the adult. There is a suggestion that the horizontal distance/shift may be smaller in the newborn monkey (33 μ compared with 43 μ for the adult), possibly indicating a thinner orientation-slab width in a brain that is smaller than adult size. In a previous study in monkeys (Hubel and Wiesel, '68), we observed that sharpness of tuning varies considerably, especially from one layer to the next. Similar variations were observed in these young visually naive monkeys. Our impression was that the cells in these animals, except for 10–15% which appeared distinctly abnormal (see below), were on the whole no less sharply tuned than are cells in the adult. Otherwise sequences such as the initial ones in the two penetrations in monkey 1, or the second sequence of the first penetration in monkey 2, in which the average value of angle/shift was less than 10°, would have been difficult or impossible to plot.

Because of the claim that in kittens a few hours of visual experience can modify or affect the subsequent orientation preference of cortical cells (Blakemore and Mitchell, '73; Pettigrew et al., '73), it is perhaps worth mentioning that minutes after the eyes were reopened the very first cell recorded in the monkey born by Cesarian section (no. 2) showed a precise orientation preference from the outset. Moreover, if any orientation was used more than any other to stimulate this cell while testing it was the cell's own optimal orientation. Yet the next cell, recorded a few minutes after the first, showed a new optimum shifted in a counter-clockwise direction, the next showed a further shift, and so on. It would be difficult to imagine that the testing procedure was in any way responsible for producing the specificities that we observed.

In the course of recording from the first three monkeys there were several groups of cells, amounting to about 10–15% of the total, that could only be driven with difficulty, or whose orientation seemed less critical than usual. On one of these occasions, at the outset of penetration 1 in monkey no. 1, the level of CO_2 in the expired air was checked and found to be excessive. Within a few moments of correcting this the cells were responding with
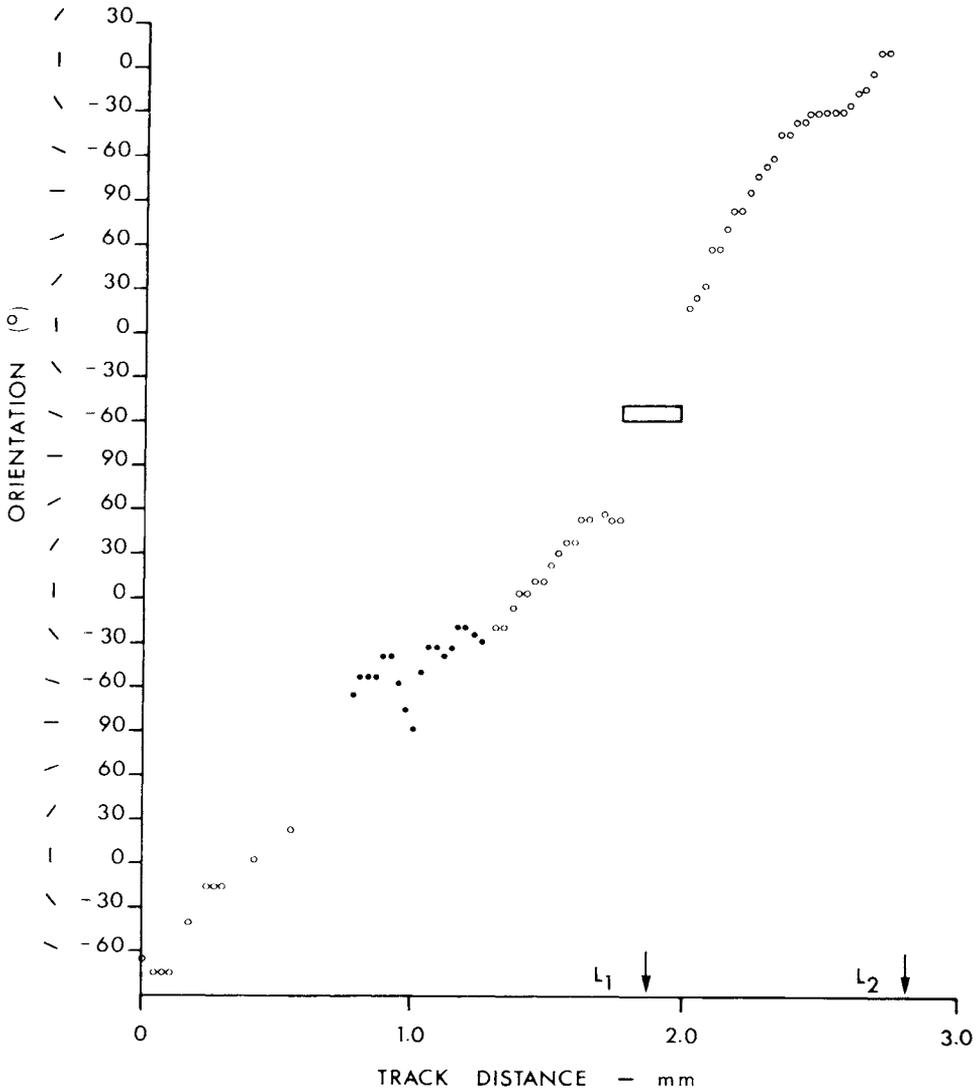
Figure 1A

Figure 1   Graphs of receptive-field orientation vs. electrode-track distance for two pene-
trations in the right striate cortex of a baby monkey whose eyes were sutured closed from the
second to the seventeenth day (when the recordings were made). A. Penetration no. 1.
B. Penetration no. 2, about 0.6 mm from no. 1 and parallel to it. C. Reconstruction of the
two electrode tracks. L_1–L_3 are lesions made to identify the tracks. Closed circles, ipsilateral
eye; open circles, contralateral eye. Open bar, contralaterally dominated activity in layer
IV C, unoriented.

an orientation precision seen in normal
adult cells. It is thus likely that at least
some of the cells were abnormal because
of the general state of the animal. On the
other hand, monkeys, like cats, when de-
prived by bilateral lid suture for several,
rather than a few, weeks have substantial
proportions of such abnormal cells (see

fig. 3, C and F); we therefore assume that
some of the abnormal cells in the present
series reflect the early stages of depriva-
tion effects. That these abnormal cells
are related to immaturity is unlikely, since
no such cells were seen in the normal
two-day-old monkey (see below).
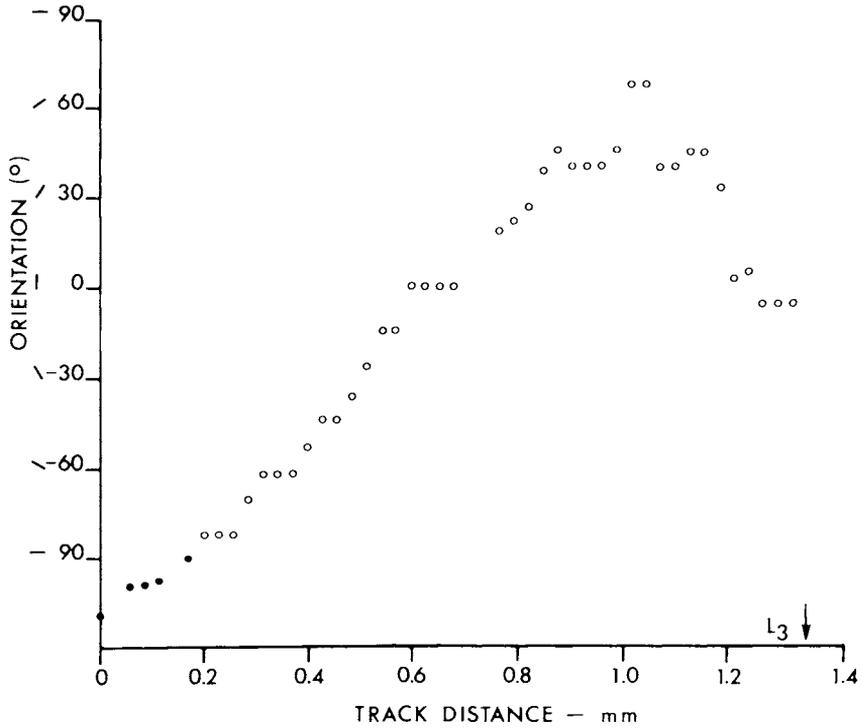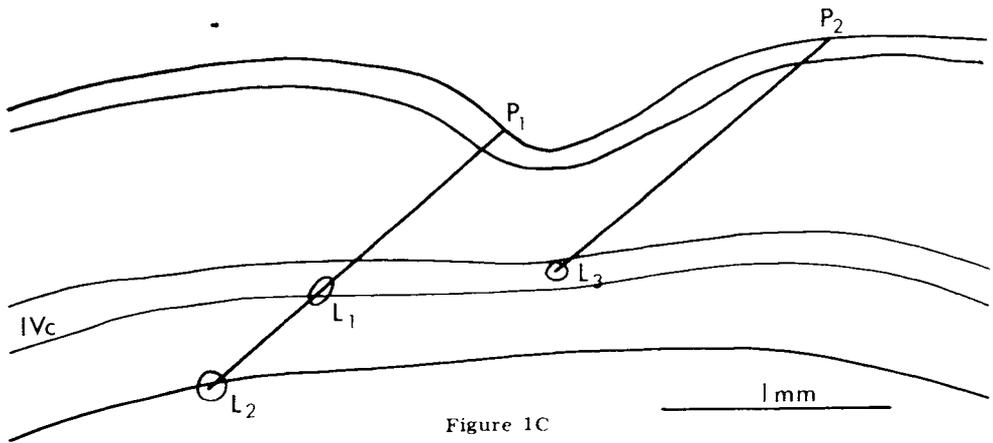   In the present experiments our major

Figure 1B

Figure 1C

aim was to establish whether or not the ordered orientation column system is present in visually naive animals, and we made no attempt to analyze receptive fields thoroughly or to make statistical comparisons between these monkeys and adults. In particular, we did not make careful measurements of receptive field size. Nevertheless, several general comments can be made concerning receptive fields. We found examples of all three receptive-field types, simple, complex, and hypercomplex. Complex cells, as in the adult, constituted the great majority of cells in the layers above and below layer IV. Simple cells were typical in firing brisk "on" or "off" responses
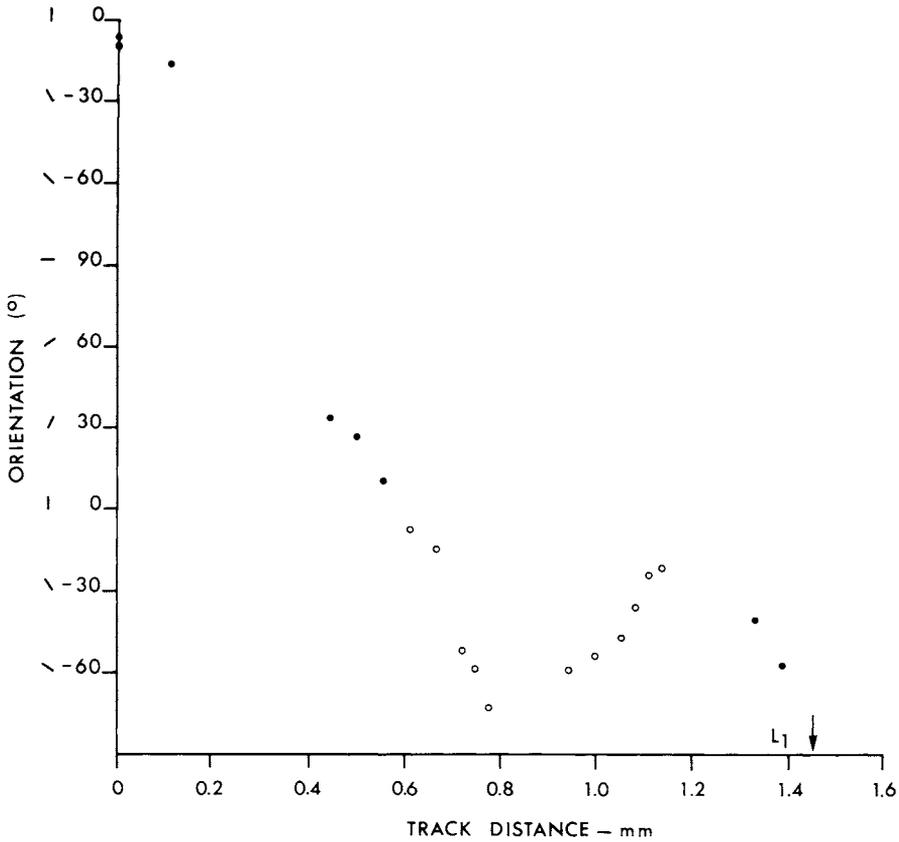
Figure 2A

Fig. 2 Graphs of receptive-field orientation vs. electrode-track distance for two penetrations in the right striate cortex of a baby monkey whose eyes were sutured closed from birth (by Cesarian Section) to the thirtieth day (when the recordings were made). A. Penetration no. 1. B. Penetration no. 2, about 0.25 mm from no. 1 and parallel to it. C. Reconstruction of the two parallel electrode tracks, about 0.3 mm apart.

to properly oriented stationary slits, dark bars, or edges. Orientation specificity to stationary stimuli, which we have also seen in visually inexperienced kittens, is of some interest in view of the assertion (Barlow and Pettigrew, '71; Pettigrew, '74) that it is direction specificity rather than orientation specificity that is present in visually naive kittens.

In figures 1 and 2, the shifts in eye preference indicated by the periodic switching from contralateral eye (open circles) to ipsilateral eye (closed circles) and back indicate that the system of ocular-dominance columns develops by innate mechanisms and is present either at birth or within three to four weeks of birth. It

would be worthwhile to test this further by anatomical methods (Hubel and Wiesel, '72).

What was very different in these two monkeys, compared with normal adults, was the overall degree of mixing of influence from the two eyes. Figure 3, A, B, and C shows ocular-dominance histograms for the three visually naive animals, as compared with the histogram for a normal three-week-old control (fig. 3D) and for the adult (fig. 3E). Compared with the normal monkey, the three deprived animals show a marked reduction in the number of cells that could be binocularly influenced. The few binocular cells that were found seemed quite normal, with
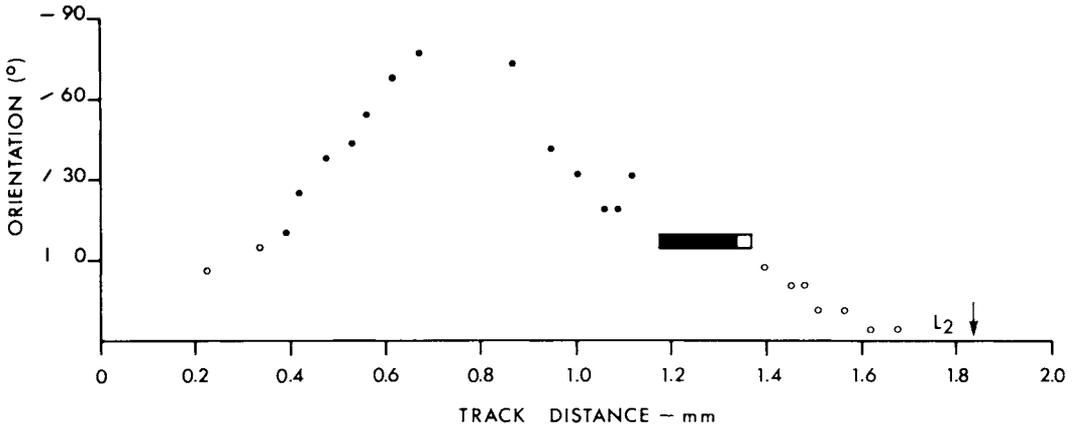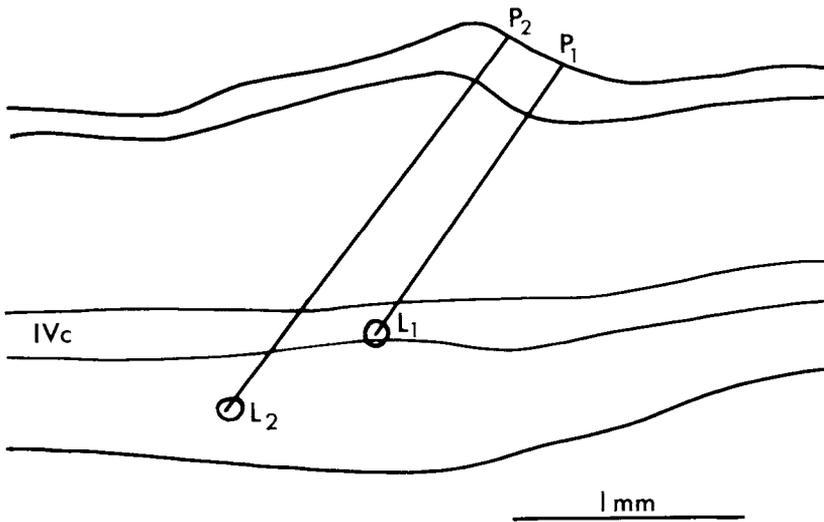
Figure 2B

Figure 2C

fields in the two eyes in corresponding positions and precisely tuned to the same orientation. We did not examine these cells using simultaneous stimulation of the two eyes. Taken at face value, the results suggest that binocular deprivation in the first three to four weeks has a markedly adverse effect on the convergence of influence of the two eyes on cortical cells. This is supported by figure 3F, which shows a marked reduction in binocular cells in an animal in which both eyes were sutured from the third week to the seventh. Figures 3D and 3F together indicate that

three weeks of closure in a baby monkey can lead to a marked decline in binocularly driven cells.

Despite this evidence, it seemed imperative to record from a newborn monkey to be sure that binocular cells were present, and to check, if possible, for the existence of orientation specificity. We accordingly recorded from 23 cells in a two-day-old rhesus monkey. The histogram (fig. 4A) shows the presence of binocular cells with about the same ocular dominance distribution as in the adult. In this monkey, cells were as precisely oriented

BINOCULAR   CLOSURE   2 17 days
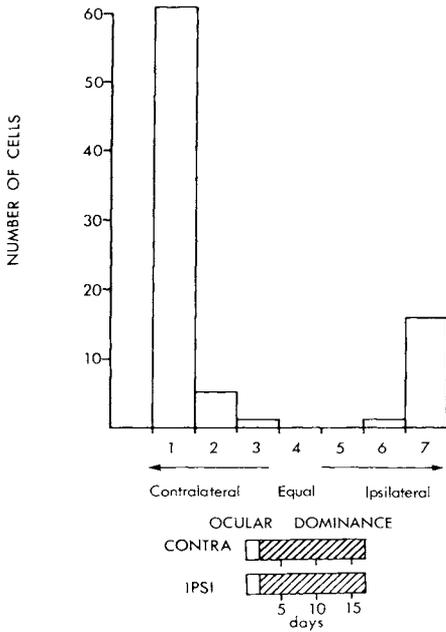
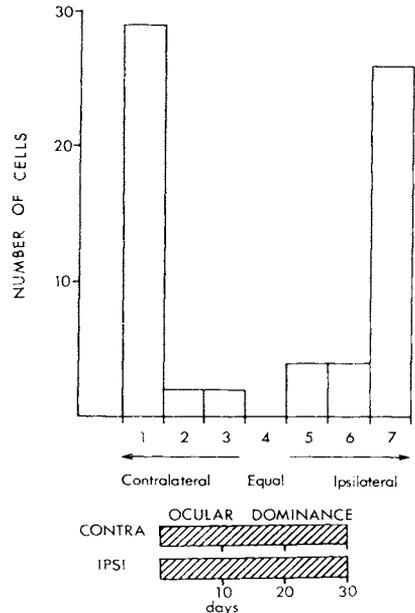BINOCULAR   CLOSURE   0   30 days

Figure 3A

Figure 3B

Fig. 3   Ocular-dominance histograms for the different monkeys. A. Monkey no. 1, binocular closure 2–17 days (table 1). B. Monkey no. 2, binocular closure 0–30 days (Cesarian section). C. Monkey no. 3, binocular closure 2–38 days. D. Monkey no. 4, normal 21-day-old monkey. E. Ocular-dominance histogram for 1116 cells in area 17 in 28 normal adult (and juvenile) monkeys. F. Monkey no. 5, binocular closure 21–49 days. 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. Shaded areas at the bottom of each histogram indicate period during which one or other eye was closed. Shaded areas in the histograms themselves represent cells that gave abnormal responses, for example, a lack of orientation specificity or unusual sluggishness. Dotted bins to the right of the histograms C and F represent cells that failed to respond to either eye.

as in the normal three-week-old monkey. A computer-generated graph of average number of impulses versus slit orientation from a complex cell is shown in figure 4B; besides showing a very sharp tuning this cell responded to downward, but not at all to upward, movement. This graph indicates a high degree of specificity, but of course by itself it does not prove the presence of orientation specificity as distinct from directional specificity. Since the cell gave very little response to stationary stimuli, that criterion could not be used to differentiate the two types of specificity.

Small moving spots, on the other hand, evoked no responses; consistent responses were seen only to lines one-third to one-half the width of the field, and the responses improved steadily with increasing line length, suggesting that the cell was indeed selective for line orientation. In every way the behavior of this cell was typical of that seen in upper layer cells in adult monkeys.

During this penetration there were several sequences of regular shifts in orientation. For the binocular cells the positions of the fields in the two eyes seemed in
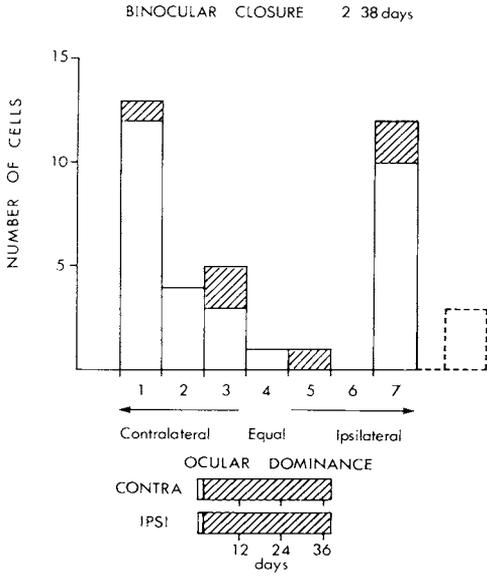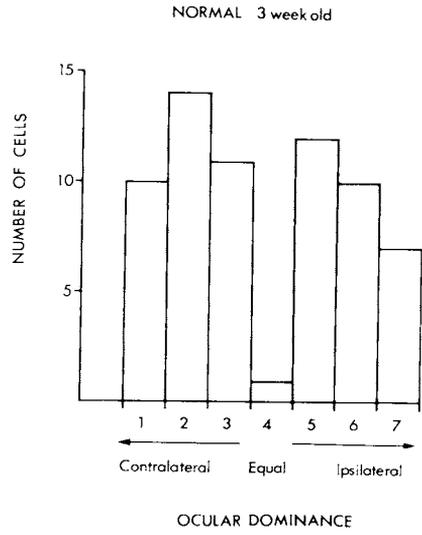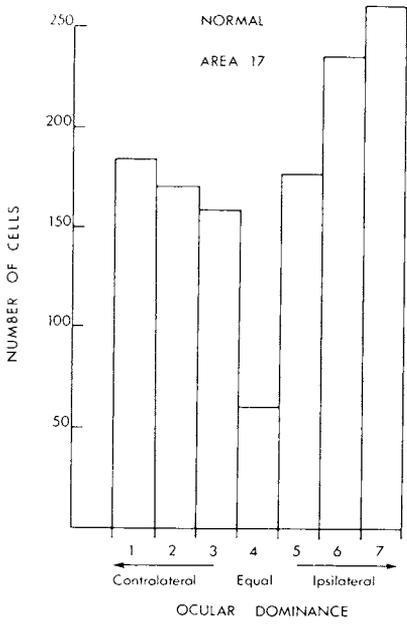
BINOCULAR CLOSURE 2 38 days

NUMBER OF CELLS

Contralateral Equal Ipsilateral

OCULAR DOMINANCE

CONTRA

IPSI

12 24 36
days

Figure 3C

NORMAL 3 week old

NUMBER OF CELLS

Contralateral Equal Ipsilateral

OCULAR DOMINANCE

Figure 3D

NORMAL
AREA 17

NUMBER OF CELLS

Contralateral Equal Ipsilateral

OCULAR DOMINANCE

Figure 3E

BINOCULAR CLOSURE 21 49 days

NUMBER OF CELLS

Contralateral Equal Ipsilateral

OCULAR DOMINANCE

CONTRA

IPSI

16 32 48
days

Figure 3F

Fig. 4A   Ocular-dominance histogram for 23 cells in a normal two-day-old macaque monkey.

ordered system of orientation columns seen in adult monkeys is innately determined and not the result of visual experience early in life. Just as striking as the ordered sequences of orientation shifts was the precision with which the orientations of cells could be determined; evidently a newborn monkey is in this respect virtually mature. This is perhaps not surprising since already at birth a macaque monkey observes and follows objects. Anatomical studies on the birth days of cells in monkey visual cortex likewise indicate that, compared with other species, the macaque at birth is already well-developed (Rakic, '74).

exact correspondence, and to within a few degrees the optimal stimulus orientations were identical. In these respects the cells were no less specific than cells in the adult monkey. Though it is not possible to make a detailed comparison between newborn cats and monkeys, given such a small sampling of cells, we were struck by the absence, in the two-day-old monkey, of unresponsive, very sluggish, or non-oriented cells in the upper and lower layers, in view of the presence of such cells in the ten-day-old kitten.

The cat, in contrast, is visually very immature at birth. It does not open its eyes for about the first ten days of life, and at that time the optic media are quite cloudy, so that the fundus cannot be visualized. The cortex is likewise anatomically immature (Cragg, '72). Presumably this relative immaturity of the newborn kitten contributes to the difficulties one finds in observing orientation specificity. Nevertheless, the adult cat, like the monkey, has a well-ordered system of orientation columns (Hubel and Wiesel, '63a, '74, fig. 13). The individual cells, except perhaps for those in layer 4C, are also remarkably similar in their basic properties in the two species. The similarity in the two visual systems increases our confidence that the orientation specificity we saw in some cells in an eight-day-old kit-

DISCUSSION

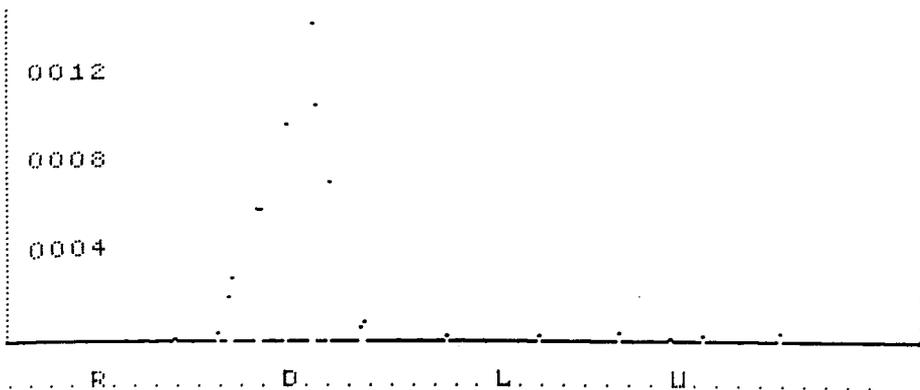The present results show that the highly

Fig. 4B   Computer graph, plotted on-line, of average response in impulses/stimulus (roughly 10 stimuli for each point) vs. orientation. Each stimulus consisted of a long narrow slit (6° × 1/4°) automatically swept in one direction across the receptive field in the orientation indicated. U = up. L = left. D = down. R = right. In addition to showing a high degree of orientation selectivity, this cell was completely unidirectional in its responses.

ten was genuine (Hubel and Wiesel, '63b), that its absence in other cells is a matter of maturation, and that the development of orientation specificity with all its orderliness is similarly determined in the two species, i.e., genetically.

At present this confidence is not shared by some others in the field (Barlow and Pettigrew, '71; Blakemore and Van Sluyters, '74; Pettigrew, '74). While is seems to be generally agreed that specificity of responses is present in some cells in newborn kittens, this has been said to take the form of a selectivity to direction of movement of virtually any shape of stimulus, whereas selectivity to line orientation is absent at birth and develops only with experience (Barlow and Pettigrew, '71). The present position of these authors is unclear, however, since both Pettigrew ('74) and Blakemore ('74) appear now to have found orientation specific cells in visually naive kittens. We have recently extended our experiments on visually naive kittens and have observed cells whose responses to a moving specifically oriented line improve as the line is lengthened and which also respond to the line if it is stationary, but only in the proper orientation (Hubel and Wiesel, unpublished). This is probably convincing enough evidence for orientation specificity as opposed to a directional specificity of the type seen in rabbit retina or cat tectum. In newborn monkeys the columnar arrangement seems to be identical to that found in the adult, and it is difficult to imagine that we are observing two distinct sets of cells, in newborn monkeys and in adults, arranged in the same architectural pattern, especially when their responses seem to be so similar.

An incidental and somewhat surprising finding in the present study was the marked decline in binocularly activated cells following a few weeks of binocular deprivation. The resulting ocular dominance histogram is very similar to that resulting from strabismus in cat (Hubel and Wiesel, '65) and in monkey (Hubel and Wiesel, unpublished; also Baker et al., '74). In binocularly deprived kittens there was some decline in the proportion of binocular cells in the middle groups, but certainly no change comparable to that seen in the present monkeys (Wiesel and

Hubel, '65). This lack of any marked decline in binocular cells after binocular deprivation complicated the interpretation of the kitten squint histograms, as resulting simply from a chronic lack of synchronous input from the two eyes onto single cells (Hubel and Wiesel, '65); here it was necessary to add the stipulation that there be some on-going input from single eyes. In the monkey, this extra condition seems not to be necessary — apparently a simple lack of synchrony is enough.

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