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EFFECTS OF VISUAL DEPRIVATION ON THE DEVELOPMENT OF THE MONKEY'S LATERAL GENICULATE NUCLEUS

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SUMMARY

1. We have studied the physiological properties of cells in the deprived layers of the lateral geniculate nucleus (l.g.n.) in monkeys monocularly deprived from birth for up to 27 weeks, and compared them with results from the non-deprived layers in the same animals and in a series of normal animals.

2. Despite the relative shrinkage of cell bodies in the deprived layers, units were easily isolated, were visually responsive and could readily be classified as linear (X) or non-linear (Y) by means of tests of spatial summation. The laminar distribution of cell types and the proportion of Y cells did not seem to be affected by deprivation.

3. The patterns and latencies of discharge produced by contrast-reversing gratings did not differ grossly between deprived and non-deprived cells. The peak firing frequencies for drifting gratings were also similar. The degree of surround antagonism (though very variable from cell to cell) seemed unaffected by deprivation.

4. Most surprising of all, there was little or no deficit in the spatial resolution of the receptive fields of deprived cells. Recordings were always taken ipsilateral to the deprived eye, and neural 'acuity' tended to be slightly lower in the deprived laminae than the non-deprived. However, this nasal/temporal asymmetry in spatial resolution was not obviously more pronounced than in normal animals.

5. Neural 'acuity' was not abnormally low in either contralateral or ipsilateral layers in the l.g.n. of an animal binocularly deprived from birth until a year of age.

6. We have not examined chromatic properties or temporal characteristics adequately to say whether they are affected by deprivation.

7. Paradoxically, although the post-natal maturation of visual acuity in normal monkeys seems to be mainly limited by peripheral factors, deprivation (which causes a profound defect of behavioural acuity) does not seem to interfere substantially with physiological development of the retina or the geniculate nucleus.

INTRODUCTION

A human baby deprived of normal visual stimulation in one eye (whether through cataract, ptosis, patching or some other cause) can suffer later in life from a condition called *amblyopia*, a profound defect of vision, characterized by reduced visual acuity

in the deprived eye, even if the retinal image is subsequently re-established and the eye itself appears entirely normal (Awaya, Sugawara & Miyake, 1979; Vaegan & Taylor, 1979). Much experimental work in kittens and monkeys points to the visual cortex as a possible site of the pathological change underlying amblyopia: after occlusion of one eye for a few days or less during a sensitive period early in life, afferent axons from the deprived laminae of the lateral geniculate nucleus (l.g.n.) establish abnormally small terminal fields in the striate cortex and cortical neurones become physiologically dominated by input from the non-deprived eye (see Blakemore, Garey & Vital-Durand, 1978; LeVay, Wiesel & Hubel, 1980; Blakemore, Vital-Durand & Garey, 1981; Swindale, Vital-Durand & Blakemore, 1981; Sherman & Spear, 1982; Frégnac & Imbert, 1984).

The extent to which these effects of deprivation on the visual cortex might simply reflect more peripheral anomalies is a subject of considerable current interest. Prolonged deprivation causes slight shrinkage of ganglion cells in the cat retina (Leventhal & Hirsch, 1983) and can affect the morphology of their axon arborizations in the l.g.n. (Sur, Humphrey & Sherman, 1982). The physiological characteristics of deprived cat retinal ganglion cells are, however, normal (Sherman & Stone, 1973), and the spatial resolution of their receptive fields is unaffected (Kratz, Mangel, Lehmkuhle & Sherman, 1979; Cleland, Mitchell, Gillard-Crewther & Crewther, 1980).

In monkeys reared in continuous darkness for up to 6 months retinal histology appears normal (Hendrickson & Boothe, 1976). However, even the naked eye can immediately distinguish the deprived layers in a section through the l.g.n. of a long-term monocularly deprived cat or monkey, because the cells are smaller than those in the non-deprived layers and they stain less densely (Wiesel & Hubel, 1963; Guillery & Stelzner, 1970; Headon & Powell, 1973; von Noorden, 1973). The effect of monocular deprivation from birth on the growth of primate l.g.n. cells is actually rather complex: the relative shrinkage of cells in the deprived layers, which has the appearance of a simple arrest of growth (Vital-Durand, Garey & Blakemore, 1978) involves initial hypertrophy in the non-deprived layers followed by shrinkage of all cells (Headon, Sloper, Hiorns & Powell, 1985). Despite these substantial effects on perikaryal size and staining, deprivation does not seem to interfere with the post-natal development of the dendritic trees of monkey l.g.n. cells (Wilson & Hendrickson, 1981) nor with synaptic organization in either kitten or monkey l.g.n. (Winfield & Powell, 1980; Winfield, Hiorns & Powell, 1980; Wilson & Hendrickson, 1981).

There has been no previous study of the physiological effects of deprivation on the primate l.g.n. and the descriptions of the responses of deprived neurones in the cat are somewhat contradictory, ranging from no obvious defects at all (Shapley & So, 1980) to 'functionally moribund' neurones (Ikeda, Plant & Tremain, 1977). Wiesel & Hubel (1963) originally reported that the majority of cells in the deprived l.g.n. layers of the monocularly deprived cat 'appeared normal' but a few were rather sluggish in their responses and had unusually large receptive field centres.

Sherman, Hoffmann & Stone (1972) found a specific reduction in the proportion of Y cells recorded in the binocular segment of the deprived layers. Although this result has been confirmed in several subsequent studies, Shapley & So (1980) failed to find any paucity of Y cells and Eysel, Grusser & Hoffmann (1979) found a normal ratio

of Y to X units when recording from deprived axons in the optic radiation. Any deficit seen in the l.g.n. itself might, then, be due to a micro-electrode sampling bias, since the larger Y cell bodies shrink relatively more than X cells as a result of deprivation (Garey & Blakemore, 1977; Friedlander, Stanford & Sherman, 1982). However, Friedlander & Stanford (1984) have recently reported a dearth of Y cells in the deprived laminae, even when recording with fine micropipettes.

Further evidence for specific effects of deprivation on Y cells in cat l.g.n. comes from Friedlander *et al.*'s (1982) correlation of structure and function by means of intracellular recording and horseradish peroxidase injection: they found some deprived l.g.n. neurones with morphology typical of Y cells to be unresponsive, sluggish or even X-like in their receptive field properties.

Maffei & Fiorentini (1976) described a defect in spatial resolution for deprived cat l.g.n. cells. Lehmkuhle, Kratz, Mangel & Sherman (1978, 1980) and Mower & Christen (1982) also reported that prolonged deprivation affects the 'acuity' of l.g.n. X cells, but Shapley & So (1980) and Derrington & Hawken (1981) found no such deficit. Finally, according to Sireteanu & Hoffmann (1979) the reduction in neuronal 'acuity' is mainly restricted to cells in lamina A1, ipsilateral to the deprived eye, merely exaggerating a natural tendency of cells in layer A1 to be inferior in resolution to those in layer A.

With these conflicting results on the cat in mind, we have now examined the effects of deprivation on the physiological development of the monkey l.g.n.

Table 1. Experimental procedures and numbers of X and Y cells

				Numbers of cells				
				Parvocellular layers		Magnocellular layers		
Rearing procedure	Monkey	Age at recording		X cells	Y cells	X cells	Y cells	Total
Right eye closed from day of birth	P7911	4 days	Left eye	29	0	10	1	40
			Right eye	21	0	9	2	32
	P7913	12 days	Left eye	25	0	0	1	26
			Right eye	19	0	0	0	19
	P7910	24 days	Left eye	28	1	2	3	34
			Right eye	23	0	2	0	25
	P7909	70 days	Left eye	18	0	5	1	24
			Right eye	23	0	6	0	29
	P7907	189 days	Left eye	19	0	17	0	39
			Right eye	24	0	11	1	36
Binocularly deprived from day of birth	F8405	358 days	Left eye	14	0	0	0	14
			Right eye	5	0	2	0	7
Normal vision until 44 days then binocularly deprived	P7903	195 days	Left eye	24	1	7	0	32
			Right eye	27	0	6	0	33

METHODS

We have already described our methods for rearing monkeys, recording in the anaesthetized, paralysed preparation, generating visual stimuli and analysing responses (Blakemore & Vital-Durand, 1986). Five animals were monocularly deprived from the day of birth: they were placed in a dark box soon after birth and transported to the laboratory where the right eye was closed by separately suturing together the conjunctival flaps and the trimmed lid margins under I.V. Althesin anaesthesia (Blakemore & Van Sluyters, 1975). One monkey (F8405) was binocularly deprived from birth until recording at 358 days of age, and a further animal (P7903) was reared normally until 44 days and then had the lids of both eyes closed until recording at 195 days. These deprived animals were examined daily and in no case did a 'window' opening develop in the sutured lids.

The fused eyelids were re-opened under general anaesthetic (Althesin, I.V.) during preparation for recording. Ophthalmoscopic examination revealed no obvious abnormality of the cornea, the internal optics of the eye or the retinal fundus in any animal. The corneae were covered with contact lenses and 4 mm diameter artificial pupils, and additional spherical lenses were used to correct refractive error, which was assessed by both direct ophthalmoscopy and by varying the lenses to optimize the spatial performance of individual l.g.n. cells (Blakemore & Vital-Durand, 1986). None of the monocularly deprived animals was obviously anisometropic and in no case was there a striking difference in the size of the two eyes when they were subsequently measured (see Fig. 16 of Blakemore & Vital-Durand, 1986). The durations of deprivation employed here were shorter than those shown by Raviola & Wiesel (1978) to induce myopia and excessive growth of the eye.

RESULTS

In this paper we describe the properties of 141 cells recorded in the deprived layers of the l.g.n. in animals that had been monocularly deprived until recording at 4, 12, 24, 70 and 189 days of age, and compare them with 163 neurones recorded in the non-deprived layers of these same animals (see Table 1) and 228 cells studied in a series of normal monkeys (see Table 1 of Blakemore & Vital-Durand, 1986). We also examined 65 units from the l.g.n. of the monkey (P7903) that was normally reared until 44 days and then binocularly deprived until 195 days and 21 l.g.n. cells in F8405, a cynomolgus monkey (*Macaca fascicularis*) binocularly deprived from birth until 358 days of age.

We always recorded on the right side of the brain in case any defect in performance might be restricted to the deprived laminae on the side ipsilateral to the closed eye, as Sireteanu & Hoffmann (1979) have reported for the cat.

General observations

To our surprise, we saw no obvious qualitative abnormalities amongst neurones in the deprived layers. All cells we isolated responded to visual stimuli and could be classified as on- or off-centre and as X or Y (Blakemore & Vital-Durand, 1986). The strength of the antagonistic surround is very variable even for normal l.g.n. cells (Kaplan & Shapley, 1982; Hicks, Lee & Vidyasagar, 1983; Derrington & Lennie, 1984; Blakemore & Vital-Durand, 1986) and we could see no consistent difference in this property between deprived and non-deprived layers.

Despite the paleness of staining and the smaller mean size of cells in the deprived layer of the monocularly deprived animals, it was not especially difficult to isolate units, even in the animal (P7907) deprived for 27 weeks. Fig. 1 *A* is a photomicrograph of the right l.g.n. in this animal, which shows the abnormal histological appearance of the deprived layers. An electrode track that passed through the l.g.n. at this level

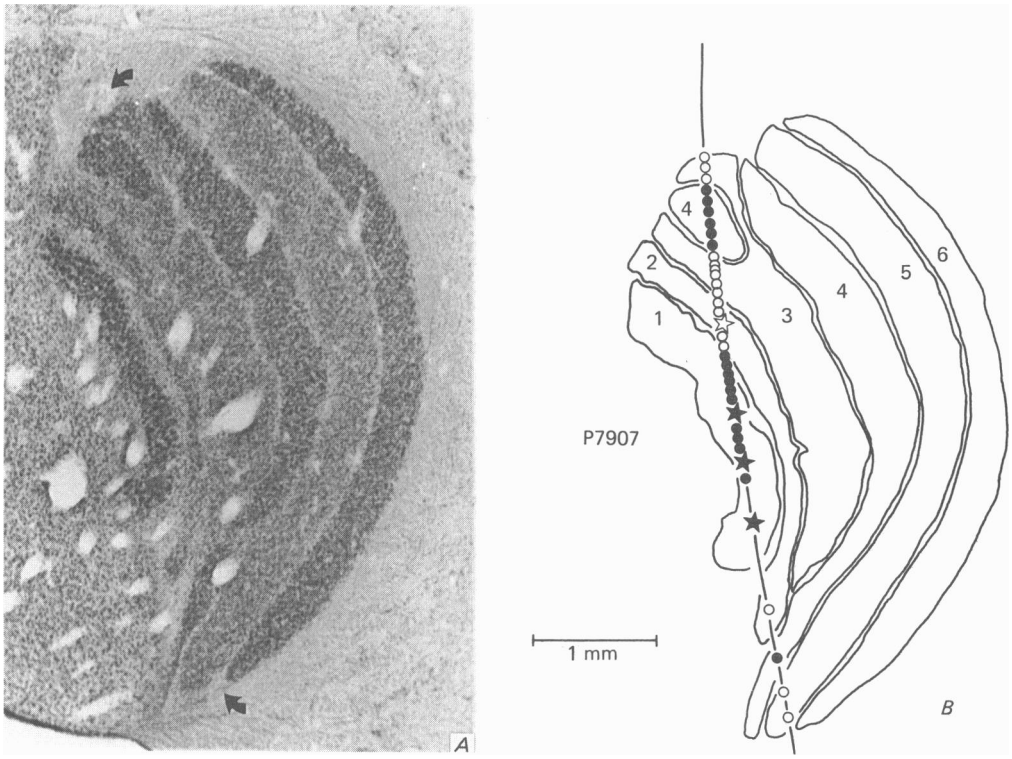

Fig. 1. This is a reconstruction of the first penetration through the right l.g.n. of monkey P7907, which had been monocularly deprived by closure of the lids of the right eye since the day of birth until recording at 189 days. The pale staining of the deprived layers 2, 3 and 5 is immediately evident in the photomicrograph of the coronal section very close to the penetration, shown in *A*. The arrows point to two small electrolytic lesions made by passing current through the electrode tip to mark the point at which it entered and left the l.g.n. on this track. The penetration itself is reconstructed on the drawing of the l.g.n., seen in *B*. Positions at which units were isolated are shown as symbols (circles for X cells, stars for Y cells; filled for left-eye cells, open for right-eye). For the first half of this track, we tried to isolate as many units as possible but after about 3 mm in the l.g.n. we deliberately drove on, recording just one or two cells at each change of eye dominance. Four Y cells were isolated in this penetration, one of them in the deprived layer 2.

is reconstructed in Fig. 1*B*, where the symbols plot the positions at which cells were recorded. The open symbols are for neurones driven through the right (deprived) eye and filled symbols represent left-eye cells. For about the first 3 mm of this track within the l.g.n. we tried to isolate as many cells as possible and there was no obvious difference in the density of units between deprived and non-deprived layers, whether parvocellular of magnocellular.

Patterns of discharge and linearity of spatial summation

We collected histograms of spike discharge in response to stationary, square-wave modulated, phase-reversing sinusoidal gratings, displayed on the television screen at various positions (spatial phases) with respect to the receptive field, in order to

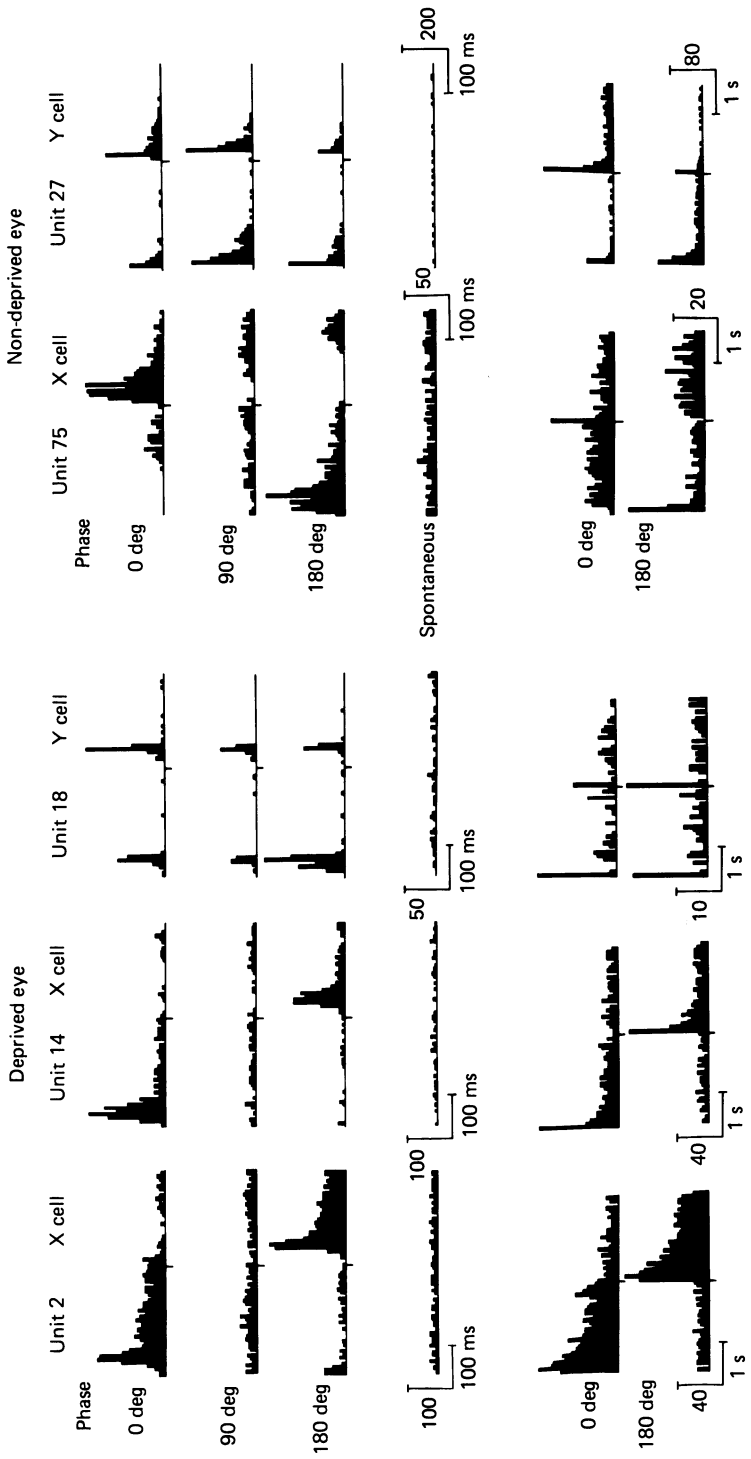

Fig. 2. For legend see opposite.

perform a null position test of spatial summation and hence to classify neurones as linear (X) or non-linear (Y) (see Blakemore & Vital-Durand, 1986). Fig. 2 shows sample histograms for five cells recorded in monkey P7907 (monocularly deprived for 189 days).

There were no obvious over-all differences between deprived and non-deprived cells in the levels of spontaneous or evoked discharge, nor in the general patterns of response. For instance, in Fig. 2, unit 2 (selected as being quite representative of X cells in the deprived parvocellular layers) had a fairly well sustained response, particularly evident in the two bottom histograms for a 0·25 Hz temporal frequency of contrast reversal. Unit 14 was the most transient X cell recorded in the deprived parvocellular layers in this animal (but it was no more phasic in its responses than unit 75, a parvocellular X cell driven through the non-deprived eye). Unit 18, recorded in layer 2, had the highly transient, second-harmonic pattern, characteristic of a Y cell, with no null position.

All 110 units recorded in the deprived parvocellular layers of the monocularly deprived animals were X cells and so too were the majority of magnocellular neurones, as in normal animals (see Blakemore & Vital-Durand, 1986). In the track shown in Fig. 1*B*, three Y cells (★) were recorded, intermingled with many X cells, in the non-deprived layer 1 and, even though the electrode passed for only a short distance through layer 2, a Y cell (unit 18; ☆; responses illustrated in Fig. 2) was

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Fig. 2. These histograms illustrate responses from five representive cells recorded in monkey P7907, which had been monocularly deprived until recording at 189 days of age. The first three cells (units 2, 14 and 18) had receptive fields in the deprived eye while the other two (units 75 and 27) were recorded in non-deprived layers. The X cells (units 2, 14 and 75) all came from parvocellular layers, while the Y cells (units 18 and 27) were isolated in the magnocellular layers. The first three histograms for each unit (80 sweeps, 7 ms bin width) show responses to a stationary horizontal grating of 0·75 contrast being phase-reversed at 2·1 Hz. The calibration bars show the firing frequency in impulses/s (vertical) and the time scale (horizontal). The averaging computer was triggered at the start of each full cycle of phase reversal and the tick below the middle of each histogram indicates the moment of contrast reversal in the middle of the temporal period. The position of the entire display was shifted across the receptive field in small steps to perform a 'null position test' (see Blakemore & Vital-Durand, 1986). The three sample histograms for each unit represent responses at three different phase angles of the display with respect to the receptive field. At phases of 0 deg and 180 deg (with the individual bars of the grating centred on the receptive field) all the units gave clearly detectable responses: the X cells discharged during the half period of the sweep when a bar of the appropriate contrast lay on the receptive field centre; the Y cells produced transient, second-harmonic responses after each contrast reversal. At the 90 deg phase position the border between a light and dark bar of the grating presumably exactly bisected the receptive field, so that contrast reversal produced no net change in luminous flux on the centre or the surround. At this 'null position' none of the X cells produced a detectable response but both Y cells still had a clear second harmonic pattern of discharge. The histograms marked 'spontaneous' were collected under identical conditions but with no pattern displayed on the screen. The bottom pair of histograms for each unit shows responses for contrast-reversing gratings at the 0 deg and 180 deg phase positions with a temporal frequency of reversal of 0·25 Hz, and they thus illustrate the ability of these units to maintain discharges when exposed to a stationary grating for a time of 2 s. There seemed to be no obvious consistent differences in the patterns of response or the maximum firing frequencies between deprived and non-deprived cells.

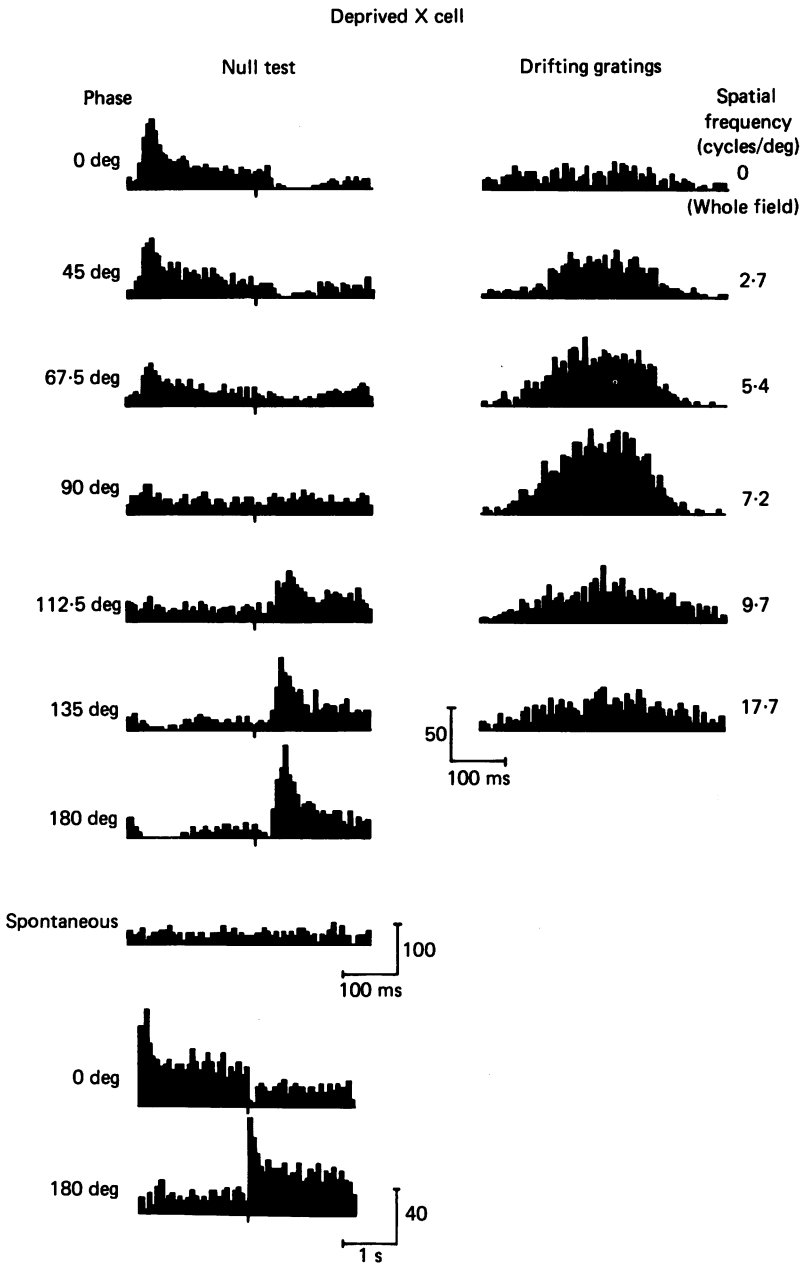

Fig. 3. Discharge histograms illustrating responses to phase-alternating gratings (on the left) and drifting gratings (on the right) for unit P7907/1, an X cell recorded in the deprived layer 3 of the monkey that had been monocularly deprived until recording at 189 days of age. The stimulus conditions for the null position test were as described for Fig. 2 (80 sweeps, 7 ms bin width, 2·1 Hz temporal frequency of square-wave modulation). Responses are shown at seven different phase angles of the display, with respect to the receptive field: the cell had a clear null position at the 90 deg phase (compare the histogram marked 'spontaneous' generated with no grating present on the screen). The

also isolated there. In all monocularly deprived animals, just three (9·7 %) out of the thirty-one deprived magnocellular cells recorded were Y cells, and two of those were in the youngest animal, deprived for only 4 days. In the non-deprived magnocellular layers of the same animals nine out of forty-three cells (21 %) were Y (see Table 1). But for the comparable data from layer 2 of the five normal animals only one out of eleven cells (9·1 %) was Y (see Table 1 of Blakemore & Vital-Durand, 1986). These numbers are too small for statistical significance to be assessed but there is certainly no evidence for a dramatic change in the proportion of Y cells as a result of deprivation.

Spatial properties

We had expected that, after prolonged deprivation, cells in the deprived l.g.n. layers would be sluggish in their responses, and would have larger than normal receptive field centres with reduced spatial resolution for drifting gratings, especially in the foveal representation. To our surprise we saw no convincing change in any of these properties as the electrode moved from non-deprived to deprived layers.

In monkey P7907, deprived from birth for more than six months, the first l.g.n. cell recorded was in the deprived layer 3 (see Fig. 1) and its receptive field lay 1·2 deg from the fovea of the right eye. On the left of Fig. 3 is a series of histograms showing the null position test for this unit, which was typical of the sample from this animal: it was an X cell, with modest spontaneous activity, a clear null (90 deg phase), and brisk, quite well maintained discharges for optimally positioned gratings (see bottom two histograms).

On the right side of Fig. 3 are sample histograms of responses to drifting gratings (0·75 contrast, 2·1 Hz temporal frequency) of various spatial frequencies. Each histogram has a duration equal to one temporal period and therefore contains the response to one complete cycle of the grating. The cell gave little response above spontaneous level for whole-field modulation of the screen (spatial frequency = 0) but the response grew in amplitude as spatial frequency was increased up to 7·2 cycles/deg and then fell, although there was clearly a small fundamental-frequency response even at 17·7 cycles/deg. The full response *versus* spatial frequency function, illustrated in Fig. 4, is comparable in every respect to data from X cells from the foveal representation in normal animals of similar age (see Fig. 15 of Blakemore & Vital-Durand, 1986).

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bottom two histograms on the left also show responses to a phase-alternating grating but at a temporal frequency of 0·25 Hz, illustrating that this cell was able to maintain responses quite well.

For the records on the right, the receptive field was stimulated with a horizontal grating of 0·75 contrast, drifting upwards at 2·1 Hz, and the averaging computer was synchronized to the temporal frequency of drift. Thus, each sweep contains the modulated response produced by passage across the receptive field of one complete spatial period of the grating. The maximum discharge has been adjusted in position to fall roughly at the middle of the sweep. The spatial frequency of the grating was varied, as shown (zero spatial frequency indicates whole-field modulation of the screen with no grating present). This cell produced its maximum modulated response at about 7 cycles/deg and it continued to respond up to about 20 cycles/deg.

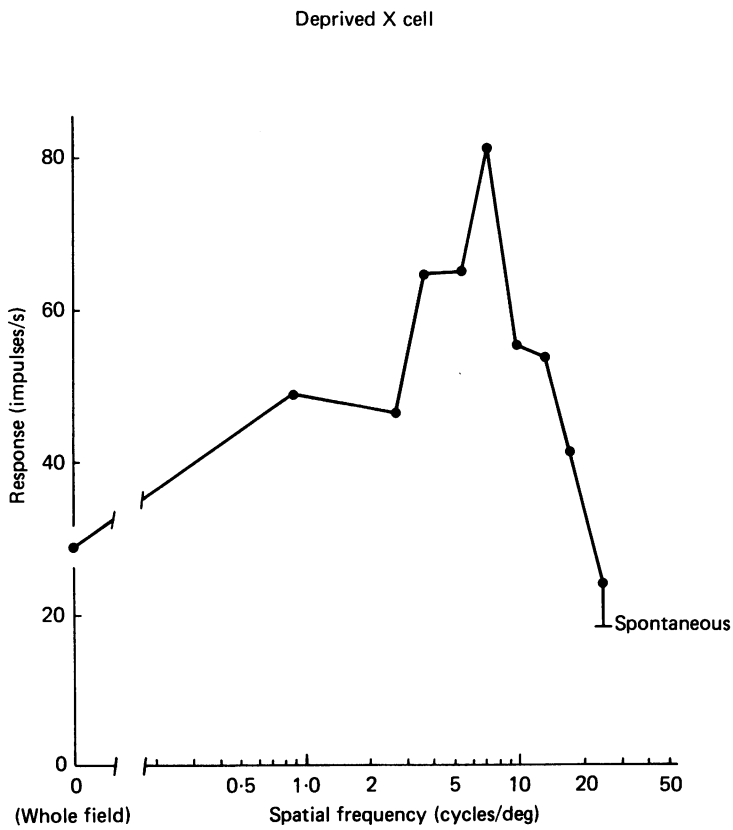

Fig. 4. This graph plots the full response *versus* spatial frequency function for the deprived X cell (P7907/1) for which sample histograms are reproduced in Fig. 3. The receptive field was stimulated with drifting gratings (2·1 Hz temporal frequency, 0·75 contrast) of various spatial frequencies (0 = whole-field modulation). The ordinate plots the maximum discharge frequency, measured from the peak of the modulated response. At the high spatial frequency end, a line is extrapolated down from the last data point to a horizontal bar that indicates the average spontaneous discharge frequency. This cell had a vigorous peak response, pronounced low-frequency attenuation, a narrow band width and a cut-off spatial frequency above 20 cycles/deg. Comparison with comparable response functions from non-deprived cells (see Fig. 15 of Blakemore & Vital-Durand, 1986) suggests that this cell, despite continuous deprivation, had quite normal spatial properties.

In order to see whether there might be a deficit in spatial performance restricted to a certain part of the visual field or to cells of a particular class, we analysed the resolution of all cells as a function of the eccentricity of their receptive fields. Fig. 5, which plots these data on a logarithmic ordinate for non-deprived (*A*) and deprived cells (*B*) from monkey P7907 reveals no striking defects in the deprived layers (although there are insufficient data to say anything about the performance of Y cells). However, just as in normal animals (Derrington & Lennie, 1984; Blakemore & Vital-Durand, 1986) there was a tendency for performance through the contralateral eye to be slightly better than through the ipsilateral. For the animal whose data appear in Fig. 5*A* and *B*, the mean resolution of X cells with receptive fields within 2 deg of the fovea was lower through the ipsilateral (deprived) eye than through the contralateral. Indeed, the difference just reached statistical significance; but so it did

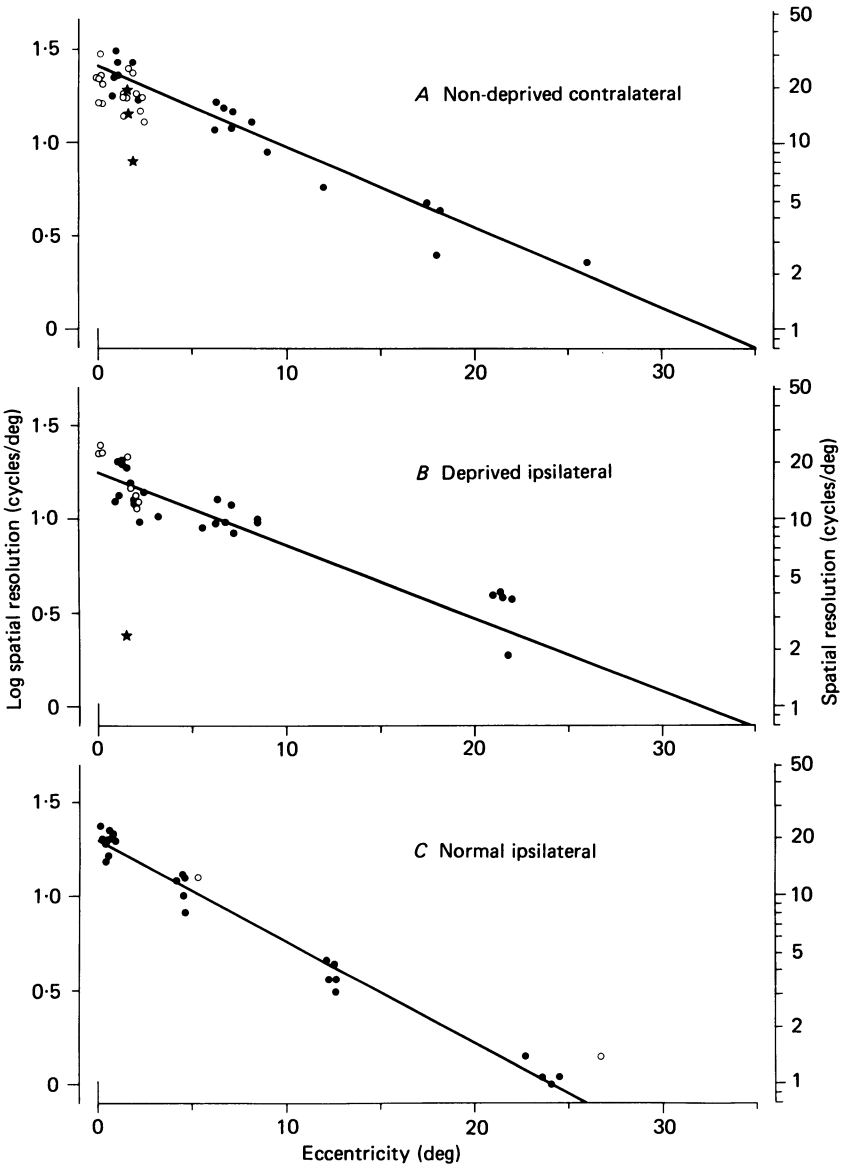

Fig. 5. Spatial resolution is plotted on a logarithmic ordinate against the eccentricity of the receptive field, zero being the centre of the fovea. Parvocellular X cells, ●; magnocellular X cells, ○; magnocellular Y cells, ★. The continuous lines are regression functions ($y = e^{(mx+c)}$) for the parvocellular X cells alone (there were insufficient data for regression lines to be fitted for the other cell types). *A*, results from the laminae connected to the *non-deprived* contralateral (left) eye for P7907, which had been monocularly deprived until 189 days of age. *B*, results from the *deprived* layers of the l.g.n. in P7907, connected to the ipsilateral (right) eye. *C*, comparable data from the ipsilateral (right-eye) laminae of a *normal* monkey, P7905, aged 191 days. Clearly, deprivation has not substantially reduced the spatial performance of neurones in the deprived layers.

for two of the four normal animals, 150 days or more of age (see Fig. 14 of Blakemore & Vital-Durand, 1986).

The magnocellular X cells recorded in this animal (○ in Fig. 5) all had their receptive fields close to the fovea, but parvocellular X cells (●) were studied over a sufficient range of eccentricity for regression lines to be fitted (according to the equation $y = e^{(mx+c)}$). There was little difference between these functions for the deprived, right eye and the non-deprived, left eye in this animal. For comparison, data from the *non-deprived* right eye of a normal monkey of almost identical age (P7905, 191 days) are reproduced in Fig. 5*C*. There are too few data points for the peripheral visual field to justify quantitative comparison: in particular the small difference between deprived and non-deprived ipsilateral-eye samples, for the few data points beyond an eccentricity of 20 deg (compare Fig. 5*B* and *C*), may well be due to the fact that the two sets of receptive fields lay on different meridians. Certainly there is no evidence of a gross defect in spatial resolution for cells in the deprived layers.

Results from the entire series of animals are displayed in Table 2 and Fig. 6. Here we consider only the spatial resolution of all X cells with receptive fields centred within 2 deg of the middle of the fovea. Data from magnocellular and parvocellular X cells are pooled because, just as in normal monkeys (see Blakemore & Vital-Durand,

TABLE 2. Spatial resolution of X cells with receptive fields in the central 2 deg of the visual field (n = number of cells)

		Mean spatial resolution ± S.E. of mean (cycles/deg)					
		Left eye (contralateral)		Right eye (ipsilateral)		Resolution of best cell (cycles/deg)	
Normal animals	Age	Mean ± S.E.	(n)	Mean ± S.E.	(n)	Left eye	Right eye
V7912	New-born	3·57 ± 0·35	(11)	3·57 ± 0·41	(5)	5·2	4·9
P7904	150 days	21·24 ± 0·94	(10)	18·91 ± 1·54	(7)	24·0	24·8
P7905	191 days	23·04 ± 1·67	(8)	19·81 ± 0·73	(10)	27·5	23·4
R8004	433 days	27·01 ± 1·19	(7)	22·37 ± 1·87	(6)	31·7	30·8
P24	> 5¼ years	26·37 ± 1·23	(10)	24·55 ± 1·64	(13)	34·0	35·2
Monocularly deprived animals		Non-deprived		Deprived			
		Mean ± S.E.	(n)	Mean ± S.E	(n)	Non-deprived	Deprived
P7911	4 days	4·17 ± 0·17	(10)	3·36 ± 0·24	(8)	5·0	4·2
P7913	12 days	4·16 ± 0·36	(11)	4·37 ± 0·44	(10)	6·0	7·0
P7910	24 days	6·91 ± 0·32	(12)	5·28 ± 0·36	(11)	8·4	8·3
P7909	70 days	10·51 ± 0·86	(22)	8·76 ± 0·74	(28)	17·6	18·6
P7907	189 days	21·67 ± 1·08	(19)	17·61 ± 1·07	(15)	31·2	24·7
Binocularly deprived from birth		Contralateral left eye deprived		Ipsilateral right eye deprived			
		Mean ± S.E.	(n)	Mean ± S.E.	(n)	Left eye	Right eye
F8405	358 days	23·06 ± 1·57	(9)	18·53 ± 1·69	(7)	33·2	25·6
Binocularly deprived from 44 days							
P7903	195 days	17·19 ± 1·12	(14)	16·7 ± 0·86	(16)	23·6	23·0

1986), there was no evidence in any animal for an over-all difference in resolution between them (see Fig. 5*A* and *B*). Table 2 lists the mean resolutions for all such central X cells, in left-eye and right-eye layers, for all the animals (as well as the resolutions of the very best X cells found in each of these samples). Comparison of mean performance in contralaterally driven (left-eye) and ipsilaterally driven laminae shows a tendency for the former to be slightly superior, especially amongst the older animals, but this difference was no more pronounced in the monocularly deprived than in the normal animals.

The most informative comparison to make is, then, between right-eye laminae alone from deprived and normal animals and this is done graphically in Fig. 6. Open circles plot, as a function of age, the mean spatial resolution (+1 S.E. of mean) for foveal X cells in the right-eye laminae of normal monkeys and the filled circles show the results for the deprived animals. Data for the oldest deprived right eye (plotted at 358 days on the abscissa) come from the animal *binocularly* deprived from birth. It can be seen that the mean resolution of deprived neurones improves steadily with age, by a factor of about 6·5 over the age range studied, and the curve does not seem substantially displaced from that for the right eyes of normal animals.

In Fig. 6 we also plot the value of spatial resolution for the very best cell encountered, using open triangles for right-eye neurones from normal monkeys and filled triangles for the best cells from deprived right-eye laminae. For comparison, filled squares show the values of neuronal 'acuity' for the best left-eye cell (all visually experienced) in each normal and monocularly deprived animal. Again there was no difference between deprived and normal right-eye cells, and the best right-eye cell recorded was similar in spatial performance to the best left-eye neurone in each monkey, even if monocularly deprived.

Visual latency

For all cells in which we collected histograms of responses for a full range of spatial positions for a phase-alternating grating we measured the latency of the discharge elicited by the contrast reversal of an optimally positioned grating, as already described (Blakemore & Vital-Durand, 1986). The results for cells recorded in the deprived layers of the monocularly deprived animals are plotted in Fig. 7, where the continuous lines show the envelope of latencies for non-deprived neurones from animals of different ages (from Fig. 11 of Blakemore & Vital-Durand, 1986).

Amongst deprived cells, just as for normal ones, there is a tendency for latency to decline during the first few weeks of life and, especially in older animals, for the latencies of magnocellular neurones to be shorter on average than those of parvocellular cells. The data points for deprived cells generally lie within the envelope of normal data; there is no evidence for an effect of deprivation on the visual latencies of l.g.n. cells.

Binocular deprivation

One cynomolgus monkey (F8405) had the lids of both eyes closed within about 1 h of birth and was then binocularly deprived until recording at almost a year of age. In this animal we concentrated mainly on the striate cortex (C. Blakemore & F. Vital-Durand, in preparation) but we also recorded twenty-one l.g.n. cells. All

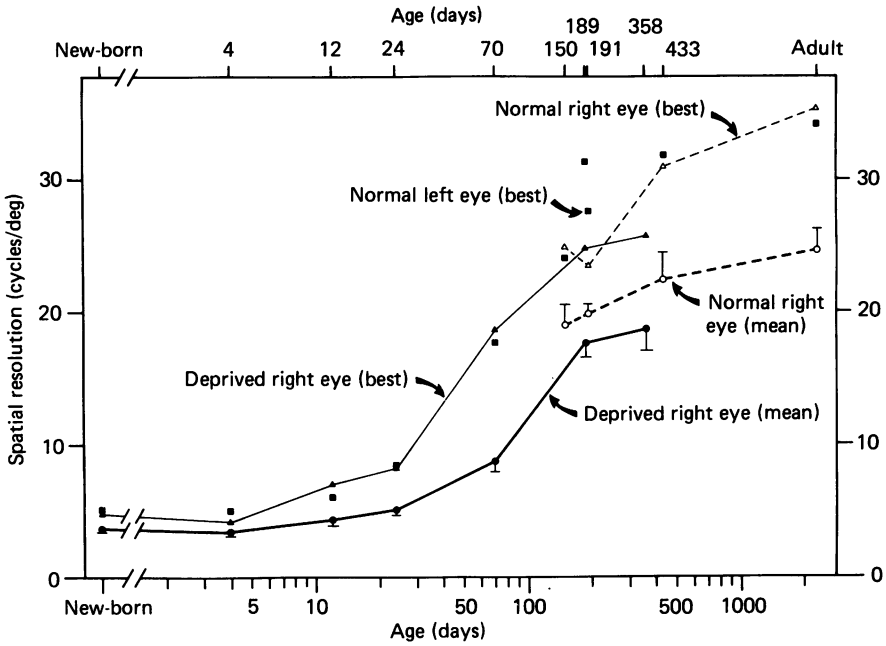

Fig. 6. Spatial resolution is plotted as a function of age (on a logarithmic abscissa) for all X cells (parvocellular and magnocellular) with receptive fields centred within 2 deg of the middle of the fovea, for the entire series of animals. The open circles joined by dashed thick lines show the mean (+1 S.E. of mean) neural 'acuity' for such foveal X cells connected to the ipsilateral (right) eye in normal monkeys. The filled circles, joined by thick lines, plot the mean resolution for cells connected to the *deprived* ipsilateral eye in the series of monocularly deprived animals, as well as data from right-eye cells in the new-born animal and in the long-term, continuously binocularly deprived animal (plotted at 358 days on the abscissa). Clearly, the mean resolution of these foveal cells increases considerably with age, despite deprivation, and there does not appear to be any obvious discontinuity between the data from deprived and non-deprived right-eye cells. For each normal animal an open triangle (joined by thin dashed lines) shows the spatial resolution of the best right-eye cell encountered in the sample. Filled triangles, connected with thin lines, show the best deprived right-eye cells. Again, there is no suggestion that performance was worse in deprived than in normal animals. Filled squares show the 'acuity' of the best cell found in laminae connected to each non-deprived left eye.

were X cells (only two were magnocellular) and, despite the prolonged period of deprivation their spatial properties seemed quite normal (see Table 2). The best cell recorded had an 'acuity' of more than 32 cycles/deg and the mean resolutions for foveal X cells in both right-eye and left-eye layers were roughly in line with comparable data from normal animals of similar age. In particular, the mean acuity for left-eye foveal cells was 23·06 cycles/deg (S.E. of mean 1·57; $n = 9$) compared with 27·01 cycles/deg (S.E. of mean 1·19; $n = 7$) for the left-eye X cells from a normal rhesus monkey (R8004), almost 11 weeks older (Table 2).

Before we had a clear picture of how little effect even continuous deprivation has on the physiological development of the l.g.n., we started to plan experiments on the effect of allowing an initial period of normal visual experience to see whether this might 'protect' the l.g.n. from any effects of subsequent deprivation. We began, then, with a single animal, P7903, binocularly deprived from 44 days until recording

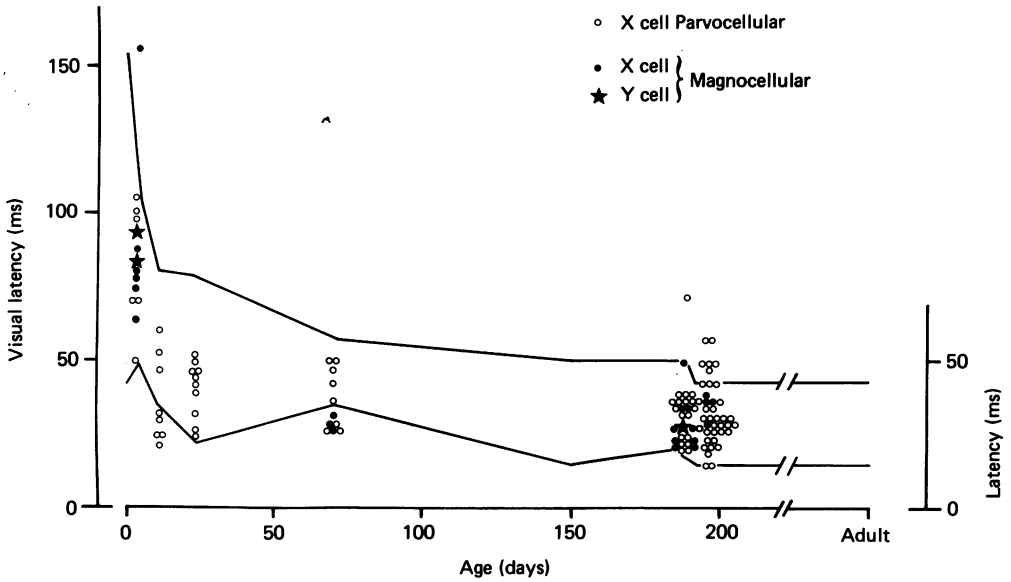

Fig. 7. The change of latency for visual stimulation is plotted as a function of age for all l.g.n. neurones recorded in the deprived layers of monocularly deprived animals, for which a full set of histograms was collected. In each case, latency was measured from histograms for a rapidly phase-reversing grating (2·1 Hz) optimally positioned over the receptive field to produce the maximum modulated discharge. The measure taken was the time from phase shift of the pattern to the first bin of the elicited discharge that contained more spikes than any bin in the histogram of spontaneous activity. Data from parvocellular neurones are plotted with open symbols and those from magnocellular cells with filled symbols, circles for X cells and stars for Y cells. The continuous lines, reproduced from Fig. 11 of Blakemore & Vital-Durand (1986), show the envelope of all latencies for cells in non-deprived layers. The visual latencies of most deprived cells lie within the normal range.

at 195 days. We recorded 65 l.g.n. cells in this animal (see Table 1) and they seemed quite normal in their properties, including the spatial resolution of cells in the foveal representation area (Table 2).

DISCUSSION

Our conclusions are simple though surprising. For the characteristics that we examined, monocular deprivation of pattern vision for up to 27 weeks and binocular deprivation for almost a year had no obvious effect on the physiological properties of monkey l.g.n. neurones. The general receptive field properties of cells, their visual latencies, their levels of spontaneous activity, their peak firing rates, their capacity to maintain discharges and, most unexpected, their ability to resolve grating stimuli seemed little affected, if at all, by deprivation. As a note of caution we must emphasize that there are some important properties that we did *not* determine with sufficient precision to allow us to be certain that they were uninfluenced by deprivation. In particular, the chromatic selectivity and temporal characteristics of

cells, which we looked at only cursorily, certainly deserve further study. We had the impression that, on the whole, deprived l.g.n. cells are not quite as good as normal cells in their ability to follow high temporal frequencies of drift or contrast reversal of gratings. Derrington & Hawken (1981) in fact found a slight reduction in mean peak temporal frequency for l.g.n. cells from a dark-reared cat (but no such effect in the deprived laminae of monocularly deprived cats).

One of the most consistent findings in studies of the deprived l.g.n. laminae of monocularly deprived cats is a reduction in the proportion of recorded Y cells (e.g. Sherman *et al.* 1972; Geisert, Spear, Zetlan & Langsetmo, 1982; Friedlander & Stanford, 1984), although it must be said that Shapley & So (1980) were unable to replicate this effect and its interpretation, in any case, remains a question of debate (Eysel *et al.* 1979; Friedlander *et al.* 1982). Unfortunately the proportion of Y cells (classified on the basis of their non-linearity of spatial summation) is very low in the normal primate l.g.n., even when the magnocellular laminae are considered alone (see Blakemore & Vital-Durand, 1986). We encountered very few Y cells in the deprived lamina 2 of our animals, but they were just as rare in lamina 2 of the series of *normal* animals. There might conceivably be subtle effects of deprivation in the monkey on the numbers of Y cells, on their responsiveness (as Derrington & Hawken, 1981, found in the cat), on their spatial properties, or on their structure–function relations, but our data are inadequate to permit us to comment on these possibilities. Recently Sesma, Irvin, Kuyk, Norton & Casagrande (1984) reported the effects (or rather lack of effects) of monocular deprivation on the l.g.n. of a New-World primate, the bush baby, *Galago*. They too encountered no difficulty in recording neurones in the deprived layers and no obvious change in the proportions of the various cell types. They even mention that the spatial properties of deprived neurones were normal.

In their original study of the l.g.n. in monocularly deprived cats, Wiesel & Hubel (1963) described a small number of cells in the deprived laminae with unusually weak inhibitory surrounds, and Ikeda *et al.* (1977) reported a general failure of development of the surround mechanism for the few visually responsive cells that they found with receptive fields in the occluded portion of the temporal retina in kittens reared with surgical convergent squint. In the normal monkey l.g.n., the strength of the surround, revealed by the reduction of response to achromatic gratings of low spatial frequency, is very variable (Kaplan & Shapley, 1982; Hicks *et al.* 1983; Derrington & Lennie, 1984). In the deprived laminae of our monocularly deprived monkeys the proportion of cells with strong surrounds (see Fig. 4) seemed quite normal.

The maturation of spatial resolution for l.g.n. X cells in normal monkeys follows much the same time course as the behavioural improvement in acuity (Blakemore & Vital-Durand, 1986). Since visual acuity through the deprived eye is severely impaired after monocular deprivation (Harwerth, Smith, Boltz, Crawford & von Noorden, 1983), we expected that the spatial resolution of l.g.n. cells in the deprived laminae, especially in the foveal representation, would similarly be poor. If this had been the case, deprivation amblyopia could have been explained in terms of interference with the development of the peripheral mechanisms that normally limit acuity in the monkey. However, even though we deliberately recorded ipsilateral to the deprived eye, where Sireteanu & Hoffmann (1979) found effects on the acuity of l.g.n. cells in the cat, we found no obvious defect in spatial resolution even in the

oldest monocularly deprived animal, nor in the monkey binocularly deprived until almost a year of age. The receptive fields with the highest spatial resolution in the very central fovea of the right eye were, in every case, very close in performance to the best of the normal left-eye fields (Figs. 5 and 6). The mean acuity of receptive fields in the central 2 deg of the visual field was slightly worse for the right eye than the left in the three oldest monocularly deprived animals, but this was also the case for the normal monkeys (see Blakemore & Vital-Durand, 1986 and Table 2) and for the binocularly deprived animal; it presumably simply reflects the slight difference in dimensions of the dendritic fields of ganglion cells in nasal and temporal retina (Perry, Oehler & Cowey, 1984).

It would be interesting to record in the l.g.n. contralateral to the deprived eye in monocularly deprived monkeys, in case there are effects on the performance of neurones there, but we are confident, on the basis of our present results, that the spatial characteristics of receptive fields mature considerably in the absence of normal visual stimulation.

In the preceding paper (Blakemore & Vital-Durand, 1986) we argued that there must be a neural component in the maturation process, even though 'passive' changes in optical quality, size of the eye and foveal cone mosaic are likely to contribute to the post-natal improvement of resolution of primate l.g.n. cells (and hence behavioural acuity). Presumably deprivation does not interfere with the non-neural factors, and the present results suggest that whatever the neural component is (increase in the strength of excitatory driving and/or reduction in synaptic convergence at some point) it too matures without patterned visual stimulation. In this context it is gratifying to see that, despite the obvious effect of monocular deprivation on the size and staining characteristics of the perikarya of l.g.n. cells in cat and monkey, their dendritic morphology and the ultrastructural appearance of the synapses on them seem unaffected (Winfield & Powell, 1980; Winfield *et al.* 1980; Wilson & Hendrickson, 1981). In fact the sizes of l.g.n. cell bodies, in a variety of experimental conditions, are well related to the dimensions of their axonal territories in the striate cortex (Vital-Durand *et al.* 1978; Swindale *et al.* 1981; Headon *et al.* 1985); so, the growth or shrinkage of an l.g.n. cell body may merely reflect the metabolic demands of its axon terminals and may tell one almost nothing about its physiological properties.

Paradoxically, then, although peripheral factors appear to play a large part in limiting the normal slow post-natal improvement of behavioural acuity in primates, even prolonged deprivation, which precipitates a gross deficit in visual acuity, seems to have little or no effect on these peripheral processes. Presumably the neural defect underlying the acuity loss in deprivation amblyopia lies central to the l.g.n.

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