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SPATIAL AND TEMPORAL PROPERTIES OF CAT GENICULATE NEURONES AFTER PROLONGED DEPRIVATION

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SUMMARY

1. Extracellular recordings were made from the dorsal lateral geniculate nucleus of monocularly deprived, dark-reared and normal cats. The spatial and temporal properties of the neurones were studied.

2. The mean acuity of X-cells with receptive fields within 3 degrees of the area centralis was 3·9 c/degree for deprived eye cells from monocularly deprived cats, compared with 3·8 c/degree for normal cells.

3. The mean activity of X-cells with receptive fields within 4 degrees of the area centralis was 4·3 c/degree for a dark-reared cat compared with 4·0 c/degree for a normal cat.

4. The peak response rates of X-cells to their best spatial frequency were determined. The mean values for the normal, monocularly deprived and dark-reared populations were all similar.

5. Measurement of the temporal frequency tuning of a number of cells was made. The mean peak temporal frequency for the dark-reared X-cells was lower than for monocularly deprived or normal X-cells.

6. The results are discussed with reference to the location of the primary neural deficit induced by visual deprivation.

INTRODUCTION

In the cat monocular deprivation of vision during development produces an almost complete loss of striate cortical cells with receptive fields in the deprived eye (Wiesel & Hubel, 1963*b*), a severe impairment of the behaviourally determined visual capacity (Wiesel & Hubel, 1963*b*, 1965*b*; Dews & Wiesel, 1970), and a reduction in visual acuity (Giffin & Mitchell, 1978). Prolonged binocular deprivation results in a general reduction in responsiveness and specificity of cortical neurones (Wiesel & Hubel, 1965*a*). The spatial frequency tuning of cortical neurones from binocularly deprived cats is also impaired (Derrington, 1980). Visual acuity is decreased following binocular deprivation, although there may be considerable recovery following the resumption of normal visual experience (Timney, Mitchell & Giffin, 1978).

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The first study of the effect of visual deprivation on the lateral geniculate nucleus (LGN) (Wiesel & Hubel, 1963*a*) found considerable cell shrinkage in the deprived laminae, with some cells showing abnormally sluggish responses. Until quite recently it was widely held that the major neurophysiological deficit after visual deprivation was at the level of the striate cortex. However, further physiological effects of monocular deprivation have now been found in the LGN: cells from the deprived laminae have significantly reduced spatial resolution (Maffei & Fiorentini, 1976; Lehmkuhle, Kratz, Mangel & Sherman, 1980). Sireteanu & Hoffmann (1979) have reported that the deprivation effects found after monocular deprivation are restricted to the lamina ipsilateral to the deprived eye (A1), whilst Shapley & So (1980) have reported that deprivation produces no discernible effect.

Similar, but more severe, behavioural and physiological deficits have also been reported after experimentally induced convergent strabismus in cats (Ikeda & Wright, 1976; Ikeda & Jacobson, 1977; Ikeda, Plant & Tremain, 1977; Jacobson & Ikeda, 1979), which also affects the development of retinal ganglion cells (Ikeda & Tremain, 1979). These authors suggest that strabismus exerts its effect by defocusing the area centralis of the squinting eye, thereby depriving it of the high spatial frequencies to which X-cells are most responsive. Rearing kittens with daily administration of atropine eye drops, which produces a blurred retinal image, results in a deficit similar to that produced by convergent strabismus (Ikeda & Tremain. 1978).

In this paper we describe the spatial and temporal properties of LGN cells recorded in normal, monocularly deprived and dark-reared cats. A brief account of some of these results has already been published (Derrington & Hawken, 1980).

METHODS

Deprivation

Two kittens were deprived of vision, monocularly, by lid-suture. Deprivation was begun before the time of natural eye opening and lasted until the day of recording 4 or 6 months later. Animals were carefully checked each day for any slight openings in the sutured eye-lids and in these animals no such 'windows' were observed. Binocular deprivation was attained by dark-rearing. The duration of the dark-rearing was 18 months and the kitten was brought out of the dark on the day of the acute experiment. The deprivation procedures were identical to those described by Blakemore & Van Sluyters (1975).

Recording

Normal and deprived cats weighing between 1 and 2·5 kg were prepared for recording using the procedure described by Derrington & Fuchs (1979) with the exception that during recording anaesthesia was maintained by I.V. injections of urethane (250 mg/kg loading dose and 25–50 mg/kg.hr thereafter). Artificial ventilation was carried out using room air. Expired carbon dioxide was monitored and maintained at 4–4·5%. Single cells were recorded in the LGN using glass-coated tungsten micro-electrodes (Merrill & Ainsworth, 1972), with 4–8 μm exposed tips. The receptive field of each isolated cell was projected onto the centre of an oscilloscope screen on which sinusoidal gratings were displayed using the method of Schade (1956) as described by Derrington & Fuchs (1979). The mean luminance of the screen was 200 cd/m^2, and it subtended 7·5 × 6 degrees at the viewing distance of 2 m. Cats were fitted with zero-power contact lenses with 2 mm pupils, refracted ophthalmoscopically and fitted with supplementary lenses to focus the display screen. Refraction was checked by changing lenses to obtain the highest acuity value for central X-cells. The following data were collected under computer control.

Spatial frequency tuning

Each cell was tested with a standard set of gratings of twelve spatial frequencies ranging from 0·18 to 8·0 c/degree (in 0·5 octave steps), a zero spatial frequency (temporal modulation of a uniform field) and a blank (uniform screen with no temporal modulation), in random order. The drift rate was 4 Hz, which is close to the optimum for most cells (Derrington & Fuchs, 1979). Response histograms to 30 cycles of each stimulus were collected; the blank collection was over the same period, and with the same averaging cycle as for each of the temporally modulated stimuli. The average modulation in firing rate at 4 Hz (F1) and the mean firing rate (F0) during the presentation of each stimulus were calculated using a Fast Fourier Transform (FFT) program. Smooth curves relating response (F1 or F0) to spatial frequency were drawn through the data points after smoothing (3 point moving average weighting by 0·17, 0·66, 0·17) by interpolating with a cubic spline algorithm (Pennington, 1970). From the smoothed curves we obtained estimates of: (1) corner frequency, the high frequency at which the response had fallen to half-height; (2) acuity, the highest spatial frequency at which the amplitude of F1 was fifteen counts greater than the value of F1 for the blank (X-cells), or the spatial frequency at which either F0 or F1 was fifteen counts greater than the blank (Y-cells).

Null phase test

The non-linearity of spatial summation characteristic of Y-cells is most easily shown by the null phase test (Hochstein & Shapley, 1976). A grating of spatial frequency *ca.* 0·5 octaves below the resolution limit for the cell was presented reversing in phase. The responses to thirty presentations were accumulated in a histogram. Comparison of the responses at eight different spatial phases covering 1 cycle showed whether the cell showed a null phase (X-cell) or a frequency-doubled response (Y-cell).

Temporal frequency tuning

Temporal frequency tuning was carried out using a moving grating of optimum spatial frequency (to within 0·5 octaves) and of contrast 0·5. Histograms of the average response to either 15 sec or 15 cycles of drift (whichever took longer) were collected with the grating drifting at frequencies between 0·5 and 32 Hz. Average modulation of firing rate at the drift frequency of the grating was measured using the FFT and used to construct a temporal frequency tuning curve.

RESULTS

In this report we present quantitative data on 119 LGN neurones recorded from four kittens. For spatial frequency tuning we obtained thirty X-cells from the deprived lamina of the two monocularly deprived kittens and forty X-cells from the non-deprived lamina of the two monocularly deprived kittens and the normal kitten, and sixteen X-cells from the dark-reared kitten. All the receptive fields were within 8 degrees of the area centralis.

X/Y classification

Cells were classified as X or Y by visual inspection of the peristimulus time histograms (Derrington & Fuchs, 1979). Fig. 1 illustrates responses of X-cells (Fig. 1*A*) and Y-cells (Fig. 1*B*) cells from animals reared under the different conditions. The spatial frequency of the gratings used for the test was close to the corner frequency (see Methods) for the individual cells. There is no discernible difference between the X-cells in each condition. The cells all had their receptive fields within 2 degrees of the area centralis. The X-cells all show null responses (by definition) and had corner frequencies greater than 3·0 c/degree while the Y-cells all show frequency doubling and had corner frequencies of less than 1 c/degree.

We found no difficulty in isolating X- or Y-cells in the deprived lamina of the

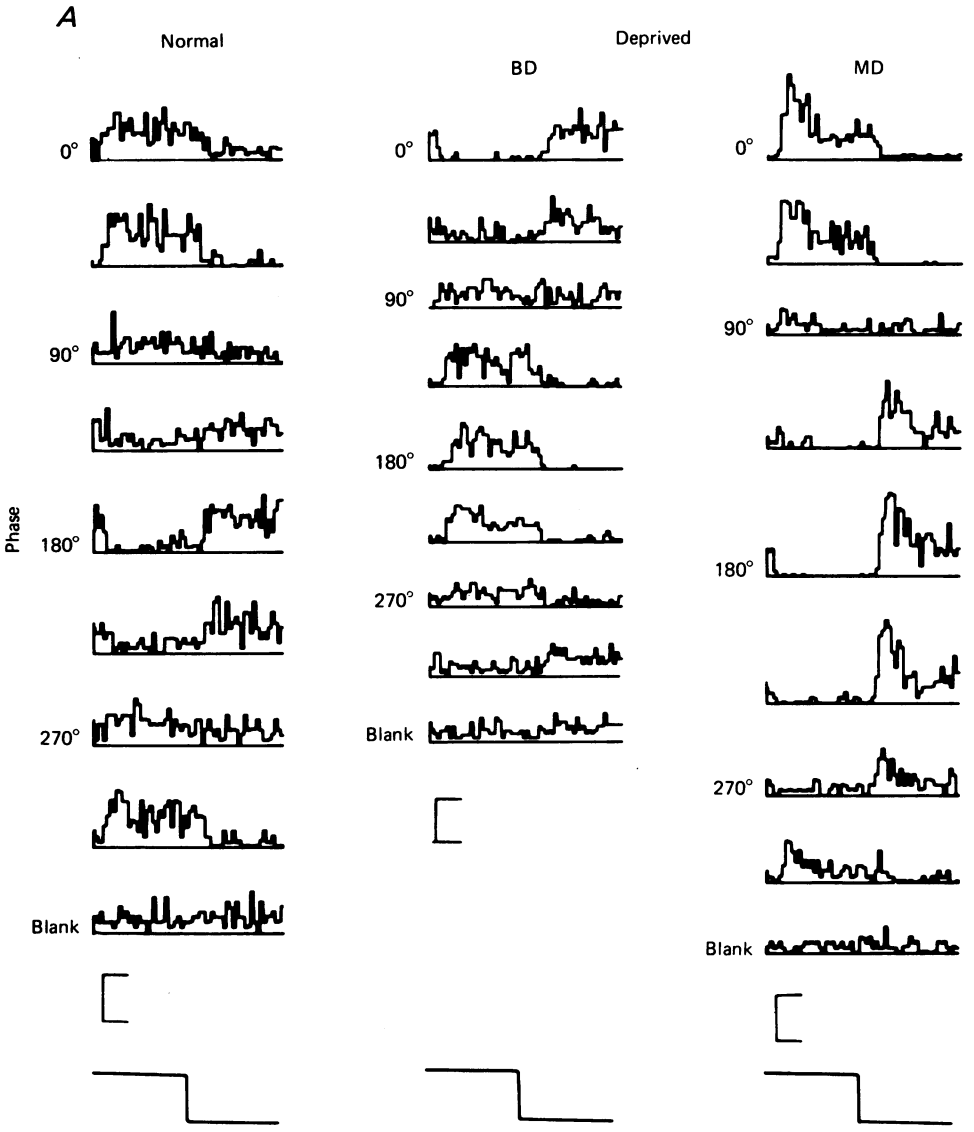


Fig. 1. For legend see facing page.

monocularly deprived cats or in the LGN of the dark-reared cat. Further, the response amplitudes of X-cells to square wave modulation of the stationary gratings used in the X/Y test were not noticeably different in the three examples shown (Fig. 1*A*). Similarly, the mean peak response rates of X-cells from the normal or deprived cats to stimulation with drifting gratings at their preferred spatial frequency were not significantly different (Table 1). On the other hand the mean Y-cell peak response from the normal cat is greater than the means of the Y-cells from the deprived or normal lamina of the monocularly deprived cats or from the dark-reared cat, and in fact these differences are significant (Table 1).

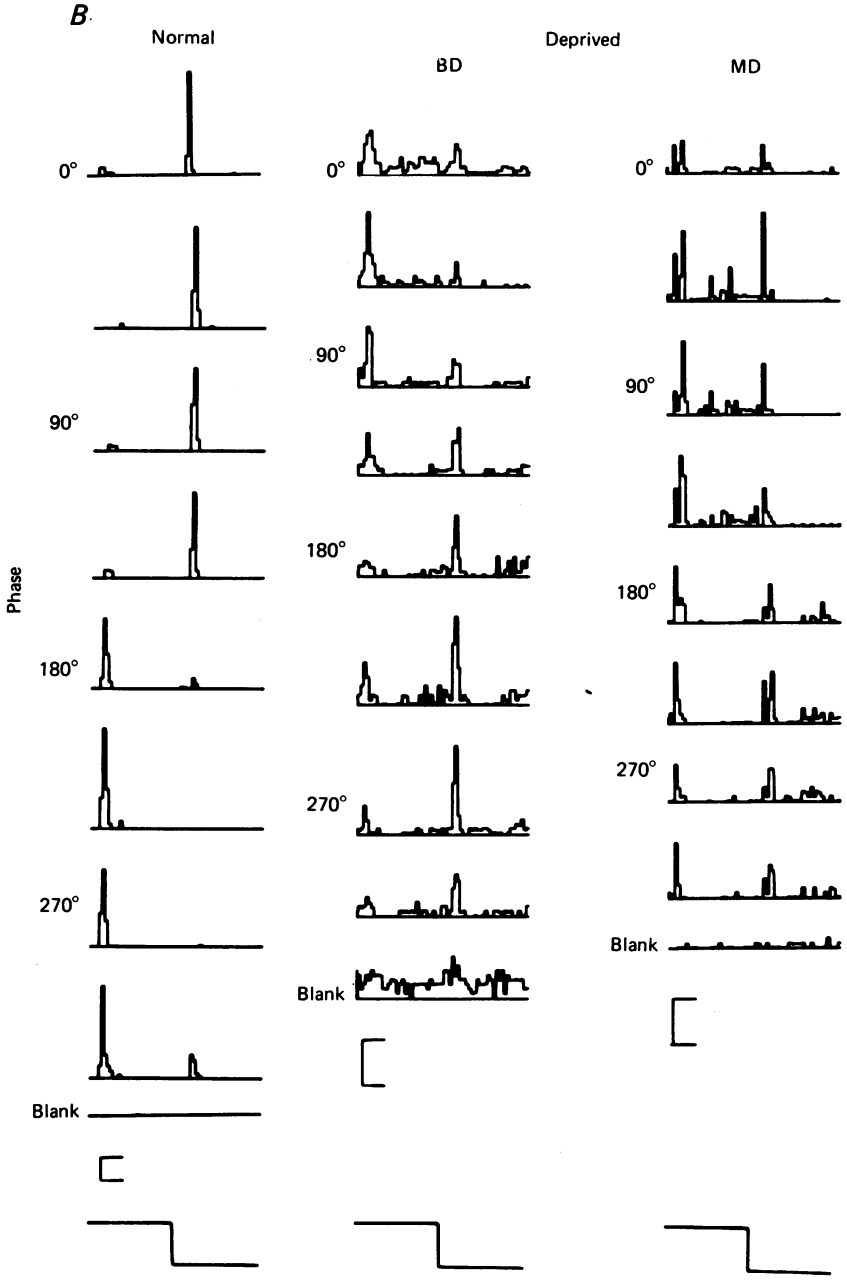
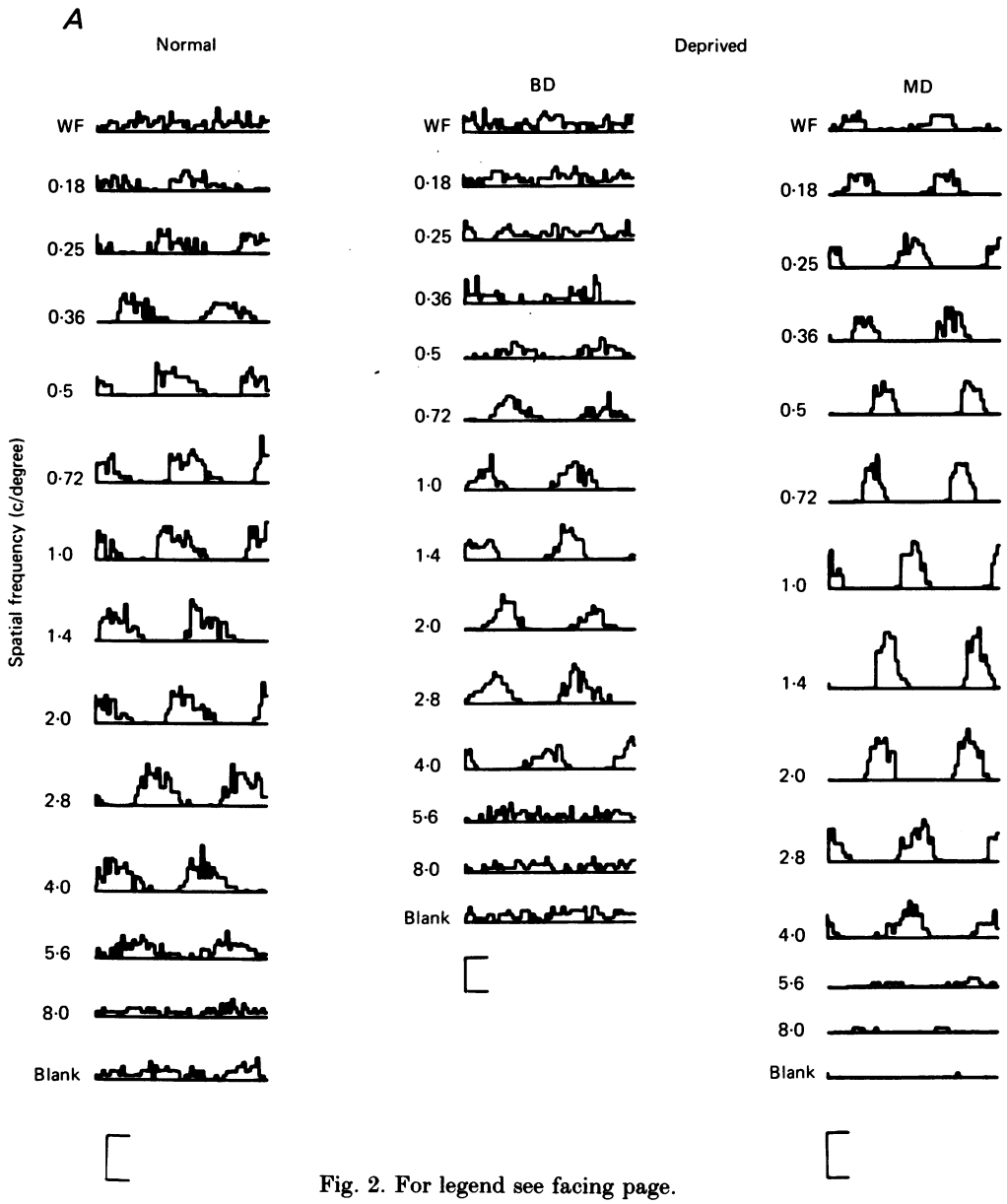


Fig. 1. *A*, the null phase test for three X-cells from animals reared normally (column 1), binocularly deprived (BD, column 2) and monocularly deprived (MD, column 3). The normal and the MD cells had on-centres while the BD cell was off-centre. Each cell shows a null response at about 90 and 270 degrees. *B*, the same test as in *A*, showing the responses of three Y-cells from normal and deprived animals. The calibration for each set of histograms is shown directly under each blank. Vertical represents 40 impulses/sec, horizontal 80 msec. Immediately under each calibration bar is shown the temporal wave-form of the stimulus; up is on.

Spatial frequency

The acuity of cells was measured from response histograms. Fig. 2 gives examples of the response histograms from normal and deprived eye cells to the range of spatial frequencies used. The X-cells all show modulated responses up to at least 4 c/degree (Fig. 2*A*). The Y-cell from the monocularly deprived kitten responds up to 2·0 c/degree with modulation and shows an unmodulated increase in mean rate at 2·8 c/degree, a feature seen in a number of Y-cells and representing the contribution of non-linearities of spatial summation. The other Y-cells in the examples do not respond above



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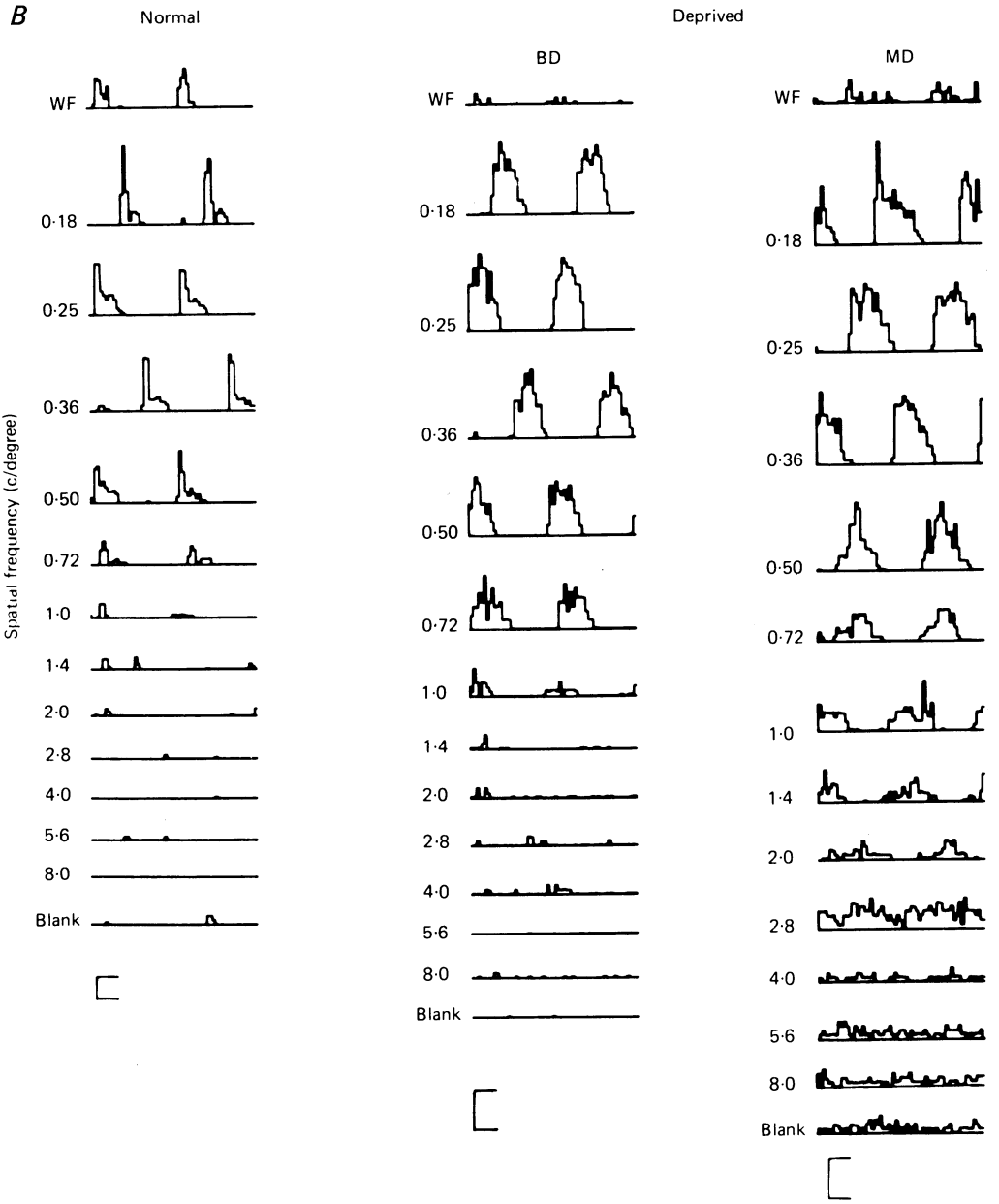

Fig. 2. *A*, response histograms of X-cells to 2 cycles of gratings of different spatial frequencies. The first histogram (WF, whole field) represents the response to temporal modulation of a uniform field. The last histogram represents the response to a uniform field not modulated. The intervening histograms give the response to gratings of the spatial frequency shown to the left of the histogram. All the cells had receptive fields within 2 degrees of the area centralis. *B*, response histograms of Y-cells to 2 cycles of gratings in the same pattern as described in *A*. All cells had receptive fields within 2 degrees of the area centralis. Calibration as for Fig. 1.

1·0 c/degree (Fig. 2*B*). The peak X-cell responses are all above 1 c/degree while the peak Y-cell responses are seen at less than 0·5 c/degree.

For quantitative estimates of the spatial tuning of visual neurones it is normal to measure contrast sensitivity functions rather than response functions (Enroth-Cugell & Robson, 1966; Movshon, Thompson & Tolhurst, 1978*a*, *b*), although in visual cortical cells at least, response and sensitivity functions are similar in shape (Movshon *et al.* 1978*c*). Since no such comparisons exist for LGN neurones and since our definition of acuity is arbitrary, we thought it worthwhile to compare the acuity values obtained from sensitivity and response measures. Fig. 3 shows a contrast sensitivity curve and a response curve from the same cell; in this case the general shape of the curves is the same and the acuity values are identical. The inset graph on Fig. 3 shows

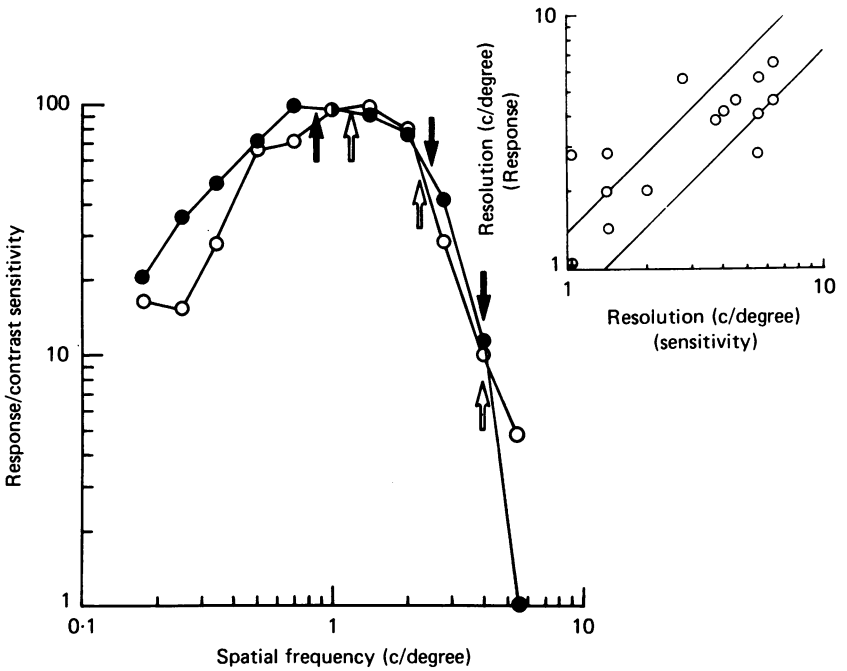

Fig. 3. A comparison between the contrast sensitivity function (open circles) and the response function (filled circles) for an X-cell from the deprived lamina of a monocularly deprived cat. The scales have been adjusted so that the peak values are equal. Filled and open arrows indicate, for response and sensitivity curves respectively (from left to right), best frequency, corner frequency and acuity. The inset shows the correlation between the acuity values measured on the two types of curve for seventeen cells.

TABLE 1. The peak firing rates in response to the best spatial frequency for X- and Y-cells from normal and deprived LGN neurones

	Peak firing rate (impulses/sec)	
	X-cells (mean ± S.D.)	Y-cells (mean ± S.D.)
Normal	129 ± 27 (17)	243 ± 55 (8)
Monocularly deprived	111 ± 32 (15) } 119 ± 37 (22)	139 ± 30 (8) } 143 ± 29 (11)
	136 ± 44 (7) }	152 ± 25 (3) }
Dark-reared	122 ± 41 (16)	155 ± 44 (13)

Number of observations in parentheses.

a comparison of the two methods on a sample of eighteen cells; the correlation is good ($r = 0{\cdot}77$, d.f. = 17). It seemed justified, then, to use the response histograms to obtain a measure of acuity. We chose response because it is much more quickly measured, allowing a greater sample of neurones to be collected from each animal.

Acuity distributions

It is well established that in normal animals the spatial resolution of X-cells decreases with eccentricity, especially for the central 10 degrees (Ikeda & Wright, 1976; So & Shapley, 1979). Fig. 4 shows acuity plotted against eccentricity for samples of normal and deprived LGN cells. We have pooled the neurones recorded from the normal animal and from the non-deprived laminae of the two monocularly deprived cats, and compared them with those recorded from the deprived laminae. There is no difference between the distributions.

Especially important is the fact that the cells of the deprived lamina that are close to the area centralis have high acuity values. The mean values for X-cells within 3 degrees of the area centralis are not significantly different ($3{\cdot}8 \pm 0{\cdot}7$ c/degree for the normal and $3{\cdot}9 \pm 0{\cdot}8$ c/degree for the deprived eye cells; $P > 0{\cdot}1$, Student's t test). Comparison of the acuity values for the normal and the dark-reared animal is made in Fig. 4*B*. Again it is clear that there is no difference in the distributions (mean values of 4·0 for the normal and 4·3 for the dark-reared animal, for cells within 4 degrees of the area centralis). We did not attempt to make comparisons between the Y-cell acuities as our samples were relatively small.

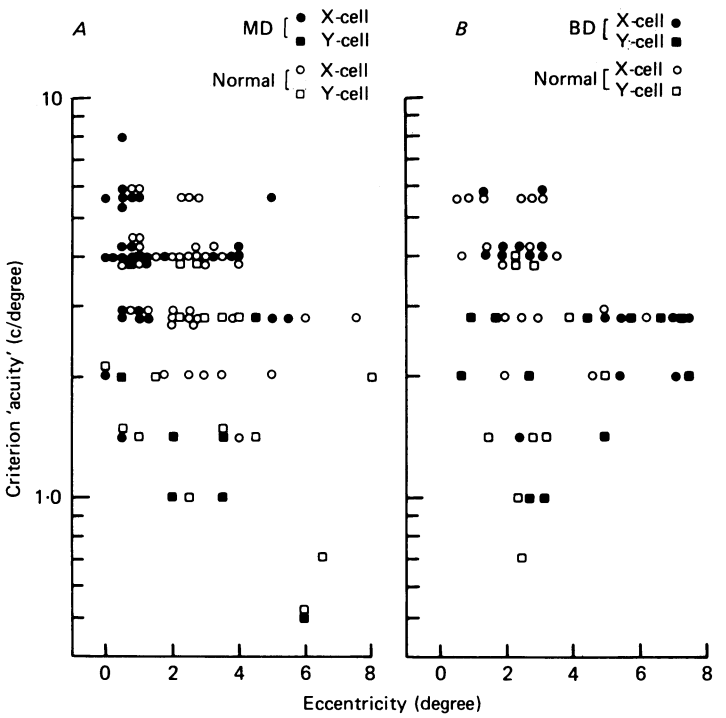

Fig. 4. *A*, comparison of acuities of neurones from the normal and deprived laminae. The neurones from the normal animals and from the experienced eye of the monocularly deprived (MD) cats have been pooled as the normal sample. *B*, comparison of acuities of neurones from normal and dark-reared (BD) cats.

Receptive field organization

It is clear that one of the functional differences between retinal ganglion cells and LGN relay neurones is an increase in the strength of the inhibitory surround (Hubel & Wiesel, 1961). We have found that for some central X-cells the response falls to zero at low spatial frequencies, indicating complete surround inhibition. Wiesel & Hubel (1963*a*) reported that some of the neurones recorded in the deprived laminae had weaker surrounds compared with cells from the non-deprived laminae. Similarly, Ikeda, Tremain & Einon (1978) found a lack of development of the inhibitory surround in kittens reared with convergent squint (induced at 3 weeks).

We could find no evidence for any lack of development of the surround in either dark-reared or monocularly deprived kittens. Fig. 5 shows the tuning curves for three cells, one from each of the three rearing conditions, where there is a complete low-frequency cut at 0·18 c/degree. For any one penetration, within a single lamina, where cells had overlapping receptive field centres, there was considerable variation in the degree of low-frequency attenuation. Some cells showed little low-frequency cut while others showed much stronger cuts. This was a feature of penetrations in all cats and did not depend on the rearing conditions.

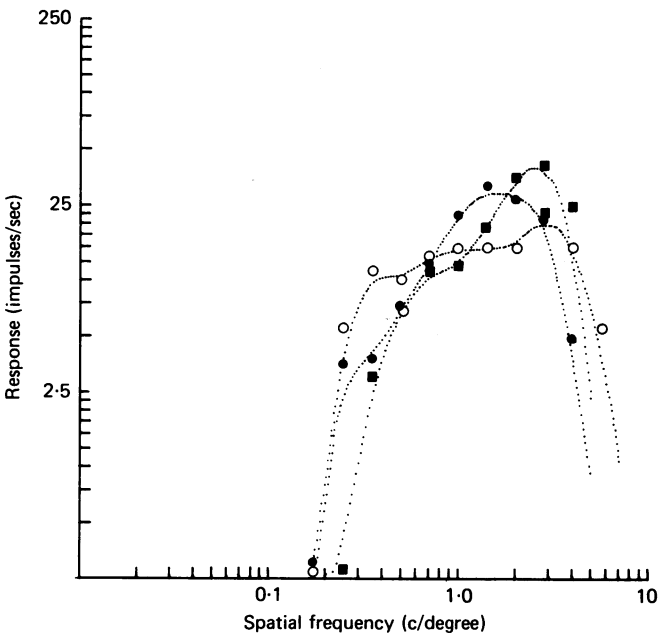

Fig. 5. Spatial frequency tuning curves from three X-cells from normal (open circles), dark-reared (filled squares) and monocularly deprived (filled circles) cats. All three neurones show complete low-frequency attenuation at 0·18 c/degree, indicating complete surround inhibition.

Temporal frequency tuning

X- and Y-cells in both normal and deprived LGN laminae responded to gratings drifting at rates between 0 and 32 Hz, with most cells responding throughout this range. We determined the temporal frequency tuning of a few cells from each animal:

the mean peak temporal frequency for X-cells from the deprived laminae of the monocularly deprived cats was 11·4 Hz ($n = 8$), which is very similar to the mean of the normal laminae (10·8 Hz; $n = 16$), but the X-cells from the dark-reared cat for which we determined temporal frequency showed a preference for lower temporal frequencies (mean 4·3 Hz; $n = 6$).

The mean peak temporal frequency of Y-cells from the normal laminae was 17·4 Hz compared with 13·4 Hz for deprived laminae of the monocularly deprived cats and 11·2 Hz for the dark-reared cat. Although there is some reduction in the peak frequency of cells from the deprived cats there is also considerable variation within each group such that these values are not significantly different.

DISCUSSION

Our findings suggest that deprivation, monocular or binocular, does not alter the spatial properties of X-cells in the deprived lamina of the LGN. For monocularly deprived cats the acuity values of the sample of X-cells from the normal and deprived lamina overlap (Fig. 4*A*) and the mean acuity values for the central 3 degrees are not significantly different. In fact, the highest value we found, 8 cycles/degree, was from the deprived lamina. Neurones with acuity values greater than 5 cycles/degree were found in both normal and deprived laminae, which is in good agreement with the values found by others for LGN (Ikeda & Wright, 1976) and retina (Ikeda & Tremain, 1979; Cleland, Harding & Tulunay-Keesey, 1979) of normal adult cats. Furthermore the acuity values of neurones within 2–3 degrees of the area centralis match quite well with the behaviourally determined visual acuity in normal cats (Giffin & Mitchell, 1978; Jacobson & Ikeda, 1979). In contrast the behaviourally determined acuity of 4-month-old monocularly deprived cats measured through the deprived eye has an asymptote at 2·45 cycles/degree, compared with the non-deprived eye which shows an acuity of 6·7 cycles/degree (Giffin & Mitchell, 1978). Our monocularly deprived kittens were 4 and 6 months old at the time of recording and therefore comparable with the cats tested behaviourally by Giffin & Mitchell (1978).

Our finding that the acuity of LGN X-cells is not altered by monocular deprivation is supported by Shapley & So (1980) but is at variance with other studies that report acuity deficits in the deprived laminae (Maffei & Fiorentini, 1976; Lehmkuhle *et al.* 1980). In the monkey monocular deprivation does not result in an acuity deficit in the deprived laminae of the LGN (Blakemore & Vital-Durand, 1980).

Not only have we found that there is no deficit in acuity of deprived X-cells but the peak response rates to their preferred stimulus do not differ from those attained by non-deprived cells, suggesting that there is no change in responsiveness to the input from the deprived retinal ganglion cells which are also normal (Kratz, Mangel, Lehmkuhle & Sherman, 1979; Cleland, Mitchell, Gillard-Crewther & Crewther, 1980). Similarly the mean peak temporal frequency did not appear to be altered by deprivation.

It is clear that monocular deprivation in the cat results in a permanent behavioural deficit in acuity through the deprived eye (Giffin & Mitchell, 1978), but the neural locus of this deficit is still unresolved. After 4–6 months of monocular deprivation few cortical neurones respond to the deprived eye (Wiesel & Hubel, 1963*b*), there is

a reduction in the zone of termination of afferents from the deprived lamina of the LGN in the cortex (Shatz & Stryker, 1978) and those neurones that do retain functional input are often weakly driven (Kratz, Spear & Smith, 1976). We would propose that the neural locus of the loss of acuity seen after monocular deprivation is cortical in origin, and is possibly due to a severe reduction in density of deprived-eye geniculate afferents in the cortex. The loss of acuity found in non-alternating esotropic cats (Jacobson & Ikeda, 1979) has a neural locus in the retina (Ikeda & Tremain, 1979) and therefore seems to be an entirely different condition from monocular deprivation.

Binocular deprivation

As for monocular deprivation, we found no deficit in acuity of X-cells from the LGN of the dark-reared cat when they were compared with the cells from the normal cat (Fig. 4*B*). Nor did there appear to be any difference in the level of responsiveness of X-cells from the dark-reared cat compared with the normal (Table 1). We did find that the peak response rate of Y-cells was reduced when compared with the normal (Table 1), although the deprived Y-cells were not sluggish. We had no difficulty in isolating Y-cells in the dark-reared cat; of the twenty-six cells isolated, with receptive fields located within 8 degrees of the area centralis, ten (38%) were Y-cells. Thus we did not find a specific loss of Y-cells such as has been reported by Kratz, Sherman & Kalil (1979), but it should be noted that we used the null phase test to classify cells whereas Kratz and co-workers used a number of tests, and this may explain the differences in the results.

The cortical effects of dark-rearing are quite severe. Some neurones do not respond to visual stimuli (Leventhal & Hirsch, 1980), while others show deficits in their spatial properties (Derrington, 1980) and tend to lack the orientation specificity seen in neurones from normally reared cats (Leventhal & Hirsch, 1980). Initially the behavioural consequences of dark-rearing are severe, with the animals appearing almost blind, but with relatively intense training the acuity can improve and animals develop normal visually guided behaviour (Timney, Mitchell & Giffin, 1978). The cortical and initial behavioural deficits seen in dark-reared cats do not seem to be a consequence of a deficit at the level of the LGN and, as we have suggested for monocular deprivation, possibly are cortical in origin.

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