Brain Research, 172 (1979) 545–551

Retinal X- and Y-cells in monocularly lid-sutured cats: normality of spatial and temporal properties

KENNETH E. KRATZ, STUART C. MANGEL, STEPHEN LEHMKUHLE and S. MURRAY SHERMAN*

Department of Anatomy, Louisiana State University School of Medicine, New Orleans, La. 70112 and (S.C.M., S.L. and S.M.S.) Department of Physiology, University of Virginia School of Medicine, Charlottesville, Va. 22908 (U.S.A.)

(Accepted April 26th, 1979)

The electrophysiological effects of prolonged neonate monocular lid suture upon the cat's dorsal lateral geniculate nucleus are at least two-fold. First, there is a reduction in the proportion of Y-cells encountered with microelectrodes in the laminae receiving input from the deprived eye[12,14]. This reduction occurs central to the optic tract. That is, the proportion of retinal Y-cells encountered in the retina and optic tract is not altered by monocular lid suture[13]. Second, there is a decrease in the spatial resolution of X-cells within these same deprived laminae[5,9,10]. Spatial resolution is defined here as the highest spatial frequency stimulus to which the cell will respond. In the present report we provide evidence that this decrease in spatial resolution of geniculate X-cells is not matched by similar changes in retinal X-cells. Therefore, this deprivation-induced deficit also primarily occurs central to the optic tract.

We used standard, extracellular recording techniques to measure spatial and temporal contrast sensitivity functions of single retinal cells in normal and monocularly lid-sutured cats. These functions not only provide accurate estimates of spatial and temporal resolution, but also elucidate the cell's sensitivity to stimulus changes produced throughout the range of spatial and temporal frequencies to which the neurons can respond (see below). Deprived cats had the lids of one eye sutured closed under general anesthesia at 5–8 days of age, and they were used for recording after they had reached adulthood (7–8 months of age). Our recording procedures have been described in previous publications and will only be briefly summarized here[6,8,12]. The animals were prepared for recording under Halothane anesthesia mixed in 50% N_2O–50% O_2 and were maintained for recording with a 70% N_2O–30% O_2 mixture. The cats were paralyzed with Flaxedil (5 mg/kg/h) and curare (0.5 mg/kg/h) mixed in lactated Ringers with 5% dextrose, and were artificially respired with end-tidal CO_2 maintained at 4.0%. Sutured eyes were opened during the initial surgical preparation.

* To whom correspondence should be addressed at: Department of Anatomical Sciences, State University of New York at Stony Brook, School of Basic Health Sciences, Health Sciences Center, Stony Brook, N.Y. 11794, U.S.A.

The pupils of both eyes were dilated with 1% atropine sulfate, and the nictitating membranes retracted with 10% phenylephrine hydrochloride. Each cornea was protected with a zero power contact lens which was opaque except for a centrally located, artificial pupil of 3 mm diameter. We performed retinoscopy and chose appropriate spectacle lenses as needed to focus the retinae at 57 cm. Varnish-coated tungsten microelectrodes or NaCl-filled micropipettes (20–50 MΩ at 500 Hz) were stereotaxically placed into the optic tract to measure extracellular potentials of ganglion cell axons. Bipolar stimulating electrodes were placed stereotaxically to straddle the optic chiasm. Receptive fields were plotted with a hand-held projector, and a battery of tests were employed to classify the cell as X or Y[2–4,6,8,12].

Contrast sensitivity functions. Spatial and temporal contrast sensitivity functions were measured with vertically oriented, counterphased, sine-wave gratings. The spatial functions plot spatial frequency of the grating (number of grating cycles per degree of visual angle) vs contrast sensitivity. Contrast is defined as $(L_{max}-L_{min})/(L_{max}+L_{min})$ where L_{max} and L_{min}, respectively, are the maximum and minimum luminance values across the grating. Contrast sensitivity is defined as the reciprocal of contrast threshold (i.e. the inverse of the minimum grating contrast necessary to evoke a modulated response from the neuron). The temporal functions plot temporal frequency (counterphase rate: sine-wave or square-wave modulated alternation of light and dark bars) vs contrast sensitivity. The gratings were generated on an oscilloscope screen (P-31, blue-green phosphor) with techniques that allowed independent manipulation of contrast, spatial phase, spatial frequency and temporal frequency[1,11]. The display was positioned 57 cm from the nodal point of the eye being tested and was 4° × 6° in size. Average luminance, defined as $1/2\ (L_{max}+L_{max})$, was held constant at 33 cd/sq. m, and contrast was variable between 0.0 and 0.6.

Following initial mapping on a tangent screen, the oscilloscope display was positioned so that the receptive field was centered on the grating pattern. For measurement of contrast sensitivity functions, the gratings were always positioned to maximize the neuronal response*. Spatial contrast sensitivity functions were obtained at a counterphase rate of 2.0 cycles per second. The spatial resolution of the cell was measured by setting the grating at 0.6 contrast and increasing the spatial frequency until the cell's evoked response was no longer modulated. The highest spatial frequency that evoked a modulated response was taken as the cell's spatial resolution. The contrast threshold of the cell was then measured at a number of lower spatial

* For X-cells, a grating position (spatial phase angle) could always be found which would evoke virtually no response, and this is the 'null position'. This position was located and frequently rechecked as spatial frequency was changed. For the contrast sensitivity functions, we shifted the gratings by 90° in spatial phase from the null position. At low spatial frequencies, Y-cells exhibit a 'fundamental' response (i.e. a modulated response at the same temporal frequency as the counterphase rate), as well as a 'second harmonic' response (i.e. a modulated response at twice the fundamental frequency). The fundamental portion of the response exhibits a null position, while the second harmonic portion does not. At low spatial frequencies, we placed the grating 90° from the null position of the fundamental response. At higher spatial frequencies, only the second harmonic response is present, and this is independent of spatial phase. Therefore, at higher spatial frequencies grating position is no longer a relevant variable[3,4].

frequencies by decreasing contrast in a step-wise fashion until modulation of the neuronal response was no longer detectable. Temporal contrast sensitivity functions were derived at the spatial frequency to which the cell exhibited the lowest contrast threshold. Temporal resolution was determined at a contrast of 0.6 by increasing temporal frequency until the cell's modulated response was no longer discriminable. The highest temporal frequency that evoked a modulated response was taken as the cell's temporal resolution. Contrast thresholds were then measured at a number of lower temporal frequencies. The contrast thresholds were determined from the audio-monitor output, but we often verified these values with computer-generated histograms which related firing rate to the stimulus cycle.

We measured the neuronal activity of 13 X-cells and 25 Y-cells from the optic tracts of 10 normal cats, plus 52 X-cells and 22 Y-cells from the optic tracts of 5 monocularly sutured cats. Of the cells sampled in the deprived cats, 29 X-cells and 15 Y-cells were from the lid-sutured eye, the remaining were from the non-deprived eye. Spatial resolution was measured in all of the above cells. Complete spatial contrast sensitivity functions were collected for 13 of the normal cells (5 X-cells and 8 Y-cells), 12 of the non-deprived cells (10 X-cells and 2 Y-cells), and 37 of the deprived cells (25 X-cells and 12 Y-cells). We first measured the spatial properties of the retinal cells in the present study. As a result, temporal information from the above-mentioned sample was collected only on 42 X-cells (9 normal, 10 non-deprived, 23 deprived) and 43 Y-cells (23 normal, 5 non-deprived, 15 deprived). Temporal resolution was measured on all of these, while complete temporal contrast sensitivity functions were collected on 11 normal cells (3 X-cells and 8 Y-cells), 10 non-deprived cells (8 X-cells and 2 Y-cells) and 31 deprived cells (20 X-cells and 11 Y-cells). All of the cells reported in the present study had their receptive field centers located within 35° from the area centralis (see Fig. 1). No differences on any measures were observed between retinal X-cells in normal cats and those from the non-deprived eye of the lid-sutured cats (see Fig. 1A, B). Similarly, no differences were seen between the normal and non-deprived Y-cells. Therefore, normal and non-deprived data are pooled in most of the subsequent analyses.

X-cells. A scatter plot of spatial resolution for normal, non-deprived, and deprived X-cells is illustrated in Fig. 1A (see also Fig. 1C). The spatial resolution of the normal, non-deprived cells averages 2.4 ± 1.0 cycles per degree (here and subsequently, this refers to mean $\pm$ S.D.), and the spatial resolution of deprived X-cells is 2.2 ± 0.8 cycles per degree. These values are not reliably different ($P > 0.1$ on a Mann–Whitney U-test). This similarity between the spatial properties of deprived and normal, non-deprived retinal X-cells is further supported by a comparison of the average spatial contrast sensitivity functions for these two groups. As illustrated in Fig. 2A, the average contrast sensitivity for deprived retinal X-cells is indistinguishable from that of normal, non-deprived retinal X-cells.

Although we failed to find an effect of lid suture on retinal X-cells, the spatial resolution of deprived geniculate X-cells is approximately one half that of their normal, non-deprived counterparts at all eccentricities[9]. The difference in effect of deprivation on retinal and geniculate X-cells is illustrated in Fig. 1C. Note that while

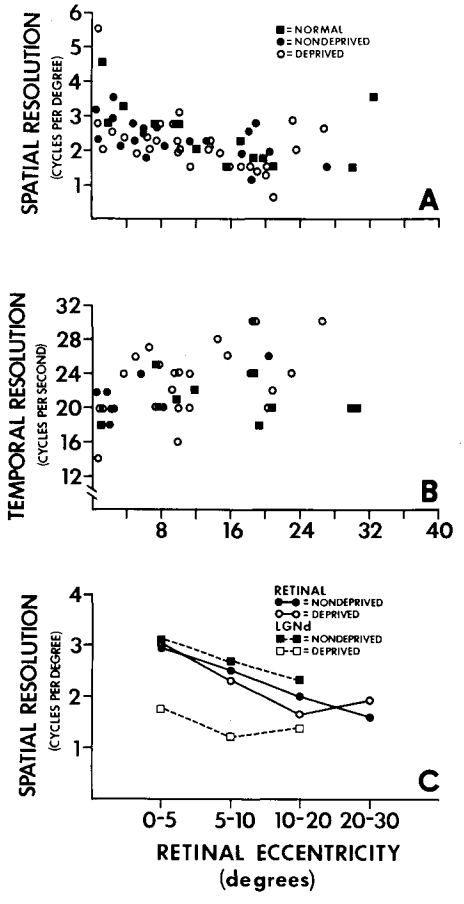

Fig. 1. Spatial and temporal resolutions of retinal X-cells plotted as a function of retinal eccentricity (degrees of visual angle from area centralis). These resolutions were measured using a counterphased, sine-wave grating of 0.6 contrast (see text for details and definitions). A: spatial resolution vs retinal eccentricity of retinal X-cells in normal cats, plus non-deprived and deprived X-cells in monocularly lid-sutured cats. B: temporal resolution vs retinal eccentricity of retinal X-cells in normal cats, plus non-deprived and deprived X-cells in monocularly lid -sutured cats. C: mean spatial resolution of normal, non-deprived, and deprived retinal and geniculate (LGNd) X-cells plotted as a function of eccentricity groups. Normal and non-deprived data are pooled and labelled NONDEPRIVED. Geniculate data, taken from ref. 9 were not available for the 20–30° eccentricity group. Cell numbers for A, B can be obtained from the text. For C, numbers for each group in each of the eccentricity ranges, central to peripheral are: non-deprived retinal: 11, 8, 11, and 4; deprived retinal: 5, 9, 10, and 5; non-deprived geniculate: 31, 28, and 15; deprived geniculate: 5, 16, and 16.

the spatial resolution of the deprived geniculate cells is significantly lower than for normal, non-deprived geniculate cells at each eccentricity group, the spatial resolution of deprived retinal cells is not statistically different from that of normal, non-deprived geniculate X-cells at any eccentricity group. Further, at each eccentricity group the mean spatial resolution of deprived retinal cells is higher than that of deprived geniculate cells. Except for the 10–20° eccentricity group, these samples are statistically different ($P < 0.01$ on a Mann–Whitney U-test).

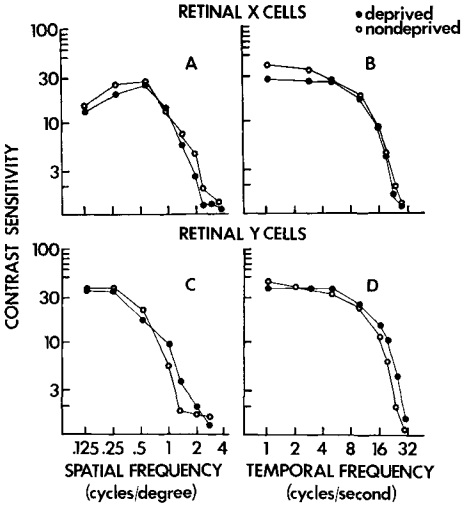

Fig. 2. Average spatial and temporal contrast sensitivity functions for retinal X- and Y-cells in normal and monocularly lid-sutured cats. Data from normal cats and from the non-deprived eye in lid-sutured cats are pooled and are labelled non-deprived. These curves were determined by averaging the contrast sensitivity values (1/threshold) for individual cells at various spatial and temporal frequencies. The number of cells on which these curves are based can be obtained from the text. A: average spatial contrast sensitivity functions for retinal X-cells. B: average temporal contrast sensitivity functions for retinal X-cells. C: average spatial contrast sensitivity functions for retinal Y-cells. D: average temporal contrast sensitivity functions for retinal Y-cells.

Fig. 1C also shows that, for the area centralis representation (0–5°), the loss of spatial resolution seen for geniculate X-cells could not be accounted for by deficits in their retinal counterparts. This result contrasts with those reported in a recent abstract by Ikeda and Tremain[7]. They described a loss of resolution for retinal X-cells representing the area centralis in strabismic cats. Perhaps had we measured a larger sample of deprived X-cells from area centralis, we would have seen a subtle deprivation effect, and perhaps strabismus somehow affects development of retinal ganglion cells more than does lid suture. Otherwise, we cannot account for this discrepancy.

As in the lateral geniculate nucleus[9], we observed no effect of lid suture on the temporal properties of retinal X-cells. The average temporal resolution of our sample of normal, non-deprived retinal X-cells is 21.8 $\pm$ 3.1 cycles per second, as compared to 22.9 $\pm$ 4.0 cycles per second for deprived cells (see Fig. 1B), and these values are not statistically different ($P > 0.1$ on a Mann–Whitney U-test). The average temporal contrast sensitivity function for both non-deprived (including normal) and deprived retinal X-cells are indistinguishable for all temporal frequencies (see Fig. 2B).

Y-cells. We found the proportion of retinal Y-cells from the sutured eye of deprived cats to be nearly the same as that from the non-deprived eye (34% and 23%, respectively; $P > 0.1$ on an χ^2-test), and this confirms an earlier observation[13]. Furthermore, the spatial and temporal properties of retinal Y-cells are also unaffected by lid suture. The spatial resolution of our total sample of normal, non-deprived retinal Y-cells (1.8 $\pm$ 0.7 cycles per degree) is indistinguishable from that observed for

deprived retinal Y-cells (1.8 ± 0.8 cycles per degree; $P > 0.1$ on a Mann–Whitney U-test). The average spatial contrast sensitivity function for each group virtually overlaps one another (see Fig. 2C). Likewise, the mean temporal resolution of normal, non-deprived retinal Y-cells is not different from that of their deprived counterparts (24.1 ± 3.7 vs 27.7 ± 3.7 cycles per degree; $P > 0.1$ on a Mann–Whitney U-test), and their average temporal contrast sensitivity functions are indistinguishable (Fig. 2D)*. Our failure to find an effect of deprivation on the spatial and temporal properties of retinal Y-cells matches our failure to find such effects on the remaining deprived Y-cells in the lateral geniculate nucleus (unpublished observations).

Conclusions. In general, we were unable in the present series of experiments to detect an effect of early monocular lid suture upon the spatial or temporal response properties of retinal X- or Y-cells. This finding is consistent with the results of earlier studies, which also failed to uncover any retinal abnormalities following lid suture[13,15]. Neither the functional loss of geniculate Y-cells nor the decrease in spatial resolution of geniculate X-cells following neonate monocular lid suture can be accounted for by similar deficits in the retina or optic tract. Therefore, both of these effects of deprivation must primarily occur central to the optic tract.

This work was supported by NIH Grant EY 01565 and NSF Grant BNS77-06785. K.E.K. and S.L. were supported by USPHS Individual Postdoctoral Fellowships DE 07037 and EY 05238, respectively. S.M.S. was supported by USPHS Research Career Development Award EY00020.

1 Campbell, F. W. and Green, D. G., Optical and retinal factors affecting visual resolution, *J. Physiol. (Lond.)*, 181 (1965) 576–593.
2 Enroth-Cugell, C. and Robson, J. G., The contrast sensitivity of retinal ganglion cells of the cat, *J. Physiol. (Lond.)*, 187 (1966) 517–552.
3 Hochstein, S. and Shapley, R. M., Quantitative analysis of retinal ganglion cell classifications, *J. Physiol. (Lond.)*, 262 (1976) 237–264.
4 Hochstein, S. and Shapley, R. M., Linear and non-linear spatial subunits in Y cat retinal ganglion cells, *J. Physiol. (Lond.)*, 262 (1976) 265–284.
5 Hoffmann, K.-P. and Sireteanu, R., Interlaminar differences in the effects of early and late monocular deprivation on the visual acuity of cells in the lateral geniculate nucleus of the cat, *Neurosci. Lett.*, 5 (1977) 512–552.
6 Hoffmann, K.-P., Stone, J. and Sherman, S. M., The relay of receptive field properties in the dorsal lateral geniculate nucleus of the cat, *J. Neurophysiol.*, 35 (1972) 518–531.
7 Ikeda, H. and Tremain, K. E., Amblyopic retinal ganglion cells in the area centralis of cats reared with convergent squint, *Neurosci. Lett.*, Suppl. 1 (1978) S391.
8 Kratz, K. E., Webb, S. V. and Sherman, S. M., Electrophysiological classification of X- and Y-cells in the cat's lateral geniculate nucleus, *Vision Res.*, 18 (1978) 1261–1264.
9 Lehmkuhle, S., Kratz, K. E., Mangel, S. C. and Sherman, S. M., An effect of early monocular lid suture upon the development of X-cells in the cat's lateral geniculate nucleus, *Brain Research*, 157 (1978) 346–350.

* It is interesting to note that while the average temporal resolution of retinal Y-cells and geniculate Y-cells, 24.1 ± 3.7 vs 21.3 ± 0.9, respectively, are equivalent, the average temporal resolution of retinal X-cells is significantly greater than that of their geniculate counterparts (21.8 ± 3.1 vs 11.8 ± 0.7, respectively; $P < 0.01$ on a Mann–Whitney U-test; see ref. 9 for data from geniculate neurons).

10 Maffei, L. and Fiorentini, A., Monocular deprivation in kittens impairs the spatial resolution of geniculate neurones, *Nature (Lond.)*, 264 (1976) 754–755.
11 Shapley, R. M. and Rossetto, M., An electronic visual stimulator, *Behav. Res. Meth. Instr.*, 8 (1976) 15–20.
12 Sherman, S. M., Hoffmann, K.-P. and Stone, J., Loss of a specific cell type from the dorsal lateral geniculate nucleus in visually deprived cats, *J. Neurophysiol.*, 35 (1972) 532–541.
13 Sherman, S. M. and Stone, J., Physiological normality of the retina in visually deprived cats, *Brain Research*, 60 (1973) 224–230.
14 Sherman, S. M., Wilson, J. R. and Guillery, R. W., Evidence that binocular competition affects the postnatal development of Y-cells in the cat's lateral geniculate nucleus, *Brain Research*, 100 (1975) 441–444.
15 Wiesel, T. N. and Hubel, D. H., Effects of visual depriviation on the morphology and physiology of cells in the cat's lateral geniculate body, *J. Neurophysiol.*, 26 (1963) 978–993.