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An effect of early monocular lid suture upon the development of X-cells in the cat's lateral geniculate nucleus

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Following neonate monocular lid-suture, the proportion of Y-cells encountered with microelectrodes in the cat's lateral geniculate nucleus is abnormally low[9]. However, to our knowledge, no physiological effects of lid-suture have yet been described for X-cells. Indeed, across a variety of tests, including visual and electrical stimulation, there seemed to be no discernible effect of deprivation upon geniculate X-cells[9].

Several laboratories have recently reported that cells in the deprived laminae (i.e. receiving direct input from the deprived eye) exhibit a deficit in spatial resolution[3,7]. Although these published results were not analyzed separately for X- and Y-cells, they suggested that a more sensitive measure, such as sensitivity to high spatial frequencies, might reveal an effect of monocular deprivation on the development of X-cells. We measured in normal and monocularly deprived cats the responses of X-cells to spatial sine-wave gratings that were varied in spatial and temporal frequency. We found that the spatial resolution of deprived X-cells was reduced, whereas their sensitivity to temporal changes was unimpaired.

Our general methods of receptive field analysis have been described in detail elsewhere[4,5,9], and will be briefly summarized here. Normally reared adult cats served as controls. Each monocularly deprived cat had the lids of one eye sutured shut at 5–8 days of age and kept closed (with frequent inspection) until the recording session at which time the cat was > 9 months of age. We used varnish-insulated, tungsten microelectrodes (20–30 MΩ at 500 Hz) to measure extracellular potentials from single geniculate cells in laminae A and A1. The cats were anesthetized (halothane followed by N_2O/O_2), paralyzed (infusion of Flaxedil and curare), artificially respirated, and maintained at an end-tidal CO_2 level of 4.0%. The sutured eyes of deprived cats were opened at the time of the recording session. Atropine sulfate and Neosynephrine were instilled in the eyes, and the corneas were fitted with contact lenses which included 3 mm diameter artificial pupils. Retinoscopy was used to ensure that both retinae were

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conjugate with a CRT placed 57 cm from the eyes. Bipolar stimulating electrodes were inserted to straddle the optic chiasm.

The diameter and the sign (i.e. on or off) of the receptive field center was determined with hand plotting techniques. After the field was plotted, a battery of tests was used to classify the cell as X or Y[4,5]. Counterphased, vertical, sine-wave gratings were then employed to determine neuronal sensitivity to temporal and spatial modulation. These gratings were generated on a CRT by standard techniques[1], which permitted independent control of spatial and temporal frequency (i.e. counterphase rate). The CRT display was 4° by 6°, and had an average luminance of 33 cd/sq.m. The contrast $(L_{max}-L_{min})/(L_{max}+L_{min})$ was fixed at 0.61. We positioned the CRT so that the receptive field was located in the center of the grating display. The grating was first placed in the null position (i.e., the horizontal position for which the inhibitory and excitatory influences of the counterphased grating on the neuron summed to zero; cf. ref. 2), and then the phase of the grating was shifted by 90° with respect to this null position in order to maximize the neuronal response. The phase of the grating was often adjusted in this fashion to ensure that small eye movements had not displaced the position of the receptive field.

Spatial resolution (i.e., the highest spatial frequency to which the cell responded) was first measured at a counterphase rate of 2 Hz. This was accomplished by increasing the spatial frequency until the cell's evoked response, as determined from the audio monitor, ceased to follow the temporal modulation of the grating. This estimate of spatial resolution was compared for several cells with an estimate derived from computer-generated histograms which measured firing rate as a function of the stimulus cycle. These comparisons indicated that our estimates derived from the audio monitor were generally indistinguishable from estimates derived from the histograms. After the spatial resolution of the cell was determined, we measured the contrast threshold at lower spatial frequencies. The results of this experiment will be reported in a later paper.

The spatial frequency at which the lowest contrast threshold was obtained was then used to measure responses to varying temporal frequencies. Temporal resolution (i.e., the highest counterphase rate to which the cell responded) was measured by increasing the temporal frequency until no modulation of the neuronal discharge was observed. Again, the estimates derived from the audio monitor were generally indistinguishable from the estimates based on computer-generated histograms.

We measured the spatial resolution of 37 X-cells in 8 normal cats and 48 X-cells in 6 monocularly deprived cats; of these latter cells, 30 were from deprived laminae. We measured the temporal resolution for 25 normal, 26 deprived, and 14 non-deprived X-cells. As in previous studies[9,11], we found few Y-cells in deprived laminae, but since we concentrated in this study on obtaining data from as many X-cells as possible, our ratios of Y- to X-cells are unreliable.

There was no significant difference between normal and non-deprived X-cells for either spatial or temporal resolution (see Fig. 1). Therefore, we combined these two groups in subsequent analyses. For the limited region of visual field in which receptive fields were located, we found no correlation between receptive field location and either

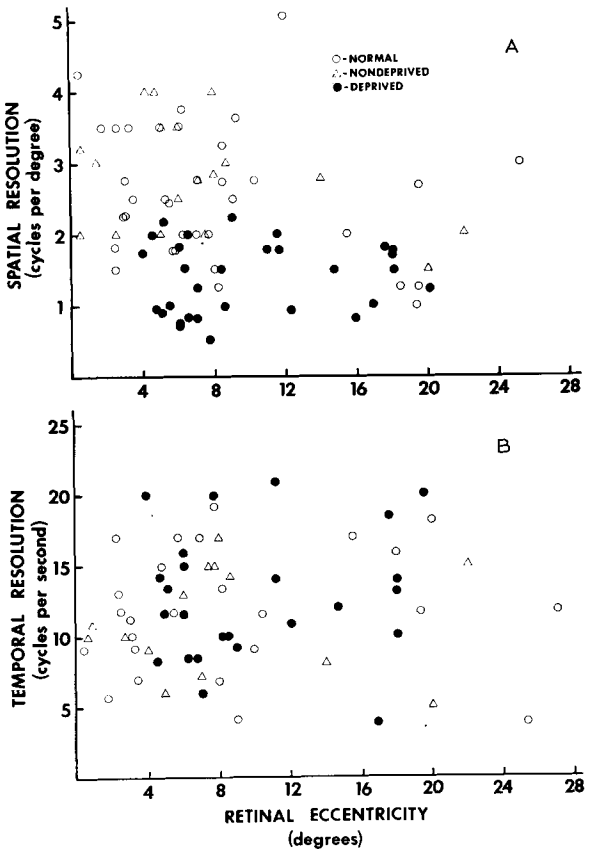

Fig. 1. Spatial and temporal resolution of X-cells as a function of retinal eccentricity (i.e., distance from the area centralis of the receptive fields). Spatial and temporal resolution were measured using a counterphase sine-wave grating with 0.61 contrast. Spatial resolution is defined as the highest spatial frequency (cycles/degree) to which the cell responded using 2 Hz temporal modulation. Temporal resolution is defined as the highest counterphase rate (cycles/sec) to which the cell responded. For temporal resolution we used the spatial frequency for which the cell is most sensitive (see text). Cells from normal cats are represented by open circles; cells from monocularly deprived cats by open triangles (from the non-deprived laminae) and by filled circles (from the deprived laminae). A: spatial resolution as a function of retinal eccentricity. B: temporal resolution as a function of retinal eccentricity.

spatial or temporal resolution (see Fig. 1). We thus pooled data irrespective of receptive field location. Finally, we observed no differences for X-cells among normal and non-deprived laminae A and A1; likewise effects in deprived laminae A and A1 were indistinguishable*. Consequently, in the ensuing analysis, our comparisons are between deprived and normal, non-deprived laminae.

At lower spatial frequencies, no difference was noted between responses of

* R. Sireteneau and K.-P. Hoffmann (personal communication) do report that the acuity losses for X-cells are more severe in deprived lamina A1 than in deprived lamina A (see also ref. 3). We cannot explain this difference between our results and theirs.

deprived and normal, non-deprived X-cells. However, the deprived X-cells failed to respond to higher spatial frequencies. In Fig. 1A, spatial resolution is plotted as a function of retinal eccentricity for normal, non-deprived, and deprived X-cells. Spatial resolution for the normal, non-deprived X-cells was 2.63 $\pm$ 0.92 c/deg*, whereas the value for deprived X-cells was 1.37 $\pm$ 0.53 c/deg. The difference between these means was statistically significant ($P < 0.001$ on a Mann–Whitney U-test). These data were also analyzed by calculating the mean spatial resolution for deprived and non-deprived X-cells for each monocularly deprived cat and comparing the differences between these means across the 6 cats. The outcome of this analysis also revealed a significant difference between deprived and normal, non-deprived X-cells ($P < 0.001$ on a correlated t-test).

An obvious increase in receptive field center diameter did not accompany this loss of spatial resolution for the deprived X-cells. In agreement with a previous report[9], we found no difference between field sizes for deprived X-cells (0.48 $\pm$ 0.13°) and normal, non-deprived X-cells (0.50 $\pm$ 0.24°). This is somewhat surprising, since for normal, non-deprived X-cells we observed a weak, negative correlation ($r = -0.49$; $P < 0.001$) between field size and the highest spatial frequency to which the cell responded[2]; for the limited sample reported here no such correlation was observed for the deprived X-cells. Perhaps properties other than receptive field size are important for spatial resolution, and these other properties are susceptible to early lid-suture.

Fig. 1B shows temporal resolution as a function of retinal eccentricity for normal, non-deprived, and deprived X-cells. The temporal resolution for the normal, non-deprived X-cells was 11.58 $\pm$ 4.34 Hz, and for deprived X-cells was 12.57 $\pm$ 4.54 Hz. The difference between these means was not statistically significant ($P < 0.01$ on a Mann–Whitney U-test). Moreover, analysis of the mean temporal resolution for each cat as a single datum, as described above for spatial resolution, did not uncover a reliable difference between deprived and non-deprived X-cells.

In addition, we compared spatial and temporal resolution in an attempt to determine if the two measures were related. For all groups of X-cells (normal, non-deprived, and deprived), there was no correlation between the highest spatial and temporal frequencies to which a cell responded. Also, as noted above, spatial resolution is more susceptible to the effects of early eyelid suture than is temporal resolution. These two findings suggest the possibility that different mechanisms govern spatial and temporal properties of X-cells.

Taken together, these results indicate that X-cell development is affected by monocular deprivation. The deficits, however, are less severe for X-cells than for Y-cells. Whereas Y-cells in deprived laminae seem functionally lost following monocular deprivation (refs. 9, 11, and present study), deprived X-cells exhibit deficits only in spatial resolution; they respond normally to lower spatial frequencies and display normal temporal modulation. The effect of monocular deprivation may differ for X- and Y-cells in other ways. For instance, the loss of Y-cells is confined to the binocular

* These and subsequent values signify the mean $\pm$ standard deviation.

segment[6]. This suggests that the loss of Y-cells is due to an imbalance during development in the competitive interaction between central connections related to the two eyes (i.e. binocular competition; cf. ref. 8). We do not yet know if the effect of monocular deprivation on X-cells is restricted to the binocular segment, and would thus be related to binocular competition. In addition, the effect of deprivation on Y-cells is not seen in the retina, since retinal ganglion Y-cells are found in normal numbers following lid suture[10]. It is possible that the loss of spatial resolution exhibited by geniculate X-cells reflects an abnormality seen among retinal X-cells. Experiments are currently underway in our laboratory to address these issues.

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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 Hoffmann, K.-P. and Sireteneau, 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) 171–175.
4 Hoffmann, K.-P., Stone, J. and Sherman, S. M., Relay of receptive field properties in dorsal lateral geniculate nucleus of the cat, *J. Neurophysiol.*, 35 (1972) 518–531.
5 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.*, (1978) in press.
6 Lin, C.-S. and Sherman, S. M., Effects of early monocular eyelid suture upon development of relay cell classes in the cat's lateral geniculate nucleus, *J. comp. Neurol.* (1978) in press.
7 Maffei, L. and Fiorentini, A., Monocular deprivation in kittens impairs the spatial resolution of geniculate neurones, *Nature (Lond.)*, 264 (1976) 754–755.
8 Sherman, S. M., Guillery, R. W., Kaas, J. H. and Sanderson, K. J., Behavioral, electrophysiological and morphological studies of binocular competition in the cat, *J. comp. Neurol.*, 158 (1974) 1–18.
9 Sherman, S. M., Hoffmann, K.-P. and Stone, J., Loss of a specific cell type from dorsal lateral geniculate nucleus in visually deprived cats, *J. Neurophysiol.*, 35 (1972) 532–541.
10 Sherman, S. M. and Stone, J., Physiological normality of the retina in visually deprived cats, *Brain Research*, 60 (1973) 224–230.
11 Sherman, S. M., Wilson, J. R. and Guillery, R. W., Evidence that binocular competition affects the post-natal development of Y-cells in the cat's lateral geniculate nucleus, *Brain Research*, 100 (1975) 441–444.