The functional significance of X and Y cells in normal and visually deprived cats

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The so-called X cells in the retino-geniculostriate pathway have been suggested to be important in the analysis of spatial patterns in the visual scene, whereas Y cells have been considered responsible for detecting temporal change. In this article Murray Sherman suggests that this is too simplistic a way of differentiating these cells, and that a more appropriate differentiation can be drawn from their developmental history: he concludes that the development of X cells is governed by a non-competitive mechanism, and Y cells by a mechanism involving binocular competition.

Studies of cats raised with visual deprivation have been a popular and fruitful enterprise which effectively dates back to the studies of Wiesel and Hubel in the 1960s. There are two good reasons for this. First, the kitten's visual pathways are an excellent system for studies of neuroplasticity and neural development. Secondly, the visual system of the cat is organized in many critical ways like that of man (see Fig. 1) and, therefore, cats raised with visual deprivation are a useful 'model' for clinical problems of vision, such as amblyopia (poor vision) due to developmental deficits in the central pathways.

I shall try to explain briefly in this account what studies of geniculate cells in cats raised with monocular eyelid suture can tell us about neuroplasticity, neural development, and the aetiology of certain types of clinical amblyopia. This treatment is necessarily very restricted, and will not cover more subtle forms of visual deprivation, nor will it deal with the vast literature on cortical physiology in visually deprived cats. I will also be quite speculative, to give something of the flavour of how we might account both for mechanisms of neuroplastic development and for the neural basis of amblyopia.

Normal X and Y cells

Let us first consider some principles of the functional organization of the lateral geniculate nucleus in normal cats, before monocularly deprived cats are discussed. The retino-geniculocortical pathways are described in Fig. 1. We now know that these pathways can be subdivided into at least two parallel portions, one containing 'X' cells, the other 'Y' cells. Normally, geniculate X and Y cells can be recorded in roughly equal proportions. The functional significance of this dichotomy for cortical neurophysiology or visual perception is far from clear, but since these cells seem to be affected by early visual deprivation, it is worth speculating a bit about their functional roles in normal cats. Since, compared with Y cells, X cells generally have smaller receptive fields, respond better to stationary targets, but less vigorously to quickly moving ones, and are concentrated in the centre of the retina, they are often suggested to be more important for analysis of spatial patterns in the visual scene, whereas Y cells cover temporal patterns. Other suggestions have also been made.

Based on recent experiments from several laboratories, including our own, we have proposed for X and Y cells a very different functional dichotomy which may be particularly relevant for visual development[7,8]. We derived spatial or temporal *contrast sensitivity functions* for a population of geniculate X and Y cells. That is, we adjusted the contrast of a grating (Fig. 2) of sinuosoidal luminance profile, alternating in phase (dark and light bars being regularly interchanged), until a threshold response was obtained: to higher contrasts, the cell responded clearly to each phase alternation; and to lower contrasts, no response was evident. These threshold values were determined for a set of spatial fre-

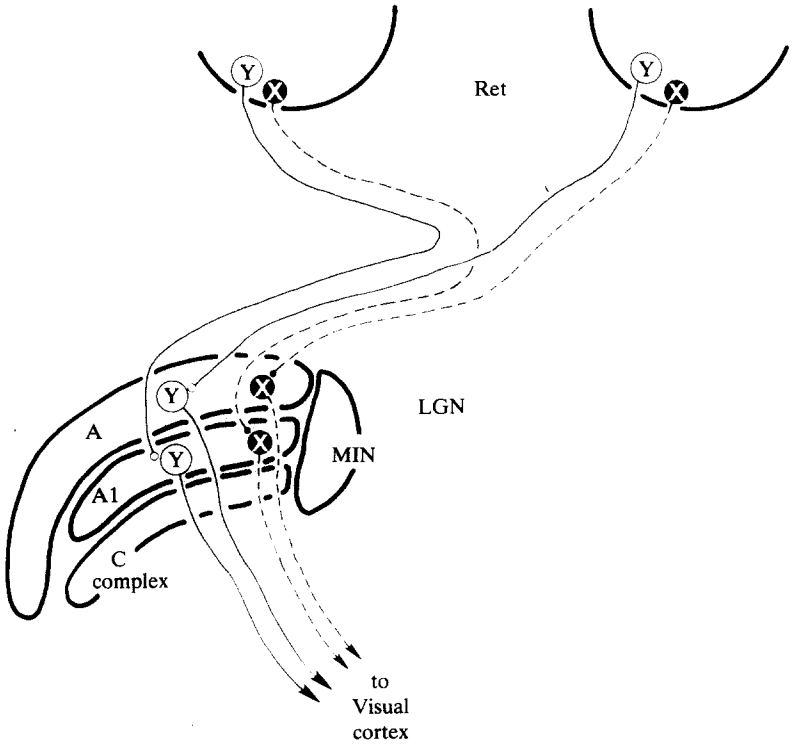

Fig. 1. Retino-geniculocortical pathways in the cat. The lateral geniculate nucleus (LGN) *is shown in coronal section. Detailed pathways, showing X and Y cells, are indicated only for laminae A and A1. Most studies have concentrated on these laminae, which represent a reasonably matched pair, one from each eye. The laminae in the C complex and the medial interlaminar nucleus* (MIN) *also possess neurones which receive retinal afferents and project axons to visual cortex.* Ret: *retina.*

quencies (i.e. grating cycles per degree of visual angle) and temporal frequencies (rate of counterphase displacement) in order to construct contrast sensitivity functions (Fig. 3). These functions can be viewed as neuronal 'transfer functions' that predict how well each cell transmits information contained in the various spatial and temporal frequencies of a visual scene.

The value of this sort of approach stems from linear systems analysis, or Fourier analysis. If one were to move a photometer across a complex visual scene, the variations in intensity with position would produce a complicated waveform which nonetheless could be described in terms of its pure component (sine-wave) frequencies. In other words, the spatial patterns in any scene can be synthesized by appropriate combinations of sine wave gratings.

Analysis of spatial patterns

By way of analogy, it may be useful to consider here the more familiar analysis of sound stimuli. A sound or noise can be represented by a waveform, often complex, which describes the air pressure changes as a function of time. Any such sound can be synthesized by appropriate linear combinations of pure tones, for which the air pressure changes with time are sinusoidal. Furthermore, the quality of reproduction in a hi-fi system depends not simply on the highest sound frequencies which can be amplified, but on the relative amplification of each frequency. Relative differences in amplifications of different tones would lead to distorted sound reproduction.

The same principles apply to analysis of spatial patterns. Any visual scene can be reconstituted by appropriate superposition of various spatial frequencies; and a description of the response of a neurone or visual system to visual stimuli requires knowledge of its response to a range of spatial frequencies (i.e. the contrast sensitivity or transfer function) and not just the highest frequency resolvable. Often this latter measure (visual acuity) is all that is obtained in clinical settings.

The value of functions that describe visual performance for low, as well as high, spatial frequencies has been emphasized by recent psychophysical studies which illustrate the importance of the low frequencies for form vision. In fact, basic form information seems to reside in the low spatial frequencies, whereas the high frequencies carry fine details and set the limits on our visual acuity[6]. Our everyday experience attests to this. Defocusing (caused by forgetting to wear spectacles, by a poorly focused camera, etc.) selectively attenuates contrast of the high spatial frequencies and has relatively little effect on transmission of low frequencies. We can easily recognize basic shapes with a moderately defocused image, but can no longer resolve the fine details. Diffusion of an image (caused, for instance, by viewing through waxed paper, fogged spectacles, half a ping-pong ball, etc.) attenuates contrast for all spatial frequencies fairly equally. If diffusion of an image sufficiently attenuates the contrast of low spatial frequencies, spatial vision is severely hampered. In fact, the same visual scene can be degraded by defocus or diffusion so that the higher spatial frequencies are more attenuated by the former, and lower frequencies by the latter. Forms in such a scene are more readily appreciated after defocus than after diffusion, and this emphasizes the importance of the low spatial frequencies for basic form vision. In Fig. 7 of their 1978 paper, Hess and Woo demonstrate these phenomena[4].

Knowledge of the range of stimulus frequencies to which neurones are sensitive can thus provide insights regarding their role in analyzing the stimulus. Fig. 3 shows the representative functions for geniculate X and Y cells. Differences between these cells at higher spatial frequencies (where X cells are slightly more sensitive) and all temporal frequencies (where Y cells are slightly more sensitive) are not terribly compelling and, in fact, considerable overlap in these parameters exists between X and Y cell populations[7,8]. On the other hand, dramatic differences are apparent in sensitivity to the low spatial frequencies which are so crucial to form information. Y cells respond vigorously to such patterns,

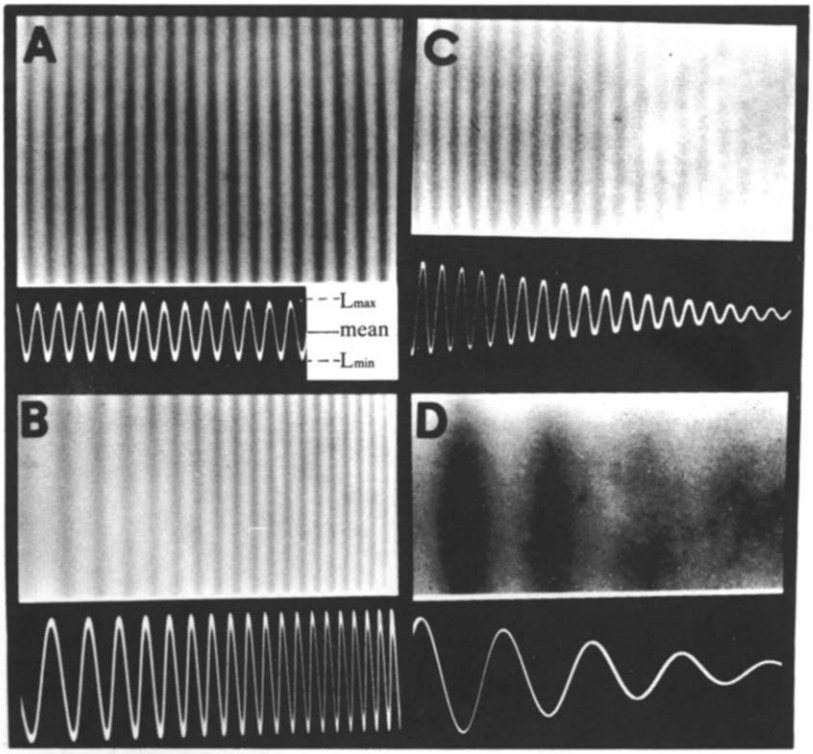

Fig. 2. Stimuli for determination of contrast sensitivity functions (cf Fig. 3). (A) *Sine-wave grating. Above is a photograph of a sine-wave grating with its luminosity profile below. The spatial frequency of the grating is defined as the number of grating cycles per degree of visual angle; contrast is the difference between maximum and minimum luminance divided by their sum [i.e. $(L_{max} - L_{min})/(L_{max} + L_{min})$]; average luminance (mean) is half the sum of maximum and minimum luminance [i.e. $(L_{max} + L_{min})/2$]. The grating is counterphased sinusoidally by reducing contrast to zero, then increasing it to its former value in such a way that bright and dark half cycles have been interchanged, then the process is reversed, etc.; the average illumination remains constant during such counterphasing. For a given spatial frequency and counterphase rate (Hz), maximum contrast is adjusted until a threshold neuronal response is obtained.* B *and* C *illustrate the appearance of changing spatial frequency and contrast.* (B) *Sine-wave grating (upper) of fixed contrast, but with increasing spatial frequency from left to right. This is indicated by the luminosity profile (lower).* (C) *Sine-wave grating (upper) of fixed spatial frequency and average luminance, but with decreasing contrast from left to right. This is indicated by the luminosity profile (lower). Notice that, although the grating exists throughout the field, its contrast is too low for grating detection in the left portion of the photograph.* (D) *Same as* C, *but for a lower spatial frequency.*

whereas X cells are fairly insensitive. For these reasons, we suggested that the functional difference between X and Y cells is not based on spatial/temporal differences. Rather, Y cell pathways may be used to analyse basic spatial forms, and X cell pathways add important details (i.e. better acuity, stereopsis, etc.)[7,8].

It must be emphasized that this is just another hypothesis and should not be mistaken for an established viewpoint. However, this would explain why striate cortical lesions in the cat, which remove X pathways (geniculate X cells project exclusively to striate cortex), but leave much or most of the Y pathways (geniculate Y cells project extensively to extrastriate, as well as striate, cortex), produce an animal with excellent form vision and only a slight loss in visual acuity[1]. One could also predict from this hypothesis that the rudimentary form vision exhibited by lid-sutured cats using their deprived eye indicates serious deficits in their Y pathways. As discussed below, the Y pathways seem particularly sensitive to early lid suture.

Effects of early lid suture on X and Y cells

It is useful to consider the differential effects of early visual deprivation upon geniculate X and Y cells against this theoretical framework. Two preliminary points can be made. First, the major effects of lid suture seem to occur central to the optic tract, since no major anatomical or physiological deficits in deprived eyes have as yet been found among retinal ganglion cells or their axons†. Secondly, the deficits described below exhibit the same general 'critical period' first established by Hubel and Wiesel for the kitten's striate cortex. That is, the geniculate cells exhibit a plastic period for only the first few postnatal months, during which their properties can be changed by lid suture, but after which lid suture has little or no effect.

In cats raised with one eye sutured, we found, using recording methods, that normal geniculate laminae (i.e. connected to the non-deprived eye) contained roughly equal numbers of X and Y cells, but that Y cells in deprived laminae were rare[11]. Apparently, the bulk of Y cells failed to develop, or perhaps even degenerated in the deprived condition. Deprived X cells, on the other hand, seemed normal, but on closer inspection had a very subtle deficiency: they were insensitive to the highest stimulus spatial frequencies which activate normal X cells, but at lower spatial frequencies, and at all temporal frequencies, their sensitivity was indistinguishable from normal X cells[8]. Correlates for this more dramatic effect of lid suture upon geniculate Y cells than upon X cells are also seen from anatomical studies, although the precise relationship between the physiological and anatomical results is not yet clear[3,9].

Binocular competition and deprivation

Another interesting difference between the effect of lid suture upon X and Y cells is their pattern within deprived laminae. The lateral geniculate nucleus, like most visual structures, contains a precise, orderly, point-to-point map of visual space, and this permits us to divide it into binocular and monocular segments[3,10,11]. The binocular segment represents that portion of the nucleus which maps the central portion of the visual field seen by both eyes. The monocular segment maps the extreme peripheral crescent of visual field seen by only the contralateral eye. Consequently, binocular interactions are likely to occur only in the binocular segment of the nucleus.

When deprived laminae are divided into binocular and monocular segments, the pattern of X and Y cell deficits is quite different (Fig. 4). Y cells with apparently normal response properties occur in normal numbers in the deprived monocular segment, and their apparent loss is limited to the binocular segment[8,11]. We can explain this by suggesting that Y cells related to each eye compete with one another during development, and the advantage conferred to the non-deprived Y cells permits them to dominate during development. Perhaps patterned stimuli evoke higher peak firing rates in the non-deprived Y cells. This allows these cells to develop cortical connections at the expense of their deprived counterparts, and the latter subsequently fail to develop or atrophy. It is this unbalanced competitive development, and not the deprivation *per se*, that retards the deprived Y cell development, and this in turn explains why these cells can develop normally in the deprived monocular segment where they do not suffer the deleterious consequences of being placed at a competitive disadvantage[3,10,11].

Deprived X cells, on the other hand, are equally affected (i.e. insensitive to higher spatial frequencies) in both binocular and monocular segments[8]. This suggests that binocular competition does not play the crucial role in X cell development that it does for Y cells, and some non-competitive deprivation mechanism applies instead. For instance, perhaps the reduced peak firing rates directly prevent these cells from developing or maintaining high spatial frequency sensitivity, and relative activity among the non-deprived X cells is irrelevant.

Not only is the degree of abnormality quite different between deprived X and Y cells, but also the developmental mechan-

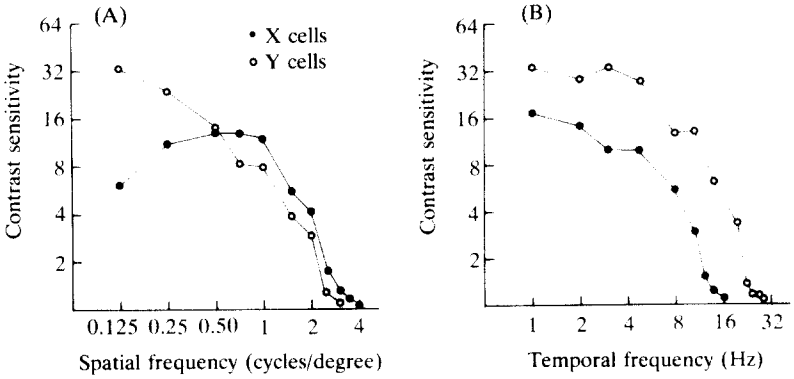

Fig. 3. Average contrast sensitivity functions for geniculate X and Y cells[3]. All the cells had receptive fields within 10° of the area centralis. *The points have been averaged from functions for individual X and Y cells. Standard error bars have been omitted for clarity, but the illustrated differences between the cell classes are statistically significant. The vertical axes represent the inverse of the contrast needed to evoke a threshold response from the cell at the indicated spatial or temporal frequency.* (A) *Spatial functions averaged for 30 X and 19 Y cells. These were obtained at a counterphase rate of 2 Hz. On average, X cells were slightly more sensitive to higher spatial frequencies, but overlap existed here (i.e. some Y cells more sensitive than some X cells). At lower spatial frequencies, dramatic qualitative differences without overlap were evident: Y cells were sensitive to such stimuli, whereas X cells were not.* (B) *Temporal functions averaged for 23 X and 14 Y cells. These were obtained for each cell at the spatial frequency for which the cell was most sensitive. The differences between classes were slight, with considerable overlap. Y cells seemed more sensitive, on average, to all temporal frequencies, but even this difference must be qualified. Had the same higher spatial frequency been used to obtain these temporal functions, the average differences between X and Y cells would disappear or even reverse, since sensitivity is generally lower for Y cells than for X cells at such higher spatial frequencies.*

†Although Ikeda, in this issue of *Trends in Neuro-Sciences*, reports changes in the retina of cats with convergent squint.

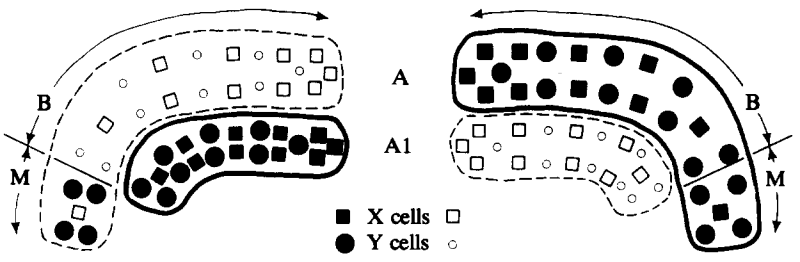

Fig. 4. Summary diagram of lateral geniculate nucleus laminae A *and* A1 *in a monocularly deprived cat. Deprived laminae are represented by dashed outlines, and the binocular* (B) *and monocular* (M) *segments are shown. Normal X and Y cells are indicated by solid symbols, and the abnormalities caused by deprivation, by open symbols. For deprived X cells, the inability to develop sensitivity for the highest spatial frequencies occurs equally in the monocular and binocular segments. For deprived Y cells, the deprivation effects are essentially limited to the binocular segment. Few normal Y cells are found there, but in the deprived monocular segment, these cells occur in normal numbers with normal properties. From such data, we conclude that development of X cells is governed by a non-competitive mechanism, and development of Y cells by a mechanism involving binocular competition (see text).*

isms involved seem different. The observation that Y cells are more affected by monocular lid suture than are X cells might have something to do with the more serious consequences of being at the short end of a competitive mechanism. In addition, the later postnatal development of Y cells[2] could contribute to their special susceptibility.

Functional and clinical implications

The above results pertain to rearing with lid suture. The lids are effective diffusers, and thus little or no spatial patterns can be present during development. Remember that defocusing is a different matter, since only higher spatial frequencies (or finer details) are attenuated. The low spatial frequencies (or larger shapes) available in a defocused image should provide excellent stimulation for Y cells, but not for X cells (Fig. 3). One might then predict that rearing conditions which provide a defocused retinal image, such as myopia, anisometropia, or certain forms of strabismus, would not affect Y cell development and would affect only those X cells which normally develop sensitivity to spatial frequencies high enough to be attenuated by the defocus. Furthermore, such early deprivation of high spatial frequencies should permit development of fairly good form vision with reduced acuity, since most Y cells would develop normally. Most of these predictions have, in fact, been described for cats reared with strabismus or otherwise defocused images[5].

Finally, this might serve to explain some of the variability observed in clinical studies of amblyopia. Some forms of amblyopia are characterized by fairly good vision, but reduced acuity, and these patients presumably have good sensitivity for low spatial patterns. Other forms of amblyopia are characterized by much worse vision, and these patients presumably have reduced sensitivity for all spatial frequencies. Much of the data from cat X and Y cells might apply here. First, we now know that retinal and geniculate cells in many mammals, including monkeys, can be divided into classes whose basic properties are indistinguishable from cat X and Y cells. Thus, there is every reason to believe that the human visual system is also constructed of X and Y pathways. Secondly, the Y pathways seem to be sufficient for basic form vision (remember that cats with striate cortical lesions have excellent form vision[1]). Thus, a visual environment which permits normal development of the Y pathways is consistent with reasonable form vision. Distortions created by lid occlusion and cataracts, which attenuate all spatial frequencies to which Y cells are sensitive, would prevent their normal development and result in severe amblyopia. Distortions created by defocusing (myopia, anisometropia, certain forms of strabismus), and which thus have considerable low spatial frequency stimuli, would permit normal development of the Y pathways and somewhat affect development of the X cell pathways. A patient suffering from such conditions would have reduced acuity, but might still be able to appreciate forms reasonably well.

Conclusions

This account must be recognized for what it is: a limited and speculative treatment of the function of X and Y cells in normal and amblyopic vision. Many questions still require answers. What is the true functional significance of the X/Y dichotomy? Why do some pathways (Y cells) seem to develop by a competitive mechanism, while others (X cells) do not? What environmental parameters are necessary to confer a competitive advantage to non-deprived Y cells, and how is this manifested in neuroplastic development? Similarly, what are the links between the deprived environment and non-competitive development of X cells? Answers to these questions are not only of inherent interest to neurobiologists, but they might also provide a clearer understanding of amblyopia and other clinical problems.

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