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Models of the Visual Cortex
Edited by D. Rose and V. G. Dobson

CHAPTER 8

Parallel W-, X- and Y-cell pathways in the cat: a model for visual function

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INTRODUCTION

The model of functional significance presented here is based on studies of cats and deemphasizes the role of the striate cortex in basic-form vision. The gist of the hypothesis is outlined below; it has been described in more detail elsewhere (Sherman, 1985). It is organized around the W-, X- and Y-cell pathways (for reviews and other terminology, see Rodieck, 1979; Stone, Dreher and Leventhal, 1979; Lennie, 1980; Sherman and Spear, 1982; Sherman, 1985). These are three major, parallel pathways that start in the retina, are integrated through the lateral geniculate nucleus and innervate the various areas of the visual cortex. Figure lc,d shows that the 'visual cortex' receiving direct geniculate afferents represents some 10 to 20 separate, retinotopically mapped regions in addition to the striate cortex (Tusa, 1982; Raczkowski and Rosenquist, 1983).

It is clear that these W-, X- and Y-cell pathways are fairly independent of one another through the lateral geniculate nucleus (Cleland, Dubin and Levick, 1971; Hoffmann, Stone and Sherman, 1972; Wilson, Rowe and Stone 1976), and cells of the striate cortex seem also to belong primarily to just one of these pathways (Bullier and Henry, 1979a, 1970b, 1979c; Tanaka, 1983a, 1983b). Any such division for the extrastriate visual areas is presently unclear. In principle, any cortical cell's innervation can be traced peripherally to one or more of these pathways. Thus the use of the term 'W-cell pathway' includes all neurons having innervation that can be traced to retinal W-cells, and likewise for the X- and Y-cell pathways. Because we cannot at present delineate these pathways through all areas of cortex, the meaning of the

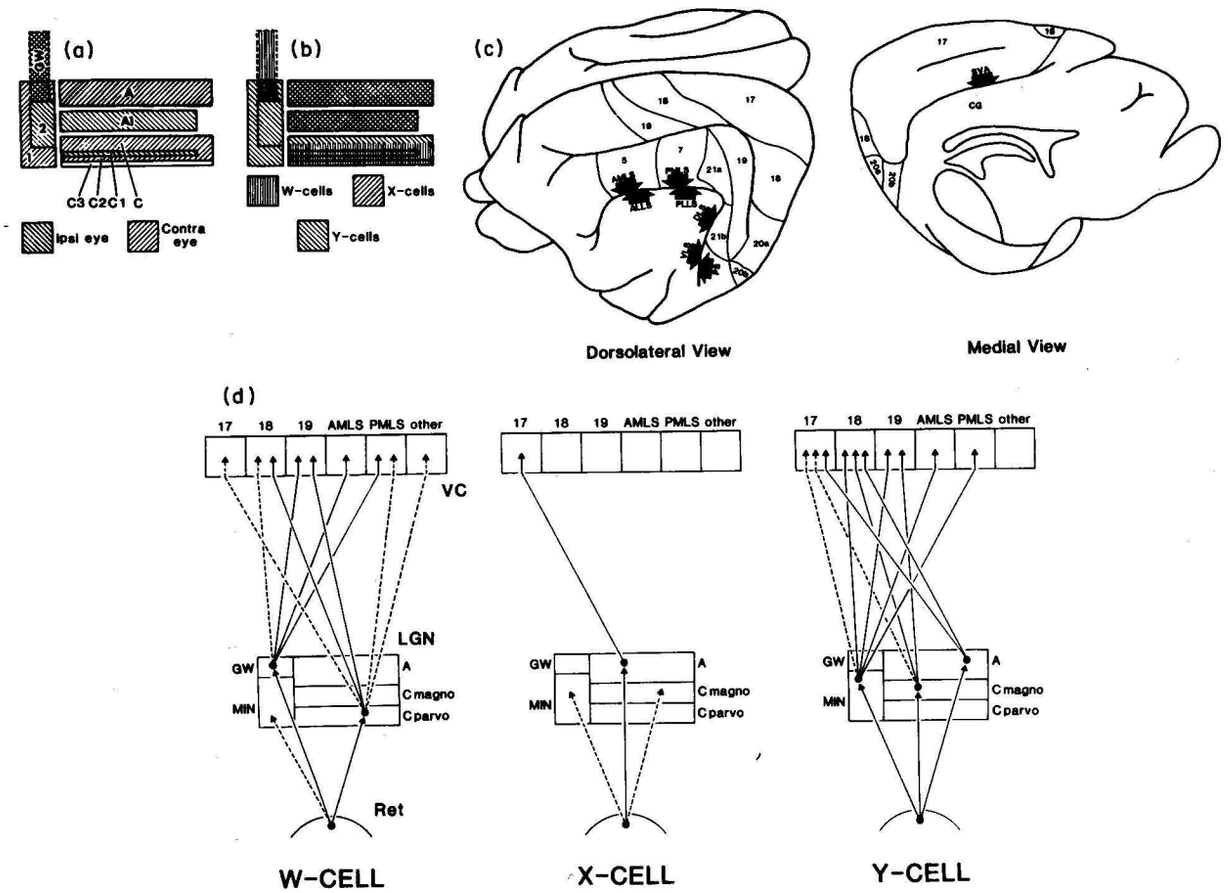


FIGURE 1 Schematic representation of the W-, X- and Y-cell pathways among the divisions of the lateral geniculate nucleus and visual cortex. (a) Laminar arrangements of the right lateral geniculate nucleus according to ocular input as schematically shown in a coronal view. Illustrated are laminae A, A1, C, C1, C2, C3, the medial interlaminar nucleus (1 and 2; lamina 3, which is innervated by the contralateral temporal retina, is not shown because it occupies a more rostral position) and the geniculate wing (GW). (b) Same view of the nucleus as in (a) but showing the main locations of W-, X- and Y-cells. Not shown are the possible presence of W-cells in the medial interlaminar nucleus and rare X-cells in the medial interlaminar nucleus and C-laminae. (c) Visual cortical areas in the cat as shown in dorsolateral (left) and medial (right) views of the left hemisphere. In addition to the nine areas designated by Brodmann numbers (5, 7, 17, 18, 19, 20a, 20b, 21a, 21b) are nine additional areas (AMLS, PMLS, VLS, ALLS, PLLS, DLS, CG, PS, SVA). The abbreviations are: AMLS, anterior medial lateral suprasylvian area; PLMS, posterior medial lateral suprasylvian area; VLS, ventral lateral suprasylvian area; ALLS, anterior lateral lateral suprasylvian area; PLLS, posterior lateral lateral suprasylvian area; DLS, dorsal lateral suprasylvian area; CG, cingulate gyrus; PS, posterior suprasylvian area; SVA, splenial visual area. Thirteen of these areas (17, 18, 19, 20a, 20b, 21a, 21b, AMLS, PMLS, VLS, ALLS, PLLS and DLS) seem to be purely visual and exhibit retinotopic organization. The remaining five (5, 7, CG, PS, SVA) have some visual neurons but may not be exclusively visual, and no retinotopic organization has yet been demonstrated for any of them. (Redrawn from Tusa, 1982; Raczkowski and Rosenquist, 1983). (d) Schematic summary diagram of W-, X- and Y-cell pathways from the retina through the lateral geniculate nucleus to various areas of visual cortex as shown in (c). Abbreviations: Ret, retina; LGN, lateral geniculate nucleus; A, A-laminae; Cmagno, magnocellular lamina C; Cparvo, parvocellular C-laminae; GW, geniculate wing; MIN, medial interlaminar nucleus; VC, visual cortex; 17, area 17; 18, area 18; 19, area 19; AMLS and PMLS, as noted in (c); other, areas 20a, 20b, 21a and 21b plus ALLS, VLS, PLLS and DLS. Solid lines represent relatively dense projections and dashed lines represent relatively sparse projections. See Sherman (1985) for details of the derivation of these connections.

terms for W-, X- and Y-cell pathways is necessarily vague beyond the lateral geniculate nucleus.

It is useful to consider the functional significance of each of these parallel W-, X- and Y-cell pathways rather than the more traditional, hierarchical approach that ascribes functional roles for the lateral geniculate nucleus, striate cortex, etc. The hypothesis presented below suggests that basic form vision is largely a function of the Y-cell pathway, particularly of its extrastriate zones of innervation, whereas the X-cell pathway, including the striate cortex, is concerned chiefly with other functions, such as raising spatial resolution from that provided by the Y-cell pathway, providing for stereopsis, etc. No specific role can yet be suggested for the W-cell pathway (however, see Stone, Dreher and Leventhal, 1979).

RESPONSE PROPERTIES OF W-, X- and Y-CELLS

With few exceptions, each geniculate W-, X- and Y-cell seems to receive its innervation from a few retinal ganglion cells of the same class, and the response properties of these geniculate neurons are essentially the same as those of their retinal counterparts (Cleland, Dubin and Levick, 1971; Kaplan, Marcus and So, 1979). Details of these properties are beyond the scope of this chapter and they have already been recently reviewed (Rowe and Stone, 1977; Rodieck, 1979; Stone, Dreher and Leventhal, 1979; Lennie, 1980; Sherman and Spear, 1982; Sherman, 1985). For the purposes of the theoretical framework constructed here, only certain response properties need be elaborated. W-cells are so poorly responsive to visual stimuli (Sur and Sherman, 1982a; Thibos and Levick, 1983) that basic analysis of the visual scene most plausibly falls to the X- and Y-cell pathways. A major difference between X- and Y-cells is that the former are more responsive to higher spatial frequencies whereas the latter respond better to lower ones (Lehmkuhle *et al.*, 1980; Thibos and Levick, 1983; Troy, 1983). Thus the Y-cell pathway is likely to be most concerned with analysis of the lower spatial frequencies in the visual scene, and analysis of fine spatial details is left to the X-cell pathway. This, of course, is speculation based on response properties of neurons in anesthetized, paralyzed cats.

MORPHOLOGICAL PROPERTIES OF W-, X- AND Y-CELLS

In both the retina and the lateral geniculate nucleus, W-, X- and Y-cells are morphologically distinct from one another (for the retina: Wassle, 1982; for the lateral geniculate nucleus: Friedlander *et al.*, 1981; Stanford, Friedlander and Sherman, 1983). The details and implications of these structure/function relationships can be found elsewhere (Friedlander *et al.*, 1981; Wassle, 1982; Stanford, Friedlander and Sherman, 1983). These relationships permit the

derivation by anatomical criteria of the numbers and distributions of W-, X- and Y-cells, thereby avoiding the sampling problems inherent in electrophysiology (cf. Friedlander *et al.*, 1981).

Retina

Ganglion cell density peaks near the area centralis, but this density function is steeper for X-cells than for W- or Y-cells (Fukuda and Stone, 1974; Leventhal, 1982, Wassle, 1982). While relative numbers thus depend somewhat on eccentricity, to a first approximation, X-cells represent roughly 50 to 60 per cent. of all retinal ganglion cells and Y-cells represent roughly 5 per cent. (Fukuda and Stone, 1974; Wassle, 1982; Williams and Chalupa, 1983). Every retinal X- and Y-cell projects to the lateral geniculate nucleus (Fukuda and Stone, 1974; Bowling and Michael, 1980; Illing and Wassle, 1981; Sur and Sherman, 1982b). Of the remaining retinal ganglion cells (i.e. W-cells), roughly 40 per cent. project to the lateral geniculate nucleus (Illing and Wassle, 1981; Leventhal, 1982). Thus about 15 to 20 per cent. of retinal ganglion cells participate in the W-cell pathway. By this analysis, the W- to X- to Y-cell ratio among ganglion cells that innervate the lateral geniculate nucleus is approximately 3:10:1.

Lateral geniculate nucleus

As noted in Fig. 1a,b, the cat's lateral geniculate nucleus is a laminated structure, and the distribution of ocular input as well as of W-, X- and Y-cells varies with lamination (Hickey and Guillery, 1974; Wilson, Rowe and Stone, 1976; Kratz, Webb and Sherman 1978; Guillery *et al.*, 1980). X-cells are nearly exclusively limited to the A-laminae, although these cells may rarely be found in the C-laminae and medial interlaminar nucleus. Y-cells abound in the A-laminae, magnocellular lamina C (i.e. the dorsal tier of lamina C) and the medial interlaminar nucleus. W-cells are found in the parvocellular C-laminae (i.e. those ventral to magnocellular lamina C) and possibly the geniculate wing and medial interlaminar nucleus.

The X- to Y-cell ratio of the A-laminae is roughly 2:1 (LeVay and Ferster, 1977; Friedlander *et al.*, 1981; Leventhal, 1982; Friedlander and Stanford, 1984), and when the C-laminae and medial interlaminar nucleus are considered, the geniculate X- to Y-cell ratio probably approaches 1:1. This is dramatically different from the 10:1 ratio in the retina. Estimates of geniculate W-cell numbers are not presently available. Sur and Sherman (1982b) have described a possible substrate for this amplification of the Y-cell pathway (see also Bowling and Michael, 1980): retinal X-cell axons typically innervate only lamina A or A1 in small zones, whereas those of Y-cells branch to innervate lamina A or A1 in large zones (5 to 10 times larger

than those of X-cells) plus the medial interlaminar nucleus and, if from the contralateral eye, lamina C.

Visual cortex

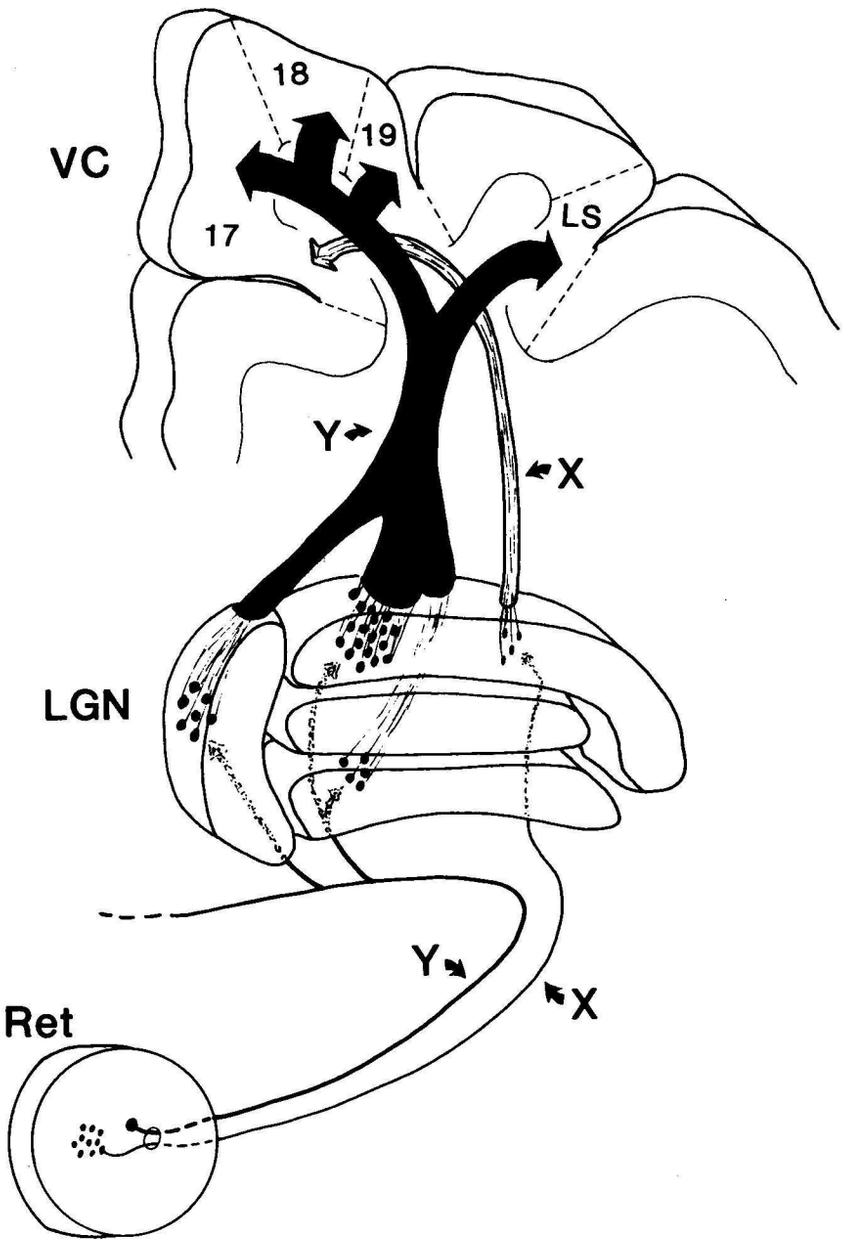
Figure 1d summarizes the probable projections of the geniculocortical limbs of the W-, X- and Y-cell pathways (for further details, see Raczkowski and Rosenquist, 1983; Sherman, 1984). The X-cell projection is limited to the striate cortex, while those of W- and Y-cells innervate many extrastriate regions in addition to the striate cortex.

The projections of individual X- and Y-cell axons to the striate cortex in some ways resemble the patterns of their retinogeniculate counterparts (Ferster and LeVay, 1978; Gilbert and Wiesel, 1983; Humphrey, Sur and Sherman 1982). Most X-cell axons innervate layer 4 ventrally in a single, small patch that may be limited to one ocular dominance column (e.g. Shatz, Lindstrom and Wiesel 1977); Y-cell axons innervate layer 4 dorsally in several, larger patches that may represent several ocular dominance columns of the same eye. Both axon classes also sparsely innervate layer 6. In addition, most of the Y-cell axons branch to innervate area 18 (Stone and Dreher, 1973; Geisert, 1980) in extensive zones (Humphrey, Sur and Sherman, 1982). Thus the Y-cell pathway may again be relatively amplified by geniculocortical projections. However, as noted above, it is not yet clear to what extent neurons in the various visual areas are members of one or more of these W-, X- and Y-cell pathways.

Summary of X- and Y-cell pathways

Figure 2 summarizes the organizational principles for the X- and Y-cell pathways as described above. (Insufficient data are available for the W-cell pathway for it to be included in such a schematic diagram.) The pathway beginning with X-cells, which represent the majority of retinal ganglion cells, innervates only a portion of a single area of the visual cortex (i.e. striate cortex). In contrast, the pathway beginning with Y-cells, which represent a

FIGURE 2 Hypothetical and schematic diagram of the retino-geniculo-cortical X- and Y-cell pathways; for simplicity, only pathways from the contralateral eye are illustrated. Each retinogeniculate and geniculocortical Y-cell axon branches to innervate many more neurons than does each of the analogous X-cell axons. Also, the X-cell pathway is essentially limited to the A-laminae and area 17, whereas the Y-cell pathway occupies most regions of the lateral geniculate nucleus and visual cortex. Consequently, a small minority of retinal ganglion cells (Y-cells) come to dominate the visual cortex whereas the much greater number of retinal ganglion cells (X-cells) come to control much less cortical tissue. For details and the functional significance of this schema, see the text.



small minority of retinal ganglion cells, dominates geniculocortical innervation, particularly with regard to extrastriate cortical areas. The morphological basis for this relative shift in central emphasis between the X- and Y-cell pathways may be the larger, more extensively arborized innervation patterns of individual Y-cell axons compared to those of X-cell axons.

BEHAVIORAL CORRELATES FOR THE W-, X- AND Y-CELL PATHWAYS

A variety of quite different functional roles have been suggested for the W-, X- and Y-cell pathways (Ikeda and Wright, 1972; Stone, Dreher and Leventhal, 1979). However, it is most difficult to test these suggestions, because of the lack of a robust linking hypothesis between behavior and neurophysiology (for details, see the discussion in Sherman, 1985). How, for instance, does one link the animal's ability to discriminate circles from triangles with different axonal conduction velocities amongst neuronal classes?

Contrast-sensitivity functions may provide a potentially useful link between behaviour and neurophysiology. These functions can be determined psychophysically for the behaving animal and neurophysiologically for individual neurons. Comparisons between behavior and physiology are thus *relatively* straightforward. Interpretation of these comparisons is nonetheless risky and requires a number of dubious assumptions. Two such assumptions are that a straightforward relationship exists between contrast sensitivity of individual neurons and that of the behaving animal, and that different physiological conditions (i.e. anesthetized and paralyzed versus alert and behaving) do not significantly affect contrast sensitivity. Despite such serious provisos, some useful insights can be gained by these measures of contrast sensitivity. For simplicity, only spatial functions at low temporal rates of modulation (1 to 2 Hz) are considered (for other temporal parameters, see Blake and Camisa, 1977; Lehmkuhle, Kratz and Sherman, 1982).

Sprague and his colleagues (Sprague *et al.*, 1977; Berkley and Sprague, 1979) have shown that bilateral removal of striate cortex has surprisingly little effect on the cat's visual capacity beyond a 25 to 50 per cent. acuity loss. Lehmkuhle, Kratz and Sherman (1982) recently confirmed and extended this with psychophysical measures of spatial contrast sensitivity. The sensitivity losses attributed to striate cortex lesions were limited to higher spatial frequencies, and no other postoperative deficits were noted. However, Kaye, Mitchell and Cynader (1981) report that binocular depth perception may be virtually lost to cats with bilateral lesions of areas 17, 18 and part of 19, despite the small losses of visual acuity and basic form vision suffered by these cats. Much larger cortical lesions, which significantly encroach into the extrastriate areas of the visual cortex, must be made before the animal's visual performance is clearly impaired beyond a simple loss of acuity (Sprague *et al.*, 1977).

These data are most interesting in the context of Fig. 1d. An ablation limited to the striate cortex removes the X-cell pathway from cortical representation, while much of the W- and Y-cell pathways remain. It thus follows that neither the X-cell pathway nor the striate cortex is necessary for reasonable form vision, although these may be necessary for maximum visual acuity and stereopsis. It seems likely that the W-cell pathway, because of its poor responsiveness, is not responsible for the remaining visual capacity. While this disregard for W-cell function may well prove incorrect, and many important functions not yet tested in destriate cats may appear in future studies, the tentative conclusion is that the remaining Y-cell pathway is sufficient for excellent form vision. Therefore, only after sufficiently large cortical lesions that destroy the bulk of the Y-cell inputs will severe visual losses in basic form vision result.

Similar psychophysical data have also been obtained from cats reared from birth with deprivation of visual forms by eyelid suture (monocular or binocular) or dark rearing. Such cats develop serious abnormalities in their Y-cell pathway. (Sherman and Spear, 1982; Friedlander, Stanford and Sherman, 1982; Sur, Humphrey and Sherman, 1982). Recent behavioral studies of their contrast sensitivity offer interesting correlates between their ambylopia and Y-cell deficits (Blake and DiGianfillipo, 1980; Lehmkuhle, Kratz and Sherman, 1982). The visually deprived cats suffer sensitivity losses at all spatial frequencies. Thus their ambylopia is not simply an acuity loss, and indeed their sensitivity losses are greater for lower than for higher spatial frequencies. This seems to relate well to the abnormalities of the Y-cell pathway, since Y-cells are especially sensitive to the lower spatial frequencies.

Two further points can be drawn from the psychophysical data. First, spatial resolution alone may not be as good an index of visual performance as is sensitivity to lower spatial frequencies. Indeed, binocularly deprived cats have slightly better resolution than do the normally reared, destriate cats (Lehmkuhle, Kratz and Sherman, 1982), but the deprived cats exhibit a clearly inferior visual performance. Second, the observation that normally reared, destriate cats see better than do visually deprived cats implies that deficits limited to the striate cortex, no matter how severe, cannot account for the ambylopia of these visually deprived cats. A more parsimonious explanation for their ambylopia relates to the deficits among their geniculate Y-cells: as can be appreciated from Fig. 1d and 2, deficits here will produce widespread effects in many areas of the visual cortex.

COMPARISON BETWEEN CATS AND MONKEYS

These studies of cats place greater emphasis for the neural substrates of pattern vision on the extrastriate Y-cell pathways and less on the X-cell pathway and striate cortex than is usually the case. One may wonder how this conclusion relates to monkeys, especially since striate cortex lesions

render monkeys practically blind (cf. Weiskrantz, 1972; Miller, Pasik and Pasik, 1980). A detailed discussion of the monkey's retino-geniculo-cortical pathways is inappropriate here, but certain points are briefly considered below.

As is the case in cats, the monkey's retino-geniculo-cortical pathways are organized into several, parallel neuronal streams (Hubel and Wiesel, 1972; Dreher, Fukuda and Rodieck, 1976; Bullier and Henry, 1980; Leventhal, Rodieck and Dreher, 1981; Blasdel and Lund, 1983; Weber *et al.*, 1983). Although many reports have emphasized basic similarities between these pathways in the monkey and the W-, X- and Y-cell pathways in the cat, the details of any such homology or analogy between species is a matter of debate (see Sherman, 1985).

It is clear in any case that the vast majority of geniculate neurons in the monkey project exclusively to the striate cortex (Tigges, Tigges and Perachio, 1977; see also Wong-Riley, 1976; Yukie and Iwai, 1981), a condition quite unlike that in the cat, for which an extensive extrastriate projection from the lateral geniculate nucleus exists. A striate cortex lesion in monkeys thus destroys nearly all of the geniculocortical input, including practically the total of any presumed Y-like pathway. As noted above, such monkeys are nearly blind without the striate cortex, while destriate cats see well. Nearly all of the geniculocortical projection must be destroyed in cats to produce an animal comparably blind to the destriate monkey. Perhaps the key to understanding the consequences of striate cortex lesions among mammalian species has less to do with striate cortex *per se* and more to do with the extent of damage to the geniculocortical innervation, and particularly to the Y-cell pathway in cats and its counterparts in other species.

CONCLUSIONS AND HYPOTHESIS

From the psychophysical studies of cats cited above, it follows that sensitivity to lower spatial frequencies may be sufficient and necessary for reasonable pattern vision. Recent psychophysical studies of human vision tend to support this: basic form information seems to be carried by the lower spatial frequencies, whereas the higher ones add detail and maximize resolution (Kabrisky *et al.*, 1970; Ginsburg, 1978; Hess and Woo, 1978).

A consideration of the spatial response properties of W-, X- and Y-cells, the visual performance of visually deprived and destriate cats and the projection patterns of the W-, X- and Y-cell pathways (Figs. 1d and 2) lead to the following hypothesis. The Y-cell pathway, with its unique sensitivity to the lower spatial frequencies, is the neural substrate for basic spatial vision. A cat with good sensitivity to lower spatial frequencies and a reasonably intact

Y-cell pathway (e.g. a normally reared cat with or without the striate cortex) displays reasonable spatial vision, whereas a cat with poor low frequency sensitivity and a deficient Y-cell pathway (e.g. a monocularly or binocularly deprived cat) exhibits serious amblyopia. The X-cell pathway (including the striate cortex), with its superior sensitivity to higher spatial frequencies, adds detail and raises acuity to the basic analysis performed by the Y-cell pathway; the X-cell pathway and striate cortex may also be essential to stereopsis. No specific role can yet be suggested for the W-cell pathway, but due to its relative unresponsiveness, it may play some unspecified but minor role in conscious visual perception (cf. Stone, Dreher and Leventhal, 1979). The above must be recognized for the speculative and incomplete hypothesis that it is.

This hypothesis can now be considered with respect to the central connections of X- and Y-cells (Fig. 2). Few Y-cells exist in retina, perhaps because the encoding of lower spatial frequencies requires relatively few peripheral elements. However, the primacy to spatial vision of these lower frequencies requires that considerable cerebral cortex be devoted to their analysis. Thus the Y-cell pathway is amplified centrally with widespread axonal connections, resulting in its relative dominance at the cortical level. The role and organization of the X-cell pathway is complementary. To extract the finest spatial detail from a visual scene requires a large number of peripheral elements to encode the higher spatial frequencies. X-cells thus abound in retina. However, the presumed secondary importance of these higher spatial frequencies to basic form vision results in an X-cell pathway that has narrowly distributed axonal connections and is channelled through a portion of a single area of the visual cortex.

Finally, this hypothesis, by playing down the role of the X-cell pathway in basic-form vision, also plays down this role for the striate cortex. For cats, this follows logically from the good spatial vision still evident after destruction of the striate cortex. Since destriate monkeys are practically blind, this secondary role for the striate cortex may seem inappropriate. However, the results of striate cortex lesions in monkeys may have more to do with a near-total destruction of geniculocortical input, including all of any monkey counterpart to the cat's Y-cell pathway, than with the loss of the striate cortex *per se*.

ACKNOWLEDGMENTS

The author's research has been supported by grants EY03038 and EYO3604 from the United States Public Health Service. The author thanks P. Palam for typing the manuscript.

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Models of the Visual Cortex
Edited by D. Rose and V. G. Dobson

CHAPTER 9

Local log polar frequency analysis in the striate cortex as a basis for size and orientation invariance

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When an object moves across the visual field its image stimulates an ever-changing array of retinal receptors. If the observer is to recognize it as the same object in spite of these variations, this variable retinal input must be transformed into a unique pattern of neural activity that defines the object. There are two current models of form encoding: (a) an abstract, structural or propositional representation of the object, typically a list of the object's features and their interrelations, or (b) an analogue representation, typically a transformation onto a new set of dimensions where form information is invariant to changes in input size, position and orientation (for a further discussion of analogue versus structural models see Sutherland, 1973; Pylyshyn, 1973; Kosslyn, 1980).

A structural or propositional representation reduces the form to be identified to a list of primitive elements and the structural relations between them. If the primitives are, for example, lines (contours) and angles, the edges must first be extracted and then the relations between them determined. Pattern classification is based on structure and the descriptions of the primitive features do not necessarily specify their size, orientation or position. As a result, this type of encoding permits representations that are, in a very simple way, invariant with respect to the size, orientation and position of the overall pattern.

In the other model, stimulus patterns are transformed into analogue representations that do not vary with the size, orientation or position of the input. Following the original work of Schade (1956), Campbell and Robson (1968) proposed that the visual system performs a Fourier analysis on the