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PARALLEL PATHWAYS IN THE CAT'S GENICULOCORTICAL SYSTEM: W-, X-, AND Y-CELLS

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The classic view of functional organization in the central visual pathways requires all neural processing relevant to conscious perception to be funnelled serially through the geniculostriate pathways. These pathways were thought to be fairly homogeneous at each level and were regarded as a sort of "initial common pathway" analogous to the "final common pathway" concept of the motoneuron.

This view of the visual pathways was more or less successfully challenged by and replaced with the concept of "parallel processing." This challenge originated from two lines of research. One is the research initiated by Sprague, Diamond, Schneider, and their colleagues (Sprague and Meikle, 1965; Sprague, 1966; Schneider, 1969; Ware *et al.*, 1974; Sprague *et al.*, 1977), research that demonstrated the importance for vision of pathways outside and organized in parallel with the geniculostriate pathways [see Sprague *et al.* (1973, 1981) for reviews of this]. The second line of research is the growing body of evidence that even the retino-geniculo-cortical pathways are organized into at least three parallel, distinct, and independent neural chains. These are referred to as the W-, X-, and Y-cell pathways, and Table I summarized some of the differences among W-, X, and Y-cells (Enroth-Cugell and Robson, 1966; Cleland *et al.*, 1971; Hoffmann *et al.*, 1972; Stone and Fukuda, 1974; Wilson *et al.*, 1976; Hochstein and Shapley, 1976a,b; Lehmkuhle *et al.*, 1980; see Lennie, 1980, for a recent review).

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TABLE I

Functional Properties of W-, X-, and Y-Cells

	W-Cells	X-Cells	Y-Cells
Axonal conduction velocity	Slow	Medium speed	Fast
Receptive-field organization	Concentric (center/surround) or diffuse	Concentric	Concentric
Spatial summation	Linear or nonlinear	Linear	Nonlinear
Receptive-field size	Large	Small	Large
Response to standing contrast	Tonic or phasic	Tonic	Phasic
Contrast sensitivity	Generally poor	Good to lower and higher spatial frequencies	Good to higher spatial frequencies

I. PROJECTIONS OF THE W-, X-, AND Y-CELL PATHWAYS

Figure 1 shows a simplified schematic wiring diagram of the cat's retino-geniculo-cortical pathways. W-, X-, and Y-cells in the retina project respectively and fairly exclusively to geniculate W-, X-, and Y-cells,* and these in turn project axons to visual cortex. Therefore, the geniculocortical input represents three distinct, parallel pathways. The degree to which these pathways remain distinct after they reach cortex is not at all clear. There is, however, some evidence from striate cortex in cats and monkeys that suggests the continued independence of these pathways (Hoffmann and Stone, 1971; Stone and Dreher, 1973; Bullier and Henry, 1979a,b,c, 1980).

As indicated in Fig. 1, the lateral geniculate nucleus is a laminated structure. The two dorsal laminae, A and A1, are a reasonably matched pair. Each receives retinal input from one or the other eye, their retinotopic maps are in register so that lines perpendicular to the lamination represent points in visual space [i.e., the "projection lines" of Bishop *et al.* (1962); see also Sanderson (1971a,b)], and practically all of the neurons found there are X- or Y-cells (Wilson *et al.*, 1976). The A laminae X-cells project exclusively to cortical area 17, while the Y-cells project to both areas 17 and 18, typically via branching axons (Stone and Dreher, 1973; Geisert, 1980).

The C complex is comprised of several laminae, termed C, C1, C2, and C3 as one proceeds dorsoventrally (Hickey and Guillery, 1974). Laminae C and C2 are innervated by the contralateral eye; lamina C1 is innervated by the ipsilateral eye; and lamina C3 appears to receive no direct retinal afferents. The dorsal tier of lamina C contains many Y-cells and perhaps some X-cells, and the remainder of the C complex represents a nearly exclusive W-cell population (Wilson *et al.*, 1976). The C laminae have a wide distribution of projections to posterior cortex that encompasses virtually all of the known visual areas, including areas 17, 18, 19, and the lateral suprasylvian cortex (LeVay and Gilbert, 1976; Geisert, 1980).

The medial interlaminar nucleus includes at least two laminae, one representing each eye. Practically all neurons there are Y-cells, although some W- and X-cells have also been reported (Mason, 1975; Kratz *et al.*, 1978; Dreher and Sefton, 1979). Guillery *et al.* (1980) have recently described an anterior and medial extension to the medial interlaminar

**Retinal X-cells project almost exclusively to the lateral geniculate nucleus. Retinal W- and Y-cells, however, also project to other structures, such as the superior colliculus.*

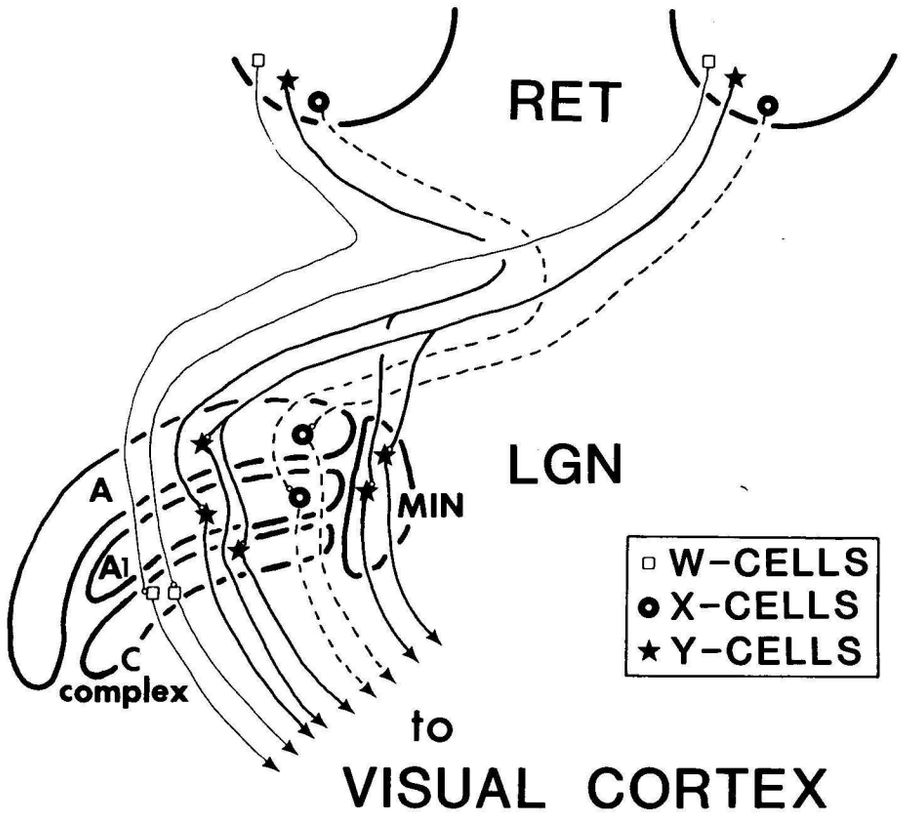


Figure 1. Simplified wiring diagram of the cat's retino-geniculo-cortical pathways. These pathways can be broken down into three parallel, fairly independent systems involving W-, X-, and Y-cells. This diagram shows the general distribution within the lateral geniculate nucleus of W-, X-, and Y-cells, but some details have been omitted for simplicity (see text). Y-Cells are also found in the dorsal portion of lamina C (the most dorsal lamina in the C complex of laminae; see text), and both X- and W-cells can be found in the medial interlaminar nucleus (MIN).

nucleus that receives fine optic tract fibers and therefore might contain mostly W-cells. Projections of the medial interlaminar nucleus to cortex are roughly as extensive as are those of the C laminae and include inputs to areas 17 (probably), 18, 19, and the lateral suprasylvian cortex (Rosenquist *et al.*, 1974; Geisert, 1980).

Consequently, X-cells are found exclusively or nearly so in the A laminae, and project exclusively or nearly so to area 17. Y-Cells are found in the A laminae, the medial interlaminar nucleus, and the dorsal part of lamina C; and these cells project widely to visual cortical areas. W-Cells are found in the C laminae and perhaps in the medial interlaminar nucleus, and these cells also project widely to visual cortical areas.

II. FUNCTIONAL PROPERTIES OF W-, X-, and Y-CELLS.

The significance of the functional organization of these parallel pathways is not at all clear. What follows is a speculative and incomplete discussion of the functional significance of W-, X-, and Y-cells, and this speculation should not be mistaken for widely held dogma.

Most hypotheses assume that the W-, X-, and Y-cell pathways analyze somewhat different aspects of the visual scene and that these analyses are synthesized at some as yet unknown central structure to produce an overall neural representation of the visual environment. Inferences concerning these differential analyses are usually drawn from different response properties of W-, X-, and Y-cells (see Table I). As just one common example, it has been suggested (e.g., Ikeda and Wright, 1972, 1975) that X-cells, by virtue of their small receptive fields, preference for stationary or slowly moving targets, concentration in the area centralis, tonic and linear responses, etc., analyze spatial patterns. Conversely, Y-cells, because of their larger fields, prevalence in peripheral retina, responsiveness to fast target movements, phasic and nonlinear responses, etc., analyze temporal patterns. W-Cells are often ignored or relegated to a minor role in conscious visual perception, both because of their generally sluggish responses and also because we simply do not yet know very much about the response properties of these cells (see also below). Other rather different speculations have also been suggested (cf. Stone *et al.*, 1979; Lennie, 1980), and one of these is presented in more detail below (cf. Sherman, 1979; Lehmkuhle *et al.*, 1980).

A. W-CELLS

As with other hypotheses, this one has no clear role for W-cells. Their function is something of a mystery. This is clearly a weakness in any hypothesis, because W-cells are numerous and have widely distributed projections to visual cortex. Most of the specific processing for conscious vision is tentatively attributed to X- and Y-cells, but as we learn more about W-cells, much or most of our working hypothesis may be altered.

B. X- and Y-CELLS

A good deal of our hypothesis concerning roles for X- and Y-cells derives from the contrast sensitivity measurements reported by Lehmkuhle *et al.* (1980). These measurements can be made with stimuli consisting of sine wave gratings in the following manner.* These gratings are generated and displayed on a cathode ray tube. The spatial frequency, temporal frequency, and constrast of these gratings are continuously altered. Spatial frequency is the number of grating cycles per degree of visual angle. Temporal frequency is the rate, in cycles per second, at which the grating is counterphased. During counterphasing, the bright and dark regions of the grating are exchanged in a sinusoidal manner [see Fig. 2 of Sekuler *et al.* (1978)]. Contrast is defined as $(L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min} are, respectively, the maximum and minimum luminance values across the grating. Contrast is altered by changing L_{max} and L_{min} equal amounts in opposite directions, and thereby the mean luminance, $(L_{max} + L_{min})/2$, is held constant. Contrast sensitivity is determined by changing the contrast for a given spatial and temporal frequency until a threshold response from the neuron is obtained; the inverse of this contrast at threshold is the contrast sensitivity. Contrast sensitivity functions can then be constructed by plotting contrast sensitivity as a function of spatial and/or temporal frequency.

** Square wave gratings, comprised of parallel black and white stripes, may be more familiar to most readers. The luminosity profile of such a grating (i.e., the change in brightness as one moves across the grating) can be represented by a square wave. A sine wave grating is quite similar, the major difference being that its luminosity profile is a sine wave.*

The value of these functions is that they illustrate neural sensitivity to a wide range of spatiotemporal variables and not just the resolution limits.* There is a theoretical usefulness to such information that derives from Fourier (or linear systems) analysis and synthesis. That is, any complex waveform can be synthesized by the combination of sine waves appropriately chosen for phase (i.e., relative position), frequency, amplitude (i.e., contrast), and mean luminance; and it is conversely possible to analyze any complex waveform in terms of its component sine waves. Since visual scenes, in black and white, can be depicted as luminosity changes with position, and this describes a complex wave form, Fourier analysis applies here. In other words, visual scenes can be analyzed and synthesized in terms of their sine wave grating components [see Braddick *et al.* (1978), and Sekuler *et al.* (1978) for a more complete discussion of this].

The contrast sensitivity functions obtained from psychophysical or neurophysiological data should thus be viewed with this in mind. Figure 2 illustrates "typical" X- and Y-cell functions, which are actually the average sensitivity values plotted for ten X- and ten Y-cells with receptive fields within 10° of the area centralis. The cell-to-cell variability in these sensitivity measures is not shown, but the following generalizations can be formulated in spite of this variability (cf. Lehmkuhle *et al.*, 1980). For spatial functions (Fig. 2, upper), Y-cells show a monotonic decrease in sensitivity with increasing spatial frequency, whereas X-cells are most sensitive to middle frequencies with decreasing sensitivity to higher and lower frequencies. Except at lower spatial frequencies (where Y-cells are always more sensitive than X-cells), X- and Y-cell sensitivity values largely overlap. There is a slight tendency for X-cells to show better spatial acuity at lower temporal frequencies (Fig. 2, upper right). Figure 2, lower, summarizes the temporal sensitivity functions. Both X- and Y-cells show decreasing sensitivity with increasing temporal frequency, but considerable overlap exists depending somewhat on spatial frequency.

The main and only dramatic difference between X- and Y-cells from these functions occurs at low spatial frequencies: here Y-cells are relatively sensitive and X-cells are not. This is interesting in the context of the importance of low spatial frequencies for form vision. Considerable visual information is carried by low spatial frequencies, while the higher frequencies add certain details and raise spatial

*Spatial resolution or acuity is the highest spatial frequency to which the cell can respond (likewise for temporal resolution). Resolution, then, is one point on a constrast sensitivity curve.

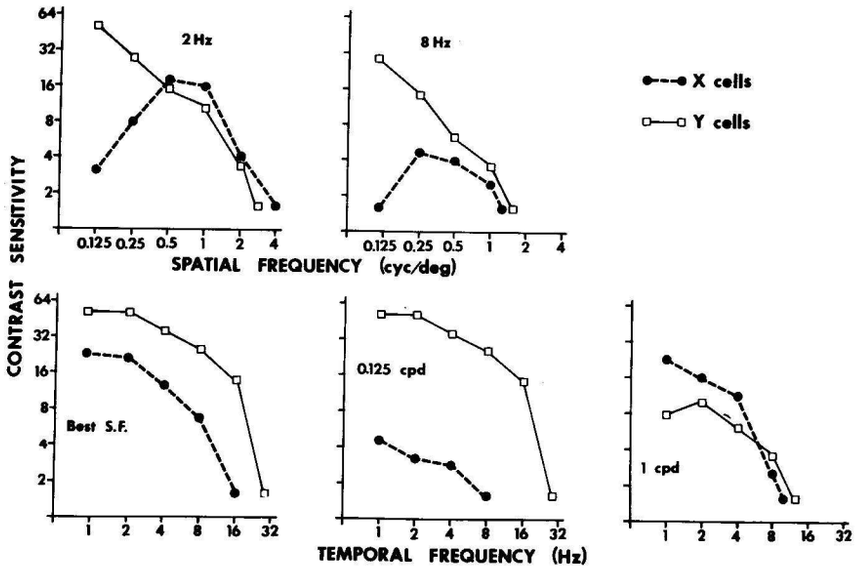


Figure 2. Composite contrast sensitivity functions for ten geniculate X- and ten geniculate Y-cells with receptive fields within 10° of the area centralis. These composite functions were derived by plotting the mean contrast sensitivity values for ten neurons at each spatial or temporal frequency. The small cell-to-cell variability is not shown. The upper curves represent average spatial functions at the two temporal frequencies indicated. The lower curves represent average temporal functions at the best spatial frequency (Best S.F.) plus the two other spatial frequencies indicated. The best spatial frequency is that which for each cell is most sensitive and is always higher for X-cells than for Y-cells.

acuity (Kabrisky *et al.*, 1970; Hess and Woo, 1978). Perhaps, then, the Y-cell system is involved in a basic form analysis while the X-cell system, particularly for low temporal frequencies, permits greater spatial resolution. X- and Y-cells both contribute to analysis of temporal patterns, and their

relative contribution depends greatly upon the spatial frequency content of the stimulus (Sherman, 1979; Lehmkuhle *et al.*, 1980).

Independent support for this hypothesis comes from the behavioral studies of Berkley and Sprague (1979). They tested cats before and after bilateral ablations to areas 17 and most of 18. Such a lesion effectively abolishes practically all X-cell projections to cortex, while many Y-cells (and W-cells) project outside of these areas (see above), and these W- and Y-cell pathways are consequently spared. Cats with these lesions demonstrate remarkably good vision after the ablations. In fact, on most tests of visual capacity, they seem normal; only on certain tests of spatial acuity are deficits seen. These observations, then, are consistent with the suggestion that Y-cells are sufficient for excellent form vision. Nonetheless, the speculative nature of this suggestion, especially in the context of our relative ignorance of W-cell properties, must be emphasized.

III. MORPHOLOGY OF W-, X-, and Y-CELLS

It has been clear for many years that geniculate neurons in the cat are morphologically quite heterogeneous. Guillery (1966) used Golgi impregnation techniques to characterize four different neuron classes based on soma size, dendritic size and shape, and dendritic appendages (see also Tombol, 1969; Famiglietti, 1970; LeVay and Ferster, 1977; Updyke, 1979).

A key question is the extent to which morphological differences in these geniculate cells correspond to functional classes (i.e., W-, X-, and Y-cells). Not only is the structural basis of function of great general interest, but such a structure/function correlation would greatly enhance our knowledge of W-, X-, and Y-cells. Until now, one could identify these cells in the lateral geniculate nucleus only by electrophysiological means, and this in turn limits study of these neurons narrowly to that discipline. In other words, one is unable to apply multidisciplinary morphological, pharmacological, etc., approaches with any confidence to the study of geniculate W-, X-, and Y-cells.

Just one example of the value of morphological correlates for these functional neuron classes relates to the actual distribution of these cells. Because of the uncontrolled biases of electrode sampling, it is not possible to determine the actual distribution of neurons from their electrophysiologically recorded samples. However, considerable indirect evidence from retina has led to a hypothesis for structure/function relationships of W-, X-, and Y-cells there (Boycott and Wassle,

1974; Cleland *et al.*, 1971). This in turn has led to fairly complete distributional maps of these cells within the retina, maps based on soma sizes and devoid of electrode sampling biases (Fukuda and Stone, 1974; Wassle *et al.*, 1975; Stone, 1978). Obviously, it would be most interesting to be able to obtain similar geniculate maps for comparison.

Thus, for many reasons, we decided to obtain direct evidence of the structure/function relationships for geniculate W-, X-, and Y-cells in the cat. Our approach involved the use of recording micropipettes filled with horseradish peroxidase (HRP). With these electrodes, we could classify and study a geniculate neuron with standard electrophysiological techniques, penetrate the cell for intracellular recording, and iontophorese HRP into the cell. The HRP rapidly invades the entire dendritic tree and often the axonal arborization as well. Subsequent histochemistry permits a detailed morphological analysis of the physiologically defined neuron. We have successfully performed such experiments on W-, X-, and Y-cells in the cat's lateral geniculate nucleus (Friedlander *et al.*, 1979, 1981; Stanford *et al.*, 1981).

Before describing the results, it is worth considering the two possible outcomes and their implications. First, no structure/function relationship might have been found. Since geniculate W-, X-, or Y-cells receive exclusive retinal input, respectively, from W-, X-, or Y-cells (cf. Cleland *et al.*, 1971), it is possible that all of the characteristic distinctions among these pathways are determined by retinal circuitry. Geniculate neurons might simply relay these distinctions with no further differential processing, and thus geniculate W-, X-, and Y-cells might not possess morphology distinct from one another. The second possibility is that these geniculate cells do differ morphologically. This, in turn, would suggest that differences among the W-, X-, and Y-cell pathways recur in the lateral geniculate nucleus. In fact, our evidence, based on over 60 neurons, strongly supports this latter possibility.

Figure 3 shows camera lucida drawings of a typical W-, X-, and Y-cell. These cells were physiologically classified and then filled with HRP. Although a certain amount of structural heterogeneity was seen for each functional class, the main differences between these classes were quite consistent.

A. W-CELLS

Our sample of W-cells is still quite small and is limited to the C laminae. Each W-cell has morphology quite distinct from any X- or Y-cell. The W-cell somata are medium in size (75-322 μm^2 in cross-sectional area, with a mean of 188 μm^2; all soma measurements given below are in cross-sectional area). The dendrites are extremely fine and sinuous, and they display an exceedingly rich branching pattern. The dendritic trees are always oriented in a plane parallel to the geniculate lamination, and thus orthogonal to the "projection lines" described by Sanderson (1971a,b).

These W-cells have all been confirmed as relay cells by virtue of antidromic activation from electrical stimulation of visual cortex and/or a filled axon that can be traced into the optic radiation. Some of the filled axons provide collateral innervation via fine branches to the perigeniculate nucleus. Perigeniculate neurons, in turn, send a rich axonal plexus through the geniculate laminae (Ahlsen and Lindstrom, 1978), thereby establishing a feedback neuronal circuit just above lamina A (see also below).

B. X-CELLS

Our sample of X-cells is limited to the A laminae. In many ways, X-cells resemble W-cells rotated through 90° around an anteroposterior axis. X-Cell somata are medium-sized (68-420 μm^2; mean, 219 μm^2). The dendrites are fine, sinuous, and tend to be oriented orthogonal to the laminae. No X-cell dendrite was ever seen to cross a laminar border, despite the observation that some X-cell dendritic trees extend dorsoventrally through nearly all of lamina A or A1. Many X-cell axons also contribute fine collaterals to the perigeniculate nucleus.

A striking feature of most X-cells is the rich distribution of complex appendages along the dendrites. These appendages often look like clusters of grapes growing from the dendritic shafts (cf. Guillery, 1966). Many cells with such dendritic morphology have been presumed to be interneurons based on Golgi impregnation (Tombol, 1969; LeVay and Ferster, 1977; Famiglietti and Peters, 1972). Much to our surpise, we found that many of the HRP-filled X-cells with morphology characteristic of "interneurons" could be antidromically activated from cortical stimulation and are thus relay neurons.

C. Y-CELLS

We found Y-cells to be the largest neurons in the lateral geniculate nucleus, with somata ranging in size from 238 to 935 μm^2 (mean, 493 μm^2). The Y-cell dendrites are coarse, fairly straight, and have few appendages. The dendritic tree typically has a cruciate appearance with approximate spherical symmetry. Unlike X-cells, every Y-cell identified as a relay neuron has some dendrites that cross laminar borders. Indeed, one Y-cell with a soma located in lamina A was excited exclu-

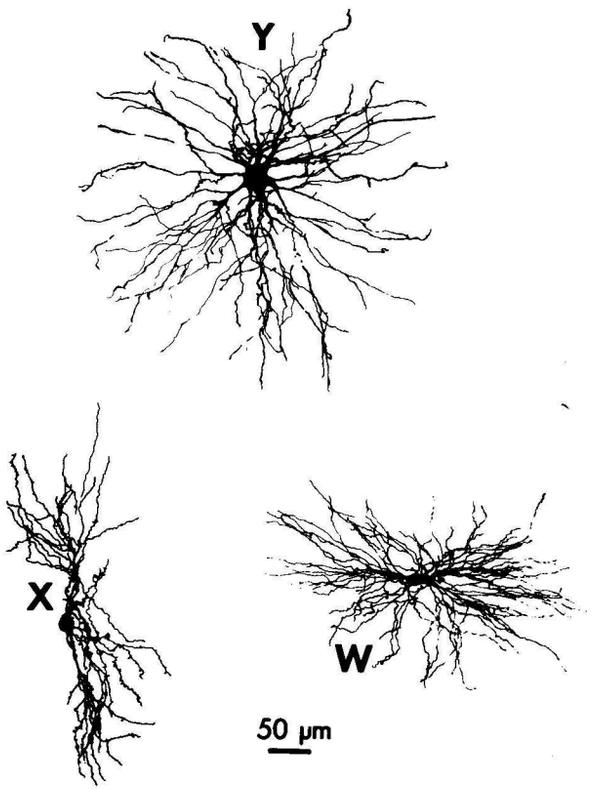


Figure 3. Camera lucida drawings of a typical W-, X-, and Y-cell identified physiologically and injected with HRP. The scale is oriented parallel to the geniculate laminae.

sively by the ipsilateral eye, presumably through optic tract terminals located on the peripheral, translaminar dendrites in lamina A1. The location of the soma and proximal dendrites thus may not always predict the functional inputs to a neuron. The entire dendritic tree should be considered. Finally, the Y-cell axons nearly always provide collateral input to the perigeniculate nucleus.

IV. IMPLICATIONS OF THE STRUCTURE/FUNCTION RELATIONSHIPS

Three main conclusions, involving interneuronal circuitry, electrode sampling biases, and implications for central connections in the W-, X-, and Y-cell pathways can be drawn.

A. INTERNEURONS

A cell type has been characterized by Golgi impregnation that has a small soma, fine, sinuous dendrites, and many, complex appendendages all along the dendrites (i.e., the class 3 cell of Guillery, 1966). This cell type is generally considered to be exclusively an interneuron (Tombol, 1969; LeVay and Ferster, 1977; Famiglietti and Peters, 1972). However, we have unambiguously identified some cells with these morphological features as relay cells. This at least implies that one cannot isomorphically identify interneurons with class 3 morphology. On the other hand, we cannot conclude either that interneurons do not exist or that no class 3 cells are interneurons. Perhaps the concept of geniculate interneurons as a special class should be reconsidered.

It is possible that many (class 3) cells subserve both interneuronal and relay cell functions; that is, perhaps they contribute both to local circuitry through dendrodendritic or axonal connections and still project an axonal branch to cortex. It is also possible that true interneurons for the lateral geniculate nucleus have somata elsewhere. For instance, perigeniculate neurons are an excellent candidate for functional interneurons since they receive collateral input from geniculate relay cells and project a dense axonal plexus to the geniculate laminae.

B. ELECTRODE SAMPLING

It is generally assumed that larger neurons are more likely to be sampled by a microelectrode than are smaller ones. Humphrey and Corrie (1978) suggested that sampling probability is linearly proportional to soma volume. Our sample of HRP-filled X- and Y-cells from the A laminae is sufficiently large to test this suggestion by comparing the soma size distribution

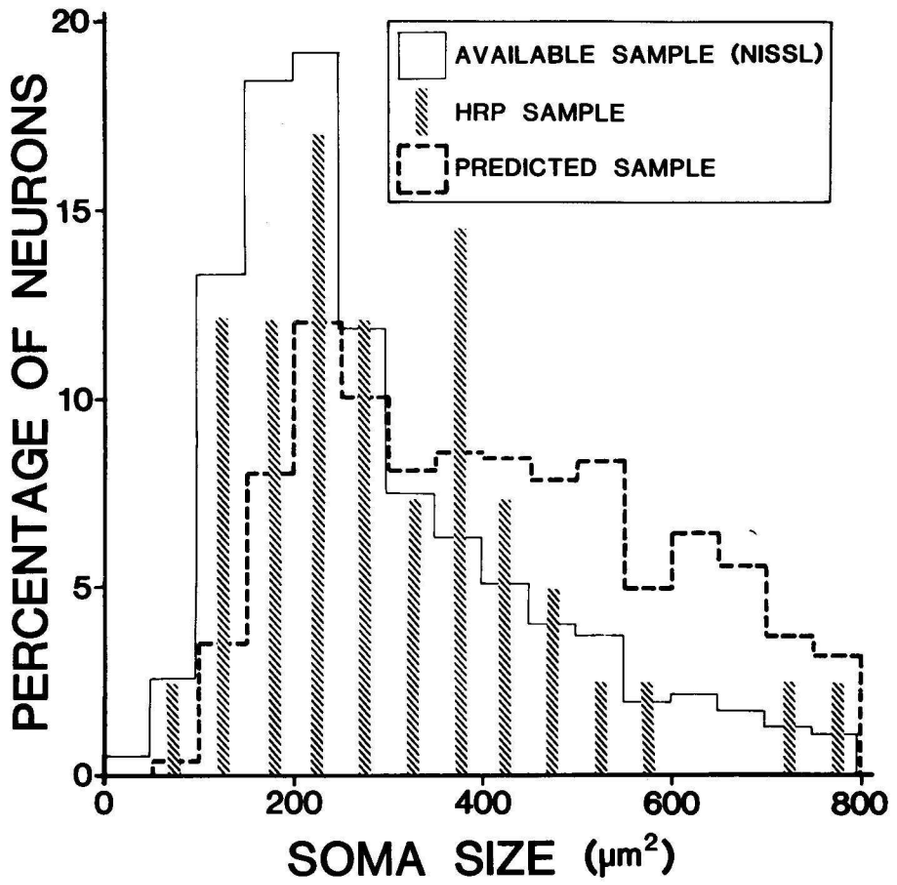


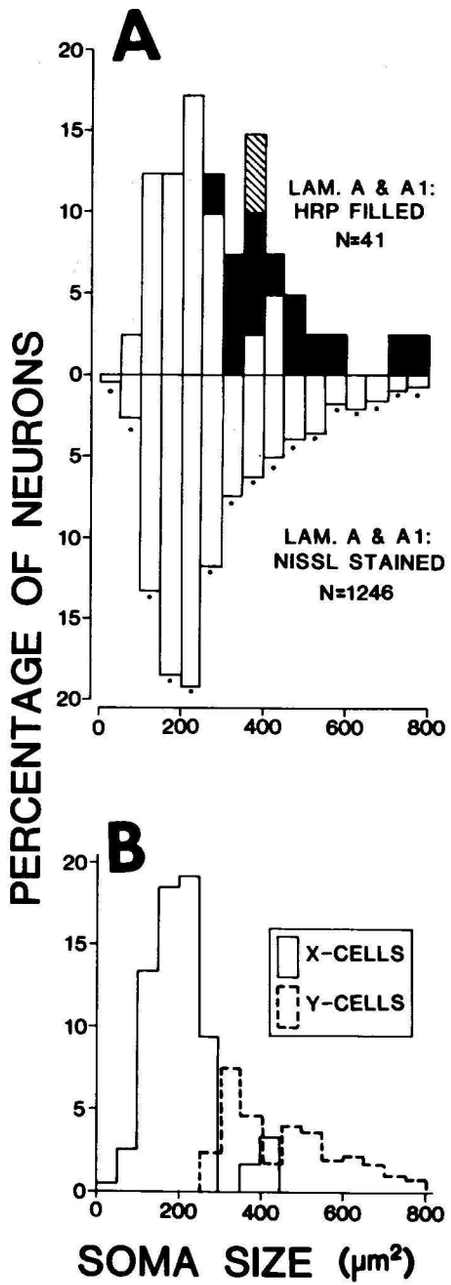
Figure 4. Soma size histograms for laminae A and A1 derived from Nissl stained sections that represent the same tissue in which HRP-filled neurons were located. The available sample is obtained from 1246 neurons in 11 cats. The HRP sample represents 41 physiologically identified and HRP-filled cells from the same 11 cats. The predicted sample is derived by placing the available (Nissl) sample through an algorithm whereby the percentages for each bin reflect a recording probability based upon soma volume (see text). Note that the predicted sample overrepresents larger somata at the expense of smaller somata, thereby producing an expected electrode sampling bias in favor of larger somata. However, the actual HRP sample is not statistically different from the available sample ($p > 0.2$ on a χ^2 test) but does differ from the predicted sample ($p < 0.001$ on a χ^2 test). We thus found no evidence of electrode sampling biases based on upon soma size.

available to the A laminae with the distribution of cells recorded and recovered in our experiments (Friedlander *et al.*, 1981).

Figure 4 represents such an analysis by superimposing three frequency hisograms (see also Fig. 5): the available A laminae sample, based on Nissl-stained material; the HRP-filled sample, which represents the actual electrode sample; and the electrode sample predicted by an algorithm whereby the probability of recording a neuron is proportional to its soma volume. Note that the predicted sample overrepresents available larger cells and underrepresents the smaller ones. Interestingly, our actual (HRP) sample does not differ statistically from the available (Nissl) sample, but is significantly different ($p < 0.001$ on a χ^2 test) from the predicted sample. In other words, we found no evidence for electrode sampling based on soma size, although other factors could well contribute to such sampling biases [see Friedlander *et al.* (1981) for a detailed discussion of this]. Furthermore, it is possible to compare the separate X- and Y-cell soma size distributions from our HRP sample with that of the available Nissl distribution (Fig. 5A) to estimate the distributions that actually exist for X- and Y-cells (Fig. 5B). This analysis places the X- to Y-cell ratio at 1.5 or 2 to 1. In retina, this ratio is typically placed closer to 5 or 10 to 1 (Fukuda and Stone, 1974; Cleland *et al.*, 1975; Wassle *et al.*, 1975; Stone, 1978). It has frequently been assumed that Y-cell percentages recorded electrophysiologically in the lateral geniculate nucleus are overestimates due to larger Y-cell somata, and that the actual geniculate X- to Y-cell ratio is more like that seen in retina (cf. So and Shapely, 1979). Our evidence suggests a more limited role for any such sampling that might favor Y-cells or larger somata in the lateral geniculate nucleus.

C. *CENTRAL CIRCUITRY*

The different morphology of geniculate W-, X-, and Y-cells is consistent with the notion that additional differences in functional circuitry for these pathways occur at the lateral geniculate nucleus. It is difficult to be specific about the nature of these functional differences, and it is not at all clear how many of the morphological differences represent epiphenomena without functional implications. However, the relative distributions of the X- and Y-cells discussed in the above section suggest at least one specific difference for geniculate X- and Y-cell circuitry.



In the A laminae, the X- to Y-cell ratio is probably no more than 2 to 1. Since Y-cells (but not X-cells) are also frequently found in the medial interlaminar nucleus and dorsal tier of lamina C, the overall geniculate X- to Y-cell ratio probably approximates 1 to 1. In retina, the probable ratio is 5 to 10 X-cells for every Y-cell (Fukuda and Stone, 1974; Cleland *et al.*, 1971; Wassle *et al.*, 1975; Stone, 1978). Thus, retinogeniculate circuitry greatly enhances neuron numbers in the Y-cell pathway relative to those in the X-cell pathway. Given the retinal and geniculate X- to Y-cell ratios, the presumably limited number of geniculate W-cells (Wilson *et al.*, 1976), the limited optic tract axon convergence onto single geniculate neurons (Cleland *et al.*, 1971), and the roughly fivefold increase in geniculate neuron numbers compared to retinal ganglion cell numbers (Sanderson, 1971b), one can roughly estimate that each retinal X-cell projects to four geniculate X-cells, but that each retinal Y-cell projects to 20-30 geniculate Y-cells [Fig. 6 and Friedlander *et al.* (1981)]. Which, if any, of the morphological differences between geniculate X- and Y-cells might contribute to this presumably different divergence ratio is not at all clear.

V. CONCLUSIONS

Any complete explanation of the central visual pathways, at least in cats, must take into account the W-, X-, and Y-cell pathways that relay information from retina to cortex along three parallel, largely independent streams. In other words, not only do extrageniculate pathways to visual cortex exist in parallel with geniculocortical pathways, but even the latter pathways are a complicated array of parallel circuits.

The functional implications for vision of W-, X-, and Y-cells are unclear and speculative at best. Little is known

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FIGURE 5. Soma size distribution for cells in laminae A and A1 representing the same data as shown in Fig. 4. (A) Comparison of HRP-filled neurons (upper) with the Nissl stained sample from the same tissue (lower). The two distributions are quite similar. In the upper histogram, X-cells are indicated by open bars, Y-cells by filled bars, and the unclassified cells by cross-hatched bars. (B) Separate X- and Y-cell distribution calculated from the histograms in (A). The two physiologically unclassified cells are not considered. Each bin in the X- and Y-cell distributions was obtained by multiplying the Nissl-stained percentage in that bin by the relative fraction of X- or Y-cells occupying that bin. From this, we estimate that 35% of A laminae neurons are Y-cells.

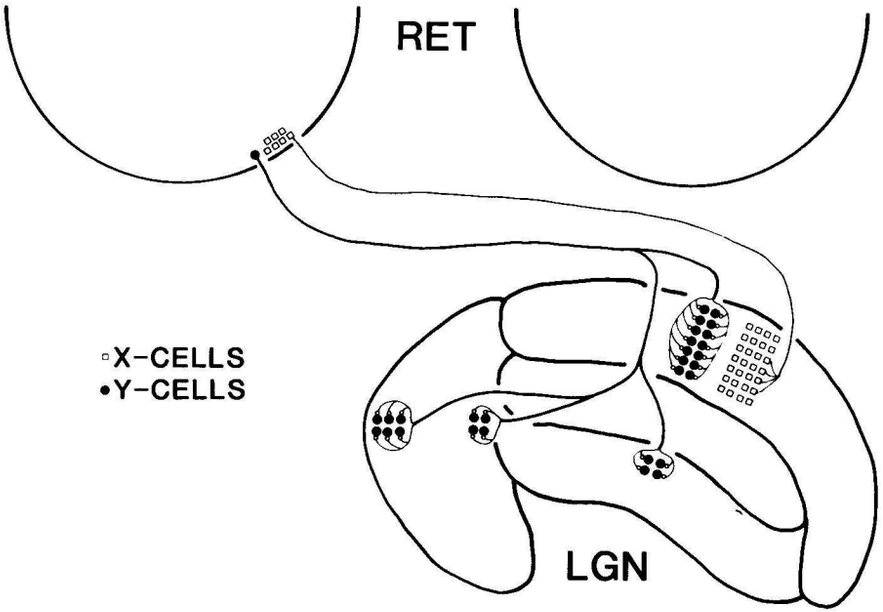

Figure 6. Schematic wiring diagram to illustrate the apparently larger divergence among Y-cell retinogeniculate connections than among those of X-cells (see text).

about the W-cell pathway, but more evidence is available from X- and Y-cells. From this, a speculative and tentative working hypothesis can be generated. This states that Y-cells perform a basic spatial analysis of the visual world while X-cells concentrate upon finer spatial details to raise acuity. Several other quite different hypotheses have also been proposed.

W-, X-, and Y-cells have been studied morphologically at the level of the lateral geniculate nucleus, and each of these functional classes has distinct morphological characteristics. This suggests that differences among these pathways are not limited to differences in retinal circuitry. Furthermore, these anatomical data provide a relative estimate of X- and Y-cell numbers. X- and Y-cells are roughly equal in numbers in the lateral geniculate nucleus despite the relative preponderance of X-cells in the retina. Retinogeniculate circuitry, then, seems to enhance connections in the Y-cell pathway. This may not be surprising if indeed Y-cells play as important a role for spatial vision as suggested above.

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