I. Introduction

Our contemporary understanding of the mammalian retinogeniculocortical pathways rests largely on the pioneering work of Hubel and Wiesel (1962, 1965). Their receptive field studies of single cells in cats emphasized the serial and hierarchical organization of these pathways. Hubel and Wiesel (1962, 1965) concluded that, as the hierarchy is ascended from retinal ganglion cells to neurons of the lateral geniculate nucleus, to and through cells that represent the presumed hierarchical levels of visual cortex (e.g., simple, complex, and hypercomplex cells), receptive field properties become more complex and specific for stimulus parameters. They suggested that this increasing complexity and specificity is the process by which the visual system abstracts and analyzes features of the visual environment. Each local portion of visual space is thus analyzed by a single chain of neurons from the retina through the lateral geniculate nucleus to the visual cortex.

Although certain aspects of this hypothesis have been challenged and some modifications of it have been required to accommodate new observations made during the past two decades, it still serves as the major theoretical framework for research into the neuronal organization of the mammalian visual pathways. Perhaps the major theoretical challenge to this hypothesis stems from evidence that emphasized the parallel organization of these pathways. Actually, two complementary and important concepts of such parallel organization have emerged. The first, elucidated originally by Sprague (1966), Diamond and Hall (1969), and Schneider (1969), emphasized the functional significance of multiple thalamocortical pathways (e.g., retinogeniculocortical and retinotectothalamocortical). This type of parallel processing is not considered further here (for reviews of this, see Sprague *et al.,* 1981; Diamond, 1982). The second type of parallel processing, which is the focus of the rest of this article, is the parallel organization evident within the retinogeniculocortical pathways. That is, at least three separate, functionally independent, retinogeniculocortical pathways have been identified. These have been called the W-, X-, and Y-cell pathways, although other terminology has also been used.

A. Terminology

A brief clarification of the terminology used here is in order. It is generally accepted that X- and Y-cells are each a fairly homogeneous neuronal class, based on morphological and physiological properties, and that each can be distinguished from W-cells (e.g., Rodieck, 1979; Stone *et al.,* 1979;

Lennie, 1980b; Sherman and Spear, 1982; Rodieck and Brening, 1983). However, W-cells, at least in the retina, are not homogeneous and almost certainly represent several distinct classes (Rodieck, 1979; Rodieck and Brening, 1983). "W-Cell" here refers to retinal ganglion or geniculate neurons that are neither X- nor Y-cells. The term W-cell is preferred, despite its shortcomings, over others suggested for the various classes thought to be subsumed by this phrase for two reasons. First, it is not yet clear how many classes (and thus terms) apply to these cells, nor has it yet been demonstrated beyond a reasonable doubt that retinal W-cells are not a single class with considerable variability. Second, this article is mainly concerned with retinogeniculocortical pathways, and as will be noted later, the subset of W-cells that is involved in this pathway may well prove to be a single class.

Several alternate terms have been used in the classification of retinal ganglion and geniculate cells. It is not always clear that these are isomorphic with one another or to the "W-, X-, and Y-cell" terminology used here. However, to a first approximation, the following terms are more or less interchangeable (Enroth-Cugell and Robson, 1966; Cleland *et al.*, 1971; Cleland and Levick, 1974a,b; Fukada and Saito, 1972; Hoffmann *et al.*, 1972; Stone and Hoffmann, 1972; Stone and Fukuda, 1974; Hochstein and Shapley, 1976a; Stevens and Gerstein, 1976; Bullier and Norton, 1979a,b). For W-cells these are "sluggish," "sluggish-sustained," or "sluggish-transient." For X-cells these are "sustained," "brisk-sustained," "tonic," "group II," "heterogeneous," or "linear." For Y-cells these are "transient," "brisk-transient," "phasic," "group I," "homogeneous," or "nonlinear." The "W-, X-, and Y-cell" terminology is used here because it is the one most commonly used and widely accepted. It is a neutral terminology that by itself conveys no implicit suggestion as to functional significance (Rowe and Stone, 1977). Also, while "W-cell" will probably be replaced with several other terms when these cells are unambiguously classified, it is preferred as a conservative alternative until such classification is available.

B. Hypothesis for Significance of W-, X-, and Y-Cell Pathways

It has often been suggested that these W-, X-, and Y-cell pathways independently analyze different aspects of the same visual scene, and that these different analyses are combined to form the neural representation of the visual environment. Thus, instead of a single hierarchical chain of neurons to represent each portion of visual space, at least three such

functionally distinct chains do so independently and in parallel, each chain responsible for a particular feature (e.g., form, movement, color, brightness, and depth or distance).

The purpose of this article is to describe a hypothesis for the functional organization of these W-, X-, and Y-cell pathways in cats. The hypothesis can be summarized as follows. Y-Cells are responsible for the analysis of basic forms and represent a sufficient and probably necessary pathway for good form vision, whereas X-cells provide higher spatial resolution to the basic form analysis accomplished by the Y-cell pathway. These suggestions derive from consideration of X- and Y-cell response properties, the anatomical organization of the X- and Y-cell pathways, and psychophysical studies of experimental cats with different levels of abnormality in the X- and Y-cell pathways. No detailed, specific hypothesis can be provided as yet for the W-cell pathway, but by reason of poor W-cell responsiveness and relative lack of influence of W-cells on neurons in visual cortex, this pathway may play a minor role in conscious perception of visual patterns (see also Stone *et al.,* 1979).

This hypothesis has already appeared for the X- and Y-cell pathways in a brief and superficial form (Sherman, 1979, 1982; see also Sherman and Spear, 1983). A consideration of other mammalian species, including primate, will also be included. The hypothesis is speculative and incomplete. It is offered in the spirit of providing a theoretical framework for existing data and perhaps also directing future investigations. Because detailed reviews of W-, X-, and Y-cells have already appeared (Rodieck, 1979; Stone *et al.,* 1979; Lennie, 1980b; Sherman and Spear, 1982, 1983), this article will simply summarize some of the major features of these neuronal classes.

II. General Overview of the Visual Pathways

The focus of this article is the retinogeniculocortical pathways, which represent the largest well-defined portion of the visual system; however, other clearly important pathways exist. Some of these extrageniculate pathways will be considered here in the context of geniculate pathways. For reviews of these pathways, see Rodieck (1979), Sherman and Spear (1982), Rosenquist *et al.* (1982), and Raczkowski and Rosenquist (1983).

The largest terminus of retinofugal fibers is the dorsal division of the lateral geniculate nucleus (hereafter, unless otherwise noted, "lateral geniculate nucleus" refers only to this dorsal division), and most of the remaining retinal fibers terminate in the superior colliculus. Other sites of termination include the ventral division of the lateral geniculate nucleus

(in the thalamus), regions of the pretectum, the accessory optic nucleus (in the midbrain tegmentum), and the suprachiasmatic nucleus (in the hypothalamus). Other brain stem visual pathways strongly implicated in sensory processing include those from the midbrain to the thalamus. The superior colliculus projects to the medial portion of the lateral posterior nucleus as well as to portions of the lateral geniculate nucleus; the parabigeminal nucleus (also located in the midbrain) projects to portions of the lateral geniculate nucleus, and the pretectal nuclei project visual fibers to the pulvinar nucleus as well as to portions of the lateral geniculate nucleus.

Tusa and colleagues (reviewed in Tusa *et al.,* 1981; Tusa, 1982) have elucidated many separate, retinotopically organized visual areas of cerebral cortex (see Fig. 1), and each of these receives input from the lateral geniculate, lateral posterior, and/or pulvinar nuclei (see Table I). Also, rich interconnections exist among these visual areas, and large projections have been described from many of these areas to the midbrain and visual thalamus. The central visual pathways are obviously complexly interconnected and functionally interdependent. Indeed, further research may continue to increase the number of distinct visual areas of cortex. For instance, Olson and Graybiel (1981) and Mucke *et al.* (1982) described a visual area in the ventral bank of the anterior ectosylvian sulcus; this is not shown in Fig. 1. Any attempt, such as the present article, to suggest the functional organization of a subset of these pathways, such as the retinogeniculocortical pathways, needs to be recognized for the simplification that it is.

III. Physiological Classification of W-, X-, and Y-Cells

Retinal ganglion and geniculate cells in the cat can be functionally classified into at least three main groups, called W-, X-, and Y-cells. However, as noted in Section I,A, the W-cell term probably subsumes several distinct groups that are arbitrarily thrown together. In any case, these ganglion cell classes represent the peripheral point of departure for any consideration of the W-, X-, and Y-cell pathways, because very little is yet known related to any differences in retinal circuitry that applies to these neuronal classes (but see Hochstein and Shapley, 1976a,b; Kolb, 1979). The available evidence suggests that each geniculate neuron receives retinal input from a small number of W-, X-, or Y-cells, with practically no mixture of classes among the retinal afferents (for X- and Y-cells, see Cleland *et al.,* 1971; Hoffmann *et al.,* 1972; for W-cells, this must be inferred from Cleland *et al.,* 1975b; Wilson *et al.,* 1976; Bowling

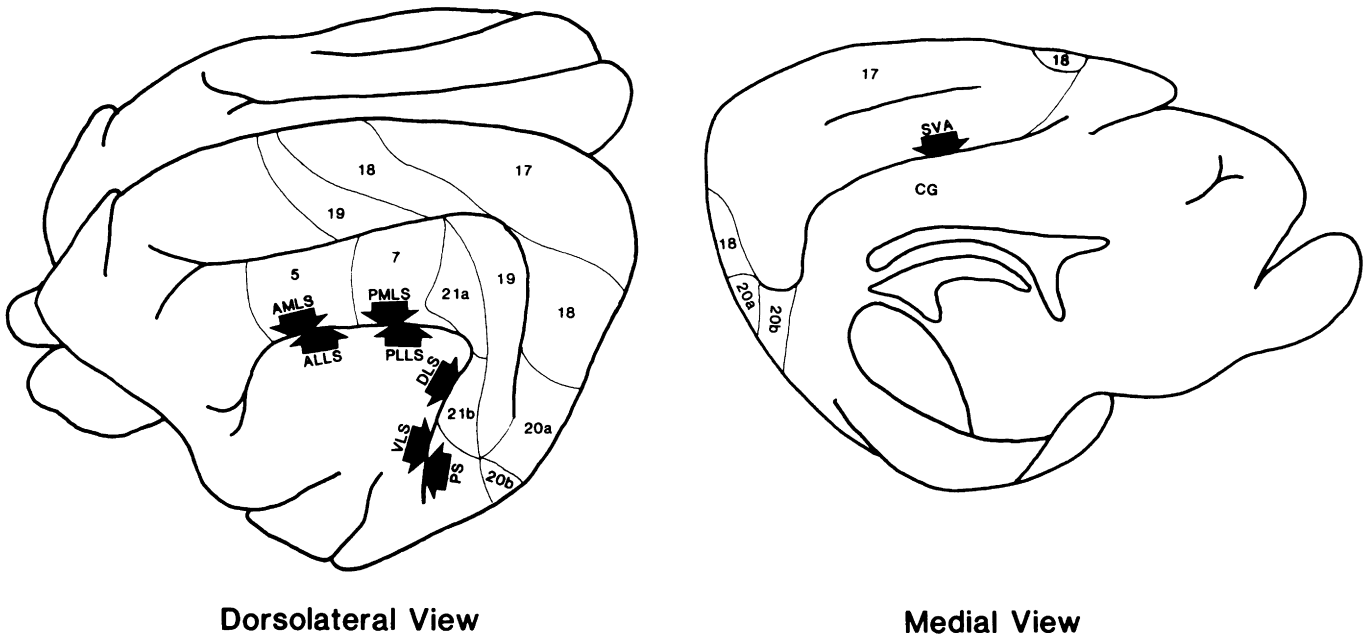

FIG. 1. Visual cortical areas in the cat as shown in dorsolateral and medial views of the left hemisphere. In addition to the nine areas designated by Brodmann numbers (5, 7, 17, 18, 19, 20a, 20b, 21a, 21b) are nine additional areas abbreviated as follows: AMLS, anterior medial lateral suprasylvian area; PMLS, 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 *et al.*, 1981; Tusa, 1982; Symonds *et al.*, 1981; Raczkowski and Rosenquist, 1983.)

TABLE I
INNERVATION OF VISUAL CORTICAL AREAS[a]

Subcortical afferent pathways[b]	Cortical areas[c]																	
	17	18	19	20a	20b	21a	21b	AMLS	PMLS	VLS	ALLS	PLLS	DLS	5	7	CG	PS	SVA
Retina → LGN (A,A1) →	+++	+++																
Retina → LGN (C_m) →	+	++	+++															
Retina → LGN (C_p) →	+	++	+++	+	+	+	+		+	+		+	+					
Retina → LGN (MIN) →	+	+++	+++					++	++									
Retina → LGN (GW) →		++	++					++	++									
Visual cortex → LP_l →	++	++	+++	+++	+++	+++	+++	+++	+++	+		+	+					
Retina → SC → LP_m →			+	++	++	+	+		+	+++	+++	+++	+++					
Retina → PT → pulvinar →			++	+	++	+	+							+++	+++	+++	+++	+++
Retina → PT → CLN →		++	++	+	+	+	+	+	+	+	+	+	+	+	+	+		
CLN → claustrum →	+++	+++	+++	+++	+++	+	+	+	+	+	+	+	+	+	+			

[a] Adapted from Raczkowski and Rosenquist (1983) and Rosenquist (1984).

[b] Abbreviations for subcortical afferents: A,A1, laminae A and A1; CLN, central lateral nucleus; C_m, magnocellular lamina C; C_p, parvocellular C laminae; GW, geniculate wing; LGN, lateral geniculate nucleus; LP_m and LP_l, medial and lateral divisions, respectively, of the lateral posterior nucleus; MIN, medial interlaminar nucleus; PT, pretectum; SC, superior colliculus. For abbreviations of cortical areas, see Fig. 1.

[c] Key: +, Light innervation; ++, moderate innervation; +++, heavy innervation.

and Michael, 1980, 1984; Sur and Sherman, 1982a,b; Leventhal, 1982). It is thus possible to refer to geniculate W-, X-, or Y-cells as those neurons receiving retinal input from W-, X-, or Y-cells, respectively. Indeed, except for subtle differences (Hubel and Wiesel, 1961; Sanderson *et al.*, 1971; Suzuki and Takahashi, 1973; Bullier and Norton, 1979a; Kaplan *et al.*, 1979; So and Shapley, 1981), response properties of geniculate neurons closely match those of their retinal inputs (Cleland *et al.*, 1971). Details of these response properties in the retina and the lateral geniculate nucleus can be found elsewhere (Kuffler, 1953; Hubel and Wiesel, 1961; Enroth-Cugell and Robson, 1966; Cleland *et al.*, 1971, 1975b; Hoffmann *et al.*, 1972; Fukada and Saito, 1972; Stone and Hoffmann, 1972; Cleland and Levick, 1974a,b; Fukuda and Stone, 1974; Stone and Fukuda, 1974; Bullier and Norton, 1979a,b; Hochstein and Shapley, 1976a,b; Stevens and Gerstein, 1976; Wilson *et al.*, 1976; Lehmkuhle *et al.*, 1980a; Lennie, 1980a; Sur and Sherman, 1982a, 1984; Thibos and Levick, 1983; Troy, 1983; for reviews, see Rodieck, 1979; Stone *et al.*, 1979; Lennie, 1980b; Sherman and Spear, 1982, 1983) and are summarized in the following paragraphs.

A. Measurement of Response Properties Used in Classification

Before considering response properties of W-, X-, and Y-cells, it is worth describing the two related approaches used to describe neuronal responses to visual stimuli. The first is the classic use of geometric stimuli like bars and spots to plot the structure of the receptive field. Neuronal response is measured as a function of stimulus shape, position, and contrast to determine this structure.

The second approach focuses on the neuronal response to stimuli consisting of one-dimensional sine wave gratings (Cornsweet, 1970; Braddick *et al.*, 1978; Sekuler *et al.*, 1978) that are drifted or sinusoidally counterphased. Such gratings are characterized by a homogeneous luminosity profile along one axis (typically vertical) and a sinusoidal profile along the orthogonal axis (usually horizontal). The stimulus contrast is defined by the luminance values of the peak (L_{max}) and trough (L_{min}) of the sinusoidal luminance profile as $(L_{max} - L_{min})/(L_{max} + L_{min})$. Mean luminance is $\frac{1}{2}(L_{max} + L_{min})$. Spatial frequency is the number of stimulus cycles of the sine wave luminance profile per degree of visual angle. Temporal frequency in cycles per second or hertz (Hz), for a drifting grating, is the drift speed in degrees per second multiplied by the spatial frequency in cycles per degree. For a counterphased grating, this value is simply the counterphase rate. Figure 2 illustrates the spatial and temporal luminance changes for a sinusoidally counterphased sine wave grating. Finally, the

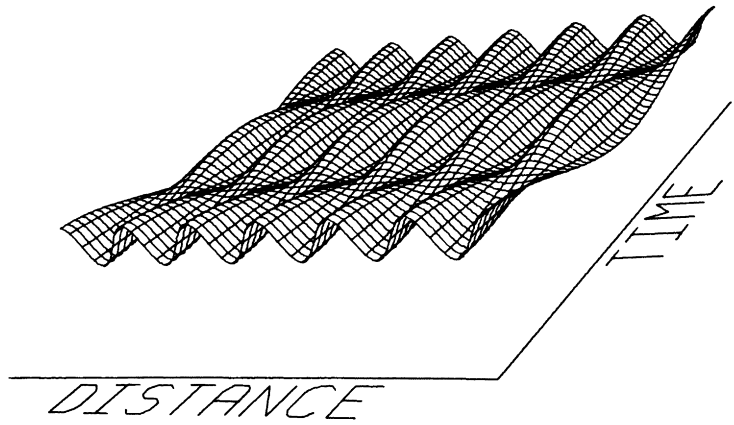

FIG. 2. Luminance profile in space and time for a sinusoidally counterphased sine wave grating. Luminance is plotted on the *Z* axis. Along the spatial axis, the luminance profile is always sinusoidal, although contrast changes with time such that no contrast is evident at certain times. Along the temporal axis, troughs of luminance become peaks, and vice versa, with a sinusoidal temporal profile. Spatial and temporal frequency can be independently adjusted. Note that mean luminance remains constant during the modulation. (From Sekuler *et al.*, 1978, with permission of the authors.)

spatial (or temporal) phase angle describes the relative spatial (or temporal) position of the grating as a fraction of a complete spatial (or temporal) stimulus cycle of 360°. For instance, a spatial phase difference of 90° between two otherwise equivalent gratings means that they are spatially offset by one-quarter of a spatial cycle. Typically, the neuronal response is plotted as a function of contrast, spatial, and/or temporal parameters. The minimum contrast needed to evoke a threshold response from the neuron can be measured as a function of spatial and temporal parameters, and contrast sensitivity is defined as the inverse of the minimum contrast needed to evoke a threshold response. One can plot either the contrast sensitivity or the response (at a fixed, generally high, contrast) as a function of spatial or temporal frequency. Because response and sensitivity are closely related and their respective functions similar in form for those retinal and geniculate neurons thus far studied (cf. Lehmkuhle *et al.*, 1980a; So and Shapley, 1981), the two measures are often considered interchangeable and are often termed spatial or temporal tuning functions.

Such response measures evoked by sinusoidal stimuli permit the use of linear systems analysis (including Fourier analysis), and the advantages of such an analysis have been described previously (Cornsweet, 1970; Braddick *et al.*, 1978; Sekuler *et al.*, 1978). Briefly, as Fig. 3 illustrates, any complex waveform can be created by the linear addition of sine waves

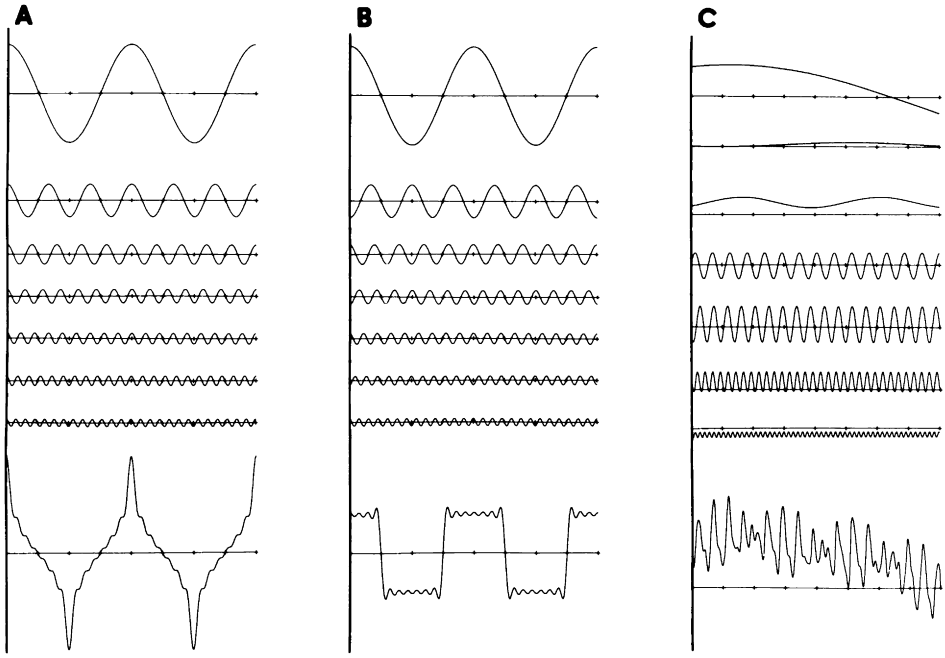

FIG. 3. Examples of Fourier analysis and synthesis. The bottom row shows three complex waveforms synthesized from the linear addition of seven different sine waves. Amplitude and frequency are in arbitrary units. (A) Formation of an approximately triangular waveform from sine waves. If the top sine wave has frequency F with amplitude A, the succeeding ones are $3F$ with $\frac{1}{3}A$, $5F$ with $\frac{1}{5}A$, $7F$ with $\frac{1}{7}A$, $9F$ with $\frac{1}{9}A$, $11F$ with $\frac{1}{11}A$, and $13F$ with $\frac{1}{13}A$. A precise triangle wave would continue to have odd components added, and the nth component would have frequency nF and amplitude A/n. Note that the peaks and troughs of the top sine wave are lined up with peaks and troughs of others, and this establishes their phase relationships. (B) Formation of an approximately square waveform from sine waves. Note that the only difference between this and (A) is the phase relationships of the component sine waves. Here, the peaks and troughs of the top sine wave are lined up with peaks and troughs of the third, fifth, and seventh sine waves, but not with the troughs and peaks of the second, fourth, and sixth sine waves. Phase is thus an important parameter in Fourier synthesis. (C) Formation of arbitrary, complex waveform from seven different sine waves that differ in both modulation amplitude and mean amplitude, in frequency, and in phase. Given enough sine waves with appropriate parameters, any complex waveform can be so analyzed and synthesized.

appropriately chosen for phase, frequency, modulation amplitude (or contrast), and mean amplitude. The importance of phase is emphasized in the comparison between Fig. 3A and B, in which the only difference in the component sine waves is one of phase, yet the resultant complex waveforms are quite different. The determination of the component sine waves of a complex waveform is Fourier analysis, and the creation of a complex

waveform from the linear addition of sine waves is Fourier synthesis. Since the luminosity of any visual scene can be described along any dimension as a complex waveform of luminosity versus distance across the scene, the luminosity values of any scene can be analyzed or synthesized in terms of its component sine wave gratings. These sine wave gratings thus represent a basic visual stimulus, and a description of a neuron's responsiveness to a range of sine wave stimuli provides a useful first approximation of the neuron's responsiveness to more complex stimuli. Because Fourier analysis depends on the linear addition of sine waves, this analysis works well for neurons that respond linearly to visual stimuli (i.e., the response to two simultaneously presented stimuli equals the sum of the responses to each alone) and poorly for neurons that respond nonlinearly.

In practice, two measures have proved most useful in the analysis of retinal and geniculate cell responsiveness: a measure of response linearity and determination of sensitivity (or responsiveness) as a function of spatial or temporal frequency. Spatial linearity is determined by the neuron's sensitivity to the spatial phase of a counterphased grating, as shown by Fig. 4A. A neuron with linear spatial summation exhibits a response that varies sinusoidally with spatial phase, the period of variation being equal to a spatial cycle of the stimulus. Although many forms of nonlinearity are possible, a retinal or geniculate neuron with nonlinear summation tends to exhibit a response that is not phase dependent in this manner, and in practice, is often phase independent (Fig. 4B). Linearity of temporal summation is determined by the Fourier components of the response to a counterphased grating (Fig. 5). A linear response is one that occurs at the fundamental temporal frequency of the stimulus frequency (Fig. 5A), and a nonlinear response occurs at higher harmonics (usually the second harmonic) of the stimulus frequency (Fig. 5B). That is, modulation of a linear response is sinusoidal at the same frequency as the stimulus, while a nonlinear response is modulated at higher harmonics, often manifested as a "frequency-doubled" (i.e., twice the stimulus frequency) response.*

* Movshon *et al.* (1978) have shown that some visual cells with more complex receptive fields than retinal ganglion or geniculate cells (e.g., cortical neurons) may require more sophisticated tests to determine their linear or nonlinear summation properties. What has been described here may not generally apply to visual neurons other than retinal ganglion and geniculate cells in the cat. Even for these simpler retinal ganglion and geniculate neurons, two different types of nonlinearities can exist that should be distinguished from one another. In practice, the noticeable frequency doubled response, which seems to result from full-wave rectification in spatial pooling of inputs to the cell under study, results in a prominent second harmonic component (plus other higher order, even components) in the response (Hochstein and Shapley, 1976b). However, if a "linear" cell's mean or spontaneous discharge level is too low to permit complete expression of a fundamental, sinusoidal re-

The second measure, spatial or temporal tuning functions, simply plots contrast sensitivity or response as a function of spatial or temporal frequency. The response measure plotted can be either the linear (fundamental) or nonlinear (usually a second harmonic) component of the neuron's response as a function of spatial or temporal frequency. Figure 6 shows spatial contrast sensitivity functions representative of geniculate W-, X-, and Y-cells, and Fig. 7 shows the analogous temporal functions. Figure 8 shows analogous spatial response functions for retinal X- and Y-cells.

B. W-Cell Response Properties

W-Cells were recognized as a distinct and major class (or classes) of retinal and geniculate neurons only during the last 5–10 years, and consequently relatively little is known about them. In the retina, they comprise a heterogeneous physiological group that has led some authors (Cleland and Levick, 1974a,b; Rodieck, 1979; Rodieck and Brening, 1983) to conclude that several distinct neuronal classes actually occupy the W-cell grouping. However, limited evidence from geniculate W-cells (Sur and Sherman, 1982a; Stanford *et al.*, 1983) suggests that these may be a single functional class that displays considerable functional variation. Thus, we can tentatively conclude that the subset of retinal W-cells that innervates the lateral geniculate nucleus and participates in the retinogeniculocortical W-cell pathway may be a single neuronal class. Preliminary evidence suggests that the other retinal "W-cells," which innervate other brain stem structures—for example, the superior colliculus (Hoffmann, 1973), ventral division of the lateral geniculate nucleus (Spear *et al.*, 1977), and pretectum (Hoffmann and Schoppmann, 1975—do indeed form separate neuronal classes (see Rodieck, 1979; Rodieck and Brening, 1983).

W-Cells can be distinguished from X- and Y-cells by a number of response properties (see Table II). W-Cells have the slowest axonal conduction velocities among retinal ganglion cells and geniculate neurons. Most geniculate W-cells have a classic, antagonistic center–surround receptive

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sponse to a stimulus (i.e., the trough of the response is cut off at zero response, since a negative response cannot be exhibited), the result is a half-wave rectification of the response. Fourier analysis of this, too, yields second and higher order, even harmonics, but such a response in terms of cell classification would be regarded as linear (Movshon *et al.*, 1978a). Full- and half-wave rectification in the response can still be distinguished, because the former has little or no power in the odd harmonics, whereas the latter does. Thus, if a ratio is computed between the sizes of the second harmonic and fundamental components of response, a low ratio indicates relative linearity, with the possibility of half-wave rectification, and a high ratio indicates relative nonlinearity, with full-wave rectification (Hochstein and Shapley, 1976a; Movshon *et al.*, 1978a).

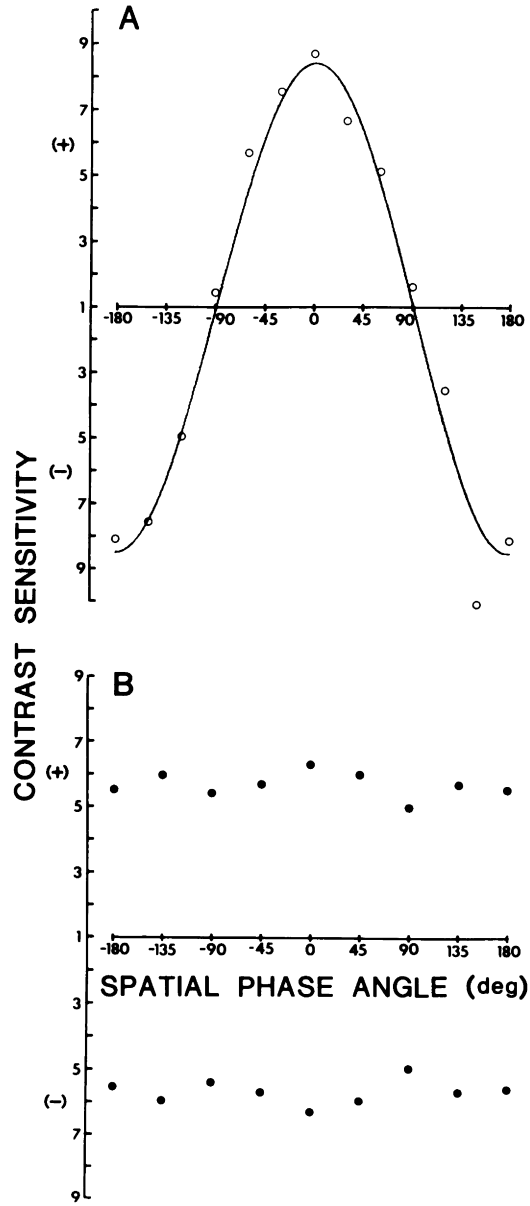


FIG. 4. Contrast sensitivity versus spatial phase angle for two geniculate neurons. (A) Linear W-cell, showing a sinusoidal sensitivity to the phase of a sine wave grating of 0.2 cycles/degree counterphased at 2 Hz. The response occurs at the fundamental counterphase frequency, and negative values imply a response 180° shifted in *temporal* phase from a positive response. At spatial phase angles of ± 90° the neuron exhibits minimal response; these are the "null positions" for the grating. (B) Nonlinear W-cell, showing little or no phase sensitivity to a 0.1 cycles/degree sine wave grating counterphased at 2 Hz. The response shows frequency doubling (i.e., it occurs at twice the counterphase rate), and thus each point is plotted twice as a positive and negative value. (From Sur and Sherman, 1982a.)

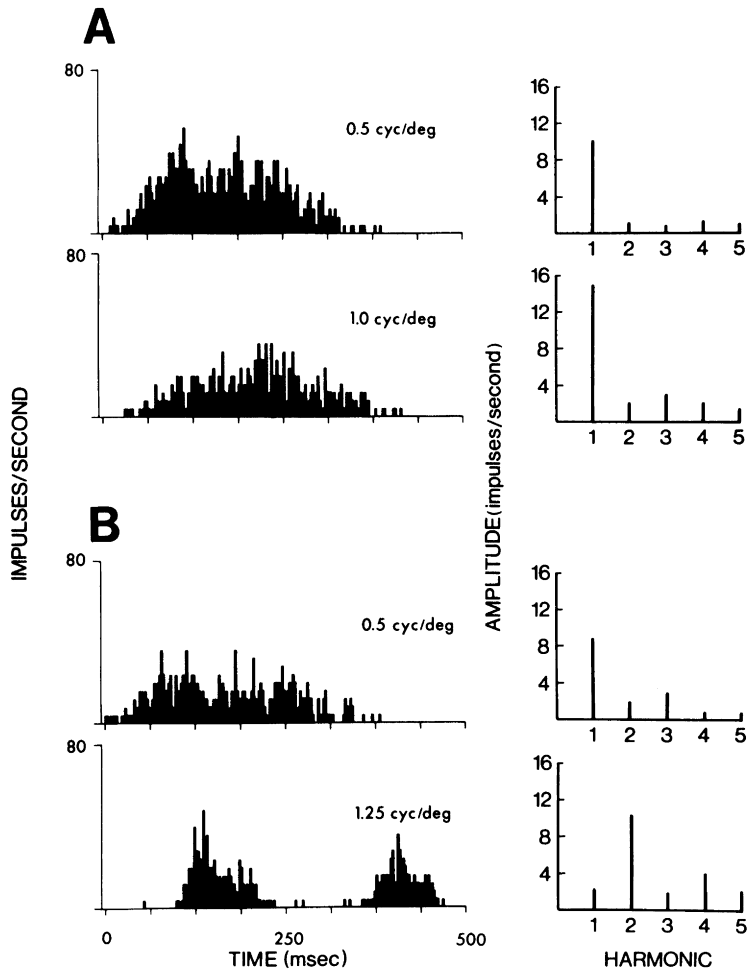


FIG. 5. Responses to counterphased gratings of a linear and nonlinear cell in the lateral geniculate nucleus. On the left are shown average response histograms to a single cycle of a sine wave grating counterphased at 2 Hz; the spatial frequency of each is also indicated. On the right is shown the first five Fourier components of this response, the first component equaling the 2-Hz counterphase rate of the grating. (A) Responses of an X-cell (linear cell). At both the lower and higher spatial frequencies, the response is dominated by the fundamental Fourier component. (B) Responses of a Y-cell (nonlinear cell). At lower spatial frequencies (upper), the response is linear and dominated by the fundamental Fourier component. At higher spatial frequencies (lower), for which the linear component is less sensitive (Fig. 6C), the response is nonlinear and dominated by higher harmonics, mostly the second harmonic. (From Mangel *et al.*, 1983).

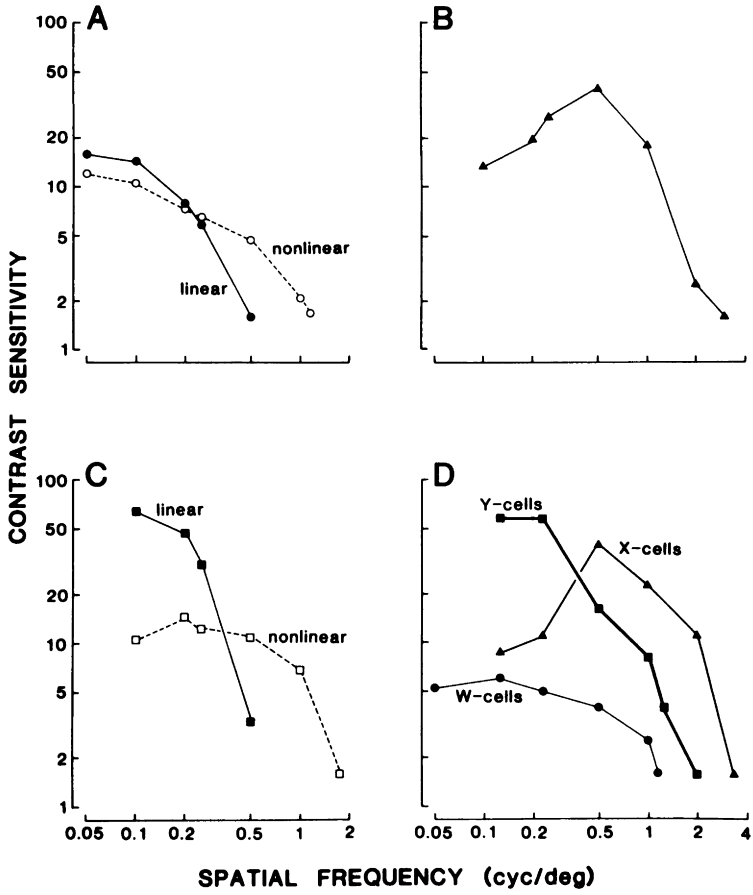


FIG. 6. Spatial contrast sensitivity functions for W-, X-, and Y-cells from the lateral geniculate nucleus. All cells illustrated had receptive fields between 5° and 15° of the area centralis. These functions were generated by measuring contrast sensitivity as a function of spatial frequency to sine wave gratings that were sinusoidally counterphased at 2 Hz. (A) Functions for two W-cells in the parvocellular C-laminae. One responded linearly and the other did not. Thus, the function in the latter case was generated from a second harmonic response (see Fig. 5B). These W-cell examples represent relatively responsive W-cells. (B) Function for a typical X-cell in the A-laminae. (C) Function for a typical Y-cell in the A-laminae. Two components are seen: a linear component that is more sensitive to lower spatial frequencies, and a nonlinear component (second harmonic response) that is more sensitive to higher spatial frequencies. The linear component is sensitive to spatial phase, and the nonlinear component is not (Fig. 4). The nonlinear component was generated at a spatial phase position of the grating for which no linear response was evident (i.e., the "null" position). (D) Mean contrast sensitivity functions for 10–15 cells of each class. No distinction is made here between linear and nonlinear responses. At least at 2 Hz, on average, W-cells are relatively insensitive to all spatial frequencies, X-cells are the most sensitive to higher spatial frequencies (and thus have the best resolution), and Y-cells are the most sensitive to lower spatial frequencies.

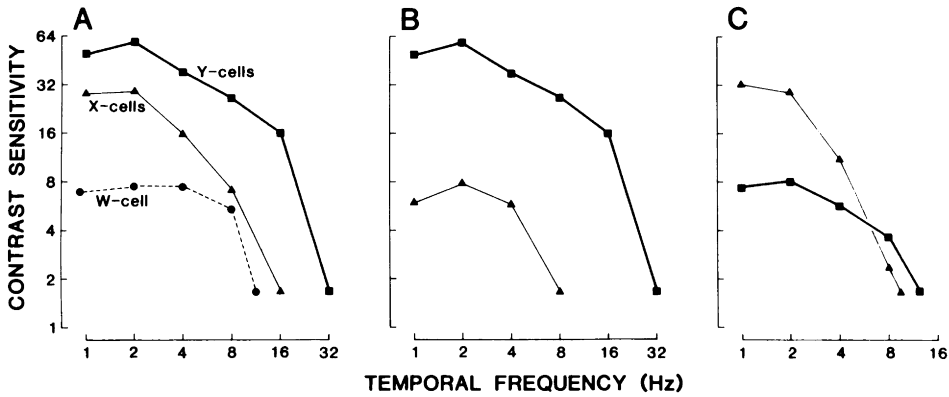


FIG. 7. Temporal contrast sensitivity functions for W-, X-, and Y-cells from the lateral geniculate nucleus. For a given spatial frequency of a sine wave grating, contrast sensitivity is plotted as a function of the sinusoidal counterphase frequency. Shown are mean data from the same X- and Y-cells as are illustrated in Fig. 6D plus a single W-cell (similar population data are not presently available for W-cells). (A) Functions in response to the spatial frequency to which the cell was most sensitive. This is a higher spatial frequency for X-cells than for W- and Y-cells (see Fig. 6D). (B) Functions taken at the same lower spatial frequency of 0.125 cycles/degree. (C) Functions taken at the same higher spatial frequency of 1.0 cycle/degree. Only at these higher spatial and lower temporal frequencies do X-cells tend to exhibit better contrast sensitivity than do Y-cells.

field arrangement, with either an ON center and OFF surround or OFF center and ON surround, and these receptive fields are relatively large. Some W-cells respond tonically to appropriate standing contrasts (e.g., a bright spot centered in an ON center field or a dark spot centered in an OFF center field), and others respond in a phasic manner. Likewise, some W-cells sum spatial and temporal parameters linearly, and others do so nonlinearly (Fig. 4). W-Cells exhibit poor and inconsistent responsiveness to visual stimuli, which has led some authors to name these cells "sluggish" (Cleland and Levick, 1974a,b; Thibos and Levick, 1983). Probably related to this, contrast sensitivity functions of these cells (Fig. 6) demonstrate poor sensitivity that is nearly a log unit worse than that for X- or Y-cells. W-Cells are most sensitive to lower spatial and temporal frequencies (Figs. 6 and 7) and exhibit poor spatial or temporal resolution, which is defined as the highest spatial or temporal frequency to which the neuron responds. Finally, W-cells with center–surround receptive field organization can be distinguished from X- and Y-cells by the following test (Cleland and Levick, 1974a): an ON center W-cell fails to respond to a dark spot removed from its center, and an OFF center W-cell likewise fails to

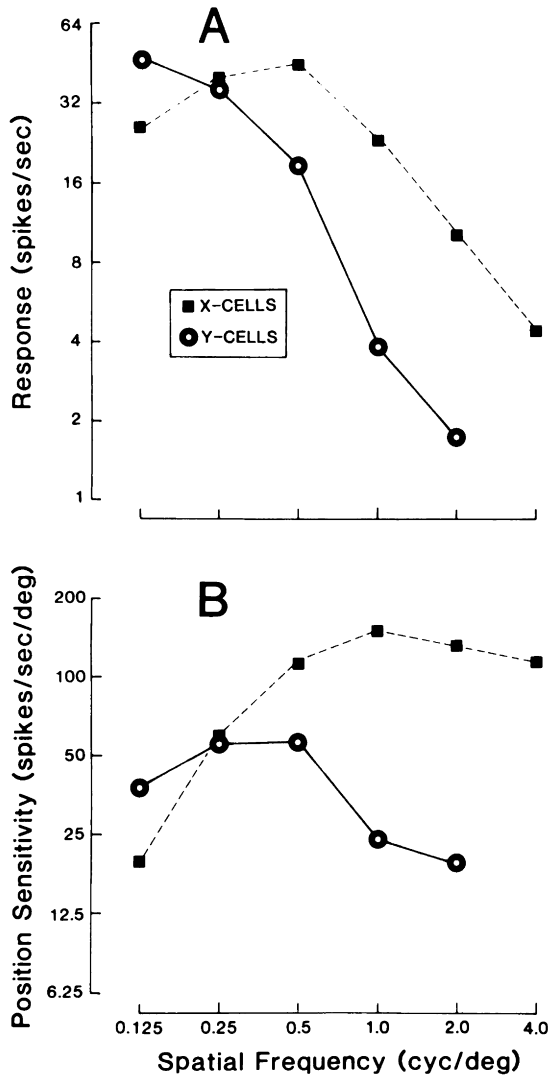


FIG. 8. Spatial tuning and position sensitivity functions for retinal ganglion X- and Y-cells averaged as in Fig. 6 and 7. The functions were obtained from 13 X- and 14 Y-cells in response to sine wave gratings drifted at 2 Hz. (A) Average spatial-tuning functions for X- and Y-cells. These represent the fundamental response component as a function of spatial frequency. (B) Average position sensitivity functions for X- and Y-cells. These represent maximum spatial phase or position sensitivity as a function of spatial frequency. This sensitivity equals $2\pi \cdot F_1 \cdot \mathrm{SF}$, where F_1 is the fundamental response component at the spatial frequency (SF) under study. (Data taken from Sur and Sherman, 1984.)

TABLE II
PROPERTIES OF RETINAL AND GENICULATE W-, X-, AND Y-CELLS

Property	W-Cells[a]	X-Cells	Y-Cells
Axonal conduction velocity	Slow	Medium	Fast
Spatial and temporal summation properties to visual stimuli	Some linear, others nonlinear	Linear	Linear to lower spatial frequencies, nonlinear to higher ones
Receptive field organization	Mostly center–surround[a]	Center–surround	Linear center–surround with small nonlinear subunits distributed throughout
Receptive field size	Large	Small	Medium
Contrast sensitivity	Poor	Good to medium and higher spatial frequencies	Excellent to lower spatial frequencies
Spatial resolution	Poor	Excellent	Linear component fair, nonlinear component good
Temporal resolution	Poor	Fair	Good
Approximate retinal ratio	10–20%[a]	75–85%	5–7%
Approximate LGN ratio	10%[a]	40–50%	40–50%

[a] Here we refer only to the subset of W-cells that seem to be involved in retinogeniculate innervation (see text). This includes mainly cells with center–surround receptive fields.

respond to removal of a centered bright spot; X- and Y-cells respond vigorously to such stimuli.

The observation just made refers to those W-cells that appear to project to the lateral geniculate nucleus. However at least four other neuronal types have been distinguished among the cat's retinal ganglion cells. These are clearly not X- or Y-cells and may be functionally distinct from the W-cells described earlier (Stone and Fabian, 1966; Rodieck, 1967; Stone and Hoffmann, 1972; Cleland and Levick, 1974a,b; Stone and Fukuda, 1974). These all have very slowly conducting axons and generally poor or inconsistent responses to visual stimuli. These four general types include (1) cells that are differentially sensitive to different wavelengths of light (2) cells that are sensitive to the direction of stimulus motion (3) cells that are inhibited by any contrast located in the receptive field, and (4) cells that are excited by any contrast in the receptive field. The color-coded cells exhibit receptive fields with a classic center–surround organization, but the last three have diffusely organized fields with no obvious center–surround arrangement. These four types of ganglion cells that do not seem to form a prominent input to the lateral geniculate nucleus are not further considered in this article.

C. X-Cell Response Properties

X-Cell axons conduct at velocities intermediate between the slower ones of W-cells and the faster ones of Y-cells. Receptive fields of X-cells have a classic center–surround organization and are smaller than those of W- and Y-cells. X-Cells generally exhibit tonic responses to standing contrasts as well as linear summation in response to visual stimuli. These cells respond briskly and sensitively to most visual stimuli. However, spatial contrast sensitivity or response functions (Figs. 6 and 8) show that these cells are most sensitive to middle spatial frequencies, since their sensitivity falls off for lower and higher ones. Generally, X-cells are most sensitive to lower temporal frequencies (Lehmkuhle *et al.,* 1980a), although there may be a sensitivity peak near 2–4 Hz (Lennie, 1980a). The best spatial resolution of X-cells, which occurs at low temporal frequencies, generally exceeds that of W- and Y-cells (Figs. 6 and 7). The best temporal resolution of X-cells (at middle spatial frequencies) falls between the poorer values of W-cells and better ones of Y-cells (Fig. 7). However, Fig. 7 shows that at higher spatial frequencies, X-cells exhibit better temporal resolution than do Y-cells, and at higher temporal frequencies, Y-cells exhibit better spatial resolution than do X-cells. W-Cells are consistently worst on these measures.

From spatial-tuning functions similar to those in Figs. 6 and 8, it is

possible to infer the cell's maximum sensitivity to small changes in stimulus position or spatial phase, which we call "position sensitivity." For drifting gratings at constant temporal frequency, this phase or position sensitivity (in spikes per second per degree) equals the product of 2π, the spatial frequency, and the amplitude of the fundamental response component at that frequency (Sur and Sherman, 1984). Since for these cells only the fundamental response component is sensitive to spatial phase (Hochstein and Shapley, 1976a), it is only this component that can confer phase sensitivity to the cell. Figure 8 plots this for retinal X- and Y-cells. The greatest position sensitivity is exhibited by X-cells at higher spatial frequencies. At lower ones, Y-cells are more sensitive than are X-cells, although this sensitivity is generally less than that observed for X-cells at higher frequencies.

D. Y-Cell Response Properties

Among retinal ganglion cells and geniculate neurons, Y-cells have the fastest-conducting axons. Y-Cells tend to have receptive fields intermediate in size between the larger ones of W-cells and smaller ones of X-cells. Y-Cells generally respond transiently to standing contrasts and are sensitive to most visual stimuli.

Y-Cells show a complex pattern of response linearity to visual stimuli: they have both linear and nonlinear response components, each of which exhibits characteristic response properties (Hochstein and Shapley, 1976b; Lehmkuhle *et al.,* 1980a; So and Shapley, 1981). The linear component is most sensitive to lower spatial frequencies and exhibits spatial resolution that is slightly better than that of W-cells but much poorer than that of X-cells (Figs. 6 and 8). Also, as noted earlier and shown in Fig. 8, the fundamental response component provides better position sensitivity for Y-cells than for X-cells only at lower spatial frequencies. The nonlinear component, which is relatively insensitive to lower spatial frequencies, is more sensitive than the linear component to higher spatial frequencies. Indeed, the nonlinear component is nearly as good as X-cells in terms of spatial resolution (Fig. 6). These and similar data led Hochstein and Shapley (1976b) to propose a two-part model for the Y-cell receptive field. One part consists of a linear, center–surround component that is relatively large to account for the relatively poor spatial resolution of the linear response. The second part is a collection of small, nonlinear subunits scattered throughout the center and surround to account for the relatively good spatial resolution of the nonlinear responses. No data have yet been published regarding the separate contributions of the linear and nonlinear response components to temporal contrast sensitivity func-

tions. However, at low spatial frequencies, for which the linear component dominates, Y-cells exhibit better temporal resolution than do W- or X-cells (Fig. 7). Also, at all spatial frequencies Y-cells are generally more sensitive to lower temporal frequencies than to higher ones (Fig. 7; and Lehmkuhle *et al.*, 1980a), although there may be a moderate sensitivity peak near 2–4 Hz (Lennie, 1980a).

E. Summary of W-, X-, and Y-Cell Response Properties

Table II and Figs. 6–8 summarize many of the functional properties that distinguish W-, X-, and Y-cells from one another. Axonal conduction velocities increase from W-cells to X-cells to Y-cells, and receptive-field sizes tend to increase from X-cells to Y-cells to W-cells. Generally, X-cells respond tonically to standing contrasts and Y-cells respond in a phasic manner; some W-cells are tonic and others are phasic. X- and Y-cells respond much better and more consistently to most visual stimuli than do W-cells. X-Cells and some W-cells exhibit predominantly linear response summation to visual stimuli. Other W-cells respond nonlinearly. Y-Cells have both linear and nonlinear response components, the former being more sensitive to lower spatial frequencies and the latter to higher ones. As shown by Figs. 6 and 7, W-cells respond relatively poorly at all temporal and spatial frequencies. At lower spatial and higher temporal frequencies, Y-cells are the most responsive neurons. Conversely, X-cells are the most responsive neurons at higher spatial and lower temporal frequences, particularly if only linear response components are considered. Finally, X-cells display their best position sensitivity at higher spatial frequencies, and this sensitivity generally exceeds that exhibited by Y-cells (Fig. 8). All of these response features suggest that Y-cells are important for the analysis of lower spatial frequencies and X-cells become increasingly important for higher ones, a distinction that will be reiterated in the consideration of the role these neuronal classes play in visual perception.

IV. Anatomical Organization and Distribution of the W-, X-, and Y-Cell Pathways

Until relatively recently, studies of the W-, X-, and Y-cell pathways were by necessity essentially unidimensional. Since these neuronal classes could be identified only by electrophysiological criteria, knowledge about them was largely confined to their response properties. As a

first step toward a multidisciplinary approach to the study of these pathways, a number of investigators have attempted to establish the morphological correlates of these cell types. Such a multidisciplinary approach, which ultimately should include a range of biological disciplines such as pharmacology, biophysics, biochemistry, and embryology, is needed not only for a thorough understanding of these pathways, but also because any single approach without validation from others is subject to difficulties of interpretation. For instance, the uncertainties of electrode sampling render doubtful any attempt to describe the distributions of the W-, X-, and Y-cell pathways. If these distributions can be verified anatomically, they can be more surely specified. Indeed, the anatomical correlates of the W-, X-, and Y-cell pathways to be described here have greatly enhanced our understanding of the functional organization of these pathways.

A. Retina

1. Morphological Classification of Ganglion Cells

Nearly a century ago, Ramón y Cajál (translated in Rodieck, 1973) drew attention to the different morphological types of ganglion cells in the cat retina that could be discerned from Golgi impregnations. Mainly on the basis of dendritic branching patterns in the inner plexiform layer, he described some 20–30 classes. Unfortunately, this classification cannot be readily correlated with the physiological classification of W-, X-, and Y-cells.

Boycott and Wassle (1974) also used the Golgi technique to provide the first hypothesis of specific morphological correlates for W-, X-, and Y-cells. They described alpha, beta, and gamma morphological types (see Fig. 9) and suggested from indirect evidence that these represent Y-, X-, and W-cells, respectively. *Alpha* cells have the largest somata, fairly extensive dendritic arbors, and the thickest axons. *Beta* cells have medium-sized somata, small but densely branched dendritic arbors, and axons of intermediate thickness. *Gamma* cells, according to the original description of Boycott and Wassle (1974), have the smallest somata, extensive but sparsely branched dendritic arbors, and the thinnest axons. One analysis of optic nerve axons has successfully demonstrated these components of the axon diameter spectrum: a small-diameter mode probably belonging to gamma-cell axons, a medium-diameter mode probably belonging to beta-cell axons, and a large-diameter tail probably belonging to alpha-cell axons (Williams and Chalupa, 1983).

Other morphological types have been described that have somata in the

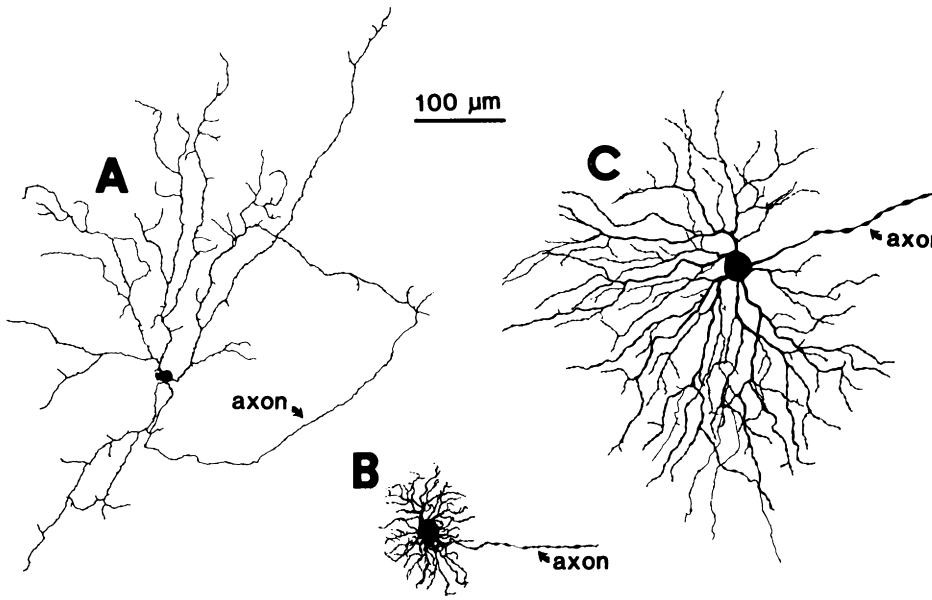


FIG. 9. Camera lucida drawings of ganglion cells in the retina as viewed in a flat mount. Each neuron was intracellularly filled with HRP after physiological identification. (A) W-Cell with gamma morphology; (B) X-cell with beta morphology; (C) Y-cell with alpha morphology. (From Stanford and Sherman, 1984.)

beta-cell range but that are clearly not beta cells. These may be variants of gamma cells [e.g., the *delta* cells of Boycott and Wassle (1974) and the medium-sized *gamma* cells of Stone and Clarke (1980)], or they may represent other morphological classes [e.g., the *epsilon, g1,* and *g2* cells of Leventhal (1982)]. At present, it is no easier to decide how many morphological classes are subsumed within the "gamma"-cell population (i.e., neither alpha nor beta cells) than it is to decide how many physiological classes are represented by "W-cells" (i.e., neither X- nor Y-cells).

The best published evidence for correlations among morphological and physiological types is the series of experiments by Wassle and colleagues (Cleland *et al.,* 1975a; Wassle *et al.,* 1975, 1981a,b; Peichl and Wassle, 1981; Wassle, 1982), which make a strong case that alpha cells are Y-cells. The evidence that beta cells are X-cells and that gamma cells are W-cells is rather less direct and secure. The more direct approach of labeling a single physiologically identified cell with an intracellular injection of Lucifer yellow or horseradish peroxidase (HRP) has produced preliminary data that largely support these correlations (Saito, 1983; Stanford and Sherman, 1984). This has shown that alpha cells are Y-cells, beta cells are

X-cells, and most gamma cells are W-cells. More data of this sort should eventually establish the structure–function correlations quite firmly.

2. *Distribution of Cell Types*

A number of laboratories have made use of the structure–function correlates just described to survey with histological techniques the distribution of the W-, X-, and Y-cell classes across the retina (Boycott and Wassle, 1974; Fukuda and Stone, 1974; Cleland *et al.*, 1975a; Wassle *et al.*, 1975, 1981b; Stone, 1978; Peichl and Wassle, 1979; Illing and Wassle, 1981; Leventhal, 1982; Williams and Chalupa, 1983). These proposed distributions must be qualified partly because of a degree of uncertainty in the structure–function correlates, particularly for W- and X-cells, and partly because of a degree of controversy regarding the estimated values for the distributions (Fukuda and Stone, 1974; Wassle *et al.*, 1981a,b; Wassle, 1982; Leventhal, 1982). Indeed there is as yet no agreement regarding the actual number of ganglion cells, regardless of classification (Hughes and Wassle, 1976; Hughes, 1981; Stone, 1978; Stone and Campion, 1978). Nonetheless, these distributions offer the best approximation of W-, X-, and Y-cell patterns across the retina independent of electrode-sampling problems. Of approximately 200,000 ganglion cells, roughly 5% are alpha cells (or Y-cells), one-half to two-thirds are beta cells (or X-cells), and one-third to one-half are gamma, delta, epsilon, g1, and g2 cells (or W-cells). Of this last group of presumed W-cells, only about 40% (or roughly 15–20% of the ganglion cell total) appear to project to the lateral geniculate nucleus (Illing and Wassle, 1981; Leventhal, 1982).

The relative ratios of cell types vary with eccentricity. The density of both X- and Y-cells peaks at the area centralis, but this peak is much sharper for X-cells. Thus, the relative ratio of X- to Y-cells, which on average is roughly 10:1, decreases with increasing eccentricity from the area centralis (Hoffmann *et al.*, 1972; Fukuda and Stone, 1974; Wassle *et al.*, 1975, 1981a; Peichl and Wassle, 1979, 1981; Wassle, 1982; Leventhal, 1982). W-Cell density is fairly uniform across the retina with a slight increase along the horizontal streak, which is an elongated horizontal region passing through the area centralis (Rowe and Stone, 1976).

3. *Central Projections*

Every retinal X- and Y-cell and an as yet unspecified subset of W-cells projects to the lateral geniculate nucleus (Fukuda and Stone, 1974; Bowling and Michael, 1980, 1984; Illing and Wassle, 1981; Leventhal *et al.*, 1980a,b; Sur and Sherman, 1982b; Rowe and Dreher, 1982). As noted

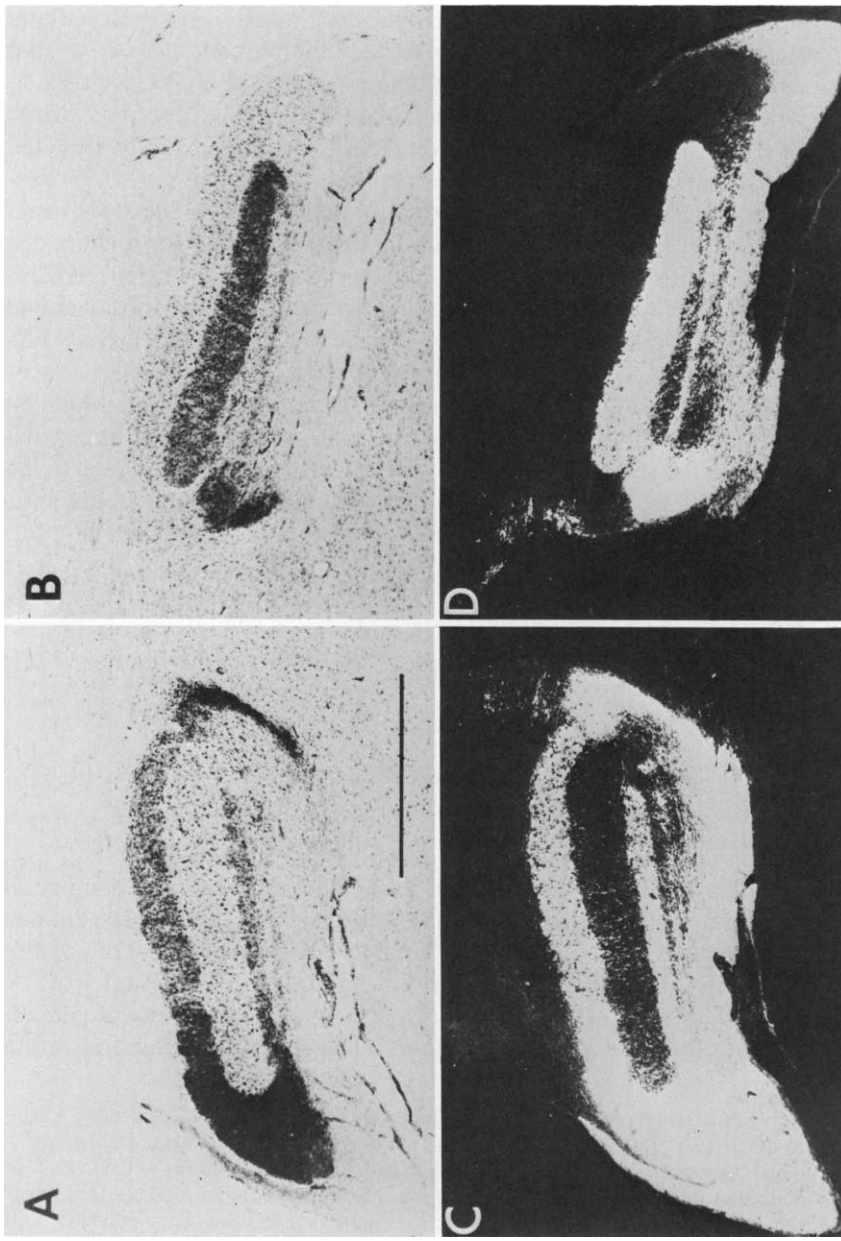
above, retrograde labeling of retinal ganglion cells from HRP injections into the lateral geniculate nucleus (Illing and Wassle, 1981; Rowe and Dreher, 1982) suggests that roughly 40% of the W-cells project to that nucleus. The details of the retinogeniculate projection of W-, X-, and Y-cells with respect to the various geniculate laminae is described in the following section. A meager projection from X-cells seems to be directed outside the lateral geniculate nucleus (Fukuda and Stone, 1974). Horseradish peroxidase labeling of individual X-cell axons in the optic tract occasionally reveals an axonal branch that can be traced for a short distance beyond the lateral geniculate nucleus (Sur and Sherman, 1982b), and some X-cell input to the midbrain has been suggested (Hoffmann and Stone, 1973; Leventhal *et al.*, 1980b; Wassle and Illing, 1980). Single Y-cell axons branch to innervate the lateral geniculate nucleus, superior colliculus, and perhaps other brain stem sites (Bowling and Michael, 1980; Wassle and Illing, 1980; Sur and Sherman, 1982b). Different populations of W-cells seem to innervate the lateral geniculate nucleus, the superior colliculus, the ventral division of the lateral geniculate nucleus, the pretectum, and perhaps other brain stem sites (Hoffmann, 1973; Fukuda and Stone, 1974; Cleland *et al.*, 1975b; Wilson *et al.*, 1976; Spear *et al.*, 1977; Leventhal *et al.*, 1980a,b). The retinogeniculate W-cells apparently have larger somata on average than do those W-cells that innervate extrageniculate structures (Leventhal *et al.*, 1980a,b; Leventhal, 1982; Rowe and Dreher, 1982).

B. Lateral Geniculate Nucleus

1. Gross Topography

a. Lamination. The cat's lateral geniculate nucleus is a laminated structure, and as Figs. 10 and 11A and B illustrate, the laminae are defined in terms of ocular input (Hickey and Guillery, 1974; Guillery *et al.*, 1980). The contralateral nasal retina innervates laminae A, C, C2, and 1 of the medial interlaminar nucleus (which is a subdivision of the lateral geniculate nucleus), and the geniculate wing.* The ipsilateral temporal retina

* Guillery *et al.* (1980) have called this retinofugal terminal zone the "geniculate wing," although others (e.g., Leventhal *et al.*, 1980a) have called this the "retinal recipient zone" of the pulvinar. One can logically define the (dorsal) lateral geniculate nucleus as that collection of neurons that receives direct retinal input and projects to cerebral cortex. This region would thus better be called "geniculate wing" rather than a division of the pulvinar. Note that, by this reasoning, lamina C3 of the lateral geniculate nucleus should indeed not be considered a part of that nucleus, because it receives no direct retinal input (Hickey and Guillery, 1974).



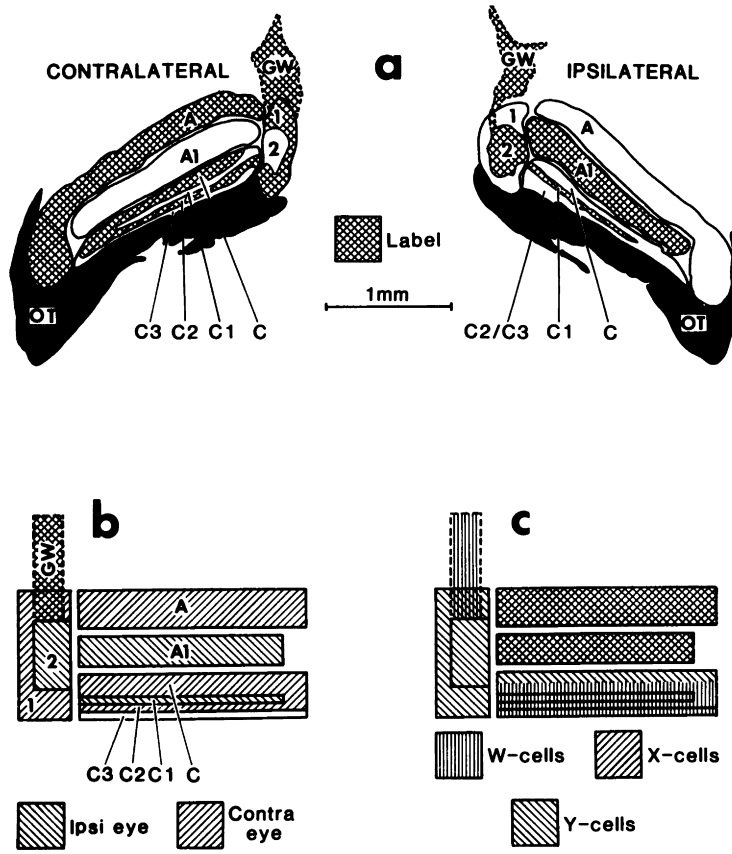


FIG. 11. Laminar arrangements of the cat's lateral geniculate nucleus. (a) Camera lucida drawings of the sections shown in Fig. 10, with autoradiographic label from the right eye cross-hatched. The contralateral eye innervates laminae A, C, C2, and 1 (of the medial interlaminar nucleus), and the geniculate wing (GW). The ipsilateral eye innervates laminae A1, C1, and 2 (of the medial interlaminar nucleus), and the geniculate wing. Thus, neither eye innervates lamina C3, and the geniculate wing is the only geniculate region to receive innervation from both eyes. (b) Schematic representation of ocular inputs in relation to the laminae. (c) Schematic representation of W-, X-, and Y-cell inputs and distributions in relation to the laminae (see text for details).

FIG. 10. Photomicrographs of coronal sections through the left and right lateral geniculate nuclei of a cat. The cat previously had an injection of tritiated proline placed into its right eye, and these sections were treated for autoradiography. (A) and (C) Bright-field and dark-field photomicrographs, respectively, of the same view of the left nucleus. (B) and (D) Bright-field and dark-field photomicrographs, respectively, of the same view of the right nucleus. Inputs from the right (injected) eye are labeled darkly in the bright-field views, and brightly in the dark-field views. Figure 11 shows the laminar relationships of these sections. The scale in (A) is 1 mm and applies as well to (B)–(D).

innervates laminae A1, C1, and 2 of the medial interlaminar nucleus, and the geniculate wing. Thus, the geniculate wing is the one region that receives binocular input, and lamina C3 is the one lamina that appears to receive no direct retinal afferents (Fig. 11B). Not shown in Figs. 10 and 11A and B is lamina 3 of the medial interlaminar nucleus (Guillery *et al.*, 1980; Rowe and Dreher, 1982), because it occupies a more caudal region than is illustrated there. Lamina 3 is innervated by the contralateral temporal retina and thus maps the "wrong" hemifield.

b. Retinotopic Organization. The lateral geniculate nucleus exhibits a precise point-to-point map such that neighboring geniculate neurons have receptive fields adjacent to each other in visual space. The retinotopic maps are best understood for the A- and C-laminae (Laties and Sprague, 1966; Sanderson 1971a). These laminae are stacked in register such that a line of cells oriented perpendicular to the laminar borders (or across the short axis of each lamina) maps the same single point in visual space. These have been termed the "projection lines." The vertical meridian of the visual field (which, in the retina, passes vertically through the area centralis) is mapped at the medial edge of the A- and C-laminae, and lateral locations along these laminae map progressively more peripheral visual field. Note, for example, that lamina A extends further laterally than does lamina A1 (Figs. 10 and 11A and B), because the nasal retina (which innervates lamina A) extends further from the vertical meridian than does the temporal retina (which innervates lamina A1). Finally, vertical directions in visual space are represented by anteroposterior directions in the nucleus such that more elevated (or less elevated) visual coordinates are mapped more posteriorly (or anteriorly). Maps in the medial interlaminar nucleus and geniculate wing are understood in less detail and have only recently been described (Guillery *et al.*, 1980).

The visuotopic map in the lateral geniculate nucleus, while continuous, is distorted by the fact that more neural tissue is devoted to more central visual regions than to more peripheral ones. This distortion has been called the "magnification factor." For instance, near the anteroposterior middle of the nucleus where the horizontal midline of the visual field is represented, the medial half of lamina A maps only the central 5° of visual field, and the lateral half maps the remaining 85–90° of visual field.

Sanderson (1971b) has suggested that this distortion is a reflection of that already present among ganglion cells, since these are more densely aggregated nearer the area centralis. Optical constraints of the eye and the predominant direction of information flow across the layers through the retina require that ganglion cells be located at or very near their receptive field positions. Thus regions that require more neurons for more detailed analysis (e.g., the area centralis) must have a greater density of cells. The

lateral geniculate nucleus (and other visual areas of the brain) have no such optical constraints and are thus able to form neural circuits in the framework of a fairly uniform density of neurons. This could result in retinal regions of greater ganglion cell density being represented by larger volumes of geniculate tissue with constant neuronal density. Magnification factors such as that seen in the lateral geniculate nucleus might thus occur.

Of course, if one wishes to relate ganglion cell density to magnification factor in a given brain locus (e.g., lateral geniculate nucleus, superior colliculus, or one of the visual cortical areas), one must include only the subset of ganglion cells that participate in innervation of that locus. For instance, magnification factor of the geniculate A-laminae, which contain X- and Y-cells but not W-cells (see later), should be compared with some combination of the density distribution of retinal X- and Y-cells; for superior colliculus, magnification factor should be compared against the combined density of retinal Y-cells and those W-cells that innervate the superior colliculus. To date, such comparisons have not been made in any systematic fashion, although a superficial comparison of the visuotopic map for the A-laminae (Sanderson, 1971a) with alpha and beta ganglion cell density distributions (Peichl and Wassle, 1979; Leventhal, 1982) suggest the plausibility of this hypothesis.

2. *Afferent Input*

a. Retinal Afferents. As mentioned before, most retinal ganglion cells, including every X- and Y-cell and many W-cells, project to the lateral geniculate nucleus. This projection has a strong differential laminar pattern. Figure 11C shows the laminar distribution of geniculate W-, X-, and Y-cells, which in turn reflects laminar differences in the retinogeniculate projection along these pathways (Fig. 12). Most information relevant to these laminar differences in afferent projection patterns stems from physiological studies of single geniculate neurons, since each of these neurons seems to receive input from a single class of ganglion cell. These studies have largely focused on the A-laminae (Cleland *et al.,* 1971; Hoffmann *et al.,* 1972; So and Shapley, 1981; Lehmkuhle *et al.,* 1980a), although several studies of the C-laminae (Cleland *et al.,* 1975b; Wilson *et al.,* 1976; Sur and Sherman, 1982a) and laminae 1 and 2 of the medial interlaminar nucleus (Mason, 1975; Kratz *et al.,* 1978; Dreher and Sefton, 1979) have been reported. Laminae A and A1 contain a mixture of X- and Y-cells without W-cells. The dorsal part of lamina C contains Y-cells and perhaps some W- and X-cells (Wilson *et al.,* 1976; Friedlander *et al.,* 1981), and the remainder of the C-laminae contain only W-cells (Wilson *et*

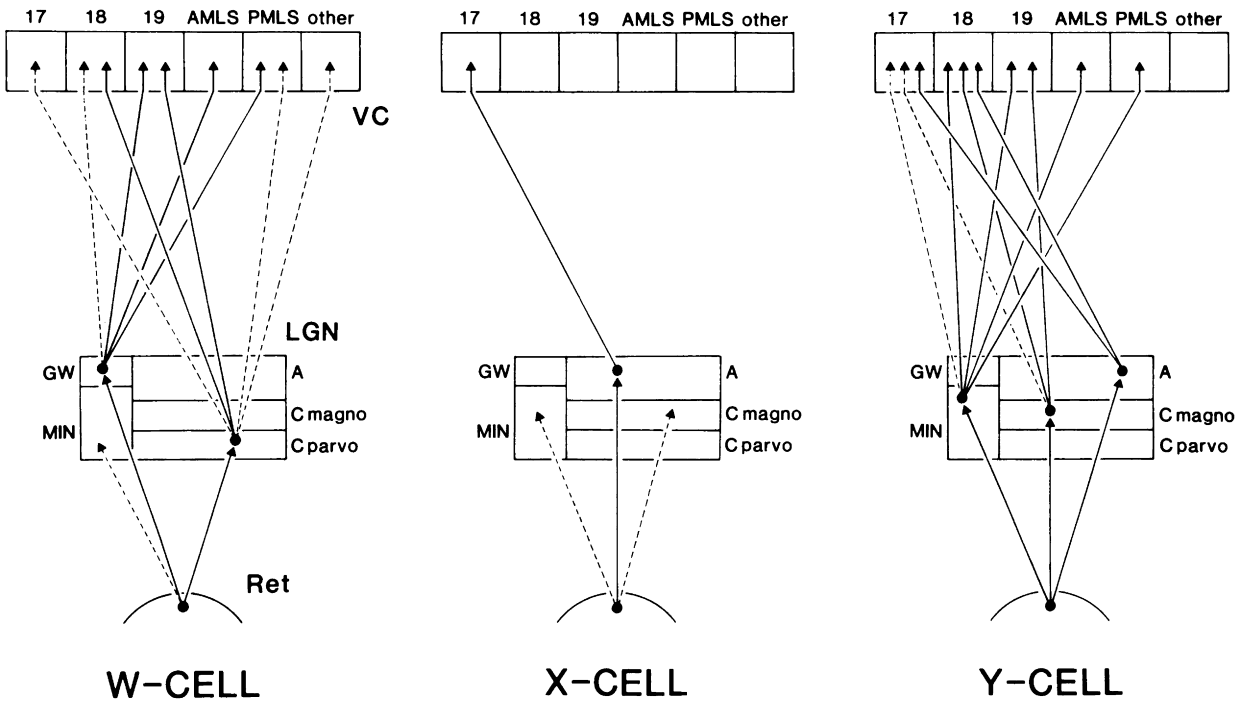


FIG. 12. Schematic summary diagram of W-, X-, and Y-cell pathways from retina through the lateral geniculate nucleus to various areas of visual cortex (for further details, see Fig. 1 and Table I). Abbreviations: Ret, retina; LGN, lateral geniculate nucleus; A, A-laminae; Cmagno, magnocellular lamina C; Cparvo, parvocellular C-laminae; GW, geniculate wing; MIN, medial interlaminar nucleus; VC, visual cortex; 17–19, areas 17–19; AMLS, anterior medial lateral suprasylvian area; PMLS, posterior medial lateral suprasylvian area; other, areas 20a, 20b, 21a, and 21b plus the ventral lateral suprasylvian, posterior lateral lateral suprasylvian, and dorsal lateral suprasylvian areas. Solid lines represent relatively dense projections, and dashed lines represent relatively sparse projections.

al., 1976; Stanford *et al.,* 1981, 1983; Sur and Sherman, 1982a). The dorsal part of lamina C that contains Y-cells has large somata and is termed magnocellular lamina C; the remainder of the C-laminae, which contain only W-cells, has small somata and is termed the parvocellular C-laminae. Laminae 1 and 2 of the medial interlaminar nucleus predominantly contain Y-cells, although rare W- and X-cells may also exist there (Mason, 1975; Kratz *et al.,* 1978; Dreher and Sefton, 1979; Rowe and Dreher, 1982). No recordings from the geniculate wing and lamina 3 of the medial interlaminar nucleus have yet been reported, but indirect anatomical evidence suggests that the former contains mostly W-cells, and the latter, mostly Y-cells (Guillery *et al.,* 1980). Figure 12 summarizes our current, somewhat incomplete understanding: retinal W-cells innervate the parvocellular C-laminae, the geniculate wing, and possibly the medial interlaminar nucleus; X-cells innervate the A-laminae and possibly magnocellular lamina C and the medial interlaminar nucleus; and Y-cells innervate the A-laminae, magnocellular lamina C, and the medial interlaminar nucleus.

Several laboratories (Bowling and Michael, 1980, 1984; Sur and Sherman, 1982b) have labeled with HRP individual, physiologically identified, optic tract axons to illustrate the pattern of single-cell terminations in the lateral geniculate nucleus. Figure 13 shows examples for an X-cell axon and a Y-cell axon. X-Cell axons innervate essentially only lamina A or A1, depending on the eye of origin, and every X-cell axon does so. The terminal fields are relatively small and densely packed with terminal boutons that represent the retinal synapses (Robson and Mason, 1979; Hamos *et al.,* 1983). An occasional X-cell axon emits a collateral branch that sparsely innervates magnocellular lamina C or the medial interlaminar nucleus, but even for these the number of terminal boutons outside of the A-laminae represent less than 1% of the number in the A-laminae (Sur and Sherman, 1982b). Finally, most X-cell axons have a branch that bypasses the lateral geniculate nucleus and approaches the brachium of the superior colliculus (Sur and Sherman, 1982b); what, if any, extrageniculate structures these axons innervate is open to question (but see Hoffmann and Stone, 1973; Leventhal *et al.,* 1980; Wassle and Illing, 1980). Every Y-cell axon innervates lamina A or A1. The typical Y-cell terminal volume for the A-laminae is 5–10 times larger with roughly 3 times as many boutons as the typical X-cell terminal region (Sur and Sherman, 1982b). Also, most Y-cell axons branch to innervate densely the medial interlaminar nucleus, and, if from the contralateral eye, magnocellular lamina C. Clearly, each Y-cell axon much more extensively innervates the lateral geniculate nucleus than does each X-cell axon. Virtually all Y-cell axons continue past the lateral geniculate nucleus to innervate other

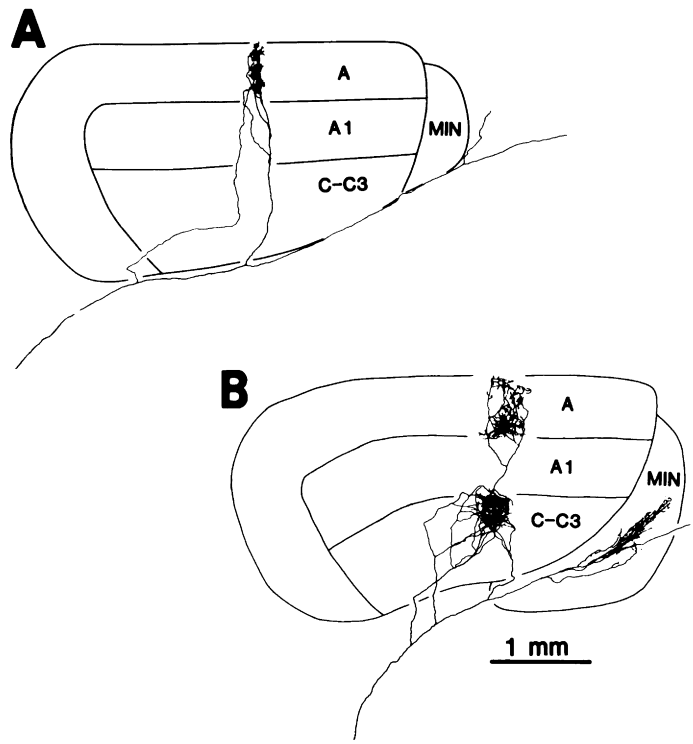


FIG. 13. Camera lucida drawings of terminal patterns for retinogeniculate axons as viewed in the coronal plane. Each axon was intracellularly filled with HRP after physiological identification, and each of these drawings was reconstructed from several consecutive 100-μm-thick sections. (A) X-Cell axon; (B) Y-cell axon. Abbreviations: A, Al, and C–C3, laminae; MIN, medial interlaminar nucleus. (Unpublished data from M. Sur and S. M. Sherman; see also Sur and Sherman, 1982b.)

brain stem sites, particularly the superior colliculus (Bowling and Michael, 1980). There are as yet no published descriptions of successfully labeled W-cell axons.

b. Extraretinal Afferents. Although this lateral geniculate nucleus is the largest terminus of retinofugal projections, this nucleus also receives afferent input from areas 17, 18, 19, and PMLS of the visual cortex (Beresford, 1962; Guillery, 1967; Garey *et al.,* 1968; Hollander, 1970, 1972; Niimi *et al.,* 1971; Kawamura *et al.,* 1974; Updyke, 1975, 1977, 1981), the perigeniculate nucleus (Alhsen and Lindstrom, 1978), the midbrain (Niimi *et al.,* 1970; Graybiel, 1972; Graham, 1977; Graybiel and Berson, 1980; Torrealba *et al.,* 1981), and probably portions of the brain stem reticular formation, including the locus coeruleus (see reviews by

Singer, 1977; Burke and Cole, 1978; see also Rogawski and Aghajanian, 1980). The perigeniculate nucleus is a collection of neurons lying just dorsal to lamina A, and perigeniculate neurons receive input from axon collaterals of geniculocortical relay cells as these axons pass en route to cortex (Dubin and Cleland, 1977; Ahlsen *et al.,* 1978; Friedlander *et al.,* 1981; Stanford *et al.,* 1983). The perigeniculate nucleus is also innervated by cerebral cortex (Niimi *et al.,* 1971; Updyke, 1975, 1977) and possibly also to a very minor degree by the retina (Laties and Sprague, 1966; Ide, 1982). The midbrain afferents terminate mainly in the C-laminae and medial interlaminar nucleus, while the other afferents seem to innervate all geniculate subdivisions.

The retinal input seems functionally dominant, since it powerfully excites geniculate target neurons and response properties of geniculate cells so closely match those of their retinal inputs (Hubel and Wiesel, 1961; Cleland *et al.,* 1971; Hoffmann *et al.,* 1972; Bullier and Norton, 1979a, Kaplan *et al.,* 1979; So and Shapley, 1981). However, retinal synapses comprise only about one-fifth of the synapses found in the lateral geniculate nucleus (Guillery, 1969), although it is not known what proportion of the remainder originates from sources extrinsic or intrinsic to the nucleus. Cortical input seems also to be excitatory (Kalil and Chase, 1970; Tsumoto *et al.,* 1978) but much less powerfully so than the retinal input, and activity of the perigeniculate neurons probably inhibits geniculate cells (Lindstrom, 1982). Because perigeniculate cells receive input from a geniculocortical relay cells, this presumed inhibition represents a feedback loop. The actions of the other inputs to the lateral geniculate nucleus are presently unknown.

3. Geniculate Neuronal Classes

As noted already, response properties of geniculate neurons closely resemble those of retinal ganglion cells, because each geniculate neuron seems to receive retinal input from very few (or one) ganglion cells of a single W-, X-, or Y-cell, ON or OFF center class. Consequently, nearly every geniculate neuron can be classified as a W-, X-, or Y-cell.

a. Relay Cells and Interneurons. A different classification of geniculate neurons is that of relay cells and interneurons. The former possess axons that project to cortex, whereas the latter have axons that are strictly intrinsic to the lateral geniculate nucleus. It should be noted that many relay cells contribute to local geniculate circuitry by means of axon collaterals (Friedlander *et al.,* 1981; Stanford *et al.,* 1983), and thus the potential for local circuits can theoretically exist without interneurons. Also, perigeniculate cells can be considered as interneurons, since they form a feedback loop from relay cells back to the lateral geniculate nu-

cleus, but strictly speaking, their somata are outside of the lateral geniculate nucleus.

Estimates of the percentage of interneurons with somata within the lateral geniculate nucleus range from practically none (Lin *et al.,* 1977) to roughly 25% (LeVay and Ferster, 1979; Geisert, 1980). The discrepancy and source of uncertainty stem from the fact that attempts to demonstrate the presence of interneurons are based on negative evidence or the inability to demonstrate an extrinsic axon. Physiologically, this usually results from a failure to activate the recorded geniculate neuron antidromically from electrical stimulation of the cortex (e.g., Dubin and Cleland, 1977) and anatomically from a failure to label cells retrogradely with markers (such as HRP) injected into cortex (e.g., LeVay and Ferster, 1977, 1979). It is not yet safe to conclude that every relay cell can be antidromically stimulated from cortex or that each will retrogradely transport HRP; such observations may not unambiguously identify interneurons.

Two more recent lines of evidence further confuse the issue. First, Friedlander *et al.* (1981) injected HRP into physiologically identified geniculate cells (see also later). They found some cells that could not be antidromically activated from cortex but that clearly possessed axons projecting to cortex. They also reported cells that had morphological features normally associated with interneurons but that were antidromically activated from cortex. Likewise, Meyer and Albus (1981) retrogradely labeled cells with morphological features usually associated with interneurons from HRP placed into visual cortex. Second, Fitzpatrick *et al.* (1984) found that virtually all geniculate cells could be labeled either retrogradely from HRP placed into cortex or with an antibody to glutamic acid decarboxylase (GAD), which is a synthetic enzyme for the presumed inhibitory transmitter, γ-aminobutyric acid (GABA). No cell was labeled for both substances. It seems implausible, though possible, that only those relay cells that failed to transport HRP retrogradely also contain GAD (e.g., Einstein *et al.,* 1983). Perhaps because of their short axons, interneurons do not generate action potentials (as is the case for many retinal interneurons) and could consequently have been overlooked in the physiological recordings on which Friedlander *et al.* (1981) based their sample. In any case, although the presence of interneurons seems most likely, it is still based on circumstantial evidence. Because every recorded cell apparently receives direct retinal afferents and can be classified as a W-, X-, or Y-cell (cf. Dubin and Cleland, 1977), and because the vast majority of geniculate neurons are in any case relay cells that can be similarly classified, the ensuing discussion is organized around these neuronal classes.

b. Structure–Function Correlates. As was the case for retina, attempts to establish structural correlates for geniculate W-, X-, and Y-cells began with studies of Golgi-impregnated neurons. In such a study of the A- and C-laminae, Guillery (1966) noted four general morphological classes, although he pointed out that the plurality of impregnated neurons in his sample could not be placed into any of these four classes. Nonetheless, other workers used a variety of indirect approaches to suggest the correlation of each of these four morphological classes with W-cells, X-cells, Y-cells, or interneurons (Wilson *et al.,* 1976; LeVay and Ferster, 1977).

Structure–function correlates have subsequently been established with the more direct approach of HRP iontophoresis into physiologically identified geniculate neurons (Friedlander *et al.,* 1979, 1981; Stanford *et al.,* 1981, 1983). From these data, Fig. 14 summarizes many of the morphological features of geniculate W-, X-, and Y-cells in the A- and C-laminae. This sort of structure–function correlation has not yet been extended to neurons of the medial interlaminar nucleus or the geniculate wing. W-Cells were found in the parvocellular C-laminae and have small somata, thin axons, and fairly thin dendrites. The dendrites occasionally have complex appendages and often are beaded or varicose in appearance. Their dendritic arbors are roughly disk-shaped and oriented parallel to the geniculate laminar borders, and typically part of each arbor crosses laminar borders. X-Cells were found in the A-laminae and have small somata, intermediate-sized axon diameters, and thin dendrites. For most X-cells, the dendrites are rather sinuous and have numerous stalked appendages. Their dendritic arbors are cylindrical, with the long axis oriented perpendicular to the laminar borders (i.e., along the previously mentioned projection lines), and each arbor is wholly contained within lamina A or A1. As noted earlier, several X-cells that were confirmed as relay cells had morphological features previously associated with interneurons (Friedlander *et al.,* 1981). Y-Cells were found in the A-laminae and magnocellular lamina C. These have large somata, thick axons, and thick, fairly straight dendrites. A few simple spinelike appendages extend from some of the dendrites. The dendritic arbors tend to display approximately spherical symmetry, and some dendrites of each Y-cell cross laminar borders.

4. Relative Numbers of Geniculate W-, X-, and Y-Cells

A number of factors conspire to confound estimates of the relative numbers of geniculate W-, X-, and Y-cells. These factors include the

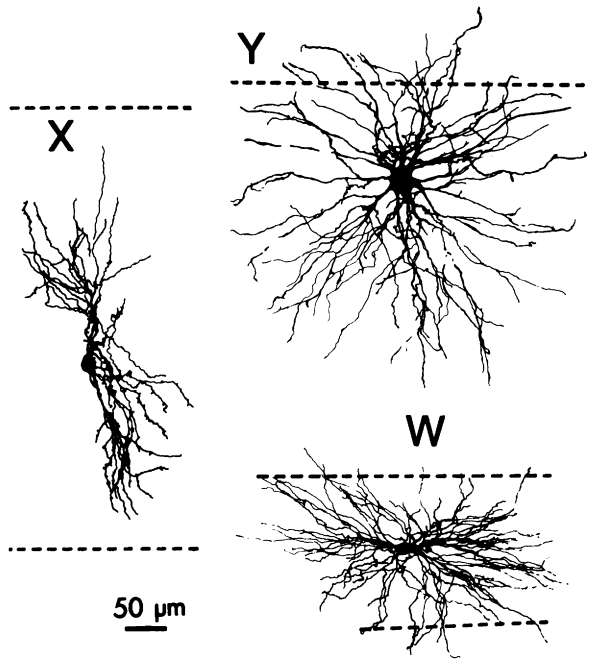


FIG. 14. Camera lucida drawings of a W-cell, X-cell, and Y-cell in the lateral geniculate nucleus as viewed in the coronal plane. The location and orientation of laminar boundaries are also shown relative to each cell. Each neuron was intracellularly filled with HRP after physiological identification, and each was reconstructed from several consecutive 100-μm-thick sections. The W-cell was located in lamina C2 and/or C3 (laminar borders here were determined by autoradiography following an injection of tritiated proline into the ipsilateral eye), the X-cell was located in lamina A, and the Y-cell was located in lamina A1. (From Stanford *et al.*, 1983.)

differential distributions of these cell classes with laminar location (Fig. 11C), differential distributions with receptive-field eccentricity (cf. Hoffmann *et al.*, 1972), and uncertainties regarding the interpretation of electrophysiological data due to uncontrolled electrode-sampling biases. Nonetheless, the available evidence to be outlined suggests that, at least for X- and Y-cells, the geniculate ratios are quite different from those in retina. This, in turn, suggests an important role for retinogeniculate circuitry beyond a simple relay of visual information. That is, this circuitry alters the relative weight of the geniculocortical limbs of these parallel pathways compared to their representation among the retinogeniculate limbs.

a. W-Cells. Estimates of relative W-cell numbers are especially tenuous because so few relevant data are available. Wilson *et al.* (1976), in an electrophysiological study of the A- and C-laminae, reported that only 11% of the neurons recorded were W-cells. Although it is often suggested that neurons with small somata (i.e., W-cells) are underrepresented in physiological samples, studies that have combined physiological and morphological analyses of single neurons (Friedlander *et al.,* 1981; Stanford *et al.,* 1983) suggest that little or no such underrepresentation exists for the A- and C-laminae. However, while W-cells may represent a small neuronal segment of these laminae, their unknown numbers in the geniculate wing and medial interlaminar nucleus render uncertain any estimate of their overall proportion in the lateral geniculate nucleus.

b. X- and Y-Cells. Two separate lines of evidence offer rather similar estimates for the X- to Y-cell ratios in the A-laminae. First, LeVay and Ferster (1977) showed that a particular morphological type, the class 1 cell described by Guillery (1966), represents roughly one-third of the neurons in these laminae. Friedlander *et al.* (1981) subsequently demonstrated that nearly all of these class 1 cells are Y-cells, although some Y-cells have other morphological features. Thus, the evidence of LeVay and Ferster (1977) suggests an X- to Y-cell ratio of no more than 2:1. Second, in an analysis of A-laminae neurons, Friedlander *et al.* (1981) compared the soma size distributions of their HRP-labeled X- and Y-cells with those seen in Nissl preparations, and from this deduced an X- to Y-cell ratio of roughly 2:1. Since Y-cells are far more numerous than are X-cells in magnocellular lamina C and the medial interlaminar nucleus, these authors suggested that the overall X- to Y-cell ratio in the lateral geniculate nucleus approaches unity.

This estimate of a geniculate X- to Y-cell ratio approaching 1:1 contrasts sharply with the retinal estimate of roughly 10:1. If these estimates are correct, and it is important to remember that neither the retinal nor the geniculate estimates are confirmed, then the retinogeniculate innervation patterns must be quite different for the X- and Y-cell pathways. That is, each retinal Y-cell axon must innervate nearly 10 times as many geniculate neurons on average as does each X-cell axon. A consideration of the relative numbers of retinal ganglion cells and geniculate neurons led Friedlander *et al.* (1981) to suggest that each retinal Y-cell axon on average innervates 30–40 geniculate neurons, whereas each X-cell axon innervates only two to four cells. As shown in Fig. 13, morphological analysis of single X- and Y-cell optic tract axons (Bowling and Michael, 1980; Sur and Sherman, 1982b) is consistent with this suggestion, since a typical Y-cell axon branches to innervate a zone of the lateral geniculate nucleus

that is roughly an order of magnitude larger than the zone innervated by a typical X-cell axon.

Regardless of the specifics of retinogeniculate circuitry, these retinal and geniculate estimates of X- and Y-cell numbers suggest a powerful relative amplification of the Y-cell pathway in this circuitry. This relative amplification forms one of the bases of the hypothesis to be presented here for X- and Y-cell functioning.

5. *Central Projections*

Figure 12 summarizes the main features of the geniculocortical projections. The many different target areas in the cerebral cortex are indicated in terms of both the W-, X-, and Y-cell pathways and the different geniculate laminae. Many of the data represented here for the W-, X-, and Y-cells are indirect and inferred from a combination of pathway-tracing studies that reveal the geniculocortical projection for each lamina (Garey and Powell, 1967; Rosenquist *et al.,* 1974; Hollander and Vanegas, 1977; Garey and Blakemore, 1977; Lin and Sherman, 1978; Itoh *et al.,* 1979; Leventhal, 1979; Geisert, 1980; Raczkowski and Rosenquist, 1980, 1983; Tong *et al.,* 1982) plus a knowledge of the laminar distribution of W-, X-, and Y-cells.

a. W-Cells. Geniculate W-cells seem to contribute to the innervation of every cortical area that receives geniculate afferents. The most prominent of the presumptive W-cell projections innervates areas 18, 19, and the AMLS and PMLS areas of the lateral suprasylvian cortex (for details of this terminology, see the legend to Fig. 1; and Symonds *et al.,* 1981; Tusa *et al.,* 1981; Tusa, 1982). As noted already, it is not yet clear that these W-cells form a homogeneous neuronal class. For instance, W-cells of the C-laminae may prove to be distinct from those thought to exist in the geniculate wing. Different classes of W-cell could thus have distinct patterns of geniculocortical innervation.

It is also not clear to what extent the W-cell innervation of multiple visual areas reflect multiple innervation of several areas by single branching axons or differential innervation of single areas by different pools of W-cells. Geisert (1980) has obtained evidence that many individual C-laminae neurons, which are presumably W-cells, innervate multiple cortical areas.

b. X-Cells. A combination of evidence, both electrophysiological (Stone and Dreher, 1973; Mitzdorf and Singer, 1978, 1980; Bullier and Henry, 1979a–c) and anatomical (Ferster and LeVay, 1978; Gilbert and Wiesel, 1979; Humphrey *et al.,* 1984a,b), demonstrates that geniculate X-

cells nearly exclusively innervate the striate cortex (area 17). While it is diffcult to exclude the possibility of some direct extrastriate input from geniculate X-cells, it seems safe to conclude that, if such a projection exists, it is exceedingly sparse.

c. Y-Cells. Like W-cells, Y-cells seem to innervate many areas of visual cortex. Relatively dense Y-cell input seems to exist for areas 17, 18, 19, plus the AMLS and PMLS areas of the lateral suprasylvian cortex. Both electrophysiological (Stone and Dreher, 1973) and anatomical (Geisert, 1980) data indicate that many individual Y-cells of the A-laminae innervate both areas 17 and 18 via branching axons, although only a minority of Y-cells do so (Humphrey *et al.,* 1984a,b). It is not clear to what extent the multiple terminal zones of geniculocortical Y-cells from magnocellular lamina C and the medial interlaminar nucleus result from an analogous pattern of branching axons.

It follows from the preceding discussion that the small minority of retinal ganglion cells that are Y-cells (roughly 5%) innervates a much larger fraction of geniculate relay cells (see earlier). These geniculate Y-cells, in turn, innervate a large region of many areas of visual cortex. In contrast, the majority of retinal ganglion cells that are X-cells have a geniculocortical representation that is limited to only one area, area 17, of visual cortex. This contrast between the X- and Y-cell pathways will be considered again later.

C. Visual Cortex

Because this article focuses on the W-, X-, and Y-cell pathways and because so little is presently known regarding the manner by which the various areas of visual cortex process information from these pathways, the discussion of visual cortex will be brief and somewhat narrowly limited. For a more general consideration of mammalian visual cortex, the reader is directed to several publications (Henry, 1977; Gilbert, 1977, 1983; Kaas, 1978, 1980; Hubel and Wiesel, 1977; Van Essen, 1979; Diamond, 1979; Lund *et al.,* 1979; Merzenich and Kaas, 1980; Lund, 1981; Tusa *et al.,* 1981; Tusa, 1982).

As noted earlier and illustrated in Fig. 1, no fewer than 13 distinct visual areas of cerebral cortex have been mapped in the cat, and Fig. 12 summarizes the distribution of geniculocortical W-, X-, and Y-cell inputs to these areas. Others not yet completely mapped may also exist, such as areas 5, 7, CG, PS, and SVA of Fig. 1 and the anterior ectosylvian area (Olson and Graybiel, 1981; Mucke *et al.,* 1982). Nearly all of the data relevant to

intracortical processing of these separate geniculate inputs derives from studies of the striate cortex.

1. Striate Cortex

a. Cell Types. The main morphological cell types found in striate cortex, and indeed throughout neocortex, are stellate cells, pyramidal cells, and fusiform cells (O'Leary, 1941; Lorente de No, 1949; Sholl, 1955; Lund, 1973; Lund *et al.,* 1979). Stellate cells have small, star-shaped somata and small but densely branched dendritic arbors. Their axons usually ramify locally, although Gilbert and Wiesel (1983) have described several spiny stellate cells with axons that travel up to 2 mm along the cortical layers (see also Martin and Whitteridge, 1984). Pyramidal cells have large, pyramid-shaped somata with the apex pointing toward the pial surface. A single long apical dendrite ascends from the apex, often with branches, and equally long basilar dendrites fan out from the base of the soma in a direction more or less parallel to the pial surface. The axon derives from the base of the soma and typically but not always enters the white matter, although branches often contribute to intracortical circuitry (Gilbert and Wiesel, 1983). Fusiform cells have a variety of shapes but are often elongated with tufts of dendrites emanating from each end of an ovoid-shaped soma. The axon usually enters white matter after emitting locally ramifying collaterals. Other rarely encountered cellular shapes have also been described (e.g., Peters and Regidor, 1981). Thus, stellate cells are thought to be the major class of cortical interneuron, whereas pyramidal and fusiform cells represent the major cortical efferents.

The two generally recognized physiological cell classes of striate cortex, simple and complex cells, were originally described by Hubel and Wiesel (1962). These classes are defined in terms of their receptive field properties. In two general ways, simple and complex receptive fields are strikingly different from those of geniculate neurons. These cortical cells usually have binocular receptive fields (i.e., a receptive field for the homonymous portion of each retina). These cells also tend to be particularly selective for the shape or orientation of visual stimuli and often for the direction of moving targets. The major differences between simple and complex cells are twofold: first, simple cells tend to have separate, spatially offset ON or OFF discharge zones (i.e., discharges at onset or offset of a small spot stimulus), while complex cells tend to have a single ON–OFF discharge zone (i.e., discharges at onset and offset of a small spot stimulus); second, simple cells tend to show fairly linear summation within their discharge zones while complex cells do not. The more subtle

differences between simple and complex cells are beyond the scope of this article (for reviews, see Henry 1977; Stone *et al.,* 1979; Lennie, 1980b; Sherman and Spear, 1982; Dean and Tolhurst, 1983).

Precisely how these morphological and physiological cell classes relate to one another and to the W-, X-, and Y-cell pathways is a matter of intense interest and some controversy. Earlier suggestions that stellate cells are simple cells and pyramidal cells are complex cells (Kelly and Van Essen, 1974) seem not to be borne out by subsequent data (Gilbert and Wiesel, 1979; Lin *et al.,* 1979; Martin and Whitteridge, 1984), suggesting no relationship between these pairs of physiological and morphological classes. Likewise, earlier suggestions that X-cells innervate simple cells while Y-cells innervate complex cells (Hoffmann and Stone, 1971) have been discarded in view of evidence that individual simple and complex cells can receive X- or Y-cell input, but not both (Bullier and Henry, 1979a–c). Interestingly, these latter studies suggest that a given simple or complex cell is part of the X- or Y-cell pathway and that no significant convergence of these pathways occurs in striate cortex (see also Mullikin *et al.,* 1981; Tanaka, 1983a,b; Ferster and Lindstrom, 1983; Martin and Whitteridge, 1984). Although anatomical data clearly implicate W-cell input to striate cortex, little physiological evidence of this input has been seen (Mitzdorf and Singer, 1978, 1980; Bullier and Henry, 1979a–c; Tanaka 1983b). In combination with the poor responsiveness of geniculate W-cells, this suggests a rather limited influence of the W-cell pathway on striate cortex, and perhaps other areas of visual cortex as well.

b. Lamination. Like other regions of neocortex, the striate cortex is composed of six layers aligned parallel to the pial surface and numbered I–VI from the pial surface to the white matter. These layers generally differ in the composition of their cellular elements, although each cell type can be found in any layer. Layer I is mainly a cell-poor, synaptic plexiform layer. Stellate cells tend to concentrate in layers II and IV, pyramidal cells in layers III and V, and fusiform cells in layer VI (O'Leary, 1941; Sholl, 1955; Lund *et al.,* 1979). Also, simple cells are concentrated in deep layer III, layer IV, and layer VI, whereas complex cells are numerous in all layers except layers I and IV (Hubel and Wiesel, 1962; Gilbert, 1977; Leventhal and Hirsch, 1978).

Another important feature of the cortical layering is the distinctive laminar arrangement of the afferents to striate cortex, the best studied among these being the geniculocortical afferents (Rosenquist *et al.,* 1974; LeVay and Gilbert, 1976; Ferster and LeVay, 1978; Leventhal, 1979; Gilbert, 1983; Humphrey *et al.,* 1984a,b). Most of these afferents terminate in layer IV, although substantial inputs exist to layers I, lower layer

III, and layer VI. W-Cells seem to terminate predominantly in layer I, lower layer III, and the layer V–VI border; X-cells, in the lower half of layer IV (i.e., layer IVb) and layer VI, although substantial X-cell input is also seen in upper layer IV (i.e., layer IVa); and Y-cells, in the upper half of layer IV (i.e., layer IVa) and layer VI. Thus, there is limited overlap in the laminar distribution of geniculocortical W-, X-, and Y-cell terminals. Iontophoresis of HRP into single X- or Y-cell axons (Gilbert and Wiesel, 1979; Humphrey *et al.,* 1984a,b) has shown that each typically innervates both layers IV and VI; also, as is the case for retinogeniculate axons, the Y-cell axons innervate a much larger volume of area 17 than do the X-cell axons (see also Ferster and LeVay, 1978). Typically, each Y-cell axon seems to innervate several ocular dominance columns (see later), whereas each X-cell axon seems to limit its innervation to a single such column. No morphological description of single W-cell geniculocortical axons has yet been published.

c. Columnar Organization. Hubel and Wiesel (1962) first demonstrated the columnar organization of the cat's striate cortex. That is, the functional unit of this cortex seems to be a column several cells in diameter that extends vertically across the layers.

Two related columnar systems have been clearly demonstrated, and others have been suggested. First are the orientation columns (Hubel and Wiesel, 1962; Albus, 1979; Schoppmann and Stryker, 1982): cells within a column are selective for the same stimulus orientation in visual space (e.g., vertical), whereas cells in a neighboring column share the same, slightly different preferred orientation (e.g., 10° from vertical). There is an orderly progression of preferred orientations as neighboring columns are sampled across cortex. The second columnar system is for ocular dominance (Shatz *et al.,* 1977; Shatz and Stryker, 1978). Alternating patches of layers IV and VI that are roughly 500 μm in width receive geniculocortical input related strictly to one eye or the other (i.e., either from laminae A, C, 1, etc., or from laminae A1, 2, etc.). Although most cells of area 17 are binocular, ocular dominance columns nonetheless signify cortical zones in which one or the other eye has the dominant input. Also, many of the layer IV simple cells only have monocular fields, and the dominant eye for these matches the cells' location with respect to the ocular dominance columns (Shatz and Stryker, 1978). Hubel and Wiesel (1977) defined the "hypercolumn" as the slab of cortex that contains adjacent ocular dominance columns plus the full cycle of orientation columns necessary to map all stimulus orientations around the clock; each slab extends through all the layers and occupies roughly 1 mm^2 of cortical surface. In addition to these types of functional columns, for which a wealth of evidence is

available, limited data suggest that columnar or laminar arrangements may also exist for other functional properties, such as spatial-frequency tuning and stereopsis or target distance from the eyes (Blakemore, 1970; Maffei and Fiorentini, 1977; Tootell *et al.,* 1980; Tolhurst and Thompson, 1982).

2. *Extrastriate Visual Areas*

Although receptive-field studies have been reported for many of the extrastriate areas of visual cortex, including areas 18, 19, and PMLS (Hubel and Wiesel, 1965, 1969; Dreher and Cottee, 1975; Spear and Baumann, 1975; Camarda and Rizzolatti, 1976; Orban and Callens, 1977; Sherk, 1978; Movshon *et al.,* 1978; Guedes *et al.,* 1983; von Grunau and Frost, 1983), few of these offer data that can be readily interpreted in the context of the W-, X-, and Y-cell pathways. Figure 12 summarizes a somewhat speculative treatment of the direct geniculocortical pathways. Those to extrastriate cortex involve only W- or Y-cells, because the X-cell input is essentially limited to area 17. However, since area 17 projects to many other regions of visual cortex, this raises the possibility that the X-cell pathway is well represented and important throughout extrastriate visual cortex.

Several studies offer preliminary clues that such an indirect X-cell input to areas 18 and 19, if it exists at all, is not of enormous import. First, electrical stimulation is often used to determine the conduction velocity of the geniculocortical afferents that are part of the pathway leading to the innervation of a cortical cell. W-, X-, and Y-cell input can be inferred from afferent conduction velocity, and such data from neurons in areas 18 and 19 have failed to reveal significant X-cell input, either direct or indirect via area 17 (Tretter *et al.,* 1975; Dreher *et al.,* 1980; Harvey, 1980), although failure to find indirect inputs from electrical stimulation may be of limited significance. Second, functional removal of area 17 by ablation or cooling has surprisingly little effect on response properties of area 18 neurons (Dreher and Cottee, 1975; Sherk, 1978; but see Donaldson and Nash, 1975), which suggests that the W- and/or Y-cell inputs normally dominate the functional properties of area 18. Unfortunately, no published data address the possible role of indirect X-cell inputs via area 17 to extrastriate visual areas other than areas 18 and 19. Although this is a substantial qualification, the X-cell pathway in cortex may nonetheless be largely limited to area 17.

Even within area 17, the importance of the X-cell pathway may be limited. This is suggested by Malpeli's study (1983) of neuronal response

properties in striate cortex during reversible blockade of geniculate lamina A. This blockade was effected by iontophoresis of cobaltous chloride into lamina A, a procedure that essentially eliminates from striate cortex all X-cell and probably most Y-cell input representing the contralateral eye. During such blockade, little effect was seen on receptive field properties from the contralateral eye for most area 17 cells in supragranular layers and many in layer V. Normal activity here must depend on W- and Y-cell inputs (although the responsiveness of these cortical cells seems greater than can plausibly be supported by W-cell input alone) from routes outside lamina A, such as via the C-laminae, medial interlaminar nucleus, or more circuitous pathways.

D. Summary

The somewhat speculative picture painted here for the functional organization of the W-, X-, and Y-cell pathways suggests that they remain largely parallel through much of the visual cortex and that the relative cortical representations of these pathways does not reflect their retinal distribution. Every retinal X- and Y-cell innervates the lateral geniculate nucleus. X-Cells are dominant in the retina, but their central representation can be followed only to the A-laminae of the lateral geniculate nucleus and from there to area 17 of visual cortex. The relay of X-cell information from area 17 to extrastriate cortex remains a possibility that has yet to be demonstrated. Y-Cells, which represent a small minority of retinal ganglion cells, innervate increasingly large neuronal pools in the lateral geniculate nucleus and visual cortex. It is likely that most of the visual cortical areas are dominated by the Y-cell pathway. Least is known about the W-cell pathway, but only a subset of retinal W-cells is related to geniculocortical pathways. Geniculate W-cells probably innervate most or all areas of visual cortex (Fig. 12). However, their importance to cortical function is difficult to gauge, although limited electrophysiological evidence suggests weak functional input to striate cortex.

It thus appears that the functional organization of the central visual pathways is such that a small minority of retinal ganglion cells (Y-cells) may come to dominate cortex, while the vast majority (X- and W-cells) may play a relatively minor role in cortical function. It should be noted that the presumed minor roles for W- and X-cells differ, since X-cells powerfully influence cells in a limited region (area 17) while W-cells seem to influence cells weakly throughout most of visual cortex. These conclusions are far from firm and require considerably more data than are presently available to assess the relative importance of the W-, X- and Y-cell pathways to the many areas of visual cortex.

V. Perceptual Correlates for W-, X-, and Y-Cells

A. Qualifications in Interpreting Behavioral Data

Large gaps persist despite attempts to relate the behavioral visual capacities of cats with the response properties of their visual neurons. For instance, most behavioral data have until recently consisted of a stimulus–response measure, the ability to learn to discriminate among various geometric shapes (e.g., Smith, 1938; Winans, 1967; Spear and Braun, 1969; Doty, 1971, 1973; Sprague *et al.*, 1977), that is difficult to relate to most neuronal receptive field properties. This gap has been bridged somewhat with the introduction of psychophysical techniques that make use of a stimulus–response paradigm similar to a paradigm used neurophysiologically. That is, a cat's contrast sensitivity to sine wave gratings can be psychophysically established as a function of spatial and temporal frequency by determining the minimum contrast needed for the cat to detect the grating (Blake and Camisa, 1977; Blake and DiGianfillipo, 1980; Lehmkuhle *et al.*, 1982, 1984). This is analogous to the contrast sensitivity functions that have been described already for visual neurons.

Even with this most favorable condition for deriving correlations between behavior and neurophysiology, several important qualifications and assumptions must be noted. First, it is not at all clear how one correlates a contrast threshold for a cell with that determined psychophysically. The techniques used to determine the cellular and psychophysical thresholds require different and somewhat arbitrary measures of responsiveness. Second, the animals' states (alert behavior versus anesthetized and paralyzed) are quite different during the psychophysical and neurophysiological determinations. Third, it is not clear what measure of neuronal responsiveness relates to the psychophysical thresholds. For instance, if, as is often assumed, the most sensitive cells for a given stimulus set the psychophysical threshold, then less sensitive neurons such as W-cells (see Figs. 6 and 7) should play little or no role in behavioral contrast sensitivity under normal conditions. As noted later, normal cats are sensitive to stimuli of sufficiently low contrast that few if any W-cells would respond to that stimulus. Thus, W-cells may contribute significantly to vision only for suprathreshold, higher-contrast targets, and measurements of behavioral contrast sensitivity functions cannot address such a hypothetical suprathreshold function. Many other difficulties with these correlations between behavior and neurophysiology could also be listed.

Finally, while spatial contrast sensitivity functions determined psychophysically for a subject may be of inherent interest, it is not yet clear how these functions relate to the quality of form or spatial vision of which

the subject is capable. Form vision can be defined as the ability to detect and recognize the spatial content of visual stimuli. While the definition of form vision may be straightforward, its measure is not. The most widely used measure of form vision has been one of spatial acuity, but it is now clear that this is inadequate (see later; see also Hess and Howell, 1977; Ginsburg, 1978; Berkley and Sprague, 1979; Lehmkuhle *et al.*, 1982). The other widely used measure of form vision is imprecise and depends on the ability to discriminate or recognize arbitrarily defined stimuli, such as circles versus crosses for cats and faces for humans. Although imprecise, this latter operational measure for the quality of form vision leads to interesting parallels between spatial vision deficits and deficient spatial contrast sensitivity functions. These parallels will be described in some detail here, but it is important to remember that these parallels reflect a limited evaluation of the quality of form vision.

Despite these qualifications, some surprisingly clear correlations emerge between a comparison of the neurophysiological and behavioral data based on contrast sensitivity functions. This section will therefore concentrate on these functions for normal cats and cats with experimental manipulations that interfere with the W-, X-, or Y-cell pathways.

B. Normal Cats

Blake and Camisa (1977) first reported spatial and temporal contrast sensitivity functions of normal cats and interpreted these results in the context of X- and Y-cell pathways. [W-Cell participation in geniculocortical innervation was not known when Blake and Camisa (1977) reported their results, and in any case, the insensitivity of W-cells makes it unlikely that they are significantly involved in the behavioral thresholds of the sort measured.] A description of the parameters of spatial and temporal frequency can be found in Section III,A; the value of sensitivity is simply the inverse of the minimum contrast needed for the cat to detect the stimulus (i.e., the threshold contrast). Figure 15 shows spatial functions at different temporal frequencies, including stationary presentation (△), ON–OFF flicker at 1.5 Hz (□), and ON–OFF flicker at 10 Hz (○). Note that, for both stationary presentation and flicker at the lower temporal rate, sensitivity peaks at middle spatial frequencies and falls off for higher and lower ones. At the higher flicker rate, the sensitivity monotonically drops with increasing spatial frequency.

Blake and Camisa (1977) reasoned as follows. Y-Cells would dictate sensitivity to higher temporal rates as well as to lower spatial frequencies (regardless of rate), because X-cells are less sensitive to such stimuli. On the other hand, X-cells would determine the sensitivity to the higher

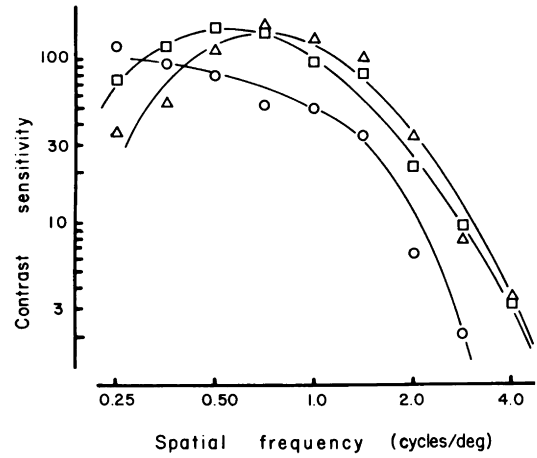


FIG. 15. Psychophysically determined contrast sensitivity as a function of spatial frequency for a normal cat. Functions are shown for stationary presentation of a sine wave grating (△), ON–OFF flicker (i.e., interchanging of the grating with a uniform field of equal average luminance) at 1.5 Hz (□), and ON–OFF flicker at 10 Hz (○). (From Blake and Camisa, 1977, with permission of the authors.)

spatial frequencies at lower rates. Figures 6 and 7 support this reasoning. Thus, the psychophysical function at 10 Hz would be Y-cell dominated, which explains why there is no sensitivity loss to lower spatial frequencies (Fig. 6). At 1.5 Hz, the significant X-cell activity would raise sensitivity to all but the lower spatial frequencies (Fig. 6), which explains why the behavioral sensitivity function at that rate peaks around the middle spatial frequencies.

C. Cats with Cortical Lesions

1. Lesions to Striate Cortex

From Fig. 12 it should be clear that a bilateral removal of area 17 in cats effectively eliminates all cortical representation of the X-cell pathway and spares much of the W- and Y-cell pathways. Doty (1971), and Sprague and colleagues (Sprague, 1966; Sprague *et al.*, 1976, 1977, 1981; Berkley and Sprague, 1978, 1979; Berlucchi and Sprague, 1981) were the first to establish that lesions limited to area 17 and parts of area 18 produce remarkably mild deficits in visually guided behavior. Visual deficits were limited to suprisingly small reductions in spatial resolution (including moderate losses in orientation and grating resolutions and a marked loss

in vernier acuity), while visual capacities on a wide range of other visual tasks were affected little or not at all by the lesions. Thus, by the operational measure of form vision noted in Section V,A, these cats without area 17 and the X-cell pathway exhibit excellent form vision despite reduced acuity. Also, Kaye *et al.* (1981) reported that although bilateral lesions of areas 17, 18, and part of 19 had surprisingly little effect on a cat's acuity, these lesions almost totally eliminate binocular depth discrimination. While area 17 and the X-cell pathway do not seem essential for basic form vision, they might be needed for other functions beyond inproved acuity, such as stereopsis or a variety of visually guided behaviors not yet tested in destriate cats.

Lehmkuhle *et al.* (1982) confirmed and extended some of these observations by obtaining preoperative and postoperative contrast sensitivity functions for destriate cats. The lesion affects sensitivity only to higher spatial frequencies and lower temporal ones (Fig. 16). At higher rates little or no difference between preoperative and postoperative performance could be detected. The contrast sensitivity found after bilateral removal of striate cortex almost certainly reflects activity in the remaining Y-cell pathways.

A more detailed consideration of Y-cell response properties further supports this conclusion. As described in Section III,D and illustrated in Fig. 6C, Y-cell responsiveness can be divided into a linear component, which dominates at lower spatial frequencies, and a nonlinear component, which dominates at higher spatial frequencies (Hochstein and Shapley, 1976b; Lehmkuhle *et al.,* 1980a). The linear component is sensitive to the spatial phase, or position, of the stimulus, whereas the nonlinear component is not (see Fig. 4; and Hochstein and Shapley, 1976b). Thus, while the nonlinear response component can signal the presence of a stimulus, the linear component is needed to signal precise stimulus position (see also, Sur and Sherman, 1984). In normal cats, for which X-cells probably determine psychophysical thresholds at higher spatial frequencies, spatial resolution of both stimulus presence and stimulus position is signaled by the same linear response mechanism. If removal of the X-cell pathway by a bilateral area 17 ablation leaves Y-cells to determine spatial resolution, one would expect a greater deficit in spatial resolution for stimulus position than for stimulus presence. That is, compared to Y-cells, X-cells are much more sensitive to position or spatial phase (Fig. 8) and only moderately more sensitive to higher spatial frequencies (Lehmkuhle *et al.,* 1980a; So and Shapley, 1981). As noted before, destriate cats suffer more of a resolution loss for vernier acuity, which requires positional information to determine the spatial offset of line segments, than for simple grating resolution, which requires only information about the presence or absence of the stimulus (Berkley and Sprague, 1979).

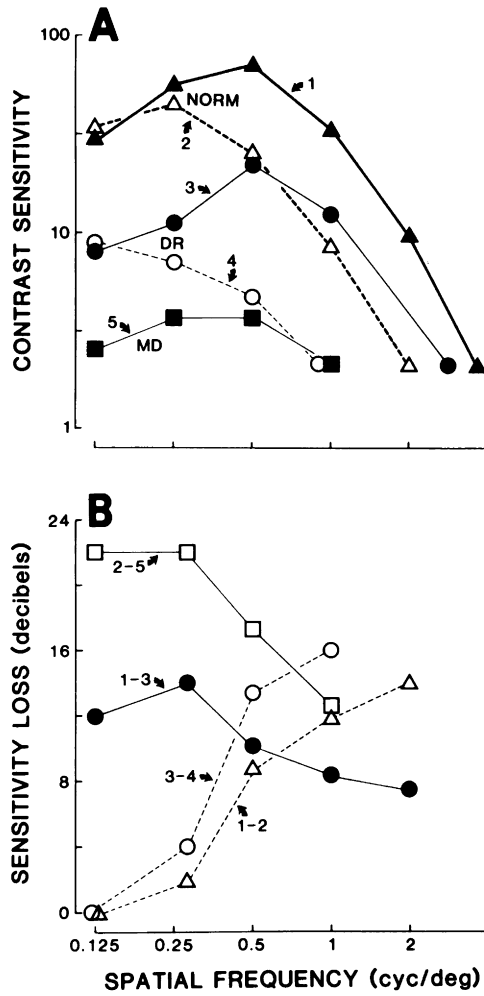


FIG. 16. Psychophysically determined contrast sensitivity of cats as a function of spatial frequency. The stimuli consisted of sine wave gratings counterphased at 1.0 or 1.5 Hz. (A) Contrast sensitivity functions for five types of cats; each curve represents an average from two subjects. (▲, △) Data from the same two normally reared cats before (curve 1) and after (curve 2) bilateral removal of cortical area 17 and part of area 18. (●, ○) Data from the same two dark-reared cats before (curve 3) and after (curve 4) bilateral removal of cortical area 17 and part of area 18. (■, curve 5) Data from the deprived eyes of two cats reared with monocular lid suture. (With their nondeprived eyes, these cats exhibited sensitivity indistinguishable from that of the normal cats.) (B) Differences in sensitivity (sensitivity loss) between various pairs of curves in (A) as a function of spatial frequency. Sensitivity loss was computed in decibels as 20 times the logarithm of the ratio of the higher to the lower sensitivity. Where differences are attributed mostly to X-cell losses (i.e., lesions to area 17; curves 1 minus 2 and 3 minus 4), sensitivity losses mostly occur at higher spatial frequencies. Where differences are attributed mostly to Y-cell losses (i.e., normal versus dark reared and normally reared with lesions to area 17 versus monocularly deprived; curves 1 minus 3 and 2 minus 5), sensitivity losses mostly occur at lower spatial frequencies. (Redrawn from Lehmkuhle *et al.*, 1982, 1984.)

While this does offer an interesting correlation between the visual capacity of cats and of their X- and Y-cells, it would be better to have available a detailed psychophysical analysis of spatial phase or position sensitivity for normal and destriate cats.

The surprisingly normal visual capacity of cats after removal of striate cortex suggests that the X-cell pathway is not necessary for basic form vision. The remaining Y-cell and perhaps W-cell pathways seem sufficient for excellent form vision, albeit with a reduced level of spatial resolution.

2. *Lesions to Extrastriate Cortex*

Although no one has yet reported contrast sensitivity measurements of cats with lesions of extrastriate areas of visual cortex, Sprague *et al.* (1977) have provided a description of visual behavior in such cats that can be tied in a general way to the W-, X-, and Y-cell pathways. Bilateral lesions that include area 17 and extend to most of area 18 do not interfere with basic form vision (Spear and Braun, 1969; Sprague *et al.,* 1976, 1977, 1981). Only when the lesions encroach significantly into area 19 and the lateral suprasylvian visual areas does pattern vision become severely compromised (Sprague *et al.,* 1977, 1979; Baumann and Spear, 1977; Loop and Sherman, 1977; Berlucchi and Sprague, 1981). Interpreted in the context of Fig. 12, it follows that a substantial loss in all of the geniculocortical pathways is needed to preclude reasonable form vision. It should also be noted that such lesions also destroy the projection zones of the extrageniculate visual thalamus (e.g., retinotectothalamocortical pathways; cf. Berlucchi and Sprague, 1981).

D. Cats Raised with Visual Deprivation

There have been several psychophysical studies of contrast sensitivity of cats raised with various forms of visual deprivation, particularly with lid suture and dark-rearing. Because the status of the X- and Y-cell pathways, and to a lesser extent the W-cell pathway, has been assessed in such cats, these data permit further correlates between neurophysiology and behavior. The neurological status of visually deprived cats has been reviewed by Movshon and Van Sluyters (1981) and Sherman and Spear (1982).

1. *Monocularly Sutured Cats*

a. Deficits in the Visual Pathways. In monocularly sutured cats, retinal ganglion cells of all classes respond fairly normally to visual stimuli (Sherman and Stone, 1973; Kratz *et al.,* 1979a; Cleland *et al.,* 1980).

However, a substantial deficit develops in the Y-cell pathway that is apparent in all appropriate regions of the lateral geniculate nucleus receiving Y-cell afferents from the deprived eye (Sherman *et al.,* 1972; for a review of this subject, see Sherman and Spear, 1982). Because of the pattern of geniculocortical innervation (Fig. 12), a failure of geniculate Y-cells to develop properly would affect practically all of the known visual areas of cortex. Apparently, much of the loss of geniculate Y-cells is due to the failure of many Y-cell axons from the deprived retina to innervate geniculate cells properly (Friedlander *et al.,* 1982; Sur *et al.,* 1982). On the other hand, deprived geniculate X-cells develop fairly normal responsiveness to visual stimuli, although there may be a deficit in their spatial resolution (Lehmkuhle *et al.,* 1980b; Shapley and So, 1980; Derrington and Hawken, 1981; Mower and Christen, 1982; Mangel *et al.,* 1983). Interestingly, the Y-cell deficits are limited to the deprived binocular segment of the lateral geniculate nucleus,* since Y-cells in the deprived monocular segment develop normally (Sherman *et al.,* 1972, 1975b; Lehmkuhle *et al.,* 1980b). However, the subtle deficit claimed for deprived geniculate X-cells, a loss of resolution, is found equally in the binocular and monocular segments (Lehmkuhle *et al.,* 1980b). No studies have specifically tested responsiveness of deprived W-cells, although histological measurements of the deprived parvocellular C-laminae suggest little or no deficit for these neurons (Hickey, 1980; Murakami and Wilson, 1980; Leventhal and Hirsch, 1983).

Presumably correlated to this pattern of geniculate deficits are recordings of evoked potentials in cortical areas 17 and 18 that reveal a dramatic loss of Y-cell input and much less of a loss of X-cell input (Snyder and Shapley, 1979; Mitzdorf and Singer, 1980; Jones and Berkley, 1983; Freeman *et al.,* 1983). That is, there is a much greater loss of the faster-conducting input that exhibits peak sensitivity to higher temporal and lower spatial frequencies. While X-cell input may reach layer IV of area 17 (Shatz and Stryker, 1978), the fact that nearly all cells beyond layer IV are insensitive to visual stimulation of the deprived eye (Wiesel and

* The binocular segment of visual field is that central portion normally viewed by both eyes; the monocular segments are those peripheral portions that are normally viewed only by the ipsilateral eye. Temporal retina sees only binocular segment, and monocular segment is viewed by the most peripheral nasal retina. For the cat, the binocular segment is the central 90° of visual field, whereas each monocular segment is represented roughly 45 to 90° laterally from the fixation point. Because the visual field is retinotopically mapped onto the lateral geniculate nucleus and areas of visual cortex, it is possible to define binocular and monocular segments of these structures. For example, the geniculate A-laminae have both segments represented: the monocular segment is mapped where lamina A extends laterally beyond lamina A1, and the binocular segment is mapped in lamina A1 and the corresponding portion of lamina A.

Hubel, 1963; Shatz and Stryker, 1978; and many others) suggests that the X-cell pathway is eventually lost as well within the level of striate cortex. W-Cell input to visual cortex is difficult to demonstrate with these techniques, even in normal cats.

Deficits due to visual deprivation have also been described in visual regions other than the lateral geniculate nucleus and striate cortex. However, most primary deficits seem to occur in the geniculocortical pathways, since these other deficits are largely secondary to those in the geniculocortical pathways (for a more detailed discussion of the primary sites of deprivation-induced deficits, see Sherman and Spear, 1982). Consequently, many of the neural abnormalities due to rearing with monocular suture may have as their basis the failure of geniculate Y-cells to develop normally.

b. Behavioral Deficits. Although some early reports suggested that a monocularly sutured cat using its deprived eye was practically blind (Wiesel and Hubel, 1963, 1965), later studies succeeded in demonstrating some rudimentary visual capacity for that eye (Ganz and Fitch, 1968; Dews and Wiesel, 1970; Rizzolatti and Tradari, 1971; Spear and Ganz, 1975), particularly its monocular segment (Sherman, 1973; Sherman and Sprague, 1979).

Figure 16A shows the psychophysically determined contrast sensitivity for the deprived eye (Lehmkuhle *et al.,* 1982). Severe sensitivity losses are evident for all spatial frequencies, particularly lower ones (Fig. 16B). This is consistent with the substantial abnormalities among geniculate Y-cells and also among area 17 neurons that presumably reflect deficits in the X-cell pathway as well. It seems likely that the additional visual deficits of the deprived eye versus those seen in the destriate cats (e.g., sensitivity losses to lower spatial frequencies) correlate with the added loss of the Y-cell pathway due to the deprivation. It is not clear whether the extremely limited spatial vision of the deprived eye reflects a fairly normal geniculocortical W-cell pathway, fairly normal W- and Y-cell subcortical pathways (cf. Hoffmann and Sherman, 1974), or some normal development of geniculocortical pathways in the deprived monocular segment (Guillery and Stelzner, 1970; Sherman, 1973; Sherman *et al.,* 1974; Wilson and Sherman, 1977). Incidentally, on all tests of visual performance, these cats using the nondeprived eye exhibit normal visual capabilities (Dews and Wiesel, 1970; Sherman, 1973; Lehmkuhle *et al.,* 1982).

2. Binocularly Deprived Cats

Two types of binocularly deprived cats have been extensively studied: one raised with binocular lid suture and the other raised in total darkness.

Although these are clearly different rearing conditions and there may well be significant differences among their neuronal abnormalities, for the purposes of this article they will be treated together because of their obvious similarities (see Sherman and Spear, 1982, for a more complete discussion of these forms of binocular deprivation).

a. Deficits in the Visual Pathways. As is the case with monocular suture, retinal ganglion cells after binocular suture seem normal (Sherman and Stone, 1973); these cells have not yet been studied in dark-reared cats. Following both forms of binocular deprivation, a substantial deficit is seen among geniculate Y-cells in both monocular and binocular segments (Sherman *et al.,* 1972; Kratz *et al.,* 1979b; see Sherman and Spear, 1982, for the significance of the differences in the pattern of deficits following monocular and binocular deprivation). Geniculate X-cells respond fairly normally in these cats (but see Mower *et al.,* 1981; Kratz, 1982), and the effects of binocular deprivation on W-cells have not yet been studied. Many cells in striate cortex remain binocularly responsive after this deprivation, although their normal specificity for stimulus orientation and direction of movement is largely absent (Wiesel and Hubel, 1965; Pettigrew, 1974; Blakemore and Van Sluyters, 1975; Buisseret and Imbert, 1976; Fregnac and Imbert, 1978; Watkins *et al.,* 1978; Leventhal and Hirsch, 1980). Leventhal and Hirsch (1980) have interpreted this pattern of cortical physiology in terms of fairly normal development of X-cell input with more serious abnormalities in Y-cell input. Although the relevant data for binocularly deprived cats are relatively sketchy, they suggest serious abnormalities in the Y-cell pathway and fairly normal development of the X-cell pathway. As is the case with monocular deprivation, deficits outside of the geniculocortical pathways may be secondary to those occurring in these pathways (e.g., Hoffmann and Sherman, 1975).

b. Behavioral Deficits. Many papers have emphasized the seriously deficient form vision in binocularly deprived cats (Wiesel and Hubel, 1965; Sherman, 1973; Blake and DiGianfillipo, 1980; Lehmkuhle *et al.,* 1982, 1984), and this is supported by studies of their contrast sensitivity. Figure 16 shows similar psychophysical functions and sensitivity losses for binocularly sutured and dark-reared cats (Lehmkuhle *et al.,* 1982). Sensitivity losses are seen for all spatial frequencies, especially for lower ones. This is a similar pattern to that seen after monocular suture, although the sensitivity losses are less severe after binocular deprivation.

The difference in sensitivity between binocularly and monocularly deprived cats may be due to a less abnormal X-cell pathway in the former than in the latter. As noted before (Sections V,D,1,a and V,D,2,a), the deprived X-cell pathway is completely disrupted in area 17 of monocularly sutured cats, but, according to Leventhal and Hirsch (1980), may

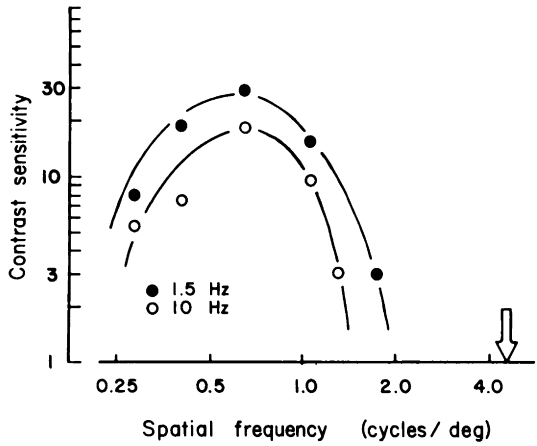


FIG. 17. Psychophysically determined contrast sensitivity as a function of spatial frequency for a dark-reared cat. Stimuli consisted of a sine wave grating sinusoidally counterphased at 1.5 Hz (●) or 10 Hz (○). The arrow along the abscissa indicates the high-spatial-frequency intercept seen in normal cats to the 1.5-Hz stimulus. (From Blake and DiGianfillipo, 1980, with permission of the authors.)

largely survive intact in area 17 of binocularly deprived cats. Indeed, Blake and DiGianfillipo (1980) have provided evidence that the reduced contrast sensitivity of dark-reared cats is mostly due to remaining X-cell activity. Unlike the case in normal cats (see Blake and Camisa, 1977; and Fig. 15), dark-reared cats exhibit attenuation to lower spatial frequencies both at low and high temporal rates (Fig. 17). It thus seems that Y-cell activity, which exhibits no sensitivity reduction at lower spatial frequencies, is not available to dominate the behavioral responses at higher temporal rates after dark-rearing, a situation that does occur in normal cats. Indeed, removal of striate cortex in these cats (and thus any useful X-cell function) seriously compromises the contrast sensitivity of these cats, and the losses are evident mainly in higher spatial frequencies as is the case in normally reared cats with such lesions (Fig. 17; and Lehmkuhle *et al.*, 1984).

E. CONCLUSIONS

Figure 16 suggests several interesting conclusions. First, the behavioral data correlate in a general way with what is known of the functional status of W-, X-, and Y-cells in normal, cortically lesioned, and visually deprived cats. These correlations by no means prove a cause-and-effect relationship, but they seem worth pursuing.

Second, the general visual capabilities of these cats correlate much more accurately with their sensitivity to lower spatial frequencies than to higher ones. Thus, cats with good sensitivity to lower spatial frequencies (e.g., normal and destriate cats) have excellent form vision, and those with poor sensitivity to these frequencies (e.g., monocularly and binocularly deprived cats) have at best rudimentary form vision. Sensitivity to higher spatial frequencies is less crucial to basic form vision than is sensitivity to lower frequencies. Indeed the dark-reared cats on average have slightly better spatial resolution (i.e., sensitivity to higher spatial frequencies) than do the destriate cats (Fig. 16), yet the destriate cats have obviously superior form vision. Clearly, spatial resolution alone is an inadequate and often misleading measure of overall visual performance. These data suggest that sensitivity to the lower spatial frequencies is necessary and sufficient for excellent form vision and that sensitivity to the higher spatial frequencies adds an appreciation of fine detail and raises resolution. This conclusion has already been reached for human visual performance (Kabrisky *et al.,* 1970; Ginsburg *et al.,* 1976; Ginsburg, 1978; Hess and Garner, 1977; Hess and Howell, 1977; Hess and Woo, 1978).

Finally, even though the vast majority of studies of the cat's central visual pathways in normal and visually deprived cats have concentrated on striate cortex, Fig. 16 illustrates some of the logical limitations of these studies. The excellent form vision of destriate cats makes it rather obvious that area 17 is not essential to this behavioral capability. Also, the fact that destriate cats have significantly better form vision than do visually deprived cats implies that deprivation-induced deficits seen in striate cortex (or the X-cell pathway), no matter how severe, cannot account for the behavioral deficits in the deprived cats. Obviously, severe deprivation-induced abnormalities must exist outside and independent of any seen in area 17 (or the X-cell pathway), and a likely source of these deficits are the geniculate Y-cells that innervate so many regions of visual cortex. While studies of cat striate cortex are obviously useful in understanding the geometry of connections in a part of the brain, the functional significance of these connections has yet to be elucidated.

VI. Hypothesis for the Functional Organization and Role of the W-, X-, and Y-Cell Pathways

The dearth of information about the W-cell pathway makes it difficult to ascribe any specific function to this pathway. However, the poor and inconsistent responses of W-cells, their large, diffuse receptive fields, and the inability of many investigators to demonstrate a powerful influence of

the W-cell pathway on neurons in striate cortex suggest that these cells do not play a significant role in basic form vision. No specific role for the W-cell pathway can yet be suggested (but see Stone *et al.,* 1979), and this is obviously a weakness in the hypothesis. Much more knowledge of W-cells is needed. Also, the possibility exists that the reported insensitivity of W-cells is an artifact of the physiological preparation (e.g., due to anesthesia or paralysis) and that these cells are normally responsive and crucial to normal pattern vision.

However, most attention regarding functional significance for spatial vision has focused on X- and Y-cells. Figures 6 and 8 summarize several major differences between these neuronal classes regarding their responses to spatial visual patterns. Y-Cells are considerably more responsive or sensitive to lower spatial frequencies, whereas X-cells are more responsive to higher ones and generally more sensitive to changes in position or spatial phase. Evidence from psychophysical studies cited in Section V underscores the primacy of lower spatial frequencies to form vision. Indeed, it has been suggested (Kabrisky *et al.,* 1970; Ginsburg *et al.,* 1976; Ginsburg, 1978; Hess and Woo, 1978) that basic form information is carried by the lower spatial frequencies and that the higher ones merely add detail to the basic forms. Thus, a loss of higher frequencies is not nearly so devastating to form vision as is a loss of lower ones (Fig. 16). From this and a comparison of response properties (Figs. 6 and 8), the following hypothesis logically emerges: *the Y-cell pathway is responsible for analysis of basic forms, and the X-cell pathway adds detail and raises spatial resolution and position sensitivity to this basic form analysis.*

This hypothesis for X- and Y-cell function differs significantly from many others, the most prominent and popular of which suggests that X-cells analyze spatial patterns while Y-cells analyze temporal patterns (Ikeda and Wright, 1972; Kulikowski and Tolhurst, 1973; Stone *et al.,* 1979). Other hypotheses have also been suggested (e.g., Lennie, 1980b; Troy, 1983). Most of these other hypotheses emphasize the relative paucity of Y-cells versus X-cells in the retina to argue for the relatively minor role in vision for Y-cells compared to X-cells. Implicit in these arguments seems to be the notion that the X-cell pathway remains dominant with respect to the Y-cell pathway throughout the lateral geniculate nucleus and visual cortex. One key to the hypothesis presented in the present article is the evidence that, compared to the X-cell pathway, the Y-cell pathway dominates the visual cortex, at least partly because of dramatically different extents of axonal arborizations between X- and Y-cell axons along these pathways.

The behavioral evidence summarized in Figs. 16 and 17, while far from definitive, clearly supports the hypothesis presented here rather than the

separation into spatial processing for X-cells and temporal processing for Y-cells, or indeed any major role in basic form vision dependent on X-cells. Essentially complete interruption of the X-cell pathway by area 17 lesions does not destroy spatial vision, as these other hypotheses would suggest. Conditions in which significant Y-cell activity exists (e.g., normal and destriate cats) provide excellent form vision. Conditions in which the Y-cell pathway is deficient (e.g., monocular and binocular deprivation) result in poor form vision, even in the case of dark-reared cats that may have fairly normal X-cell activity (Fig. 17). These data suggest but by no means prove that the Y-cell pathway is necessary and sufficient for good form vision.

The importance attributed by this hypothesis to Y-cells seems at first glance to be at variance with the low percentage of Y-cells in the retina (see earlier). As noted already and summarized schematically in Fig. 18, the Y-cell pathway starts as a small minority of retinal ganglion cells, captures a much larger fraction of geniculate neurons, and becomes a dominant input to the many areas of visual cortex. In contradistinction, the X-cell pathway starts as the majority of retinal ganglion cells, becomes a much smaller fraction of geniculate neurons, and influences perhaps a half or less of a single area (area 17) of visual cortex.

This difference in the functional connections and relative importance of the X- and Y-cell pathways at peripheral and central levels actually fits neatly with the hypothesis of X- and Y-cell function suggested in this article. Note here that peripheral and central refers to hierarchical stages of processing rather than to locations in the visual field. In order to encode the lower spatial frequencies at the sensory periphery or retina, relatively few neurons are needed. Thus, few Y-cells need exist in the retina. However, the importance of these lower spatial frequencies to form analysis dictates that most of the visual cortex be devoted to them. Thus, a tremendous amplification of the Y-cell pathway occurs centrally. In order to encode the higher spatial frequencies peripherally in the retina (e.g., to maximize spatial resolution and position sensitivity), many more neurons are needed than are required for the lower frequencies. Thus, X-cells abound in retina. However, since the X-cell pathway is used to add detail to a basic form analysis already provided by the Y-cell pathway, relatively little cortex is devoted to X-cells. Thus, relatively little divergence and amplification occurs centrally in the X-cell pathway.

This hypothesis for the functional organization and significance of the W-, X-, and Y-cell pathways is little more than a sketchy notion that might be useful as a theoretical framework against which to test future data. There are many untested assumptions and gaps in our knowledge. Nonetheless, this hypothesis does serve to unify a large and diverse body

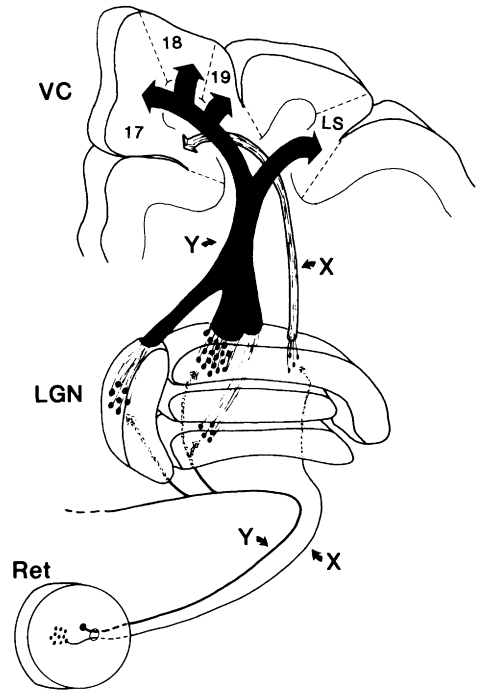


FIG. 18. Hypothetical and schematic diagram of the retinogeniculocortical X- and Y-cell pathways; for simplicity, only pathways from the contralateral eye are illustrated. VC, Visual cortex; LGN, lateral geniculate nucleus; Ret, retina. Each retinogeniculate and geniculocortical Y-cell axon branches 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 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 text.

of presently available data even if future experimentation might require its abandonment.

VII. W-, X-, and Y-Cells in Mammalian Species Other Than the Cat

All of the discussion in the previous sections has been limited to the functional organization of the cat's retinogeniculocortical pathways. A natural question is, how generally are these organizational features found in other species? More specifically, do neurons and pathways homolo-

gous to W-, X-, and Y-cells and their pathways even exist in species other than the cat? Despite several years of interest in these and related questions, clear answers have yet to emerge.

A. Homology and Classification

Ideally, one would like to determine if in species other than cats neurons and pathways exist that are homologous to W-, X-, and Y-cells and their pathways. Campbell and Hodos (1970) have thoroughly discussed the concept of homology in the nervous system and define the term as follows: "Structures and other entities are homologous when they could, in principle, be traced back through a geneological series to a stipulated common ancestral precursor irrespective of morphological similarity" (Campbell and Hodos, 1970, p. 358). In other words, primate homologs to cat X- and Y-cells must have evolved from cell classes in an ancestor that was also ancestral to cats, and these same ancestral X- and Y-cells must have evolved into those classes recognized as X- and Y-cells in cats. Direct determination of homology is impractical, since extinct ancestral species cannot be studied, and indirect determinations of homology from living species require much more evidence of possible retinal and geniculate cell classes across mammalian species than is presently available. Instead of this, most studies have concentrated on more limited aspects of the similarities in the physiology and morphology of neurons and pathways across species, and this reflects analogy. Analogy can be defined as "correspondence between structures or entities due to similarity in function whether or not they can be traced to a stipulated common precursor" (Campbell and Hodos, 1970, p. 359). Too many examples of analogy from convergent evolution exist to distinguish between homology and analogy when such similarities are noted between neuronal types.

While the question of homology versus analogy must be put aside, at least for the present, it is still of considerable interest to determine the extent to which the central visual pathways of different species, including primates and humans, are organized functionally like the cat's. The conclusion one reaches in such phylogenetic comparisons usually reflects the manner by which one classifies neurons.

As a hypothetical example, consider the classification of Y-cells. In the cat such cells can be characterized both by fast axonal conduction and by nonlinear spatial and temporal summation of certain visual stimuli. If a cell type in another species possesses fast axonal conduction (a Y-cell characteristic) but linear summation of visual stimuli (an X-cell characteristic), such a cell might be identified as a Y-cell if conduction velocity were considered to be the "essential" characteristic or as an X-cell if

linearity of summation were considered to be "essential." Since the choice of "essential" features to establish homologies or analogies is artificial and arbitrary, it seems better to rely on a range of characteristics for classification of cell types (cf. Rowe and Stone, 1977). As Campbell and Hodos (1970) note, "nature has not provided us with a 'touchstone' for the recognition of homology" (p. 362). If neuronal types in two species share most of a constellation of properties and have relatively few differences, these cell types could be considered functionally similar, and their differences could be viewed as relatively minor properties for which strong evolutionary pressures to conform did not exist. If cell types in two species do not share a majority of properties, the hypothesis of homology or analogy would not be supported. Many of these problems of establishing similar cell types are exemplified in comparisons between cats and primates.

B. Primate Visual System

A detailed description of the primate visual system is beyond the scope of this article. Instead the focus will be on a brief overview of the classification in primates of retinal and geniculate neurons into categories that can be compared to W-, X-, and Y-cells in the cat. Studies of primate retinal ganglion cells have suggested a threefold division into classes with properties in some ways similar to those of the cat's W-, X-, and Y-cells (deMonasterio and Gouras, 1975; deMonasterio, 1978a–c; Schiller and Malpeli, 1977), but the main points about these pathways can be made from a consideration of the lateral geniculate nucleus.

1. Lateral Geniculate Nucleus

a. Monkeys. In the monkey this nucleus is composed of a dorsal collection of several laminae of smaller cells called the parvocellular laminae, a ventral pair of magnocellular laminae with larger cells, and neurons in the interlaminar zones and in the "S"-laminae lying ventral to the magnocellular laminae. Several groups have suggested that the parvocellular cells are X-like, the magnocellular are Y-like, and the remainder (interlaminar and S-laminae) are W-like. In favor of this classification are the following observations (Hubel and Wiesel, 1972; Dreher *et al.,* 1976; Sherman *et al.,* 1976; Leventhal *et al.,* 1981; Fitzpatrick *et al.,* 1981, 1983; Weber *et al.,* 1983; Blasdel and Lund, 1983). Larger retinal ganglion cells with rapidly conducting axons (somewhat like cat alpha cells) project to the cells in the magnocellular laminae. These geniculate cells have larger receptive fields, respond well to rapidly moving targets, and exhibit tran-

sient responses to visual stimuli. Also, these geniculate cells project to layer IVC-alpha of area 17, which is the dorsal half of the major geniculate recipient zone and presumably corresponds to the Y-cell termination in the dorsal half of layer IV of the cat. The cells in the parvocellular laminae are innervated by more slowly conducting axons of smaller ganglion cells (somewhat like cat beta cells), have smaller receptive fields, respond poorly to rapidly moving targets, exhibit sustained responses to visual stimuli, and innervate layer IVC-beta of area 17, which is just ventral to the magnocellular terminal zone and presumably corresponds to the X-cell termination in the ventral half of layer IV of the cat. Least is known about the interlaminar and S-laminae cells, but like W-cells in the cat, these cells project to layers I and III of striate and extrastriate cortex.

However, in several important ways, only some of which are outlined here, these comparisons can be criticized. First, no one has yet reported response properties for neurons in the S-laminae or the interlaminar zones, so evidence for the W-cell analogy is particularly thin. Second, the parvocellular (but not magnocellular) laminae of many or most monkeys (e.g., rhesus monkeys) are dominated by cells selective for color, a property not associated with cat X-cells. However, some monkeys (e.g., owl monkeys) may not have significant wavelength sensitivity among parvocellular neurons. Third, tests of spatial and temporal linearity (Kaplan and Shapley, 1982) indicate that all parvocellular and many of the magnocellular cells sum linearly, an X-cell property. The remainder of magnocellular cells sum nonlinearly, as do Y-cells. This has led Kaplan and Shapley (1982) to suggest that the magnocellular cells as a group are analogous to X- and Y-cells of the cat intermixed as in the A-laminae and that the parvocellular cells represent a class for which no clear analogy exists in the cat. However, Derrington and Lennie (1984) and Sherman *et al.* (1984) have recently suggested that these magnocellular cells as a population are actually continuously variable for the property of linearity and that the division into linear (X) and nonlinear (Y) classes is an arbitrary division of a continuum; on average, magnocellular cells exhibit greater nonlinearity than do parvocellular cells. Also, it should be noted that W-cells in the cat can be either linear or nonlinear (Sur and Sherman, 1982a), so that these properties are not uniquely linked to X- or Y-cells.

Obviously, it is not at all clear what, if any, specific analogies exist in the monkey for the cat's X- and Y-cells. On balance, many similarities can be listed for an X- and Y-cell analogy to parvocellular and magnocellular cells, respectively. The chief problem with this conclusion is that certain details of the spatial and temporal summation properties are not equivalent between X-cells and parvocellular cells or between Y-cells and magnocellular cells. However, it seems possible that the "linear" magno-

cellular cells may be analogous to Y-cells that never developed or evolved powerful nonlinear subunits. In kittens, these subunits develop relatively late, so that immature Y-cells are often rather linear (Wilson *et al.,* 1982; Mangel *et al.,* 1983). Perhaps in this regard, the linear magnocellular cells of the monkey are similar to immature Y-cells in the cat.

b. Galogos. A similar argument has been made by Norton and Casagrande (1982) for geniculate neurons in the galago, or bush baby. This prosimian primate has three pairs of geniculate laminae: a pair with small cells that exhibit response properties rather like W-cells, a pair with medium-sized cells that exhibit response properties, including linear summation, rather like X-cells, and a pair with large cells that exhibit response properties rather like Y-cells, although most exhibit linear summation. Norton and Casagrande (1982) concluded that the last type represents neurons more like Y-cells without nonlinear subunits than like X-cells.

2. *Functional Correlates*

A consideration of psychophysical data from monkeys in the context of their presumptive analogs to W-, X-, and Y-cell pathways offers interesting parallels to the cat. In monkeys, the projection of nearly all parvocellular and magnocellular cells (e.g., all presumptive X-like and Y-like neurons, regardless of which analogy proves correct) is limited to area 17 (Tigges *et al.,* 1977; Hendrickson *et al.,* 1978). Thus nothing comparable is seen in monkeys to the massive extrastriate projection of geniculate Y-cells of the cat, which may be taken as another criticism of the proposed analogy between cat Y-cells and monkey magnocellular cells. However, cells of the monkey's S-laminae and interlaminar zones plus perhaps a small minority of parvocellular and magnocellular cells exhibit an extrastriate projection (Wong-Riley, 1976; Yukie and Iwai, 1981; Benevento and Yoshida, 1981; Fitzpatrick *et al.,* 1981), perhaps analogous to the cat's W-cell pathway. Thus a bilateral ablation of area 17 in a monkey, which severely compromises the animal's spatial vision (Weiskrantz, 1972; Schilder *et al.,* 1972; Keating, 1980; Dineen and Keating, 1981), would completely eliminate nearly all cortical representation of presumptive X-like and Y-like cells. Miller *et al.* (1980) have shown the devastating effects of such a lesion on the animal's contrast sensitivity (Fig. 19).

Perhaps the reason that striate cortex is essential to satisfactory form vision in monkeys and not in cats is that all or nearly all of the cortical representation of the Y-cell pathway passes through this area in monkeys but not in cats. The main difference between species is not area 17 per se but rather the pattern of Y-cell projections. As long as significant Y-cell projections remain (the destriate cat), excellent form vision results, but

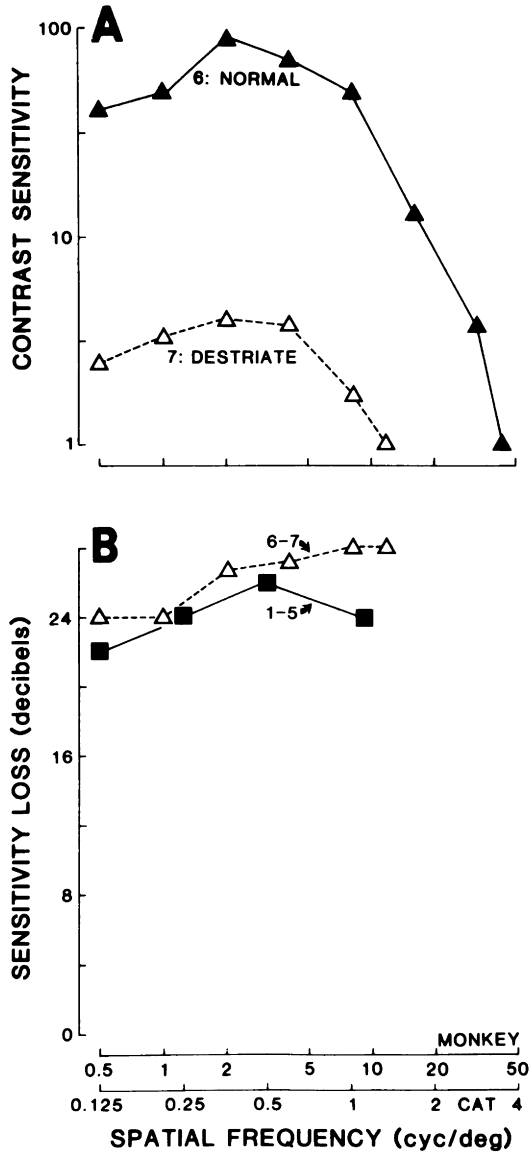


FIG. 19. Average of psychophysically determined contrast sensitivity as a function of spatial frequency for four rhesus monkeys. The stimuli consisted of stationary sine wave gratings that had to be discriminated from a gray target of equal luminance. (A) Spatial contrast sensitivity functions before (curve 6) and after (curve 7) bilateral removal of area 17. (Curves 1–5 appear in Fig. 16.) (B) Sensitivity loss as a function of spatial frequency (cf. Fig. 16). Compared are the losses of monkeys due to area 17 lesions (curve 6 minus 7) and those of cats due to rearing with monocular deprivation (curve 1 minus 5 from Fig. 16). Note the similarity in these losses that may be attributed to similar losses of geniculocortical X- and Y-cell pathways. (Data for rhesus monkeys redrawn from Miller *et al.*, 1980.)

when the Y-cell pathway is substantially interrupted (the visually deprived cat and destriate monkey), extremely poor vision results. Figure 19B shows the similarity in deficits between the destriate monkey and monocularly deprived cat. In both animals, subcortical pathways and/or W-cell pathways reaching cortex are presumably the major substrates for the remaining visual capacity.

3. Conclusions

Clearly, the primate's retinogeniculocortical pathways are organized into at least three parallel and largely separate pathways. It is not yet possible to decide whether this represents a pattern similar to the cat's W-, X-, and Y-cell pathways, and if so, what the precise homologies or analogies are. It might prove particularly interesting to discern primate analogs to the cat's Y-cell pathway, given the importance this article has suggested for the Y-cell pathway's role in the cat's visual capacities. However, one candidate for geniculate Y-like cells in monkeys and *Galago* species (i.e., cells of the magnocellular laminae) often exhibits linear summation and does not possess an extrastriate projection. Perhaps this neuronal class, which in the cat may be the latest to develop ontogenetically and is most susceptible to the postnatal visual environment (see review in Sherman and Spear, 1982), exhibits more variation in properties across species than do other classes. In any case, if Y-like cells do exist in the monkey's geniculostriate pathways, the difference in behavioral consequences of striate cortex ablation between cats and monkeys can be readily explained by the hypothesis presented in this article for Y-cell function and the differences in geniculocortical Y-cell projection patterns between cats and monkeys.

C. Other Mammalian Species

In general, insufficient data are available to be certain that neurons analogous to W-, X-, and/or Y-cells exist in other mammalian species, but in those species studied, it seems clear that retinal ganglion cells and/or geniculate neurons are organized into functionally distinct classes. Furthermore, some of the functional differences are remarkably similar to those found among cat W-, X-, and Y-cells. Mammalian species other than primates for which such differences have been reported include the tree shrew (Sherman *et al.,* 1975a), rat (Fukuda *et al.,* 1979; Lennie and Perry, 1981), and rabbit (Caldwell and Daw, 1978; Molotchnikoff and Lachapelle, 1978; So, 1983). While a positive statement cannot yet be made, the available evidence does not rule out the notion that the parallel

organization of W-, X-, and Y-cell pathways seen in the cat is a general mammalian feature.

It should be noted that data from the tree shrew are somewhat at variance with some of the specific speculations just outlined. In this species, little or no extrastriate component exists in the geniculocortical projection (Diamond *et al.,* 1970; Harting *et al.,* 1973), yet form vision remains excellent after complete removal of area 17 (Snyder and Diamond, 1968; Killackey *et al.,* 1971; Ware *et al.,* 1972). Thus, although monkeys and tree shrews exhibit a similar pattern of geniculocortical connections, the behavioral consequences of striate cortex lesions are quite different between these species. The excellent form vision of the destriate tree shrew has been attributed to retinocolliculothalamocortical pathways that provide visual input to extrastriate cortex independently of the geniculostriate projection. The tree shrew superior colliculus is remarkable for its size,* and Norton (1982) has suggested that collicular neurons in tree shrews have response properties similar in many ways to those of Y-cells in cats. In any case, this serves as an example of the difficulty in inferring the functional significance of visual pathways in different species from notions developed in cats.

VIII. General Conclusions

This article has focused on the division of the cat's retinogeniculocortical system into W-, X-, and Y-cell pathways. A number of independent lines of research have suggested a functional hypothesis for these pathways. This hypothesis is incomplete. It is intended as a theoretical framework for present data and should be tested for future validation or dismissal.

Least is known specifically about the W-cell pathway, but largely because of the poor responsiveness of W-cells, this pathway is not assigned a specific role in conscious visual perception (see also Stone *et al.,* 1979). This is the weakest part of the hypothesis and the most likely one to require change. The Y-cell pathway is assigned the most prominent role in form vision. This pathway with its cortical representation seems sufficient and probably necessary for reasonable spatial vision. The X-cell pathway is assigned a role in maximizing spatial acuity and position sensitivity,

* Norton (1982) has pointed out that the ratio of volumes of the superficial gray layer of the superior colliculus and the lateral geniculate nucleus is 6 for tree shrews and only 0.2 for monkeys. By this measure the collicular pathways versus the geniculocortical pathways are roughly 30 times more prominent in tree shrews than in monkeys.

thereby providing greater detail in the analysis of the visual scene than that provided by the Y-cell pathway. The X-cell pathway may also play a crucial role in stereopsis. This hypothesis is substantially different from previous suggestions for these pathways, particularly those pertaining to X- and Y-cells (cf. Ikeda and Wright, 1972; Stone *et al.,* 1979; Lennie, 1980b).

There is still considerable controversy and confusion regarding the homologs or analogs of W-, X-, and Y-cells in species other than the cat. While it is clearly premature to extend this hypothesis to other species, it does offer an attractively simple explanation for some of the different deficits caused by cortical ablations. For instance, removal of the striate cortex in cats leaves much of the Y-cell pathway relatively undisturbed, and good spatial vision results. The same cortical lesion in monkeys obliterates the presumptive Y-like pathway, and poor spatial vision ensues. However, so many obvious differences can be seen between the cat's and the monkey's (and other species') neurons, it is quite possible that no specific analogy to W-, X-, and Y-cells exists outside of cats.

Whether or not correct, the hypothesis presented here offers a different way of interpreting ablations or other disruptions (e.g., abnormal development) of the visual system. One should of course attend to specific anatomical levels or areas of cortex damaged, but attention should also be directed to abnormalities in the W-, X-, or Y-cell pathways irrespective of the anatomical level or cortical area affected.

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