Cat and monkey retinal ganglion cells and their visual functional roles

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Retinal ganglion cells, the integrative-output neurons of the retina, can be sorted into functional classes. In the cat, two ganglion cell classes are labelled X and Y. These are distinguished by the different retinal subnetworks that provide their input. X cells are driven by a single linear receptive field center mechanism. Y cells receive center and surround signals and additional signals from nonlinear subunits in their receptive fields. Both X and Y cells are highly sensitive to contrast. X cells project almost exclusively to the A or A1 layers of the lateral geniculate nucleus (LGN). Y cell axons terminate in the A or A1 layers and also the more ventral C layers, and also the superior colliculus. In the monkey, P cells connect the retina to the parvocellular layers of the LGN, have small receptive fields, are wavelength-selective, and are insensitive to contrast. M cells are ganglion cells that send axons to the magnocellular layers of the LGN, are not wavelength-selective, have somewhat larger receptive fields than P cells, and are very sensitive to contrast. Comparisons between cat and monkey ganglion cell classes reveal several important similarities between M cells and X cells.

Different types of retinal ganglion cells, the output neurons of the retina, project in parallel, separately and independently, from the retina to the brain. Each of these cell types, or classes, is distributed throughout the retina. Therefore, activity across the population of cells in each one of the classes forms a representation of the world as seen by that type of cell. Previously, one might have conceived of the eye as an optical device with a sensitive film (the retina) from which neural images were transmitted to the brain. Now this concept must be modified to include the idea that the retina is made up of many neural films overlaid on one another, with each transmitting a separate filtered version of the optical image formed by the eye.

In the cat, two of the known functional classes of retinal ganglion cells, denoted the X and Y types[1–3], are believed to be of the greatest importance for pattern perception. This is because of their high sensitivity to spatial patterns[4,5], and because of their direct connection to the lateral geniculate nucleus (LGN) which relays visual information to the primary visual cortex[2,6,7]. The X cells are most sensitive to fine detail. Y cells respond most vigorously to coarse patterns and abrupt changes in diffuse illumination. The function of these neurons can be understood by considering how they act as filters of spatial and temporal stimuli from the environment. The differences in filtering characteristics imply that the different cell types are connected to basically different retinal neural pathways.

One of the important questions for present research in this field is whether primates, including humans, have visual pathways organized, like the cat's, into X and Y retinocortical channels. This question has been studied extensively in the retina of macaque monkeys. Macaque retinal ganglion cells can also be sorted into cell classes[8–10]. The crux is whether or not the macaque's ganglion cell classes are functionally similar to the cat's X and Y classes. We will summarize the evidence indicating that primate M cells, which project to the magnocellular layers of the LGN, are functionally similar to X cells. P cells, ganglion cells that form the input to parvocellular LGN, are functionally different from cat X cells and appear to be a primate specialization for colour vision.

Spatial and temporal filtering and the X/Y classification

We begin by discussing the cat X and Y classes and then will compare the monkey's P and M cells with X and Y. To categorize retinal ganglion cells according to their visual functions, one needs to know how they combine signals from different photoreceptors. A way to answer this question is to examine the linearity of spatial summation of neural signals[1,11]. A sinusoidal grating pattern, shown in Fig. 1, is a useful tool for this task. If a ganglion cell is simply adding up neural signals, and there is no difference in the time course of the response from the different signal sources, then positions can be found at which introduction and withdrawal of

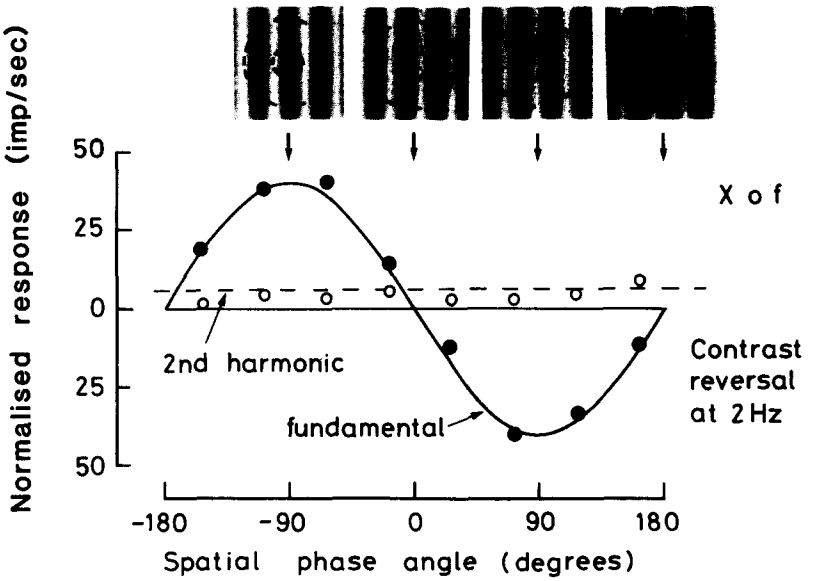

Fig. 1. *The amplitude of an X cell's response is a sinusoidal function of spatial phase. The stimulus was a sinusoidal grating undergoing sinusoidal contrast reversal in time. Small patches of a sine grating are shown. The fundamental Fourier component of the response is plotted as filled circles, while the second harmonic component is plotted as empty circles. When the grating is at −90 or 90 degrees spatial phase, a peak or trough of the sine grating lies over the middle of the receptive field and produces peak response. At −180, 0 and 180 degrees of spatial phase, the response amplitude is zero because zero crossing of the grating pattern lies over the midpoint of the receptive field, as indicated in the insets. These are data from a cat off-center X cell*[4].

the grating produce no response[1]. At these null positions the grating is placed so that introduction of the pattern produces as much net positive signal from one side of the cell's receptive field as it produces net negative signal from the other side of the field; the two signals of equal magnitude but opposite sign cancel when added. Null positions can be found for X cells, but not for Y cells[1]. Furthermore, the responses of X cells follow a sinusoidal function of spatial phase[12] as illustrated in Fig. 1. This spatial phase (position) dependence is a consequence of linearity of spatial summation[12].

The responses of Y cells have a peculiar dependence on spatial phase (position)[13]. To understand it, one can analyse the ganglion cell's impulse rate in response to sinusoidal modulation of the stimulus. An X cell's impulse rate modulation is at the temporal frequency of modulation of the stimulus[4,12,14]. A Y cell's response contains two components: (1) a linear component at the temporal modulation frequency of the stimulus, the fundamental; (2) a non-linear component at twice the frequency of the stimulus, the second harmonic. The fundamental component of the Y cell's response varies sinusoidally with spatial phase like an X cell's, but the second harmonic magnitude does not vary with spatial phase. If one measures and graphs fundamental and second harmonic response magnitudes vs. spatial frequency, the two curves intersect (Fig. 2). This intersection is what has been called the Y cell signature[15]. The spatial phase invariance and the high spatial frequency resolution of the nonlinear, second harmonic response shown in Fig. 2 imply that there must be many receptive field subunits, each of which pools photoreceptor signals over a small area. Then subunit signals are summed by the Y cell after a non-linear transduction[13].

Where is the non-linearity located? Non-linear systems analysis revealed that the Y subunit non-linearity must be embedded in the network of the retina between photoreceptors and ganglion cells[16]. Results on intraretinal recording from bipolar and amacrine cells in cold-blooded vertebrates, e.g. catfish[17], carp[18], and mudpuppy[19], indicate that some amacrine cells combine signals from bipolar cells by means of a non-linear transduction. The results on Y cells are consistent with the idea that the non-linear transduction in the cat retina also is located at the bipolar–amacrine connection.

The X/Y dichotomy is not based on a single property of linear or non-linear filtering, but rather on evidence of linear spatial filtering measured across a wide range of spatial frequencies, in the case of the X cells, or of the Y cell signature, as shown in Fig. 2, in the case of the Y cells. The procedure for determining whether a cell is X or Y thus requires the measurement of a cluster[20,21] of spatial filtering properties.

The different receptive field mechanisms of X and Y cells must contribute to their different roles in the cat's perception. Y cell centers have about three times poorer spatial frequency resolution than neighboring X cells, but Y cell subunits resolve patterns about as well as nearby X cells[7,13,22]. The array of subunits excites a Y cell whenever a pattern moves or changes over a wide area of the retina. Y cells therefore send an increased signal to the brain whenever a pattern is present, but they indicate its location in an imprecise manner. X cells are accurate about location. Central X cells can give a maximally modulated response when a grating pattern is moved from a null position by as little as 0.1 degree of visual angle, a change in position of about 20 μm on the retina.

Other physiological properties of X and Y cells

There are several other physiological and anatomical properties of cat X cells which differentiate them from cat Y cells, besides spatial filtering characteristics. A Y cell's response to a bright step of light on a dim background is more transient than is an X cell's[2]. This sustained-transient distinction seems to be much more apparent at high contrast than low[23,24]. Y cells respond better to large targets and to higher target

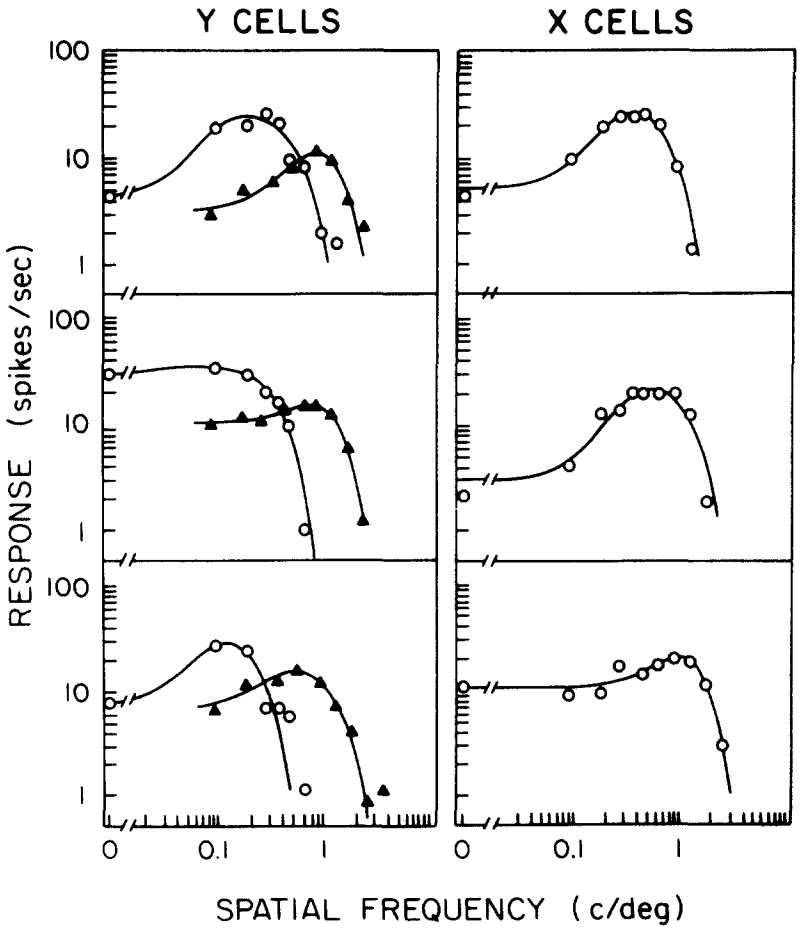

Fig. 2. *Spatial frequency responses of cat X and Y cells: linear filtering in X cells and the Y-cell signature. Fundamental response amplitudes to drifting sine gratings are plotted as empty symbols and second harmonic amplitudes in response to grating contrast reversal are drawn as filled triangles. The data are from cat X and Y LGN cells[7], but identical data have been taken from X and Y ganglion cells. The X cells have almost no second harmonic component. The Y cell second harmonic response curve crosses the fundamental response curve at high spatial frequency; this is the Y-cell signature[15].*

velocities than X cells[2,25]; this is due, at least qualitatively, to the larger receptive field centers of Y cells[2,7,13,22,25,26]. X and Y cells are both highly sensitive to contrast[4,26,27].

The average conduction velocity of Y cell axons in the optic nerve and tract is higher than that of X axons[2,3,7,28]. The average conduction velocity for X axons between optic nerve and chiasm is about 18 m s^{-1} (Refs 7, 21, 28). The estimated average velocity for Y axons is more variable because of measurement difficulty; values between 30 and 70 m s^{-1} have been reported[7,21,28]. These velocity differences cause rather small latency differences at the lateral geniculate nucleus between X and Y afferent input of about 1 to 2 m s^{-1} in comparison to a common visual latency for both X and Y cells of 30–40 m s^{-1} (Ref. 24) in the light adapted state.

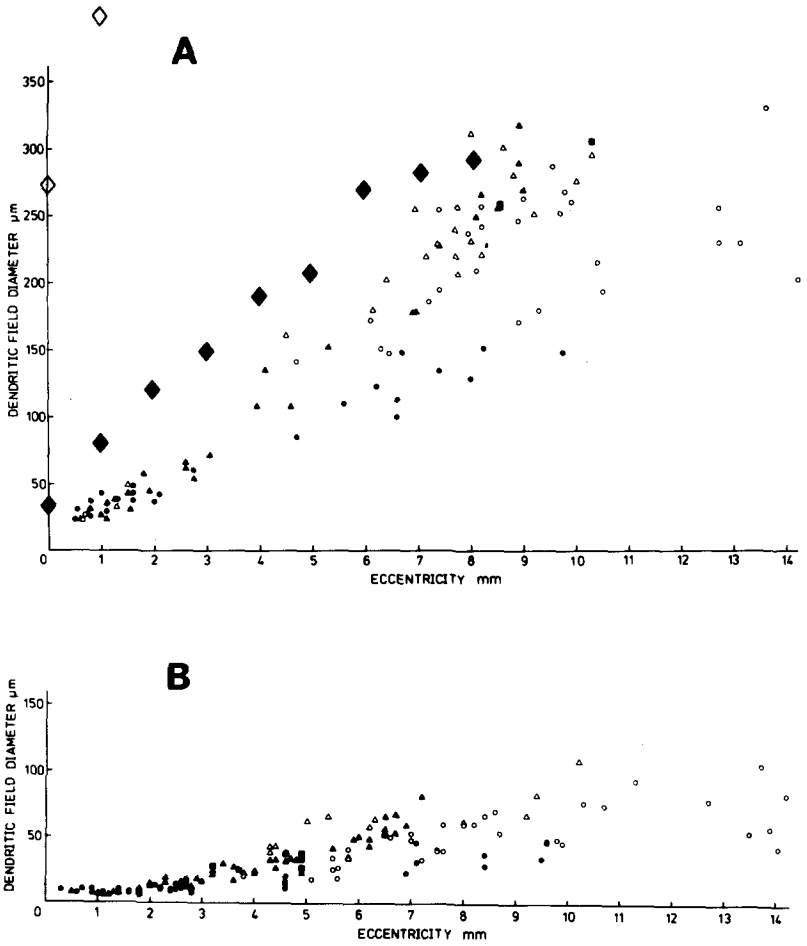

Fig. 3. *Distributions of ganglion cell dendritic field size with retinal eccentricity in monkey and cat. In* (**A**), *data from monkey M (empty and filled circles and triangles) cat alpha (empty diamonds) and beta (filled diamonds) ganglion cells are plotted. The M cell data*[51] *were obtained from HRP injection into the optic nerve and observation of the dendritic fields of retrogradely filled neurons. The cat alpha and beta cell data were obtained from Golgi stained retinae*[36]. *Boycott and Wässle's data have been corrected for shrinkage. In* (**B**), *data for P cells are plotted*[51]. *These were obtained also with the HRP retrograde labelling technique.*

W cells

W cells[22,25], which are all cat ganglion cells not classifiable as X or Y[25,29,30], are probably composed of several classes of cells[20,21,25,29–31]. Many of these cells have axons with a slow conduction velocity. One particular class of W ganglion cells in the cat is especially interesting for trans-species comparisons with macaques. This is the class of colour-coded units[32], which react to visual stimuli in a manner similar to blue-on, yellow-off colour-opponent cells in monkey. In cat the colour-coded cells project to the C laminae of the LGN[30,32], and to the superior colliculus[30]. The corresponding cell type in the monkey projects only to the parvocellular layers of the LGN[9,33–35].

Morphology of cat ganglion cells and central projections

The morphology of the dendritic trees of cat ganglion cells has been found to correlate well with the physiological classifications[36–39]. The large ganglion cells denoted alpha cells are certainly Y cells. Probably most of the ganglion cells with medium sized cell bodies and smaller dendritic trees, denoted beta cells, are X cells. The variation of dendritic field size with retinal eccentricity of the alpha and beta cells[36,37] is like the variation in receptive field center size of Y and X cells (Fig. 3)[22,26], although the correspondence of the receptive field center to dendritic field is not exact.

The morphology and central connections of cat retinal ganglion cells is illustrated in Fig. 4. X cells connect primarily with the A or A1 layer of the LGN[22,38–42]. Y cell axons typically have many collaterals and most if not all project to A or A1, and also C laminae of the LGN, as well as to the superior colliculus[29,38,40–42]. The pattern of central connections is important to keep in mind for cat–monkey comparisons.

Ganglion cell classes in the monkey

Visual neurophysiological study of the macaque monkey is especially interesting to students of human vision because the visual performance of macaques is very similar to that of humans. There are similarities between X and Y cell classes in cat and ganglion cell classes in monkey, but there is an ongoing debate about which monkey ganglion cells are most like cat X cells and which like Y cells. Table I presents the trans-species comparison of cat X and Y and monkey P and M cells.

There are three clear subdivisions of monkey ganglion cells. The most numerous type is the P cell[8–10]. The P cell will give sustained responses to light when the wavelength is at the peak of the cell's spectral sensitivity curve. However, P cells respond phasically to white light or other broad-band illumination[10]. They have a concentric center-surround organization, and often the surround has a different action spectrum from that of the center, giving the cell colour-opponent properties in response to stimuli that cover center and surround[33,34]. P cells send axons only to the four dorsalmost parvocellular laminae of the LGN[9,35,43].

Another major class of monkey ganglion cells is the group we call M (Ref. 8). These ganglion cells have concentric center–surround receptive fields[10]. They respond in a transient

TABLE I.

	Cat X	Cat Y	Monkey P	Monkey M
Relative				
Relative receptive field center size	smaller	larger	smaller	larger
Relative axonal conduction velocity	slower	faster	slower	faster
Dendritic field diameter	smaller	larger	smaller	larger
Absolute				
Non-linear subunit input	No	Yes	No	No M_X Yes M_Y
Axonal conduction velocity	18 m s^{-1}	50 m s^{-1}	13 m s^{-1}	21 m s^{-2}
Colour opponency	No	No	Yes	No
Central receptive field size	0.1°	0.3°	0.01°	0.06°
Projection pattern to brain	Unbranched	Branched	Unbranched	Unbranched
Peak cell density mm^{-2}	4500	200	29 600	3700
Contrast gain	High	High	Low	High

manner to a step of broad-band illumination, in this way resembling the P cells. The time course of their response to monochromatic or highly coloured light has been little investigated, but may be transient or sustained[8,43]. M cells show little overt wavelength selectivity[34] though recent work on their target cells in the LGN[44] suggests that they may receive antagonistic signals from different cones. Their axons project mainly to the magnocellular layers of the LGN[9,35,43], though there is a small fraction of M cells which projects also to the superior colliculus[35].

A third class contains all those ganglion cells that are neither M nor P and has been referred to as the rarely encountered class[35,45]; ganglion cells in this odd-bins group resemble some of the W cells in the cat[30]. None have been found to be wavelength selective[45,46]. This group provides the bulk of the retinal input to the superior colliculus[35,46].

Spatial summation and filtering in monkey ganglion cells

If one uses drifting grating patterns or temporally modulated spots that fill the receptive field, one measures response versus contrast curves in monkey and cat ganglion cells like those shown in Fig. 5. For cat X cells, and monkey M cells, the response rises steeply with contrast at low contrast and begins to saturate when stimulus contrast exceeds 0.1 (Refs 24, 43). For monkey P cells, the response versus contrast curve is much shallower and is approximately a straight line up to a contrast of 0.64 (Ref. 43). The contrast gain for each cell is the limiting slope of the curve at low contrast. The steeper curves of X and M cells indicates that they have a higher contrast gain than P cells.

It is reasonable to test for linear signal summation at contrasts where the cell's response is proportional to contrast. When this is done, as many as 80% of the M cells behave like X cells in response to grating contrast reversal. Their response amplitudes vary sinusoidally with spatial phase, and their response is predominantly at the fundamental temporal modulation frequency of the stimulus[43]. This result is consistent with the finding that about 80% of magnocellular neurons, the targets of M cells in the LGN, also are X-like in this respect[47,48]. A small fraction of M ganglion cells and their magnocellular target cells were found to behave like Y cells; they had the same Y-cell signature as Y cells in the cat[43,47,48]. However, it has also been reported that there is a continuum in amount of nonlinearity among magnocellular LGN neurons, implying that there are not two distinct groups of magnocellular neurons[27,49]. This could mean that there is an X/Y continuum among monkey M ganglion cells, and this important subject will require more experiments.

When tested for linear signal summation, almost all P ganglion cells are X-like as are their LGN targets, the parvocellular neurons. However, P

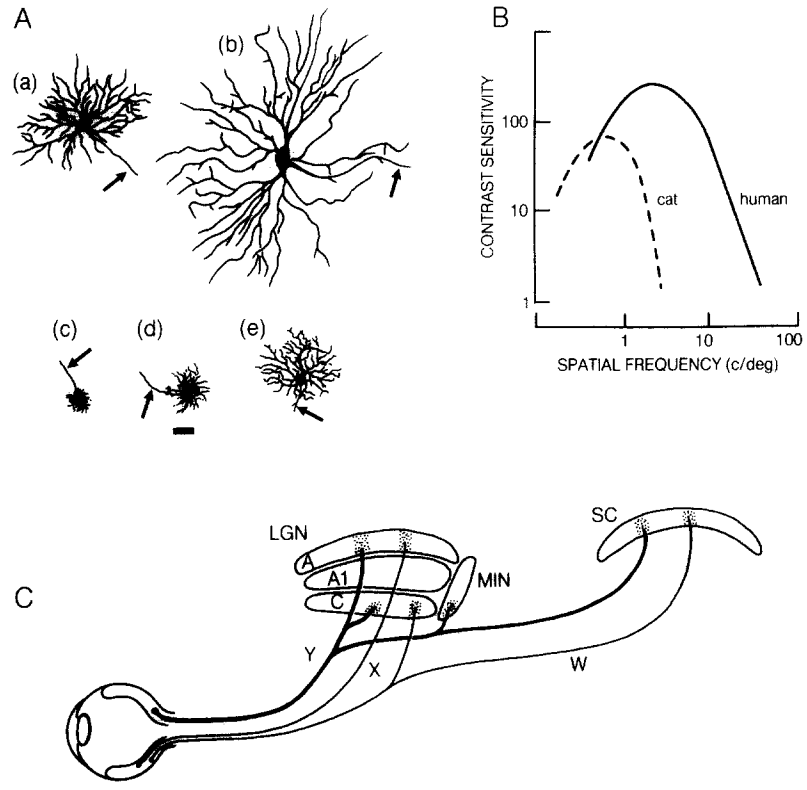

Fig. 4. *Morphology and projections of cat retinal ganglion cells.* **(A)** *Golgi-stained ganglion cells from the cat retina. (a) and (b) are alpha(Y) cells at 1.2 mm and 8.3 mm from area centralis[36]. (c), (d) and (e) are beta(X) cells at 1.2, 2.9 and 10 mm, respectively, from the area centralis[36]. The arrows indicate axons. The scale bar is 50 μm.* **(B)** *Cat and human contrast sensitivity for sine gratings as a function of spatial frequency. The reciprocal of the contrast needed for detection of a sine grating at each spatial frequency is plotted[67].* **(C)** *Crossed retinal projection for the different classes of retinal ganglion cell[38–42]. The W class is heterogeneous and illustrated is a typical W cell. SC is the superior colliculus and MIN is the medial interlaminar nucleus.*

cells are very unlike cat X cells in their contrast gain and other visual characteristics.

The P neurons have the smallest receptive field centers[10,34]. Near the fovea the radius of the smallest fields may be as little as 0.01 deg and the average is 0.03. The average radius of foveal M cell centers is 0.06 deg. In the cat, the smallest X cell centers in the area centralis have radii of about 0.1 deg[26]. Central Y cells have centers with radii about 0.3 deg. Thus, in terms of spatial filtering properties, the cells most similar to each other are the cat X cells and the monkey M cells. It is noteworthy that the radii of the P cell centers do not vary much with eccentricity within the central 5 deg[10].

Morphological properties of monkey ganglion cells

There have been recent advances in knowledge about the morphologies, central connections, and retinal distributions of monkey ganglion cells[41,50–52], and some of this new information is summarized in Fig. 6. P ganglion cells have the smallest dendritic trees and are most numerous. M cells have much larger dendritic trees and are much sparser. (In the terminology of Perry and Cowey[50,51], M cells were called Pα for primate alpha, while P cells were called Pβ for primate beta. This earlier nomenclature should now be dropped on account of Table I and Fig. 3, and the taxonomic arguments to follow.) The dependences of dendritic tree diameter on retinal eccentricity for the two types of monkey ganglion cell are shown in Fig. 3, together with the corresponding dependences for alpha and beta cells in the cat. It can be seen immediately upon inspection that the only two cell types to have a similar dendritic field dependence on retinal eccentricity are the cat beta(X) cells and the monkey M cells. Actually, the cat X, Y and monkey M cells have a similar dependence on eccentricity if the cat Y cell data are scaled down by a constant factor. However, the monkey P cells, in particular those with the characteristic morphology of midget ganglion cells[53], do not resemble the other cell types in dependence of dendritic tree diameter on eccentricity because there is a central retinal zone within which the dendritic trees of monkey P cells are approximately invariant with eccentricity, unlike all the other cell classes.

Trans-species comparisons

There are two main proposals for grouping monkey ganglion cells in correspondence with cat ganglion cells. The original idea was that P cells were functionally similar to X cells and M cells were similar to Y cells. This idea originated from experimental results on parvocellular and magnocellular LGN neurons[54] and was then applied to their retinal inputs[9,10]. This hypothesis was based on the following considerations: (1) P cells and X cells were the ganglion cells with the smallest receptive fields, and dendritic trees, at each retinal locus in each retina; (2) M cells and Y cells had the axons which were fastest for their respective species; (3) the response of P cells was more sustained than that of M cells, just as the response of X cells was more sustained than that of Y cells. In each case, the argument is based on relative properties between the two cell classes.

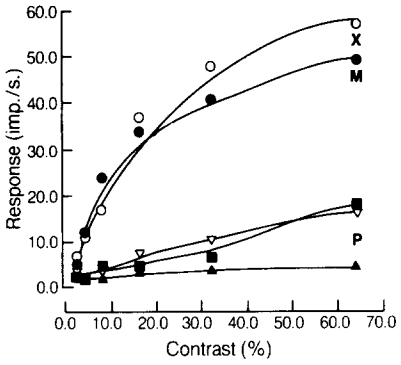

Fig. 5. *Contrast-response functions of cat and monkey retinal ganglion cells. The P cell data are plotted with filled symbols: filled triangles, filled inverted triangles and filled squares. The M cell data are from an X-type M cell and are plotted with filled circles. The cat X cell (empty circles) was an on-center X. All these data were taken from retinal ganglion cell S-potentials recorded in the LGN of the respective species. The monkey data were obtained from a rhesus monkey (R. Shapley and E. Kaplan, unpublished observations).*

A completely different proposal has been advanced on the basis of visual and spatial filtering characteristics[43,47]. This is the idea that M cells and their magnocellular targets are actually composed of two subgroups which correspond to X and Y cells. The more numerous M_X variety projects to the magno-X cells, while the less numerous M_Y type cell projects to the magno-Y cells. Part of this proposal is that the monkey P cell group has no exact functional equivalent in the cat, but is a hyperplasic enlargement of the colour-coded class of cat ganglion cells that project to the C-laminae. This proposal is based on the following considerations: (1) a large majority of magnocellular neurons and their M cell inputs are X-like in terms of spatial summation and spatial filtering; (2) a small fraction of magnocellular neurons and M cells have the Y-cell signature; (3) all monkey ganglion cells have transient responses to white light and most have more or less sustained responses to monochromatic light; (4) the contrast gain of M cells is comparable to that of X and Y cells in the cat[43,47] and is about ten times greater than the contrast gain of parvocellular neurons and P cells; (5) P cells and their LGN targets, the parvocellular neurons, may be wavelength-selective while cat X cells are not; and (6) most M cells make synaptic contacts only with magnocellular neurons in the LGN, while almost all cat Y axons branch three or four times and contact neurons in A and C layers in LGN and in superior colliculus[28,30]. Arguments for the second hypothesis rest mainly on absolute comparisons of visual capabilities of neurons from monkey and cat. Comparisons of relative and absolute properties for X,Y,P and M cells are given in Table I. The new morphological evidence in Fig. 3 on size scaling of dendritic field with eccentricity lends support to the second hypothesis.

The weight of the evidence is against one proposed functional equivalence: monkey P cells and cat X cells. These two classes differ in the following important ways: receptive field size distribution with eccentricity, dendritic tree diameter's dependence on eccentricity, contrast gain, wavelength selectivity, and conduction velocity.

Function of monkey ganglion cells in vision

Rather than ending with tortuous taxonomy, we will finish with a discussion of the relation of M and P cells to vision. First we discuss pattern and then colour vision.

Consider the functional consequences of the striking difference in contrast gain[43,47] and contrast sensitivity[27] between P and M cells. The behavioral contrast sensitivity of monkeys and man is several times higher than that of P cells[55,56]. It has been proposed that probability summation among as few as ten P cell target neurons could allow P cell signals to contribute to perceptual sensitivity[27]. However, probability summation among hundreds of P cells would be required. The high gain and high sensitivity of the M cell pathway are probably important for pattern perception at low contrasts at low to intermediate spatial frequencies. At

high contrast the P cells may contribute to extending the dynamic range of vision, because the M cell responses will saturate (Fig. 5).

The dependence of the local spatial scale of the visual system on retinal eccentricity is another piece of evidence that indicates the functional importance of M cells for pattern vision. The entire spatial frequency response function, not just the high frequency tail, varies with retinal eccentricity. Psychophysical experiments on retinal inhomogeneity in man have shown that the local space scale appears to increase roughly in proportion to the distance from the fovea[57–59]. M cells show such a spatial scaling of dendritic tree and receptive field size (see Fig. 3), but the peculiar flat portion of the P cell curve within 2 mm (or 10 deg) of the fovea is inconsistent with psychophysical spatial scaling.

The properties of the P cells are, we believe, related to their role in colour vision. The most curious feature of the P cells is the small size of their receptive fields. Small fields are good for acuity, but the P cells do not seem especially highly resolving, because their contrast gains are so low. Furthermore, it has recently been shown that human colour perception is a low-gain, low resolution system[60]. It is possible, as presented below, that the small fields of P cells may be necessary for wavelength selectivity.

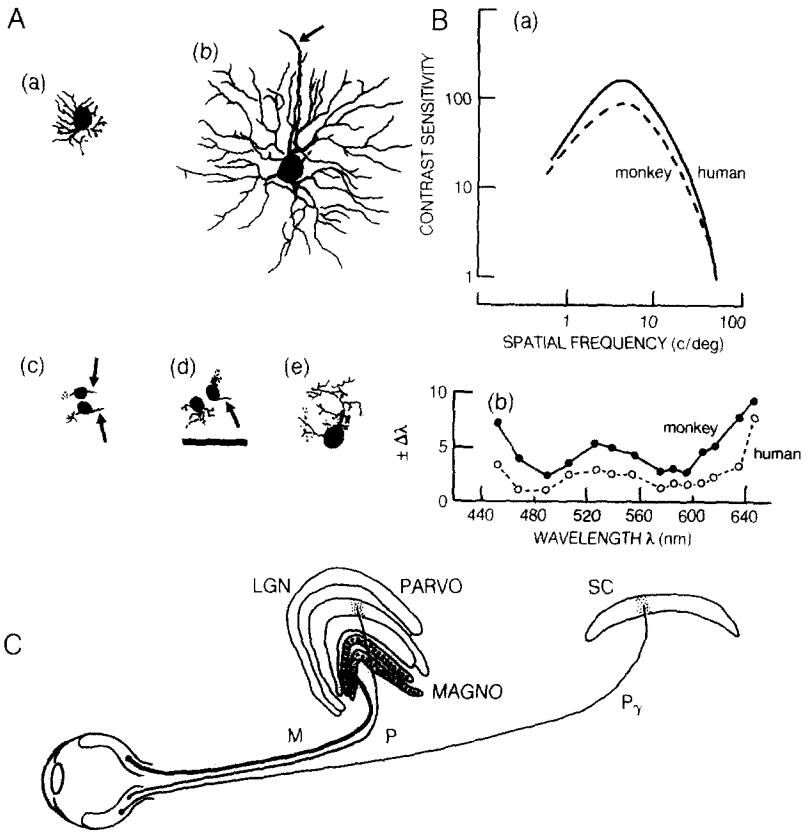

Fig. 6. *Morphology and central connections of retinal ganglion cells in the macaque monkey.* **(A)** *HRP filled monkey ganglion cells. (a) and (b) are M cells 1 and 8 mm from the fovea. (c), (d) and (e) are P cells at 1, 3 and 8 mm from fovea. The arrows indicate axons. The scale bar is 50 μm. Note the difference in scale from Fig. 4.* **(B)** *Contrast sensitivity functions and wavelength discrimination functions for monkey and man. (a) shows the reciprocal of the contrast needed for detection of a sine grating at each spatial frequency[55] and (b) shows the wavelength difference required for a wavelength change just to be noticeable[55]. The vertical and horizontal scales of (b) are in nanometers.* **(C)** *Diagram of the crossed retinal projections of monkey retinal ganglion cells to the LGN and superior colliculus (SC)*[41,50,51].

Wavelength specificity, small P cell fields, and the hit-or-miss hypothesis

The small sizes of the receptive fields of 'midget' P cells could be explained if the only way red (560 nm) and green (530 nm) cones could be connected specifically to bipolar cell were by one-to-one synaptic contacts. Suppose that the synaptic terminals of red and green cones near the fovea are virtually indistinguishable during development. Then bipolar cells that contacted many cones would be unable to pick out only the green cones, and their receptive field centers would receive mixed red and green input. This could lead to less precise and in the limit to no wavelength specificity. One solution would be one-to-one contacts; these would guarantee wavelength specificity of the bipolar cells. Then one also must suppose that foveal and parafoveal P cells are forced to contact only a single bipolar cell, preserving the wavelength specificity. We call this speculation the hit-or-miss hypothesis: wavelength specificity conferred on bipolar cells by connecting to only a single cone, and preserved in ganglion cells by connecting only to one bipolar. We speculate further that peripheral red cones are preferred over green in connecting to bipolar cells, and that peripheral P cells are no longer constrained to make contacts only with one bipolar cell.

This hypothesis receives some support from the peculiar variation of dendritic field sizes of P cells with retinal eccentricity (Fig. 3) together with the known variation of wavelength selectivity in P cells with eccentricity. The P cells on the retina may be separated into two groups: those within 1.6 mm of the fovea where the P cell dendritic field is constant in extent, and those beyond 1.6 mm, where dendritic field size gradually increases with eccentricity. In terms of colour vision, the cells within the inner 1.6 mm area are almost all colour opponent cells[34]. However, in the area outside 1.6 mm, many of the P cells are not colour opponent, but are hidden opponent cells dominated by red cone input[61,62]. On the monkey's retina 1.6 mm corresponds to about 8 deg of visual angle.

One might expect that some difference would show up in human colour vision in the same region of retinal eccentricity where the monkey's P cells change from colour opponent to hidden opponent. This expectation is confirmed. The ability to see a full range of colour is restricted to central vision. While it is possible with the use of large stimuli to elicit colour sensation from the peripheral retina, it is impossible to elicit perceptions of saturated colours and particularly saturated greens[63]. The deterioration of colour perception starts about 10 deg out from fovea[64]. Zrenner and Gouras guessed that poor peripheral colour vision might be related to the absence of green photoreceptors in the periphery of the retina[62]. However, psychophysical evidence on the variation of spectral sensitivity and cone sensitivity with eccentricity rules out such an idea[63,65,66]. The ratio of red to green cones is approximately invariant with retinal position. The difficulty with peripheral colour perception is comprehensible in

terms of the hit-or-miss hypothesis. In the periphery, where the hit-or-miss strategy is abandoned by the retina, P cells become predominantly red cone-dominated, hidden-opponent cells. Such cells are poorly stimulated by light with a greenish hue and therefore such light loses its chromatic effectiveness in the periphery.

Conclusions

Cat X cells handle fine detail and are important for pattern detection while Y cells signal change and movement. Macaque monkey M cells report about fine detail and are important for pattern detection. Macaque P cells carry information about colour and about fine detail at high contrast. Trans-species comparisons may clarify or obscure these fundamental facts.

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