Pergamon

0042-6989(95)00002-X

Vision Res. Vol. 35, No. 16, pp. 2359–2369, 1995
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0042-6989/95 $9.50 + 0.00

Cortical Simple Cells Can Extract Achromatic Information from the Multiplexed Chromatic and Achromatic Signals in the Parvocellular Pathway

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Received 7 December 1992; in revised form 6 December 1994

P cells, which carry both achromatic and chromatic information, are largely responsible for achromatic acuity and contrast sensitivity. The P cell achromatic information must be separated from the chromatic information to be useful. Cortical simple cells are well suited to the extraction of achromatic information by spatial bandpass filtering. Bandpass filtering of Type I P cells by cortical simple cells yields an achromatic signal with a residual chromatic response. The bandpass model makes predictions in accord with existing physiological data and explains the role of a heretofore puzzling class of cortical cells, which have bandpass tuning for both achromatic and chromatic modulations. The model is shown to be related to a previously postulated class of ideal detectors. Finally, the model is used to make a number of physiological and psychophysical predictions.

Color Luminance Modelling Parvo Simple cell

INTRODUCTION

A large majority of LGN cells serving central vision are Type I P (parvo) cells (Lennie, 1980). These cells have concentric receptive fields with the center and surround driven by units of different spectral sensitivity (Wiesel & Hubel, 1966; De Valois & Pease, 1971). The P cell Type I receptive field responds to both chromatic and achromatic stimuli, rendering the total signal ambiguous, and that has led some to doubt that P cells play a major role in visual perception (Marr, 1982). However, numerous studies show that P cells are responsible for both visual acuity and color vision, and that these cells underlie detection for most of the threshold spatiotemporal achromatic and chromatic contrast sensitivity surfaces (Kelly, 1983; Merigan & Eskin, 1986; Schiller, Logothetis & Charles, 1990). Clearly, both the chromatic and achromatic signals carried by Type I P cells are used by the cortex. Previous papers examined the extraction of chromatic information from P cells by lowpass filtering (Billock, 1991; Billock, Vingrys & King-Smith, 1994). It has also been postulated that achromatic information could be cortically extracted by spatial bandpass filtering, although some chromatic crosstalk would occur (Billock, Ingling & Grigsby, 1989; Billock, 1991; Kingdom & Mullen, in press). Here, the properties of a spatial bandpass filtering process are shown to be in agreement with a class of cortical simple cells that have bandpass tuning for both chromatic and achromatic stimuli (Thorell, De Valois & Albrecht, 1984). This bandpass filtering model, implemented as a series of derivatives, resembles a class of ideal detectors that could detect bandlimited achromatic signals in lowpass chromatic "noise" (Martel & Mathews, 1961). The presence of chromatic crosstalk in this achromatic system may have implications for some types of psychophysical color/luminance interactions.

THEORY

The response properties of linear cells can be inferred from their receptive fields. Ingling and Martinez (1983a, b, 1985) have shown that the P cell Type I receptive field can be modelled as the sum of two receptive fields—one sensitive to chromatic fields, the other sensitive to achromatic variations. To illustrate this, Ingling and Martinez decompose an r + g− receptive field using the algebraic identity $AX - BY = (A + B)(X - Y)/2 + (A - B)(X + Y)/2$. Let R and G be the spectral sensitivity of the cone types driving the

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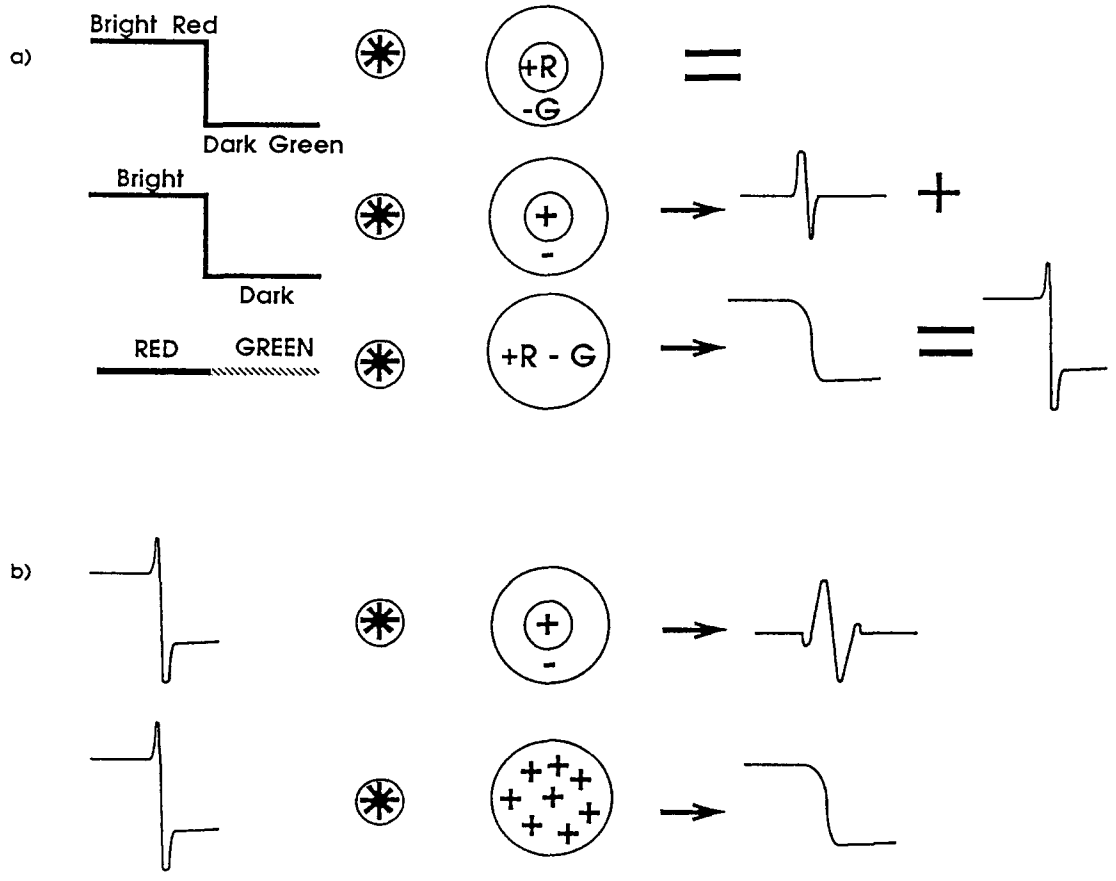

FIGURE 1. Basic notion behind matched spatial filtering (from Billock, 1991). (a) The response of a Type I P cell to a signal of mixed chromatic and achromatic information. The convolution of a bright red/dark green edge with an r+g− Type I cell is equivalent to the convolution of a bright/dark edge with an achromatic bandpass filter (resembling a Type III receptive field) plus the convolution of a red/green edge with a color opponent lowpass filter (resembling a Type II receptive field). (b) The total output of the r+g− Type I cell can be filtered to retrieve the achromatic and chromatic information. A bandpass filter (top line) eliminates the low frequency chromatic information, leaving a signal similar to the original encoded achromatic information. This particular filter is matched to the exact properties of the original encoder (including radial symmetry). More realistic cortical filters are oriented in space and many have more excitatory and inhibitory sidebands in their receptive fields. Also shown (bottom line) is the corresponding chromatic extraction mechanism—a lowpass filtering operation matched to the lowpass chromatic encoding stage.

center and surround. C and S are the point or line spread functions of the center and surround respectively. Then:

$$RC_{enter} - GS_{urround} = (R + G)(C - S)/2 + (R - G)(C + S)/2. \quad (1)$$
$$\text{(achromatic term)} \qquad \text{(chromatic term)}$$

If the modulation transfer functions for the center and surround are lowpass filters, equation (1) states that the P cell response to chromatic information is encoded by a lowpass filter, and the response to achromatic information is encoded by a bandpass filter (Ingling & Martinez, 1983a, b, 1985). Although it may seem biologically implausible that chromatic and achromatic information would be transmitted in the same ganglion cell, it has been found experimentally that both signals are present in Type I cells (De Valois & Pease, 1971). The Type I cell's frequency multiplexed signal is a mixture of mostly chromatic information at lower spatial frequencies and mostly achromatic information at higher spatial frequencies. [Note, throughout this paper, unless otherwise specified, the terms chromatic and achromatic information refer to the information encoded by the lowpass and bandpass terms of the P cell described by equation (1).] In electrical engineering, multiplexed signals are often separated by using filters matched to the frequency sensitivity of the encoders. The analogous approach for the parvocellular system is to construct cortical cells with receptive fields matched to the spatial properties of the chromatic and achromatic terms in equation (1), and to use these cells as labelled "matched" filters for chromatic and achromatic information (Billock *et al.*, 1989; Billock, 1991). Figure 1(b) illustrates the operation (in the spatial domain) of labelled matched filtering. Although the matched filter is an "ideal detector" in the sense of extracting as much of the desired signal as possible (Green & Swets, 1974) matched filtering is not optimal in separating the two multiplexed signals, because the achromatic bandpass filter has some response to the lowpass filtered chromatic signal. Therefore, one way to improve on matched filtering is to use

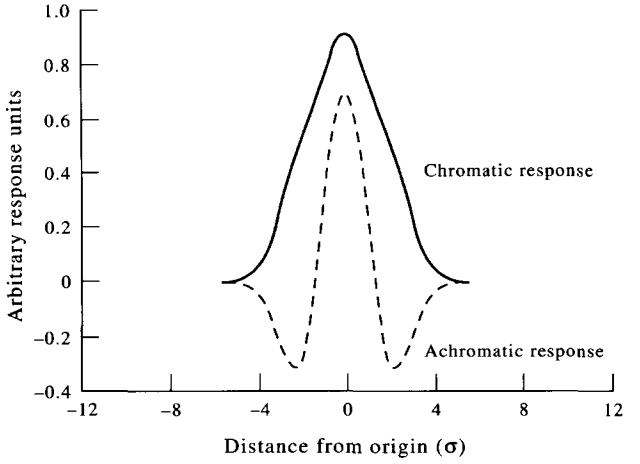

FIGURE 2. P cell line weighting functions for achromatic and chromatic stimuli. The achromatic line weighting function is formed by offset differences of Gaussians representing the center and surround and can be modelled as the second derivative (Laplacian) of the Gaussian representing the center. The chromatic line weighting function is obtained by adding the center and surround responses as in equation 1. This yields a Gaussian-like line spread function with a space constant of about 1.83 times greater than the center's space constant.

filters with less response to low frequency chromatic information.

Many cortical cells have narrower bandwidths than LGN cells and are tuned to relatively high spatial frequencies (De Valois, Albrecht & Thorell, 1982). That is, cortical cells behave like bandpass filtered versions of their LGN afferents. This spatial bandpass filtering process can be modelled by selective excitatory and inhibitory combinations of neighboring LGN afferents (Hubel & Wiesel, 1962; Young, 1985, 1991; Soodak, 1986; Hawken & Parker, 1987). The same mechanisms which provide cortical cells with their restricted spatial frequency tuning might provide the basis for improved separation of the achromatic and chromatic signals. The relationship between these cortical receptive fields and P cell receptive fields provides a simple model of spatial bandpass filtering to recover luminance signals. This model employs the fact that LGN receptive fields mapped for achromatic stimuli resemble second derivatives of Gaussians and cortical simple cell receptive fields resemble higher order derivatives of Gaussians (Young, 1985, 1987, 1991; Stork & Wilson, 1990). In addition to being excellent models for receptive fields, derivatives of lowpass functions are a convenient model for bandpass filtering (Kelly, 1975) and other kinds of visual processing (Adelson & Bergen, 1991). Consider the P cell receptive field for achromatic stimuli, modelled by Young (1987) as a difference of offset Gaussians (DOOG). Let the center and the offset surrounds be represented by $N_{\sigma,m}$ (a Gaussian with space constant of σ and mean m). Then, the line spread function of an on-center P cell is

$$\mathrm{DOOG}_{\sigma,m}(x) = -N_{\sigma,m-a\sigma}(x) + 2N_{\sigma,m}(x) - N_{\sigma,m+a\sigma}(x) \qquad (2)$$

where $N_{\sigma,m}(x) = (\sigma\sqrt{2\pi})^{-1}\exp[-\{x-m\}^2/2\sigma^2]$.

If the center and surround have similar space constants and if the mean of the surrounds is offset from the center by about 2σ, then some useful simplifications result (see the Appendix for a discussion of the assumptions of this model and the consequences of relaxing

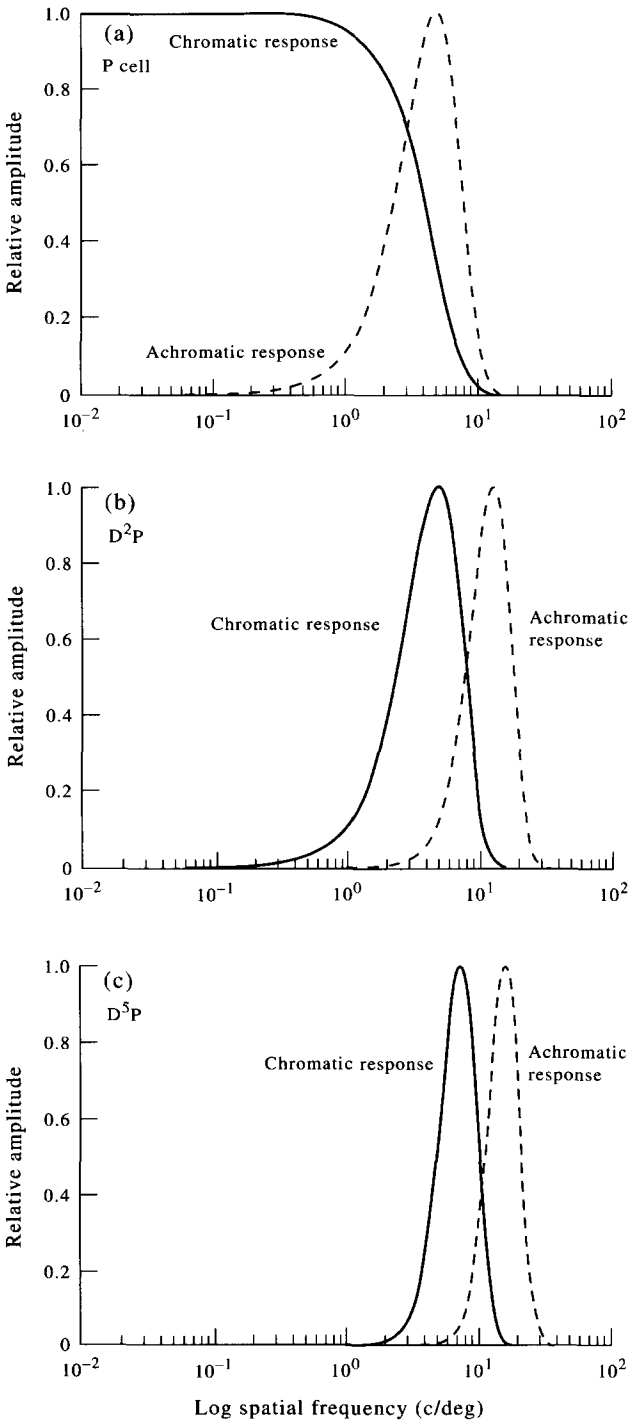

FIGURE 3. (a) Spatial frequency tuning of an LGN P cell for achromatic and chromatic stimuli. (b, c) Spatial frequency tuning for achromatic and chromatic stimuli of some spatial bandpass luminance extraction filters (the second and fifth local derivatives of the P cell array). Note that as the filters become more bandpass (higher orders of differentiation), the tuning for chromatic and achromatic stimuli become similar, as found by Thorell *et al.* (1984). Thus, these cells labeled for achromatic information respond vigorously to laboratory produced high contrast, high frequency chromatic gratings. The space constant (σ) is 0.025 deg for all three units.

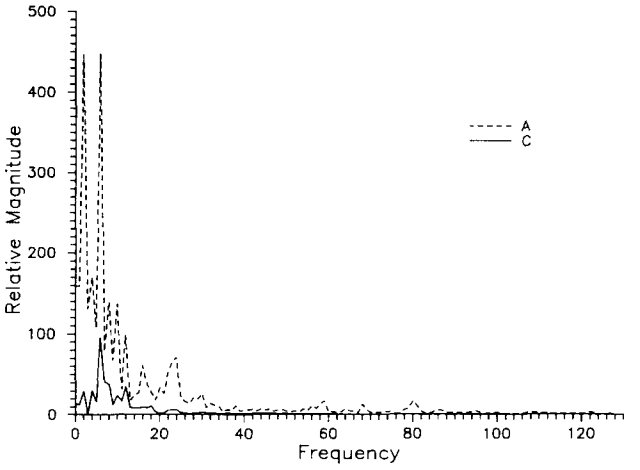

FIGURE 4. Plot of the average of the achromatic "A" and chromatic "C"power spectra in 4 natural scenes. Reproduced from Derrico and Buchsbaum (1991) with permission from J. Derrico.

these assumptions). In particular, the achromatic term is equivalent to the second derivative (Laplacian) of a Gaussian, and the chromatic term is well fit by a Gaussian with a space constant approximately 1.83 times the original σ of the center (see Fig. 2), and equation (1) becomes

$$2RC_{\sigma,m}(x) - GS_{\sigma,m\pm 2\sigma}(x) = 0.5(R+G)D^2C_{\sigma,m}(x) + (R-G)C_{1.83\sigma,m}(x) \quad (3)$$
(achromatic term) (chromatic term)

Let $H_\sigma(\omega)$ be the Fourier transform of $C_\sigma(x)$ and $\omega = 2\pi f$, where f is spatial frequency. Note that the transform of a Gaussian is a Gaussian and that the nth derivative of a transform is the product of ω^n and the transform (Arfken, 1970). Then, the amplitude spectrum of the P cell in equation (3) is

$$F^{-1}\{P_{r+g}\} = 0.5(R+G)\omega^2 H_\sigma(\omega) + (R-G)H_{1.83\sigma}(\omega) \quad (4)$$

where $H_\sigma(\omega) = \exp[-2(\pi\sigma f)^2]$.

Young (1985, 1991) has modelled the achromatic response of cortical simple cells as higher order derivatives of Gaussians. The spatial weighting function of these derivatives can be represented as the product of a Gaussian and an nth order Hermite polynomial (yielding a function with $n+1$ positive and negative subregions; Abramowitz & Stegum, 1965; Young, 1985). Young (1985) showed that operators similar to D^nG filters can be constructed by weighted differences of offset second derivative-like LGN afferents (see Appendix for a brief discussion). It has often been speculated that simple cell receptive fields are constructed by weighted sums and differences of LGN afferents (Hubel & Wiesel, 1962; Soodak, 1986; Hawken & Parker, 1987).

The tuning of a cortical cell created by bandpass filtering an array of P cells [by taking the nth derivative of equation (4)] to extract achromatic information is

$$F^{-1}\{D^nP\} = 0.5(R+G)\omega^{n+2}H_\sigma(\omega) + (R-G)\omega^n H_{1.83\sigma}(\omega) \quad (5)$$
(achromatic response) (chromatic crosstalk)

Equation (5) shows that the achromatic and chromatic response of these cortical filters resemble differential operators, but the achromatic term is two orders of differentiation higher than the chromatic term, and the chromatic term has a larger space constant than the achromatic term. The chromatic and achromatic tuning functions of some cortical differential filters described by equation (5) are plotted in Fig. 3(b, c) (these functions are normalized to facilitate comparison of tuning; absolute gain of these filters grows with order of differentiation). The chromatic response is crosstalk—an unavoidable consequence of the frequency overlap of the center + surround and center − surround filters used by the encoding Type I cells. Differentiation minimizes chromatic crosstalk by eliminating the low frequencies where most of the chromatic information is concentrated, and shifting the peak of the chromatic response to where little real world chromatic information is located (Derrico & Buchsbaum 1991). Figure 4 shows the average relative achromatic and chromatic information content of 4 color scenes studied by Derrico and Buchsbaum. They found that the chromatic information is confined to lower spatial frequencies relative to achromatic information. As Fig. 5 shows, higher level derivatives of P cells have little response to low spatial frequency chromatic information, and therefore emphasize achromatic information.

A physiological correlate of bandpass luminance filtering

Equation (5) states that a cortical cell built by lateral inhibition of LGN afferents has bandpass sensitivity to both chromatic and achromatic information, even though designed to emphasize the achromatic. Such a cell would be sensitive to high spatial frequency chromatic gratings. Thorell *et al.* (1984) recorded from a class of cells in striate cortex that have simple or complex receptive fields and bandpass tuning to both chromatic and achromatic stimuli. This cell type has also been reported by Lennie, Krauskopf and Sclar (1990). The dual bandpass tuning of these cells is predicted by the spatial frequency filtering model shown in equation (5), but is difficult to reconcile with cancellation models of hue and luminance demultiplexing (which predict cortical cells with only chromatic or achromatic tuning, see Discussion). Equation (5) leads to some predictions about the relative tuning of the chromatic and achromatic responses that can be compared to Thorell *et al.*'s (1984) results.

(1) Bandwidth predictions. The bandwidth of a D^nP filter is (Young, 1985):

$$BW = [2\pi/(n+k)]^{1/2} \quad (6)$$

where $k = 2$ for the achromatic response and $k = 0$ for

chromatic response (see above). Equation (6) means that cortical luminance detectors with bandpass tuning for achromatic and chromatic stimuli should have narrower bandwidths for achromatic than for chromatic stimuli. This was the case for the cells measured by Thorell *et al.* [see Fig. 6(a) and 7], who found that the average chromatic bandwidth was 1.56 octaves, compared to an achromatic bandwidth of 1.34 octaves, a significant difference ($P < 0.02$; Thorell *et al.*, 1984). Note that if n is large, $1/n \approx 1/(n+2)$, so the ratio of achromatic bandwidth should be closer to 1.0 for cells with narrow chromatic bandwidths than for cells with broad chromatic bandwidths. A test of this prediction is shown in Fig. 7, which plots the logarithm of the achromatic/chromatic bandwidth of Thorell's cells as a function of chromatic bandwidth. The dashed line in the figure is the prediction of equation (6) (with no free parameters), which is effectively a straight line with a slope of -0.112. This is in good agreement with a linear regression fitted to Thorell *et al.*'s data, which had a slope of -0.128 ($r = -0.439$, d.f. $= 71$, $P < 0.0001$).

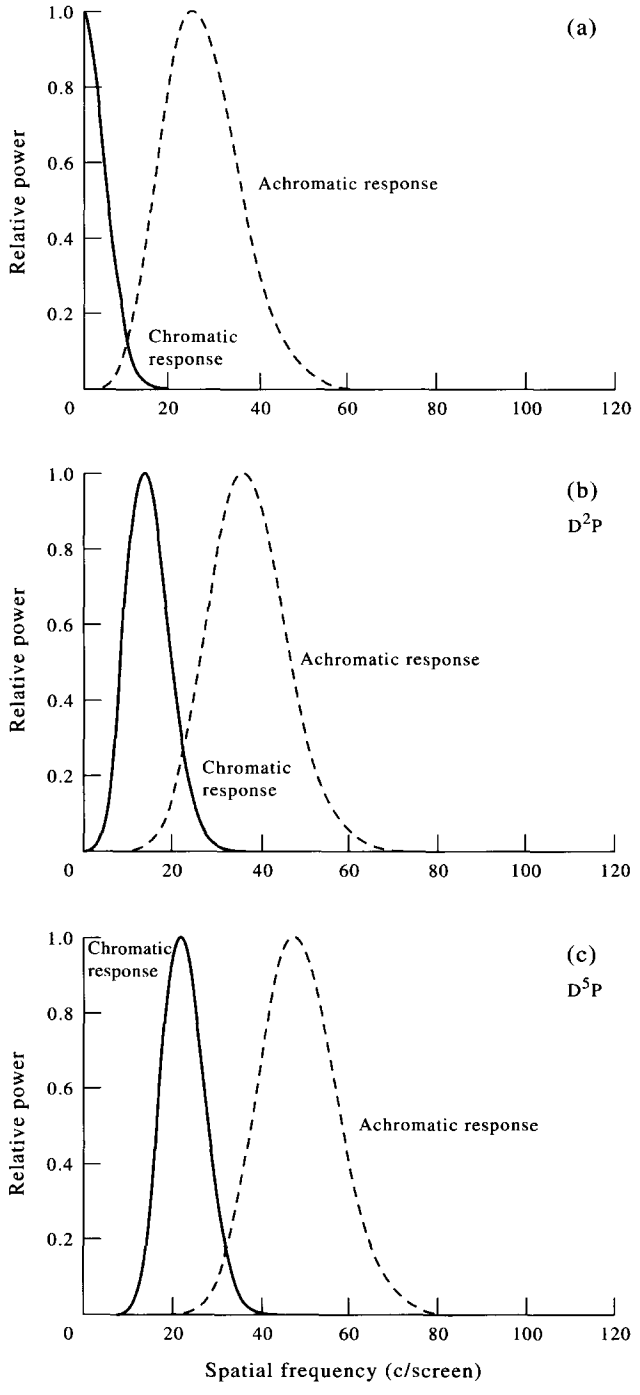

FIGURE 5. Power spectrum of chromatic and achromatic responses of the units of Fig. 3, recomputed for comparison with Fig. 4, by assuming that 1 pixel subtends 0.0083 deg. Power spectra of cortical units are easily computed with equation (5), by doubling $n + k$. Compare tuning of units to the power spectra of the natural scenes in Fig. 4. Note that higher level achromatic filters suffer less from chromatic crosstalk because the peak frequency responses of these cells are shifted to higher frequencies, where there is less chromatic information content.

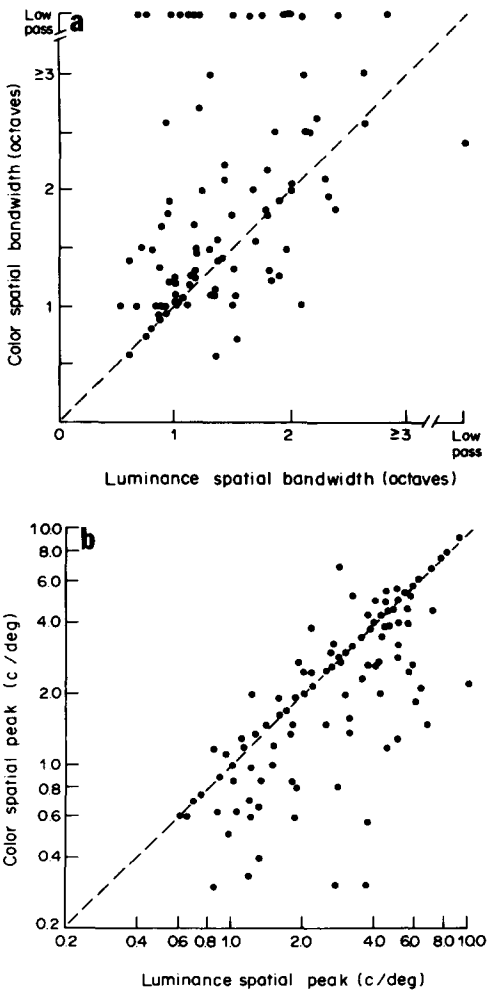

FIGURE 6. Scatterplots of chromatic and achromatic response properties of 110 simple, complex and concentric (LGN-like) cortical cells studied by Thorell *et al.* (1984). Reproduced by permission of L. Thorell. (a) Scatterplot of chromatic and achromatic spatial frequency bandwidth. (b) Scatterplot of frequency of peak chromatic and achromatic response in the same cells.

(2) Peak frequency prediction. The peak frequency of a D^nP operator is (Young, 1985):

$$f_{max} = \sqrt{(n+k)}/(2\pi\sigma). \quad (7)$$

Since peak frequency increases with the order of differentiation and decreases with the space constant, the chromatic response should peak at lower frequencies than the

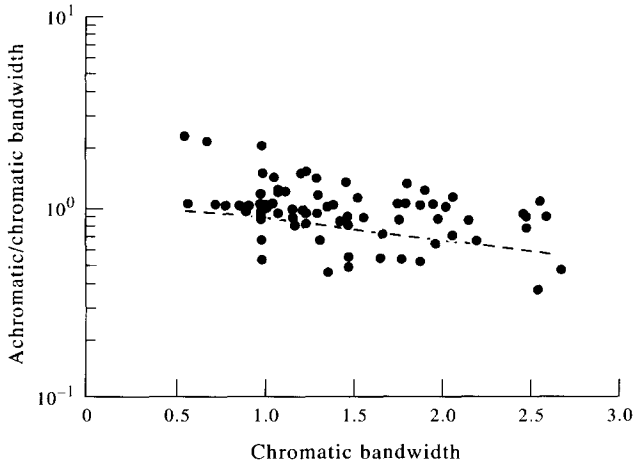

FIGURE 7. The model predicts that tuning for chromatic and achromatic stimuli will be more alike for cells with narrow chromatic bandwidths than for cells with broad chromatic bandwidths. The solid points show the ratio of achromatic to chromatic bandwidth for 73 digitizable cells in Fig. 6(a) with bandpass tuning for both. The dashed curve shows the prediction of equation (6) (no adjustable parameters). Although the data scatter is considerable ($r = -0.430$), the model's prediction captures the trend of the data.

achromatic response. This was generally the case for the cells measured by Thorell *et al.* [see Fig. 6(b)], who found the mean peak frequency of the color response was 2.63 ± 1.82 (SD) c/deg compared to the average achromatic response of 3.5 ± 2.4 c/deg, a significant difference ($P < 0.05$; Thorell *et al.*, 1984).

Figures 6 and 7 contain data from cells with simple, complex, and concentric receptive fields. Thorell *et al.* (1984) found that simple and complex cells are similar in their joint tuning to chromatic and achromatic stimuli (although complex cells tend to peak at higher frequencies). Although the theory above applies specifically to simple cells, it is likely that a similar theory applies to complex cells (see the Discussion and Appendix for treatment of the nonlinearities that would arise in this context).

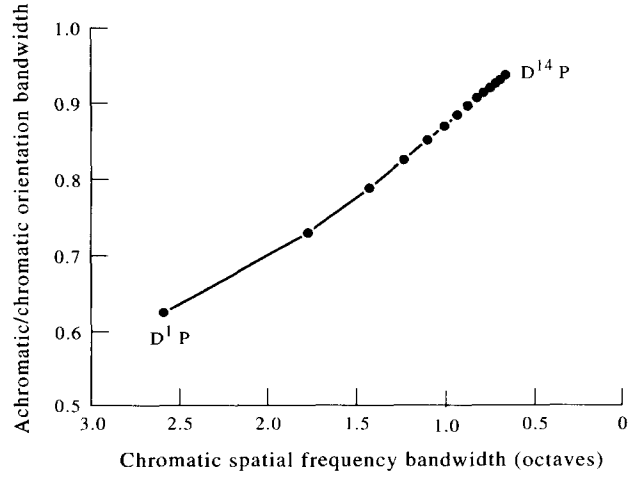

FIGURE 8. Prediction of chromatic and achromatic orientation tuning of cortical cells sensitive to both. As order of differentiation rises, spatial frequency bandwidth for chromatic information narrows and orientation tuning for chromatic and achromatic stimuli become more alike. Points are for 14 model cortical cells whose effect on the P cell signal (and the original optical image) ranges from little bandpass filtering (D^1P) to a great deal of bandpass filtering ($D^{14}P$).

DISCUSSION

Comparison of spatial frequency filtering and other demultiplexing schemes

Several investigators have advanced another model of demultiplexing the achromatic information in P cells (Lennie, 1984; Martinez-Uriegas, 1985, 1990; Lennie & D'Zmura, 1988; Derrico & Buchsbaum, 1991; Mullen & Kingdom, 1991; De Valois & De Valois, 1993). This model is based on the fact that the various P cell subtypes (e.g. P_{r+g-}, P_{r-g+}, P_{g+r-}, and P_{g-r+}) all carry similar chromatic and achromatic signals, the difference being in the relative phases and polarities of the signals. By appropriate combinations of these cells, either the hue or luminance signal can be completely cancelled. Equations (8)–(11) illustrate cancellation filtering using just two cell subtypes. Other, combinations are possible (Martinez-Uriegas, 1994):

$$P_{+r-g} = 1/2(R + G)(C - S) + 1/2(R - G)(C + S) \quad (8)$$

$$P_{+g-r} = 1/2(R + G)(C - S) + 1/2(G - R)(C + S) \quad (9)$$

so

$$P_{+r-g} + P_{+g-r} = (R + G)(C - S) \quad (10)$$

$$P_{+r-g} - P_{+g-r} = (R - G)(C + S). \quad (11)$$

This is a perfect recovery of achromatic and chromatic information. This method seems to imply that both receptive fields occupy the same region of space, but the method can be made to work with overlapping receptive fields using weighted averages. The mathematics of these operations are similar to bandpass and lowpass filtering (see Billock, 1991) and recovery can be imperfect—even for cancellation—under some circumstances.

Cancellation is a clever and elegant approach that seems well suited to the known classes of LGN cells. However, it seems unlikely, both on psychophysical and physiological grounds, that cancellation filtering is used by the cortex. Several lines of psychophysical and physiological evidence suggest that cancellation actually works better than the process used by the cortex. If precisely implemented, cancellation leads to complete separation of chromatic and achromatic signals, and therefore is not a useful predictor of psychophysical data on color and luminance interactions. For example, Lu and Fender (1972) report that the luminance contrast required to fuse random dot stereograms is wavelength dependent. This result is predictable from both nonlinear (Russell, 1979) and linear filtering models (Billock, 1987; Billock *et al.*, 1989), but not from models that completely cancel the chromatic signal. Moreover, spatial frequency filtering is a better predictor of cortical cell receptive fields than cancellation. For example, the physiology and anatomy of double opponent cell formation are incompatible with cancellation algorithms, but can be explained by spatial frequency filtering (Billock, 1991).

Also, as discussed above, spatial frequency filtering predicts an entire class of cortical cells—the dual tuned units found by Thorell *et al.*—which do not fit into the cancellation framework at all. As Mullen and Kingdom (1991) have pointed out, in the cancellation framework these cells appear to remain multiplexed and their signals are still ambiguous. Only in the context of spatial frequency filtering for the extraction of achromatic information (affected by chromatic crosstalk) do these cells make sense.

Recently, demultiplexing models have been advanced that implicitly or explicitly combine cancellation and filtering. One origin of these models was Martinez-Uriegas's (1990, 1994) observation that if stimuli are modulated in only one direction, the importance of nonsuperposition of cancelling receptive fields is reduced by organizing the cancelling receptive fields along the axis of modulation. This results in a simple cell-like receptive field whose chromatic and achromatic response is highly dependent on orientation (Martinez-Uriegas, 1994; Kingdom & Mullen, in press). Although originally motivated by cancellation ideas, this organization is implicitly a bandpass filter, using multiple LGN subtypes where the present model employs excitatory and inhibitory connections. The weight that each connection is given depends on whether the cortical cell is being tuned for a particular filter characteristic or if cancellation is being optimized (Kingdom & Mullen, in press). There are some potential advantages to these approaches. For example, by making use of multiple LGN cell subtypes, problems of irregular or inadequate sampling are reduced. Irregular sampling could be a problem for the model discussed above, making the achromatic extraction of each cortical cell probabilistic. While it is clearly possible to incorporate multiple LGN cell types into filtering models, this is not the route that seems to be followed in creating cortical double opponent receptive fields (Billock, 1991). It may be true for the cells described by Thorell *et al.* (1984) although, as discussed above, operations on just one subtype of geniculate cell suffice.

Role of nonlinearities

The modeling described above neglects the role of nonlinearities. Many studies show that simple cells behave like linear mechanisms followed by a nonlinearity [usually rectification, over-rectification, or half-squaring; see Heeger (1992a, b) for a review]. There are two lines of psychophysical evidence that these nonlinearities affect demultiplexing. (1) Lu and Fender's (1972) data on stereopsis of near-equiluminance random dot stereograms was initially explained by a computationally intensive feature detection algorithm that detects the luminance zero crossings superimposed on chromatic information (Russell, 1977). However, the same data could be explained by linear spatial filtering followed by a rectifier, even with a very low threshold (Billock, 1987; Billock *et al.*, 1989). (2) Billock *et al.* (1994) report a subject with optic nerve hypoplasia (a congenital reduction in the numbers of otherwise normal retinal ganglion cells) who violates Bloch's law for temporal integration of equiluminous green but not red spots. Perimetry and other data suggest a congenital loss of retinal ganglion cells subserving detection of green spots relative to equiluminous red. Billock *et al.* (1994) found that the violation in Bloch's law could be modeled if the equiluminous spot detection pathway consisted of low-pass spatial filtering of like-spectrally opponent Type I cells, followed by rectification and temporal integration over some observation window. The number of pooled Type I cells determines the amplitude of the net signal relative to the threshold of the rectifier. If the signal is on the order of the threshold, high-amplitude-short-duration stimuli are more effective than equal energy low-amplitude-long-duration stimuli in getting past the rectifier threshold. A possible benefit for a rectifying nonlinearity in a demultiplexing mechanism may be inferred from Lubin (1991) who notes that communication engineers use filtering followed by rectification to reduce noise and crosstalk (a process known as coring). Lubin found that the best results are obtained if multiple spatial frequency channels are used to set the thresholds of each other's rectifiers (adaptive coring).

Psychophysical predictions—masking of achromatic by chromatic gratings

Chromatic gratings are potent maskers of achromatic gratings (almost as effective as achromatic gratings in masking achromatic gratings; De Valois & Switkes, 1983; Switkes, Bradley & De Valois, 1988). It is easy from equations (5)–(7) to see why. The cortical filters that extract achromatic information from the combined chromatic and achromatic signals have a strong chromatic response [the second term in equation (5)]. This unwanted crosstalk is minimized in real world scenes when processed by higher order differential operators, because the effect of differentiation is to move the filter's peak response to higher frequencies (equation (7)] and to narrow its bandwidth [equation (6)], thus shifting the filter into a frequency region where there is little chromatic information (in natural images) to process (recall Figs 4 and 5; see Derrico & Buschbaum, 1991). This shift leaves the achromatic extraction mechanism sensitive to high spatial frequency chromatic gratings (which, appropriately, look achromatic; van der Horst & Bouman, 1969). As n becomes large, the effect of n and $n+2$ in equations (5)–(7) become similar: e.g. for higher order derivatives, the achromatic tuning and chromatic tuning become more alike and masking becomes a problem. Equation (5) could be used to predict the masking of achromatic gratings by chromatic gratings, if the parameters n and σ in equation (5) were fit to a large representative sample of simple cells. Unfortunately, Thorell *et al.*'s (1984) single unit data are apparently no longer available. However, it is possible to make a simpler prediction based on equations (5)–(7). Cortical cells with high peak frequencies for achromatic gratings tend to have narrower bandwidths than cells with lower peak frequencies (De Valois *et al.*, 1982). Equations (5)–(7) therefore imply that cells with high

peak frequencies for color would tend to have similar frequency tuning for chromatic and achromatic stimuli (the strength of this trend is dependent on variations in σ). Consequently, there should be a tendency for chromatic masking of achromatic gratings to be least effective for low mask frequencies, as reported by Switkes *et al.* (1988).

Another interesting aspect of Switkes *et al.*'s (1988) masking data is the lack of facilitation for detection of luminance gratings by low contrast chromatic masks. Facilitation is often found for other masking conditions and is usually attributed to a contrast nonlinearity which is accelerating at low contrasts and saturating at high contrasts. Facilitation is expected for low chromatic contrasts because low contrast color would act as a "pedestal" raising the achromatic contrast into the accelerating portion of the contrast nonlinearity's operating range. To account for the lack of facilitation, Switkes *et al.* (1988) have postulated more complicated models involving chromatic inhibition of the luminance mechanism. A similar result could be obtained by adaptive coring (Lubin, 1991) if activity in the chromatic extraction mechanism (Billock, 1991; Billock *et al.*, 1994) affected the properties of the achromatic extraction mechanism's contrast nonlinearity.

A physiological prediction—orientation tuning for achromatic stimuli narrower than for chromatic stimuli

Young (1985) has found that the orientation tuning of the Nth derivative of a Gaussian is $\cos^n(\theta)$. (This result assumes that the receptive field's profile in the orthogonal direction is a Gaussian distribution with the same space constant as the differentiated Gaussian; Young, 1985.) The orientation tuning of the cortical cells modelled here as derivative of Gaussian filters, should be proportional to $\cos^{n+k}(\theta)$ where θ is in degrees, $k = 2$ for achromatic stimuli and $k = 0$ for chromatic stimuli. Therefore, orientation tuning will be tighter for achromatic stimuli than for chromatic stimuli. Also, as n becomes large, $\cos^n(\theta)$ becomes similar to $\cos^{n+2}(\theta)$, therefore cells with narrow spatial frequency bandwidths will have tighter orientation bandwidths as well, for both achromatic and chromatic stimuli. Elfar and De Valois (1992) report similar orientation tuning for chromatic and achromatic stimuli in cells tuned to both. Figure 8 shows a prediction for the ratio of the achromatic and chromatic orientation bandwidths as a function of chromatic spatial frequency bandwidth. Since there is no published data on the joint spatial frequency and orientation chromatic and achromatic tuning of a large set of cortical cells, Fig. 8 will serve as a future test of this model.

Similarity of spatial frequency filtering to an "ideal detector"

Instead of viewing the demultiplexing problem as the separation of two signals, we could reconceptualize the problem as follows: the cortex is trying to detect a bandlimited achromatic signal in lowpass shaped chromatic noise. Martel and Mathews (1961) have shown that bandlimited signals in lowpass noise can be reconstructed perfectly (even for infinitely low signal-to-noise ratios) if the detector can differentiate the waveform an infinite number of times. In general, the ideal detector consists of the sum of a correlation filter and $N - 1$ derivatives of the stimulus envelope. Usually, the correlation filter is the most important term, but as the noise increases, the role of the higher order derivatives becomes more important. For the P cell system, the correlation term would be well modelled by taking the second derivative of the LGN response (since P cells are second derivative operators for achromatic stimuli, and correlation is equivalent to convolution for symmetric operators). The $N - 1$ local derivatives of the P cell response are equivalent to the output of cortical cells built up out of weighted sums and differences of P cells. It is interesting that Martel and Mathews believed that their detector would have no application in perception, but in 1961 there were no indications of multiple bandpass filters in the visual system.

SUMMARY

In summary: (1) There is a problem with retrieving the achromatic information encoded by Type I LGN P cells. These cells carry both chromatic and achromatic signals, making the overall signal ambiguous. (2) Much evidence showing the Type I achromatic signal is used by the cortex, requires that there exist a cortical decoder. (3) The P cell achromatic signal is shaped by a bandpass filter, while the chromatic signal is shaped by a lowpass filter, suggesting that achromatic signals could be extracted by bandpass spatial filtering. (4) Bandpass filtering of P cells yields an achromatic signal and a chromatic crosstalk term. The frequency tuning of these terms correspond to a class of cortical cells (Thorell *et al.*, 1984) with bandpass sensitivity to both chromatic and achromatic stimuli. (5) The correspondence between cortical cell properties and the properties of the postulated achromatic filters suggests that these cortical cells are labelled bandpass filters for achromatic information and that the chromatic response of these cells is simply the result of crosstalk. Although lack of high spatial frequency chromatic information in natural scenes may normally limit the chromatic response of this channel, it does suggest a mechanism (in addition to chromatic form mechanisms insensitive to achromatic contrast) by which chromatic information may contribute to processing of spatial form. It also suggests a mechanism for some psychophysical color/luminance interactions and for the achromatic appearance of high spatial frequency chromatic gratings. (6) These results are not predictable from chromatic cancellation algorithms that are highly efficient at removing chromatic information from P cell signals. Less efficient chromatic cancellation algorithms resemble bandpass filters. (7) The bandpass filters for extracting achromatic information resemble local derivatives of the P cell array, a result that provides a connection to ideal observer theory. (8) The model can

be reinforced or falsified by some proposed physiological and psychophysical tests.

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Acknowledgements—This work was supported by NIMH 5T32MH19116-06 and by a National Research Council–U.S. Army Aeromedical Research Laboratory Research Award. I thank Thomas Harding, Frederick Kingdom, Victor Klymenko, Edmond Mesrobian, Richard Young, and an anonymous reviewer for helpful suggestions.

APPENDIX

The model developed in the Theory section rests on certain assumptions. None of these assumptions is crucial—relaxing any one would not change any of the predictions qualitatively—however, these assumptions greatly simplify the analysis. Here, each assumption is specified and its consequences addressed.

Assumptions in modelling retinal or geniculate units

The retinal analysis is based on the assumption that receptive fields (and their MTFs) can be modelled by a difference of lowpass functions. Two common models for X-like cells are the DOG (Difference Of Gaussians) and DOOG (Difference Of Offset Gaussians) models. In the DOG model the Gaussians have the same mean, but different space constants. Marr (1982) found that if the surround is given a space constant about 1.6 times larger than the center, then the resultant receptive field closely resembles the weighting function of a second derivative (Laplacian) of a Gaussian. However, a similar result is obtained if the concentric surround is replaced by multiple Gaussians, with space constants about the same size as the center Gaussian, and means about 2 space constants away from the center (the DOOG model). These are not unreasonable assumptions. Young (1987) found that Type I receptive fields were best fit with surrounds that did not completely extend through the center. This is was in keeping with De Monasterio's (1978) careful receptive field mapping of Type I cells which clealy showed a multimodal surround, with little surround response at the very center of the Type I receptive field, but rather peaking at some distance to either side of the center. Similarly, Reid and Shapley (1992), in their study of color sensitive ganglion cells, found Type I cells with doughnut shaped surrounds of different spectral sensitivity to their concentric centers. However, suppose that real P cells were more like DOGs than DOOGs. DOG modelled P cells would still be spatial bandpass derivative-like operators when the surrounds subtract from the center, and lowpass Gaussian-like operators when the surrounds add to the center. Not even the use of the Gaussian distribution is crucial. Taking the difference of nearby operators is a local derivative-like operation [see Ratliff's (1965) discussion of the difference equation approach, Kelly's (1975) model using derivatives of exponentials, or Budrikis' (1973) application of lateral inhibition to a variety of lowpass operators]. No matter what lowpass function the model begins with, the result of lateral inhibition or differentiation is to increase the slope of the low frequency response by the order of differentiation (Arfken, 1970; Bracewell, 1986).

Another assumption is that the center and surround are balanced so that the DOOG or DOG operator has no DC response. This seems to be the case for the visual system as a whole, because the spatial contrast sensitivity function has little DC response. It is convenient to model cells that have properties representative of the ensemble of cells, because (in a pseudolinear system) the convolution of such a cell with a stimulus is equivalent to the response properties of the entire ensemble firing in unison (Ratliff, 1965). However, it is possible to model the properties of individual cells that are not "average". In the frequency domain, if the center and surround are not balanced, the effective order of differentiation [n in equation (4)] is reduced (Kelly, 1975). Alternately, the DC term can be modelled by replacing the Laplacian with a Helmholtzian (a Laplacian of a Gaussian plus a Gaussian, see Young, 1985, 1987). A similar situation can arise for some "achromatic" stimuli. Equation (1) (which represents the case of a r+g− cell) and the equations that follow assume that the effective stimulus for the chromatic term is a chromatic grating produced by the addition in counterphase of red/black and green/black gratings. This grating is isoluminant for the cell if both the red and green bars produce equal total activity in the R-cone driven center and G-cone driven surround. It follows that the effective stimulus for the achromatic term is a yellow/black grating of identical contrast, produced by shifting the red/black and green/black gratings into phase. This is how Thorell *et al.* (1984) produced their achromatic and chromatic stimuli. Depending on the chromaticity of the yellow, an achromatic stimulus can produce a chromatic response). Only for stimuli that fall on the cell's neutral point is there no chromatic response (Ingling and Martinez, 1983b; Kingdom & Mullen, in press).

Cortical modeling assumptions

The cortical model employed in this paper assumes some kind of bandpass filtering process. Most simple bandpass filters have a f^n dependence at low frequencies, a process most easily modelled by assuming a derivative-like process, with n orders of differentiation. To approximate this, a cortical operator is assumed—D^nP—which approximates the local derivative of the output of the P cell array. This can be modelled by a derivative of Gaussian model like that developed by Young (1985, 1991), if D^nP is treated as roughly equivalent to $D^{n+k}G(\sigma)$, where k is the retinal order of differentiation, approximately 2 for achromatic and 0 for chromatic stimuli, and σ is larger (by a factor of about 1.83) for chromatic stimuli, because the P cells act like lowpass filters on the chromatic signal.

Young suggested that a sensible model for implementing higher level derivatives in the cortex is to form weighted differences or sums of offset second derivative LGN afferents (for related models of simple cells see: Hubel & Wiesel, 1962; Soodak, 1986; Hawken & Parker, 1987). Equations (A1a–d), modified from Young (1985), show how to construct several higher level derivative-like filters from linear combinations of LGN cells. Let D^nP be the nth derivative (at $x = 0$) of the on-center P cell array, each element of which has a line spread function of $DOOG_{\sigma,m}(x)$.

$$D^0P(x) \approx DOOG_{\sigma,m}. \tag{A1a}$$

$$D^1P(x) \approx -DOOG_{\sigma,m-\sigma} + DOOG_{\sigma,m+\sigma}. \tag{A1b}$$

$$D^2P(x) \approx -DOOG_{\sigma,m-2\sigma} + 2DOOG_{\sigma,m} - DOOG_{\sigma,m+2\sigma}. \tag{A1c}$$

$$D^3P(x) \approx -DOOG_{\sigma,m-3\sigma} + 3DOOG_{\sigma,m-\sigma} - 3DOOG_{\sigma,m+\sigma} + DOOG_{\sigma,m+3\sigma} \tag{A1d}$$

The weights on the DOOGs are obtained by a binomial expansion, and correspond to a Gaussian distribution of connection strengths as a function of distance from the center of the filter (Young, 1985). This results in derivative-like operators whose weighting functions and frequency tuning have the same qualitative features as the D^nP operators whose weighting functions are formed by the products of Gaussians and Hermite polynomials. However, D^nP operators have the same range as their underlying Gaussian, while the operators derived in equation (A1) have a spatial range that grows with the effective order of differentiation. For the purposes of this paper it does not really matter which model is employed so long as a low frequency f^{n+k} dependence can be assumed. (The predictions of the model are reliant on the ratio $f^{n+k}G(\sigma)/f^nG(a\sigma)$, so the nuances of extended DOOGs vs D^nP cancels out.) If necessary however, the two models could be reconciled using any one of the following approaches: (1) The extended

DOOG model could be forced into correspondence with the D^nP model by using the weights and offsets in equation (A1) as fitting constants. (2) The D^nP model could be forced into correspondence with the extended DOOG model by computing the tuning functions for both and then modifying the space constant (σ) in equation (5) until the two fit. Shiftable numerical tuning functions for the first six DOOGs are available in Mesrobian (1992). (3) A more general analysis using arbitrarily placed and weighted LGN units could be employed (see Soodak, 1986; Hawken & Parker, 1987; Kingdom & Mullen, in press). However, any realistic subunit analysis model will have to be based on retinal units that are bandpass for achromatic contrast and lowpass for chromatic stimuli. Other models based on differencing or differentiating such units will give results qualitatively similar to those in this paper, because they will be filtering units that are already more filtered for achromatic contrast than chromatic.

Cortical nonlinearities will have little effect on these results. Evidence for rectification, over-rectification and half-squaring in simple cells exists (Heeger, 1992a, b; Movshon, Thomson & Tolhurst, 1978; Tadmor & Tolhurst, 1989). Simple half-wave rectification results in truncated sinusoids whose amplitude and phase are unchanged (Heeger, 1992). Both over-rectification and half-squaring have the effect of narrowing the response function of the cell relative to what would be predicted from the Fourier transfer function of the impulse response function (or alternately, if the amplitude response is Fourier transformed, extra sidebands appear in the inferred receptive field). This needs to be taken into account when reconciling modeling of space domain and frequency domain data. However it has little effect on the predictions of the model for the relative tuning of chromatic and achromatic information, since the effects of over-rectification and half-squaring will be similar and in the same direction for both (for half-squaring the effect will be the same as adding 2 to the order of differentiation for both the chromatic and achromatic terms, based on the two extra sidebands shown in Heeger, 1992b).