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Separating colour and luminance information in the visual system

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Abstract—In our visual world we can distinguish with ease between chromatic and luminance contrasts. However, in our retinae most neurones are responsive to both chromatic and luminance changes and therefore send ambiguous or 'multiplexed' information to the higher visual centres. Psychophysical evidence suggests that some cortical process must subsequently separate out this information into its chromatic and luminance components. The purpose of this communication is to review and critically evaluate the different existing schemes for doing this. To assist in this evaluation a linear systems analysis is employed in which model cortical neurones are imputed with the property of providing information about either colour or luminance. It is concluded that there is currently no unified scheme available to explain a separation of colour and luminance information in the visual system. Some theoretical considerations and most promising approaches to solving the problem are noted, but it is suggested that there may be definite limits to the ability of the visual system to achieve complete separation of colour and luminance from the retinal signal.

1. INTRODUCTION

The spectral and intensive content of reflected light is our main source of information about the world around us. The variations in wavelength across the image arise principally from changes in the spectral reflectance of objects and thus inform us about material changes in the world. Variations in intensity arise either from changes in (luminance) reflectance or changes in the condition of illumination (e.g. from shading and shadows). They thus inform us about changes in material (reflectance), structure (e.g. shape from shading), and illumination (e.g. shadows). The spatial pattern of illumination of objects can vary considerably over space and time, causing changes in local luminance contrasts both at object borders and within object surfaces and thus it would make sense for the visual system to be able to distinguish between colour and luminance contrasts precisely in order to distinguish material from illumination changes.

The idea that the visual system possesses separate mechanisms for processing luminance and colour information was first implicit in Hering's (1920) opponent-colour

theory, later developed quantitatively by Hurvich and Jameson (1955). Hering argued that colour appearance involved combinations of three independent opponent processes: black-white (i.e. brightness), red-green and yellow-blue (both chromatic). More recently support for the notion of separability of colour-luminance mechanisms within the visual system has come from a variety of different sources. In the psychophysical literature, the existence of separable colour and luminance mechanisms is indicated by the lack of subthreshold summation between colour and luminance contrast (Switkes *et al.*, 1988; Cole *et al.*, 1990; Mullen and Losada, 1994; but see Gur and Akri, 1992 for the contrary result), and by the lack of cross masking between colour and luminance in studies which use broad band noise masks (Gegenfurtner and Kiper, 1992; Losada and Mullen, 1995).

Adaptation studies and spatial masking studies have addressed the extent to which these mechanisms remain independent at suprathreshold contrasts, or whether either may have some reduced sensitivity to contrast in the cross condition. Independence has been demonstrated most convincingly in the failure to find significant cross adaptation between colour and luminance stimuli (Krauskopf *et al.*, 1982; Bradley *et al.*, 1988). In the masking studies the results have been equivocal, and limited interactions are likely at high mask contrasts. Switkes *et al.* (1988) find significant masking of luminance contrast detection by colour, although not vice versa, whereas Mullen and Losada (1994) find some cross masking in both conditions confined to high contrasts. Gegenfurtner and Kiper (1992) and Losada and Mullen (1995) using noise masking report independence of colour and luminance contrast except at high noise spectral densities. There are a number of studies which have demonstrated facilitation for the detection of colour contrast by suprathreshold levels of luminance contrast under a wide variety of conditions (Hilz and Cavonius, 1970; Hilz *et al.*, 1974; Switkes *et al.*, 1988; Cole *et al.*, 1990; Mullen *et al.*, 1992). However, the facilitation observed in these studies is believed to be due to higher-order effects such as the demarcating of the chromatically defined region of interest by the facilitating luminance discontinuity and is not explained by luminance contrast and chromatic contrast directly stimulating a common detection mechanism (Cole *et al.*, 1990; Eskew *et al.*, 1991), or the detection of local chromaticity changes in the stimulus (Mullen and Losada, 1994). Thus the evidence from facilitation studies is consistent with the underlying independence of colour and luminance.

Three further lines of evidence support the presence of separate mechanisms encoding colour and luminance. First Legge *et al.* (1990) find no additive interaction between suprathreshold levels of colour and luminance for speed of reading of text. Second, recent studies of patients with cerebral achromatopsia, in which localized cortical brain damage leads to a dramatic loss of colour sensation, have shown that the ability to discriminate pure luminance contrasts has been preserved (Heywood *et al.*, 1987). Third, it has been shown that the visual system is deficient at associating colour-only and luminance-only elements to extract a contour, whereas the same contour is readily perceived if the association required is between like elements only (McIlhagga and Mullen, 1995).

Taken together, these lines of evidence support the position that cortical mechanisms exist which independently process colour and luminance information, though it is

likely that there are also mechanisms which are simultaneously sensitive to both colour and luminance. Since the purpose of this communication is to consider various schemes for implementing colour-luminance separability at the physiological level, the physiological evidence for colour-luminance separability will be considered as part of the discussion below.

Given that information about colour contrast and luminance contrast can be separately represented, the question arises as to how this may be achieved? To capture both intensive and spectral information, we possess three classes of photoreceptors (cones). All three are sensitive to light energy, but are differentially sensitive to wavelength. However, because cone responses are univariant with respect to wavelength and quanta, they cannot provide unambiguous information about the composition of each stimulus dimension. The first stage toward obtaining this information is to sum the outputs of the different cone types to provide information about luminance, and difference their outputs to provide information about the spectral content of the image (Sperling and Harwerth, 1971; King-Smith and Carden, 1976). Currently, how these processes give rise to separate colour and luminance information is not fully understood, in spite of the considerable advances that have been made in our understanding of retinal and early cortical organisation.

In this communication we critically examine the existing computational schemes that have previously been suggested for separating chromatic and luminance information. To evaluate those schemes based directly on neurophysiology we have employed a linear systems analysis to describe the properties of model cortical neurones that are implicated in such schemes, we point out the schemes' limitations as well as a number of their behavioural consequences. It is not our intention in this paper to describe a completed project but rather to point to the theoretical considerations and most promising approaches to solving the problem.

Before examining the various schemes for separating the chromatic and intensive content of images, we examine the first stage in the post-receptoral processing of colour information in the retina, and in doing so make explicit the assumptions we are making concerning the nature of the output of chromatic and luminance information from the retina to the higher visual centres.

2. MULTIPLEXING IN RETINAL GANGLION CELLS

Most ganglion cells (about 80%) in the foveal region of the primate retina show single cone opponency, that is they are excited by light of one wavelength and inhibited by light of another. These cells, known anatomically in primates as midget ganglion cells (Rodieck *et al.*, 1985) or physiologically as P-cells in monkeys (Shapley and Perry, 1986), therefore possess the property that in principle allows them to provide unambiguous information about wavelength. However, they are also sensitive to luminance contrast (Wiesel and Hubel, 1966; DeValois and Pease, 1971; Gouras and Kruger, 1979), and their small size and relative numerosity suggests they are most likely to be the principal conveyers of information about fine spatial detail (Perry *et al.*, 1984). Thus, like the photoreceptors themselves, they perform a 'double-duty'

by carrying information about both colour contrast and luminance contrast. This is sometimes referred to as 'multiplexing' (Ingling and Martinez, 1983a,b; 1985; Mullen and Kingdom, 1991).

In their elegant analysis of the primate P-cell, Ingling and Martinez (1983a,b; 1985) have shown that its multiplexing property is an inevitable consequence of the fact that it has both cone opponency and spatial opponency. Their argument can be best illustrated by considering the two-dimensional profile of a difference-of-Gaussian (DOG) approximation to the receptive field of a P-cell fed exclusively by M (medium wavelength sensitive) and L (long wavelength sensitive) cones. The majority of P-cells in the primate retina are of this variety (DeMonasterio *et al.*, 1975). The unit is illustrated schematically in Fig. 1a, and Fig. 1b shows the point-spread-function (PSF) of the unit in response to achromatic stimulation. The unit in Fig. 1 consists of an excitatory centre fed by L cones, and an inhibitory surround fed by a mixture of L and M cones in the ratio of $2L:1M$. The cone opponent property of the unit results from the fact that the centre and surround will have different spectral sensitivities. However, because of the close spectral overlap in M and L cone sensitivity, light of more or less any given spectral composition will always stimulate both the centre *and* surround regions of the receptive field. Thus the unit will be sensitive to stimuli of uniform colour but modulated in intensity across space. In other words the unit may be considered to have both a cone subtractive $[3L-(2L+M)]$ component with low-pass spatial characteristics, and a cone additive, $[3L+(2L+M)]$ component with band-pass spatial characteristics to its response (see Ingling and Martinez, 1983a,b; 1985).

Figures 1c and 1d illustrate the two- and Fig. 1e the one-dimensional spatial frequency response functions, or amplitude spectra, of the unit to two types of stimuli, 'chromatic' and 'luminance' gratings. The chromatic grating is a red-green (RG) grating and consists of two components, a red and a green sinusoidal grating, 180 degrees out of phase. The amplitudes of the two components are chosen such as to produce equal outputs (a 'silent substitution') in the summed quantal absorptions of the L and M cones in the P-cell unit, taking into account the proportions and weightings of the two cone types. The resulting grating is thus 'isoluminant' for this particular model P-cell. The achromatic (ACHR) grating modulates the L and M cones in equal proportions and in phase, and could thus be any of the colours that lie on the tritanopic confusion line for which L and M cone activation are equal. In each 2-D spectrum spatial frequency is on a log axis and radiates outwards from the centre, while orientation is encoded as angle about the origin, which in this case is arbitrary. For the chromatic, RG grating (Fig. 1c), the spatial tuning of the unit is low-pass with a relatively poor response to high spatial frequencies. For the ACHR grating (Fig. 1d), the spatial tuning is more band-pass with a relatively good response to high spatial frequencies. These characteristics of the P-cell have been discussed previously by Ingling and Martinez (1983a,b; 1985).

Full details of the calculation of the two-dimensional MTFs for the model P-cell unit shown in Fig. 1 as well as the combination P-cell units described in the later sections are given in the Appendix.

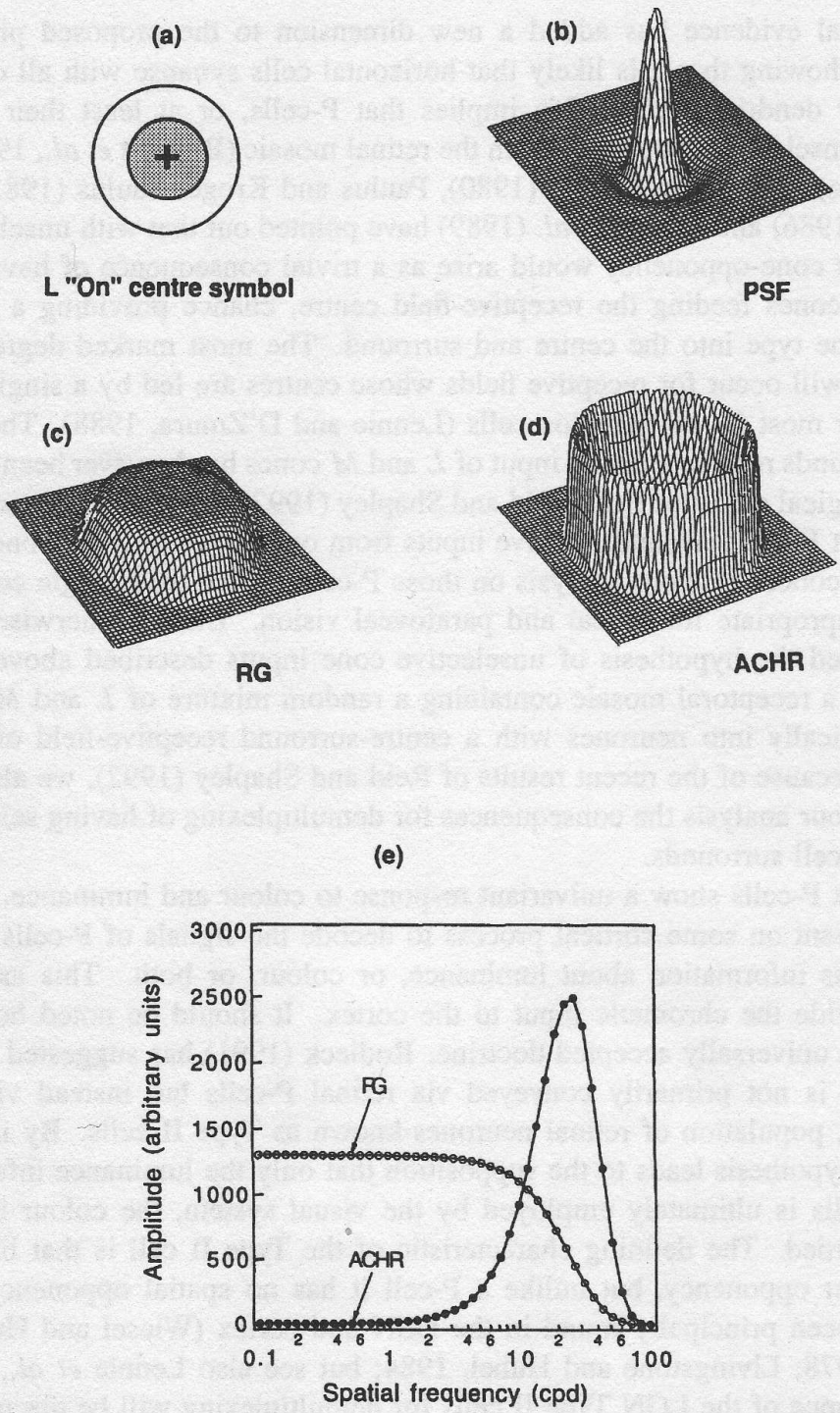

Figure 1. Properties of a model P-cell. (a) Symbol for an 'On' centre P-cell whose receptive-field centre is fed by a single *L* (long-wavelength-sensitive) cone. The symbol is only schematic and is not meant to accurately represent the relative sizes of the centre and surround of the P-cell. (b) The PSF (point-spread-function) of the P-cell in response to achromatic light. The P-cell is modeled as a DOG (Difference of Gaussian). See Appendix for details. (c) and (d) give the two-dimensional MTFs (modulation transfer functions) in response to isoluminant RG (red-green) gratings and luminance modulated ACHR (achromatic) gratings respectively. As in subsequent figures, spatial frequency is on a log axis radiating outward from the centre of each plot and orientation of the stimulus is coded by angle, with vertical gratings represented on the x-axis. The graph in (e) shows the one-dimensional MTFs for the RG and ACHR gratings.

Anatomical evidence has added a new dimension to the proposed properties of P-cells by showing that it is likely that horizontal cells synapse with all cones types within their dendritic field. This implies that P-cells, or at least their surrounds, receive an unselective cone input from the retinal mosaic (Boycott *et al.*, 1987; Wassle *et al.*, 1989a). Moreover, Lennie (1980), Paulus and Kroger-Paulus (1983), Shapley and Perry (1986) and Lennie *et al.* (1989) have pointed out that with unselective cone connectivity cone-opponency would arise as a trivial consequence of having a small number of cones feeding the receptive-field centre, chance providing a differential input of cone type into the centre and surround. The most marked degree of cone-opponency will occur for receptive fields whose centres are fed by a single cone, the situation for most foveal ganglion cells (Lennie and D'Zmura, 1988). The view that P-cell surrounds receive a mixed input of L and M cones has however been challenged by physiological evidence from Reid and Shapley (1992). Their evidence supports the position that P-cell surrounds receive inputs from only L, or only M cones. In what follows we concentrate our analysis on those P-cells which have single cone centres, which is appropriate for foveal and parafoveal vision. Unless otherwise stated we have assumed the hypothesis of unselective cone inputs described above, in which cones from a receptoral mosaic containing a random mixture of L and M cones are fed topologically into neurones with a centre-surround receptive-field organisation. However, because of the recent results of Reid and Shapley (1992), we also consider in much of our analysis the consequences for demultiplexing of having selective cone inputs to P-cell surrounds.

Given that P-cells show a univariant response to colour and luminance, it is therefore incumbent on some cortical process to decode the signals of P-cells to provide unambiguous information about luminance, or colour, or both. This assumes that P-cells provide the chromatic input to the cortex. It should be noted however that this is not a universally accepted doctrine. Rodieck (1991) has suggested that colour information is not primarily conveyed via retinal P-cells but instead via a different, sparser, population of retinal neurones known as Type II cells. By implication, Rodieck's hypothesis leads to the supposition that only the luminance information in retinal P-cells is ultimately employed by the visual system, the colour information being discarded. The defining characteristic of the Type II cell is that like a P-cell it has colour opponency, but unlike a P-cell it has no spatial opponency. Type II cells have been principally found in the LGN and cortex (Wiesel and Hubel, 1966; Michael, 1978; Livingstone and Hubel, 1984; but see also Lennie *et al.*, 1990) and the significance of the LGN Type II cells for demultiplexing will be discussed in the next section. Rodieck's argument rests on the assertion that the LGN Type II cells exist in sufficient number to account for colour vision, and critically that they receive projections only from Type II cells in the retina. Retinal Type II cells have been found by DeMonasterio and Gouras (1975), DeMonasterio (1978) and most recently by Reid and Shapley (1992). The numbers reported in the first two studies are very small, namely 3% (DeMonasterio and Gouras, 1975) and 1.6% (DeMonasterio, 1978), while Reid and Shapley (1992) report that 39% of the neurones they studied have the Type II arrangement. While Rodieck's (1991) hypothesis is an interesting one, it must remain speculative while the reported proportions of Type II retinal cells are

so inconsistent and for the most part so low. However, even if future studies reveal more numerous retinal Type II cells, there still remains the issue as to how the cortex would discard the strong component of the P-cell response which arises from its response to colour contrast, such that the luminance component of its response could be represented unambiguously.

To summarise, the analysis that follows makes the following assumptions and imposes the following restrictions. First, we assume that retinal P-cells are the principal source of chromatic information for the cortex and that they also provide luminance information, especially at high spatial frequencies and low temporal frequencies. Second, we assume a 2 : 1 ratio of L to M cones in the retinal mosaic. Third, we have restricted our analysis to single cone centre P-cells. Fourth, while we have assumed that P-cell surrounds receive a mixed cone input for some aspects of our analysis, we have examined the consequences for demultiplexing of having selective cone inputs to P-cell surrounds in all cases where it could be critical. We now go on to consider the various demultiplexing schemes.

3. MODELS OF DEMULTIPLEXING

3.1. Demultiplexing using spatially superimposed receptive-field pairs

This mechanism for demultiplexing the M/L filter response has been suggested by Lennie and D'Zmura (1988), Martinez and Kelly (1989) and by Mullen and Kingdom (1991). The basic idea is illustrated in Fig. 2a. This figure shows that the addition of pairs of spatially superimposed single-opponent units, with selective cone inputs to centre and surround, will provide two types of operator: one carries the additive signal (Fig. 2a i and ii) and the other carries the cone opponent signal without spatial opponency (Fig. 2a iii and iv). The cone additive luminance sensitive mechanism will have band-pass spatial characteristics whereas the cone subtractive mechanism will be spatially low-pass. The scheme shown in Fig. 2a shows units constructed from either 'On' or 'Off' centre P-cells whose centres are fed by a single cone type, and this is consistent with the view supported by morphological primate data that each cone feeds both an 'On' and an 'Off' centre ganglion cell (Wassle *et al.*, 1989b). Note that this scheme's potential for demultiplexing the colour and luminance components of individual P-cell signals is not contingent on there being selective cone inputs to the surrounds of the P-cells, as in Fig. 2a. The scheme would also work if the cone inputs to the P-cell surrounds were mixed.

A crucial problem with this scheme lies in its requirement of spatially superimposed receptive fields with different cone inputs into the receptive-field centre. Complete spatial superimposition of receptive fields with different cone centre types is impossible to achieve for a single cone layer, and is of course impossible whether or not the cone inputs to the receptive-field surrounds are selective or not. Superimposition could be effectively achieved (although never completely) only for large receptive fields which pool large numbers of cones, and in which the cone inputs to the centre were selective.

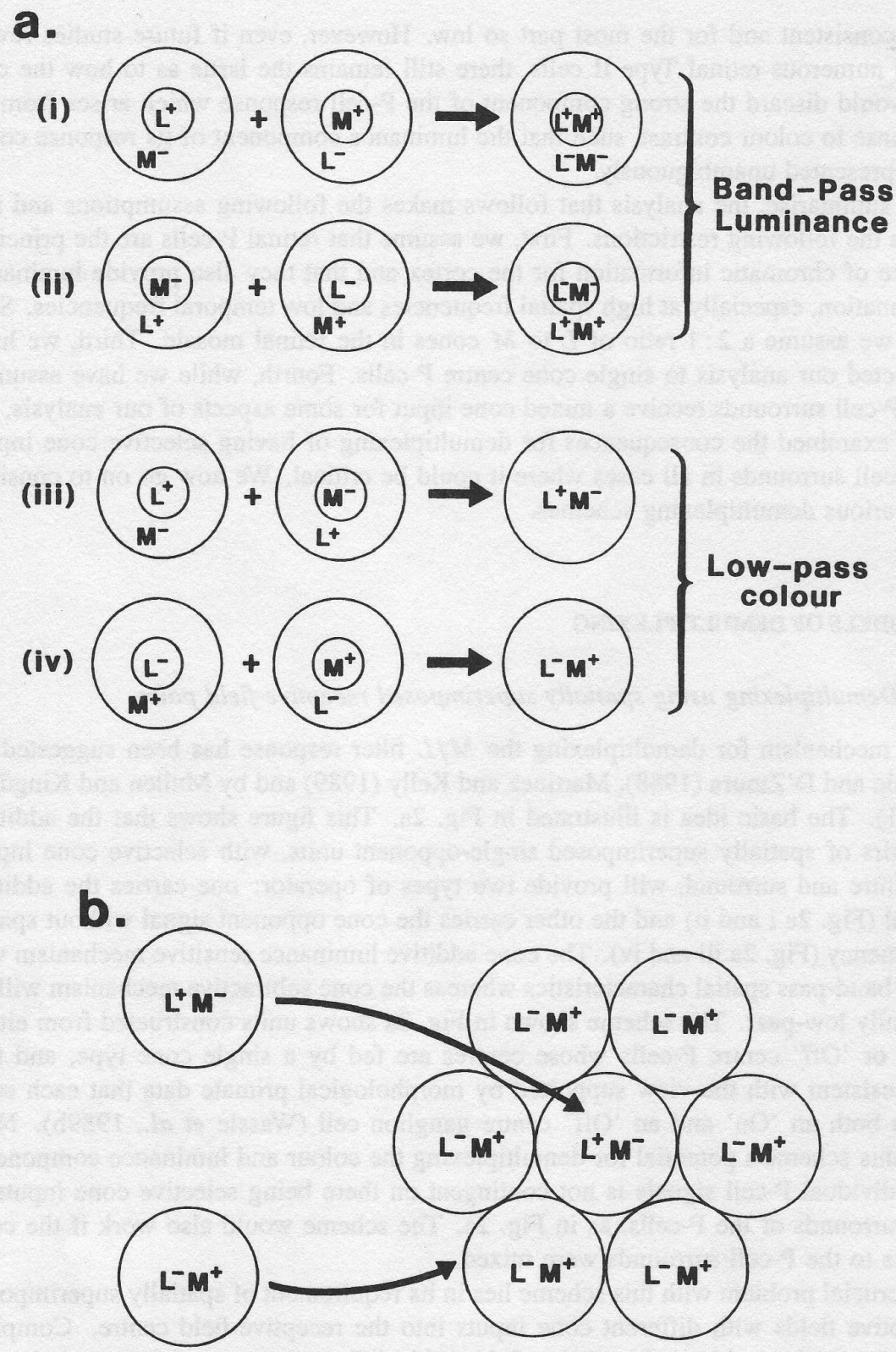

Figure 2. A scheme for demultiplexing using spatially superimposed receptive fields. In (a) the four units on the right hand side are each produced by linear summation of pairs of superimposed P-cell units. In (i) and (ii) the result is respectively an On- and an Off-centre luminance unit, in (iii) and (iv) respectively $L-M$ and $M-L$ chromatic units. A similar set of units to i–iv could be produced by subtraction rather than addition. (b) shows how a double-opponent unit could be constructed from (a.iii) and (a.iv). Adapted from Mullen and Kingdom (1991).

Despite these problems it is interesting to note that there is evidence for the existence in the visual system for units similar to all of those shown in Fig. 2a. As we noted earlier, there exist in the LGN and cortex colour-opponent units without spatial opponency which are termed Type II units (Wiesel and Hubel, 1966; Michael, 1978; Livingstone and Hubel, 1984; but see also Lennie *et al.*, 1990). It has been proposed that these Type II units provide the input to dual opponent cells in the cortex, as shown in Fig. 2b (Michael, 1978; Bertulis and Glezer, 1984) though this has recently been disputed (Billock, 1991 and see below). Dual opponent cells are reported in layer 4 of striate cortex (Gouras, 1974; Michael, 1978) and the cytochrome oxidase blobs of layers 2 and 3 (Livingstone and Hubel, 1984). The question is: how could these chromatically sensitive units in the LGN and cortex be constructed without recourse to spatial superimposition of their P-cell inputs? In the next section, we attempt to answer this question. We begin by illustrating the failure of demultiplexing for the combination of outputs of two adjacent rather than superimposed P-cells. We then examine the possibility that the effective demultiplexing provided by units with the Type II and double-opponent organisation could be constructed from the P-cell matrix without recourse to a spatial superimposition model.

3.2. Demultiplexing by pooling adjacent receptive fields

In Figs 3 and 4 we examine the chromatic and luminance responses of various hypothetical filters constructed by pooling the outputs of P-cells whose centres are fed by a single cone, and whose centres lie adjacent to one another in the retinal matrix. The P-cells are thus pooled with the highest sampling density possible given the constraint of a single cone layer. In computing the MTFs of the combination P-cell units to the RG gratings shown in these and the following figures, the amplitudes of the red and green components are chosen to produce equal outputs in the response of L and M cones across the cone population as a whole, assumed to exist in the ratio of $2L:1M$. The stimulus is thus 'isoluminant' for the cone-additive $(2L + M)$ response averaged across the population of P-cells, but will not be necessarily isoluminant for each individual P-cell.

Figure 3 illustrates the result of applying the model of demultiplexing described earlier and illustrated in Fig. 2, but to pairs of receptive fields which are not spatially superimposed, but whose single cone centres lie adjacent to each other in order to give the largest degree of overlap between the receptive fields as possible. Contrary to the situation when the pairs of P-cells were hypothetically superimposed (Fig. 2a), the combinations in Fig. 3 fail to give 'pure' chromatic and luminance signals. Instead, they are highly responsive to both chromatic and luminance modulation at virtually all orientations and have thus failed to demultiplex the P-cell signals.

Figure 4a illustrates the result of combining a larger number of single cone centre P-cells using the sign-covaries-with-cone-centre-type rule, the rule ostensibly designed to provide unambiguous information about colour contrast. This is essentially the scheme suggested by Gouras (1991) for extracting a relatively pure colour signal from the P-cell layer. The resulting filter is now relatively less responsive to luminance contrast compared with combining just two P-cells as in Fig. 3a. A more

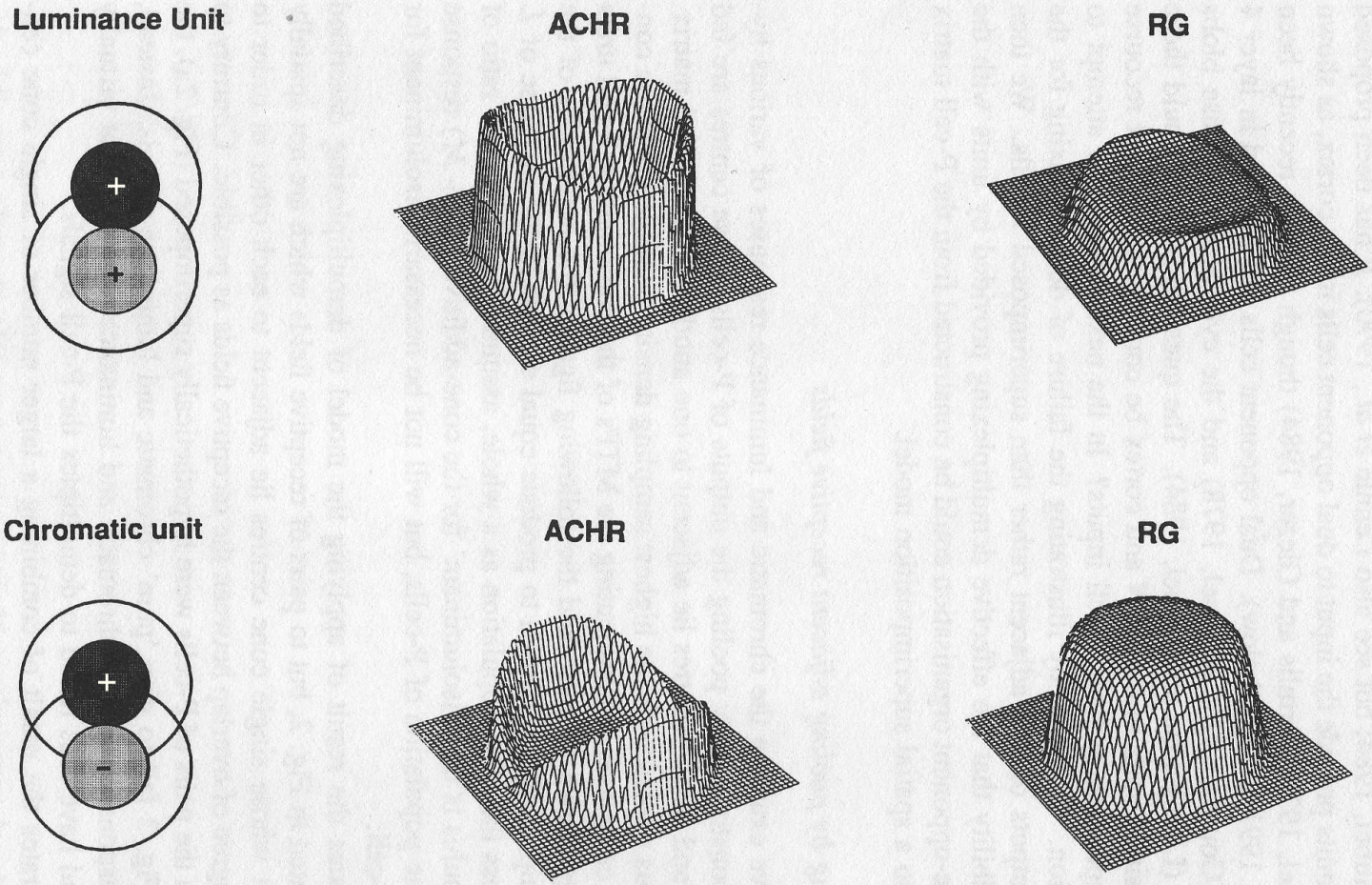

Figure 3. The result of applying the demultiplexing scheme described in Fig. 2 but for non-overlapping pairs of model P-cell receptive fields whose receptive-field centres lie adjacent to each other in the retinal matrix. *L* cone centre P-cells are dark grey, *M* cone centre P-cells light grey. (+) 'On-centre', (−) 'Off-centre'. Next to each pair are shown the computed 2-D MTFs in response to luminance modulated ACHR (achromatic) and isoluminant RG (red-green) gratings. Both types of unit are highly responsive to both types of grating.

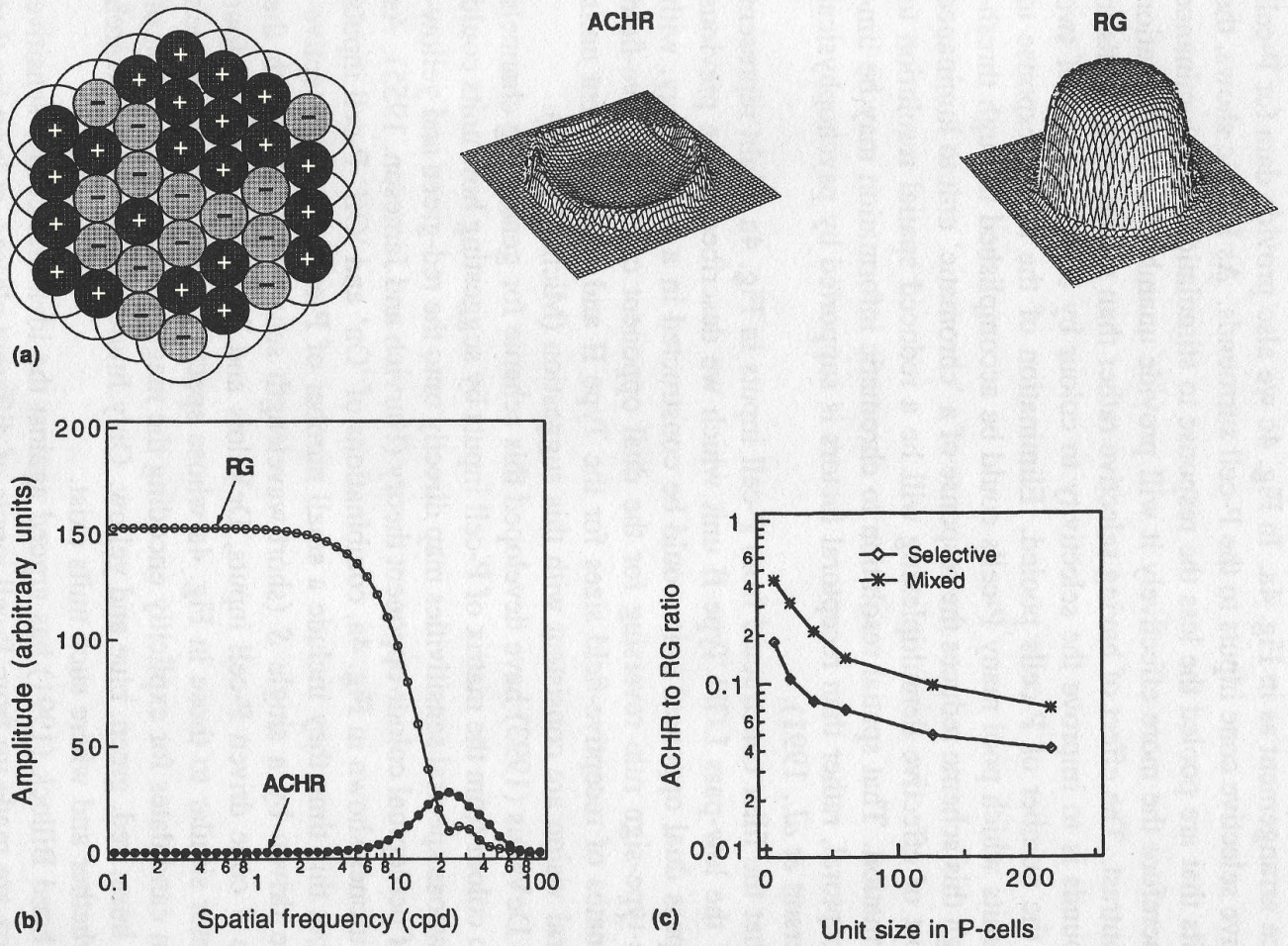

Figure 4. (a) The result of pooling a large number of adjacent P-cells using the sign-covaries-centre-cone-type rule in order to extract information about colour contrast. The relatively 'clean' chromatic response of such units, at least to the luminance modulated ACHR gratings is illustrated in (b). This gives 1-D MTFs computed by averaging across all stimulus orientations and across 10 sample filters of the type shown in (a) but with randomized cone-centre-type inputs. (c) illustrates the relative response to ACHR and RG gratings as a function of the number of P-cells that are pooled. Results for both selective and mixed cone inputs to P-cell surrounds are shown.

quantitative analysis of the relative responses to chromatic and luminance contrast is given in Fig. 4b. This shows the MTFs averaged across all orientations and across 10 sample units each with a random allocation of single cone centre P-cell types taking into account the $2L:1M$ ratio. Finally Fig. 4c shows how the relative peak amplitude response to ACHR and RG stimulation of units of the type shown in Fig. 4a varies with the number of P-cell inputs. The P-cells are always pooled to produce a hexagonal lattice arrangement as in Fig. 4a. In Fig. 4c we also provide data for P-cell inputs which have selective cone inputs to the P-cell surrounds. As Fig. 4c shows, the more P-cell units that are pooled the less the response to stimulation from luminance contrast, and therefore the more effectively it will provide unambiguous information about colour contrast. The effect of having selective rather than mixed cone inputs to the P-cell surrounds is to improve the selectivity to colour by about a factor of two irrespective of the number of P-cells pooled. Elimination of the small response to luminance for units which pool many P-cells could be accomplished through thresholding. Although this scheme reduces the response of a 'chromatic' unit to luminance contrast, the cost of effective demultiplexing will be a reduced spatial resolution to chromatic information. That spatial resolution to chromatic information may be limited by post-receptoral, rather than receptoral factors is supported by psychophysical evidence (Anderson *et al.*, 1991).

We suggest that the filter constructed from P-cell inputs in Fig. 4a might represent the structure of the low-pass LGN Type II unit which we described in the previous section. Band-pass dual opponent units could be constructed in a similar way, with the cone-centre-type-sign rule reversing for the dual opponent cell's receptive-field surround. Estimates of receptive-field sizes for the Type II and dual-opponent units in primate central vision are consistent with this suggestion (Michael, 1978).

DeValois and DeValois (1993) have developed this scheme for generating channels sensitive only to colour from the matrix of P-cell inputs by suggesting how units could be constructed whose spectral sensitivities map directly onto the red-green and yellow-blue channels of perceptual colour-opponent theory (Hurvich and Jameson, 1955). As in the model neurones shown in Fig. 4a, combinations of 'On' and 'Off' P-cell inputs are employed, but this time they include a small number of P-cells whose receptive-field centres are driven by a single S (short-wavelength sensitive) cone. With the inclusion of the S cone driven P-cell inputs, DeValois and DeValois generated four classes of operator similar to those in Fig. 4a whose spectral sensitivities were such as to make them candidates for explicitly encoding the magnitude of the sensation of the four unique hues: red, green, blue and yellow. Only future physiological research will establish whether and where such units exist.

On the other hand Billock (1991) has argued against the idea that colour sensitive cells in the cortex are made up from P-cell inputs of different classes, at least for that class of cortical cells known as dual-opponent cells. Arguing directly from the pharmacological and neurophysiological evidence he instead asserts that dual-opponent cells are constructed entirely from just *one* class of P-cell input. In the example he gives to illustrate his model a dual-opponent unit is made up entirely from $L+$ centre, $M-$ surround $(L-M)$ Type I inputs. The centre of the dual-opponent cell's receptive field receives excitatory connections and the surround inhibitory connections from

this one type of input. As Billock (1991) points out, such a system of pooling information from just one class of P-cell unit from across the retina low-pass filters the P-cell information. Although of course the dual-opponent cell is a band-pass filter, its relatively large receptive-field centre would mean that it would preserve much of the low spatial frequency chromatic signal from the P-cell inputs while losing much of the higher spatial frequency band-pass luminance signal. Billock (1991) recognizes that pooling the outputs of $L+$ centre $M-$ surround units across the retina is mathematically equivalent to pooling a mixture of $L+$ centre $M-$ surround and $M-$ centre $L+$ surround units. However, if the surround of the P-cells has a mixed cone input there will be no exact equivalence. A dual-opponent unit constructed from P-cells with mixed cone surrounds of just the $L+$ centre type will be less sharply tuned in spectral sensitivity than one constructed from a mixture of $L+$ centre and $M-$ centre types. A more sharply tuned response would then require higher-order units which compared the outputs of dual-opponent units each constructed from only $L+$ centre, or $M+$ centre P-cell inputs. It is of course quite possible that a variety of dual-opponent cells exist, some constructed from Type II units (Michael, 1978; Livingstone and Hubel, 1984), themselves either constructed from mixed P-cell inputs or just one type of P-cell input (Livingstone and Hubel, 1984; Billock, 1991) and some dual-opponent cells from just one class of P-cell as Billock (1991) has suggested.

3.3. Demultiplexing via orientation selectivity

It is universally accepted that the output of retinal ganglion cells is the basis for the construction of orientationally tuned cortical units such as simple cells (Hubel and Wiesel, 1968) and it is therefore valuable to consider whether this arrangement can provide unambiguous information about luminance contrast. Since Martinez-Uriegas (1990) has suggested that *both* chromatic and luminance contrast information could be unambiguously separated by orientationally tuned cortical units, we next examine the potential role of orientation selectivity for the extraction of both types of information.

For a one-dimensionally modulated stimulus of given orientation, the net result of stimulating a row of adjacent receptive fields which lie along the axis of orientation will be the same as if the receptive fields were spatially superimposed (assuming linear summation). This basic principle suggests that demultiplexing could occur via orientationally tuned neurones which receive their inputs from rows of adjacent simple opponent neurones. Martinez-Uriegas (1990) has described just such a scheme. The rules suggested by Martinez-Uriegas (1990) for allocating the sign of each P-cell input based on its cone centre type in order to produce cortical units sensitive exclusively to luminance or colour are the same as those used for the units in Fig. 2a. Here we consider in detail the role that orientational selectivity might play in providing unambiguous information about luminance, since orientation selectivity in cortical neurones has principally been associated with neurones responsive to luminance defined stimuli.

In Fig. 5 we illustrate a hypothetical unit constructed from three adjacent columns of P-cell units, in which the rule which allocates the sign of each P-cell unit reverses for the two flanking strings. We have considered two different models for the allocation of weights to each P-cell in the unit. The Gaussian model produces the most

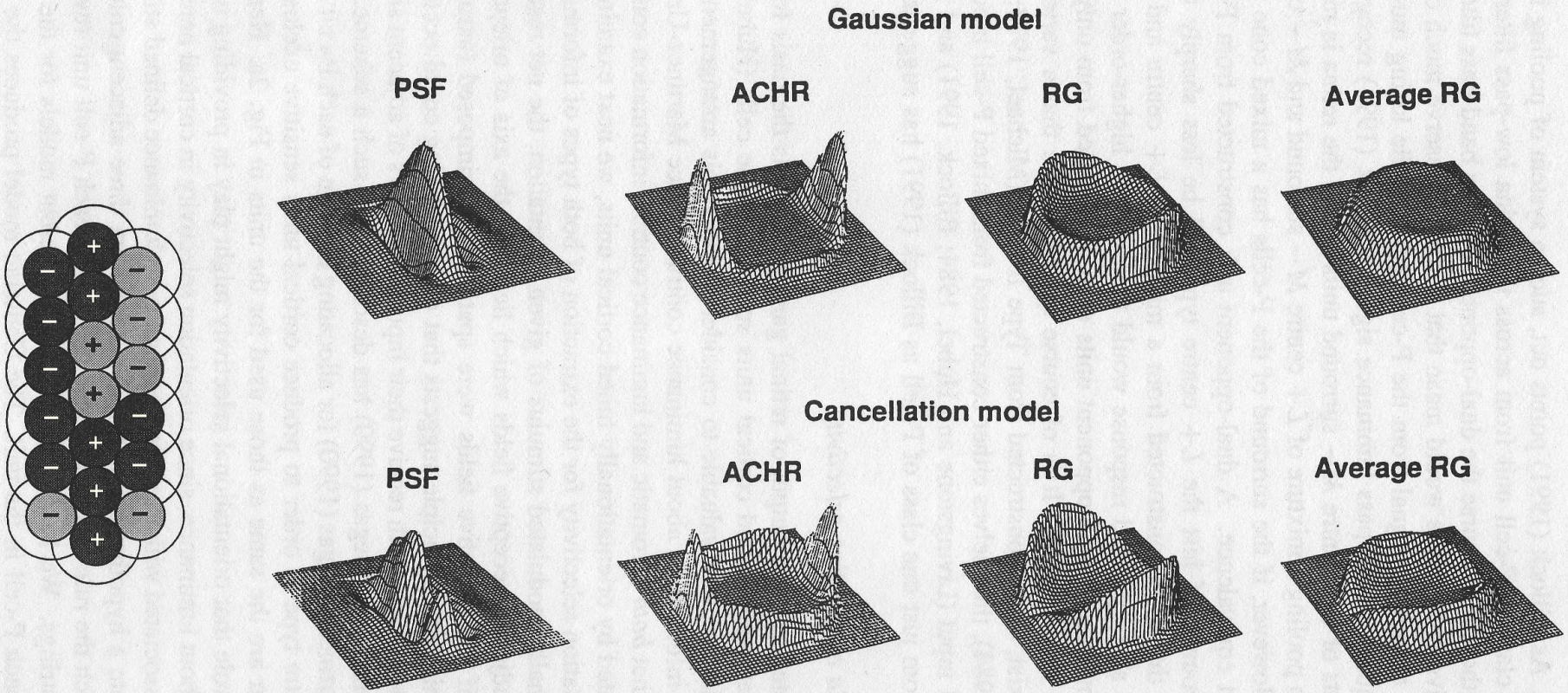

Figure 5. The limitations of extracting luminance information via orientational selectivity. The luminance unit illustrated is constructed under two models. In the Gaussian weighting model, the weightings of the P-cell inputs have been multiplied by a Gaussian along the *long* axis of the unit, and this results in the close resemblance of the unit's PSF to the even-symmetric Gabor profile of many simple cells. In the Cancellation weighting model the weightings have been adjusted to null the response to vertical RG gratings, as in the model of Martinez-Uriegas (1990). This null response to vertical RG gratings can be seen in the RG MTF surface plot. In both models the weightings have also been adjusted to produce a 'balanced' unit (centre weightings equal surround weightings). The average RG surface plots show MTFs to RG stimulation averaged over 20 sample units each with random P-cell type inputs. The MTFs in response to RG gratings under either model show significant responses with broad orientational and spatial-frequency tuning.

physiologically realistic model cortical units, while the Cancellation model represents the most ideal method for extracting achromatic information based on orientational selectivity. The Gaussian model weights each P-cell by a Gaussian function along the *long* axis of the unit with a space constant of 0.27 times the overall length of the unit when length is defined as the number of P-cells along the unit's central axis. This produces a unit whose point-spread-function (PSF) to achromatic light closely resembles the two-dimensional even-symmetric Gabor profile found for many cortical simple cells in cat cortex (Marcelja, 1980; Field and Tolhurst, 1986; Jones and Palmer, 1987). The Gaussian model is also similar to that proposed by Hawken and Parker for monkey cortical neurones (Hawken and Parker, 1987, 1991) with the difference that in Hawken and Parker's model the LGN inputs have unbalanced receptive fields, resulting in a DOG rather than Gabor like profile for the simple cell's receptive field. The Cancellation model on the other hand adjusts each P-cell weighting in order to null the response of the unit to RG gratings at the unit's preferred orientation (vertical), as implied in the model proposed by Martinez-Uriegas (1990). In both the Gaussian and Cancellation models the weights of the flanking P-cells have been adjusted to equal the weights of the centre P-cells, thus making the units 'balanced'. The MTFs in Fig. 5 are calculated for the unit shown, except for the average MTFs to RG stimulation which are calculated as averages of 25 MTFs taken from sample units each with a random allocation of cone-centre-types.

Comparison of the MTFs for RG versus ACHR gratings for the unit in Fig. 5 reveals significant responses to chromatic stimulation under either the Gaussian or Cancellation model. Although the Cancellation model eliminates responses to vertical RG gratings as intended, it nevertheless shows significant responses to RG gratings at almost all other orientations. Moreover, the unit is more broadly tuned for RG stimulation in both orientation and spatial frequency than for ACHR stimulation. Hence one must conclude that demultiplexing has not occurred at the level of the single model unit illustrated in Fig. 5, irrespective of how the weightings of its P-cell inputs are adjusted.

A more quantitative analysis of the relative responses to RG and ACHR stimulation of model units such as those in Fig. 5 is provided in Fig. 6, which describes the effect of increasing the number of P-cells combined along the long axis of the unit. In Fig. 6 we also compare the effects of selective and mixed cone inputs to the P-cell surrounds. The graphs in Fig. 6 show how the relative peak and relative mean amplitude of the model unit's response to RG and ACHR stimulation varies as a function of the length of the unit. The peak and mean amplitude in each condition is calculated from a 2D MTF which was the average of 20 sample unit MTFs, each sample unit generated with a random allocation of cone centre type. The only constraint on the allocation of cone centre types was in the case of the Cancellation model where it was required that at least one L cone centre and at least one M cone centre P-cell occurred within each column of P-cells in the unit. This constraint was necessary to ensure that a null response to horizontal RG gratings could always be achieved. Values on the ordinate of each graph in Fig. 6 which are greater than unity imply a larger response to RG stimulation, whereas values less than unity imply a larger response to ACHR stimulation. Inspection of the two left-hand graphs in Fig. 6

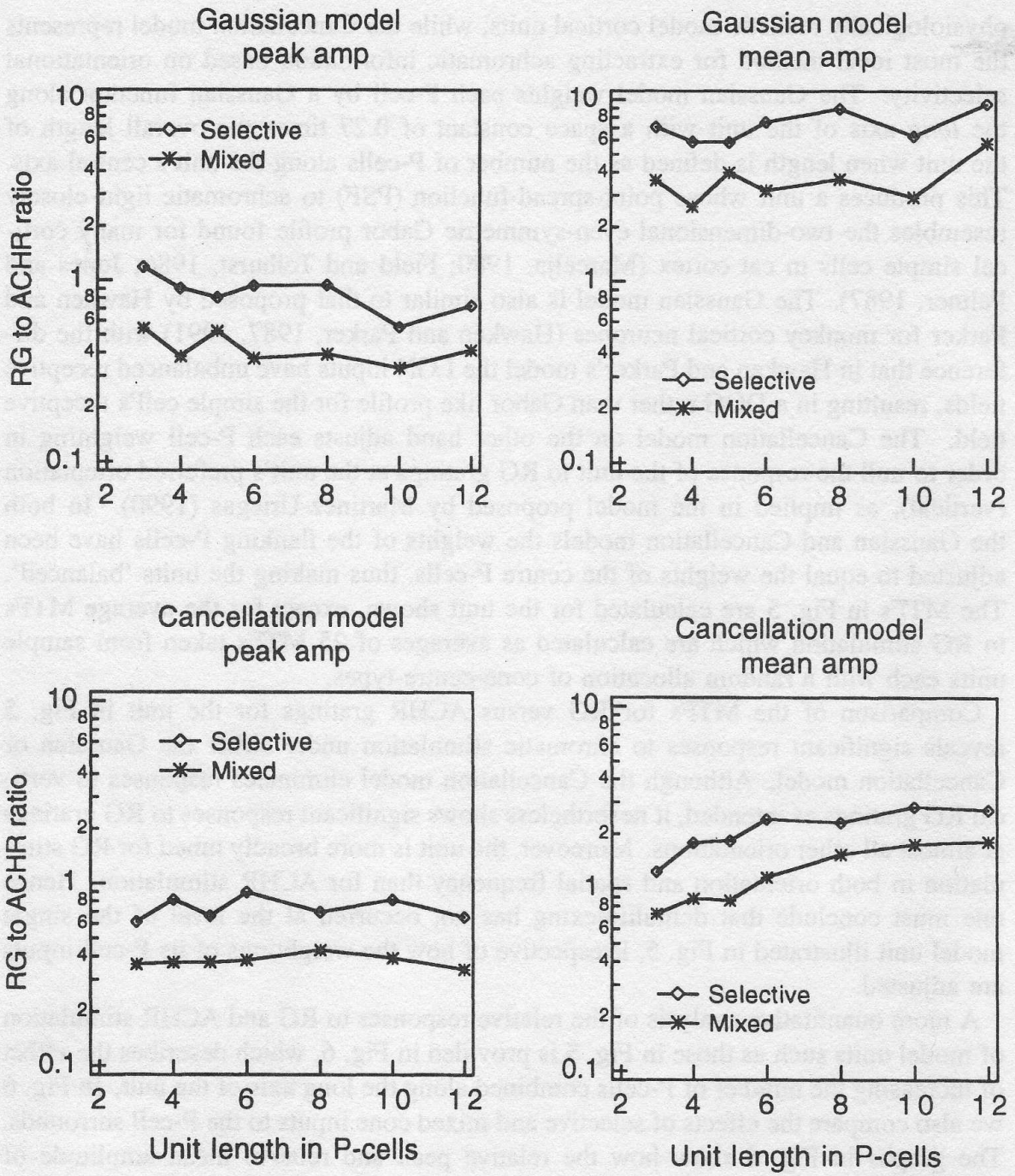

Figure 6. Quantitative analysis of model luminance units illustrated in Fig. 5. The graphs show how relative responses to RG versus ACHR gratings varies as the number of P-cells along the axis of the unit increases, according to both the Gaussian and Cancellation models. Each data point represents the average values over 20 sample luminance units each with a random input of P-cell types. The two left-hand graphs show how the peak amplitude varies with the length of the unit, according to the two types of weighting model. The two right-hand graphs show how the mean amplitude, calculated across all orientations and spatial frequencies, varies with the length of the unit.

show that for both the Gaussian and Cancellation models, units of nearly all lengths give a higher peak amplitude response to ACHR compared to RG gratings (the RG to ACHR ratio is less than 1) and this is to be expected from units which combine P-cells

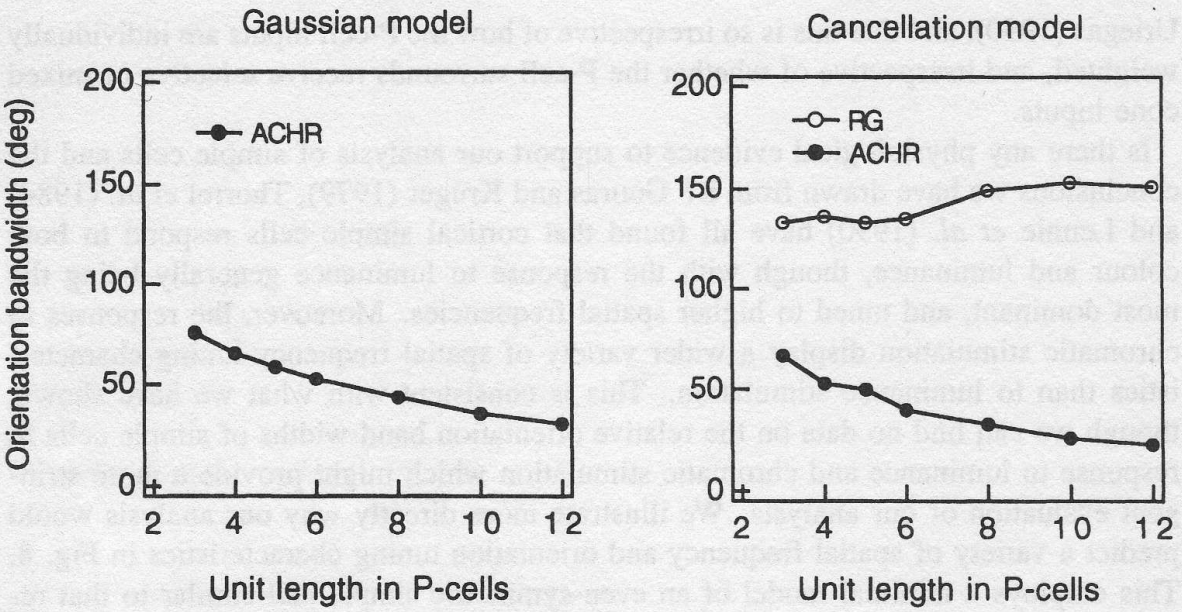

Figure 7. Orientation bandwidths of the model simple cells as a function of the length of the unit, for ACHR and RG stimulation, and for both Gaussian and Cancellation weighting models. Orientation bandwidth is defined as the width at half height of the peak response in the mean MTF as calculated for Fig. 6. Note that in the Gaussian model no data are shown for the RG gratings, because of an almost complete absence of orientational tuning, as can be seen in the RG surface plots in Fig. 5. Data are identical for both selective and mixed cone inputs to P-cell surrounds.

without concern for their cone centre type and which are therefore designed to be ostensibly sensitive to luminance rather than colour contrast. There is however little effect of filter length on the relative response to RG and ACHR stimulation. Selective, as opposed to mixed, P-cell surrounds render the units relatively more sensitive to RG stimulation, as we also found for the chromatic units in Fig. 4a. The right-hand pair of graphs show that the relative mean amplitude response is actually greater for RG compared with ACHR stimulation at almost all lengths of unit and the difference increases slightly with the length of unit. The reason for this last, seemingly counter-intuitive, result becomes apparent when one examines the orientation bandwidths of the model units shown in Fig. 7. As the unit increases in length the orientation bandwidth for ACHR stimulation decreases as one would expect (i.e. it becomes more sharply tuned for orientation) and this has the effect of decreasing its *average* response calculated across all orientations. On the other hand the orientation bandwidth for RG stimulation either remains isotropic as in the case of the Gaussian model (e.g. see Fig. 5 top right surface plot), or increases with the length of the unit in the case of the Cancellation model. Thus the relative mean amplitude to ACHR stimulation decreases with the length of the unit. We found no difference in the orientation bandwidths of units constructed from P-cells with selective and mixed P-cell surrounds in any of the conditions we examined.

In summary, although our analysis is based on idealized models of simple cells it nevertheless reinforces the conclusion that combining P-cells into oriented simple cell units without additional neural processing is unlikely to be sufficient for providing unambiguous information about luminance contrast, as proposed by Martinez-

Uriegas (1990), and that this is so irrespective of how the P-cell inputs are individually weighted, and irrespective of whether the P-cell surrounds receive selective or mixed cone inputs.

Is there any physiological evidence to support our analysis of simple cells and the conclusions we have drawn from it? Gouras and Kruger (1979), Thorrel *et al.* (1984) and Lennie *et al.* (1990) have all found that cortical simple cells respond to both colour and luminance, though with the response to luminance generally being the most dominant, and tuned to higher spatial frequencies. Moreover, the responses to chromatic stimulation display a wider variety of spatial frequency tuning characteristics than to luminance stimulation. This is consistent with what we have shown, though we can find no data on the relative orientation band-widths of simple cells in response to luminance and chromatic stimulation which might provide a more stringent evaluation of our analysis. We illustrate more directly why our analysis would predict a variety of spatial frequency and orientation tuning characteristics in Fig. 8. This employs a minimal model of an even-symmetric simple cell similar to that recently suggested by Watson and Ahumada (1989). All the units in Fig. 8 show the same bandpass response to luminance contrast but reveal a variety of spatial tuning characteristics to chromatic contrast.

We have shown on theoretical grounds that under the assumption of linearity simple cells are unlikely to be able to provide unambiguous information about luminance contrast. Are there any non-linear processes, however, which might assist in demultiplexing? One possibility is cross-orientation inhibition, implicated directly in neurophysiological studies of cat simple cells (Morrone *et al.*, 1982; Bonds, 1989; Nelson, 1991) and incorporated in recent computational models of contrast normalization in cortical neurones (e.g. Heeger, 1992). Cross-orientation inhibition is the suppression of neuronal responses to preferred stimuli by stimuli at orientations which presented alone would not stimulate the neurone. In Figs 5, 7 and 8 we demonstrated very broad orientation tuning of our model simple cells to RG gratings. Cross-orientation inhibition might be expected to at least reduce the responsivity of simple cells to stimuli with a chromatic component because a broad range of neurones tuned to other orientations to that of the stimulus would respond and as a consequence reduce the response by mutual inhibition.

Another way in which demultiplexing might be assisted is through the operation of mechanisms of contour extraction acting on the output of prestriate neurones. An important class of current models of contour extraction involve excitatory connections between cells whose receptive-field axes line up along curved lines and inhibitory connections between nearby cells whose receptive-field axes do not (e.g. Zucker *et al.*, 1989; Parent and Zucker, 1989; Gigus and Malik, 1991). This could have the effect of reducing the response to 'unwanted' chromatic stimulation at orientations to which the simple cells are not ostensibly tuned and would be particularly effective if the weights of the P-cell inputs to the cell were adjusted as in the Cancellation model illustrated in Figs 5 and 6. Without direct experimental evidence, however, the suggestion that cross-orientation-inhibition or contour-extraction mechanisms might reduce sensitivity to 'unwanted' chromatic contrast in cortical neurones remains purely speculative.

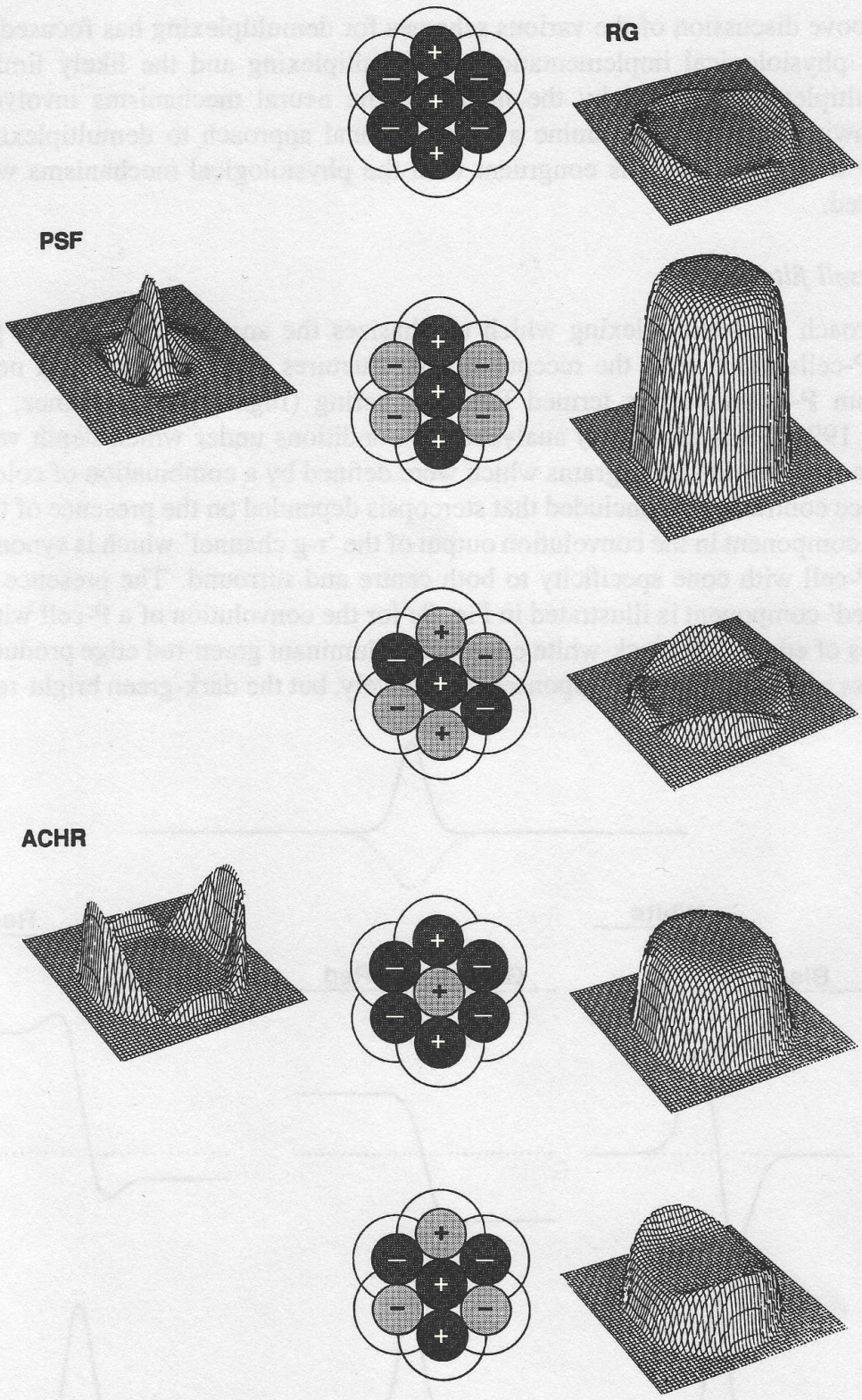

Figure 8. Various model even-symmetric simple cells constructed from a single hexagon of P-cell inputs with non-selective cone-centre-type inputs. As in Fig. 5, the PSF of the filters to achromatic stimulation have an even-symmetric Gabor profile. All filters show the same band-pass response to luminance modulated ACHR gratings, but their responses to isoluminant RG gratings show a variety of spatial tuning characteristics.

The above discussion of the various schemes for demultiplexing has focused on the possible physiological implementation of demultiplexing and the likely limitations to demultiplexing imposed by the nature of the neural mechanisms involved. In the following section we examine a computational approach to demultiplexing and consider to what extent it is congruent with the physiological mechanisms we have considered.

3.4. Russell filtering

An approach to demultiplexing which emphasizes the analysis of the filter properties of P-cells rather than the receptive-field structures of putative cortical neurones built from P-cell inputs is termed Russell filtering (Ingling and Martinez, 1983b; Billock, 1991). Russell (1979) analyzed the conditions under which depth was perceived in random-dot-stereograms which were defined by a combination of colour and luminance contrast. He concluded that stereopsis depended on the presence of the 'enhanced' component in the convolution output of the 'r-g channel' which is synonymous with a P-cell with cone specificity to both centre and surround. The presence of this 'enhanced' component is illustrated in Fig. 9c for the convolution of a P-cell with various types of edge. The black-white edge and isoluminant green-red edge produce pure band-pass and pure low-pass responses respectively, but the dark-green bright-red edge

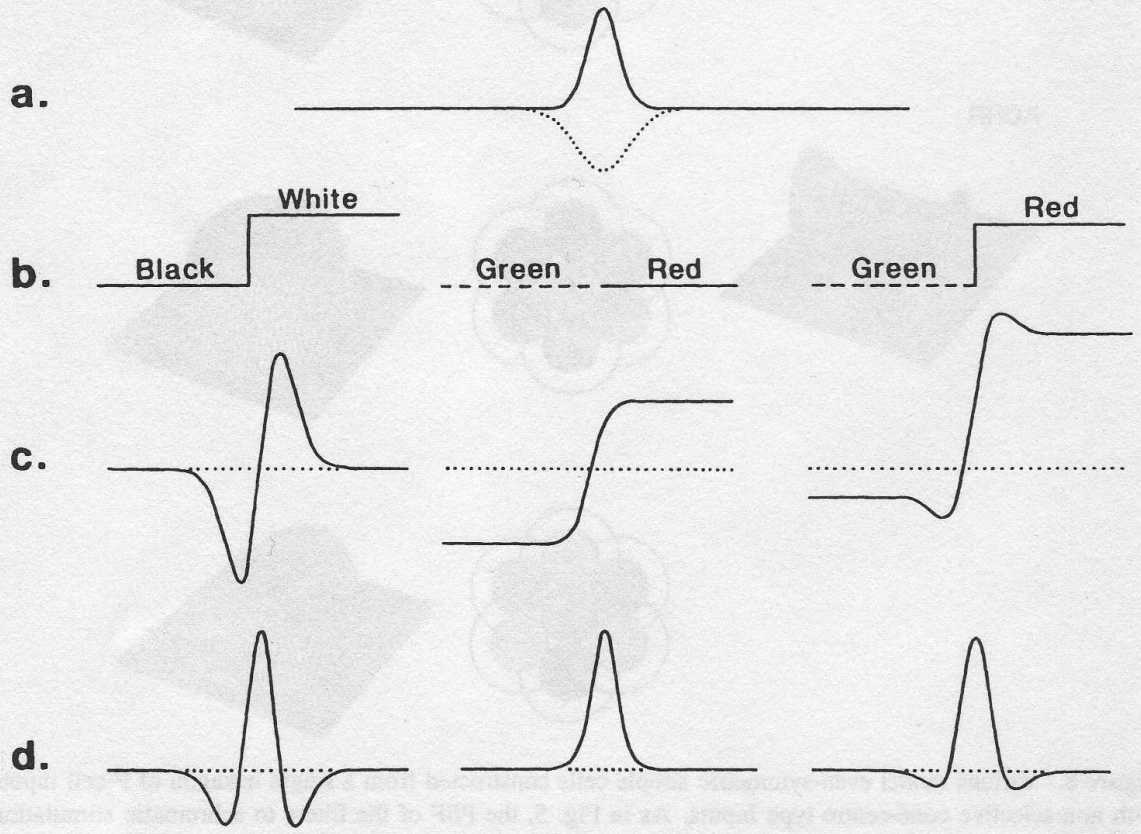

Figure 9. Response of a model P-cell unit to various edges. (a) 1-D PSF of both centre and surround of unit to achromatic light; (b) achromatic black-white edge (left) isoluminance red-green edge (middle), red-green edge with luminance contrast (right); (c) convolution response profile of unit; (d) first derivative of convolution response profile.

which combines both colour and luminance contrast produces a convolution response with both band-pass and low-pass characteristics. According to Russell, when the band-pass component is sufficiently strong to produce the two 'bumps' in the convolution response for the dark-green bright-red edge, stereopsis is possible. Ingling and Martinez (1983b) suggest that this criterion could be used to demultiplex the r-g channel output. They argue that a band-pass filter applied to the P-cell response would discard the dc component attributable to the chromatic content of the stimulus, thus providing relatively unambiguous information about colour contrast. Similarly low-pass filtering of the P-cell output could provide the chromatic content (Billock, 1991).

In theory the success of Russell filtering depends on the extent to which the spatial tuning of the putative band-pass and low-pass filters each fall exclusively within the pass-bands of the P-cell's response to luminance contrast and colour contrast respectively. Given the sizable overlap between the luminance and colour tuning functions of individual P-cells this would not seem to be a realistic scheme, for example requiring extremely narrow-band band-pass filters to extract pure luminance contrast information from P-cells. The chromatic unit illustrated in Fig. 4a and the model simple cells in Figs 5 and 8 respectively low-pass and band-pass the P-cell output to a good degree of approximation and thus can be considered as physiologically plausible Russell filters. Their demultiplexing capability can in theory be enhanced beyond that which filtering alone is capable by virtue of the inclusion of cancellation (at least to a degree) between different cone-centre-type P-cell inputs. Nevertheless our analysis has shown the limitations of the demultiplexing abilities of these units, particularly in the case of the model simple cells. The limitations of Russell filtering have thus already been considered in the context of its likely physiological implementation in the schemes discussed earlier.

This completes our analysis of possible schemes for separating the colour and luminance components of the image by the primate visual system. Before drawing conclusions, however, we will consider possible reasons why the visual system contains post-receptoral neurones which carry multiplexed information.

4. WHY DEMULTIPLEXING?

One obvious solution to the problem of coding colour and luminance given the univariant nature of cone responses would be for the retina to possess two overlapping layers of different cones types. Two classes of post-receptoral neurones would then be required, one to sum and one to difference (assuming a receptor transduction non-linearity) the output of overlapping pairs or groups of cones at each retinal location to provide luminance and chromatic information respectively. Why, therefore, is the retina organized in such a way that a single cone layer provides information to post-receptoral P-cell neurones which carry a multiplexed signal?

One argument follows from the general principle that the retina is organized so as to minimize the amount of redundant image information that is carried to the higher visual centres (Barlow, 1980; Srinivisan *et al.*, 1982; Buchsbaum and Gottschalk, 1983; Derrico and Buchsbaum, 1991). Derrico and Buchsbaum (1991) have argued that the

receptive-field structure of a P-cell is designed precisely to achieve this goal. Using decorrelation techniques with natural images they conclude that two operators are needed to represent efficiently the available information, one which is cone-opponent and spatially low-pass, the other achromatic and spatially band-pass. P-cells combine both types of operator in one and thus reduce the required channel capacity in two ways: firstly by removing information that is redundant in the chromatic and luminance domains and secondly by multiplexing the information that remains to be transmitted.

Another reason is that multiplexing may simply reflect the priority that the visual system places on detecting luminance, rather than colour contrast. Recent speculations on the evolution of trichromacy are relevant to this issue. Mollon (1989) has argued on the basis of recent molecular genetic evidence from Nathans *et al.* (1986) that, prior to the evolutionary development of trichromacy, a primordial, 'blue-yellow' dichromatic system existed in which the retina contained a small number of *S* cones and a substantial majority of a putative cone type whose spectral sensitivity lay within the region of the present *L* and *M* cones. Under such retinal organization the majority of ganglion cells in the primordial system would have received inputs from just one cone type and these would therefore have signaled only luminance contrast. One possibility therefore is that the primordial middle-to-long wavelength cone type was replaced by a random mixture of *L* and *M* cones with little or no restructuring of the retina. If so, the resulting multiplexing property in the *L* and *M* P-cell response became the inevitable consequence of introducing cone-opponency into a system which previously detected mainly luminance contrast. In theory maximum sensitivity to luminance contrast would be retained in the new system by continuing to pool the signals from all the cones that lay within the P-cell's receptive field, even if this meant a less than optimal cone-opponent signal otherwise achieved through selective wiring. On the other hand, selective wiring of cones into the P-cell centres and surrounds would strengthen the cone-opponent signal at the expense of the response to luminance contrast.

5. CONCLUSION

From a consideration of all the approaches to demultiplexing described above we offer the following conclusions.

1) Models of demultiplexing involving spatial superimposition of P-cell receptive-field pairs are untenable.

2) For middle-to-low spatial-frequency stimuli, chromatic information can be obtained reasonably unambiguously from units which pool the outputs of a large number of P-cells whose receptive-field centres are fed by a single cone. If P-cells with different cone centre types are pooled, then the sign of each P-cell input must covary with the cone centre type. If the cone inputs to P-cell surrounds are selective rather than mixed, then the demultiplexing property of the chromatically sensitive units is enhanced. Thresholding would also provide a cleaner chromatic response. The pooling of P-cells into chromatically sensitive units will, however, limit chromatic resolution.

3) Information about luminance contrast is unlikely to be provided unambiguously at the level of linear simple cell units in the cortex. The effect of selective as opposed to mixed cone inputs to P-cell surrounds will render simple cell units even less able to provide a pure luminance signal. It is possible that demultiplexing to extract achromatic information might be improved at the cortical level either by cross-orientation inhibition between cortical neurones or through the operation of contour extraction mechanisms.

Finally, to what extent is our analysis of the behaviour of model cortical cells consistent with the psychophysical literature on colour-luminance separability that we summarized in the Introduction? Our finding that our model cortical simple cell units failed to provide unambiguous information about luminance contrast might suggest a neural basis for some of the colour-luminance masking interactions that have been observed (Switkes *et al.*, 1988; Gegenfurtner and Kiper, 1992; Mullen and Losada, 1994). However, as we pointed out in the Introduction, the psychophysical literature clearly points to the existence of separable mechanisms for coding colour and luminance in addition to mechanisms sensitive to both. We must therefore conclude that the neural basis for separability must occur beyond the early cortical level.

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APPENDIX

Calculation of combination model P-cell MTFs in response to colour and luminance gratings

We employed a DOG (Difference of Gaussian) approximation to the PSF (point spread function) of the model P-cells:

$$\mathrm{PSF}(x, y) = \exp\left(-\frac{x^2+y^2}{2\sigma^2}\right) - \frac{1}{R^2}\exp\left(-\frac{x^2+y^2}{2\sigma^2 R^2}\right), \tag{A1}$$

where σ is the space constant of the receptive-field centre and R the ratio of space constants of the surround to centre mechanisms. R was set to 1.6 and σ to 24 arcmin.

In computing the MTF of a model P-cell it is useful to consider the centre and surround mechanisms separately. The Hankel Transform defines the Fourier Transform of a radially symmetric function, and for the centre mechanism this is given by

$$F(s)_{\mathrm{cen}} = \int_0^{2\pi}\int_0^{\theta} r\exp\left(-\frac{r^2}{2\sigma^2}\right)\exp(-2\pi j s)\,\mathrm{d}r\,\mathrm{d}\theta, \tag{A2}$$

where r is radial distance, θ angle, s is radial spatial frequency and $j = \sqrt{-1}$. Solving Eqn (A2) gives

$$F(s)_{\mathrm{cen}} = 2\pi\sigma^2\exp\left(-2\pi^2\sigma^2 s^2\right). \tag{A3}$$

Since we are interested in the MTFs of units made up of a number of model P-cell inputs distributed in space, we use the shift theorem (Bracewell, 1986, p. 244) to compute the 2-D Fourier Transform of the centre mechanism when shifted by an amount a, b from the origin. We set the centre-to-centre spacing of adjacent P-cells to 30 arcmin, and the P-cell inputs were always organized in a hexagonal lattice arrangement. Expressing spatial frequency now instead in Cartesian coordinates u, v, the shifted 2-D Fourier Transform is given by

$$F(u, v, a, b)_{\text{cen}} = 2\pi\sigma^2 \exp\Big(-2\pi^2\sigma^2\big(u^2+v^2\big)\Big) \exp\big(-2\pi j(au+bv)\big), \quad \text{(A4)}$$

and for the surround mechanism

$$F(u, v, a, b)_{\text{sur}} = -2\pi\sigma^2 \exp\Big(-2\pi^2\sigma^2R^2\big(u^2+v^2\big)\Big) \exp\big(-2\pi j(au+bv)\big). \quad \text{(A5)}$$

Note both the inclusion of R (ratio of surround to centre space constants) and the negative prefix in Eqn (A5). The negative prefix reflects the inhibitory nature of the surround mechanism.

Equations (A4) and (A5) can be expressed in terms of their individual cosine and sine amplitude spectral components, $A(u, v, a, b)$ and $B(u, v, a, b)$, thus:

$$A(u, v, a, b)_{\text{cen}} = 4\pi\sigma^2 \exp\Big(-2\pi^2\sigma^2\big(u^2+v^2\big)\Big) \cos\big(2\pi(au+bv)\big), \quad \text{(A6)}$$

$$B(u, v, a, b)_{\text{cen}} = 4\pi\sigma^2 \exp\Big(-2\pi^2\sigma^2\big(u^2+v^2\big)\Big) \sin\big(2\pi(au+bv)\big), \quad \text{(A7)}$$

$$A(u, v, a, b)_{\text{sur}} = -4\pi\sigma^2 \exp\Big(-2\pi^2\sigma^2R^2\big(u^2+v^2\big)\Big) \cos\big(2\pi(au+bv)\big), \quad \text{(A8)}$$

$$B(u, v, a, b)_{\text{sur}} = -4\pi\sigma^2 \exp\Big(-2\pi^2\sigma^2R^2\big(u^2+v^2\big)\Big) \sin\big(2\pi(au+bv)\big). \quad \text{(A9)}$$

To calculate model P-cell responses to isoluminant RG (red-green) gratings, the following terms must now be defined.

$L_{\lambda 1}$ = the response of an L cone to light of wavelength $\lambda 1$,
$L_{\lambda 2}$ = the response of an L cone to light of wavelength $\lambda 2$,
$M_{\lambda 1}$ = the response of an M cone to light of wavelength $\lambda 1$,
$M_{\lambda 2}$ = the response of an M cone to light of wavelength $\lambda 2$.

The wavelengths $\lambda 1$ and $\lambda 2$ refer to the two sinusoidal components, the green (G) and red (R) components, which when 180 degrees out of phase produce the RG (red-green) grating. The two selected wavelengths were 526 nm and 602 nm, respectively. This wavelength pair was employed in the measurement of chromatic contrast sensitivity by Mullen (1985). The responses of the L and M cones to these wavelengths were calculated from Smith and Pokorny's (1975) cone sensitivity functions, normalized to

that of the M cone in response to the 526 nm stimulus. The resulting values were $L_{\lambda 1} = 0.65$; $L_{\lambda 2} = 0.704$; $M_{\lambda 1} = 1.0$; $M_{\lambda 2} = 0.33$. Four more parameters must also be defined:

$$\begin{aligned} p_{\mathrm{L}} &= \text{the proportion of } L \text{ cones in the population,} \\ p_{\mathrm{Lcen}} &= \text{the proportion of } L \text{ cones in a given P-cell centre,} \\ p_{\mathrm{Lsur}} &= \text{the proportion of } L \text{ cones in a given P-cell surround,} \\ Q &= \text{the ratio of amplitudes of the R and G components } (\lambda 2/\lambda 1). \end{aligned}$$

The value of Q, the ratio of amplitudes of the red and green components in the RG gratings, was calculated to produce an isoluminant stimulus using Eqn (A10) below. Isoluminance was defined as that ratio of R to G amplitudes which produces an equal quantum catch in the total population of L and M cones. Thus:

$$\begin{aligned} Q = p_{\mathrm{L}} L_{\lambda 1} + (1 - p_{\mathrm{L}}) M_{\lambda 1} \\ p_{\mathrm{L}} L_{\lambda 2} + (1 - p_{\mathrm{L}}) M_{\lambda 2}. \end{aligned} \tag{A10}$$

In the case of model P-cell units with mixed surrounds, p_{L} in Eqn (A10) was set to 0.6667 and Q was thus calculated to be 1.323. For the model P-cells with selective surrounds, p_{L} in Eqn (A10) was set to 0.5 in order that isoluminance was definable for the combination P-cell units themselves, and this resulted in a value of Q of 1.301. The cosine and sine amplitude spectra of the response of a single P-cell to an RG grating is then computed by combining Eqns (A6)–(A9) with the above defined parameters. The result is

$$\begin{aligned} A(u, v, a, b)_{\mathrm{RG}} = {} & A(u, v, a, b)_{\mathrm{cen}} p_{\mathrm{Lcen}} L_{\lambda 1} + (1 - p_{\mathrm{Lcen}}) M_{\lambda 1} \\ & - Q\left(p_{\mathrm{Lcen}} L_{\lambda 2} + (1 - p_{\mathrm{Lcen}}) M_{\lambda 2}\right) \\ & + A(u, v, a, b)_{\mathrm{sur}} p_{\mathrm{Lsur}} L_{\lambda 1} + (1 - p_{\mathrm{Lsur}}) M_{\lambda 1} \\ & - Q\left(p_{\mathrm{Lsur}} L_{\lambda 2} + (1 - p_{\mathrm{Lsur}}) M_{\lambda 2}\right). \end{aligned} \tag{A11}$$

Note that the terms for the surround mechanism are all positive because the negative sign indicating an inhibitory surround has already been prefixed in Eqn (A5) and Eqns (A6)–(A9).

The change in sign preceding all terms with $\lambda 2$ reflects the 180 degrees phase difference between the red and green components.

For the achromatic (ACHR) gratings, the cosine amplitude spectrum is:

$$A(u, v, a, b)_{\mathrm{ACHR}} = k\left(A(u, v, a, b)_{\mathrm{cen}} + A(u, v, a, b)_{\mathrm{sur}}\right), \tag{A12}$$

where k is a scaling factor set to a value of 0.755, the mean value of $L_{\lambda 1}$, $QL_{\lambda 2}$, $M_{\lambda 1}$ and $QM_{\lambda 2}$.

Equations for the *sine* amplitude spectra, $B(u, v, a, b)_{\mathrm{RG}}$ and $B(u, v, a, b)_{\mathrm{ACHR}}$ can be similarly defined.

To calculate the amplitude spectra of a *combination* P-cell unit the individual P-cell cosine amplitude spectra must be summed separately to that of their sine amplitude spectra, taking into account each P-cell's position in space with respect to the origin, cone composition of both the centre and surround and polarity ('On' or 'Off' centre). Thus

$$A(u, v)_{\mathrm{RG}} = \mathrm{sgn}\,(i)\, A\big(u, v, ai, bi, p_{\mathrm{Lcen}.i}, p_{\mathrm{Lsur}.i}\big)_{\mathrm{RG}}, \tag{A13}$$

$$B(u, v)_{\mathrm{RG}} = \mathrm{sgn}\,(i)\, B\big(u, v, ai, bi, p_{\mathrm{Lcen}.i}, p_{\mathrm{Lsur}.i}\big)_{\mathrm{RG}}, \tag{A14}$$

where N is the total number of model P-cells input to the filter, a_i and b_i represents the coordinate position of the ith P-cell input, $p_{\mathrm{Lcen}.i}$ and $p_{\mathrm{Lsur}.i}$ the proportion of L cones respectively in the centre and surround of the ith P-cell input and sgn (i) the polarity of the ith P-cell, where sgn $(i) = +1$ for an 'On' centre P-cell and -1 for an 'Off' centre P-cell. Expressions for cosine and sine amplitude spectra for combination model P-cells in response to RG ($A(u, v)_{\mathrm{RG}}$ and $B(u, v)_{\mathrm{RG}}$) and ACHR ($A(u, v)_{\mathrm{ACHR}}$ and $B(u, v)_{\mathrm{ACHR}}$) are similarly computed.

Finally the MTFs of the combination P-cell filters to the two types of stimulus (RG and ACHR) are then given by the Pythagorean sum of the respective cosine and sine amplitude spectra:

$$\mathrm{MTF}\,(u, v)_{\mathrm{RG}} = \left[A(u, v)^2_{\mathrm{RG}} + B(u, v)^2_{\mathrm{RG}}\right]^{1/2}, \tag{A15}$$

$$\mathrm{MTF}\,(u, v)_{\mathrm{ACHR}} = \left[A(u, v)^2_{\mathrm{ACHR}} + B(u, v)^2_{\mathrm{ACHR}}\right]^{1/2}. \tag{A16}$$

Note that if the phase spectra were required they can be computed by taking the arctan of the ratio of the sine to cosine amplitude spectra.