J. Physiol. (1984), **357**, *pp.* 241–265
With 15 *text-figures*
Printed in Great Britain

CHROMATIC MECHANISMS IN LATERAL GENICULATE NUCLEUS OF MACAQUE

BY A. M. DERRINGTON*, J. KRAUSKOPF† AND P. LENNIE‡
From the Laboratory of Experimental Psychology, University of Sussex, Brighton, England

(*Received 3 February 1984*)

SUMMARY

1. This paper introduces a new technique for the analysis of the chromatic properties of neurones, and applies it to cells in the lateral geniculate nucleus (l.g.n.) of macaque. The method exploits the fact that for any cell that combines linearly the signals from cones there is a restricted set of lights to which it is equally sensitive, and whose members can be exchanged for one another without evoking a response.

2. Stimuli are represented in a three-dimensional space defined by (a) an axis along which only luminance varies, without change in chromaticity, (b) a 'constant B' axis along which chromaticity varies without changing the excitation of blue-sensitive (B) cones, (c) a 'constant R & G' axis along which chromaticity varies without change in the excitation of red-sensitive (R) or green-sensitive (G) cones. The orthogonal axes intersect at a white point. The isoluminant plane defined by the intersection of the 'constant B' and 'constant R & G' axes contains lights that vary only in chromaticity. In polar coordinates the constant B axis is assigned the azimuth 0–180 deg, and the constant R & G axis the azimuth 90–270 deg. Luminance is expressed as elevation above or below the isoluminant plane (−90 to +90 deg).

3. For any cell that combines cone signals linearly, there is one plane in this space, passing through the white point, that contains all lights that can be exchanged silently. The position of this 'null plane' provides the 'signature' of the cell, and is specified by its *azimuth* (the direction in which it intersects the isoluminant plane of the stimulus space) and its *elevation* (its angle of inclination to the isoluminant plane).

4. A colour television receiver was used to produce sinusoidal gratings whose chromaticity and luminance could be modulated along any vector passing through the white point in the space described. The spatial and temporal frequencies of modulation could be varied over a large range.

5. When stimulated by patterns of low spatial and low temporal frequency, two groups of cells in the *parvocellular* laminae of the l.g.n. were distinguished by the locations of their null planes. The null planes of the larger group were narrowly distributed about an azimuth of 92·6 deg and more broadly about an elevation of 51·5 deg, which suggests that they receive opposed, but not equally balanced, inputs

* Present address: Department of Psychology, Durham University, Durham, England.
† On leave from: AT&T Bell Laboratories, Murray Hill, NJ 07974, U.S.A.
‡ Present address and address for correspondence: Center for Visual Science, University of Rochester, Rochester, NY 14627, U.S.A.

from only R and G cones. These we call R–G cells. The null planes of the smaller group were narrowly distributed about an azimuth of 178·4 deg and an elevation of 76·7 deg, which suggests that these cells receive inputs from B cones almost equally opposed by some combined input from R and G cones. We call these B–(R & G) cells. No cells were found that lacked chromatic opponency.

6. By assuming that the spectral sensitivities of the macaque's cones are like those of man's, the azimuths and elevations of the null planes can be transformed by the use of Smith & Pokorny's (1975) fundamental spectral sensitivities to yield the weights attached by each cell to signals from the three classes of cone. This representation shows that cells that receive inputs from B cones have these inputs opposed by varying combinations of inputs from R and G cones.

7. Raising the spatial frequency of a grating systematically reduced the elevations but did not systematically alter the azimuths of the null planes of parvocellular units. This change, which was more pronounced for R–G than for B–(R & G) units, shows that the constituent opponent mechanisms are not spatially co-extensive.

8. Increasing the temporal frequency of modulation (up to 15 Hz) systematically, but only slightly, reduced the elevations of the null planes of parvocellular units.

9. When stimulated by patterns of low spatial and temporal frequency, the elevations of the null planes of *magnocellular* units were clustered around 23·2 deg, with broadly distributed azimuths. The elevations of the null planes dropped to 9·7 deg as spatial frequency was raised, which suggests that the receptive fields are both spatially and chromatically opponent. Changes in temporal frequency up to 15 Hz had little effect on receptive field organization.

10. An analysis of cone contributions to the receptive fields of magnocellular units shows that R and G cones contribute differentially to the centre and surround of most of them. Some units appear to receive signals from B cones.

INTRODUCTION

The macaque's retina contains three types of cone photoreceptors that have different absorbance spectra (Bowmaker, Dartnall & Mollon, 1980). At later stages in the visual pathway the signals from these three classes of cones are combined in chromatically opponent mechanisms. All are agreed that chromatic opponency is a distinctive feature of many ganglion cells in the macaque's retina (Gouras, 1968; De Monasterio & Gouras, 1975) and relay cells in its lateral geniculate nucleus (l.g.n.) (De Valois, Abramov & Jacobs, 1966; Wiesel & Hubel, 1966), although published observations suggest a great diversity of chromatic properties. This is to be contrasted with psychophysical evidence (particularly from Krauskopf, Williams & Heeley, 1982) that points to the existence of just two types of chromatically opponent mechanism in man.

One reason for the variation in the physiological characteristics may be that the techniques generally used to determine the chromatic properties of cells are very sensitive to the particular conditions under which the measurement is made (e.g. state of chromatic adaptation, temporal and spatial properties of the stimulus). In this paper we introduce a new method to characterize neurones in the l.g.n. under uniform conditions that permits a simple expression of their chromatic properties. We show

that cells fall naturally into distinct and rather homogeneous groups: two chromatically opponent classes in the parvocellular layers and a separate magnocellular group.

METHODS

The experiments were undertaken on seven *Macaca fascicularis* and one *Macaca mulatta*, all of which also provided material for the preceding paper, which describes the preparation and recording.

As a preliminary the receptive field was characterized by its response to coloured spots on different backgrounds (as described in the previous paper), by the application of the test for linear spatial summation, and by measurement of contrast sensitivity at different spatial frequencies. For many units we also had time to examine the temporal contrast sensitivity and spatio-temporal interaction using the display and techniques described in the preceding paper.

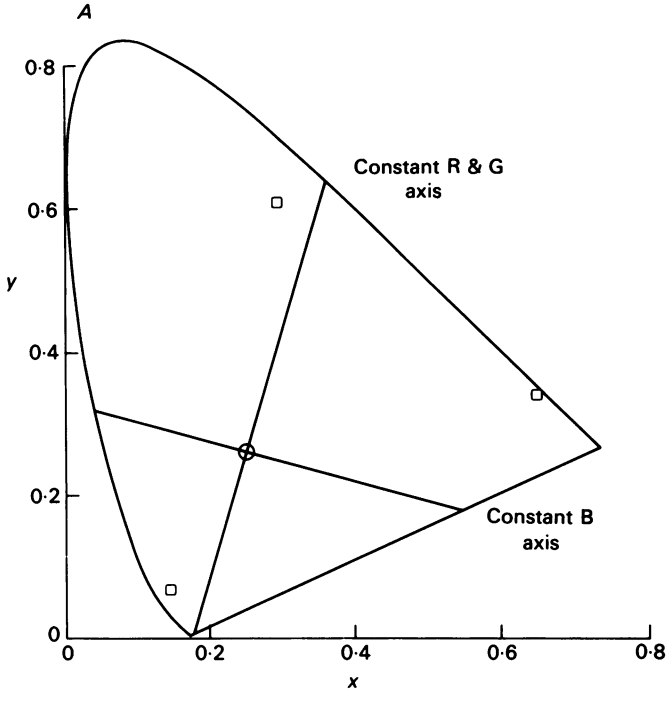
Principle of the analysis

Consider a cell whose receptive field is made up of two antagonistic mechanisms that have different spectral sensitivities. Suppose that each mechanism sums linearly the signals from one or more classes of cone (evidence supporting the assumption of linearity will be presented subsequently), then providing that the adaptive state of that mechanism is not disturbed, its response to a light of any spectral composition and fixed intensity can be matched exactly by the response to a light of any other spectral composition, suitably adjusted in intensity. Thus interchanging such stimuli, which we call 'silent substitution pairs', will produce no change in the response of the mechanism. Similarly, if responses of the two mechanisms that make up the receptive field are combined additively to generate the response of the cell, there will be silent substitution pairs for the *cell* that, in general, differ from those for the constituent *mechanisms*. Because different combinations of cone signals will require different spectral mixtures for matched responses, the silent substitution pairs for a particular cell provide a distinctive 'signature' that reflects its spectral sensitivity.

For any cell there is an infinity of silent substitution pairs, so we need to find some succinct way of representing its chromatic signature. Since the significant parameters of such pairs are chromaticity and intensity, it might seem natural to represent them using a space formed by adding an intensive dimension to the C.I.E. chromaticity diagram (Fig. 1*A*). We chose instead to use a chromaticity coordinate system introduced by MacLeod & Boynton (1978) because its axes correspond to the 'cardinal directions' of colour space identified by Krauskopf *et al.* (1982), and in addition are the directions of best response expected of l.g.n. cells on simple physiological assumptions that we introduce below.

Along one axis of this space (the 'constant B' axis) the signal from blue-sensitive (B) cones is constant while signals from red-sensitive (R) and green-sensitive (G) cones co-vary so as to keep their sum constant. The second ('constant R & G') axis is a line along which the signals from R and G cones are constant and only that from B cones varies. We add to these two dimensions a third dimension of luminance (or radiance) variation. Signals from all three cone classes vary proportionally along this dimension. In this space a change in chromaticity along the constant B axis from white towards red is assigned a direction 0 deg, and along the constant R & G axis towards yellow–green is assigned 90 deg. The opposite ends of these axes are assigned the directions 180 deg and 270 deg, respectively (Fig. 1*B*). In directions orthogonal to this chromaticity plane, increasing luminance is assigned a direction of 90 deg and decreasing luminance a direction of −90 deg. In what follows we assume (in keeping with psychophysical evidence) that luminosity depends only upon the suitably weighted sum of signals from R and G cones. This does not imply that movement along the luminance axis has no effect on B cones; it implies only that in any (isoluminant) plane orthogonal to the luminance axis the sum of signals from R and G cones is constant.

Consider the responses of an R–G cell (that is, one that receives opposed inputs from R and G cones) to variations in colour of a spatially uniform field. It will respond best to stimuli that vary along the constant B axis but, more important for our analysis, it will not respond to modulations along the line of constant R & G excitation nor, if the antagonistic mechanisms are well



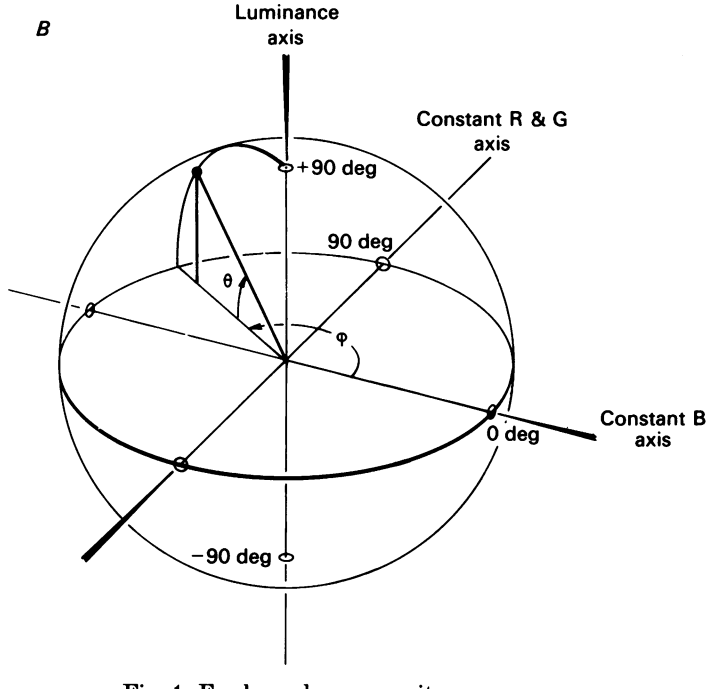


Fig. 1. For legend see opposite.

balanced, along the luminance axis: in the former case this is because signals from neither R nor G cones vary, in the latter case because the variations in signals from R and G cones are equal and opposite.

Similarly, a B–(R & G) cell (which receives opposed inputs from B cones on the one hand and R and G cones on the other) will respond to modulation along a constant R & G line and will not respond to modulation along either of the other two axes. It will fail to respond to modulation along the constant B axis because the signal from B cones is unchanging and the R & G input, assumed to be the sum of the signals from the R and G cones, is by definition constant in the isoluminant plane. The cell will not respond to modulation along the luminance axis because changes in the signal from B cones are cancelled by the changes in R & G signal from R and G cones.

In what follows we use the expressions R–G (or G–R) and B–(R & G) (or (R & G)–B) to denote classes of chromatically opponent unit, where the first term in the expression refers to the excitatory mechanism. Where it is not important to distinguish between R–G and G–R cells, or between B–(R & G) and (R & G)–B cells, we use only the expressions R–G and B–(R & G).

Finally, a 'luminance' cell, which sums the signals of R and G cones, will respond best to luminance modulation and not at all to modulations along either of the other two axes. It will be silent to modulation along the constant R & G axis because signals from the R or G cones never change, and it will not respond to modulation along the constant B axis because the sum of the R and G signals is constant.

Thus, we have established for each of these canonical cells that there is a direction of best response and two orthogonal axes that define a plane within which modulation is ineffective. Because responses sum linearly, the response to modulation in any direction can be calculated by vector addition of the responses along the coordinate axes. Hence modulation along any line within the plane defined by two axes of silent modulation will also be silent. Each ideal cell thus has a direction of best response and a 'silent modulation plane' or 'null plane' orthogonal to it.

Cells with other distributions of cone inputs can be considered as being composed of sums of cells of the three linearly independent classes just discussed because the outputs of cells are assumed to be linear sums of the signals from the cones that drive them. It follows that any cell will have an axis of maximal response and a null plane orthogonal to it. The location of either the null plane or the axis of maximal response characterizes the chromatic properties of the cell and either can serve as the chromatic signature; we have chosen to use the coordinates of the null plane.

The assumption of linear summation of cone signals implies that the amplitude of response to modulation along any vector in our stimulus space will be proportional to the component of that vector resolved along the axis of maximal response, i.e. to the sine of the angle between the vector and the null plane. The response is therefore given by:

$$R = K\{\sin\theta \,.\, \cos\theta_0 - \cos\theta \,.\, \sin\theta_0 \,.\, \sin(\phi - \phi_0)\}, \tag{1}$$

where R is the response amplitude in impulses s^{-1}, K is a scale factor, θ is the elevation of the vector, θ_0 is the elevation of the null plane, ϕ is the azimuth of the vector, ϕ_0 is the azimuth of the null plane (see Fig. 1*B* for the definitions of azimuth and elevation). From eqn. (1) we see that the amplitude of the response will be a sinusoidal function of vector rotation in any plane that contains the white point; in the null plane the amplitude is zero.

Fig. 1*A*, C.I.E. chromaticity diagram showing the coordinates of the red, green and blue phosphors (squares), the white point about which all stimuli were modulated (circle) and the 'constant B' and 'constant R & G' lines that form two of the axes of the colour space used in the present experiments. *B*, chromaticity space in which the 'constant B' and 'constant R & G' axes define an isoluminant plane, centred on the white point. The constant B axis is assigned the direction 0 deg, the constant R & G axis 90 deg. The third axis passes orthogonally through the isoluminant plane at the white point. The direction of any line that passes through the white point is specified by its *azimuth* (angle ϕ, which can take values between 0 and 360 deg) and its *elevation* (angle θ, which can take values between −90 and 90 deg). The colour space can be thought of as a sphere with the white point at its centre; the azimuth and elevation of a point can be thought of as its longitude and latitude respectively.

Visual stimuli

A television display is the most convenient means of producing stimuli whose spatial and temporal properties are to be continuously varied. For the present experiments we employed a domestic colour television receiver (Sony KV 1207), modified to allow signals to be fed directly to the d.c.-coupled amplifiers that controlled the voltages of the red, green and blue cathodes of the cathode ray tube. Red, green and blue signals could be independently varied, if necessary taking new values on each horizontal line displayed. Successive frames, each of which contained 220 lines, were interlaced at 60 Hz. One-dimensional patterns (usually gratings) could be modulated in time or made to move by changing the signals on each frame of the display. Magnocellular neurones (but not parvocellular ones) respond to flicker at the rate at which the display was refreshed (cf. Fig. 12, Derrington & Lennie, 1984). In the present work this was manifest as an entrainment of the maintained discharge, without apparent effect upon the responsiveness to the stimuli presented during experiments.

A PDP 11/34 computer generated the red, green and blue signals and delivered them to the display via an interface designed by W. J. Kropfl of Bell Laboratories. The interface controlled the frame and line scans, and contained buffers to hold the separate red, green and blue signals, which were delivered simultaneously to the display (via 12-bit digital-to-analog converters) each time a new line was generated. The relationships between applied voltage and the luminances of the phosphors were non-linear, so compensating non-linearities were introduced into the signals. Inverse transforms of the voltage *versus* luminance relations for the three primaries were incorporated in look-up tables that were used by the computer program that ran the display. The correction was checked at intervals during the course of the experiments, and found to be satisfactory, but we cannot exclude the possibility that short-term fluctuations in the voltage–intensity relationship, of the kind described by Rodieck (1983), have added some variance to our results.

The chromaticity coordinates of the three phosphors (provided by the manufacturer, and checked for one television set) are shown as squares on the diagram in Fig. 1*A*; that of the white point as an open circle. This point is obtained when each phosphor is driven to half its maximum luminance and has no theoretical significance. A line passing through the white point and the tritanopic co-punctal point (Walraven, 1984) defined the constant R & G axis of our colour space. While changing chromaticity along the constant R & G axis, variations in the amount of blue primary were matched by compensatory changes in the red and green primaries to ensure that luminance remained constant. Lines of constant B cone excitation intersect the chromaticity diagram at $x = 1{\cdot}0$, $y = 0$. It was computationally convenient to construct a constant B axis along which changes in chromaticity were produced by varying only the proportions of the red and green primaries, keeping luminance constant. This line passes through the white point and the coordinate $x = 1{\cdot}19$, $y = 0$, and in our colour space is 0·55 deg from the correct axis, a quite negligible change for the present purposes.

For the experiments described here, we used grating patterns whose spatio-temporal modulation about the white point could be varied along any direction in this three-dimensional space. These patterns were viewed from 5·4 m, at which distance the screen subtended 2·1 by 2·7 deg. Its space–time averaged luminance was 300 cd m^{-2}. A unit vector along the luminance axis provided a Michelson contrast of 1·0 in each primary. A unit vector through the white point in the isoluminant plane cannot be as simply defined, because in that plane there is no single dimension along which the stimulus varies. For practical purposes the unit vector in the isoluminant plane was defined as the modulation produced by the maximum excursion from the white point obtainable from the blue primary, since this was the least luminous of the three. For all experiments described here cells were stimulated by modulations of amplitude 0·89 units.

Analysis of response

In most experiments stimuli were modulated sinusoidally in time at 3·75 Hz (a value chosen to be near the peak of the temporal contrast sensitivity function). Different stimuli, each presented for 1 s, were randomly interleaved and peristimulus time-histograms (p.s.t.h.s) that had a bin width of 16·7 ms were formed from the recorded discharges. The amplitude and phase of the response to a stimulus were obtained by extracting the 3·75 Hz component from the Fourier transform of the histogram. The early part of the histogram, which sometimes contained transients, was discarded in the analysis.

RESULTS

Parvocellular laminae

Most parvocellular units have concentrically organized receptive fields, with centre and surround that have different spectral sensitivities (Wiesel & Hubel, 1966). For these 'type I' units, and also for 'type II' units, which have chromatically but not spatially opponent receptive fields, a spatially uniform field whose chromaticity varies in time should be a very effective stimulus.

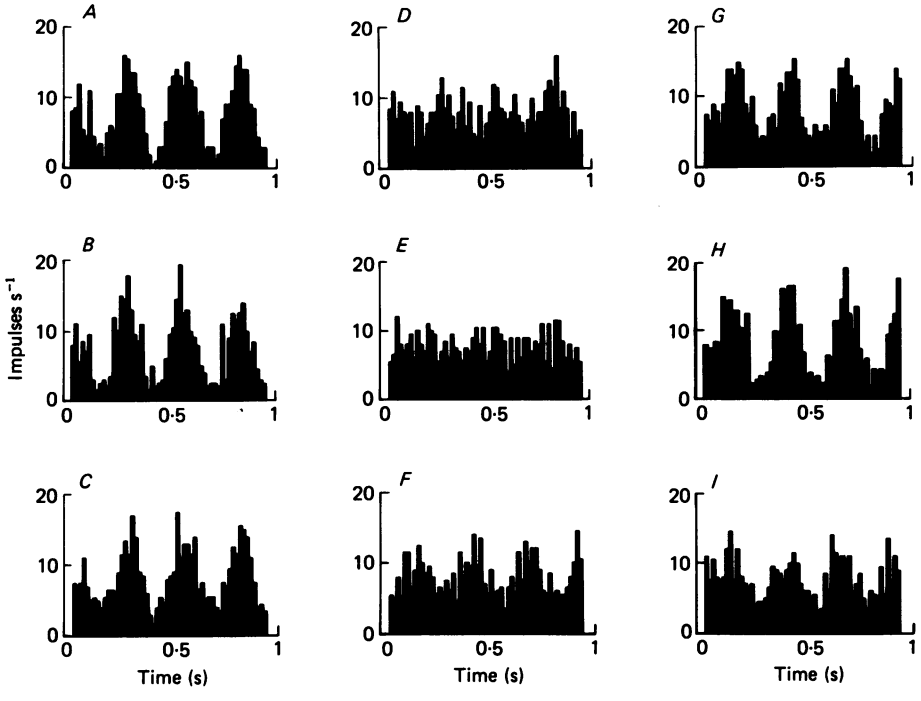


Fig. 2. Peristimulus time-histograms (p.s.t.h.s) of responses to temporal modulation of the chromaticity of a spatially uniform field. For all responses drawn here the modulation was confined to the isoluminant plane (elevation 0 deg); successive records show the effect of changing the azimuth of the direction along which chromaticity was modulated, from 0 deg (*A*) to 180 deg (*I*) in steps of 22·5 deg. Note the change in phase of the response as it passes through the null near 90 deg. Temporal frequency 3·75 Hz; bin width, 16·7 ms; thirty responses accumulated per histogram.

Analysis of null planes. Because eqn. (1) has three unknowns (K, θ_0, ϕ_0) one can, in principle, establish the azimuth and elevation of the null plane by measuring the amplitudes of responses to stimuli modulated along just three vectors that pass through the white point. In practice we used stimuli modulated along many directions, so that the assumptions underlying our analysis could be more easily examined.

Fig. 2 shows p.s.t.h.s of the responses of a type I unit to spatially uniform fields modulated at 3·75 Hz along vectors spaced at 22·5 deg intervals in the isoluminant

plane. The amplitude of response varies progressively with vector rotation, passing through a null (where the phase is reversed) in the region of 90 deg. This direction defines the azimuth of the null plane, and it could be determined precisely by finding the phase of the sinusoid that best describes the variation of response amplitude with vector direction. Similarly, the elevation of the null plane could be found by

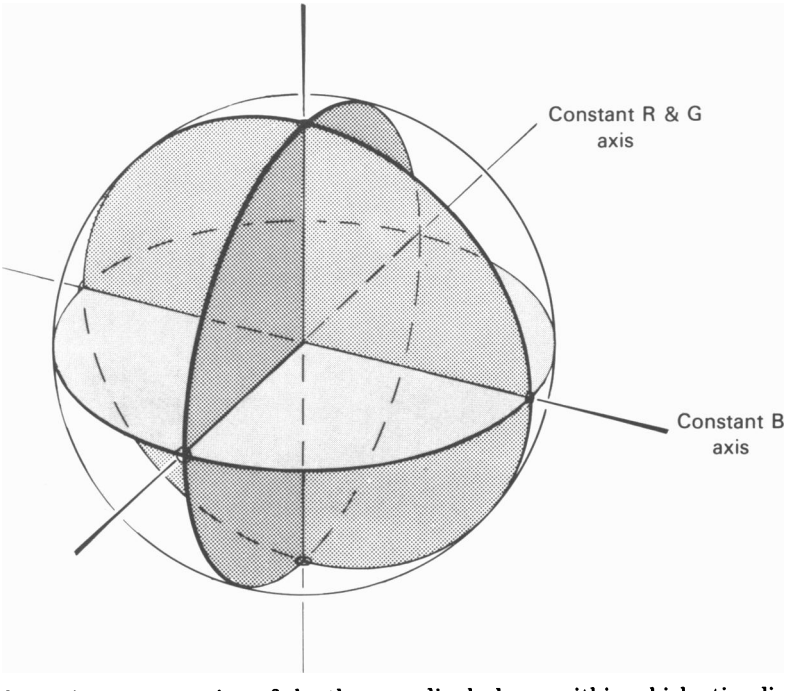


Fig. 3. Schematic representation of the three cardinal planes within which stimuli were modulated in the experiments to establish the position of the null plane for each cell. Within each plane stimuli were modulated along vectors that passed through the white point and were spaced at 22·5 deg intervals.

modulating stimuli along vectors in a vertical plane passing through the isoluminant plane at the azimuth giving the best response. However, it was generally more efficient to find the azimuth and elevation in a single comprehensive experiment in which spatially uniform fields were modulated in time along vectors that lay in three planes passing through the white point. One plane was isoluminant, the others both orthogonal to it, each passing through a cardinal axis in the isoluminant plane. Within each plane stimuli were modulated at 3·75 Hz along nine vectors spaced 22·5 deg apart, as shown schematically in Fig. 3. Each stimulus was presented thirty times, in trials lasting 1 s, randomly interleaved with trials on which other stimuli were presented, and p.s.t.h.s of responses to all stimuli were accumulated concurrently.

Fig. 4*A*, *B*, and *C* shows, for one unit, how response amplitude (the magnitude of the Fourier component at the frequency of modulation) varied with direction of modulation in each of the three planes. If the cell meets our assumption of linearity then response amplitude should vary sinusoidally with vector direction in each plane. The smooth curves drawn through the points are the best-fitting solutions to eqn. (1)

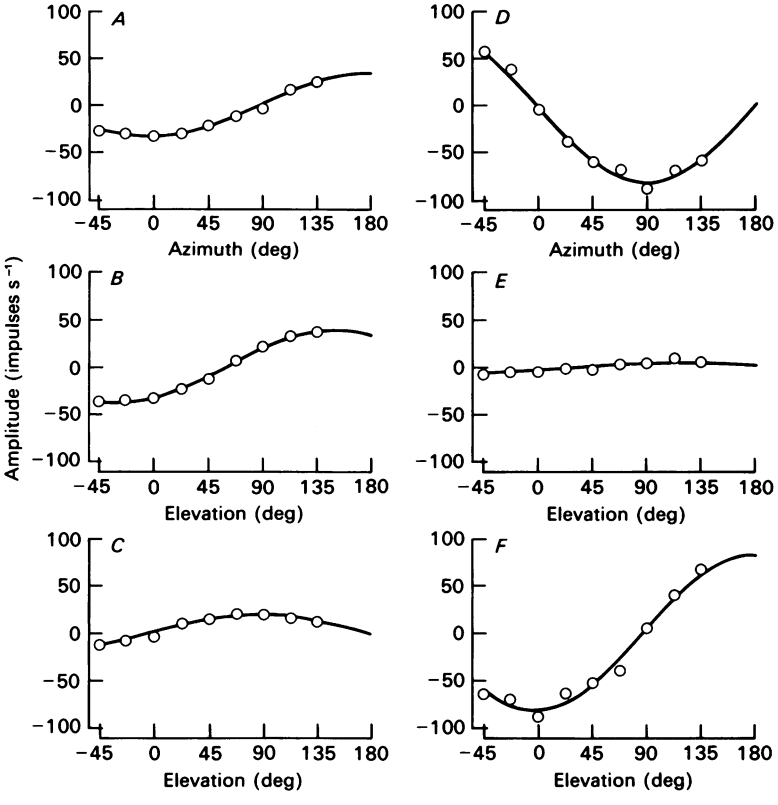


Fig. 4. Variation of response amplitude with direction of stimulus modulation in the three planes illustrated in Fig. 3. Measurements made using spatially uniform fields, modulated at 3·75 Hz, obtained from two parvocellular units (*A*, *B* and *C*) and (*D*, *E* and *F*). Modulation depth was 0·89 (see Methods for definition). *A* and *D*, amplitude of response to modulation in the isoluminant plane (defined by the constant B axis and the constant R & G axis). *B* and *E*, amplitude of responses to modulation in an orthogonal plane (defined by the constant B axis and the luminance axis). *C* and *F*, amplitude of response to modulation in an orthogonal plane defined by the constant R & G axis and the luminance axis. Measurements shown in *A*, *B* and *C* were all obtained in a single experimental run, and the smooth curves are generated from the best-fitting solution to eqn. (1). Similarly for *D*, *E* and *F*. Amplitudes of responses were obtained from Fourier transforms of the p.s.t.h.s, and are shown as negative when the phase of the response was greater than 180 deg.

found by the minimizing routine STEPIT. The fit of the sinusoid is clearly very good, giving a r.m.s. error of 3·5 %; the absence of distortion constitutes a satisfactory test of our assumption of linearity. (Gielen, van Bisbergen & Vendrik (1982) provide rather different evidence for linearity.) For this unit the azimuth of the null plane was 87·5 deg and its elevation −41 deg. Results obtained from another unit are shown in Fig. 4*D*, *E* and *F*. The points here are equally well fitted by eqn. (1), but the azimuth and elevation of the null plane are 178 deg and −83 deg respectively.

101 parvocellular units were subjected to this experiment, and in Fig. 5*A* the elevations of their null planes are plotted against the azimuths (in this graph

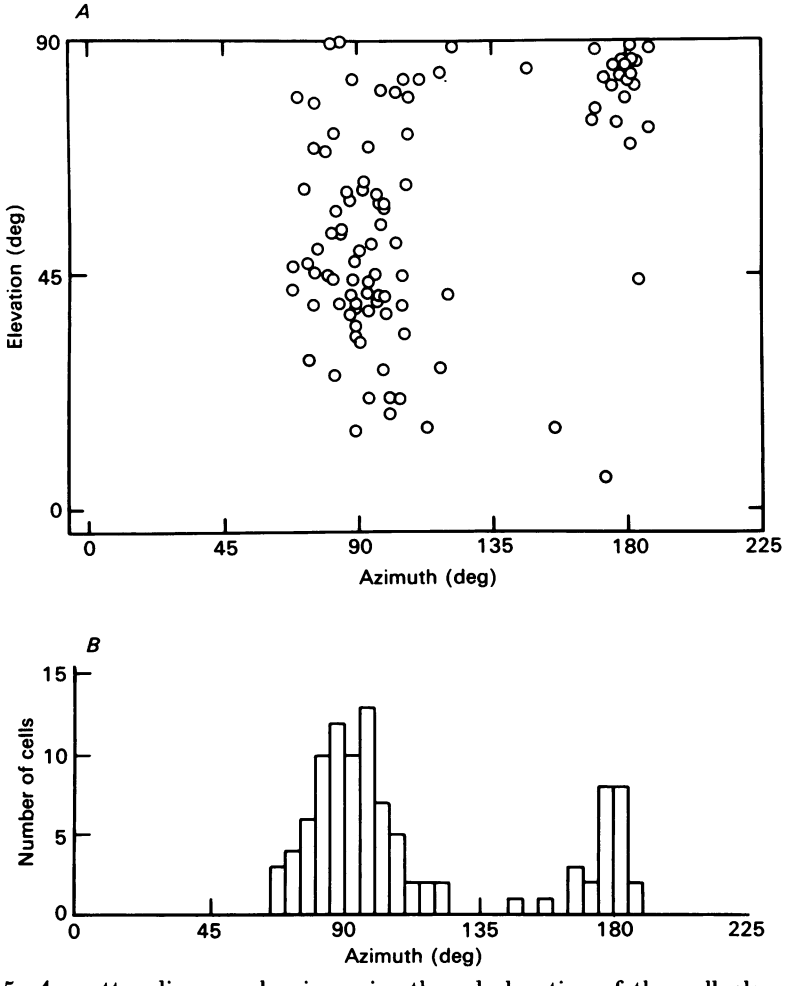


Fig. 5. *A*, scatter diagram showing azimuth and elevation of the null plane of each parvocellular unit subjected to the experiment of Figs. 3 and 4. Elevations are plotted without regard to sign. *B*, distribution of azimuths.

elevations have been plotted without regard to sign). Fig. 5*B*, which shows the distribution of azimuths, emphasizes that there are two quite distinct clusters of cells, a large one with properties represented by the unit of Fig. 4*A*, *B* and *C*, and a smaller one with the properties represented by the unit of Fig. 4*D*, *E* and *F*. The mean azimuth of the larger group is 92·6 deg (S.D. 13·8 deg) and its elevation 51·5 deg (S.D. 19·4 deg), so the mean null plane passes obliquely through the isoluminant plane almost along the constant R & G axis. For the smaller group the azimuth is 178·4 deg (S.D. 5·4 deg) and the elevation 76·7 deg (S.D. 18·0 deg), so the null plane passes steeply through the constant B axis. It should be noted that the relative numbers of units in the two groups shown in Fig. 5 do not represent the frequencies with which they are normally encountered; in one animal we deliberately sought units belonging to the smaller group.

Fig. 5 reveals a group of cells with properties close to those expected of 'ideal' B–(R & G) cells, and a group that has many of the properties expected of R–G cells, although the opponent mechanisms of cells in the latter group appear not to show the fine balance of antagonism expected of the 'ideal' units. Fig. 5 provides no evidence for the existence of a third group of cells that might form the substrate of the 'luminance' channel; the isoluminant plane is the null plane for such a group, so its constituent cells would be expected to have elevations of 0 deg.

The variation in the positions of the null planes revealed by these experiments must be considered an upper bound to the variation that would be found at a given position in the retina of one animal.

Analysis of cone contributions. The azimuth and elevation of the null plane characterize a cell in terms of its response to lights. An alternative way to represent the signature of a cell is by the weights it attaches to inputs from the three classes of cone. This representation provides rather more information about the organization of physiological mechanisms.

The spectral sensitivities of the three classes of human cones are now known relatively precisely from psychophysical experiments (Smith & Pokorny, 1975), and microspectrophotometric work (Bowmaker *et al.* 1980) suggests that those of *M. fascicularis* and *M. mulatta* are very similar. In the following analysis we assume them to be the same. Knowing these spectral sensitivities one can calculate directly what modulation of the signal in any class of cone will be produced by modulating a stimulus along any vector in our colour space.

R cones have a null plane with azimuth 90 (the constant R & G axis) and elevation −3·1 deg; G cones have a null plane with azimuth 90 and elevation 5·28 deg; B cones have a null plane with azimuth 0 and elevation 42·57 deg. For stimuli modulated within the isoluminant plane about the white point used in the present experiments the maximum attainable modulation of R cone signals was 0·057 (along the constant B axis), of G cone signals 0·094 (also along the constant B axis) and of B cone signals 0·917 (along the constant R & G axis).

The signature of a cell can be expressed in terms of the weights it attaches to the modulation of signals from the three classes of cone as:

$$A = w_r M_r + w_g M_g + w_b M_b, \tag{2}$$

where A is the amplitude of the fundamental component of response, in impulses s^{-1}, M_r, M_g and M_b are modulations of R, G and B cone signals, w_r, w_g and w_b are the weights assigned to the modulated signals from R, G and B cones.

The weights w_r, w_g and w_b can be estimated from the solution of eqn. (2) that best fits the observations obtained in the experiment of Fig. 4. Fig. 6 shows the best-fitting estimates of the weights attached to signals from three classes of cone by each cell represented in Fig. 5. In this plot the weights are normalized by dividing each by the sum of the absolute weights attached to R, G and B signals. Thus:

$$W_r = w_r/(w_r + w_g + w_b)$$

and similarly for W_g and W_b. Since the absolute values of the normalized weights sum to unity they can all be represented on a plot of W_g against W_r, in which W_b is implicitly given.

In this representation units that are driven only by R and/or G cones lie along the diagonals connecting unit values on the axes. Cells that receive opposed inputs only from R and G cones will lie on the diagonals in the second and fourth quadrants; neurones that receive signals of the same polarity from only R and G cones will lie on the diagonals in the first and third quadrants. It is clear from Fig. 6 that two

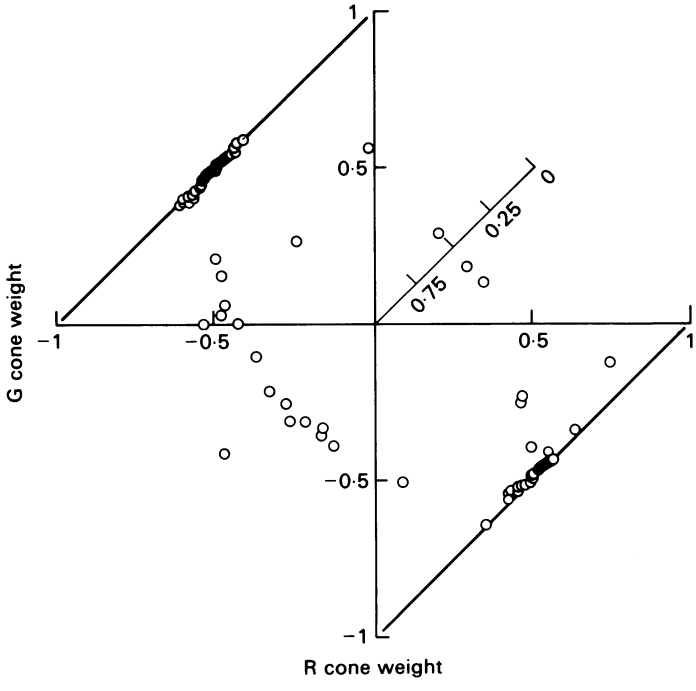


Fig. 6. Scatter diagram showing the weights attached to signals from R and G cones by each parvocellular unit in Fig. 5. Weights are normalized such that $w_r + w_g + w_b = 1$. Points representing cells that receive inputs only from R and G cones will lie along the diagonals that connect unit values on the axes; R–G or G–R cells will lie on the positive diagonals, R & G cells on the negative diagonals. Cells that receive inputs from B cones are represented by points that lie inside the unit diagonals. The magnitude of the weight attached to signals from B cones is constant along lines perpendicular to these diagonals. A scale of B cone weights is given for the upper right quadrant, and may be equivalently applied to corresponding diagonals in the other quadrants.

substantial groups of cells (R–G and G–R) receive opposed inputs from only R and G cones, and that for most cells the R and G cones provide inputs of nearly equal weight. Cells that provided the substrate of the 'luminance' mechanism, with equally weighted inputs from R and G cones, would lie in the first or third quadrants at the coordinates 0·5, 0·5 or −0·5, −0·5. There is apparently no such group of cells in the parvocellular layers of the macaque's l.g.n.

Cells that are substantially influenced by B cones will lie inside the diagonals that connect unit values. Were the signal from B cones opposed by a signal contributed

equally by R and G cones, points would lie at −0·25, −0·25 (for B–(R & G) units) and 0·25, 0·25 (for (R & G)–B units). Both sorts of unit exist (the former being more numerous) but there are also units that receive substantial input from B cones opposed by unequal mixtures of inputs from R and G cones. In units driven by B cones, much of the variability in the weights is probably due to variations in pre-retinal absorption of short wave-lengths. Macular pigmentation varies greatly with eccentricity, and from animal to animal. We have made no attempt to compensate for the effects of this, but any selective absorption of short wave-lengths will appear as some R or G cone signal acting with the same sign as that from B cones.

Null planes versus cone weights. The chromatic properties of units have been summarized in two ways: by the loci of their null planes and by the weights they attach to signals from the three classes of cone. The first provides a functional description, the second a mechanistic one. Both methods reveal the same classes, but give seemingly different accounts of the variability within groups; for example, the standard deviation of the elevations of the null planes of R–G units is 19·4 deg, while almost all of them have cone weights whose absolute values lie between 0·4 and 0·6. The relationship between the elevation of the null plane of an R–G unit and the weights it attaches to signals from cones is given by:

$$\theta_{rg} = \text{atan}\{(W_r \,.\, \sin\theta_r + W_g \,.\, \sin\theta_g)/(w_r \,.\, \cos\theta_r + w_g \,.\, \cos\theta_g)\},$$

where θ_r and θ_g are −3·1 and 5·28, the elevations of the null planes for R and G cones, respectively.

For R–G units $W_g = W_r - 1$, and because the null planes for R and G cones lie so close together a small mismatch between W_r and W_g will bring about a large shift in the elevation of the null plane of the R–G unit: the elevation of the null plane peaks sharply at a value of ±90 deg as W_r approaches ±0·5, and falls to less than 20 deg if W_r is less than 0·4 or greater than 0·6.

The null plane of the B cones has an elevation of 42·57 deg, and in a B–(R & G) cell its opposing mechanism has a null plane of elevation close to 0 deg. Because the elevations of these null planes are so far apart, a small mismatch in the weights attached to the two mechanisms has a relatively small effect on the elevation of the null plane of the B–(R & G) unit.

Sensitivity to chromatic modulation. Our assumption of linearity, demonstrated by the results of Fig. 4, requires that, within the range used in our experiments, the amplitude of response be proportional to the depth of modulation of the stimulus. (In the preceding paper (Derrington & Lennie, 1984) this is verified for responses to achromatic gratings.) We can therefore compare the sensitivities of different units by calculating what stimulus would be required to elicit a criterion response. From an analysis of the amplitudes of component frequencies in the maintained discharge it was established that a response of about 11 impulses s^{-1} would be detected on about 50% of occasions with a false-positive rate of 2%. We then calculated what stimuli would elicit this response. Since we have no simple metric for modulation in the isoluminant plane, we have expressed sensitivities of cells in the units defined in Methods. Along the constant B axis, R–G cells had thresholds distributed about a mean of 0·552; the human observer's threshold for a comparable stimulus was about

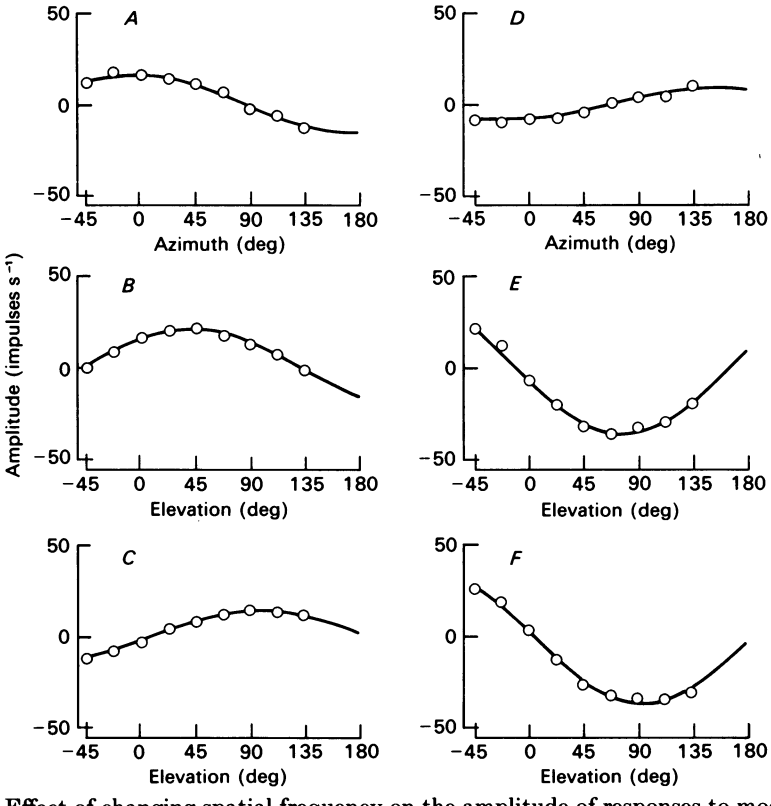


Fig. 7. Effect of changing spatial frequency on the amplitude of responses to modulation along vectors in the three planes illustrated in Fig. 3. *A*, *B* and *C*, spatially uniform field, modulated sinusoidally at 3·75 Hz; *D*, *E* and *F*, sinusoidal grating of 4·25 cycles deg^{-1} (the optimum spatial frequency when the grating was achromatic) moving at 3·75 Hz. Other details as for Fig. 4.

0·019. B–(R & G) units stimulated by modulation along the constant R & G axis had thresholds distributed about a mean of 0·209; the human observer could detect a modulation of 0·032.

Influence of spatial frequency

The hypothesis being explored by our experiments is that the responses of parvocellular units depend upon the additive combination of signals from two antagonistic mechanisms. Any experimental manipulation that changes the balance of signals in these mechanisms will alter the sensitivity of the cell, and therefore its signature. Most parvocellular units have receptive fields with centre–surround organization, so the balance between the sensitivities of the antagonistic mechanisms can be quite simply altered by changing the spatial frequency of stimuli. As spatial frequency is raised from zero (uniform field) the sensitivity of the surround falls before that of the centre. Consequently, the spectral sensitivity of the cell changes with spatial frequency, and there is a concomitant change in the orientation of the null plane.

Fig. 7 shows the results of an experiment in which stimuli were modulated along vectors in three planes in our colour space, first using a spatially uniform field flickering at 3·75 Hz (Fig. 7*A*, *B* and *C*), then using a sinusoidal grating moving at 3·75 Hz (Fig. 7*D*, *E* and *F*); the spatial frequency used (4·25 cycles deg^{-1}) was that to which the cell was most sensitive when stimulated by achromatic gratings. Raising

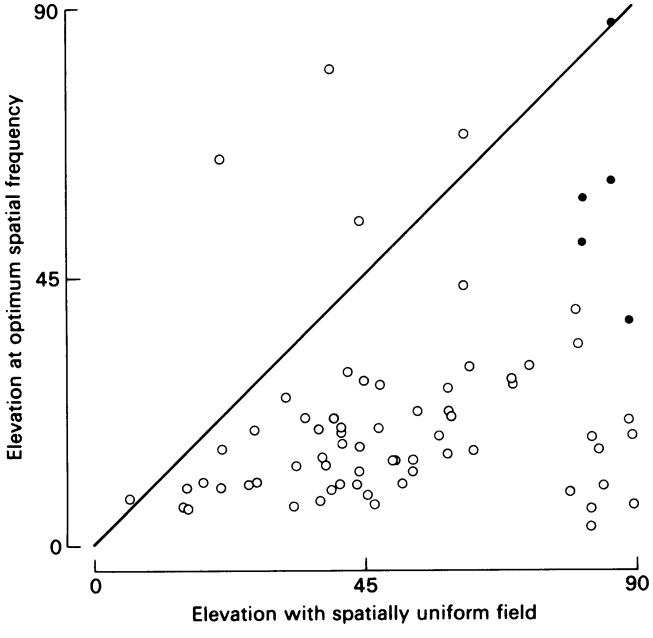


Fig. 8. Scatter diagram showing the effect on the elevation of the null plane of changing spatial frequency from 0 cycle deg^{-1} (uniform field) to that which would be optimum were the cell stimulated by achromatic gratings. For each cell elevation for the optimum spatial frequency is plotted against elevation for a uniform field. Open circles, R–G units; filled circles, B–(R & G) units. A change in spatial frequency from 0 cycle deg^{-1} to optimum reduces the elevation of the null plane (and increases the responsiveness to luminance modulation) in most units. This implies that the opponent mechanisms differ in their spatial distribution of sensitivity.

the spatial frequency from 0 to 4·25 cycles deg^{-1} impaired the response to modulation in the isoluminant plane and improved the responses to modulation in the orthogonal planes. The elevation of the null plane moved from −30 to 7 deg and its azimuth moved from 84 to 69 deg, as spatial frequency was raised. For most units the change in spatial frequency had a marked effect upon the elevation of the null plane, but a small and unsystematic effect on the azimuth. Fig. 8 shows, for seventy units (including five driven by B cones), the elevation of the null plane measured with gratings of optimum spatial frequency plotted against the elevation obtained with a spatially uniform field. Signatures of R–G units are plotted as open circles, those of B–(R & G) units as filled circles. Almost without exception increases in spatial frequency bring about changes in the elevation of the null planes.

The fact that a change in spatial frequency alters the position of the null plane

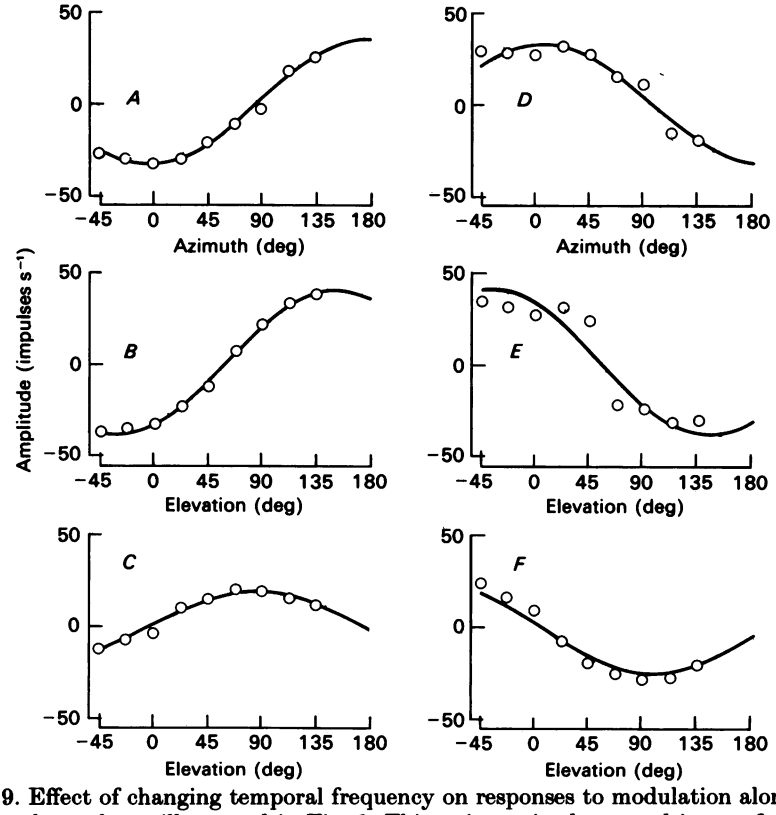


Fig. 9. Effect of changing temporal frequency on responses to modulation along vectors in the three planes illustrated in Fig. 3. This unit received opposed inputs from R and G cones. *A*, *B* and *C*, spatially uniform field modulated sinusoidally at 3·75 Hz; *D*, *E* and *F*, spatially uniform field modulated sinusoidally at 15 Hz. The reversal in the phase of response with change in temporal frequency is a consequence of our assigning negative amplitude to responses of phase greater than 180 deg. It does not reflect a reversal of receptive field properties. Other details as for Fig. 4. Variations in temporal frequency up to 15 Hz have little effect upon the chromatic properties of the cell.

of nearly all units means that these units have receptive fields that are chromatically *and* spatially opponent (i.e. they are 'type I' cells of Wiesel & Hubel, 1966). The implication of Fig. 8 is that units (particularly R–G ones) become more sensitive to luminance contrast and less sensitive to chromatic contrast as spatial frequency is raised. If, by raising spatial frequency, the centre mechanism in R–G units could be isolated perfectly, we would expect the elevation of the null plane to lie between −3·1 deg (the elevation of the null plane for R cones) and 5·28 deg (the elevation of the null plane for G cones). B–(R & G) units appear to be less affected, but it should be remembered that the null plane for B cones is 42·57 deg, and that is the asymptotic elevation expected for the null plane of any B–(R & G) cell that has a centre driven by B cones.

Influence of temporal frequency

The preceding paper provides evidence that in units with receptive fields that have centre–surround organization the surround is relatively less effective at high temporal

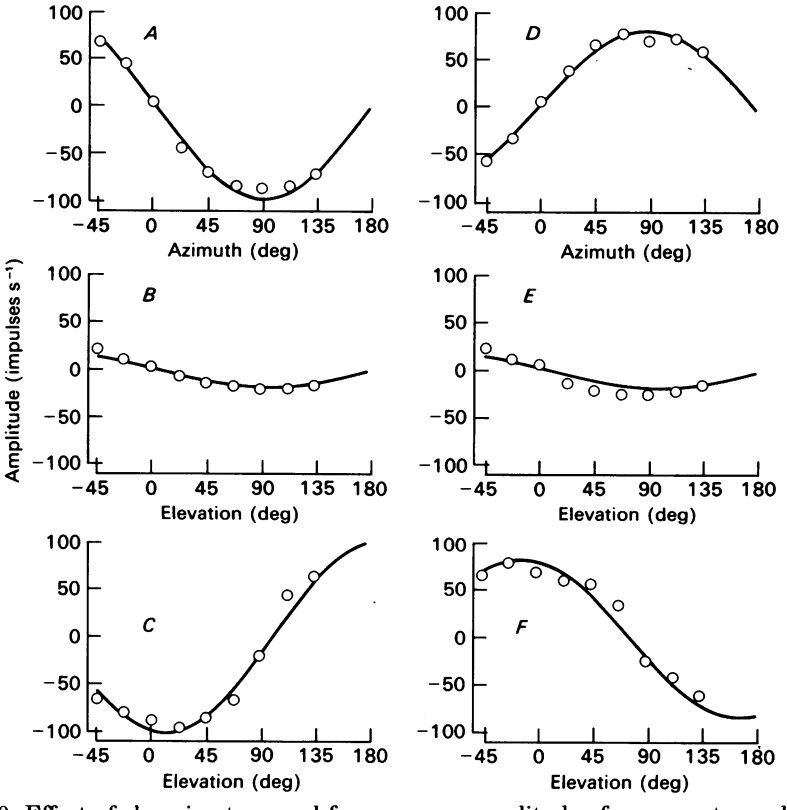


Fig. 10. Effect of changing temporal frequency on amplitude of response to modulation along vectors in the three planes illustrated in Fig. 3. This unit received inputs from B cones opposed to inputs from R and G cones. *A*, *B* and *C*, spatially uniform field modulated sinusoidally at 3·75 Hz; *D*, *E* and *F*, spatially uniform field modulated sinusoidally at 15 Hz. The reversal in the phase of response with the change in temporal frequency results from our assigning negative amplitude to responses of phase greater than 180 deg. It does not reflect a reversal of receptive field properties. Other details as for Fig. 4.

frequencies. We would therefore expect variations in temporal frequency to alter the signature of the cell. The highest temporal frequency that could be produced by our apparatus was 15 Hz; Fig. 9 compares, for one R–G unit, the amplitude of responses to modulation of a spatially uniform field along vectors in three planes at 3·75 Hz (Fig. 9*A*, *B*, and *C*) and 15 Hz (Fig. 9*D*, *E* and *F*). Raising the temporal frequency has no effect upon the azimuth, but slightly reduces the elevation of the null plane, from 41 to 34 deg, which suggests that, over the range of temporal frequencies studied, centre and surround have rather similar dynamics. Fig. 10 shows results from a similar experiment undertaken on a B–(R & G) unit; again, the effect of changing temporal frequency is small (the elevation fell from 70 to 68 deg). The results for all parvocellular units on which measurements were made are summarized in Fig. 11, in which the elevation of the null plane at 15 Hz is plotted against the elevation at 3·75 Hz (there were only small and unsystematic effects upon the azimuth). For both R–G and B–(R & G) units the elevation of the plane is lowered by raising temporal frequency, but only slightly. Our results on this point are consistent with those of

Gielen *et al.* (1982), but not with the observation of Gouras & Zrenner (1979) that, when excited by 15 Hz square-wave flicker, parvocellular units lose their chromatic opponency.

Magnocellular neurones

All magnocellular neurones have spatially opponent receptive fields, and some (type IV units) also show weak chromatic opponency (Wiesel & Hubel, 1966). We might therefore expect magnocellular units to be distinguished from parvocellular

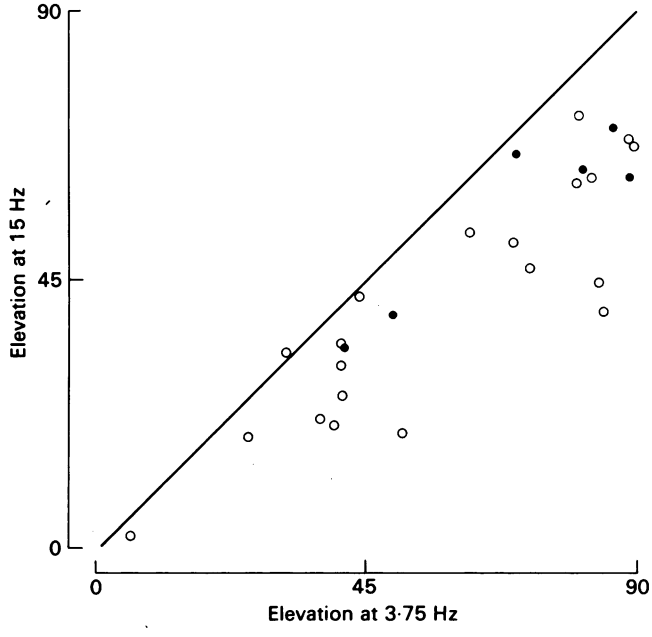


Fig. 11. Scatter diagram showing the effect of changing temporal frequency on the elevations of the null planes of parvocellular units. Open circles, R–G units; filled circles, B–(R & G) units. The elevation of the null plane is reduced with the change in temporal frequency from 3·75 to 15 Hz, although the effect is not large.

ones by having rather poor sensitivity to modulation of chromaticity. Fig. 12*A*, *B* and *C* shows, for one unit, how the amplitude of response varies with direction of modulation of a spatially uniform field in three orthogonal planes that pass through the white point. Unlike most parvocellular cells, this unit responds well to modulation out of the isoluminant plane but poorly to stimulus modulation within it. Fig. 13*A* shows, for all magnocellular units on which measurements were made using uniform fields, the elevation of the null plane plotted against its azimuth. Azimuth values are broadly distributed, and elevations, mostly lower than those of parvocellular units (shown in Fig. 5), are distributed about a mean of 23·2 deg. One consequence of representing our stimuli in a spherical coordinate system is that the azimuth of the null plane becomes undefined when elevation is 0 deg. Units identified as 'type IV' from preliminary observations (indicated by filled circles in Fig. 13*A*) do not form a distinct subgroup when driven by uniform fields.

Schiller & Colby (1983) found that the abrupt exchange of diffuse red illumination for diffuse green illumination evoked a discharge from magnocellular neurones, no matter what the relative luminances of the lights. A non-linearity of this kind should be evident as a second harmonic (F_2) component in the response to modulation of chromaticity, and we examined this in the twenty-five cells on which the experiment of Fig. 12*A*, *B* and *C* was undertaken. A second harmonic component was discernible

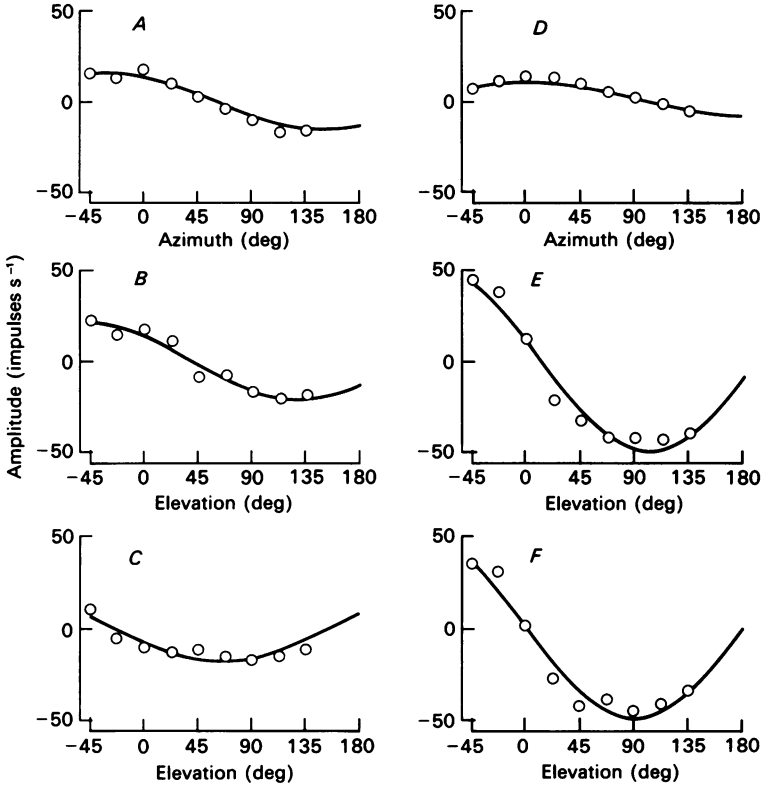


Fig. 12. Variation of response amplitude of a magnocellular unit with direction of stimulus modulation in the three planes illustrated in Fig. 3. *A*, *B* and *C*, measurements made using a spatially uniform field modulated at 3·75 Hz; *D*, *E* and *F*, measurements made using a grating of spatial frequency 1·51 cycles deg^{-1} (the optimum when the grating was achromatic). Other details as for Fig. 4

in the averaged responses of five units, but it was always much smaller than the fundamental component, and its amplitude did not vary systematically with direction of modulation in the isoluminant plane. Units that gave rectified responses to modulation of chromaticity were those that showed the clearest non-linearities of spatial summation (see preceding paper), so the mechanisms that generate rectified responses may possess some degree of chromatic opponency.

Fig. 12*D*, *E* and *F* shows the results obtained when the experiment of Fig. 12*A*, *B* and *C* was undertaken with moving gratings of optimum spatial frequency rather than uniform fields. Increasing spatial frequency from 0 to 1·51 cycles deg^{-1}, which decreases the relative weight of the surround mechanism, greatly increases the

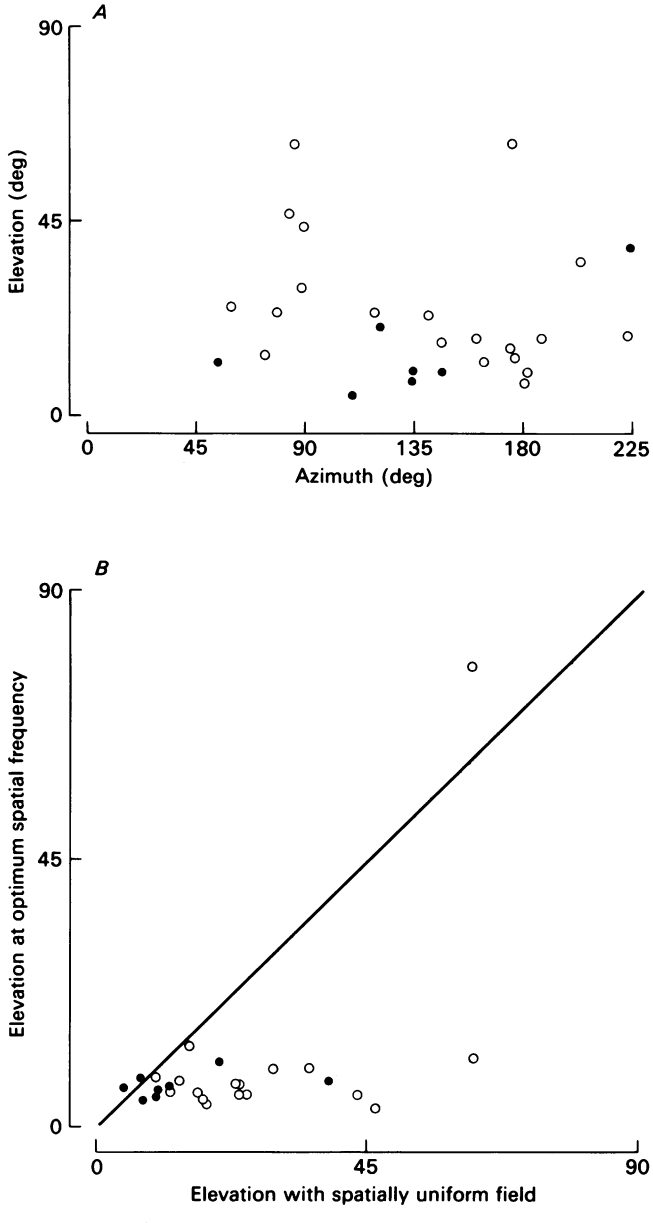


Fig. 13. *A*, scatter diagram showing the azimuths and elevations of the null planes of magnocellular units studied with spatially uniform fields modulated at 3·75 Hz. Elevations are plotted without regard to sign. Open circles mark units provisionally identified as 'type III', filled circles units provisionally identified as 'type IV'. *B*, scatter diagram showing the effect of changing spatial frequency on the elevations of the null planes of magnocellular units. Open circles, type III units; filled circles, type IV units. Optimum spatial frequencies were established from contrast sensitivity curves obtained with achromatic gratings.

amplitude of responses to stimulus modulation out of the isoluminant plane, and changes the elevation and azimuth of the null plane from 26 to 5 deg and from 59 to 93 deg respectively. The effect of changing spatial frequency was studied on twenty-five magnocellular units; there were no systematic changes in the position of the azimuth of the null plane but in all but two cells its elevation was reduced

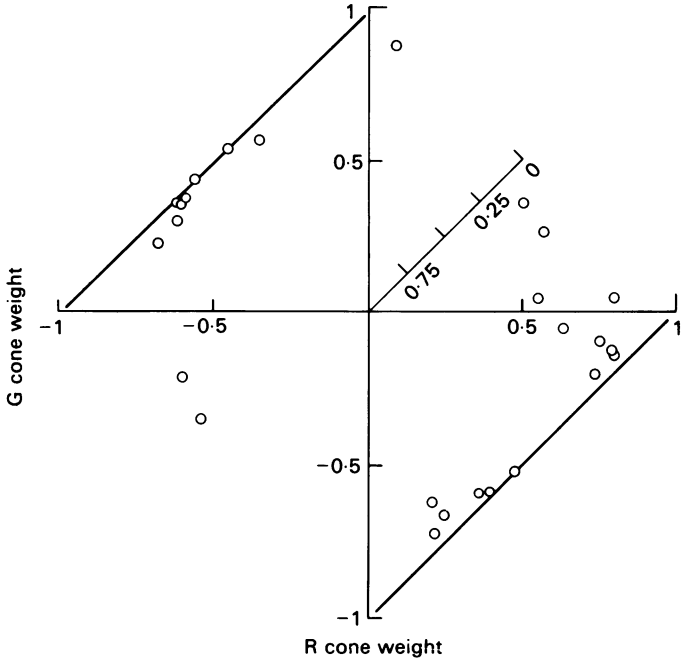


Fig. 14. Scatter diagram showing the weights attached to signals from R and G cones by each magnocellular unit in Fig. 13*A*. Weights are normalized such that $w_r + w_g + w_b = 1$. Other details as for Fig. 6.

(from a mean of 23·2 to 9·7 deg). This is shown in Fig. 13*B*, where the elevation of the null plane obtained using the optimum grating is plotted against the elevation obtained using a uniform field. Had centre and surround the same spectral sensitivities, we should have expected the points to be scattered along the 45 deg diagonal. They fall almost along the abscissa, which demonstrates that magnocellular units have receptive field mechanisms that are both chromatically and spatially opponent. An analysis of the relative weights contributed by the three classes of cones is given in Fig. 14 using the conventions introduced in Fig. 6. It shows that most magnocellular units have opposed inputs from R and G cones, although these inputs are much less well balanced than those of parvocellular units (cf. Fig. 6) and many units receive some input from B cones.

If centre and surround have different temporal properties, it should be possible, by changing the temporal frequency at which measurements are made, to alter the position of the null plane. The experiment of Fig. 12*A*, *B* and *C* was undertaken on nine magnocellular units at temporal frequencies of 3·75 and 15 Hz; the change of temporal frequency brought about no systematic change in either the azimuth or the elevation of the null plane.

DISCUSSION

Classes of parvocellular neurone

Our results suggest that parvocellular neurones fall into only two classes, one (R–G units) that receives opposed inputs from R and G cones, the other (B–(R & G)) that receives inputs from B cones opposed to variously weighted inputs from R and G cones. All R–G units have null planes that pass through the isoluminant plane close to the constant R & G axis (azimuth 90 deg), but the elevations are spread around a mean of 51·5 deg, which suggests that in most units one cone type contributes greater weight than the other. Fig. 5 does not tell us how the two types of cone contribute to centre and surround, but that information is obtained by establishing the azimuth and elevation of the null plane with a grating that isolates the centre. (The spatial frequency of this grating equals or exceeds that which gives the greatest contrast sensitivity for achromatic gratings.) For all but five R–G units an increase in spatial frequency reduced the elevation of the null plane, by an amount proportional to its initial height (Fig. 8). This demonstrates that the R and G cones contribute differentially to centre and surround. Cells with weak chromatic opponency are probably those identified by Wiesel & Hubel (1966) as 'type III'; they are not qualitatively distinguishable from the colour-opponent 'type I' cells. Within our sample of cells (all drawn from within 10 deg of the fovea) there was no indication that the degree of chromatic opponency varied with eccentricity.

B–(R & G) units, which are much less frequently encountered than R–G ones, have null planes that pass through the isoluminant plane close to the constant B axis (azimuth 0 deg) with elevations that are clustered near 90 deg. If the position of the null plane is established with a grating rather than a uniform field, the azimuth is not systematically altered, and the elevation is decreased (Fig. 8, filled circles), which suggests that for most of these units the spatial distributions of the opposing mechanisms differ.

Our results differ from those of earlier investigators in showing that parvocellular units fall into only two groups and in showing that these groups have rather uniform chromatic properties. One way to represent this uniformity is to confine ourselves to the isoluminant plane and establish for each cell what monochromatic light could be silently substituted for a white light of equal luminance. This monochromatic light defines the 'neutral point' of a cell and provides a chromatic signature that may be compared with that obtained by other workers (e.g. De Valois *et al.* 1966; Wiesel & Hubel, 1966). The monochromatic neutral point of a cell can be derived from our results by plotting the azimuth of the null plane on the C.I.E. chromaticity diagram and projecting a line from the white point through the azimuth to the spectrum locus. Fig. 15 shows a C.I.E. chromaticity diagram on which lines connecting the white point to the average azimuth (± 1 S.D.) have been projected to the spectrum locus. For R–G units the average neutral point is 558 ± 4 nm and for the B–(R & G) units it is 492 ± 3 nm. This spread is much smaller than that found by earlier investigators, and it is worth considering what features of our experiments give rise to it.

Two factors probably explain the greater consistency of our results. First, in our experiments the stimuli were modulated about a fixed white point, and the variations in signals arriving at the opponent site were relatively small, so the opponent

mechanism was only modestly perturbed about some equilibrium state. Moreover, the highest temporal frequency used was 15 Hz, so any small differences in time of arrival of signals would be of little consequence. When the signals from cones are large, and/or the equilibrium of the opponent site is disturbed, we might expect much less linear behaviour. Large signals can reach the opponent site if a uniform field is suddenly presented to the dark-adapted eye, or if one class of cone is substantially

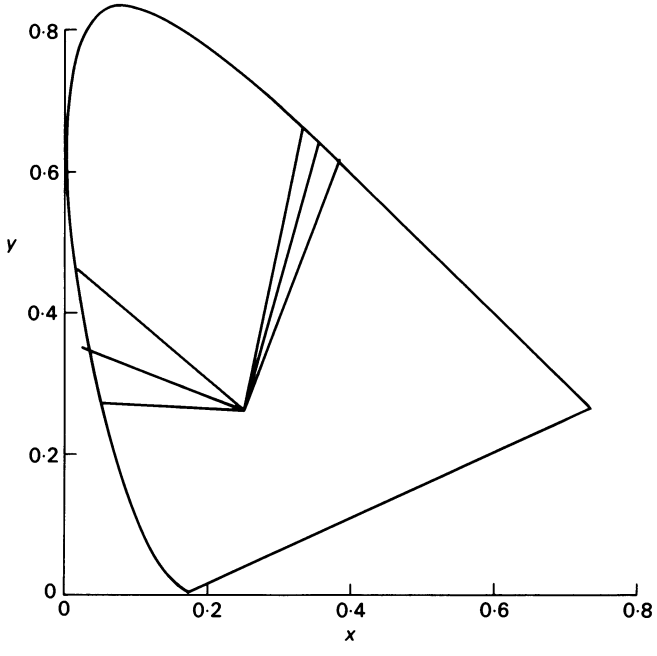


Fig. 15. C.I.E. chromaticity diagram showing the mean azimuth (± 1 S.D.) of the null planes of the two groups of parvocellular neurones revealed by the present experiments. These lines have been projected to the spectrum locus to provide an estimate of the range of monochromatic lights that could be silently substituted for the white light used in our experiments. For the R–G cells the neutral point is 558 ± 4 nm; for the B–(R & G) units it is 492 ± 3 nm.

desensitized by chromatic adaptation. Under these circumstances the opponent site may combine signals non-linearly.

Secondly, special circumstances arise when stimuli are modulated in the isoluminant plane along the constant R & G or constant B axes. Modulation along a constant R & G line produces a constant quantum catch in both R and G cones, so if inputs to the opponent site arise only in R and G cones the opponent site will receive steady signals, *no matter what the temporal properties or sensitivities of the earlier pathways.* Modulation along a constant B axis produces a constant quantum catch in the B cones and a constant total catch in the R and G cones, so a B–(R & G) opponent site should receive a steady signal.

Magnocellular cells

These have null planes whose elevations are mostly low and whose azimuths are distributed uniformly (Fig. 13*A*). The analysis of cone contributions to receptive fields (Fig. 14) suggests no principle by which the cells might be grouped, although it provides clear evidence of chromatic opponency in most of them. The opposed inputs are substantially segregated in centre and surround, because the elevation of the null plane drops almost to zero when a grating, rather than a spatially uniform field, is used to measure it. Our quantitative results do not support Wiesel & Hubel's (1966) division of the cells into 'type III' (spatially but not chromatically opponent) and 'type IV' (spatially opponent, with a surround that is particularly sensitive to longer wave-lengths). Rather, the evidence suggests that virtually all magnocellular units have chromatically opponent receptive fields in which the antagonistic mechanisms are segregated spatially.

Roles of different classes of neurones

Results obtained from the experiments of this paper suggest that only parvocellular neurones have the chromatic properties required for colour vision. In the preceding paper the argument was made that parvocellular neurones that receive signals from R and G cones could underlie psychophysically measured contrast sensitivity. These units do not meet the specification of the canonical R–G opponent cell or of the canonical luminance cell (their null planes lie neither in the isoluminant plane nor in an orthogonal plane passing through the constant R & G axis), but they respond well to modulation of chromaticity at low spatial frequencies and modulation of luminance at high spatial frequencies. They are therefore likely to be doing 'double duty' in providing signals about both the chromatic and the spatial properties of stimuli. Such an arrangement, already suggested by the work of Wiesel & Hubel (1966) and discussed by Ingling & Martinez (1983), would make economical and efficient use of the limited capacity of the optic nerve: spatial-temporal changes in chromaticity are well encoded at low but not at high spatial frequencies, and spatio-temporal changes in luminance are well encoded at high but not at low spatial frequencies. Psychophysical observations (Krauskopf *et al.* 1982) provide evidence that the 'luminance' and 'chromatic' mechanisms are independently adaptable, so the chromatic and luminance signals, ambiguously represented in the responses of a parvocellular neurone, must be separated later, possibly in striate cortex. (It is perhaps worth pointing out that no units in the l.g.n. could be adapted or 'habituated' by prolonged exposure to any of the stimuli used in our experiments.)

The B–(R & G) opponent cells must have a major role in colour vision, but their rarity and very low sensitivity to achromatic gratings (preceding paper) argue against their being important for spatial vision. Their axes of best response lie along the constant R & G line; one of the cardinal directions identified in the experiments of Krauskopf *et al.* (1982), but clearly different from the 'unique yellow–unique blue' direction most associated with the activity of the 'yellow–blue' opponent mechanism (Hurvich & Jameson, 1957).

Magnocellular units (and the ganglion cells that drive them) have in the past been thought strong candidates for the achromatic mechanism (De Monasterio & Schein, 1980), but their chromatic opponency, their larger receptive fields and their relatively

sparse coverage of the fovea make this unlikely. A more promising role for magnocellular units is that they contribute to a specialized system for detecting moving objects: they are substantially more sensitive than parvocellular units to stimuli of high temporal frequency (preceding paper), and their large receptive fields and high contrast sensitivity make them well suited to detecting the small flux changes produced by fast-moving objects. Moreover, there is a fairly direct projection from their site of termination in layer 4cα, via layer 4b, to the middle temporal region, which Movshon, Adelson, Gizzi & Newsome (1984) have recently shown contains neurones with receptive fields that are especially well suited to extract information about the movement of objects.

R. M. Boynton, J. D. Mollon, D. Y. Teller and Q. Zaidi kindly commented upon the manuscript. This work was supported by grants from the Medical Research Council (979 500) and the National Eye Institute (EY 04440) to P.L. A.M.D. held a Beit Memorial Fellowship.

REFERENCES

Bowmaker, J. K., Dartnall, H. J. A. & Mollon, J. D. (1980). Microspectrophotometric demonstration of four classes of photoreceptor in an old world primate, *Macaca fascicularis*. *Journal of Physiology* **298**, 131–143.

De Monasterio, F. M. & Gouras, P. (1975). Functional properties of ganglion cells of the rhesus monkey retina. *Journal of Physiology* **251**, 167–195.

De Monasterio, F. M. & Schein, S. J. (1980). Protan-like spectral sensitivity of foveal Y ganglion cells of the retina of macaque monkeys. *Journal of Physiology* **299**, 385–396.

De Valois, R. L., Abramov, I. & Jacobs, G. H. (1966). Analysis of response patterns of LGN cells. *Journal of the Optical Society of America* **56**, 966–977.

Derrington, A. M. & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *Journal of Physiology* **357**, 219–240.

Gielen, C. C. A. M., van Gisbergen, J. A. M. & Vendrik, A. J. H. (1982). Reconstruction of responses of colour-opponent neurones in monkey lateral geniculate nucleus. *Biological Cybernetics* **44**, 211–221.

Gouras, P. (1968). Identification of cone mechanisms in monkey ganglion cells. *Journal of Physiology* **199**, 533–547.

Gouras, P. & Zrenner, E. (1979). Enhancement of luminance flicker by colour-opponent mechanisms. *Science* **205**, 587–589.

Hurvich, L. M. & Jameson, D. (1957). An opponent-process theory of color vision. *Psychological Review* **64**, 384–404.

Ingling, C. R. & Martinez, E. (1983). The spatiochromatic signal of the r–g channel. In *Colour Vision*, ed. Mollon, J. D. & Sharpe, L. T., pp. 433–444. London: Academic Press.

Krauskopf, J., Williams, D. R. & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research* **22**, 1123–1131.

MacLeod, D. I. A. & Boynton, R. M. (1978). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America* **69**, 1183–1186.

Movshon, J. A., Adelson, E. H., Gizzi, M. S. & Newsome, W. T. (1984). The analysis of moving visual patterns. *Experimental Brain Research* (in the Press).

Rodieck, R. W. (1983). Raster-based colour stimulators. In *Colour Vision*, ed. Mollon, J. D. & Sharpe, L. T., pp. 131–144. London: Adacemic Press.

Schiller, P. H. & Colby, C. L. (1983). The responses of single cells in the lateral geniculate nucleus of the rhesus monkey to color and luminance contrast. *Vision Research* **23**, 1631–1641.

Smith, V. C. & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research* **15**, 161–171.

Walraven, P. L. (1974). A closer look at the tritanopic convergence point. *Vision Research* **14**, 1339–1343.

Wiesel, T. N. & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology* **29**, 1115–1156.