An account of responses of spectrally opponent neurons in macaque lateral geniculate nucleus to successive contrast

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Coloured surfaces in the normal environment may be brighter or dimmer than the mean adaptation level. Changes in the firing rate of cells of the parvocellular layers of macaque lateral geniculate nucleus were studied with such stimuli; chromatic mixtures briefly replaced a white adaptation field. This paradigm is therefore one of successive contrast. Families of intensity-response curves for different wavelengths were measured. When taking sections at different luminance ratios through these families of curves, strongly opponent cells displayed spectrally selective responses at low luminance ratios, while weakly opponent cells had higher chromatic thresholds and responded well to stimuli at higher luminance ratios, brighter than the adaptation field. Strength of cone opponency, defined as the weight of the inhibitory cone mechanism relative to the excitatory one, was thus related to the range of intensity in which cells appeared to operate most effectively. S-cone inputs, as tested with lights lying along tritanopic confusion lines, could either be excitatory or inhibitory. Families of curves for different wavelengths can be simulated mathematically for a given cell by a simple model by using known cone absorption spectra. Hyperbolic response functions relate cone absorption to the output signals of the three cone mechanisms, which are assumed to interact linearly. Parameters from the simulation provided estimates of strength of cone opponency and cone sensitivity which were shown to be continuously distributed. Cell activity can be related to cone excitation in a trichromatic colour space with the help of the model, to give an indication of suprathreshold coding of colour and lightness.

Introduction

Most objects differ from one another in the spectral composition of light reflected from them, so that for a given patch of retina, with successive fixations, changes in both intensity and spectral composition occur, some spectral mixtures being darker and some brighter than the mean adaptation level. This situation is therefore different from the conditions often used in visual experiments in which stimuli are briefly added upon a background. A better experimental approximation to the normal viewing situation can be achieved by substituting light stimuli of
differing luminance for an achromatic background simulating the mean adaptation level of the normal environment. Stimuli thus differ in luminance ratio and in spectral composition relative to the background. This stimulus situation is one of successive contrast; with the addition of a surrounding illuminated area simultaneous contrast may also be provided (Valberg et al. 1985).

In the case of the cone-opponent neurons of the primate visual system, superimposition of stimuli onto white or chromatic backgrounds has been used to isolate and identify cone mechanisms providing input to a cell (Wiesel & Hubel 1966; Gouras 1968; de Monasterio & Gouras 1975; de Monasterio et al. 1975). Cells of the parvocellular layers (PCL) of the macaque lateral geniculate nucleus (LGN) are almost all wavelength selective, commonly being excited by light of some wavelengths and having their activity suppressed by light of other wavelengths (DeValois 1965; Wiesel & Hubel 1966; Creutzfeldt et al. 1979). The activity of such cells presumably forms the basis for psychophysical colour estimation. However, the distinct ‘red–green’ and ‘yellow–blue’ channels postulated by opponent-colour theory to exist in primate vision (Hering 1920; Jameson & Hurvich 1955; Hurvich & Jameson 1957) are far from being established by neurophysiological methods. The paradigm of superimposing stimuli on a background, and the variety of connections of different cone types with opponent cells in the retina and in the LGN, has obscured any relationship between single cells and hypothetical physiological opponent ‘channels’, an uncertainty reflected in the different classification schemes proposed at one time or another (DeValois 1965; Wiesel & Hubel 1966; Creutzfeldt et al. 1979). One recent approach has attempted to directly relate cell responses to cone excitation space (Derrington et al. 1984). The approach we have used is similar in principle. However, the use of optical stimulation techniques instead of a colour television display enabled us to explore a much wider range of chromaticities and relative luminances.

Using the successive contrast situation, we have measured the responses of PCL cells of macaque LGN to stimuli of different wavelengths and sizes over a 5 log unit range of luminances. In a previous paper responses of LGN cells to stimuli of varying radiance presented on a white background were described by a simple model based on the spectral absorption of the cone pigments, and assuming firstly, a function known to describe receptor behaviour and secondly, linear interaction between cone mechanisms (Lee et al. 1983). Here a similar model is used to account for responses under successive contrast conditions, when luminance ratio is used as an intensity measure. The wide variety of stimuli used enabled us to generate a general description of cell behaviour in terms of this simple model.

A preliminary account of some of these results may be found in Valberg et al. (1983).

**Methods**

Monkeys (19 Macaca fascicularis and 2 M. mulatta) were anaesthetized with an intramuscular injection of ketamine hydrochloride (10–20 mg kg⁻¹). After standard surgical procedures, a craniotomy was performed over one LGN and a tungsten–in–glass microelectrode lowered into the nucleus. Further anaesthesia
Successive contrast and cell responses in macaque LGN

was maintained by respiring the animal with a 75% / 23.4% / 1.6% N₂O/O₂/CO₂ mixture with the addition of either 0.4–0.8% halothane to the gas mixture or the addition of 0.5–1.0 mg kg⁻¹ h⁻¹ barbiturate or 6 mg kg⁻¹ h⁻¹ etomidate (Hypnomidate; Janssen) to a continuous infusion of Ringer's solution (ca. 50 ml kg⁻¹ d⁻¹), together with gallamine triethiodide (5 mg kg⁻¹ h⁻¹) to paralyse the eye musculature. Electrocardiogram and electroencephalogram were monitored continuously. The latter showed predominantly synchronized activity. End-tidal pCO₂ was kept near 4% by adjusting the rate and depth of respiration. Temperature was kept near 37.5 °C.

The pupils were dilated by topical instillation of atropine, and contact lenses approximately matching the corneal curvature were fitted. Accessory lenses were used to focus a tangent screen 57 or 28 cm from the eyes onto the retina. Artificial pupils (6 mm diameter) were used. The eyes were irrigated every few hours. The fundus and fovea of each eye were back-projected onto the tangent screen. After the experiment animals were killed with an overdose of barbiturate. On a few occasions lesions were placed in the geniculate to confirm recording sites; in these cases the animal was perfused with formol saline and the brain subjected to standard histological treatment (see Hicks et al. 1983).

Stimulation and recording

Sustained, wavelength-dependent responses characterize cells of the PCL of the LGN so that entry of the electrode into the nucleus is unmistakable. From the sequence of changes in ocularity, and later the change in unit response properties as the magnocellular layers are encountered, it is possible to be confident during recording of the electrode site within the nucleus. After isolation of the activity of a single cell, its receptive field location was plotted with hand-held stimuli and its spectral responsiveness approximately determined. Receptive fields were usually parafoveal (5–15° eccentricity).

A three-channel system back-projected visual stimuli onto the tangent screen, which was of a material for which the angle of view had little effect on stimulus intensity. One channel provided a white adaptation field (4 × 5° or 8 × 10°; 110 cd m⁻²; 3100 td; CIE chromaticity co-ordinates (x, y) = (0.404, 0.410)) which was centred over the receptive field. Around this adaptation field the screen was usually dimly lit (1 cd m⁻²) but a fourth projector could be used to add a larger adaptation field surrounding the central one (Valberg et al. 1985).

Stimuli that were used consisted of fields the same size as the adaptation field or small spots or annuli. Stimuli were usually projected for 300 ms, replacing the adaptation field which was present during the 1200 ms interstimulus intervals. Shutters in the projector beams controlled this alternation. Motor-driven, 10-location filter wheels before each of the stimulus projectors allowed a wide variety of stimulus configurations. Filters were Schott NaI interference filters (bandwidth at half-maximum 50 nm) or Kodak Wratten filters.

Several series of stimuli were used. (a) A colour series consisting of eight gelatine

† 1 td (troland) is the retinal illumination when a luminance of 1 cd m⁻² is seen through a pupil of area 1 mm². For light of wavelength 580 nm, taking transmission losses into account: 1 td = 0.003 cd sr⁻¹ m⁻² = 10⁷ quanta s⁻¹ mm⁻² approximately.
filters equated for luminance by addition of neutral density filters. This was used for initial screening of cells’ responsiveness. (b) An intensity series covering 2.7 log units in 0.3 log unit steps. Wavelength and luminance range were adjusted by interference or neutral density filters elsewhere in the beam. (c) Purity series were usually generated by mixing white light and light passed through an interference filter. Insertion of ascending and descending series of neutral density filters in the two filter wheels allowed series of equal luminance but varying saturation to be produced, or series lying along tritanopic confusion lines.

Stimulus series were each presented ten times and cell responses averaged. For plotting of stimulus–response curves, the mean firing rate during the total response, excluding the first 45 ms, was measured and maintained activity with the adaptation field subtracted. The result was plotted against the ratio of stimulus \((L)\) to field \((L_a)\) luminance. The first 45 ms were excluded since a variable transient was sometimes present; such transients are seldom present when stimuli move across the retina (Lee et al. 1979). We also did analyses including the initial transient; resulting curves differed little.

All photometric and colorimetric values were computed from the spectral transmission of the filters and the spectral power distribution of the projector light. The only direct photometric measurement was that of the luminance of the white projector light (with a spot photometer, Photo Research). Other luminances were computed with the \(\text{cie } 10^\circ V_{\lambda}\) function. A more extensive description of these calculations is given elsewhere (Valberg et al. 1987).

Results

Measurement of cell responses

We show here some typical examples of response histograms and their evaluation, taken from a sample of ca. 425 cells from the pL. Figure 1a, b contain responses to a series of wide-field stimuli of different spectral compositions. The first stimulus is achromatic, followed by a series of equiluminous chromatic stimuli of dominant wavelengths shown. The penultimate stimulus consisted of the removal of the adaptation field and the last a white stimulus ten times more luminous than others in the series. When the adaptation field was present between stimuli (figure 1a), the first, equiluminous white stimulus fails to evoke a response. For this cell, long-wavelength stimuli then gave an excitatory response while shorter wavelengths suppressed activity. In comparison, in figure 1b, when stimuli were presented on a dark background, the cell became more broadly tuned spectrally. The cell would thus have been classified as \(+Y-B\) by DeVlooi (1965), although as it received only M- and L-cone input, it cannot discriminate between white, yellow and blue stimuli along a tritanopic confusion line, or WL by Creutzfeldt et al. (1979) (the cell gave an excitatory response to a wide band of long wavelengths). In terms of receptive field organization it was a red on-centre cell (Wiesel & Hubel 1966).

We classified cells in terms of receptive field organization using hand-held stimuli and in terms of general spectral responsiveness with the aid of histograms such as those of figure 1a, b. In the following, cells will be specified in terms of both centre–surround structure and spectral responsiveness.
Figure 1. The general characteristics of cell responses and the way they were measured is shown here. (a, b) Responses of a WL cell to a series of equiluminant stimuli of different dominant wavelengths, indicated at top. In (a), the stimuli, which subtended $4^\circ \times 5^\circ$, were alternated with an equiluminant ($110 \text{ cd m}^{-2}$) white adaptation field of the same size, as sketched above. In (b), the stimuli were alternated with a dark background, as sketched. Stimuli were presented for 300 ms and inter-stimulus interval was 1200 ms. For each histogram, the series of stimuli were each presented ten times. Bin width was 15 ms. The cell gives an excitatory response to long wavelengths; spectral tuning becomes broader when stimuli alternate with a dark background. In (c), for the same cell, intensity–response functions were measured. The histogram shown was obtained with light of 621 nm dominant wavelength alternated with the white field. Intensity was incremented in 0.3 log unit steps, as sketched above. The net firing rate is plotted below, the luminance ratio between stimulus ($L$) and white field ($L_a$) being the independent variable.
When intensity and dominant wavelength were systematically varied, descriptions of cell behaviour were obtained as in these examples of families of curves from two cells of the green (a) and red (b) on-centre types. For each cell, original histograms are shown, the dominant wavelengths of the lights used being indicated. The families of points derived from these two cells are shown in the two graphs in the lower part of the figure. The curves are least-squares best fits to responses using the model described in the text. The dominant wavelengths used (and their symbols) are shown with each curve.

**Figure 2.**
Histograms such as those of figure 1a give only a limited view of responsiveness at one intensity level. Intensity–response curves at different wavelengths were measured to specify cell behaviour more extensively. An example of one such curve is shown in figure 1b for the same neuron. A 621 nm (dominant wavelength) stimulus field was substituted for the adaptation field, the luminance ratio being increased in 0.3 log unit steps as sketched at the top of the figure. At the lowest luminance ratio, maintained firing is suppressed. With increasing luminance, the cell gave an increasingly vigorous response, reaching saturation at a ratio of 0.3. The firing rate during the response is plotted below, the curve being fitted by eye. Repeating such measurements at different wavelengths gave families of curves for each cell.

Figure 2 shows examples of such families of curves for two cells. In figure 2a a green on-centre cell is shown. With stimuli on a dark background it gave an excitatory response to a wide-band of short wavelengths (WS-cell (Creutzfeldt et al. 1979)). In the two original histograms, obtained using the successive contrast paradigm, a vigorous excitatory response occurs at 463 nm, but there is only a response at high intensity to 589 nm, except for a phasic off-response. Such responses were usually small, very phasic and varied substantially from cell to cell of similar type; they may be due to differences in latency of opponent mechanisms and we do not analyse them further here. Firing rates as a function of luminance ratio are plotted as points below.

At very low luminance ratios, below 0.01, a suppression of maintained firing occurs due to removal of the adaptation field, the chromatic content of the stimulus being below threshold. With increasing luminance ratio, an excitatory response appeared, though at 589 nm a very intense stimulus was required. Curve slope and maximal response is dependent on spectral composition.

The same format is used to illustrate the response of the cell in figure 2b, which was of the red on-centre type, giving an excitatory response to a wide-band of long wavelengths (WL cell). Low luminance ratios caused a decrease in maintained activity, and then wavelengths above 572 nm caused a vigorous response as luminance increased. With short wavelengths, i.e. 463 nm, the response of the cell can only be measured until maintained firing has been abolished. With an achromatic stimulus a curve of shallow slope passes through zero at a luminance ratio of one, when stimulus and adaptation field are identical; a similar curve was measured with 572 nm, these lights lying close to a tritanopic line. For 621 nm repeat measurements were taken. The variability in response magnitude shown, about 10%, was typical.

**Simulation of cell responses**

Responses of wavelength-opponent cells could be accounted for on the basis of a simple model. We have chosen six cells as examples of those frequently encountered, making up perhaps 90% of the total sample. Taking cone absorption spectra from the revised data of Estevez (1979; personal communication) and Wyszecki & Stiles p. 618 (1982), which are similar to the absorption spectra of individual cones as measured by Bowmaker et al. (1980); (see Valberg et al. (1987)), we assume receptor outputs follow hyperbolic functions of the form

\[ Q = Q_{\text{max}} S^n / (S^n + \sigma^n) \]
Here, $S$ is proportional to absorption by a receptor mechanism, the constant $\sigma$ is the absorption giving a half-maximum response, $n$ is an exponent and $Q$ is response of the receptor mechanism. Such response functions were first applied to primate cones by Boynton & Whitten (1970) and Valeton & van Norren (1984) with $n = 0.7$. We further assume responses measured could be expressed by linear sums and differences of hyperbolic response functions. There are thus two free parameters per cone mechanism, $\sigma$ and $Q_{\text{max}}$.

For any given cell, we first tried to account for its responses on the basis of M- and L-cone mechanisms alone. In certain cases an S-cone contribution was also obviously necessary. Free parameters were adjusted until the least square error was minimized, either using a search routine devised by one of us (Tryti 1985) or a pseudo-Gauss–Newton procedure (BMDF statistics package). Both methods yielded similar parameters. A more extensive justification of the assumptions underlying the model is given elsewhere (Valberg et al. 1987).

The curves of figure 2 are those derived from the simulation. Both these neurons' responses could be accounted for on the basis of M- and L-cones alone, $+M-L$ in the case of figure 2a and $+L-M$ for figure 2b. A reasonable agreement between data points and fitted curves is apparent. The relative order of the curves for different wavelengths is reproduced, as is the curve for an achromatic stimulus. It is remarkable that the relatively complicated families of curves of such cells can be simulated so closely. For optimal wavelengths, a slight decrease in response magnitude at high intensities was present both in data and model curves.

Constants derived from the simulation are listed in table 1. Estimates of maximum cone mechanism outputs are of the order of several hundred spikes per second while the half-saturation constants are expressed as the luminance ratio of an achromatic stimulus which would produce half-maximal excitation. Estimates of goodness of fit are also included. The root mean square residual error in impulses s$^{-1}$ is given, as is the percentage of variance in the data left unaccounted for by the model, about 6–10%. With a variability of about 10% in repeated

Table 1. Parameters derived from simulation of cell responses

<table>
<thead>
<tr>
<th>cell type</th>
<th>green on-centre (WS)</th>
<th>red on-centre (WL)</th>
<th>green off-centre (NS)</th>
<th>red-green type II (NL)</th>
<th>blue on-centre (NS)</th>
<th>yellow-blue type II</th>
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<tr>
<td>figure</td>
<td>$2a$</td>
<td>$2b$</td>
<td>$3a$</td>
<td>$3b$</td>
<td>$4a$</td>
<td>$4b$</td>
</tr>
<tr>
<td>$\sigma_M$</td>
<td>1.38</td>
<td>0.38</td>
<td>0.09</td>
<td>0.07</td>
<td>--</td>
<td>7.26</td>
</tr>
<tr>
<td>$\sigma_L$</td>
<td>1.44</td>
<td>0.44</td>
<td>0.11</td>
<td>0.11</td>
<td>0.43</td>
<td>14.9</td>
</tr>
<tr>
<td>$\sigma_S$</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>0.48</td>
<td>20.1</td>
</tr>
<tr>
<td>$Q_{M,\text{max}}$ (impulses s$^{-1}$)</td>
<td>508</td>
<td>-575</td>
<td>208</td>
<td>-160</td>
<td>--</td>
<td>338</td>
</tr>
<tr>
<td>$Q_{L,\text{max}}$ (impulses s$^{-1}$)</td>
<td>-463</td>
<td>625</td>
<td>-234</td>
<td>139</td>
<td>-199</td>
<td>-147</td>
</tr>
<tr>
<td>$Q_{S,\text{max}}$ (impulses s$^{-1}$)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>138</td>
<td>-236</td>
</tr>
<tr>
<td>mean square error (impulses s$^{-1}$)</td>
<td>8.5</td>
<td>8.7</td>
<td>6.1</td>
<td>6.5</td>
<td>11.6</td>
<td>9.6</td>
</tr>
<tr>
<td>residual variance (%)</td>
<td>9.5</td>
<td>5.0</td>
<td>10.6</td>
<td>9.4</td>
<td>7.5</td>
<td>4.2</td>
</tr>
</tbody>
</table>

Half-saturation constants are expressed as that ratio of achromatic light causing half excitation.
measurements of the same intensity series, this suggests some of the residual variability arose from experimental sources.

The two cells of figure 2 were typical of WS and WL, or green and red on-centre units. In both, the excitatory cone mechanism appeared to dominate, as seen from the excitatory asymptote at high luminance ratios and as mirrored in the larger excitatory cone mechanism maxima in the simulations. Such cells would thus be termed weakly cone opponent by Gouras & Zrenner (1981). Other neurons demonstrated stronger cone opponency and two examples are shown in figure 3 which includes original histograms, data points and fitted curves; responses of both could be accounted for by input solely from M- and L-cones.

The cells in figure 3 differed in several respects from those in figure 2. Removal of the adaptation field led to an increase in firing which was then modulated by the chromatic stimuli. Chromatic thresholds tended to be lower than with cells such as those shown in figure 2. Most striking however was the non-monotonic nature of intensity–response curves; with excitatory wavelengths, a maximum response was reached at a luminance ratio of 0.1 or below and thereafter increasing stimulus intensity caused responses to decline.

Classification of such cells with conventional stimuli on a dark background revealed them to give excitatory responses to a narrow band of short or long wavelengths (NS and NL; Creutzfeldt et al. 1979). In terms of receptive field organization, they were, with some exceptions, red or green off-centre cells or red–green opponent type II cells (Wiesel & Hubel 1966).

As shown elsewhere (Lee et al. 1983), non-monotonic intensity–response curves may be accounted for by linear opponent cone interactions, due to the nonlinear nature of cone intensity–response curves. This is also so in the simulated curves of figure 3, which account for the data well. In figure 3a +M–L cone inputs were assumed and in figure 3b +L–M. Cone mechanism maxima and half-saturation constants tended to be rather lower than with cells such as those in figure 2. Root mean square deviations were somewhat smaller than with weakly cone opponent cells largely due to the weaker responses usually obtained from such neurons, for goodness-of-fit estimated from residual variance was similar. Although cells such as those in figures 2 and 3 were common, intermediate cases were also frequent. The idea that a continuum of cone opponency exists (Zrenner & Gouras 1983) was supported by our observations on a population of cells, as shown below.

Evidence of the influence of the S-cone was present in about 20% of the cells encountered. In most cases, comparison of intensity–response curves for wavelengths lying along tritanopic confusion lines showed very marked differences in responsiveness; excitatory S-cone inputs in 15% of cells and inhibitory S-cone inputs in 3.5% of cells could be identified in this way, presentation of series of equiluminous tritanopic mixtures providing confirmatory evidence (Valberg et al. 1986a). In some instances, synergistic M-cone and S-cone excitation appeared to be present in green on-centre cells.

Two examples where S-cone influence was strong are shown in figure 4. In figure 4a data from a neuron with strong excitatory S-cone input are simulated assuming antagonistic inhibition from L-cones. The neuron was of the NS type or blue on-centre. The distinctive feature of such cells was a more vigorous response
Figure 3. Two examples of families of curves from two strongly cone-opponent cells, in (a), a green off-centre, in (b), a red–green type II. The format is as in figure 2. For each cell, original histograms are shown, the dominant wavelengths of the lights used being indicated. Curves are again least-squares best fits.
Figure 4. Examples of families of curves from two cells receiving S-cone inputs, excitatory in (a), inhibitory in (b). The format is as in figure 2. Dominant wavelengths are as indicated. Curves are again least-squares best fits.

to 435 nm than other wavelengths, and a much stronger response to wavelengths lying at the short-wavelength end of tritanopic confusion lines, e.g. 435 nm relative to 550 nm. Such responses can only be simulated assuming excitatory inputs from S-cones. The simulations provide a reasonable description of the data, but for blue on-centre cells as a whole, it was difficult to tell from simulations if inhibition originated in M- or L-cones or both.

Retinal ganglion cells with inhibitory input from S-cones were found by de Monasterio & Gouras (1975) but their significance has been discounted (Gouras & Zrenner 1981). We found a small but significant population of these cells, some
Figure 5. Families of curves from examples of two rare cell types, in (a), for a cell with L-cone excitation and M- and S-cone inhibition and in (b) a cell responding at lower luminance ratios to wavelengths at the spectral extremes than in mid-spectrum. The curves in (a) are the best fit which could be obtained. Although the experimental results are approximately reproduced, the fit is not as good as in figures 2-4. The cell in (b) could only be poorly simulated; the curves are drawn by eye and labelled individually.

20 out of 567 (3.5 %), although the sampling uncertainties of microelectrodes make the reliability of this proportion uncertain. Such cells usually possessed type II receptive field organization. Figure 4b shows data and simulation for one of these cells. A strong response is present to 572 nm, while little response occurs to an achromatic stimulus, in contrast to the +L-M cell of figure 2b where responses to 572 nm and an achromatic stimulus are similar. This suggests an inhibitory S-cone input since these lights lie close to a tritanopic confusion line. Responses of these cells could be modelled assuming excitatory M-cone and inhibitory S-cone inputs, with in some cases a weak inhibitory L-cone also being present. Chromatic
mixtures along other tritanopic confusion lines confirmed the S-cone inhibitory input to these cells (Valberg et al. 1986a).

The involvement of S-cones with other combinations of receptor inputs was described by de Monasterio & Gouras (1975). We also encountered such instances, which constituted ca. 2% of the total sample. Two examples of these rare cells are shown in figure 5.

Families of curves in figure 5a, b were obtained from well-isolated units studied over an extended period of time with good reproducibility on repeat measurement. The neuron of figure 5a gave vigorous excitatory responses at long wavelengths, indicating an excitatory L-cone input. However, the vigorous excitatory response to 572 nm, which lies close to a tritanopic confusion line relative to a white stimulus, suggests S-cone inhibition. Comparison of responses to lights along a deuteranopic confusion line indicates M-cone inhibition as well. Figure 5b shows a family of curves from a neuron in which excitatory responses were obtained from the spectral extremes with little response at mid-spectrum except at very high intensities. Comparison of responses to wavelengths lying along tritanopic confusion lines suggests excitatory input from L- and S-cones opposed by an M-cone inhibitory input. Cells such as those in figure 5 generally posed problems for the simulation. This can be seen from the curves of figure 5a which were the best fit which could be achieved. Although the order of the curves is reproduced with excitatory L-cone and inhibitory M- and S-cone inputs, the fit is poor. The response of the cell of figure 5b could not be modelled without assuming some nonlinear cone interaction. Curves have been drawn through the points by eye, with wavelengths as indicated.

In conclusion, we have been able to account for responses of cone opponent cells, to a first approximation at least, on the basis of a simple model with plausible assumptions.

Spectral tuning curves

By taking sections through the curves of figures 2, 3 and 4 one may plot spectral responsiveness as a function of wavelength at different luminance ratios, as shown in figure 6. Responsiveness was estimated at four different luminance ratios, interpolating between actual data points, while the solid curves show that predicted by the model. Responsiveness of the cells of figure 2a, b is shown in figure 6a, b, that of cells of figure 3a, b in 6c, d, and that of figure 4a, b in 6e, f.

Cells of figure 6a–d received only M- and L-cone inputs. The two cells of figure 6e, f have quite different spectral response properties with crossover points closer to 500 nm. For these cells, as well as those in the upper part of the figure, the simulated curves provide a good approximation to the data, further confirming the postulated cone inputs to each cell.

All cells in figure 6a–d tend to have a crossover point between excitation and inhibition around 570 nm, though crossover point is luminance ratio dependent. Comparing figure 6a with figure 6c and figure 6b with figure 6d, the order of the curves for different luminance ratios is quite different. For weakly opponent cells (figure 6a, b) spectral band width broadens with increasing luminance ratio, while with strongly opponent cells the opposite is the case. This has a consequence that
Figure 6. Spectral responsiveness plotted against dominant wavelength for the cells of figures 2, 3 and 4. Sections were taken at luminance ratios as indicated, firing rates being read off from straight-line connection of the measurement points. The figure illustrates that M–L cone opponent cells differ little in spectral selectivity in the successive contrast situation, but differ in the luminance ratio range in which they respond. Cells with S-cone inputs (e, f) display different spectral responsivity under successive contrast.
Figure 7. Responses of four cells to stimuli of different dominant wavelengths, either alternated with an equiluminant white adaptation field or with a dark background. The four cell types are as indicated and the dominant wavelengths of each stimulus are displayed above each histogram set. Spectral responsiveness is different with and without the white adaptation field. With the white field, the crossover from excitatory to suppressive responses occurs near 570 nm for all cells.
at low luminance ratios more strongly opponent cells give the most vigorous responses while at higher ratios weakly opponent cells respond better. This effect is clearly reproduced in the simulated curves, and thus is a result of variation in sensitivity and balance of cone mechanisms among cells. Under these successive contrast conditions, therefore, it may be more appropriate to view the difference between weakly and strongly opponent cells (or narrow- and wide-band cells as tested with stimuli on a dark background) in terms of their operating range in colour space.

When stimuli were presented on a dark background (not shown), the cells of figure 6c, d were spectrally narrow-band (classifiable as +B−Y or +R−G; DeValois (1965)), due to their strong cone opponency, while those of figure 6a, b were spectrally wide-band (+G−R or +Y−B), being only weakly cone opponent. However, it is apparent from the data and curves that this difference in bandwidth of spectral responsiveness disappears in the successive contrast stimulus situation, giving way to a characteristic difference in response to relative luminance.

The tendency for weakly and strongly opponent M/L cells to acquire a crossover point near 570 nm in the successive contrast situation is further illustrated in figure 7, in which examples of cells similar to those in figures 2 and 3 are included. The histograms were recorded with a series of equiluminous stimuli of different dominant wavelengths as in figure 1a, b.

The excitatory responses of the cell of figure 7a are extended to longer wavelengths when lights alternate with a white field in comparison with presentation upon a dark background (cf. responses to 551 nm). Also, for the cell of figure 7d there is a tendency for the crossover point to shift towards 570 nm, the vigorous response to 586 nm on a dark background disappearing in the successive contrast condition, indicating a decrease in spectral bandwidth. The spectral responsiveness of cells in figures 7b, c is changed less. These changes in spectral responsiveness are likely to be due to some adaptive effect of the white field. Relative to a dark background some change in cone sensitivity and balance may occur, causing spectral selectivity to alter.

These changes in spectral responsiveness are comparable to those found by Marrocco & DeValois (1977). A similar change in spectral responsiveness occurs when stimuli are presented on the 100 cd m⁻² background (Crook et al. 1987), indicating that the change is due to the photopic adaptation conditions rather than successive contrast per se. Results of Marrocco & DeValois (1977) were qualitatively similar to those presented here within the limited intensity range they tested, except that we found very few pCl cells with V₁₀ λ sensitivity, in contrast with their finding of a large proportion of such cells. A lack of cells with S-cone inputs would also be apparent from their results.

Cone inputs and their relative strengths

It is generally agreed that the majority of wavelength-opponent cells receive input from only M- and L-cones, and we were able to simulate behaviour of about 75% of neurons reasonably well solely on the basis of these cone inputs. These opponent mechanisms participate in a variety of receptive field structures, so that in the case of +L−M cells either red on-centre, green off-centre or type II red-
green-opponent fields may result. The degree to which these field structures form a continuum is uncertain, but in terms of cone opponency \textit{per se} with large field stimuli, it seems likely that a continuum exists. This is illustrated in figure 8, in which we summarize parameters derived from simulations of 146 cells.

Half-saturation constants given an indication of the sensitivity of the M- and L-cone mechanisms in the successive contrast situation. In figure 8a, b are plotted values of half-saturation constants for cells with $+ L-M$ and $+ M-L$ cone inputs respectively. These values are highly correlated. The distribution of half-saturation constants appears continuous. Weakly opponent, WS and WL cells, usually corresponding to green and red on-centre units, are indicated by open symbols and strongly opponent, NS and NL cells, usually corresponding to red or green off-centre cells or type II cells, are indicated by filled symbols. A lower half-saturation constant indicates lower chromatic thresholds, and such cells produce a chromatically coded signal at lower luminance ratios relative to the adaptation field. NS and NL cells tended to show lower constants than WS and WL cells. Thus, this analysis of half-saturation constants over the cell population supports the notion that narrow-band cells respond optimally at lower luminance ratios whereas wide-band cells have an optimum response range at higher luminance levels relative to the adaptation field.

We interpret the correlation between half saturation constants as indicating that these mechanisms are closely balanced under neutral adaptation conditions with a white adaptation field. The sensitivity of opponent cells to chromatic adaptation may thus stem from the large changes in responsiveness which may be wrought by relatively small changes in half-saturation constants. It has proved possible to simulate the effects of chromatic backgrounds by assuming proportional, von Kries-type differential adaptation of the individual cone mechanisms (Valberg & Lee, unpublished observations).

The other free parameter for each cone mechanism are $Q_{L_{\text{max}}}$ and $Q_{M_{\text{max}}}$, which may be viewed as the weighting of cone mechanisms received by a particular cell. The distribution of the ratios $Q_{L_{\text{max}}}/Q_{M_{\text{max}}}$ for cells receiving excitatory L-cone inputs and $Q_{M_{\text{max}}}/Q_{L_{\text{max}}}$ for cells receiving the converse are shown in figure 8c, d. Ratios greater than one indicate the excitatory cone mechanism was dominant and ratios less than one indicate a more powerful inhibitory mechanism. There is a continual distribution of relative cone weights, so that for those cells classed as weakly opponent, WL or WS (open areas), or red or green on-centre, the excitatory mechanism is dominant and for strongly opponent, NL and NS cells the inhibitory mechanism displays stronger antagonism. The distinction between weakly and strongly opponent ganglion cells thus receives some quantitative support here.

The parameter distributions of figure 8 are capable of accounting for the different features observed in the families of luminance–response curves in figures 2–5, and we can give a qualitative description of the way the model accounts for cell activity.

The two main factors determining cell behaviour are half-saturation constants and the relative weights of the opponent mechanisms. Higher sensitivity (i.e. lower half-saturation constants) leads to lower chromatic thresholds under these
Figure 8. A comparison of parameters for cells receiving solely M and L-cone inputs. In (a) (+L-M) and (b) (+M-L), half-saturation constants derived from simulation are closely correlated. Filled circles indicate narrow-band, mostly off-centre cells when stimuli were projected upon a dark background; open circles indicate wide-band, on-centre cells. In (c) and (d) the ratios of cone mechanism weights are compared. Filled and open areas indicate narrow- and wide-band cells respectively. The comparisons show both half-saturation constant and relative cone weights are continuously distributed, with a continuous transition from strongly to weakly opponent.

conditions; such cells carry a chromatic signal when a spectral mixture is a good deal darker than the adaptation level. Cells with high sensitivity are generally strongly opponent, leading to a disinhibition to removal of the adaptation field and highly non-monotonic intensity response curves. Cells with weaker opponency, less sensitive in the successive contrast situation, are excited by achromatic stimuli and thus their activity is reduced by removal of the adaptation field. Owing to the dominance of the excitatory cone mechanism, they continue to give a chromatic signal at high luminance ratios.
Successive contrast and cell responses in macaque LGN

Discussion

The aim of the present experiments was to describe responses of colour-selective cells in the monkey visual pathway under conditions of successive contrast, similar to those occurring in the natural environment, where colours may be either brighter or dimmer than a mean adaptation level. This is reflected in colour schemes such as the Munsell system, in which samples consist of both light and dark colours.

In our experimental situation, spectral stimuli replaced a white adaptation field, mimicking mean adaptation level, and they could be lighter or darker than the field, as might occur with successive fixations in the awake animal. At least for M/L cone opponent cells, we show here that cells with different strengths of cone opponency, defined as the strength with which the inhibitory mechanism opposes the excitatory one, may play a differential role in encoding such light and dark colours; weakly opponent cells respond optimally at high luminance ratios, to lighter colours, and strongly opponent cells at low luminance ratios, to darker colours. Cells receiving S-cone input, which may be excitatory or inhibitory, provide the additional dimension of colour space.

Although there are several layers of synaptic interaction within the retina, with ample possibility of feedback, we have been able to show that cell responses can be modelled in a relatively simple way, despite the apparent complexity of the sets of curves in figures 2–4. Cone output is related to pigment absorption using a saturating hyperbolic function (Naka & Rushton 1966) which has found wide use in visual physiology and psychophysics. Opponent mechanisms then interact linearly. A very similar model has been employed in a description of human colour scaling within Euclidean geometry (Seim & Valberg 1985), suggesting some features of chromatic coding may be related to physiological events at rather peripheral levels of the visual pathway.

An advantage of this approach is that it is possible to assess relative contributions of cone mechanisms unaltered by chromatic adaptation. In so far as constants derived from the model are realistic assessments of cone inputs, there is a continuum of opponency between M and L cones, varying between weakly and strongly opponent. As mentioned above, strength of opponency, and the accompanying differences in half-saturation constants would appear to be an important parameter determining the chromatic signal carried by different cells, so that the continuum of cells serves to code chromatic information over a larger range of intensities relative to the mean adaptation level than would be possible for single cells.

The constants used in the model are unlikely to be those of individual cones however. The constants found for a given cone mechanism must also result from summation of inputs from individual cones with different weights, with external factors, such as surround illumination (Valberg et al. 1985), also being capable of modifying these constants. Despite these complexities, under fixed adaptation conditions the model is able to predict cell responsiveness.
Models of opponent cell activity and psychophysics

A first attempt to relate the activity of cone-opponent cells to models of colour vision was based on experiments in which stimuli were projected upon a dark or dim background, and relied on the clustering around 500 or 600 nm of the crossover point from excitatory to inhibitory responses, which led to the suggestion that different cell types related to Hering opponent channels (DeValois 1965). However, the location of such crossover points are labile and a poor indication of the cone inputs a cell receives (de Monasterio & Gouras 1975). A bimodal distribution of crossover points would be expected from a population of cells receiving inputs solely from M- and L-cones when the balance of cone inputs changes in a continual manner. Qualitatively this can be understood by considering the rate of change of M- and L-cone inputs relative to one another. This reaches a maximum in between the absorption peaks of the pigments, i.e. between 535 and 570 nm. Thus with a continual change in cone balance, this spectral region will be under-represented in the crossover point distribution. Thus classification schemes based on crossover points give, rather than an indication of cone inputs, an indication of the strength of cone opponency, given the rarity of S-cone inputs to cells.

A more sophisticated approach to relating cell activity with psychophysics has been applied by Derrington et al. (1984) who sinusoidally modulated the phosphors of a colour television monitor about the white point. They found responses of all cells could be accounted for on the basis of M/L cone opponency or opponency between S-cones and some combination of M- and L-cones, assuming a model in which output of each cone mechanism was linearly related to absorption by the photopigment, with cone mechanisms then combining linearly. Cell activities could thus be described in terms of a space in which M/L cone-opponent and tritanopic axes provide the chromatic dimensions.

Our experiments were conceptually very similar, except that the optical system used for stimulation enabled a much wider range of intensities to be explored than with a television monitor. Although cone output may be linearly related to absorption with small signals, with large signals cone output follows a hyperbolic function (Boynton & Whitten 1970; Valeton & van Norren 1983), and we found this function necessary to account for our results. However, when we converted the constants we found to the relative cone input weights \( W_r \) and \( W_g \) of Derrington et al. (1984), a similar distribution to theirs was found.

As well as those neurons receiving strong S-cone excitation and inhibition opposed by one or both of the other cones, we found rare cells with other cone combinations (figure 5), as described by de Monasterio & Gouras (1975). Indeed, although Derrington et al. (1984) classified cells entirely as R-G and B-Y opponent, inspection of their figure 6 shows some cells with other combinations. The functional significance of such rare cells is obscure. They may simply be the result of aberrant connectivity, but since one can distinguish lights lying along tritanopic confusion lines throughout the CIE diagram, it is possible that cells such as those in figure 5 aid discrimination in regions in which other neurons are inactive.

It should be stressed that the principle of colour opponency in the visual system
as developed by Hering (1920) and subsequent workers (Jameson & Hurvieh 1955; Hurvieh & Jameson 1957) is not analogous to cone opponency found in the primate visual system. For example, a red–green opponent channel does not correspond in axis direction to M–L cone opponency. However, this argument does not of course lessen the validity of the theoretical treatment of Buchsbaum & Gottschalk (1984) who demonstrate an opponent formulation is optimal for transmission of chromatic information.

We have stressed strength of cone opponency as an important feature in chromatic signal processing rather than receptive field organization. Through the centre–surround organization of cone opponency, its strength depends on stimulus size (Wiesel & Hubel 1966). As much colour psychophysics is carried out with relatively large stimuli, this emphasis may be justified. However, centre–surround organization may be significant under other circumstances, such as tasks involving processing of spatial information.

The model presented here is likely to be useful in understanding mechanisms underlying colour vision in a normal daylight environment. It has been used to predict cell responses to light of differing saturation (purity) and it has been possible to reconstruct an equidistant colour space fairly well simply by linear combination and transformation of cell activities (Valberg et al. 1986b). As far as threshold tasks are concerned, the model can be used to account for thresholds for chromatic stimuli presented on a white background (Crook et al. 1987). Such representations are thus of help in finding constant relations and correlates between cell responses, and sensory magnitudes and colour discrimination.

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