

Temporal-chromatic interactions in LGN P-cells

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Abstract

We studied the interaction between the chromatic and temporal properties of parvocellular (P) neurons in the lateral geniculate nucleus (LGN) of macaque monkeys. We measured the amplitudes and phases of responses to stimulation by spatially uniform fields modulated sinusoidally about a white point in a three-dimensional color space, at a range of temporal frequencies between 1 and 25 Hz. Below about 4 Hz, temporal frequency had relatively little effect on chromatic tuning. At higher frequencies chromatic opponency was weakened in almost all cells. The complex interactions between temporal and chromatic properties are represented by a linear filter model that describes response amplitude and phase as a function of temporal frequency and direction in color space along which stimuli are modulated. The model stipulates the cone inputs to center and surround, their temporal properties, and the linear combination of center and surround signals. It predicts the amplitudes and phases of responses of P-cells, and the change of chromatic properties with temporal frequency. We used the model to investigate whether or not the chromatic signature of the surround in a red–green cell could be estimated from the change in the cell's chromatic properties with temporal frequency. Our findings could be equally well described by mixed cone surrounds as by pure cone surrounds, and we conclude that, with regard to temporal properties, there is no benefit to be gained by segregating cone classes in center and surround.

Keywords: P-cells, Lateral geniculate nucleus (LGN), Macaque monkey, Chromatic properties, Temporal properties

Introduction

The psychophysical limits on temporal resolution depend on the color composition of the visual stimulus (Kelly & van Norren, 1977; Noorlander et al., 1981, 1983; Noorlander & Koenderink, 1983), being generally lower for chromatically modulated stimuli than for achromatically modulated ones. Pattern-induced flicker colors, demonstrated by Benham's top, point to the importance of spatiotemporal interactions in color vision. These phenomena are observed at relatively low temporal frequencies to which the different classes of cones respond very similarly, so they probably arise at, or beyond, the color-opponent site. The two opponent mechanisms in a P-cell's receptive field are contained in its center and surround. Center and surround have different dynamics (Gielen et al., 1982; Smith et al., 1992), so we expect the chromatic properties of P-cells to depend on temporal frequency.

By characterizing the interaction between the temporal and chromatic properties of a cell, we hoped to learn a good deal how the different classes of cones contribute to the surround. In and near the fovea each P-cell receives center input from a single cone (Dowling & Boycott, 1966; Boycott & Dowling, 1969; Boycott & Hopkins, 1991; Calkins et al., 1994). The receptive field would

therefore be color-opponent even if the surround drew indiscriminately on inputs from all classes of cones. Anatomical (Wässle et al., 1989) and physiological (Dacey & Lee, 1995) evidence favors this possibility, for horizontal cells, which probably form the receptive-field surround (Mangel, 1991), do not draw their inputs from a single class of cone. Moreover, Lennie et al. (1991) showed that the chromatic properties of the P-cells studied by Derrington et al. (1984) could be satisfactorily explained by assuming that surrounds drew mixed inputs from L- and M-cones. Other work that has explored both spatial (Reid & Shapley, 1992) and temporal (Smith et al., 1992) properties of P-cells has argued against this possibility. The issue might be resolved if, from detailed measurements of the chromatic and temporal properties of a cell, we could separately estimate the temporal properties of center and surround, then (knowing that the center receives input from a single cone type) find the chromatic signature of the surround.

Previous studies of P-cells disagree about the effect of temporal frequency on the chromatic properties of cells. Gouras and Zrenner (1979) reported that P-cells lose their chromatic opponency at frequencies above about 15 Hz. Lee and coworkers (Lee et al., 1989*b*, 1990, 1994; Smith et al., 1992; Yeh et al., 1995) and Gielen et al. (1981, 1982) found clear but less substantial effects of temporal frequency in this range; Derrington et al. (1984) found small effects of temporal frequency up to 15 Hz. To try to resolve this question, we have made detailed measurements of the temporal characteristics of P-cells driven by modulations of chromaticity and luminance along several directions passing through a white point. We have applied to these measurements an analytical model

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that describes the temporal and chromatic properties of center and surround. Center and surround act as linear temporal filters whose signals are combined in an opponent mechanism. Our approach is like that used by Smith et al. (1992), but is applied to different kinds of measurements.

Methods

We recorded the discharges of P-cells in the lateral geniculate nucleus (LGN) of three *Macaca nemestrina* that weighed between 3.0 and 4.5 kg. These animals were also studied in the preceding paper (Lankheet et al., 1998), which describes the preparation and methods for recording from single units. That paper also provides details of visual stimulation and the methods used to find a neuron's chromatic signature. Although we recorded from both red-green cells and blue-yellow cells, this paper discusses only red-green ones.

All stimuli were spatially uniform fields modulated sinusoidally in chromaticity and/or luminance about some steady adaptation level (the white point). The stimuli were always very much larger than receptive fields and covered them fully.

After initial measurements that identified the kind of cell (on-/off-center, and the chromatic signature), we measured responses to modulations of chromaticity/luminance along six directions in color space at five temporal frequencies ranging from 1.2 Hz to 24.9 Hz. For red-green cells, stimuli were confined to the plane defined by the L-M axis and the achromatic axis (azimuth fixed at 0 deg, see Fig. 1, preceding paper). Thus, chromaticities were fully defined by the elevation only. Elevations were equally spaced from +90 to -90 deg (an elevation of 0 deg provided isoluminant modulation, an elevation of + or -90 purely achromatic modulation). Elevation and temporal frequency formed a two-dimensional matrix of stimuli from which each stimulus, plus a blank, was presented for 2 s, 20 times, in random order. After completing these measure-

ments, we checked the stability of the recording by repeating the initial measurements that characterized the cell.

Results

The measurements described in Methods were completed on 17 red-green P-cells, seven of which were red-center and ten green-center. Similar but less detailed measurements were made on a further 27 neurons.

Fig. 1 shows the set of poststimulus time histograms (PSTHs) of responses obtained from a red off-center cell. At low temporal frequencies and for achromatic modulation (90-deg elevation), the response was in counterphase with the stimulus, identifying the cell as off-center. To isoluminant modulation (0-deg elevation) with phase referred to the "red" direction along the L-M axis, the cell also responded in counterphase at low temporal frequencies. It is therefore classified as a red off-center cell. Characterized with stimuli modulated at 4 Hz, the cell had a preferred elevation of -70.9 deg and a preferred azimuth of 192.5 deg.

At all temporal frequencies and elevations, P-cells responded with approximately sinusoidal modulation of discharge rate at the frequency of stimulation. The harmonic distortion was generally small. For the unit in Fig. 1, the amplitudes of second, third, and fourth harmonic components of response, expressed as multiples of the fundamental, were 0.36, 0.21, and 0.13. The harmonic distortion factor, defined as the square root of the sum of squares of these ratios (up to the 5th harmonic), was 0.43, on average. Similar values were found for other cells. Moreover, the harmonic distortion did not vary consistently with elevation, temporal frequency, or amplitude of the response. Responses can therefore be well-characterized by the first harmonic (linear) component of the discharge captured in the histograms.

Fig. 1 shows that both elevation and temporal frequency of modulation affect response amplitude and phase. These influences

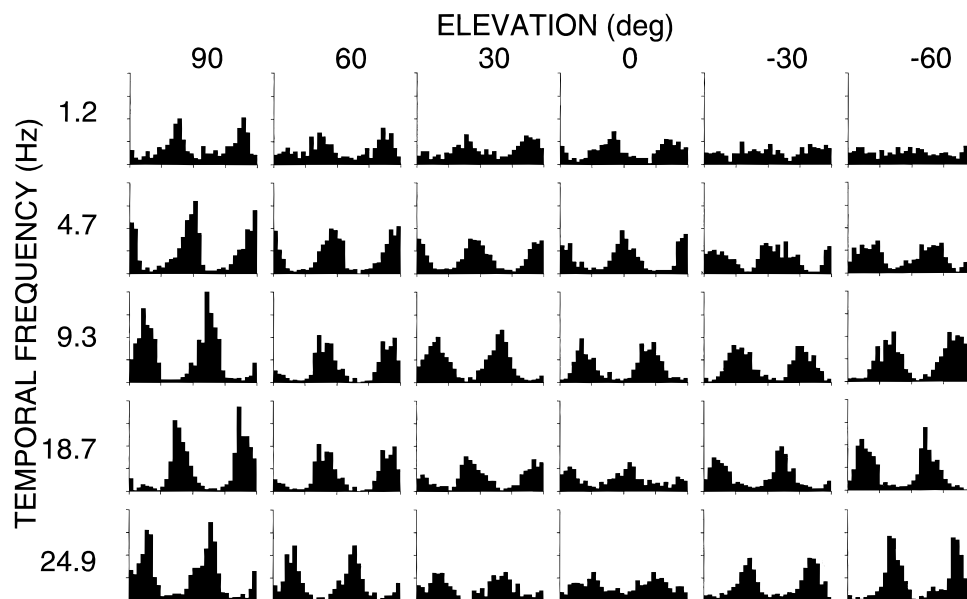


Fig. 1. Poststimulus time histograms of the responses of a red off-center cell to stimuli modulated at different temporal frequencies (rows) along different directions in color space (columns). Stimuli were spatially uniform fields modulated sinusoidally along a vector through the white point. The azimuth was fixed at 0 deg (L-M axis), confining stimuli to a plane orthogonal to the S-axis. Each panel shows the response folded to two cycles of the sinusoidal stimulus. The ordinate in each panel spans a response amplitude of 80 spikes/s.

are more easily seen in Fig. 2, which shows how amplitude and phase vary with temporal frequency, for different elevations. This data set is typical of ones obtained from P-cells, and reveals substantial interaction of chromatic and temporal variables, even at low temporal frequencies. For isoluminant modulations (elevation 0), the amplitude curves have a bandpass characteristic, with a maximum at 6–10 Hz. For modulations along elevations of 90-deg and 60-deg amplitude declined little or not at all up to a frequency of 25 Hz, whereas for modulation along the L–M axis amplitude always declined regularly as frequency was raised above 10 Hz. The drop in amplitude at low frequencies varied more among cells, but also depended on stimulus elevation. For the cell in Fig. 2, the greatest fall at low frequencies occurred for elevations of -30 and -60 deg. The elevation for which the low-frequency cut was steepest was related to a cell's preferred elevation, which varied considerably among cells. Tuning to low elevations implies balanced input from L- and M-cones and thus corresponds to maximal cancellation at low frequencies for achromatic modulations. Phase lags increased progressively with temporal frequency, with a slope that depended on stimulus elevation. This is seen most easily in Fig. 2C, which shows the phase lag relative to that for achromatic modulation. The extra phase shifts, which were observed in all cells, become larger at higher frequencies. Phase shifts were most substantial at elevations of -60 , -30 , and 0 deg.

These examples show that chromatic properties change considerably with temporal frequency. The nature of the change is shown directly in Fig. 3, which displays, for a red off-center cell (A) and a green off-center cell (B), amplitudes and phases of responses as a function of stimulus elevation at each temporal frequency. Symbols represent measurements, and the continuous lines show the behavior of the linear center-surround model described in a following section. All amplitudes are defined to be positive, and sign reversals are therefore expressed in the phase of response. For red center cells phases increase with elevation; for green center cells phases decrease with elevation. The steep parts of the phase curves are aligned with the minima of the amplitude curves.

At low temporal frequencies the amplitudes varied approximately sinusoidally with elevation, and phases changed rapidly, by about 180 deg, around the amplitude minima. Center and surround signals are presumably in counterphase, and cancel at the minima. This behavior agrees with that previously reported by Derrington et al. (1984) and can be well fitted by their model that describes a cell's response as the linear sum of contributions from different cone classes. At higher temporal frequencies the amplitudes clearly do not vary sinusoidally with elevation, indicating more complex interactions between cone inputs. These reflect differences between the temporal characteristics of center and surround mechanisms. Different temporal filters or different time delays will lead to frequency-dependent phase shifts between center and surround signals, and will affect both the amplitude and the phase of the cell's response. Presumably, center and surround signals are no longer in exact counterphase. As a result, the responses at different elevations can be predicted only by vector summation of the signals from center and surround. Thus, even though both center and surround signal amplitudes vary sinusoidally with elevation, their different phase characteristics cause the response of the cell to vary nonsinusoidally with elevation.

A model of chromatic-temporal interaction

The simple linear model used by Derrington et al. (1984) and in the preceding paper predicts that response amplitude will vary sinu-

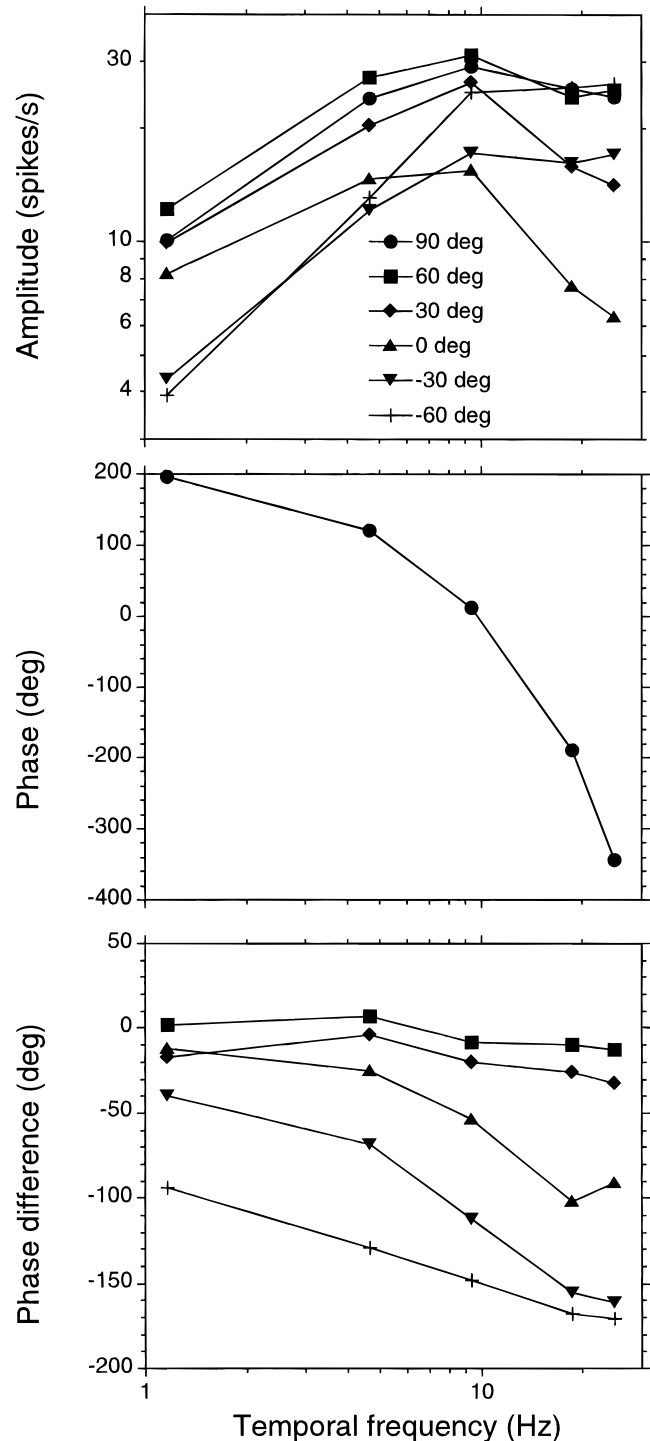


Fig. 2. Change of response amplitude and phase with temporal frequency, for a red off-center cell. A: Variation of amplitude with temporal frequency, for stimuli modulated along the elevations identified in the legend. The azimuth of modulation was fixed at 0 deg. B: Variation in the phase of the response to achromatic modulation with temporal frequency. C: Differences between the phases of responses to stimuli modulated along different elevations, and the phase of response to achromatic modulation (B). Amplitudes and phases were obtained by Fourier transform of the first harmonic component of the response histograms shown in Fig. 1.

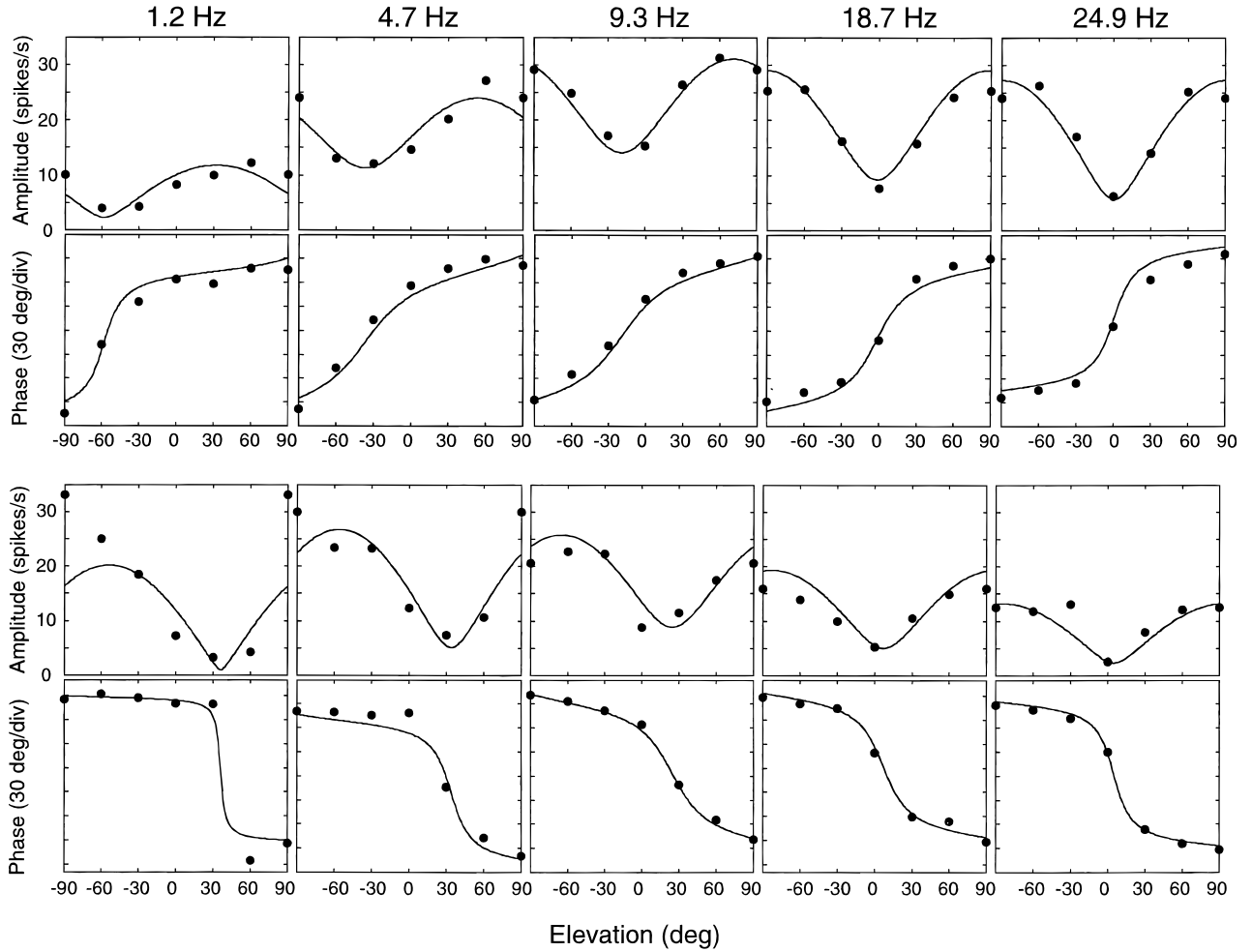


Fig. 3. Response amplitude and phase as a function of stimulus elevation, at different temporal frequencies. A: Red off-center cell (91ab). B: Green off-center cell (91d). Symbols show responses measured at azimuth 0 deg. Continuous lines are fits of the linear model described in the text. The model was fitted to each complete data set in a single operation. Table 1 shows the best-fitting values of the parameters.

soidally with elevation, but does not capture the change in chromatic characteristics at high temporal frequencies. To describe how chromatic properties change with increasing temporal frequency, and to help us understand the temporal and chromatic properties of center and surround mechanisms separately, we have developed a more general model in which the response of the cell reflects the combination of signals from a center and a surround mechanism, each of which has its own amplitude and phase characteristics. The aim was to derive the amplitude and phase characteristics shown in Figs. 1–3.

The model is summarized in Fig. 4. We assume that both center and surround are univariant, and linear. Their responses to sinusoidal stimulation are therefore described fully by their amplitudes and phases. The temporal characteristics of center and surround are described by a series of first-order high-pass and low-pass RC filters. The high-pass characteristic represents the action of early (and nonlinear) mechanisms of light adaptation that attenuate low-frequency signals, and are probably common to both center and surround pathways (Lankheet et al., 1993). Together with the center-surround antagonism that is expressed for some directions of stimulus modulation, this accounts for the low-frequency loss of responsivity. The high-pass filtering is characterized by two pa-

rameters, the time constant (τ_{HP}) and the number of filters in series (N_{HP}). For a single high-pass RC filter, the amplitude attenuation and corresponding phase shift are given by

$$\text{Amplitude} = \frac{1}{\sqrt{\left(\frac{1}{2\pi f\tau_{\text{HP}}}\right)^2 + 1}}$$

$$\text{Phase} = \arctan \frac{1}{2\pi f\tau_{\text{HP}}}$$

For multiple stages the amplitude attenuations are multiplied and the phase shifts are added.

The high-frequency loss of responsivity is modeled by a series of low-pass RC filters. The time constants set the corner frequency, i.e. the temporal frequency at which responses start to decline. The time constants of the multiple filter stages in each mechanism can either be the same, or can be spaced at regular, logarithmic intervals. The amplitude attenuation and phase shift brought about by a single low-pass filter are coupled and are described by

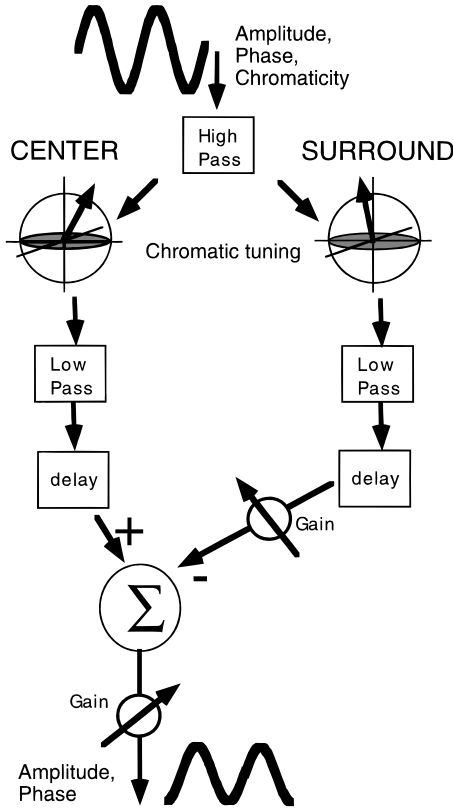


Fig. 4. Schematic representation of a model that describes the combination of signals from center and surround. Center and surround are linear, and generate sinusoidal signals in response to sinusoidal modulation of stimuli. The amplitudes and phases of center and surround signals can be attenuated by chromatic filtering and by temporal filtering. Signals from each mechanism are subject to transport delays, and are combined by subtraction at the opponent site, taking phase differences into account. The gain of the surround is always smaller than that of the center. See text for details.

$$\text{Amplitude} = \frac{1}{\sqrt{(2\pi f\tau_{LP})^2 + 1}}$$

$$\text{Phase} = -\arctan 2\pi f\tau_{LP}$$

For multiple stages the amplitude attenuations are multiplied and the phase shifts are added.

We allow the number of filters N_{LP} and the time constant (τ_{LP}) to differ between center and surround, resulting in different attenuations and phase lags. In addition to the phase shift caused by temporal filtering, center and surround can have transport delays that are temporal frequency-independent. The surround delay is constrained to be larger than the center delay, as characterized in cat ganglion cells (Derrington & Lennie, 1982; Enroth-Cugell et al., 1983; Frishman et al., 1987) and those of macaque (Lee et al., 1989a; Yeh et al., 1995).

Since center and surround are linear mechanisms, their chromatic properties are characterized by their preferred azimuths (Az_{pref}) and elevations (El_{pref}). The amplitude of the signal generated by each mechanism varies sinusoidally with the elevation (El) and azimuth (Az) of stimulus modulation in any plane (Derrington et al., 1984):

$$\text{Amplitude} = \sin El \sin El_{pref} + \cos El \cos El_{pref} \cos(Az - Az_{pref})$$

We assume that the center mechanism receives input from a single class of cone, so the preferred azimuth and elevation can be fixed for that class. The surround's preferred elevation can be varied between the preferred elevations of the L- and M-cones, to reflect different mixtures of cone inputs. This affects only response amplitudes of center and surround, not their response phases.

Differences between the temporal filters (or transport delays) or chromatic properties of center and surround affect the amplitudes and phases of their inputs to the opponent site, but introduce no distortion. The sensitivity of the surround in relation to the center is described by a gain factor, g_s , constrained to be less than 1. The amplitude and phase of response are found by vector addition of center and surround signals, using the following formula for two vectors with amplitude A_c and A_s and phase Ph_c and Ph_s :

$$\text{Amplitude} = S\sqrt{A_c^2 + A_s^2 - 2A_cA_s \cos(Ph_s - Ph_c)}$$

$$\text{Phase} = Ph_s + \arctan\left(\frac{A_c \sin(Ph_c - Ph_s)}{-A_s + A_c \cos(Ph_c - Ph_s)}\right)$$

The parameter S describes a cell's overall sensitivity.

The parameters of the model were estimated by minimizing concurrently the mean-squared error of the fit to both the amplitudes and phases of responses. The minimizing routine STEPIT was used to estimate the set of model parameters that best fitted the amplitude and phase data. Amplitude and phase were given equal weight in the fit by minimizing the product of mean-squared errors. It was important to minimize amplitude and phase errors simultaneously. Amplitude or phase characteristics alone can be fitted with a wide range of parameter values, but because phases depend partly on the amplitude attenuation of the RC filters and partly on fixed time delays, the parameter values are much more constrained when amplitudes and phases are fitted concurrently.

The model results shown in Fig. 3 (solid lines) were derived by assigning pure L- or M-cone input to both center and surround. The time constants, number of filters, center and surround delays, and the gains were free parameters. Table 1 lists the parameters that were allowed to vary in fitting the sets of 60 data points for each cell. To prevent discontinuities in the parameter space, we did not constrain the number of filters to be integer values. This has no consequence for the validity of the model.

With a single set of parameter values, we satisfactorily describe the temporal properties and the chromatic properties of P-cells, and their interactions. The model describes response phase well: for the data sets shown in Fig. 3 the mean phase error was 10.0 (A) and 7.4 deg. (B); for most cells it was well below 15 deg. The model also provides a reasonable account of the variation of response amplitude with elevation and temporal frequency. Mean errors were 1.8 (A) and 3.0 (B) spikes/s. Such errors as there are result from failure to represent irregularities in the measurements rather than from a systematic discrepancy between model and data.

Table 1 shows the values of parameters used to fit the measurements in Fig. 3. For one cell (A), the center and surround dynamics differed in both temporal filtering and transport delays. For the other cell (B), center and surround had the same low-pass filtering, but different transport delays. Similar results were obtained from all 17 cells on which we completed these measurements. For some cells the different temporal properties of center and surround were best described by a transport delay of several milliseconds, for others by different filtering properties, or a combination of the two.

The model describes comprehensively the factors that determine the temporal and chromatic properties of P-cells. Because it

Table 1. Parameter values for model fits^a

	Cell 91ab (red off-center)		Cell 91d (green off-center)	
	Pure surround	Mixed surround	Pure surround	Mixed surround
High-pass filtering				
τ_{HP}	8.11 ms	14.8 ms	5.6 ms	5.8 ms
N_{HP}	0.50	0.43	0.22	0.27
Low-pass filtering				
$\tau_{LP\ center}$	12.5 ms	12.0 ms	6.5 ms	7.8 ms
$N_{LP\ center}$	6.0	8.0	6.0	7.0
$\tau_{LP\ surround}$	20.5 ms	12.0 ms	6.5 ms	7.8 ms
$N_{LP\ surround}$	6.0	8.0	6.0	8.0
Spacing time constants (log units)				
Delay center	47.3 ms	43.5 ms	28.7 ms	26.4 ms
Delay surround	56.7 ms	46.0 ms	34.8 ms	32.5 ms
Gain (S)	187 spikes/s	341 spikes/s	111 spikes/s	178 spikes/s
Relative gain surround (g_s)	0.88	0.94	0.71	0.77
RME phase	10.02 deg	10.70 deg	7.40 deg	7.31 deg
RME amplitude	1.76 spike/s	1.68 spikes/s	3.01 spikes/s	2.87 spikes/s

^aBest-fitting values of parameters for the fit to the two sets of results shown in Fig. 3. The first and third columns show values obtained assuming pure cone input to the surround. For the red off-center cell in Fig. 3A (91ab), center and surround have elevations -94.8 and -80.9 , respectively. For the green off-center cell in Fig. 3B (91d), center and surround have elevations of -80.9 and -94.8 deg, respectively. These values correspond to the preferred directions for single classes of cones. The second and fourth columns show results for a surround that receives input from a luminance mixture of L- and M-cones, i.e. a preferred elevation of $90/-90$ deg. Changing the composition of inputs to the surround changes the best-fitting values of parameters but does not increase the residual mean error (RME).

has several free parameters, it enables us to describe temporal-chromatic interactions fairly completely. We exploited this for two purposes. First, we characterized succinctly the interaction between a cell's chromatic properties and its temporal properties, expressed through the change of the preferred elevation with temporal frequency. Second, we investigated whether this description of spatio-temporal interactions constrains the chromatic properties of the surrounds well enough to distinguish surrounds that receive pure cone input from those that receive mixed cone input.

Preferred elevation as a function of temporal frequency

The model delivers a useful summary of the effects of temporal frequency on the chromatic properties of cells. Fig. 5 shows how preferred elevation depends on temporal frequency. The curves are derived from best fits of the model to sets of responses (like those shown in Fig. 3) obtained from 17 red-green cells, seven on-center (upper group) and ten off-center ones (lower group).

The effect of temporal frequency varied from cell to cell, although in all cases the preferred elevation increased progressively with increasing temporal frequency. Some cells, especially those that at low temporal frequencies preferred high elevations (and by implication have a dominant center), showed little change of preferred elevation with increasing temporal frequencies. A few cells showed a substantial change in preferred elevation even below 5 Hz. Between these extremes lay the largest group, among which elevation changed in the frequency range between 7 and 20 Hz. For most cells the change of chromatic tuning was fairly gradual, but in a few the change was abrupt, spanning a range of 70 deg between about 6 and 12 Hz. Cells with low preferred elevations (sensitive to isoluminant modulations) always showed substantial changes of preferred elevation with increasing temporal frequency.

Estimating cone inputs to the surround

If the model fit sufficiently constrains the unknown parameter values, we can resolve the composition of the cone input to the surround of the red-green receptive field—whether the surround draws its input from a single class of cone, or from both L- and M-cones.

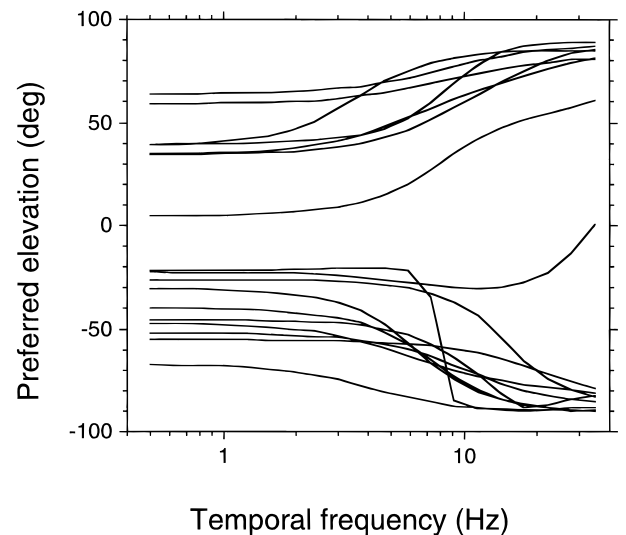


Fig. 5. The change of preferred elevation with temporal frequency, for 17 red-green P-cells (seven on-center and ten off-center). Preferred elevations were found by fitting the model to the sets of responses, and finding the elevation that yielded the largest amplitude response (without regard to phase). Lines for on-center cells lie in the upper part of the figure; lines for off-center cells lie on the lower part.

The change in a cell's preferred elevation with increasing frequency depends both on the different temporal properties of center and surround and on their chromatic signatures. With sufficiently tight constraint on its temporal parameters, our model can place bounds on the chromatic signature of the surround and thereby put bounds on the proportions in which L- and M-cones provide input to it.

The fits shown in Fig. 3 were obtained with center and surround elevations constrained to reflect pure cone input to each. We also examined fits obtained with the surround elevation fixed at values that reflected different mixtures of L- and M-cone inputs, ranging from pure input arising in a single class of cone to a mixture in the proportions that define the luminosity function. Since the temporal parameters of center and surround were not known *a priori*, the time constants, number of filters, and delays were initially allowed to vary freely. Similarly, the relative gain for the surround and the overall gain were free parameters. With these few constraints, the results were simple and clear: our measurements could be fitted equally well with surround elevation fixed anywhere in the range examined. We found no systematic increase or decrease of the fitting error with change in the surround elevation. The second and fourth columns in Table 1 show the parameter values obtained for mixed surrounds. The residual mean errors (RME, bottom lines in Table 1) were as small as, or smaller than, those for a pure surround. This was true for both red center cells and green center cells. Changes in the surround's preferred elevation could be compensated perfectly by changes in relative gain, delay (Fig. 3A) or temporal filtering, or a combination of these. Thus, without additional constraints on the values of parameters, pure- and mixed-cone surrounds account equally well for the temporal-chromatic interactions. We return to this issue in the Discussion.

Discussion

Change of chromatic properties with temporal frequency

Our measurements reveal a complex relationship between the chromatic and temporal characteristics of P-cells. The amplitude and phase of a cell's response vary with temporal frequency in ways that depend on the chromatic properties of the stimulus. The amplitude characteristic for chromatically modulated stimuli is band-pass; for achromatic stimuli, it is generally high-pass within the range of temporal frequencies we studied, and presumably declines at frequencies above 30 Hz. The phase of response changes progressively with increasing temporal frequency, but more for chromatically modulated stimuli than for achromatically modulated ones. For a cell in which center and surround have different spectral sensitivities, our model explains this behavior by heavier low-pass filtering of surround signals than center signals, and a longer delay in the transport of surround signals to the opponent site.

The chromatic properties of a red-green cell are succinctly represented by its preferred elevation. In most neurons the preferred elevation increases substantially with temporal frequency, although usually not until the frequency rises above about 7 Hz. Our model suggests that the change results from both a differential delay of center and surround signals, which increases the phase difference at higher temporal frequencies, and from stronger temporal filtering of surround signals. The latter causes the amplitude of the surround signal to decline more rapidly with increasing temporal frequency and also contributes to the phase shift between center and surround. The upshot is decreased antagonism between center and surround, so the preferred elevation shifts more toward that for the center mechanism, converging on the preferred eleva-

tion of either the L- or the M-cone. In our color space these preferred elevations lie at 99.1 deg and 85.2 deg, respectively.

Our results broadly agree with those of earlier studies (Gouras & Zrenner, 1979; Derrington et al., 1984; Lee et al., 1989*a,b*) that have explored how the chromatic properties of P-cells vary with temporal frequency. Like the earlier studies, we found substantial variation among cells in the effects of increasing temporal frequency, though unlike Gouras and Zrenner (but in agreement with Lee et al.) we found few cells that changed from color-opponent to nonopponent at frequencies below 15 Hz. Some cells showed little change with temporal frequency up to 15 Hz, but in most we saw a conspicuous change in chromatic properties with increasing temporal frequency. The cells we characterized, especially those with low preferred elevations, showed larger changes of preferred elevation than were previously reported by Derrington et al. (1984). Part of the discrepancy might arise from the different ways in which the preferred elevations were estimated in the two studies. Derrington et al. assumed similar dynamics for center and surround and algebraic summation of cone signals. We took different dynamics into account and used vector summation of signals. The different approaches, however, cannot account fully for the differences observed. Part of the discrepancy might be due to sampling.

Cone inputs to the surround

Two earlier studies have explored the mix of L- and M-cone signals in the surround. In simulating the results obtained by Derrington et al. (1984), Lennie et al. (1991) could not distinguish pure and mixed cone inputs. Reid and Shapley (1992) explored the local spatial distribution of cone inputs to the P-cells' receptive fields and found that inputs from the two classes of cones were segregated in center and surround. The receptive fields studied by Reid and Shapley were very much larger than those examined here, and might have represented a different population of cells.

Our results could be fitted equally well with a model that assumes pure cone input or mixed cone input to the surround. From a similar analysis, Smith et al. (1992) found that the temporal characteristics of red center cells, but not green center cells, were described more accurately by assuming pure cone than mixed cone input to the surround. (Differences in behavior resulting from pure *versus* mixed surrounds are smaller for green center cells than for red center cells, due to the larger weight of L-cones in a luminance mixture.) We found that for both red and green center cells the data could be perfectly fitted by either mixed or pure surrounds. The discrepancy between studies might reflect different constraints imposed on the models they used: Smith et al. fitted independently the results obtained at each temporal frequency. Our measurements at all temporal frequencies were fitted in a single operation, so our procedure imposes the constraint that the amplitude and phase of both center and surround signals must vary regularly with change of temporal frequency. The filter parameters, the transport delay, and the gain parameters were however free to vary.

The change in a cell's chromatic properties with temporal frequency provides too little information to estimate the chromatic signature of its surround. This does not reflect unreliable or noisy measurements, but rather a more interesting and fundamental constraint that a range of values among different parameters can bring about exactly the same behavior. To confirm this, we generated a noise-free data set by fitting the model to the data in Fig. 2. With surround elevation fixed at each of a range of values, we then examined the fit of the model to the synthetic data set. A perfect fit

was obtained for a pure cone surround as well as for a surround with the spectral sensitivity of the luminosity function.

It might be argued that our failure to capture the chromatic signature of the surround results from our model permitting too many degrees of freedom for the temporal properties of center and surround. There is good reason to believe that the temporal properties arise jointly from transport delays and filtering delays, and we believe both must be represented in the fit. We can, however, explore tighter constraints on the temporal characteristics of the surround, and ask whether doing that confines the possible values of the surround's chromatic signature. If we can measure the temporal characteristics of the surround in isolation, these can be fixed in making the final fit. Given that the center receives input from a single cone class, the surround can be isolated by confining stimulus modulations to the null-plane for the center cone. The temporal properties of the isolated surround can then be determined, and their values fixed in the final fit. We examined this using a noise-free data set generated by the model. We found, however, that even with the surround's temporal properties fixed, the model still confounded the chromatic properties of the surround with other unknown parameters in the fit. In particular, the surround's elevation could be traded against its relative gain in relation to the center. We conclude that any variation in temporal characteristics with the mixture of cone inputs to the surround can be duplicated by physiologically plausible changes in the values of other relevant parameters.

It is undoubtedly more expensive to build receptive-field surrounds that draw on pure L- or M-cone input than it is to build surrounds that draw inputs indiscriminately from all L- and M-cones within their compass. Our inability to distinguish a cell that receives surround input from L-cones only or M-cones only and a cell that receives surround input from both L- and M-cones suggests that, at least for shaping the temporal-chromatic characteristics of a cell, nothing is to be gained by this expenditure.

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