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# THE PHYSIOLOGICAL BASIS OF HETEROCHROMATIC FLICKER PHOTOMETRY DEMONSTRATED IN THE GANGLION CELLS OF THE MACAQUE RETINA

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SUMMARY

1. Heterochromatic flicker photometry is a way of measuring the spectral sensitivity of the human eye. Two lights of different colour are sinusoidally alternated at, typically, 10–20 Hz, and their relative intensities adjusted by the observer until the sensation of flicker is minimized. This technique has been used to define the human photopic luminosity, or $V_\lambda$, function on which photometry is based.

2. We have studied the responses of macaque retinal ganglion cells using this stimulus paradigm. The responses of the phasic ganglion cells go through a minimum at relative radiances very similar to that predicted from the $V_\lambda$ function. At this point, defined as equal luminance, an abrupt change in response phase was observed. A small residual response at twice the flicker frequency was apparent under some conditions.

3. The spectral sensitivity of parafoveal phasic cells measured in this way corresponded very closely to that of human observers minimizing flicker on the same apparatus.

4. Minima in phasic cell activity were independent of flicker frequency, as is the case in the psychophysical task.

5. The response minima of phasic cells obey the laws of additivity and transitivity which are important characteristics of heterochromatic flicker photometry.

6. As the relative intensities of the lights were altered responses of tonic, spectrally opponent cells usually underwent a gradual phase change with vigorous responses at equal luminance. The responses of tonic cells treated individually or as a population could not be related to the $V_\lambda$ function in any meaningful way.

7. We conclude that the phasic, magnocellular cell system of the primate visual pathway underlies performance in the psychophysical task of heterochromatic flicker photometry. It is likely that other tasks in which spectral sensitivity conforms to the $V_\lambda$ function also rely on this cell system.

## INTRODUCTION

Flickering stimuli are readily generated with simple equipment, and the history of psychophysical studies of flicker reaches back beyond the 19th century (Kelly, 1972). One technique of importance is heterochromatic flicker photometry which is used to

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determine the spectral sensitivity of a human eye. It was largely on the basis of results obtained with this method that the human photopic luminous efficiency function, $V_\lambda$, was defined by the Commission Internationale de l'Eclairage (C.I.E.) in 1924 (see Wyszecki & Stiles, 1982). This function has acquired major importance as a basis for physical light measurement; it has formed 'the basis of photopic photometry for over 50 years' (Wyszecki & Stiles, 1982). With this function, radiometric units are converted to photometric units.

In heterochromatic flicker photometry, lights of differing spectral composition are alternated at, say, 10 Hz, and the subject has to adjust their relative radiances until the sensation of flicker is minimized or abolished. The two spectral mixtures are then defined as of equal luminance for that observer (or equal sensation luminance; see Kaiser, 1988). To define a spectral sensitivity function, different monochromatic lights are alternated with some standard (see Boynton, 1979). The photopic $V_\lambda$ function, which peaks at 555 nm, represents an average of different sets of data obtained with this technique, together with some data obtained by other methods (see Wyszecki & Stiles, 1982).

A physiological mechanism underlying heterochromatic flicker photometry should possess the important characteristics found psychophysically. First, the mechanism should have the desired sensitivity, $V_\lambda$. Secondly, spectral sensitivity should be independent of the flicker frequency used. Psychophysically, sensitivity is independent of flicker frequency between about 5 and 40 Hz; below 5 Hz the sensation of chromatic flicker makes the task difficult. Thirdly, the linearity laws of brightness matching should be obeyed. Additivity and proportionality should be present. If stimuli $A$ and $B$ are adjusted for equal luminance by heterochromatic flicker photometry, and also $A$ and $C$, then $A$ alternated with $B/2+C/2$ should also provide a flicker minimum. This is at least approximately the case psychophysically. Also, transitivity should apply. If $A$ and $B$ are equated and also $A$ and $C$, then $B$ and $C$ should provide a minimum when directly exchanged.

The responses of neurones in the visual pathway to flickering stimuli have been studied in some detail in the cat (Enroth, 1953; Maffei, Cervetto & Fiorentini, 1970; Frascella & Lehmkuhle, 1984), but in order to obtain results relevant to human psychophysics it is necessary to turn to non-human primates. The visual system of Old World primates, for example the macaque monkey, is very similar to that of man. The spectral sensitivities of the cones of both species are almost identical (Bowmaker & Dartnall, 1980; Bowmaker, Dartnall & Mollon, 1980; Nunn, Schnapf & Baylor, 1984; Baylor, Nunn & Schnapf, 1987), and so is their psychophysical performance (DeValois, Morgan, Polson, Mead & Hull, 1974). The visual pathway contains two main cell systems; one consists of tonic, spectrally opponent retinal ganglion cells which project to the parvocellular layers of the lateral geniculate nucleus, and the other of phasic non-opponent ganglion cells which project to the magnocellular layers of the nucleus (Wiesel & Hubel, 1966; de Monasterio & Gouras, 1975; Dreher, Fukuda & Rodieck, 1976; de Monasterio, 1978; Creutzfeldt, Lee & Elepfandt, 1979; Perry, Oehler & Cowey, 1984).

Only two papers have considered the responses of these different cell types to flickering stimuli (Spekreijse, van Norren & van den Berg, 1971; Gouras & Zrenner, 1979) despite the wide variety of psychophysical paradigms which employ flicker of

one form or another. We have recorded from ganglion cells in the monkey retina using different kinds of flickering stimuli. In this report we describe the responses of macaque ganglion cells under conditions similar to those used in heterochromatic flicker photometry. We show that the properties required of a system underlying heterochromatic flicker photometry are all found in the phasic cell system whereas it is not possible to account for the psychophysical results on the basis of the tonic wavelength-opponent system.

Preliminary reports of some of these results have appeared elsewhere (Lee, Martin & Valberg, 1987). A more extensive description of the responses to flicker of these different cell types is in preparation (B. B. Lee, P. R. Martin & A. Valberg, in preparation).

## METHODS

Juvenile macaques (*M. fascicularis*, 2–3 kg) were anaesthetized with an intramuscular injection of ketamine hydrochloride (10–20 mg/kg). The animal was held in a stereotaxic frame, and one eye prepared for recording by sewing a cuff of conjunctiva to a ring. A needle was inserted into the eye about 2–3 mm behind the limbus as a guide tube for a tungsten-in-glass microelectrode which was lowered onto the retina. A flat plate on the sclera provided a socket joint about which the tube could be rotated and helped prevent loss of vitreous humour.

During surgery the animal was ventilated through a tracheal cannula with a 70%/30% $N_2O/O_2$ mixture with 1–2% halothane. After completion of surgery wound areas were infiltrated with local anaesthetic (Licocaine) and the halothane content in the inspired gas mixture reduced to 0·2–1·0%. EEG and ECG were monitored as a check on adequacy of anaesthesia. End-tidal $P_{CO_2}$ was kept near 4% by adjusting the rate and depth of ventilation. Eye movements were prevented by intravenous infusion of gallamine triethiodide (5 mg $kg^{-1}$ $h^{-1}$) together with additional fluids (3–5 ml/h). Body temperature was maintained near 37·5 °C.

A contact lens of internal radius matched to the corneal curvature protected the eye, which was focused on a tangent screen 57 cm from the animal with accessory lenses as necessary. The loci of fovea and optic disc were mapped onto the screen with the aid of a fundus camera. A 6 mm artificial pupil was usually used during recording.

We recorded from ganglion cells in the parafoveal retina, with eccentricities between 3 and 10 deg. After the electrode had penetrated the axon layer on the retinal surface, activity of a ganglion cell was isolated, and the cell type ascertained with flashing spots. Wavelength-opponent cells were usually readily identifiable by their very sustained discharge to excitatory wavelengths, while phasic cells gave to all wavelengths a transient burst of activity at moderate contrast levels. In doubtful cases thresholds to achromatic contrast were estimated by listening to responses to flashed spots over a loudspeaker. The tonic cells of the parvocellular layers of the geniculate nucleus have substantially lower sensitivity to achromatic contrast than the phasic cells of the magnocellular layers (Kaplan & Shapley, 1982; Hicks, Lee & Vidvasagar, 1983), and this difference is also characteristic of phasic and tonic ganglion cells (B. B. Lee & A. Valberg, unpublished observations). Cell responses to a standard series of equiluminous stimuli of differing dominant wavelength were recorded as an aid in cell classification.

*Visual stimulation.* Visual stimuli were generated with a three-channel optical stimulator, each having as a light source a tungsten filament lamp (Prado Universal, Leitz), providing white light with chromaticity co-ordinates $x, y = 0{\cdot}404$, $0{\cdot}410$. One channel provided a background if necessary. Crossed polaroid filters before the other two projectors and a rotating polaroid disc, placed in the combined projector beams, enabled us to sinusoidally alternate different spectral mixtures. We routinely used a 4 deg stimulus field, but frequently recorded responses with a 0·5 deg field for purposes of comparison. We chose this latter size so as to be certain of completely activating the receptive field centre without encroaching too much upon the surround. Changes in adaptation level were achieved by placing neutral density filters before the animal's eye.

Spectral composition of stimuli was adjusted with interference filters (Schott, NAL, half-bandwidth at half-height, 25 nm) and intensities could be adjusted with neutral density filters.

Filter wheels with ten slots allowed a sequence of stimuli to be pre-selected. When inserted into the stimulus beams, these wheels were controlled by a computer system which also averaged and stored unit responses. An analog output from a spot photometer (Photo Research) was also stored, to give us a record of the luminance over a cell's receptive field.

A Photo Research 702A/703A Scanning Spectrophotometer measured the luminance (2 deg) and chromaticity co-ordinates of the stimuli. The luminance levels measured with it were within 10% of those of the spot photometer. Since cell receptive fields were parafoveal, we used photometric values based on the 10 deg $V_\lambda$ curve. To do this, we calculated the spectral power distribution of the stimuli from spectral transmissions of the filters and the spectral power distribution of the projector light. Multiplying by the 2 or 10 deg $V_\lambda$ function and summing over the spectrum allowed us to calculate relative luminance, as described by Valberg, Lee & Tryti (1987). Precise comparison of the $V_\lambda$ of man and monkey has not been carried out, but the measurements which are available (DeValois *et al.* 1974) suggest they are similar. We have used the human $V_\lambda$ on the assumption it is very close to that of the monkey. This assumption is examined in the Discussion.

Responses to heterochromatic flicker were studied in two ways. Either the luminance of one component was held constant (mean 25 cd/m$^2$) and the other systematically varied, or we kept the total mean luminance of the flickering stimuli constant at 50 cd/m$^2$ while changing the luminance ratio between them. A mean luminance of 50 cd/m$^2$ corresponds to a retinal illuminance of 1400 td. Luminance elsewhere in the visual field was approximately 10 cd/m$^2$.

Cell responses to each stimulus condition were averaged over about 6 s and stored as a peristimulus time histogram. Amplitudes of responses were derived from Fourier analysis of these histograms.

## RESULTS

### *Cell responses to heterochromatic flicker*

We have recorded the responses of macaque ganglion cells to heterochromatic and luminance flicker. In the heterochromatic paradigm, two different spectral mixtures were sinusoidally alternated, and cell responsiveness measured as the relative intensities of the two components were changed. In the luminance flicker paradigm responses were recorded to a flickering light which was sinusoidally varied in intensity. It was usually possible to maintain stable recording for several hours permitting a rather extensive examination of a cell's behaviour. We recorded responses to heterochromatic flicker from forty-two phasic ganglion cells and from fifty-four tonic, spectrally opponent ganglion cells. We describe here results relevant to the psychophysical task of heterochromatic flicker photometry. A more extensive description of cell responses to the different flicker paradigms is in preparation (B. B. Lee, P. R. Martin & A. Valberg, in preparation).

In the psychophysical task of heterochromatic flicker photometry, the observer varies the relative intensities of the two flickering lights until the sensation of flicker is minimized or abolished. We searched for a physiological substrate for this task by measuring cell responses as the intensity of a test, almost monochromatic, light was varied relative to that of a reference light. Usually, a white light was used as a reference spectral mixture, but some experiments were also carried out with alternation of two monochromatic lights. Responses of phasic and tonic ganglion cells showed marked, qualitative differences with this paradigm, and Figs 1–5 contain response histograms which demonstrate these differences.

Examples of responses of a phasic off-centre and a phasic on-centre cell are shown in Figs 1 and 2 respectively, together with a sketch indicating the composition of the flicker. Each histogram contains the averaged response to one cycle of flicker at 10 Hz and, proceeding down each of the four columns in each figure, the relative

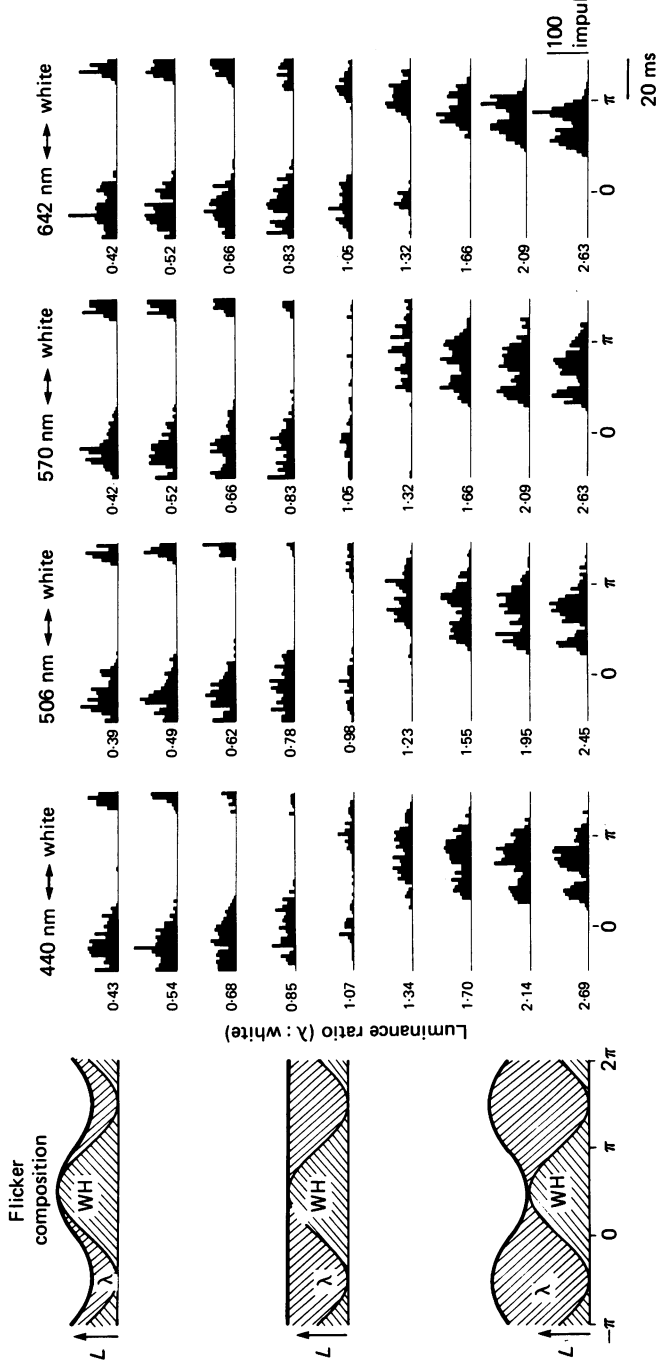


Fig. 1. Response histograms of a phasic off-centre cell to heterochromatic flicker (10 Hz, 4 deg field), the composition of which is illustrated on the left. The modulation of luminance ($L$) of each light for slightly more than one cycle of flicker is shown; the thick line shows the total luminance of the mixture. White was alternated with near-monochromatic lights of the wavelengths indicated. Each histogram represents the response to one cycle of flicker, beginning at the minimum intensity of the white component ($-\pi/2$). The luminance ratio ($\lambda$:white) is indicated for each histogram. The modulated response of the cell goes through a minimum close to a luminance ratio of one at which point an abrupt change in phase is seen. Six seconds of activity were averaged for each histogram. Bin width was 2 ms. The responses of the cells commonly 'wrap around' the end of the histogram.

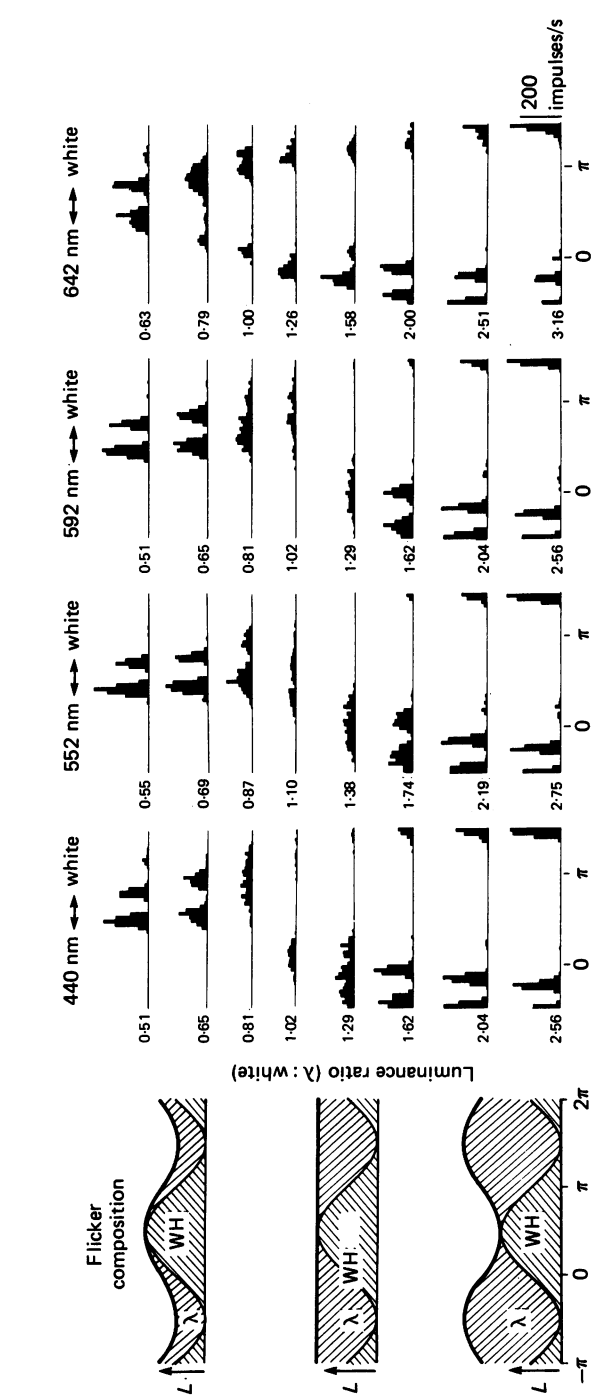


Fig. 2. Response histograms of a phasic on-centre cell to heterochromatic flicker (10 Hz, 4 deg field), the composition of which is illustrated on the left. *L* indicates luminance. White was alternated with near-monochromatic lights of the wavelengths indicated. Each histogram represents the response to one cycle of flicker, beginning at the minimum intensity of the white component ($-\pi/2$). The luminance ratio ($\lambda$ : white) is indicated for each histogram. The modulated response of the cell goes through a minimum close to a luminance ratio of one, at which point an abrupt change in phase occurs. The cell responds about a half-cycle out-of-phase to that in Fig. 1. Six seconds of activity were averaged for each histogram, and bin duration was 2 ms.

intensities of the two lights increase in 0·1 log unit steps. For each column a different wavelength was alternated with white light. Those shown were chosen from nine different wavelengths usually tested on each cell. The beginning of each histogram corresponds to the minimum intensity in the white component of the flicker.

Stimuli were calibrated in terms of the human 10 deg $V_\lambda$ function (see Methods) and the ratio of the luminance of the monochromatic to that of the white component accompany each histogram so that at a ratio of one the two lights were of equal luminance. Inspection of the histograms reveals that cell responsiveness passes through a minimum close to this ratio with all wavelengths used, although a residual response is sometimes present. As relative intensity is changed through a ratio of one, a relatively abrupt phase change occurs, so that on comparing the top and bottom histograms of each column a half-cycle phase shift is seen. The phase behaviour of the on- and off-centre cell is of course reversed.

The responses of the cells of Figs 1 and 2 were characteristic for all phasic cells studied, with clear minima close to equal luminance. Phasic cells, in this respect, formed a homogeneous population. The minimization of activity of phasic cells thus corresponds to the minimization of subjective flicker by human subjects under the same conditions.

It was seldom possible to abolish completely phasic cell responses. This was partly due to the 0·1 log unit steps used, corresponding to a change in luminance contrast of about 11 %, luminance contrast being defined as $(L_{max}-L_{min})/L_{max}+L_{min})$, with $L_{max}$ and $L_{min}$ representing maximum and minimum luminances in the flicker. The contrast threshold of phasic cells, both in the magnocellular layers of the geniculate nucleus (Kaplan & Shapley, 1982; Hicks *et al.* 1983; Derrington & Lennie, 1984) and in phasic ganglion cells (B. B. Lee, P. R. Martin & A. Valberg, in preparation), is 2–4 %, so that sometimes a small residual response at the fundamental frequency can be seen.

A residual response at twice the stimulus frequency can also be seen in Figs 1 and 2 for some wavelengths. This was especially apparent with long wavelengths, as can be seen in the 642 nm column of histograms. The frequency-doubled response was not present when the two alternating lights lay along a tritanopic confusion line (see Fig. 1, 570 nm). Along a tritanopic confusion line at equal luminance there is a modulation of only the short- (S) wavelength cones and so such spectral mixtures cannot be distinguished by a tritanopic observer.

We attribute this frequency-doubled response to a non-linearity seen on summation of middle- (M) and long- (L) wavelength cone inputs in phasic cells, and it is described in more detail elsewhere (Lee, Martin & Valberg, 1988). When such a frequency-doubled signal is of significant amplitude it might be expected to interfere with the minimization of subjective flicker by human subjects, and we argue later that this is the case.

The responses of tonic, spectrally opponent cells differed qualitatively from those of phasic cells. We were able to record from cells receiving all the cone combinations commonly observed, +M−L, +L−M, +S−(ML) and +M−S (de Monasterio & Gouras, 1975; Derrington, Krauskopf & Lennie, 1984; Valberg, Lee & Tigwell, 1986; Lee, Valberg, Tigwell & Tryti, 1987). We illustrate in Figs 3–5 results from a red on-centre cell, a green on-centre and a blue on-centre cell, the latter receiving S-cone input.

Figure 3 shows response histograms to one cycle of flicker for a red on-centre cell, three wavelengths being shown. For short (440 nm) and long (642 nm) wavelengths there is a gradual change in response phase as luminance ratio is altered, but no sign of a minimum over the range tested (note that the steps used are coarser than in Figs 1 and 2). The response to 642 nm–white flicker is in fact maximal at equal luminance. Only for 570 nm–white flicker is there no modulated response at equal luminance. These lights lie close to a tritanopic confusion line, so that if a cell received only M- and L-cone inputs, it would be unresponsive to 570 nm–white flicker at equal luminance (Derrington *et al.* 1984; Valberg *et al.* 1986).

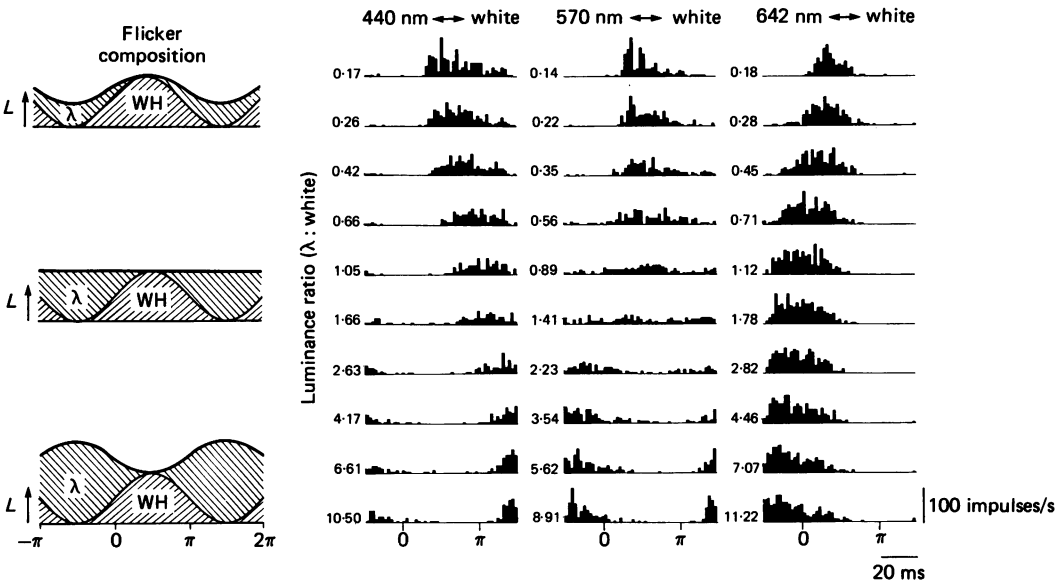


Fig. 3. Response histograms of a red on-centre cell to heterochromatic flicker (10 Hz, 4 deg field), the composition of which is illustrated on the left. *L* indicates luminance. White was alternated with near-monochromatic lights of the wavelengths indicated. Each histogram represents the response to one cycle of flicker, beginning at the minimum intensity of the white component. The luminance ratio ($\lambda$:white) is indicated for each histogram. The phase of response undergoes a gradual change without any indication of a minimum, except for 570 nm–white flicker. These lights lie along a tritanopic confusion line and so for a red on-centre cell with no S-cone input no response is to be expected. Six seconds of activity were averaged for each histogram, and bin duration was 2 ms.

A similar result is shown for a green on-centre cell in Fig. 4. Again, the cell's response is characterized by a gradual phase shift without any sign of a minimum except with 570 nm–white flicker. For some cells we ensured by taking finer steps that we were not missing a very sharp minimum in the range of ratios tested.

Examination of the histograms in Figs 3 and 4 shows that for short and long wavelengths the phase shift is in the opposite direction. Also the direction of the phase shift for a given wavelength is reversed for the two cells. The direction of the phase shift, and its reversal, is consistent with it being due to a centre–surround phase delay (Gouras & Zrenner, 1979). We investigate this effect in more detail, and at different temporal frequencies, elsewhere (B. B. Lee, P. R. Martin & A. Valberg, in preparation).

Figure 5 shows sets of histograms for a blue on-centre cell receiving S-cone input. This neurone responds most vigorously to 440 nm–white flicker, but gives a response to 570 nm–white flicker at equal luminance. This is to be expected since along a tritanopic confusion line the S-cone's excitation is modulated, causing the cell to respond.

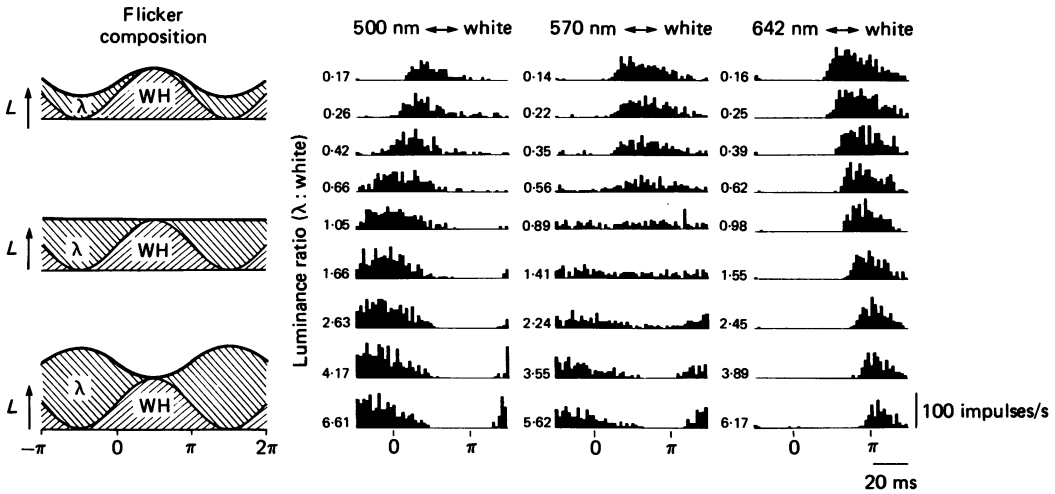


Fig. 4. Response histograms of a green on-centre cell to heterochromatic flicker (10 Hz, 4 deg field), the composition of which is illustrated on the left. *L* indicates luminance. White was alternated with near-monochromatic lights of the wavelengths indicated. Each histogram represents the response to one cycle of flicker, beginning at the minimum intensity of the white component. The luminance ratio ($\lambda$:white) is indicated for each histogram. The phase of response undergoes a gradual change without any indication of a minimum, except for 570 nm–white flicker. These lights lie along a tritanopic confusion line, and so for a green on-centre cell with no S-cone input, no response is to be expected. Six seconds of activity were averaged for each histogram, and bin duration was 2 ms.

Responses of S-cone on-centre cells were more complex than those of red or green on-centre cells, for frequency-doubled responses sometimes appeared. For 440 nm, less phase shift is visible than in Figs 3 and 4. This may be because the inhibitory cone mechanisms of blue on-centre cells lead to an off-response with achromatic flicker, which is then reinforced by an excitatory response evoked by the 440 nm flicker component as it increases in intensity. The responses to 570 nm–white flicker are not explicable on this basis, however. A frequency-doubled component is visible in the response which may indicate some kind of non-linearity.

In order to quantify cell responses, we subjected them to Fourier analysis and plotted the amplitude of the fundamental response as a function of luminance ratio. For phasic cells a sharp minimum was present close to equal luminance. In Fig. 6, responses of the cells of Figs 1 and 2 have been plotted in this way. In the top panels the amplitude of the fundamental is shown relative to the luminance ration ($\lambda$: white) of the flicker components. The cells' responsiveness goes through a sharp minimum close to a luminance ratio of one. In the lower panels, response phase is plotted in the same manner. When a luminance component is present in the flicker, the response of the on- and the off-centre cell lags behind the maximum and minimum

luminance in the flicker by about $0{\cdot}2\pi$. At low luminance contrasts this phase lag increases somewhat and there is an abrupt change in phase close to equal luminance. At this point, if the fundamental were absent, phase would be undefined, and this has been represented by the dashed lines.

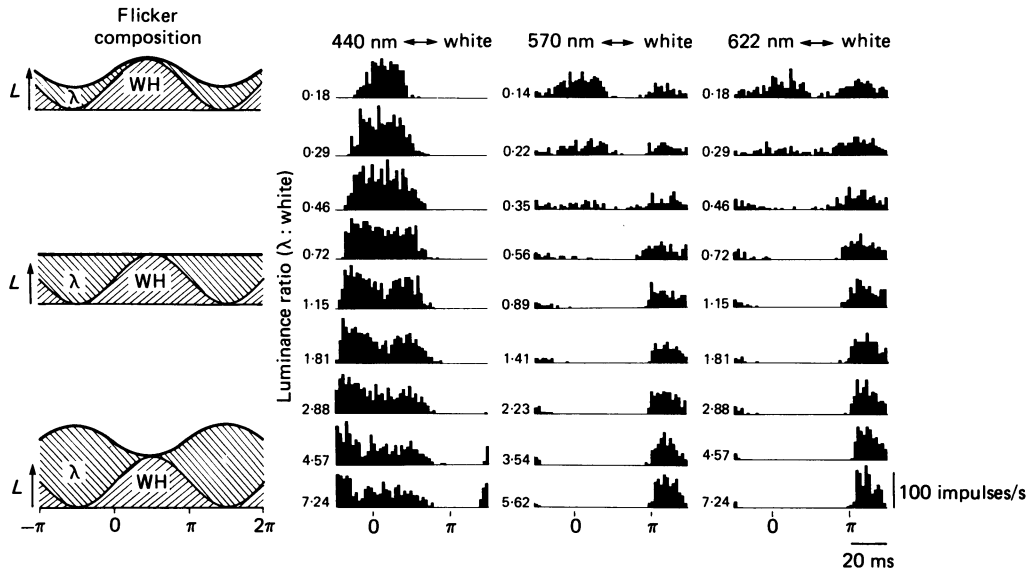


Fig. 5. Response histograms of a blue on-centre cell to heterochromatic flicker (10 Hz, 4 deg field), the composition of which is illustrated on the left. *L* indicates luminance. White was alternated with near-monochromatic lights of the wavelengths indicated. Each histogram represents the response to one cycle of flicker, beginning at the minimum intensity of the white component. The luminance ratio ($\lambda$:white) is indicated for each histogram. The phase of response undergoes a gradual change without any indication of a minimum. There is a response to 570 nm–white flicker at a luminance ratio of one, for these lights differentially activate the S-cone. Six seconds of activity were averaged for each histogram, and bin duration was 2 ms.

Figure 7 shows the same type of analysis for the cells of Figs 3–5, together with data for an extra wavelength. For the red and green on-centre cells (Fig. 7*A* and *B*) there is no indication of a minimum at equal luminance except for 570 nm–white flicker. Often, a very substantial residual response is present. Although there is a clear minimum for 570 nm–white flicker, it is much less sharply defined than for phasic cells (note that the abscissae in Figs 6 and 7 differ). The difference in slope of the descending limbs of the 570 nm–white curve between phasic and tonic cells is equivalent to the difference in contrast gain between cells of the parvo- and magnocellular layers of the lateral geniculate nucleus described by Kaplan & Shapley (1982). For the blue on-centre cell in Fig. 7*C* there is a response to both 570 nm–white flicker and to the other wavelengths at equal luminance.

Response phase of tonic cells varied much more between different wavelengths at a given luminance ratio than was the case for the phasic cells of Fig. 6, and response phase appeared to be affected by changes in luminance ratio over a very broad range. We found that increasing luminance ratio with wavelengths above 570 nm caused a

progressive phase advance in the response of red on-centre cells, and a progressive phase lag for green on-centre cells. For wavelengths below 570 nm the opposite was the case. As mentioned above, this is consistent with a centre–surround phase delay underlying these phase shifts.

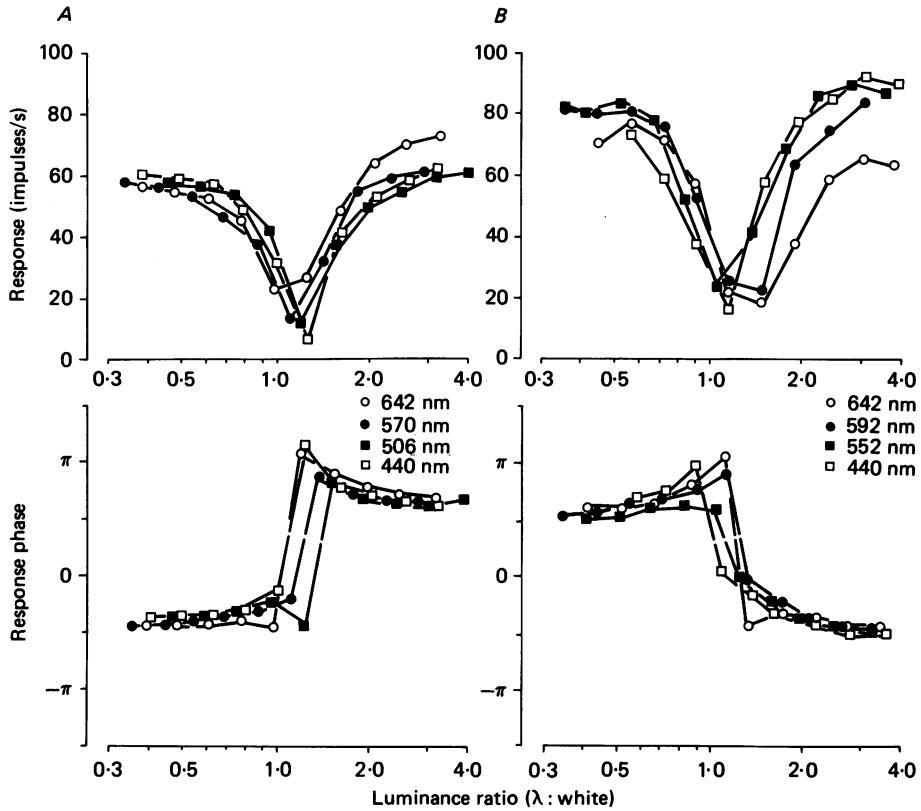


Fig. 6. Results of a Fourier analysis of the responses of phasic cells in Figs 1 and 2. Above are plotted the amplitudes of the first-harmonic components for the wavelengths indicated as a function of luminance ratio. For both cells responsiveness passes through a minimum close to a luminance ratio of one. Below, response phase is plotted against luminance ratio. An abrupt change occurs close to equal luminance. Strictly speaking, at this point phase is undefined (indicated by the breaks in the lines) and whether a phase shift of plus or minus $\pi$ is chosen is arbitrary. For clarity, we show here all shifts in one direction. An alternative method of plotting phase and cell response is shown in Fig. 11.

We conclude that the minimization of subjective flicker in heterochromatic flicker photometry finds an obvious substrate in the minimization of activity in the phasic cells which belong to the magnocellular pathway.

*Flicker photometric spectral sensitivity of phasic cells*

From curves such as those in Fig. 6 we interpolated the intensity ratios at which individual cells' activity went through a minimum. For twenty-six cells, we measured such minima throughout the spectrum. In Fig. 8*A* we compare the spectral

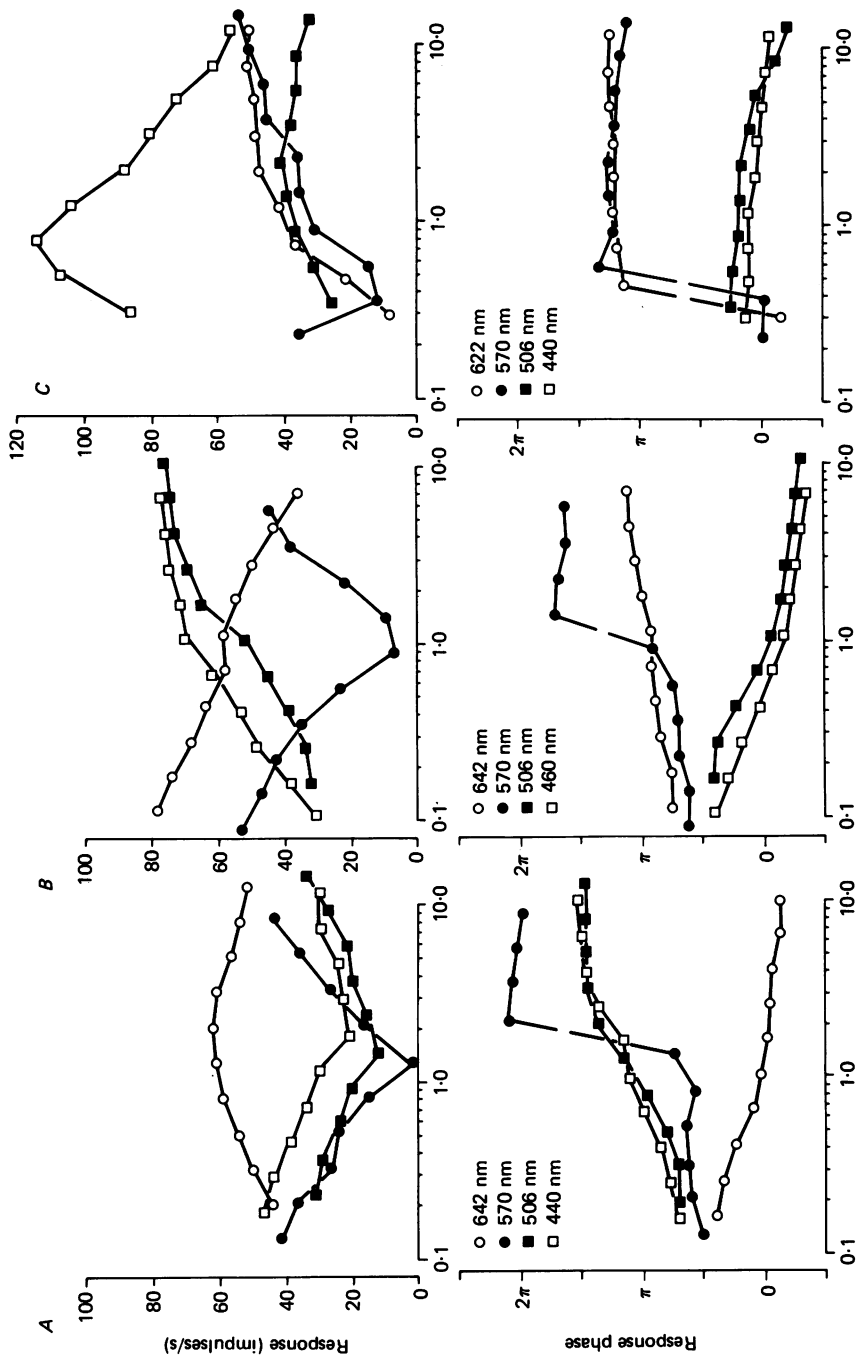


Fig. 7. Results of a Fourier analysis of the responses of tonic cells in Figs 3–5. Above are plotted the amplitudes of the first-harmonic components for the wavelengths indicated as a function of luminance ratio. For the red and green on-centre cells, responses are vigorous close to a luminance ratio of one, except for 570 nm–white flicker, when responsiveness passes through a minimum. Below, gradual changes in response phase are seen as luminance ratio is altered. For the blue on-centre cell, a significant response is apparent to 570 nm–white flicker.

sensitivity of phasic cells measured in this way with the human 10 deg $V_\lambda$ sensitivity function. The function has been changed slightly to take into account that our interference filters were not absolutely monochromatic, but this made a difference of less than 0·1 log unit except at 440 nm. The error bars indicate standard deviations. There is very good agreement between cell spectral sensitivity and the $V_\lambda$ function.

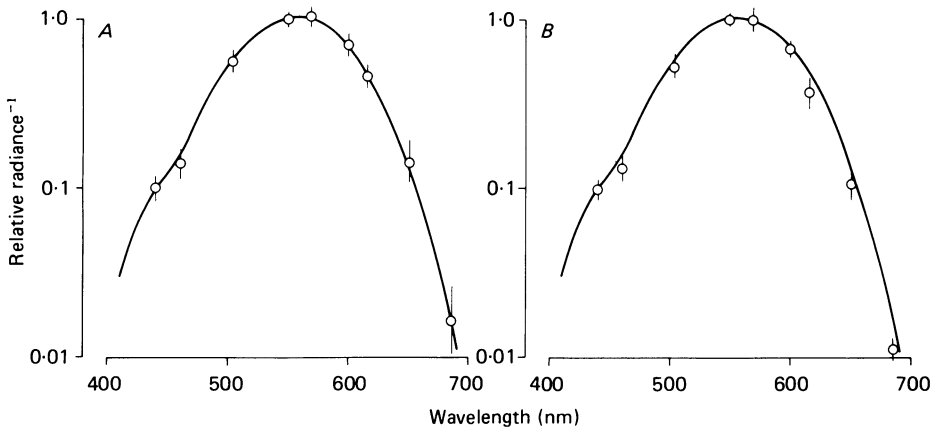


Fig. 8. *A*, spectral sensitivity of phasic cells (4 deg field) was calculated from the minima in graphs such as those in Fig. 6. The means and standard deviations from measurements at nine wavelengths on twenty-six phasic cells are indicated, and the human 10 deg $V_\lambda$ curve drawn in for comparison. The curve has been slightly modified to take into account the fact that our filters were not strictly monochromatic, but the correction is small. *B*, spectral sensitivity of nine human subjects (mean and S.D.) who were required to minimize flicker in a 4 deg field presented 10 deg parafoveally. The same corrected $V_\lambda$ curve as in *A* has been drawn through the points.

The standard deviations for wavelengths at the spectral extremes are larger than in mid-spectrum. Derrington *et al.* (1984) also reported such variation, in terms of variation of the null planes of phasic cells from the magnocellular layers of the lateral geniculate nucleus. We converted the variability we observed into their metric, and found it to be about 50 % of that observed by Derrington *et al.* (1984). Although such variation might be expected if some variability in the weighting of M- and L-cone inputs to individual phasic cells was present, the presence of second-harmonic components close to equal luminance, as shown in Figs 1 and 2, also increased the variability in phasic cell minima with wavelengths near the spectral extremes.

The 10 deg $V_\lambda$ function, although commonly used when studying parafoveal spectral sensitivity, is derived in a different way from the 2 deg function (see Wyszecki & Stiles, 1982). In order to provide comparable psychophysical results, we tested human observers on a flicker photometric task with stimuli presented at 10 deg eccentricity on temporal retina. The stimulus paradigm was identical to that used in the physiological experiments, with luminance ratio being changed in 0·1 log unit steps and the subjects reporting when flicker was minimized. Figure 8*B* shows means and standard deviations from eight normal trichromatic observers, again compared with the 10 deg $V_\lambda$ function. There is a good correspondence between the

flicker minima set by our subjects and the 10 deg function, and thus with cell spectral sensitivity.

The results in Fig. 8 show that the spectral sensitivity of phasic cells as determined by flicker photometry matches that of human observers, and thus meet this criterion for the physiological substrate of a luminance channel.

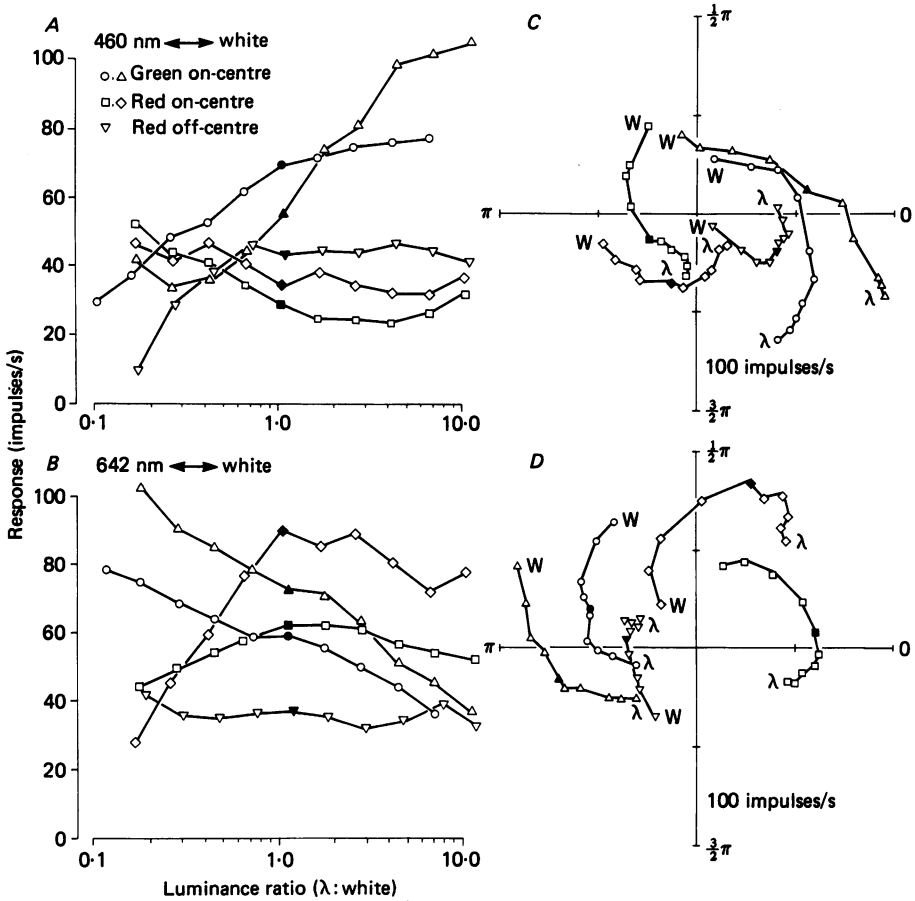


Fig. 9. Response of five tonic cells to heterochromatic flicker (*A*, 460 nm; *B*, 642 nm) at 10 Hz is plotted as a function of luminance ratio, for two wavelengths. In *C* and *D*, the same responses are plotted in polar co-ordinates together with response phase. The filled symbols represent the luminance ratios closest to one. High luminance ratios (λ:white) are designated by λ and low by W. A gradual change in phase as luminance ratio is altered, in opposite direction for the red and green on-centre cells, can be seen.

*A luminance channel from cone-opponent cells?*

Despite the steep minima observed in Fig. 6, and the excellent agreement between phasic cell sensitivity and the $V_\lambda$ function (Fig. 8), it might perhaps be argued that activity in tonic cells as a population goes through a minimum at equal luminance, and this contributes to the minimization in subjective flicker. To test if such a

hypothesis were viable we have plotted responses of five representative tonic cells in Fig. 9. In Fig. 9*A* and *B*, cell response is shown as a function of the luminance ratio between two monochromatic lights (460 and 642 nm) and white. There is no indication that activity in the sample of cells chosen would go through a minimum at equal luminance. However, it could be argued that such an analysis is not

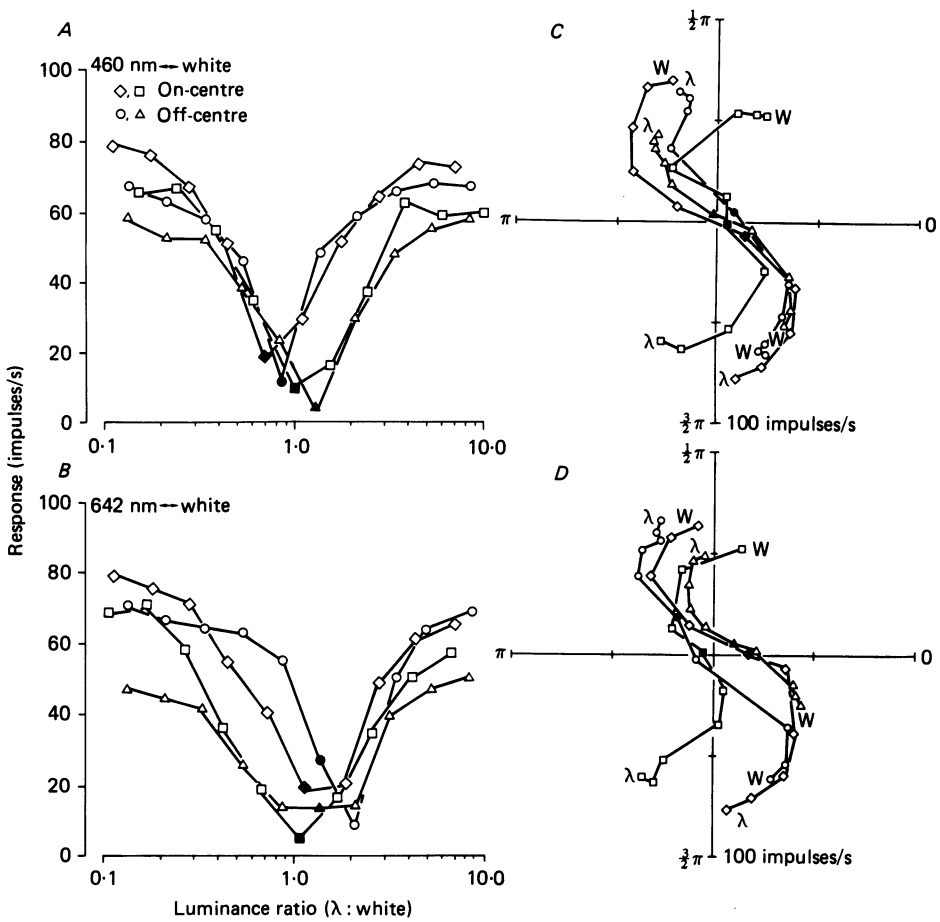


Fig. 10. Response of four phasic cells (two on-, two off-centre) to heterochromatic flicker at 10 Hz is plotted as a function of luminance ratio for two wavelengths (*A*, 460 nm; *B*, 642 nm). In *C* and *D* the same responses are plotted in polar co-ordinates together with response phase. The filled symbols represent the luminance ratios closest to one. High luminance ratios (λ : white) are designated by λ and low by W. The cells' responsiveness passes through a minimum close to a luminance ratio of one. In both sets of plots, it can be seen that the behaviour of all cells is similar.

adequate, for response phase has not been taken into account. To do so, we have transformed the same data into polar co-ordinates as shown in Fig. 9*C* and *D*. Response magnitude is represented on a radial axis and increasing phase lag is represented by an anticlockwise movement of the response vector. The symbols refer to the same cells as in *A* and *B*. For a particular curve, the low luminance ratio end

is marked by W, and the high ratio end by $\lambda$. The progressive phase change as luminance ratio varies can be seen. The filled symbols represent the responses close to a luminance ratio of one. Plotted in this way, different cell types clearly differ in their phase behaviour as luminance ratio or wavelength is varied. For the two wavelengths shown, the phase change is in opposite directions for red and green on-centre cells, and for each cell, phase changes in the opposite direction comparing 460 and 642 nm.

We attempted to find a minimum in the responsiveness of this sample population by adding the vectors for the different cells. It proved impossible to do so for several reasons. Because of the differences between cells, such vector sums usually did not behave in an orderly manner, not altering systematically as luminance ratio was changed. Also, for a given cell, responsiveness and phase were heavily dependent on the wavelength used, and the temporal frequency of flicker, so that a relative weighting for a vector sum of different cells which might produce a minimum for one condition did not lead to a minimum under other conditions.

We show in Fig. 10 a similar analysis (for the same two wavelengths, 460 and 642 nm) for two on- and two off-centre phasic cells. In Fig. 10*A* and *B*, the amplitudes of the first-harmonic components of their responses are shown to go through a minimum close to a luminance ratio of one. In the polar co-ordinates, all curves pass near the origin, and phase behaviour of different cells is fairly similar, except at high contrasts. The spiral shape of the curves is indicative of a gradually increasing phase lag as luminance contrast is reduced.

We conclude that a minimum in the activity of a population of tonic, opponent cells does not occur at equal luminance, and thus cannot contribute to the minimization of subjective flicker in heterochromatic flicker photometry. It is remarkable that subjects can minimize or abolish subjective flicker in the face of such vigorous activity in the opponent cell population, and we present elsewhere evidence that a low-pass temporal filtering of this cell pathway is likely at a higher level (B. B. Lee, P. R. Martin & A. Valberg, in preparation).

*Variation in temporal frequency*

A subject who minimizes the sensation of subjective flicker in heterochromatic flicker photometry sets the same relative intensities of the component lights for all temporal frequencies at which the task is possible. Below about 5 Hz the sensation of chromatic alternation becomes so marked as to make the task difficult. We therefore tested twelve phasic cells, to see if minima were independent of temporal frequency. Two wavelengths were chosen (506 and 622 nm), and their intensities relative to the white reference light changed as shown in Figs 1 and 2. We tested these cells at six frequencies between 1 and 40 Hz, and typical results are shown in Fig. 11.

As shown in previous figures, the responsiveness of phasic cells went through a minimum close to equal luminance. We conclude from the data shown in Fig. 11 that this minimum is independent, or almost independent of flicker frequency, down to 1 Hz. Similar results were obtained with the other ten cells. We tested about twenty tonic cells at different temporal frequencies with the same wavelengths as in Fig. 11. Response magnitude and phase changed in a complex manner.

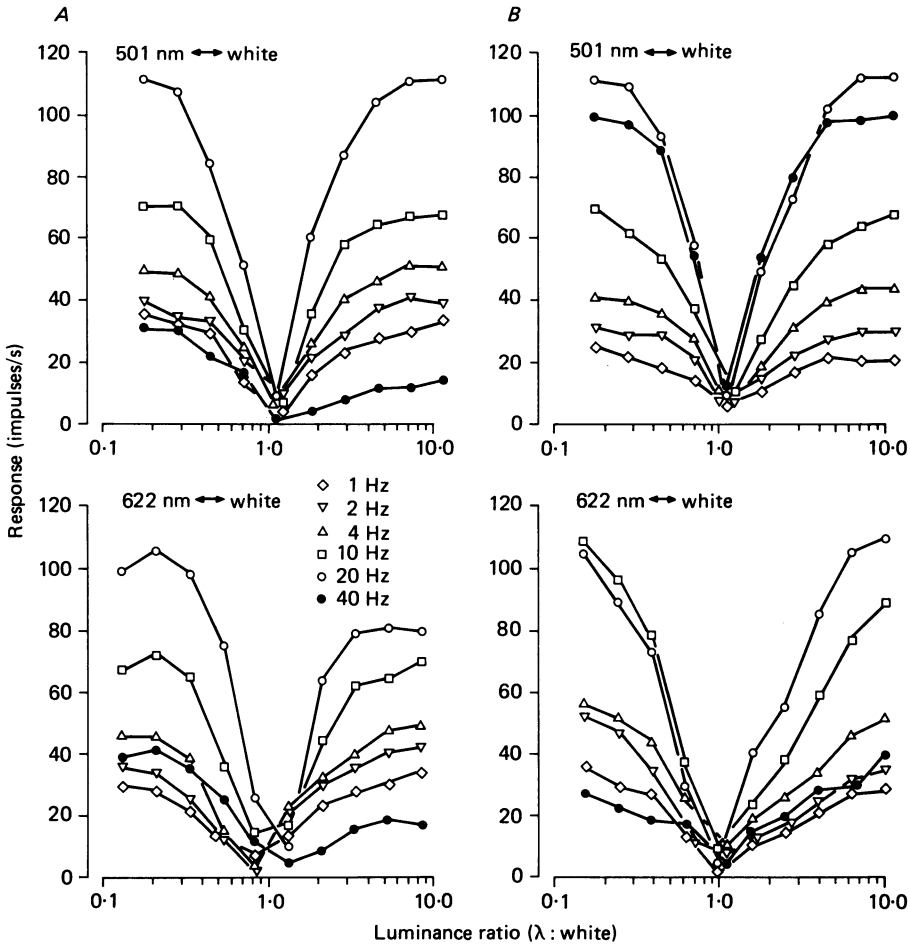


Fig. 11. Responses of two phasic cells (*A* and *B*) are plotted as a function of luminance ratio for six different temporal frequencies at two wavelengths. The minima in the cells' activity are largely independent of temporal frequency between 1 and 40 Hz.

We conclude that minimization of activity of phasic cells of the retina is sufficiently independent of temporal frequency to account for the frequency independence of results of heterochromatic flicker photometry.

*Additivity and transitivity*

Additivity is an important feature of heterochromatic flicker photometry (see Boynton, 1979), for it allows the luminosity of non-monochromatic lights to be calculated by integrating over their spectral distributions. Thus, it is necessary for this property to be demonstrable in phasic ganglion cells. We tested five phasic ganglion cells for additivity, and results from two of these cells are shown in Fig. 12.

If additivity and proportionality hold and if two wavelengths, *A* and *B*, are individually matched for luminance against a reference *C*, then the mixture $\frac{1}{2}A + \frac{1}{2}B$

should also match $C$. We alternated pairs of wavelengths with the white reference, first individually (in which case a minimum in responsiveness occurred close to a luminance ratio of one) and then as a mixture, so adjusted that each wavelength contributed half the luminance of the mixture. In the various examples in Fig. 12, it can be seen that responsiveness to the mixture, $\frac{1}{2}A+\frac{1}{2}B$, also goes through a minimum at a luminance ratio of one.

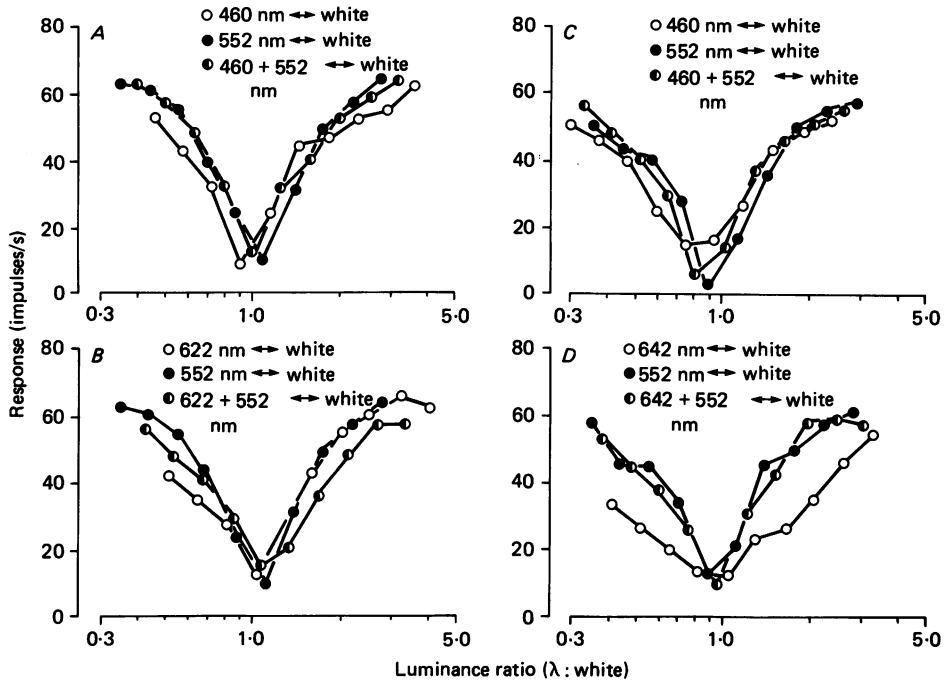


Fig. 12. A demonstration of the property of additivity for two phasic cells. Different monochromatic wavelengths were alternated with white and then an equal mixture of the two (calculated in terms of luminance) was alternated with white. In the latter instance, cell responsiveness also went through a minimum at a luminance ratio of one. Linear addition of the two monochromatic components would give this result.

A property related to additivity is transitivity. If the two wavelengths, $A$ and $B$, are matched for luminance against a reference, $C$, they should also match one another. To demonstrate transitivity we compared, for twelve phasic cells, different monochromatic lights with one another. Responses of two cells are illustrated in Fig. 13. Response magnitude when different monochromatic lights were alternated with white was minimal close to a luminance ratio of one, as expected. This was also the case when two monochromatic lights were alternated with each other.

We conclude that additivity and transitivity are displayed by phasic ganglion cells, so that these two requirements of a system underlying heterochromatic flicker photometry are met by phasic cells.

*Dependence on field size and luminance level*

Typically, field size in flicker photometry is a few degrees, but no striking changes in spectral sensitivity are observed as field size is varied. Spectral sensitivity is also

largely independent of luminance level under photopic conditions. However, at high luminance levels the task becomes difficult because of residual flicker. To confirm that the minimization of phasic cell activity with equal luminance flicker occurred independently of changes in these parameters, we carried out flicker photometry on eight phasic cells with 0·5 deg as well as with 4 deg fields, and for four cells we searched for flicker minima at 44 or 140 td as well as at 1400 td.

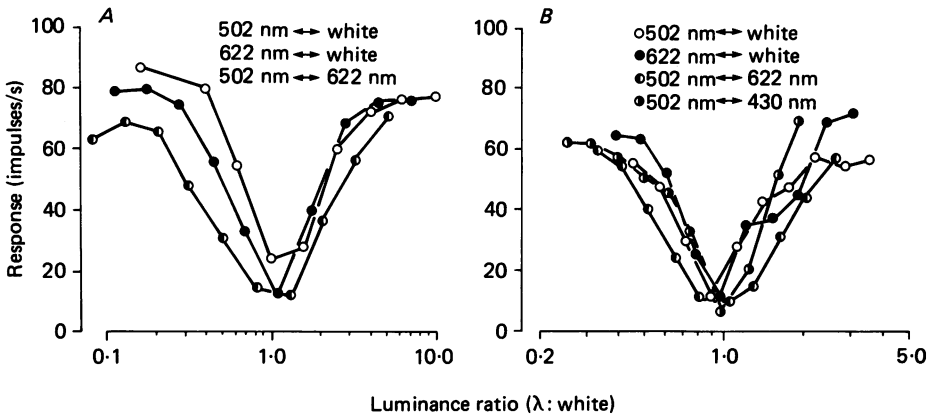


Fig. 13. Demonstration of transitivity in two phasic cells. Different monochromatic lights were alternated with the white reference and then with one another. In all cases cell responsiveness went through a minimum with a luminance ratio of one implying that if two lights each match a reference they also match one another in luminance.

With 0·5 deg stimuli, which predominantly stimulate the receptive field centre, responsivity was often greater than with 4 deg fields. This is probably because the inhibitory effect of the surround has largely been eliminated. In addition, minima were more sharply defined. This is illustrated in Fig. 14. With a 4 deg field (*A*), some variability in the location of minima is apparent in the three wavelengths shown, especially marked at 642 nm, which is displaced toward higher luminance ratios, that is more red light is needed. However, with a 0·5 deg field, this variability becomes less. This change was associated with the disappearance of the residual frequency-doubled response component when small spots are used as stimuli (Lee *et al.* 1988). This second-harmonic component appeared to shift and broaden the minima of the first-harmonic component with 4 deg fields, but when small spots were used, modulation of a cell's firing at equal luminance could be almost completely abolished. The presence of these residual responses might be related to the extent to which residual flicker disturbs flicker photometric matches. We argue below that this is the case.

Figure 14*C* shows the means and standard deviations of the sensitivities of the eight phasic cells tested with small spots, compared with the 10 deg $V_\lambda$ function. Sensitivity is little changed in comparison with Fig. 8, but standard deviation toward the spectral extremes (especially at 686 nm) has become less. A similar result was reported by Derrington *et al.* (1984).

Similarly, a decrease in mean luminance level to 44 td also resulted in a substantial attenuation of residual frequency-doubled responses (documented in Lee *et al.* 1988), so that a cell's firing was almost unmodulated at equal luminance. Spectral sensitivity at 44 td was similar to that at 1400 td, however, indicating the proportionality law holds, to a first approximation, over this range of luminances.

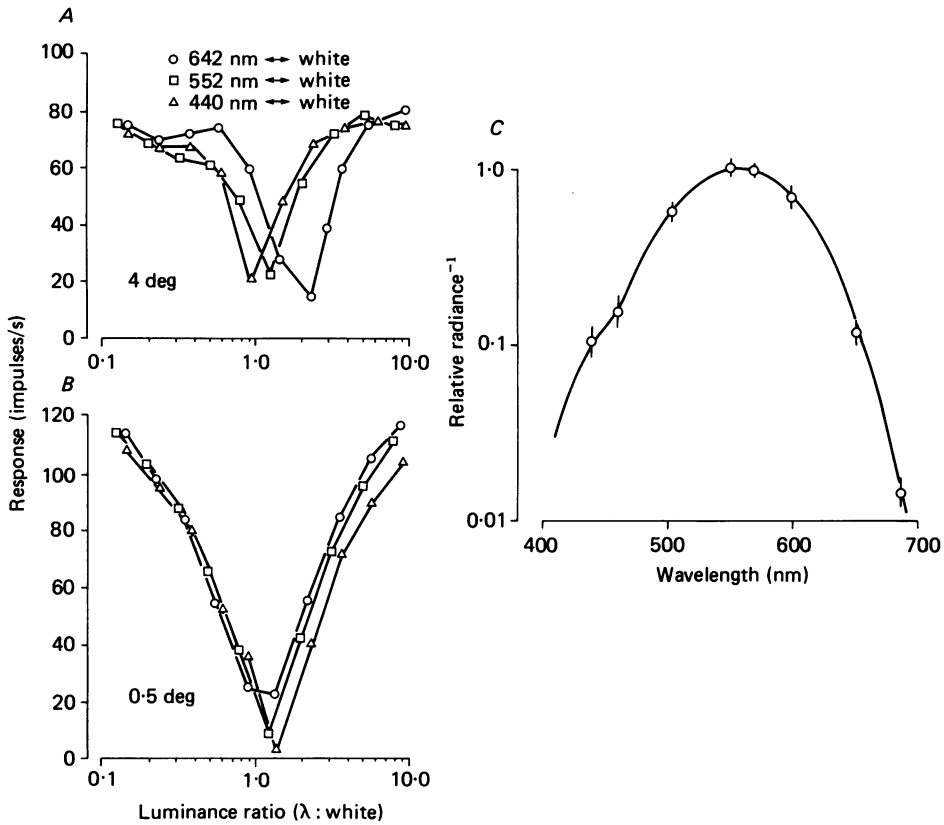


Fig. 14. Responses of a phasic cell when three different wavelengths were alternated with white, either with a 4 or a 0·5 deg stimulus field. Responses tended to be more vigorous with the smaller spot at high or low luminance ratios and minima more well defined, due to the absence of residual second-harmonic components.

## DISCUSSION

An obvious way of defining the relative luminous efficiency of two different-coloured lights would be to have an observer match them for subjective brightness. However, this procedure, known as heterochromatic brightness matching, relies on a labile subjective judgement and yields variable results. Moreover, such matches are not additive (see Boynton, 1979). Heterochromatic flicker photometry is a reliable and precise means of defining a subject's spectral luminous efficiency function which displays additivity, so that the luminance of any surface may be obtained by integrating over its spectral reflectance and the luminosity function. The 2 deg $V_\lambda$

curve was defined in 1924 largely using results from this technique, and the $V_\lambda$ function was adopted in 1931 as one of the colour-matching functions ($\bar{y}_\lambda$) of the CIE Standard Observer. The 10 deg $\bar{y}_{10\lambda}$ function (1964) was defined solely with respect to colour-matching data, but was made to conform with 10 deg flicker photometric matches at three sample wavelengths. A more extensive desciption of the background to these definitions is given in Wyszecki & Stiles (1982). It should be noted that the luminosity function makes it possible to measure light in an objective manner; it was not intended to represent the performance of an individual observer on a particular task (see Kaiser, 1988).

From a psychophysical viewpoint, the distinctive properties of heterochromatic flicker photometry led to the suggestion that it is dependent on some kind of achromatic channel, and other evidence was found to support the existence of an achromatic, non-opponent, as distinct from opponent, channel (e.g. Kelly & van Norren, 1977). Whether these psychophysically postulated channels could be correlated with distinct cell systems in the visual pathway has remained controversial.

We show here that the neurophysiological substrate of heterochromatic flicker photometry can be identified as the phasic, magnocellular system of the primate visual pathway. Minimization of activity in these cells corresponds closely to minimization of subjective flicker in human subjects (Fig. 8) over the whole spectrum. Furthermore, independence of flicker frequency, additivity and transitivity are all important properties of the psychophysical task which are also displayed by the phasic ganglion cells of the retina. A further property, proportionality (see Wyszecki & Stiles, 1982), was also found to hold by testing cells at 44 as well as at 1400 td.

Derrington *et al.* (1984) have reported results similar, in principle, to those presented here. These authors measured responses of cells from the lateral geniculate nucleus to modulation of the luminance and chromaticity of a video display. They found that the null planes of phasic cells from the magnocellular layers lay close to the equal luminance plane. This is equivalent to the minimization of cell responsiveness we observe when two different spectral combinations are alternated at equal luminance.

An alternative hypothesis for the physiological origin of the $V_\lambda$ function was put forward by Gouras & Zrenner (1979). Using square-wave luminance flicker of different-coloured lights, they found that tonic cells were colour opponent (with a spectral cross-over point in mid-spectrum) at low temporal frequencies but became broad-band in their spectral responsiveness at higher flicker frequencies. They attributed this to a difference in latency between the opponent mechanisms feeding into centre and surround. They suggested that chromatic and luminance signals could be 'multiplexed' in tonic cells in different frequency bands (the 'double duty' hypothesis). A prediction of this hypothesis would be at high temporal frequencies firing rate of tonic cells should not be modulated at a luminance ratio of one, when no luminance difference is present. We have shown that with heterochromatic flicker at 10 Hz complex changes in responsiveness and phase occur as the relative intensity of two different-coloured lights is changed. This was also so at 20 and 40 Hz (B. B. Lee, P. R. Martin & A. Valberg, in preparation). It was not the case that activity of

wavelength-opponent cells, treated either individually or as a population, goes through a minimum which might contribute to the minimization of subjective flicker at equal luminance.

We show in Figs 3 and 4 that the gradual phase shifts which occur with tonic cells with heterochromatic flicker are in opposite directions either side of 570 nm, and are also in opposite directions for red and green on-centre cells. This can be qualitatively explained as follows. If centre and surround components are represented as vectors, with achromatic luminance flicker at low temporal frequencies these vectors will be orthogonal. At higher frequencies, they are no longer orthogonal due to the centre–surround phase delay. The response vector will fall somewhere between them. Heterochromatic flicker between white and a wavelength longer than 570 nm (the tritanopic axis) will cause a rotation of the response vector in one direction as luminance ratio is increased, and between white and a wavelength shorter than 570 nm will cause rotation in the opposite direction. If for both red and green on-centre cells there is a phase delay of surround relative to centre, opposite phase changes will occur for these two cell types. A formal analysis is presented elsewhere (B. B. Lee, P. R. Martin & A. Valberg, in preparation).

Two objections may be raised to the conclusion that minimization of activity in phasic cells is responsible for subjective minimization of flicker. Firstly, the comparison in Fig. 8 assumes that the luminosity functions of man and macaque are similar. DeValois *et al.* (1974) found this to be the case, although there were some deviations at the spectral extremes in comparison with the 2 deg curve. DeValois *et al.* (1974) themselves point out, however, that their simian subjects were able to use the peripheral retina. This and a field size of more than 4 deg would lead to the reported deviations from the 2 deg curve at the spectral extremes.

The luminosity function of man is thought to be made up of a sum of M- and L-cones (see Boynton, 1979) and it seems likely that the luminosity function of the macaque is also made up of the sum of M- and L-cone sensitivities. The cones of man and macaque are virtually identical in their spectral properties (Bowmaker & Dartnall, 1980; Bowmaker *et al.* 1980; Nunn *et al.* 1984; Baylor *et al.* 1987). In view of the great similarity of man and macaque in other psychophysical tasks, such as wavelength discrimination (DeValois *et al.* 1974), and on the basis of Fig. 8, we would predict that the luminosity functions of man and macaque should be very similar. Adequate behavioural evidence on this point is still lacking, however.

Secondly, it might be thought that the residual frequency-doubled response in phasic cells at equal luminance might interfere with psychophysical performance. Schiller & Colby (1983) remarked on such responses and concluded they should limit the role of phasic cells in flicker minimization. Although they used square-wave chromatic alternation at 1 Hz, which is likely to exaggerate the frequency-doubled response due to adaptation effects, there is no doubt that such responses can be of large magnitude. We show elsewhere that they originate because of a non-linearity in M- and L-cone interaction in the receptive field surround, perhaps a saturating non-linearity of the cone mechanisms (Lee *et al.* 1988).

The amplitude of the frequency-doubled response component at equal luminance is directly related to the amplitude of cone modulation, which is in antiphase for M- and L-cones. This cone modulation is large when long wavelengths are alternated

with the white reference, and under these conditions frequency-doubled responses were substantial. It is under these conditions that subjects may experience difficulty in making flicker photometric matches, especially at high levels of retinal illumination (J. Pokorny & V. C. Smith, personal communication). In the flicker photometric experiments illustrated in Fig. 8*B* the subjects did report difficulties due to residual flicker with very long wavelengths. Decreasing retinal illumination or increasing flicker frequency, which both mitigate problems with residual flicker in the psychophysical task, also diminish the magnitude of frequency-doubled components in cell responses.

One way of reducing residual flicker is to make small phase adjustments of the flickering lights (de Lange, 1958; Walraven & Leebeck, 1964), although the effect is variable (see Stromeyer, Cole & Kronauer, 1987). We tried such small phase changes on some phasic cells, which caused changes in the residual, frequency-doubled responses. Sufficient data is not available to allow any firm conclusions, however.

We propose that frequency-doubled responses are partly responsible for residual flicker, and when they are substantial the task becomes difficult. However, signals from other sources may also contribute to residual flicker. For example, slight variation in the relative weighting of M- and L-cones among different phasic cells would make it impossible to silence all such cells at the same luminance ratio. Also, the strong responses in tonic, opponent neurones at equal luminance may also contribute to residual flicker.

Although the principles of frequency independence, transitivity, proportionality and additivity hold to a first approximation for the psychophysical task, some deviations are to be found. For example, at high retinal illuminations small additivity failures become apparent (Ingling, Tsou, Gast, Burns, Emerick & Riesenberg, 1978). It is possible that frequency-doubled responses may affect subjective flicker minima in such a way as to account for these deviations.

It is remarkable that subjects are able to minimize the sensation of flicker in the face of the very vigorous responses of opponent cells. We show elsewhere (B. B. Lee, P. R. Martin & A. Valberg, in preparation) that the sensitivity of wavelength-opponent cells to chromatic flicker approaches that of human observers at low temporal frequencies (below 4 Hz), but at high temporal frequencies opponent cells maintain high sensitivity whereas for the human observer sensitivity falls off rapidly. It is possible that at a later stage in the visual pathway a low-pass temporal filter attenuates the response of opponent cells to rapid changes in colour and/or luminance and this enables flicker photometric judgements to be made solely on the basis of phasic cell activity.

Although our results suggest that a luminance mechanism cannot be built from the responses of opponent cells at high temporal frequencies, because of the complex phase changes they show, it is possible to reconstruct an equidistant colour space, including a lightness or brightness dimension, from the sustained responses of such cells (Valberg, Seim, Lee & Tryti, 1986; Lee *et al.* 1987; B. B. Lee, P. R. Martin & A. Valberg, in preparation). Heterochromatic brightness matching may thus have a different physiological substrate to flicker photometry.

Other psychophysical tasks, for example the minimal distinct border technique, also yield the $V_\lambda$ function (Boynton & Kaiser, 1968; Wagner & Boynton, 1972). Such

tasks probably also depend on minimization of activity of the phasic, magnocellular system, and we predict that phasic cell activity would be minimized at equal luminance if tested with these techniques. Results obtained with other psychophysical detection paradigms have been interpreted in terms of chromatic mechanisms. For example, detection and discrimination of chromatic spots (Crook, Lee, Tigwell & Valberg, 1987; Valberg & Lee, 1988) can be shown to be dependent on detection by wavelength-opponent cells of different types. If detection by chromatic or achromatic mechanisms postulated psychophysically correlate with detection by different cell classes in the visual pathway then the hypothesis that wavelength-opponent cells perform 'double-duty' becomes untenable.

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