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SENSITIVITY OF MACAQUE RETINAL GANGLION CELLS TO CHROMATIC AND LUMINANCE FLICKER

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SUMMARY

1. We have studied the sensitivity of macaque retinal ganglion cells to sinusoidal flicker. Contrast thresholds were compared for stimuli which alternated only in luminance ('luminance flicker') or chromaticity ('chromatic flicker'), or which modulated only the middle- or long-wavelength-sensitive cones ('silent substitution').

2. For luminance flicker, the lowest thresholds were those of phasic, non-opponent ganglion cells. Sensitivity was maximal near 10 Hz.

3. Tonic, cone-opponent ganglion cells were relatively insensitive to luminance flicker, especially at low temporal frequencies, but were sensitive to chromatic flicker, thresholds changing little from 1 to 20 Hz. Those with antagonistic input from middle- and long-wavelength-sensitive (M- and L-) cones had a low threshold to chromatic flicker between red and green lights. Those with input from short-wavelength-sensitive (S-) cones had a low threshold to chromatic flicker between blue and green. Expressed in terms of cone contrast, the S-cone inputs to blue on-centre cells had higher thresholds than M- and L-cone inputs to other cell types.

4. Phasic, non-opponent cells responded to high-contrast red–green chromatic flicker at twice the flicker frequency. This frequency-doubled response is due to a non-linearity of summation of M- and L-cone mechanisms. It was only apparent at cone contrasts which were above threshold for most tonic cells.

5. M- or L-cones were stimulated selectively using silent substitution. Thresholds of M- and L-cone inputs to both red and green on-centre cells were similar. This implies that these cells' sensitivity to chromatic flicker is derived in equal measure from centre and surround. Thresholds of the isolated cone inputs could be used to predict sensitivity to chromatic flicker. The high threshold of these cells to achromatic contrast is thus, at least in part, due to mutual cancellation by opponent inputs rather than intrinsically low sensitivity.

6. Thresholds of M- and L-cone inputs to phasic cells were similar at 10 Hz, and were comparable to those of tonic cells, suggesting that at 1400 td cone inputs to both cell groups are of similar strength.

7. The modulation transfer function of phasic cells to luminance flicker was similar to the detection sensitivity curve of human observers who viewed the same stimulus. For chromatic flicker, at low temporal frequencies thresholds of tonic cells (red or

green on-centre cells in the case of red–green flicker or blue on-centre cells in the case of blue–green flicker) approached that of human observers. We propose the different cell types are the substrate of different channels which have been postulated on the basis of psychophysical experiments.

8. At frequencies of chromatic flicker above 2 Hz, human sensitivity falls off steeply whereas tonic cell sensitivity remained the same or increased. This implies that high-frequency signals in the chromatic, tonic cell pathway are not available to the central pathway responsible for flicker detection.

INTRODUCTION

Periodic variation in a light source produces a sensation of flicker. Change in intensity produces luminance flicker, whilst change in colour, with luminance held constant, gives rise to chromatic flicker. In some psychophysical paradigms both luminance and spectral composition may be varied. One such paradigm is heterochromatic flicker photometry, which has been used to determine the spectral sensitivity of a human observer. Results obtained with these paradigms, and with other psychophysical tasks, have led to the supposition that there exist an achromatic mechanism and one or more opponent, chromatic mechanisms, or channels, within the visual pathway (Kelly & van Norren, 1977).

The visual system of old-world primates, such as the macaque and man, contains two main cell systems. One consists of tonic, cone and wavelength-opponent retinal ganglion cells which project to the parvocellular layers of the lateral geniculate nucleus (P-pathway). The other consists of phasic, non-opponent ganglion cells which project to the magnocellular layers of the nucleus (M-pathway; Wiesel & Hubel, 1966; de Monasterio & Gouras, 1975; Dreher, Fukuda & Rodieck, 1976; de Monasterio, 1978; Creutzfeldt, Lee & Elepfandt, 1979; Perry, Oehler & Cowey, 1984). Tonic cells can be subdivided into two major groups: those which receive antagonistic input from medium- and long-wavelength-sensitive (M- and L-) cones and those which receive input from short-wavelength-sensitive (S-) cones, opposed by some combination of M- and L-cones. The opponent mechanisms of most tonic cells form cone-specific centre and surround mechanisms. Phasic cells, on the other hand, receive combined input from M- and L-cones to both centre and surround (Wiesel & Hubel, 1966; de Monasterio & Gouras, 1975; Creutzfeldt *et al.* 1979; Derrington, Krauskopf & Lennie, 1984).

The systems of man and macaque are sufficiently similar to allow comparison of physiological results from the macaque with psychophysical results from man (DeValois, Morgan, Polson, Mead & Hull, 1974; Crook, Lee, Tigwell & Valberg, 1987; Lee, Martin & Valberg, 1988). However, accounts of flicker responses of cells in the macaque visual pathway are infrequent, and usually have involved only luminance flicker (Spekreijse, van Norren & van den Berg, 1971; Gouras & Zrenner, 1979), although Derrington *et al.* (1984) did measure responses to chromatic flicker.

The possibility that the tonic and phasic cell systems could be the substrates of the different channels of psychophysics has had little unambiguous experimental support. The contrast sensitivity of phasic cells to black–white luminance gratings is much higher than that of tonic cells, and approaches the contrast sensitivity of

human observers (Kaplan & Shapley, 1982; Hicks, Lee & Vidyasagar, 1983). On the other hand, evidence such as that of Gouras & Zrenner (1979), who showed that tonic cells respond to a broad band of wavelengths at high flicker frequencies, led to the suggestion that the tonic cell population may do 'double duty' as a luminance or a chromatic channel depending on temporal frequency (Ingling & Martinez, 1983; Zrenner, 1983; Lennie, 1984).

We have studied responses of macaque retinal ganglion cells to flicker under a variety of conditions, similar to those used in psychophysical paradigms. We have shown elsewhere that it is the phasic ganglion cells of the macaque retina which underlie the task of heterochromatic flicker photometry (Lee *et al.* 1988), which is sometimes assumed to tap the activity of a 'luminance channel'. Here, we describe the contrast sensitivity of phasic and tonic cells in the macaque retina to different types of flicker at different temporal frequencies, and compare these responses to the psychophysically measured sensitivity of human observers who viewed the same stimuli. We provide strong support for the suggestion that phasic and tonic cells are the physiological substrate of detection of luminance and chromatic flicker, respectively, and may thus be related to different channels postulated psychophysically. We also provide evidence that the poor contrast sensitivity of tonic cells to achromatic luminance contrast may largely be a result of cone opponency rather than low sensitivity *per se*. Some of these results have been described briefly elsewhere (Lee & Martin, 1987).

In the accompanying paper we provide a fuller account of properties of tonic cells, especially with respect to those effects which arise due to a centre–surround latency difference (Lee, Martin & Valberg, 1989*a*).

METHODS

The activity of ganglion cells was recorded from the retinae of juvenile macaques (*M. fascicularis*). Animals were anaesthetized initially with an intramuscular injection of ketamine and thereafter with halothane in a 70–30% N_2O–O_2 mixture (1–2% during surgery, followed by 0·2–1% during recording). Local anaesthetic was applied to points of surgical intervention, especially around the eye. EEG and ECG were monitored continuously as a control for anaesthetic depth. Muscular relaxation was attained by intravenous infusion of gallamine triethiodide (5 mg kg^{-1} h^{-1}) together with *ca* 3 ml h^{-1} of dextrose Ringer solution. End-tidal P_{CO_2} was kept near 4% by adjusting the rate and depth of ventilation, and 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 positions of fovea and optic disc were ascertained with the aid of a fundus camera. A 6 mm artificial pupil was usually used. Clarity of the optic media was checked frequently, and when the smaller retinal vessels could no longer be recognized, recording from that eye was terminated, and the second eye prepared. On completion of recording the animal was killed with an overdose of barbiturate.

A cannula was inserted through the sclera, just behind the limbus, and a tungsten microelectrode was lowered through it onto the retina. Extracellular activity of a ganglion cell was isolated, and the cell type ascertained with flashed spots. Even with hand-held stimuli, 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. Cell responses to stimuli of differing dominant wavelength were then recorded as an aid to cell classification. Tonic cells with different cone inputs give very characteristic responses to such flashed stimuli at 1400 td (e.g. Lee *et al.* 1987; Crook *et al.* 1987). In doubtful cases, thresholds to

achromatic contrast were estimated; this is a reliable method of distinguishing the tonic cells in the parvocellular layers of the geniculate nucleus from the phasic cells in the magnocellular layers (Kaplan & Shapley, 1982; Hicks *et al.* 1983). We recorded from ganglion cells from parafoveal retina.

Visual stimulation. Three channels were available, each providing white light with chromaticity co-ordinates $(x, y) = (0{\cdot}404, 0{\cdot}410)$. One channel provided a background if necessary. To generate chromatic flicker, crossed polaroids were placed in each of the two stimulus channels. The beams were combined and passed through a rotating polaroid, producing a sinusoidal alternation of two wavelengths, which was then added to a background. The background was chosen to be approximately half-way between the stimulus components in terms of their chromaticity co-ordinates.

We routinely used a 4 deg stimulus field, but also recorded responses with a 0·5 deg field. Mechanical limitations restricted us to flicker frequencies up to 40 Hz. Flicker was usually around a mean luminance of 50 cd m^{-2} giving a retinal illumination of 1400 td.

Spectral composition of stimuli was adjusted with interference (Schott, NAL, 25 nm half-bandwidth at half-maximum) or gelatine (Kodak Wratten) filters. Filter wheels in each stimulus beam allowed sequences of stimuli to be pre-selected. These wheels were controlled by a computer system which also averaged and stored unit responses. An analogue output from a spot photometer (Photo Research) was also stored, to give us a record of the luminance modulation over a cell's receptive field.

A Photo Research 702A/703A Scanning Spectrophotometer provided 2 deg luminance 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 the 10 deg human photopic luminosity, or V_λ, function, basing our calibration on calculations as described by Valberg, Lee & Tryti (1987).

We express modulation depth of the stimuli in terms of the contrast produced in individual cones, that is $(S_{max}-S_{min})/(S_{max}+S_{min})$ where S is cone excitation. To calculate these values, we first integrate the product of the spectral power distribution, $P(\lambda)$, of the light with the cone fundamentals (Estevez, 1982), $s(\lambda)$, and the transmission of the filters, $\tau(\lambda)$, $(S = e\int_{390}^{760} s(\lambda)P(\lambda)\tau(\lambda)d\lambda)$, as described in Valberg *et al.* (1987). These values were normalized by the factor e to the cone excitation produced by our white light of the same luminance. We could then calculate the relative amplitudes of each cone's modulation for different filter and luminance conditions. When two lights, i and j, which produce cone excitations S_i and S_j and have the luminances L_i and L_j, are exchanged upon a background light k, which produces a cone excitation S_k and has luminance L_k, the cone contrast, C, is given by

$$C = (S_iL_i - S_jL_j)/(S_iL_i + S_jL_j + S_kL_k).$$

For luminance flicker, the projector light was modulated. For red–green flicker, we modulated between 622 and 522 nm projected upon a background of 570 nm. Here and elsewhere, these are peak wavelengths after the light had passed through all filters in the system. Using our filters, 622 and 522 nm were chosen so that for a given modulation depth a similar contrast was seen by the M- and L-cones. To test cells with S-cone input, we chose wavelengths close to a tritanopic confusion line (440 alternated with 522 nm upon a 484 nm background). These lights do not lie precisely along a tritanopic confusion line but at threshold for blue on-centre cells (and for human observers), modulation of the M- and L-cones was 1% or less. Limitations as to the amount of light available from our projector system prevented a more satisfactory choice of wavelengths, but we tested two blue on-centre cells (at a lower mean luminance) with flicker using wavelengths closer to a tritanopic confusion line, with similar results to those with the usual wavelength combination.

By appropriately adjusting the relative luminance of the stimulus beams in accordance with the equations above it was possible to choose conditions under which M- and L-cones were selectively stimulated (silent substitution). Under these conditions, modulation of the 'silent' cone was less than 5% of that of the stimulated cone.

Cell responses to each condition were averaged over about 6 s and stored as a peristimulus time histogram. Response amplitude was derived from Fourier analysis of these histograms. To measure thresholds, filter wheels were so arranged that contrast was increased in 0·2 log unit steps. A criterion of a 10 impulses s^{-1} first-harmonic amplitude was taken as threshold. With maintained activity, first-harmonic components for both tonic and phasic cells were less than 5 impulses s^{-1}.

The psychophysical sensitivity of six colour-normal observers was also tested. Thresholds were

measured at 10 deg retinal eccentricity using a forced-choice procedure. The stimulus conditions were identical to those in the physiological experiments except that the stimuli, presented in pseudo-random order, were in 0·1 log unit steps. The threshold was calculated from a 60% frequency-of-seeing criterion.

RESULTS

The great majority (90%) of the retinal ganglion cells of the macaque send their axons to the lateral geniculate nucleus (Perry *et al.* 1984). Practically all ganglion cells we encountered appeared similar in their visual response properties to cells we have encountered there (Creutzfeldt *et al.* 1979; Lee, Valberg, Tigwell & Tryti, 1987; Crook *et al.* 1987). We classified cells as phasic or tonic on the basis of the time course of their response to chromatic spots, and on the basis of estimates of their achromatic contrast sensitivities; details are given in the Methods section.

Since tonic cells characteristically receive opponent cone inputs, and phasic cells non-opponent inputs, the former should be more sensitive to chromatic flicker (when cones are stimulated out of phase) and the latter should be more sensitive to luminance flicker; the results of Hicks *et al.* (1983) and Derrington *et al.* (1984) imply such a difference. We therefore measured thresholds of fifty-eight tonic and thirty-one phasic cells, with different flicker paradigms at different flicker frequencies. Tonic cells with antagonistic input from M- and L-cone mechanisms were most commonly recorded, but seven cells with S-cone input were also studied.

Measurement of sensitivity to flicker

We estimated sensitivity from responses to different depths of modulation, and so could generate contrast–response curves. Such curves are plotted for a phasic off-centre and a tonic green on-centre cell in Fig. 1, for luminance flicker and red–green chromatic modulation at different temporal frequencies. Contrast levels have been calculated in terms of modulation in the individual cones, as described in the Methods. In the case of achromatic luminance flicker, the contrast is the same for both cones. For red–green chromatic flicker, the L-cone contrast was slightly greater (by a factor of 1·14) than the M-cone contrast. The values used are the mean of M- and L-cone contrasts.

The characteristic differences between phasic and tonic cells are exemplified by these two neurones. The phasic cell responds more vigorously to luminance flicker than the tonic cell at all temporal frequencies, the latter responding to luminance modulation only at temporal frequencies above 10 Hz. With luminance flicker, the higher contrast gain (Kaplan & Shapley, 1982) of phasic relative to tonic cells is reflected in their steeper intensity–response curves. With chromatic flicker, the opposite pattern can be seen. The green on-centre cell displays steep intensity–response curves for all temporal frequencies.

The fundamental component of the phasic cell's response is almost absent with red–green chromatic modulation, but there was a response at twice the flicker frequency. This frequency-doubled response is shown in Fig. 2. Response histograms to two cycles of each type of flicker are shown, at 10 Hz, with about 20% cone contrast in each case. To luminance flicker the first-harmonic component is apparent, while to chromatic flicker a response at twice the frequency can be seen. The

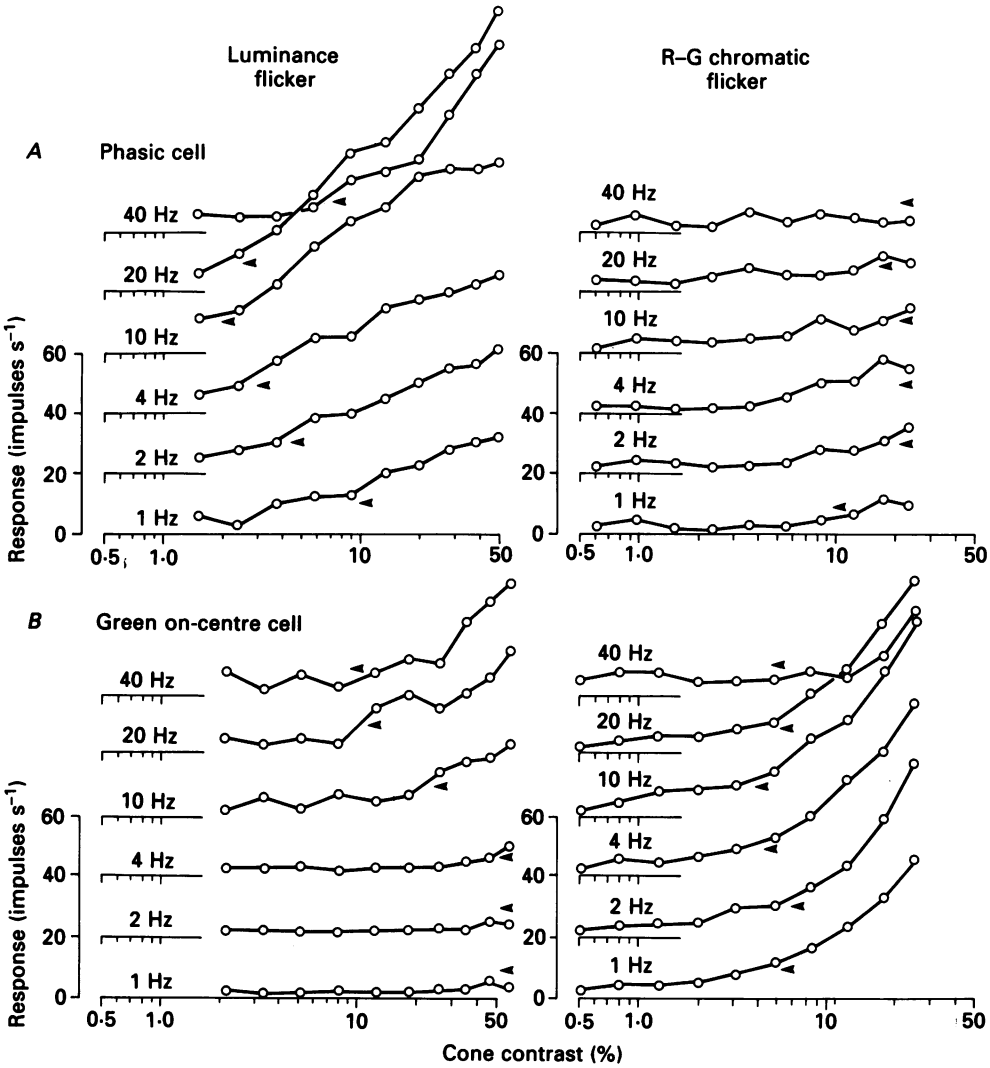

Fig. 1. Graphs of contrast against response amplitude (first harmonic) for a phasic off-centre and a green on-centre cell. Contrast is expressed in M- or L-cone modulation. These were identical for luminance flicker and approximately the same for red–green (R–G) chromatic flicker. In *A*, the phasic cell can be seen to respond well to luminance flicker, but poorly to chromatic flicker. The converse is the case for the tonic cell. The arrows indicate the points at which cell response exceeded the threshold criterion chosen (10 impluses s^{-1}).

intensity–response curves indicate that this frequency-doubled response was present at all temporal frequencies. A comparison of Figs 1 and 2 shows that a greater cone contrast was required to evoke a frequency-doubled response from the phasic cell than was needed to evoke a response from the green on-centre cell. We show elsewhere that the origin of this frequency-doubled response is in a non-linearity of

summation of M- and L-cone inputs to phasic cells. It is apparent with red–green chromatic modulation, for then M- and L-cones are modulated in counterphase (Lee, Martin & Valberg, 1989*b*). Such a frequency-doubled response was never seen in tonic cells with M- and L-cone input.

From curves such as those shown in Figs 1 and 2 we estimated cell thresholds. These thresholds, defined as a 10 impulses s^{-1} response, are indicated by the arrows on each curve. For luminance flicker, the phasic cell is maximally sensitive at 10 Hz

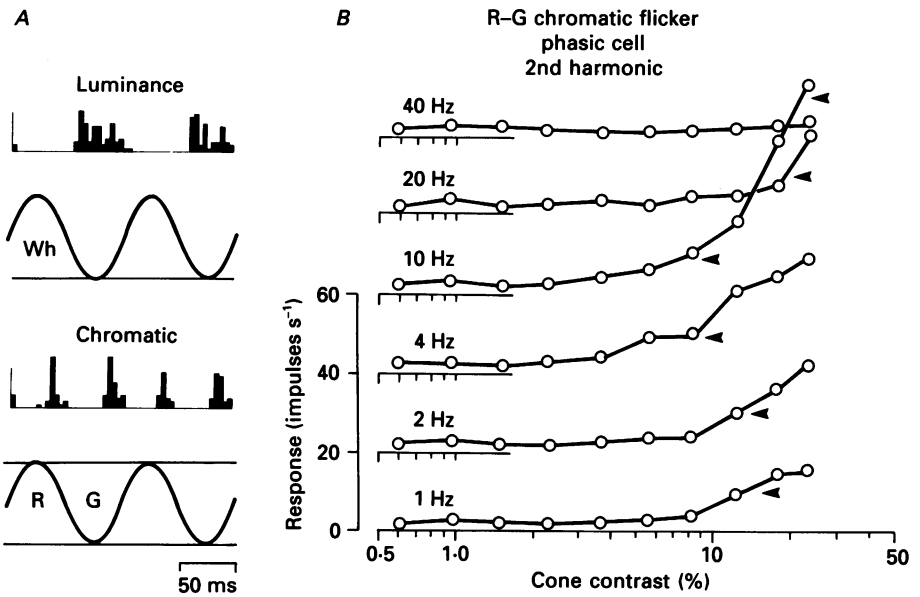

Fig. 2. Phasic cells respond to red–green (R–G) chromatic flicker at twice the flicker frequency. The histograms (two flicker cycles) compare response to luminance (white; Wh) and chromatic flicker at similar contrast (0·2). The second-harmonic amplitude for the phasic cell of Fig. 1 is plotted at right for different frequencies. Details are as in the previous figure. For histograms, amplitude calibration 50 impulses s^{-1}.

with a fall in sensitivity at lower temporal frequencies. It was more sensitive than the green on-centre over the whole frequency range tested. In contrast, with chromatic flicker, the green on-centre cell is much more sensitive than the phasic cell, with little change in sensitivity between 1 and 20 Hz.

In Fig. 3 we have summarized the average contrast sensitivities for chromatic and luminance flicker for twenty phasic cells (Fig. 3*A*) and twenty tonic cells (Fig. 3*B*) at six temporal frequencies between 1 and 40 Hz.

For achromatic luminance flicker, the mean sensitivity of phasic cells was maximal around 10 Hz, with a 3·5% contrast in each cone. With a 10 impulses s^{-1} threshold criterion, this corresponds to a contrast gain of 2·9, which is very similar to the value reported by Kaplan & Shapley (1982). Phasic cells were more sensitive than tonic cells at all frequencies tested, by a factor of at least 8 at low temporal frequencies (to which some tonic cells did not respond), and by a factor of 3–5 at higher frequencies.

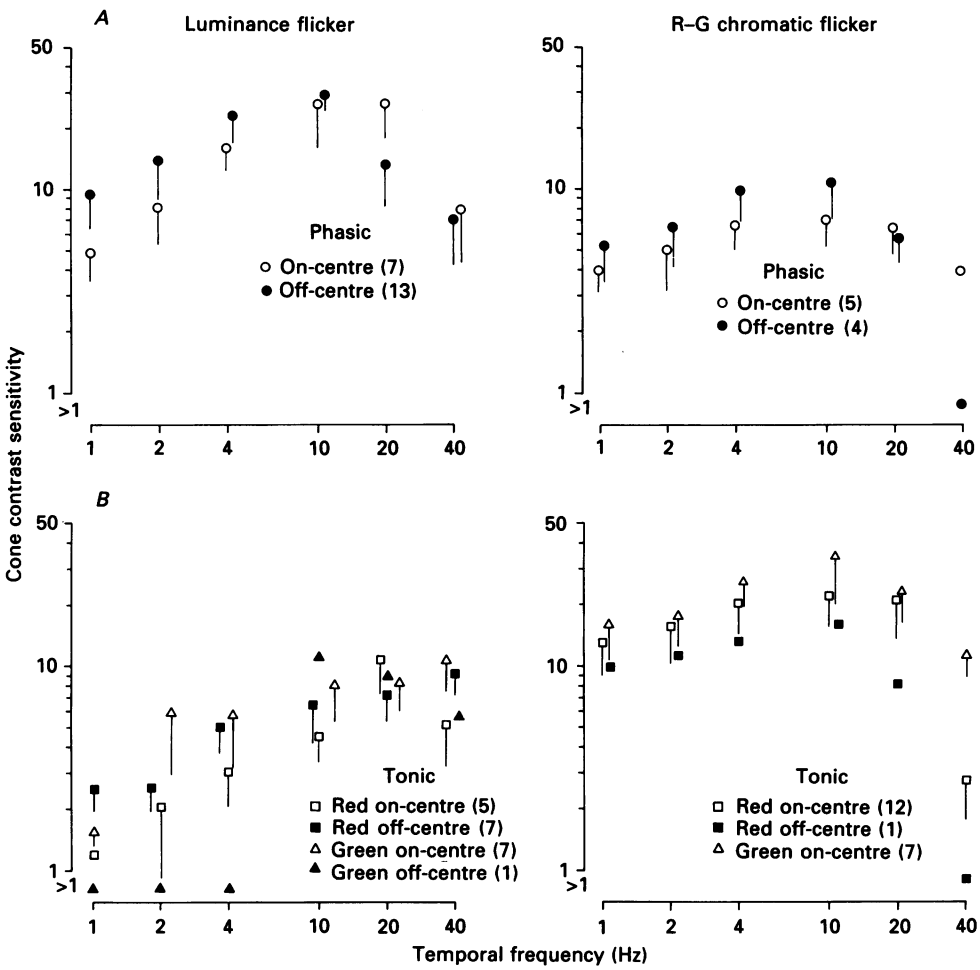

Fig. 3. Contrast sensitivity at different temporal frequencies for phasic cells, and tonic cells with M- and L-cone inputs. The twenty most sensitive cells are shown for each cell group. Bars are standard deviations. Sensitivity is expressed as the reciprocal of the M- or L-cone contrast at threshold. For red–green (R–G) chromatic flicker, the threshold of the second-harmonic Fourier component of the phasic cell response is shown.

When stimulated with red–green chromatic flicker, tonic cells were more sensitive than phasic cells at all frequencies tested. As discussed in relation to Fig. 2, phasic cells gave a frequency-doubled response and we have plotted thresholds of the second-harmonic component. Tonic cell sensitivity to chromatic flicker was maximal at 10 Hz, but fell only slightly at lower temporal frequencies. It decreased rapidly for frequencies greater than 10 Hz. We had the impression that green on-centre and red on-centre cells were more sensitive to chromatic flicker than green off-centre and red off-centre cells. However, our sample of off-centre neurones was limited. The reason for this low sampling rate is obscure. Off-centre phasic cells were encountered as often as their on-centre counterparts.

When sensitivity is plotted in terms of cone contrast modulation, as in Fig. 3,

luminance and chromatic sensitivity are directly comparable. Thus, tonic cell sensitivity to chromatic flicker exceeds phasic cell sensitivity to luminance flicker at low temporal frequencies. An equivalent psychophysical result for low spatial and temporal frequencies was reported by Mullen (1985).

It has been suggested (Derrington & Lennie, 1984; Shapley & Perry, 1986) that the high thresholds of tonic cells with achromatic modulation is due to intrinsically low sensitivity, perhaps because of small centre size, but we show here that sensitivity is high to chromatic flicker. However, centre and surround both influence sensitivity, so a way must be found to separate these contributions. This question is addressed in later sections.

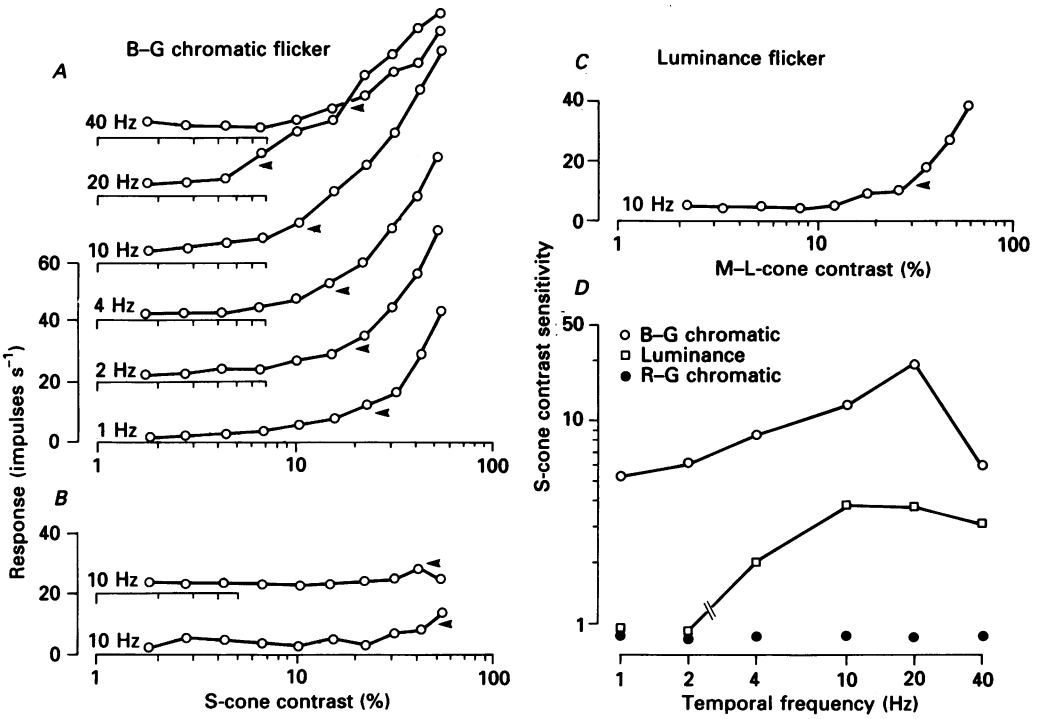

Fig. 4. In *A*, responses of a blue on-centre cell with S-cone input. Response amplitude is plotted against S-cone contrast for blue–green (B–G) chromatic flicker. The threshold criterion is shown by the arrows. In *B*, the lack of response of a phasic on-centre (upper curve) and a green on-centre cell (lower curve) to B–G flicker is shown. *C*, the weak response of the blue on-centre cell to achromatic luminance flicker. *D*, contrast sensitivity of the blue-on cell is plotted against flicker frequency for B–G flicker, R–G (red–green) flicker and achromatic flicker. For B–G flicker, sensitivity is derived from S-cone contrast. No response was present to R–G flicker. Sensitivity to achromatic flicker is low.

Responses of cells with S-cone inputs

Cells receiving input from S-cones invariably showed poor responses to luminance flicker or red–green chromatic flicker, but responded vigorously to chromatic flicker between 440 and 522 nm. These latter wavelengths lie close to a tritanopic confusion line. Figure 4 shows a typical example of one of the six cells studied with excitatory

S-cone input. The one cell we studied which had inhibitory S-cone input also responded vigorously to blue–green flicker, but was less sensitive than the blue on-centre cells. The blue on-centre cell responds vigorously over temporal frequencies up to 20 Hz (Fig. 4*A*). Thresholds are shown by arrows as in Fig. 1.

Due to technical limitations, our stimuli did not lie exactly on a tritanopic confusion line. We therefore tested a number of other cells to make sure they did not respond to blue–green flicker. Examples of a phasic on-centre (upper curve) and a green on-centre cell (lower curve) are shown in Fig. 4*B*. Neither cell responds to blue–green flicker. There was no frequency-doubled response in phasic cells (Lee *et al.* 1989*b*).

Thresholds of the blue on-centre cell to blue–green and red–green chromatic flicker, and to achromatic luminance flicker, are shown in Fig. 4*D*. With the blue on-centre cells we encountered, sensitivity to blue–green chromatic flicker was maintained up to a frequency of 20 Hz, showing that the S-cones respond to at least this frequency, as suggested by Zrenner & Gouras (1981). Further examples of blue on-centre cell sensitivity are shown in Fig. 9.

With blue on-centre cells, S-cone contrasts at threshold were typically around 20%. Such values are much higher than the M- or L-cone contrasts at threshold with other tonic cells for red–green chromatic flicker. This can be seen if Fig. 4 is compared with Figs 1 and 3.

The sensitivity of blue on-centre cells to luminance flicker was poor, as can be seen in Fig. 4. The cell shown did not respond at all to red–green chromatic flicker, although some others were weakly responsive.

Response to 0·5 deg fields

With 4 deg fields, cell sensitivity will depend on contributions from centre and surround. One way of attempting to separate these contributions is to restrict the size of the stimulus. For nine phasic cells and nine tonic cells with M- and L-cone input, we compared sensitivity with 4 and 0·5 deg fields. We chose 0·5 deg as a size which would certainly include the centre of the receptive field of parafoveal cells without encroaching too much on the surround mechanism (de Monasterio & Gouras, 1975; Crook, Lange-Malecki, Lee & Valberg, 1988). The sensitivity of two tonic and two phasic cells to different types of flicker at different temporal frequencies are shown in Fig. 5.

Reduction of stimulus size usually enhanced the sensitivity of tonic cells to achromatic luminance flicker, especially at low temporal frequencies, though the extent of the effect varied between cells. Enhanced responses of colour-opponent cells to small, achromatic spots as compared with large-field flashes is well known (Wiesel & Hubel, 1966). Of the nine phasic cells tested, four showed an increase in sensitivity to 0·5 deg spots at 10 Hz, while five showed little change in sensitivity, or even a slight decrease.

For all tonic cells, the sensitivity to red–green chromatic flicker was reduced with 0·5 deg stimuli. We attribute this to only one cone mechanism being then able to contribute to sensitivity. Phasic cells did not respond to chromatic flicker with small spots. The frequency-doubled response is largely eliminated with small stimuli (Lee *et al.* 1989*b*).

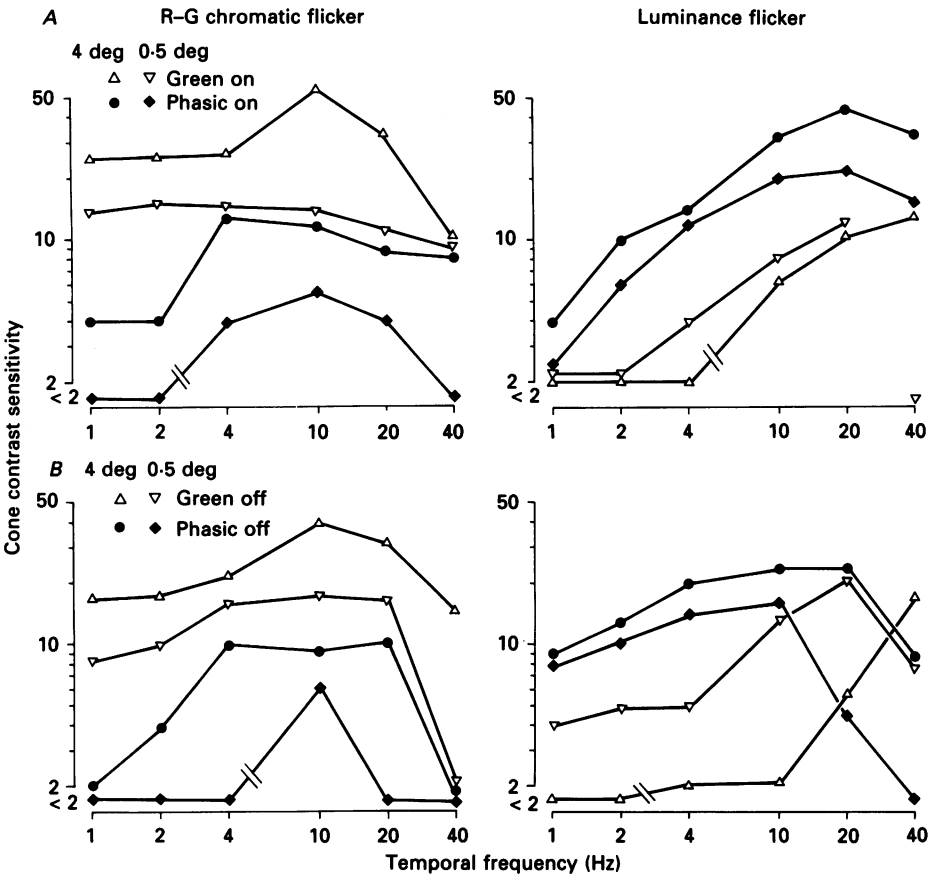

Fig. 5. A comparison of sensitivity to 4 deg and 0·5 deg stimulus fields. Results from two pairs of cells are shown; in both *A* and *B* sensitivities of one tonic and one phasic cell are compared. The left-hand panels show sensitivity to red–green chromatic flicker, the right-hand panels show sensitivity to achromatic luminance flicker. Points plotted below the bottom of the sensitivity scale indicate that the cell did not reach the threshold criterion. For the phasic cell with chromatic modulation the second-harmonic threshold is plotted.

The results found with small spots are consistent with those using grating stimuli (e.g. Kaplan & Shapley, 1982). However, to obtain a better separation of centre and surround contributions to tonic cell sensitivity, we isolated them by silent substitution.

Isolation of cone mechanisms by silent substitution

Insofar as the centre and surround of tonic cells each receive only M- or L-cone input, their contributions may be isolated by activating solely one or the other cone. This method is superior to varying stimulus size, for even with a small spot some surround involvement cannot be ruled out.

We studied eighteen tonic cells with M- and L-cone input to this type of flicker, at a variety of temporal frequencies. We also studied fourteen phasic cells. We used the

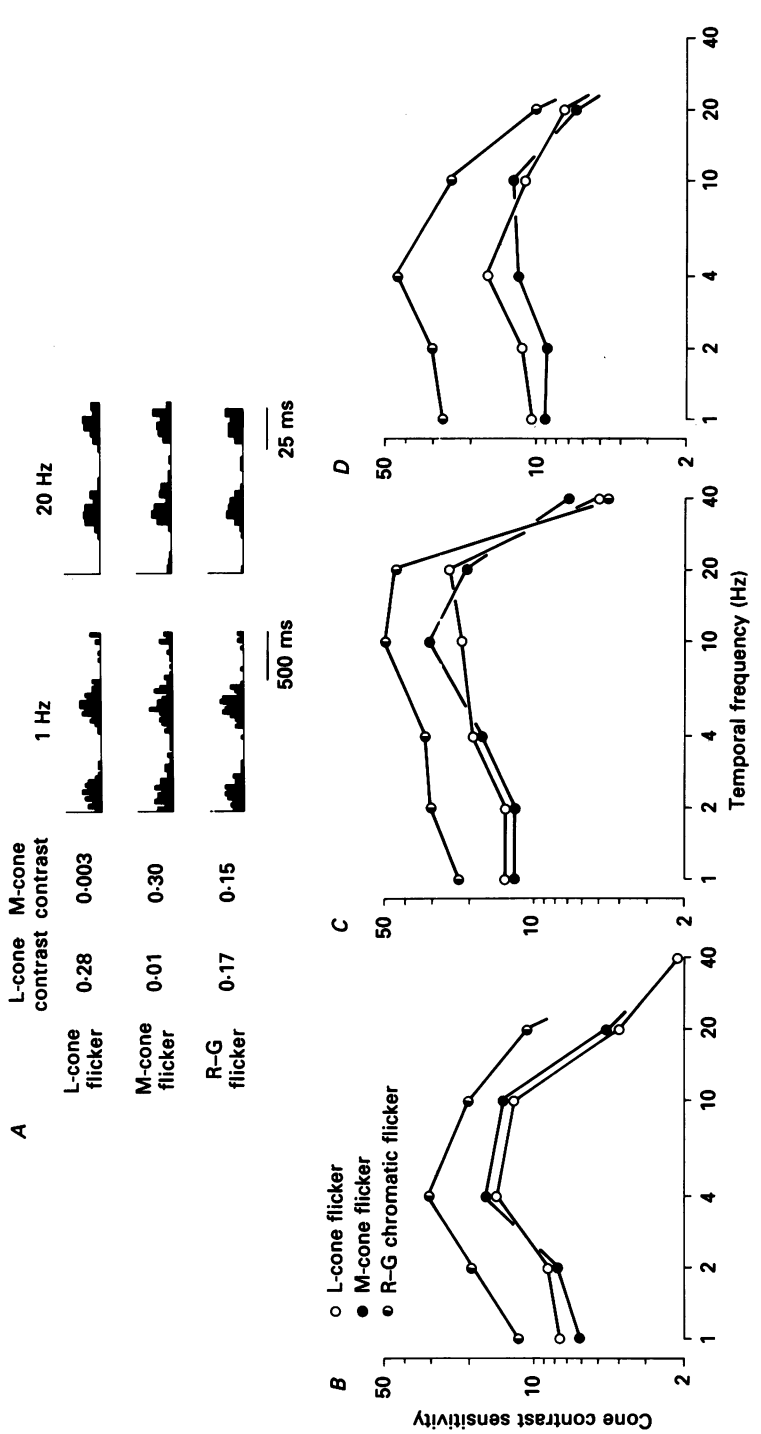

Fig. 6. Tonic cell sensitivity to M-cone and L-cone flicker. In *A*, histograms showing response to two cycles of 1 Hz and 20 Hz flicker for a red on-centre cell. Responses are summed over about 6 s of flicker. Vertical scale bar is 50 impulses s^{-1}. The top two histograms show response to L-cone flicker, the middle two to M-cone flicker, and the bottom two to red–green (R–G) chromatic flicker. The contrast of M- and L-cone mechanisms is indicated. In *B* for the same cell, sensitivity is plotted for the three conditions. It is similar for M- and L-cone flicker, while sensitivity to red–green chromatic flicker is about twice that to either cone alone, indicating a linear addition of sensitivity at threshold. *C* and *D* show the same result for two green on-centre cells.

same filter combination as with red–green chromatic flicker, but tilted the flicker axis out of the equal luminance plane so as to silence one cone type or the other. This was achieved by adjusting the luminance of one component of the flicker mixture, in accordance with the equations in the methods section. When the L-cone is silent, we will refer to 'M-cone flicker' and when the M-cone is silent to 'L-cone flicker'.

Figure 6 shows typical results from three tonic cells stimulated with M-cone flicker, L-cone flicker and with red–green chromatic flicker. In Fig. 6*A* are histograms of the response of a red on-centre cell to M-cone, L-cone and chromatic flicker at 1 and 20 Hz, with cone contrasts as indicated.

The histograms show responses of comparable amplitude, i.e. the on-response to the L-cone (centre response) is similar to the off-response to the M-cone (surround response). The response to chromatic flicker may thus derive from approximately equal contributions from each cone. This is further illustrated by the threshold measurements in Fig. 6*B–D*, the curves in *B* being for the cell in *A*, and those in *C* and *D* for two green on-centre cells. The sensitivity to red–green chromatic flicker has been derived from the average modulation of M- and L-cones at threshold, as in the previous figures.

For all three cells, thresholds to M- and L-cone flicker were very similar up to 20 Hz. This was true of all eighteen tonic cells that we tested. The cells are about twice as sensitive to red–green chromatic flicker as to M- or L-cone flicker, except at 40 Hz. This implies that tonic cell sensitivity to chromatic chromatic flicker is the sum of M- and L-cone contributions of similar weighting.

Phasic cells receive synergistic input from M- and L-cones to centre and surround; one would therefore expect that these cells' sensitivity to luminance flicker to be made up of contributions from M- and L-cones. However, for phasic cells centre and surround mechanisms are not separable by silent substitution. Responses of a phasic cell to M-cone and L-cone flicker and to luminance flicker are shown in Fig. 7*A*.

Figure 7*B–D* shows thresholds of three phasic cells. The sensitivities of the individual cone mechanisms, as tested with M- and L-cone flicker, are similar at 10 Hz. However, in contrast to tonic cells, tuning curves of phasic cells often differed for the two cone mechanisms. In particular, at low temporal frequencies thresholds for the M-cone mechanism were higher than for the L-cone mechanism. This was the case for all other phasic cells tested with 4 deg fields at 1400 td. Thresholds for luminance flicker were lower than for M-cone or L-cone flicker, as expected if M- and L-cone contributions summate to provide achromatic flicker sensitivity.

We compare sensitivity at 10 Hz to M- and L-cone flicker for all phasic and tonic cells tested in Fig. 8*A*. Cells have been divided into three groups, phasic cells, tonic cells with +M−L-cone inputs (predominantly green on-centre cells) and those with +L−M-cone inputs (mostly red on-centre cells). All three populations overlap; no significant difference was present between them. This suggests that both tonic and phasic cells receive M- and L-cone inputs of similar strength.

Although it could be argued that this analysis puts phasic cells at a disadvantage, because with 4 deg fields centre–surround antagonism could lower sensitivity, for three phasic cells we measured thresholds to M- and L-cone flicker with 0·5 deg spots but, at 10 Hz, did not find such a difference in sensitivity as to invalidate the results shown in Fig. 8*A*.

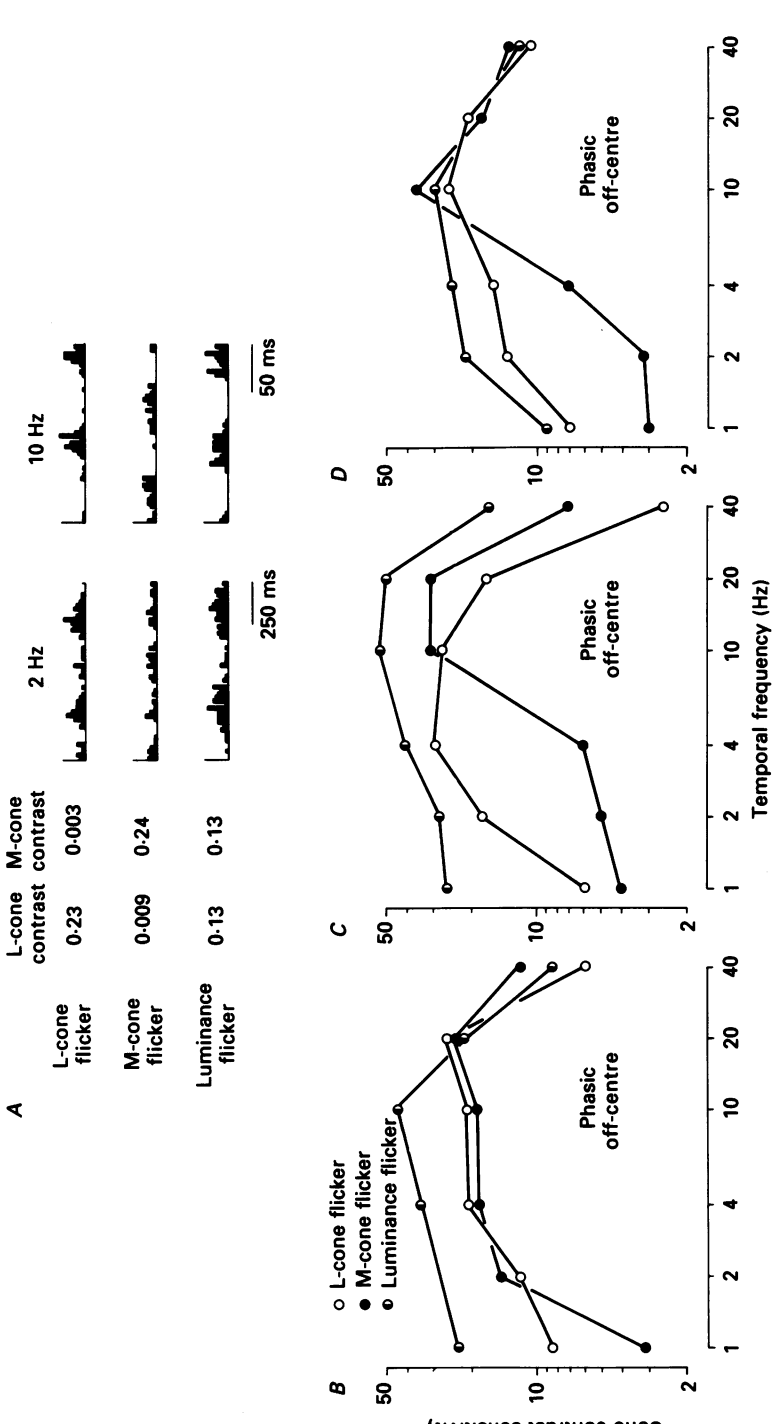

Fig. 7. Responses of phasic cells to achromatic, M- and L-cone flicker. Histograms show response to two cycles of 2 and 10 Hz flicker at cone modulation levels as indicated. Responses are summed over 6 s of flicker. The vertical scale bar is 50 impulses s^{-1}. In *B* are plotted thresholds of three phasic cells to M- and L-cone flicker and to luminance flicker. Sensitivity to luminance flicker is higher than to M- or L-cone flicker, but generally not by a factor of two.

Secondly, as in Fig. 6, M- and L-cone thresholds are similar for red and green on-centre cells, indicating that centre and surround have about the same sensitivity, despite their large difference in diameter. If sensitivity to chromatic flicker is equally derived from centre and surround (Valberg *et al.* 1987), the low sensitivity of tonic cells to luminance flicker can be interpreted as a result of mutual cancellation by the opponent mechanisms rather than low sensitivity of the cone input to the centre.

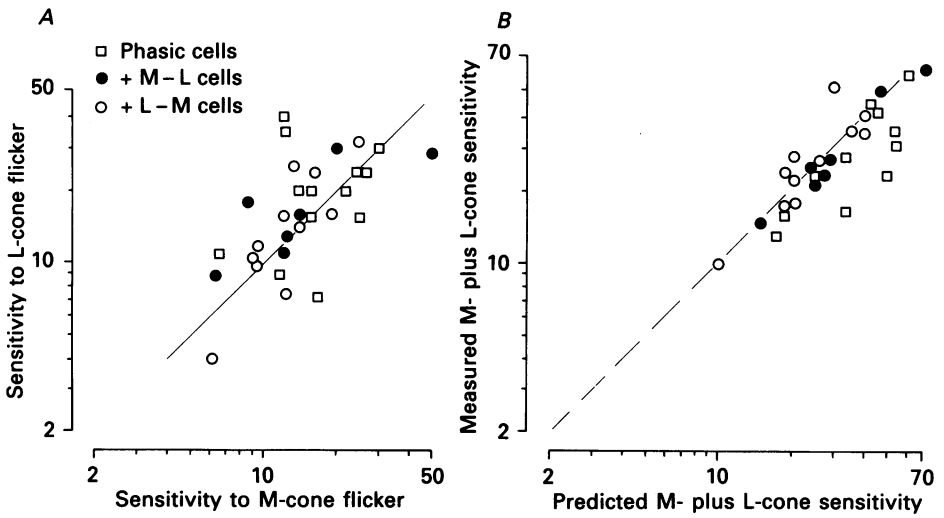

Fig. 8. *A*, the sensitivities (at 10 Hz) of tonic and phasic cells to M- and L-cone flicker is compared. The line indicates equal sensitivity. +M−L and +L−M cells were mostly green on-centre and red on-centre cells respectively. Sensitivity of phasic and tonic cells is similar. In *B*, sensitivities to red–green chromatic flicker for tonic cells, and to luminance flicker for phasic cells, is predicted from M- and L-cone flicker sensitivities. Additivity is indicated by the line. Tonic cells cluster long the line, but for phasic cells points tend to fall below the line, indicating a degree of subadditivity.

Sensitivity of tonic cells to M- and L-cone flicker was correlated ($r = 0{\cdot}66$, $n = 18$, $P < 1\%$). This is not entirely unexpected, for roughly equal cone weightings are necessary to account for such cells' suprathreshold responses (Derrington *et al.* 1984; Lee *et al.* 1987; Valberg *et al.* 1987).

It is of interest how well cell thresholds can be predicted from M- and L-cone flicker sensitivity. If inputs sum linearly, then tonic cell thresholds to chromatic flicker, and phasic cell thresholds to luminance flicker, should be given by the sum of M- and L-cone flicker sensitivities. Predicted sensitivity is plotted against measured sensitivity in Fig. 8*B* for 10 Hz stimulation. A line has been drawn with a slope of one to indicate additivity. Tonic cells cluster very close to this line. For phasic cells, points tend to fall below the line. This indicates a degree of subadditivity, so that sensitivity to luminance flicker was not as high as that predicted from a sum of sensitivity to isolated M- and L-cone flicker.

The ratio of predicted to measured sensitivity was calculated to test if this difference reached significance. A ratio of one would indicate perfect additivity. The mean ratio for tonic cells was 0·99 ($n = 18$, S.E.M. $= \pm 0{\cdot}043$). For phasic cells, it was

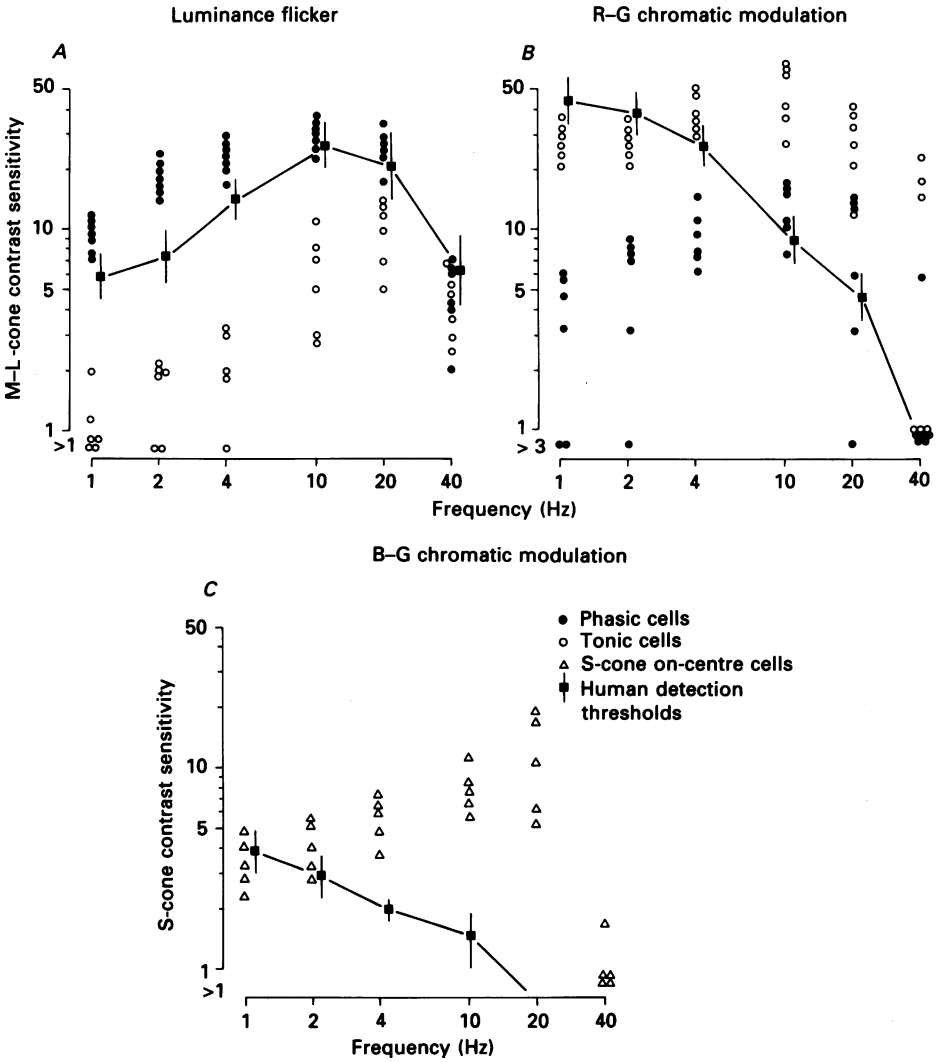

Fig. 9. Sensitivity of six human subjects to luminance, red–green (R–G) chromatic and blue–green (B–G) chromatic flicker is plotted against temporal frequency, and compared with the most sensitive cells encountered. Phasic cell sensitivity is broadly similar to human sensitivity for luminance flicker. For chromatic flicker, M-/L-cone opponent cells are almost as sensitive as human observers at low temporal frequencies, but whereas human observers become rapidly less sensitive above 2 Hz, cell sensitivity remains high. For blue–green flicker, a similar difference is present. Only blue on-centre cells responded to this condition.

1·31 ($n = 11$, S.E.M. $= \pm 0{\cdot}11$) which indicates a significant ($P < 2\%$) degree of additivity failure. The frequency-doubled responses shown in Fig. 2 are also an example of non-additivity.

Comparison of cellular with psychophysical sensitivity

Human sensitivity to luminance flicker is maximal about 10 Hz, while to chromatic flicker it is maximal at 1 Hz or below (de Lange, 1958; Kelly & van

Norren, 1977; Swanson, Ueno, Smith & Pokorney, 1987). We measured thresholds of six human subjects to luminance and chromatic flicker using identical stimulus conditions to those used for cells. Stimuli were viewed parafoveally (10 deg) to permit comparison with thresholds of parafoveal ganglion cells.

In Fig. 9, we compare thresholds of the most sensitive phasic and tonic cells found with the mean sensitivities of the human observers. For luminance and red–green chromatic flicker, sensitivity is expressed as L- or M-cone contrast, while for blue–green chromatic flicker, S-cone contrast sensitivity is shown.

Human thresholds are as expected from the literature. The sensitivity of individual phasic cells to luminance flicker is comparable to human sensitivity at all temporal frequencies tested. A striking divergence between psychophysical and physiological data is observed for chromatic flicker. For red–green and blue–green chromatic flicker, individual tonic cells approach human sensitivity below 4 Hz. Unlike the psychophysical results, however, tonic cell sensitivity increases slightly up to 10 or 20 Hz, whereas human sensitivity decreases dramatically. This quite remarkable divergence suggests that high-frequency signals from tonic cells are not available to the detection mechanism.

DISCUSSION

The study of flicker sensitivity was given a systematic basis by de Lange (1958), who was the first to recognize that sinusoidal (as opposed to rectangular) variation in luminance or chromaticity makes the performance of the visual system readily amenable to linear systems analysis. Although early studies of the cat's visual system often employed flickering stimuli (Enroth, 1953; Cleland & Enroth-Cugell, 1966; Maffei, Cervetto & Fiorentini, 1970; Grüsser, 1971), sinusoidal gratings have largely superseded flicker in visual neurophysiology. Nevertheless, flickering stimuli are still employed in many psychophysical experiments, and those of de Lange (1958) and Kelly & van Norren (1977) originally led to the suggestion that the different temporal modulation sensitivities for chromatic and luminance flicker reflect the properties of different chromatic and achromatic channels. We show elsewhere (Lee *et al.* 1988) that the channel responsible for human performance in heterochromatic flicker photometry can be identified with the phasic, magnocellular system in the primate visual pathway. In this paper, we discuss the cell systems most likely responsible for detection of chromatic and luminance flicker.

The sensitivity of phasic ganglion cells to achromatic, luminance flicker was superior to that of tonic ganglion cells, as expected from earlier results using black–white gratings (Kaplan & Shapley, 1982; Hicks *et al.* 1983). On the other hand, sensitivity to red–green chromatic flicker was substantially higher in those tonic ganglion cells with antagonistic M- and L-cone inputs than in phasic ganglion cells. This result is consistent with observations of Derrington *et al.*(1984) who used suprathreshold stimulation.

The relation between cell and psychophysical sensitivity

As discussed at length elsewhere (Crook *et al.* 1987), comparison of physiological results from the macaque and psychophysical results from man must be undertaken

with some caution. Nevertheless, behavioural tests on the macaque have proved its performance to be sufficiently like that of man to permit such comparison (DeValois *et al.* 1974).

The sensitivity of phasic ganglion cells to luminance flicker is adequate to account for human thresholds at all the temporal frequencies we studied. The sensitivity of tonic ganglion cells of different types approached human sensitivity to red–green and blue–green chromatic modulation at low temporal frequencies; at higher frequencies cell sensitivity was *superior* to that found psychophysically. These results strongly support the viewpoint that different channels, as identified psychophysically in flicker experiments (Kelly & van Norren, 1977), can be identified with the phasic and tonic cell systems. They go against the idea that tonic cells can do 'double duty' as a chromatic channel at a low temporal frequency and a luminance channel at high frequencies (Zrenner, 1983; Kelly, 1983).

S-cone contrast sensitivity of blue on-centre cells was substantially lower than sensitivity of other classes of tonic cells to red–green or M- or L-cone flicker. This corresponds to the larger Weber fraction of the π-mechanisms associated with the S-cones, in comparison with those associated with M- and L-cones (Stiles, 1946).

Phasic ganglion cells respond to red–green chromatic modulation, with a residual response at twice the fundamental frequency. This has its origin in some non-linearity in M- and L-cone summation, for it is not present with flicker along a tritanopic confusion line, such as blue–green flicker (Lee *et al.* 1989*b*). This response might relate to psychophysical reports that a luminance mechanism intrudes into chromatic flicker detection at 6–8 Hz. This is visible in the original experiments of de Lange (1958), and has been discussed in more detail by Swanson *et al.* (1987). The frequency-doubled component disappears when the stimulus is restricted to the receptive field centre, or at low levels of retinal illumination. Psychophysical results (Swanson *et al.* 1987) also fail to reveal intrusion of a luminance mechanism under these latter conditions.

Tonic cells were much more sensitive than human observers to chromatic flicker at high temporal frequencies. The observation of vigorous, modulated tonic cell responses to a 10 Hz stimulus not visible to a human observer was very striking. When human observers carry out flicker photometric matches, they presumably can do so because the vigorous, modulated responses of tonic cells are not perceived.

It is likely that at some later stage in the visual system, perhaps in primary visual cortex, high temporal frequency modulation in tonic cells is discarded. One mechanism would be a low-pass temporal filter, but other possibilities exist. It seems plausible that high-frequency components are also discarded centrally when tonic cells respond to achromatic flicker or under other stimulus conditions. It is thus difficult to see how tonic cell responses to achromatic flicker at 20 or 40 Hz could contribute to flicker detection, when with the same frequencies red–green chromatic flicker is not seen.

Why are high-frequency components in tonic cells' signals not used perceptually? One possibility is that, since their spectral responsiveness changes with increasing flicker frequency (Gouras & Zrenner, 1979; Lee *et al.* 1989*a*), their chromatic signal is no longer reliable; it cannot be used for assessment of chromatic composition.

Nevertheless, it could be argued that the response of these cells to rapid change

might be useful for motion and form perception. However, it has become evident in recent years that phase is an important parameter in visual analysis (Julesz & Schumer, 1983). In the accompanying paper we show that with flicker stimuli, the response phase of tonic cells (and thus the timing of the signal they provide) is variable, depending on both chromatic and temporal parameters (Lee *et al.* 1989*a*). Phase information therefore may be not reliably transmitted by tonic cells. On the other hand, phase information from phasic cells does not show this variability with different spectral composition and temporal frequency, and this may indicate why the luminance system plays such an important role in, for example, motion perception (Ramachandran & Gregory, 1978; Cavanagh, Tyler & Favreau, 1984), where velocity information is presumably encoded in terms of response phase.

Sensitivity of cone inputs to tonic and phasic cells

Early measurements of the centre size of tonic cells' provided diameters of less than 7 min of arc in the central 20 deg of retina (de Monasterio & Gouras, 1975). This would be consistent with the notion that such ganglion cells receive, through the midget system, input from just one cone (Boycott & Dowling, 1969). However, recent measurements in macaque, both in the geniculate nucleus (Blakemore & Vital-Durand, 1986) and on retinal ganglion cells (Crook *et al.* 1988), have shown that the visual resolution of tonic and phasic cells to achromatic gratings is similar, so that for tonic cells in parafoveal retina, resolution is much inferior to that expected on the basis of their reported centre size. In contrast, for cat ganglion cells, the relation between centre size and visual resolution is well established (Peichl & Wässle, 1979). One possible explanation (Hicks *et al.* 1983; Derrington & Lennie, 1984; Shapley & Perry, 1986) is that small receptive field centres are intrinsically insensitive so that resolution is degraded.

This argument is rendered unlikely by the results reported here. Using silent substitution, which we have termed M- and L-cone flicker, we have been able to show that the contribution of these two cones to a cell's chromatic flicker sensitivity is very similar, and that M- and L-cone inputs to green and red on-centre cells are similar in strength to those to phasic cells. Tonic cell centre mechanisms are thus not particularly insensitive. To an achromatic stimulus, the centre of a phasic cell (summing both cones) should only be twice as sensitive as that of a tonic cell (summing only one).

It is possible that tonic cell centre size is larger than previous estimates, for technical objections can be raised to the conclusions of both de Monasterio & Gouras (1975) and Derrington & Lennie (1984). Centre diameter measured from area–threshold curves yielded larger values than these earlier reports (Crook *et al.* 1988). However, this would be inconsistent with the assumption that many red or green on-centre ganglion cells have a centre consisting of only one cone. The resolution of this interesting issue remains unclear.

The ability to predict sensitivity of tonic cells to chromatic flicker from M- and L-cone sensitivities is consistent with linear cone summation to these cells (Derrington *et al.* 1984; Lee *et al.* 1987; Valberg *et al.* 1987). For phasic cells and luminance flicker, perfect additivity of M- and L-cones was not found. Together with frequency-doubled responses to chromatic flicker, this indicates a non-linearity of M- and

L-cone summation to phasic cells, so that the phasic, magnocellular pathway cannot be viewed as one in which straightforward linear summation of M- and L-cone inputs occurs.

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