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THE PHYSIOLOGICAL BASIS OF THE MINIMALLY DISTINCT BORDER DEMONSTRATED IN THE GANGLION CELLS OF THE MACAQUE RETINA

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SUMMARY

1. The minimally distinct border method involves setting the relative radiances of two adjacent, differently coloured fields until the border between them is minimally distinct. At these radiance settings, the two fields are found to be of equal luminance. The task shares with flicker photometry all the requirements of a photometric method.

2. We have recorded responses of macaque ganglion cells to such borders moved back and forth across the receptive field; the size of the luminance step across the border was systematically varied.

3. Phasic ganglion cells gave transient responses to such borders, consisting of an increase or decrease in firing rate depending on direction of luminance contrast and cell type (on- or off-centre). Tonic ganglion cells gave sustained responses dependent on chromatic contrast across the border.

4. An analysis of phasic cell responses showed a minimum near equal luminance, suggesting their signal could readily support the minimally distinct border task. We could not devise a scheme whereby tonic cells could support the task.

5. Spectral sensitivity of phasic cells, determined from their minima, closely resembled the 10 deg luminous efficiency function, as required of a mechanism underlying the psychophysical performance.

6. For phasic cells, the minimum was independent of movement speed, and hence of eye movement velocity under natural viewing conditions.

7. Proportionality, additivity and transitivity are found psychophysically with the minimally distinct border method. All these properties were also exhibited by phasic cell responses.

8. Residual responses were present in individual phasic cells to equal-luminance borders, probably due to a non-linearity of M- and L-cone summation. The

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amplitude of residual response depended on the wavelengths on either side of the border, and was zero for pairs of lights lying along a tritanopic confusion line. These residual responses could be correlated with residual border distinctness at equal luminance as reported psychophysically.

9. There was some variability in spectral sensitivity among phasic cells, and this could be described in terms of variability in weighting of the middle- and long-wavelength cone inputs to each cell. With equal-luminance borders, the residual response of the phasic cell population will thus be made up of the residual responses from individual cells and a contribution due to variation in spectral sensitivity among cells.

10. The responses of phasic ganglion cells thus form the physiological substrate of psychophysical performance on the minimally distinct border task. These cells also provide a residual signal to equal-luminance borders which correlates with residual distinctness. This implies that their activity is strongly related to border and contour perception, and that they play a major role in form vision.

INTRODUCTION

Borders between objects can be recognized by differences in either luminance or colour. If the ratio of intensities across a border between two colours is adjusted, at some ratio the border becomes least distinct (Frauenhofer, 1824; Liebmann, 1927; Boynton & Kaiser, 1968). The minimally distinct border method of heterochromatic photometry is based on this result. A subject adjusts the relative radiances of two differently coloured fields until the border between them is minimally distinct. The minimum is found to occur when the sensation luminances (Kaiser, 1988) of the two fields are equal. If monochromatic wavelengths are tested against a reference light, the spectral sensitivity curve so obtained closely resembles Judd's modification to the CIE (Commission Internationale de l'Eclairage) photopic luminous efficiency function (V_λ; Wagner & Boynton, 1972).

The human luminous efficiency, or V_λ function, was defined by the CIE in 1924 as a standard for the spectral sensitivity of the human observer, with a correction being proposed by Judd in 1951 (see Kaiser, 1973). Much of the data used to derive the V_λ function were obtained using the technique of heterochromatic flicker photometry. It has been shown that the minimally distinct border method shares with flicker photometry all the characteristics of a photometric technique. Not only are the spectral sensitivity curves derived from the two techniques similar, but linear properties such as additivity (Boynton & Kaiser, 1968), proportionality (Ingling, Tsou, Gast, Burns, Emerick & Riesenberg, 1978) and transitivity (Ward & Boynton, 1974) are also common to both of them.

The border strength at the minimum depends on the colours on either side of the border. With different monochromatic wavelengths tested against white, residual distinctness is high for long wavelengths, very low near 570 nm and then increases again at short wavelengths (Kaiser, Herzberg & Boynton, 1971). Residual distinctness can be described in terms of the difference in excitation between the middle- (M-) and long-wavelength (L-) cones across the border (Valberg & Tansley, 1977; Tansley & Valberg, 1979). When this is zero, as is the case with tritanopic pairs of lights between which there is a difference only in S-cone excitation, the border is

very indistinct (Valberg & Tansley, 1977) and seems to 'melt' (Tansley & Boynton, 1976), although more recent psychophysical investigations have shown that S-cones do make a small contribution to border distinctness (Kaiser & Boynton, 1985; Boynton, Eskew & Olson, 1985).

In the old-world primate, such as the macaque and man, there are two main cell systems in the visual pathway. Tonic, cone- and wavelength-opponent retinal ganglion cells project to the parvocellular layers of the lateral geniculate nucleus (P-pathway). Phasic, non-opponent ganglion cells 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 divided into two groups. The majority received antagonistic input from medium- and long-wavelength-sensitive (M- and L-) cones. The minority receive input from short-wavelength-sensitive (S-) cones, opposed by some combination of M- and L-cones. The opponent mechanism of most tonic cells form cone-specific centre and surround mechanisms. Phasic cells 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).

We have shown elsewhere that phasic, M-pathway cells form the physiological substrate for human performance on the heterochromatic flicker photometry task (Lee, Martin & Valberg, 1988). We show here that minimization of activity in this pathway also underlies psychophysical minimization of border distinctness. Furthermore, due to a non-linearity in M- and L-cone summation (Lee, Martin & Valberg, 1989*a*) phasic cells can give a residual response to a moving border on either side of which are colours of equal luminance. The strength of this residual response is correlated with residual distinctness ratings of human subjects. Thus, the phasic M-pathway would seem to play a key role in border perception.

A preliminary report of these results has been published (Lee, Martin, Kaiser & Valberg, 1989).

METHODS

Ganglion cell activity was recorded from the retinae of juvenile macaques (*M. fascicularis*). Animals were anaesthetized initially with an intramuscular injection of ketamine and thereafter with halothane or isofluorane in a 70%–30% N_2O–O_2 mixture (1–2% during surgery, and 0·2–1% during recording). Local anaesthetic was applied to points of surgical intervention. EEG and ECG were continuously monitored as a control for anaesthetic depth. Muscular relaxation was maintained 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 and of appropriate power to focus the eye on a black-projection tangent screen 57 cm from the animal was fitted. Positions of fovea and optic disc were ascertained with the aid of a fundus camera. A 2 mm artificial pupil was 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.

Details of recording technique and cell classification are given in Lee, Martin & Valberg (1989*b*). Briefly, after extracellular activity of a ganglion cell was isolated, the cell type was determined using flashed spots. Cell responses to stimuli of different equiluminous colours were then recorded as an aid to cell classification. 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, Lee & Vidyasagar, 1983). We recorded from ganglion cells from parafoveal retina.

Visual stimulation. Two orthogonally mounted Leitz Prado projectors provided white light with CIE chromaticity co-ordinates $(x, y) = (0{\cdot}404, 0{\cdot}410)$. The 'white' light used was thus slightly yellowish, An edge could be generated in two ways. For one of them, a front surface silver coating was deposited on one-half of an optically flat piece of glass, to give a straight and sharp mirror boundary. An anti-reflective coating was then added. The glass was set at 45 deg in the stimulus beams. Thus combined, the beams of the two projectors passed through a focusing lens and were then reflected off a front surface-silvered mirror mounted on a galvanometer, which provided stimulus movement. The image of the mirror edge on the tangent screen could be moved as desired under computer control. The edge could also be generated using razor blades appropriately mounted in each projector beam, the beams then being combined in a beam splitter. Both methods provided an edge which was almost artifact free for foveal viewing by a human observer. Adjusting the razor blades was tedious, however, and they were only used in tests for chromatic aberration effects.

The spectral composition of each field was adjusted with interference filters (Schott, NAL, 50 nm bandwidth at half-maximum). Neutral-density filter wheels in each stimulus beam allowed the intensities of each field to be changed. These wheels were controlled by the computer system which moved the mirrors and averaged and stored unit responses. A Photo Research 702A/703A Scanning Spectrophotometer provided the radiance distribution (390–760 nm) and the 2 deg luminance and chromaticity co-ordinates of the stimuli. Wavelengths cited are peak radiances so measured. Since cell receptive fields were parafoveal (4–15 deg eccentricity), we based our calibrations on the 10 deg luminosity function, as described by Valberg, Lee & Tryti (1987). With the 2 mm artificial pupil, the retinal illuminance was usually about 80 trolands (td).

For additivity experiments, a third projector was installed and its beam combined with that of the test beam with a beam splitter. This allowed us to mix two wavelengths on one side of the border in any given proportion.

Cells' receptive fields were centred on a 5 deg stimulus aperture across which the edge was moved. To reduce chromatic adaptation effects resulting from the same colour being present over the receptive field for several seconds, and to speed data collection, we usually restricted movement amplitude to 1 deg. This may be appropriate, because during fixation on an edge by human subjects eye movement amplitude is restricted. Observations with larger movement amplitudes yielded similar results.

For each condition, cell responses to a series of relative intensities across the edge were measured, the range being adjusted to straddle the point of equal luminance. Usually, when different monochromatic wavelengths were tested against a white reference, the radiance on the white side of the border was kept constant. For a few phasic cells, we also measured spectral sensitivity by adjusting radiance on both sides of the border so as to keep mean luminance constant. There was no difference in the results obtained. Fourteen to twenty responses to each edge movement were averaged and stored as a peristimulus time histogram of 128 bins. For clarity of illustration, a resolution of 64 bins is shown in the figures. An analog 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.

For phasic cells, response amplitude was measured in a window (80 ms at 4 deg s^{-1}) centred on the peak excitatory response to the maximal contrast (see Fig. 1). Maintained activity (derived from the mean of twenty bins at the beginning and twenty bins at the end of the histogram) was then subtracted. Negative responses thus reflect a suppression of maintained activity. The responses of tonic cells were so sustained (see Fig. 5) that a different procedure had to be adopted. Mean firing rates over thirty bins before and after the edge passed over the receptive field centre were measured and the difference between these values used as the cell's response.

RESULTS

We recorded responses to moving borders from thirty-eight phasic ganglion cells and twenty-four tonic cells, classified using the usual tests (Lee *et al.* 1989*b*). For each combination of colours, ten different luminance ratios across the border were tested.

Usually, it was possible to study the same cell for several hours, so that we could test under a variety of conditions. We also investigated the effect of stimulus velocity and mean luminance level and made control observations to rule out a significant effect of chromatic aberration.

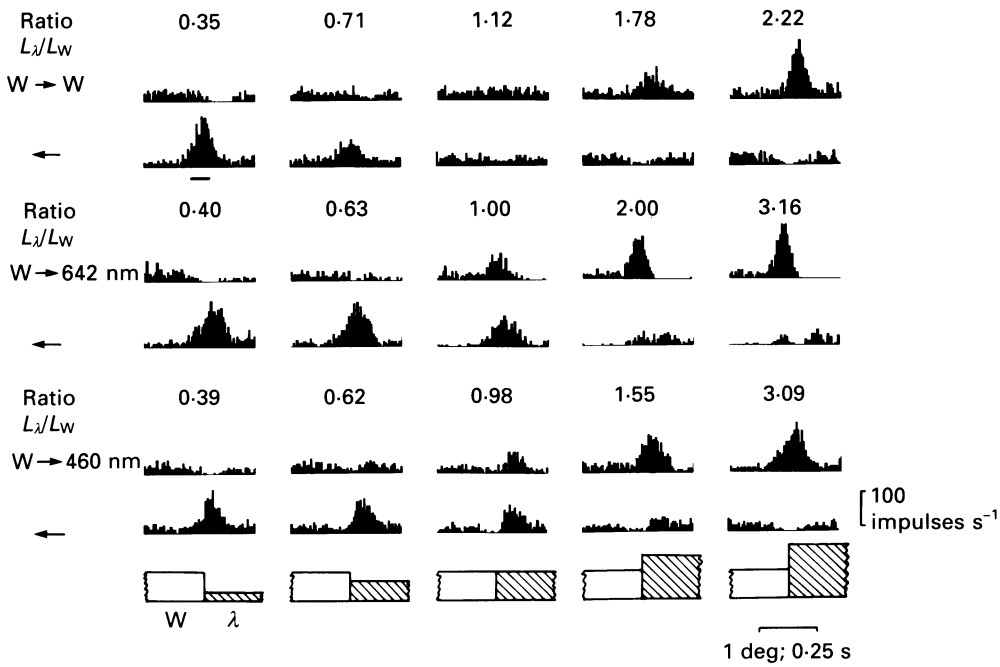

Fig. 1. Responses of a phasic on-centre cell to moving borders, of which the composition is indicated on the left-hand side, recorded with various luminance ratios (L_λ/L_W) across the edge, as indicated by the numbers above each pair of histograms. Each pair represents responses to back and forth movement of the edge (see arrows). The cell gives a transient increase in firing to a luminance increment. At a luminance ratio of one (equal luminance), there is no residual response with an achromatic border (W–W), but in the other two conditions (W–λ) a residual response can be seen. Each response averaged from twenty sweeps, sixty-four bins shown at 8 ms per bin, movement speed 4 deg s^{-1}. Window width used is demonstrated by the line under the first histogram. Average retinal illuminance *ca* 80 td. Below each column is sketched the relative luminances of the white (open) and coloured (hatched) fields either side of the border.

Phasic cells responded to an edge moving across the receptive field with a transient change in firing rate, although for a few cells there was some change in maintained firing rate associated with long wavelengths (Wiesel & Hubel, 1966). Responses of tonic cells were very sustained. Responses of these different cell types and their quantification are described in the following sections.

Border responses of phasic cells

For each cell, responses to a border between achromatic fields were recorded. Then responses to borders made up of a white field juxtaposed with different chromatic fields were tested. Typical results for an on- and off-centre cell are shown in Figs 1 and 2 respectively. In each figure, the two top rows of histograms represent responses

to back and forth movement of an achromatic border, the next two rows to movement of a white–642 nm border and the lower rows to movement of a white–460 nm border. For each border, five of the ten luminance ratios tested are shown here. The luminance ratio between the test and the white reference field is indicated above each pair.

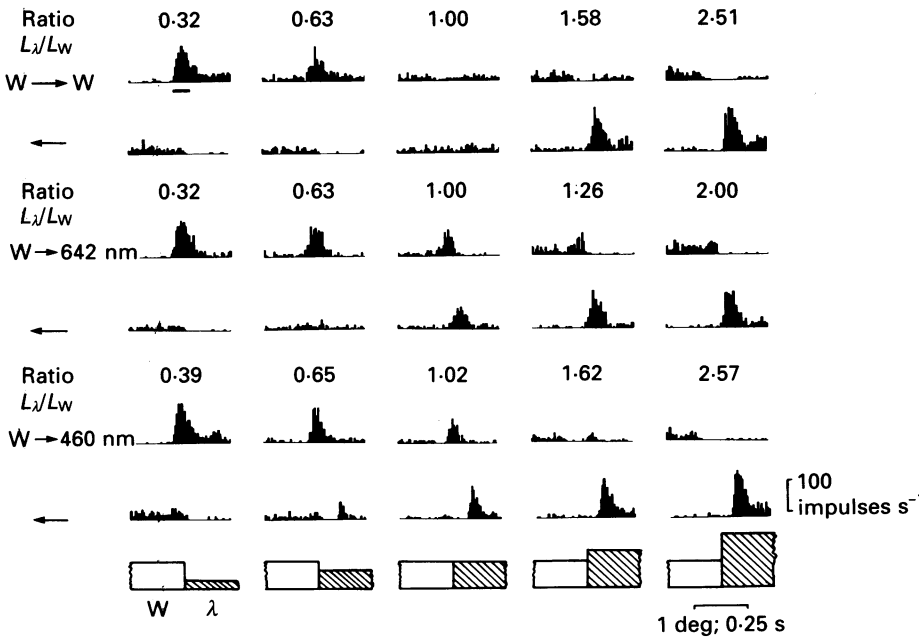

Fig. 2. Responses of a phasic off-centre cell to moving borders as in Fig. 1. The cell gives a transient increase in firing to a luminance decrement.

With an achromatic edge, which can be viewed as a control condition, the on-centre cell responds to an incremental step with an increase in firing and to a decremental step with a depression of maintained activity. The opposite pattern is present for the off-centre cell. At a luminance ratio of one, no response is present; this is necessarily so, for in this case both sides are identical and the border is not visible. In the other two conditions, a similar pattern is seen in that responses diminish as the luminance ratio approaches unity. However, near a ratio of one an excitatory response is apparent to *both* directions of border movement, for both the on- and the off-centre cell. For a given cell, these responses are approximately equal in magnitude near equal luminance. Such residual responses were seen in every phasic cell. Their amplitude was dependent on the stimulus colours producing the border. We subsequently describe this effect in more detail.

To quantify responses, we took the firing rate in a window (indicated in Figs 1 and 2) and fixed its position from a histogram in which a vigorous excitatory response was present. The same window position was then used for responses in other histograms in the series. Maintained firing rate was subtracted. Wavelength-dependent changes in maintained firing were sometimes observed, usually manifested as a decrease associated with long-wavelength fields (Wiesel & Hubel, 1966). We

therefore derived maintained firing estimates from an average of values obtained at the beginning and end of each histogram, i.e. from an average of the maintained firing to the colours on either side of the edge.

Figure 3*A* and *B* shows response curves obtained from the cells of Figs 1 and 2 respectively. In addition to the three conditions shown in those figures, the response to a white–570 nm border has been plotted. We have chosen to use luminance ratio for the abscissa to allow comparison with psychophysics, where border distinctness is minimal with a luminance ratio of one.

In each panel, the curves represent the two movement directions, and it can be seen that these curves cross close to a ratio of one, i.e. at equal luminance. For the achromatic and white–570 nm conditions, when this occurs there is zero response, reflecting the fact that no residual response was present, as shown for the achromatic conditions in Figs 1 and 2. For the other two conditions, although the curves intersect close to a ratio of one, a significant residual response was present. From the dashed line extended onto the abscissa, we derived the residual response, q, and we could estimate the discrepancy between the curve intersection and the luminosity function. A necessary assumption is that no significant direction selectivity was present in phasic cells. Responses to achromatic contrast showed no indication of such direction selectivity.

Results virtually identical to those in Fig. 3 were found with all thirty-eight phasic cells tested. When no residual response is present, it is clear that the phasic M-pathway is not modulated, and could thus readily underlie a human subject's performance when setting minimal distinctness. When a residual response is present, a minimal signal at equal luminance could also be derived from the phasic cell system (as may be seen from Fig. 3).

Although not apparent in Fig. 3, off-centre cells gave significantly larger responses to a small luminance decrement than did on-centre cells to the same luminance increment. In terms of the percentage contrast, defined as $(L_{max}-L_{min})/(L_{max}+L_{min})$, required to produce a 10 impulses s^{-1} firing rate increment, mean values were 4·0% for off-centre cells ($n = 15$, S.D. = 1·5%) and 6·2% for on-centre cells ($n = 14$, S.D. = 2·3%). This difference is significant at the 1% level (t test). Psychophysical sensitivity to light decrements is generally higher than to light increments (e.g. Boynton, Ikeda & Stiles, 1964; Short, 1966), and this difference between on- and off-centre cell sensitivities could underlie this phenomenon.

Spectral sensitivity of phasic cells derived from border responses

For twenty-two cells we recorded responses for eight different wavelengths bordering the white reference field. From plots as in Fig. 3 we compared spectral sensitivity of phasic cells with that expected from the 10 deg luminosity function. Sensitivities were calculated relative to stimulus radiance measured with a scanning spectrophotometer. The comparison is shown in Fig. 4. Correspondence between phasic cell sensitivity and the V_λ function is acceptable. This is in accord with previous measurements of phasic cell spectral sensitivity using heterochromatic flicker photometry (Lee *et al.* 1988).

We conclude that minimization of border distinctness by human observers could be due to minimization of activity in phasic ganglion cells.

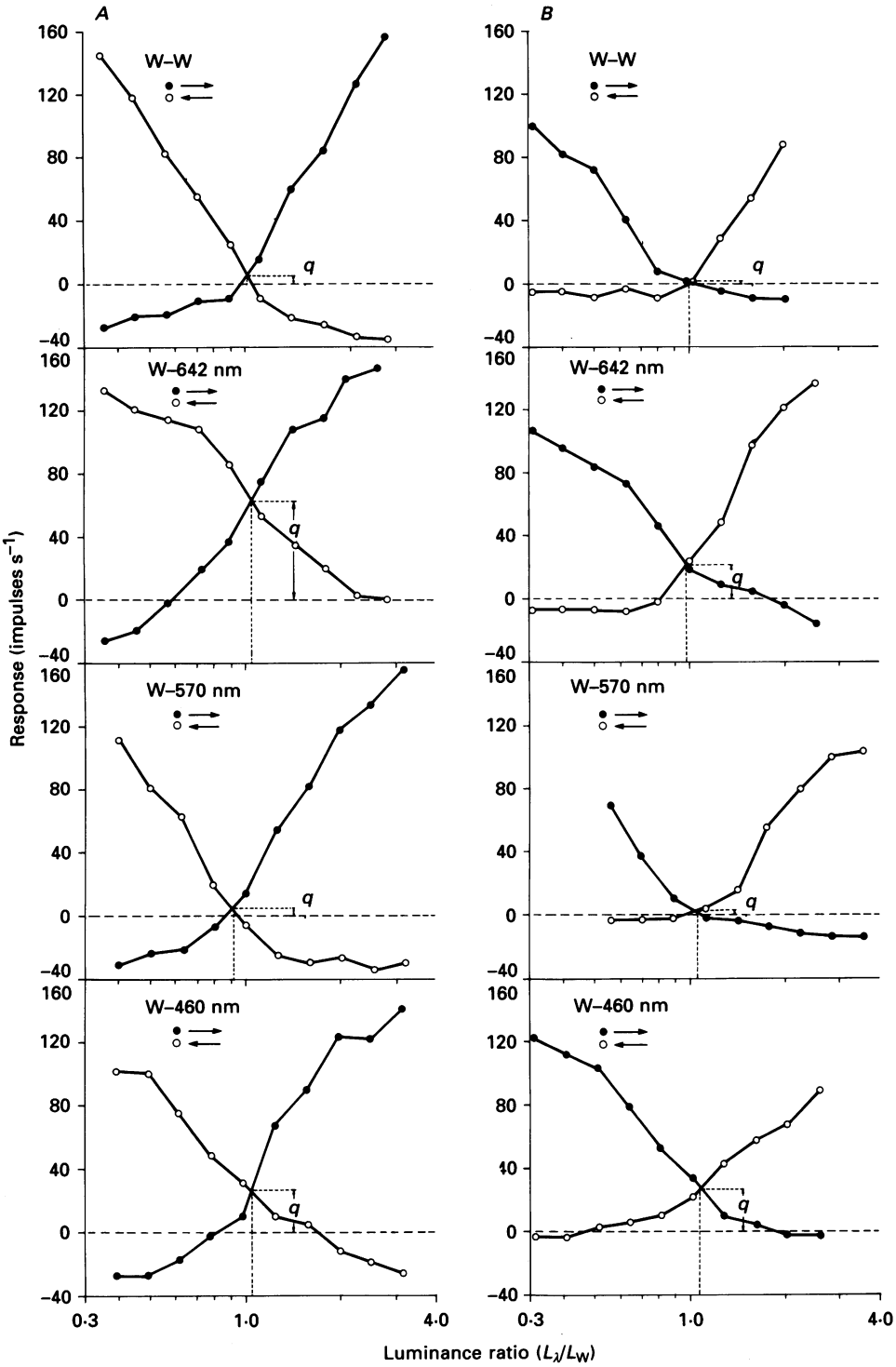

Fig. 3. For legend see facing page.

Can residual responses be due to an optical artifact?

For a subject to perform the minimally distinct border task, the edge between the two fields must be free of optical artifact. One way of testing this is to make the two fields the same colour, and see if their intensities can be adjusted until the field is uniform. We did this with our stimuli. A small artifact was just barely detectable using foveal fixation with the mirror edge but not with the razor blades. With parafoveal viewing, the stimulus field appeared uniform with either system.

A further source of artifact is chromatic aberration within the eye itself. This can be compensated with an achromatizing lens (e.g. Powell, 1981), but the positioning of such a lens on the optic axis is critical, which obviates its use in animal experiments. Nevertheless, we consider it unlikely that any artifact due to chromatic aberration gave rise to residual responses. A number of arguments support this view.

Firstly, large residual responses were observed with borders between 570 and 642 nm lights, but no residual responses were observed with borders between 510 and 440 nm, this latter pair lying close to a tritanopic confusion line. A longitudinal chromatic aberration of 0·3 dioptres would be expected in the former case, and a greater aberration of 0·7 dioptres in the latter (Charman & Jennings, 1976).

Secondly, for five cells we deliberately introduced optical artifacts into the stimulus by separating or overlapping the images of the razor blades which formed the border (see Methods). An artifact subtending 1·5 min of arc did not generate a response but generally an artifact subtending 3 min of arc did do so. This is consistent with the visual resolution of parafoveal phasic cells (Crook, Lange-Malecki, Lee & Valberg, 1988). A chromatic aberration of at least one dioptre would be required to produce an artifact of this magnitude (Gubisch, 1967; Charman & Jennings, 1976).

Thirdly, substantial residual responses were observed after defocusing the image (by 1–2 dioptres). This might be expected to smear out any aberration artifact. The effect of such defocusing was to broaden the peaks associated with phasic cell responses, but the luminance ratio at which a minimum response was present was unaffected. This may correspond to the observation that with blurred borders, spectral sensitivity of human subjects performing the minimally distinct border task is unaffected (Lindsey & Teller, 1989).

Fourthly, a chromatic aberration artifact consisting of some kind of luminance

Fig. 3. Plots of response magnitude against luminance ratio for the cells of Fig. 1 (*A*) and Fig. 2 (*B*), measured from the 80 ms peak response (ten bins). The location of this window was fixed from histograms in which the most vigorous response was present. Maintained firing was then subtracted to give response amplitude (abscissa). The two movement directions are indicated by the open and filled symbols. Luminance ratio is in terms of the 10 deg luminosity function. Four conditions are shown, the three in Figs 1 and 2 and one with 570 nm–white borders. As a luminance ratio of one is approached for either movement direction, responses decrease in size. Curves for the two movement directions intersect near a ratio of one. For the W–642 nm and the W–460 nm conditions there is a significant residual response at this curve intersection. We have used the point of curve intersection as an indication of the cell's spectral sensitivity. Deviation from the luminosity function is measured by dropping a perpendicular onto the abscissa. The residual response is measured from the distance q as shown.

perturbation in the retinal image would be expected to induce opposite patterns of response in on- and off-centre cells. With such pairs of cells, recorded sequentially from the same retinal region, no such reciprocal behaviour was observed.

Together, these arguments make response artifacts due to chromatic aberration unlikely. We conclude that residual responses arise from a non-linearity of M- and L-cone summation, as observed in responses of phasic cells to heterochromatic flicker (Lee *et al.* 1989*a*).

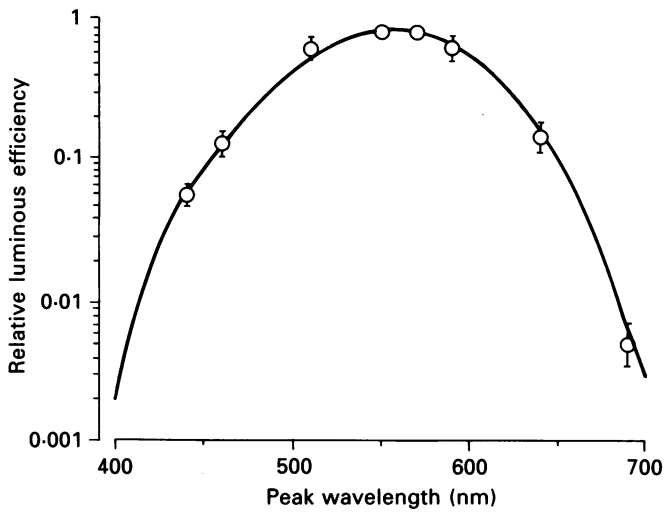

Fig. 4. Spectral sensitivity of phasic cells has been calculated from curve intersections as in Fig. 3, and is here compared to the human 10 deg luminosity function, calibrated with respect to radiance measurements of the stimuli. Means and standard deviations from twenty-two phasic cells are shown; where the latter are not visible, they are smaller than the symbols. The agreement is satisfactory.

Border responses of tonic cells

Tonic cells produced vigorous responses to chromatic borders which depended on the stimulus conditions and cell type. However, the response profiles were quite different from those exhibited by phasic cells. Examples of green on-centre, red on-centre and blue on-centre cells are seen in Figs 5–7. We explored a larger range of contrasts across the border with tonic than with phasic cells, 0·2 instead of 0·1 log unit steps being used.

Figure 5*A* shows responses of a green on-centre cell to borders between white and 642, 570 and 460 nm. Responses to the 642–white and 460 nm–white borders are vigorous, with a substantial response near a luminance ratio of one. To the 570 nm–white border, the response is smaller, and there is no response near a ratio of one. This is to be expected, for 570 nm and white lights lie close to a tritanopic confusion line, and so only cells with S-cone input will respond to such a border at equal luminance (see Fig. 7).

The sustained character of the response required us to quantify responses in a different way than for phasic cells. The difference in firing rate in 120 ms windows set before and after the edge passed over the receptive field was used, as indicated in the

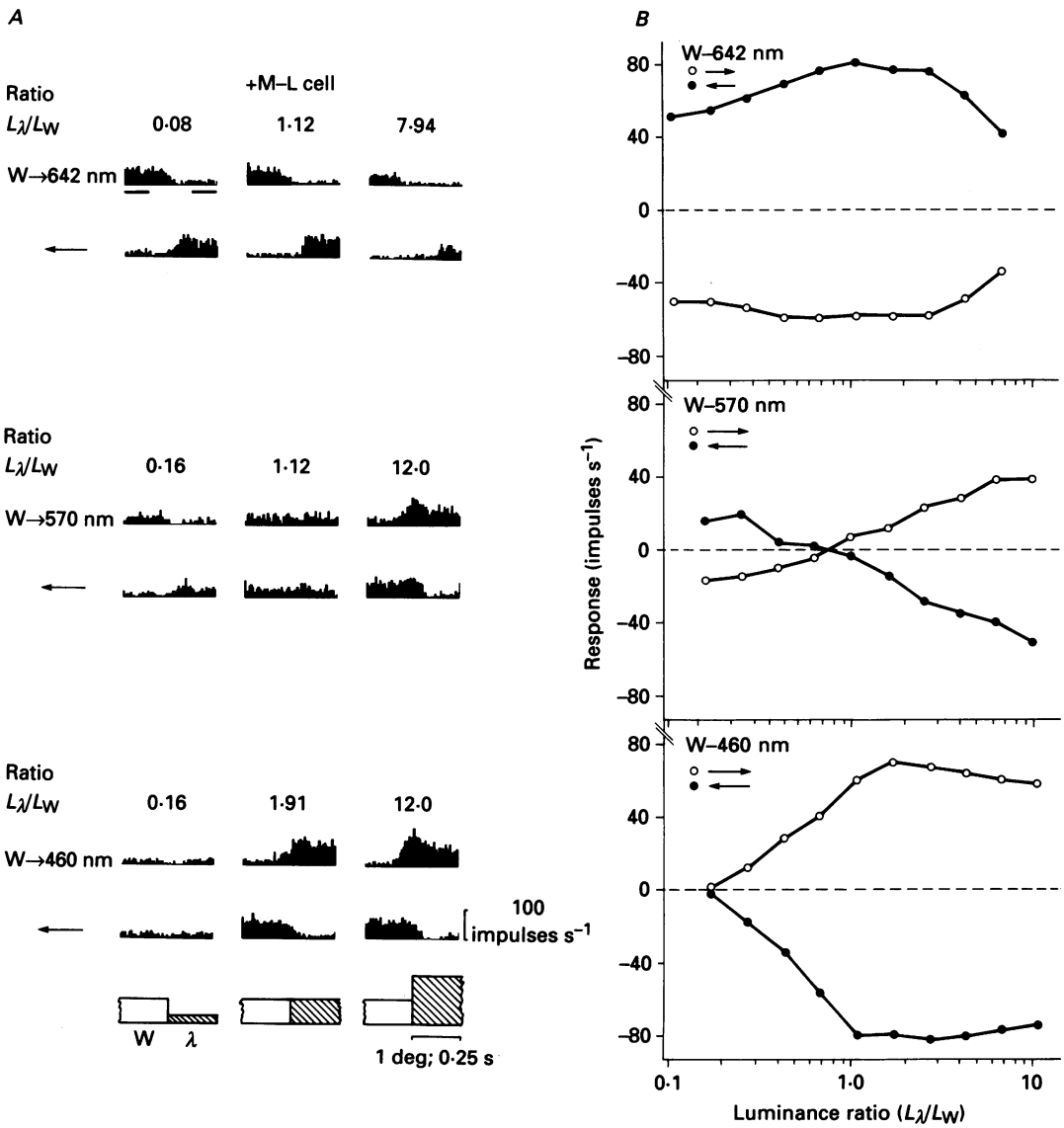

Fig. 5. *A*, responses of a green on-centre cell to moving borders as in Fig. 1. The cell gives a sustained change in firing depending on luminance ratio and the chromatic change across the edge. For the W–642 nm condition, the cell's firing increases in response to the white field, for the W–570 nm the response is weak, whereas for W–460 nm the cell fires in response to the chromatic field. *B*, response plots as in Fig. 3, except the difference in firing rate before and after the edge passed across the field is used. Lines indicate windows used. Note abscissa compressed by a factor of two relative to Fig. 3. For W–642 nm and W–460 nm no indication of a minimum close to a ratio of one is visible. For W–570 nm, the curves intersect close to a ratio of one. This is to be expected from a cell without S-cone input.

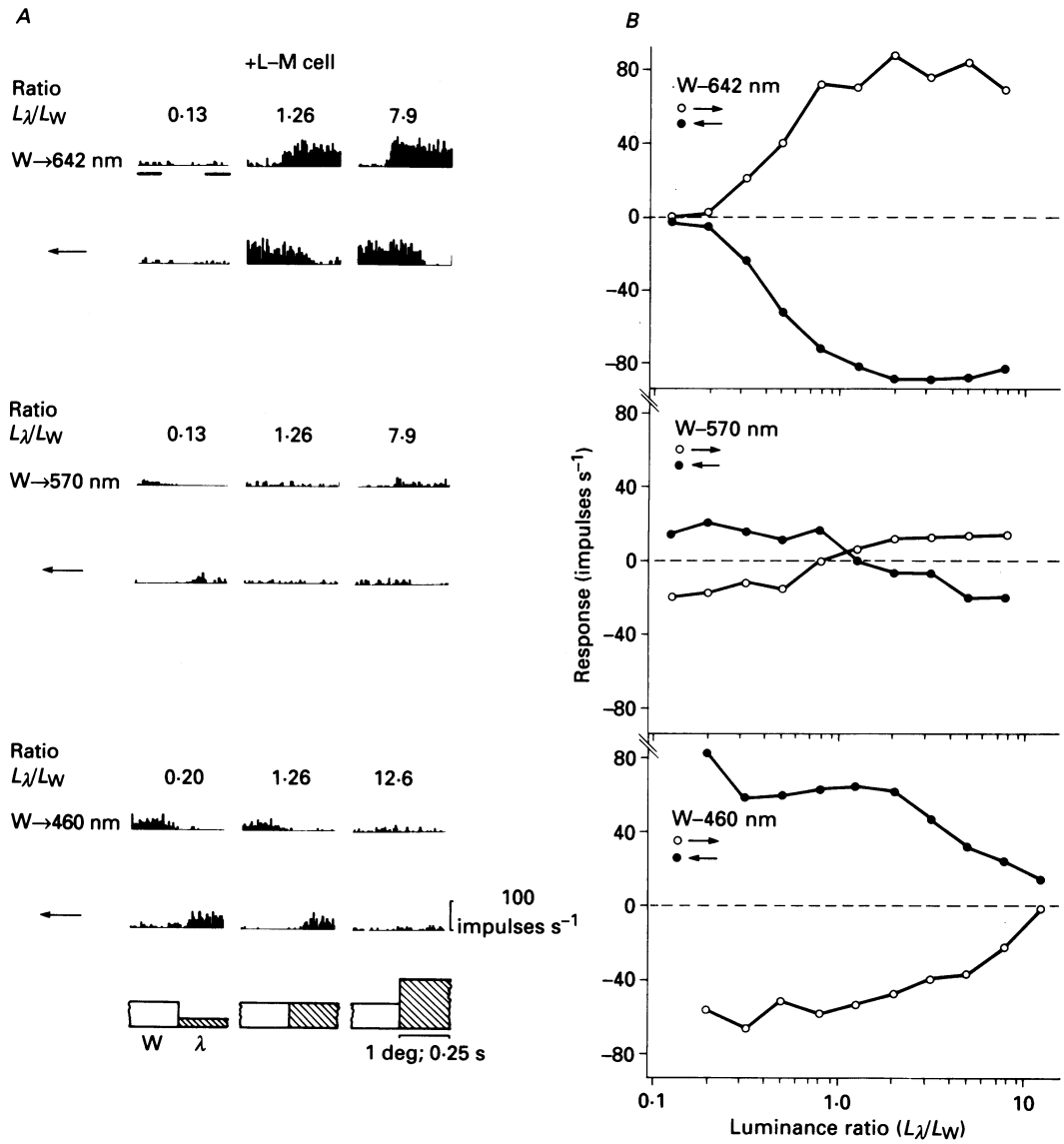

Fig. 6. *A*, responses of a red on-centre cell to moving borders as in Fig. 1. The cell gives a sustained change in firing depending on luminance ratio and the chromatic change across the edge. The pattern of response is the reverse of that of the green on-centre cell in Fig. 5. For the W–642 nm condition, the cell's firing increases in response to the chromatic field, for the W–570 nm the response is weak, whereas for W–460 nm the cell fires in response to the white field. *B*, response plots as in Fig. 5. Again, for W–642 nm and W–460 nm there is no indication of a minimum close to a ratio of one.

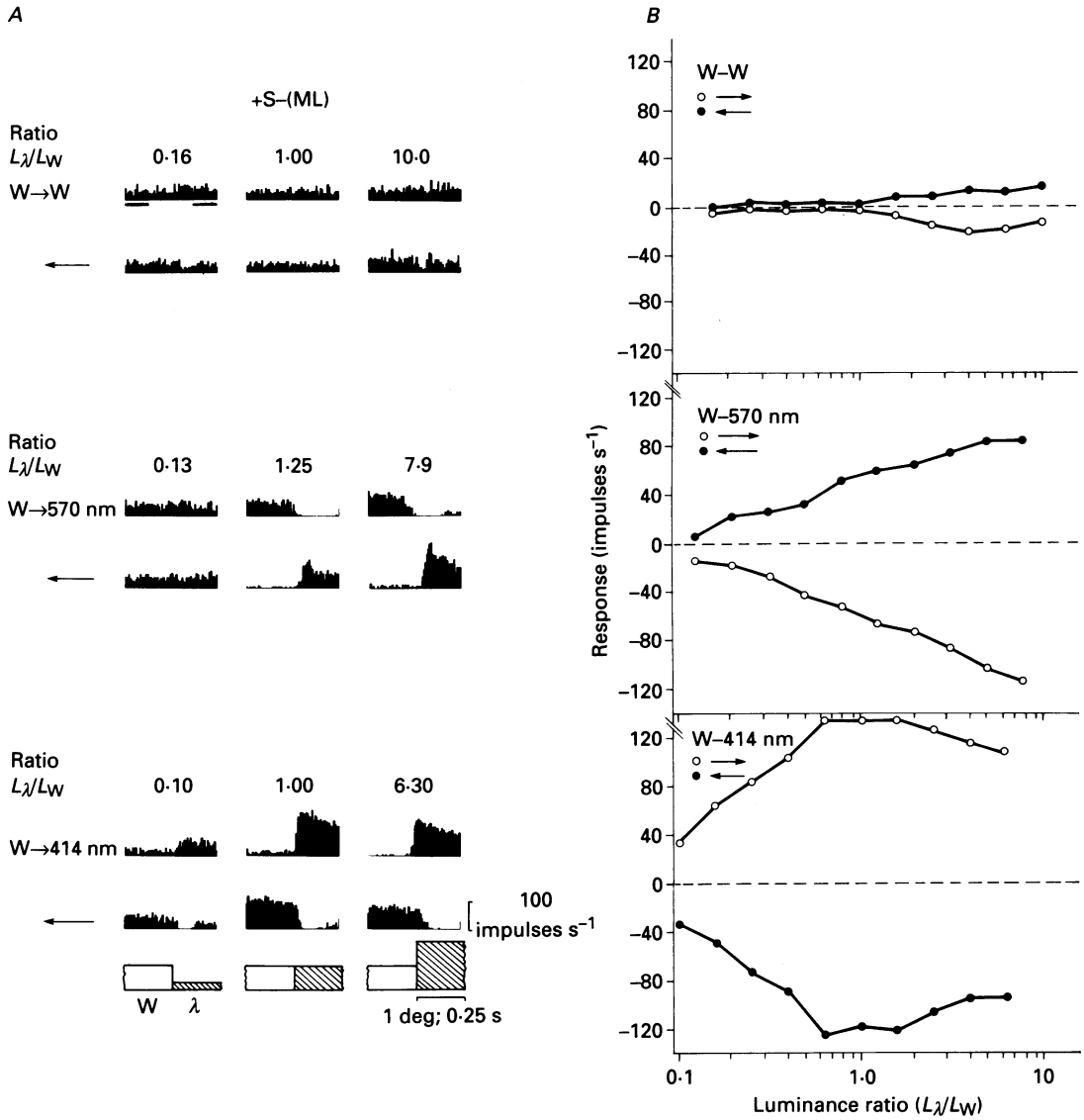

Fig. 7. *A*, responses of a blue on-centre cell to moving borders as in Fig. 1. The cell gives a sustained change in firing depending on luminance ratio and the chromatic change across the edge. For the achromatic condition, the cell's response is weak, but for W–570 nm the response is vigorous, the cell firing in response to the white field. For W–414 nm there is a vigorous response to the 414 nm field. *B*, response plots as in Fig. 5. For W–570 nm, a vigorous response is present. This is to be expected from a cell with S-cone input.

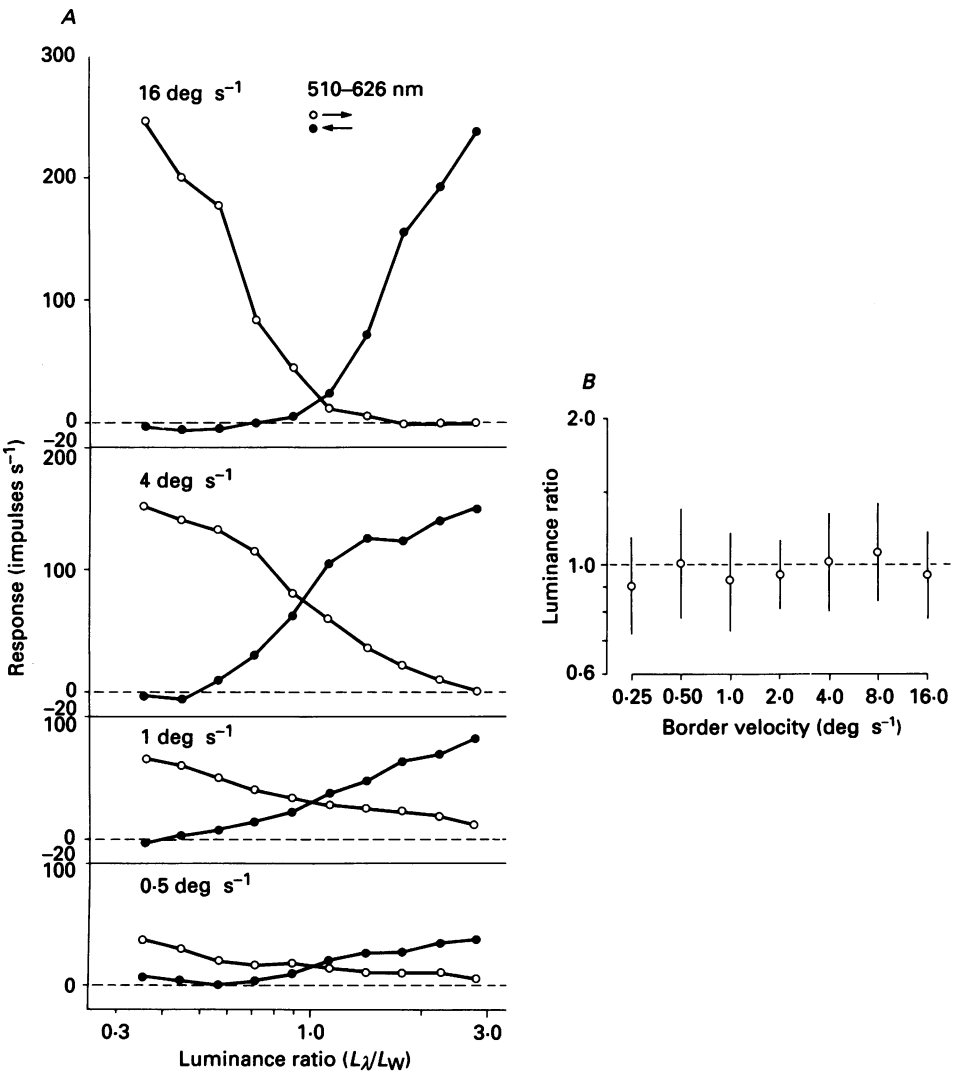

Fig. 8. *A*, responses of a phasic on-centre cell at different velocities of edge movement, using the same format as in Fig. 3. A 510–626 nm edge was used. Response amplitude (and also residual response) is dependent on velocity but in all cases the curves intersect close to a ratio of one. *B*, means and standard deviations for seven cells of deviations from the luminosity function (measured from curves as in *A*) as a function of movement speed. No systematic trend is apparent. The size of standard deviation reflects systematic deviations from the luminosity function from cell to cell, rather than systematic trends with velocity in individual cells.

upper left histograms in Figs 5–7. This would neglect any sharp transient response as the border passes across the field, but such transients were seldom observed except at high luminance ratios. This may be verified by inspection of Figs 5–7.

Responses so measured are plotted against luminance ratio in Fig. 5*B*, for the green on-centre cell. Note that the abscissa is compressed by a factor of two in

comparison with Fig. 3. To the 642 nm–white border, the cell's rate of discharge is increased when the white side of the border is over the receptive field, while to the 460 nm–white border, the chromatic field evokes the higher discharge rate. Around a luminance ratio of one, the cell's firing rate does not change rapidly as this ratio is altered. An analysis of a red on-centre cell is shown in Fig. 6. The behaviour seen is opposite to that of the green on-centre cell, i.e. the cell's discharge rate was increased by the 642 nm field and decreased by the 460 nm field.

The curves for the 570 nm–white border were very similar to those obtained with an achromatic border, as expected for a cell without S-cone input. For an achromatic border, much weaker responses to a given achromatic contrast were observed than in phasic cells, as predicted from the difference in achromatic contrast sensitivity of these two cell groups (Kaplan & Shapley, 1982; Hicks *et al.* 1983; Derrington & Lennie, 1984; Lee *et al.* 1989*b*). To evoke a 10 impulses s^{-1} change in firing rate, on average 29·9% luminance contrast was required for tonic cells ($n = 15$), compared with 5·6% for phasic cells ($n = 29$, on- and off-centre cells combined).

In the case of blue on-centre cells, a different pattern was present (Fig. 7). An extremely vigorous response to a 414 nm–white border can be seen, and there is also a vigorous response to a 570 nm–white border at equal luminance, the higher discharge rate being to the white side of the border. Thus, cells with S-cone input provide a signal at borders between tritanopic pairs of lights. The cell's response to achromatic contrast is weak. It is of interest that the response to the 570 nm–white border is sharply defined, although psychophysical evidence suggests that visual resolution of the S-cone system (and by implication 'sharpness' of edge responses) is poor. The other blue on-centre cell studied extensively also showed such a sharp change in discharge rate.

The response of twenty-four tonic cells to different border conditions was studied. The general patterns of response observed always resembled those in Figs 5–7. The curves shown resemble those found in a successive contrast situation, when chromatic stimuli abruptly replace a white adaptation field (Lee, Valberg, Tigwell & Tryti, 1987; Valberg *et al.* 1987). For example, in these earlier experiments, a red on-centre cell responded to replacement of an adaptation field with a 642 nm stimulus even when the luminance of the 642 nm field was much lower than that of the field. Responses then increased rapidly with luminance ratio to saturate at or before a ratio of one. This resembles the curve shown in Fig. 6.

It is not immediately obvious how such responses as seen in Figs 5–7 could correlate with, or be used as a substrate for, the setting of minimal border distinctness by a human observer. However, it could be argued that a combination of signals from different tonic cells with L- and M-cone inputs could somehow provide a suitable signal. We believe there are strong arguments against this possibility, and these are mustered in the Discussion.

The effect of stimulus velocity

On fixation of a small target, slow drifts of the eyes are on average a few minutes of arc in extent and several minutes of arc per second in speed (see Hallett, 1986, for review). Taking into account the increase in receptive field size with eccentricity, we chose a movement amplitude of 1 deg, and a movement speed of 4 deg s^{-1}. However,

if phasic cells underlie the setting of a minimally distinct border, it is necessary that such minima as seen in the curves of Fig. 3 be independent of drift velocity.

Spectral sensitivity of three phasic cells was tested at two or three different speeds. Differences were small. For six cells, responses to a red–green (510–626 nm) border were measured at seven speeds from 0·25 to 16 deg s^{-1}, and representative curves for one cell are shown in Fig. 8*A*. The amplitude of the response is dependent on temporal frequency and a marked residual response was present. Nevertheless, the curve intersection always occurs close to a luminance ratio of one. For the seven cells, in Fig. 8*B* mean deviation from equal luminance at the minima is plotted as a function of temporal frequency. No systematic trend is present. Standard deviations are *ca* 0·2 log units, but this reflected systematic differences in spectral sensitivity from cell to cell, rather than any systematic changes in individual cells with stimulus velocity.

If minimization of a signal derived from the phasic, M-pathway underlies the minimally distinct border task, then this minimization can be carried out independent of image velocity across the retina. Since drift movements during fixation presumably occur at any angle relative to a static border position, this invariance is a necessary requirement of any such underlying mechanism.

Tests of photometric linearity

It is basic to photometry that linearity laws be obeyed. The laws of transitivity, proportionality and additivity were tested on phasic cells and found to hold.

Transitivity refers to the requirement that if a light A is matched with B, and A with C, then B and C should also form a match. This held for phasic cells. We have shown that when different monochromatic lights are tested against a white reference light, minima occur close to a luminance ratio of one. When two monochromatic wavelengths form the border (Fig. 8), minima also occur close to a ratio of one. For nine cells a large variety of combinations of different wavelengths were tested. Although the residual response varied according to the particular wavelengths used, in every case minimum response occurred close to equal luminance. Thus, transitivity is displayed by phasic cell border responses.

Proportionality means that if lights A and B form a match, then αA and αB also do so, α being a constant of proportionality. We tested four cells at different retinal illuminances with a red–green border, and results from two of them are shown in Fig. 9. In A, curves are shown for four illuminance levels. At 25, 80 and 800 td, minima are apparent close to a ratio of one, with a substantial residual response being present, as in Fig. 8. At 8 td, the minimum has shifted to the right, indicating a decreased sensitivity to 642 nm relative to 510 nm. This can also be seen in the cell of Fig. 9*B*, and similar results were found in the other two cells. Rod intrusion becomes apparent in phasic cells recorded from the magnocellular layers of the geniculate nucleus at about 20 td (Virsu & Lee, 1983; Virsu, Lee & Creutzfeldt, 1987), and it is likely that the shift at 8 td is due to rod intrusion.

Proportionality is present psychophysically over a wide range of illuminances down to less than 10 td (Ingling *et al.* 1978). However, with foveal viewing of the border, rod intrusion at 8 td may be less likely, although some small deviations from proportionality found by Ingling *et al.* (1978) may be attributable thereto. In any

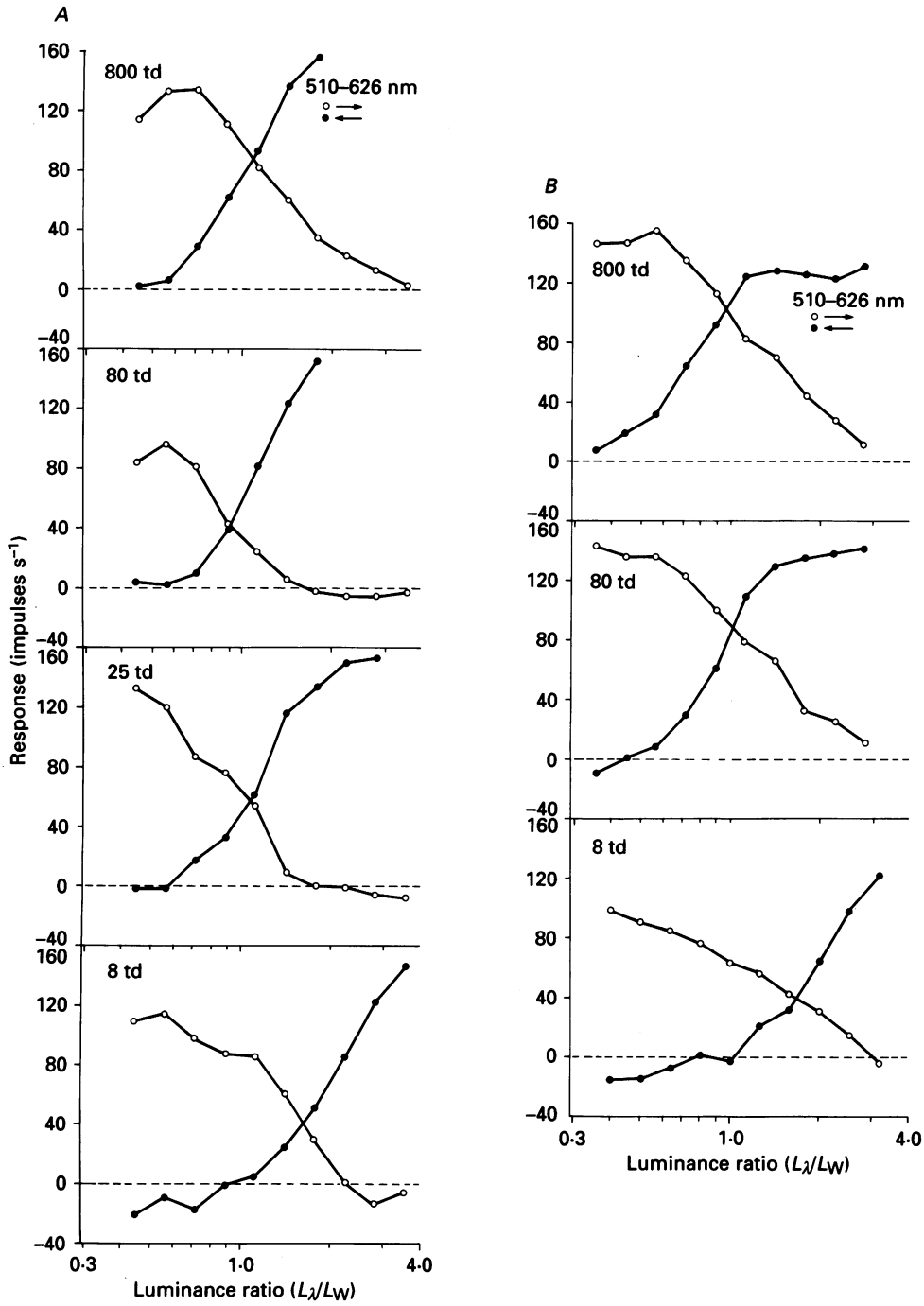

Fig. 9. Curves measured at different retinal illuminances for two cells, for a 510–626 nm edge. Format as in Fig. 3. Curve intersections occur close to a ratio of one, except at 8 td. We attribute this deviation to rod intrusion. At 25 td and above, the curves intersect close to a ratio of one.

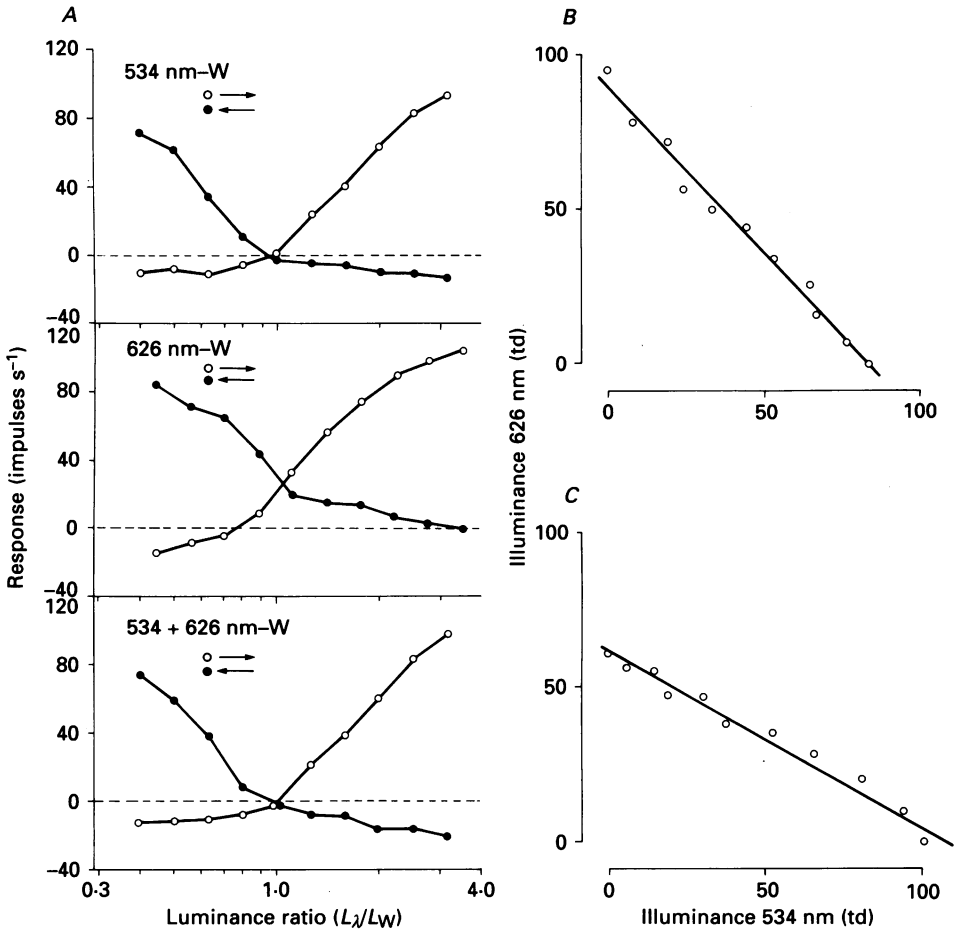

Fig. 10. *A*, curves demonstrating a test of additivity on a phasic cell. Format as in Fig. 3. For the 534 nm–W and the 626 nm–W condition, curve intersections occur close to a ratio of one. With a mixture of the two wavelengths (half-and-half in terms of the 10 deg luminosity function), the curve intersection also occurs close to a ratio of one. *B* and *C*, a more extensive test of additivity on two phasic cells, 534 and 626 nm being mixed in various proportions and apposed to a white field. The troland values at the curve intersections are plotted against one another for the two wavelengths. Additive behaviour is indicated by the linear relationship apparent. Least-squares regression lines are shown. For the cell in *B*, the slope of the regression line is −1·06, from which may be deduced the cell had a sensitivity very close to the luminosity function. In *C*, the slope is less than unity (−0·56), indicating that the cell was more sensitive to long wavelengths than expected from the luminosity function.

event, at retinal illuminances above 20 td proportionality would appear to hold for phasic ganglion cells.

Additivity implies, for example, that if light *A* is matched with *B* and *C*, it will also match $B/2+C/2$. A psychophysical demonstration of additivity was one of the first

indications that the minimally distinct border task could be viewed as a photometric technique (Boynton & Kaiser, 1968).

Boynton & Kaiser (1968) tested additivity with mixtures of red and green lights making a border with a white reference field. A similar experiment was performed on nine phasic cells. We mixed 534 and 626 nm light in different proportions, and measured cells' responses. An example of results from one cell is shown in Fig. 10*A*. Two sets of curves were obtained with each wavelength alone, and the third set with them mixed in equal proportion by luminance. A minimum can be seen close to equal luminance in all three graphs, indicating that additivity held.

For seven cells we tested a number of mixtures. We calculated the amounts of red and green (measured in trolands) at the cells' minima. Results from two cells are plotted in Fig. 10*B* and *C*. For the cell in *B*, spectral sensitivity was very close to the luminosity function; with red or green alone, a similar troland value was found at the minimal response. The cell in *C* was somewhat more sensitive to long wavelengths and required fewer trolands of red than of green light to achieve the minimum (see below). However, with the different combinations a linear relationship describes the data points well in both cases, indicating that additivity was present. The results in Fig. 10*B* and *C* provide strong evidence that photometric additivity is a property of phasic cells' responses.

In summary, transitivity, proportionality and additivity are demonstrable in the responses of cells of the phasic M-pathway. This is consistent with performance in the minimally distinct border task being dependent on this system.

Variability in spectral sensitivity between phasic cells

Variability in cells' spectral sensitivity was greater with lights towards the spectral extremes than in mid-spectrum. We noted that an increased sensitivity to long wavelengths was usually associated with decreased sensitivity to short wavelengths, and *vice versa*. This was not obviously related to retinal eccentricity; such variability was observed between successively recorded cells. At equal luminance, this variability would contribute to the residual signal from the population of phasic cells, adding to the signal arising from residual responses of individual cells.

One source of this variability may lie in relative strengths of M- and L-cone inputs to individual cells; it is generally assumed that the luminosity function is made up of a sum of these cone types (see Boynton, 1979). We attempted to determine how far variability between cells could be described by variability in relative weights of the M- and L-cones.

If for a given cell the response is minimal when a white field of luminance L_W borders a chromatic field of wavelength λ and luminance L_λ, then

$$(aR_\lambda + bG_\lambda) L_\lambda = (aR_W + bG_W) L_W, \tag{1}$$

or

$$\frac{L_W}{L_\lambda} = \frac{(aR_\lambda + bG_\lambda)}{(aR_W + bG_W)}, \tag{2}$$

where R_W, G_W and R_λ, G_λ are the L- and M-cone excitations generated by unit luminance for the white and chromatic lights respectively, a and b represent input

weights of the L- and M-cones to the cell. If R_λ and G_λ are normalized such that $R_W = G_W = 1$, becoming R' and G', then

$$\frac{L_W}{L_\lambda} = \frac{(a/bR' + G')}{(a/b+1)}. \tag{3}$$

a/b is the ratio of L- to M-cone weights. Following the normalization, $R_W + G_W = R' + G' = 2$ so that

$$\frac{L_W}{L_\lambda} = \frac{(a/b-1)}{(a/b+1)}R' + \frac{2}{(a/b+1)}. \tag{4}$$

In so far as systematic deviations from the luminosity function in a particular cell can be accounted for by variation in L/M cone weighting, then the ratio L_W/L_λ (the reciprocal of the values derived as in Fig. 3), at which the cell's response is minimal, should be linearly related to the excitation of the L-cone, R', normalized to L-cone excitation by the white reference light. Relative cone excitations generated by the different interference filters were calculated as described in Valberg *et al.* (1987). The measured ratio L_W/L_λ was plotted against R' for the different wavelengths tested for the twenty-two cells for which spectral sensitivity data were available. Examples of three successively recorded cells are shown in Fig. 11*A–C*.

In *A* is shown one cell in which spectral sensitivity was similar to the luminosity function while in *B* and *C* are shown two extreme examples in which the L- or M-cone appeared to dominate the cells' sensitivity. In *B* and *C*, significant correlations between R' and L_W/L_λ were present. Straight-line relationships fitted the data satisfactorily, consistent with a constant ratio a/b, or constant cone weights, when different wavelengths were tested. A positive slope indicates $a/b > 1$, and therefore that the L-cone input is dominant. A line parallel to the x-axis indicates $a = b$, and that a cell's spectral sensitivity deviated little from the luminosity function. A negative slope $a/b < 1$ indicates that the M-cone is dominant.

For twenty of the twenty-two cells, straight-line relationships as in *A–C* appeared to hold. The ratio a/b was calculated for each cell and its distribution is shown in Fig. 11*D*. The hatched bars indicate those cells for which the correlation coefficient reached the 5% significance level. For nine cells, the ratio a/b fell between 0·67 and 1·5, which generally did not represent a systematic deviation from V_λ sensitivity. All the other thirteen cells showed systematic deviations from V_λ sensitivity, which could be described on the basis of the weights shown. It should be stressed that the ratio a/b provides a *relative* measure of the ratio of L- to M-cone input, since values are normalized to cone excitations generated by the white field. The luminosity function itself is considered to be made up of contributions from the L- and M-cones in a ratio of 2:1 (Walraven, 1974), but this factor is not taken into account here.

Derrington *et al.* (1984) also reported variability in relative cone weights to phasic cells of the magnocellular layers of the geniculate nucleus. However, it is difficult to directly compare our results to theirs, since their analysis was based on fitting suprathreshold responses to a linear model incorporating inputs from all three cone types. We found no evidence for a contribution from S-cones. However, the ranges of M- to L-cone weightings found appear comparable.

From Fig. 11 it would appear that although on average phasic ganglion cell

spectral sensitivity corresponds closely to the luminosity function, an inter-cell variability is present, and that this is systematically related to wavelength. It is not clear if this variability is due to differences in the number of cones providing input, or due to differences in gain at the synapses between cone and ganglion cell. It is also

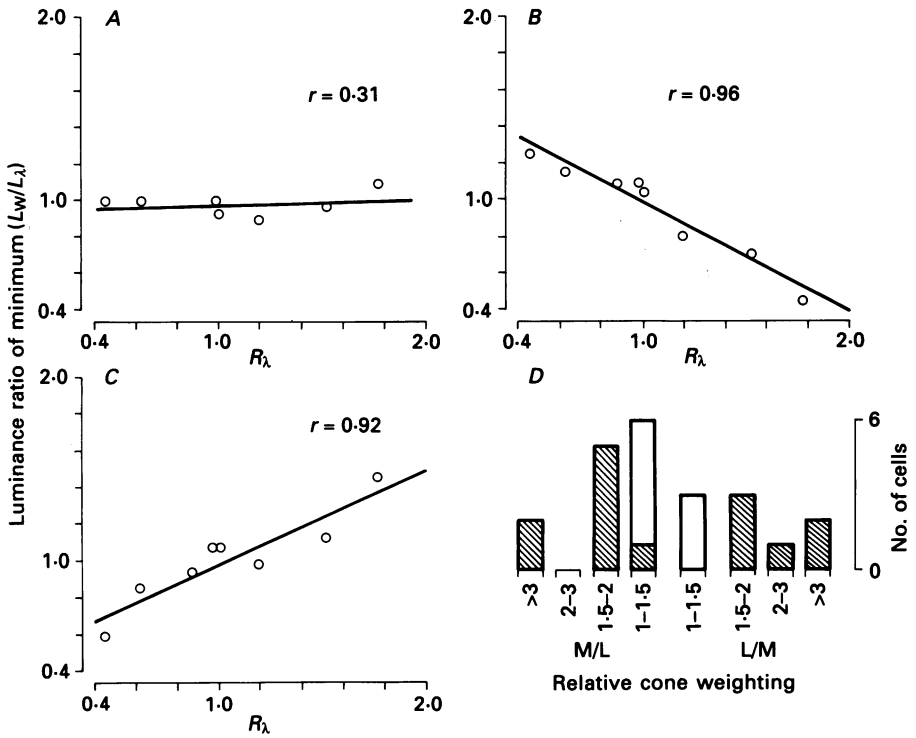

Fig. 11. An analysis of inter-cell variability in spectral sensitivity in terms of possible variability in cone weighting. *A–C*, for borders of various wavelengths with white, deviation from the luminosity function as measured from curve intersections (note linear axis) plotted as a function of relative L-cone excitation, as derived in the text. *A*, little significant deviation from the luminosity function. *B* and *C*, examples of the most extreme deviations observed. From the slopes of such curves we estimated the relative cone weightings necessary to produce such deviations. The distribution of these cone weightings is shown in *D*. The hatched cells are those for which correlation coefficients reached the 5% significance level.

unknown how far centre and surround mechanisms each contribute to this variability, and how far any non-linearity, such as is manifest in residual responses, may also play a role. Whatever its origin, the variability may be of functional significance in that any equal-luminance pattern will generate a response in some members of the phasic cell population, over and above the residual responses of individual cells.

Residual responses at equal luminance

Every phasic cell gave a residual response to both directions of border movement with some combinations of lights on either side of the border, and we argue above

that this is most unlikely to arise from an optical artifact. In Fig. 12 are plotted residual responses (the value q derived from curves such as those in Fig. 3) for different wavelengths when tested against the white reference field. Representative samples of on- and off-centre cells are shown. There is substantial variability between

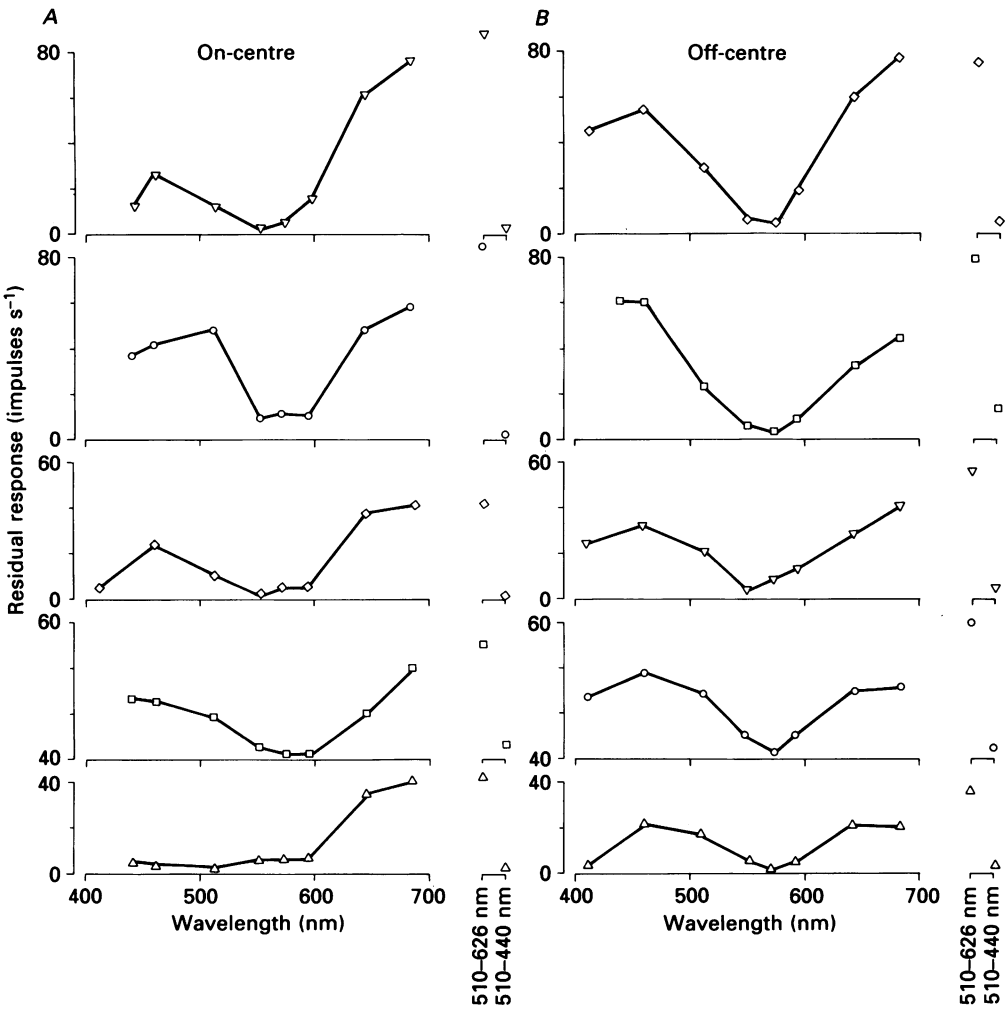

Fig. 12. Amplitude of residual responses for five on-centre and five off-centre cells, derived from the measures q in Fig. 3. Amplitudes are shown for different wavelengths forming a border with a white field, and for two additional combinations (510–626 nm and 510–440 nm). The amplitude of the residual response varies from cell to cell, but the general shape of the relationship is similar from cell to cell. With 510–626 nm, the residual response is always large; with 510–440 nm it is always small.

cells in the amplitude of residual responses, and there is some variability in the relative amplitudes of residual responses at short *versus* long wavelengths. However, the general shapes of the curves are similar from cell to cell. Also shown are residual responses to green–red (510 *versus* 626 nm) and tritanopic blue–green (440 *versus* 510 nm) borders. In every instance, the former combination gives a large residual

response, and the latter almost no residual response (consistent with a lack of S-cone input).

With heterochromatic flicker, at equal luminance phasic cells give rise to a frequency-doubled response, which can be attributed to a non-linearity of M- and L-

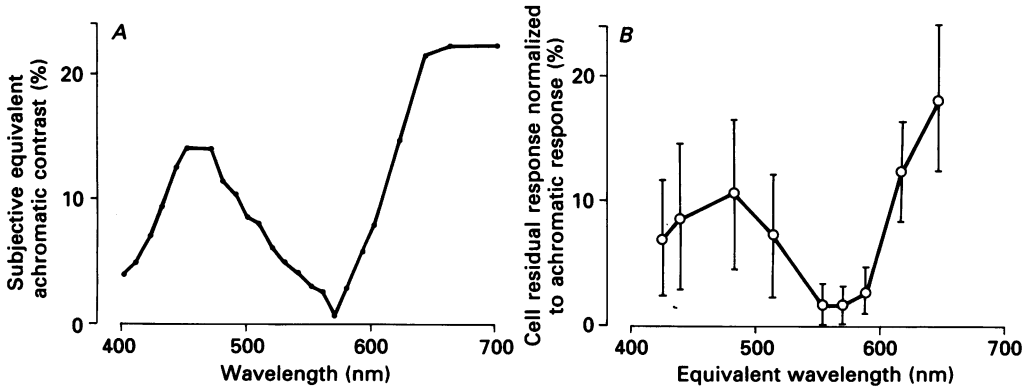

Fig. 13. *A*, residual distinctness, estimated by a human observer when different monochromatic lights bordered onto an isoluminant white field, plotted as a function of wavelength, scaled relative to distinctness of an achromatic contrast. In *B*, the data points show residual responses (mean, S.D., $n = 21$) of phasic cells, scaled for each individual cell relative to its response to an achromatic contrast of 20%. Because our filters were not monochromatic, it was necessary to calculate the equivalent wavelength producing the same ratio of M–L cone excitations to make the comparison. Cell responses resemble psychophysical data in both shape of the function and its absolute magnitude.

cone summation (Lee *et al.* 1989*a*). The amplitude of this frequency-doubled response was maximal for long wavelengths alternated with a white reference, all but absent for 570 nm, and increasing again towards the short-wavelength end of the spectrum. In addition, the frequency-doubled response with heterochromatic flicker was vigorous with red–green flickering lights, and absent for blue–green flicker, these latter lights lying along a tritanopic confusion line. The results in Fig. 12 thus resemble these earlier results.

The significance of these residual responses lies in their relation to residual distinctness assessed by human observers after they have set heterochromatic borders to a minimum (see Boynton, 1978, for review). This residual distinctness is high for long wavelengths tested against a white field, very low near 570 nm, increases towards 450 nm and then decreases once more. Residual distinctness has been quantified in terms of the equivalent achromatic contrast, either by direct matching or by a scaling technique (Ward & Boynton, 1974). We had available to us each cell's response to an achromatic border, and so could normalize each cell's residual responses to that cell's response to an achromatic contrast. We can then compare the psychophysical and physiological data. This comparison is shown in Fig. 13, psychophysical data being taken from Tansley (cited in Boynton, 1978; Valberg & Tansley, 1977). Since our interference filters were not monochromatic, we have calculated the monochromatic wavelength which would produce the same M/L cone ratio, and plotted the physiological data as a function of these equivalent wavelengths.

The mean residual responses of phasic cells resemble the psychophysical data in that they bear a similar relation to wavelength and are of comparable amplitude, in terms of equivalent achromatic contrast. Cell standard deviations are substantial, due to the variability in residual response seen in Fig. 12. It is of note that in both psychophysical and physiological data, there is a *decrease* in residual signal at very short wavelengths, indicating it to be related only to the differential activity of the L- and M-cones. Thus, phasic cells not only provide a signal which can mediate performance on the minimally distinct border task, but they also provide a signal which may account for residual distinctness perceived after a subject has carried out the minimization.

DISCUSSION

Minimization of the distinctness of a border between two differently coloured fields was first proposed as a photometric method by Frauenhofer (1824; Pease, 1987), who compared different sections of a prism spectrum with a reference light. However, when the photopic luminosity function was defined in 1924, it was largely on the basis of results from an alternative method, heterochromatic flicker photometry (see Kaiser, 1973). In this latter technique, two lights are rapidly alternated, and the subject is required to adjust their relative intensities until the sensation of flicker is minimized or abolished. Human spectral sensitivity curves obtained by the two methods are very similar, whereas those delivered by other techniques (e.g. heterochromatic brightness matching) are substantially different (Wagner & Boynton, 1972).

The minimally distinct border technique has acquired new relevance due to recent interest in human psychophysical performance with equal-luminance patterns. Liebmann (1927) was the first to stress the peculiar perceptual characteristics of such borders, noting that in the 'critical zone', borders appeared to 'melt' or 'flicker', and figure–ground relationships were lost. Recent experiments have focused on degradation of performance with equal-luminance patterns specific to particular tasks (Lu & Fender, 1972; Cavanagh, Tyler & Favreau, 1984). Although there has been speculation as to the relative roles of the M- and P-pathways in such tasks (Livingstone & Hubel, 1987), direct electrophysiological evidence has been lacking.

It is relevant to ask if our classification of ganglion cells reliably distinguished those belonging to the M- and P-pathways. We are confident this was the case. Firstly, although early reports (Wiesel & Hubel, 1966) noted broad-band cells in the parvocellular layers of the geniculate, at photopic levels almost all these cells respond optimally to modulation close to or in the equal-luminance plane (Derrington *et al.* 1984; Lee *et al.* 1987), indicating cone and spectral opponency. This behaviour is consistent with responses to equal-luminance borders of the cells we identified as tonic. Secondly, we used criteria for cell classification very similar to those we have used previously to distinguish cells of the parvocellular and magnocellular layers of the geniculate nucleus.

We have recently shown that heterochromatic flicker photometry has as a physiological substrate the ganglion cells of the phasic M-pathway (Lee *et al.* 1988). The evidence presented here strongly suggests that this pathway also underlies the

minimally distinct border task, as might be expected from the similar psychophysical characteristics of these methods. From cell responses such as those in Fig. 3, it is readily possible to devise a scheme whereby minimization of phasic cell activity could serve as a substrate for human performance on this task. The spectral sensitivity curve so defined (Fig. 4) is very similar to the human luminosity function, and linear properties such as additivity, transitivity and proportionality are also demonstrable. For additivity, each individual cell displayed this property, although there was some variability in spectral sensitivity from cell to cell (i.e. variability in the slopes in graphs such as those in Fig. 10*B* and *C*). One would nevertheless expect additivity from the cell population as a whole. Lastly, minimization of phasic cell responses is independent of stimulus velocity across the retina. This is analogous to the independence of temporal frequency shown by phasic cell minima in heterochromatic flicker photometry (Lee *et al.* 1988).

The presence of residual responses makes the comparison between physiology and psychophysics not quite as straightforward as in heterochromatic flicker photometry. For the flicker task, the first harmonic component of both on- and off-cells' responses went through a minimum close to equal luminance, although a small residual, frequency-doubled component could be observed at equal luminance. This differs from the situation with border responses. Both on- and off-cells gave residual responses at equal luminance. Consider, then, the introduction of a luminance decrement to the border. On-centre cells would then respond less vigorously and off-centre cells more vigorously. It is thus necessary to postulate a mechanism *comparing* signals from on- and off-centre cells. Such a comparison would be carried out by cortical cells with even-symmetric receptive fields (Movshon, Thompson & Tolhurst, 1978) derived from on- and off-centre input. Such a receptive field structure is of course a zero-crossing detector. Alternative central neuronal mechanisms could be readily derived, however.

We conclude that the phasic M-pathway has all the characteristics necessary to support performance on the minimum distinct border technique. We now discuss if similar characteristics could be derived from responses of tonic cells.

Derivation of an achromatic signal from tonic cells?

Tonic cells with only M- and L-cone inputs did not respond to a moving border at equal luminance when it was made up of pairs of lights lying along a tritanopic confusion line. Thus, their behaviour under this condition resembled that of phasic cells. However, as expected from their low achromatic contrast sensitivity (Kaplan & Shapley, 1982; Hicks *et al.* 1983), with such pairs of lights tonic cells were relatively insensitive to changes in luminance ratio away from equal luminance, and thus they would seem poorly suited to aid in setting minimal distinctness. Phasic cells, with their comparatively higher contrast sensitivity, would provide a more sensitive mechanism for this purpose.

Of more interest is a border made up of red and green lights. We have shown in Figs 8 and 9 that phasic cells could support psychophysical performance with this condition. We attempted to see if some combination of tonic cells could also provide an adequate substrate for psychophysical performance. At first sight, this seems unlikely. Figure 14 shows responses of four tonic cells (two red on-centre, two green

on-centre) plotted against luminance ratio across a red–green border. All cells gave a vigorous, almost saturated, response at equal luminance, so that many tonic cells' responses did not change significantly as luminance ratio varied around a ratio of one; this is especially apparent in the green on-centre cells of Fig. 14. Such change would be necessary to derive from tonic cells' information relevant for minimally distinct border settings.

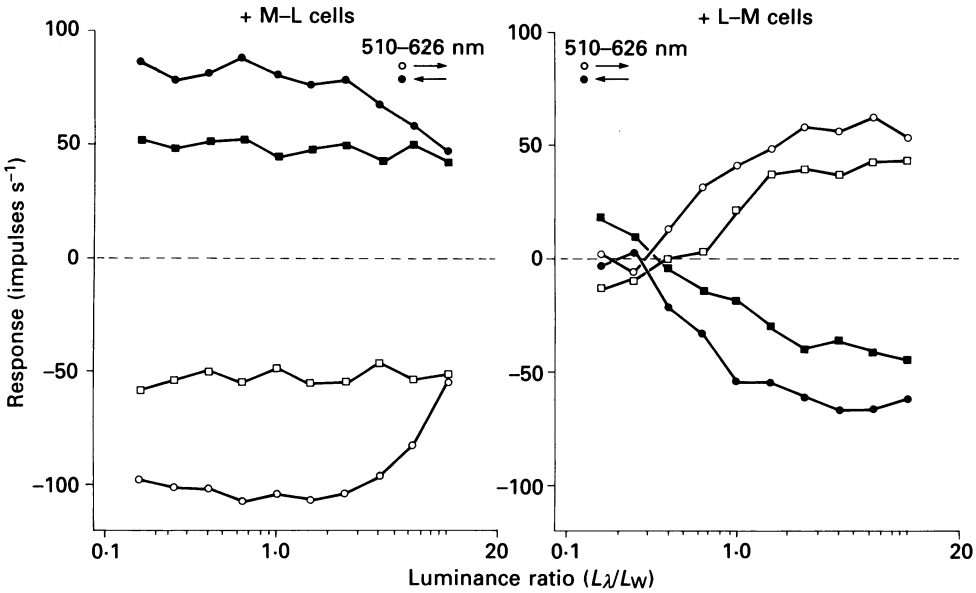

Fig. 14. Response plots as in Fig. 5*B*, for two green on-centre and two red on-centre cells for a 510–626 nm edge. It is difficult to derive a signal from this population of cells which might underlie minimization of border distinctness.

Nevertheless, it might be argued that other tonic cells' output could be combined to deliver a relevant signal. We attempted to construct such a model. Although for a given pair of lights a satisfactory weighting of tonic cell inputs might be found, a different pair would require a change in such weightings. Such a scheme would not seem realistic.

It has been proposed that an achromatic channel could be derived from tonic, opponent cells by spatiotemporal filtering of their signal and that the form of these cells' responses should be taken into consideration (Ingling & Martinez, 1983, 1985). Such response shapes as they predicted were observed. For example, with red–green equal-luminance edges, a change in firing rate occurred without any transient 'overshoot'. This is because centre and surround mechanisms act synergistically in evoking responses to such an edge. With a substantial luminance imbalance, a transient 'overshoot' component sometimes became apparent, probably because of lateral inhibition arising from centre–surround antagonism. Ingling & Martinez (1983, 1985) proposed that extraction of such components could lead to an achromatic border response from the tonic cell population. However, it is unlikely

such a mechanism would be useful for the minimally distinct border task. With a red–green border, as the luminance ratio is changed away from equal luminance, centre–surround antagonism can only occur after the luminance ratio has altered to such an extent to exceed the ratio at which silent substitution occurs. Depending on the wavelengths used, this requires a considerable luminance imbalance, corresponding with the red–green borders we used to at least 40% luminance contrast. Standard deviations when subjects make minimally distinct border settings are usually only a few per cent (Kaiser, 1971). Secondly, such a mechanism would not function if the edge were blurred, since spatial antagonism would no longer be pronounced. Psychophysically, the task is still possible with blurred edges (Lindsey & Teller, 1989), and phasic cell minima still occurred close to equal luminance.

It should be stressed that although an achromatic channel suitable for use in the minimally distinct border task cannot be derived from tonic cells, construction of a brightness dimension in a colour scaling system can be derived from their responses (Valberg, Seim, Lee & Tryti, 1986; Valberg *et al.* 1987).

Significance of residual responses

A response of phasic cells of the M-pathway to an equal-luminance colour exchange was first reported by Schiller & Colby (1983). It is observed as a frequency-doubled response with heterochromatic flicker, and can be ascribed to a non-linearity of M- and L-cone summation, which probably originates in the surround mechanism of phasic cells (Lee *et al.* 1989*a*). With flicker, the amplitude of the frequency-doubled response is directly related to the difference in excitation of M- and L-cones. The residual responses of phasic ganglion cells to moving equal-luminance borders appear to be another manifestation of this non-linearity.

With an equal-luminance border, the amplitude of residual response from the population of phasic cells will depend not only on residual responses in individual cells, but also on variability in spectral sensitivity between different cells. We have quantified this variation for our cell sample in Fig. 11 on the basis of variability in cone weighting. A residual signal from this source will vary with wavelength, being zero with tritanopic pairs of lights and high with, for example, a red–green border. Thus, a direct relationship with the M- and L-cone difference signal would again be expected.

From the cell sample in Fig. 11*D* and using curves such as those in Fig. 3, we estimated the relative sizes of residual signals at equal luminance due to variation in spectral sensitivity among the population of phasic cells, in comparison with the residual response of individual phasic cells shown in Fig. 13. The latter was about twice the size of the former. Although it is probably unjustified to assume that the residual response of the population can be predicted by simple addition of these two effects, it would seem likely that both could be of behavioural significance.

The significance of the residual response lies in its relevance to residual distinctness measured psychophysically. Residual distinctness is dependent on the colours on either side of the border (Liebmann, 1927; Kaiser *et al.* 1971). The |L−M| cone excitation difference, or tritanopic purity, is the critical determinant of residual distinctness, not only for different wavelengths measured against white but for all

other possible combinations of colours (Valberg & Tansley, 1977; Tansley & Valberg, 1979). For pairs of lights for which |L−M| is zero, i.e. tritanopic pairs, residual distinctness is extremely low (Tansley & Boynton, 1976).

Psychophysical residual distinctness can be expressed in terms of equivalent achromatic contrast. Residual responses of phasic cells were normalized to their responses to achromatic contrast. For the two sets of data, both the shape of the curve and the amount of the equivalent achromatic contrast were comparable. Given the large variability in the magnitude of residual distinctness ratings of human subjects (although all show the same-shaped curve; Valberg & Tansley, 1977), and in phasic cell residual responses, the significance of the resemblance between the physiological and psychophysical data in Fig. 13 should not be overestimated. Nevertheless, it is clear that the residual signal from phasic cells could make a major contribution to residual border distinctness.

Implications for form perception

We conclude that psychophysical minimization of border distinctness relies on minimization of phasic M-pathway activity and that these cells provide a signal which is correlated with residual distinctness seen by subjects after they have set a minimum. Recent interest in the role of chromatic and achromatic pathways in pattern perception has been stimulated by the recognition that performance on many psychophysical tasks is degraded with equal-luminance patterns. This is so for motion perception (Cavanagh *et al.* 1984), vernier acuity (Morgan & Aiba, 1984) and fine stereopsis (Lu & Fender, 1972), amongst other tasks. All these deficits can be interpreted in terms of a failure in border perception due to poor responses in the phasic M-pathway. Reintroduction of a small degree of luminance contrast immediately restores performance. This is relatively difficult to account for with some achromatic mechanism based on tonic cell activity, but is a natural consequence of behaviour of phasic cells as shown in Fig. 3.

Ability to perform the above tasks is seldom wholly abolished at equal luminance. We propose at least some of this 'residual performance' derives from residual responses of phasic cells. The difference in stereopsis with equal-luminance patterns depending on the size of the elements (Lu & Fender, 1972; Comerford, 1974) would be consistent with this interpretation. With fine patterns, residual responses of phasic cells would be small since their centres appear to sum cone signals linearly (Lee *et al.* 1989*a*). With coarse patterns, residual responses would be available for stereopsis.

We would predict that 'residual performance' with equal-luminance patterns should resemble results from the minimally distinct border task. It should be directly related to the |L−M| cone excitation difference, and should thus show a predictable dependence on the wavelength combinations used, and should be maximally equivalent to about 20% achromatic contrast.

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