J. Physiol. (1975), **251**, *pp.* 197–216
With 10 *text-figures*
Printed in Great Britain

TRICHROMATIC COLOUR OPPONENCY IN GANGLION CELLS OF THE RHESUS MONKEY RETINA

BY F. M. DE MONASTERIO, P. GOURAS AND D. J. TOLHURST*

From the Section of Neurophysiology, Laboratory of Vision Research, National Eye Institute, National Institutes of Health, Department of Health, Education and Welfare, Bethesda, Md. 20014, U.S.A.

(*Received 24 December 1974*)

SUMMARY

1. Two hundred and eleven colour-opponent ganglion cells were studied in the central 10° of the retina of the rhesus monkey, to determine the inputs which they were receiving from different cone mechanisms. Spectral-sensitivity measurements in the presence of neutral and coloured backgrounds showed that 24% of these cells appeared to receive input from all three cone mechanisms.

2. In 3% of the cells, the red-sensitive cone mechanism opposed the blue- and green-sensitive ones. In 18% of the cells, the blue-sensitive cone mechanism opposed the green- and red-sensitive ones. In 3% of the cells, the green-sensitive cone mechanism opposed the blue- and red-sensitive ones.

3. In 12% of the cells receiving opponent green- and red-sensitive cone inputs, responses from the beta-band of the red-sensitive cone mechanism could be detected and distinguished from blue-sensitive cone input.

4. All cells receiving blue-sensitive cone input appeared to be trichromatic. The retinal distribution of cells with trichromatic input and that of cells with beta-band responses seemed to parallel the availability of blue-sensitive cones in the retinal area being considered.

5. The results indicate that trichromatic interactions in the macaque visual system begin in the retina.

INTRODUCTION

A large number of cells in the visual system of the rhesus monkey show colour-opponent responses; these cells are excited by some wave-lengths and are inhibited by others. Colour-opponent cells in the retina (Gouras,

* On leave from The Physiological Laboratory, Cambridge, CB2 3EG, U.K.

1968) and lateral geniculate nucleus (Wiesel & Hubel, 1966; De Valois, 1973) have been reported to receive only dichromatic input, some cells only from green- and red-sensitive cones and other cells either from blue- and green- or from blue- and red-sensitive cones. Studies of the visual cortex (Gouras, 1970; Dow, 1974) have found cells which seem to receive trichromatic input, e.g. inhibitory input from green-sensitive cones and excitatory input from both blue- and red-sensitive cones.

The finding of a cortical trichromatic organization and of a subcortical dichromatic organization could indicate a central reorganization of the processing of colour information. This paper shows, however, that many colour-opponent ganglion cells in the rhesus monkey retina receive input from all three cone mechanisms, indicating that trichromatic interactions begin in the retina.

METHODS

These have been described in a preceding paper (De Monasterio & Gouras, 1975). Much of the evidence in this report consists of spectral threshold curves (action spectra) obtained in the presence of neutral and coloured backgrounds. In many cells, each coloured background was used at two adaptation levels. One, very intense, usually suppressed responses mediated by a given cone mechanism. The other level of adaptation was intense enough to permit the study of cone inputs, but not as strong as to eliminate the responses mediated by the cone mechanism selectively affected by the background light. Such moderately intense backgrounds were used whenever only one background adaptation level was employed, to facilitate measurements of peak sensitivities, curve shapes and normalization of action spectra in different regions of the spectrum. All threshold measurements were obtained two minutes after the introduction of a new background light. The presentation of all coloured backgrounds was preceded by a short exposure to a moderately intense white background.

Throughout this report the abbreviations B, G, R, C, Y and M stand respectively for blue, green, red, blue and green (cyan), green and red (yellow) and blue and red (magenta) cone input to the cells. The terms blue, green and red cones refer to the cone types containing the 445 nm, 535 nm and 570 $nm_{\lambda max}$ pigment, respectively. Centre–surround organization is represented as centre/surround; in those abbreviations not separated by a slant line (/), no spatial organization is implied. + and − stand respectively for excitatory and inhibitory responses.

RESULTS

Evidence for trichromatic opponent input was found in twenty-seven cells out of a sample of 211 ganglion cells with colour-opponent responses. An additional twenty-three cells were suspected of having trichromatic input, but they were not studied in enough detail to permit a thorough identification of trichromacy. Since only three types of cone appear to be present in the primate retina (Brown & Wald, 1964; Marks, Dobelle & MacNichol, 1964), only three simple opponent combinations are possible: green-magenta (GM), blue-yellow (BY) and red-cyan (RC). All three

combinations were found, the retinal distributions of the cells being shown in Table 1.

Green-magenta cells

Seven cells were suggestive of having GM input, but only five cells of this type were sufficiently studied to identify conclusively a trichromatic combination. Three cells received excitatory input from the green-cone mechanism and inhibitory input from both blue- and red-cone mechanisms.

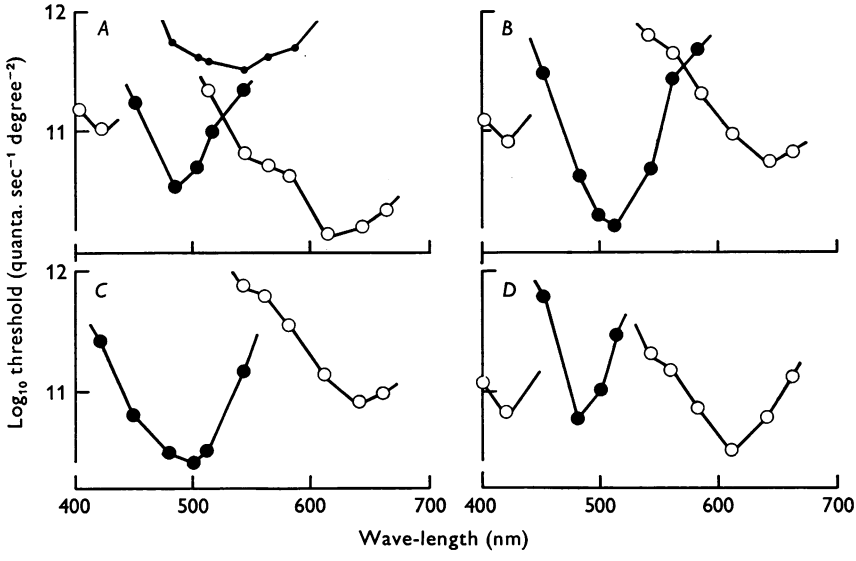

Fig. 1. Action spectra from a G − /M + cell, eccentricity 5°. *A*: data obtained with a 0·05° (small circles) and a 2° (large circles) spot, in the presence of a white background of 0·9 $\log_{10}$ cd/m². *B*: red background (11·6 $\log_{10}$ quanta sec^{-1} deg^{-2}), 2° spot. *C*: magenta background (11·8 $\log_{10}$ quanta sec^{-1} deg^{-2}), 2° spot. *D*: yellow background (11·5 $\log_{10}$ quanta sec^{-1} deg^{-2}), 2° spot. In these and following action spectra, filled symbols represent inhibitory responses and open symbols excitatory responses. Stimulus *on* for 400 msec, once per second. Adapting backgrounds continuously present.

In the other cells the opposite configuration was found. The cells had a centre–surround organization and the centre of the receptive field received input only from the green-cone mechanism, while the surround received antagonistic input from both red- and blue-cone mechanisms.

Fig. 1 shows action spectra of a G − /M + cell, obtained on a neutral and various coloured backgrounds. On a white background (Fig. 1*A*) a small spot elicited only inhibitory responses in the middle of the spectrum (small circles). A large spot, in addition to these responses, also elicited excitatory responses in the blue and red ends of the spectrum (large circles); three minima are clearly observed in the action spectrum at 420,

480 and 610 nm, suggesting three different cone inputs. To differentiate and identify each mechanism it was necessary to obtain action spectra on at least three coloured backgrounds. On a moderately intense red background (Fig. 1*B*), the sensitivity of the long wave-length mechanism was depressed, while that of the middle and short wave-length mechanisms was increased, despite the fact that the latter two mechanisms were opposing each other. On a magenta background (Fig. 1*C*), the sensitivity of the mid-

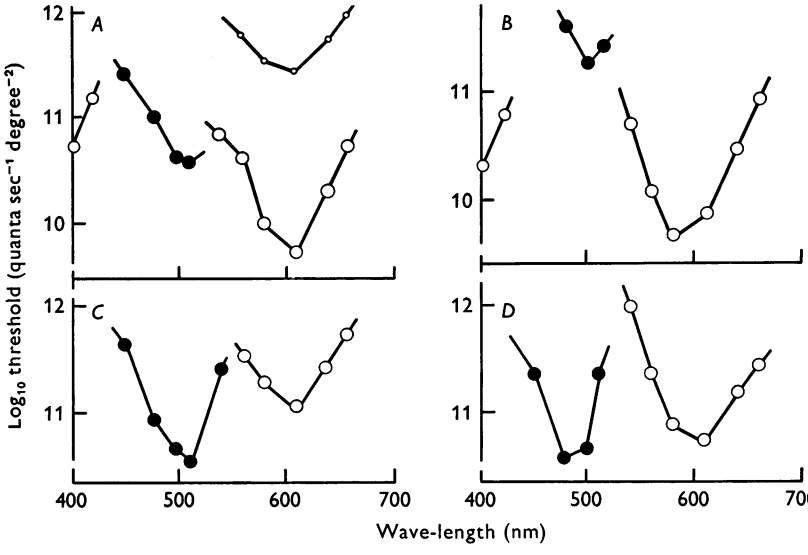

Fig. 2. Action spectra from an Rβ+/G− cell, eccentricity 1·5°. *A*: white background of 1·0 $\log_{10}$ cd/m²; small circles: spot of 0·08°; large circles: spot 2°. *B*: blue background (11·5 $\log_{10}$ quanta sec^{-1} deg^{-2}), spot 2°. *C*: red background (11·6 $\log_{10}$ quanta sec^{-1} deg^{-2}). *D*: yellow background (11·8 $\log_{10}$ quanta sec^{-1} deg^{-2}). Other parameters as in Fig. 1.

spectral mechanism was increased while that of the long and short wave-length mechanisms was decreased. Finally, on a yellow background (Fig. 1*D*), the long and mid-spectral mechanisms had lower sensitivity than on a neutral background, whereas the sensitivity of the short wave-length mechanism was increased. These results indicate that the three mechanisms represented input from blue, green and red cones.

The possibility that the short wave-length responses could be due to rod input can be excluded by the fact that these responses still remained in the presence of a sufficiently strong white background (30 cd/m²) and also on a red background on which a strong white background was superimposed; in both cases rod sensitivity should have been depressed (Gouras, 1967). The red-cone pigment has a secondary absorption peak at about 380 nm (Marks *et al.* 1964, their fig. 2), the *beta band*, which arises from the 11-cis

configuration of the chromophoric group. The presence of excitatory responses at 420 nm on a red background and their absence on a blue background (not shown in Fig. 1), allow us to eliminate the possibility that the 420 nm minimum could have been produced by beta-band absorption. In fact, all GM cells showed a noticeable increase in the sensitivity of the blue-cone mechanism on red backgrounds (see also De Monasterio & Gouras, 1975, their fig. 5; Gouras, 1970, his fig. 1).

Short wave-length responses due to beta-band absorption of the red-cone mechanism, mimicking a blue-cone input were recorded from nineteen GR cells in different parts of the retina. β-Band responses were more frequently observed in GR cells with a surround mediated by the red-cone mechanism (G/R_β), than in those mediated by the green-cone mechanism (R_β/G). Action spectra of an R_β/G cell are shown in Fig. 2. On a white background (Fig. 2*A*) a small spot elicited only excitatory responses in the 560–600 nm region; a large spot elicited mid-spectral inhibitory responses flanked by excitatory ones. Responses at 400 nm were enhanced by a blue background (Fig. 2*B*) and abolished by red and yellow backgrounds (Figs. 2*C*, *D*), the opposite to the behaviour of a GM cell. All G/R_β cells required large spots or annuli to show beta-band responses. R_β/G cells near the foveola required small spots for such responses, but towards the perifovea large spots were required.

Blue-yellow cells

In thirty-eight ganglion cells the short wave-length mechanism peaked at 450 nm and could be identified as blue-cone input. Five cells had a non-concentric (co-extensive) receptive-field organization and thirty-five cells showed a centre-surround organization. In the latter group, seventeen cells had blue-cone input to the centre (fourteen on-centre and three off-centre) and sixteen cells had blue-cone input to the surround (ten on-surround and six-off-surround).

Fig. 3 shows action spectra from a Y+/B− cell. On a white background (Fig. 3*A*) a small spot elicited only excitatory responses in the middle and long wave-lengths (small circles). A large spot elicited inhibitory responses in the short wave-lengths and excitatory responses in the remainder of the spectrum (large circles). The presence of a minimum at 450 nm on a white background, however, is not sufficient evidence of blue-cone input (Beauchamp & Lovasik, 1973; De Monasterio, Gouras & Tolhurst, 1975). The position of this minimum must be examined on various coloured backgrounds, affecting the red- and green-cone mechanisms to different degrees. On yellow and red backgrounds (Figs. 3*B*, *D*), the sensitivity of the inhibitory mechanism was increased but its minimum remained at 450 nm. In addition to the relative increase in sensitivity at 500–510 nm,

these backgrounds also increased sensitivity at 420 nm. A magenta background (Fig. 3*C*) eliminated inhibitory responses above 450 nm, showing that the 450 nm minimum was not due to a green-cone mechanism displaced to short wave-lengths by strong red-cone opponency; if the cell had been a GR cell, this minimum would have been shifted towards 500–540 nm on a magenta background (cf. De Monasterio *et al.* 1975).

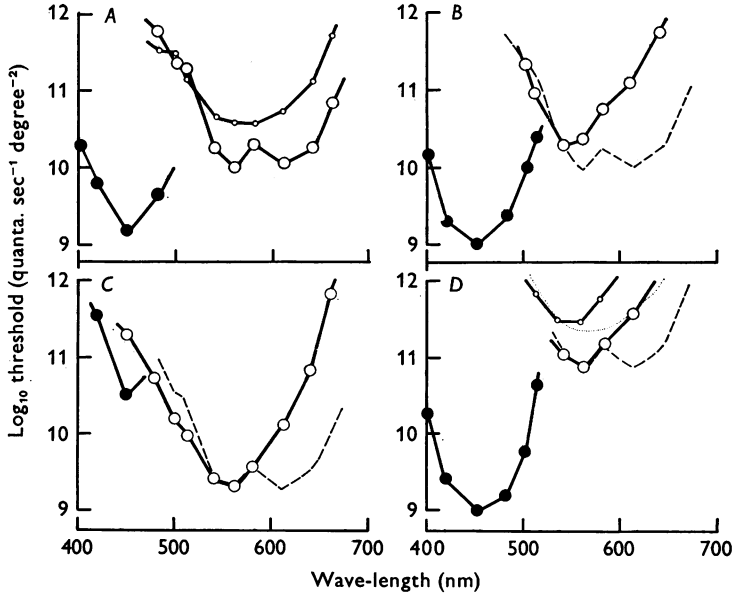

Fig. 3. Action spectra from a Y + /B − cell, eccentricity 6°. *A*: white background of 0·9 $\log_{10}$ cd/m²; small circles: spot 0·08°; large circles: spot 2°. *B*: yellow background (11·6 $\log_{10}$ quanta sec^{-1} deg^{-2}), spot 2°. *C*: magenta background (11·5 $\log_{10}$ quanta sec^{-1} deg^{-2}), spot 2°. *D*: red background (10·0 $\log_{10}$ quanta sec^{-1} deg^{-2}), spot 0·08°; (12·0 $\log_{10}$ quanta sec^{-1} deg^{-2}), spot 2°. Dashed curves in *B*, *C* and *D* represent action spectrum for 2° spot of *A*; dotted curve in *D* represents action spectrum for 0·08° spot of *A*; these action spectra have been displaced along the ordinate. Other parameters as in Fig. 1.

The overlap and broadness of the spectral sensitivity of the green- and red-cone mechanisms make it difficult to decide whether one or both of these mechanisms oppose the blue-cone input from action spectra obtained solely in the presence of a white background. If only one cone mechanism were involved, a red background would only shift the action spectrum on the intensity axis and would not modify the shape of the long wave-length side of the curve, as compared to that on a white background, since the blue-cone mechanism influences this region minimally if at all. This was

found to be the case for RG cells and it is illustrated in Fig. 4. The upper part of the figure shows action spectra of the long wave-length mechanism and their envelope on a white background in 11 GR cells. Fig. 4*B* shows curves for the same cells obtained on a moderately intense red background,

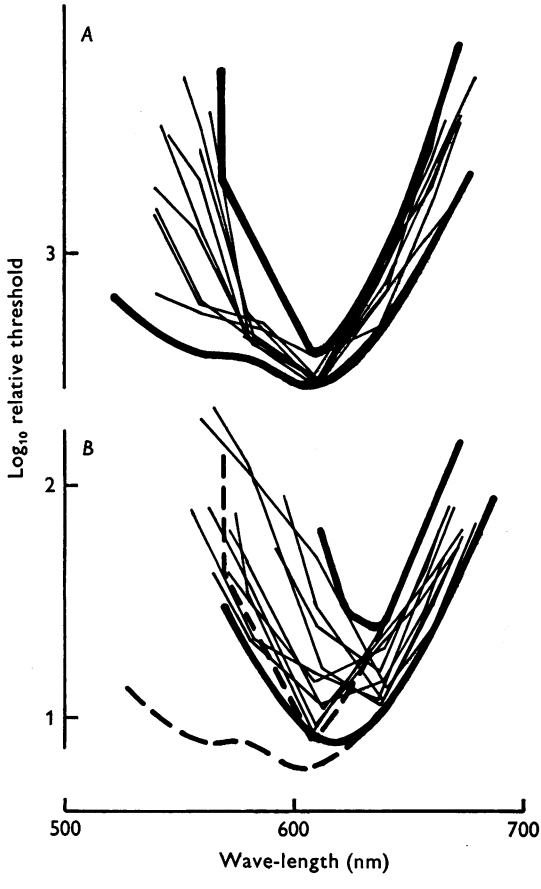

Fig. 4. Spectral distribution of the long wave-length mechanism of 11 GR cells in the presence of a neutral (*A*) and a red (*B*) background. Action spectra have been displaced along the ordinate and superimposed in the 600–660 nm region. Thicker lines represent the envelopes of these action spectra. Interrupted lines in *B* represent the envelope of *A*.

the dashed lines representing the envelope of Fig. 4*A*. Both envelopes are superimposable in the 600–660 nm region, suggesting that only one type of cone mechanism mediated these responses.

If both red- and green-cone mechanisms contribute to the opponent mechanism in BY cells, the long wave-length side of action spectra ob-

tained on a white background might differ from that obtained on a red background, since the latter will affect the green- less than the red-cone mechanism. This is shown in Fig. 3*D*, where the dashed curve represents the action spectrum on a white background with a large spot and the

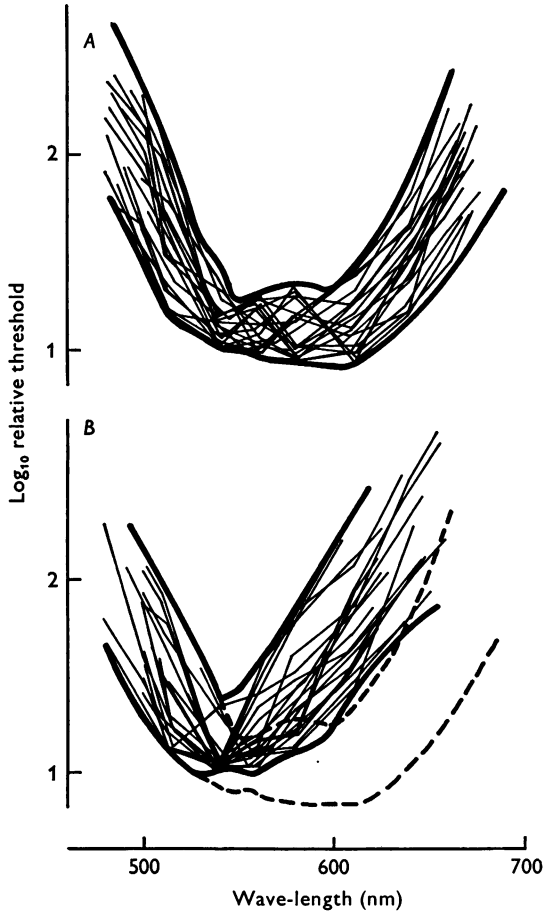

Fig. 5. Spectral distribution of the long wave-length mechanism of nineteen BY cells in the presence of a neutral (*A*) and a red (*B*) background. Action spectra have been displaced along the ordinate and superimposed in the 500–540 nm region. Thicker lines represent the envelopes of these action spectra. Interrupted lines in *B* represent the envelope of *A*.

dotted one with a small spot (Fig. 3*A*). Similar results were obtained on a yellow background (Fig. 3*B*). Fig. 5*A* shows action spectra of the long wave-length mechanism and their envelope on a white background in nineteen BY cells. Fig. 5*B* shows curves of the same cells obtained on a

moderately intense red background, the dashed lines representing the envelope of Fig. 5*A*. Both envelopes are superimposable in the 500–540 nm region but not at longer wave-lengths. These results are quite different from those of Fig. 4, and indicate that at least two cone mechanisms opposed the blue-cone mechanism in BY cells.

Action spectra obtained on neutral and coloured backgrounds were compared with red- and green-cone nomograms of the macaque (*apud* Abramov, 1968) and also with a curve generated by the addition of these two cone nomograms; this 'yellow' nomogram was almost identical to the red-cone one in the 600–660 nm region. Fig. 6 shows a comparison of these nomograms (interrupted lines) with the envelopes of Fig. 5. There is good fitting for the red-cone and 'yellow' nomograms on the long wave-length side of the white-background envelope. The green-cone nomogram (Fig. 6, dotted line) does not fit this envelope, suggesting that the responses were not due to green-cone input *alone*. On the other hand, this nomogram fits the red-background envelope well, while the red-cone and the 'yellow' nomograms fail to fit. These results support the previous evidence that both red- and green-cone mechanisms mediated the curves obtained in the presence of a white background.

Action spectra of BY cells showed an indentation at about 540–560 nm in 60 % of the cells (23/38), which can be observed in Fig. 3*A*. This indentation is also observed in the upper boundary of the envelope of Fig. 5*A*; it coincides with the point of departure of the red-background envelope from the white-background envelope (Fig. 5*B*) and it matches an indentation found at 540–560 nm on a curve generated by subtraction of the red- and green-cone nomograms and based on absolute values.

Red-cyan cells

We often recorded from cells in which the mechanism antagonistic to the red-cone mechanism had a minimum at about 450 nm on some backgrounds, but the minimum was shifted to higher wave-lengths on other background. These minima might suggest combined input from green and blue cones. The minimum of the green-cone mechanism, however, can be shifted to short wave-lengths by strong red-cone opponency (see De Monasterio *et al.* 1975, their fig. 3; see also Beauchamp & Lovasik, 1973) and can be confused with a blue cone input. The minimum at 450 nm must be demonstrable on backgrounds markedly desensitizing the red-cone mechanism. It is difficult, then, to suggest that this minimum corresponds to a displaced green-cone mechanism, *provided there is a monotonic reciprocal relation between colour-opponency and desensitization.*

To examine this relation we have measured how much the minimum of the shorter wave-length mechanism had been shifted by opponency from the longer wave-length mechanism in 110 cells with supposedly dichro-

matic RG input (Fig. 7). The spectral locus of this minimum was plotted against the ratio of the sensitivities of these cone mechanisms. The data were obtained with various stimulus sizes and on various coloured backgrounds, as well as on neutral backgrounds. Data obtained on a yellow

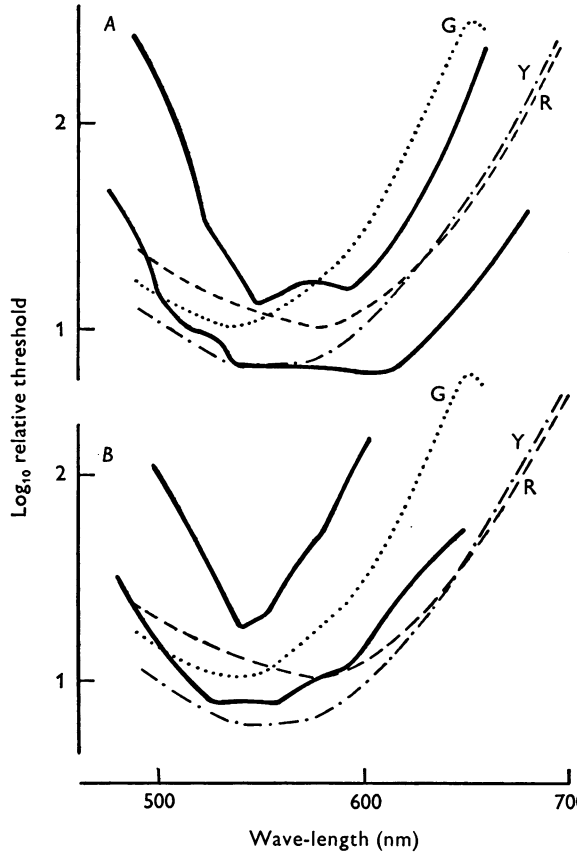

Fig. 6. *A*: envelope of the spectral distribution of the long wave-length mechanism of nineteen BY cells in the presence of a white background (same as Fig. 5*A*). *B*: envelope of the spectral distribution of this mechanism in the presence of a red background (same as Fig. 5*B*). The interrupted lines represent the red (R, – – – –) and green (G, · · · ·) cone nomograms and a 'yellow' nomogram (Y, –·–·) obtained by the addition of the previous nomograms. Cone nomograms based on Abramov (1968). The curves have been vertically displaced to fit the nomograms.

background, which is most likely to reveal a blue-cone input, are represented by open symbols; all other backgrounds by filled symbols. GR_{β} cells, which are less likely to receive strong blue-cone input, are represented by squares; other GR cells by circles. The distribution of the data, though

scattered, indicates a monotonic reciprocal relation between the amount of desensitization of the red-cone mechanism and the spectral locus of the minimum of the green-cone mechanism. In most cells, whenever the red-cone mechanism had been markedly desensitized (e.g. abscissa values above 1·0 log unit), the minimum of the shorter wave-length mechanism was located close to the minimum of the green-cone nomogram, 535 nm, as might be expected in GR cells. Provided the relation is indeed monotonic, as Fig. 7 shows, any significant departure from this relation indicates that more than one cone mechanism is involved in the mechanism opposing the red-cone mechanism.

The spectral relation between the interacting mechanisms on a yellow background deviated significantly from the observed relation in at least

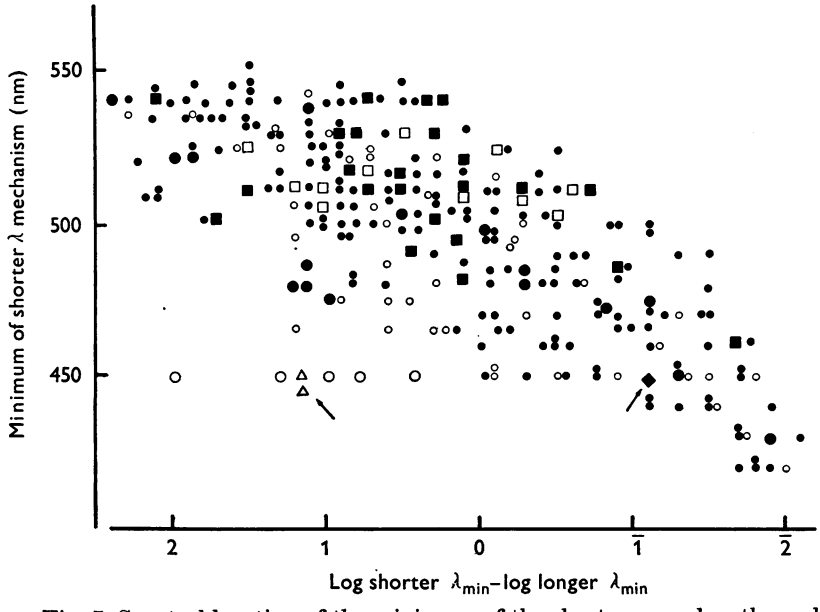

Fig. 7. Spectral location of the minimum of the shorter wave-length mechanism plotted against the ratio of sensitivities of the shorter and longer wave-length mechanisms in 110 cells supposedly receiving GR input only. Data obtained with various stimulus sizes and on various backgrounds. Open symbols: yellow background; filled symbols: all other backgrounds. Squares represent GR_β cells, while circles represent other GR cells. Most cells (small circles) follow a monotonic reciprocal relation between opponency and desensitization: the more the longer wave-length mechanism had been desensitized, the more the minimum of the shorter wave-length mechanism approached the location of the minimum of the green-cone nomogram (535 nm). Five cells deviated from this relation by different amounts (large open circles). These cells received RC input. Arrows point to the RC cells illustrated by Beauchamp & Lovasik (1973, triangles), and by Dow (1974, diamond). See text.

three cells (large open circles in Fig. 7). Action spectra of two such cells are shown in Figs. 8 and 9. The receptive-field centre of these cells received input from the red-cone mechanism, while the surround received combined antagonistic input from both green and blue cones. Results on a white background (Figs. 8*A*, 9*A*), gave no clear indication of the nature of the cone mechanisms involved. On red and magenta backgrounds (Figs. 8*B–C*, 9*B–C*), input from the green-cone mechanism is evident, the minimum of

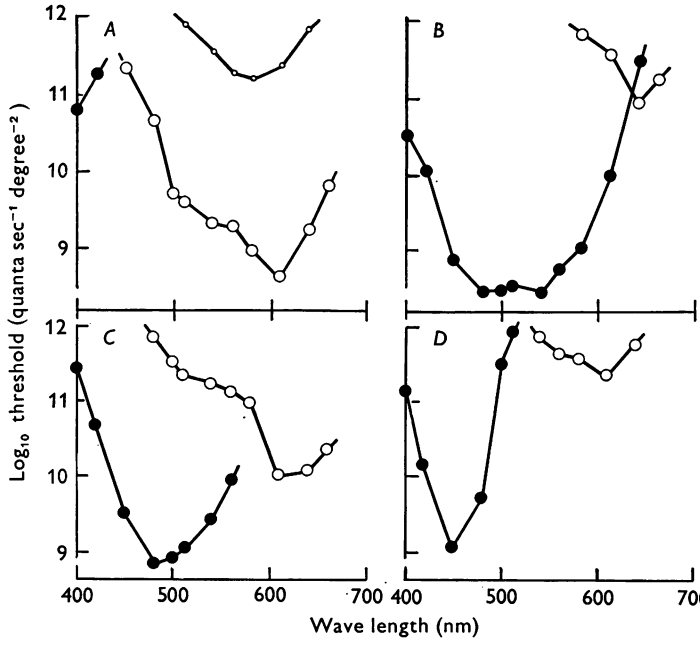

Fig. 8. Action spectra from an R+/C− cell, eccentricity 7°. *A*: white background of 0·9 $\log_{10}$ cd/m²; small circles: spot 0·08°; large circles: spot 2°. *B*: red background (11·6 $\log_{10}$ quanta sec^{-1} deg^{-2}), spot 2°. *C*: magenta background (11·2 $\log_{10}$ quanta sec^{-1} deg^{-2}), spot 2°. *D*: yellow background (12·0 $\log_{10}$ quanta sec^{-1} deg^{-2}), spot 2°. Other parameters as in Fig. 1.

its action spectrum being at about 490 nm. On a yellow background (Figs. 8*D*, 9*D*), however, there was a pronounced minimum at 450 nm despite the marked reduction in the sensitivity of the red-cone mechanism, indicating blue-cone input.

The short wave-length side of the mechanism opposing the red-cone one in these cells was also examined on backgrounds affecting the blue- and green-cone mechanisms to different degrees. If the shorter wave-length mechanism received cyan input, changes in the shape of the curves might be evident. Fig. 10 shows a comparison of action spectra of the cells

illustrated in Figs. 8 and 9, obtained in the presence of yellow (filled circles) and magenta (open circles) backgrounds. Only one of the cells described above (Fig. 9) did show an obvious change in the shape of the curves. The other two cells, despite their pronounced minima at 450 nm (e.g. Fig. 8*D*) did not show obvious modifications in the 400–450 nm region of action spectra on red, yellow and magenta backgrounds. Had these two cells received more or less equally strong input from both blue and green

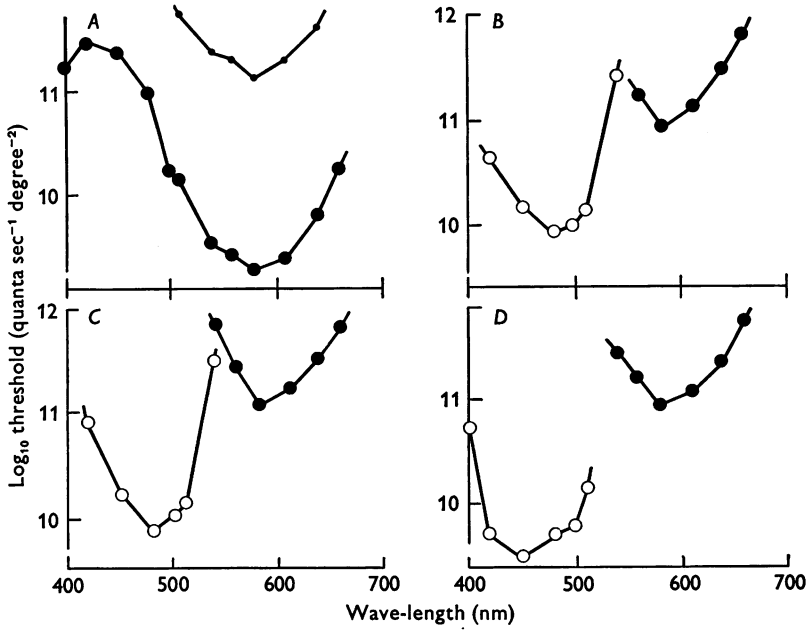

Fig. 9. Action spectra from an R−/C+ cell, eccentricity 5°. *A*: white background of 1·0 $\log_{10}$ cd/m²; small circles: spot 0·08°; large circles: spot 3°. In the presence of this background this cell had concealed colour opponency (De Monasterio *et al.* 1975). *B*: red background (11·6 $\log_{10}$ quanta sec^{-1} deg^{-2}). *C*: magenta background (11·6 $\log_{10}$ quanta sec^{-1} deg^{-2}). D: yellow background (11·6 $\log_{10}$ quanta sec^{-1} deg^{-2}). Spot of 3° in *B*, *C* and *D*. Other parameters as in Fig. 1.

cones, it would be expected that the curves would be narrower on magenta than on the other backgrounds (Fig. 10). But if one of the cone inputs was much weaker than the other, modifications of the shape of the curves might not be noticeable and trichromacy, although present, might not be detected by this single test. Our results indicate that these two cells received a much stronger input from blue cones than from green cones to the shorter wave-length mechanism. Similar findings have been reported in ganglion cells of the goldfish retina (Beauchamp & Lovasik, 1973), where some RC

cells had a rather similar contribution from the two mechanisms, while other RC cells received stronger blue-cone input. For comparison, we have included in Fig. 7 (triangles) the RC cells described by Beauchamp & Lovasik (1973, their figs. 2 and 3); the spectral relation between the interacting mechanisms on a yellow background in these two cells matches that observed in the RC cells of our sample. Two other cells appeared to receive RC input, but they were not studied in enough detail to conclusively identify such input.

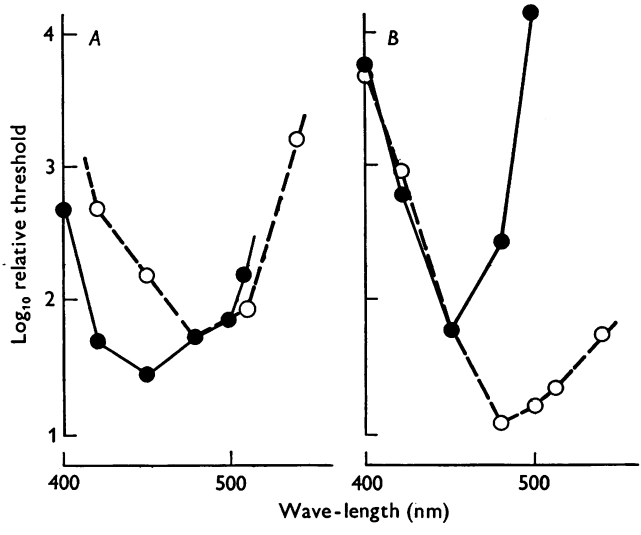

Fig. 10. Comparison of the spectral distribution of the shorter wave-length mechanism of two RC cells in the presence of a yellow (filled circles) and a magenta (open circles) background. These data are the same as Figs. 9*C–D* (*A*) and 8*C–D* (*B*). The curves have been displaced along the ordinate and superimposed by eye.

TABLE 1. Retinal distribution across the central 10° of the retina of 211 colour-opponent ganglion cells. For abbreviations see Methods

	Retinal eccentricity		
Type	0–05°	0·5–2°	2–10°
GR*	27	50	65
GR_β†	9	6	4
GM	1	1	5
RC	—	2	3
BY	10	14	14

* G/R or R/G cells. † G/R or R/G cells with beta-band responses from the red-cone mechanism.

DISCUSSION

Evidence for trichromatic opponent input to single neurones in the macaque visual system is scarce. No claim of trichromacy has been made previously at the retinal level, but studies of the more central parts of the system have reported single cells with trichromatic input. GM cells have been described in the visual cortex (Gouras, 1970; Dow, 1974) and in the lateral geniculate nucleus (Padmos & Norren, 1975). De Valois & Jones (1961) reported 'green-on, purple-off' cells in this nucleus but there is no indication that they ruled out rod input or β-band absorption by the red-cone mechanism. When appropriate tests to exclude such inputs are done, the identification of a GM cell is rather unassailable due to the different polarities of the cell responses and spectral response peaks. In contrast with GM cells, the blue-and green-cone inputs to RC cells have the same polarity and considerable spectral overlap. In addition, the blue-cone input to RC cells is probably antagonized by the β-band of the red-cone mechanism (see below); consequently, the backgrounds used to separate blue- from green-cone inputs must desensitize the red-cone mechanism to a similar extent, to avoid differences in the amount of β-band opponency in the 400–420 nm region. For these reasons, combined input from blue and green cones will not be obvious and is more difficult to demonstrate. RC cells have been reported in the visual cortex (Gouras, 1970; Dow, 1974) and the lateral geniculate nucleus (Padmos & Norren, 1975). None of the cortical studies have ruled out the possibility that the putative blue-cone input was, in fact, a green-cone input. This is illustrated in Fig. 7, where the diamond represents the cell labelled as RC by Dow (1974, his fig. 16*c*); the cell has a relation between sensitivity ratio and shorter wave-length minimum more indicative of an RG than an RC input. It is also difficult to understand why the yellow background did not increase the sensitivity of the putative blue-cone mechanism in the 400–450 nm region (as compared with that on no background), but increased the sensitivity of the 510–540 nm region.

Gouras (1968) and Wiesel & Hubel (1966), studying the retina and lateral geniculate nucleus respectively, reported 'blue on-centre' cells; the opponent mechanism was labelled as the green-cone mechanism, but no conclusive proof for the labelling was given. De Valois (1965) and De Valois, Abramov & Jacobs (1966) studying the lateral geniculate nucleus, and Marroco (1972) studying the retina, labelled cells with cross-over (neutral) points below 560 nm either as '$+B-Y$' or as '$+Y-B$'. Abramov (1968) attempted to identify the cone mechanisms in these cells, comparing suprathreshold averaged responses obtained by De Valois *et al.* (1966) and by Abramov (1968) with modified nomograms of red and green cones. Only

the 586–656 nm region was examined. He concluded that the longer wave-length responses from these cells were mediated only by the red-cone mechanism and that the inputs to these cells were strictly dichromatic, derived from blue and red cones.

Both these conclusions may be questioned. No compelling evidence is available to demonstrate that the cells analysed by Abramov were in fact BY cells and not RG cells, e.g. chromatic adaptation with backgrounds selectively desensitizing to different extents the green and red-cone mechanisms. A cross-over point below 560 nm (or elsewhere) is insufficient evidence to distinguish between BY and RG cells, even in the presence of a yellow background (cf. De Monasterio *et al.* 1975), and especially in spectral response curves not based on a threshold–response criterion. No analysis was done on the shorter wave-length responses to determine the nature of their cone input. In fact, several observations indicate that many cells classed as BY on the basis of a 560 nm cross-over point are probably RG cells (De Monasterio *et al.* 1975). In addition, averaged responses of '+Y−B' cells show a peak at 610 nm for the longer wave-length mechanism (De Valois *et al.* 1966, their fig. 10); it has been claimed that this mechanism received red-cone input and that the peak excitation was shifted from 570 nm (λ_{max} of the red-cone mechanism) to 610 nm solely on the basis of opponency from the blue-cone mechanism (De Valois, 1973, p. 222), which is practically unresponsive at wave-lengths as low as 520 nm (Abramov, 1968, his fig. 1; Brown & Wald, 1964, their fig. 3; Daw, 1973, his fig. 1; Marks *et al* 1964, their fig. 2) and – according to De Valois (1973, p. 223) – should not have any influence at the lowest wave-length examined by Abramov, which was 586 nm. The comparison between a red-cone nomogram and a 'yellow' nomogram, generated by the addition of the red and green-cone nomograms, shows that they differ only in the first point (586 nm) of the region examined by Abramov, and then only by 0·1–0·2 log units (see Fig. 6). It is difficult to believe that an analysis based on suprathreshold responses could have distinguished red- from *combined* red- and green-cone input on the basis of a single point at the beginning of the examined region, where the influence of the blue-cone mechanism seems controversial. In fact, the averaged longer wave-length responses of these 'BY' cells *only* failed to fit the green-cone nomogram at 586 nm (at a 95% confidence level) but, curiously, not at longer wave-lengths (Abramov, 1968, his table 3) where one would expect larger differences between the red- and green-cone mechanisms (cf. Abramov, 1968, his fig. 1).

It should be stressed that the synergistic cone mechanisms in cells with trichromatic input do not necessarily contribute in equal amounts. Thus, two RC cells received a blue-cone input stronger than the green-cone one, and in two GM cells the blue-cone input was much weaker than the red-

cone one. Similar results were obtained in BY cells. In most cells, a yellow background caused modifications in the 600–660 nm region of action spectra similar to those shown in Fig. 5*B*. In other cells, however, the curves either did not show such modifications or showed them in the 500–560 nm region. Since this background affected more or less equally the 510–700 nm band, the above results suggest that the red- and green-cone mechanisms might contribute in different amounts to BY cells. As a consequence, either of these mechanisms might apparently be missing in analyses not using selective chromatic adaptation, mostly in those based on suprathreshold responses where response saturation effects can occur.

Retinal distribution

Our sample of cells with identified trichromatic input represents 13% (27/211) of the recorded population of colour-opponent cells with sustained responses. This percentage is probably an underestimate of the frequency of cells receiving obvious input from all three cone mechanisms. Only half of our BY cells were studied in enough detail to demonstrate a trichromatic input, and it is probably reasonable to assume that all of the thirty-eight were similarly organized. In addition, RG cells recorded in earlier experiments were not adequately studied on a yellow background, thus precluding the eventual identification of a blue-cone input. Including those cells in which trichromacy was suspected but not conclusively identified (19 BY, 2 GM and 2 RC cells), the total percentage represents 24% (50/211), probably still an underestimate. In relation to retinal distribution, proven trichromatic cells represented *ca.* 13% (6/47) in the foveola, 12% (9/73) in the fovea and 13% (12/91) in the perifovea. Similar distributions for proven and suspected cells were 23% (11/47), 23% (17/73) and 24% (22/91), respectively.

Although the total distribution was rather flat across the central 10° of the retina, some distributions clearly appeared to be correlated with retinal eccentricity (Table 1). GR_β cells predominated toward the foveola and diminished toward the perifovea, whereas GM and RC cells had the opposite distribution. This is clearly seen, for example, between fovea and perifovea where GR cells have the same relative frequency, but GR_β and GM-RC cells have mirror image frequencies. All of these cells had receptive-field centres mediated by either the green- or the red-cone mechanism. If one considers a GR_β cell as a GR one in which no blue-cone input is present in an amount strong enough to occlude β-band responses, and GM or RC cells as GR ones in which blue-cone input is strong enough so as to be observable, the above distributions bear a relation with the relative availability of blue cones in the retinal area being considered. This is supported

by the observation that all cells in which blue-cone input could be detected were probably trichromatic. Toward the foveola, where blue cones are supposedly less numerous (Wald, 1967), GR_β cells represented 24% (9/37) of the cells with 'red' or 'green' centres, becoming less frequent in the fovea (10%, 6/59) and still less in the perifovea (5%, 4/77). In contrast, GM and RC cells represented 3% (1/37), 5% (3/59) and 10% (8/77) in those three respective areas, predominating in the perifovea where blue cones are relatively more frequent (Wald, 1967).

The above distributions suggest that GR_β, GR, GM and RC cells represent a basic GR configuration with different amounts of blue-cone contribution. This can be observed in Fig. 7. The minimum of the shorter wave-length mechanism in GR_β cells (open squares), in the presence of a yellow background, was always above 510 nm, while that of GR cells (open small circles) showed large variations, between 420 and 550 nm. This minimum was at 450 nm in RC cells (open large circles), but the cells showed variations in the ratio of sensitivity between the longer and shorter wavelength mechanisms on a yellow background. Since blue-cone input is at least weak in GR_β cells and it can be detected in RC cells, these results support the possibility of different amounts of blue-cone contribution among these cells. This is also suggested by the fact that 'typical' GR cells do not show obvious β-band responses in the presence of neutral backgrounds. In some cells this could be due to strong green-cone opponency, precluding a 400 nm red-cone input. In many cells, however, the green cone mechanism did not show strong opponency and did not extend beyond 420 or even 450 nm on a neutral background. In these cases it is conceivable that a cone mechanism other than the green-cone one was opposing β-band responses, namely blue-cone opponency. This is supported by the fact that in some GR cells, β-band responses were disclosed by an adequately intense blue background (although in other cells this did not occur and may be related to red-cone desensitization through β-band absorption; see Daw, 1973) and because perifoveal GR_β cells required larger stimuli to show these responses than foveolar cells. Thus, *concealed* blue-cone input opposing both red- and green-cone inputs and strong enough to occlude β-band responses, could explain at least some of the 'typical' GR cells. From this point of view, whenever such input becomes strong enough to be detected, GR cells would become either GM or RC cells, according to the polarity of the channel carrying the blue-cone information to the cell. This type of interaction implies that most colour-opponent ganglion cells may have input from all three cone mechanisms, even though it may not be obvious in most cells. In fact, earlier experiments using colour-matching techniques in single cells of the lateral geniculate nucleus (De Valois, 1965) suggested that many GR cells

received a concealed blue-cone input, although this view has apparently since been abandoned (e.g. De Valois, 1973).

Such chromatic interactions are most probably taking place before the ganglion cell level in the retina. This is supported by the fact that a red background increased the sensitivity of responses mediated by the blue-cone mechanism in GM cells, indicating blue-red cone opponency. Similar results have been obtained in broad-band cells with colour-opponent responses (cf. De Monasterio & Gouras, 1975, their fig. 12). In addition, the decrease of sensitivity at 540–560 nm in the action spectra of most BY cells, matching a similar decrease in a curve obtained by subtracting the red-cone and green-cone nomograms and based on absolute values, is suggestive of green-red cone opponency. The observed blue-red cone opponency in GM cells and the possible green-red cone opponency in BY cells, where these two pairs are synergistic at the ganglion cell level, indicate that such opponency probably occurs before the ganglion cells. It could very well result from antagonistic interactions between the cone themselves, each cone type inhibiting the other two.

We are grateful to R. Gunkel for preparing the contact lenses. We appreciate the technical contributions of B. Shellman and J. Jones. We would like to thank P. Padmos and D. V. Norren for access to their manuscript. F. M. M. was supported in part by Conselho Nacional de Pesquisas and Fight for Sight, Inc., N.Y., fellowships. D. J. T. thanks the Wellcome Trust for a travel grant.

REFERENCES

ABRAMOV, I. (1968). Further analysis of the response of LGN cells. *J. opt. Soc. Am.* **58**, 574–579.

BEAUCHAMP, R. D. & LOVASIK, J. V. (1973). Blue mechanism response of single goldfish optic fibers. *J. Neurophysiol.* **36**, 925–939.

BROWN, P. K. & WALD, G. (1964). Visual pigments in single rods and cones of the human retina. *Science, N.Y.* **144**, 45–52.

DAW, N. (1973). Neurophysiology of color vision. *Physiol. Rev.* **53**, 571–611.

DE MONASTERIO, F. M. & GOURAS, P. (1975). Functional properties of ganglion cells of the rhesus monkey retina. *J. Physiol.* **251**, 167–195.

DE MONASTERIO, F. M., GOURAS, P. & TOLHURST, D. J. (1975). Concealed colour opponency in ganglion cells of the rhesus monkey retina. *J. Physiol.* **251**, 217–229.

DE VALOIS, R. L. (1965). Analysis and coding of color vision in the primate visual system. *Cold Spring Harb. Symp. quant. Biol.* **30**, 567–579.

DE VALOIS, R. L. (1973). Central mechanisms of color vision. In *Handbook of Sensory Physiology*, vol. VII/3, part B, ed. JUNG, R. Berlin, Heidelberg, New York: Springer-Verlag.

DE VALOIS, R. L., ABRAMOV, I. & JACOBS, G. H. (1966). Analysis of response patterns of LGN cells. *J. opt. Soc. Am.* **56**, 966–977.

DE VALOIS, R. L. & JONES, A. E. (1961). Single cell analysis of the organization of the primate color-vision system. In *The Visual System: Neurophysiology and Psychophysics*, ed. JUNG, R. & KORNHUBER, H. Berlin, Goettingen, Heidelberg: Springer-Verlag.

DOW, B. M. (1974). Functional classes of cells and their laminar distribution in monkey visual cortex. *J. Neurophysiol.* **37**, 927–945.

GOURAS, P. (1967). The effects of light adaptation on rod and cone receptive field organization of monkey ganglion cells. *J. Physiol.* **192**, 747–760.

GOURAS, P. (1968). Identification of cone mechanisms in monkey ganglion cells. *J. Physiol.* **199**, 537–547.

GOURAS, P. (1970). Trichromatic mechanisms in single cortical neurons. *Science, N.Y.* **168**, 489–492.

MARKS, W. B., DOBELLE, W. H. & MACNICHOL, E. F. JR. (1964). Visual pigments of single primate cones. *Science, N.Y.* **143**, 1181–1182.

MARROCO, R. T. (1972). Responses of monkey optic tract fibers to monochromatic lights. *Vision Res.* **12**, 1167–1174.

PADMOS, P. & NORREN, D. V. (1975). Cone systems interaction in single neurons of the lateral geniculate nucleus of the macaque. *Vision Res.* **15**, 617–699.

WALD, G. (1967). Blue-blindness in the normal fovea. *J. opt. Soc. Am.* **57**, 1289–1301.

WIESEL, T. N. & HUBEL, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *J. Neurophysiol.* **29**, 1115–1156.