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THRESHOLDS TO CHROMATIC SPOTS OF CELLS IN THE MACAQUE GENICULATE NUCLEUS AS COMPARED TO DETECTION SENSITIVITY IN MAN

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SUMMARY

1. The relation between wavelength and psychophysical threshold for chromatic spots on a white background provides evidence for the existence of chromatic channels in the primate visual system. To find the physiological substrate of this task, we compared increment thresholds of different cell types in the macaque lateral geniculate nucleus with human psychophysical thresholds to the same stimuli, using two spot sizes, 4 and 0·4 deg.

2. At different wavelengths, different opponent cell classes in the parvocellular layers of the nucleus were most sensitive, so that at long wavelengths (> 600 nm) red on-centre cells were most sensitive, while at short wavelengths (< 500 nm) S-cone, blue on-centre cells were most sensitive, from 500 to about 550 nm green on-centre cells being most sensitive. A rare cell type with inhibition from S-cones was most sensitive at about 570 nm, although its maximum contrast increment sensitivity was poor compared with that of other cell types. Variation in strength of cone opponency caused a considerable range in threshold in each of the opponent cell classes of the parvocellular layers.

3. On- and off-centre cells from the magnocellular layers were more sensitive than opponent cells to white and yellow spots (as is the case with achromatic gratings).

4. With different wavelengths and spot sizes, the most sensitive cells found approached (to within 0·1–0·3 log units) human psychophysical sensitivity, suggesting that the most sensitive cells available may underlie detection.

5. Measurements of psychophysical chromatic discrimination thresholds, both with nearly monochromatic spots and with spots of differing saturation (purity), support this hypothesis. When magnocellular cell sensitivity corresponded to psychophysical threshold, a suprathreshold stimulus, capable of activating opponent cells, was required for chromatic discrimination.

INTRODUCTION

Measurement of thresholds for detection of spots upon a background is a common probe when studying mechanisms of visual function, either in neurophysiological

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experiments or in human psychophysics. If thresholds of a human subject are measured when both spot and background are chromatic, it is possible to isolate different chromatic (π) mechanisms (Stiles, 1959). With a white background, a graph of spot radiance at threshold against wavelength shows three peaks, with maxima around 460, 530 and 610 nm, and this multi-humped curve has been interpreted as the envelope of the sensitivities of the different chromatic mechanisms (Sperling & Harwerth, 1971; King-Smith & Carden, 1976).

The visual system of old-world primates (for example, the macaque monkey) is similar to that of man, both in terms of the absorption spectra of the visual pigments (Bowmaker & Dartnall, 1980; Bowmaker, Dartnall & Mollon, 1980; Nunn, Schnapf & Baylor, 1984) and in terms of anatomy of the visual pathway. Psychophysically the two species are also similar (DeValois, Morgan, Polson, Mead & Hull, 1974). In the visual pathway of the macaque, and most probably of man, there exist two main cell systems, one consisting of tonic, wavelength- and cone-opponent ganglion cells which project to the parvocellular layers (p.c.l.) of the lateral geniculate nucleus (l.g.n.) and the other made up of phasic, non-opponent cells which project to the magnocellular layers (m.c.l.) of the l.g.n. (Wiesel & Hubel, 1966; de Monasterio & Gouras, 1975; Dreher, Fukuda & Rodieck, 1976; de Monasterio, 1978; Creutzfeldt, Lee & Elepfandt, 1979; Perry, Oehler & Cowey, 1984).

In view of the psychophysical results, it might be supposed that cells of different types underlie detection under different stimulus conditions. The first to measure spot thresholds in monkey l.g.n. were Wiesel & Hubel (1966), but they, and subsequent authors, were mainly concerned with identifying cone inputs or studying receptive field organization. An additional complication is that most psychophysical measurements have used background adaptation levels sufficiently high (above 1000 troland) to eliminate rod intrusion while physiological experiments have generally employed lower retinal illumination levels.

To provide a more direct comparison between psychophysical and cell sensitivities, we measured thresholds of l.g.n. cells to chromatic and achromatic spots upon a 100 cd/m^2 white background, and compared these thresholds with those of human subjects detecting the same stimuli. Under different stimulus conditions, different cell types, either p.c.l. or m.c.l., were most sensitive, with in each case some neurones approaching psychophysical thresholds in sensitivity. Thus different cell types may support detection under the different conditions.

METHODS

Physiological experiments. Macaques (*Macaca fascicularis*, 2–4 kg) were anaesthetized with an intramuscular injection of ketamine hydrochloride (10–20 mg/kg) and tracheal and venous cannulae inserted. After fixation in a stereotaxic frame, a craniotomy was performed over the left l.g.n. End-tidal P_{CO_2} was maintained near 4% and rectal temperature at 37·5 °C. Continuing anaesthesia was maintained by 0·5–1·0% halothane in a 70:30% N_2O:O_2 gas mixture, e.e.g. and e.c.g. being continuously monitored as a check on depth of anaesthesia. After termination of recordings, animals were killed with an overdose of barbiturate. In those animals in which lesions were placed to confirm recording sites, perfusion with a fixative enabled histological treatment.

The pupils were dilated by instillation of atropine sulphate and eye movements prevented by infusion of 5 mg/(kg h) of gallamine triethiodide together with 2–3 ml dextrose Ringer solution per hour. Contact lenses fitted to the corneal curvature and cushioned with artificial tear fluid were

installed together with artifical pupils (6 mm diameter). A screen 57 cm distant from the animals' eyes was brought into focus on the retinae with accessory lenses. Regular irrigation of the eyes and rest periods with closed lids helped prevent clouding of the eye optics. Cell activity was recorded through a microelectrode lowered into the l.g.n. Passage of the microelectrode from p.c.l. into m.c.l. is accompanied by characteristic changes in cell response properties (Hicks, Lee & Vidyasagar, 1983). After classification in terms of receptive field organization (red on-centre, green on-centre, etc.) by means of hand-held stimuli, spectral responsiveness and intensity–response curves were recorded to a series of wide-field stimuli flashes (Lee, Valberg, Tigwell & Tryti, 1987). S-cone inputs were confirmed by means of stimuli lying along tritanopic confusion lines (Valberg, Lee & Tigwell, 1986*a*).

The cell sample (107 p.c.l. and 49 m.c.l.) was obtained from five animals, and is a subset of a larger group of cells subjected to a variety of other measurements. Receptive fields were parafoveal, between 5 and 15 deg eccentricity.

Visual stimulation. Stimuli were back-projected onto a translucent screen, made from a material for which intensity was not strongly dependent on viewing angle. Stimuli and background were generated with a three-channel optical system, one channel providing the background, the other two various stimulus configurations. The light sources for each channel were tungsten filament lamps, providing white light with CIE chromaticity co-ordinates $(x, y) = (0{\cdot}404, 0{\cdot}410)$. A constant white background of 110 cd/m^2 (retinal illuminance, 3100 troland) was present. Spots of different sizes were generated with metal slides in the stimulus beams; wavelength composition was altered with interference filters (Schott, Mainz, NAL).

Stimulus intensities were calibrated by multiplying the spectral power distribution of the projector light with the transmision curves of the filters, to give relative radiance, and then multiplying by the CIE 1964 10 deg V_λ function (the photopic luminosity function) to obtain relative luminance. Absolute luminance was calculated by reference to luminance of the white light. A Photo Research 702A/703A scanning spectrophotometer was used to check luminances and chromaticities of the chromatic stimuli; discrepancies between calculated and measured values were less than 0·1 log unit (for further details see Valberg, Lee & Tryti, 1987).

To measure cell thresholds, we constructed intensity–response curves for different wavelengths and spot sizes using motor-driven wheels holding ten neutral-density filters (in steps of 0·2 or 0·3 log units) to give an ascending series of stimulus intensities. Individual stimuli were presented for 300 ms with a 1200 ms interstimulus interval. Single-unit activity was averaged over five or ten presentations of the same stimulus. With a bin duration of 15 ms, responses to a whole series were stored in one histogram of 1000 bins. To measure responses, for magnocellular cells firing rate in the peak three bins (45 ms) of the response was calculated and for parvocellular cells the mean firing rate over the entire response was calculated. After subtraction of maintained activity, intensity–response curves were plotted and thresholds defined as a 10 impulse/s increment in firing rate, as illustrated in the Results section.

Psychophysical experiments. With human subjects, the filter wheels held neutral-density filters covering a 1 log unit range in 0·1 log unit steps but in random order. Overall intensity was adjusted with filters elsewhere in the beam so that this range straddled threshold. Subjects pressed a button if the spot was detectable. Frequency-of-seeing curves were constructed and the 50% level taken as detection threshold. False positives were very rare. Three naive subjects with normal colour vision were used. Thresholds were reproducible within and between observers to within about $\pm 0{\cdot}1$ log units or less. Chromatic discrimination thresholds were measured with a two-alternative forced-choice procedure. A chromatic and a white spot, normalized to their respective thresholds, were presented in random order, and subjects were required to identify the coloured one. Initially below detection threshold, intensity was increased in 0·1 log unit steps until discrimination threshold was reached.

RESULTS

Measurement of cell thresholds

With a steady white background of 3100 troland, we flashed spots of increasing intensities (0·2 or 0·3 log unit steps) upon neuronal receptive fields. Responses to such

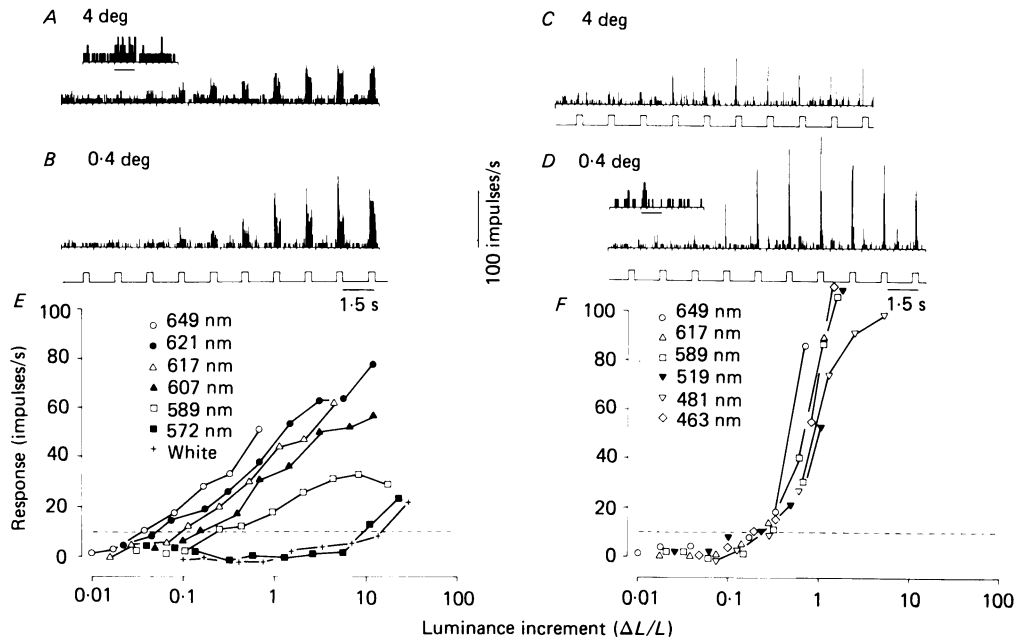

Fig. 1. *A–D*, histograms (1000 bins, binwidth 15 ms, average of five sweeps) of response of p.c.l. red on-centre cell (*A* and *B*, 621 nm stimulus) and m.c.l. on-centre cell (*C* and *D*, 484 nm stimulus) to 4 deg (*A* and *C*) and 0·4 deg (*B* and *D*) spots. In each sweep ten stimuli were presented, increasing in intensity in 0·3 log unit steps. Background in this and subsequent Figures was 110 cd/m². Response increases with stimulus contrast; in *D*, a 0·5 log unit filter was removed from the stimulus beam, so the histogram is moved the appropriate distance to the right. The dimmest stimulus in *A* and *B* was of contrast 0·011 and in *C* of 0·07. In *A* and *D*, insets are magnified versions of the third response in the relevant stimulus series, in both cases just exceeding threshold. The bars indicate the stimuli. Magnification: *X*-axis, ×3: *Y*-axis, ×2 in both cases. *E* and *F*, plots of response (after subtraction of maintained activity) against contrast for different wavelengths for the cell of *A* and *B* with 4 deg stimuli (*E*) and for the cell of *C* and *D* with 0·4 deg spots (*F*). Threshold is highly dependent on wavelength for the red on-centre cell in *E* but contrast threshold is almost wavelength independent for the m.c.l. in *F*. The threshold criterion of 10 impulses/s is indicated by the dashed line.

series, typical of those obtained from p.c.l. and m.c.l. cells, are shown in Fig. 1*A*, *B* and *C*, *D*, respectively. Responses from a red on-centre cell are shown in Fig. 1*A* for large spots (4 deg) and in *B* for small spots (0·4 deg), both of dominant wavelength 621 nm. With weak stimuli, no response is present but with increasing intensity a response is evoked which eventually saturates. With a small spot, threshold is higher, but the response of the cell then rises more steeply with increasing intensity.

Figure 1*C* and *D* shows similar histograms for an on-centre m.c.l. cell, with spot sizes of 4 and 0·4 deg, respectively. In Fig. 1*D*, a 0·5 log unit filter had been removed from the stimulus beam, and the histogram is shifted the appropriate amount to the right. The very transient response contrasts with the sustained p.c.l. cell discharge. Although threshold is lower with the larger spot, with the small spot a steeper intensity–response relation is apparent and responses have a longer time course; these effects are due to the activation of the surround with larger stimuli.

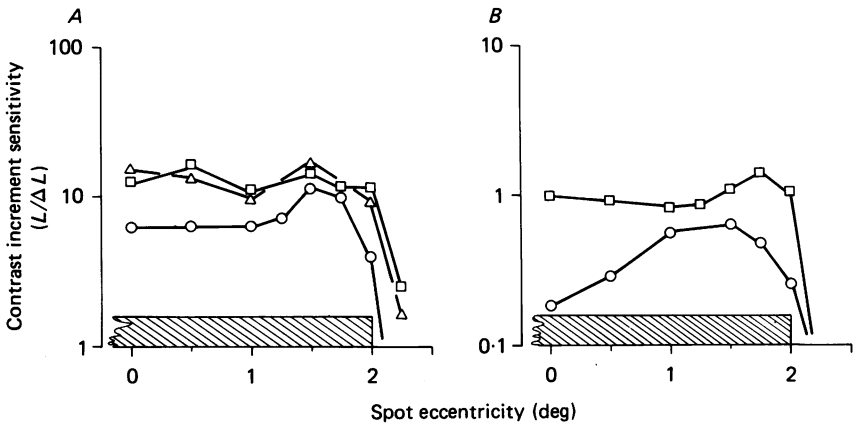

Fig. 2. *A*, contrast increment thresholds ($L/\Delta L$) with 4 deg white spots of three on-centre cells as a function of spot eccentricity relative to receptive field centre. The shaded area on the abscissa indicates the extent of the spot. For two cells, spot location did not much affect sensitivity (although affecting response magnitude to suprathreshold stimuli). For the third cell, higher sensitivity is present when the centre is close to the spot's edge. For all three cells peak sensitivity is similar to that shown in Fig. 3*C*. *B*, sensitivity of two red on-centre cells measured with the same paradigm. Note the ordinate axis scale is different in *A* and *B*.

Cell firing rates (for p.c.l. cells the mean during the whole response, for m.c.l. cells the mean in the peak) were plotted against luminance contrast increment. We chose to use luminance (10 deg V_λ function) as an intensity measure rather than radiance; this is necessary to allow comparison with contrast sensitivity to white spots. This assumes of course that the V_λ functions of man and monkey are similar. To a first approximation this is so (DeValois *et al.* 1974); possible differences in the V_λ functions of the two species are taken up in the Discussion.

Sets of curves for the p.c.l. cell (with 4 deg stimuli) and for the m.c.l. cell (with 0·4 deg stimuli) are drawn in Fig. 1*E* and *F*. A firing rate increment of 10 impulses/s was chosen as threshold, read off where the intensity–response curves intersect with the dashed lines. To give an indication of a cell response discriminable as suprathreshold, the insets in Fig. 1*A* and *D* were magnified versions of the first responses to exceed criterion.

For the p.c.l. cell, contrast threshold is clearly strongly wavelength dependent, with the highest incremental sensitivity with long-wavelength stimuli. For the m.c.l. cell, contrast sensitivity is independent of wavelength, as expected if the spectral sensitivity of phasic ganglion cells approximates the 10 deg photopic luminosity function (de Monasterio & Gouras, 1975; de Monasterio, 1978).

Threshold is dependent on the criterion firing rate chosen. A response of 10 impulses/s was generally clearly distinct from maintained activity, and could be heard on the audio monitor. Based on variability in maintained firing, it was possible to estimate the firing rate which, on a single presentation, was equal to an increment of two standard deviations above the maintained activity. This ranged between 3 and 8 impulses/s, so a 10 impulses/s criterion was a rather conservative estimate.

Both p.c.l. and m.c.l. cells demonstrate centre–surround organization (Wiesel & Hubel, 1966). In a series of experiments in which we measured area–threshold curves,

we found a range of equivalent centre sizes from 0·10 to 0·5 deg for both p.c.l. and m.c.l. cells with parafoveal receptive fields (B. B. Lee, D. A. Tigwell & A. Valberg, unpublished observations). These values are similar to those of Wiesel & Hubel (1966). We chose as standard stimulus sizes 4 and 0·4 deg spots, the latter filling the field centre of most cells.

Area–threshold curves sometimes showed a threshold increase as larger spots encroached upon the surround. The action of the surround of the m.c.l. cell in Fig. 1*C* might be deduced from the shorter response time course and lower response magnitude in comparison with Fig. 1*D*, and such effects were observed in all m.c.l. cells. For the large-spot comparison with psychophysical thresholds, we chose m.c.l. cells in which the actual threshold increase was small. Nevertheless, it might be argued that the location of the spot relative to the receptive field centre, i.e. whether it was centred or eccentric, might affect thresholds in a significant way. We therefore measured thresholds of fifteen cells to white spots located eccentrically relative to the field centre, and examples of three phasic m.c.l. on-centre cells are shown in Fig. 2*A*. Contrast increment sensitivity is plotted as a function of spot eccentricity. For two cells, spot location made little difference to sensitivity, until the spot actually fell outside the centre. The third cell showed an increased sensitivity when its centre was close to the edge of the spot, and this may be attributed to centre–surround interaction. Such cells showing contour enhancement presumably would also be able to aid in detection.

Figure 2*B* shows thresholds of two red on-centre cells with the same paradigm; note that the ordinate scale differs from that in *A*. For one of them, spot eccentricity has little effect on threshold, but for the other sensitivity is enhanced if the field centre is close to the spot's edge. In both cases, sensitivity is much less than in Fig. 2*A*, however.

Sensitivity of p.c.l. cells was measured for those wavelengths evoking an excitatory response. With wavelengths causing a suppression of p.c.l. firing, thresholds were often difficult to determine due to the low maintained activity of many neurones. The threshold for evoking an excitatory off-response from p.c.l. cells was significantly higher (0·6–1·0 log units) than for on-inhibition. In those few cells with higher maintained firing, thresholds for on-inhibition were similar to those for on-excitation for cells with reciprocal cone inputs.

For m.c.l. off-centre cells, off-excitation and on-inhibition became apparent at similar contrast levels. Peak firing rates at stimulus-off were thus plotted for these m.c.l. cells.

Thresholds of different cell types

Of the cone combinations providing input to opponent p.c.l. cells, four are frequently encountered at the retinal and geniculate level (de Monasterio & Gouras, 1975; Derrington, Krauskopf & Lennie, 1984; Lee *et al.* 1987; Valberg *et al.* 1987), those showing antagonism between long- (L) and middle- (M) wavelength cones, either +L−M or +M−L, and those showing antagonism between S-cones and some combination of the other two. S-cones may be excitatory or inhibitory (Valberg *et al.* 1986*a*). None of the rare cells with other combinations of cone inputs were encountered during these experiments.

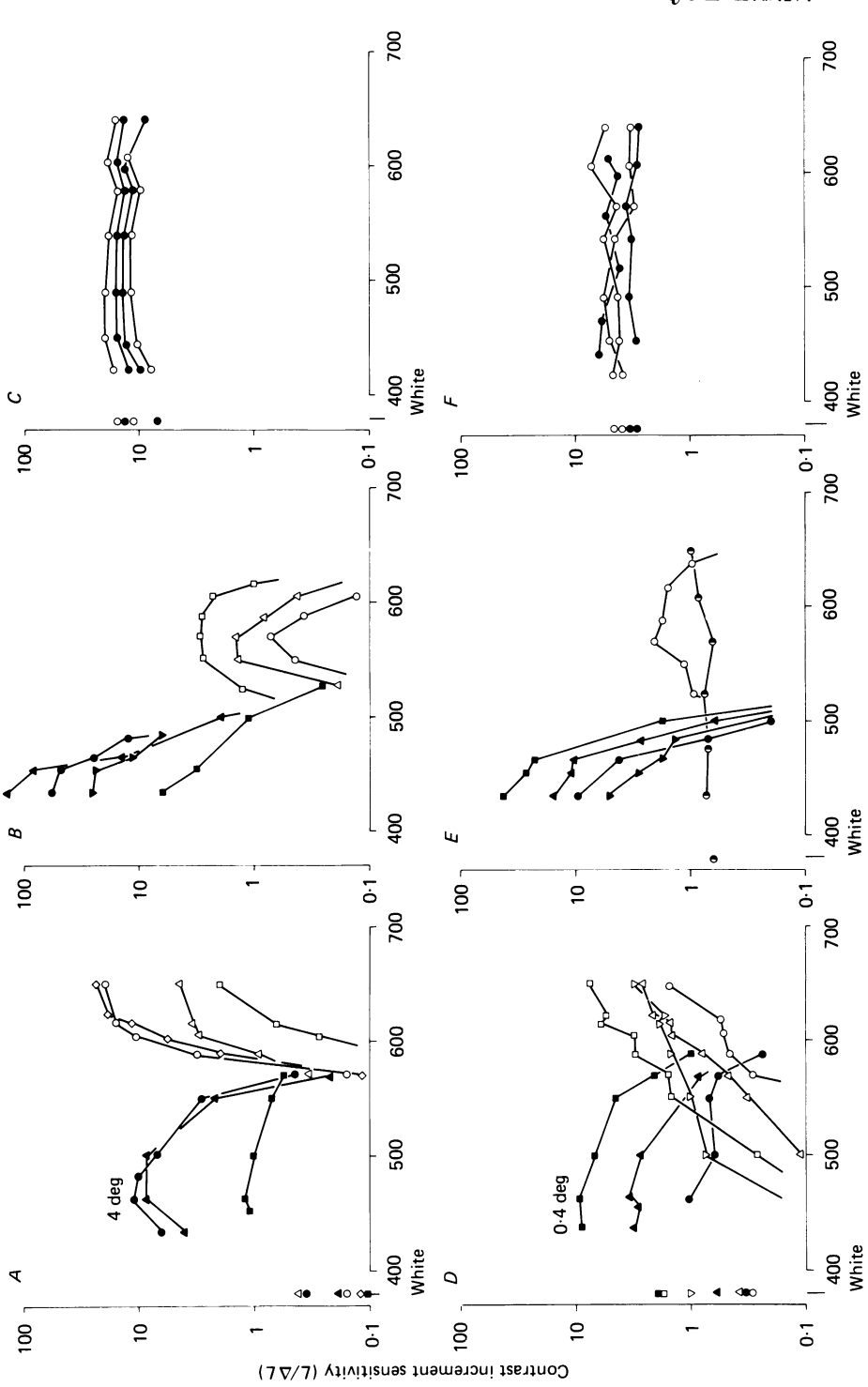

Fig. 3. *A*, thresholds ($L/\Delta L$) of M/L opponent cells to 4 deg stimuli. Cells were chosen to show the range of thresholds encountered. Open symbols refer to cells with excitatory L-cone input, filled symbols with excitatory M-cone input. White spot thresholds are indicated at the left. *B*, threshold to 4 deg stimuli of cells with S-cone input, either excitatory (filled symbols) or inhibitory (open symbols). A range of thresholds is again apparent. These cells seldom gave responses to white spots. *C*, thresholds to 4 deg spots of m.c.l. cells, two on- (○), two off-centre (●). *D*, thresholds of M/L opponent cells to 0·4 deg spots. Different cell samples were employed in *D*–*F* in comparison with *A*–*C*. A decrease in spot size is accompanied by a broadening of spectral sensitivity especially for the red on-centre cells. *E*, thresholds to 0·4 deg spots of cells with S-cone input. A decrease in sensitivity is present especially with S-cone (blue) on-centre cells. Half-filled circles are thresholds of rare non-opponent p.c.l. cell, which gave no response to large spots. *F*, thresholds to 0·4 deg spots of m.c.l. cells.

Cells with +L−M cone inputs may be of the red on-centre or, more rarely, green off-centre type or type II (Wiesel & Hubel, 1966). Similarly, green on-centre cells were the more common +M−L cells. Red on-centre cells are usually more weakly inhibited by M-cones, and thus weakly opponent (Zrenner & Gouras, 1983), and were classifiable as +Y−B (DeValois, 1973) or WL (Creutzfeldt *et al.* 1979) with stimuli presented upon a dark background. Other cells with +L−M inputs were more strongly inhibited by M-cones, classifiable as +R−G (DeValois, 1973) or NL (Creutzfeldt *et al.* 1979). Such cells were commonly type II or green off-centre.

Thresholds of M/L cells displaying a range of opponency are plotted in Fig. 3*A*, large field stimuli being used (4 deg). For all +L−M cells (open symbols), incremental contrast sensitivity was highest at the longest wavelengths tested and fell steeply below 600 nm. Also indicated to the left are the sensitivities to a white spot. A considerable range of threshold sensitivities is present. At a dominant wavelength of 649 nm, incremental sensitivity varied from 50 to 2 with a geometric mean of 8·3, thirty-three cells being tested. This variability, observed even between successively recorded cells, was associated with cell type. Weakly opponent, red on-centre cells were the most sensitive, with strongly opponent cells, such as red-green type II cells, being less sensitive.

All cells were also tested with large-field flashes on a dark background. Red on-centre cells were much more broad-band under these conditions, corresponding to the +Y−B class of DeValois (1973). Thus, the difference in spectral bandwidth between +Y−B and +R−G disappears at higher adaptation levels, as it does in the successive contrast situation (Marocco & DeValois, 1977; Lee *et al.* 1987).

Cells with +M−L cone inputs also varied in threshold, as seen in the examples of Fig. 3*A*. At 463 nm, sensitivity varied from 20 to 0·05, with a geometric mean of 1·9 ($n = 18$). Weakly opponent, green on-centre cells were the most sensitive, with strongly opponent type II or red off-centre cells being least sensitive; four such cells did not give an excitatory response on a 100 cd/m^2 background with the intensities available. On a dark background, weakly and strongly opponent cells would have been classified as +G−R or +B−Y (DeValois, 1973) or WS and NS (Creutzfeldt *et al.* 1979) on the basis of bandwidth. With a 100 cd/m^2 background, all +M−L cells have a crossover of around 570 nm.

Figure 3*B* shows contrast sensitivities at different wavelengths for cells receiving S-cone input, as proven with stimuli lying along tritanopic confusion lines (Valberg *et al.* 1986*a*). S-cone on-centre cells were very sensitive to short wavelengths, with sensitivity falling rapidly at about 500 nm. Again a range of sensitivities is present, from 200 to 4 at 435 nm (geometric mean 18, $n = 11$). Lastly, in Fig. 3*B* are three neurones with inhibitory S-cone input, excitation coming from M-cones. Such cells are rare, both in the retina (de Monasterio & Gouras, 1975) and in the l.g.n. (Valberg *et al.* 1986*a*). They have a peak sensitivity at around 570 nm, but are relatively insensitive. All cells with S-cone inputs were very insensitive to white spots.

Figure 3*C* shows sensitivities of m.c.l. cells to wide-field stimuli. Incremental sensitivity was largely wavelength independent, as expected, for the sensitivity of most phasic cells approximates the photopic luminosity function (de Monasterio, 1978). Sensitivity ranged from 7·8 to 25 (mean with white spots, 14).

With small spots, a broadening of spectral sensitivity of p.c.l. type I cells occurs

due to the selective activation of the cone mechanism supplying the centre (Wiesel & Hubel, 1966). This broadening is seen in Fig. 3*D*, in which thresholds for 0·4 deg spots are plotted against wavelength, although it is of variable extent and most apparent in red on-centre cells. A decrease in sensitivity at the spectral extreme in comparison with 4 deg fields was present for red on-centre cells (mean at 649 nm, 2·5, $n = 20$) but was not universal in green on-centre neurones (mean at 463 nm, 2·0, $n = 6$).

For S-cone on-centre cells a reduction in sensitivity is also present (Fig. 3*E*; mean 10·4, $n = 6$), as expected from the large centres of such cells. Spectral sensitivity of only one +M−S cell was tested with small spots. Little sensitivity decrement with small spots was seen. This corresponds to our experience with area–threshold curves with such cells, which indicates that they are type II with relatively small fields (Valberg *et al.* 1986*a*) and co-extensive centre and surround.

Two tonically responding cells from the p.c.l. were tested which were not spectrally selective, and one of them is shown in Fig. 3*E*. These neurones gave no response to 4 deg stimuli, and were relatively insensitive to small spots.

Figure 3*F* displays sensitivity curves for m.c.l. cells with small spots. A decrease in sensitivity is present in comparison with large fields (mean for white spots 4, $n = 27$), and incremental sensitivity is not wavelength dependent.

Comparison of sensitivities to white spots in Figs 3*A–C* and *D–F* shows that a higher sensitivity was found in m.c.l. cells than in p.c.l. cells, especially with large stimuli (mean for m.c.l. cells 14, $n = 11$; for p.c.l. cells 0·3, $n = 23$, with fifteen p.c.l. cells failing to respond in the intensity range available). This difference in sensitivity is analogous to the marked difference in contrast sensitivity between p.c.l. and m.c.l. cells when achromatic gratings are used as stimuli (Kaplan & Shapley, 1982; Hicks *et al.* 1983). With small spots, the difference becomes less marked (mean sensitivity 4 for m.c.l. cells, $n = 27$; mean 0·49 for p.c.l. cells, $n = 23$) but is still significant.

From the results presented in Fig. 3 it is clear that under different stimulus conditions, different cell types possess the greatest sensitivity. We now compare these thresholds with psychophysical data.

Comparison of neurophysiological and psychophysiological thresholds

In most studies of psychophysical thresholds stimuli have been presented foveally (King-Smith & Carden, 1976). Since our cell receptive fields were parafoveal, human thresholds were measured with stimuli at 10 deg eccentricity on the temporal retina. The spot sizes used, 4 and 0·4 deg, correspond roughly to the 1 and 0·1 deg stimuli King-Smith & Carden (1976) presented foveally, after the magnification factor is taken into account (Virsu & Rovamo, 1979). For these two spot sizes, Fig. 4 shows psychophysical detection thresholds at different wavelengths; the same stimuli and filters were used as in the physiological experiments. In Fig. 4*A*, where relative radiance is used as an intensity measure, with 4 deg stimuli sensitivity peaks around 460, 530 nm and a shoulder near 610 nm are present. With 0·4 deg stimuli, the sensitivity curve approaches more closely the photopic luminosity function, except at short wavelengths. This can be seen more clearly in Fig. 4*B*, where points have been replotted in terms of luminance contrast increment thresholds, together with the threshold for a white stimulus. With large stimuli, a very high sensitivity is

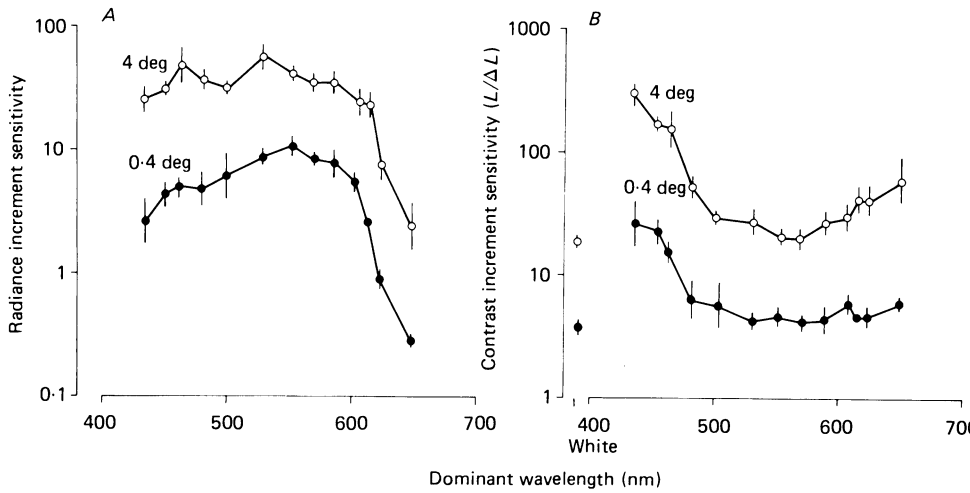

Fig. 4. Psychophysical thresholds for 4 deg (○) and 0·4 deg (●) spots on a 110 cd/m² background. Thresholds represent 50% frequency-of-seeing, stimuli being presented for 300 ms on the temporal retina at 10 deg eccentricity. Shown are means and standard deviations of two measurements by each of three naive subjects. Standard deviations were 0·03–0·14 log units. *A*, thresholds are plotted on a relative radiance scale. *B*, thresholds converted to luminance contrast (sensitivity $L/\Delta L$) with threshold to a white spot also shown.

present at short wavelengths, and to a lesser extent at long wavelengths. Sensitivity is less in mid-spectrum, but does not fall below the sensitivity for a white spot.

These results are similar to those of King-Smith & Carden (1976) with foveal stimuli; with such stimuli, 1 and 0·12 deg in size, we also obtained similar results. A distinct peak at 610 nm is not so apparent in our data, perhaps because of the yellowish projector light used as background.

Figure 5 compares cell and psychophysical thresholds. In Fig. 5*A* and *B* the thin line indicates psychophysical measurements from Fig. 4, the dashed line the envelope of the most sensitive of p.c.l. cells, and the thick continuous line the envelope of m.c.l. cell sensitivities. With differing wavelength and spot size, the threshold of the most sensitive cells approaches that found psychophysically. At wavelengths below 500 nm, S-cone on-centre cells are most sensitive, and at long wavelengths above 600 nm, L-cone, red on-centre cells. Between 500 and 550 nm, the most sensitive p.c.l. cells are of the green on-centre type. M.c.l. cells approach psychophysical sensitivity for white spots, as is the case for achromatic gratings (Kaplan & Shapley, 1982; Hicks *et al.* 1983). Also, around 570 nm with a 4 deg stimulus, where a dip in the p.c.l. sensitivity envelope is apparent, m.c.l. cells constitute the most sensitive population. With small spots, cell thresholds also approach psychophysical levels. Due to the broadening of spectral sensitivity of opponent cells, the dip in the p.c.l. sensitivity is less marked. In Fig. 5*C* and *D*, the data are replotted in terms of radiance, separate sensitivity curves being shown for each cell type.

King-Smith & Carden (1976) measured both detection and chromatic discrimination thresholds. If cone-opponent cells were able to mediate detection, then spot colour might be discriminable at threshold. We also made such tests; a white and a

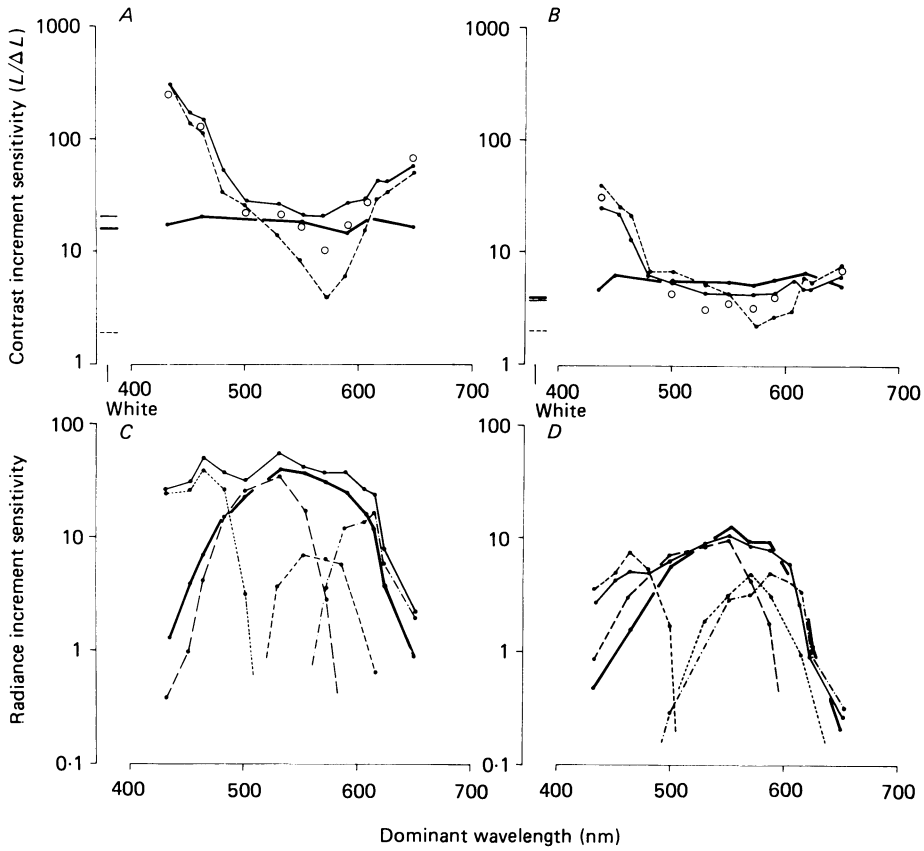

Fig. 5. Comparison of psychophysical (thin continuous line) and envelope of p.c.l. (dashed lines) and m.c.l. (thick continuous line) sensitivities for 4 deg (*A*) and 0·4 deg (*B*) spots. The most sensitive cells approach psychophysical sensitivity, either p.c.l. (at the spectral extremes) or m.c.l. (for white and 570 nm spots). Circles are chromatic discrimination thresholds between chromatic and white spots (normalized in intensity relative to threshold) presented in a two-alternative, forced-choice situation. These are similar to detection thresholds except about 570 nm. In *C* and *D*, data replotted in terms of relative radiance increment, with envelopes for each p.c.l. cell type drawn separately.

chromatic spot were adjusted in intensity to be just below threshold, and then both were increased in intensity (in 0·1 log unit steps) until the chromatic spot could be distinguished. The circles of Fig. 5*A* and *B* are these measurements. With 4 deg stimuli at long and short wavelengths detection and discrimination thresholds are similar, while at 570 nm the chromatic stimulus must be suprathreshold to be discriminable, confirming the observations of King-Smith & Carden (1976). This is the low point in the p.c.l. sensitivity envelope, and we propose that in this spectral region suprathreshold stimulation is necessary to activate opponent cells capable of carrying chromatic information.

On the assumption that macaque physiology is comparable to that of man, we propose detection of the stimuli used could be based on detection by the most sensitive cells available.

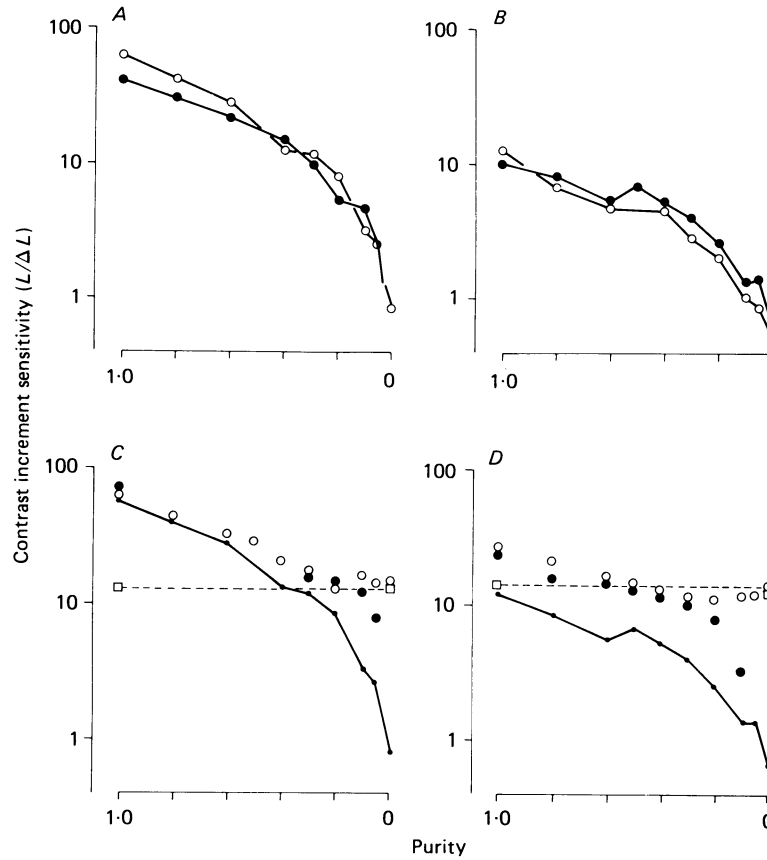

Fig. 6. The relation between threshold and stimulus purity with 4 deg spots for two red on-centre cells (*A*, dominant wavelength 649 nm) and two green on-centre cells (*B*, dominant wavelength 531 nm). Threshold increases rapidly at low purities. *C* and *D*, comparison of p.c.l. (continuous line) and m.c.l. (dashed line) cell thresholds with psychophysical detection (○) and chromatic discrimination (●) thresholds. Discrimination and detection thresholds are similar down to low purities where discrimination threshold begins to fall more rapidly. At a purity of 0·05 a 530 nm stimulus could not be distinguished from white. The open squares indicate m.c.l. sensitivities.

Variation in stimulus purity

If m.c.l. cells underlie detection of white spots and p.c.l. cells of chromatic spots except near 570 nm, then when spots of differing saturation are used, at some saturation detection by one cell type should give way to detection by the other. For example, with a 649 nm spot, certain red on-centre cells are most sensitive, but as saturation is decreased by adding white to the stimulus, at some point red on-centre cells might be expected to become less contrast sensitive than m.c.l. cells. Up to this point, detection and chromatic discrimination thresholds would be identical but thereafter a suprathreshold stimulus might be required to allow chromatic discrimination.

In one experiment we measured cell thresholds of eighteen neurones to 4 deg spots of differing saturations; unfortunately only red and green on-centre cells were en-

countered, which were tested with spots of dominant wavelengths of 649 and 531 nm, respectively. Figure 6*A* and *B* shows contrast thresholds of two of the most sensitive red on-centre cells (Fig. 6*A*) and two of the most sensitive green on-centre cells (Fig. 6*B*), plotted against stimulus purity, defined as $L_\lambda/(L_\lambda + L_W)$ where L_λ is the luminance of the chromatic component and L_W the luminance of the white light in the stimulus. Sensitivity decreases slowly at first with decreasing purity and then more rapidly to reach a sensitivity to white spots more than 1 log unit lower than to the chromatic stimulus.

Thresholds of human subjects to the same stimuli are compared with cell thresholds in Fig. 6*C* and *D*. Both detection and discrimination thresholds were measured, using the same paradigms as with monochromatic stimuli; discrimination thresholds were mainly measured at low purities, where a difference between detection and discrimination thresholds might be expected. With decreasing purity, detection thresholds increased slowly for 649 nm (Fig. 6*C*) and for 531 nm (Fig. 6*D*) until a threshold level similar to that for white spots was reached. At lower purities, discrimination thresholds became higher than detection thresholds, this being most marked for 531 nm spots.

The shape of the p.c.l. cell threshold curves (continuous lines) is similar to the decline in psychophysical discrimination sensitivity, but the most sensitive cell was for both wavelengths about 0·2–0·3 log units less sensitive than the psychophysical values. It is possible that a larger cell sample may have yielded more-sensitive neurones. The open squares indicate m.c.l. sensitivity, which is expected to be independent of purity.

The more rapid decline in opponent cell sensitivity at low purity parallels the rapid decline in chromatic discrimination sensitivity at low purities. Thus, the experiments shown in Fig. 6 provide support for the hypothesis that the most sensitive cell available can provide a basis for detection and under conditions where m.c.l. cells are most sensitive, discrimination and detection thresholds are different, p.c.l. cells underlying the discrimination task.

Variability in parvocellular layer cell sensitivity

Responsiveness of p.c.l. cells may be quantified by means of a model describing and predicting cell behaviour (Lee, Virsu & Elepfandt, 1983; Lee *et al.* 1987; Valberg *et al.* 1987). Output of each cone mechanism follows a saturating hyperbolic function (Naka & Rushton, 1966) of the form

$$Q = Q_{max} S^n/(S^n + \sigma^n),$$

where Q indicates cone mechanism output, Q_{max} its maximum, σ the half-saturation constant, with S being proportional to pigment absorption. An exponent, n, was set to 0·75. Cone mechanisms interact linearly. Families of intensity–response curves obtained in a successive contrast stimulus paradigm (when stimuli alternate with a 100 cd/m^2 adaptation field) can be accounted for using this model (Lee *et al.* 1987; Valberg *et al.* 1987). Each cone mechanism has available two free parameters, Q_{max} and σ, and these parameters were optimized using a least-squares criterion.

This model may be used to predict cell responses to spectral mixtures when stimuli are alternated with an adapting field (Valberg *et al.* 1987). It approximately predicted

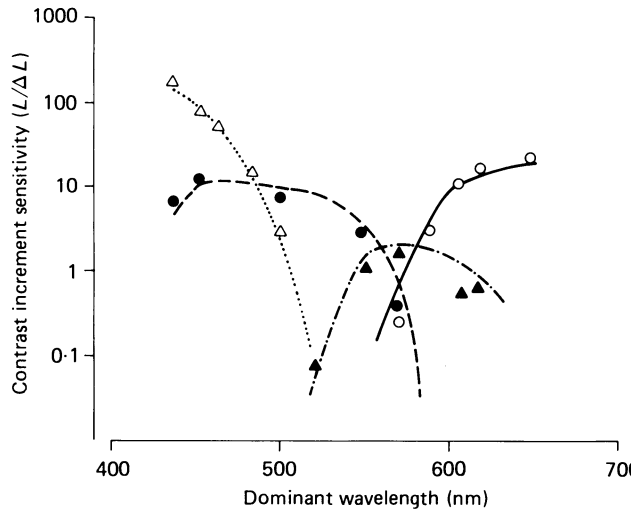

Fig. 7. Comparison for examples of each cell type of the relation between threshold and wavelength with predicted curves based on a model of cell behaviour (described in text). For S-cone on-centre cell (dotted curve) excitation from the S-cone and inhibition from the M-cone was assumed, for the green on-centre cell (dashed curve) excitation from M-cone and inhibition from L-cone, for the red on-centre cell (continuous line) the converse, and for the mid-spectral cell, excitation from M-cones and inhibition from S-cones. Good agreement at threshold is present. In other cells predictions as to threshold always fell within 0·3 log units of the measured value.

threshold behaviour in the experiments described here. Figure 7 shows empirical measurements compared with derived spectral sensitivity curves from the same neurones. The agreement is satisfactory at threshold, although deviations were present at higher response amplitudes. Independent of whether the model provides a valid description of cell response, the form of the curves relating incremental contrast sensitivity to wavelength can be derived from interaction of the different combinations of cone mechanisms present in different cell types.

DISCUSSION

The variety of cell types in the macaque retina and l.g.n. is much richer than in the cat, a species without significant colour vision. The variety of cone combinations and receptive field organization to be found makes for variation in area–threshold behaviour. We have evaded this problem by restricting the stimulus conditions employed, to allow comparison with psychophysical thresholds with the same stimuli, a more extensive exploration of threshold variation with receptive field structure not being attempted.

Among opponent cells receiving similar cone inputs, there was considerable variation in threshold with the same stimulus. In comparison, m.c.l. cells displayed less variation, especially with small spots, and in this respect would seem a more homogeneous population. The reason for threshold variability among opponent cells appears to be related to the strength of opponent inhibition. Strongly opponent cells

respond optimally to chromatic stimuli dimmer than an adaptation field in the successive contrast situation (Valberg, Seim, Lee & Tryti, 1986*b*; Lee *et al.* 1987; Valberg *et al.* 1987), so that strongly and weakly opponent cells may be useful in encoding spectral information at a range of luminances darker and brighter than the mean illumination level. Threshold variation can be expected on the basis of variability in opponency.

Legitimacy of the comparison of cell and behavioural thresholds

Formulation of linking hypotheses between physiological and psychophysical processes must be undertaken with some care (Teller, 1984), though a correlation of physiological and psychophysical thresholds involves a class A hypothesis of Brindley (1960), and thus is justifiable. Nevertheless, several assumptions are implicit in the comparisons made here.

Firstly, it is assumed that macaque and man are comparable species as far as their spectral sensitivities are concerned. DeValois *et al.* (1974) found the photopic luminosity function of the macaque to be similar to that of man, though there were some deviations between macaque and human functions at the spectral extremes. At 450 nm the macaque was about 0·3 log units more sensitive than a human observer, and at 650 nm about 0·2 log units more sensitive. However, as DeValois *et al.* (1974) themselves point out, in their animal experiments it was likely that the animals were able to use their peripheral retinae, which would result in such increased sensitivity at the spectral extremes. In any event, possible differences between man and macaque are smaller than the relevant differences in sensitivities between different cell types; S-cone on-centre cells were 1 log unit more sensitive than other types at 450 nm.

DeValois *et al.* (1974) also found wavelength and saturation discrimination functions of man and macaque to be very similar. Furthermore, the sensitivity of the visual pigments is almost identical in the two species (Bowmaker & Dartnall, 1980; Bowmaker *et al.* 1980; Nunn *et al.* 1984). Finally, Sperling, Crawford & Espinoza (1978) tested macaques on an identical paradigm to that used here, and found a sensitivity curve with three peaks, as in man. We conclude that colour vision in man and macaque is sufficiently similar to warrant our comparisons.

A further assumption is that anaesthesia did not affect cell thresholds. Transmission from retina (where anaesthetic effects might be expected to be minimal) to geniculate is fairly linear (Lee, Virsu & Creutzfeldt, 1983) so error from this source is unlikely to be great. We also assume the cell sample to be representative, in that a larger sample would not have thrown up much more sensitive neurones. Those recorded were, however, typical of a much larger group (over 1000) recorded in other experiments. Lastly, we assume that a 10 impulses/s firing rate increment is equivalent to 50% frequency-of-seeing. In view of these assumptions, a discrepancy of, say, 0·2–0·3 log units between psychophysical and physiological thresholds is unlikely to be significant. However, our results show striking differences between cell types of much greater magnitude.

We usually restricted our measurements to spots centred over the receptive field. In the case of m.c.l. cells, which often have strong surrounds, one objection might be that cells with fields close to the edges of the spot might have been more sensitive.

We tested some cells with such eccentrically positioned spots (Fig. 2) and demonstrated that contour enhancement may be present in some m.c.l. cells, as well as in some p.c.l. cells. Such m.c.l. cells, with receptive fields close to the edge of the spot, approached in sensitivity those of Fig. 3*C*, and could also aid in detection. Opponent cells with fields close to the spot's edge were substantially less sensitive to achromatic spots.

The physiological results shown here differ from those of Sperling *et al.* (1978) who tried to correlate macaque psychophysical performance with simultaneously acquired physiological data. Macaque psychophysical threshold curves were similar to those of man, but little cell data is provided by these authors. The one red on-centre cell shown did not approach psychophysical sensitivity at long wavelengths, although it fell into the range of sensitivities found here. However, Sperling *et al.* (1978) observed at least one broad-band, presumably m.c.l., cell with high sensitivity, especially at short wavelengths, and attributed psychophysical thresholds to such cells. S-cone input to phasic ganglion cells, which project to the m.c.l. (Perry *et al.* 1984), is rare (de Monasterio, 1978), and we found no m.c.l. cells with an enhanced sensitivity at short wavelengths attributable to such input. In any case, it is difficult to see how a single cell type could form a basis for chromatic discrimination, where participation at threshold of several cell types would seem to be necessary.

Psychophysical thresholds are dependent on spot duration as well as spot size, although the latter is the more important variable (King-Smith & Carden, 1976). Due to the difference in time course of p.c.l. and m.c.l. responses, one might expect that input of the former to some central mechanisms capable of temporal integration might be more severely affected by shortening flash duration than the latter. King-Smith & Carden (1976) measured temporal integration at detection threshold and found it to be minimal near 570 nm, which would be consistent with phasic m.c.l. cells being involved in detection at this wavelength.

Cell types and chromatic channels

Our results show that the three peaks in sensitivity at 460, 530 and 610 nm (Fig. 5*C*) reflect thresholds of different cell types, and thus may be due to different 'chromatic channels', if S-cone, M-cone and L-cone on-centre cells can be so named. The cell sensitivity curves of Fig. 5*C* and *D* are indeed similar to those postulated by King-Smith & Carden (1976). With white and 570 nm spots, the phasic, magnocellular system is likely to underlie detection. On the other hand, from the results of Fig. 5*B* and *D*, the idea that the V_λ-like sensitivity with small spots is attributable to some kind of achromatic mechanism appears to be an oversimplification. Finkelstein & Hood (1984) found, and we confirm, that the colour of small spots is discriminable at threshold, which makes detection by an achromatic channel alone unlikely. Physiologically, thresholds for phasic and tonic cells were similar with small spots except at short wavelengths (below 480 nm) so both could contribute to detection, with opponent cells allowing chromatic discrimination.

It is difficult to predict how the palette of most sensitive cells might change under different conditions, for example chromatic adaptation. Such cases must be studied physiologically on an individual basis. For example, it is possible that cellular chromatic discrimination thresholds may underlie MacAdam ellipses; the envelope of

p.c.l. sensitivities in Figs 5 and 7 transforms to a contour resembling a MacAdam ellipse about the white point.

The difference between detection and chromatic discrimination thresholds, near 570 nm and with desaturated stimuli, is consistent with the hypothesis that when phasic cells are the most sensitive, they may set detection threshold, but chromatic discrimination requires activation of cone-opponent neurones. If the threshold of opponent cells is lower than or equal to that of phasic cells, then discrimination and detection thresholds are identical.

Under the different stimulus conditions tested here, different cell types have the lowest threshold, with the most sensitive cells approaching in sensitivity psychophysical thresholds. This would argue against probability summation playing a large role under our stimulus conditions. Although such summation is likely in tasks involving detection of spatial patterns (for example, Graham, 1977), these effects are small (0·1–0·3 log units) in chromatic discrimination tasks (see Wyszecki & Stiles, 1982). Indeed, Stiles (1967) reported inhibitory interaction between chromatic channels at threshold. M.c.l. cells were at least a factor of 10 more sensitive than p.c.l. cells to white spots, as is the case with achromatic gratings (Kaplan *et al.* 1982; Hicks *et al.* 1983). A difference in sensitivity of this magnitude would be unlikely to be made up by probability summation or some kind of averaging among p.c.l. cells, for then one might expect such a mechanism to be operative with chromatic spots as well, yet the most sensitive p.c.l. cells then approached psychophysical threshold levels. However, it remains possible that summation among the most sensitive cells might occur to a limited extent. Commonly, the most sensitive cells found were 0·1–0·3 log units less sensitive than a human observer, leaving such a possibility open.

The sensitivity curves of Fig. 3 bear a superficial resemblance to channels required by opponent-colour theory (Hering, 1920; Hurvich & Jameson, 1957). However, M/L cells do not operate along the axis required of a Hering type, red–green opponent channel, and although phasic cells may be involved in some detection tasks, their phasic responses and limited dynamic range make them unsuitable as a counterpart for an achromatic brightness channel. It is possible to reconstruct colour scaling systems quite well, however, assuming a linear combination of opponent cell outputs alone (Valberg *et al.* 1986*b*).

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