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SPECTRAL AND ORIENTATION SPECIFICITY OF SINGLE CELLS IN FOVEAL STRIATE CORTEX OF THE VERVET MONKEY, *CERCOPITHECUS AETHIOPS*

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SUMMARY

1. The spectral sensitivity, orientation specificity and inhibitory surround of seventy-three cells were studied in the vervet monkey. The eye was in the dark or illuminated with steady white or spectral light. The cells were in the striate cortex corresponding to the foveal representation. Nearly all the cells gave on- or on/off-responses.

2. More than a third of the cells (41 %) responded over a narrow spectral band, in the blue, green, yellow or red section. Three quarters of them were orientation specific with flanking inhibitory surround and half of these were of the 'stopped-end' variety as well. The effect of the wavelength of the background indicated that only a half were activated by such excitatory–inhibitory colour pairs as have been described in the geniculate nucleus.

3. A third of the cells (36 %) responded to most colours but with the greatest response to green, yellow or red. Less than half were orientation specific. Unlike the narrowband cells, the response decreased with the intensity of the light. Two thirds were activated by the excitatory-inhibitory colour pairs that have been described in the geniculate nucleus.

4. In both groups of cells the wave-length of the spectral peak could be different when the stimuli were weak compared with when they were strong.

5. One quarter of the cells (23 %) gave on/off-responses to all spectral flashes; half were not orientation specific. The difference in orientation specificity between narrow- and broadband cells is significant ($P < 0{\cdot}01$).

INTRODUCTION

Although the responses to coloured stimuli of single cells in the area of foveal representation in the striate cortex of monkey have been described, there is little agreement as to what the findings show. In previous work about a third of single cells were found to respond over a narrow range of the spectrum when diffuse flashes were given (Andersen, Buchmann & Lennox-Buchthal, 1962; Lennox-Buchthal, 1965). Other workers used spectral stimuli defined with respect to position and movement. Thus, Hubel & Wiesel (1968) found only a few cells that responded to specific coloured stimuli and some of them did so in a way never seen in the geniculate nucleus (Wiesel & Hubel, 1966). Dow & Gouras (1973) and Gouras (1974) reported that cells were either 'colour-coded' or 'spatial-coded' but rarely both. Yates (1974) and Poggio, Baker, Mansfield, Sillito & Grigg (1975) found half the cortical cells to be luminosity and half chromatic cells.

In the study reported here we confined the flashes to the centre of the receptive field of single cells in the foveal striate cortex of the vervet monkey and found the location, the dimensions and orientation of the slit or square that gave the best response. The optimal spectral stimuli and background illumination were then established. Most of the cells that responded over a narrow band of the spectrum required a precisely oriented and dimensioned slit to respond.

An abstract of the findings was presented at the XVth Scandinavian Congress of Physiology and Pharmacology, Århus, Denmark, 16–19 August 1976 (Bertulis, Guld & Lennox-Buchthal, 1976).

METHOD

Animals. The animals were twelve vervet monkeys, *Cercopithecus aethiops pygerythrus.* Several weeks before experiments the animals were anaesthetized, a circular bone flap 1·5 cm in diameter was lifted on the right, over the cortical region corresponding to the foveal representation (Guld & Bertulis, 1976), and a plastic chamber filled with sterile bone wax was fixed to the skull with methacrylate cement. Experiments were then performed for 6–8 hr at about weekly intervals for up to 2 months. When the animal was killed, the position of the chamber over the striate cortex was verified histologically.

Recording of potentials. The micro-electrodes were 0·3 mm platinum/iridium wire coated with glass and platinized at the tip to give a tip of about 3 μm^2 and an impedance of 10–100 MΩ. The impedance was measured in saline and then repeatedly in the cortex, as the peak voltage across the tip of the electrode when a 1 msec rectangular current pulse of less than 10^{-9} A was applied (Guld, 1974). The electrodes were fixed in a microdrive device in the lid of the chamber (modified from Andersen & Laursen, 1959). A transducer attached to the electrode measured how far in microns the electrode was advanced (Petersen & Butterfield, 1968).

Action potentials were amplified by an amplifier with neutralized input capacitance (Guld, 1974), the frequency range used being 300–5000 Hz (6 db attenuation). The ground electrode was placed in the mouth. Potentials were displayed on an oscilloscope with a 500 msec sweep and, via a delay line (Nissen-Petersen, Guld & Buchthal, 1969), on a 10 msec sweep; the stimulus flash was recorded on another beam. Each sweep was photographed (example in Fig. 4).

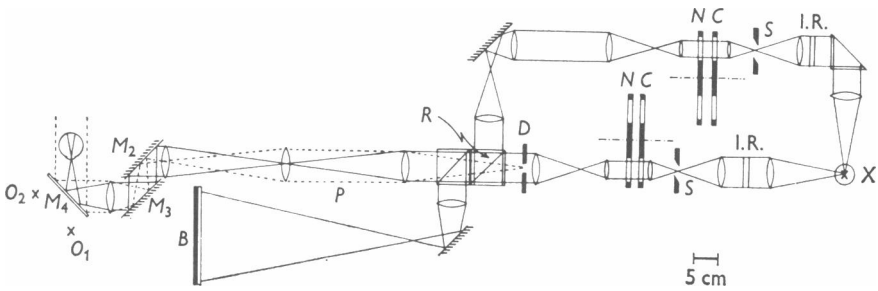

Fig. 1. Light stimulator. Two light paths from the light source, one for background illumination and one for the flashed stimulus (slit or square). The light source was a 450-W Xenon arc (*X*). Two similar light paths (thin lines) were led from it, each with an infrared filter (I.R.), a magnetic shutter (*S*), a wheel with twenty neutral filters (*N*) to vary intensity and one with a neutral and nineteen narrowband filters (*C*) to deliver a 10° circular background illumination that covered the area of the spot (upper paths), and a 'spot' (lower path) of variable shape up to 3° × 3°, determined by the rectangular diaphragm (*D*). The two paths were combined at cube *R* and the beam was led through a periscope (*P*). The crater of the Xenon bulb was focused on the cornea to give Maxwellian view. The variable diaphragm (*D*, light path shown by dashed lines) was focused on the retina and imaged on a screen (*B*), such that 1 cm corresponded to 1° of visual angle. The angle of incidence at the eye and thus the position of the spot on the retina was changed by mirrors M_2, M_3, M_4 mounted on a goniometer (Fig. 2). The retina was seen through a half-mirror M_4 when the observer's eye was placed at O_1; the stimulus was seen from O_2. The diagram is drawn to scale (5 cm line). The principal lenses were achromats, 31·5 mm in diameter.

Apparatus to deliver flashes and background illumination. The two optical paths, one for the test flash and one for background illumination, are shown in Fig. 1 and described in the legend. The neutral filters (Baird-Atomic B-1) passed a band about 7 nm wide at half-transmission. Peak transmissions were at 410–670 nm in steps of 10–20 nm. The spectral transmission of each filter in the flash channel was calibrated with a monochromator and photomultiplier and in the background channel with a spectrophotometer. The light through each filter was calibrated repeatedly with a photometer (United Detector Technology 40 A) both in units of energy and in photometric units.

The flash beam passed through a variable rectangular diaphragm to illuminate the retina with a slit or square of at most 3° by 3°. The slit could be rotated by a motor and moved by micrometer screws to any position on the 10° background field.

The animal's head was positioned to place the pupil at the focal point of the mixed beams and the beam of light was directed about the central axis of the eye by a light goniometer (Fig. 2). The neutral and colour wheels were moved by stepping motors and any combination of filters could be inserted electronically.

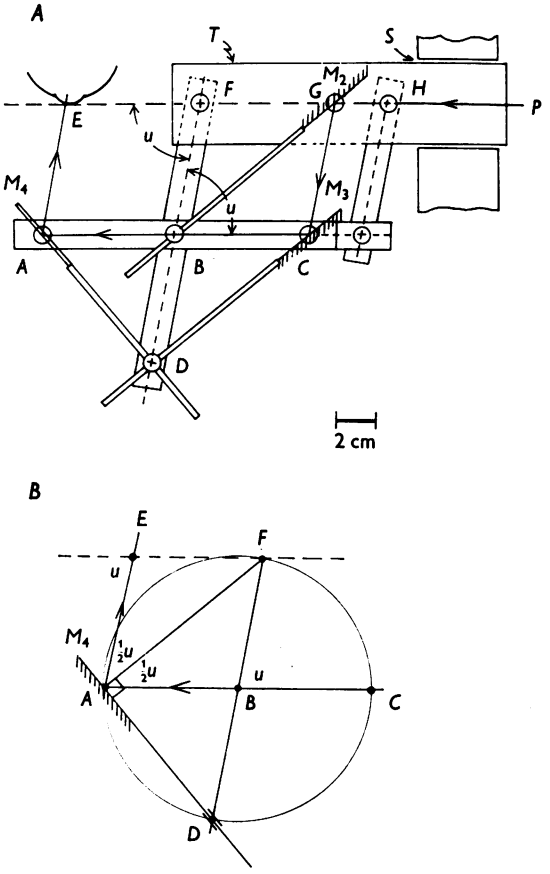

Fig. 2. *A*, shows the goniometer used to direct the light paths about the anterior nodal point of the eye and thus to different positions on the retina. The goniometer tilted mirrors M_2, M_3, M_4 so light from the periscope (Fig. 1) entering at P was directed through the pupil at E at any angle of incidence in the visual field. Rotation of tube T in bearing S around the axis PE determined one angular co-ordinate of the stimulus in the visual field. The second co-ordinate was determined by the angle u in the system of broad bars mounted on T by bearings at F and H. The distances between the bearings at A, B, C, D, F and G were equal. As shown in *B*, D moved on the perimeter of a circle and tilted mirror M_4 by the thin rod AD. Thus light along CA was reflected in direction AE parallel to FD, i.e. at an angle u from the incident beam. M_2 and M_3 were tilted similarly by rods BG and DC. The angular co-ordinates in the visual field were set by worm gears.

Procedure. For each acute experiment lasting 6–8 hr, the animal was anaesthetized with ketamine hydrochloride, intubated, established on artificial respiration adjusted to keep end-tidal CO_2 at 5·2–5·5%, paralysed with continuous I.V. gallamine triethiodide (Flaxedil[R]) and D-tubocurarine in 0·9% NaCl solution and kept on a N_2O/O_2 mixture (75/25%). The pupil was dilated with homatropine 1%, a contact lens (Guld & Bertulis, 1975) placed on the eye, the spot placed on the centre of fovea in the middle of the background field, and a platinized micro-electrode lowered into the cortex through bone wax and unopened dura. When action potentials from a cell were picked up, the colour, position, size and orientation of the slit or spot that gave the best response were found. The slit was varied in length and width to test for the presence of an inhibitory surround and the 'stopped-end effect' but no systematic effort was made to establish the type of receptive field of the cell by other means. Then the colour and illuminance of the background illumination were set. A combination of colour and illuminance of the spot and background was chosen as a reference to check at any time in a programme whether the cell was still responding as it did when it was found, or whether the position of the spot should be re-adjusted.

The standard series of stimuli was run by a PDP-8 computer (Digital Equipment Co.); 200 msec flashes were delivered at intervals of 2 sec. Two identical flashes were given through a neutral and eight narrowband filters at four to seven levels of equal photopic illuminance ($\pm$ 0·1 log unit adjusted from the human C.I.E. curve), of the order of 200–10,000 trolands. Throughout a run, the eye was either in the dark, or was illuminated with a steady white or spectral light (470, 550, 580, 630, and in later experiments, 510 nm) that covered 10° of visual angle including the area covered by the flash. The background illuminance was adjusted to be equal from the human photopic sensitivity curve. The effect of changing the illuminance of the background was recorded in all the early experiments; later an illuminance was found that gave the best response and the series run at that level, of the order of 400–1000 trolands (td). Other programmes were run as indicated by the spectral responsiveness of the cell displayed by the on-line computer write-out. When the series were finished the slit or square was traced (on *B*, Fig. 1). Since the cells could be held for 1–4 hr, recordings were usually made from two to three cells in each penetration.

The number of potentials in each 10 msec during the flash and the following 300 msec was written out on-line by the computer (Fig. 3). The latency and number of potentials during and after the flash were measured from film and from the computer write-out and were plotted as a function of relative quanta and of illuminance (C.I.E. photopic curve).

RESULTS

This report concerns seventy-three adequately studied cells in the region of the striate cortex corresponding to the foveal representation of twelve vervet monkeys.

Receptive fields

Responses were evoked by flashing stationary slits or square spots. About half the receptive fields of all cells were within 1° of the centre of the fovea, half were at 1·2–2°, and only three were at 3°. Cells encountered in the same penetration had overlapping receptive fields, though the optimal orientation of the slits rarely coincided. The optimal size of the slits was as small as 0·05°–0·1° × 0·2°. The largest slit was 0·2° × 2°.

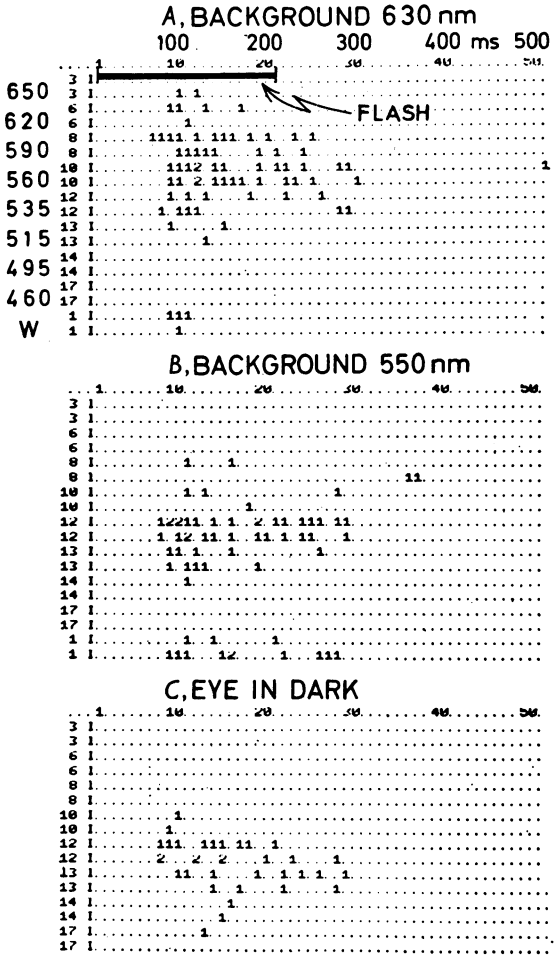

Fig. 3. An on-line computer write-out of the number of potentials in each 10 msec period (indicated by dots) during and after each 200 msec flash. The wave-lengths and code numbers are on the left. The flashes were of equal photopic illuminance (3·5 $\log_{10}$ trolands (td), C.I.E. curve). *W* is white. Unlike responses of geniculate cells, the on-response continued into the off-period. *A*, the precisely oriented slit, 0·1 × 0·3°, was flashed on a red background (3·0 $\log_{10}$ td). The peak number of potentials in the response was at 560 and 590 nm but there were a few potentials at a wave-length as short as 515 and as long as 650 nm. *B*, the spot was flashed on a green background (3·0 $\log_{10}$ td); the largest response was at 535 nm and the total range was less, 495–590 nm. *C*, when the eye was in the dark, the potentials were fewer, the largest response was at 535 nm, the range 460–560 nm and there was no response to white flashes.

Cells (thirty) that responded over a narrow spectral band

Response. The cells had little spontaneous activity; they gave on-responses (Fig. 4), the latency of which increased with decreasing intensity of the light. The number of potentials did not change uniformly with diminishing intensity; in half the cells the number decreased and in the rest it increased, remained level or fluctuated.

Off-responses were usually insignificant or absent. The largest off-response was usually at the same or nearly the same wave-length that

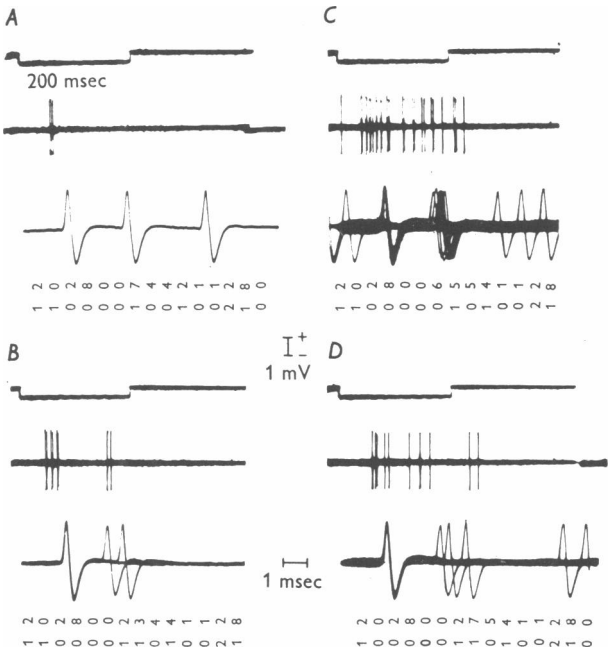

Fig. 4. Four responses of a narrowly responsive cell (positive, upward). These forms of response were seen frequently in cells in this category. *A*, the on-response had few potentials and the cell had little spontaneous activity (the only potentials the cell discharged in a 2 sec period were the three displayed on the middle and lower traces). *B*, the on-response could have an early and a late component. *C*, the on-response sometimes continued uninterruptedly into the period after the flash and it could be impossible to distinguish the onset of the off-response, unless an off-response sometimes came clearly after the on-response, as it does in *D*. Top trace, the 200 msec flash, which served as calibration of time for the middle trace, on which the potentials are displayed; bottom trace, the potentials on a fast time base, the sweep triggered by the potentials which are displayed after a delay (Nissen-Petersen *et al.* 1969). The numbers below each picture code the wave-length and intensity of the flash and of the background illumination, the amplification and the protocol number.

evoked the largest on-response. Opponent-colour responses, i.e. an on-response to some wave-lengths and an off-response to others, were seen with some backgrounds in eight cells. There were four among the five blue-sensitive cells and four among the sixteen red-sensitive ones. No yellow- or green-sensitive cell had opponent-colour properties.

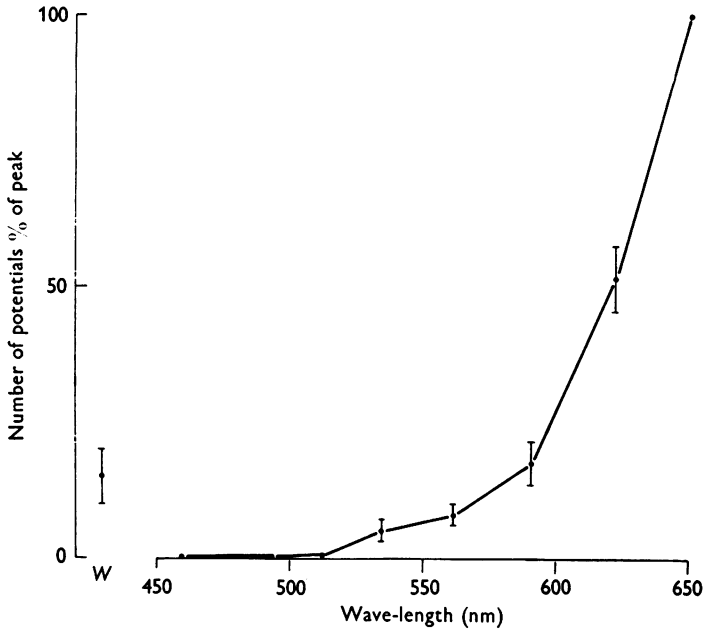

Fig. 5. The mean on-response of sixteen red-sensitive cells to flashes at different wave-lengths. At each wave-length, two flashes were given at each of five levels of equal photopic illuminance (C.I.E. curve). All these cells responded with the greatest number of potentials to 650 nm flashes, and the number at other wave-lengths is given as % of the peak number. The vertical bars give the S.E. of the mean. *W* is white.

Spectral responsiveness (Table 1, left; Figs. 5, 6). The spectral responsiveness was measured as the number of potentials in the on-response to flashes adjusted to be of equal brightness from the human photopic sensitivity curve. Red-sensitive cells (sixteen) gave the largest response to 650 nm flashes, the longest wave-length used (Fig. 5). Yellow-sensitive cells (five) responded maximally at 590 nm, the only yellow light used routinely; green-sensitive cells at 560 (three) or 535 nm (one) (Fig. 3); blue-sensitive cells (five) gave their greatest response at 495 nm (Fig. 6). In each group there was at least one cell that gave a large response to only

two narrow filters (peak transmission 20–30 nm apart). Most cells (eighteen of twenty-four) responded to white flashes but the response was sparse (Figs. 3, 5, 6).

Spectral sensitivity. The lowest intensity (relative quantal energy) of a flashed stimulus that just evoked a response was at the same wave-length that evoked the peak number of potentials in only eleven of twenty-seven

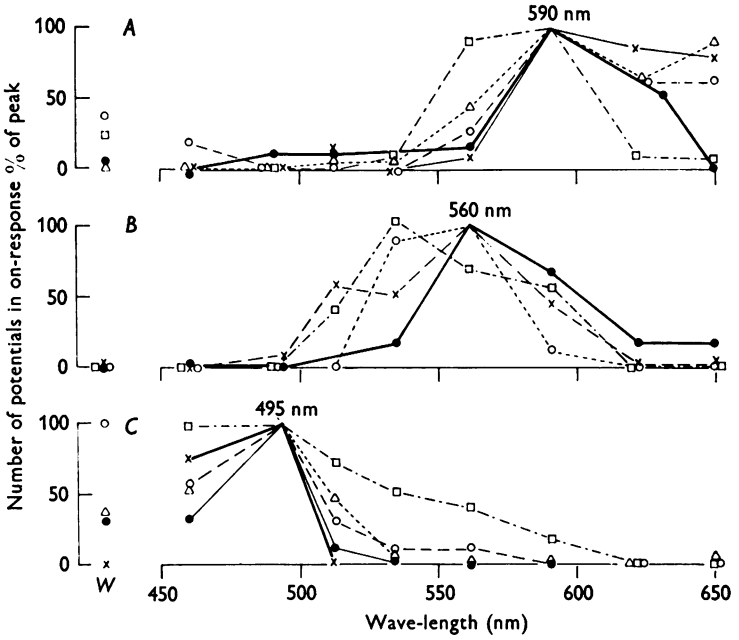

Fig. 6. *A*, the on-response of five yellow-sensitive cells, *B*, four green- and *C*, five blue-sensitive cells to flashes at different wave-lengths. For each wave-length two flashes were given at each of five levels of equal photopic illuminance (C.I.E. curve). The peak number of potentials is taken as 100% and the number at other wave-lengths is given as % of the peak number. The narrow interference filters had peak transmission about 30 nm apart and there was one cell in each group that responded to only two adjacent filters, shown by the heavy line. *W* is white.

cells (Table 1). The discrepancy was the rule for the red-sensitive cells (all had peak response at 650 nm): only one had its lowest threshold at 650 nm, three had their lowest threshold at 620 nm and ten gave few potentials when the flashes were green or yellow but these potentials appeared at lower intensities than did the responses to red (Fig. 7). Thus, at low levels of light intensity the spectral peak was shifted towards the photopic peak of sensitivity.

Most yellow- and all green-sensitive cells had the lowest threshold at the same wave-length as the greatest response (Table 1). Of the blue-sensitive cells, two of five had the lowest threshold at a shorter wave-length than that for the largest response.

Effect of the wave-length of the background. The background was a steady light centred on the fovea; it covered 10° including the area of the flash. The illuminance of the backgrounds was equal, adjusted from the human

TABLE 1. Cells that respond over a narrow spectral band. Wave-length for the peak number of potentials and for the lowest threshold

Wave-length for peak response		Wave-length for lowest threshold							
nm	No.	460	495	535	560	590	620	650	Unknown
460	0	—	—	—	—	—	—	—	—
495	5	2	**3**	—	—	—	—	—	—
535	1	—	—	**1**	—	—	—	—	—
560	3	—	—	—	**3**	—	—	—	—
590	5	—	—	—	1	**3**	—	—	1
620	0	—	—	—	—	—	—	—	—
650	16	—	—	—	4	6	3	**1**	2
	30								**11/27**

The wave-length for the peak response and for the lowest threshold coincided in eleven of twenty-seven cells (shown in bold type).

TABLE 2. Wave-length of the background that increased the response of narrow-band cells

Wave-length for largest response			Wave-length of the backrground for best response				
nm	Colour	No.	470	510	550	575	630
		A complementary colour					
495	Blue	1	—	—	—	1	—
535, 560	Green	3	—	—	—	—	3
590	Yellow	2	2	—	—	—	—
650	Red	6	—	—	6	—	—
		Opposite end of the spectrum from that for peak response					
495	Blue	3	—	—	—	—	3
650	Red	3	3	—	—	—	—
		Same wave-length as for peak response, or close to it					
495	Blue	1	—	1	—	—	—
560	Green	1	1	—	—	—	—
590	Yellow	3	—	—	1	1	1
650	Red	7	—	—	—	5	2

photopic sensitivity curve. The response of twelve of thirty cells was increased by a background of a complementary colour (Table 2). Six red-sensitive cells responded best when the background was green, and three green-sensitive cells when it was red. Two yellow-sensitive cells responded best when the background was blue and one blue-sensitive cell when it was yellow.

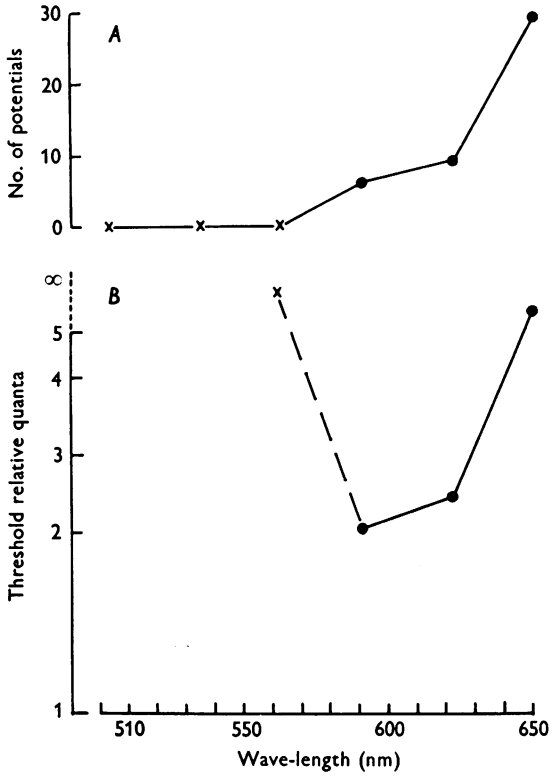

Fig. 7. To show the discrepancy between the spectral peak for the largest response and for the lowest threshold of a red-sensitive cell. The peak number of potentials was given at 650 nm, the lowest threshold at 590 nm. *A*, the number of potentials for different wave-lengths at equal levels of photopic illuminance (C.I.E. curve). Ordinate, linear scale. ×, indicates no response. *B*, the threshold as a function of relative quanta. Ordinate, logarithmic scale.

The response of six out of thirty cells was increased when the colour of the background was at the opposite end of the spectrum from that for peak response (Table 2). Three red-sensitive cells responded best when the background was blue and three blue-sensitive cells when it was red. In these cases the effect was most marked when the wave-length of the

background was furthest from that of the effective stimulus and became less as it approached that at which the cell responded best.

The response of twelve of thirty cells was increased by a background of the same, or nearly the same, wave-length as evoked the greatest response (Table 2): seven red-sensitive cells responded best when the background was 630 or 575 nm; three yellow-sensitive cells when it was 630, 575 or 550 nm; one green-sensitive cell when it was blue; and one blue-sensitive cell responded best when the background was 510 nm.

TABLE 3. Spectral responsiveness and orientation-specificity of cells in the foveal striate cortex

	Mainly on-response to a spectral band		On/off to all colours
	Narrowband	Broadband peak at G, Y or R	Broadband no peak
No.	30	26	17
Orientation specific	22 (73 %)	9 (35 %)	8 (47 %)
Flanking inhibition alone	11	7	6
Flanking inhibition + stopped-end	11	2	2
Not orientation specific	7 (23 %)	17 (65 %)	8 (47 %)
Inhibitory surround	2	10	2
No inhibitory surround	2	4	1
Inhibitory surround not tested	3	3	5
Unknown orientation specificity	1 (3 %)	0	1 (6 %)

The difference in orientation-specificity between narrow- and broadband cells is significant ($P < 0{\cdot}01$).

G, green; Y, yellow; R, red.

Orientation specificity. Of the twenty-nine cells tested, twenty-two responded only to a slit with a particular width and orientation and eleven of them stopped responding when the slit was lengthened ('stopped-end effect') (Table 3). The proportion of narrow band cells found to be orientation specific is significantly higher than that of broadband cells ($P < 0{\cdot}01$). In general, when the width of an optimally dimensioned slit was doubled, the cell stopped responding. The orientation of the slit was critical; most cells responded only if the orientation was less than 10° from the optimal one. If the cells tolerated a deviation of more than $\pm 45°$, they were not classified as orientation specific. Seven cells responded to a square and two of them responded less to a large square, i.e. there was an inhibitory surround.

Cells (twenty-six) that responded over a broader band of the spectrum but still showed a spectral maximum

Response. These cells had little spontaneous activity; they gave on-responses with a mean of 50% more potentials than narrowband cells. The latency increased and the response decreased with decreasing intensity, i.e. the responses were graded according to the intensity of the flashes, except at the highest intensities used, when the number decreased and the latency tended to be longer ('over-loading').

The response of these cells was to all wave-lengths but it was not the same, for photopically equated flashes, across the spectrum. These cells

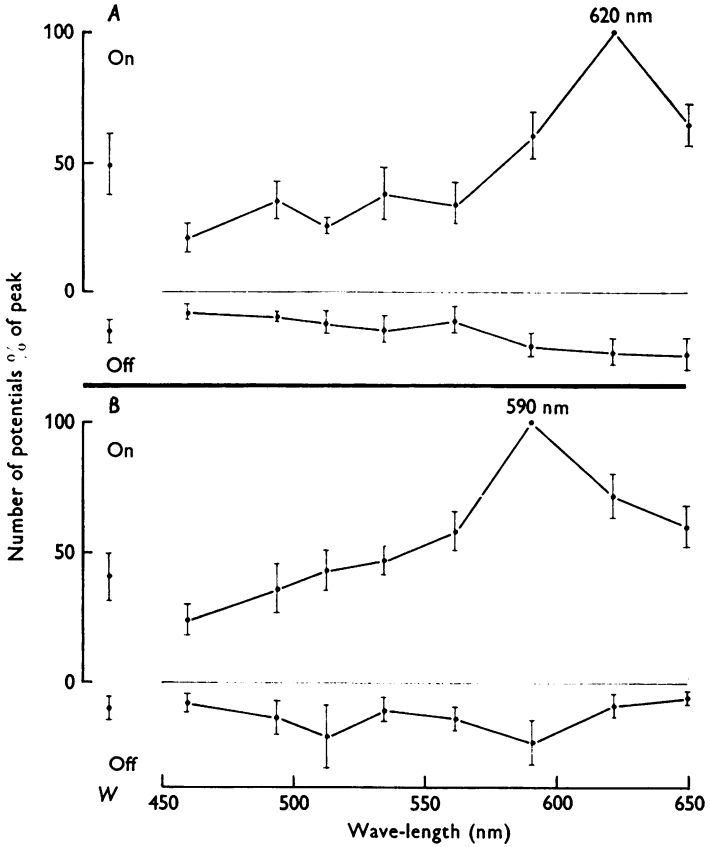

Fig. 8. Mean on/off-responses to flashes at different wave-lengths of cells that responded across the spectrum: *A*, with peak response to red 620 nm (seven); or *B*, to yellow 590 nm (eight). The peak number is taken as 100 and responses to other wave-lengths are expressed as % of the peak number. The vertical bars give the S.E. of the mean. *W* is white.

responded maximally at middle and long wave-lengths. The cells that responded mainly to yellow or red could give a fairly prominent off-response, some to the wave-length that evoked the greatest on-response and some to green (Fig. 8). The cells that responded mainly to green gave few potentials after the flash, or the on-response continued without pause after the flash, making it difficult to identify a response to the end of the flash. None of these cells gave opponent-colour responses.

TABLE 4. Cells that responded over a broader spectral band but with a spectral peak. Wave-length for the largest response and for the lowest threshold

Wave-length for largest response		Wave-length for lowest threshold							
nm	No.	495	515	535	560	590	620	650	Unknown
495	0	—	—	—	—	—	—	—	—
515	1	—	—	—	1*	—	—	—	—
535	4	1†	—	—	1*	1	—	—	1
560	3	—	—	2†	**1**	—	—	—	—
590	8	—	—	3†	1*	**2**	1	—	1
620	7	—	—	2†	1*	1*	**2**	—	1
650	3	—	—	—	2*	—	—	—	1
	26							5/22	

The wave-length at the maximal response and at the lowest threshold coincided in five of twenty-two cells (shown in bold type).

* Threshold closer to the photopic peak of sensitivity than the largest response.

† Threshold closer to the scotopic peak of sensitivity than the largest response.

Spectral responsiveness (Fig. 8). The spectral responsiveness was measured as the number of potentials in the on-response to flashes adjusted to be of equal brightness from the human photopic sensitivity curve. Of the ten red-sensitive cells (Table 4, left), only three gave the largest response at 650 nm; all the others gave the largest response at 620 nm. All eight yellow-sensitive cells responded with most potentials to 590 nm flashes. The green-sensitive cells responded mainly at 560 or 535 nm and one cell had a stable peak at 515 nm. The cells responded to white flashes, the mean being about half of the peak response (Fig. 8).

The peak response of the green-sensitive cells could vary and shift to a different wave-length in the green portion of the spectrum or less often in the yellow or red band. The shifts seemed to occur with changes in the colour or illuminance of the background, or occasionally with small changes in the position of the spot.

Spectral sensitivity. The lowest intensity (relative quantal energy) of a flashed stimulus that just evoked a response was at the same wave-length

that evoked the peak number of potentials in only five out of twenty-two cells (Table 4). The lowest threshold of seven cells was closer to the photopic peak of sensitivity, whereas eight cells had the lowest threshold closer to the scotopic peak than was the greatest response. Two cells had the lowest threshold at a longer wave-length than the peak response, away from the photopic peak.

Effect of the wave-length of the background. The response of sixteen out of twenty-six cells was increased when the background was green (550 nm), whether the cell's peak response was at green, yellow or red. In all, the response of half the cells (fourteen out of twenty-six) was increased when the colour of the background was complementary to that at the peak response: eight red-sensitive cells when the background was green, three green-sensitive cells when it was red and three yellow-sensitive cells when it was blue or blue-green. The response of eleven cells was increased when the colour of the background was the same as or close to that at peak response: one red-sensitive cell when it was red; five green-sensitive cells when it was green (four) or yellow; and five yellow-sensitive cells when it was green (four) or yellow. Finally, one red-sensitive cell responded best when the background was blue. Thus eighteen out of twenty-six (69 %) were activated by excitatory/inhibitory colour pairs that have been described in the geniculate nucleus (see Discussion).

Orientation specificity. Of these cells, nine of twenty-six were orientation-specific (Table 3). This is a significantly smaller proportion than that of narrowband cells. Three quarters of the cells without orientation specificity had an inhibitory surround, an insignificant difference compared with the four of seven cells in the other two groups ($P > 0{\cdot}1$).

Cells (seventeen) that responded to flashes of all colours and white

Seventeen cells had moderate to much spontaneous activity. They responded with a profuse discharge both during and after flashes of all or most wave-lengths and white. Cells in this group were not uniform. The response of some was flat across the equal-luminosity spectrum, whereas others had a smaller response either at the blue or at the red end of the spectrum. The response of some cells increased with increasing intensity, whereas the response of others changed little, or even decreased at the highest illuminance used. Some of these cells were little affected by the wave-length of the background, whereas the response of others was depressed at the wave-length of the background. A more detailed analysis of these cells is underway.

Like broadband cells with a spectral peak, half of these cells were orientation specific (Table 3). The difference from narrowband cells is significant ($P < 0{\cdot}01$).

Location of receptive fields

The receptive fields of half the cells that responded mainly or solely over a restricted spectral band lay within 1° from the centre of the fovea and half at 1·2–2°. The receptive fields of only four of sixteen cells that responded to flashes of all colours were within 1° from the centre of fovea and twelve were at 1·2–2°. The difference is not significant ($0{\cdot}1 > P > 0{\cdot}05$).

Depth below the first cell

Of the narrowband cells and of the cells that responded to a broader band, two thirds lay in the 0·6 mm below the first cell. Of the cells that responded to all colours, only a quarter were in the first 0·6 mm. The difference in depth between cells with a narrow or broad spectral peak and those that responded to all colours is significant ($P < 0{\cdot}05$).

DISCUSSION

In our sample of cells in the foveal striate cortex of monkey, more than a third gave mainly on-responses solely over a narrow band of the spectrum, in agreement with our previous studies (Lennox-Buchthal, 1962, 1965; Andersen *et al.* 1962). The main finding in this study, that most cells that responded over a narrow band of the spectrum required a precisely oriented and dimensioned slit to respond, is at variance with that of Dow & Gouras, who found foveal cortical cells to be either 'spatial-coded' or 'colour-coded' but rarely both (10 %, Dow & Gouras, 1973; 28 %, Gouras, 1974). The discrepancy can perhaps be explained by the fact that we had little difficulty in holding cells; for Dow & Gouras (1973) supposed that, although they recorded rather few, such cells might be numerous: 'the small spike size, difficulty in isolation and general fastidiousness of these cells suggest them to be more common than the small numbers might imply'. We have no explanation for another discrepancy: half the cells we found that responded across the spectrum were not orientation-specific, whereas cells that were either not 'colour-coded' (Dow & Gouras, 1973) or 'luminosity cells' (Poggio *et al.* 1975), were mainly orientation specific.

It has been assumed (Dow & Gouras, 1973; Gouras, 1974) that the narrowband cells are in fact 'colour-opponent'. The effect we saw of changing the wave-length of the background did not support this contention. When a coloured background increased the response of a narrowband cell, we supposed the cell to have been inhibited by that colour. Then the response of only twelve out of thirty cells was increased by a background of an opponent colour ($R^{+}G^{-}$, $Y^{+}B^{-}$ or vice versa, De Valois, 1972).

Our findings differ as well from previous reports (Dow & Gouras, 1973;

Gouras, 1974; Yates, 1974; Poggio *et al.* 1975) of many 'opponent-colour' cells in or close to the striate area of foveal representation. We found only eight in the group of thirty cells that responded over a narrow spectral range (and none in the other groups) and most of them did not respond precisely as has been described. The on-response found within a restricted spectral band was in fact on/off and the rare pure off-response was usually to all colours but was greatest at another region of the spectrum. We interpret our findings as indicating that features of cortical organization modify the signals that arrive from the geniculate nucleus (Guld & Lennox-Buchthal, 1968). In view of this finding, the spectral responsiveness of cortical cells can hardly be attributed to more peripheral mechanisms, such as one or the other type of cone, as has been assumed by Dow & Gouras (1973; Gouras, 1974).

TABLE 5. Excitatory–inhibitory pairs of colours: narrowband cells in the foveal striate cortex (this study) and cells in the geniculate nucleus (references 1, 2)

Striate No. of cells	Geniculate (Reference)	Excitatory colour	Inhibitory colour
1	0	Blue	Blue-green
0	(1)	Blue	Green
1	(2)	Blue	Yellow
3	0	Blue	Red
1	(1)	Green	Blue
0	0	Green	Green
0	0	Green	Yellow
3	(1, 2)	Green	Red
2	(2)	Yellow	Blue
1	(1)	Yellow	Green
1	0	Yellow	Yellow
1	0	Yellow	Red
3	0	Red	Blue
6	(1, 2)	Red	Green
5	0	Red	Yellow
2	0	Red	Red
30			

References: (1) Wiesel & Hubel, 1966; (2) De Valois, 1972. Total: colour pairs of cells in both the striate cortex and geniculate nucleus, fourteen; in the striate cortex alone, sixteen.

Hubel & Wiesel (1968) described some responses to colour of cortical cells that could not be explained unless several geniculate cells projected to the same cortical cell. Gouras (1974) also reported that 'in contrast to cells in the geniculate nucleus many (striate) cells receive centre–surround antagonism from the *same* cone mechanism'. We have seen similar cells and have tried to estimate how frequent they are. One half of the narrow-band cells in the cortex were activated by excitatory–inhibitory colour

pairs that seem not to have been described in the geniculate nucleus (Table 5), confirming the conclusion that features of cortical organization are implicated (Guld & Lennox, 1968; this study). That cortical cells behave differently to cells in the geniculate nucleus casts doubt on the validity of explanations of psychophysical phenomena in terms of findings in the geniculate nucleus (De Valois, Jacobs & Jones, 1963).

Our findings, too, can be criticized for failing to explain psychophysical phenomena. Possibly much information as to colour is derived from secondary projection to Zeki's fourth visual area (Zeki, 1973, 1974). On the other hand, such orientation- and colour-specific neurones as we found could well mediate the colour- and orientation-contingent after-effects first described by McCollough (1965).

Since we did not see (with few exceptions) manifest 'colour-opponency' as it has been described in the geniculate nucleus (De Valois *et al.* 1963; Wiesel & Hubel, 1966; De Valois, 1972), we can hardly have been recording from geniculostriate fibres. Even the cells that responded across the spectrum, and lay 1·0 mm or more below the first unit, gave on/off-responses to all colours, whereas Wiesel & Hubel (1966) found that geniculate cells had either an on- or an off-response depending on the colour of the stimulus but rarely gave on/off-responses.

Other workers (De Valois *et al.* 1963; De Valois, 1972; Poggio *et al.* 1975) have used the number of potentials evoked by a flash as a measure of the spectral sensitivity of a cell and to do so may be justified in the case of the geniculate nucleus. In the striate cortex, however, the spectral locus that evoked most potentials was the same as that of lowest threshold in only sixteen of forty-nine cells. The wave-length at which the threshold was lowest was closer to the photopic or to the scotopic peak of sensitivity (depending on the cell's responsiveness) than the wave-length that gave the most profuse response. Thus, the afferent input to the cell can be different when the light is weak (at threshold) and when it is strong (peak response). In view of this fact, it is inevitable that our findings differ somewhat from those of others, who used mainly threshold intensities of light (Hubel & Wiesel, 1968; Dow & Gouras, 1973; Gouras, 1974; Poggio *et al.* 1975).

It is not clear how many of the 'tuned' and 'colour-opponent' cells (Poggio *et al.* 1975) correspond to the cells in our sample that responded only over a narrow band of the spectrum. If the correspondence is close, then the findings are at variance: one fifth were simple and none was hypercomplex (Poggio *et al.* 1975) whereas in our sample more than a third were simple and more than a third hypercomplex. In agreement with Yates (1974) and Poggio *et al.* (1975) more than half the cells we found were, or probably were, 'luminosity' cells.

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