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IDENTIFICATION OF CONE MECHANISMS IN MONKEY GANGLION CELLS

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SUMMARY

1. Blue, green, and red sensitive cone mechanisms have been studied in two types of on-centre ganglion cells in the Rhesus monkey's retina.

2. One type of cell receives signals from both green and red sensitive cone mechanisms, both of which excite in the centre and inhibit in the periphery of the cell's receptive field. These cells discharge transiently to maintained stimuli of any wave-length and are called *phasic*.

3. The second type of cell receives excitatory signals from only one cone mechanism, either blue, green or red sensitive, in the centre, and inhibition from another cone mechanism in the periphery of its receptive field. These cells discharge continuously to maintained stimuli of appropriate wave-length and are called *tonic*.

4. Tonic cells outnumber phasic cells although both are found adjacent to one another throughout the retina. Phasic cells are relatively more common toward the periphery and tonic cells relatively more common toward the fovea.

INTRODUCTION

Cone vision of the Rhesus monkey resembles that of man (Grether, 1939; De Valois, 1965*a*; Sperling, Sidley, Dockens & Jolliffe, 1968). Blue, green and red absorbing cone receptor cells have been found in this monkey's retina (Brown & Wald, 1963; Marks, Dobelle & MacNichol, 1964). Similar cone mechanisms have also been detected electrophysiologically from single neurones in the lateral geniculate nucleus of monkeys (De Valois, 1965*b*; Wiesel & Hubel, 1966). At this stage in the visual system classes of cells are found which receive either spatially or spectrally antagonistic cone mechanisms.

It would be interesting to know what retinal organization underlies the cone signals which arrive at the lateral geniculate nucleus. The present

study examines this problem by determining the retinal distribution and receptive field organization of ganglion cells of the Rhesus monkey, receiving signals from blue, green and red sensitive cone mechanisms. An abstract mentioning some of these results has been published (Gouras, 1968).

METHODS

The methods were similar to those of previous studies (Gouras & Link, 1966; Gouras, 1967). Responses of ganglion cells were detected by introducing fine glass micropipette electrodes into the retina of monkeys (*Macaca mulatta*) anaesthetized with sodium pentobarbitone. Light stimuli were obtained from a xenon arc lamp providing two independent beams, presented to the eye in Maxwellian view. The area, timing, energy, wave-length and retinal position of the stimuli obtained from these beams could be controlled independently. One beam was the test, the other the adapting stimulus. The receptive field centre of each ganglion cell was determined by placing a 0·0004 mm^2 spot over the retinal area that produced the strongest response. Movements of 0·02 mm or less were sufficient to reduce markedly the effectiveness of such spots. Thresholds to this and larger spots or an annulus, placed concentrically over the receptive field of each cell, were based on the energy of monochromatic light which produced a response from the cell at least 90 % of the time. These test stimuli were usually 100 msec in duration and were repeated every second. The retina was maintained in a light-adapted state and thresholds were always determined in the presence of an adapting light, completely covering the cell's receptive field and of sufficient energy to raise rod thresholds above those of cones (Gouras, 1967). Either one of three wave-length bands was used as the adapting light, obtained from Corning sharp cut glass filters, 2408 (red), 3482 (yellow) and 5543 (blue). The approximate energies of these adapting lights in $\log_{10}$ quanta/sec. mm^2 retina were 11·2, 11·5 and 11·0, respectively. Thresholds were determined about a minute or longer after any change in the adapting light.

RESULTS

Phasic cells. Figure 1 illustrates how slightly suprathreshold responses of an on-centre ganglion cell to a test stimulus (610 nm) change in the presence of either a red (above) or blue (below) adapting light. After a transient depression at the onset of either adapting light, the responses reappear within a period of 5–10 sec. The responses of such cells, to even relatively small spots of light, are brief, lasting less than the duration of the stimulus. There is no maintained discharge to diffuse adapting lights of any wave-length. Because of their brief responses to maintained stimuli, such cells have been called *phasic*.

Figure 2 shows how the receptive field organization of such a cell, tested with both 456 and 610 nm stimuli, changes with the wave-length of the adapting light. In the presence of the blue adapting light, the cell is more sensitive to 610 nm than to 456 nm stimuli. The red adapting light reduces this difference by decreasing the thresholds to 456 nm and increasing those to 610 nm, similarly throughout the receptive field. Under all conditions, the cell's thresholds are lower to small than to large spots.

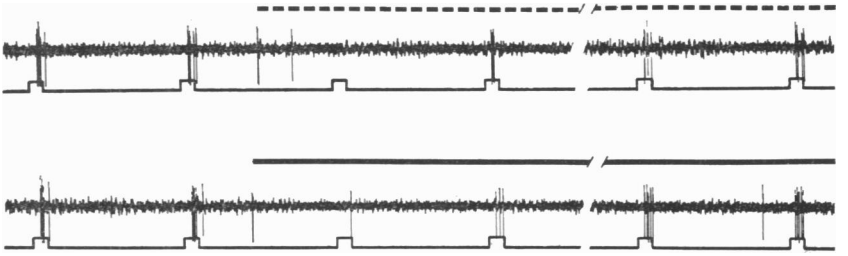

Fig. 1. Responses of a phasic on-centre cell to a 0·004 mm² test spot (610 nm) centred in its receptive field before and after turning on a red adapting light (dashed line above) in the upper, and blue adapting light (continuous line above) in the lower oscillograph. The responses shown after the break in the oscillographs have been obtained 9–10 sec after the start of the adapting light. The photocell's response to the test stimulus, 100 msec in duration and presented every second, is below the cell's responses. Positivity is upwards.

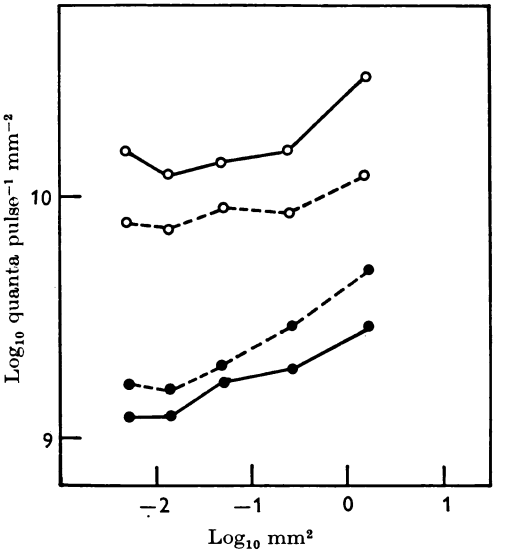

Fig. 2. Thresholds of a phasic on-centre cell in $\log_{10}$ of the number of quanta in the light pulse/mm² of retina (610 nm, ●; 456 nm, ○) to concentric spot stimuli of different sizes ($\log_{10}$ mm² of retina) in the presence of the red (---) and blue (—) adapting light.

Figure 3 shows the action spectra of three such cells obtained in the presence of the red (open symbols) and blue (filled symbols) adapting lights. The red adapting light raises the thresholds to long more than to short wave-length stimulation; the blue adapting light does the converse. In the former case, the action spectra resemble the π_4 and, in the latter, the π_5 mechanism of Stiles (1959).

Tonic cells. Figure 4 (above) shows how an on-centre ganglion cell,

receiving excitatory signals from a red sensitive cone mechanism, responds to a 610 nm test stimulus in the presence of the red and blue adapting lights. The blue adapting light tends to inhibit the cell and, during this time, the test stimulus strongly excites the cell. The red adapting light continuously excites the cell and, during this time, the test stimulus is

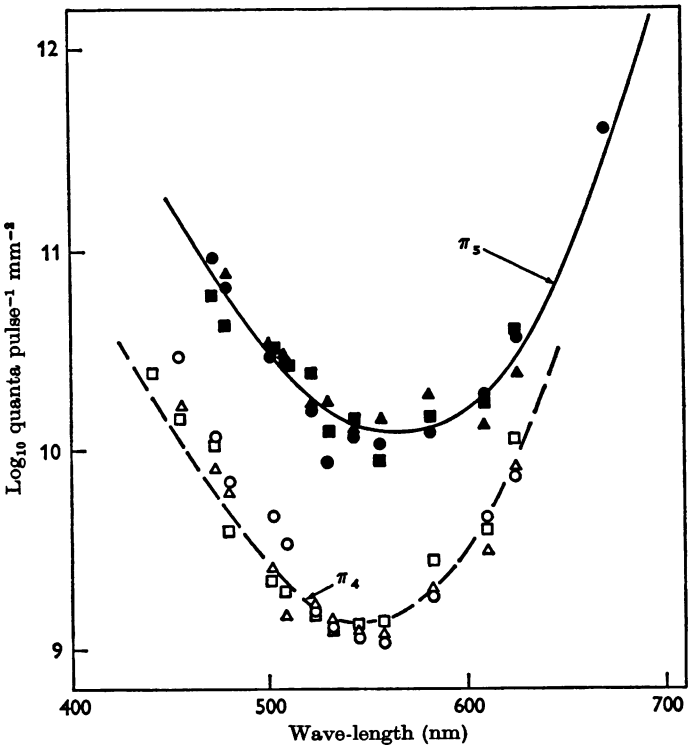

Fig. 3. Thresholds of 3 phasic on-centre cells in log $_{10}$ relative quanta for different wave-lengths in nanometers in the presence of the red (open symbols) and blue (filled symbols) adapting light. Thresholds of each cell have been shifted vertically so that the thresholds at 531 nm coincide. The dashed and continuous lines are the π_4 and π_5 mechanisms of Stiles (1959), respectively.

ineffective. These cells, in contrast to phasic ones, discharge continuously to maintained stimuli of appropriate wave-length and, consequently, have been called *tonic*.

Figure 4 (below) shows how two such tonic on-centre cells, one (spikes of large amplitude) receiving excitatory signals from a red, the other (spikes of small amplitude) receiving excitatory signals from a green sensitive cone mechanism, behave in the presence of the same adapting lights. The red adapting light tends to excite the former and inhibit the

latter cell. The blue adapting light does the converse. The test stimulus (610 nm) excites the cell which is being inhibited and tends to inhibit the cell which is being excited by the adapting light. The unresponsiveness of the excitatory mechanism in the presence of an excitatory adapting light is not due to overstimulation of these ganglion cells because the frequency of firing elicited by such an adapting light is lower than the excitatory response to the test stimulus.

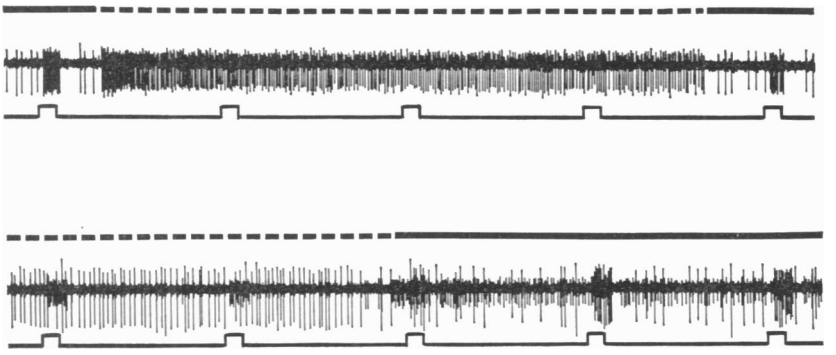

Fig. 4. Upper set of oscillographs shows the responses of a tonic on-centre cell, receiving excitatory signals from a red sensitive cone mechanism, to a 0·004 mm² test spot (610 nm), centred in its receptive field, in the presence of the blue (continuous line above) and red (dashed line above) adapting light. Lower set of oscillographs shows the responses of two tonic on-centre cells, one (spikes of large amplitude) receiving excitatory signals from a red, the other (spikes of small amplitude) receiving excitatory signals from a green sensitive cone mechanism, to a 1·54 mm² test spot (610 nm), placed over the centres of the receptive fields of these two cells, in the presence of the same adapting lights. A photocell's response to the stimulus, 100 msec in duration and presented every second, is below the cells' responses. Positivity is upwards.

Figure 5 shows the action spectra of such a cell determined with both small and large spot stimuli in the presence of the blue and then the red adapting light. With the blue adapting light, thresholds are lower and excitation is produced at all wave-lengths. The action spectra obtained with small and large spots are similar with their lowest thresholds toward the red end of the spectrum. With the red adapting light, weak responses are obtained with the large spot, which elicits excitation at long and inhibition at short wave-lengths. Under these circumstances the cell is more sensitive to an annulus of the same area, which produces inhibition at all wave-lengths (Fig. 5). This inhibitory mechanism has its lowest threshold in the green region of the spectrum. Other cells are found in which the action spectra of these excitatory and inhibitory mechanisms are reversed.

Figure 6 shows the action spectra of the excitatory mechanism of thirteen such cells, nine receiving excitatory signals from a red and four from a green sensitive cone mechanism, the former obtained in the presence of the blue and the latter in the presence of the red adapting light. The action spectra are narrower than the π_5 and π_4 mechanisms of Stiles (1959), respectively. The lowest thresholds of the red sensitive mechanism are at approximately 590 nm, displaced toward long wavelengths in comparison to π_5. The lowest thresholds of the green sensitive mechanism are at approximately 530 nm, displaced toward short wavelengths in comparison to π_4.

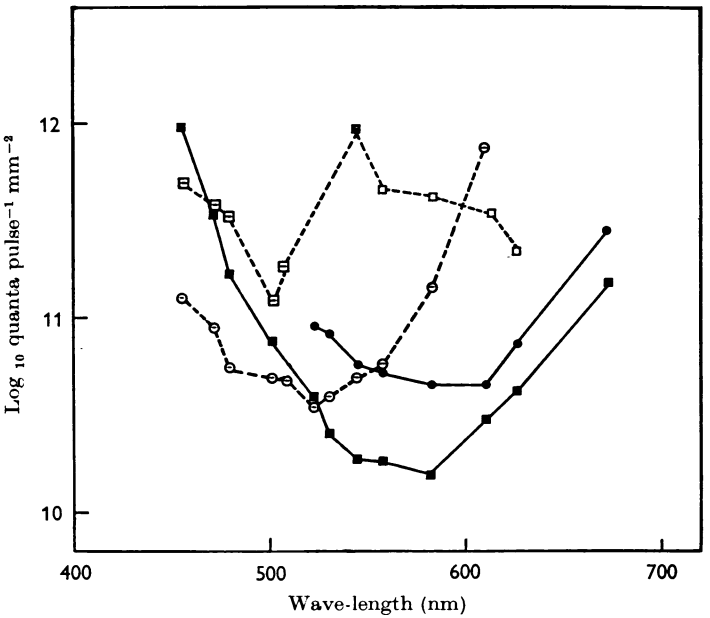

Fig. 5. Thresholds of a tonic on-centre cell in $\log_{10}$ of the number of quanta in the light pulse/mm² of retina at different wave-lengths in nm to a 0·004 mm² (●) and a 1·54 mm² (■, □) test spot and an annulus (○) in the presence of the red (---, □, ○) and blue (—, ●, ■) adapting light. The horizontal line within some of the open symbols indicates that the response at threshold is inhibition; otherwise the threshold response is excitation.

Blue sensitive cells. Tonic on-centre cells, receiving excitatory signals from only a blue sensitive cone mechanism, are also found. Figure 7 shows the responses of such a cell to 442 (above) and 610 (below) nm stimuli in the presence and absence of a strong yellow adapting light. In the presence of the adapting light only the 442 nm stimulus affects the cell. This excitatory response is momentarily suppressed by removal of the adapting light. Even after this transient effect subsides, the response to 442 nm remains

weaker in the absence than in the presence of the adapting light. In the absence of the adapting light, 610 nm inhibits the cell. Such cells discharge continuously to maintained stimulation with blue light and are also called tonic.

Figure 8 shows the action spectra of the excitatory and inhibitory mechanisms influencing such a cell, the former determined in the presence of the yellow and the latter in the presence of the blue adapting light. The excitatory mechanism has its lowest threshold at approximately 450 nm. Beyond about 530 nm, thresholds are determined by the inhibitory mechanism even in the presence of the yellow adapting light. This inhibitory mechanism has its lowest threshold at approximately 540 nm.

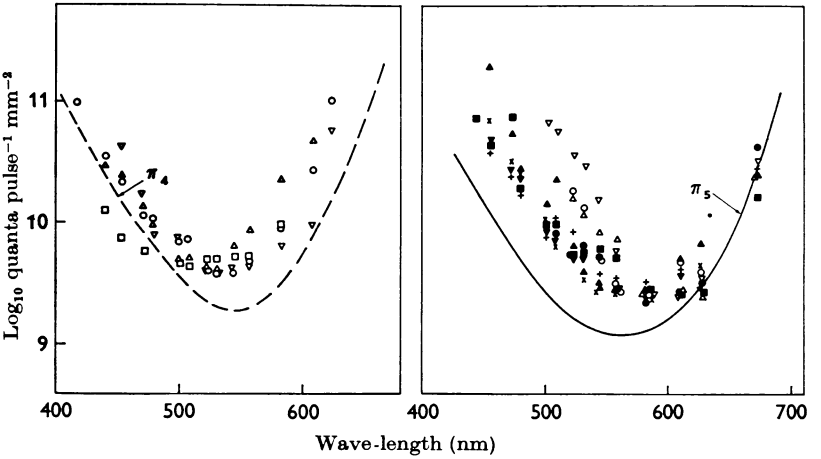

Fig. 6. Thresholds of the excitatory mechanism of thirteen tonic on-centre cells in $\log_{10}$ relative quanta at different wave-lengths in nanometers for either 0·004 or 1·54 mm² spots centred in the receptive field of each cell. The open symbols on the left are for four cells, excited in the presence of the red, and the symbols on the right for nine cells, excited in the presence of the blue adapting light. Thresholds of each cell on the left have been shifted vertically so that the thresholds at 523 nm coincide; those on the right have been made to coincide at 583 nm. The dashed and continuous lines are the π_4 and π_5 mechanisms of Stiles (1959), respectively.

Figure 9 shows the action spectra of seven such tonic and three phasic cells determined in the presence of the yellow adapting light. In addition, the latencies of these threshold responses are included for the phasic and three of the tonic cells. The action spectra of the blue sensitive mechanism resembles the π_1, π_3 mechanisms of Stiles (1959) and the latencies of the responses of this mechanism at threshold are approximately 50 msec. At wave-lengths longer than about 530 nm, where π_1 and π_3 differ, thresholds are determined by the antagonistic cone mechanism and response latencies at threshold are comparatively short. In the presence of the same yellow

adapting light, no evidence of a blue sensitive mechanism is found in the phasic cells. The latencies of these responses at threshold are the same at all wave-lengths and similar to those of the inhibitory mechanism affecting the blue sensitive cells. The differences in the latencies of these responses at threshold seem due to the fact that the yellow adapting light affects the red and green much more than the blue sensitive cone mechanism (Gouras, 1967).

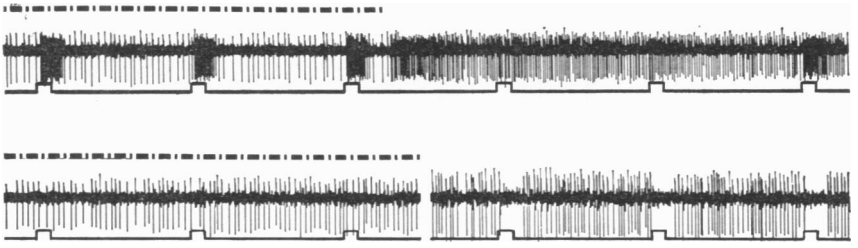

Fig. 7. Responses of a tonic on-centre cell, receiving excitatory signals from a blue sensitive cone mechanism, to a 1·54 mm² test spot, 442 nm (above) and 610 nm (below), centred in the cell's receptive field in the presence (on the left, dashed line above) and absence (on the right) of the yellow adapting light. The responses to 442 nm show the behaviour of the cell immediately after the adapting light has been turned off. A photocell's response to the test stimulus, 100 msec in duration and presented every second, is below the cell's responses. Positivity is upwards.

Figure 10 shows the responses of a phasic and a blue sensitive tonic cell to identical stimuli from three different regions of the spectrum. The phasic cell is excited by all the stimuli but most weakly by 419 nm. The tonic cell is only excited by the 419 nm stimulus.

Retinal organization of phasic and tonic cells. Phasic and tonic cells are found directly adjacent to one another within the retina. Figure 11 shows responses of a phasic and a tonic cell recorded simultaneously, while the wave-length of the adapting light is changed. The phasic cell (spikes of large amplitude) is excited periodically by a small spot (610 nm) centered in its receptive field, in the presence of either the red or blue adapting light. Except for an initial transient, the phasic cell is not excited by the adapting lights. The tonic cell (spikes of small amplitude), which receives excitatory signals from a green sensitive cone mechanism, is excited continuously by the blue and inhibited by the red adapting light.

Figure 12 shows thresholds of the excitatory mechanism of phasic and tonic on-centre ganglion cells to concentric spot stimuli of different sizes. The phasic cells have been studied in the presence of the red adapting light. The tonic cells have been studied in the presence of an adapting light of wave-length appropriate to suppress selectively the antagonistic surround

mechanism. The receptive field centres of phasic cells appear to be smaller than those of tonic cells. Tonic cells, receiving excitatory signals from either red or green sensitive cone mechanisms, have smaller receptive field centres than those receiving excitation from the blue sensitive mechanism. The tonic cells, which show less spatial summation than the others in each group, also tend to be closer to the fovea.

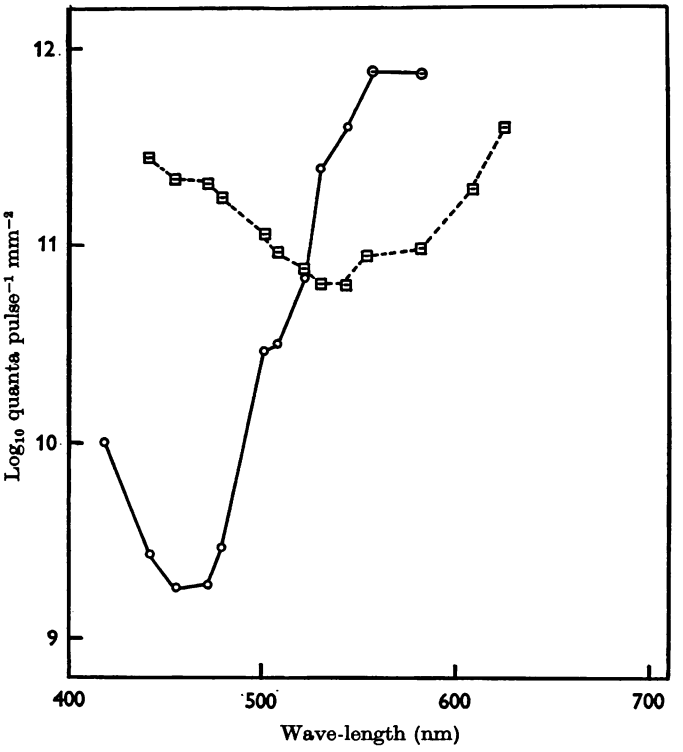

Fig. 8. Thresholds of a tonic on-centre cell in $\log_{10}$ of the number of quanta in the light pulse/mm^2 of retina at different wave-lengths in nanometers for a 1·54 mm^2 spot centred in the cell's receptive field. Thresholds for the excitatory (circles connected by continuous lines) and inhibitory mechanisms (squares connected by dashed lines) have been obtained in the presence of the yellow and blue adapting lights, respectively. A horizontal line within the symbol indicates an inhibitory response at threshold; otherwise the threshold response is excitation.

Figure 13 shows the retinal distribution of 72 phasic and tonic on-centre ganglion cells. Although both cells are found throughout the retina, tonic cells outnumber phasic ones. Phasic cells are relatively more common toward the periphery and tonic cells relatively more common toward the fovea.

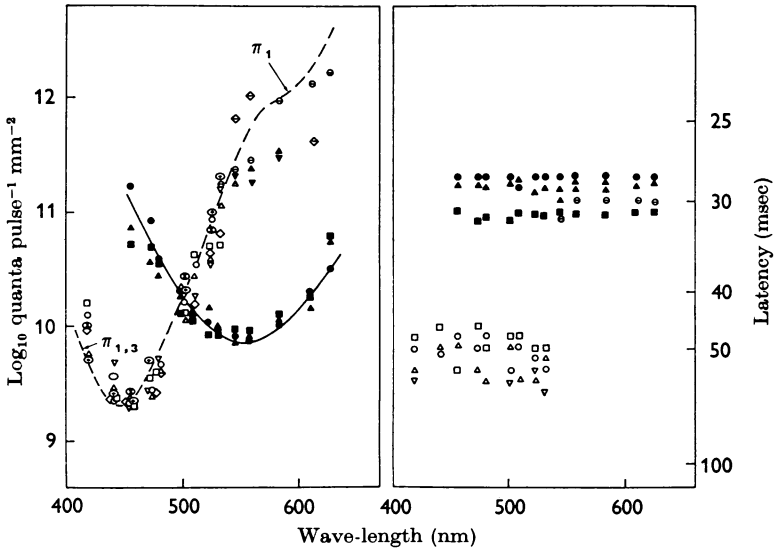

Fig. 9. Thresholds (left) in log $_{10}$ relative quanta for 10 on-centre cells, seven tonic (open symbols) and three phasic (filled symbols), and latency at threshold on a reciprocal scale of msec for the phasic and three of the tonic cells at different wave-lengths in nm and obtained in the presence of the yellow adapting light. The test stimulus, centred in each cell's receptive field, is either 0·25 or 1·54 mm^2 for the tonic and 0·004 mm^2 for the phasic cells. Thresholds of each tonic cell have been shifted vertically so that the thresholds at 456 nm coincide; those of the phasic cells have been made to coincide at 531 nm. The horizontal line within some of the open circles indicates that the response at threshold is inhibition; otherwise the threshold response is excitation. The dashed line is the π_1, π_3 mechanism of Stiles; the continuous line is the Commission Internationale de l'Eclairage (C.I.E.) photopic luminosity function.

DISCUSSION

Phasic and tonic cells. The cone system in the Rhesus monkey's retina communicates with the lateral geniculate nucleus through two types of on-centre ganglion cells. One type receives signals from both green and red sensitive cone mechanisms, both of which are excitatory in the centre and inhibitory in the periphery of the cell's receptive field. Signals from blue sensitive cones cannot be detected in these cells. The action spectra of the green and red sensitive mechanisms resemble the π_4 and π_5 mechanisms of Stiles (1959), respectively. The thresholds of either of these two mechanisms can be elevated selectively by chromatic adaptation, allowing the other to determine the sensitivity of the ganglion cell. These cells have been called phasic because they are excited only briefly by prolonged stimulation of any wave-length. Because of this phasic behaviour, such cells appear to transmit only the earliest excitatory signals which reach

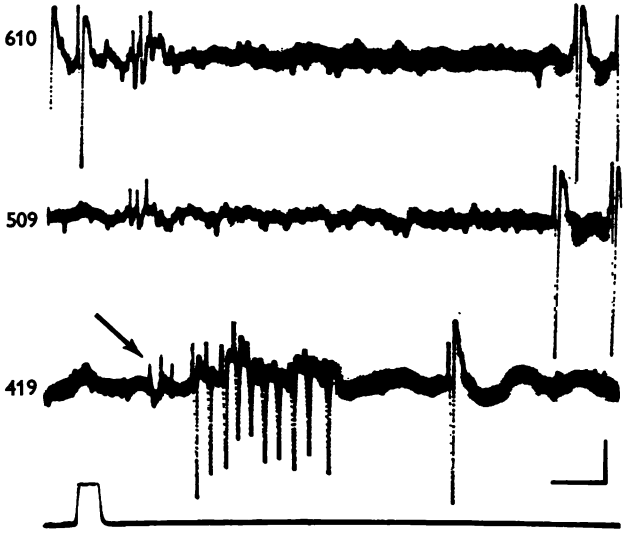

Fig. 10. Responses of 2 on-centre cells, one phasic (spikes of small amplitude) and the other tonic, receiving excitatory signals from a blue sensitive cone mechanism (spikes of large amplitude), to a 1·54 test mm² spot placed over the centres of the receptive fields of both cells. The numbers on the left signify the wave-length in nanometers of the stimulus. The arrow points to the response of the phasic cell to 419 nm stimulation. The photocell's response to the test stimulus is the lowest oscillograph. The calibration signifies 0·20 mV vertically and 20 msec horizontally. Positivity is upwards.

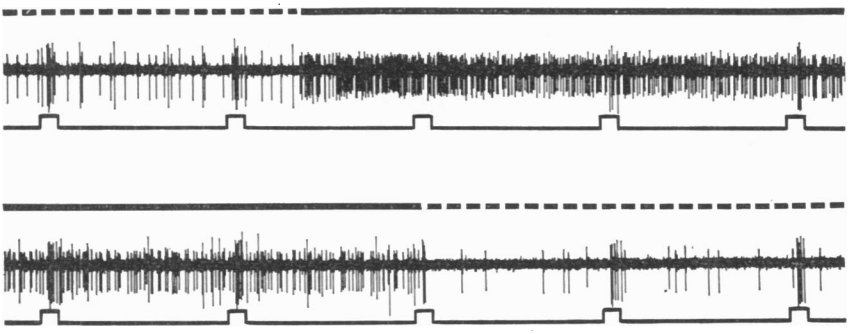

Fig. 11. Responses of a phasic on-centre cell (spikes of large amplitude) to a 0·004 mm² test spot centred in the cell's receptive field in the presence of the red (dashed line above) and the blue (continuous line above) adapting light. A neighbouring tonic on-centre cell (spikes of small amplitude), receiving excitatory signals from a green sensitive cone mechanism, responds to the adapting lights. The photocell's response to the test stimulus is below the cells' responses. Positivity is upwards.

them, either from red or green sensitive cones, and to exclude subsequent ones. Rod signals, which are also received by these cells, are handled similarly (Gouras & Link, 1966; Gouras, 1967).

The other type of cell receives excitation from only one cone mechanism

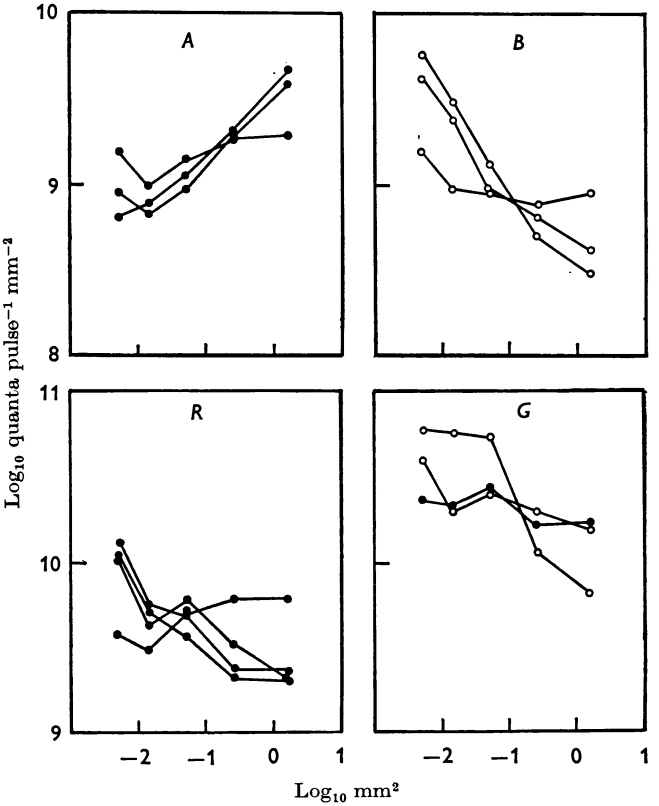

Fig. 12. Thresholds in $\log_{10}$ of the number of quanta in the light pulse/mm^2 of retina for the excitatory mechanism of three phasic (*A*) and thirteen tonic on-centre cells to concentric spot stimuli of different sizes ($\log_{10}$ mm^2 of retina) and centred in the receptive field of each cell. Among the tonic cells, four receive excitatory signals from a red (*R*), three from a green (*G*) and three from a blue (*B*) sensitive cone mechanism. Thresholds for groups *A* and *G* have been determined in the presence of the red, group *R* in the presence of the blue and group *B* in the presence of the yellow adapting lights. The wave-length of the test stimulus is either 610 (●) or 456 (○) nm.

in the centre and inhibition from another in the periphery of its receptive field. The excitation comes from either a blue, green or red sensitive mechanism. The action spectrum of the former resembles the π_1, π_3 mechanism of Stiles. The action spectra of the other two mechanisms are narrower than the π_4 and π_5 mechanisms of Stiles, respectively. This

narrowing may be due to the fact that the chromatic adaptation used does not completely separate these two spectrally overlapping, antagonistic mechanisms. Nevertheless, chromatic adaptation selectively raises the thresholds of each of the cone mechanisms which converge on such ganglion cells. These cells respond strongly in the presence of an adapting light which selectively suppresses the antagonistic surround mechanism. The absence, or perhaps weakness, of surround antagonism from the same cone

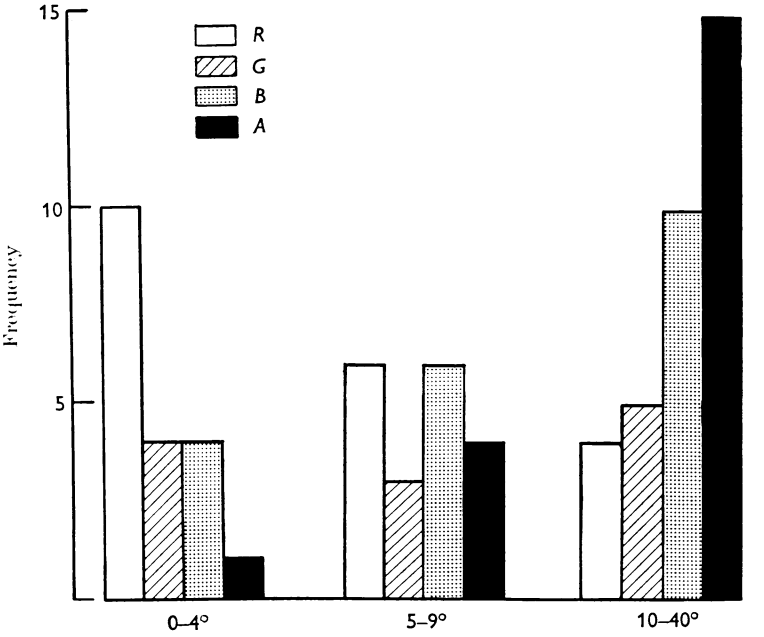

Fig. 13. Frequency of types of on-centre cells found in different regions of the retina, measured in degrees from the fovea (1 degree = 0·28 mm). Phasic cells are group *A*; tonic cells receiving excitatory signals from red, green, and blue sensitive cone mechanisms are group *R*, *G*, and *B*, respectively.

mechanism which controls the centre of the receptive field may enable such cells to respond continuously to maintained stimuli of appropriate wave-length. Because of such maintained responses, these cells have been called tonic.

A major characteristic in the organization of cone vision at the monkey's lateral geniculate nucleus, i.e. classes of cells, receiving either spatially (Wiesel & Hubel, 1966), or spectrally (De Valois, 1965*b*; Wiesel & Hubel, 1966) antagonistic mechanisms, is already determined in the retina. The spectrally antagonistic mechanisms have different spatial distributions, suggesting that this cell type may function in form as well as colour perception. This is supported by the fact that such retinal cells predominate

toward the fovea where both form and colour vision are most highly developed.

Midget system. By light microscopy, Polyak (1941) separated primate ganglion cells into two main groups. The cells in one group have relatively extensive dendritic ramifications and contact a number of bipolar cells. The cells in the other group, called monosynaptic or individual ganglion cells, have a more restricted dendritic spread and synapse directly with a midget bipolar cell, receiving signals from a single cone. Polyak (1941) thought that the latter group, which was relatively more common toward the fovea, represented the majority of ganglion cells in primate retina. Tonic cells may belong to this group for the following reasons: each tonic cell receives signals from only one cone mechanism in the centre of its receptive field; they are the most common cell type in the central retina and become relatively more common toward the fovea; they seem to be smaller than phasic cells because their extracellular discharges are usually of lower amplitude.

Against this hypothesis is the fact that the receptive field centres of tonic cells are not everywhere the same, and are larger than what would be expected if each cell receives signals from a single cone. The size of the receptive field centre of a ganglion cell depends upon the strength of the antagonistic surround. The same ganglion cell, for example, has a smaller receptive field centre in the light- than in the dark-adapted retina because of differences in the effectiveness of the antagonistic surround (Barlow, Fitzhugh & Kuffler, 1957; Gouras, 1967). It is difficult to study the receptive field centre of a tonic cell in the presence of an adapting light which excites the central mechanism. On the other hand, the central mechanism can be readily examined in the presence of an adapting light which strongly suppresses the antagonistic surround, as has been done in the present study. Under these circumstances, light scattered from the periphery on to the centre of the receptive field becomes more effective and may be responsible for lowering the thresholds of tonic cells to large spot stimuli. Phasic ganglion cells, whose receptive field organization prevents any separation of the surround from the centre mechanism by chromatic adaptation, show, contrastingly, relatively small receptive field centres.

Blue sensitive mechanism. The absence of blue sensitive cone signals in phasic ganglion cells may underlie some unusual characteristics, observed psychophysically in man. The human blue sensitive cone mechanism differs from the red and green sensitive ones in having a higher Weber fraction, a lower visual acuity, greater spatial summation and a lower flicker fusion frequency (Brindley, Du Croz & Rushton, 1966). The last property, in particular, may depend on the fact that this receptor mechanism transmits its signals to the brain exclusively through tonic ganglion cells, which

appear less suited to follow rapid changes in retinal illumination than phasic cells. The distribution of phasic cells across the retina may explain why cone flicker fusion frequencies increase away from the fovea (Lythgoe & Tansley, 1929).

Stiles (1949) and more recently Das (1964) have observed that the sensitivity of the blue sensitive mechanism of human vision decreases transiently after an adapting light, which had been suppressing the other cone mechanisms, had been turned off. Under similar conditions the response of the blue sensitive cone mechanism in ganglion cells is also transiently reduced. Such an effect could occur if the blue sensitive mechanism adapted slightly more slowly than the other cone mechanisms, a possibility that has already been suggested for man (Du Croz & Rushton, 1966).

I thank Miss Mary Hoff and Dr Ralph D. Gunkel for their valuable assistance.

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