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THE EFFECTS OF LIGHT-ADAPTATION ON ROD AND CONE RECEPTIVE FIELD ORGANIZATION OF MONKEY GANGLION CELLS

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SUMMARY

1. Receptive fields of perifoveal ganglion cells have been measured by determining threshold for eliciting a just detectable response using either concentric spot stimuli centred on the receptive field or small spot stimuli in different parts of the receptive field at various states of retinal adaptation and with stimuli selected to separate rod from cone function.

2. Light-adaptation decreases the sensitivity, latency and duration of threshold responses throughout the receptive field of a ganglion cell.

3. With all patterns of retinal stimulation and states of adaptation, threshold signals of the rods reach a ganglion cell later and those of the cones earlier than approximately 50 msec after a light stimulus.

4. In the more dark-adapted retina threshold rod and cone signals can be transmitted to the brain by the same or by neighbouring ganglion cells but not simultaneously; in the light-adapted state only the cone signal is transmitted.

INTRODUCTION

The duplex theory of vision depends on the fact that there is considerable independence in the threshold sensations mediated by the rod and cone systems of the retina. This independence cannot be due to a complete separation of the neural channels mediating these two sensations, since rod and cone signals have been detected in single neurones within the visual system of many animals with duplex vision. In the Rhesus monkey, for example, this has been observed both in the lateral geniculate body (De Valois, Smith, Kitai & Karoly, 1958; Wiesel & Hubel, 1966) and the retina (Gouras, 1965).

Rod and cone signals arriving at a ganglion cell in the dark-adapted monkey's retina have different latencies, which prevent them from acting

at the same place simultaneously (Gouras & Link, 1966). This difference in retinal delay time may be responsible for some of the independence in the threshold sensations mediated by these two receptor systems. The present work examines this hypothesis by studying threshold rod and cone signals arriving at perifoveal ganglion cells in the Rhesus monkey's retina from different regions of the cell's receptive field and at various levels of retinal adaptation. An abstract describing some of these results has been presented (Gouras, 1967).

METHODS

The methods were similar to previous studies (Gouras & Link, 1966; Gouras, 1966). Responses of single ganglion cells were recorded by fine glass micropipette electrodes from the perifoveal retina of monkeys (Macaca mulatta), anaesthetized with pentobarbital sodium at a rate of 20 mg/kg every 2–3 hr. Monochromatic lights from two separate beams of an Xenon arc lamp were used to stimulate the retina in Maxwellian view. The area, timing, energy, wave-length and retinal position of the stimuli obtained from these beams could be independently controlled. One beam was the test, the other, the adapting stimulus. A 10 msec test stimulus was presented every 1 or 2 sec in the following ways, either as a concentric spot or an annulus centred over the receptive field of a ganglion cell or as a 0·045 mm^2 spot placed in different positions in the receptive field. The spots used in the former method measured 0·004, 0·015, 0·045, 0·25, 1·54 mm^2 and the annulus, 1·54 mm^2 on the retina. A 24·6 mm^2 stimulus, which was not exactly centred over the receptive field, was also employed. The energy and wave-length of these stimuli were changed respectively by neutral density and narrow band interference filters. Ten different wave-lengths extending from 419 to 672 nm were used in the test beam. Two wave-lengths, 610 and 419 mm, were scotopically balanced so as to have equal effects on the rod receptors. The adapting beam covered 24·6 mm^2 of retina and was controlled by a hand-operated shutter. Either one of two different wave-length bands, obtained from Corning sharp cut glass absorption filters, 2418 and 3484, were used in the adapting beam. Filter 2418 transmits 80 % beyond 640 nm, 37 % between 599 and 610 nm, less than 0·5 % below 579 nm and appears red; filter 3484 transmits 80 % beyond 574 nm, 37 % between 527 and 544 nm, less than 0·5 % below 507 nm and appears yellow. The approximate energies in these adapting stimuli were determined in quanta/mm^2 of retina by photometrically balancing them with monochromatic light of similar hue (626 and 583 nm) obtained from the narrow band interference filters in the test beam which had already been standardized with a calibrated thermopile and galvanometer.

Responses were recorded from ganglion cells after the retina had been dark-adapted for 20 min or longer. The centre of the receptive field of each cell was found by determining the region with the lowest threshold to the 0·004 mm^2 spot. Threshold was considered to be the first detectable and consistent change in the cell's discharge frequency elicited by removing 0·1 or 0·3 neutral density units of filtering from the test beam. Responses were recorded on electromagnetic tape around and for some range above threshold for each condition, first in the dark-adapted state and then in the presence of background lights. For the scotopically balanced stimuli, thresholds were determined first for one, then for the other wave-length before the spatial pattern was altered. A few minutes were allowed for the ganglion cell to adjust to a change in background illumination before thresholds were judged. The responses were later photographed from the electromagnetic tape in order to evaluate the entire discharge pattern and to measure latencies.

RESULTS

Threshold responses to spots of different sizes. Figure 1 shows how threshold and response speed at threshold (reciprocal latency) of an on-centre ganglion cell, tested with concentric spot stimuli of different sizes, change with retinal adaptation. In the dark-adapted state thresholds and response speeds at threshold are relatively low. Light-adaptation increases both thresholds and threshold response speeds throughout the receptive field and this effect is greater for larger than for smaller spot

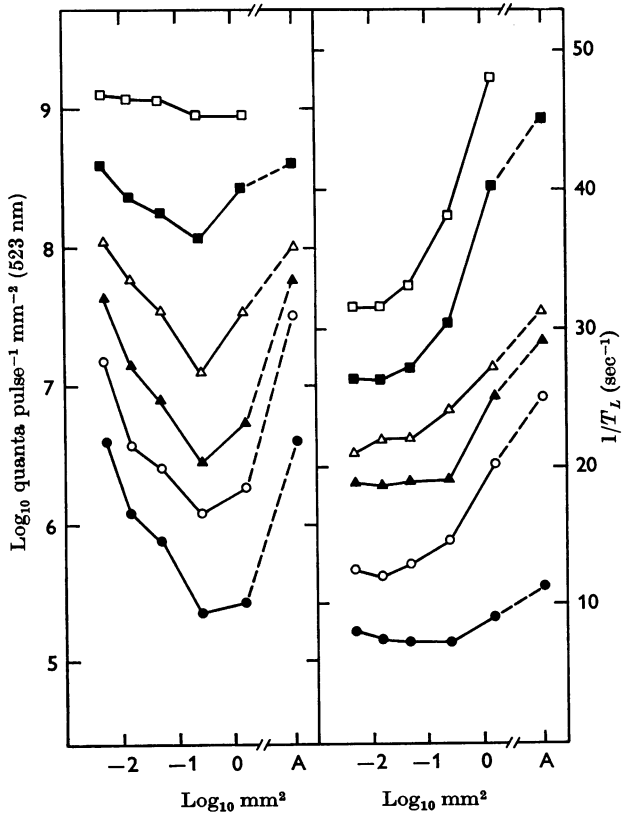

Fig. 1. Thresholds (left) in $\log_{10}$ of the number of quanta (523 nm) in the light pulse/mm^2 of retina and reciprocal latencies ($1/T_L$) of threshold responses (right) for different spot sizes (mm^2 of retina) and an annulus (A) at different levels of retinal adaptation for an on-centre cell with its receptive field centre 2·5 mm above and 0·5 mm nasal to the fovea. The symbols signify the energy of the red adapting light in $\log_{10}$ quanta/sec.mm^2 of retina: ●, $-\infty$; ○, 8·5; ▲, 9·1; △, 9·7; ■, 10·6; □, 11·5. The area of the annulus is equal to that of the largest spot and the data for these two test stimuli are connected by an interrupted line. With the strongest adapting light no response could be obtained with the annulus.

stimuli. It appears that the greater the amount of antagonistic surround in proportion to receptive field centre that is stimulated, the faster will the threshold response be. This is well demonstrated by the response speeds at threshold for the annular stimulation in Fig. 1. Figure 2 illustrates that large spots produce not only faster but briefer threshold responses than small spots.

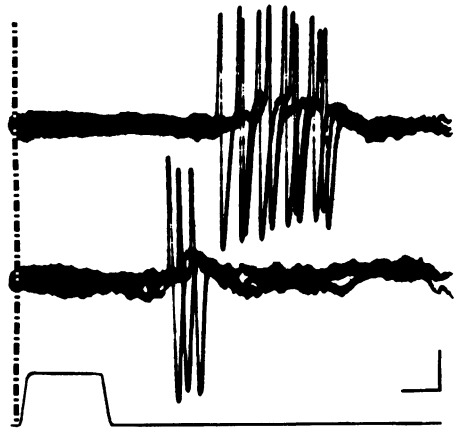

Fig. 2. Threshold responses to a spot, 0·045 mm² (above), and 24·6 mm² (below), centred over the receptive field of an on-centre cell, 2 mm superior and 1 mm temporal to the fovea. The energy of the stimuli are $\log_{10}$ 10 quanta/pulse.mm² of retina at 523 nm and of the red adapting light $\log_{10}$ 11·5 quanta/sec.mm². Three responses to every stimulus are superimposed in each oscillograph to provide some measure of temporal variability. The photocell's response to the stimulus can be seen below. The calibration signifies 0·5 mV vertically and 5 msec horizontally. Positivity is upwards.

Small spot receptive fields. Figure 3 shows how threshold and response speed at threshold of an on-centre cell, tested with a 0·045 mm² spot in different parts of its receptive field, change with retinal position and adaptation. Thresholds and response speeds are lowest in the centre of the receptive field and both increase progressively with more eccentric stimulation. Light adaptation increases thresholds and response speeds at threshold throughout the receptive field.

Figure 4 illustrates threshold responses of this cell at different levels of retinal adaptation. In the dark-adapted state, the responses are late, prolonged and show considerable temporal variability. This is more apparent with central than with eccentric stimulation. As light-adaptation increases the responses become faster, more compact and less variable throughout the receptive field.

Rod and cone receptive fields. Figure 5 shows how thresholds and response speeds at threshold of four on-centre ganglion cells, in the same region

of dark-adapted retina change with size of concentric spot stimulation using scotopically balanced lights (419 and 610 nm). The thresholds to the large spots are lowest and relatively similar from cell to cell. These responses must be due to the rods alone, since both thresholds and response

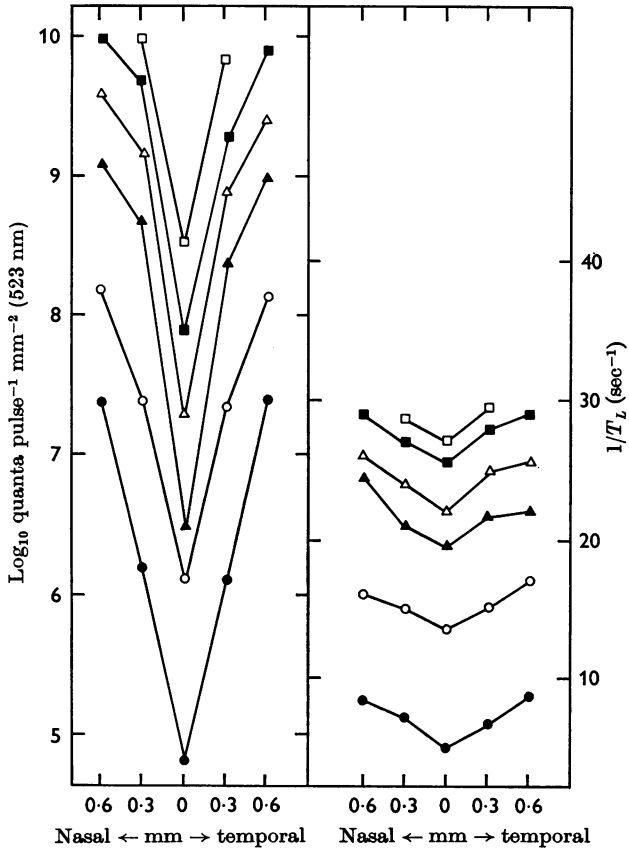

Fig. 3. Thresholds (left) in $\log_{10}$ of the number of quanta (523 nm) in the light pulse/mm^2 of retina and reciprocal latencies ($1/T_L$) of threshold responses (right) for a 0·045 mm^2 test spot placed in the centre and then 0·3 and 0·6 mm on both sides of the centre of the receptive field along the horizontal meridian of an on-centre cell with its receptive field centre 2 mm superior and 1 mm temporal to the fovea. The symbols signify the energy of the red adapting light in $\log_{10}$ quanta/sec. mm^2 of retina: ●, $-\infty$; ○, 9·1; ▲, 9·7; △, 10·3; ■, 10·9; □, 11·5.

speeds at threshold are identical for the scotopically balanced stimuli. The thresholds rise with smaller spots and in some cells more to 419 than to 610 nm. The latter change is accompanied by a doubling in the speed of the threshold responses to 610 nm and must be due to the intrusion of the cones.

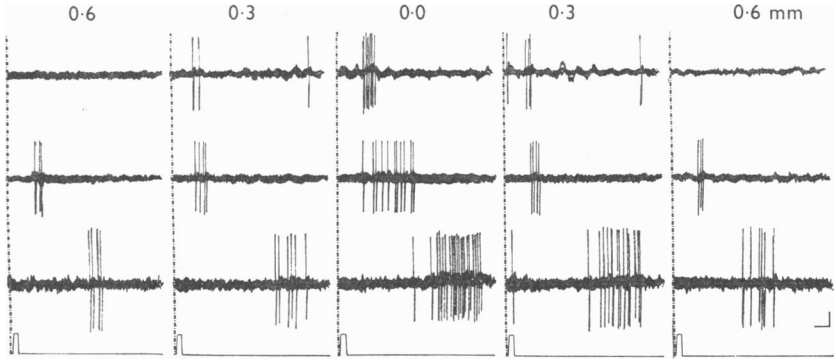

Fig. 4. Threshold responses of the cell, from which the results of Fig. 3 were obtained, to the 0·045 mm² spot placed centrally (0·0) and at various distances off the centre of the receptive field (nasal to the left; temporal to the right) and at three different levels of retinal adaptation. The energy of the red adapting light in $\log_{10}$ quanta/sec.mm² of retina are 11·5 (upper set), 10·3 (middle set) and $-\infty$ (lower set). The energy of the threshold test stimuli in $\log_{10}$ quanta/pulse.mm² at 523 nm can be obtained from Fig. 3. Three responses to every stimulus are superimposed in each oscillograph to provide some measure of temporal variability. The photocell's response to the stimulus can be seen below. The calibration signifies vertically 0·25 mV for the lower set and 0·5 mV for the other two sets of responses and 20 msec horizontally for all traces. Positivity is upwards.

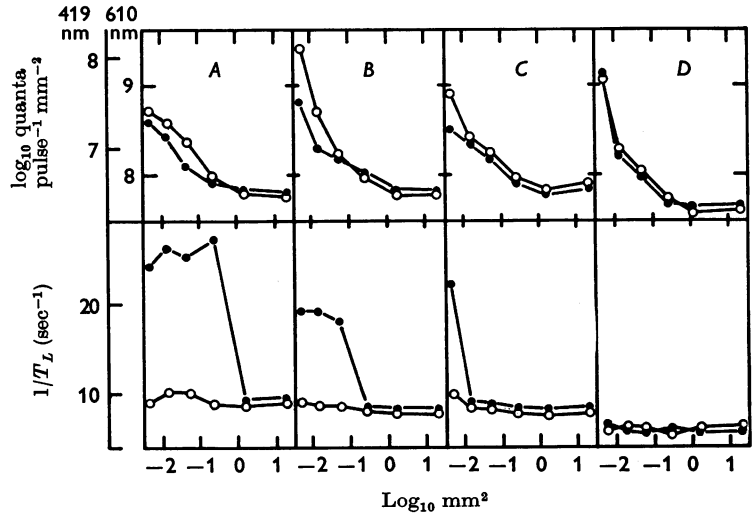

Fig. 5. Thresholds (above) in $\log_{10}$ of the number of quanta in the light pulse/mm² of retina and reciprocal latencies ($1/T_L$) of threshold responses (below) to concentric spot stimulation (mm² of retina) using scotopically balanced stimuli (419 nm, ○; 610 nm, ●) of four on-centre cells, whose receptive field centres are in the same region of the retina, 3·5 mm above and 1 mm nasal to the fovea.

Figure 6 shows how light-adaptation changes the receptive field organization of one of the cells of Fig. 5. Light-adaptation increases the threshold of the scotopically balanced stimuli but much more for the short than for the long wave-length end of the spectrum. Response speeds at threshold also increase and somewhat more for larger than for smaller spot stimuli. In contrast to the dark-adapted state, response speeds at threshold now become similar for 419 and 610 nm stimulation for all spot sizes. These responses must be due to the activation of cones.

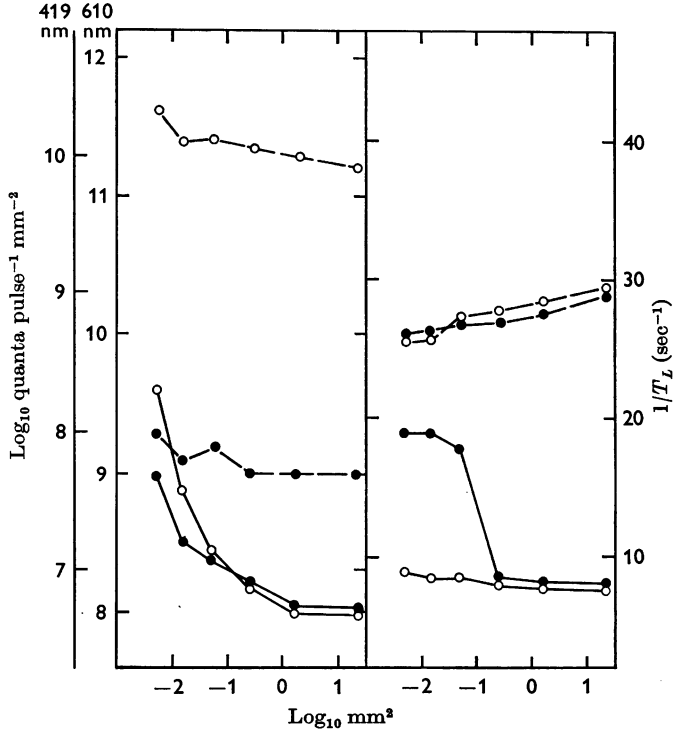

Fig. 6. Thresholds (left) in $\log_{10}$ of the number of quanta in the light pulse/mm^2 of retina and reciprocal latencies ($1/T_L$) of threshold responses (right) to concentric spot stimulation (mm^2 of retina) using scotopically balanced stimuli (419 nm, ○; 610 nm, ●) in the dark-adapted (—) and light-adapted (---) state for cell *B* of Fig. 5. The energy of the yellow adapting light is $\log_{10}$ 9·7 quanta/sec.mm^2 of retina.

Figure 7 shows how the same degree of light-adaptation changes the spectral sensitivity for eliciting a threshold response from such a cell using a 0·004 mm^2 spot centred in its receptive field. In the dark-adapted retina this action spectrum resembles the C.I.E. (Commission Internationale d'Eclairage) scotopic luminosity curve except at the long wave-length end

of the spectrum. When the spectral sensitivity resembles that of a rod mechanism, response speeds at threshold are correspondingly slow. The threshold responses to long wave-length stimulation, which do not match the rod curve, are about twice as fast as the others. In the light-adapted state the action spectrum shifts entirely to the C.I.E. photopic luminosity curve and all response speeds increase. A stronger adapting light further increases both thresholds and response speeds at threshold but similarly throughout the spectrum. The light-adapted thresholds are considered to be the result of cone action entirely.

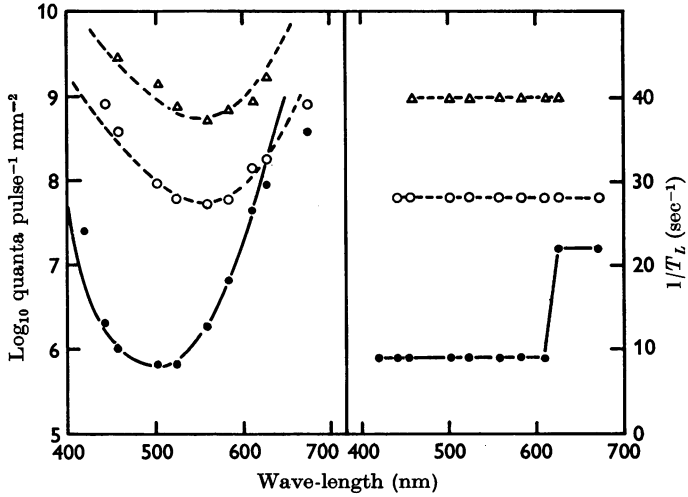

Fig. 7. Thresholds (left) and response speeds at threshold (right) for different wave-lengths of stimulation using a 0·004 mm² spot centred in the receptive field of an on-centre ganglion cell, located 0·5 mm below and 0·6 mm temporal to the fovea. The symbols indicate the energy of the adapting yellow light in $\log_{10}$ quanta/sec. mm² of retina (●, $-\infty$; ○, 9·7; △, 10·9). The continuous and hatched lines (left) are the C.I.E. scotopic and photopic luminosity functions, respectively.

Figure 8 (below) shows the responses of a perifoveal ganglion cell to scotopically balanced stimuli at and slightly above threshold in the dark-adapted state. At threshold the responses of the cell are similar for the scotopically balanced stimuli; with slightly stronger stimulation, latency becomes much shorter to the longer wave-length stimulus. The later component of the responses to both stimuli remains similar. The early component in the response to the long wave-length stimulus is due to the cones; the later component in the responses to both stimuli is due to the rods (Gouras & Link, 1966). Figure 8 (above) shows the cell's response at and slightly above threshold in the light-adapted state. These responses have a much shorter latency but remain quite similar at and above threshold. The stimuli are

no longer scotopically equivalent, however, since the energy of the short wave-length stimulus must be increased a thousand times, whereas that of the long wave-length stimulus must be increased only 8 times the energy required for threshold in the dark-adapted state.

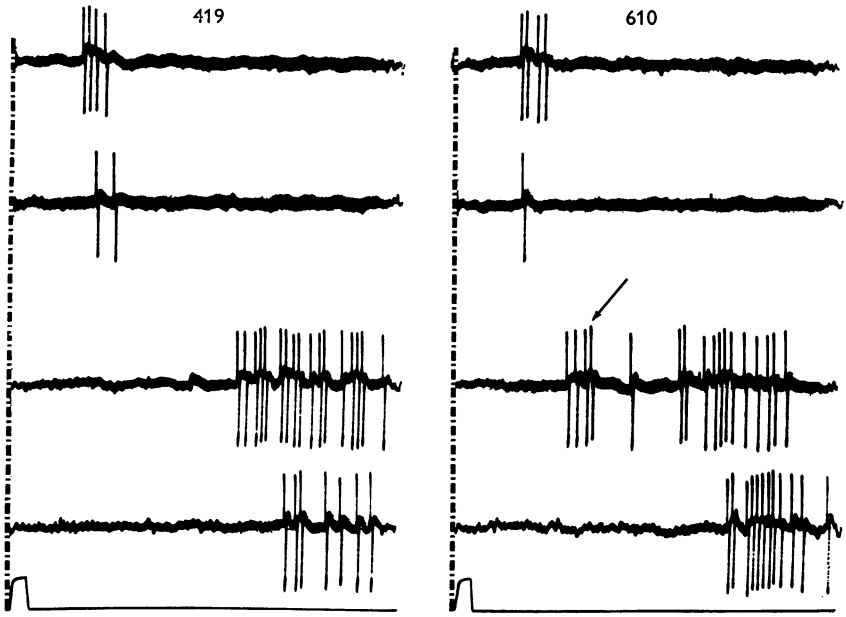

Fig. 8. Responses of an on-centre ganglion cell with its receptive field centre 0·3 mm above and 3 mm temporal to the fovea with stimuli from both ends of the spectrum (419 nm, left and 610 nm, right). The stimulus is a 0·015 mm^2 spot centred in the cell's receptive field. The lower set of four responses have been obtained in the dark-adapted retina with scotopically balanced stimuli. The energies of the stimuli for the lowermost responses in this set are approximately threshold and are $\log_{10}$ 7 for 419 nm and $\log_{10}$ 8·3 for 610 nm in $\log_{10}$ quanta/pulse. mm^2 of retina. The responses shown immediately above these traces have been obtained by doubling the energy of these threshold stimuli. The arrow indicates the intrusion of cone responses. The upper set of four responses have been obtained in the presence of a yellow adapting light of $\log_{10}$ 10·9 quanta/sec. mm^2 of retina. The energy of the stimuli for the lowermost responses of this set are again threshold and are $\log_{10}$ 10 for 419 nm and $\log_{10}$ 9·2 for 610 nm in $\log_{10}$ quanta/pulse. mm^2 of retina. The responses shown immediately above these traces have also been obtained by doubling the energy of these threshold stimuli. The duration of each trace is 0·2 sec. The vertical calibration for the lowermost responses of Fig. 4 can also be applied here. Positivity is upwards.

Figure 9 is a plot of the log. light energy of stimulation versus the average of the response speeds of all the cells in Figure 5 around and somewhat above threshold for the various spot sizes and at different states of retinal adaptation. The response speeds fall into two distinct groups,

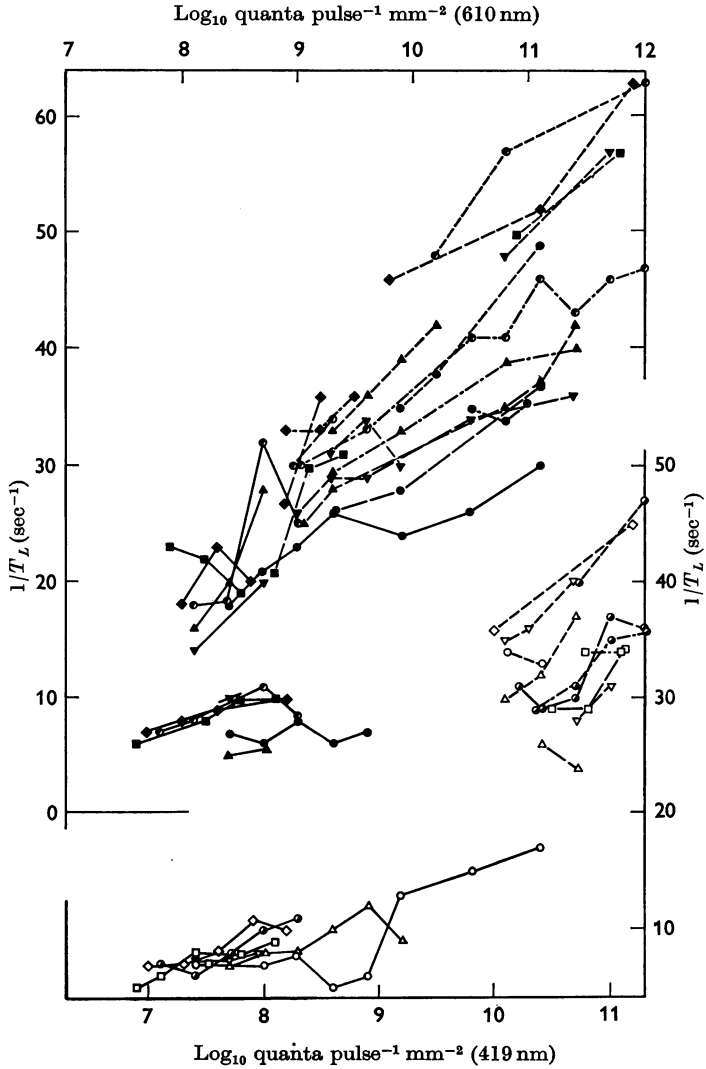

Fig. 9. Relation of reciprocal latency ($1/T_L$) to the $\log_{10}$ of the number of quanta in the light pulse/mm² of retina near and above threshold averaged for all the cells of Fig. 5 at different states of retinal adaptation and with concentric spot stimuli of different sizes using scotopically balanced stimuli (419 nm, open symbols and ◑; 610 nm, closed symbols and ◐). The left ordinate and the upper abscissa correspond to the 610 nm symbols; the right ordinate and the lower abscissa to the 419 nm symbols. The symbols signify the spot sizes (mm² of retina): 0·004 mm² (●, ○); 0·015 mm² (▲, △); 0·045 mm² (▼, ▽); 0·25 mm² (■, □); 1·54 mm² (◇, ◆); 24·6 mm² (◐, ◑). The connecting lines signify the energy of the adapting yellow light in $\log_{10}$ of the number of quanta/sec.mm² of retina: —, $-\infty$; — —, 9·7; —·—, 10·3; - - - -, 11·5.

one slow, the other fast. The slow responses, which occur only in the dark-adapted state and are the same for scotopically balanced stimuli, must be due to the rods alone. These responses become faster with stronger stimulation but are lost in the presence of the weakest background light. The faster group of responses, on the other hand, is better obtained with 610 than with 419 nm and becomes more apparent in the light-adapted retina. The shift from the slow to the fast group of responses is abrupt for both wave-lengths. After this shift, the relation between response speed

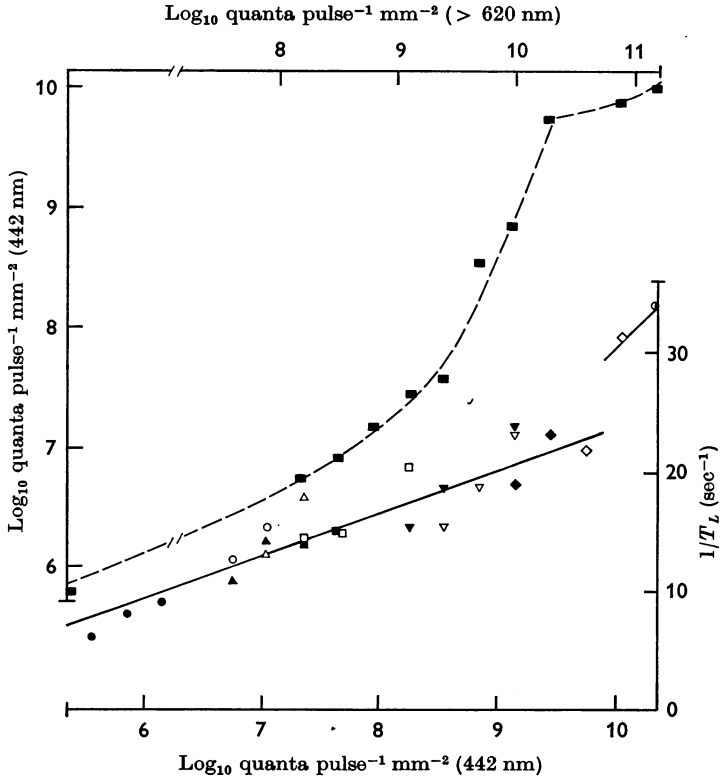

Fig. 10. Relation of thresholds (■) in $\log_{10}$ of the number of quanta/pulse.mm^2 of retina (442 nm) and the energy of the red adapting light in $\log_{10}$ of the number of quanta/sec.mm^2 of retina shown by the left ordinate and the upper abscissa respectively and relation of reciprocal latency ($1/T_L$) and the $\log_{10}$ number of quanta/pulse.mm^2 of retina (442 nm) near and above threshold at different states of retinal adaptation shown by the right ordinate and the lower abscissa respectively for an on-centre cell with its receptive field centre about 3·5 mm above and 1·5 mm nasal to the fovea. The test stimulus is 0·045 mm^2 on the retina and centred over the receptive field of the cell. The following symbols apply to the reciprocal latencies ($1/T_L$) and signify the $\log_{10}$ number of quanta/sec.mm^2 of retina in the adapting beam: ●, $-\infty$; ○, 8·2; ▲, 8·5; △, 8·8: ■, 9·1; □, 9·4; ▼, 9·7; ▽, 10·0; ◆, 10·3; ◇, 10·9; ◑, 11·2.

and log. light energy is parallel for both wave-lengths and must be due to a similar mechanism, determined by the cones.

Light-adapted rod responses. Rod responses can be obtained in some cells in the light-adapted state by using short wave-length test stimuli and long wave-length adaptation. Figure 10 shows how the thresholds and threshold speeds of ganglion cell responses mediated by the rods change with light-adaptation. At first thresholds increase gradually and then more steeply with brighter backgrounds and this is accompanied by faster response speeds at threshold until, with the brightest backgrounds, cone activity abruptly appears. Even when rod thresholds are higher, the response speeds of the rods are slower than those of the cones. The shortest latencies of threshold rod responses detectable at the ganglion cell are about 50 msec. Threshold responses of shorter latencies must be due to the cones entirely.

DISCUSSION

The receptive field of a perifoveal ganglion cell in the Rhesus monkey's retina appears to be organized into two superimposed fields, one determined by the rods, the other by the cones. The rod field has greater spatial summation so that ganglion cells in the dark-adapted retina are always driven at threshold by the rods, when relatively large spots are used. This advantage of the rods over the cones decreases as the size of the stimulus is reduced so that the thresholds of some cells in the dark-adapted state can be determined by the cones with small spots and by the rods with larger spots without changing the wave-length of stimulation. Under these conditions spectral sensitivity curves based on ganglion cell thresholds will depend upon the spatial characteristics of the stimulus. Regardless of spot size, however, threshold rod signals arrive at the ganglion cell later and threshold cone signals earlier than 50 msec after the light stimulus.

As retinal illumination increases, thresholds and response speeds at threshold increase over the entire receptive field of a ganglion cell. This occurs for both the rod and cone systems converging upon the cell. Light-adaptation increases rod much more than cone thresholds but even when rod thresholds are higher, their response latencies at the ganglion cell remain longer than those of the cones. Therefore at threshold just as with suprathreshold stimuli (Gouras & Link, 1966) rods and cones do not contribute simultaneously to a ganglion cell's response and this is as apparent in the light- as in the dark-adapted state. Because the cone system is so much faster than that of the rods under all circumstances, it manages to control ganglion cell function whenever stimuli are sufficient to excite it.

Responses to large or eccentric spots or to annuli tend to be faster and briefer than those to central stimulation and this is more apparent in the light- than in the dark-adapted retina. This greater speed appears to stem from the fact that with the former stimuli, the central area of the receptive field must be stimulated more strongly in order to overcome the antagonistic surround. The fact that central responses can be obtained at all to such stimuli implies that the responses from the surround are not as fast as central ones, an observation already made in the rabbit retina (Barlow, Hill & Levick, 1964). As a result of such time factors, a ganglion cell's responses to either different size spots or to a spot in different parts of its receptive field are seldom similar, even if the cell's thresholds to these stimuli are identical.

Several hypotheses proposed to explain why the spatial resolving power of vision increases with the amount of light entering the eye, postulate that stronger stimulation brings more neural units into action (Hecht, 1928; Pirenne & Denton, 1952). This idea receives some support from the present study, since ganglion cell thresholds in the same retinal area are not identical. Resolution does not increase continuously with retinal illumination, however, but reaches a maximum when the brightness of the test object is near that of the background (Craik, 1939). A decrease in the effective size of the central region of the receptive field of ganglion cells as found in the cat can provide some explanation for this effect (Barlow, Fitzhugh & Kuffler, 1957). In the monkey retina light-adaptation also reduces the effective size of the receptive field centre and in this case part of the change is clearly due to a shift from rod to cone function.

Although light-adaptation reduces the sensitivity, it does not decrease the spatial resolving power of vision. Correspondingly, light-adaptation raises the threshold for obtaining a ganglion cell response but the threshold response ultimately obtained is as fast and as, or perhaps more, accurate than that produced by this same stimulus in the dark-adapted state. If spatial resolution depends upon some central mechanism which discriminates differences in the timing of impulses arriving from a number of different ganglion cells, then light-adaptation would be expected to have either no effect or perhaps slightly improve this function. Similarly, an increase in the temporal resolving power of vision found in the light-adapted eye (Lythgoe & Tansley, 1929) may also depend upon the greater speed and shorter persistency of light-adapted ganglion cell responses.

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

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