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RESPONSES OF SINGLE RODS IN THE RETINA OF THE TURTLE

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SUMMARY

1. The responses of rods in the retina of the turtle, *Chelydra serpentina*, have been studied by intracellular recording.

2. The identification of rods as the origin of the recorded responses has been confirmed by marking with Procion Yellow.

3. The response to a small spot of light was a hyperpolarization which increased with increasing light intensity. For dim, small diameter stimuli, the shape of the rod response was similar to that of cones but 2 × slower and 2 × larger in amplitude. The time integral of the rod response to a dim, small diameter flash is, therefore, approximately 4 × greater than the integral of the cone response.

4. The shape of the rod response depended on the pattern of retinal illumination as well as stimulus intensity. Enlarging the area of illumination increased the peak amplitude and delayed repolarization following a light step. The area of retina which influenced the response was approximately 200 μm in radius.

5. It is concluded that for dim light the responses of rods are larger than those of cones because of (i) a greater response to direct illumination and (ii) an enhancement of response by interaction from a large retinal area.

INTRODUCTION

The retinae of most vertebrates contain two classes of photoreceptors, rods and cones (Hannover, 1840; Kölliker, 1852). Considerable evidence indicates that rods mediate vision in dim light and cones mediate vision in bright light (Schultze, 1866; for a review see Pirenne, 1962). Recently the intracellular responses of cones have been determined (for a review see Tomita, 1972). Although the responses of rods have also been reported

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(Toyoda, Hoshimoto, Anno & Tomita, 1970; Grabowski, Pinto, & Pak 1972), the origin of the great sensitivity of rod vision has not been apparent. The subject of this report is the receptive field properties and kinetics of rod responses in the turtle retina. These are compared with the properties of cones previously reported by Baylor, Fuortes & O'Bryan (1971). The comparison indicates that the greater sensitivity of a rod can be attributed to a greater response to direct illumination and to enhancement by interaction from a large area of neighbouring retina.

METHODS

Experiments were performed on the isolated eye cups of turtles, *Chelydra serpentina*, whose carapace lengths were 8–14 in. The properties of cones were determined to be similar to those previously studied by Baylor *et al.* (1971) in the turtle *Pseudemys scripta elegans*. *C. serpentina* was used in this study because its rods are more numerous than in *P. scripta elegans* (Underwood, 1970).

The stimulating and recording procedure has been previously described (Schwartz, 1973). Rods were stimulated with 500 nm and red cones with 615 nm light obtained by inserting narrow-band interference filters into the light path. The maximum irradiance delivered to the retina was $5{\cdot}2 \times 10^{13}$ quanta cm^{-2} sec^{-1} and was attenuated with neutral density filters calibrated in optical density units (O.D.). The absolute value of membrane potential was uncertain due to the unfavourable properties of the high resistance pipettes (200–400 MΩ) used. Therefore, all voltages are reported as a change from the membrane potential during the dark.

RESULTS

The cell of origin of the recorded responses was identified by intracellular injection of Procion Yellow. Four cells were marked and identified as rods (see Pl. 1).

Responses to small diameter stimuli

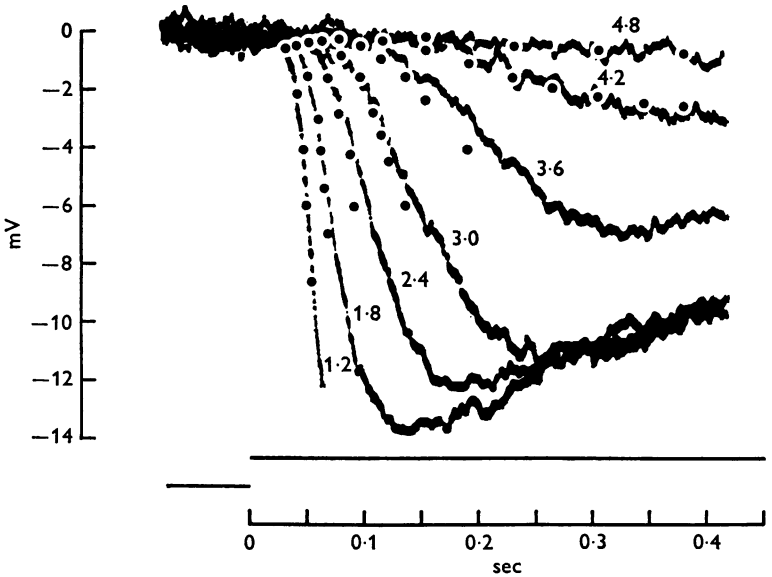
Rods responded with a hyperpolarization which increased with increasing light intensity; superimposed responses to different intensities of light covering a circle 100 μm in diameter are shown in Text-fig. 1.

The time course of rod responses were compared to cone responses by fitting the initial phase of the responses with an equation of the form (Fuortes & Hodgkin, 1964, eqn. (10)).

$$V = B\tau I[1 - C(u, n+1)]. \quad (1)$$

V is voltage; B is a coefficient with the dimension of potential/(light quantity/unit area); I is light intensity; $C(u, n+1)$ is the cumulative Poisson distribution of $n+1$ terms with $u = t/\tau$ where t is time and τ is a time coefficient. Possible physical systems which yield this equation have been discussed by Borsellino & Fuortes (1968). The responses of cones in the retina of *P. scripta elegans* have been previously fitted to this equation (Baylor *et al.* 1971). I found that the cone responses of *C. serpentina*

were best fitted with $n = 6$ and $\tau = 24 \pm 3{\cdot}1$ msec (average of eight cells) Rod responses were best fitted with $n = 6$ and $\tau = 47 \pm 8{\cdot}4$ msec (average of seven cells). Values predicted by eqn. (1) are superimposed on to the responses of Text-fig. 1 for comparison. It can be seen that by increasing the value of the time coefficient, τ, an equation describing the onset of cone responses also adequately describes the onset of rod responses. The shape of cone and rod response to small spots of *dim* illumination therefore differ only by a scale factor.



Text-fig. 1. Rod responses to steps of light. Superimposed responses to steps of light of increasing intensity (as indicated) covering a circle 100 μm in diameter. Downward deflexion is a hyperpolarization. For comparison are superimposed values calculated from eqn. (1) with $n = 6$, $\tau = 48$ msec and $B = 1920\ \mu\text{V/quanta}\ \mu\text{m}^{-2}$.

To compare the magnitude of rod and cone responses, it is necessary to have a convenient measure of response size. A frequent measure is the scaled amplitude* which may be defined for a step of light as

$$A_s \equiv \frac{V_{max}}{I} = B\tau. \qquad (2)$$

The scaled amplitude for a flash is analogously defined and by taking the

* The term 'scaled amplitude' is preferred to the previously used term 'sensitivity' (e.g. Fuortes & Hodgkin, 1964) so that the latter may be reserved for perception and psychophysical experiments where it is defined as the inverse of a threshold stimulus.

derivative of eqn. (1) and noting that the peak response occurs at $t = (n-1)\tau$,

$$A_t \equiv \frac{V_{\max}}{Q} = \frac{B\upsilon^{\upsilon}e^{-\upsilon}}{\upsilon!}, \tag{3}$$

where $\upsilon = (n-1)$ and Q is the quantity of light, $Q = I\Delta t$. Another measure of response size is gain which may be defined for a step as

$$G \equiv \frac{\int_0^{\infty} V\mathrm{d}t}{I\Delta t} = B\tau. \tag{4}$$

A similar definition for a flash yields the same result. The scaled amplitude differs for a flash or step, whereas gain is the same for both and is independent of stimulus duration.

Gain can be easily estimated by noting that eqns. (2) and (4) yield the same result. The coefficient B for a dim, 100 μm diameter stimulus was, for rods, 1650 μV/quanta μm^{-2} (average of eight cells) of 500 nm light, and, for red cones, 770 μV/quanta μm^{-2} (average of ten cells) of 615 nm light. With these values and values for τ, the gain for rod responses is approximately 4 × greater than for cone responses. This difference occurs over the range of intensities for which eqn. (1) applies. For voltage changes greater than approximately 2 mV, however, the observed responses increase amplitude less than proportional to light intensity (see also Text-fig. 3B) and, therefore deviate from eqn. (1) with a concomitant decrease in gain. A similar effect is seen in the responses of cones (Baylor *et al.* 1971) and can be attributed to a form of gain control (for a discussion see Fuortes & Hodgkin, 1964).

The maximum response following the effective absorption of a single photon, V^*, can be calculated from eqn. (3) if the quantity of incident light is rescaled to the quantity of light effectively absorbed by a single receptor. Thus,

$$V^* = \frac{V_{\max}}{Q} = \frac{B\nu^{\nu}e^{-\nu}}{\nu!\ \sigma\ (1-10^{-\epsilon\rho\eta})},$$

where η is the probability for an absorbed photon isomerizing a photopigment molecule (= 0·62, Dartnall, 1972), ϵ is the specific extinction coefficient (= 0·014 μm^{-1}, Liebman & Entine, 1968), ρ is the length of the outer segment ($\cong$ 25 μm) and σ is the cross-sectional area ($\cong$ 50 μm^2). For both rods and cones in the turtle retina

$$\frac{\nu^{\nu}e^{-\nu}}{\nu!\ \sigma\ (1-10^{-\epsilon\rho\eta})} \cong 0{\cdot}011\ \mu m^{-2}.$$

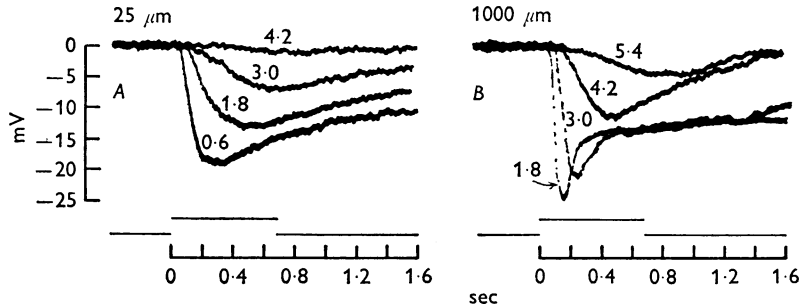
Therefore the peak response following the absorption of one photon is estimated to be 8·7 μV in a cone and 18 μV in a rod.

It is assumed above that all of the light which enters the broad base of the inner segment is directed into the narrow outer segment. Tansley & Johnson (1956) have demonstrated that a large fraction of the light incident on the inner segment is

indeed 'funnelled' to the outer segment. However, cones cannot funnel all of the incident light into their outer segments (O'Brien, 1951; Enoch, 1963). This inability gives rise to the psychophysical Stiles–Crawford effect. A similar phenomenon also occurs in the cones of the turtle *Clemmys japonica* (Pautler, 1967). Therefore, the estimate of V^* for cones must be corrected for their inability to collect all of the incident light. Model studies indicate that when the axis of illumination is normal to the retinal surface, cones collect perhaps half of the incident light (O'Brien, 1951). With this consideration, the responses following the absorption of a single photon in rods and cones have nearly the same peak amplitude (20 μV/quanta) but differ in time scale.

The added effect of illumination in the surround

In addition to the effect of direct illumination, rod responses were altered by illumination of the surround. In Text-fig. 2 are superimposed the records of responses elicited by different relative intensities of stimuli 25 and 1000 μm in diameter. The responses evoked by the two stimuli are different indicating that illumination of the surround modified the response. In order to understand what actions illumination of the surround exerted on the central cell, it is necessary to compare responses to stimuli of different diameter which each delivered the same light to the impaled rod.



Text-fig. 2. Responses to short steps of light covering small or large areas. *A* shows superimposed records of responses to different relative intensities (as indicated) covering a circle 25 μm in diameter. *B* is a similar experiment performed on the same cell with a circle of light 1000 μm in diameter. The responses evoked by the two stimuli are different. However, to compare responses it is necessary to know the amount of light attenuation at the centre of the 25 μm diameter stimuli due to scatter within the retina. After correcting for attenuation due to scatter (see text and Text-fig. 3), the response to a 1000 μm, 5·4 O.D. light is larger than to a 25 μm, 4·2 O.D. light even though the 1000 μm diameter light is 4 × *dimmer*.

It is therefore necessary to know the attenuation of light at the centre of small diameter stimuli due to scatter within the retina (see Baylor & Fuortes, 1970).

The loss of light due to scatter was estimated by the method illustrated in Text-fig. 3. Responses were determined for a 25 μm diameter spot placed at several dis-

tances from the impaled cell. The peak amplitude of the response as a function of distance across the vitreal surface was plotted as in Text-fig. 3*A*. It is assumed that for this small spot the response was determined essentially by the light impinging directly upon the impaled rod, interactions within this area being regarded as negligible (it is shown below that the total area of interaction was at least 100 × greater than the area covered by this light). Because response amplitude was not proportional to light intensity, this relationship does not indicate the distribution of light at the receptor layer. However, the amount of light reaching the impaled rod can be estimated by knowing the relationship of intensity to response amplitude when the 25 μm spot was centred (Text-fig. 3*B*). By projecting each point in Text-fig. 3*A* to the continuous curve in Text-fig. 3*B*, the light intensity reaching the impaled rod when the stimulus was placed off-centre can be estimated and replotted as in Text-fig. 3*C*.

The distribution of light can also be predicted by the 'circular coverage' or P function (tabulated values may be obtained from Masters, 1954; see also Baylor *et al.* 1971):

$$P\left(\frac{a}{\sigma},\frac{x}{\sigma}\right) = \int_0^{2\pi}\int_0^{a} N\left(\frac{x}{\sigma}\right) r\,dr\,d\theta,$$

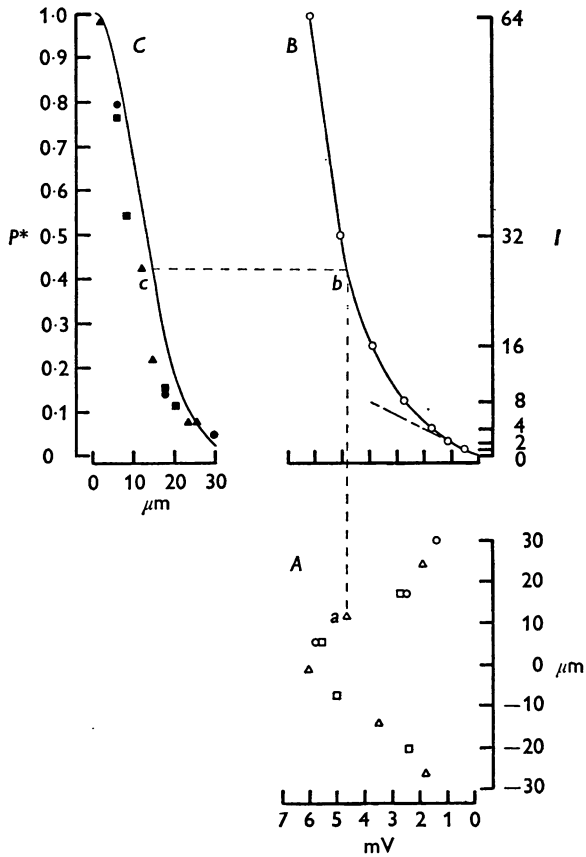


Fig. 3. For legend see facing page.

where x is the distance from the centre of a uniform circle of illumination of radius a and $N(x/\sigma)$ is the normal density function with space coefficient σ. The P function was fitted to the observed data by adjustment of the space coefficient. The solid line in Text-fig. 3*C* expresses the normalized value, P^*, of this function when the light is a 25 μm diameter spot blurred at the receptor layer with a space coefficient of 10 μm. The curve agrees reasonably well with the reconstructed light intensities of Text-fig. 3*C*. For a space coefficient of 10 μm the light intensity at the centre of a 25 μm image is determined from the table of the P function to be reduced to 27 % of the nominal value; the intensity at the centre of a 100 μm image is unattenuated.

It should be noted that if enhancement of response amplitude due to interactions from neighbouring retina (see below) were not, as assumed, entirely negligible for the small diameter stimulus used, then the responses of Text-fig. 3*A* would be determined by both scattered light and interaction in which case the space coefficient for scatter alone would be less than 10 μm and the attenuation even less than estimated.

With the above corrections, it was possible to compare stimuli which delivered the same light to the impaled rod but different quantities of light to the surround. A difference in time course of the rod response occurred if 100 and 1000 μm spots were compared even though both delivered the same light at the centre of the image. No adjustment of intensity could make the responses to 100 and 1000 μm spots coincide over their entire time course (Text-fig. 4). Enlarging the area of illumination added a transient increase

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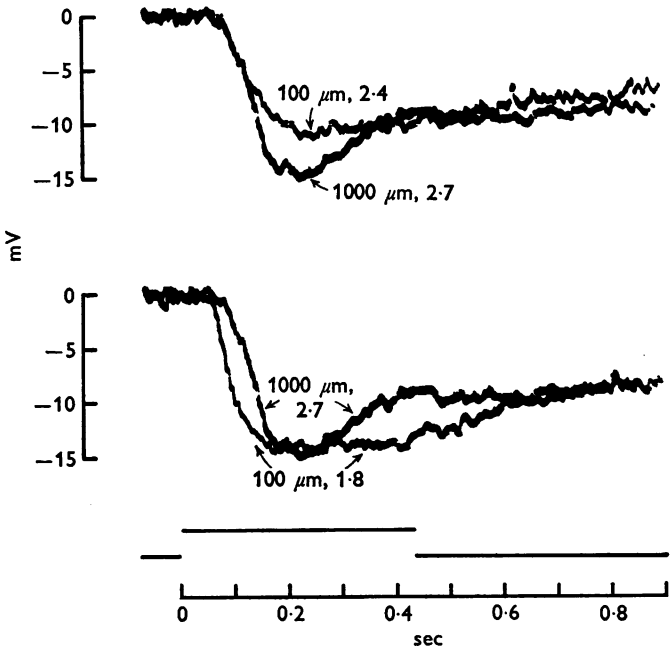
Text-fig. 3. Estimation of the loss of light from the centre of small diameter stimuli due to scatter within the retina. *A* (lower right): peak amplitude of response as a function of distance from the centre of a 25 μm diameter spot. Intensity was constant. The spot was moved from the centre to the right (○), from right to left (△) and finally from left to right (□). The spot was then recentred; the peak amplitudes of response for different light intensities were then determined and plotted in *B* (upper right). By projecting each point in *A* on to the continuous curve in *B* (for example, line *ab*), the intensity of light reaching the impaled rod when the spot was placed off-centre can be determined and is replotted in *C* (for example, by line *bc*). The continuous line in *C* expresses the normalized value of the 'circular coverage' function, P^*, for a 25 μm diameter spot with a space coefficient of 10 μm. This estimate of the space coefficient indicates that scatter reduced the light intensity at the centre of the 25 μm diameter spot to 27 % of the nominal value and that light at the centre of a 100 μm diameter spot was unattenuated.

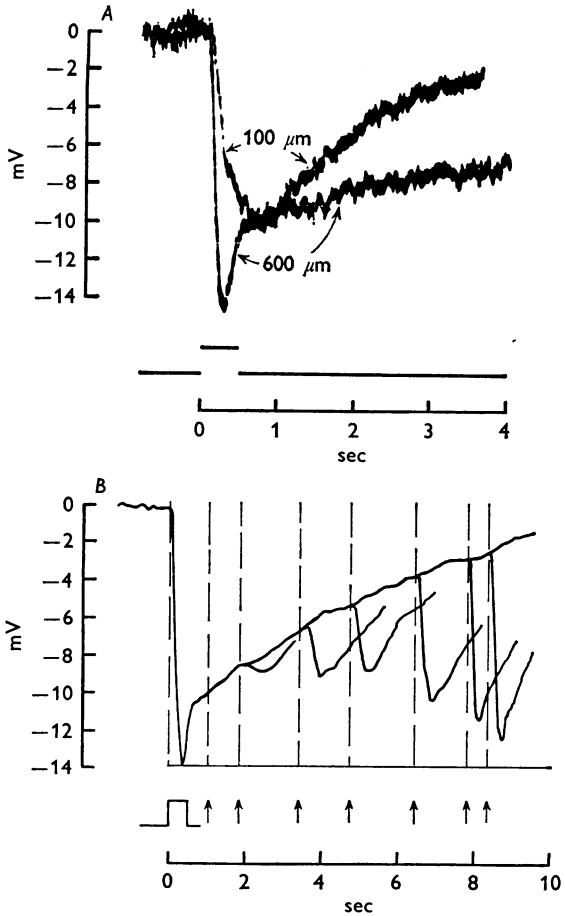
The observed amplitudes of *B* deviate from a simple proportionality to light intensity (straight line through the origin) for responses greater than 1·2 mV. An estimate of scaled amplitude (see text) indicates that this voltage was achieved by a flash containing 60 absorbable photons. This is in agreement with the estimate of Penn & Hagins (1972) for the linear range of extracellular photocurrent responses of rat rods. The present experiments also demonstrate that response amplitude continues to increase non-linearly over several additional decades of increasing light intensity (see also Text-fig. 2). Similarly Penn & Hagins (1972, p. 1093), citing unpublished observations, state that 'the saturating level for rod photocurrent responses can be raised by several factors of 10 in an appropriate ionic environment'.

in the peak of the response and delayed recovery following the stimulus (Text-fig. 5*A*). In contrast, enlarging the area of a non-saturating light, modified cone responses as previously described by Baylor *et al.* (1971) and did not significantly delay their recovery following the stimulus. The delay in recovery was a striking difference between rod and cone responses.

During the slow recovery phase, the response to a second stimulus was decreased. In Text-fig. 5*B* the large diameter stimulus was followed after a variable time interval by a second, identical stimulus. The second stimulus produced no response at a short interval; as the interval was lengthened and repolarization from the first response became more complete, the amplitude of the response to the second stimulus increased; after complete repolarization the initial response amplitude could be obtained.



Text-fig. 4. Responses to small or large stimuli cannot be made to coincide by an adjustment of intensity. If responses with equal time of onset are compared (above), the response to the larger diameter stimulus reaches a greater peak amplitude. If responses with equal peak height are compared (below), the response to the larger diameter stimulus is delayed and after reaching peak amplitude decreases to a plateau even before the light is terminated. The same response to a 1000 μm diameter spot is shown in the two sets of traces. Response shape changed when the radius was enlarged from 50 to 500 μm. Therefore interactions occurred over a distance greater than 50 μm. In additional experiments it was consistently observed that response shape changed as the spot was enlarged up to a radius of 200 μm and then did not change as the spot was further enlarged.



Text-fig. 5. *A*: stimuli of different area which each present the same light to the impaled rod differ in peak amplitude and time course of recovery following the light. Enlarging the area of illumination added a transient increase in the peak of the response (as indicated also in Text-fig. 4). Following the offset of the light, the response to a 100 μm spot repolarized more rapidly than that to a 600 μm spot. *B*: during the time of delayed recovery following a large diameter spot the response to a second stimulus was depressed. The Figure summarizes responses to eight stimulus conditions. The large spot of *A* was first repeated on a slower time base. In the seven successive trials two identical light steps (600 μm diameter, 3·0 O.D.) were given at a variable time interval. Responses to the first stimulus of each pair superimposed. The second stimulus (each presented at a time indicated by an arrow) produced no response at the shortest interval. As the interval was lengthened and repolarization from the first response became more complete, the amplitude of response to the second stimulus increased; after complete repolarization the initial response amplitude could be obtained. The light intensity was non-saturating; the peak amplitude of response to a 600 μm, 1·8 O.D. light was 18 mV.

The responses of Text-figs. 4 and 5 indicate that the area of retina which influenced a rod response was large compared to a 50 μm radius. It was consistently observed that enlarging a spot from 50 to 200 μm radius changed the response shape markedly and that no additional change occurred when the spot was enlarged from 200 to 800 μm radius. It therefore seems likely that interaction extends to a distance of 200 μm from the impaled rod. Further, light on the far periphery (from 200 to 800 μm from the impaled rod) is apparently without effect. By comparison, cone responses are enhanced by cone-cone interaction when a central spot is enlarged up to 70 μm radius and are inhibited by a feed-back from horizontal cells when the area of illumination is enlarged up to 800 μm radius (Baylor *et al.* 1971; see also Fuortes, Schwartz & Simon, 1973). Rods, therefore, differ from cones in receptive field organization.

DISCUSSION

Rod responses differ from cone responses in time scale, gain and receptive field properties. Rods increase response amplitude over a range of light intensity to which cones also give large responses; however, for small diameter, dim spots, rod responses are 2 × slower, 2 × larger in amplitude and, consequently, possess a gain approximately 4 × greater than cone responses. The larger gain of rods versus cones probably enables them to more effectively modulate the release of transmitter at low levels of irradiance. In addition the rod response to direct illumination is modified by interactions occurring within a 200 μm radius which add a transient increase in the peak of the response and delay recovery following a stimulus. This lateral interaction further increases response size to dim light.

The properties of rods may be compared with the sensitivity of rod mediated vision as determined by psychophysical experiments. For a large diameter stimulus, the threshold for seeing in the peripheral retina is 500–1000 × lower than in the fovea (see Baumgardt, 1972). The difference is usually attributed to an absence of rods from the fovea and to their presence in the periphery. This difference in sensitivity is greatly reduced, however, when small diameter stimuli are compared (Craik & Vernon, 1941; Crawford, 1947; Rushton & Cohen, 1954). For sufficiently small test-fields, the thresholds of foveal and extra-foveal regions differ by less than 10 × (Baumgardt, 1949; Arden & Weale, 1954; Weale, 1958). The sensitivity of rod vision is therefore increased by areal summation which has been claimed to occur over a radial distance of at least 150 μm (see Baumgardt, 1972). Similarly, in the turtle retina, the rod response to a small spot is approximately 4 × greater than that of cones and is greatly enhanced by interaction from a large neighbouring area.

In psychophysical experiments, increasing the area of illumination also slows the rate of subsequent dark adaptation (Craik & Vernon, 1941). The difference has been attributed to a 'neural adaptation' (Dowling, 1963; Rushton, 1965) mediated by interaction from neighbouring retina. The site of the interaction has been uncertain. But Grabowski *et al.* (1972) have recorded from rods and suggested that a form of desensitization unrelated to the bleaching of photopigment occurs within the rods themselves. The present experiments demonstrate that areal desensitization of rod mediated vision occurs, in part, within the rods. In addition, retardation of recovery following moderate intensity light may explain the fate of the rod response during photopic vision.

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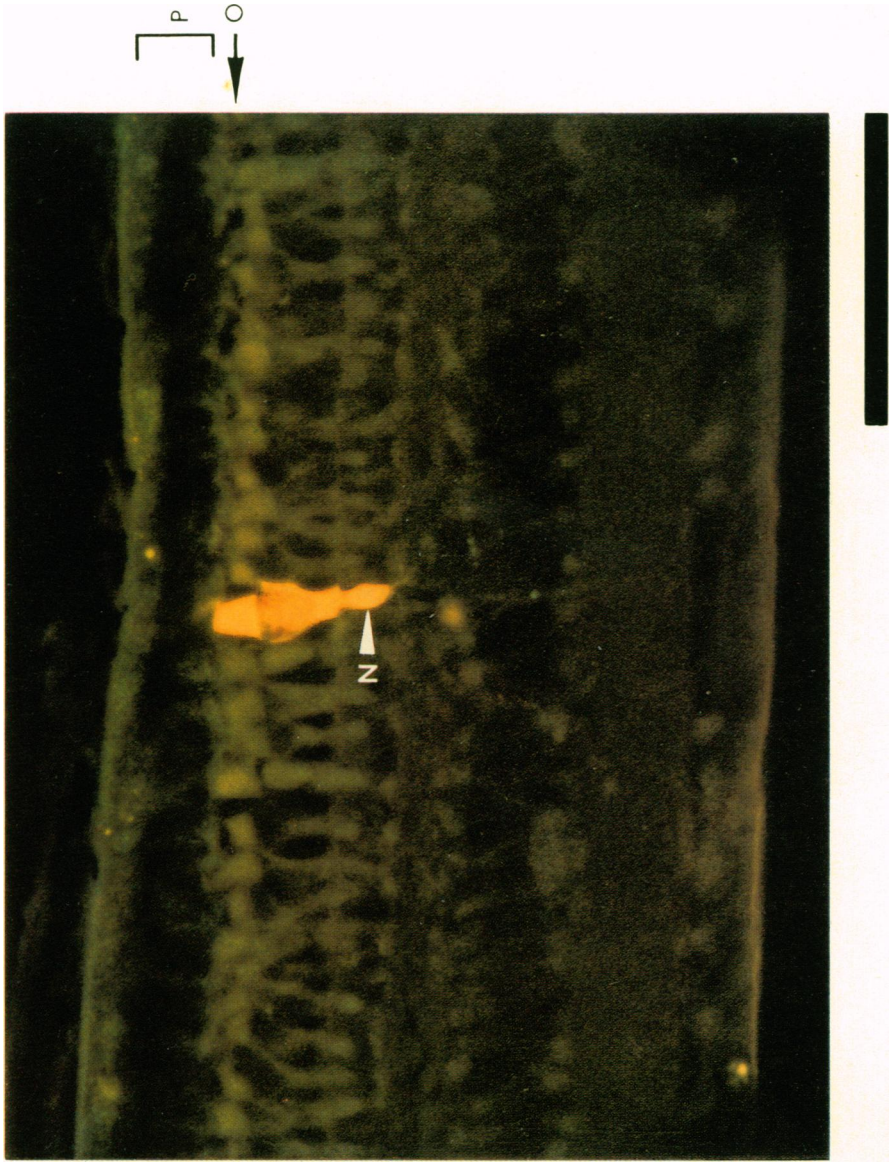
EXPLANATION OF PLATE

Photomicrograph of a cross-section of retina to show the origin of responses. The fluorescent dye Procion Yellow M4R was injected into a cell giving the responses described. The cell is identified as a rod by its absence of an oil droplet, the low position of its nucleus, and the simple structure of its synaptic base (a very small piece of which was included in an adjacent section). The outer segment is obscured by pigment epithelium. P, pigment epithelium; O, level of the cone oil droplets; N, nucleus of the injected rod. The bar indicates a distance of 100 μm.



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