LIGHT-EVOKED ELECTRICAL POTENTIALS FROM THE EYE AND OPTIC NERVE OF STROMBUS: RESPONSE WAVEFORM AND SPECTRAL SENSITIVITY

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The neural processing of visual information by the retina is reflected in the light-evoked extracellular retinal potentials (electroretinogram or ERG) and the discharge pattern of the concomitant afferent impulses in the optic nerve fibres. The waveform of the ERG is often fairly complex, since it represents the summed activity of a large number of different neurons; this activity can include the photic stimulation of receptors, and synaptic excitation and inhibition (Brown, 1968; Werblin & Dowling, 1969). Examining the ERG and its relation to the optic nerve activity which encodes the visual information can help to reveal the underlying neural mechanisms (Kennedy, 1964). Molluscan eyes, which exhibit a vast range of anatomical complexity (Charles, 1966), have proven amenable to the electrophysiological investigation of these mechanisms (see Discussion for examples and references).

The eyes of strombid gastropods (family Strombidae) are well formed and conspicuous; within the phylum Mollusca, except for those of cephalopods and heteropods, they are among the largest and most complex (Charles, 1966). The eye of the strombid Strombus luhuanus, as will be shown in this paper, exhibits complex electrical responses to photic stimulation. The eye is also of unusual interest because it permits the examination of the ontogeny of these responses during development, since Strombus readily regenerates a new and apparently normal eye following amputation. As the regenerate develops, its electrical responses progressively assume the complexities of the responses of the mature eye. This will be considered in more detail in a separate communication (Gillary, in preparation).

The present report concerns light-evoked electrical activity in the mature eye and optic nerve of Strombus. It focuses on the waveform of the ERG, its spectral sensitivity and dependence on dark adaptation, temperature, and stimulus intensity, and its relation to the patterned discharge of afferent impulses. The results indicate that the eye contains a single visual pigment and that its response to photic stimulation reflects complex intra-retinal neural interactions which involve excitation, inhibition, and oscillatory 'off' activity. Preliminary reports of some of the results have appeared elsewhere (Gillary, 1971, 1972).

METHOD

Mature Strombus luhuanus, with shell lengths of about 4 cm, were collected at depths of 5–30 ft near the Eniwetok Marine Biological Laboratory in the Marshall Islands, imported to Hawaii, and maintained in marine aquaria. Prior to experimenta-
tion animals were anaesthetized by immersion in a 7.3% solution of magnesium chloride to facilitate amputation of the eye and eyestalk. Two types of preparation were used for electro-physiological recording. For the recording of only retinal potentials, the eye was amputated with a small attached stump of eyestalk. For the simultaneous recording of the retinal response and afferent action potentials, the eye and its attached branches of optic nerve were dissected free from the eyestalk. Before recording, the preparations were allowed to recover from the dissection in sea water for at least an hour. While such preparations were usually used within 12 h, they could continue to yield apparently normal electrical responses to photic stimulation for several days. No differences were observed between the responses of the above preparations and those prepared without the aid of magnesium chloride anaesthesia.

During an experiment the preparation was immersed in sea water whose temperature was continuously monitored with a telethermometer and controlled with the aid of a Peltier thermo-electric cooling assembly. The ERG was recorded via a suction electrode with a glass tip about a millimeter in diameter, which was applied to the corneal surface of the eye. (For the last two records of Text-fig. 1, it was applied to the back of the eye.) This signal was led to a D.C. pre-amplifier. To record afferent action potentials, a suction electrode with a fine glass tip (50 μm dia. or less) was applied to a branch of the optic nerve several millimeters from the eye; this signal was led to a low-level differential pre-amplifier with input blocking capacitors. The amplified signals were displayed on a cathode-ray oscilloscope and photographed.

Light from the high-intensity quartz-iodide bulb of the photic stimulator was passed through heat filters and could be focused on the preparation, which was oriented so that light entered the pupil of the eye. The intensity of the stimulus was varied by means of neutral density filters placed in the light path and its spectral composition was altered with second-order interference filters combined with absorption filters to eliminate unwanted transmission peaks. The light intensity incident on the preparation was calibrated with a radiometer; the maximum intensity of white light used, as in Text-figs. 2-4 and 8, was 10⁶ ergs/cm²/sec. The temporal characteristics of the stimuli were varied by means of an electromechanical shutter and monitored by a photocell in the path of the light.

In addition to the light delivered via the photic stimulator the preparation could receive simultaneous adapting illumination from a second source of white light combined with a heat filter. For the studies requiring chromatic adaptation this source was used to deliver either blue light, passed through a No. 47B Kodak Wratten filter with a transmission peak at 435 nm, or red light with wavelengths greater than 580 nm, passed through a No. 25 Kodak Wratten filter. The intensity of the adapting illumination was varied with neutral density filters.

The brief anatomical description of the eye and optic nerve of Strombus included in this paper is based on the examination of dissected living material, light microscopy of stained serial sections of paraffin-embedded and epon-embedded specimens, and electron microscopy of thin sections (H. and E. Gillyary, unpublished). The photomicrographs in Plate 1 are of a section from an epon-embedded eye fixed with glutaraldehyde and stained with Azure II-Methylene Blue. A more detailed description of the anatomical methods and of the anatomy and ultra-structure of the eye of Strombus will be presented in a separate publication.
RESULTS

Anatomy

The eyes of Strombus, as large as two millimeters in diameter, are situated at the distal ends of retractile anterior eyestalks which are over a centimetre in length. Light enters the eye and impinges on its retina after passing through the transparent structures of the eye. These include the cornea, a pupil surrounded by a non-muscular iris, a rigid spheroidal lens, and a gelatinous vitreous body (Pl. 1 A). The multilayered retina is erect in contrast to the inverted retinas of vertebrates (Pl. 1 B). Nearest the cornea is a layer of rhabdome composed of the distal segments of more than $10^6$ photoreceptors. Each distal segment is made up of microvilli, as is usual for gastropods, rather than lamellae derived from cilia, as in the distal retinas of pelecypods (Charles, 1966; Eakin, 1972). Peripheral to the distal segments is a region containing dark pigment granules mostly contained within cells lacking outer segments. This is followed by a nuclear layer; the elongated nuclei of the cells bearing dark pigment are distinguishable from those of the photoreceptors. Nearest the peripheral collagenous capsule is a rich meshwork of neuropile. The retina is innervated by numerous twigs of the optic nerve which converge to form progressively larger and fewer trunks as they run along the eyestalk to the cerebral ganglion. Whether the optic nerve fibres are the axons of receptors has not yet been established (see Discussion).

Electroretinogram

General waveform. The ERG exhibited several distinct components illustrated in Text-fig. 1. If a dark-adapted eye was illuminated by a brief flash (e.g. 0.1 sec duration), a cornea-negative potential was evoked whose amplitude often exceeded 10 mV. This ‘on’ potential was often monophasic (Text-fig. 1A) but under certain conditions (described in the next three sections) it exhibited two distinct peaks before returning to the baseline (Text-fig. 1B). If the eye received prolonged illumination (e.g. for more than 5 sec), the large cornea-negative potential declined during the stimulus to a
smaller 'steady-state' potential which persisted for the duration of the stimulus and returned to the baseline after illumination ceased (Text-fig. 1 C, D). The amplitude of this steady-state potential was depressed by prior adaptation with light whose intensity exceeded that of the stimulus; this indicates that this ERG component is not a stimulus artifact. Following the initial 'on' peak, the ERG amplitude from a light-adapted eye often fell below the steady-state value before levelling off (Text-fig. 1 E). Occasionally an ERG evoked from an eye below 20 °C by a prolonged stimulus of high intensity had more than two 'on' peaks (Text-fig. 1 F). The ERG recorded from the back of the eye exhibited the same general waveform as the corneal ERG but had opposite polarity (Text-fig. 1 G, H).

After stimulation ceased, these cornea-negative potentials were often followed by relatively small regular oscillations which were usually less than 0.1 mV in amplitude (e.g. Text-fig. 1 C–F). Their frequency and amplitude tended to decrease gradually in the absence of stimulation (e.g. note the oscillations preceding the response of Text-fig. 1 C after approximately a minute in darkness); they often persisted in the dark for more than 20 min following illumination. These oscillations were inhibited during the cornea-negative potentials described above (e.g. Text-fig. 1 C).

The presence of each of the above ERG components depended on the stimulating conditions. How the ERG was affected by stimulus intensity, dark-adaptation time, temperature, and the wavelength of light incident on the retina will be considered below.
Text-fig. 3. Effects of stimulus frequency on ERG. (A) Four records from single preparation. Upper trace, ERG; lower traces monitor 0.1 sec stimuli of equal intensity. (22 °C) The record of A₄ is identical to that of Text-fig. 2 A₄. It is duplicated for comparison with A₂—A₄ which are typical ‘steady-state’ responses (see text) to repetitive stimulation at respective frequencies of 2, 6 and 60 per min. (B) Plots of amplitude (●—●) and latency (○—○) (as in Text-fig. 2 B) determined from records in A plus two others not shown. (Data from A₁ is plotted to left of abscissa break).

Stimulus intensity. Text-fig. 2 illustrates the effects of stimulus intensity on the ERG evoked by a brief flash. The relationship between the amplitude of the ERG and the stimulus intensity was S-shaped; above a threshold, which depended on the extent of light adaptation, the amplitude increased with intensity until it reached a maximum. After the maximum of the amplitude had been reached the duration of the ‘on’ component of the ERG continued to increase with intensity. When stimuli with progressively increasing intensities were delivered to the eye at regular intervals, the amplitude of each response increased in proportion to the logarithm of the stimulus intensity over a range of more than a log unit. The latency of the ERG decreased as the stimulus intensity increased. This decrease continued even after the ERG amplitude had reached its maximum. For brief flashes of fixed intensity, the ERG amplitude increased with increasing stimulus duration (records not shown), as it did with increasing intensity, provided that this duration did not exceed the latency to the peak of the ERG.

Repetitive stimulation and adaptation. If a dark-adapted eye was repetitively stimulated at constant frequency with flashes of fixed intensity and duration, the ERG amplitude progressively declined to a steady-state value. As illustrated in Text-fig. 3, higher frequencies of repetitive stimulation resulted in a greater decrease in amplitude, which was accompanied by only a slight increase (not necessarily significant) in the latency to half the maximum ERG amplitude (Text-fig. 3 B). These effects are probably
Text-fig. 4. Effects of temperature on ERG. A. Four sequential ERGs from a single preparation held at 33 °C and stimulated at 3 min intervals with successive intensities having unit log increments. (Except for temperature, preparation and test sequence identical to that for Fig. 2 A₁-A₄.) The stimulus preceding A₁ was below threshold; the ERG amplitude of A₄ was maximal. Arrows indicate cessation of 0.1 sec stimuli (and shutter artifacts) for both A and B. B. Two consecutive ERGs from same preparation at 9 °C, stimulated with ascending intensities as in A. The stimulus intensity for B₁ is the same as that for A₄; that for B₂ is a log unit greater. The lower traces of B₁ and B₂ are continuous with the ends of their respective upper traces. C. Intermittent sequential ERGs from a single preparation (different from that of A) stimulated at 3 min intervals with flashes of constant intensity and duration (0.1 sec) as the temperature was gradually varied. The respective temperatures during each test were 33, 17 and 13 °C. Vertical calibration of C₂ and C₃ is identical. (See text for details.)

related to the greater light adaptation resulting from the higher frequency of stimulation; longer intervals between stimuli permitted greater dark adaptation and larger responses. The frequency of repetitive stimulation also affected the relative amplitudes of the two 'on' peaks of the ERG. While the amplitudes of both peaks declined with increasing stimulation frequency, the rate of decline of the second peak was greater than that of the first.

Temperature. The ERG was markedly dependent on temperature (Text-fig. 4). The effects of stimulus intensity on the responses of a single preparation held at either 33 or 9 °C are illustrated in Text-fig. 4 A and B (cf. also Text-fig. 2 A). Increasing the temperature decreased the latency and duration of the response and increased the frequency of the repetitive 'off' potentials. Raising the temperature also significantly lowered the threshold of the cornea-negative 'on' response. For example, at 33 °C a sizeable cornea-negative response was evoked (Text-fig. 4 A₄) at an intensity two log units below that which failed to produce one at 9 °C (Text-fig. 4 B₁), although repetitive cornea-positive potentials were elicited.
Light-evoked electrical potentials of Strombus -0.5 -1.0 -1.5 -2.0 0 400 500 600 Wavelength (nm)

Text-fig. 5. ERG spectral sensitivity. Sensitivity is the reciprocal of the light intensity required to evoke an ERG amplitude equal to that evoked by a 500 nm stimulus of constant duration (0.1 sec) and intensity (approx. 20 ergs/cm², sec) which evoked an ERG of approximately one-half the maximum amplitude. The data points were determined from 26 consecutive 0.1 sec stimuli of various wavelengths and intensities, delivered every 6 min. The sensitivity to 500 nm light was compared with that to each of the other 10 wavelengths in a random sequence. The curve is Dartnall's nomogram with a maximum absorption at 485 nm. (27 °C.)

When a series of repetitive stimuli of constant intensity, duration and frequency was delivered to a dark-adapted preparation, the ERG amplitude declined to a 'steady state', as described previously (see Text-fig. 3). At lower temperatures, considerably lower frequencies were required to evoke a criterion 'steady-state' amplitude. This is probably due to a slower rate of dark adaptation at the lower temperatures.

When stimuli of 0.1 second duration and constant intensity were presented at regular 3 min intervals while the temperature was continuously varied, the maximum amplitude of the evoked ERG was reached between 27 and 32 °C, and progressively declined as the temperature was raised or lowered beyond this. (This temperature optimum is approximate to the natural ambient temperature for the Strombus used in these studies. The ERGs of other gastropods, Otala and Aplysia, have exhibited similar optima below 20 °C (Gillary & Wolbarsht, 1967; Jacklet, 1969) which more closely correspond to the temperatures of their more temperate habitats.) The response failed reversibly beyond the range of 9–39 °C. This failure below 9 °C was probably caused by the depressed rate of dark adaptation mentioned above, since a dark-adapted preparation could respond below 9 °C. The latency progressively decreased with increasing temperature over the whole range of response, and the frequency of repetitive 'off' potentials increased with a $Q_{10}$ of more than four between 13 and 23 °C. Text-fig. 4C presents three ERGs from such an experiment; they show that temperature also affected the relative amplitudes of the two 'on' peaks. At higher temperatures the second peak was larger than the first; consequently, the optimum temperature of the
Text-fig. 6. Effect of chromatic adaptation on ERG spectral sensitivity. Sensitivity is the reciprocal of the light intensity required to evoke an ERG of constant amplitude, approximately half of the maximum response. The data points were determined from the ERGs evoked in a single eye by 78 consecutive 0.1 sec stimuli of various wavelengths and intensities. The spectral sensitivity was determined nine different times, under different conditions of light adaptation, in the sequence indicated by the data point numbers (i.e. 1 was first, 2 second, etc.). Twice (i.e. for 3 and 7) the sensitivity to 480 nm light alone was determined. For the remaining seven, the relative sensitivity to 430, 480 and 545 nm light was determined using a test sequence designed to compare most accurately the relative sensitivity to 430 and 545 nm light. Before each determination, the preparation was allowed to dark-adapt for 20 min; the interval between tests within a determination was 5 min. Determinations were made either with no intentional adapting illumination (1, 3, 5, 7, 9), or with continuous red adapting light (2, 8) or with blue adapting light (4, 6). Each of the curves is Dartnall’s nomogram for a pigment with maximum absorption at 485 nm. (28 °C. See text for further details.)

first peak was lower than that of the second. This effect was seen whether the temperature was increasing or decreasing.

Wavelength. The studies described so far employed stimuli of white light. ERGs evoked by monochromatic (narrow band) light of various wavelengths were identical to those evoked by white light in terms of the general waveform of the ERG, its relation
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Text-fig. 7. Simultaneous ERG and optic nerve response to intermittent prolonged stimuli. A. Continuous records during the presentation of three successive stimuli of white light. The preparation was dark-adapted for 3 min prior to the stimulus in A. Upper trace, superimposed ERG and stimulus monitor (rapid upward deflexion indicates the onset of illumination, and rapid downward deflexion its cessation); lower trace, AC-recorded optic nerve response. (23 °C.) B. Successive records to stimulation at wavelengths of 520 and 440 nm. The relative intensities were adjusted to evoke equal responses. Each stimulus was preceded by more than 2 min of darkness. Preparation and recording conditions as in A.

to stimulus intensity, and its response to adaptation. The spectral sensitivity curve exhibited a maximum at about 485 nm and corresponded well to the Dartnall nomogram (Dartnall, 1953) for a single visual pigment (Text-fig. 5). This peak was not shifted by chromatic adapting illumination of sufficient intensity to depress the sensitivity by more than a log unit (Text-fig. 6) or by changes in temperature between 14 and 33 °C.

Optic nerve response

Photic stimulation of the preparation evoked impulses in optic nerve fibres; such impulses were abolished by crushing the nerve between the eye and the recording site. Text-fig. 7 illustrates this optic nerve discharge and its concomitant ERG during sustained illumination. Such stimuli often evoked one or two phasic ‘on’ bursts of impulses in both large and small fibres, and a tonic ‘on’ response of small impulses (often largely obscured by baseline noise). The abrupt cessation of stimulation frequently evoked an ‘off’ response of repetitive bursts of these large impulses. Each ‘off’ burst appeared to contain repetitive impulses from several fibres. The bursts tended to be phase-locked to the repetitive ‘off’ potentials of the ERG and usually
coincided with the rapid cornea-positive phase of each oscillation. Prolonged illumination tonically inhibited the large impulses (Text-fig. 7A). The general pattern of neural response was unaffected by the wavelength of light between 400 and 600 nm (e.g. Text-fig. 7B).

Text-fig. 8 illustrates several effects of varying the intensity and frequency of brief stimuli on the ERG and optic nerve response. When presented with a dim flash, the dark-adapted preparation gave strong repetitive ‘off’ discharges, in phase with the oscillations in corneal potential, in the absence of a distinct cornea-negative ‘on’ potential (Text-fig. 8A). Higher stimulus intensities evoked a cornea-negative response (Text-fig. 8B). The ‘on’ response of small fibres in the optic nerve (poorly visible in the figure) continued throughout the cornea-negative phase of the ERG and the repetitive ‘off’ bursts of large impulses occurred only after the ERG returned to the baseline. Repetitive stimulation at constant intensity caused a decrease in the amplitude and duration of the cornea-negative phase of the ERG and a concomitant decrease in the latency of the onset of the repetitive ‘off’ bursts (Text-fig. 8C). This implies that the onset of the ‘off’ impulses is more directly related to the duration of the cornea-negativity than to the stimulus duration.
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DISCUSSION

The ERG of Strombus exhibited two separable ‘on’ peaks, a steady-state potential, and repetitive ‘off’ oscillations. Optic nerve afferents exhibited phasic and tonic ‘on’ activity, photic inhibition, and repetitive ‘off’ activity. These contrast with the optic responses of stylommatophoran gastropods such as Otala and Helix whose ERGs have exhibited a relatively simple monophasic waveform without ‘off’ oscillations and whose optic nerves have yielded only ‘on’ activity (Gillary & Wolbarsht, 1967; Hermann & Goldman, 1967; Gillary, 1970). The greater complexity of the electrical activity of Strombus eyes suggests that they are capable of a higher degree of visual information processing. This processing appears to involve photoexcitation, adaptation, inhibition, and synaptic excitation. The evidence for this will be discussed shortly.

One complexity which appears to be lacking is a mechanism for colour vision. The spectral sensitivity curve of the ERG corresponded closely to the Dartnall nomogram for a single visual pigment with an absorption maximum of 485 nm, and its peak failed to be shifted by chromatic adaptation. This implies that only a single visual pigment is present in the eye (Kennedy, 1964). Furthermore, the qualitative similarity of both the ERG and the optic nerve response to stimuli of different spectral compositions suggests that colour-coded cells are lacking. These spectral sensitivity data for Strombus are similar to those obtained for other molluscs which appear to possess single visual pigments with absorption maxima between 470 and 505 nm; these include cephalopods (Hamasaki, 1968; Wells, 1966) pelecypods (Wald and Seldin, 1968; McReynolds & Gorman, 1970b; Mpitsos, 1973) and gastropods (Gillary & Wolbarsht, 1967; Dennis, 1967; Hughes, 1970; Berg & Schneider, 1972).

Certain general inferences can be made regarding the cellular origin of the ERG components. In other molluscan eyes light-evoked cornea negativity has been associated with the depolarization of receptors whose distal segments are composed of microvilli, and with ‘on’ optic nerve activity (Hagins, Zonana & Adams, 1962; Hagins 1965; Gillary & Wolbarsht, 1967; Eakin & Brandenburger, 1967; Land, 1968; Jacket, 1969; McReynolds & Gorman, 1970a). By analogy, the initial ‘on’ peak of the ERG of Strombus probably arises from receptor depolarization and is associated with the excitation of certain optic nerve afferents. The cornea-negative steady-state potential evoked by sustained illumination also seems to reflect receptor depolarization and to be linked with the excitation of tonic ‘on’ fibres in the optic nerve. The reduction in amplitude of this steady potential below that of the first ‘on’ peak may be due to adaptation of the receptors and possibly also to synaptic inhibition. The light-evoked cornea-negativity also seems related to the inhibition of ‘off’ fibre activity. The ‘off’ activity of the optic nerve probably reflects a release from light-evoked inhibition. This inhibition is very likely synaptic, as in the eye of Hermisenda (Dennis, 1967; Alkon & Fuortes, 1972), rather than primary (Hartline, 1938; Kennedy, 1960; Land, 1968; McReynolds & Gorman, 1970a; Wiederhold, MacNichol & Bell, 1973; Mpitsos, 1973) since no distal retina or receptors with ciliary outer segments such as those of pelecypods have been found in the eye of Strombus.

The origin of the second ‘on’ peak of the ERG is still uncertain. The differential effects of light adaptation and temperature on the relative sizes of the two ‘on’ peaks indicate that they are caused by two temporally separated processes. The first may be
associated with photoreceptor excitation, and the second with a synaptic process. Perhaps two depolarizing events give rise to the two peaks, or perhaps a cornea-positive notch due to retinal inhibition or receptor hyperpolarization divides an otherwise monophasic cornea-negativity into two peaks. (Under certain conditions these processes may vary rhythmically to produce ERGs with more than two peaks.) Graded light-evoked potentials in other molluscan retinas also appear to be due to at least two separate processes with different sites of origin and adaptational properties (Tasaki, Oikawa & Norton, 1963; Jacklet, 1969; Alkon & Fuortes, 1972).

The small repetitive cornea-positive ‘off’ potentials of the ERG are similar to oscillations which appear in the ERGs of cephalopods (Bullock, 1965). In Strombus each burst of repetitive ‘off’ impulses in the optic nerve fibres tended to coincide with or just precede a cornea-positive oscillation; however, the oscillations could occur in the absence of recorded impulse activity. Perhaps the ‘off’ oscillations of the ERG reflect rhythmic excitatory or inhibitory synaptic events.

The repetitive ‘off’ bursts of impulses in the optic nerve of Strombus resemble those recorded from the distal nerve of Pecten by Hartline (1938), who attributed the synchrony of impulses within each burst to interaction between the primary receptors. The ‘off’ impulses of Strombus might also occur in bursts because of excitatory cross-coupling, either synaptic or electrotonic, between retinal units. Excitatory electrotonic coupling between retinal receptors in Hermissenda resulted in their tendency to discharge in synchrony (Dennis, 1967). Similar coupling between retinal units is suggested by the synchronous discharges seen in the optic nerves of other gastropods (Jacklet, 1969; Patton & Kater, 1972).

The anatomy of the retina offers potential sites for the neural processes mentioned above. The receptors are presumed to be excited by the absorption of light by visual pigment in their distal segments. The layer of neuropile offers ample opportunity for excitatory and inhibitory synaptic interactions. There is not yet evidence for second-order neurones in the retina. In other molluscs the retinal photoreceptors are apparently primary neurones whose axons run via the optic nerve directly to the brain (Young, 1962; Bullock, 1965, Eakin & Brandenburger, 1967; Newell & Newell, 1968; Eakin & Brandenburger, 1970). If this is also true for Strombus, lateral interaction between the receptors seems likely. Intraretinal potentials are currently being recorded with microelectrodes to determine the cellular origin of the potentials described above.

**SUMMARY**

1. The cornea-negative ERG of the eye of Strombus exhibited two distinct ‘on’ peaks, a steady state during sustained illumination, and small rhythmic oscillations following the cessation of stimulation.
2. In certain afferent optic nerve fibres, illumination evoked phasic and tonic ‘on’ responses; others, whose activity was inhibited by light, responded with repetitive ‘off’ bursts which tended to occur in phase with the rhythmic ERG oscillations.
3. Spectral sensitivity studies indicate the presence of a single visual pigment with a peak absorption of about 485 nm.
4. The effects on the response of temperature and stimulus intensity and frequency were also examined.
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5. The results indicate photo-excitation and synaptic inhibition of the receptors, and excitatory coupling between them.

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REFERENCES


**EXPLANATION OF PLATE**

**PLATE I**

Light micrographs of eye and retina. (A) Mid-sagittal section (approx.) through eye. *c*, cornea; *l*, lens; *v*, vitreous body; *r*, retina; *on*, branches of optic nerve (indicated by arrows). Note branch on right penetrating capsule. Rectangle indicates magnified region in B. (B) Enlargement of retina in (A). *ds*, distal segments; *p*, pigment layer; *nu*, nuclear layer; *n*, neuropile; *c*, capsule, *on*, optic nerve.