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CLASSES OF LIGHT-EVOKED RESPONSE IN THE RETINA OF *STROMBUS*

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SUMMARY

Two general classes of light-evoked responses were recorded intracellularly from the retina of *Strombus luhuanus*. In one class, retinal illumination caused depolarization, the amplitude of which was graded with light intensity. In the other, it produced hyperpolarization and concomitant inhibition of repetitive action potentials.

There were two types of depolarizing waveform. Each was associated with a different type of intracellular recording site, characterized on the basis of electrical properties in the dark. In general, the type of response with a more rapid rate of decay was recorded from a site which exhibited a lower resting potential, higher input resistance, and longer 'membrane charging time.'

The two depolarizing responses and the hyperpolarizing response apparently each arose from a different type of neurone. The depolarizing types, at least one of which is a photoreceptor, apparently give rise to the cornea-negativity of the electroretinogram and 'on' activity in the optic nerve fibres. The hyperpolarizing type apparently mediates 'off' activity in the optic nerve.

INTRODUCTION

The retina of *Strombus luhuanus*, a marine gastropod, can contain more than 10^5 neurones and exhibits a distinct rhabdomeric layer, as well as layers of cell nuclei and neuropile (Gillary, 1974). Ultrastructural studies have shown that the retina is comprised predominantly of three morphologically distinct cell types (Gillary & Gillary, 1979). One type has relatively large distal segments with long microvilli which comprise the bulk of the rhabdomeric layer; this cell is apparently a photoreceptor. A second cell type appears to be glial, while a third type, apparently neuronal, is characterized by numerous short microvilli at its apical end. Afferent fibres run from the retina to the central nervous system via an optic nerve.

Previous reports have described the extracellularly recorded electrical activity of the eye and optic nerve of this species (Gillary, 1974, 1977). Illumination of the retina produces at least two cornea-negative 'on' components in the electroretinogram (ERG), and 'on' activity in a relatively large population of optic nerve fibres; cessation

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of illumination produces rhythmic 'off' oscillations in the ERG, and bursts of 'off' impulses in a smaller population of fibres.

In the present study, intracellular recordings were made from individual neurones in the retina of *Strombus luhuanus*, to aid in understanding how the mature eye functions at the cellular level and to provide a basis for future studies on the regenerating eye (following amputation of the eye of this species, a new and apparently normal one is regenerated quite rapidly in its place; Gillary, 1972). A preliminary report of some of the results has already been published (Quandt & Gillary, 1975).

METHODS

Adult *Strombus luhuanus* were collected and maintained as described previously (Gillary, 1974). The isolated eye was placed in sea water, which is similar in ionic composition to *Strombus* haemolymph (Little, 1967), and the retina exposed by dissection under dim red or white light. This involved peeling away part of the retina from the vitreous body, to which the rhabdomeric layer tends to adhere. Muscle fibres were often removed from the back of the eye to prevent light-evoked retinal movement (Gillary, 1977). The preparation was then pinned to a Sylgard block and orientated in a recording chamber (containing sea water at *ca.* 21 °C) to permit impalement of the retina with microelectrodes. Impalement was facilitated by transillumination with red light (passed through a Kodak Wratten 25 filter). However, following impalement, except for intentional photic stimuli, the preparation was kept in darkness to minimize the effects of light adaptation.

Intracellular recordings were obtained with glass microelectrodes filled with 3 M-KCl, with resistances which ranged from 15 to 100 MΩ and time constants of less than 1 ms. The extracellular retinogram was sometimes recorded simultaneously via a glass capillary (tip outer diam. *ca.* 0·8 mm) filled with sea water, which was pushed up against the vitreous body adhering to most of the retinal surface. Electrodes were connected to high-input impedance d.c. preamplifiers and were displayed and recorded by conventional methods.

To determine the input resistances and 'charging time' (defined later) of the various intracellular recording sites, brief pulses (usually less than 50 ms in duration) of constant current were passed through the recording microelectrode via a bridge circuit (Mentor N-950 or WPI M-701). Currents were usually less than 0·1 nA, although currents ranging as high as 2 nA were used on occasion.

To stimulate the retina with light, the entire retinal surface was illuminated with white light from a tungsten element. The light was passed through a filter to absorb infra-red radiation, and intensity was varied with neutral-density filters. The maximum intensity at the retina was 400 J m^{-2} s^{-1} although intensities considerably below this were more usual. The experimental procedures used in the present studies have been described elsewhere in greater detail (Quandt, 1976).

RESULTS

Types of intracellular response. All cells impaled – more than 300 – responded to illumination. Six hyperpolarized in response to light; the rest depolarized. For a given impalement, depolarizations fell into one of two categories, distinguishable on the basis of rate of repolarization after a flash of high intensity (i.e. one which evoked response amplitudes greater than half the maximum). One type repolarized rapidly (*ca.* 25 mV/s, Fig. 1 A), while the second type repolarized slowly (*ca.* 10 mV/s, Fig. 1 B). Evidence to be presented below indicates that these two types of response arise from different intracellular recording sites, with different electrophysiological characteristics.

Action potentials were absent from the depolarizing responses in all except three cells – which had resting potentials of about −40 mV and action potentials of up to 15 mV in amplitude (Fig. 1 C). For some cells the depolarizing responses were as great as 40 mV in amplitude, and could exceed the level of zero transmembrane potential (Fig. 1 D). The light-evoked depolarizations often exhibited more than a single peak (e.g. Fig. 1 B). Such complexities in waveform are considered elsewhere (Quandt, 1976) and will not be considered in this paper.

Two examples of cells which hyperpolarized in response to illumination are shown in Fig. 1 E and F. These cells had resting potentials of −50 to −60 mV and exhibited spontaneous action potentials prior to stimulation which were inhibited during the light-evoked hyperpolarizations. After stimulation, there was often a brief increase in the frequency of the action potentials (Fig. 1 E, F), and occasionally rhythmic bursts of action potentials associated with periodic oscillations in potential. We have no more detailed information about these cells because we encountered them so rarely.

Resting potentials. Fig. 2 shows the distribution of stable resting potentials recorded in the dark from cells giving depolarizing responses. The distribution appears to be bimodal and could be divided into two groups. One, with resting potentials less negative than −50 mV, had a mean value of −26 mV ± 10 mV S.D. ($n = 88$) (and was designated group I); the other, with resting potentials more negative than −50 mV, had a mean value of −75 ± 7 mV S.D. ($n = 204$) (and was designated group II). 'Type I' penetrations tended to yield light-evoked responses with relatively rapid decay rates, similar to those of Fig. 1 A and D, while 'type II' penetrations generally exhibited responses with slower rates of decay, such as that of Fig. 1 B. This suggests that the two types of responses were recorded from different types of recording site, a hypothesis which is supported by other evidence presented below.

Application of intracellular current. Type I and type II recording sites differed in their electrical characteristics determined by the passage of transmembrane current via the recording microelectrode. One such difference was in the 'charging time', which is defined as the time for the potential in response to an abruptly initiated, constant current (see Methods) to attain 85% of its maximum, steady-state value (Fig. 3 A). The distribution of these measurements is shown in Fig. 3 B. Recording site I exhibited a mean charging time of 24·4 ± 21·6 ms S.D. ($n = 13$), while site II had a mean charging time of 0·4 ± 0·1 ms S.D. ($n = 10$).

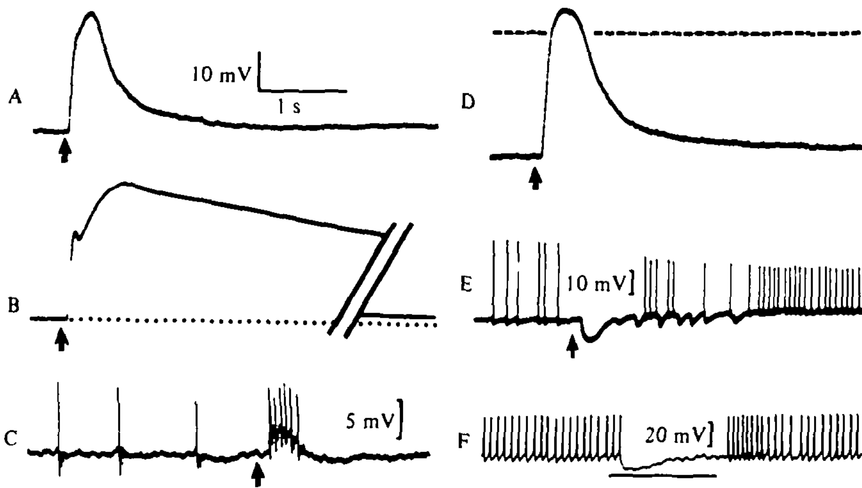

Fig. 1. Types of light-evoked intracellular potential recorded from the retina of *Strombus*. The arrows in (A)–(E) indicate the onset of a 0·1 s photic stimulus; the bar in (F) monitors a stimulus of longer duration. In this and all subsequent figures, transmembrane depolarization is upwards. The vertical calibration in A applies also to (B) and (D). (A) Depolarizing response from a cell with a −35 mV resting potential ('type I' response, see text). (B) Response from a cell with a −75 mV resting potential ('type II' response). The break in (B) is 23·5 s. Note the difference between the rates of repolarization of (A) and of (B). (C) Depolarizing response from a cell with −40 mV resting potential, exhibiting light-evoked action potentials. (D) Type I depolarization which overshoots 0 mV transmembrane potential (indicated by broken line). (E, F) Examples of light-evoked hyperpolarizations and concomitant inhibition of spontaneous action potentials. The resting potentials of the cells in (E) and (F) were −50 and −60 mV, respectively. (Action potentials in (C) and (E) were retouched for clarity.)

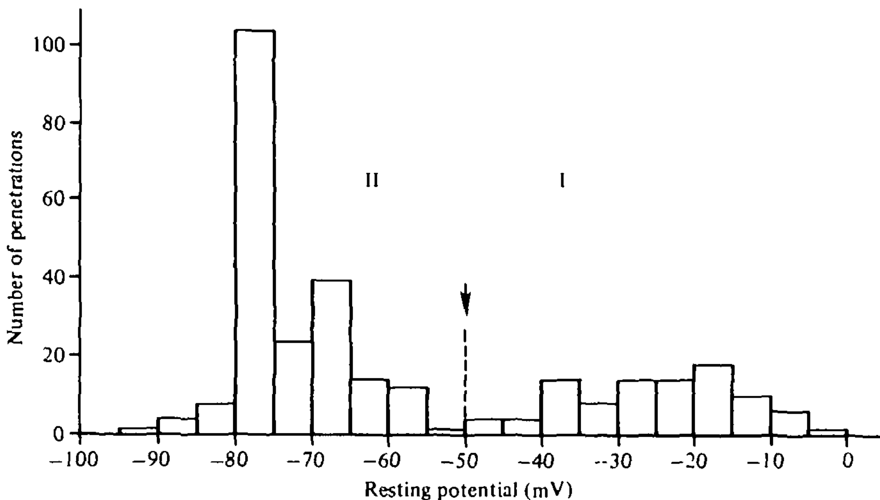

Fig. 2. Bimodal distribution of resting potentials in the dark from penetrations which yielded light-evoked depolarizations. Penetrations yielding resting potentials more negative than −50 mV (arrow) tended to yield 'type I' responses. Those yielding resting potentials more positive than −50 mV tended to yield 'type II' responses.

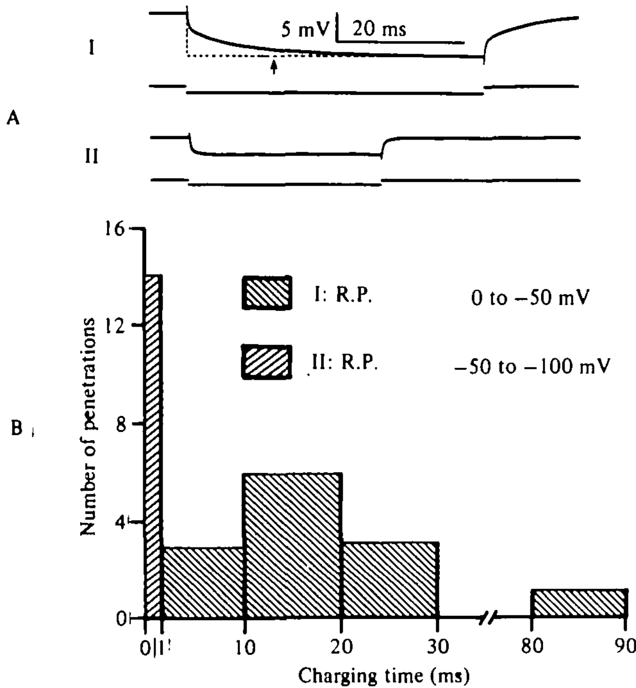

Fig. 3. Charging times determined at recording sites I and II in the dark. (A) For records I and II, respectively, the upper traces indicate the voltage in response to constant −0·1 nA currents passed via the recording electrode and monitored in the lower traces. The resting potential for record I was −25 mV; that for record II was −75 mV. The potential across the electrode resistance was balanced out with an active bridge circuit. The 'charging time' (indicated for I by the arrow) is the time taken for the potential to attain 85 % of its maximum displacement. (B) Distribution of charging times. Note that the type II recording sites are correlated with relatively short charging times, while those for the type I sites tend to be considerably longer.

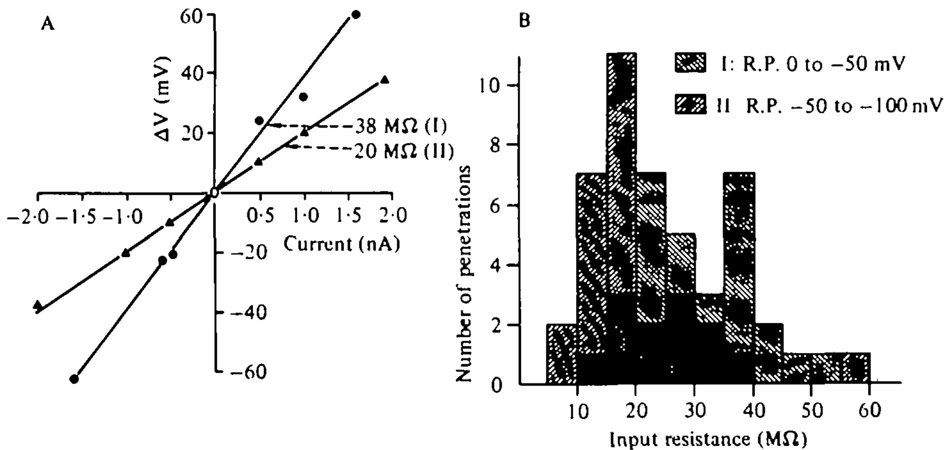

Fig. 4. Input resistances determined for recording sites I and II in the dark. (A) Amplitudes of the steady state change in membrane potential (ΔV) plotted as a function of constant current applied through the recording electrode. The potentials across the electrode resistance were balanced out with an active bridge circuit. ●, Data from a representative type I recording site (resting potential −27 mV); ▲, from a type II site (resting potential −70 mV). Note that the input resistance is constant over the range of potentials presented. (B) Distribution of input resistances. Note that the lower input resistances tend to be correlated with the type II recording site, and the higher input resistances, with the type I sites.

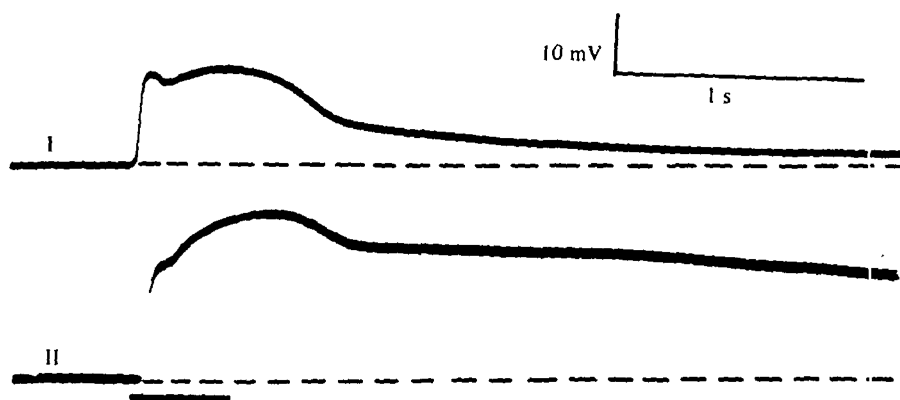

Fig. 5. Type I and type II light-evoked depolarizations recorded simultaneously from the same retina. I indicates record from a type I recording site; II indicates a type II recording site. The bar below II monitors the photic stimulus for both traces. Broken lines indicate resting potentials. Note the differences between the respective waveforms, including differences in the second phase of depolarization, as well as in the rates of repolarization.

Values for input resistance determined for impaled cells in the dark also differed between recording sites I and II. For both sites, the resistance did not vary with the current injected within a range of ± 2 nA (Fig. 4A). The distribution of the values for input resistance is shown in Fig. 4B. Recording site I had a mean value of 34 ± 17 MΩ S.D. ($n = 19$), while that of site II was 22 ± 9 MΩ S.D. ($n = 34$).

Waveform of depolarizations. In one series of experiments, two microelectrodes were used to impale simultaneously, in a given retina, two different cells with respective characteristics of the type I and type II recording sites, in order to compare more accurately the waveforms of the light-evoked depolarizations from these sites. An example of this is shown in Fig. 5. While the latencies of the two types of response were approximately the same, the potential from the type II site was more prolonged than that of the type I site, as a consequence of its lower rate of repolarization. Both recording sites were in the same region of the retina, upon which the incident light intensity was uniform, so it is unlikely that the differences in waveform were due to differences in photic stimulation.

The markedly different rates of repolarization of the two types of depolarizing response evoked by high light intensities provided a reliable criterion for distinguishing between the two types of response, and this enabled response waveform to be correlated with other recording site parameters. For example, a correlation was found with resting potential in the dark. The mean resting potential for 79 penetrations which yielded rapidly decaying light-evoked potentials was -26 ± 11 mV S.D. while the values for 181 penetrations which yielded slowly decaying depolarizations was -76 ± 7 mV S.D. These mean values are comparable to those presented earlier which were obtained by separating the resting potentials into those above -50 mV and those below it (Fig. 2).

Relation of response to ERG. The electroretinogram (ERG) recorded extracellularly from the retina can exhibit a complex waveform which represents the summed responses of a number of retinal cell types (Brown, 1968). Fig. 6 illustrates the

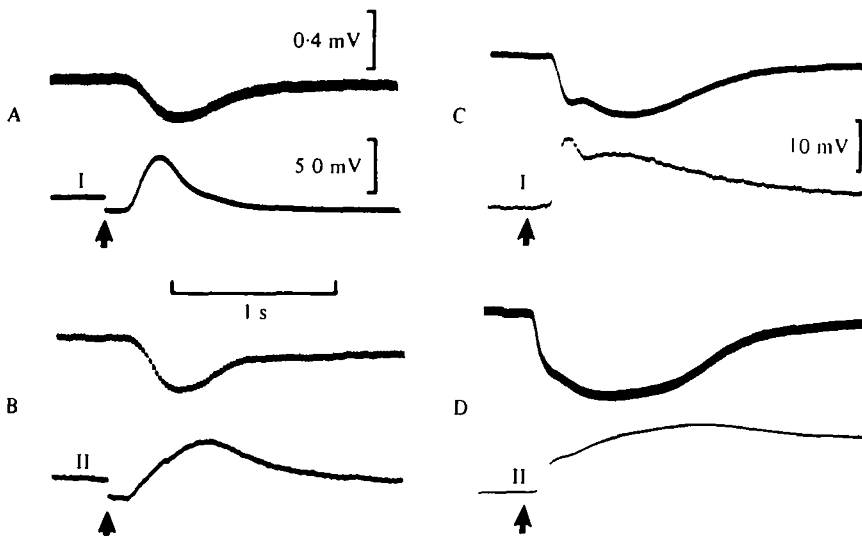

Fig. 6. Comparison of the waveforms of the light-evoked depolarizations, recorded intracellularly, with those of the ERG recorded simultaneously with an extracellular electrode. For (A)–(D) the upper traces are ERG's and the lower traces simultaneously recorded intracellular potentials. I and II identify the type of recording site. Each arrow indicates the onset of wide-field retinal illumination which continues throughout the remainder of the record. The vertical calibration mark for the upper trace in (A) applies also to the upper traces of (B)–(D), that for the lower trace in (A) applies also to the lower trace in (B), and that for the lower trace in (C) applies also to the lower trace in (D). (A) and (B) are from the same retina under similar conditions of stimulation. (C) and (D) are from different retinas. Note that the ERG is similar to but not identical to either type of intracellular potential.

relationships of the ERG waveform of *Strombus* to the depolarizing responses from recording sites I and II. Although the waveforms of the ERG and simultaneous intracellular potential tended to be similar, the ERG generally peaked after the maximum of potential from recording site I (Fig. 6A), and before the maximum from recording site II (Fig. 6B). The results are compatible with the view that the ERG reflects the combined depolarizations from both recording sites I and II.

Electrode position. Usually the position of the tip of the microelectrode within the retina could not be clearly determined. However, on several occasions, a cell was impaled with the electrode tip clearly positioned in the rhabdomeric layer, which is comprised primarily of the distal segments of photoreceptors. When this occurred, the electrical properties and responses were characteristic of recording site I. In addition, several impalements which were clearly deep within the retina (i.e. near the capsule) exhibited characteristics of the type II recording site.

Depolarizing recording sites and possible cell damage. The above results indicate that there were two intracellular recording sites which gave rise to the light-evoked depolarizations. Recording site I typically had a resting potential of −26 mV, an input resistance of 34 MΩ and a charging time of 24 ms. Following a depolarization to intense illumination, repolarization to the resting potential in the dark was relatively fast (*ca.* 25 mV/s). In contrast, recording site II exhibited a more negative resting potential (typically −75 mV), a lower input resistance (*ca.* 22 MΩ) and a very much

smaller charging time (*ca.* 0·4 ms), and the repolarization of the membrane following an intense stimulus was relatively slow (*ca.* 10 mV/s or less).

It seems highly unlikely that the different electrical characteristics of the two sites were due to cell damage by the impaling electrode. Although the resting potentials associated with recording site I were low compared with those of site II, they were stable over periods greater than half an hour and are within the physiological range of those recorded from other molluscan retinas (Hagins, Zonana & Adams, 1962; Tomita, 1968; McReynolds & Gorman, 1970*b*; Chase, 1974). In addition, site I exhibited higher values for input resistance and charging time than site II; both of these would be expected to be decreased by microelectrode damage. Furthermore, the light-evoked potentials recorded from site I attained amplitudes which were comparable to those of site II, a finding not to be expected if site I were really a damaged site II. Finally, if site I did represent a site II with damage or deterioration, one might expect the characteristics of site II to change at least occasionally to those of site I during impalement, but this was never seen.

DISCUSSION

The depolarizing light-evoked potentials of *Strombus* are like those of other molluscan photoreceptors which possess microvilli (Hagins *et al.* 1962; Tomita, 1968; Mauro & Baumann, 1968; Jacklett, 1969; McReynolds & Gorman, 1970*a*; Mpitsos, 1973; Alkon & Fuortes, 1972; Chase, 1974). In the squid retina, illumination of the distal segments of the photoreceptors causes localized inward current, photoreceptor depolarization and a cornea-negative ERG (Hagins *et al.* 1962). The retina of *Strombus* also exhibits a cornea-negative ERG, intracellular light-evoked depolarizations, and photoreceptors with prominent distal segments bearing microvilli, suggesting that illumination may cause inward transmembrane current in the distal segments of *Strombus* photoreceptors. This is further supported by results not presented in this paper (Quandt, 1976; F. N. Quandt & H. L. Gillary, in preparation). For example, the light-evoked depolarizations are resistant to magnesium ion inhibition and so probably do not arise as a consequence of chemical synaptic transmission. In addition, decreases in input resistance accompany the light-evoked depolarizations, the polarity of which can be reversed by applied depolarizing current (F. N. Quandt & H. L. Gillary, in preparation). These observations indicate that ionic conductance changes in the photoreceptor membranes underlie the generation of the light-evoked depolarizations, as they apparently do in other photoreceptors (Millechia & Mauro, 1969; Brown *et al.* 1970; McReynolds & Gorman, 1970*b*; Detwiler, 1976).

Whereas there is some morphological evidence that the retinal photoreceptors of certain gastropods give rise directly to optic nerve fibres (Eakin & Brandenburger, 1967; Stensaas, Stensaas & Trujillo-Cenoz, 1969), it is still uncertain whether this occurs in *Strombus*. In *Strombus*, the intracellularly recorded light-evoked depolarizations typically lacked concomitant action potentials, such as those recorded from the optic nerve (Gillary, 1974). However, these may simply have failed to invade the recording site from a relatively remote zone of impulse initiation.

The hyperpolarizing responses to light almost certainly arise from a type of cel

which is distinct from those yielding depolarizing responses. Certain gastropod photoreceptors which typically depolarize in direct response to light can also exhibit hyperpolarization mediated by inhibitory synaptic input from neighbouring photoreceptors (Dennis, 1967; Alkon & Fuortes, 1972). However, evidence for this in *Strombus* has not been seen; in the absence of externally applied current, cells which exhibited light-evoked depolarizations never gave hyperpolarizing responses under a wide variety of stimulating conditions, and those cells which were hyperpolarized by light never yielded light-evoked depolarizations. Another difference which suggests that the hyperpolarizing responses arise from a separate cell type is that 'spontaneous' action potentials in the dark could always be recorded from hyperpolarizing cells, but only very rarely from depolarizing cells.

Certain molluscan retinas contain two types of photoreceptors: those which are depolarized by light and those which hyperpolarize in direct response to photic stimulation (McReynolds & Gorman, 1970*a*; Mpitsos, 1973). The latter type are said to exhibit 'primary inhibition' (Land, 1968) and are capable of generating 'off' responses in the optic nerve. While the optic nerve of *Strombus* exhibits 'off' responses to light, certain evidence indicates that such responses are due to inhibitory synaptic input from neurones excited by light, rather than to primary photic inhibition (Gillary, 1974, 1977).

The evidence presented indicates that the light-evoked depolarizations arise from two separate intracellular recording sites. While it is uncertain as to whether these sites lie in two separate types of cell or in two different parts of the same cell, the former hypothesis seems more plausible since the potentials at the two sites are quite different, both in the dark and during illumination. If the two recording sites were in different parts of a single type of photoreceptor, the cell would require a space constant considerably shorter than its actual length. While an accurate value for such a space constant has not been determined for *Strombus* photoreceptors, that for squid photoreceptors has been found to be 250–400 μm during the response to light (Hagins *et al.* 1962; Hagins, 1965), and one would expect the value to be even larger in the dark, since the membrane resistance then is higher. If this value for the squid is similar to that for a typical *Strombus* photoreceptor, different regions of the latter would be expected not to be able to exhibit simulateneously large differences in potential, since the photoreceptors are less than 200 μm in length (Gillary, 1974).

The observation that the light-evoked depolarizations recorded from either type of intracellular recording site can reach a maximum amplitude of 40 mV also argues against the view that the two sites lie in electrically remote regions of the same cell. If the receptor potential were generated in one region of the cell (e.g. the distal segment), one would expect the potential at an electrically remote region of the cell to be greatly attenuated, unless some voltage-dependent amplification near this latter site occurred. However, no evidence for such a process has been found, by examining either the current voltage relations of the two sites, or the results of voltage-clamp experiments, described elsewhere (Quandt, 1976; F. N. Quandt & H. L. Gillary, in preparation). The above considerations therefore tend to favour the hypothesis that the two recording sites lie in two different types of retinal cell.

As mentioned in the Introduction, morphological studies on the retina of *Strombus* indicate that it contains two types of neurone (Gillary & Gillary, 1979). One type,

evidently a photoreceptor, has rhabdomeric distal segments as long as 100 μm. The other type terminates in numerous short microvilli and may be a second type of photoreceptor. If the two recording sites do lie in two different cell types, such morphological differences may help to explain the different electrical properties of the recording sites. For example, the greater charging time of recording site I, which apparently indicates a larger input capacitance, may reflect a more extensive cell surface, such as that conferred by a large distal segment. The electro-physiological differences of the recording site may also reflect differences regarding the extent of coupling of the two cell types to other cells. Further studies employing intracellular staining techniques (Kater & Nicholson, 1973) are expected to clarify the morphological basis of the two types of intracellular recording site in the retina of *Strombus*.

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