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INCREMENTAL RESPONSES TO LIGHT RECORDED FROM PIGMENT EPITHELIAL CELLS AND HORIZONTAL CELLS OF THE CAT RETINA

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SUMMARY

1. Rod-dependent incremental responses were recorded intracellularly in both pigment epithelial cells and horizontal cells of the cat retina. They were elicited by test flashes which were superimposed on background flashes after a delay.

2. In pigment epithelial cells smaller test responses were produced as background intensity was raised. The incremental sensitivity function was linear for about 1·4 log units, with a slope of 0·86, and the approach of saturation occurred at about 2·5 log td scotopic.

3. The amplitude of pigment epithelial test responses could be estimated from the dark-adapted amplitude–log intensity function obtained with single flashes. Test flashes produced the voltage increment predicted by the slope of this function just above the point on the curve equal to the background intensity. The pigment epithelial response to a test flash, therefore, is the response expected if the background were presented alone and made more intense by the amount of the test flash.

4. Rod-dependent incremental sensitivity functions of horizontal cells closely resembled the ones obtained from pigment epithelial cells.

5. It was concluded that the adaptive effects observed in pigment epithelial cells originated in individual rods. These effects arose from the compressive nature of the dark-adapted amplitude–intensity function. In horizontal cell responses these effects may be modified by the failure of the background response to maintain its initial voltage.

INTRODUCTION

It has been difficult to perform experiments on the mammalian retina *in situ* which provide information about rod photoreceptor activity. Intracellular recordings from these cells have not yet been achieved.

Furthermore, the extracellular rod receptor potential is difficult to isolate from the *c*-wave of the local electroretinogram (LERG) (Brown & Watanabe, 1962*a*, *b*). There are also severe limitations to the inferences which can be made about rod activity from recordings at more proximal retinal levels, because of signal transformations between the rods and the recording site.

At present the recording of intracellular pigment epithelial responses in the cat offers a moderately direct way of studying rod activity. The experiments can be performed with intact retinas and cone activity does not interfere with the responses (Steinberg, Schmidt & Brown, 1970). In addition, apart from its integration through a slow time constant, rod activity probably has not been further modified so that the responses represent the summed activity of individual rods (Schmidt & Steinberg, 1971).

This work began with the observation that background lights produced a rapid desensitization of the pigment epithelial response; an adaptive effect which must have originated in the rods. The present paper describes this effect and compares it to the adaptation produced by backgrounds in rod-dependent horizontal cell responses.

METHODS

The preparation and maintenance of the cat, recording technique from the intact eye, and conditions of stimulation have been described in previous publications (Steinberg, 1969*a*, *b*). Additional information pertaining to the study of intracellular pigment epithelial responses was provided in the accompanying paper (Schmidt & Steinberg, 1971) and in an earlier publication (Steinberg *et al.* 1970).

Incremental responses were elicited by circular test spots of light presented against concentrically placed circular backgrounds. Intracellular responses can be maintained for only a limited period of time, so steady backgrounds were not used because of the time needed to readapt between stimulus presentations or to return to the dark-adapted state. Instead, both the test (ΔI) and background (I) were flashed. A stimulus presentation consisted of the onset of a background flash which, in different experiments, was followed by onset of a test flash at a delay of 1·9–3·9 sec. Background flashes were 5·5–6·5 sec in duration. The test flash was temporally placed so that the complete test response could be readily distinguished from the background response. Horizontal cell test responses were elicited with 0·5 sec flashes. Within the range of delays used, the amplitude of the test responses was constant as a function of the delay from the onset of the background. Pigment epithelial test responses were elicited by 2·6 sec flashes, which were long enough to bring the test response to a plateau level.

Background levels were increased in 0·5–1·0 log steps. At each background level, test intensities were increased in 0·2–1·0 log steps as required by the particular experiment. In order to minimize residual adaptive effects, time elapsed between presentations of stimulus sets (background and test) was lengthened as the background levels were raised.

The test stimuli were obtained from the stimulus beam of the dual-beam ophthalmoscope using an electromagnetic shutter with a 1·0 msec rise and fall time. In the

study of horizontal cell responses, background flashes were produced by a glow modulator tube (Sylvania R1131C), driven by a pentode current amplifier and triggered from a Grass stimulator. These flashes reached full incandescence and full nigrescence in 0·1 msec, and peak current through the tube was never greater than 50 mA. In the pigment epithelial experiments background flashes were provided by a tungsten filament lamp (colour temperature 2850° K), turned on and off by a relay triggered from a Grass stimulator. Full incandescence and nigrescence were reached in about 200 msec. The slow 'on' and 'off' of these background flashes did not hinder the experiment because the test flashes always came on after both the lamp and the background response had reached steady-state levels. Illuminances of the background flashes were estimated by comparing their effectiveness in eliciting scotopic components of the LERG with that of test flashes which had been calibrated photometrically (Schmidt & Steinberg, 1971).

RESULTS

Responses from pigment epithelial cells

In order to study rod-dependent incremental responses from pigment epithelial cells, it was not essential to use long wave-length backgrounds as in the method of Aguilar & Stiles (1954). This is because the cones do not appear to contribute to pigment epithelial responses in the cat (Steinberg *et al.* 1970). Most horizontal cell responses, on the other hand, exhibit contributions from both the rods and cones (Brown & Murakami, 1968; Steinberg, 1969*c*) so that long wave-length backgrounds must be used to suppress the cone responses. In studying pigment epithelial incremental responses, long wave-length backgrounds of 620 nm were only used so that the results could be directly compared with those from horizontal cells.

Fig. 1 shows pigment epithelial responses to blue test spots of 440 nm presented against five intensities of an orange background of 620 nm. The background response increased in amplitude as background intensity increased and reached a 15 mV ceiling at between 2·8 and 3·7 log td scotopic. The test response increased in amplitude with increases in test intensity at each intensity of background. As background intensity was raised, its suppressive effect on the test response can be observed in the diminution in amplitude of the responses to test flashes of equal intensity. For example, the response to a 1·6 log td scotopic flash progressively decreased at backgrounds greater than 0·9 and was just visible at 2·3 log td scotopic; while the response to a 2·2 log td scotopic test flash can just be seen at a background of 2·8 log td scotopic. The 3·7 log td scotopic background was sufficiently intense to suppress responses to bright test flashes. For example, a 3·5 log td scotopic test flash produced a 15 mV response when presented alone, but produced no response when presented against the 3·7 log td scotopic background.

In Fig. 2*A* these test responses have been plotted as a function of test intensity at each level of background. As background intensity increases, the functions are displaced toward the right and retain their shape except for a tendency to bend over at high backgrounds (2·3, 2·8).

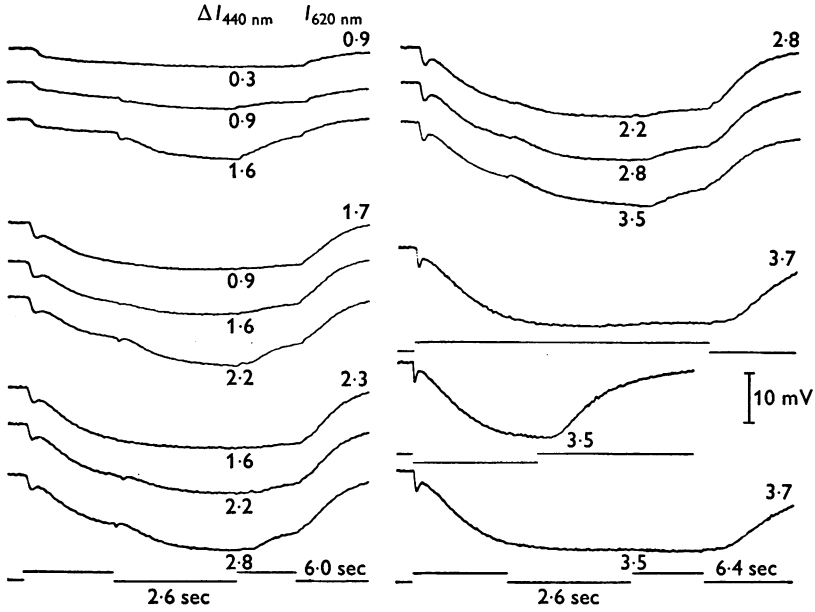

Fig. 1. Intracellular responses from a pigment epithelial cell to blue test flashes of 440 nm presented against orange background flashes of 620 nm. The background ($I_{620\,nm}$) and test ($\Delta I_{440\,nm}$) spots both were 2·0 mm in diameter and were concentrically placed on the retina. The background had a duration of 6·0 sec at background intensities of 0·9–2·3 and 6·4 sec at higher intensities. The test flash began 1·9 sec after the onset of the background and had a duration of 2·6 sec, long enough for the test response to reach a plateau. Two separate responses appear in each record, a test response and a background response. The intensity of the background flash increased from above downwards as indicated in the right margins in log td scotopic. At each background intensity, the test intensity also increased from above downwards as indicated beneath each test response. Negative responses are displayed downward in all Figures of this paper.

Fig. 3 is a double log plot of test *v.* background intensity derived from the data in Fig. 2, plus data from two other cells studied under the same stimulus conditions. The curve drawn by hand through the data points traces the test intensity required to produce a constant response of 3·0 mV as background intensity increased. Similar curves were obtained with lower voltage criteria (0·5–2·5 mV). The curve is linear for about 1·4 log units and has a slope of 0·86. The approach of saturation is indicated by the increase in slope at about 2·5 log td scotopic.

Fig. 4 illustrates, for a different cell, how rod-dependent responses also can be studied using a blue-green background of 496 nm. The background response reached a 16·0 mV ceiling at between 2·7 and 4·0 log td scotopic and even a very intense test flash of 4·2 log td scotopic did not elicit a response at a background of 4·0 log td scotopic. The amplitude–log intensity curves of Fig. 2*B* were obtained from the data of Fig. 4 and

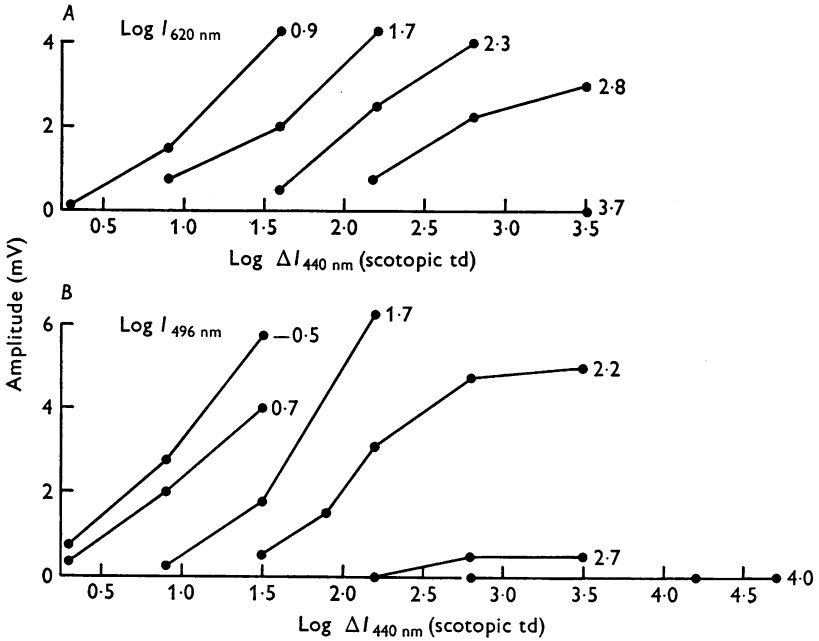

Fig. 2. Amplitudes of test responses from pigment epithelial cells plotted as a function of test intensity (log ΔI) for each level of background. The curves in *A* were derived from the responses presented in Fig. 1, and those in *B* from the responses partially presented in Fig. 4. To obtain the amplitude of the test response, the background response, measured when the background was presented alone, was subtracted from the maximum voltage reached during the test flash. The background intensity is indicated in log td scotopic at the top of each curve.

resembled the curves obtained with orange backgrounds in Fig. 2*A*, but saturation of the response was more clearly observed in Fig. 2*B* because the test responses reached their amplitude ceilings at backgrounds of 2·2 and 2·7 log td scotopic.

In analysing the suppressive effect of background illumination it was found that the amplitudes of incremental responses could be estimated from the amplitude–log intensity function obtained with single flashes in the dark-adapted retina. Test flashes produced the voltage increment predicted by the slope of the dark-adapted amplitude–intensity function

just above the point on the curve equal to the background intensity. Thus if I and ΔI are presented simultaneously in the dark-adapted retina they will produce a response V_0 equal in amplitude to the response produced by a single flash I_0, where $I_0 = I + \Delta I$. Let us assume that V_0 exactly equals the sum $\Delta V + V$ produced when the test flash is presented against the background after a delay. Both V and V_0 can be obtained from the dark-adapted curve, and the differences between these voltages should equal the ΔV obtained by experiment.

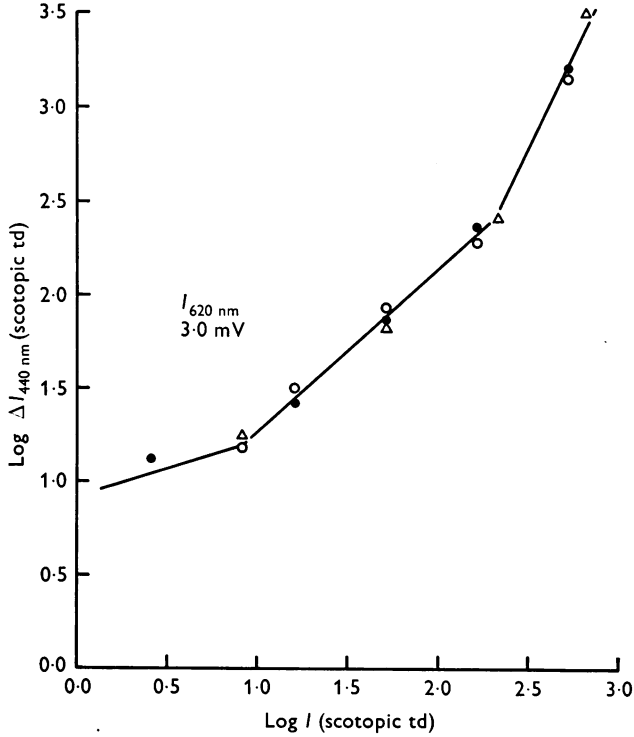

Fig. 3. Log test intensity ($\Delta I_{440\,nm}$) plotted as a function of log background intensity ($I_{620\,nm}$) for a 3·0 mV pigment epithelial response. The curve was drawn by hand through data points obtained from three pigment epithelial cells in two retinas.

Fig. 5 shows these predictions for the dark-adapted amplitude–log intensity function presented in Fig. 7 of the accompanying paper (Schmidt & Steinberg, 1971). The responses were obtained with blue flashes of 440 nm, 4·6 sec in duration. The inset in Fig. 5 shows the construction, from the dark-adapted curve, of ΔV as a function of ΔI at various levels of I (see the legend of Fig. 5 for more detail). The series of curves on the left were derived in this manner and the filled circles plot ΔV as the increment

in voltage above V at 0·5 log steps of background intensity. The line segment placed underneath the first point of each curve designates V for each level of background. As ΔI increases the curves converge on the dark-adapted function since ΔI approaches I_0.

In Fig. 6, predicted ΔV–log ΔI functions are compared with those obtained by experiment for the data presented in Figs. 2*B* and 4. The open circles specify V, at increasing levels of I, and the dark-adapted amplitude–log intensity function was drawn through these points. The

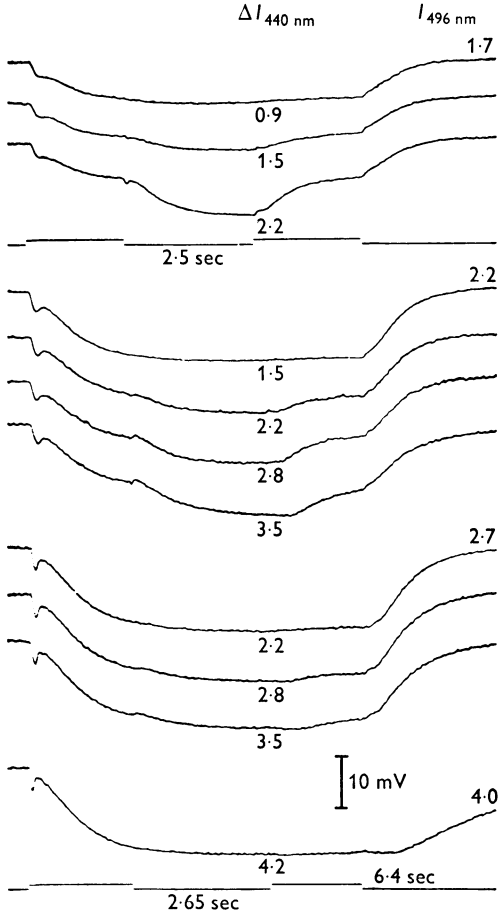

Fig. 4. Intracellular responses from a pigment epithelial cell to blue test flashes of 440 nm presented against blue-green background flashes of 496 nm. The background ($I_{496\,nm}$) and test ($\Delta I_{440\,nm}$) spots both were 2·0 mm in diameter and were concentrically placed on the retina. The background had a duration of 6·4 sec. The test flash began 1·9 sec after the onset of the background and had a duration of 2·5 sec at $I_{496\,nm}$ 1·7, and 2·65 sec at all other intensities of background. Otherwise the conditions are the same as in Fig. 1.

continuous curves are the predicted ΔV–log ΔI functions for the backgrounds used in this experiment, calculated and plotted as in Fig. 5. The closed circles are the actual ΔV responses obtained by experiment and replotted from Fig. 2*B* as the increment above V. Notice that these points

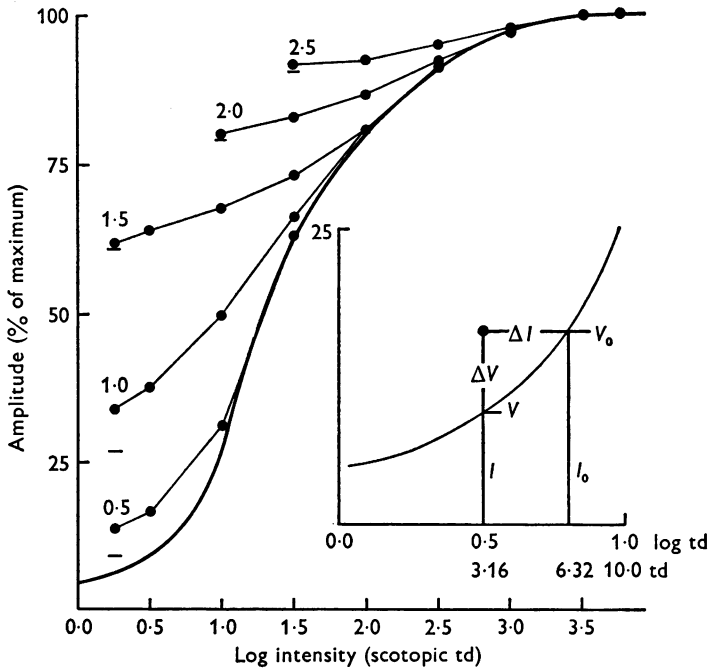

Fig. 5. Predictions of test response amplitude from a dark-adapted amplitude–log intensity function. The continuous curve is the dark-adapted amplitude–log intensity function taken from Fig. 7 of the accompanying paper (Schmidt & Steinberg, 1971). The responses had been elicited in a dark-adapted retina by blue flashes of 440 nm, which were 4·6 sec in duration. The filled circles are the predicted amplitudes of ΔV at 0·5 log unit steps of background intensity. The ΔV's are plotted as voltages above the background response, V. The amplitude of the background response, V, is designated by a line segment placed underneath the first point of each curve. The inset illustrates the construction of ΔV. In this example, both ΔI and I were 0·5 log td scotopic, their sum I_0 equals 6·32 td scotopic (0·8 log td scotopic). The perpendiculars at I and I_0 intersect the curve at V and V_0 and ΔV is the increment in voltage produced by ΔI. This voltage, ΔV above V, has been plotted at ΔI = 0·5 log td scotopic.

approximately follow the predicted curves. Similar results were obtained in three additional cells. It appears, therefore, that the response ΔV to a flash ΔI presented against a background is the same as would be obtained if the background flash were presented alone and simply made more intense by the quantity ΔI.

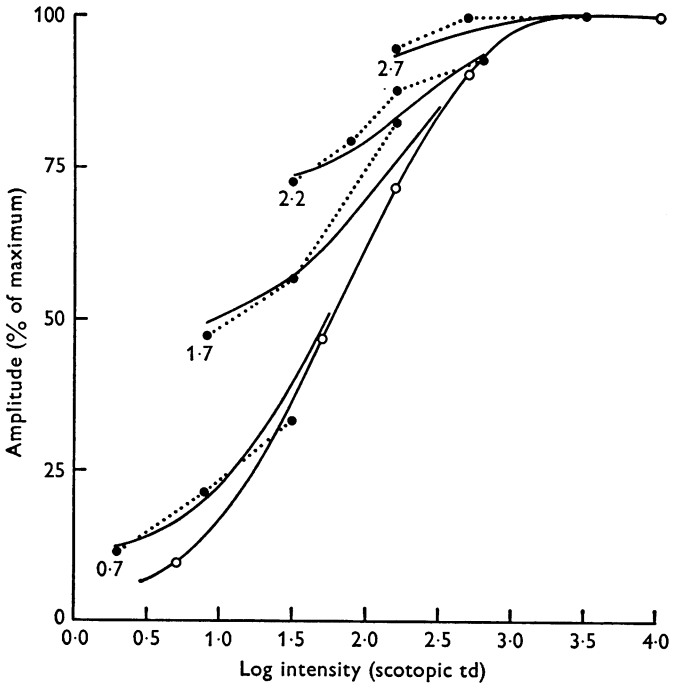

Fig. 6. Predicted and experimentally obtained test response amplitudes for the pigment epithelial cell of Fig. 4. The open circles are background response amplitudes for each intensity of background. The continuous curve drawn through these points was used to construct test response amplitudes according to the method given in the inset of Fig. 5. These points were then connected by a smooth curve at each background intensity. The filled circles connected by dotted lines are the experimentally obtained test response amplitudes replotted from Fig. 2*B* as the voltage above the background response.

Responses from horizontal cells

In most horizontal cells both the rods and cones contributed to the response. This was established using blue and orange flashes and examining the responses according to criteria previously described (Steinberg, 1969*b*, *c*). Long wave-length backgrounds were used, therefore, so that rod-dependent incremental responses could be followed over the widest possible range.

Fig. 7 shows part of a typical response-series to blue test flashes of 433 nm against orange backgrounds of 615 nm. Since the orange background elicited a strong response from the cones, the background responses continue to grow at high background intensities. The adaptive effect of the background upon rod-dependent test responses can be seen in the decrease

in the amplitude of test responses at test intensities which did not produce a significant cone response (2·0 and 2·5 log td scotopic). Saturation of the rod-dependent response is indicated at a background of 2·7 log td scotopic by the minimal increase in test response amplitude as a function of test

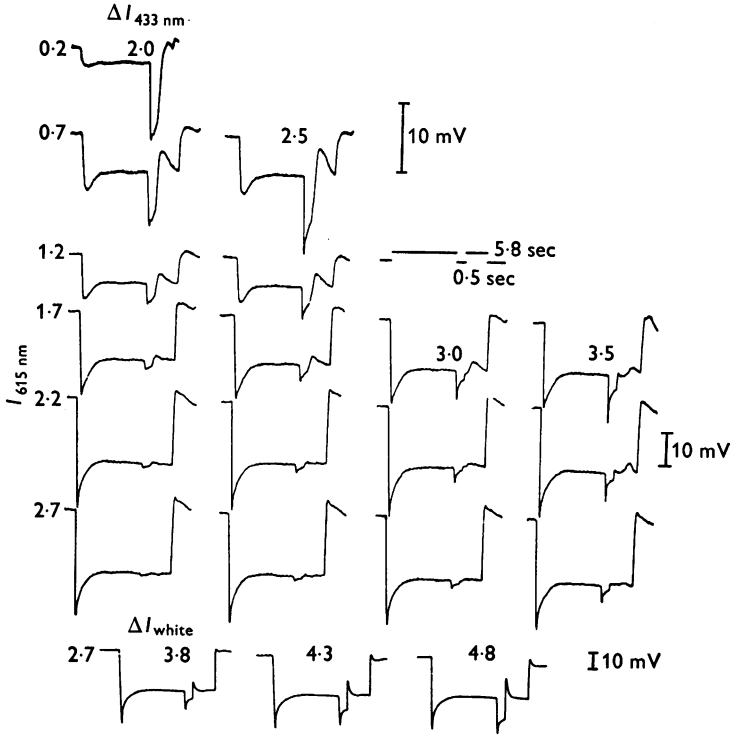

Fig. 7. Intracellular responses from a horizontal cell to blue test flashes of 433 nm presented against orange background flashes of 615 nm. The responses of this cell were determined by both the rods and cones. The background ($I_{615\,nm}$) was 2·0 mm in diameter while the concentrically placed test spot ($\Delta I_{433\,nm}$) had a diameter of 1·2 mm. The duration of the background was 5·8 sec and the test flash began 3·9 sec after the onset of the background and had a duration of 0·5 sec. The responses are arranged in horizontal rows at a constant intensity of $I_{615\,nm}$ and in vertical rows at a constant intensity of $\Delta I_{433\,nm}$. The test responses in the bottom row were elicited by flashes of 'white' light (colour temperature 2850° K) in order to achieve higher photopic intensities. Note that the gain of the amplifier was halved in horizontal rows 3–6 and again in the bottom row.

intensity. The cone-dependent test response first clearly appeared at a test intensity of 3·0 log td scotopic as a rapid decay following the 'off' of the test flash. It grew larger at $I_{615\,nm}$ 2·7 when test intensity was further increased by the change to a 'white' test flash.

Fig. 8 shows the test response amplitude plotted as a function of log test intensity at each intensity of background. As with pigment epithelial responses, the curves displaced towards the right as background intensity increased and bent over at high intensities (2·2, 2·7).

To compare the adaptive effects observed here with those from pigment epithelial cells, it was not possible to plot ΔV above V (Fig. 6), because the cone contribution to the background response of horizontal cells could not

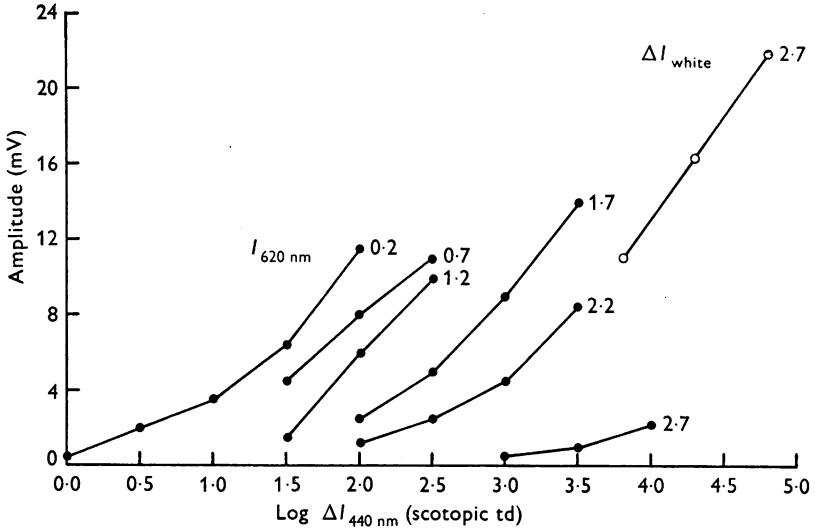

Fig. 8. Amplitudes of test responses from a horizontal cell plotted as a function of test intensity (log ΔI) for each level of background. These curves were derived from the responses presented in Fig. 7. To obtain the amplitude of the test response, the maintained voltage in response to I was subtracted from the peak voltage in response to ΔI. Both voltages were measured from the base line. The background intensity is indicated for each curve in log td scotopic.

be easily distinguished from the rod contribution. The comparison could be made by plotting log test flash intensity *v.* log background intensity for a rod-dependent criterion response.

Fig. 9 shows this function for the horizontal cell of Fig. 7. It was assumed that the small criterion response of 2·25 mV was almost completely rod-dependent within this range of intensities. The curve drawn through the data points had a slope of 0·88 over a 2·0 log range. Above this level the approach of saturation was indicated by the sharply steeper slope. This function was almost identical with the one obtained from pigment epithelial cells studied under similar conditions (Fig. 3), except that the linear portion extended to a lower intensity of background.

Figs. 10 and 11 present data from a unique cell whose responses did not show a cone contribution even at high photopic intensities. Otherwise, the response characteristics were similar to those of S-potentials which exhibit both rod and cone contributions, and which have been identified by intracellular dye injection as originating from horizontal cells (Steinberg & Schmidt, 1970). It is assumed, therefore, that the all-rod response is also generated by a horizontal cell, but the positive identification must be deferred until other cells of this type are injected with dye.

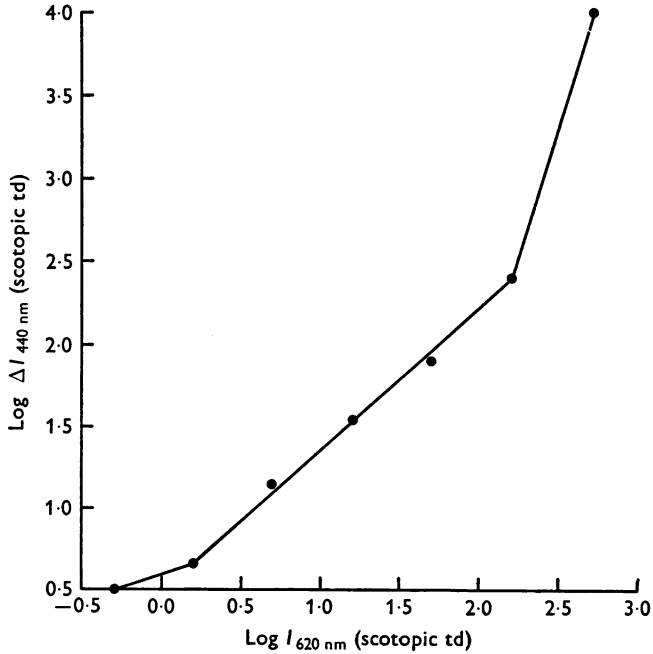

Fig. 9. Log test intensity ($\Delta I_{440\,nm}$) plotted as a function of log background intensity ($I_{620\,nm}$) for a constant amplitude horizontal cell response. The curve was drawn through data points obtained from Fig. 7, for a 2·25 mV peak response.

Fig. 10 shows the response as a function of intensity with blue flashes of 440 nm and orange flashes of 620 nm. As expected when only one type of receptor contributes, the responses to both wave-lengths have the same form. The long latencies and slow rise and fall times identify these receptors as the rods (Brown & Murakami, 1968; Gouras, 1966; Gouras & Link, 1966; Steinberg, 1969*b*, *c*). One amplitude–log intensity function fitted both sets of data points and the function reached a ceiling at an intensity which saturated the rods (2·5–3·5 log td scotopic).

As with pigment epithelial cells, rod-dependent incremental responses could be studied using blue-green backgrounds. In Fig. 11 the responses

have been superimposed at each of three backgrounds. At the lowest background intensity, 0·2 log td scotopic, the test response markedly increased in amplitude and reached 28·0 mV. At a much higher background intensity of 2·1 log td scotopic the test response still increased with intensity but reached a ceiling of only 6·4 mV. At a still higher background of 3·1 log td scotopic, a test response could not be elicited because the background

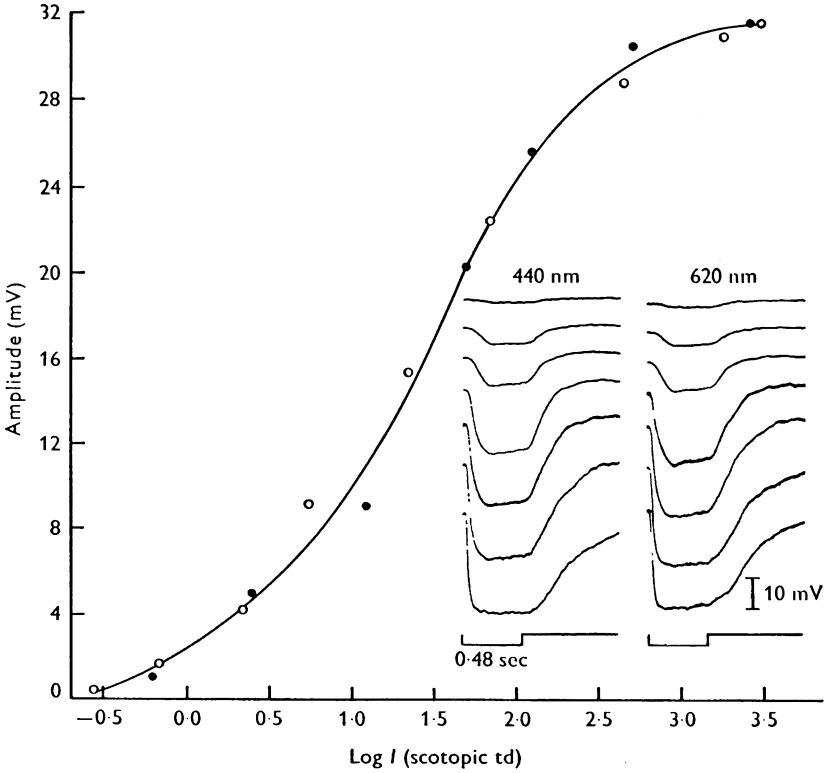

Fig. 10. Intracellular responses from a horizontal cell which were determined exclusively by rods. The inset shows responses as a function of intensity with blue (440 nm) and orange (620nm) flashes. They were obtained in a dark-adapted retina with a stimulus spot diameter of 0·9 mm and at a flash duration of 0·48 sec. The amplitude at 440 nm (●) and 620 nm (○) has been plotted as a function of log intensity for the responses presented in the inset. The amplitudes were measured base line to peak and a single curve has been drawn through both sets of data points.

response had reached the amplitude ceiling. An increase in test intensity above the intensity which produced an amplitude ceiling produced the rod after-effect, both with the dim background (0·2) at a test intensity of 2·2 log td scotopic and, more prominently, with the bright background (2·1) at test intensities greater than 2·2 log td scotopic.

The 32·0 mV ceiling reached by $\Delta V + V$ at a background intensity of 0·2 log td scotopic is greater than the 29·4 mV ceiling reached by either $\Delta V + V$ at 2·1 log td scotopic, or V alone at 3·1 log td scotopic. It is not known if this difference is a function of the conditions of stimulation, or whether it resulted from a change in response sensitivity.

Because of the limited range of background intensities, the adaptive effects observed here could be compared with those from pigment epithelial cells only for the case of response saturation. Thus $\Delta I + I$, which is suffi-

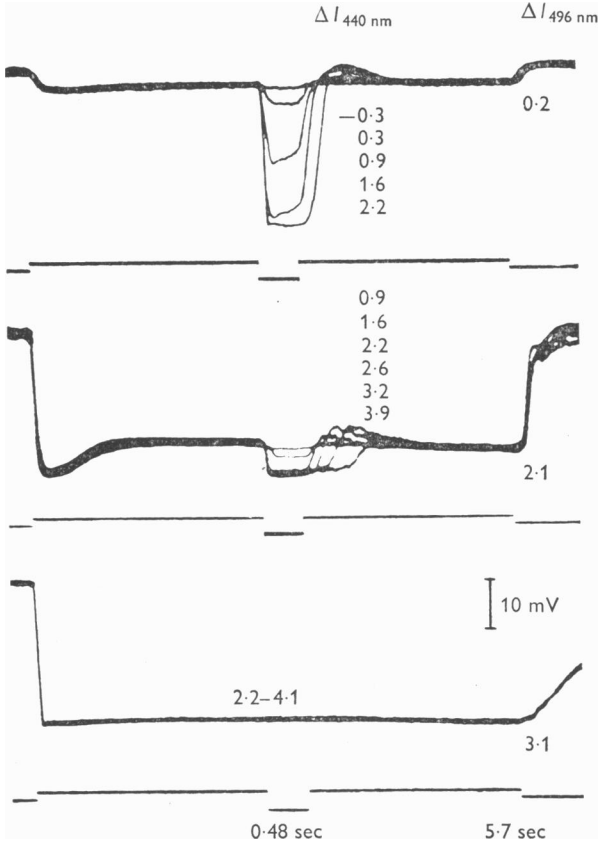

Fig. 11. Intracellular responses from a horizontal cell to blue test flashes of 440 nm presented against blue-green backgrounds of 496 nm. The responses of this cell were determined exclusively by the rods. The background ($I_{496\,nm}$) and test ($\Delta I_{440\,nm}$) spots were both 2·0 mm in diameter and were concentrically placed on the retina. The background had a duration of 5·7 sec. The test flash began 2·7 sec after the onset of the background and had a duration of 0·48 sec. The responses to both test and background were superimposed at each intensity of background. The intensity of the background flash is indicated in the right margin in log td scotopic. At each background intensity the intensity of the test flash increased in log td scotopic as indicated near each set of responses.

cient to saturate, should be constant at all levels of I, and equal to a single flash I_0 which saturates the response in the dark-adapted retina. In this experiment, however $\Delta I + I = 162$ td scotopic with the dim background (0·2) and almost twice that amount, 284, with the bright background (2·1). Since the bright background alone was almost at the saturating intensity obtained with the dim background (126 *v.* 162 td) the additional intensity came from adding test flashes which were too bright. In fact, ΔI was five times the predicted value at the amplitude ceiling for $\Delta V + V$. In effect, test responses still occurred at test intensities which brought $\Delta I + I$ above the predicted level.

The extension of the test response range at a background of 2·1 log td scotopic originates from the failure of the background response to maintain its initial amplitude. The background response of 29·0 mV was almost at the amplitude-ceiling, and if it had been maintained, only a very small test response could have occurred. The voltage fell 22 % from the peak, however, to a maintained level of 23·0 mV. The test responses now added to this lower voltage and bright test flashes brought $\Delta V + V$ to the ceiling. Notice that raising the background to 3·1 log td scotopic also brought the maintained voltage up to the amplitude-ceiling and produced the rod after-effect. The failure to hold the initial voltage means that the background has a suppressive effect on the test response which is less than predicted.

Intracellular recordings from vertebrate photoreceptors also show the fall-off from the initial peak voltage (Toyoda, Nosaki & Tomita, 1969; Werblin & Dowling, 1969; Baylor & Fuortes, 1970). In cat horizontal cells it is difficult to assess which portion of the fall in voltage originates in the rods and which in the horizontal cell, since the peak:maintained ratio varies from cell to cell and with recording conditions (high ratios in poor penetrations). It would appear, however, that the rather low peak:maintained ratio of the responses in Figs. 10 and 11 originated in the rods. If the fall in voltage originated in the horizontal cell and not in the rods, then the test responses (Fig. 11) would have increased in duration before $\Delta V + V$ reached a ceiling voltage, because $\Delta I + I$ was sufficiently intense to bring the rod output to its ceiling. This assumes that the after-effect, recorded from this cell, originates in the rods. Instead, the test responses first increased in duration at levels of ΔI which brought $\Delta V + V$ to a ceiling, suggesting that the rod output had also fallen from its peak.

DISCUSSION

Pigment epithelial cells associate with the distal ends of the rods by virtue of the close apposition of membranes from rod outer segments and pigment epithelial apical processes. Since it is unlikely that pigment epithelial responses are influenced by neural processing proximal to the photoreceptors, the adaptive effects described above must originate in the rods. In the same way, area summative effects from the proximal retina

should not influence pigment epithelial responses, so that these adaptive effects must originate in individual rods.

The adaptive effects reported here for rod-dependent pigment epithelial responses resemble those identified in cone late receptor potentials of cynomolgus macaque monkeys by Boynton & Whitten (1970). They showed that a power law relation between amplitude and intensity, and the presence of receptor saturation, lead to a compression of response amplitude as intensity increases, and it is this which determines test response amplitude. Because the relation between amplitude and intensity is non-linear, the number of quanta needed to produce a criterion response increases as a function of the number of quanta already absorbed; thus as background levels are raised, more quanta are needed to produce the same test responses. Bleaching becomes a second important factor at high intensities. The rod adaptive mechanism found in pigment epithelial responses also arises from the compressive nature of the relation between response amplitude and intensity (Schmidt & Steinberg, 1971). Bleaching is not a significant factor with rod responses in these experiments, for 6·0 sec background flashes, which bring the response to an amplitude-ceiling, bleach only very small amounts of pigments, $< 0{\cdot}1\,\%$ at 3·0 log td scotopic (Rushton, 1961).

Adaptation in rod-dependent responses from horizontal cells probably results from the same mechanism, since both the dark-adapted amplitude–intensity functions and the incremental sensitivity functions are similar to those obtained from pigment epithelial cells. Naka & Rushton (1966) already have shown that incremental responses from fish horizontal cells for a single pigment system can be predicted from the amplitude–intensity function with zero background, where the background and test stimuli act as a single flash to produce a voltage equal to the sum of the background and test responses. In the present work, in addition, the fall-off of the voltage to a lower maintained value at a critical intensity of background extends the dynamic range of the incremental responses. This is the same mechanism described by Naka & Kishida (1966) for receptor responses from the insect compound eye (Apis drone).

At more proximal locations in the cat retina scotopic responses from ganglion cells (Barlow, 1965; Sakmann & Creutzfeldt, 1969; Daw & Pearlman, 1969) and from components of the LERG (Ford, 1969; Rodieck & Ford, 1969) reach amplitude-ceilings at the same level reported here and in the accompanying paper, 2·5–3·5 log td scotopic (Schmidt & Steinberg, 1971). Also, incremental sensitivity functions of pigment epithelial cells do not differ significantly from those at more proximal locations of the cat retina, at background levels of 0·0–3·5 log td scotopic (Barlow, 1965; Daw & Pearlman, 1969; Ford, 1969); the slope of the function in ganglion

cells (Sakmann & Creutzfeldt, 1969), horizontal cells and pigment epithelial cells of cat often being less than 1·0. This is not to exclude the possibility that other adaptive mechanisms act proximal to the rods, for example, the contribution to adaptation which is made by the center-surround receptive field organization of ganglion cells (Barlow & Levick, 1969; Sakmann & Creutzfeldt, 1969).

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REFERENCES

AGUILAR, M. & STILES, W. S. (1954). Saturation of the rod mechanism of the retina at high levels of stimulation. *Optica acta* **1**, 59–65.

BARLOW, H. B. (1965). Optic nerve impulses and Weber's law. *Cold Spring Harb. Symp. quant. Biol.* **30**, 539–546.

BARLOW, H. B. & LEVICK, W. R. (1969). Changes in the maintained discharge with adaptation level in the cat retina. *J. Physiol.* **202**, 699–718.

BAYLOR, D. A. & FUORTES, M. G. F. (1970). Electrical responses of single cones in the retina of the turtle. *J. Physiol.* **207**, 77–92.

BOYNTON, R. M. & WHITTEN, D. N. (1970). Visual adaptation in monkey cones: recording of late receptor potentials. *Science, N.Y.* **170**, 1423–1426.

BROWN, K. T. & MURAKAMI, M. (1968). Rapid effects of light and dark adaptation upon the receptive field organization of S-potentials and late receptor potentials. *Vision Res.* **8**, 1145–1171.

BROWN, K. T. & WATANABE, K. (1962*a*). Isolation and identification of a receptor potential from the pure cone fovea of the monkey retina. *Nature, Lond.* **193**, 958–960.

BROWN, K. T. & WATANABE, K. (1962*b*). Rod receptor potential from the retina of the night monkey. *Nature, Lond.* **196**, 547–550.

DAW, N. W. & PEARLMAN, A. L. (1969). Cat colour vision: one cone process or several? *J. Physiol.* **201**, 745–764.

FORD, R. W. (1969). The cat electroretinogram to incremental stimuli. Doctoral dissertation, University of Sidney.

GOURAS, P. (1966). Rod and cone independence in the electroretinogram of the dark-adapted monkey's perifovea. *J. Physiol.* **187**, 455–464.

GOURAS, P. & LINK, K. (1966). Rod and cone interaction in dark-adapted monkey ganglion cells. *J. Physiol.* **184**, 499–510.

NAKA, K. I. & KISHIDA, K. (1966). Retinal action potentials during dark and light adaptation. In *Functional Organization of the Compound Eye*, ed. BERNHARD, C. G., pp. 251–266. New York: Pergamon Press.

NAKA, K. I. & RUSHTON, W. A. H. (1966). S-potentials from luminosity units in the retina of fish (Cyprinidae). *J. Physiol.* **185**, 587–599.

RODIECK, R. W. & FORD, R. W. (1969). The cat local electroretinogram to incremental stimuli. *Vision Res.* **9**, 1–24.

RUSHTON, W. A. H. (1961). Rhodopsin measurement and dark-adaptation in a subject deficient in cone vision. *J. Physiol.* **156**, 193–205.

SAKMANN, B. & CREUTZFELDT, O. D. (1969). Scotopic and mesopic light adaptation in the cat's retina. *Pflügers Arch. ges. Physiol.* **313**, 168–185.

SCHMIDT, R. & STEINBERG, R. H. (1971). Rod-dependent intracellular responses to light from the pigment epithelium of the cat retina. *J. Physiol.* **217**, 71–91.

STEINBERG, R. H. (1969*a*). Comparison of the intraretinal *b*-wave and d.c. component in the area centralis of cat retina. *Vision Res.* **9**, 317–331.

STEINBERG, R. H. (1969*b*). Rod and cone contributions to S-potentials from the cat retina. *Vision Res.* **9**, 1313–1329.

STEINBERG, R. H. (1969*c*). Rod-cone interaction in S-potentials from the cat retina. *Vision Res.* **9**, 1331–1344.

STEINBERG, R. H. & SCHMIDT, R. (1970). Identification of horizontal cells as S-potential generators in the cat retina by intracellular dye injection. *Vision Res.* **10**, 817–820.

STEINBERG, R. H., SCHMIDT, R. & BROWN, K. T. (1970). Intracellular responses to light from the cat's pigment epithelium: origin of the electroretinogram *c*-wave. *Nature, Lond.* **227**, 728–730.

TOYODA, J., NOSAKI, H. & TOMITA, T. (1969). Light-induced resistance changes in single photoreceptors of Necturus and Gekko. *Vision Res.* **9**, 433–463.

WERBLIN, F. S. & DOWLING, J. E. (1969). Organization of the retina of the Mudpuppy, Necturus maculosus. II. Intracellular recording. *J. Neurophysiol.* **32**, 339–355.