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LIGHT ADAPTATION IN THE PHOTORECEPTOR OF THE CRAYFISH, *PROCAMBARUS CLARKI*

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OVER the past decade considerable progress has been made in the elucidation of factors responsible for light adaptation in arthropod visual systems. In the eccentric cell of the lateral eye of Limulus, FUORTES (1959) has shown that ultimately the effect of illumination is to reduce the cell's membrane resistance. More recently, FUORTES and HODGKIN (1964) have proposed an electrical analogue of the photoreceptor. The model is based upon the assumption that the time scale of the response to light is proportional to the leakage resistance, R, of a linear filter with n stages of exponential delay between the input and output. The sensitivity, however, is proportional to R^{n-1}.

A different approach was taken by NAKA and KISHIDA (1966) who studied the primary photoreceptor (i.e. retinular cell) in the eye of the Apis drone. Light adaptation was considered in terms of its influence on the empirical Fechner relationship, $V = \log(1+\Delta I)$, where V is the peak response amplitude and ΔI the stimulus intensity. The effect of a change in the state of adaptation, resulting from exposure to a background light, is to shift the V-log$I$ function along the intensity scale.

The purpose of this investigation was to examine the V-log$I$ relationship and obtain a quantitative estimate of light induced changes in sensitivity in a crustacean eye. The results lead to a modification of the Fechner relationship which is capable of describing light induced desensitization under steady state conditions.

MATERIALS AND METHODS

Eyes of the crayfish, *Procambarus clarki*, were studied in either the excised or intact condition. When the eye was removed it was bisected in the lateral plane and the ventral half was mounted dorsal side up in a bath of VAN HARREVELD's (1936) solution. This preparation had the advantage of permitting clear visualization of the ommatidium in which the microelectrode was inserted and direct stimulation of the penetrated retinular cell, thus avoiding the problems associated with stimulation through the dioptric apparatus (i.e. pigment migration). Its disadvantage lay in the tendency of the preparation to decay after 2 or 3 hr. For experiments requiring longer periods of time, the eye was studied in its natural position with its circulation intact. To minimize movement, the exoskeleton of the eye cup was glued to the carapace with Eastman 910 adhesive and the carapace, tail and limbs were firmly clamped. The electrode was inserted through a small hole (approximately 200 μ) drilled in the cornea. The electrodes were glass micropipettes filled with 2·8 M KCl, having tip resistances of 40–100 M Ω. Connections to ground and to the micropipette were of silver-silver chloride wire. The electrode was connected to a standard

microelectrode amplifier (Medistor 35-A), possessing a cathode follower at its input and a feedback circuit to minimize stray capacitance. From here the signal was led to one channel of a dual beam oscilloscope (Tektronix 502A) and tape recorder. The stimulus was monitored with a photodiode whose output was recorded on a second channel of the oscilloscope and tape recorder.

Response amplitude was determined by the peak displacement of the membrane potential. Estimates of the rate of rise were obtained from the slope of the rising phase of the response measured at the earliest possible point of the rapidly accelerating phase. For very small responses discrete fluctuations in membrane potential limited the accuracy of this measurement considerably. With larger response amplitudes estimates of the rate of rise were obtained to a reasonable degree of accuracy and reliability (less than a 5 per cent disparity upon repetition of the measurement).

Two quartz iodide lamps (Sylvania 500Q/CL) were used as adapting and stimulating sources. The latter was housed behind an electromechanical shutter which opened in less than 10 msec. The power to the lamps was monitored and maintained at a constant level. The filament of the stimulus was projected on to one end of a 1/4 in. dia. fiber optic light guide through a silvered mirror with a transmittance of 60 per cent. The adapting light was reflected from the mirror surface and focused to the same point. At the opposite end of the light guide an optical stop and a small microscope condensing lens were used to focus a 200 μ circular spot on the preparation. Stimulus intensity was attenuated by means of calibrated neutral density filters inserted between the lamps and the mirror.

RESULTS

NAKA and KUWABARA (1959) have shown that in the crayfish eye relatively large responses to illumination may be recorded extracellularly with microelectrodes. These responses may be either monophasic or diphasic with an initial rapid component in either the positive or negative going direction. The waveform is largely dependent upon the location of the microelectrode. The monophasic potentials recorded in this manner are usually of 5–10 mV in amplitude and may be recorded in the presence of a d.c. potential presumably associated with the basement membrane. Similar observations were made in the present study. More recently, however, EGUCHI (1965) has succeeded in penetrating cells within the ommatidia which yield relatively stable resting potentials of 30–60 mV and positive going (i.e. depolarizing) responses to illumination of 30–50 mV. It was therefore assumed that an electrode was located within a retinular cell when these criteria were obtained. Figure 1 illustrates the changes observed in the response of a cell as the stimulus intensity was varied over a range of 3 log units. At low intensities the response rises sigmoidally to a value that is maintained for the duration of the stimulus. Termination of the light is accompanied by an exponential decay toward the resting potential. As the intensity is raised both the amplitude and rate of rise increase. Furthermore, at higher intensities it was fairly common to observe either a prepotential as shown in Fig. 1 or an inflection in the early portion of the rising phase. The larger responses decay either more or less rapidly than those in Fig. 1 to a d.c. level that is maintained for the duration of the stimulus.

To obtain a precise index of the V-log$I$ relationship a number of experiments were performed in which stimuli were presented at 90-sec intervals to fully dark adapted eyes. The intensity was varied randomly or in an ascending order until at least ten observations were obtained at each level. In Fig. 2 the results of two such experiments are compared

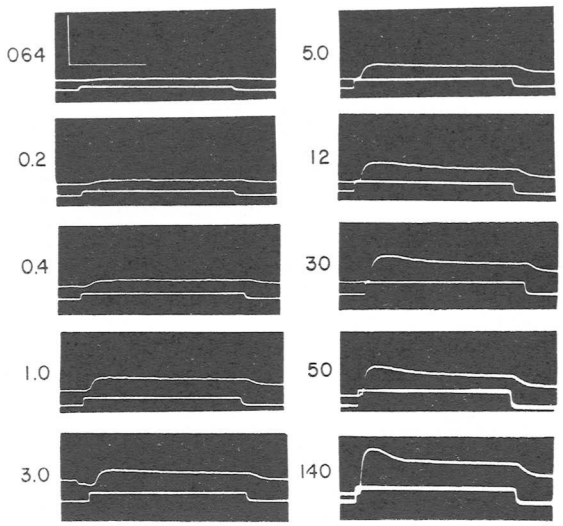

FIG. 1. Intracellularly recorded receptor potentials. Stimulus duration is given by lower trace of each pair while stimulus intensity in candles/ft² is indicated at the left of each frame. Calibration marks: 30 mV, 1 sec.

by plotting their relative response magnitudes ($\Delta V/V$max) as a function of the stimulus intensity ΔI (scaled logarithmically). The two sets of data points come from different preparations. The distributions of points along the two curves clearly indicate a smaller variability of response magnitude to a given stimulus when the intensity is varied in a constant order. This is to be expected from the fact that each stimulus is presented in the same position in the light adaptation cycle resulting from previous stimuli. With either

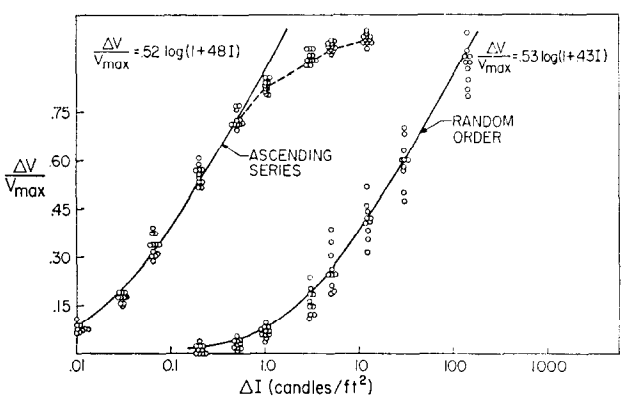

FIG. 2. Relative response magnitude ($\Delta V/V$max) as a function of the log ΔI for two different preparations. The smooth curves represent the adjacent equations. *Ascending series* and *random order* are the modes of stimulus presentation.

method the variability is greatest in the so-called dynamic range of the V-log$I$ curve in which small fluctuations in sensitivity have the largest influence on the response. This dynamic range generally covers 1·7 log units of intensity while the entire observable response range typically exceeds 4·0 log units. As shown in Fig. 2 the relationship between

response magnitude and stimulus intensity can be approximately described by the empirical Fechner relationship:

$$\Delta V/V\max = a \log(1 + K\Delta I) \quad (1)$$

in which $\Delta V/V\max$ is the relative response amplitude, a is an empirically derived constant from the slope of the linear portion of the curve and K determines the position of the function along the intensity scale. In 25 preparations in which the value of a has been determined it has fallen in the range of 0·44–0·56 with a mean of 0·50. The value of K, however, is proportional to the sensitivity of the preparation and may vary considerably with the state of adaptation and from one preparation to another. The latter source of variability may in part be due to differences in spectral sensitivity among the various retinular cells studied. WALD (1968) has obtained evidence suggesting that the crayfish retina may contain at least two populations of color receptors with peak sensitivities at 435 and 565 mμ.

If the sensitivity of the cell is such as to permit saturation of the response mechanism by the available stimulus intensities one invariably observes a gradual approach of the V-log$I$ function to the saturated response level. At the upper segment of the curve, therefore, the data depart from the empirical Fechner curve (Fig. 2, curve on left) suggesting that the latter is at best an approximation of the stimulus response relationship. An attempt to account more precisely for the shape of this function is presented in the discussion.

As noted above changes in response amplitude are associated with changes in the rate of rise. The relationship between relative response amplitude and the log of the relative rate of rise ($R_t/R_t\max$) is illustrated in Fig. 3a. Since the plot so closely resembles the function relating response magnitude to stimulus intensity an equation analogous to (1) was fitted to the data. The solid line in Fig. 3a thus represents the relationship:

$$\Delta V/V\max = b \log(1 + JR_t/R_t\max) \quad (2)$$

in which b and J are constants analogous to a and K respectively. Similar curves have been fitted to the data of twelve other preparations and in all cases equation (2) furnishes a relatively close approximation of the observed relationship. Furthermore the constants b and J generally remain invariant despite large shifts in sensitivity associated with light and dark adaptation. The fit shown in Fig. 3a is quite typical and includes an illustration of the fact that the relative rates of rise tend to be slightly less than predicted at the upper end of the curve.

Neglecting this disparity one can formulate the relationship between the relative rate of rise and the stimulus intensity by substituting the right hand side of equation (2) for the relative response amplitude in equation (1) and solve for $R_t/R_t\max$:

$$R_t/R_t\max = [(1 + K\Delta I)^{a/b} - 1]/J \quad (3)$$

The fit of this relationship to the experimental data is demonstrated on a log-log plot in Fig. 3b. Again the approximate nature of the underlying Fechner relationship is apparent. The limiting slope of equation (3) is a/b whereas the relative rates of rise show signs of saturation at the upper end of the response range.

When the eye is permitted to dark adapt after exposure to an intense flash, the response to a second flash increases as a function of time in darkness. This relationship was examined in the lateral eye of Limulus by BENOLKEN (1962) who observed that recovery is an exponential function of the duration of dark adaptation. A similar relationship is obtained in the crayfish eye (Fig. 4). As the intensity or duration of the flash was increased the initial rapid recovery phase was retarded and the total time to complete dark adaptation

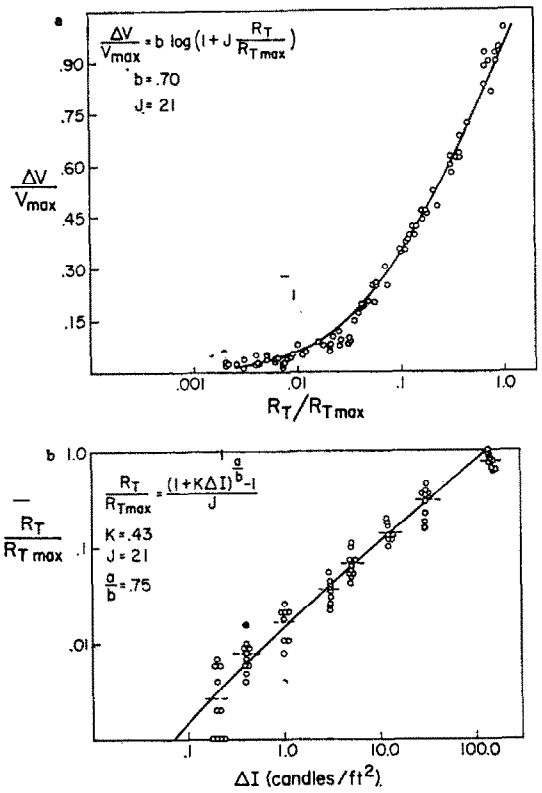

FIG. 3. A. Relative response amplitude as a function of the relative rate of rise (scaled logarithmically). The smooth curve represents the adjacent equation. Data obtained from same cell as right hand curve of Fig. 1.

B. Relative rate of rise as a function of stimulus intensity on log-log coordinates. Smooth curve represents adjacent equation. Data as in A.

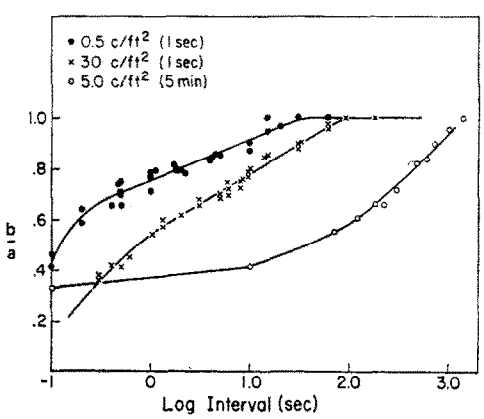

FIG. 4. Recovery during dark adaptation as a function of log of inter-stimulus interval. Ordinate is the response amplitude to the second (*b*) of a pair of flashes (*a*, *b*) divided by the response to *a*. For the two curves on the left both *a* and *b* were presented for each determination and were of 1 sec duration. When the adapting stimulus was of 5 min duration (curve on the right) *a* was presented only once and *b* (1 sec duration) was presented at the intervals shown.

lengthened. When intense adapting lights of 5–10 min duration were used the recovery phase extended over several hours (WALD, 1968). At the termination of such a stimulus the membrane potential generally showed an initial rapid fall toward the resting level which was followed by a much slower stage of recovery (i.e. after depolarization). Furthermore, since the period to complete recovery was adequately long it was possible to observe the changes in sensitivity by means of the V-log$I$ relationship. The raw data from one such experiment are illustrated in Fig. 5. In order to maintain the baseline close to

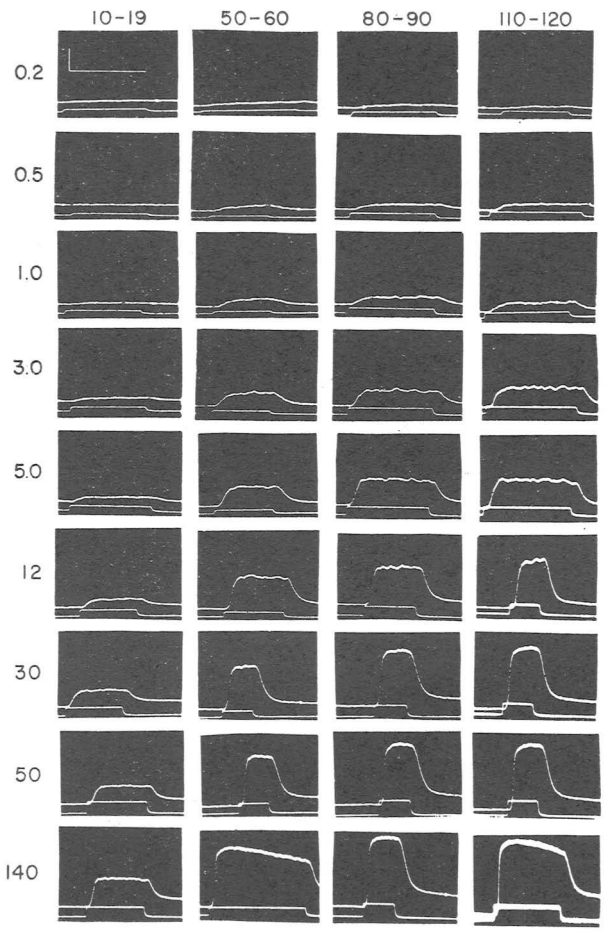

FIG. 5. Intracellularly recorded receptor potentials at the four durations of dark adaptation indicated (in min) above each column. The stimulus intensity in candles/ft² is given at the left of each row. The stimulus duration was more than 1 sec at the lowest intensities but shortened at higher intensities to minimize adaptation due to test stimuli. Calibration marks: 10 mV and 1·0 sec.

the bottom of the film the d.c. shift accompanying dark adaptation is not shown, but it should be noted that 5 min after the offset of the adapting light the membrane resting potential was 32 mV. Dark adaptation was accompanied by a gradual repolarization such that by the end of 2 hr the resting potential exceeded 50 mV. The course of this repolarization could only be determined approximately since the membrane tends to be somewhat

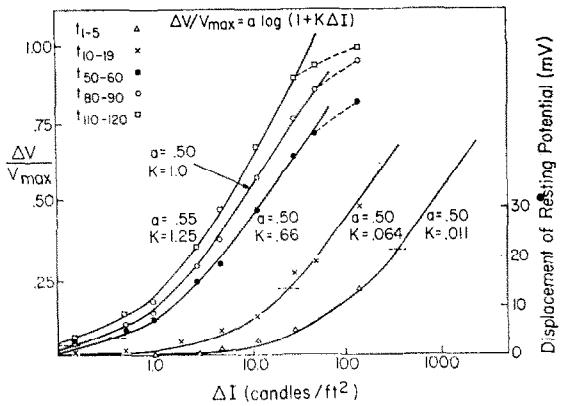

FIG. 6. Relative response amplitude as a function of log I for five durations of dark adaptation. Except for curve on the extreme right points obtained from same data as Fig. 5. Smooth curves represent equation (1) with constants as indicated. Horizontal dashed lines through each function refer to ordinate on the right.

unstable during prolonged periods of dark adaptation. Figure 6 is a V-log$I$ plot derived from the data of Fig. 5. The resting potential displacement at the time of each determination is represented by a horizontal line through the function which should be read with reference to the ordinate values on the right hand side of the figure. The smooth curves representing equation (1) were fitted to the data with the values a and K as indicated. The plot demonstrates that during the 2 hr of dark adaptation the slope, a, of the Fechner function remains reasonably constant while its position on the intensity scale, K, shifts to lower intensities by more than 2 log units.

Another aspect of visual adaptation is the desensitization of a system observed in the presence of an adapting light. Using intracellular recording techniques in the isolated eye, a number of attempts were made to observe the V-log$I$ function over a wide range of adapting intensities. After a 10 min exposure to a moderate adapting light, however, recovery time often exceeded half the lifetime of a good preparation (about 3 hr). Complete recovery was deemed necessary since it is possible as in the case of the human observer that the desensitizing effects of a previous and a contemporary exposure to illumination are additive (RUSHTON, 1965). Intracellular studies of isolated eyes had therefore to be limited to a somewhat narrow range of weaker adapting lights.

Experiments with eyes in situ

To extend these studies to the desired range of adapting intensities it was necessary to use the second preparation described in the methods section. Furthermore, an extracellular approach was also required to obtain the necessary degree of stability. Figure 7a and b represent recordings obtained with this technique. In all instances the electrode was placed in the crystalline cone layer just anterior to the approximate location of the retinular cell bodies. With the electrode in this position the response is considerably smaller than those obtained intracellularly and of the reversed polarity. Aside from these two characteristics other details of the waveform are reasonably well preserved. The preparation remained normally responsive to light and was capable of full recovery from light adaptation for at least the 6 hr required to perform an experiment. After each exposure, recovery was monitored by the response to a constant stimulus of 1·0 sec duration. Exposure to another

adapting light was initiated only after the test response surpassed the criterion of 95 per cent of the response amplitude observed in complete dark adaptation. Figure 7a illustrates the responses to the adapting steps. Test stimuli were presented as soon as the response to the adapting step obtained a stable d.c. level.

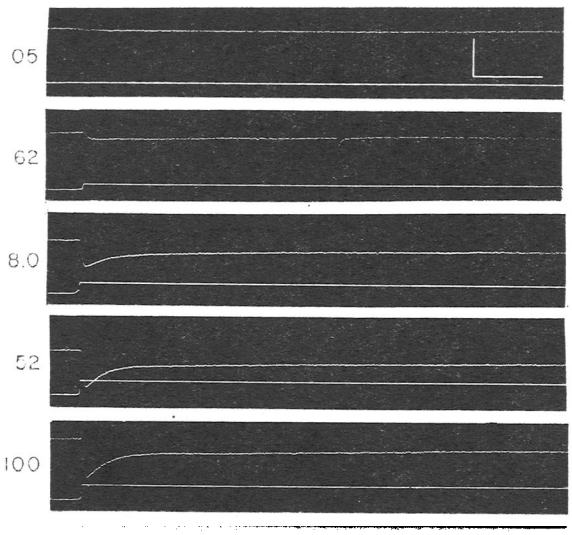

FIG. 7a. Extracellularly recorded responses of the intact eye to steps of light at the indicated intensities. The lowest adapting step (0·005 cd/ft²) is not shown. Calibration marks: 5 mV and 1 sec.

The responses to the superimposed test stimuli are presented in Fig. 7b. The lowest adapting intensity (not shown in Fig. 7a) was less than that required to elicit the smallest detectable response, yet the sensitivity of the cell was clearly altered by its presence as indicated in the plot of $\Delta V/V\text{max}$ against the log ΔI in Fig. 8. A similar observation has been made in the eye of *Limulus* (MACNICHOL, 1958). The smooth curves of Fig. 8 represent equation (1) fitted to the data at each adapting intensity. The value of a was 0·55 while K varies by a factor of 350 across the range of adapting intensities. The d.c. shift (relative to $V\text{max}$) associated with each adapting light is indicated by the dashed horizontal line drawn through each function. This line thus represents the amount by which the function should be vertically raised if one is interested in the total depolarization ($V + \Delta V/V\text{max}$) associated with each stimulus. For the moment let us consider the functions relating ΔV to ΔI. One way of interpreting this data is to arbitrarily choose a criterion response level, ΔV, and determine the stimulus magnitude, ΔI, required to elicit this response at the various background intensities, I. If the values for ΔI are obtained by interpolating along the Fechner curve then the effect of varying the criterion, ΔV, is to generate a family of parallel functions relating ΔI to I. The result of this manipulation is indicated by the solid curves in Fig. 9. The dashed lines represent the result of the same manipulation using criteria of $V + \Delta V$.

The functions are most simply described by a modified form of an equation developed by BARLOW (1957) to deal with psychophysical data of a similar nature. This equation may be written:

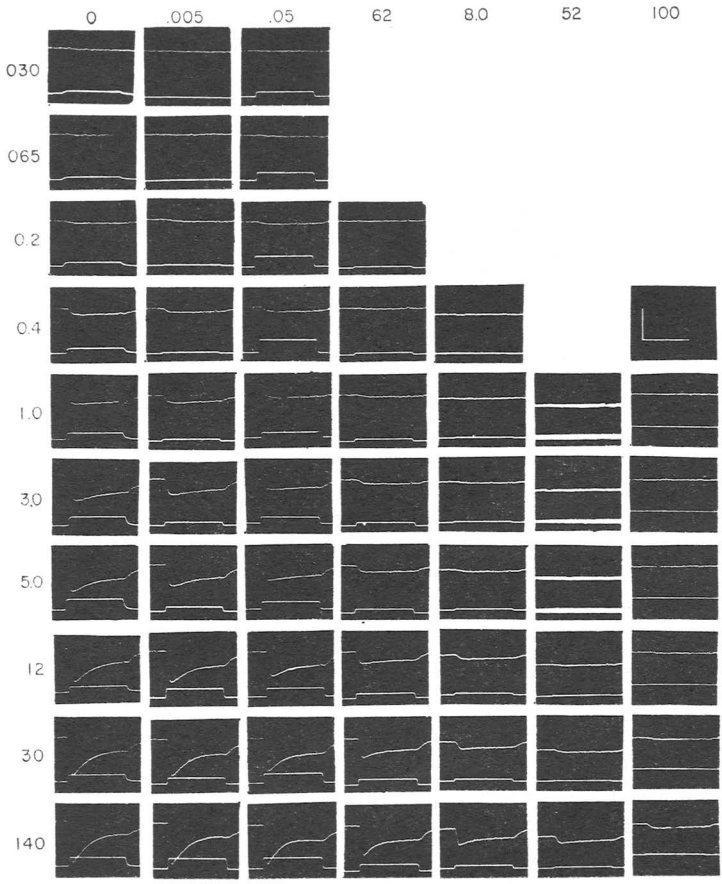

FIG. 7b. Responses to stimuli superposed on the steps presented in Fig. 7a. The adapting intensity in cd/ft² is indicated above each column of responses. The intensity of the test stimulus is given at the left of each row. Calibration marks: 5 and Vm 1 sec.

$$\Delta I = A(1 + I/I_d)^n \tag{4}$$

in which A is the fully dark adapted value of I to reach criterion (i.e. the absolute threshold) and I_d is an estimate of the receptor noise level. I_d is expressed in units of illumination in Fig. 9 on the assumption that the receptor noise is equivalent to a constant background illumination. It is determined by the point at which the horizontal asymptote extended from A intersects with the linear portion of the ΔI function. The value of n is the slope of the straight line segment of the function. In the illustrated experiment n would take on values of 0·61 for criteria of ΔV and 0·53 for criteria of $V + \Delta V$.

An alternative method of interpreting these data is in terms of K from equation (1). Since K is directly proportional to the sensitivity and ΔI inversely so, the reciprocal of K is plotted on the same coordinates as ΔI to facilitate comparison. The similarity of the functions is not surprising since K reflects an average value of ΔI on a given V-log$I$ function. Substituting $1/K$ for ΔI in equation (4) one obtains:

$$K = K_o/(1 + I/I_d)^n \tag{5}$$

in which K_o is the value of K with the eye in the dark adapted state.

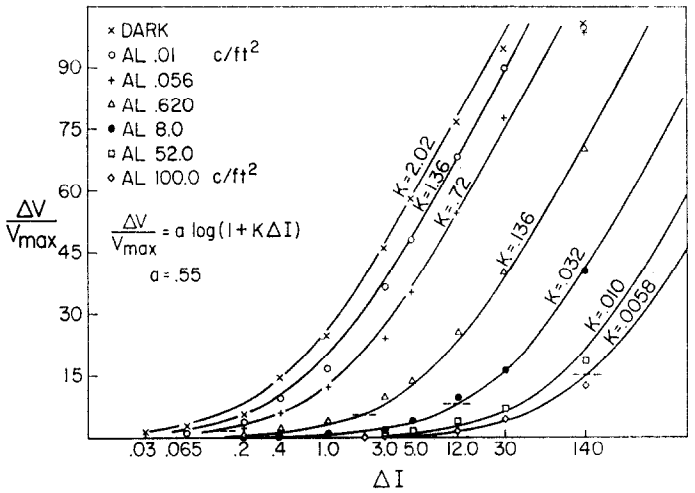

FIG. 8. V-log$I$ plot derived from Fig. 7b. The height of the dashed lines indicates the d.c. displacement relative to Vmax (from Fig. 7a) upon which the test responses were superposed. The smooth curves represent equation (1).

From equations (1) and (5):

$$\Delta V/V\text{max} = a \log[(1 + \Delta IK_o)/(1 + I/I_d)^n] \tag{6}$$

we obtain a modified form of the empirical Fechner relationship which can be extended to steady state conditions of light adaptation. The description of this experiment and the manipulations carried out apply equally well to intracellular studies although the observable range of I was limited to less than 3 log units in these instances. Since the predictive value of this equation depends upon the constancy of a, K_o, I_d, and n their values for 5 similar experiments are presented in Table 1.

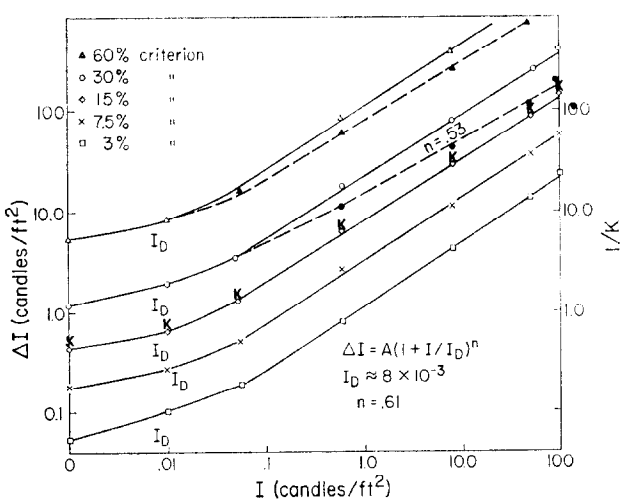

FIG. 9. The log ΔI required to elicit a criterion response as a function of log I for the indicated criterion values of ΔV (as shown in the symbol legend) and $V + \Delta V$ (same symbols, filled). The values, K, refer to the right hand ordinate. See text for discussion of other details.

TABLE 1. VALUES OF CONSTANTS IN EQUATION (6) OBTAINED IN FIVE PREPARATIONS

Preparation #		a	K_o	I_d(candles/ft²)	n
*	22	0·44	3·57	6×10^{-2}	0·73
*ic	33	0·45	2·22	$1{\cdot}5 \times 10^{-2}$	0·58
	45	0·48	4·28	3×10^{-3}	0·55
	63	0·48	3·91	$3{\cdot}5 \times 10^{-3}$	0·51
	66	0·55	2·02	8×10^{-3}	0·61

* Data obtained from an isolated eye.
ic Data obtained with an intracellular electrode.

DISCUSSION

The finding that response magnitude is related to the log of the stimulus intensity while rate of rise is somewhat more linearly related to intensity is not unique to the crayfish retinular cell. FUORTES and HODGKIN (1964) observed that the initial events associated with the generator potential of the Limulus eccentric cell were likewise linearly related to intensity. Similar results have been obtained in a receptor as far removed from these as the Pacinian corpuscle (GRAY and SATO, 1953).

In the eccentric cell of Limulus evidence has been obtained suggesting that the generator potential arises from the summation of discrete changes in membrane conductance whose number is directly proportional to the number of photons absorbed (FUORTES and YEANDLE, 1964; DODGE, KNIGHT and TOYODA, 1968). On the basis of this assumption it is possible to account for the precise form of the V-log$I$ relationship. Since the light responses of the crayfish photoreceptor give no indication of overshooting the membrane resting potential it is reasonable to postulate that light absorption results in a nonspecific increase in membrane conductance. A similar first approximation was hypothesized by CASTILLO and KATZ (1954) with regard to the endplate of the neuromuscular junction. So long as the receptor potential, ΔV, is very small relative to the resting potential the number of discrete changes in membrane resistance, m, should be given by $\Delta V/v_1$ where v_1 is the mean amplitude of the spontaneous discrete fluctuations in membrane potential. For larger values of m summation with respect to ΔV is nonlinear (MARTIN, 1955) and a correction factor must be introduced such that:

$$m = \Delta V/v_1(1 - \Delta V/V\text{max})^{-1}$$

assuming m is proportional to ΔI and solving for $\Delta V/V$max:

$$\Delta V/V\text{max} = \Delta I v_1/(V\text{max} + \Delta I v_1) \tag{7}$$

Since neither the calibration of the source nor any estimate of v_1 (in the present experiment) is of sufficient accuracy to warrant an attempt at a precise curve fit the functions generated by equation (7) for three hypothetical values of v_1 are illustrated in Fig. 10 along with the data of 6 cells. The one instance in which the observed function clearly departs from the predicted shape of the curve (data curve on right hand side of Fig. 10) is probably an artifact of the available intensity range. The data are therefore consistent with the view that light absorption results in the formation of discrete membrane short circuits. It should be noted, however, that the analogy drawn between the photoreceptor membrane and the muscle endplate is not meant to imply that there is an intermediate step, such as a chemical transmitter, between the absorption of light by a photopigment and the presumed increase in membrane conductance. It is equally possible that the pigment is

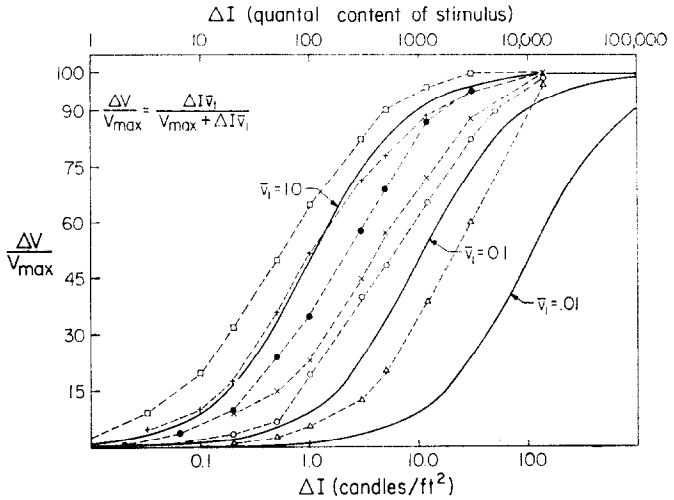

FIG. 10. V-log$I$ plot for 6 dark adapted preparations (dashed lines). Smooth curves represent adjacent equation for the indicated values of v_1. Arbitrary light intensity units of the upper abscissa refer to the solid curves.

located in the membrane, and that the increase in membrane conductance is directly associated with a particular stage in the thermal degeneration of the photopigment.

Light adaptation

Although equation (4) is well suited to a description of human psychophysical data (BARLOW, 1957) its application in the present context has certain implications which should be avoided. As originally stated by Barlow the relation between ΔI and I is written:

$$\Delta I = (I + I_d)^{1/2} \cdot K(a\tau/F)^{1/2} \tag{8}$$

where K is the signal to noise criterion for a threshold response (in a psychophysical determination) and a, τ and F are parameters of ΔI. In complete darkness one obtains:

$$A/(I_d)^{1/2} = K(a\tau/F)^{1/2} \tag{9}$$

where A is the absolute threshold. Thus it is possible to express the relation between ΔI and I in terms of A and I_d:

$$\Delta I = A(1 + I/I_d)^{1/2} \tag{10}$$

The crucial assumption in this formulation is that a psychophysically measured threshold is a statistical judgement based upon a signal to noise discrimination. The exponent, 1/2, arises from the fact that quantal fluctuations in the absorption of light (i.e. noise) are proportional not to I but to its square root. In the present experiment the functions were obtained by applying a constant criterion response level to the V-log$I$ function, not a constant signal to noise ratio. A study of the latter would certainly be necessary if one were concerned with the informational content of the receptor response. This investigation has been restricted to light induced changes in receptor sensitivity, *per se*. The results indicate that receptor sensitivity is proportional to I^n (where $0{\cdot}50 < n < 0{\cdot}75$) for at least 4 log units above threshold. To what extent does I^n reflect changes in the effective stimulus (due to isomerization of some proportion of photopigment) or changes in the responsiveness of the receptor membrane? The influence of the latter variable is yet to be investigated under steady state conditions of light adaptation. BURTT, CATTON and

COSENS (1966) observed that after the onset of an adapting light, changes in the slow potential response of the locust eye are mirrored by fluctuations in sensitivity. In the present study d.c. shifts in membrane potential were observed during both dark and light adaptation. In both instances changes in sensitivity were roughly proportional to the displacement of the resting potential. Similar observations have been made in the eye of the dragonfly (NAKA, 1960) and the eye of the bee (NAKA and EGUCHI, 1961). Presumably these d.c. shifts are related to steady state or very slow changes in membrane conductance that accompany adaptation. A study of light induced changes in membrane conductance and its relationship to the responsiveness of the membrane should therefore be informative for evaluating stimulus induced attenuations in receptor sensitivity. For this purpose and those mentioned earlier efforts are presently underway to measure the membrane resistance under the various experimental conditions considered thus far.

In a theoretical discussion of the classical ΔI function RUSHTON (1965) argued that the relationship between ΔI and I could be predicted by assuming an underlying V-log$I$ relationship in the human retina. He went on to show that his psychophysical observations were consistent with this view. This report presents a demonstration of the fact that a somewhat modified form of the same relationship can be observed in a primary photoreceptor. The finding raises an interesting question of a comparative nature. It is generally assumed that there is a close analogy between the vertebrate rods and cones and the arthropod retinular cell. Rushton, however, has made an excellent case for the view that adaptation in the human retina is strictly a function of the receptor summation pool (i.e. at least one synapse removed from the site at which the receptor response is generated). In both the crayfish and the bee (NAKA and KISHIDA, 1966), however, adaptation appears to be a characteristic of the primary receptors themselves.

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Abstract—Receptor potentials of retinular cells in the eye of the crayfish, *Procambarus clarki*, were studied with the aid of microelectrodes. Recordings were obtained with the eye excised using intracellular leads or with the eye in situ, using an extracellular approach. The V-log$I$ relationship was observed as well as a somewhat more linear relationship between stimulus intensity and rate of rise. It was shown that a close approximation of the V-log$I$ relationship can be predicted on the assumption that increases in light intensity result in a proportional increase in the number of discrete membrane resistive changes. The effect of light adaptation is to shift the empirically determined Fechner curve to a position of lowered sensitivity on the intensity scale. The slope of the curve is relatively unaffected by this shift. Recovery during dark adaptation is accompanied by a shift in the opposite direction. In both cases reductions in sensitivity are accompanied by decreases in the membrane resting potential. If a constant criterion, ΔV, is imposed on the empirical Fechner functions observed during light adaptation, it is possible to determine the relationship between a threshold intensity, ΔI, and the intensity of the adapting light, I. It was observed that ΔI increases as I (where $0{\cdot}50 < n < {\cdot}75$) for at least four and one-half log units above threshold. The results suggest a modification of the empirical Fechner relationship which may be extended to conditions of light adaptation.

Résumé—On étudie avec des microélectrodes les potentiels de récepteurs des cellules rétinulaires de l'oeil de l'écrevisse, *Procambarus Clarki*. Pour les enregistrements sur les yeux excisés, on emploie des conducteurs intracellulaires, et extracellulaires pour les yeux in situ. On observe la relation V-log$I$, et aussi une relation plus linéaire, entre l'intensité du stimulus et la vitesse d'accroissement de la réponse. On montre qu'une bonne approximation de la relation V-log$I$ peut être prévue si on admet que des accroissements d'intensité lumineuse produisent un accroissement proportionnel du nombre de changements discrets dans la résistance de la membrane. L'effet de l'adaptation à la lumière déplace la courbe de Fechner déterminée empiriquement vers une moindre sensibilité sur l'échelle d'intensité. La pente de la courbe est relativement peu affectée par ce déplacement. La récupération durant l'adaptation à l'obscurité est accompagnée d'un déplacement dans la direction opposée. Dans les deux cas les réductions de sensibilité sont accompagnées par des diminutions du potentiel de repos de la membrane. Si on impose un critérium constant, ΔV, aux fonctions empiriques de Fechner observées durant l'adaptation à la lumière, il est possible de déterminer la relation entre un seuil d'intensité ΔI et l'intensité I de la lumière d'adaptation. On constate que ΔI varie comme I^n (ou $0{,}50 < n < 0{,}75$) pendant au moins 4,5 unités logarithmiques au-dessus du seuil. Ces résultats suggèrent une modification de la relation empirique de Fechner, qui pourrait être étendue aux conditions d'adaptation à la lumière.

Zusammenfassung—Die Rezeptorpotentiale der Netzhautzellen des Flußkrebses *Procambarus clarki* wurden mit Hilfe von Mikroelektroden untersucht. Beim exstirpierten Auge wurden die Ableitungen mittels intrazellulärer Zuführungen und in situ durch extrazelluläre Methoden gewonnen. Es wurde sowohl der V-log$I$-Zusammenhang, als auch eine etwas mehr lineare Relation zwischen Reizintensität und Anstiegsgeschwindigkeit festgestellt. Es wurde gezeigt, daß eine gute Annäherung der V-log$I$-Beziehung durch die Annahme vorausgesagt werden kann, daß ein Zuwachs an Lichtintensität eine proportionale Zunahme der Zahl der diskreten Widerstandsänderungen der Membran bewirkt. Helladaptation bewirkt, daß die empirisch bestimmte Fechner-Kurve zu einem Gebiet niedrigerer Empfindlichkeit auf der Intensitäts-

skala verschoben wird. Der Anstieg der Kurve wird durch diese Verschiebung relativ wenig beeinflußt. Die Erholung während der Dunkeladaptation wird von einer Verschiebung in der anderen Richtung begleitet. In beiden Fällen werden Empfindlichkeitsabnahmen von Abnahmen des Membran-Ruhepotentials begleitet. Bei Anwendung eines konstanten Kriteriums ΔV auf die empirisch bestimmten Fechner-Funktionen, wie sie bei Helladaptation beobachtet werden, kann man den Zusammenhang zwischen einer Schwellwertintensität ΔI und der Intensität des Adaptationslichts I bestimmen. Es wurde beobachtet, daß ΔI mit I über mindestens vier und eine halbe Zehnerpotenz oberhalb der Schwelle zunimmt. (Hierbei ist $0{,}50<n<0{,}75$). Die Ergebnisse legen eine Modifikation des empirischen Fechnerschen Zusammenhanges nahe, der bis zu den Bedingungen unter Helladaptation ausgedehnt werden kann.

Резюме — Рецепторные потенциалы ретинулярных клеток глаза рака (Procambarus clarki) были изучены с помощью микроэлектродов. Записи производились либо от изолированного глаза — внутриклеточно, либо же от глаза in situ— экстраклеточно. Наблюдалось отношение V-log T, так же как несколько более приближающееся к линейному отношение между интенсивностью стимула и скоростью подъема. Показано, что значительное приближение к отношению V-log T может быть предсказано при том предположении, что увеличение интенсивности света дает в результате пропорциональное увеличение числа дискретных изменений в мембранах обладающих сопротивлением. Действие световой адаптации проявляется в сдвиге эмпирически определяемой Фехнеровской кривой в позицию более низкой чувствительности на шкале интенсивности. На наклон кривой этот сдвиг не оказывает существенного влияния. Восстановление чувствительности во время темновой адаптации сопровождается сдвигом в противоположном направлении. В обоих случаях уменьшение чувствительности сопровождается понижением мембранного постоянного потенциала. Если постоянный критерий, ΔV, налагается на эмпирические Фехнеровские функции, наблюдаемые в ходе световой адаптации, то возможно определить соотношение между пороговой интенсивностью, ΔT и интенсивностью адаптирующего света, T. Наблюдалось, что ΔT увеличивается как T (где $0{,}50<n<0{,}75$), по крайней мере для четырех с половиной логарифмических единиц над порогом. Полученные результаты позволяют думать о модификации фехнеровского эмпирического отношения, которое может быть распространено на условия световой адаптации.