Local Adaptation in the Ventral Photoreceptors of *Limulus*

ALAN FEIN and J. SHERWOOD CHARLTON

From the Laboratory of Sensory Physiology, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

ABSTRACT Local adaptation was demonstrated in the ventral photoreceptors of *Limulus* using either flashes or continuous illumination. Spots of light locally desensitized the region of the photoreceptor on which they were focused. In dark-adapted photoreceptors where "quantum bumps" were clearly discernible, local adaptation of the quantum bumps was observed. Local adaptation could induce differences of threshold of 1 decade over distances of 50–80 μm. With continuous local illumination these gradients could be maintained from 2 s to 30 min. In addition, the decrease in time scale associated with light adaptation was also found to be localized to the region of illumination.

INTRODUCTION

The process whereby visual sensitivity is decreased during illumination is referred to as light adaptation. The subsequent recovery of sensitivity occurring when the illumination is turned off is called dark adaptation. Both of these processes have been shown to occur in photoreceptors of both vertebrates (for examples see: Boynton and Whitten, 1970; Grabowski et al., 1972; Dowling and Ripps, 1972; Normann and Werblin, 1974) and invertebrates (for examples see: Hartline and McDonald, 1947; Benolken, 1962; Naka and Kishida, 1965; Glantz, 1968; Fein and DeVoe, 1973). In fact, to our knowledge, both light and dark adaptation have been found to occur in every photoreceptor in which they have been sought.

A number of years ago, Hagins et al. (1962), demonstrated that the large photoreceptors of the squid could be adapted locally. They found that when the tips of squid photoreceptors were exposed to an adapting flash, the response of the tips to subsequent test flashes was initially reduced more than 10-fold, whereas the sensitivity of unilluminated parts of the same photoreceptors were not detectably affected by the adapting flash. Hamdorf (1970) observed a similar result in octopus photoreceptors. It may be that local adaptation is a property shared by all photoreceptors. If in fact this is so,

then local adaptation may reflect some fundamental process underlying transduction in photoreceptors.

We undertook the experiments described in this paper for the following reasons. First, we wanted to establish that local adaptation is found in arthropod as well as cephalopod photoreceptors. Second, we wanted to obtain more detailed information about local adaptation than was previously available. And finally we wanted to use local adaptation as a tool for investigating the transduction process. Brief accounts of some of these experiments have appeared previously (Fein, 1973; Fein and Lisman, 1975). Also Spiegler and Yeandle (1974) have presented evidence for local adaptation in *Limulus* ventral photoreceptors.

METHODS

The lateral olfactory nerves, on which the ventral photoreceptors are located, were prepared as previously reported (Fein and DeVoe, 1973). In the experiments reported here the nerves were pinned to the bottom of a small transparent chamber which had been coated with Sylgard (Dow Corning Corp., Midland, Mich.), a transparent rubbery potting compound.

Spots of light were projected up through the transparent base and onto the photoreceptors in the manner shown diagrammatically in Fig. 1 from an optical stimulator designed by E. F. MacNichol, Jr. The optical system contained two independent pathways which were essentially equivalent optically. Lens L_1 formed an image of the source filament in the plane of the electromagnetic shutter SH. Lens L_2 in turn formed an image of the filament on the projector (OB_1, a × 10 microscope objective). Stimulus intensity was controlled by a pair of counterdriven linear

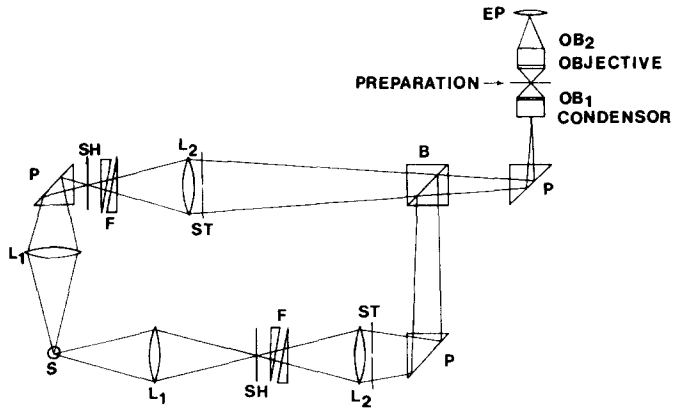


FIGURE 1. Diagram of optical stimulator. S, source; L_1, condenser lens; P, prism; SH, shutter; F, pair of counter driven linear neutral density wedges; L_2, field lens; ST, field lens aperture stop; B, combining prism; OB_1, × 10 microscope objective used as condenser of microscope; OB_2, Zeiss Achromat UD objective, × 40, 0.65 NA, 6.8-mm working distance; EP, eyepiece.

neutral density wedges, F. The projector OB_1 projected a reduced image (10-μm spot) of the aperture stop (ST, 100-μm pinhole) onto the photoreceptors. One of the pinholes was mounted on a calibrated X-Y stage in such a manner that the 10-μm spot (reduced image of pinhole) could be repeatedly positioned anywhere on the photoreceptor. All experiments were carried out under visual control at a magnification of 400 ($\times$ 10 eyepiece, EP; $\times$ 40 microscope objective, OB_2). The objective (OB_2) was a Zeiss Achromat UD, $\times$ 40, 0.65 NA with a 6.8-mm working distance (Carl Zeiss, Inc., New York). The long working distance of this objective allowed the recording microelectrode (not shown in Fig. 1) to be easily positioned for impalement of the photoreceptors.

Microelectrodes were made from dual-channel ("theta") borosilicate tubing (obtained from W. Dehn, Spencerville, Md.); these electrodes usually filled in less than a minute after injection with the appropriate solution. Most electrodes were filled with 2 M KCl and had resistances of 10–30 MΩ when measured in the artificial seawater (435 mM NaCl, 10 mM KCl, 10 mM $CaCl_2$, 25 mM $MgSO_4$, 20 mM $MgCl_2$, and 10 mM Tris, pH 7.8) that bathed the preparation. Some microelectrodes were filled with a 5% solution of Niagara Sky Blue so that the photoreceptor could be stained with the dye at the end of the experiment. We found that electrodes filled with this dye and others often clogged when we tried to eject the dye iontophoretically. Therefore we beveled our dye-filled microelectrodes in order to facilitate staining of the photoreceptors. We followed the procedure described by Werblin (1975), using an instrument designed by E. F. MacNichol, Jr.

Light scatter is a significant problem in trying to locally stimulate a photoreceptor. We have tried to minimize light scatter by having the light beams pass through as little neural tissue as possible. This was accomplished by pinning the nerve in the chamber in such a way that the photoreceptors lay on the side of the nerve rather than on top. In spite of these attempts, there still was a significant amount of light scatter. We observed that the 10-μm diameter spot of light appeared larger (15–20 μm) when focused on a photoreceptor.

Throughout this paper light intensities (I) are given as $\log_{10} I/I_o$, where I_o is the intensity of the unattenuated beam. Thresholds are given as the intensity of a test flash that elicits a criterion response of the receptor potential. Sensitivity is the reciprocal of threshold. For uniform illumination of the photoreceptor one can probably ignore light scatter and assume the stimulus intensity is uniform across the photoreceptor. However, a 10-μm diameter spot of light cannot be thought of as uniformly stimulating a limited region of the photoreceptor. Our observations of the large degree of light scatter in these photoreceptors clearly indicate that small spots of light cause a very nonuniform illumination of small regions of the photoreceptor.

RESULTS

Fig. 2 illustrates the phenomena of local adaptation. A 5-s adapting stimulus at A desensitizes the photoreceptor to a subsequent test flash at A, whereas the response to a test flash at B was nearly unaffected. A similar adapting stimulus at B desensitized the photoreceptor to a subsequent test flash at B

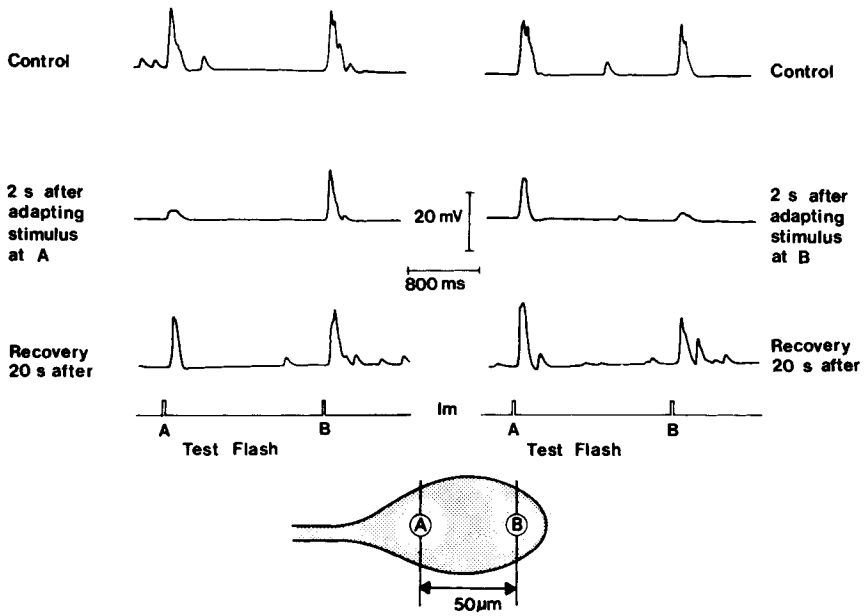


FIGURE 2. Localized densensitization produced by a local adapting light. The lower part of the figure is a schematized version of the photoreceptor, showing the two stimulus spots (see Methods) labeled A and B. The upper part of the figure shows the intracellularly recorded responses elicited by two constant intensity test flashes, one at A and one at B. The light monitor (lm) shows the time-course of the two consecutive test flashes. The adapting stimulus was the same log intensity (−2.7) as the test flash and had a duration of 5 s.

while leaving the response to a test flash at A nearly unaffected. In both cases the photoreceptor recovered from the localized adapting stimuli in about 20 s for the experiment in Fig. 2.

In Fig. 2 one can see what appear to be spontaneously evoked discrete waves of depolarization. These discrete waves of depolarization, sometimes referred to as quantum bumps, have previously been observed in *Limulus* photoreceptors as well as in other arthropod photoreceptors (Fuortes and Yeandle, 1964; Scholes, 1965; Kirschfeld, 1965; DeVoe, 1972; Millecchia and Mauro, 1969). Yeandle and Spiegler (1973) have presented evidence which indicates that the light-evoked quantum bumps observed in *Limulus* ventral photoreceptors are triggered by the absorption of single photons. These observations led us to consider whether local adaptation of individual quantum bumps could be observed. In Fig. 3 we present experimental evidence, obtained from the same photoreceptor as in Fig. 2, demonstrating the local desensitization of quantum bumps. For this experiment a dim long-duration test flash was chosen that would elicit many quantum bumps. One can see that an adapting stimulus at A significantly reduces the size of the

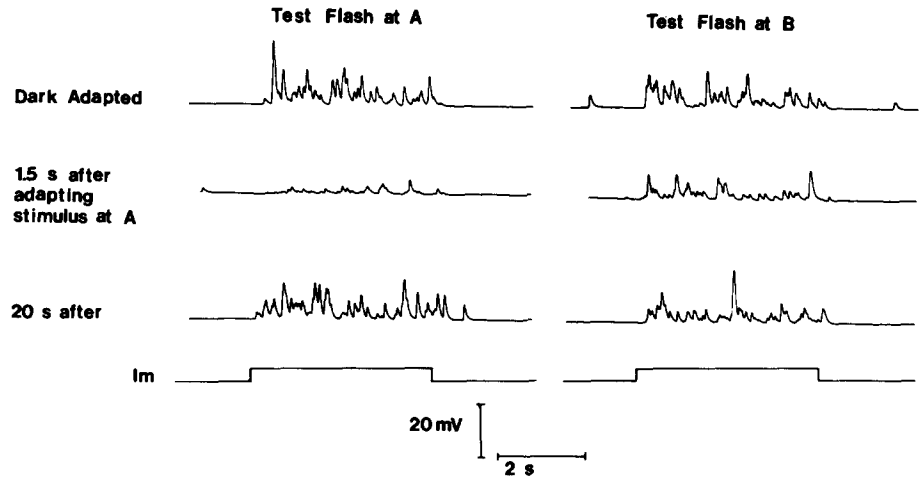


FIGURE 3. Localized desensitization of quantum bumps. These results are from the same photoreceptor as shown in Fig. 2. Positions A and B are the same as those shown in Fig. 2. In this experiment the adapting spot was fixed at A and the test spot was moved from A to B (see Methods). The light monitor (lm) gives the time-course of the test flash. The log intensity of the test flash was −4.7 and the log intensity of the adapting flash was −2.7.

quantum bumps elicited by a subsequent test flash at A. However the same adapting stimulus at A has much less effect on the size of the quantum bumps elicited by the same test flash when it is located at B.

The results presented so far qualitatively demonstrate the phenomenon of local adaptation. To deal with local adaptation quantitatively, we measured the threshold of the photoresponse with our movable test spot (see Methods) at different positions on the photoreceptor, the threshold being defined as the intensity of the test flash needed to produce a criterion response of the receptor potential. Thresholds were measured both in the dark, and under different conditions of light adaptation. The adapting stimulus was either a spot of light located at position A on the photoreceptor (see Fig. 2) or uniform illumination of the whole photoreceptor. The results of these measurements are given in Fig. 4 for the same photoreceptor as shown in Figs. 2 and 3. The O-μm position in Fig. 4 corresponds to position A in Figs. 2 and 3, the 50-μm position, to B, and the 25-μm position to a point midway between A and B. In the dark or when light adapted with uniform illumination, the threshold at different points along the photoreceptor does not differ by more than 0.2 log units (data points connected by solid lines). Thus light adaptation with uniform illumination produces nearly uniform desensitization of the photoreceptor. However, when the photoreceptor is light adapted with a local stimulus at A, the results are much different, as is shown by the data points

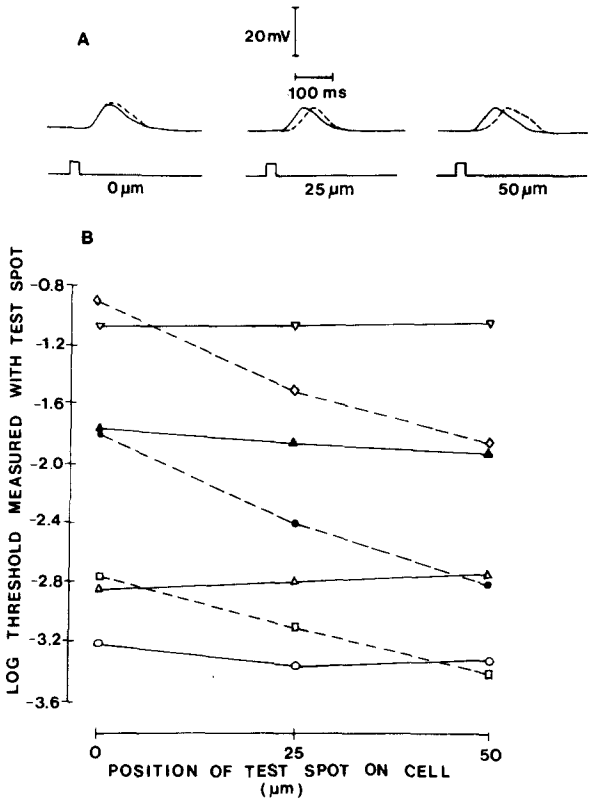


FIGURE 4. A comparison of adaptation produced by local illumination and uniform illumination. These results are from the same photoreceptor as shown in Figs. 2 and 3. The 0-μm position corresponds to position A of Fig. 2. The 50-μm position to position B and the 25-μm position to a point midway between A and B. These positions represent the center of the movable test spot (see Methods). (A) Response waveforms of threshold responses. The continuous tracing of responses correspond to the filled triangles of B. The dashed tracings of responses correspond to the filled circles of B. The lower trace gives the time-course of the stimulus flash. (B) Threshold at different positions on the photoreceptor as a function of different conditions of adaptation. The threshold was measured 2 s after the 50-ms adapting flash. The results presented correspond to a 10-mV criterion response; this large criterion was necessary because of the large size of the quantum bumps (see Figs. 2 and 3). The results remain unchanged for a criterion value in the range of 10–20 mV, the range tested in this experiment. Adapting stimulus condition: (○) Dark adapted, (◇, ●, □) 10-μm spot centered at 0-μm position, (▽, ▲, △) uniform illumination. The adapting stimulus had a duration of 50 ms. Log intensities were: (◇) 0.0, (▽) −2.3, (▲) −3.3, (●) −1.0, (△) −3.9, (□) −2.0.

connected by the broken lines. Local light adaptation produces a threshold variation across the photoreceptor, which can be as large as 1.0 log unit.

In both vertebrate and invertebrate photoreceptors the rise in threshold associated with light adaptation is associated with a decrease in the time

scale of the photoresponse (for example, see DeVoe, 1967; Fuortes and Hodgkin, 1964; Baylor and Hodgkin, 1974). In Fig. 4 A we compare the time-course of the threshold responses at similar positions of the test spot on the photoreceptor but under different conditions of adaptation. The conditions were chosen so that adaptation with either local illumination at A (filled circles Fig. 4 B) or uniform illumination (filled triangles Fig. 4 B) produced the same threshold elevation at position A. The response waveforms given by the solid lines are the threshold responses of the photoreceptor corresponding to adaptation with uniform illumination. They all have nearly the same time-course and thus can be thought of as control responses. The response waveforms given by the broken lines correspond to localized adaptation at A. At the 0-μm position where the thresholds were chosen to be the same, the response waveforms are nearly the same. However, at the 25- and 50-μm positions the response waveforms corresponding to the lower thresholds (local adaptation) have a longer time to peak. These results indicate that the changes in time scale associated with light adaptation are also localized within the photoreceptor

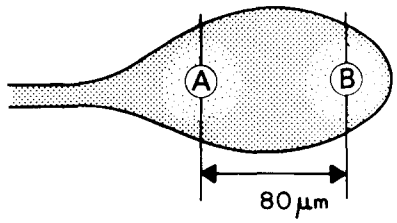
For the results presented so far the adaptation produced by an adapting flash was investigated by testing the responsiveness of the photoreceptor in the dark several seconds after the adapting stimulus. We have also investigated local adaptation with test flashes given during continuous illumination. We find that there is no *major* difference between local adaptation produced with either type of adapting stimulus. A comparison of the adaptation produced by flash illumination and continuous illumination is given in Table I, for a different photoreceptor than presented in Figs. 2–4. For each type of adaptation shown in Table I the intensity of the adapting stimulus was chosen to give the same threshold elevation at position A. These results clearly indicate that both flash illumination and continuous illumination produce localized adaptation of the photoreceptor. For the particular photoreceptor shown in Table I the continuous illumination lasted for a duration of 5 min and the threshold was measured before turning off the illumination. We have repeated this measurement in other photoreceptors for continuous illumination lasting from 2 s to 30 min and we have not observed any significant differences from the results presented in Table I.

The data presented in Table I indicate that there is a minor difference between the local adaptation produced by continuous and flash illumination. Continuous illumination with a spot at A raises the threshold at B more than does flash illumination at A. We have observed this difference in every photoreceptor in which we have investigated the phenomenon. A possible explanation for this difference may be that it is due in part to the steady depolarization and decrease in input resistance (Fein and DeVoe, 1973) associated with steady illumination. We suspect, therefore, that this differ-

TABLE I

LOG RELATIVE SENSITIVITY OF LATE RECEPTOR POTENTIAL AT POSITIONS A AND B

Condition of adaptation	Position A	Position B
Dark	2.5–2.6	2.2
Adapting spot at A (flash illumination)	1.0	2.1–2.2
Adapting spot at A (steady illumination)	1.0	1.9–2.0
Full field adaptation (flash illumination)	1.0	0.8–0.9
Dark	2.6–2.7	2.1–2.2



Sensitivity of the photoreceptor was measured with the movable test spot (see Methods). The schematized version of the photoreceptor shows the two locations of the test spot at which the sensitivity was measured. The duration of the test flash was 20 ms. For the adapting spot at A: the flash had a duration of 20 ms and log intensity of −0.9; the steady illumination had log intensity of −2.5. For uniform illumination of the photoreceptor (full field adaptation) the flash duration was 20 ms and the log intensity was −3.1.

ence would not be present if these experiments were repeated under voltage clamp.

We have directly confirmed, using intracellular staining, that all of the results we have presented are indeed properties of single photoreceptors. Fig. 5 is one example of an experiment in which we measured local adaptation and then stained the photoreceptor at the termination of the experiment.

DISCUSSION

The results presented in this paper clearly establish that local adaptation is a property of the ventral photoreceptors of *Limulus*. We have observed the different aspects of local adaptation presented in this paper in over 40 cells. In a few cells, however, the local adaptation was not as pronounced as that shown in this paper. We found that this difference could be attributed to a combination of light scatter and nonuniform sensitivity of the photoreceptor in the dark. The following example will illustrate our reasoning along these lines. Suppose that one is stimulating a photoreceptor with two (10 μm) test spots of light separated by 60 μm. Further suppose that the thresholds of the photoreceptor at the two test spots are equal but that at a central region midway between the two spots the threshold is 2 log units lower. Then if there is only 1% light scatter from these test spots onto the central region,

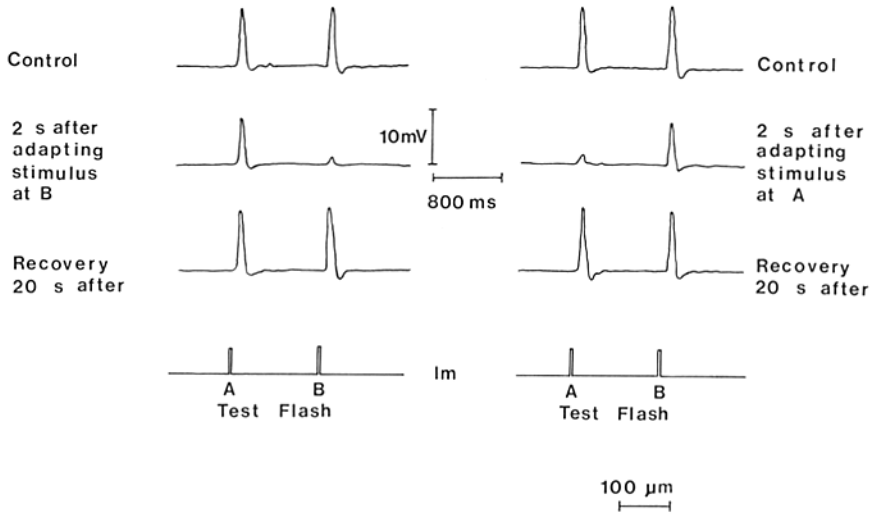


FIGURE 5. Confirmation of local adaptation with intracellular staining. The lower part of the figure is a photograph of the photoreceptor from which the results were obtained. The photoreceptor was stained with Niagara Sky Blue (see Methods) at the termination of the experiment. The arrows labeled A and B indicate the location of the two test spots on the photoreceptor. The test spots were located well within the stained region of the photoreceptor. The test spot at A had log intensity of -2.1 and the test spot at B had log intensity of -1.8. The adapting stimulus had a duration of 5 s and had log intensity of -2.1 at A and -1.8 at B.

the responses produced by the test spots will in part be due to light scattered into the more sensitive region. Thus both test spots will in part be producing a response from the same central region of the photoreceptor. Therefore adapting stimuli located at either test spot would desensitize the central

region and thereby the response produced by the other test spot. As this example shows, a nonuniform sensitivity of the photoreceptor in the dark, coupled with significant light scatter, would tend to make it difficult to demonstrate local adaptation in the photoreceptor. For the cells presented in this paper the sensitivity of the photoreceptor in the dark was within 0.6 log units at different points on the photoreceptor. In those cells in which the local adaptation was not as pronounced the sensitivity in the dark varied from 1 to 2 log units across the photoreceptor.

Dodge et al. (1968) have proposed that the photoresponse in *Limulus* photoreceptors is due to the summation of quantum bumps. They also proposed that during light adaptation the size of the individual quantum bumps decreases and during dark adaptation the quantum bumps recover in size. The results presented in Fig. 3 indicate that this "adapting bump process" is localized to the region of the photoreceptor in which the photons are absorbed.

Recently Srebro and Behbehani (1974) have suggested that what they call "rapid" adaptation has little or no spatial localization in the ventral photoreceptor of *Limulus*. They also suggested that this rapid adaptation is synonymous with the adapting bump process and mediates the light adaptation that occurs during continuous illumination. Thus their suggestions would appear to indicate that light adaptation during continuous illumination has little or no spatial localization. Our results presented in Table I are not consistent with this possibility that indicate that continuous illumination with a spot of light does produce a significant amount of local adaptation.

A component of adaptation that is correlated with pigment concentration is well known in the vertebrate retina (Dowling, 1963; Rushton, 1965; Dowling and Ripps, 1970). Therefore it might be thought that the local adaptation investigated in this paper is related to pigment bleaching in the illuminated region of the cell. However, recent experiments have shown that adaptation in the ventral photoreceptors is unrelated to the recovery of the visual pigment, measured either photometrically (Fein and Cone, 1973) or using the early receptor potential (Fein and DeVoe, 1973).

Fein and DeVoe (1973) presented several lines of evidence which indicated that adaptation in ventral photoreceptors was not controlled by the value of the membrane potential. The results presented in this paper provide additional evidence in support of this proposal. The voltage clamp studies of Millecchia and Mauro (1969) indicate that the ventral photoreceptors are essentially isopotential. Thus the continuous illumination with a spot of light (Table I) which locally adapted the photoreceptor must have certainly depolarized the whole photoreceptor. Therefore the depolarization could not be responsible for the large changes in sensitivity of the photoreceptor that are associated with light adaptation.

The experimental findings presented in Fig. 4 indicate that the decrease in time scale associated with light adaptation is localized within the photoreceptor. This result clearly shows that the change in time-course associated with light adaptation cannot be determined by a change in the membrane time constant, for if it were, it would not be localized within the photoreceptor.

The observation that steady illumination with a spot of light produces maintained local adaptation (Table I) imposes strong constraints on the possible mechanisms which may be involved in adaptation. For example, adaptation might be brought about by a change in concentration of some substance in the cytoplasm of the photoreceptor. Then local adaptation would be brought about by a local change of concentration in the cytoplasm. If this were the case we would expect diffusion to equalize the concentration throughout the cell. Many small solutes (K^+, Na^+, $SO_4^=$, sucrose, sorbitol) with the exception of Ca^{++} have diffusion coefficients in both water and cytoplasm of about 10^{-5} cm^2/s (Hodgkin and Keynes, 1957; Kushmerick and Podolsky, 1969; Hodgkin and Keynes, 1953). Such solutes would take on the average about 3 s to diffuse the 80 μm that separated the two spots in the experiment shown in Table I (Moore, 1962). However, the steady adapting light spot used in that experiment was kept on for 300 s. In one photoreceptor we measured maintained local adaptation for 30 min (1,800 s) of continuous illumination with our adapting spot. These results indicate that if changes in concentration of some substance are to be involved in adaptation then the effective diffusion coefficient of the substance in the cytoplasm must be several orders of magnitude lower than 10^{-5} cm^2/s. Thus changes in the concentration of the previously mentioned solutes are most likely not involved in adaptation.

Lisman and Brown (1972 *a*) have shown that injection of Ca^{++} reduced the response of *Limulus* ventral photoreceptors to spatially uniform illumination and have proposed that a light-induced increase in intracellular Ca^{++} concentration is a factor controlling light adaptation (Lisman and Brown, 1972 *b*). Also Hodgkin and Keynes (1957), Kushmerick and Podolsky (1969), and Orentlicher et al. (1974) have shown that the effective diffusion coefficient of Ca^{++} in axoplasm and myoplasm is considerably lower than in water. These findings coupled with the results presented in this paper led Fein and Lisman (1975) to investigate whether the injection of Ca^{++} ions into ventral photoreceptors would locally desensitize the photoreceptor. They found that indeed the injection of Ca^{++} into ventral photoreceptors did lead to localized desensitization. Therefore the results presented in this paper appear to be consistent with the calcium hypothesis of Lisman and Brown (1972 *b*).

All of the results presented in this paper show some amount of spread of the adaptation produced by local stimuli (see Fig. 4). This spread might be

due to either light scatter or the spread of some "signal" (possibly Ca^{++}) inside the photoreceptor. The data in Fig. 4 appear to indicate that both of the above-mentioned processes are at work in this photoreceptor. For example, in Fig. 4 one can compare the threshold elevation produced 50 μm away from an adapting spot (filled circles) to the threshold elevation produced by uniform illumination of the photoreceptor (open triangles, $\triangle$). Both of these stimuli (filled circles; open triangles) elevate the threshold at the 50-μm position on the photoreceptor by the same amount. Since the log intensity of the uniform illumination was -3.9 (open triangles) one would only have to suppose that 0.1% of the light contained in the -1.0 log intensity local stimuli (filled circles) was scattered to the region 50 μm away on the photoreceptor. Thus only 0.1% light scatter is needed to account for the spread of adaptation over a distance of 50 μm. This small amount of light scatter appears to be consistent with the degree of light scatter we have directly observed (see Methods). On the other hand Fig. 4 shows that an adapting spot with a log intensity of -1.0 (filled circles) is equivalent to uniform illumination with a log intensity of -3.3 (filled triangles), the equivalence being the ability of the two stimuli to raise the threshold of the photoreceptor at the 0-μm position. Thus uniform illumination is 200 times more effective in elevating the threshold at the 0-μm position than a spot of light focused there. This difference appears to be far too great to be accounted for solely by the amount of light scatter we have observed (see Methods). Taken as a whole the results presented in this paper appear to indicate that the adaptation produced by local stimulation spreads somewhat beyond the region of illumination, but the degree of spread is not so great as to eliminate gradients of sensitivity across the photoreceptor. Furthermore, these gradients of sensitivity can be maintained for up to 30 min. This interpretation is consistent with the findings of Fein and Lisman (1975). They found that the desensitization of these photoreceptors caused by intracellular calcium ion injection was largest near the injection site. That is, for large Ca^{++} injections desensitization spread to distant regions of the cell, however the desensitization was larger at the injection site. Furthermore, they measured gradients in sensitivity that lasted for up to 5 min.

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