Pigment Migration and Adaptation in the Eye of the Squid, Loligo pealei

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ABSTRACT The migration of the screening pigment was investigated in the retina of the intact squid. The action spectrum of pigment migration corresponds to the action spectrum of the visual pigment, rhodopsin, rather than to the absorption spectrum of the screening pigment. The total number of quanta required for a fixed criterion of pigment migration is the same, when the quanta are delivered over any period of time from 6 s to an hour or more. When less than 3–10% of the rhodopsin is isomerized, the screening pigment migrates out to the tips of the receptors with a time-course of 5–15 min, and back again over the same period of time. When rather more than 10% is isomerized, the outward migration takes 5–15 min, but the screening pigment does not migrate inwards, even after several hours in the dark. Indirect evidence suggests that the band of screening pigment, when it reaches the tips of the receptors, is approximately equivalent to a filter of 0.6 log units. The spectral sensitivity of the optic nerve response was measured, and was found to be broader than the absorption spectrum of squid rhodopsin in vitro; the broadness could be explained by self-screening, assuming a density of rhodopsin of 0.6 log units at 500 nm.

INTRODUCTION

The cephalopod retina contains a screening pigment, most of which is located near the basement membrane at the proximal end of the rhabdomeric segments of the receptors (Lenhossek, 1894; Cajal, 1917; Zonana, 1961; Young, 1962; Cohen, 1973). This screening pigment has been identified as omnin (Butenandt, 1959). There is evidence that part of this pigment migrates in a band to the tips of the receptors during light adaptation (Rawitz, 1891; Hesse, 1900; Hess, 1905; Glockauer, 1915; Hagins and Liebman, 1962; Young, 1963). During dark adaptation the pigment moves back again. Most of the pigment is located within the receptor cells; some of it is also located within the supporting cells (called pigment cells by Cajal), but it is not certain that
the processes of supporting cells reach as far as the tips of the receptors (Cohen, 1973). The pigment that migrates within receptors is only a portion of the total pigment within the receptor cells.

Several questions need to be answered concerning this screening pigment migration. What is the spectral sensitivity for its activation? How effective is the pigment as a filter for light reaching the rhodopsin? How does the pigment migration relate quantitatively to light and dark adaptation (Byzov et al., 1962)?

We investigated the migration of this pigment in a variety of conditions in which the intensity of illumination of the retina could be specified precisely, and the animal was, as far as possible, intact. The experiments were done on the living squid, *Loligo pealei*. The results provide some answers to the above questions. In addition, a surprising phenomenon was observed: when more than 3–10% of the rhodopsin was isomerized to metarhodopsin, those screening pigment granules that had moved out to the tips of the receptors did not move back again, even after several hours of dark adaptation.

**METHODS**

The intact squid was used. The preparation was adapted from that developed by MacNichol and Love (1961) and Wurtz (1961). The squid was placed in position during anesthesia with 0.3% urethane. It was held down on a Plexiglas platform (Rohm and Haas Co., Philadelphia, Pa.) by four pins, two through the cartilage posterior to the eyes, and two through the muscle anterior to the eyes. The cornea and iris were removed to increase the flux of light on the retina. A small piece of the muscle over the eye and optic lobe was dissected away, so that the electrode would not have to pass through it. During the experiment, the squid was not kept under anesthetic, but rested quietly. Oxygenated seawater at room temperature flowed into the mantle and past the gills. Mantle and siphon movements were normal, with an occasional siphon spurt.

A spot of 6-mm diameter on the retina (about 60° visual angle) was illuminated. The optical system (Fig. 1) had two beams, a test beam and a background beam, each provided by a Leitz Prado projector with a 85–120-mm condenser lens and no objective (E. Leitz, Inc., Sold by Opto-Matic Tools, Rockleigh, N. J.). The images of the lamp filaments were focused on the lens of the squid eye by two condenser lenses (CL), one outside the squid tank, and one underwater inside it. One beam (the test beam) had a Compur C-3 electronic shutter (S), a Kodak type M neutral density wedge (W) (Eastman Kodak Co., Rochester, N. Y.), and a holder for filters (F). The intensity of the other beam (the background beam) was varied by putting Kodak Wratten glass neutral density filters (F) in the path. In some experiments the combining mirror (M) was removed, and only the test beam was used. An aperture (A) just outside the first condenser lens defined the area of the squid retina to be illuminated. For measurements of spectral sensitivity, Baird Atomic interference filters (Baird Atomic, Inc., Bedford, Mass.) were placed in the beam.

The irradiances of the beams were measured with a radiometer (Y.S.I. Kettering...
model 65A, Yellow Springs Instrument Co., Yellow Springs, Ohio) in the plane of the squid lens, and checked by a measurement in the plane of aperture A. The most crucial results were obtained with the mirror removed, and a 490-nm interference filter in the beam. Under these conditions the irradiance of the squid lens for full brightness of the beam was 24.5 mW/cm². Considering that (a) the measurement was made in air with a spot size of approximately 3/6 inches, whereas underwater the spot size was approximately 3/8 inches; (b) the effective diameter of the squid lens was 0.16–0.2 inches, whereas the size of the illuminated spot on the retina was 0.25–0.3 inches, the irradiance of the squid retina was $24.5 \times 9 \times 0.642/25 = 3.6$ mW/cm². This figure ignores the factor for losses in the water of the tank and media of the squid eye. The interference filters and the neutral density filters were calibrated in situ with a measuring device placed in the plane of the squid lens, using a Y.S.I. radiometer for higher irradiances and a United Detector Technology pin diode (United Detector Technology Inc., Santa Monica, Calif.) for lower irradiances.

Recordings were made from the space between eye and optic lobe. The electrode was a glass coated platinum-iridium electrode (Wolbarsht et al., 1960) with 40–50 μm of the tip bare, or the glass broken in several places up to 10 μm from the tip. It was held by an insulated hypodermic needle inside a guard tube; the latter was in contact with the squid and the seawater in the squid tank and connected to ground. Signals

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**Figure 1.** Diagram of the squid tank and optical arrangement. A, aperture; CL, condenser lens; F, filter; M, mirror; OSW, oxygenated seawater; P, projector; S, shutter; W, neutral density wedge.

**Figure 2.** Oscillatory response as a function of intensity against a background of 1 μW/cm². Test flash duration 0.25 s; test beam shutter triggers oscilloscope sweep.
were fed through a preamplifier to a Tektronix 564B oscilloscope (Tektronix, Inc., Beaverton, Ore.), and heard on an audio speaker.

The wave recorded under these conditions is usually a decaying oscillatory potential lasting about 60 ms with a period of 7 ms. This oscillatory potential represents activity of the optic nerve fibers, since it is present when the optic nerve fibers are cut proximally, disconnecting the optic lobe, and is not recorded in front of the retina (Boycott et al., 1965; Tsukahara et al., 1973). The amplitude of the oscillatory potential increases rapidly with light intensity (Fig. 2) and the shape of the amplitude-intensity curve was found to be the same when measured against several different intensities of background. Consequently a criterion of $X \mu V$ is a good criterion for comparing the effect of one background with another on the response, the form of the results being independent of the value $X$. Occasionally we recorded from single optic nerve fibers, but these could not be held for the hours required by these experiments; we sometimes also recorded multiple action potentials coming from several optic nerve fibers. Most experiments in which thresholds were measured were done with a 20–25-$\mu V$ oscillatory potential as threshold criterion.

At the end of each experiment the eyes were injected with Bouin's fixative (15 parts saturated picric acid, 5 parts formaldehyde and 1 part glacial acetic acid). The squid was killed by decapitation and the eyes quickly removed from the head and immersed in Bouin's. The anterior aspect of the eye and the lens were removed, and the retina and attached optic lobe left in fixative for 12–18 h. In certain situations a discrete black spot is evident grossly in the retina as soon as it is fixed for 1 or 2 min (Fig. 3 A). This spot corresponds to the area of retina illuminated experimentally; on sections of the retina (Fig. 3 B) it is evident that the black spot is produced by screening pigment at the tips of the receptors. The spot becomes distinct after fixation because fixation makes the receptors opaque, thus obscuring the pigment at the receptor bases. When the screening pigment has migrated one-fourth of the way back from the tips the black spot is no longer seen, presumably because of light scattering in the distal receptor cytoplasm. The presence of a grossly apparent black spot in the fixed retina is therefore a reliable and convenient criterion for migration of screening pigment to the receptor tips. When illumination intensities were intermediate between those producing pigment migration and those not producing pigment migration after a given duration, a partial black spot was apparent (Fig. 3 C). This appearance presumably represents small nonuniformities in the illuminating spot that we were unable to correct.

After fixation, retinas were transferred to ethanol for serial dehydration. In most cases the most oral and caudal aspects of the retina were trimmed away and the remainder embedded in paraffin and serial sectioned at 6 $\mu m$. Every 20th section was mounted and examined unstained; when appropriate, material was stained with Cason's Mallory Heidenhain stain for retina. In cases with obvious discrete black spots indicating the area of illumination, only the part of the retina containing the spot was embedded and sectioned.

**RESULTS**

The increment threshold curve obtained from the squid retina is usually a straight line with a slope of about 1. The increment threshold curves illustrated
FIGURE 3. (A) Eyecup of a squid fixed after light adaptation to 25 $\mu$W/cm$^2$; then dark adaptation for 90 min. Black spot corresponds to area illuminated. (B) Section of retina across the edge of the illuminated area. Illuminated by white light of 25 $\mu$W/cm$^2$, then dark adapted for 32 min before fixation. (C) Eyecup of a squid fixed after light adaptation to 2 $\mu$W/cm$^2$. Illuminated area same as in Fig. 3 A; black areas represent part of area illuminated.
by Fig. 4 were obtained with flashes of light of \( \frac{1}{6} \) s. Each background was kept on continuously for 2 min while the test beam was flashes at various intensities to determine threshold, then the intensity of the background was increased by about 0.5 log unit for the next measurement. After illumination with background levels of moderately high intensity (about 5 \( \mu W/cm^2 \)) the subsequent dark adaptation is very fast, reaching absolute threshold within 5 min (Fig. 4 A). The threshold remains constant in the dark for a period of several hours. If the retina is fixed at the end of this time, the omnin in the retina is found to be concentrated near the terminal bars at the proximal end of the rhabdomeric segments of the receptors (Fig. 4 C). This is what one would expect from previous work on pigment migration in cephalopods.

A rather different result is obtained if the light adaptation goes up to higher intensity levels. Fig. 4 B shows the results in a squid where the higher background intensity was 270 \( \mu W/cm^2 \), kept on for 2 min. Dark adaptation is fast for the first 10 min and reaches a value close to the final one after 20 min. The threshold does not change very much over the next 4 1/2 h, staying at least 1.5 log units above the initial dark adapted threshold throughout this period. When the eyecup was examined grossly after fixation, a black spot could be seen on the retina, corresponding in size to the area of illumination (Fig. 3 A). When the eye was sectioned, a portion of the screening pigment was found at the tips of the receptors (Fig. 4 D). Quite frequently retinas light and dark adapted in this fashion were found to be split just below the level of the terminal bars after fixation and sectioning.

The edge of the area which had been illuminated is generally quite sharp. This can be seen in the eyecup (Fig. 3 A) and in sections through the retina (Fig. 3 B). Where pigment has migrated to the tips of the receptors, it leaves behind a sharp band of pigment at the base of the rhabdomeres (Fig. 3 B). In the fully dark adapted state, some very short fingers of pigment can usually be seen projecting from the band at the base of the rhabdomeres (Fig. 4 C). The longer fingers seen on the left in Fig. 3 B, projecting from the main band of pigment, are probably due to light scattered from the main spot of illumination to other parts of the retina.

In the normal situation, where moderate intensities of illumination are used, the time-course of pigment migration is 5–15 min for either outward or inward movement. Fig. 5 shows a series of sections through retinas that were illuminated by 450 nm light of irradiance 0.3 \( \mu W/cm^2 \) for 30 min and then left for varying periods of time in the dark before fixation. Immediately after turning the light off, the screening pigment is at the tips of the receptors (Fig. 5 A). 2 min later, some is at the tips and some has started to migrate back (Fig. 5 B). 3 min after that most of the pigment is about one-fourth way back or more (Fig. 5 C). At 10 min after the end of illumination all the pigment is more than halfway back (Fig. 5 D). At 16 1/2 min substantially all the pigment has returned (Fig. 5 E.).
Figure 4. (A) Increment threshold and dark adaptation in a squid retina adapted to moderate levels of illumination, up to 5 μW/cm². (B) Increment threshold and dark adaptation in a squid retina adapted to high levels of illumination, up to 270 μW/cm². Threshold and background intensities are expressed in terms of log microwatt per square centimeter of retinal irradiance, ignoring losses in water of squid tank and media of squid eye (C) Section through retina of Fig. 4(B) fixed at end of experiment.
One test of whether pigment migration is due to absorption of light by rhodopsin, or absorption by screening pigment is to measure the spectral sensitivity of the pigment migration. First, however, one must know the spectral sensitivity of the screening pigment and of squid rhodopsin in the retina.

Whereas the absorption spectrum of squid rhodopsin in vitro is known (Hubbard and St. George, 1958), the spectral sensitivity of the retina can be expected to be broader, because the receptors are long, and self-screening of rhodopsin is involved. The spectral sensitivity of the receptors was deduced from the action spectrum of the oscillatory potential in the optic nerve, since this consists, for the most part, of axons of receptor origin. Three sets of measurements were made on the same preparation: (a) dark adapted, at the start of the experiment, (b) against a white background sufficiently bright that the screening pigment remained at the tips of the receptors (10 mW/cm²), and (c) after 12 min of subsequent dark adaptation. The results are shown in Fig. 6, with the same curve drawn through each set of points. The fit of the points to
the curve is reasonable in each case, with the exception of the points at 650 nm, indicating that the screening pigment acts as a fairly neutral filter out to 600 nm. The curve is appreciably broader than the absorption spectrum of squid rhodopsin in vitro (Fig. 8). Application of the formulae for self-screening (Dartnall, 1957) indicates that the difference between the action spectrum and the absorption spectrum for dilute solutions can be explained if the rhodopsin has a density of 0.6 log units at 490 nm.

The presence or absence of a black spot in the fixed retina (see Methods) was used to measure the spectral sensitivity of the permanent screening pigment migration. The retina was illuminated for 2 min with monochromatic light of 450, 490, 530, 570, 610, 630, or 650 nm. The squid was then left in the dark for 15 min and the retina fixed still in the dark, and observed a few minutes later. For each wavelength at higher intensities a black spot is seen (filled circles in Fig. 7) and at lower intensities no spot is seen (open circles in Fig. 7). At intermediate intensities sometimes part of the illuminated
area is black and part is not (partly filled circles in Fig. 7). The solid curve was drawn by hand between the filled circles and the open circles, and is taken to be the spectral sensitivity for permanent screening pigment migration.

This curve can be compared with others (Fig. 8): the absorption spectrum of squid rhodopsin (Hubbard and St. George, 1958), the spectral sensitivity of the squid optic nerve response (from Fig. 6), the absorption spectrum of the screening pigment extracted in digitonin (Hagins, 1973), the absorption spectrum of the screening pigment extracted in methanol (Hagins, personal communication), and the latter screening pigment curve corrected for the rhodopsin which acts as a filter in front of it.

It is not clear whether the curve for screening pigment extracted in methanol or digitonin should be taken. However this question is outweighed by other factors. The screening pigment is very dense in the squid retina; the absorption spectrum should therefore be adjusted for self-screening, which will make the curve broader. Furthermore, the screening pigment was at the base of the receptors at the start of illumination, and did not have time to move sub-
stantially during the 2 min of illumination used for this series of experiments, so that the rhodopsin filter has to be taken into account. Clearly the spectral sensitivity for the screening pigment migration follows the rhodopsin spectral sensitivity much more closely than the screening pigment absorption spectrum in methanol corrected for the rhodopsin filter, and any adjustments for self-screening or a different solvent will take the screening pigment curve even further away.

Given that screening pigment migration results from absorption by rhodopsin, it is interesting to see whether the quanta involved have to be delivered in a short period of time, or can be spread out over long periods. For this purpose, the retina was illuminated by monochromatic light of 490 nm. The illumination was of various intensities, for various durations. The squid was left in the dark for 15 min after the end of the illumination, then the retina was fixed in the dark, and observed a few minutes later. Again, the criterion was the presence or absence of a black spot.

The results of this experiment show that \( I \times t \) is constant, for the presence of a black spot, over durations from 6 s to 6 min, and also over durations from 40 min to 200 min or more (Fig. 9). Since the time-course of screening pigment migration outwards is 5-15 min, the results can be interpreted as a single curve with \( I \times t \) constant from 6 s to 400 min, and the screening pigment acting as a filter for durations longer than 5 min. For durations of 40 min and more, the period of time during which the screening pigment was not at the tips of the receptors is a comparatively small fraction of the total period of illumination. If this interpretation of the results is correct, then the effectiveness of the screening pigment as a filter is given by the displacement of the second limb of the curve vertically in relation to the first limb of the curve. This value is 0.6 log units.

These results were all obtained by fixing the retina 15 min after the end of the illumination. In a number of other cases retinas were illuminated with various intensities and various durations, then left in the dark for longer periods, up to 5 ½ h. In general, if a retina showed a black spot at the end of 15 min in the dark for a given intensity and duration of illumination, the screening pigment was still at the tips of the receptors after several hours in the dark in other retinas illuminated for similar intensities and durations.

The amount of rhodopsin isomerized to metarhodopsin at threshold for the black spot was calculated. The retinal irradiance at threshold was 5.8 \( \mu \text{W/cm}^2 \). Taking factors of 0.5 for quantum efficiency (it must be at least 0.3, Hagins, 1965), 0.75 for percentage of light absorbed (if the rhodopsin has a density of 0.6 log units, then 25% of the light at 490 nm will be transmitted without absorption), the effective light flux is \( 6.5 \times 10^{14} \) quanta/cm\(^2\). The decadic extinction coefficient of squid rhodopsin is 40,600 liters mol\(^{-1}\) cm\(^{-1}\), giving a photosensitivity of \( 1.52 \times 10^{-16} \) cm\(^2\) (Hubbard and St. George, 1958). Therefore
this flux of light should isomerize 10% of the rhodopsin; it should isomerize more if the quantum efficiency is greater than 0.5, and less if absorption by the lens and optic media is taken into consideration.

In order to check this calculation, retinas were prepared at 4×, 10×, and 60× threshold for the black spot, dissected on ice immediately after illumination, and prepared for extraction of the visual pigment. The extract was assayed for percentage of rhodopsin compared to metarhodopsin (Sperling and Hubbard, personal communication). When the results are extrapolated back to threshold, the conclusion is that less than 3% rhodopsin was isomerized at threshold, in approximate agreement with calculations from the optics of the system.

DISCUSSION

The fact that squid retinal screening pigment migration has the spectral sensitivity of rhodopsin is important, but not surprising. Hagins and Liebman (1962) were able to elicit screening pigment migration by illuminating slices of retina with spots of light falling on the rhabdomeres, but not directly on the screening pigment. Fish and amphibia also have a retinal screening pigment that migrates, the melanin in the epithelial cells. The spectral sensitivity of melanin migration has been shown to correspond to porphyropsin for the trout (Ali and Crouzy, 1968) and to rhodopsin for the frog (Liebman et al., 1969). The spectral sensitivity of pigment migration has not previously been measured, however, for an invertebrate.

The time-course of pigment migration outward (5–15 min) agrees with the time-course found by Hagins and Liebman (1962), and other authors under less well-defined circumstances (Young, 1963). The time-course of pigment migration inward does not agree with Hagins and Liebman’s result that the pigment returns over a period of 2 h after 10–50% of the rhodopsin is bleached (in these circumstances in our experiments the pigment had not migrated inward after several hours). Whether this discrepancy is due to a difference in the preparation (isolated retina as opposed to whole animal) or temperature (10°C for Hagins and Liebman, compared to 18–20°C for this study) is not certain. When the screening pigment does migrate, the bulk of it remains at the base of the rhabdomeric segments of the receptors.

The estimate for the density of squid rhodopsin at 500 nm from the self screening effect was 0.6 log units. Taking the length of the receptors to be 300 μm, and the decadic extinction coefficient to be 40,600 liters/mol cm, the concentration of visual pigment is 0.5 mM. This compares to 1.5–2 mM in vertebrate receptors (Marks, 1963; Hagins et al., 1970; Liebman, 1972) but the pigment in vertebrate receptors occupies almost all the cross section, whereas the pigment in squid occupies less than half the cross section (Cohen, 1973). Hamdorf et al. (1968) came up with a rather higher estimate, 0.75–2
log units, for the density of rhodopsin in *Eledone moschata*, based on similar arguments. It is possible that a strict application of the Dartnall formulae for self-screening may not be correct, since quanta of 500 nm may tend to be absorbed near the tips of the receptors, and other wavelengths, such as 650 nm, may be absorbed more uniformly down the receptor. The contributions of rhodopsin molecules isomerized in different parts of the receptor to the optic nerve response may not be equal. This factor might account for the discrepancy between the spectral sensitivity of omnin migration and the spectral sensitivity of the oscillatory potential at longer wavelengths.

The finding that the screening pigment does not move back over several hours if more than 3–10% of the rhodopsin is isomerized is strange. One hypothesis is that the isomerization of this much rhodopsin leads to a chemical or membrane change in the receptor, irreversible over several hours. In a number of cases where 10% rhodopsin or more was isomerized, the retina was found to be split at the junction of the proximal and distal segments after fixation. An increase in threshold was correlated with the failure of pigment migration backwards, but the size of the increase (over 2 log units in many cases, see Fig. 4) was larger than the effectiveness of the screening pigment as a neutral density filter suggested either by the results in this paper or electron microscope pictures of the granules at the tips of the receptors (Cohen, 1973). This suggests that there is some long-term change in the state of adaptation which has to be accounted for, besides the change in the state of the screening pigment.

A second hypothesis is that there are two types of pigment granule, one of which migrates out and back in a matter of minutes, the other of which migrates out in minutes, but does not move back for several hours. This seems less attractive, because it would account only for the pigment migration, and not for the size of the associated increase in threshold. There is no evidence from the extractions made by Butenandt (1959) or Hagins (1973) for two types of granule. The fact that the pigment moves as a fairly discrete band would tend to argue against two types of motile force for the granules.

The finding that quanta delivered over a period of several hours appear to have the same effect in producing irreversible pigment migration as quanta delivered over 6 s is also strange. It has been suggested that the preparation may degenerate over several hours, so that the mechanism for the return of screening pigment is destroyed. However, this explanation predicts a vertical line rather than a 45°-line dividing the long-term points in Fig. 9. Also migration outwards was seen at intensities of 0.3 $\mu W/cm^2$ for 30 min (see Fig. 5) as was migration backwards after this. This indicates that the points at 0.3 $\mu W/cm^2$ with durations of 50 and 100 min in Fig. 9 represent retinas in which migration backwards occurred, and therefore the preparation was quite viable after 2 h.
One may also hypothesize that regeneration of rhodopsin in squid is very slow, and that more than 3–10% of the rhodopsin is never isomerized in the normal course of events. Calculations from measurements of irradiance at 10 m underwater in the Baltic Sea (the nearest latitude to Woods Hole measured, Jerlov, 1968) show that about 10% rhodopsin would be isomerized in 8 h by a squid looking at a white object. These calculations assume that the squid’s pupil was closed down to a slit of 1-mm² area, and that the screening pigment at the tips of the receptors provides a filter of 0.6 log units. Squid rhodopsin can be regenerated from metarhodopsin by light (Hubbard and St. George, 1958). There must also be a mechanism for regeneration in the dark, because the spectral sensitivities of squid rhodopsin (493 nm) and metarhodopsin (500 nm) are close together, and retinas removed from freshly caught squid contain 100% rhodopsin within the experimental error of the procedures involved. Figures on the rate of regeneration of squid rhodopsin show that it is slow (Schwemer, 1968; Kito et al., 1972; Tsukahara and Tasaki, 1972), but are not yet complete enough to allow the hypothesis to be evaluated properly. If the hypothesis is true, then the slit pupil of the squid, its screening pigment, and the tendency for it to swim fairly deep in the water in the daytime are all protective mechanisms which prevent damage to the retina from bright lights.

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