Biophys. Struct. Mech. 6, 227–232 (1980)

Biophysics of Structure and Mechanism

Absorption of Light in Photoreceptors: Effect of Waveguiding Property*

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Abstract. The effect of waveguiding property (i.e., the intensity distribution) of the photoreceptor on the number of photons absorbed in a photoreceptor has been studied. It has been found that the effect is significant only for large values of the exposure and the maximum effect is less than 11% in the case of human rod photoreceptor. In the analysis, the funnelling effect, which follows from the coupling between the interior and exterior fields, has not been considered.

Key words: Absorption – Photoreceptors – Waveguiding property.

Dartnall et al. (1936, 1938) and Dartnall (1968) studied the time variation of the light transmitted through the visual pigment solution and determined the photosensitivity of visual pigments. In the mathematical formula, derived by these authors to determine the photosensitivity of visual pigments, they assumed that the concentration of the unbleached pigments is same everywhere throughout the solution at all times during bleaching process. But if the irradiated sample is a solid instead of the solution then the above assumption will not be true. Because of this, Rabinovitch (1973) and Onderdelinden and Strackee (1973) gave a mathematical treatment for the absorption of light in solid sample taking into account the time variation of the concentration of unbleached pigments along the direction of the propagation of light. The mathematical treatment given by these authors will be valid if the intensity distribution in the plane perpendicular to the direction of incident light is uniform. But this is not true in the case of visual photoreceptors. This is due to the fact that visual photoreceptors behave like optical waveguides (Enoch 1960, 1961, 1963) which allow the light to propagate through them only as certain transversely varying intensity patterns (called modes). Similar to the solid

* Work partially supported by the Department of Science and Technology (India)
** B. D. Gupta is associated with the School of Bioscience Studies

0340-1057/80/0006/0227/$ 01.20

sample, the time variation of the concentration of unbleached pigments along the direction of the incident light (i.e., along the axis of the photoreceptor) will be present in the case of photoreceptors. This is because the visual pigments are located in the disc membranes whose planes are perpendicular to the axis of the photoreceptor. Therefore in the case of visual photoreceptors, we have axial as well as radial dependence of the intensity or the concentration. Thus the amount of light absorption in the photoreceptor will be affected by the waveguiding property of the photoreceptor. Since in the disc membrane plane, visual pigments have translational diffusional motion (Poo and Cone 1973, 1974; Liebman and Entine 1974), the contribution of the waveguiding property will depend on the translational diffusion of the molecules.

In the present paper, we have studied the maximum effect of the waveguiding property of the photoreceptor on the absorption of light in the photoreceptors. In the mathematical analysis we have not considered the funnelling effect which arises from the coupling between the exterior and interior fields (Röhler and Fischer 1971). For simplicity we have assumed that light is propagating only as the fundamental mode. This is quite a good approximation as this mode carries most of the light power (~ 90%) incident on the retina. For the analysis we have considered the following reaction model:

$$\text{Visual pigment} \rightsquigarrow \text{Photoproduct} \tag{1}$$

In the above reaction model we have assumed that no photoreversal takes place from the photoproduct. This will be true if the intermediate formed does not absorb light in the region of the wavelength of the incident light. In the bleaching reaction of rhodopsin (a photosensitive pigment in the rod photoreceptor), metarhodopsin II is an intermediate which does not absorb light having wavelength greater than 450 nm. If we choose the duration of the source greater than the life time of metarhodopsin I but smaller than that of metarhodopsin II then as the rhodopsin molecule absorbs light it will soon decay to metarhodopsin II and in that case above reaction model will be valid. It can be noted that this is the only possible reaction model in which the waveguiding property of the photoreceptor can play an important role but it should also be noted that this reaction plays an important role in the excitation of the photoreceptor. To see the maximum effect of the waveguiding property on absorption we have considered the following two cases:

i) When there is no transverse diffusion, and
ii) When there is an infinitely rapid transverse diffusion[1].

Case I: In this case the kinetic equation for the reaction model (1) can be written as

$$\frac{dR(r, x, t)}{dt} = -\gamma \varepsilon_R I(r, x, t) R(r, x, t) \tag{2}$$

1 This case is equivalent to the one if we assume that the photoreceptor does not behave like an optical waveguide (i.e., when there is no transverse dependence of the intensity)

where

$$I(r, x, t) = I(r, o, o) \exp\left[-\varepsilon_R \int_0^x R(r, x, t)dx\right] \tag{3}$$

$$I(r, o, o) = A\, J_0^2\left(U\frac{r}{a}\right) \tag{4}$$

$R(r, x, t)$ represents the instantaneous concentration of visual pigment at axial distance x from the inner-outer segment junction and at a radial distance r from the axis of the outer segment; γ represents the quantum efficiency of the reaction; ε_R (λ) represents the extinction coefficient of the visual pigment at wavelength λ; $I(r, x, t)$ represents the instantaneous intensity of the incident beam at an axial distance x and radial distance r; $I(r, o, o)$ represents the intensity distribution at the junction of the inner and outer segments (we have assumed that the intensity of the incident light does not depend on time); a represents the radius of the photoreceptor's outer segment; U represents the normalized propagation constant of the fundamental mode; A is a constant and J_0 is the Bessel function of zeroeth, order. The solution of Eq. (2) with the initial condition

$$R(r, x, t = 0) = N_0 = \text{a constant}$$

can be written as (Rabinovitch 1973)

$$R(r, x, t) = \frac{N_0\,(1 + q(x))}{w(r, x, t)} \tag{5}$$

where

$$w(r, x, t) = q(x) + e^{\gamma\varepsilon_R I(r, o, o)t}$$

$$q(x) = e^{\varepsilon_R N_0 x} - 1$$

and N_0 represents the concentration of visual pigments when all the molecules are unbleached. The number of photons absorbed in the outer segment in time t will be

$$F_1(t) = 2\pi \int_0^t \int_0^a I(r, o, o)\left[1 - \exp\left\{-\varepsilon_R \int_0^l R(r, x, t)dx\right\}\right] r\, dr\, dt\,, \tag{6}$$

where l represents the length of the outer segment.

Case II: In this case R will not depend on radial distance r. Therefore we can write

$$\frac{dR(x, t)}{dt} = -\gamma\varepsilon_R I(x, t)R(x, t)\,, \tag{7}$$

where

$$I(x, t) = I_{av} \exp\left[-\varepsilon_R \int_0^x R(x, t)dx\right]$$

$$I_{av} = \frac{2}{a^2} \int_0^a I(r, o, o) r\, dr$$

$$= A[J_0^2(U) + J_1^2(U)]\,. \qquad (8)$$

J_1 is the Bessel function of first order. The solution of Eq. (7) can be obtained similar to the case I.

In this case, the number of photons absorbed in the outer segment in time t will be

$$F_2(t) = 2\pi \int_0^t \left([1 - \exp\{-\varepsilon_R \int_0^l R(x, t)dx\}] \int_0^a I(r, o, o) r\, dr\right) dt \qquad (9)$$

The difference in the number of photons absorbed in time t in the two cases will be

$$\Delta F = F_2 - F_1$$

$$= \frac{\pi}{\gamma \varepsilon_R} \Big[2 \int_0^a \ln[1 + e^{-\beta}\{e^{\gamma \varepsilon_R I(r, o, o)t} - 1\}]\, r\, dr$$

$$- a^2 \ln[1 + e^{-\beta}(e^{\gamma \varepsilon_R I_{av} t} - 1)]\Big] \qquad (10)$$

where

$$\beta = \varepsilon_R N_0 l$$

For the analysis, human rod photoreceptor has been chosen and therefore the following values of the parameters have been used in the analysis:

γ	$= 0.67$	(Dartnall 1968)
$\varepsilon_R(\lambda_{max})$	$= 3.8 \times 10^{-16}$ cm^2/chromophore	(Pugh 1975)
β	$= 0.8$	(Alpern and Pugh 1974)
a	$= 0.5 \times 10^{-4}$ cm	(Wolken 1961)
U	$= 1.788^*$ (see footnote 2)	

2 This value has been obtained by solving the waveguide eigenvalue equation (Snyder 1969) for the normalized frequency, $V = 3.1$ which corresponds to an average photoreceptor at $\lambda = 500$ nm

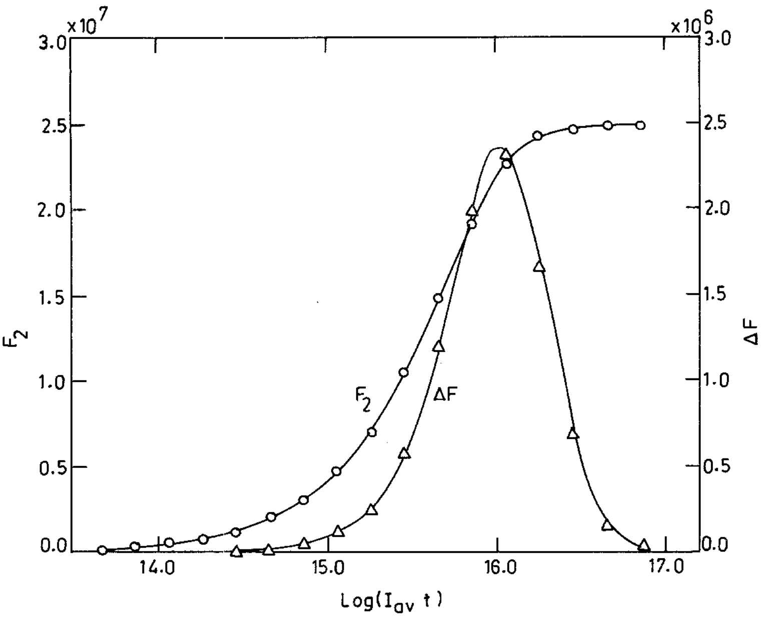

Fig. 1. Variation of F_2 (the number of photons absorbed when there is an infinitely rapid molecular diffusion or when the transverse dependence of the intensity is absent) and ΔF (the fractional difference in the number of photons absorbed) with $I_{av} \cdot t$ (the exposure)

In Figure 1 we have plotted ΔF (i.e., fractional difference in the number of photons absorbed) and F_2 (i.e., the number of photons absorbed when there is an infinitely rapid molecular diffusion or when the transverse dependence of the intensity is absent) as a function of $I_{av} \cdot t$ (i.e., exposure). It can be seen from the curve of ΔF that for $I_{av} \cdot t \leq 10^{15}$ the transverse dependence of the intensity, i.e., the waveguiding property of the photoreceptor does not play any important role in the absorption of light in photoreceptor. But as the value of $I_{av} \cdot t$ increases, the effect of transverse dependence of the intensity increases. The maximum effect has been found to be about 11% for $I_{av} \cdot t = 10^{16}$. From this one can draw the following conclusions:

(i) If we assume that photoreceptor does not behave like an optical waveguide, i.e., if we do not consider the transverse dependence of the intensity in the outer segment then the assumption will hold good if the value of exposure (i.e., the product of intensity and time) is small. As its value increases upto some particular value the validity of the assumption decreases. When $I_{av} \cdot t$ crosses that particular value the validity of the assumption increases. This is due to the occurence of saturation in the value of F_1 and F_2 (see Fig. 1).

(ii) For any value of the exposure the effect is not more than 11%. Since the translational diffusion of the molecules in the disc membrane is finite, therefore, in actual case the maximum effect will be less than 11%.

In summary, we have found that the waveguiding property of the photoreceptor affects the number of photons absorbed in the photoreceptor.

The effect is more significant for large values of exposure and its effect is less than 11% in the case of human rod photoreceptor.

Acknowledgements. The authors are grateful to Professor M. S. Sodha, Professor A. K. Ghatak, and Dr. I. C. Goyal for helpful discussions.

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Received December 6, 1979/Accepted April 14, 1980