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Absorption of Light in Photoreceptors: Transverse Incidence*

B. D. Gupta

Department of Physics, Indian Institute of Technology, Delhi
New Delhi-110016, India

Abstract. The time variation of the absorption rate (i.e., the number of photons absorbed per sec) in a photoreceptor when light is incident perpendicular to its axis has been studied for various species and different conditions. Due to the cylindrical geometry of the photoreceptor the expressions for the absorption rates become very complicated. Hence, simple approximate expressions for the absorption rates in the case of some of the species have been suggested. The present analysis will be useful in analysing the mechanism of the photoreceptor when light is incident perpendicular to the axis.

Key words: Absorption – Photoreceptors

Introduction

The absorption of light by visual pigments in a rectangular glass cell and in photoreceptors has been studied by several workers, theoretically (Dartnall et al. 1936, 1938; Dartnall 1968; Rabinovitch 1973; Onderdelinden and Strackee 1973; Gupta and Sharma 1980). In all such studies on photoreceptors light was considered to be incident along the axis of the photoreceptor but there are a number of experiments in literature in which light is incident perpendicular to the axis of the photoreceptor (Schmidt 1938; Denton 1954, 1959; Liebman 1962; Wald et al. 1963; Baylor et al. 1979; Jagger 1979); from such experimental studies various new results have been obtained (Gupta et al. 1979; Baylor et al. 1979). Also there are some experimental observations which need for their explanation the time variation of the concentrations of visual pigments for different exposures when light is incident perpendicular to the photoreceptor axis. To determine this one has to solve the kinetic equations. In the case of transverse incidence of light the kinetic equations or the expressions of

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absorption rates become very complicated due to the cylindrical geometry of the photoreceptor. Hence, one would like to have simple expressions for absorption rates which give the concentration of visual pigments.

In the present paper we have studied the time variation of the absorption rate in a photoreceptor when light is incident perpendicular to its axis for various species and different conditions. We have also suggested simple expressions for the absorption rates for some species. The present analysis will be useful in analysing the mechanism of the photoreceptor when light is incident perpendicular to the axis.

Theory

Following Gupta and Sharma (1980) we consider the following reaction model for the analysis:

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

In addition to the situations described by Gupta and Sharma (1980) this reaction also occurs if the photoreceptor is treated with hydroxylamine. In the photoreceptor visual pigments are contained in disk membranes whose planes are perpendicular to the axis of the photoreceptor. These molecules may or may not have diffusional motion depending on the conditions. Therefore, in the analysis, we have considered both the cases:

(i) When there is transverse diffusion of the molecules in the disk membranes, and

(ii) When there is no transverse diffusion, i.e., the molecules are fixed.

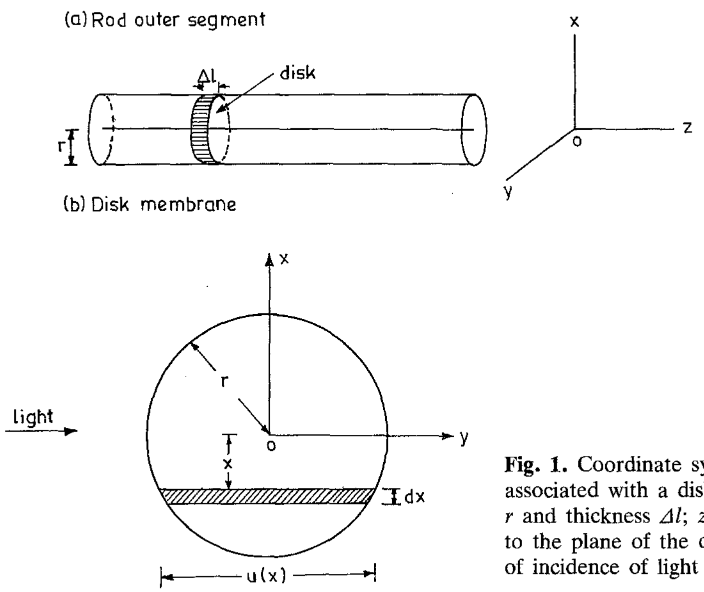

Fig. 1. Coordinate system (x, y, z) associated with a disk membrane of radius r and thickness Δl; z-axis is perpendicular to the plane of the disk while the direction of incidence of light is along the y-axis

Further, due to the cylindrical geometry of the photoreceptor the expressions for absorption rates are very complicated. However, by assuming the photoreceptor to have a square cross-section, one can obtain simple expressions for the absorption rates. The analysis using such a model is given as Case III.

Case I

Such cases occur when the photoreceptor is at room temperature. Consider a coordinate system (x, y, z) associated with a disk membrane of radius r and thickness Δl; the z-axis is perpendicular to the plane of the disk (see Fig. 1). Light is assumed to be incident along the y-axis (i.e., perpendicular to the axis of the photoreceptor). Since the width of the disk along the y-axis varies with x, the absorbance for the light propagating along the y-axis will also vary with x. Therefore, to solve the problem we consider a strip of thickness dx at a distance x from the center of the disk (see Fig. 1). The length and volume of the strip is given by

$$u(x) = 2\,(r^2 - x^2)^{1/2} \tag{2}$$

and

$$dv = u(x)\,\Delta l\,dx\,. \tag{3}$$

Consider a small portion of the beam of light falling on the area $\Delta l\,dx$ of the disk. Due to the diffusion of molecules in the disk the instantaneous concentration of the molecules will remain the same throughout the disk. Thus the number of photons absorbed in the strip per sec will be equal to $I_0 \Delta l\,dx\,(1 - e^{-\alpha_\perp(\lambda)\bar{A}(t)u(x)})$; $\bar{A}(t)$ is the instantaneous concentration of visual pigments in the disk (in chromophore per cm^3), I_0 is the intensity of the incident light (in photons per cm^2 per sec) and $\alpha_\perp(\lambda)$ is the extinction coefficient of visual pigments located in the disk for light incident perpendicular to the axis at wavelength λ (in cm^2 per chromophore). The number of photons absorbed in a disk per sec in the presence of diffusion can be written as

$$J_{PD}(t) = I_0 \Delta l \int_{-r}^{r} (1 - e^{-\alpha_\perp(\lambda)\bar{A}(t)u(x)})\,dx\,. \tag{4}$$

Thus the kinetic equation which describes the reaction model (1) for light incident perpendicular to the photoreceptor axis can be written as

$$V\frac{d\bar{A}(t)}{dt} = -\gamma J_{PD}(t)\,, \tag{5}$$

where V is the volume of the disk (in cm^3) and γ is the quantum efficiency of the reaction (1). Integrating Eq. (4) we obtain

$$J_{PD}(t) = -\pi r \Delta l I_0 [I_1(-\mu(\lambda, t)) + L_1(-\mu(\lambda, t))]\,, \tag{6}$$

where

$$\mu(\lambda, t) = 2\,\alpha_\perp(\lambda)\bar{A}(t)r\,.$$

I_1 is the modified Bessel function of first kind and of order one and L_1 is the modified Struve function. The expression for absorption rate contains $\bar{A}(t)$ and hence can be calculated only by first solving Eq. (5) for $\bar{A}(t)$. Equation (5) cannot be solved analytically and hence one has to first solve numerically to obtain $\bar{A}$ as a function of t and then calculate $J_{PD}(t)$. The calculation of $J_{PD}(t)$ also involves higher transcendental functions.

Case II

Such cases occur if the photoreceptor is at low temperature or if it is treated with glutaraldehyde (Brown 1972). In this case the concentration of visual pigments will be different at different positions. Thus, for light falling on the disk at a distance x from the center, the kinetic equation can be written as

$$\frac{dA_{xy}(t)}{dt} = -\gamma\alpha_\perp(\lambda)I_{xy}(\lambda, t)A_{xy}(t)\,, \tag{7}$$

where

$$I_{xy}(\lambda, t) = I_0 e^{-\int_0^y \alpha_\perp(\lambda)A_{xy}(t)dy}\,. \tag{8}$$

$A_{xy}(t)$ and $I_{xy}(\lambda, t)$ represent the instantaneous concentration of visual pigments and intensity at a distance y from the edge of the disk along the direction of incidence of the light and at a distance x from the center of the disk. Solving Eqs. (7) and (8) for $y = u(x)$ we obtain

$$I_x(\lambda, t) = \frac{I_0}{1 + (e^{\alpha_\perp(\lambda)A_0 u(x)} - 1)\, e^{-\gamma\alpha_\perp(\lambda)I_0 t}}\,. \tag{9}$$

If the light is incident between x and $x + dx$ (i.e., on the strip of Fig. 1) then the number of photons absorbed per second will be equal to

$$I_0 \Delta l\, dx \left[1 - \frac{1}{1 + (e^{\alpha_\perp(\lambda)A_0 u(x)} - 1)\, e^{-\gamma\alpha_\perp(\lambda)I_0 t}}\right].$$

Thus the absorption rate in the absence of diffusion can be written as

$$J_{AD}(t) = 2\, I_0 \Delta l \int_0^r \frac{(e^{\alpha_\perp(\lambda)A_0 u(x)} - 1)e^{-\gamma\alpha_\perp(\lambda)I_0 t}}{1 + (e^{\alpha_\perp(\lambda)A_0 u(x)} - 1)\, e^{-\gamma\alpha_\perp(\lambda)I_0 t}}\, dx\,. \tag{10}$$

The integral in this case also has to be evaluated numerically.

Case III

In this case we assume that the photoreceptor has a square cross-section instead of a circular one and its volume is equal to that of the actual photoreceptor. Thus, the kinetic equation in the presence of diffusion can be written as

$$V \frac{d\bar{A}(t)}{dt} = -\gamma J_s(t) , \tag{11}$$

where

$$J_s(t) = a\Delta l I_0 (1 - e^{-\alpha_\perp(\lambda)\bar{A}(t)a}) \tag{12}$$

and

$$a = \sqrt{\pi}\, r . \tag{13}$$

Using Eq. (12) we obtain

$$J_s(t) = \frac{a\Delta l I_0 (e^{\alpha_\perp(\lambda)A_0 a} - 1)\, e^{-\gamma\alpha_\perp(\lambda)I_0 t}}{1 + (e^{\alpha_\perp(\lambda)A_0 a} - 1)\, e^{-\gamma\alpha_\perp(\lambda)I_0 t}} . \tag{14}$$

In the absence of diffusion the absorption rate is equal to that in the presence of diffusion for this geometry of the photoreceptor. Thus, the absorption rates in the three different cases are given by Eqs. (6), (10), and (14) respectively of which Eq. (14) is the simplest one. The numerical results obtained in the three different cases are given in the last section.

Selection of Parameters

Gupta (1980) and Gupta et al. (1979) reported that rhodopsin is a planar absorber with a ratio of about 100 : 7 between the extinction coefficients along the long axis and perpendicular to it. In the model reported by them the plane of the chromophore is perpendicular to that of the disk and the long axis of the chromophore makes an angle of 6.6° with the plane of the disk. Using these results the extinction coefficient of the visual pigments located in the disk membrane for light incident perpendicular to the photoreceptor axis is given by

$$\alpha_\perp(\lambda) = \frac{\alpha_\parallel(\lambda)[K + (1 + \phi)/2]}{1 - \phi} , \tag{15}$$

where

$$\phi = (1 - K)\sin^2\theta ,$$

$\alpha_{\|}(\lambda)$ is the extinction coefficient of the visual pigment for the light incident along the axis, $K = 0.07$ and $\theta = 6.6°$ (Gupta 1980; Gupta et al. 1979). To see the maximum difference in the absorption rates in the three different cases we choose $\lambda = \lambda_{max}$ (the wavelength corresponding to maximum absorption). For the human eye,

Table 1

Species	r [cm]	Δl [cm]	A_0 [chromophore/cm^3]
Man[a]	0.5×10^{-4}	2.5×10^{-6}	6.38×10^{18}
Cattle	0.5×10^{-4}	2.0×10^{-6}	1.49×10^{18}
Frog	3.0×10^{-4}	1.5×10^{-6}	9.0×10^{18}

[a] The value of A_0 in the case of man has been obtained using $\beta = \alpha_{\|}(\lambda_{max})\, N_0/\pi^2 = 0.8$ (Alpern and Pugh 1974) and assuming rhodopsin to be a spherical molecule of diameter 40 Å (Wald 1954); where N_0 represents the number of rhodopsin molecules in a photoreceptor. The other parameters used to calculate A_0 are taken from Wolken (1961) and some of them are reported in Table 1

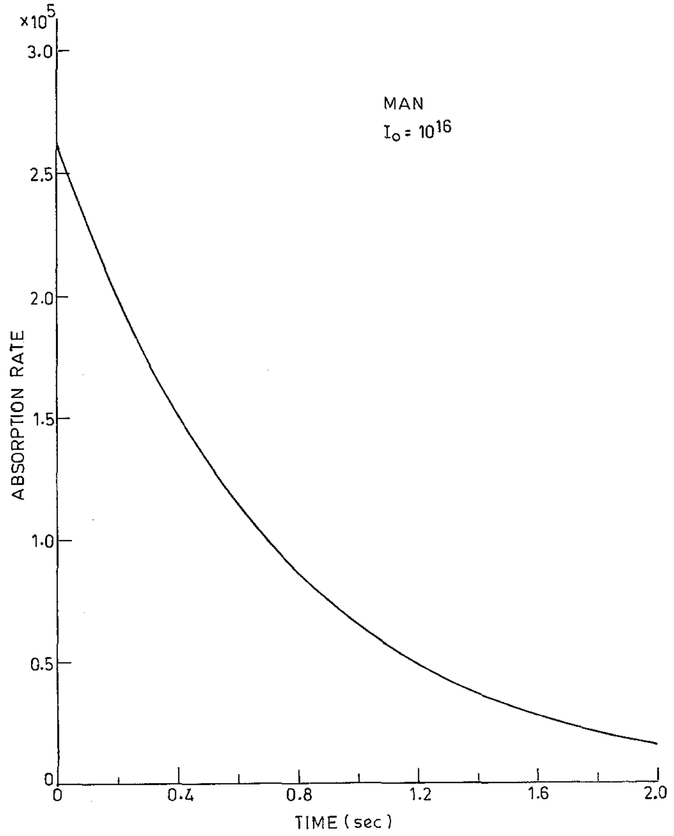

Fig. 2. Time variation of absorption rate for $I_0 = 10^{16}$ photons per cm^2 per sec in the case of man

$\alpha_{\parallel}(\lambda_{max}) = 3.8 \times 10^{-16}$ cm^2 per chromophore (Pugh 1975) which gives [using Eq. (15)],
$\alpha_{\perp}(\lambda_{max}) = 2.216 \times 10^{-16}$ cm^2 per chromophore.

In the present calculations this value of $\alpha_{\perp}(\lambda)$ will be used for all the species. The value of quantum efficiency used in the calculation is 0.67 (Dartnall 1968). The values of the other parameters used for different species are given in Table 1.

Results and Discussion

In Figs. 2, 3, and 4 we have plotted absorption rates as a function of time for $I_0 = 10^{16}$ photons per cm^2 per sec in the three different cases for man, cattle, and frog respectively. It can be seen from these figures that in the case of man and cattle the absorption rates are the same at all times in the three different cases. In the case of frog the absorption rates in the three different cases are different. Initially the absorption rate in Case I (i.e., in the presence of diffusion) is greater

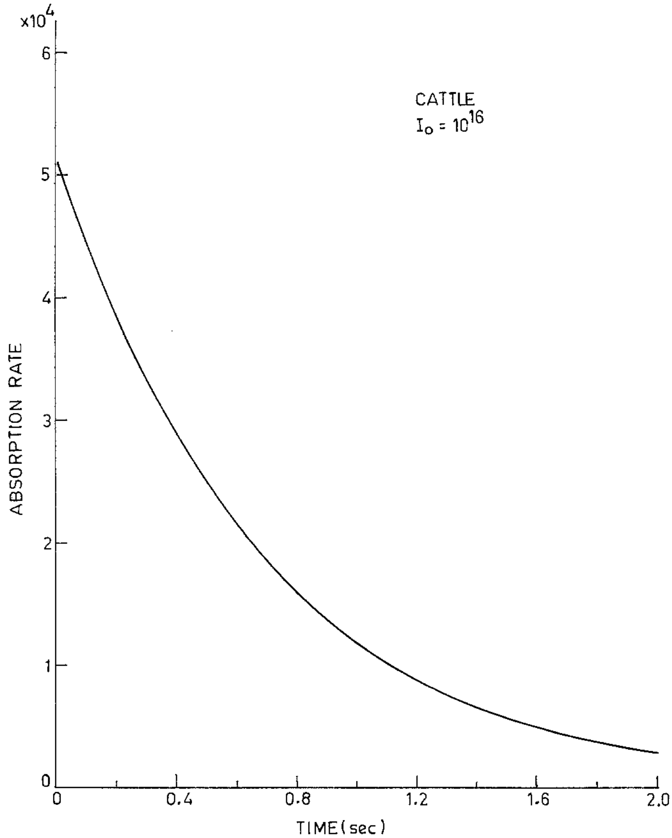

Fig. 3. Same as Fig. 2 except that it has been plotted for cattle

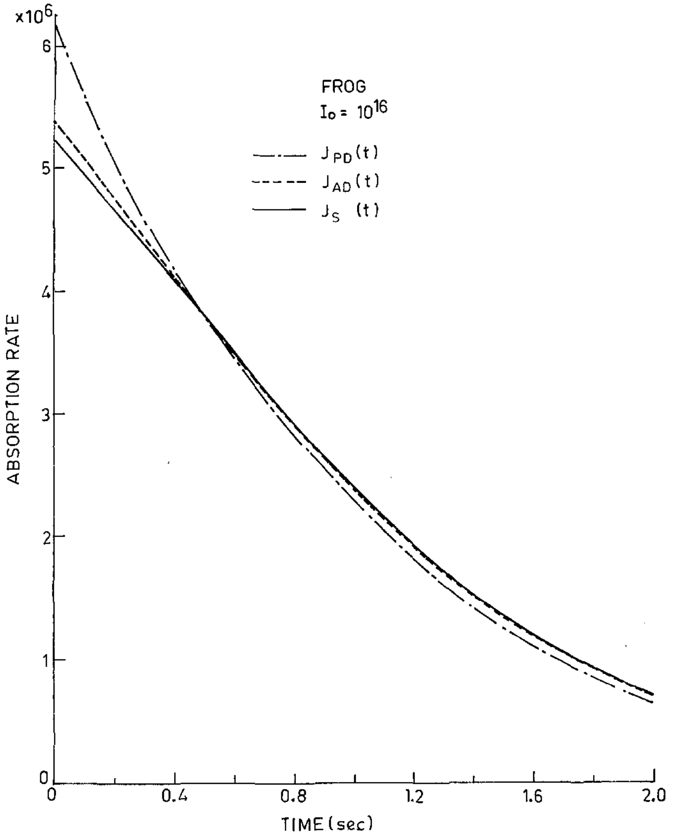

Fig. 4. Same as Fig. 2 except that it has been plotted for frog

than the absorption rate in Case II (i.e., in the absence of diffusion) which is greater than that in Case III (i.e., if the photoreceptor has square cross-section) but after sometime their order is reversed. That is, the absorption rate in Case I becomes slower than that in Case II which is slower than that in Case III. The difference between Case II and Case III is smaller than the difference between Case I and Case II. From this study one can draw the following conclusions:

(i) In order to study the mechanism of visual photoreceptors of man and cattle when light is incident perpendicular to the axis of the photoreceptor one can consider the photoreceptor to have a square cross-section of area πr^2, no matter what the temperature of the photoreceptor is or whether it has been treated with glutaraldehyde or not. In the case of frog, since the difference between the absorption rates in Case II and Case III is small, one can assume the photoreceptor to have a square cross-section only if the temperature is very low or if the photoreceptor has been treated with glutaraldehyde. For a photoreceptor of square cross-section the expression for absorption rate becomes very simple.

(ii) In the case of frog, since the difference between Case I and Case III is very large, one cannot assume photoreceptor to have a square cross-section if it is at room temperature (i.e., if the molecules have diffusional motion in the disk membrane). Therefore we see that in the case of frog and in the presence of diffusion the analysis will become very complicated.

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