

Increment Threshold as a Function of Background Illumination: Contribution of cellular adaptation

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Abstract

In the present communication we have studied the contribution of cellular adaptation in increasing the photoreceptor increment threshold as a function of background intensity in intact eye and isolated retina. In intact eye, at low level of illumination, the contribution increases with the background intensity and saturates at higher intensity. In isolated retina, the results have been found to be very much different. It is found that the contribution of cellular adaptation increases with background intensity upto a certain value and after that it decreases rapidly to reach its dark adapted value.

Key words : cellular adaptation, eye, vision

Introduction

It is well known that the background illumination causes changes in sensitivity of the rod and cone photoreceptors. Following three sensitivity regulating mechanisms have been proposed for cone photoreceptors: response compression (Boynton & Whitten 1970), pigment bleaching (Boynton & Whitten 1970) and cellular adaptation (Normann & Perlman 1979). Response compression is caused by the nonlinear relation between stimulus intensity and response. It occurs when the operating point of the photoreceptor moves to a higher position on the response curve, *e.g.* by the steady potential produced by a steady background light. Pigment bleaching causes desensitization because fewer quanta from a given stimulus are absorbed. Cellular adaptation is an active mechanism in the photoreceptor that adjusts its operating range to conform to the background illumination. In a number of species, cellular adaptation has been found to be a major factor in photoreceptor adaptation. In the literature the variation of increment threshold with background intensity in intact eye and isolated retina have been reported to be nearly the same although in intact eye the regeneration of

the visual pigment occurs while in isolated retina it does not (Dowling 1987). Due to this, in the present communication, we have studied the contribution of cellular adaptation to the increase in the threshold intensity in the presence of background illumination for both intact eye and isolated retina.

Theory

To determine the relationship between cellular adaptation and background illumination we have derived an expression for the relative threshold versus background illumination. For this we have used the following equation which describes the intensity response function of the photoreceptor (Valeton & Van Norren 1983; Pepperberg 1984).

$$\frac{V}{V_m} = \frac{I^n(1-B)^n}{I^n(1-B)^n + \sigma^n} \quad (1)$$

where V = amplitude of the flash response; V_m = maximum possible flash response; I = intensity of the flash; B = fraction of pigment bleached before the flash; σ = flash intensity that gives half maximum response and is also called adaptation parameter and n = exponent, usually between 0.7 and 1.0. The term $(1-B)$ in Equation (1) has been introduced as a correction for efficiency of quantum capture. In Equation (1) both σ and V_m depend on the background light intensity (I_B); the changes in σ reflecting the adaptation properties, the changes in V_m reflecting the response range compression. In the dark adapted state (i.e. $B = 0$ and $I_B = 0$) Equation (1) can be written as

$$\frac{V}{V_{max}} = \frac{I^n}{I^n + \sigma_0^n} \quad (2)$$

where V_{max} and σ_0 are the constants and represent, respectively V_m and σ for the fully dark adapted condition. Let V_0 , a constant be the criterion response. If I_{T_0} is the threshold intensity (i.e. the flash intensity which gives V_0 as the flash response) in the dark adapted condition then Equation (2) gives

$$(I_{T_0})^n = \frac{V_0/V_{max}}{\{1 - V_0/V_{max}\}} \sigma_0^n \quad (3)$$

In the light adapted condition i.e. in the presence of background illumination, Equation (3) becomes (also see Equation (1))

$$(I_T)^n = \frac{V_0/V_m}{(1-B)^n \{1 - V_0/V_m\}} \sigma^n \quad (4)$$

where I_T = intensity of the flash required to obtain the criterion response V_0 ; $V_m = V_{max} - V_B(I_B)$ and V_B = steady response produced by a steady background light (I_B). In most of the experiments carried out and reported in the literature $V_0/V_{max} \ll 1$, therefore, on dividing Equation (4) by Equation (3) we obtain

$$\Delta I = \frac{I_T}{I_{T_0}} = \frac{1}{(1-B)} \left\{ \frac{V_{max}}{V_{max} - (V_B + V_0)} \right\}^{1/n} (\sigma/\sigma_0) \quad (5)$$

where ΔI is the relative threshold intensity. The logarithm of Equation (5) gives

$$\log \Delta I = \log\left(\frac{1}{1-B}\right) + \log\left(\frac{\sigma}{\sigma_0}\right) + \frac{1}{n} \log\left\{\frac{V_{max}}{V_{max} - (V_B + V_0)}\right\} \quad (6)$$

This equation gives the contribution of each of the three sensitivity regulating mechanisms to the total sensitivity loss that occurs in light adaptation.

Results

To know the contribution of cellular adaptation parameter (σ), one has to know ΔI , V_B and B as a function of I_B . Normann & Anderton (1983) have studied experimentally the relation between incremental sensitivity of turtle cone photoreceptors and steady state background illumination. Their results can be expressed by the following relation

$$\Delta I = 1 + 1.7977 \times 10^{-4} I_B \quad (7)$$

where I_B has units of quanta/ μm^2 /sec. The above equation has been used in the present analysis. For V_B vs I_B relation we have used the results obtained by Baylor & Hodgkin (1974) in the same species and have used the following values of the parameters: $V_{max} = 24$ mV; $n = 0.74$ and $V_0 = 25 \mu V$. The last parameter required for calculation is the variation of B with I_B .

In intact eye the fraction of pigment bleached due to steady background of intensity I_B can be written as

$$B = \frac{1}{1 + kI_B/\phi} \quad (8)$$

where ϕ is the photosensitivity of the pigment and k is the rate constant of its regeneration. In turtle cones, $\phi/k = 1.25 \times 10^{-6} \mu m^2$ sec. In Fig. 1 we have plotted the contribution of cellular adaptation (σ) apart from pigment bleaching and response compression in intact eye. It can be seen that, at low level of illumination, the contribution of cellular adaptation to the increase in threshold increases with the background intensity and saturates at higher intensity.

In the case of isolated retina the fraction of pigment bleached due to steady light of intensity I_B can be written as

$$B = 1 - \exp(-\phi I_B t) \quad (9)$$

where t is the duration of the background illumination. For calculation we have used $\phi = 10^{-17} cm^2$ /chromosphere and $t = 1$ min (Normann & Anderton 1983). Similar to Fig. 1 we have plotted, in Fig. 2, the contributions of all the three mechanisms responsible for increase in increment threshold with background illumination in isolated retina. It can be seen that the contribution of cellular adaptation in isolated retina first increases upto a certain value of I_B and then decreases rapidly towards its dark adapted value. This is different from what has been obtained in intact eye. It can be noted that the sensitivity decrease for backgrounds upto 10^7 quanta (μm) $^{-2}$ sec $^{-1}$ is mainly caused by cellular adaptation and response compression. For the intensity greater than this the contribution of response compression saturates, the contribution of cellular adaptation starts decreasing while that of pigment bleaching increases.

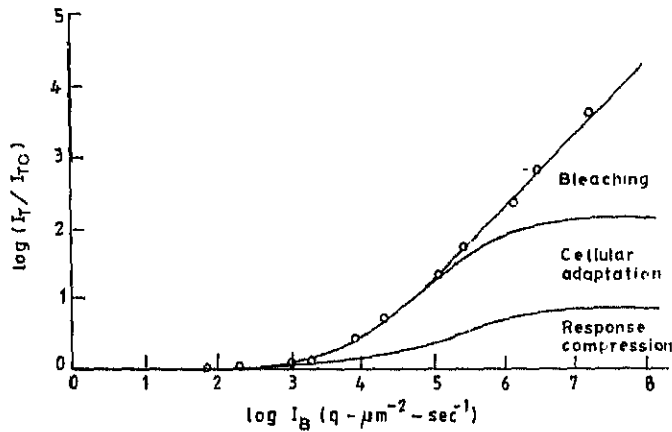


Figure 1. Increment threshold vs. intensity function. Circles are the experimental data (Normann & Anderton 1983). The contribution of each of the three sensitivity regulating mechanisms in intact eye is shown.

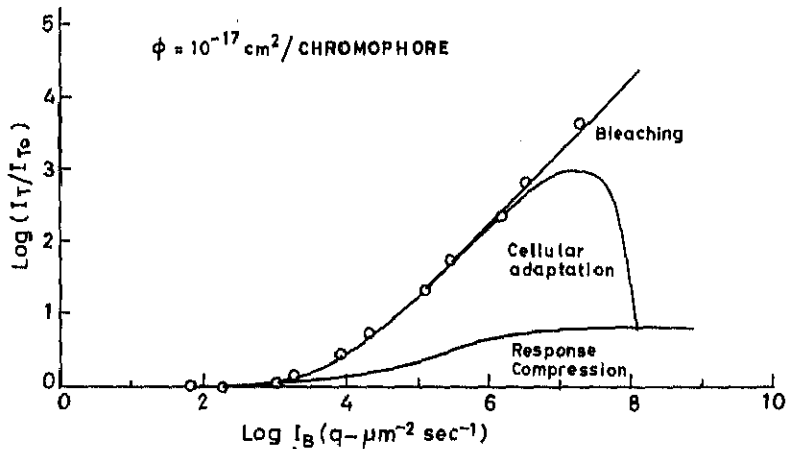


Figure 2. Same as Figure 1 except that it has been plotted for isolated retina.

Pepperberg (1984) has analysed the photoreceptor increment threshold data of isolated skate retina. To fit his theoretical results in experimental data he has used the following relation for the contribution of cellular adaptation:

$$\log\left(\frac{\sigma}{\sigma_0}\right) = \log\{1 + \theta_1 I_B(1 - B) + \theta_2 B\} \quad (10)$$

where

$$(\theta_1)^{-1} = 3.1 \text{ quanta } \mu\text{m}^{-2}\text{sec}^{-1} \text{ and } \theta_2 = 100.$$

From Equation (10) one can calculate the contribution of cellular adaptation for different values of B and I_B . For $B = 1$ (i.e. very high background intensity) it gives $\log(\sigma/\sigma_0) = 2$. If $B = 0$ and $I_B = 10^3 \text{ quanta } \mu\text{m}^{-2}\text{sec}^{-1}$ then we obtain $\log(\sigma/\sigma_0) = 2.5$ which is greater than 2; at low level of illumination $B \approx 0$ (Weinstein, Hobson & Dowling 1967). Thus the value of $\log(\sigma/\sigma_0)$ first increases upto a certain value and after that it decreases. At very high background intensity it is equal to 2. In other words it does not saturate in isolated skate retina. This supports our results obtained here on isolated retina.

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