

Purkinje Shift and Retinal Noise

THE Purkinje shift is the displacement of the maximum sensitivity of the eye towards the blue end of the spectrum at low levels of ambient illumination. It occurs in a wide variety of vertebrates, including some which possess the porphyropsin system of freshwater fishes in place of the rhodopsin system of sea-water fishes and land vertebrates; but in spite of this widespread occurrence, there is no satisfactory explanation for the advantage derived from evolving different photosensitive systems with different spectral sensitivity curves for use at high and low levels of illumination. An explanation is not to be found in the different distribution of energy in the incident light in day-time and at night, for the maximum energy of light from the Moon is slightly to the red side of the maximum for light from the Sun. Le Grand¹ suggests that rhodopsin was evolved by deep-sea fishes, for the light which penetrates deep into the sea has a maximum energy close to the peak of the absorption of rhodopsin, but a shift of the spectral sensitivity curve to the blue may enable the eye to achieve greater sensitivity for a quite different reason.

Recent work² has shown what factors control the ultimate sensitivity of detectors of radiant energy working at the limit set by radiation noise from their surroundings. In particular, it has been shown³ that the sensitivity can be greatly improved by reducing to a minimum the response of the detector to wavelengths longer than those contained in the signal. The sensitivity of the human eye is probably not limited by radiation noise, but reasons have been advanced elsewhere⁴ for believing that it may be limited by the thermal decomposition of rhodopsin molecules. de Vries⁵ pointed out that a shift of spectral sensitivity to the blue would reduce the rate of thermal decomposition, so that this may be as beneficial to the sensitivity of the eye as it is to detectors limited by radiation noise. This conclusion is reached as follows.

Stiles⁶ has shown that the spectral sensitivity curve of the human eye at the red end of the visible spectrum can be partially accounted for on the hypothesis that the photochemical change which activates a rod requires a certain definite minimum energy which is not entirely derived from a quantum of absorbed radiation, but is supplemented by

thermal energy supplied by collisions with the surrounding molecules. If thermal energy can supplement radiant energy, it is natural to suppose that, occasionally, it may be sufficient to activate a rod without the absorption of any radiation. Unfortunately, it is not possible to calculate the absolute rate of such thermal excitations; but it is possible to show how the rate would be affected by varying the minimum energy (E) required for the photochemical change which causes rod excitation. It is assumed that a change of E does not affect the availability of thermal energy to the site in the rhodopsin molecule which is linked to the mechanism of rod excitation, and that it does not change the maximum extinction coefficient of the molecules, but that it does change the position of maximum absorption (λ) so that $hc/\lambda = E$ (that is, one quantum of maximum visibility radiation provides exactly the minimum energy). Following Stiles's assumptions, the fraction of molecules (F) with energy greater than E is given by the expression:

$$F = \exp(-E/kT) = \exp(-hc/\lambda kT)$$

where h is Planck's constant, c the velocity of light, k Boltzmann's constant and T the absolute temperature. If other conditions are the same, the smallest number of quanta which must be absorbed for a given reliability of detection will be proportional to the square root of the rate of the thermal reaction, so that the threshold energy (I) is given (in arbitrary units) by:

$$I \cdot \lambda = F^{1/2} = \exp(-hc/2\lambda kT)$$

On changing E from E_0 to E_1 , the position of the peak of sensitivity changes from λ_0 to λ_1 , and the ratio of threshold energies at the two wave-lengths is given by:

$$\frac{I_1}{I_0} = \frac{\lambda_0}{\lambda_1} \exp \frac{hc}{2kT} \left(\frac{1}{\lambda_0} - \frac{1}{\lambda_1} \right)$$

For $\lambda_0 = 550 \text{ m}\mu$, $\lambda_1 = 541 \text{ m}\mu$, $I_1/I_0 = \frac{1}{2}$, so the rather surprising conclusion is reached that, in the middle of the visible spectrum, a shift of the spectral sensitivity curve by $9 \text{ m}\mu$ towards the blue allows the threshold energy to be halved. For a shift from the peak of the photopic ($560 \text{ m}\mu$) to the peak of the scotopic visibility curve ($507 \text{ m}\mu$), the theory predicts an improvement of 65 times, and for the shift from the red receptor ($580 \text{ m}\mu$) to the rods ($507 \text{ m}\mu$) an advantage of 265 times.

Wald⁷ compared the sensitivity of rods lying 8° from the fovea with the sensitivity of cones lying at the fovea, using a test stimulus 1° in diameter exposed for $1/25$ sec., and found that the rods were

