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Absorption of White Light in Photoreceptors

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The fraction F of incident light absorbed by a photoreceptor of length l has traditionally been given by $F = 1 - e^{-kl}$, where k is the absorption coefficient of the photoreceptor. Unfortunately, this widely-used expression is incorrect for absorption of the type of light most common in natural scenes—broad spectrum "white" light—and significantly over-estimates absorption. This is because the measured values of k are only valid at the absorbance peak wavelength of rhodopsin, whereas at other wavelengths (which the eye may also see) k is lower. We have accounted for the wavelength dependence of k and calculated the absorption of white light from four different natural radiant sources: the quantal irradiances of natural daylight and a patch of very blue sky, and the quantal reflections of soil and green foliage irradiated by natural daylight. Based on these results, a simple averaged correction for white light stimulation is derived, $F = kl/(2.3 + kl)$, which is valid for a wide range of k and l, and therefore applicable to both vertebrate and invertebrate photoreceptors. © **1998 Elsevier Science Ltd**

Absorption coefficient White light Photoreceptors Self-screening Visual pigment

INTRODUCTION

Near-monochromatic visible light occurs on Earth in only three situations: as bioluminescence; as down-welling light in deep water; and in the laboratory. In the vast majority of situations, eyes view scenes which reflect light of much broader spectral composition, with some wavelengths having greater quantal intensity than others (Lythgoe, 1979; Osorio & Bossomaier, 1992; Nagle & Osorio, 1993). Moreover, the spectral composition of this natural "white" light is usually broader than the range of wavelengths which can be absorbed by any particular visual pigment.

Despite the fact that white light is the normal visual stimulus, monochromatic light, because of its quantitative convenience, has been used extensively in visual research. Unfortunately, this has occasionally lead to conclusions which are not valid for vision in white light. An example of this concerns one of the fundamentals of vision, the absorption of light in photoreceptors. The photoreceptor's absorption coefficient (k), has now been determined in a number of animals, both vertebrate and invertebrate, but always at the absorbance peak wavelength (λ_{max}) of the resident visual pigment (Table 1). Whilst these measurements are by no means incorrect, they cannot be used to quantify absorption of white light, as has often been done. This is simply because wavelengths other than λ_{max}, whilst still absorbed by the visual pigment, have lower absorption coefficients. Some wavelengths are therefore absorbed at much lower rates than others. This means that at the proximal end of a very long photoreceptor almost no light of peak wavelength remains, having been almost entirely absorbed more distally. The only light remaining in any quantity would be composed of wavelengths far away from λ_{max}, with absorptions at much lower rates (Fig. 1). If it were possible to exclusively measure the spectral sensitivity of the extreme proximal photoreceptor, it would show greatest sensitivity to wavelengths for which the visual pigment shows low sensitivity. This leads to a broader spectral sensitivity for the entire photoreceptor than that predicted from the rhodopsin spectrum. This curious absorption phenomenon, which is most pronounced in long photoreceptors, is called self-screening (Brindley, 1960). Dragonflies, some of which have the longest photoreceptors known (>1.1 mm), suffer particularly from self-screening (Labhart & Nilsson, 1995).

For the sake of simplicity, it has commonly been assumed in absorption calculations (especially those pertaining to optical sensitivity) that all wavelengths incident on a photoreceptor are absorbed at the same rate per micron, this rate being specified by the absorption coefficient (k) measured at λ_{max} (e.g. Land, 1981; Mathis *et al.*, 1988; Warrant & McIntyre, 1990a; Seyer, 1992). This assumption is implicit in calculations of the fraction F of incident light which can be absorbed in a photoreceptor of length l:

$$F(l) = 1 - e^{-kl}. \quad (1)$$

This fraction is also known as the absorptance (Knowles & Dartnall, 1977: see Appendix A). For a long photo-

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TABLE 1. Known photoreceptor absorption coefficients, k

Animal	k (μm^{-1})	Reference
Vertebrates		
Skate	0.037	Cornwall, Ripps, Chappell and Jones (1989)
Bony fishes	0.023–0.035	Partridge (1990)
Deep sea fish	0.064	Partridge, Shand, Archer, Lythgoe and van Groningen-Luyben (1989)
Goldfish	0.030	Liebman (1972)
	0.028	Harosi and MacNichol (1974)
Tiger salamander		Harosi (1975)
Land phase	0.041	
Water phase	0.028	
Mud puppy		
Rods	0.029	Harosi (1975)
Cones	0.037	Liebman (1972)
Leopard frog	0.041	Harosi and MacNichol (1974); Liebman (1972)
Cane toad		Harosi (1975)
Rods (red)	0.039	
Rods (green)	0.032	
Pigeon	0.049	Bowmaker (1977)
Tawny owl		Bowmaker and Martin (1978)
Rods	0.039	
Cones	0.030	
Chicken		Bowmaker and Knowles (1977)
Rods	0.053	
Cones	0.035	
Macaque monkeys		
M. fascicularis		
Rods	0.029	Baylor, Nunn and Schnapf (1984)
Rods	0.041	Bowmaker, Dartnall and Mollon (1980)
Cones	0.035	
M. mulatta		Bowmaker, Dartnall, Lythgoe and Mollon (1978)
Rods	0.044	
Cones	0.035	
Man (rods)	0.028	Alpern and Pugh (1974)
Invertebrates		
House fly	0.005	Kirschfeld (1969)
Dronefly	0.009	Stavenga (1976)
Lobster	0.0067	Bruno, Barnes and Goldsmith (1977)
Spider crab	0.013	Hays and Goldsmith (1969)
Mantis shrimps	0.007–0.018	Cronin and Marshall (1989a,b)
Crabs	0.003–0.023	Cronin and Forward (1988)
Deep-sea shrimps		Hiller-Adams, Widder and Case (1988)
Systellaspis	0.0085	
Sergestes	0.0106	

Unless otherwise stated, all quoted vertebrate values are for rods. The absorption coefficient k should not be confused with the *specific absorbance*, D_s. Both parameters have units μm^{-1}, and are simply related through $k = 2.303 \cdot D_s$. The terminology and mathematical relationships between the various published parameters describing absorption are explained in Appendix A.

receptor, $F(l)$ approaches 1, implying that essentially all light incident on the photoreceptor is absorbed by it. $F(l)$ also depends on k, and approaches 1 more quickly for larger values of k. Absorption coefficients (at λ_{max}) have been measured a few times in invertebrates and numerous times in vertebrates (Table 1). The values determined for vertebrates are roughly five times larger than those for invertebrates living in similar light intensities (animals living in the deep sea typically have higher absorption coefficients, but the ratio of values between vertebrates and invertebrates is still *ca* 5). Setting $k = 0.035\ \mu m^{-1}$ for vertebrates, and $k = 0.0067\ \mu m^{-1}$ for invertebrates, the effect of k on $F(l)$ can readily be seen [Fig. 2(A)]. Equation (1) can also be plotted with respect to the logarithm of kl, thus giving a sigmoidal curve valid for various combinations of k and l [Fig. 2(B)], and therefore applicable to both vertebrates and invertebrates.

Even though equation (1) is valid for the absorption of monochromatic light of wavelength λ_{max}, it is invalid for the absorption of broad spectrum (white) light, the light most commonly seen by photoreceptors. This is because the equation assumes that the measured value of k is valid for all absorbed wavelengths. This leads to a considerable over-estimate of F for a given photoreceptor length (Labhart & Nilsson, 1995). For white light, a correct formulation of equation (1) must account for the fact that k is not a constant independent of wavelength. The pursuit of a correct formulation is the subject of this investigation. Despite an involved calculation, the correction turns out to be surprisingly simple.

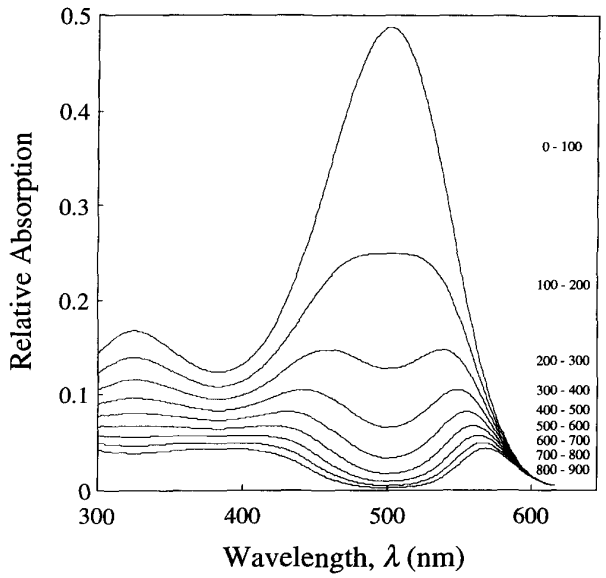

FIGURE 1. An illustration of self-screening in a photoreceptor 900 μm long. The absorbance peak wavelength (λ_{max}) of the resident visual pigment is taken as 500 nm. In the distalmost 100 μm, the absorption spectrum resembles the absorbance spectrum. In successively more proximal 100 μm segments (as indicated at right), the absorption spectrum becomes more bi-lobed in appearance, the lobes displacing further from λ_{max} with increasing depth. The wavelengths within the lobes are the only wavelengths remaining which can still be absorbed, with wavelengths around λ_{max} having already been strongly attenuated. This self-screening significantly widens the spectral sensitivity of the photoreceptor. Curves were calculated iteratively using equation (3), with $k = 0.0067\ \mu m^{-1}$, $l = 100\ \mu m$ and $A(\lambda)$ given by the SSH rhodopsin template (Appendix B).

THEORY

A statement of the problem

Equation (1) can be corrected by recognizing that k is not a constant, but rather, varies depending on wavelength (λ). In the limit of infinitesimal photoreceptor length, the dependence of k on λ exactly follows the absorbance spectrum of rhodopsin, $A(\lambda)$:

$$k(\lambda) = kA(\lambda). \tag{2}$$

Because $A(\lambda)$ has values between 0 and 1, $k(\lambda)$ has values between 0 and k. Substituting equation (2) into equation (1) yields

$$F(l, \lambda) = 1 - e^{-kA(\lambda)l}. \tag{3}$$

Equation (3) describes the *absorptance spectrum*: at any given photoreceptor length l, it is possible to calculate the fraction F of incident light of wavelength λ which is absorbed by the photoreceptor. This also assumes that k is constant along the photoreceptor's length. Imagine that the photoreceptor (of certain k and l) is receiving light from a white light source such as natural daylight (Fig. 3), and that this daylight has a quantal irradiance spectrum described by the function $I(\lambda)$. Also imagine that the photoreceptor's visual pigment has an absorbance spectrum that allows it to absorb light in a wavelength range between λ_1 and λ_2. The total number of photons Q_T available to the photoreceptor from the daylight spectrum $I(\lambda)$ is then simply (Fig. 3),

$$Q_T = \int_{\lambda_1}^{\lambda_2} I(\lambda)\, d\lambda. \tag{4}$$

At each wavelength between λ_1 and λ_2, the absorptance spectrum [equation (3)] determines how many incident photons at that wavelength are absorbed by the photoreceptor. The total number of photons Q_A absorbed by the photoreceptor is then given by (Fig. 3):

$$Q_A = \int_{\lambda_1}^{\lambda_2} I(\lambda)(1 - e^{-kA(\lambda)l})\, d\lambda. \tag{5}$$

The fraction of photons $F_w(k, l)$ absorbed by the photoreceptor from the daylight source is simply the ratio Q_A/Q_T, that is

$$F_w(k, l) = \frac{\int_{\lambda_1}^{\lambda_2} I(\lambda)(1 - e^{-kA(\lambda)l})\, d\lambda}{\int_{\lambda_1}^{\lambda_2} I(\lambda)\, d\lambda}, \tag{6}$$

where the subscript w denotes "white" light absorption. For any combination of k and l, equation (6) describes the fraction of photons from a white light source (such as daylight) that can be absorbed by a photoreceptor with an absorbance peak wavelength λ_{max}. The calculation example shown in Fig. 3 is specifically for a photoreceptor with $k = 0.0067\ \mu m^{-1}$, $l = 400\ \mu m$ and $\lambda_{max} = 500$ nm, typical invertebrate values. At a given λ_{max}, equation (6) can be used to calculate absorption as a function of $\log_{10}(kl)$, thus generating a curve of the type shown in Fig. 2(B), but now instead applicable to white light absorption. This is precisely the aim of the present investigation.

Calculation parameters

Evaluation of equations (3, 5, 6) requires an expression (called a template) describing the absorbance spectrum of rhodopsin, $A(\lambda)$. Finding suitable templates has been a subject of considerable interest over the last 30 yr [for a good review see Stavenga *et al.* (1993)], but until recently, very few easily manageable expressions have been found. Among the simplest to arrive in recent times are the templates of Partridge and De Grip (1991) and Stavenga *et al.* (1993). The Stavenga, Smits and Hoenders (SSH) template (described in detail in Appendix B) is the better of the two for our purposes, and is shown at lower left in Fig. 3. This simple and elegant template fits the absorbance bands (α, β, γ) of known rhodopsin spectra extremely well. The α and β absorbance bands are the most important for vision, and the template we will use here is based on these two bands only. The precise location of the β-band relative to that of the α-band is still unresolved, and accordingly we will hold the position of the β-band constant and set its absorbance peak wavelength ($\lambda_{max,\beta}$) at 350 nm [following the example of Stavenga *et al.* (1993)]. Most known visual pigments in the animal kingdom have an α-band with peak absorbance wavelength ($\lambda_{max,\alpha}$) lying somewhere between 350 and 625 nm (Lythgoe, 1979). To test

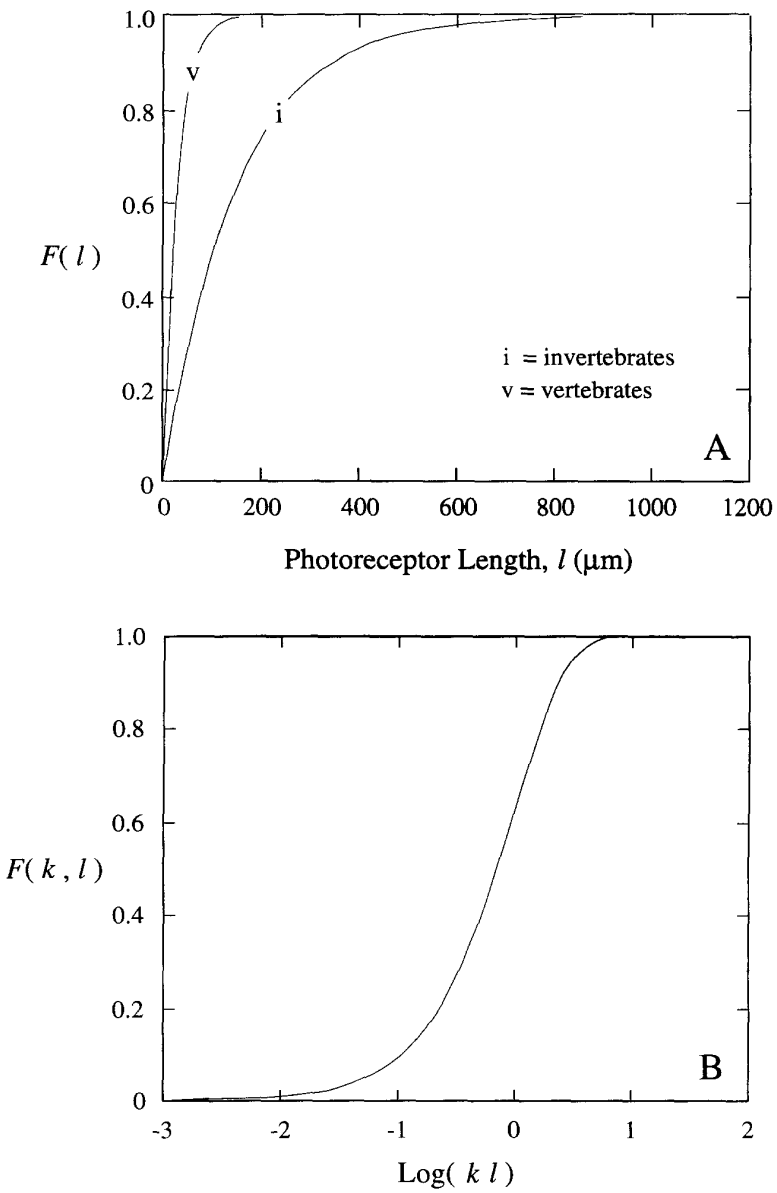

FIGURE 2. (A) The fraction of incident monochromatic light F which is absorbed by a photoreceptor of length l in vertebrates (v) and invertebrates (i). The curves result from equation (1). By virtue of having an absorption coefficient ca five times larger than that of invertebrates, vertebrates have absorption curves which rise much more steeply with l. (B) Equation (1) plotted as a function of $\log_{10}(kl)$ yields a single sigmoidal curve valid for both vertebrates and invertebrates.

the effect of wavelength on $F_w(k, l)$, we will evaluate equation (6), as a function of $\log_{10}(kl)$, at ten different values of $\lambda_{max,\alpha}$: 375, 400, 425, 450, 475, 500, 525, 550, 575 and 600 nm.

An expression for $F(l, \lambda)$ can be derived by substituting the SSH rhodopsin template [equations A(7)–A(11)] into equation (3). The spectrum $I(\lambda)$ of the "white" light source being viewed by the photoreceptor depends of course on the particular source in question. We will use four different sources:

1. The quantal irradiance of natural daylight [Fig. 4(A)];
2. The quantal irradiance of a patch of very blue sky [Fig. 4(B)];
3. The quantal reflection of soil irradiated by natural daylight [Fig. 4(C)]; and
4. The quantal reflection of green foliage irradiated by natural daylight [Fig. 4(D)].

It should be noted that most published natural spectra are energy spectra as opposed to quantal spectra. However, it is the number of photons available at each wavelength, rather than the relative energy of each wavelength, which modulates the strength of a visual signal. In order to convert an energy spectrum into a

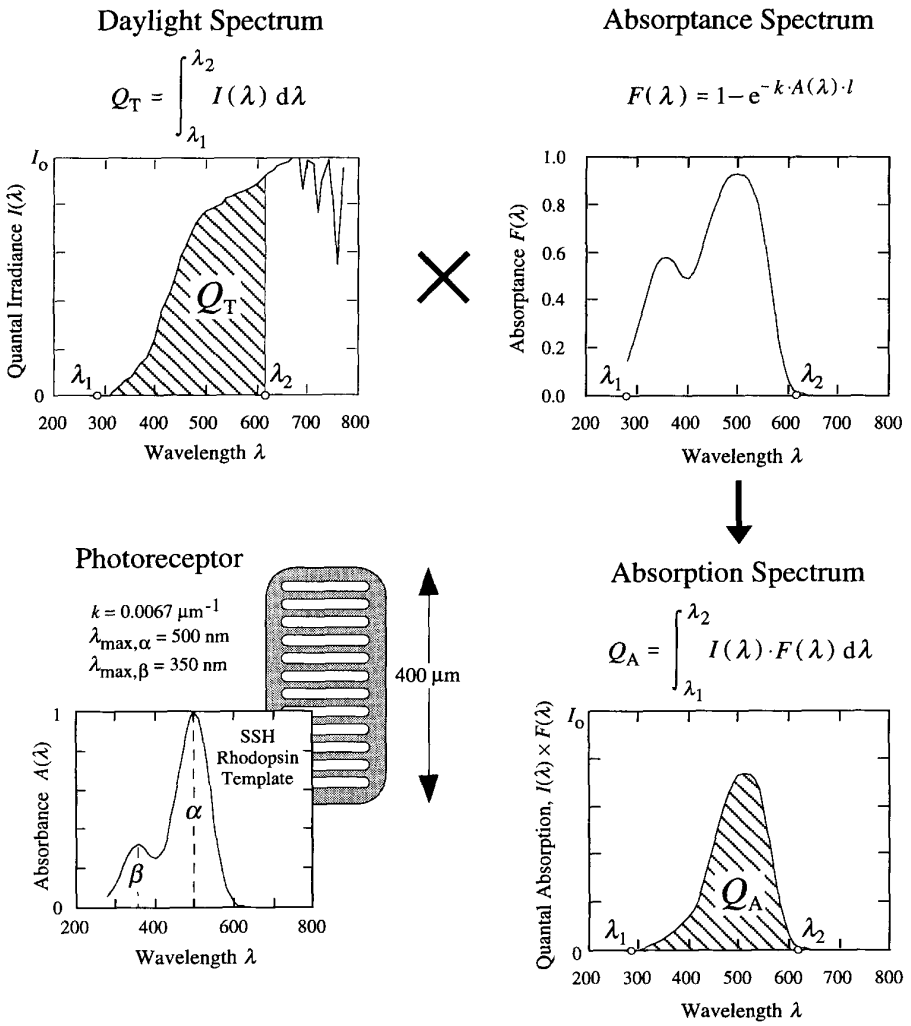

FIGURE 3. A schematic representation of the calculation embodied in equation (6). A photoreceptor (lower left) has a length of 400 μm, an absorption coefficient of 0.0067 μm^{-1} and a visual pigment whose absorption properties can be described by the SSH rhodopsin template $A(\lambda)$ (with α- and β-bands having peak absorbance wavelengths of 500 and 350 nm, respectively). This photoreceptor (which can absorb light in a wavelength range between λ_1 and λ_2) is irradiated by natural daylight (upper left) with a quantal spectrum described by the function $I(\lambda)$. Between λ_1 and λ_2 a total of Q_T photons of natural daylight are supplied to the photoreceptor. At each wavelength between λ_1 and λ_2, the photoreceptor absorbs only a fraction of that wavelength, according to equation (3). The resulting absorptance spectrum $F(\lambda)$ (upper right), when multiplied with the daylight spectrum $I(\lambda)$, determines the absorption spectrum $I(\lambda) \times F(\lambda)$ (lower right). The total number of photons absorbed by the photoreceptor is Q_A. The fraction of incident photons absorbed is Q_A/Q_T. The displayed SSH template was derived using equations (A7)–(A11). When $\lambda = 1.231\ \lambda_{max,\alpha}$, $A(\lambda) = 0.01$. This wavelength is equivalent to λ_2, the upper limit to the integration in equation (6).

quantal spectrum requires multiplication of the energy at each wavelength by that wavelength, with final normalization of the resulting curve [see Lythgoe (1979), p. 3]. The daylight and sky quantal spectra were obtained in this manner from published energy spectra (Fig. 4, caption).

Substituting $F(l, \lambda)$ and $I(\lambda)$ into equation (6) then allows us to evaluate $F_w(k, l)$. Unfortunately, the integral in equation (6) cannot be evaluated analytically, so instead we are forced to evaluate it numerically. The only remaining unknowns are the limiting wavelengths of the integration, λ_1 and λ_2. We shall set $\lambda_1 = 280$ nm. It is unlikely that light of lower than this wavelength has any meaning for vision in any animal. Even though many visual pigments are still capable of absorbing light of wavelength below 280 nm, the internal structures of the eye would almost certainly absorb such light long before it reaches the photoreceptors (Lythgoe, 1979). However, it should be noted that primates and squirrels possess yellow lens pigments which strongly absorb short wavelengths, and in these animals λ_1 is more realistically in the range 400–420 nm [review: Miller (1979)]. A convenient value for λ_2 is the wavelength for which the template drops to 1% of its maximum at its long

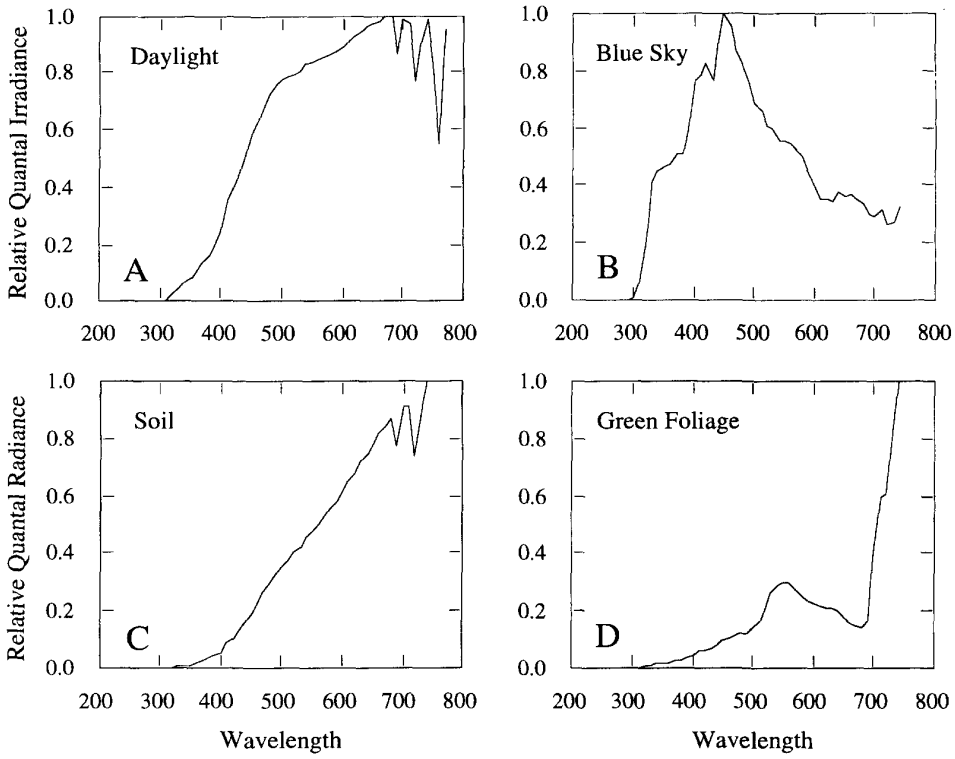

FIGURE 4. Natural quantal spectra. (A) Daylight at sea level, according to data compiled by Moon (1940). Moon's data, originally presented as an energy spectrum, was converted to a quantal spectrum via multiplication of the energy at each wavelength by that wavelength [see Lythgoe (1979), p. 3]. (B) Blue skylight, according to data compiled by Henderson and Hodgkiss (1963), converted to a quantal spectrum as in (A). The spectrum of blue skylight can be approximated by the spectrum of black-body radiator of colour temperature between 8000 K and (at least) 40 000 K, depending on the patch of blue sky in question (Henderson & Hodgkiss, 1963). The spectrum presented here is for a patch of very blue sky, with a correlated colour temperature of 34 000 K. (C) The spectrum of natural daylight reflected from soil. The reflectance spectrum of soil was obtained from Osorio and Bossomaier (1992), with extrapolation to include higher and lower wavelengths (Osorio, personal communication). The quantal spectrum of soil was obtained by multiplying the quantal spectrum of natural daylight from (A) with the reflectance spectrum of soil. (D) The spectrum of natural daylight reflected from green foliage. The unpublished reflectance spectrum of green foliage was kindly supplied by Dr Daniel Osorio of the University of Sussex. The quantal spectrum of green foliage was obtained as in (C).

wavelength end. Conveniently, for the SSH template, this wavelength is a constant multiple of $\lambda_{max,\alpha}$. In fact, $\lambda_2 = 1.231\lambda_{max,\alpha}$.

RESULTS

The absorption of light from natural radiant sources

Natural objects reflect some wavelengths of light more than others (Fig. 4; Lythgoe, 1979; Osorio & Bossomaier, 1992; Nagle & Osorio, 1993), thereby being perceived with different colours. This is partly due to the fact that natural daylight, which all natural objects reflect, is composed of longer wavelengths more than shorter [Fig. 4(A)]. In addition, the objects which reflect this daylight do not reflect each wavelength equally. Green foliage, as its name suggests, radiates significantly in the green part of the spectrum [Fig. 4(D)]. Nevertheless, even greater numbers of photons are emitted >700 nm, but due to our poor sensitivity in this part of the spectrum, we still perceive foliage as green (Osorio & Bossomaier, 1992).

We have calculated equation (6) for four different natural quantal spectra (Fig. 4):

1. The irradiance of natural daylight alone;
2. The irradiance of a patch of very blue sky;
3. Daylight reflected from soil; and
4. Daylight reflected from green foliage.

These spectra are assumed, for simplicity, to be unaltered by the passage of light through the optical media of the eye to the photoreceptors.

We will begin with a photoreceptor exposed to natural daylight [Fig. 4(A)]. Using this quantal irradiance spectrum $I(\lambda)$, equation (6) was evaluated as a function of $\log_{10}(kl)$ for varying rhodopsin peak absorbance wavelength ($\lambda_{max,\lambda}$) For comparison, the monochromatic curve [Fig. 2(B)], generated using equation (1), will also be calculated. The curves which result [Fig. 5(A)] allow

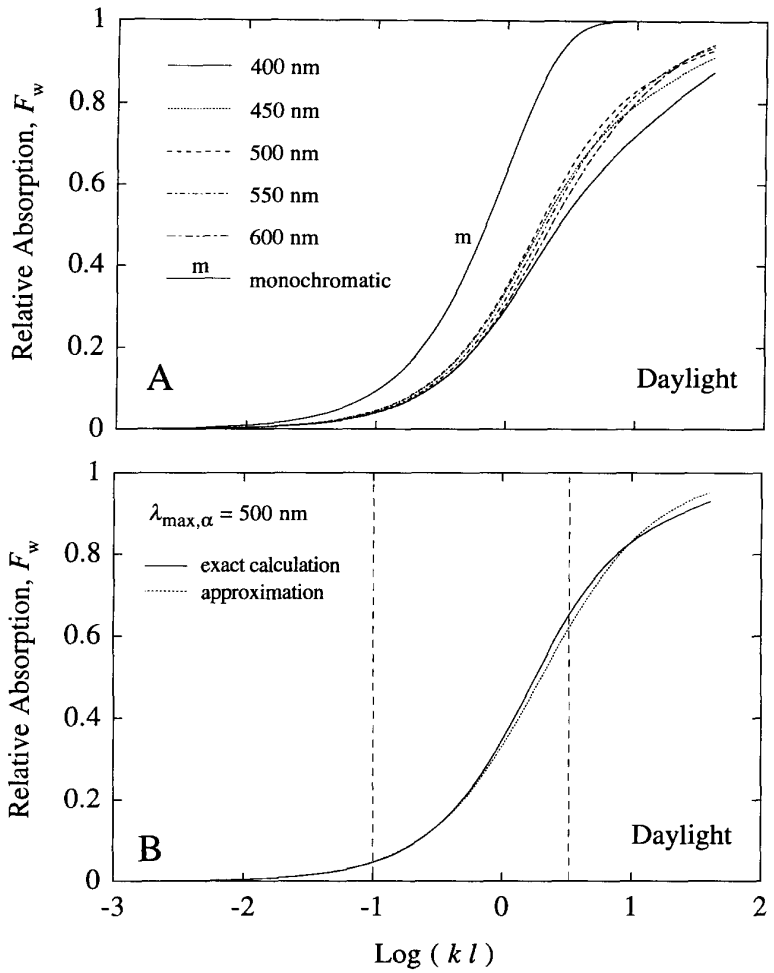

FIGURE 5. Absorption curves for natural daylight. (A) Absorption curves calculated according to equation (6) as a function of $\log_{10}(kl)$ for five different values of $\lambda_{max,\alpha}$: 400, 450, 500, 550 and 600 nm. As a comparison, the monochromatic absorption curve (*m*), calculated according to equation (1), is also shown. Notice that absorption efficiency is considerably lower for white light than for monochromatic light. (B) Absorption of daylight for $\lambda_{max,\alpha} = 500$ nm. Exact (——) and approximate (- - -) absorption (F_w) as a function of $\log_{10}(kl)$. The exact curve was calculated using equation (6). The approximate curve is a plot of equation (7) with $h = 0.30$ and $m = 1.00$. The relative difference (in %) between the exact and approximate curves always remains less than *ca* 10%, while the absolute difference (ΔF_w) is always less than *ca* 0.078. The range of the most commonly encountered $\log_{10}(kl)$ values is delineated by the vertical dashed lines (−1.0 to +0.5 log units).

determination of the fraction of natural daylight absorbed by photoreceptors (of given $\lambda_{max,\alpha}$) for any combination of l and k. For example, an insect photoreceptor of length 300 μm, absorption coefficient 0.0067 μm^{-1} and peak sensitivity to 500 nm green light has $\log_{10}(kl) = 0.3$. Inspection of the 500 nm curve in Fig. 5(A) reveals that the fraction of daylight which could be absorbed by this photoreceptor is *ca* 0.55. Longer photoreceptors and/or higher absorption coefficients lead to greater absorption of light.

The family of curves in Fig. 5(A) have two important properties:

1. They vary only moderately with $\lambda_{max,\alpha}$; and
2. They rise much more slowly with $\log_{10}(kl)$ (i.e. show much lower absorption efficiency) than the curve generated for monochromatic stimulation using equation (1).

The second of these properties is of particular interest: correction for white light stimulation produces shallower absorption curves, as recently predicted by Labhart and Nilsson (1995). This means that a vertebrate photoreceptor ($k = 0.035$ μm^{-1}) needs to be *ca* 600 μm long [i.e. $\log_{10}(kl) = 1.33$] to absorb 90% of incident daylight. In contrast, to absorb 90% of incident monochromatic light the photoreceptor need only be 65 μm long (equation (1)).

The numerical evaluation of equation (6) is time-consuming and cumbersome, and is unsuitable for easy calculations of white-light absorption. Fortunately, the information embodied in Fig. 5(A) can be simply and

TABLE 2. Best-fit parameters (m and h) for various light sources

	Daylight		Blue skylight		Green foliage		Soil	
$\lambda_{max,\alpha}$	m	h	m	h	m	h	m	h
375	0.97	0.47	0.99	0.27	0.97	0.49	0.96	0.64
400	0.98	0.43	1.01	0.22	0.97	0.45	0.97	0.57
425	1.00	0.36	1.02	0.19	0.97	0.46	0.97	0.50
450	1.00	0.31	1.03	0.18	0.97	0.49	0.98	0.44
475	1.00	0.29	1.03	0.21	0.99	0.43	1.00	0.39
500	1.00	0.30	1.03	0.25	1.00	0.33	1.00	0.37
525	1.00	0.32	1.03	0.29	1.02	0.25	1.00	0.37
550	1.00	0.34	1.02	0.36	1.02	0.22	1.00	0.37
575	1.00	0.35	1.01	0.42	1.01	0.28	1.00	0.37
600	1.00	0.36	1.01	0.47	0.97	0.51	1.00	0.36

m and h are the best-fit parameters for equation (7) which minimize the percentage relative difference between this approximation and the exact calculation of absorption [equation (6)], for a range of absorbance peak wavelengths ($\lambda_{max,\alpha}$).

accurately approximated. This approximation is so simple that calculating white-light absorption becomes a trivial affair. An equation which accurately approximates the calculated sigmoidal curve has the form

$$F_w = \frac{(kl)^m}{10^{hm} + (kl)^m}, \qquad (7)$$

where h is the value of $\log_{10}(kl)$ which yields $F_w = 0.5$, and m is the slope of the sigmoid in its central "linear" region. Via a combination of least-squares fitting and a final adjustment of parameters to minimize the relative difference (see below), the most ideal values of h and m were found for each $\lambda_{max,\alpha}$ (Table 2). For natural daylight and $\lambda_{max,\alpha} = 500$ nm, the best-fit values of h and m are 0.30 and 1.00, respectively. These values can be substituted into equation (7), and the resulting approximation plotted together with the exact calculation [Fig. 5(B)]. Even though the approximate and exact curves do not coincide completely, the percentage difference between the two curves is small over the entire range of $\log_{10}(kl)$, at no point does it exceed 10%. The *absolute* difference ΔF_w is never greater than *ca* 0.08, and is usually considerably smaller than this. It is possible to find values of h and m which reduce ΔF_w to almost nothing (such that the approximate and exact curves appear to almost overlap), but then the % difference climbs to as much as 50%, especially at values of $\log_{10}(kl)$ which are less than zero. However, within the range of $\log_{10}(kl)$ values normally encountered (−1.0 to +0.5: dashed lines in Fig. 5(B)], the % difference is <5% and ΔF_w is <0.03. In the unusual circumstance that a $\log_{10}(kl)$ value >0.5 is encountered, it is probably better to read off the appropriate value of F_w directly from the exact curve.

The absorption curves for the other three natural radiant sources (blue skylight, green foliage and soil) are superficially similar to those for daylight, being sigmoidal in shape (Fig. 6). The spectra of blue skylight and green foliage have peaks *ca* 450 and 550 nm, respectively. Photoreceptors having visual pigments with $\lambda_{max,\alpha}$ *ca* 550 nm demonstrate much greater absorption

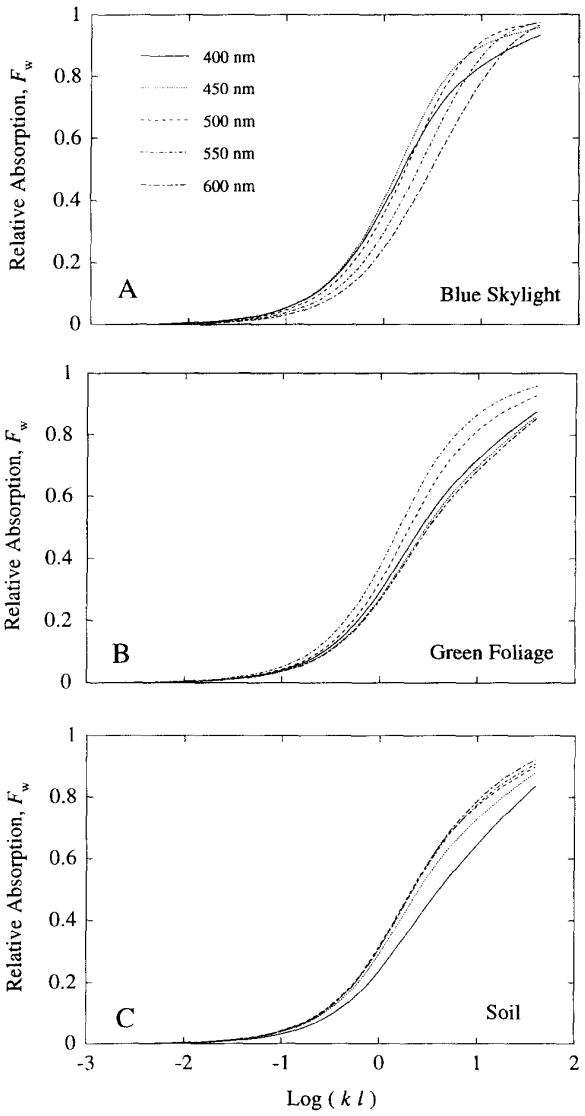

FIGURE 6. Absorption curves for blue skylight (A), daylight reflected from green foliage (B) and daylight reflected from soil (C). Curves were calculated using equation (6) as a function of $\log_{10}(kl)$ for five different values of $\lambda_{max,\alpha}$: 400, 450, 500, 550 and 600 nm.

efficiency of light reflected from green foliage than do photoreceptors with $\lambda_{max,\alpha}$ far from 550 nm [Fig. 6(B)]. The same can be said for photoreceptors absorbing blue skylight with $\lambda_{max,\alpha}$ *ca* 450 nm [Fig. 6(A)].

As with daylight, the exact curves of Fig. 6 can be approximated by equation (7). Ideal values for the parameters m and h as a function of $\lambda_{max,\alpha}$ can be found for skylight, foliage and soil in Table 2. Not all curves are as well approximated as others, with relative differences sometimes as high as 12%. Generally, however, the largest differences between the approximation and the exact calculation occur well outside the range of $\log_{10}(kl)$ normally encountered in nature: within the range, the differences are usually much smaller.

An average expression for the absorption of white light

Very often in calculations involving absorption (such as in optical sensitivity calculations: see below), the light spectrum viewed by the eye is unknown. The spectral sensitivity of the photoreceptors is also often unknown. In these cases it would be better to have some average expression for estimating white light absorption. Based on the four natural spectra and ten $\lambda_{max,\alpha}$ values presented in this study, we can average all values of m and h (Table 2), to arrive at a single average expression for the absorption of white light in photoreceptors. Doing this we obtain $m = 1.00 \pm 0.02$ and $h = 0.37 \pm 0.10$. Substitution of these values into equation (7) yields

$$F_w = \frac{kl}{2.3 + kl}, \quad (8)$$

which is a very simple expression indeed. This average expression for white light absorption provides an ideal replacement for equation (1).

DISCUSSION

Absorption of white light in photoreceptors

Photoreceptors do not absorb all wavelengths of light with equal efficiency. The wavelength most efficiently absorbed is the absorbance peak wavelength of the resident visual pigment (λ_{max}): all other wavelengths are absorbed with lower efficiency. This dependency of absorption efficiency on wavelength simply reflects the fact that the absorption coefficient k of the photoreceptor also depends on wavelength. The dependency is equivalent to that of the photopigment absorption in the limit of infinitesimal photoreceptor length. The absorption coefficient k is certainly not a constant independent of wavelength as frequently, and wrongly, assumed.

The dependence of k on wavelength has a profound effect on the absorption of white light in photoreceptors. Because of self-screening, white light is absorbed much less efficiently (equation (6)) than monochromatic light of wavelength λ_{max} [in which case absorption is described by equation (1)]. In other words, the absorption curve for white light is much shallower than that for monochromatic light (Fig. 5). The major implication of this difference is that in order to absorb a given fraction of the incident light, photoreceptors which normally absorb white light need to be longer than those that absorb near-monochromatic light. The dorsal eye foveal photoreceptors of the dragonfly *Sympetrum* are an interesting example of this (Labhart & Nilsson, 1995). Measuring 1.1 mm in length, they are the longest photoreceptors known. Being in the dorsal eye, they typically view blue skylight. According to equation (1), the photoreceptors need only be 687 μm long in order to absorb 99% of incident 420 nm light, the wavelength to which they are most sensitive. If, however, they would need to maximally absorb as many wavelengths of incident blue skylight as possible, they must be considerably longer. At a length of 1.1 mm, *Sympetrum*'s photoreceptors can absorb 83% of incident skylight, compared to just 75% had they been only 687 μm long [equation (7), with $h = 0.19$, $m = 1.02$, $k = 0.0067\ \mu m^{-1}$]. Presumably, *Sympetrum* strives to maintain as high a photon catch as possible in its dorsal eye in order to maximize visual performance (Labhart & Nilsson, 1995). It is not surprising to learn that it is precisely this part of the eye that is used to locate and pursue the small flies upon which it preys, a task that requires extremely fast, high-acuity vision.

By accounting for the wavelength dependence of k, we have derived a general average expression describing the absorption of white light in photoreceptors [equation (8)] which is valid for all animal photoreceptors containing a single rhodopsin-like photopigment, irrespective of length and absorption coefficient. Despite the complications of self-screening, equation (8) is extraordinarily simple. From the point of view of future absorption calculations, this is a great relief indeed: it is even easier to calculate absorption in white light than it is in monochromatic light! However, the expression may be inaccurate for photoreceptors where the rhodopsin template $A(\lambda)$ provides an insufficient spectral description, as in photoreceptors containing more than one rhodopsin type (e.g. the fused rhabdoms of arthropods having individual rhabdomeres with differing spectral sensitivity). This inaccuracy is probably small if the amount of one rhodopsin type is significantly greater than the amount of any other types present. Photoreceptors containing sensitizing pigments (as in fly rhabdomeres: Kirschfeld, Franceschini & Minke, 1977), may also reduce the accuracy of the expression. In all of these cases, however, an accurate evaluation of equation (6) is still possible if an appropriate template can be substituted.

Spectral windows in the natural world

Even though most visual stimuli are fairly white in spectrum, there are a number of notable exceptions, most of which occur in rather dark environments, such as in very deep water. Regardless of being salty or fresh, water is a natural spectral filter which is transparent to some wavelengths and rather absorbent of others. The range of wavelengths for which water is most transparent depends on the quality of the body of water in question [reviewed in Lythgoe (1979)]. Clear water of the open ocean is often transparent to light of peak wavelength *ca* 480 nm. The clear, deep fresh water of Lake Baikal in Siberia is transparent to light of much longer wavelength, between 550 and 600 nm (Bowmaker *et al.*, 1994). The deeper the water, the more narrowly tuned the remaining downwelling light becomes to these wavelengths (Tyler & Smith, 1970; McFarland, 1986; Goldsmith, 1990). For example, 600 m below the surface of Crater Lake in Oregon, the spectral range available to an animal is just 425 nm $\pm$ 15 nm (Tyler & Smith, 1970), which is very nearly monochromatic. Not surprisingly, the visual pigments of deep water eyes generally have λ_{max}s which are matched to these narrow wavelength ranges. This is true for both aquatic [Bridges (1972); but for an

TABLE 3. The sensitivity of eyes to white light, S_w

Species	Animal	Eye type	A (μm)	f (μm)	d (μm)	l (μm)	S_w (μm^2 sr)
H. sapiens	Man (diurnal)	Lens	3000	16700	3	30	0.133
Littorina	Marine snail	Lens	108	126	4	20	0.399
Phidippus	Diurnal spider	Lens	380	767	2	23	0.038
Vanadis	Marine worm	Lens	250	1000	6	80	0.262
Planaria	Flat worm	Pit	30	25	10	6	1.527
Bufo	Toad	Lens	5550	4714	2.5	54	2.410
Pecten	Scallop	Reflector	450	270	7.5	15	4.018
Onitis	Dung beetle	Compound	427	352	14	86	35.6
Ephestia	Nocturnal moth	Compound	340	170	8	110	38.4
Dinopis	Nocturnal spider	Lens	1325	771	20	55	100.8

Table based on data given in Land (1981, Table 5), except for *Littorina* (Seyer, 1992), *Bufo* (Mathis *et al.*, 1988) and *Oritis* (Warrant and McIntyre, 1990b). A is aperture, f is focal length, d and l are photoreceptor diameter and length. S_w was calculated using equation (10), with appropriate values for k (see text). The units of S_w (μm^2 sr) reflect the area of the pupil (μm^2) and the solid angle of visual space viewed by the photoreceptor (sr). The calculation neglects light loss due to reflection, scattering and absorption within the optical media of the eye.

exception see Bowmaker *et al.* (1994)] and marine (Loew & Lythgoe, 1978) deep water fish, as well as for crustaceans (Denys & Brown, 1982) and cephalopods (Matsui, Seidou, Horiuchi, Uchiyama & Kito, 1988). Within the narrow range of wavelengths experienced by these animals, the photoreceptor's absorption coefficient k would maintain an almost constant value. Because of this, the absorption curves of the photoreceptors would be described much more accurately by the original monochromatic absorption expression given in equation (1).

Another source of light that can be near-monochromatic is bioluminescence, which has a variety of functions including sexual communication, camouflage and prey attraction (Lythgoe, 1979). The emission spectrum of bioluminescence varies in both breadth and peak wavelength from animal to animal [reviewed by Lythgoe (1972)]. Some bioluminescence spectra have a half-width as narrow as 20 nm, which is nearly monochromatic. Other spectra are much "whiter", with half-widths of *ca* 100 nm. There are many examples of animals whose primary visual stimulus is bioluminescent in nature and whose spectral sensitivity is matched to the emission spectrum of the bioluminescence. Fireflies and harvestmen are good examples of terrestrial animals (Lall, Chapman, Trouth & Holloway, 1980a; Lall, Seliger, Biggley & Lloyd, 1980b; Meyer-Rochow & Liddle, 1988). Many marine animals also use bioluminescence (Herring, 1983). The more monochromatic the bioluminescence experienced by a photoreceptor, the more suitable is the original monochromatic absorption expression (equation (1)). However, "whiter" bioluminescence may not be white enough to be absorbed according to equation (8). In these cases, the actual absorption curve would probably lie somewhere between the curve calculated for monochromatic light [equation (1)] and that calculated for white light [equation (8)].

The optical sensitivity of eyes to white light

A much quoted and highly useful expression for determining the optical sensitivity S of an eye to an extended light source is the Land equation [Kirschfeld (1974), Land (1981): see Appendix C for a full derivation]:

$$S = \left(\frac{\pi}{4}\right)^2 A^2 \left(\frac{d}{f}\right)^2 (1 - e^{-kl}), \qquad (9)$$

where A is the diameter of the (circular) aperture through which light enters the eye, f is the focal length of the eye and d is the diameter of each photoreceptor. The term in brackets at the end is immediately recognizable as equation (1), with k and l having exactly the same meanings. The optical sensitivity is the ratio of the number of photons (at λ_{max}) absorbed by a photoreceptor to the number (at λ_{max}) emitted per steradian of solid angle from a unit area of an extended source. In other words, it is a measure of a photoreceptor's ability to capture photons when viewing an extended light source of given radiant intensity. This ability depends partly on the design of the eye, and partly on the design of the photoreceptor: photoreceptors absorb more photons when they view larger solid angles of visual space [proportional to $(d/f)^2$] through larger pupils [proportional to A^2]. S therefore has units of μm^2 steradian^{-1}.

Equation (9) has been much used to compare the optical sensitivity of eyes from different species, and has proved immensely useful. For the reasons we have discussed earlier, it unfortunately works best only for near-monochromatic stimulation. We are now in a position to modify the equation so that it becomes valid for white-light stimulation. This is simply achieved by replacing the last term in equation (9) with equation (8):

$$S_w = \left(\frac{\pi}{4}\right)^2 A^2 \left(\frac{d}{f}\right)^2 \left(\frac{kl}{2.3 + kl}\right). \qquad (10)$$

The subscript w denotes white light.

The optical sensitivity of the light-adapted human eye to white light can easily be determined using equation (10). The light-adapted human pupil has a diameter, A, of 3 mm. The cones have a diameter, d, and a length, l, of 5 and 30 μm respectively. The focal length f is 16.7 mm (Land, 1981). Using these values and $k = 0.028$ (Table 1) gives $S_w = 0.133$ μm^2 sr^{-1}. If we use equation (8), and

instead calculate the optical sensitivity of the human eye to monochromatic light, we obtain $S = 0.283\ \mu m^2\ sr^{-1}$, which is slightly more than twice S_w. Our expression for white light stimulation means that the published optical sensitivity values for animals normally experiencing white light are probably too high by a factor of about two. This does not really matter because one is rarely interested in absolute optical sensitivity values, but rather in the relative differences in optical sensitivity between different types of animals. These differences are in orders of magnitude (Land, 1981), so an alteration in optical sensitivity by a factor of two is hardly noticeable. Nevertheless, for interest, we have calculated S_w for a number of different animals normally experiencing white light. The results are given in Table 3, which is based partly on the classical table of Land (1981, Table 5), who used equation (9). As we have alluded, some animals have much greater optical sensitivity to white light than others: 4 log units of variation in S_w are evident in Table 3. Animals active in dim light typically have much greater optical sensitivity (but also much lower spatial resolution) than animals active in bright light (Land, 1981; Warrant & McIntyre, 1992).

Inspection of equation (10) reveals that the optical sensitivity of an eye depends strongly on its photoreceptor length. However, the *optimum* length of a photoreceptor also depends on the ambient light intensity. This latter relation will be treated in a forthcoming paper (Nilsson & Warrant, in preparation).

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APPENDIX A

The definitions and terminology of visual absorption

The terms and definitions which apply to visual absorption are a particularly messy area of science. Many terms have very similar names, but unfortunately very different meanings, and these confusions are sometimes encountered in the literature. The clearest published accounts are those of Knowles and Dartnall (1977, pp. 53–59) and Land (1981, p. 483), although each of these deals with the topic slightly differently. We will attempt here to summarize and synthesize these two accounts. All densities and coefficients refer to a single wavelength, in this case the absorbance peak wavelength of the visual pigment, λ_{max}.

Imagine that light of wavelength λ_{max} and intensity I_{inc} is incident on the distal end of a photoreceptor of length l and absorption coefficient k. Let the intensity of light absorbed during passage through the photoreceptor be I_{abs} and the (unabsorbed) intensity emitted from the proximal end of the photoreceptor be I_{trans}. The three intensities are simply related by

$$I_{abs} = I_{inc} - I_{trans}. \tag{A1}$$

The fraction of light (λ_{max}) absorbed, F, is

$$F = \frac{I_{abs}}{I_{inc}} = 1 - e^{-kl}, \tag{A2}$$

where we notice the inclusion of equation (1). The unitless fraction F is also called the *absorptance* and has been symbolized as J by Knowles and Dartnall (1977). Another unitless quantity, the *transmittance* (T) is simply $(1 - F)$. A(1) and A(2) can be used to define another important unitless parameter, the *optical density*, D (sometimes symbolized as A). D has been called many things in the literature including *absorbance*, *density*, *extinction* and *absorption*. It can be defined as follows:

$$D = \log_{10}\left[\frac{I_{inc}}{I_{trans}}\right] = -\log_{10}\left[1 - \frac{I_{abs}}{I_{inc}}\right] = -\log_{10}\left[e^{-kl}\right] = 0.4343kl. \tag{A3}$$

The optical density also has an alternative definition:

$$D = 0.4343\alpha cl = \varepsilon cl, \tag{A4}$$

where c is the *concentration* of visual pigment in the photoreceptor (mol l^{-1}) and α is the *extinction coefficient* (l mol^{-1} μm^{-1}). α is often replaced by the *molar decadic extinction coefficient* ε, which simply collects the constant in A(4): $\varepsilon = 0.4343\alpha$. Inspection of A(3) and A(4) also reveals that $k = 2.303\varepsilon c$. Finally, the optical density per unit length D_s (μm^{-1}), called the *specific optical density*, or *specific absorbance*, or sometimes the *unit absorbance*, is given via A(3):

$$D_s = \frac{D}{l} = 0.4343k. \tag{A5}$$

Measurements of D_s, which is a base-10 logarithmic absorption parameter, are very often quoted for photoreceptors. A(5) reveals that the absorption coefficient k (a natural logarithmic absorption parameter) is simply related to D_s via

$$k = 2.303D_s. \tag{A6}$$

APPENDIX B

The SSH rhodopsin template, A(λ)

The SSH template is an elegant and simple template derived from literature data for visual pigment spectra (Stavenga *et al.*, 1993). It assumes that these spectra consist of a summation of their absorbance bands (α, β, γ, etc.), whose shapes can be described by simple exponential functions. The resulting template fits the known absorbance spectra of photopigments astonishingly well, irrespective of the type of vitamin A upon which the pigment is based (i.e. A_1, A_2, A_3 or A_4). The exponential functions describing the α and β absorbance bands [$\alpha(\gamma)$ and $\beta(\gamma)$, respectively] are:

$$\alpha(\lambda) = A_\alpha \exp\left[-a_0 x_\alpha(\lambda)^2\left[1 + a_1 x_\alpha(\lambda) + \frac{3}{8}a_1^2 x_\alpha(\lambda)^2\right]\right], \tag{A7}$$

$$\beta(\lambda) = A_\beta \exp\left[-a_2 x_\beta(\lambda)^2\left[1 + a_3 x_\beta(\lambda) + \frac{3}{8}a_3^2 x_\beta(\lambda)^2\right]\right], \tag{A8}$$

where a_0, a_1, a_2, a_3, A_α and A_β are unitless constants, and

$$x_\alpha(\lambda) = \log\left(\frac{\lambda}{\lambda_{max,\alpha}}\right), \tag{A9}$$

$$x_\beta(\lambda) = \log\left(\frac{\lambda}{\lambda_{max,\beta}}\right), \tag{A10}$$

For a vitamin A_1 rhodopsin, $a_0 = 380$, $a_1 = 6.09$, $a_2 = 247$, $a_3 = 3.59$,

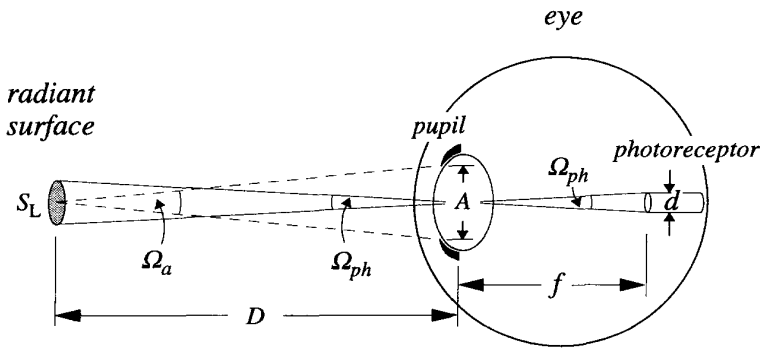

FIGURE 7. Parameters used in the derivation of equation (9). All parameters are defined and explained in Appendix C.

$A_\alpha = 1.00$ and $A_\beta = 0.29$. The wavelengths $\lambda_{\max,\alpha}$ and $\lambda_{\max,\beta}$ are the absorbance peak wavelengths of the α and β absorbance bands, respectively. A rhodopsin spectrum based predominantly on these two absorbance bands would be described by the template $A(\lambda)$:

$$A(\lambda) = \alpha(\lambda) + \beta(\lambda). \tag{A11}$$

A vitamin A1 rhodopsin template, composed of the α and β bands alone, is shown in Fig. 3 (using $\lambda_{\max,\alpha} = 500$ nm and $\lambda_{\max,\beta} = 350$ nm).

APPENDIX C

The optical sensitivity of eyes

A more extensive derivation of optical sensitivity S [equation (9)] can be found in Land (1981). All lengths are in microns. Solid angles have units of steradians (sr).

Imagine a photoreceptor of circular diameter d in the retina of an eye of focal length f and with a circular pupil of diameter A (Fig. 7). The solid angle of visual space viewed by the photoreceptor (Ω_{ph} in steradians) is given by its cross-sectional area divided by f^2 (from the definition of solid angle):

$$\Omega_{\text{ph}} = \frac{\pi}{4}\left(\frac{d}{f}\right)^2. \tag{A12}$$

Now imagine an extended luminous surface which emits L photons per second per m^2 of surface into each steradian of solid angle in space. This surface is located at a distance D from the pupil of the eye. The photoreceptor views a circular area S_{L} of the surface within the solid angle Ω_{ph} of its receptive field. This solid angle is also equivalent to S_{L} divided by D^2 (from the definition of solid angle):

$$\Omega_{\text{ph}} = \frac{S_{\text{L}}}{D^2}. \tag{A13}$$

The number of photons which enter the pupil and reach a single photoreceptor each second (E_{r}) is simply the product of the surface's intensity L, the area of surface viewed by a photoreceptor S_{L} and the solid angle subtended by the pupil at the surface (Ω_a). From the definition of solid angle, Ω_a is given by the area of the pupil divided by D^2. Thus,

$$E_{\text{r}} = LS_{\text{L}}\Omega_a = \frac{\pi}{4} L\left(\frac{S_{\text{L}}}{D^2}\right)A^2, \tag{A14}$$

and from equations (A12) and (A13),

$$E_r = LS_L\Omega_a = \frac{\pi}{4} L\Omega_{\text{ph}}A^2 = L\left(\frac{\pi}{4}\right)^2 A^2\left(\frac{d}{f}\right)^2. \tag{A15}$$

In the original formulation of equation (9), the photons which strike the photoreceptor are absorbed with a probability of $(1 - e^{-kl})$. The total number of photons absorbed by the photoreceptor, E_{abs}, is therefore given by

$$E_{\text{abs}} = L\left(\frac{\pi}{4}\right)^2 A^2\left(\frac{d}{f}\right)^2 (1 - e^{-kl}). \tag{A16}$$

Finally, the optical sensitivity S (in units of μm^2 sr^{-1}) is the number of photons absorbed per receptor, per unit luminance:

$$S = E_{\text{abs}}/L = \left(\frac{\pi}{4}\right)^2 A^2\left(\frac{d}{f}\right)^2 (1 - e^{-kl}).$$