1. Derivation of theory (detailed version)

(a) Discrimination criteria

Detection of a target against a background requires discrimination of signals from two visual channels (pixels) sampling light from the target and the background respectively (Fig. 1). We can think of these pixels as being retinal areas at least as large as a single photoreceptor, but potentially much larger. We assume that the channels being compared have identical properties. The channels may represent single photoreceptors or larger circular pools of receptors. A target channel detects a mean of N_T photons per integration time, and the corresponding mean count for a background channel is N_B. The photon counts are sums of real photons and intrinsic noise (false photons), and obey Poisson statistics [1,2], where the standard deviation is the square root of the mean. We follow Land [3] and assume a Gaussian distribution of photon samples (this approximation is good when at least one of the two signals to be compared exceeds 10 photon events). Discrimination between the signals in the two channels is possible when the difference is greater than or equal to a reliability constant R times the standard deviation of the difference (which is the square root of the sum of the two means; see Land [3]): $\left|N_T - N_B\right| \geq R\sqrt{N_T + N_B}$. The discrimination threshold is then given by:

$$\left|N_T - N_B\right| = R\sqrt{N_T + N_B} \,. \qquad (1)$$

Variables and constants are defined in Table 1 of the main paper. By developing expressions for the photon counts, we can now use the criterion to calculate maximum distance at which a target can be detected. This will have to be done separately for each type of detection task.

(b) Detection of a point source on a transparent target

This case is applicable for detection of single transparent planktonic organisms against the background space light. We assume a pair of visual channels in a camera type eye. A target channel is aimed at the bioluminescent point source, and its signal is compared to that of a channel aimed at the background next to the point source (Fig. 1). The target channel is assumed to receive all light that enters the eye from the bioluminescent point source. Because the source does not obscure the background, the target channel receives background space-light of the same intensity as that seen by the background channel. The target channel will receive an average of N_{bio} photons per integration time from the point source and N_{space} photons from the background space-light, whereas the background channel only receives N_{space} photons from the background. Each channel also generates an average of X_{ch} false photons per integration time. The total average signal in the target channel will thus be $N_T = N_{bio} + N_{space} + X_{ch}$ and in the background channel, $N_B = N_{space} + X_{ch}$. Inserting this into Eq. 1 gives:

$$\left|\left(N_{bio} + N_{space} + X_{ch}\right) - \left(N_{space} + X_{ch}\right)\right| = R\sqrt{\left(N_{bio} + N_{space} + X_{ch}\right) + \left(N_{space} + X_{ch}\right)}\,, \qquad (2)$$

which simplifies to

$$N_{bio} = R\sqrt{N_{bio} + 2N_{space} + 2X_{ch}} \,. \qquad (3)$$

Before we develop N_{bio} and N_{space}, we need to consider the angular size of the two channels. For maximum detection ability, the target channel should collect as much light as possible from the point source, and both channels should collect a minimum of background space-light. This requires that the angular size of the channels is matched to the resolution of the optical image in the eye. Assuming that aberrations are corrected well enough for diffraction-limited optics [4], the optimum visual angle of a channel is limited by diffraction. The main lobe of the diffraction pattern, the Airy disc, contains nearly all the light from a point source, and it spreads from the pupil over an angle of $2.44\lambda / nA$ radians [5], where λ is the wavelength of the stimulating light, n is the refractive index of water, and A is the diameter of the pupil (Table 1). We know that aquatic eyes typically have focal lengths of 2.55 lens radii (Matthiessen's ratio, M). Expressed in pupil diameters, the focal length, f, is $0.5MA$, and the angular diameter of the Airy disc becomes $2.44\lambda M / 2nf$ radians. If we multiply this by the focal length we obtain the actual size of the Airy disc on the retina, or $2.44\lambda M / 2n$. This means that if M is constant, the diffraction blur spot has a constant size on the retina irrespective of eye size. For a wavelength of 480 nm and M = 2.55 the Airy disc is 1.1 µm wide, and for M as high as 3, the Airy disc is still only 1.3 µm wide. But photoreceptor diameters are typically somewhat larger (d = 2-6 µm for most rods, cones and rhabdoms), which implies that realistic angular dimensions of the spatial channels should be given by actual receptor diameters rather than any theoretical optimum. We assume a Gaussian profile of the sensitivity across single receptors, where the angular half-width in visual space is d/f and the solid angle is $1.13(d/f)^2$, in contrast to the solid angle of $\pi/4(d/f)^2$ for a square angular profile [5].

Ultimately we are interested in the relationship between the pupil diameter A and the range r, and search for expressions relating these to N_{bio} and N_{space}. Following Warrant [6], optical geometry gives a photon flux density of $E/4\pi r^2$ for a point source, attenuation by water is given by $e^{-\alpha \cdot r}$ and the pupil area accepting the light is $\pi A^2/4$. The product of these factors multiplied by the efficiency q of the retina and the integration time Δt provides the desired expression of N_{bio}:

$$N_{bio} = \frac{EA^2}{16r^2} e^{-\alpha \cdot r} q\Delta t \,. \qquad (4)$$

The background space-light is an extended source, and the sensitivity [3] of a retinal channel is simply the product of the pupil area, $\pi\,(A/2)^2$, the solid angle in visual space of the channel, $1.13(d/f)^2$, and the efficiency q by which the eye detects photons. We arrive at N_{space} by multiplying the sensitivity by the radiance of the background space-light, I_{space}, and the integration time Δt:

$$N_{space} = 1.13\left(\frac{\pi}{4}\right)A^2\left(\frac{d}{f}\right)^2 q\Delta t \cdot I_{space} \,. \qquad (5)$$

We know from above that $f = \left(M \cdot A\right)/2$ and substituting this into Eq. 5 we obtain:

$$N_{space} = 1.13\left(\frac{\pi}{4}\right)A^2\left(\frac{2d}{MA}\right)^2 q\Delta t \cdot I_{space} = 3.55\left(\frac{d}{M}\right)^2 q\Delta t \cdot I_{space} \,. \qquad (6)$$

The dark noise per integration time is simply:

$$X_{ch} = X\Delta t \,. \tag{7}$$

We now want to combine Eqs. 4, 6 and 7 with Eq. 3. In order to solve for A, we square Eq. 3:

$$N_{bio}^2 = R^2\left(N_{bio} + 2N_{space} + 2X_{ch}\right), \tag{8}$$

or

$$N_{bio}^2 - R^2 N_{bio} = R^2\left(2N_{space} + 2X_{ch}\right), \tag{9}$$

which is a quadratic equation with the solution:

$$N_{bio} = \frac{R^2}{2} \pm \sqrt{\left(\frac{R^2}{2}\right)^2 + 2R^2\left(N_{space} + X_{ch}\right)} \,. \tag{10}$$

Only the positive root gives $N_{bio} > 0$, leading to:

$$N_{bio} = \frac{R^2}{2}\left(1 + \sqrt{1 + \frac{8\left(N_{space} + X_{ch}\right)}{R^2}}\right). \tag{11}$$

Now, re-arranging Eq. 4:

$$A = \sqrt{N_{bio}\frac{16r^2}{Eq\Delta t}e^{\alpha\cdot r}} \tag{12}$$

and combining with Eq. 11 gives:

$$A = \sqrt{\frac{R^2}{2}\left(1 + \sqrt{1 + \frac{8\left(N_{space} + X_{ch}\right)}{R^2}}\right)\frac{16r^2}{Eq\Delta t}e^{\alpha\cdot r}} \,, \tag{13}$$

where N_{space} and X_{ch} are given by Eqs. 6 and 7:

$$A = \sqrt{R^2\left(1 + \sqrt{1 + \frac{8\left(3.55\left(\frac{d}{M}\right)^2 q\Delta t \cdot I_{space} + X\Delta t\right)}{R^2}}\right)\frac{8r^2}{Eq\Delta t}e^{\alpha\cdot r}} \,, \tag{14}$$

which is the desired relation between A and r for detection of transparent point sources.

(c) Detection of a point-source on a black target

This case is applicable for detection of single small photophores on the body of a black opaque animal, or transparent bioluminescent plankton seen against the black body of an animal (such as with stimulated plankton bioluminescence). Here we thus assume that the target holding the bioluminescent point source is a black, rather than a transparent object (Fig. 1). For both channels, the target, in this case, interrupts the background space-light, and new light is scattered into the line of sight between the target and the observer. Even a black target will thus contribute light to a visual channel viewing it. The photon count contributed by light scattered into the line of sight, N_{black}, then replaces N_{space} in Eq. 3:

$$N_{bio} = R\sqrt{N_{bio} + 2N_{black} + 2X_{ch}}\,. \tag{15}$$

For an observer at constant depth in the sea, space-light enters the line of sight at the rate $1-e^{(\kappa-\alpha)r}$, where the diffuse attenuation coefficient κ depends on the viewing angle [7-9]. For a target at constant depth, the corresponding expression is $e^{\kappa r}-e^{\alpha r}$, but here we want to determine the space-light at the depth of the observer (from where the eye is performing the discrimination) and thus use the form $1-e^{(\kappa-\alpha)r}$ .The radiance seen in the direction of a black target then becomes $I_{space}\left(1-e^{(\kappa-\alpha)r}\right)$. To get an expression for N_{black} we substitute $I_{space}\left(1-e^{(\kappa-\alpha)r}\right)$ for I_{space} in Eq. 6:

$$N_{black} = 3.55\left(\frac{d}{M}\right)^2 q\Delta t \cdot I_{space}\left(1-e^{(\kappa-\alpha)r}\right). \tag{16}$$

We then repeat the derivation from the previous case and arrive at

$$A = \sqrt{R^2\left(1+\sqrt{1+\frac{8\left(3.55\left(\frac{d}{M}\right)^2 q\Delta t \cdot I_{space}\left(1-e^{(\kappa-\alpha)r}\right)+X\Delta t\right)}{R^2}}\right)\frac{8r^2}{Eq\Delta t}e^{\alpha\cdot r}}\,. \tag{17}$$

(d) Detection of an extended black target (silhouette) triggering bioluminescence

This case models the visibility of an animal silhouette. The animal body is assumed to be black, but may contain any number of bioluminescent point sources, either being the animal's own photophores, or transparent bioluminescent plankton triggered to emit light by the moving animal. We again assume an equal pair of visual channels, but now optimally sized to detect an extended object against the background space-light. To maximise the signal, the target channel fills the width of the object (Fig. 1), and both channels have square rather than Gaussian sensitivity profiles (all receptors in the circular pool have equal weight). We thus assume that the angular size of the visual channels (pixel) is dynamic, and suited to the object at all times. This detection strategy is chosen because it offers the best detectability with circular pixels (the actual properties of visual channels in pelagic animals is yet

unknown). The angle in visual space of such a channel is the target width T divided by its distance, T/r (radians), and with a square profile its solid angle is $(\pi/4)(T/r)^2$ (steradians). Each individual photoreceptor within the circular pool occupies a solid angle of $(\pi/4)(d/f)^2$ in visual space (see Table 1 for definition of variables). The number of photoreceptors forming a channel is then $(Tf/rd)^2$, and its diameter on the retina is Tf/r.

Even though the target itself is assumed to be black, it may contain bioluminescent point sources, but the background is just space light and no bioluminescence (Fig. 1). Modelling this way we are free to investigate both dark (E = 0) and luminous extended objects (E > 0). The signal of the target channel comes partly from target bioluminescence attenuated on its way to the eye, space-light having entered the line of sight between the target and the eye, and dark noise from the contributing photoreceptors: $N_T = N_{bio} + N_{black} + X_{ch}$, and the background channel sums background space-light and channel noise: $N_B = N_{space} + X_{ch}$.

The discrimination threshold (Eq. 1) now becomes

$$\left|(N_{bio} + N_{black} + X_{ch}) - (N_{space} + X_{ch})\right| = R\sqrt{N_{bio} + N_{black} + N_{space} + 2X_{ch}}\,, \tag{18}$$

which reduces to

$$\left|N_{bio} + N_{black} - N_{space}\right| = R\sqrt{N_{bio} + N_{black} + N_{space} + 2X_{ch}} \tag{19}$$

(we here keep the absolute value of the difference because either N_T or N_B can have the largest value, depending on the amount of bioluminescence). Note that N_{bio}, N_{black}, N_{space} and X_{ch} are in this case parameters for dynamic receptor pools, and are thus not identical to the same parameters in the point source cases.

We are now ready to work out expressions for N_{bio}, N_{black}, N_{space} and X_{ch}, which happens to be easier in the reverse order. The channel noise X_{ch} is derived as for the point source case, but here multiplied by the number of photoreceptors in the pool (see above):

$$X_{ch} = \left(\frac{Tf}{rd}\right)^2 X\Delta t\,. \tag{20}$$

With $f = MA/2$ this becomes

$$X_{ch} = \left(\frac{TMA}{2rd}\right)^2 X\Delta t\,. \tag{21}$$

The photon count from background space-light is similar to the point-source case (Eq. 5) but with T/r replacing d/f, and assuming a square rather than a Gaussian profile for the angular sensitivity, we thus replace 1.13 with $\pi/4$:

$$N_{space} = \left(\frac{\pi}{4}\right)^2 A^2\left(\frac{T}{r}\right)^2 q\Delta t \cdot I_{space} = 0.617\,A^2\left(\frac{T}{r}\right)^2 q\Delta t \cdot I_{space}. \tag{22}$$

The contribution of light entering the line of sight between the target and the eye, N_{black}, can be determined by replacing I_{space} of Eq. 22 with $I_{space}\left(1-e^{(\kappa-\alpha)r}\right)$ as in Eq. 16:

$$N_{black} = 0.617 A^2 \left(\frac{T}{r}\right)^2 q\Delta t \cdot I_{space}\left(1-e^{(\kappa-\alpha)r}\right). \tag{23}$$

The target may include bioluminescent point sources in the form of photophores on the target animal or planktonic organisms stimulated to emit light by the moving target. The total bioluminescent emission seen by the target pixel, N_{bio}, can be obtained by multiplying the expression for a single point source (eq. 4) with the total number, P, of point sources within the field of the target pixel:

$$N_{bio} = P\frac{EA^2}{16r^2}e^{-\alpha\cdot r}q\Delta t\,. \tag{24}$$

The number of point sources, P, seen by the target pixel requires specific expressions depending on the geometric distribution of photophores, or in the case of stimulated planktonic bioluminescence the expression depends on target motion direction. Different expressions for P are given in a separate section after the main derivations, and in Table 2.

We are now ready to substitute Eqs. 21-24 for X_{ch}, N_{space}, N_{black} and N_{bio} in Eq. 19 and solve for A. First, let $X_{ch} = A^2 k_{ch}$, $N_{space} = A^2 k_{space}$, $N_{black} = A^2 k_{black}$, and $N_{bio} = A^2 k_{bio}$, where

$$k_{ch} = \left(\frac{TM}{2rd}\right)^2 X\Delta t\,, \tag{25}$$

$$k_{space} = 0.617\left(\frac{T}{r}\right)^2 q\Delta t \cdot I_{space}\,, \tag{26}$$

$$k_{black} = 0.617\left(\frac{T}{r}\right)^2 q\Delta t \cdot I_{space}\left(1-e^{(\kappa-\alpha)r}\right), \tag{27}$$

$$k_{bio} = P\frac{EA^2}{16r^2}e^{-\alpha\cdot r}q\Delta t\,, \tag{28}$$

and make the substitutions in Eq. 19,

$$A^2\left|k_{bio}+k_{black}-k_{space}\right| = R\sqrt{A^2\left(k_{bio}+k_{black}+k_{space}+2k_{ch}\right)}. \tag{29}$$

Then solve for A,

$$A = \frac{R\sqrt{k_{bio}+k_{black}+k_{space}+2k_{ch}}}{\left|k_{bio}+k_{black}-k_{space}\right|}\,, \tag{30}$$

Expanding with Eqs. 25-28, and cleaning up yields:

$$A = \frac{R\sqrt{q\Delta t\left\{P\frac{EA^2}{16r^2}e^{-\alpha\cdot r} + 0.617\left(\frac{T}{r}\right)^2\left[I_{space}\left(2 - e^{(\kappa-\alpha)r}\right)\right]\right\} + 2\left(\frac{TM}{2rd}\right)^2 X\Delta t}}{\left|q\Delta t\left\{P\frac{EA^2}{16r^2}e^{-\alpha\cdot r} - 0.617\left(\frac{T}{r}\right)^2\left[I_{space}\left(e^{(\kappa-\alpha)r}\right)\right]\right\}\right|}, \quad (31)$$

which is the desired relation between A and r for detection of extended sources. For black objects without bioluminescence, the term $P\frac{EA^2}{16r^2}e^{-\alpha\cdot r}$ disappears both in the numerator and in the denominator.

(e) Detection of an extended transparent target triggering bioluminescence

Finally we consider the case where the extended target consists of triggered bioluminescence in the wake behind a moving object (Fig. 1d). This is similar to the previous case, except that the target does not block the background space-light. The signal of the target receptor then changes to $N_T = N_{bio} + N_{space} + X_{ch}$, whereas that of the background receptor remains $N_B = N_{space} + X_{ch}$. We can then substitute N_{space} for N_{black} in Eq. 19, which leads to a modification of Eq. 30:

$$A = \frac{R\sqrt{k_{bio} + 2k_{space} + 2k_{ch}}}{k_{bio}}. \quad (32)$$

This expands with Eqs. 25, 26 and 28 to

$$A = \frac{R\sqrt{q\Delta t\left[P\frac{EA^2}{16r^2}e^{-\alpha\cdot r} + 1.23\left(\frac{T}{r}\right)^2 I_{space}\right] + 0.5\left(\frac{TM}{rd}\right)^2 X\Delta t}}{P\frac{EA^2}{16r^2}e^{-\alpha\cdot r}q\Delta t}. \quad (33)$$

This expression provides the desired relation between A and r.

2. Modelling of aquatic radiance and absorption coefficients

We used values for two different water qualities, clear oceanic water [10], and coastal water [11]. For oceanic water we integrated the radiance measured at 200 m depth across a wavelength interval of 390-510 nm, multiplied with a spectral absorption curve for a 57 µm long vertebrate photoreceptor with a peak absorption coefficient of 0.035 μm^{-1} (or a 300 µm long invertebrate rhabdom with a peak absorption coefficient of 0.0067 μm^{-1}) [12,13]. The absorption peak was set to agree with the radiance peak. These calculations generated a 'visible radiance' at 200 m in oceanic water of $6.28\cdot10^{15}$ quanta m^{-2} s^{-1} sr^{-1} for down-welling light, $5.11\cdot10^{13}$ for horizontal radiance and $2.90\cdot10^{13}$ for upwelling radiance. For coastal water we used measurements from a Norwegian fiord [11] and simply calculated the difference at peak wavelength for 200 m depth and arrived at a down-welling radiance of $7.94\cdot10^{13}$ quanta m^{-2} s^{-1} sr^{-1} for down-welling radiance, and $6.46\cdot10^{11}$ quanta m^{-2} s^{-1} sr^{-1} for horizontal radiance and $3.67\cdot10^{11}$ quanta m^{-2} s^{-1} sr^{-1} for down-welling radiance. Compared to the Jerlov

classification [14], the oceanic water would most closely correspond to type I (open Pacific), and the coastal water to type III (North Sea coastal).

Attenuation with depth in oceanic water was 1.638 log units for every 100 m for down-welling radiance, 1.677 log units for horizontal radiance and 1.668 log units for up-welling radiance [10]. For coastal water we used a 100 m depth attenuation value of 2.29 log units for down-welling radiance [11], 2.34 log units for horizontal radiance, and 2.33 log units for up-welling radiance.

The beam and background attenuation coefficients (for an explanation see [9]) used for oceanic water were $\alpha = 0.0468$, and $\kappa = 0.0385$ for looking upwards, $\kappa = 0$ for horizontal viewing, $\kappa = -0.0385$ for looking downwards. The corresponding values assumed for coastal water were $\alpha = 0.3$, and $\kappa = 0.14$ for looking upwards, $\kappa = 0$ for horizontal viewing, $\kappa = -0.14$ for looking downwards.

It is important to note that the properties of coastal water can vary tremendously, and that the values used here should be taken as examples rather than typical values. Even in oceanic water, the upper 100-200 m is usually much less clear and much more variable than deeper layers. Our spectral intensity integral used to calculate I_{space} was performed for the narrow-band blue light at 200 m in oceanic water. For more shallow water, this integration will underestimate the available light intensity. Accurate modelling of vision in shallow water will require a specific spectral integral for each depth.

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