Report

Visual Reliability and Information Rate in the Retina of a Nocturnal Bee

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Summary

Nocturnal animals relying on vision typically have eyes that are optically and morphologically adapted for both increased sensitivity and greater information capacity in dim light [1]. Here, we investigate whether adaptations for increased sensitivity also are found in their photoreceptors by using closely related and fast-flying nocturnal and diurnal bees as model animals. The nocturnal bee *Megalopta genalis* is capable of foraging and homing by using visually discriminated landmarks at starlight intensities [2, 3]. *Megalopta*'s near relative, *Lasioglossum leucozonium*, performs these tasks only in bright sunshine. By recording intracellular responses to Gaussian white-noise stimuli [4, 5], we show that photoreceptors in *Megalopta* actually code less information at most light levels than those in *Lasioglossum*. However, as in several other nocturnal arthropods [6–13], *Megalopta*'s photoreceptors possess a much greater gain of transduction, indicating that nocturnal photoreceptors trade information capacity for sensitivity. By sacrificing photoreceptor signal-to-noise ratio and information capacity in dim light for an increased gain and, thus, an increased sensitivity, this strategy can benefit nocturnal insects that use neural summation to improve visual reliability at night.

Results and Discussion

Megalopta genalis is a fast-flying nocturnal sweat bee (family Halictidae) that relies on vision as one of its primary senses. This bee's well-known flight behavior [2, 14], well-documented activity periods [3], intensively studied optics [2, 15], eye anatomy [15], and neuroanatomy [16, 17] make it an appropriate model for studying how photoreceptors are adapted for vision in dim light.

We compared the performance of *Megalopta*'s photoreceptors in dim light to the performance of photoreceptors in the very closely related [18] diurnal sweat bee *Lasioglossum leucozonium*. Both species are fast flying [14] and rely to a large extent on vision for orientation and foraging. Earlier studies of photoreceptor physiology in nocturnal insects have been made either on ground-dwelling insects such as cockroaches [7, 8] and ants [9], which rely to a large extent on mechanosensory [19] or chemical [20] cues for orientation, or on slow-flying

crane flies [10, 11] and locusts [6, 21, 22], whose locomotory speed has very likely influenced receptor physiology [10, 11]. Here, we remove the confounding effects of a slow locomotory speed, widely divergent phylogenies, and the influence of other senses to study the role of darkness alone on photoreceptor performance.

We made electrophysiological recordings from single photoreceptor cells by using a light stimulus consisting of Gaussian-distributed white noise [4, 5]. From the responses we calculated the contrast gain function, $G(f)$, which reveals the amplification of the response per unit contrast and bandwidth and the photoreceptor signal-to-noise ratio (SNR). The SNR and the bandwidth define the amount of information that can be coded in a single receptor [5, 23–26].

To calibrate stimulus intensities in terms of the number of "effective photons" absorbed by the receptor per second [4, 11, 27], thus eliminating species-specific differences in the light-gathering capacities of the optics, we used a continuous dim-light stimulus to which the cell responded to individual photons (photon bumps). Such recordings also reveal a much larger photon bump amplitude in *Megalopta*'s photoreceptors (1.8 ± 0.4 mV) compared to those of *Lasioglossum* (0.9 ± 0.2 mV) (Figures 1A and 1B). This indicates that photoreceptor responses to single photons in the nocturnal *M. genalis* have a much higher signal amplification, a feature that has been noted previously in several other nocturnal arthropods [6–13].

Increased Contrast Gain in Nocturnal Photoreceptors

The contrast gain functions (Figure 2) reveal three interesting properties of nocturnal photoreceptors. First, *Megalopta*'s photoreceptors have a much narrower bandwidth than those of *Lasioglossum*. The corner frequencies of the contrast gain functions of *M. genalis* (the frequency in which the power has fallen to 50% of its maximal value [28]) change from 6.8 ± 3.1 Hz when dark-adapted at 140 effective photons per second to 21.4 ± 6.9 Hz when light adapted at 1.3×10^6 effective photons per second, whereas those of *L. leucozonium* change from 20.3 ± 6.4 Hz (dark-adapted at 180 effective photons per second) to 29.9 ± 9.2 Hz (light adapted at 1.5×10^6 effective photons per second). Second, the maximal contrast gain per unit bandwidth is similar or higher in the photoreceptors of *M. genalis* at all adapting intensities. This finding accords with previous studies on nocturnal photoreception in cockroaches in which amplification has been taken to the extreme, with the long photoreceptor axons showing spiking properties [7, 8]. Third, the maximal contrast gain per unit bandwidth does not change as markedly during light adaptation in *M. genalis* as in *L. leucozonium* (Figure 2). Our findings concur with previous photoreceptor studies of dark adaptation in diurnal flies, which reveal an increase in the gain of transduction and a slowing down of the response kinetics in order to sacrifice temporal resolution in favor of sensitivity and reliability at lower temporal frequencies in dim light [6, 25, 28–30].

Although increased transduction gain has the advantage of beneficially increasing the power of the visual signal, it also has the disadvantage of increasing the power of the visual noise. This includes photon shot noise (due to the stochastic nature

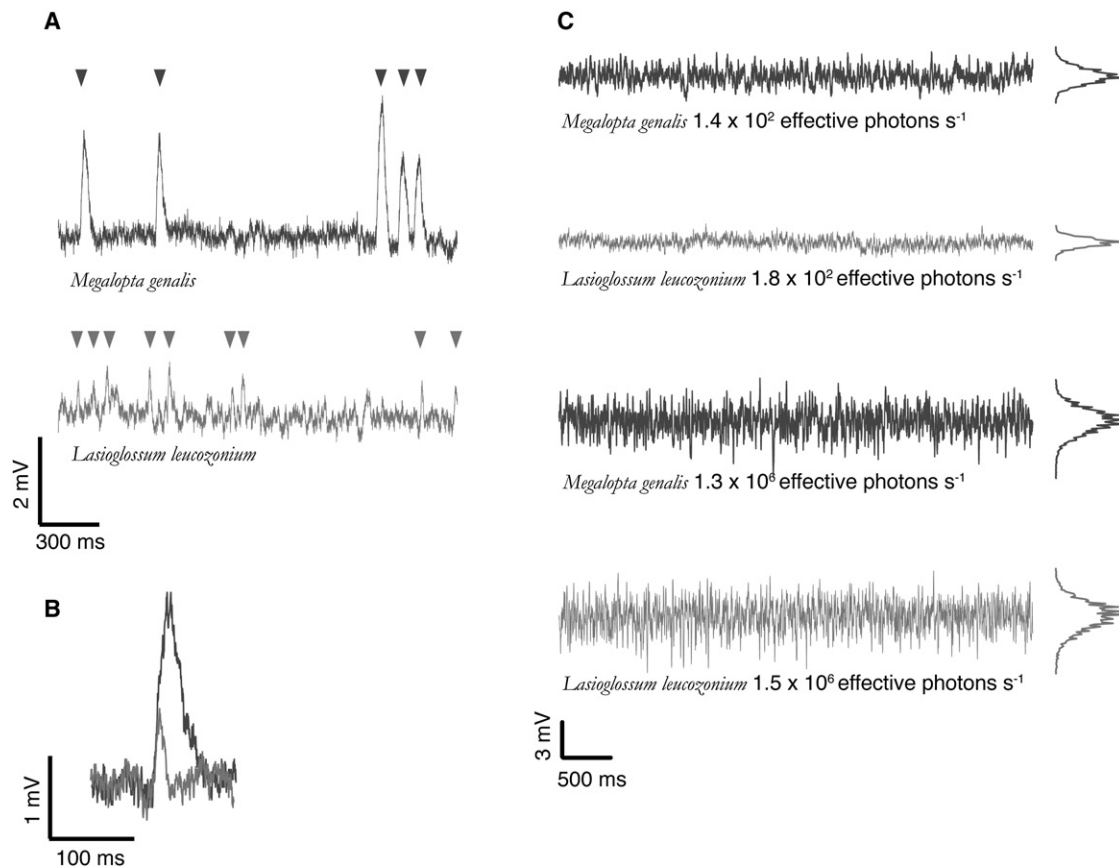*Correspondence: rikard.frederiksen@cob.lu.se

Figure 1. Photoreceptor Responses

(A) Shown are responses to single photons. Because the optics of the eyes in the two different species endow them with different sensitivities to light, we calibrated stimulus intensities at the level of the photoreceptors by recording their responses—called photon bumps (see arrowheads)—to single photons. All cells were calibrated in this way. The traces show five photon bumps recorded from a photoreceptor in *Megalopta genalis* (dark gray) and nine photon bumps recorded from a photoreceptor in *Lasioglossum leucozonium* (light gray).

(B) A detailed view of one bump of each species. Note that the bump amplitude is larger, and the bump time course much slower, in *M. genalis* (dark gray) than in *L. leucozonium* (light gray).

(C) Shown are response sequences and normalized density distributions to a white noise stimulus in *Megalopta genalis* (dark gray) and *Lasioglossum leucozonium* (light gray). Adapting intensities are indicated in effective photons per second in the panels.

of photon arrival), an inevitable constraint in nocturnal vision. The only possibility to increase the SNR is to increase the sample size, either by an increased optical sensitivity, by the pooling of signals from multiple visual channels, or by increasing the visual integration time [31, 32].

Because the hymenopteran phototransduction pathway is unknown, the extent of early biochemical signal amplification is still a matter of speculation. The large bumps (Figures 1A and 1B) and high contrast gain (Figure 2) found in *Megalopta*'s photoreceptors are likely due to the electrical properties of the photoreceptor membrane rather than to an increased early amplification in the transduction cascade: The amplification of voltage signals depends on the electrical properties of the nonphototransductive membrane, which are known to differ between species [10, 23, 33–35].

M. genalis has wide rhabdom diameters ($d = 8$ μm) [2], resulting in an increased optical sensitivity [15, 36, 37]. The large photoreceptive membranes of nocturnal insects are associated with high signaling costs. One proposed strategy to reduce this cost is to reduce the conductance of the nonphototransductive membrane [38]. The effect of this is a long membrane time constant [38] and a narrow response bandwidth. *Megalopta*'s narrow bandwidth (Figures 2 and 3)

indicates a low-pass filtering of the visual signal and a suppression of degrading high-frequency noise [11]. Thus, visual reliability in dim light is improved at low frequencies, a conclusion previously drawn for the photoreceptors of nocturnal crane flies [10, 11].

Information Rate of Nocturnal Insect Photoreceptors
Despite *M. genalis* being nocturnal, its photoreceptors do not show an intrinsically higher information rate in either bright or dim light compared to the diurnal *L. leucozonium* (Figures 3 and 4A). The information rate, R, of a photoreceptor depends on its SNR and bandwidth (see Equation 6 and Figure 3) [5, 26]. The lower information rate in the photoreceptors of *M. genalis* is due to a combination of both properties being lower in *Megalopta* than in *Lasioglossum* (Figure 3). This finding agrees well with theoretical predictions made by van Hateren [39]—neural filters tend to aquire low-pass characteristics in systems possessing a poor SNR, such as a photoreceptor in dim light.

If the recordings are instead calibrated to the external ambient intensity, we are then able to see the effects of the roughly 27 times more sensitive optics found in the compound eyes of *M. genalis* [15] (Figure 4B). It is now clear that with its more
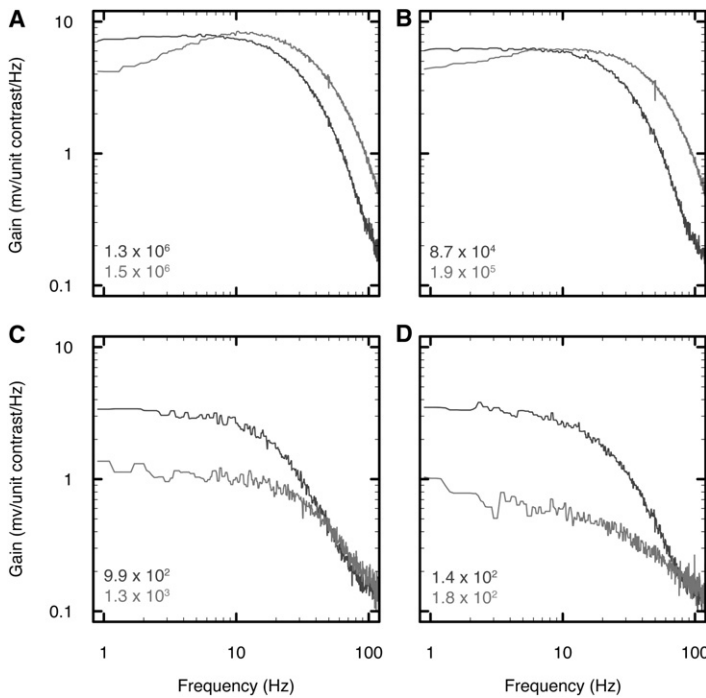
Figure 2. Average Contrast Gain as a Function of Frequency in *Megalopta genalis* and *Lasioglossum leucozonium* at Different Adapting Intensities, Indicated as Effective Photons per Second in the Panels

(A) *M. genalis* (dark gray, n = 8) 1.3×10^6 effective photons per second and *L. leucozonium* (light gray, n = 8)1.5×10^6 effective photons per second.

(B) *M. genalis* (dark gray, n = 8) 8.7×10^4 effective photons per second and *L. leucozonium* (light gray, n = 8) 1.9×10^5 effective photons per second.

(C) *M. genalis* (dark gray, n = 8) 9.9×10^2 effective photons per second and *L. leucozonium* (light gray, n = 8) 1.3×10^3 effective photons per second.

(D) *M. genalis* (dark gray, n = 8) 1.4×10^2 effective photons per second and *L. leucozonium* (light gray, n = 8) 1.8×10^2 effective photons per second. In light-adapted conditions (A and B), both species reach the same maximum contrast gain per unit bandwidth, although *L. leucozonium* has broader bandwidth and a higher corner frequency (frequency at which the power has fallen of to 50% of its maximum). In dark-adapted conditions (C and D), *M. genalis* has a much higher contrast gain per unit bandwidth.

sensitive optics, *M. genalis* can code more information in dim light. But we must stress that this effect is due to a higher optical sensitivity and is not due to an intrinsic photoreceptor adaptation.

Spatial Summation in the Lamina Ganglionaris?

At the photoreceptor level there are few cellular mechanisms that can deal with the deleterious effects of photon shot noise. The only way to reduce this type of noise is to increase the sample size. In *M. genalis* the higher optical sensitivity of the eyes is one adaptation that achieves this [15]. Another possibility is to pool responses from several photoreceptors [31, 32, 40]. By doing this, uncorrelated shot noise would be averaged out, and the signal enhanced, thus resulting in a dramatic

increase in SNR, albeit at the cost of spatial resolution [32]. The widely branching second-order cells (LMCs) of the lamina ganglionaris in *M. genalis* [16, 17] strongly suggest that these bees may be using summation to improve visual reliability in dim light [16, 17, 40]. Our data, which show increased photoreceptor contrast gain and noise, support this as the necessary solution to restore visual information.

Whether the LMCs of *M. genalis* perform spatial summation is yet to be confirmed experimentally. However, our previous anatomical [16, 17] and theoretical [2, 40] results, together with the results presented here, strongly suggest that it must occur in order to ensure visual reliability at the very dim intensities that this bee is active.
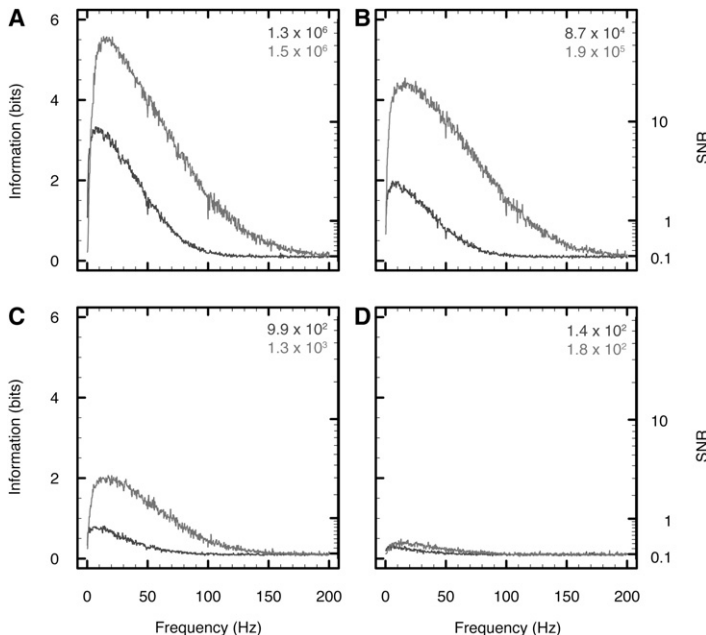
Figure 3. Average Information and SNR per Unit Bandwidth that Can Be Coded in the Photoreceptors of *Megalopta genalis* and *Lasioglossum leucozonium*

(A) *M. genalis* (dark gray, n = 8) 1.3×10^6 effective photons per second and *L. leucozonium* (light gray, n = 8) 1.5×10^6 effective photons per second.

(B) *M. genalis* (dark gray, n = 8) 8.7×10^4 effective photons per second and *L. leucozonium* (light gray, n = 8) 1.9×10^5 effective photons per second.

(C) *M. genalis* (dark gray, n = 8) 9.9×10^2 effective photons per second and *L. leucozonium* (light gray, n = 8) 1.3×10^3 effective photons per second.

(D) *M. genalis* (dark gray, n = 8) 1.4×10^2 effective photons per second and *L. leucozonium* (light gray, n = 8) 1.8×10^2 effective photons per second. The photoreceptors of *L. leucozonium* have a broader bandwidth and a higher maximum information (i.e., higher signal-to-noise ratio) than those of *M. genalis* at all adapting intensities, although when dark adapted (C and D) the amplitudes of both parameters are significantly decreased in both species. The information (left scale) was calculated as $\log_2(SNR + 1)$ [26], where the SNR is shown in $\log_{10}$ units on the right scale, which is thus stretched due to this base transform.
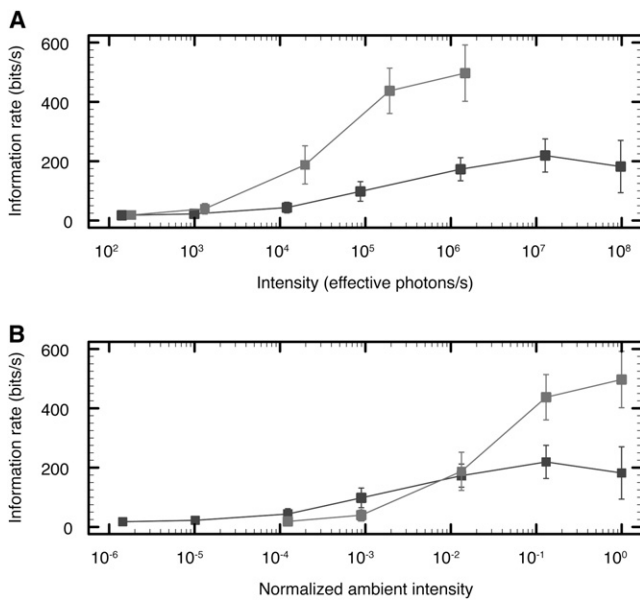
Figure 4. Average Information Rates in the Photoreceptors of *Megalopta genalis* and *Lasioglossum leucozonium*

(A) It is evident that at all intensities, calibrated as effective photons absorbed by the photoreceptor per second, *L. leucozonium* (light gray, n = 8) has a higher information rate than *M. genalis* (dark gray, n = 8). The error bars indicate the standard deviation of the average information rates. (B) When instead calibrated to external ambient intensities (10^0 being equivalent to the light intensity on an overcast day, or 180 cd/m^2), *M. genalis* (dark gray, n = 8) has a higher information rate in dim light than *L. leucozonium* (light gray, n = 8), although this is due to its 27 times more sensitive optics and is not due to an intrinsic adaptation present within the photoreceptors. The error bars represent the standard deviation of the average information rates.

were used for electrophysiological recordings from photoreceptor cells. *Lasioglossum leucozonium* was captured on the island of Öland and at Revingehed, Sweden. All bees were kept on a 12 hr light/12 hr dark cycle. All dissections were made during the light period and all recordings were made during the dark period. Although differences in naturally experienced temperatures and day lengths may have influenced our results [41], we consider them negligible for the following reasons. Both species have very well defined activity periods with well-defined light regimes—*Megalopta* only flies for about 20 to 30 min before sunrise and after sunset when it is extremely dark [3]. *Lasioglossum* is active only during the brightest hours on summer days and stops foraging as soon as there is an overcast sky (R.F. and E.J.W., unpublished data). Even though temperature has a major impact on photoreceptor physiology [41], nocturnal temperatures in the tropics differ little from those at midday during the southern Swedish summer.

Recording Procedures

In preparation for electrophysiology the bee was mounted in a plastic tube with its head protruding through a hole in one end. We fixed the head to the tube with wax. A small triangular hole was cut in the dorsal area of the eye for electrode insertion. We covered the hole with Vaseline to prevent dehydration. The indifferent electrode was inserted in the contralateral eye.

Light from a green LED (Roithner Lasertechnik, B5B-433-B525, 6600 mcd, peak transmission of 525 nm) was focused into a 5 mm wide light guide. The other end of the light guide was mounted in a cardan arm device that could be moved freely throughout the visual field of the animal. The distance between the stimulus light guide and the cornea was 50 mm (subtending an angle of 5.7° of visual space). We used quartz neutral density filters (Linos and Melles Griot) to control the offset intensity of the stimulus LED.

The recording protocol consisted of an initial 2 min of continuous constant-adapting light. After 2 min a 10 s sequence of pseudorandom Gaussian-distributed white noise [4] with a flat spectrum up to 250 Hz and a mean contrast (intensity ratio of standard deviation to mean) of 0.32 was superimposed on the adapting light. This was followed by a short period of adapting

light at the mean intensity level (1 s). The same sequence was presented 15 times. We repeated the experiment with two different pseudorandom sequences. Next, we increased the adapting intensity by about one log unit and repeated the above protocol. This procedure was continued until maximal output intensity was reached or the photoreceptor was saturated. After a successful recording sequence, the cell was allowed to dark adapt for 30 min.

The cell response was amplified with an NPI SEC-05LX amplifier. A Humbug (QuestScientific) was used to eliminate 50 Hz mains noise. Recordings were digitized at 1638.4 Hz with a National Instruments DAQCard-6036E and a laptop computer. Stimulus and acquisition software were custom written in LabVIEW 7.1 (National Instruments). The intensity output of the LED was continuously monitored by a photodiode placed at a right angle to the LED and illuminated by using a coverslip glass placed at 45° between the LED and the photodiode.

Data Analysis

All recordings we used for data analysis met the following criteria: (1) the resting potential of the cell was equal to or less than −60 mV, (2) we could record photon bumps when we presented a dim light stimulus, (3) the recording was stable during the entire recording program (a baseline drift of less than 5 mV was accepted), and (4) the cell was able to dark adapt again after the recording, signified by a return of the baseline to resting potential and the presence of bumps. Of 60 cells in 22 animals, 8 cells in *M. genalis* were used for data analysis. In *L. leucozonium*, of 21 cells from 10 animals, 8 cells met the criteria.

From each cell recording we calculated the transfer function, $H(f)$:

$$H(f) = \left\langle \frac{\langle V_{m,n}(f) \rangle_m}{C(f)_n} \right\rangle_n, \tag{1}$$

where $V_{m,n}$ is the photoreceptor voltage response to a contrast stimulus $C(f)$. Brackets $\langle \rangle_x$ indicate an ensemble average across the repetitions, x. The indices indicate repetitions of stimulus presentations: m indicates repetitions of the same stimulus sequence and n, the number of different sequences. From the transfer function we extracted the contrast gain function, $G(f)$:

$$G(f) = \text{mod}H(f). \tag{2}$$

We calculated the signal power, $S(f)$, by taking an ensemble average across the responses to the same pseudorandom contrast sequence, m, and an ensemble average across the power spectra of the averaged responses to different sequences, n:

$$S(f) = \left\langle |\langle V_{m,n}(f) \rangle_m|^2 \right\rangle_n. \tag{3}$$

The noise power spectrum was calculated by using the same responses as used in the calculation of the signal power. This was done by subtraction of the individual responses to a single contrast stimulus, n, from the calculated ensemble average across the responses to the same pseudorandom contrast sequence. The result is a number of sequences of noise. The ensemble average across the squared absolute values of these resulting sequences constitutes the noise power spectrum:

$$N(f) = \left\langle |V_{m,n}(f) - \langle V_{m,n}(f) \rangle_m|^2 \right\rangle_{m,n}. \tag{4}$$

The signal-to-noise ratio as a function of frequency, $SNR(f)$, was calculated as the ratio of the signal power to the noise power:

$$SNR(f) = \frac{S(f)}{N(f)}. \tag{5}$$

By using Shannon's formula [26], we calculated the information rate, R, of the photoreceptor:

$$R = \int_0^\infty (\log_2[SNR(f) + 1]) df. \tag{6}$$

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