

2005 Special issue

Quantifying information and performance for flash detection in the blowfly photoreceptor[☆]

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Abstract

Performance on specific tasks in an organism's everyday activities is essential to survival. In this paper, we extend information-theoretic investigation of neural systems to task specific information using a detailed biophysical model of the blowfly photoreceptor. We determine the optimal detection performance using ideal observer analysis and find that detection threshold increases with background light according to a power function. We show how Fisher information is related to the detection performance and compare Fisher information and mutual information in this task-specific context. Our detailed model of the blowfly photoreceptor enables us to detangle the components of phototransduction and analyze the sensitivity of detection performance with respect to biophysical parameters. The biophysical model of the blowfly photoreceptor provides a rich framework for investigation of neural systems.

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Keywords: Blowfly photoreceptor; Biophysical model; Ideal observer analysis; Flash detection; Fisher information; Sensitivity analysis

1. Introduction

Biological sensory organs operate under severe constraints of size, weight, structural composition, and energy resources. In many cases, the performance levels are near fundamental physical limits (Bialek, 1987). Nowhere is evolutionary pressure on information processing stronger than in visual systems, where speed and sensitivity can mean the difference between life and death. Consider fly photoreceptors, capable of responding to single photons, while successfully adapting to light up to $\sim 10^6$ effectively absorbed photons per second (Hardie & Raghuram, 2001). Relying on their visual input, flies can chase mates at turning velocities of more than 3000 s^{-1} with delay time of less than 30 ms (Borst & Haag, 2002).

The marvellous efficiency and effectiveness of neural systems motivate both scientific research to elucidate the underlying principles of biological information processing and engineering efforts to synthesize microsystems that

abstract their organization from biology (Abshire & Andreou, 2001a). It is crucial to quantify information processing in neural systems for both purposes. Developed in the 1940s (Shannon, 1948), information theory is the study of information transmission in communication systems. It has been successful in estimating the maximal information transmission rate of communication channels, *information channel capacity*, and in designing codes that take advantage of it. The usefulness of information theory in neural information processing was recognized early (Barlow, 1961; Atick, 1992; Steveninck & Laughlin, 1996). Information transmission rate has been measured in many neural systems (Borst & Theunissen, 1999), and information channel capacity has been estimated in fly photoreceptors (Steveninck & Laughlin, 1996). However, in most previous work, the system was treated as a black-box and the analysis was performed from input–output measurements. This approach provides little insight into the internal factors that limit information transmission. To address this issue, we decomposed the black-box of one extensively studied system, the blowfly photoreceptor, into its elementary biophysical components, and derived a communication model. Since information channel capacity is a fundamental property of a communication channel, we quantified the effect of individual components on information capacity in the blowfly photoreceptor (Abshire & Andreou, 2001b).

[☆] An abbreviated version of some portions of this article appeared in (Xu & Abshire, 2005a), published under the IEEE copyright.

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Although information capacity gives an upper bound on information transmission rate, it is unclear how it extrapolates to performance on specific tasks that are directly related to survival of the organism. In this work we extend the information-theoretic investigation of neural systems to task specific information using our blowfly photoreceptor model. We focus on the behaviorally relevant task of photoreceptors detecting changes in light intensity. Performance in such visual detection tasks is limited by noise intrinsic to the photon stream as well as noise contributed by transduction components within the photoreceptor. We model the response of the photoreceptor to incident flashes and determine the optimal detection performance using ideal observer analysis. We compute the detection threshold over a range of background light intensities and find that detection threshold increases with background light intensity according to a power function (Xu & Abshire, 2005b). We then derive Fisher information contained in the photoreceptor output, and show that Fisher information is directly related to the detection performance. In this sense it quantifies task specific information. We compare Fisher information and mutual information and show that Fisher information is a more relevant quantity in the context of this specific task.

Phototransduction in the blowfly photoreceptor consists of multiple stages comprising many biophysical and biochemical reactions. Many physical parameters are involved, and they interact with each other. We analyze the sensitivity of the detection performance with respect to those parameters. Examination of the blowfly photoreceptor model confirms the results of the sensitivity analysis and illustrates the roles that the parameters play in the detection task.

The remainder of the paper is organized as follows: first, we briefly describe our blowfly photoreceptor model; then, we compute the information capacity using the model; next, we analyze flash detection using ideal observer analysis; then, we relate Fisher information to optimal detection performance and compare Fisher information with mutual information; next, we describe the sensitivity analysis of detection performance; and finally we summarize our work.

2. Photoreceptor model

Vision in the blowfly begins with two compound eyes that cover most of the head. Each of the two compound eyes is composed of a hexagonal array of ommatidia.

Each ommatidium contains eight photoreceptors which receive light through a facet lens and respond in graded fashion to the incident light. Each photoreceptor has an associated waveguide, or rhabdomere, which consists of thousands of microvilli contiguous with the membrane of the photoreceptor. The rhabdomeres of photoreceptors R1–R6 form an asymmetric ring in the periphery of the ommatidium, while the rhabdomeres of photoreceptors R7 and R8 lie end to end in the center. Electrical signals from the non-spiking photoreceptor cells R1–R6 project to the large monopolar cells (LMCs) in the lamina, while R7 and R8 project to cells in the medulla (Roberts & Bush, 1981). In this investigation, we focus on photoreceptors R1–R6, which play the major role in optical sensing.

The photoreceptors communicate information about visual stimuli to LMCs through a series of signal transformations. Behaviorally relevant visual input is received as incident light on the fly's eyes. Photons are guided through the optics of the compound eyes, attenuated by an intracellular pupil mechanism, and absorbed by the photosensitive pigment, rhodopsin, in the rhabdomere. The activated pigment triggers a cascade of biochemical reactions that open light-gated ion channels in the membrane. The open channels provide a membrane conductance that allows an ionic current to flow, changing the membrane voltage. The voltage changes propagate down a short axon to the synaptic terminal in the lamina. The synaptic terminal voltage is the output of the system. Each of these transformations is associated with changes in the signal itself and the inevitable introduction of noise. Sources of noise include photon shot noise, thermal activation of rhodopsin, stochastic channel transitions, and membrane thermal noise.

We model these transformations which comprise phototransduction in the blowfly photoreceptor as a cascade of signal transformations and noise sources as shown in Fig. 1. While the photoreceptors exhibit nonlinearity at very low light levels or for large signals, their linear properties are well documented (Juusola, Kouvalainen, Järvilehto, & Weckström, 1994). We linearize these nonlinear transformations about an operating point, given by the average light intensity, and consider them as linear systems. Such analysis is expected to be accurate only when the operating point remains fixed, i.e. for small signals about a background intensity, a reasonable assumption for many visual tasks. We assume that each noise source contributes independent, additive noise at the location where it appears in Fig. 1.

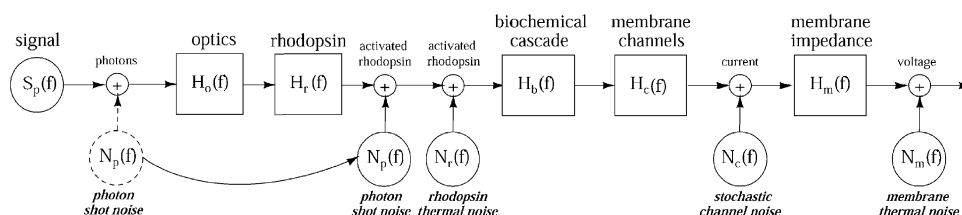


Fig. 1. Communication channel model of the blowfly photoreceptor.

Table 1
Biophysical parameters in the blowfly photoreceptor model

Description	Value(s)
Optical transmission and absorption	$C_o(I)$, η fit from data
Rhodopsin thermal isomerization rate	$\lambda_r = 10^{-11}$ events/rhodopsin/s
Biochemical cascade parameters	$h_b(I)$, $n_b(I)$, $\tau_b(I)$ fit from data
Parameters for voltage-activated K channels	$E_K = -85$ mV; $\gamma_K = 20$ pS; $N_K = 10^4$; $g_n(V)$, $L_n(V)$, $g_K(V)$ fit from data
Parameters for light-gated channels	$\tau_L = 1.8$ ms; $E_L = 10$ mV; $\gamma_L = 17$ pS; $g_L(I)$, N_L fit from data
Parameters for leakage channels	g_{leak} fit from data
Photoreceptor membrane parameters	$R = 1.0$ Ω m; $C_m = 1$ μ F/cm ² ; $C_i = 2.2$ pF; $R_i = 100$ M Ω ; $r_a = 2$ μ m; $l_a = 35$ μ m; $R_g = 25$ M Ω ; $R_b = 2$ M Ω ; $r_b = 2.5$ μ m; $l_b = 125$ μ m; SA = 40 μ m; $V_m(I)$ fit from data

Photon shot noise arises in the original photon stream, as indicated by the dashed noise source; however, it remains a Poisson source until the photons are absorbed. Thus it appears in the model as an additive noise at the location indicated by the arrow and solid noise source. The magnitude transfer functions and noise components of this model were described in (Abshire & Andreou, 2001b). The noise power at stage n is given by:

$$N_n(f) = \sum_{j=1}^m \prod_{i=k_j}^n |H_i(f)|^2 N_j(f) \quad (1)$$

where $N_j(f)$ is the power spectrum of independent noise source j entering at stage k_j , and $H_i(f)$ is the transfer function of stage i . Parameters of the model were estimated using experimental data as described in (Abshire & Andreou, 2001b) and are listed in Table 1 for reference. The extension of the model into the time domain was described in (Xu & Abshire, 2005b). The entire model allows us to compute the response of the system to stimuli in the linear operating range. We briefly introduce the noise sources and transfer functions here for use in later sections.

2.1. Photons: $N_p(f)$

The power spectral density of the photon noise, in units of (photons per s)²/Hz, is given by

$$N_p(f) = 2I \quad (2)$$

where I is the average photon arrival rate, and the factor of 2 is introduced because the spectrum is single-ended.

2.2. Optics: $H_o(f)$

The fly's eyes possess an intracellular pupil mechanism for gain control at high light intensities. We model the optical transfer function of the pupil as a transmission coefficient C_o that takes a value between 0 and 1 and depends on the background light intensity I :

$$H_o^2(f) = C_o^2(I) \quad (3)$$

2.3. Rhodopsin: $H_r(f)$ and $N_r(f)$

The transformation from photons to activated rhodopsin molecules is modelled by the transfer function $H_r(f)$

and the noise caused by thermal isomerization is modelled by $N_r(f)$:

$$H_r^2(f) = \eta^2 \quad (4)$$

$$N_r(f) = 2\lambda_r \quad (5)$$

where η is the absorption quantum efficiency and λ_r is the thermal isomerization rate. The effective photon shot noise, taking into account pupillary absorption and rhodopsin quantum efficiency, is given by:

$$N_p(f) = 2I\eta C_o(I) \quad (6)$$

2.4. Biochemical cascade: $H_b(f)$ and $N_b(f)$

Each activation of a rhodopsin molecule triggers a cascade of biochemical reactions, which cause a 'bump' response in the membrane conductance. The bump can be described by a gamma function (Wong, 1980):

$$h(t) = \frac{h_b}{n_b! \tau_b} \left(\frac{t}{\tau_b} \right)^{n_b} \exp\left(-\frac{t}{\tau_b} \right) \quad (7)$$

where h_b is the gain parameter, n_b is the shape parameter, and τ_b is the time parameter. The bump can be considered as the impulse response of the biochemical cascade to each activated rhodopsin. The transfer function is given by

$$H_b^2(f) = \frac{h_b^2}{[1 + (2\pi f \tau_b)^2]^{n_b+1}} \quad (8)$$

We do not model any noise sources contributed by the biochemical cascade, i.e. $N_b(f) = 0$.

2.5. Stochastic channels: $H_c(f)$ and $N_c(f)$

Membrane channels allow current to pass through the membrane and transform the conductance change into membrane current. Thus we have

$$H_c^2(f) = (V_m - E_L)^2 \quad (9)$$

where V_m is the membrane voltage, and E_L is the reversal potential of light-gated channels. The stochastic transition between states of a channel causes fluctuation in the number of open channels. This introduces noise in the membrane

current from all channel populations, modeled by

$$N_c(f) = \frac{4N_{ch}\gamma_{ch}^2(V_m - E_{ch})^2 n_\infty(1 - n_\infty)\tau_{ch}}{1 + (2\pi\tau_{ch}f)^2} \quad (10)$$

for channel 'ch' with time constant τ_{ch} , open probability n_∞ , single channel conductance γ_{ch} and a total population of N_{ch} independent channels.

2.6. Membrane impedance: $H_m(f)$ and $N_m(f)$

Membrane impedance is modeled as a cable with axial resistance and radial impedance contributed by light-gated channels, leakage channels, weakly active potassium channels (Koch, 1984), and membrane capacitance. Membrane current generated by the light gated channels propagates along the membrane to the synaptic terminal and is transformed into synaptic voltage. The transfer function is given by the transfer impedance Z_{tr} and the membrane thermal noise is given by output impedance Z_{out} :

$$H_m^2(f) = |Z_{tr}|^2 \quad (11)$$

$$N_m(f) = 4kT\text{Re}\{Z_{out}(f)\} \quad (12)$$

The axoplasm impedance z_a and membrane impedance z_m of a unit length compartment are given by

$$z_a = \frac{R}{\pi r^2} \quad (13)$$

$$z_m = \frac{(1 + 2\pi f L_n g_n j)/SA}{g_n + g_m - g_n C_m L_n (2\pi f)^2 + 2\pi f (C_m + L_n g_n g_m) j} \quad (14)$$

$$g_m = g_L + g_{leak} + g_K \quad (15)$$

The cell is represented by three lumped-parameter compartments, with two segments for the cell body and a third for the axon (Hateren, 1986). Z_{tr} and Z_{out} are complex functions of z_m , z_a , l_a , l_b , and load resistance. The load resistance depends on z_m , z_a , l_a , l_b , synaptic resistance R_t and capacitance C_t , gap junction resistance R_g , and resistance between lamina and receptor layer R_b .

3. Information and channel capacity

The biophysical model of phototransduction of Fig. 1 can be viewed as an additive Gaussian communication channel. Under an average power constraint $E[X^2] \leq P$, the information capacity of such a channel is $C = \max_{P(x): E[X^2] \leq P} I(X, Y)$, where $I(X, Y) = E_{P(x,y)}[\log_2(P(X, Y)/P(X)P(Y))]$ is the mutual information between two random variables (Shannon, 1948). We compute input-referred noise using the transfer functions and noise sources described above. We then use the waterfilling procedure (Cover & Thomas, 1991) to compute the information capacity of the blowfly photoreceptor.

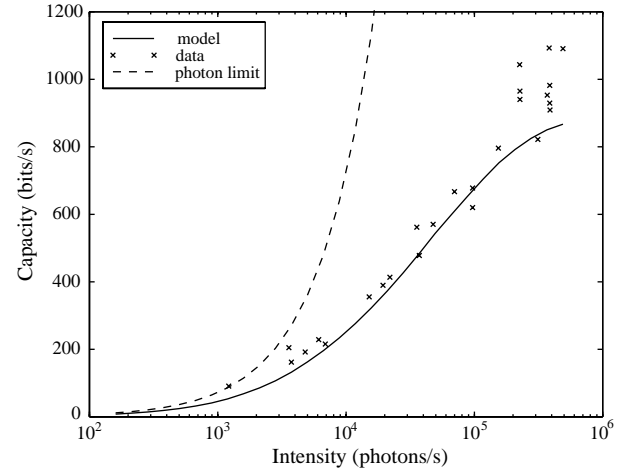


Fig. 2. Information capacity computed from our model and estimated from experimental data.

This computation was performed over a range of physiologically relevant light intensities, and the capacity is plotted as a function of incident light intensity in Fig. 2. The estimates of information capacity computed directly from physiological measurements of transfer characteristics and noise are also shown as 'x's (Steveninck & Laughlin, 1996). The dashed line shows the capacity for the case where the photoreceptor does not contribute noise, i.e., for photon shot noise only. The capacity predicted by the model corresponds closely to the capacity computed from the physiological measurements, particularly for low intensity. At high intensity, the capacity predicted by the model saturates. Biological photoreceptors do not have infinite dynamic range, so the response—and also the capacity—must eventually saturate at high intensities. We anticipate that the experimental data would confirm this trend if estimates were available at higher intensities. Furthermore, the capacity estimates have been obtained from data of five different photoreceptor cells, so the experimental estimates are scattered. Parameters of the model have been estimated independently from data reported from many different experiments and different animals (Abshire & Andreou, 2001b). As such, the model does not represent a specific photoreceptor cell whose capacity is represented by the data, so it is not surprising that it does not match the empirical estimates exactly. As model parameters vary, the capacity predicted by the model will also vary. For the data shown in Fig. 2, this variation causes the capacity predicted by the model to saturate at lower intensity than the experimental estimates. Below we investigate the sensitivity of detection performance on parameters of the model.

4. Flash detection

The channel capacity shown in Fig. 2 is an upper bound on the rate of information transmission, assuming that the signal is limited only in average power and the noise is normally distributed. It offers limited insight into how

information is actually transmitted and used in specific tasks involved in the organism's everyday activity. In order to further investigate the role of information and signal integrity in specific tasks, we study performance in the context of a simple but important visual detection task, discrimination of the presence or absence of brief flashes of light. We assume that flashes are detected under a forced choice between two alternatives, presence and absence. We apply ideal observer analysis to quantify the optimal detection performance.

4.1. Mean system response to a flash stimulus

Phototransduction is a stochastic process because of the randomness of photon arrival and the noise introduced by the physical components of the system. Responses to the same flash stimulus are different for each trial. In order to perform ideal observer analysis, we compute the mean system response to the flash stimulus. The photon arrival rate defines the background light intensity \mathcal{A} which determines the operating point of the system. For a flash of duration T and incremental intensity λ , the average number of photons comprising the flash is given by $n = \lambda T$. If we assume that the system responds linearly to each photon, for n arrivals at times t_i , $i = 1, \dots, n$, the system response will be:

$$f(t) = \sum_{i=1}^n B(t - t_i) \quad (16)$$

where $B(t)$ is the single photon response to a photon arrival at time 0. $B(t)$ varies according to the operating point of the system determined by the background light level (Wong, 1980). We compute the mean system response as the expected response to photons arriving during a flash (Xu & Abshire, 2005a):

$$\bar{m}(\lambda, t) = E[f(t)] = \lambda m'(t, T) \quad (17)$$

where $m'(t, T)$ is computed from $B(t)$ and determined by the background light level and flash duration. Therefore the mean response is a linear function of the flash intensity. This agrees with our linear model.

4.2. Ideal observer analysis of flash detection

An ideal observer is a theoretical idealization that performs a specific task in an optimal fashion, given available observations and constraints. The performance of an ideal observer on a task quantifies the best possible performance of a system as it relates to that task. Therefore, an ideal observer at different stages of a system can reveal how the system transforms signals and transmits task specific information. Furthermore, it can be used as a benchmark to evaluate the performance of a system in comparison with other systems, biological or manmade (Geisler, 2003), (Steinmetz & Winslow, 1999).

We apply ideal observer analysis to the photoreceptor model described above in the detection of flashes. One of two stimuli is presented during an interval and the subject, in this case an ideal observer, is required to select one of the two choices based on the observation during the interval. The two stimuli consist of background light alone and a light flash superimposed on the background light; the observation is a vector $\vec{v} \in \mathfrak{R}^k$, $\vec{v} = [\nu_0, \nu_1, \dots, \nu_{k-1}]$, of the membrane voltage at the synaptic terminal of the photoreceptor uniformly sampled over the interval. The ideal observer determines the presence or absence of the flash stimulus in the test interval by minimizing detection error given the observation vector.

A test statistic d is computed according to (Poor, 1994):

$$d^2 = \bar{m}(\lambda)^T \Sigma^{-1} \bar{m}(\lambda) \quad (18)$$

where $\bar{m}(\lambda)$ is the mean observation vector for a flash stimulus with duration T and intensity λ and Σ is the covariance matrix of the observation. From Eq. (17) we compute $\bar{m}(\lambda) = \lambda \bar{m}'$ where \bar{m}' is obtained by uniformly sampling the mean response $m'(t, T)$ over the interval $[0, T]$ with $m'_i = m'(i\tau, T)$, $i = 0, 1, \dots, k-1$. τ is the sampling period. $m'(t, T)$ does not vary with flash intensity for a given background level and flash duration. Therefore $\bar{m}(\lambda)$ is a function only of the flash intensity λ for a given background level and flash duration. Σ is the covariance matrix of the observation, and is a symmetric matrix. Under the assumptions that the operating point for the system remains fixed, i.e. the noise is a wide sense stationary signal, and that noise covariance is equal for background alone and background with flashes, Σ is also the covariance matrix of the noise. Furthermore, under the same assumptions, the probability of detection error can be computed according to (Poor, 1994):

$$\text{Pr}(\text{error}) = 1 - \Phi(d/2) \quad (19)$$

where Φ denotes the cumulative distribution function (cdf) of a standard normal variable.

We vary the intensity of the flash stimulus to find the threshold intensity, defined as the lowest light intensity with detection error less than or equal to 25%. Fig. 3 shows how the flash detection threshold varies as a function of background light level and stimulus duration (Xu & Abshire, 2005b). Threshold increases with background intensity according to a power function and decreases with increasing stimulus duration. The optimal performance is specified by the test statistic d , which is directly related to the detection threshold.

5. Fisher information

In statistics, Fisher information $I_F(\theta)$ is used as a measure of the amount of information that an observable random variable X carries about an unobservable parameter θ upon

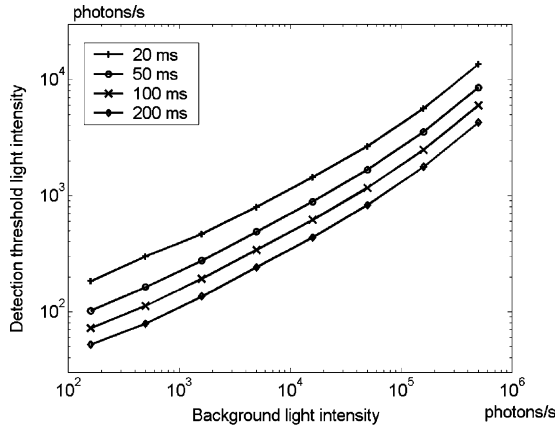


Fig. 3. Performance of the ideal observer on the flash detection task for different background light intensities and flash durations in the photoreceptor system.

which the probability distribution of X depends. It has been shown that Fisher information limits the accuracy of signal estimation according to the Cramér-Rao bound (Poor, 1994) and is defined by

$$I_F(\theta) \triangleq E \left[\left(\frac{\partial}{\partial \theta} \log P_\theta(X) \right)^2 \right] \quad (20)$$

$P_\theta(X)$ is the probability density function of X conditioned on θ . Below, we explore Fisher information in the flash detection task and relate it to the optimal detection performance from ideal observer analysis. We showed that Fisher information is equivalent to signal-to-noise ratio (SNR) in a simplified case. It is also intimately connected with signal discriminability (Xu & Abshire, 2005a). We compare Fisher information with mutual information to further demonstrate that Fisher information functions as an information measure that is directly related to performance on specific tasks.

5.1. Fisher information and detection performance

At a given background light level \mathcal{A} , the photoreceptor system can be modeled as a linear system with responses varying around the operating point set by the background level. The background level determines the single photon response $B(t)$, and together the background level and flash duration T determine the shape of the mean response. Flash intensity λ determines the magnitude of the mean response. We sample the synaptic terminal voltage during the observation interval to obtain the sampled voltage vector \vec{v} of length k . Considering the noise sources in the model described above, the observation vector follows the multidimensional Gaussian distribution:

$$P(\vec{v}|\lambda) = \frac{1}{(2\pi)^{k/2} |\Sigma|^{1/2}} \exp \left[-\frac{1}{2} (\vec{v} - \vec{m}(\lambda))^T \Sigma^{-1} (\vec{v} - \vec{m}(\lambda)) \right] \quad (21)$$

where $\vec{m}(\lambda)$ is the mean vector of \vec{v} . $\vec{m}(\lambda)$ is a function of λ for a given background light and flash duration, therefore $P(\vec{v}|\lambda)$ is determined by λ for a given background light level and flash duration. This allows us to compute the Fisher information at the synaptic terminal using the distribution of the membrane voltage vector.

$$\frac{\partial \ln P(\vec{v}|\lambda)}{\partial \lambda} = \frac{\partial}{\partial \lambda} \left[-\frac{1}{2} (\vec{v} - \lambda \vec{m}')^T \Sigma^{-1} (\vec{v} - \lambda \vec{m}') \right] \quad (22)$$

$$\begin{aligned} &= -\frac{1}{2} [-\vec{v}^T \Sigma^{-1} \vec{m}' - \vec{m}'^T \Sigma^{-1} \vec{v}] - \vec{m}'^T \Sigma^{-1} \vec{m}' \lambda \\ &= (\vec{v} - \vec{m}(\lambda))^T \Sigma^{-1} \vec{m}' \end{aligned} \quad (23)$$

$$I_F(\lambda) = \int_{\mathfrak{R}^k} P(\vec{v}|\lambda) \left(\frac{\partial \ln P(\vec{v}|\lambda)}{\partial \lambda} \right)^2 d\vec{v} \quad (24)$$

$$= \vec{m}'^T (\Sigma^{-1})^T \left[\int_{\mathfrak{R}^k} P(\vec{v}|\lambda) (\vec{v} - \vec{m}(\lambda)) (\vec{v} - \vec{m}(\lambda))^T d\vec{v} \right] \Sigma^{-1} \vec{m}' \quad (25)$$

$$= \vec{m}'^T (\Sigma^{-1})^T \Sigma \Sigma^{-1} \vec{m}' = \vec{m}'^T \Sigma^{-1} \vec{m}' \quad (26)$$

$$= \frac{1}{\lambda^2} \vec{m}(\lambda)^T \Sigma^{-1} \vec{m}(\lambda) = \frac{d^2}{\lambda^2} \quad (27)$$

Consequently we can express the detection performance in terms of Fisher information as

$$\Pr(\text{error}) = 1 - \Phi \left(\frac{1}{2} \lambda \sqrt{I_F(\lambda)} \right) \quad (28)$$

The optimal detection performance is directly related to the Fisher information available from the observation for a given stimulus. Therefore Fisher information is a measurement of the information relevant to performance in the flash detection task.

From Eq. (26) we see that Fisher information can be computed from \vec{m}' and Σ which are functions of background light level and flash duration. \vec{m}' is determined by the single photon response at the background light level of interest, and Σ is determined by the noise characteristics of the channel at the same background light level. Therefore the Fisher information in this system is a function only of the background light level \mathcal{A} , and remains the same for different flash intensities λ ; we will write it as $I_F(\mathcal{A})$ instead of $I_F(\lambda)$ from now on.

Once we define detection threshold as the flash intensity corresponding to a specific detection error, i.e. 25%, Fisher information also determines the threshold intensity, or minimum detectable flash intensity. The threshold is a function of background light level according to

$$\lambda_{\min} = \frac{d_{25\%}}{\sqrt{I_F(\mathcal{A})}} \quad (29)$$

where $d_{25\%}$ is the value of the test statistic that satisfies $1 - \Phi(d_{25\%}/2) = 0.25$. The larger the Fisher information is, the smaller the minimum detectable flash of light.

5.2. Mutual information revisited

We have shown that for the flash detection task, Fisher information is a function of the background light level; it determines the best detection performance or the minimum detectable flash intensity at a given background. Then what can mutual information tell us about the task? In the flash detection task, there are two possible stimuli, flash present (denoted by S^+) and flash absent (denoted by S^-). As discussed above, the responses R at the photoreceptor terminal are k -dimensional Gaussian distributed for both stimuli, i.e., $P(R|S^+)$ is $N(\lambda\vec{m}', \Sigma)$ and $P(R|S^-)$ is $N(\vec{0}, \Sigma)$. Σ is determined by the background light intensity. The mutual information between stimuli and responses can be written as

$$I(S, R) = H(R) - H(R|S) = H(R) - \frac{1}{2} \log_2 [(2\pi e)^k |\Sigma|] \tag{30}$$

The distribution of R is a Gaussian mixture, $1/2(N(\lambda\vec{m}', \Sigma) + N(\vec{0}, \Sigma))$ for equal probability of S^+ and S^- . It depends on both background light intensity and flash intensity so $I(S, R)$ depends on both background intensity and flash intensity as well. In this case there is no known analytic solution for $I(S, R)$. For a given background intensity $H(R|S)$ is fixed and $H(R)$ increases with flash intensity. Therefore mutual information increases monotonically with the flash intensity. However, there is no simple relationship between mutual information and detection performance, nor is there a direct method to compute the minimal detectable flash intensity from mutual information.

If we reduce the Gaussian response at the synaptic terminal to the binary decision (denoted by R^+ and R^-) produced by the ideal observer, this becomes a binary symmetric channel. The detection error P_e is given by Eq. (19). The mutual information is $1-H(P_e)$, where $H(P_e) = -P_e \log_2 P_e - (1 - P_e) \log_2 (1 - P_e)$. At detection threshold, P_e is 25%, so the mutual information is 0.1887 bit. In summary, mutual information quantifies how much information is transferred at a certain performance level, whereas Fisher information quantifies the best performance level for the task.

6. Sensitivity analysis

Phototransduction in the blowfly photoreceptor consists of multiple stages of signal transformation and additive noise which are represented by the communication channel shown in Fig. 1. We model the transfer function of each signal transformation and power spectrum of each noise source according to the biophysical mechanisms. There are

many parameters in this intricate model and they interact with each other in complicated ways. Altogether they determine the signal and noise, the Fisher information, and optimal detection performance at every stage within the system. The values for the parameters have been obtained either from reported measurements, or from estimation based on reported experimental results (Abshire & Andreou, 2001b). Thus many of them are approximations. It is important to determine how sensitive the simulation results are with respect to the accuracy of the parameters, in order to understand how well the model can predict properties of the real photoreceptor system. Sensitivity analysis also reveals the role each parameter plays in the overall task performance.

We analyse sensitivity for each parameter by varying it from 20 to 200% of its original value while holding all other parameters fixed. At each data point, we compute Fisher information at one flash intensity using Eq. (27), then compute the optimal detection threshold using Eq. (29). This is simpler than the simulation method for Fig. 3 which varied the flash intensity to find the detection threshold. We plot the optimal detection threshold as a function of each parameter for two values of the background intensity. η is the ratio of the parameter value to its nominal value. th/th_0 is the ratio of the detection threshold to its nominal value at $\eta = 1$, th_0 . The low background level is 500 photons/s, while the high background level is 5,00,000 photons/s. Signal and noise depend on many parameters, often in a nonlinear way, so these results are sometimes nonintuitive and difficult to interpret. Depending on the operating point of the system, the detection performance may improve or deteriorate as a given parameter varies. In general, the detection threshold exhibits three kinds of behavior as the parameters vary: (I) threshold is a monotonic function of the parameter; (II) threshold is a non-monotonic function of the parameter; (III) threshold is almost constant, with change of less than 1%. Table 2 shows the parameters in each group. We can gain some insight into these results by qualitative analysis of the transfer functions and noise power spectra. In lieu of an exhaustive and lengthy exposition for each parameter, we will highlight some examples from each functional group in order to illustrate their roles in determining detection performance.

Table 2
Sensitivity behavior of parameters

Group	I	II	III
Change	Yes	Yes	No
Monotonic	Yes	No	
Pupil	C_o		
Bump model	h_b, τ_b, n_b		
K activation	γ	α, β	
Channel	$N_K, \gamma_K, \gamma_L, \tau_L, E_L, G_t, E_t$	E_K	N_L
Membrane	l_b	r_b, r_a	$R_a, C_m, R_t, C_t, l_a, R_g, R_b$

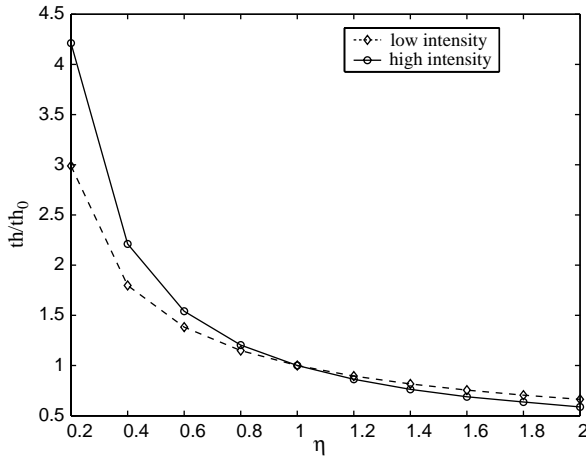


Fig. 4. The detection threshold decreases as the pupil transmission increases, shown at two values of the background light level.

6.1. Pupil transmission

When the pupil transmission increases by a factor k , the amplitude of the signal increases by k . Although the power of photon shot noise also increases by k , the power of the signal increases by k^2 , so the signal increases more than the noise. The detection performance improves and the detection threshold decreases with k as shown in Fig. 4.

6.2. Bump model parameters

The three parameters of the adapting bump model affect the signal according to Eq. (7). When h_b increases, the signal increases. When n_b or τ_b increases, the bump spreads out in time. The bump model determines the biochemical cascade transfer function, so it also affects the noise, but only photon shot noise. Since only part of the noise experiences the same gain or attenuation as the signal, the influence of the signal change dominates the detection performance. The detection threshold decreases with increasing h_b , decreasing n_b , or decreasing τ_b as shown in Fig. 5.

6.3. Potassium channel activation parameters

The potassium channel activation parameters, α , β and γ , determine the channel conductance $g_K = n_\infty \gamma_K N_K$ and dynamical parameters $g_n = \tau/L_n$ and $L_n = 1/\gamma(V_m - E_K)$ which model the voltage dependence of the potassium channels. τ is the time constant given by $1/(\alpha + \beta)$ and n_∞ is the steady state probability that the channel is open given by $\alpha/(\alpha + \beta)$. When α increases, τ decreases, n_∞ increases, g_n decreases, g_K increases, and g_m increases. By inspection of Eq. (14), we see that the numerator decreases and the denominator can either increase or decrease. Therefore it is hard to predict the overall effect on z_m . The situation is similar for β . The detection threshold can increase or decrease with increasing α or β depending on the operating

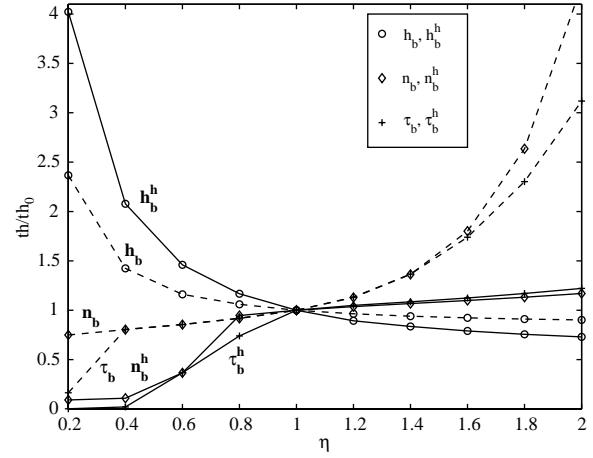


Fig. 5. The detection threshold decreases as h_b increases and n_b or τ_b decreases, at two values of the background intensity (solid line and superscript h indicates high background level).

point. The threshold behaves differently for γ . When γ increases, L_n decreases. Since τ is fixed, g_n increases. g_K is fixed because n_∞ is fixed. By inspection of Eq. (14), we now see that the real part of the denominator of z_m increases. This means that the membrane impedance decreases, so the signal has a larger leakage through the membrane. Consequently, the detection threshold increases with γ as shown in Fig. 6.

6.4. Channel parameters

Additional channel parameters include the total number of channels, unit conductance per channel, time constant, and reversal potential for each type of channel. When N_K or g_K increases, g_m increases and the membrane impedance z_m decreases, so there is higher membrane leakage. The detection threshold is expected to increase, as confirmed by simulation (results not shown).

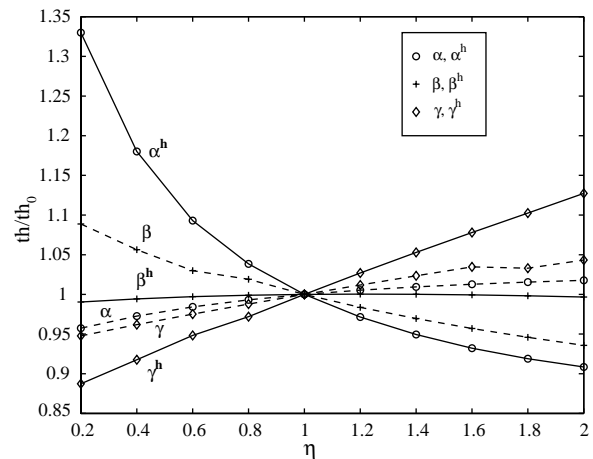


Fig. 6. While the detection threshold may either increase or decrease with α and β , it increases monotonically with γ , at two values of the background intensity (solid line and superscript h indicates high background level).

6.5. Membrane parameters

Most of the membrane parameters have little effect on the detection threshold, so they are in group III. Membrane parameters determine the membrane transfer function and membrane thermal noise. Thermal noise is negligible compared with other sources of noise. The signal and noise are transformed by the same membrane transfer function, equally amplified or attenuated. Therefore the detection performance at the synaptic terminal varies little with these parameters.

7. Summary

In this paper, we have extended the information-theoretic investigation of neural systems using the framework provided by a detailed biophysical model of the blowfly photoreceptor. We applied ideal observer analysis to flash detection using the model. We then demonstrated that Fisher information quantifies performance in this specific task and compared it with mutual information. In addition, we analyzed the sensitivity of detection performance to further investigate the contributions of biophysical parameters. We conclude that Fisher information is a powerful analytical tool for understanding task-specific performance and that the biophysical model of phototransduction is a powerful predictive tool for relating biophysical structure to functional performance.

Acknowledgements

This material is based upon work supported by the National Science Foundation under Grant No. 0238061.

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