

Threshold Detection of Intensity Flashes in the Blowfly Photoreceptor by an Ideal Observer

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Abstract

Detection of intensity flashes in the blowfly photoreceptor is limited by photon noise in the input signal as well as noise contributed by transduction components within the photoreceptor. Our analysis uses an ideal observer and a model of blowfly phototransduction to compute the threshold for optimal detection of intensity flashes as background intensity varies. We find that detection threshold increases with background light intensity according to a power function, that the threshold for low light levels is limited mainly by the photon noise, and that the threshold at high light levels is limited mainly by the channel noise.

Keywords: Blowfly photoreceptor; Biophysical model; Ideal observer; Two-Alternative Forced Choice (2-AFC); Detection threshold

1. Introduction

Noise limits the ability of any physical system to accurately represent and process information. For a linear system operating under a signal power constraint, the presence of noise imposes an upper limit on the rate of information transmission through that system, known as the *information channel capacity*. Information capacity provides a fundamental measure of system performance, particularly for peripheral sensory systems that are used in many different tasks. Whereas capacity provides an upper bound on mutual information, it is unclear how capacity

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extrapolates to performance on specific tasks that are directly related to survival of the organism. In this work we present a framework which incorporates the biophysics and noise mechanisms underlying phototransduction to analyze task specific performance in the blowfly photoreceptor. Similar work has been previously reported for rod photoreceptors [13] and cortical neurons [10].

We extend our study of information transmission in the blowfly photoreceptor [1] by analyzing the photoreceptor's ability to detect changes in light intensity. Performance in visual detection tasks is limited by noise intrinsic to the photon stream as well as noise contributed by transduction components within the photoreceptor. Using an ideal observer for a two alternative forced choice (2-AFC) task [3, 13], we determine the optimal detection performance for a detailed biophysical model of blowfly phototransduction [2]. We model the response of the photoreceptor to incident stimuli that are intensity flashes of varying strength, and compute detection error of the ideal observer under the assumptions that noise is normally distributed and remains the same whether the stimulus is present or absent. We define the light intensity corresponding to 25% detection error as the detection threshold, and determine how the detection threshold varies with background light intensity. We find that detection threshold increases with background light intensity according to a power function. The threshold at low light levels is limited mainly by the photon noise, and the threshold at high light levels is limited mainly by the channel noise.

The remainder of the paper is organized as follows: Section 2 describes the model of the blowfly photoreceptor, Section 3 describes the ideal observer analysis, Section 4 presents our results, and Section 5 summarizes the work.

2. Photoreceptor model

Blowfly photoreceptors communicate information about visual stimuli to other neurons through a series of signal transformations. Photons are guided through the optics of the compound eye, attenuated by an intracellular pupil mechanism, and absorbed by the photosensitive pigment rhodopsin. The activated pigments trigger 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. Each of these transformations is associated with deterministic and stochastic changes in the signal. 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 [6], their linear properties are well documented [7]. 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 [9, 12]. We assume that each noise source contributes independent, additive noise at the location where it appears in Fig. 1.

The magnitude transfer functions and noise components of this model were described in [2]. Parameters of the model are estimated using data from [4, 5, 7, 8, 15] as described in [2]. In the present work the model is extended into the time

domain in order to apply ideal observer analysis. At each background light level, the transfer functions corresponding to optics, rhodopsin, and membrane channels are pure amplitude scaling factors. The time response is determined by the biochemical cascade and the membrane impedance. The impulse response of the biochemical cascade is described by a gamma function [16]. The membrane impedance is modeled according to cable theory as a photoreceptor cell loaded at its synaptic terminal by gap junctions to five other photoreceptors looking into the same direction in space [4]. Its impulse response is computed from the magnitude and phase of its transfer function. The entire model allows us to compute the response of the system to any stimulus in the linear operating range.

3. Ideal observer analysis

An ideal observer is a theoretical observer that performs a specific task in an optimal fashion, given available observations and constraints. The performance of an ideal observer on a task can be used to quantify the best possible performance of the system as it relates to that task. Therefore, ideal observer analysis on 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 artificial.

We apply ideal observer analysis to the photoreceptor model described above in a 2-AFC task. A 2-AFC task presents one of two stimuli in an interval and requires the subject, in this case an ideal observer, to select one of the two choices based on the observation during the interval. In the present work the two stimuli consist of background light alone and a light flash superimposed on the background light; the observation is the membrane voltage at the synaptic terminal of the photoreceptor over the interval. In each interval of the test, the observation signal is sampled

uniformly in time to generate an observation vector X , $X = [x_0, x_1, \dots, x_{n-1}]^T$. We

define the covariance matrix K , $K = E[(X - E[X])(X - E[X])^T]$, where $E[\cdot]$

denotes the expectation operator. A test statistic d is computed by [11]:

$$d^2 = (m_1 - m_0)^T K^{-1} (m_1 - m_0)$$

where m_0, m_1 are mean observation vectors for the background and flash stimulus respectively, computed from the membrane voltage at the synaptic terminal of the model photoreceptor in the absence of noise. Note that the test statistic d depends on the difference between m_1 and m_0 , so we only need to compute the small signal response for the flash stimulus relative to the background stimulus.

Under the assumptions that the operating point for the system remains fixed, i.e. the noise is a wide sense stationary (WSS) signal, and that noise covariance is equal for background and flashes, the noise covariance function $C_\tau(t)$ may be computed from the inverse Fourier transform of the power spectral density (PSD) of the membrane voltage noise. $C_\tau(t)$ is then used to generate the covariance matrix K , where $K_{i,j} = C_\tau(|i - j| \Delta t)$ and Δt is the sample interval. Consequently K is a symmetric matrix because the covariance of the noise at two sample points depends only on their time difference. Furthermore, under the same assumptions, the probability of detection error can be computed by [11]:

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

where Φ denotes the cumulative distribution function (cdf) of a standard normal variable. We sweep 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%. If we consider each detection outcome as the output of a binary symmetric channel with

input determined by the presence of a flash, then a fixed amount of information (0.1887 bit) is conveyed at the detection threshold during each interval.

4. Results

We use ideal observer analysis to find detection thresholds at different background light levels and different stimulus durations. The mean observation vector for the flash stimulus is computed using the model described above. The time response at each background light level is determined by the biochemical cascade and the membrane impedance, represented by the impulse responses from the photoreceptor model. Other transduction components are amplitude scaling factors. Fig. 2 shows the impulse response of the biochemical cascade and of the membrane impedance at a background light level of 5000 photons/s.

The total impulse response of the system is determined by convolving the impulse responses of the biochemical cascade and the membrane impedance, then scaling it with the responses from other transduction components in the system. We compute the noise PSD at each background light level using the noise sources and transfer functions of the photoreceptor model, and generate the corresponding noise covariance matrix.

A flash stimulus is represented by a square pulse; its amplitude is given in terms of photon arrival rate (photons/s). The system response to the flash is obtained by convolving the square pulse and the system impulse response (derivation similar to Campbell's theorem). It is equivalent to the system response to a discrete impulse train representation. Fig. 3 shows the system responses to flash stimuli of 20 ms and 100 ms at the background level 5000 photons/s.

Fig. 4a shows the detection thresholds as a function of background light intensity for three cases: total noise, which comprises all noise sources of the photoreceptor

model described above; photon noise, which uses only the photon shot noise; and other noise, which uses only the noise contributed by transduction components within the photoreceptor. Detection threshold including all noise components increases with background light intensity according to a power function. This result is consistent with previous work in vertebrate vision [14]. The detailed biophysical model allows us to separately consider the effects of input and system noise. The threshold for low light levels is limited mainly by the photon noise, and the threshold at high light levels is limited mainly by the stochastic channel noise. Fig. 4b shows the fraction of the total noise contributed by different noise components, which agrees with the detection threshold results – photon noise is dominant at low light levels and channel noise becomes significant at high light levels.

We also see from Fig. 5 that detection threshold decreases monotonically with increasing stimulus duration.

5. Conclusions

We performed ideal observer analysis for a 2-AFC detection task using a linearized model of the blowfly photoreceptor. We find that the detection threshold for light flashes increases with background light intensity according to a power function. At low and high light intensities we find that the performance is limited by input noise and transduction noise respectively.

In prior work [2] we used a model of the blowfly photoreceptor to compute information capacity of the photoreceptor system. This work extends the previous results into the framework of evaluating task specific performance. Ideal observer analysis provides a way to measure the best possible performance given the available observations and constraints. This optimal performance is specified by the test statistic d , which directly determines the detection threshold and provides a

comparison for the detection performance of different systems or a system at different operating points. This work establishes the basis for further investigation into the communication and computation tradeoffs in a biological system – that is, whether the biological system is optimized to achieve a higher information transmission rate or better performance on specific tasks.

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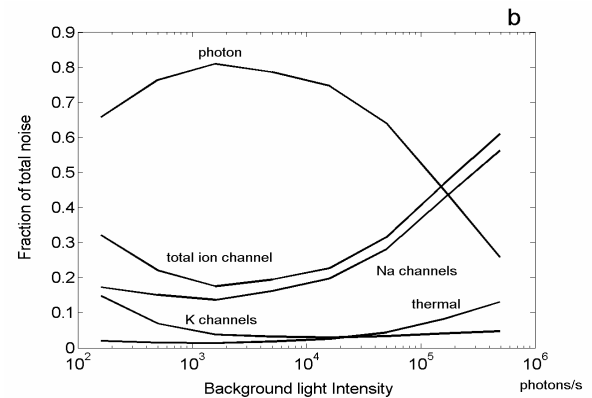
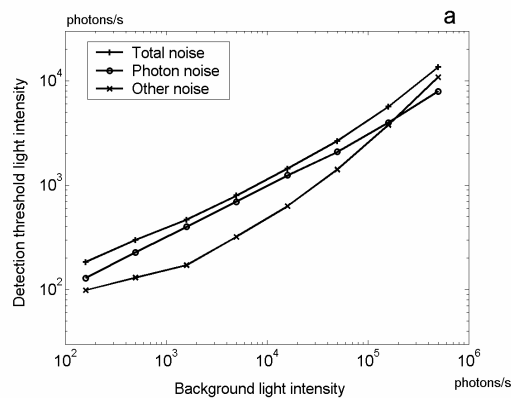
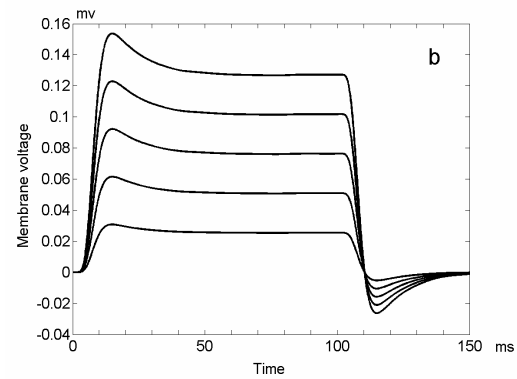
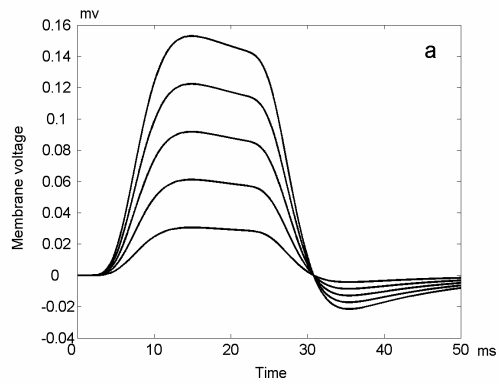
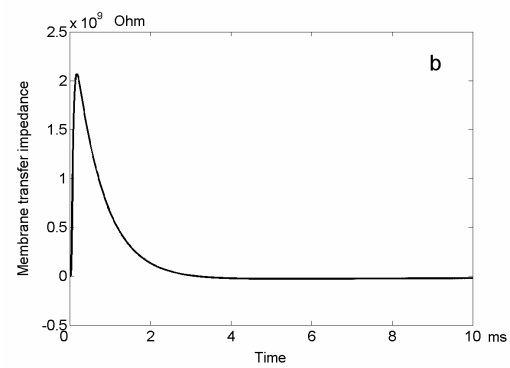
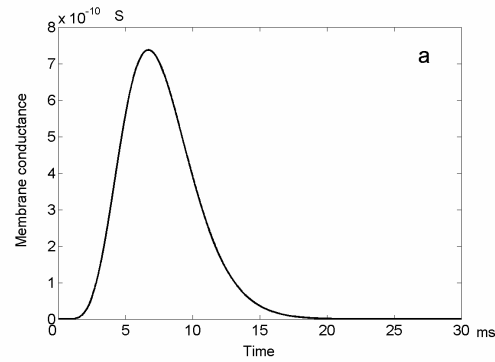
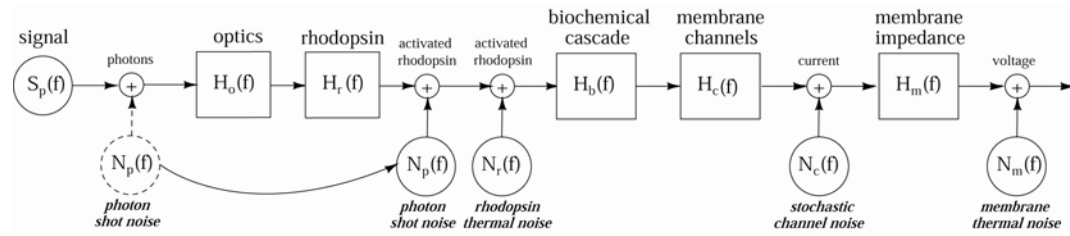
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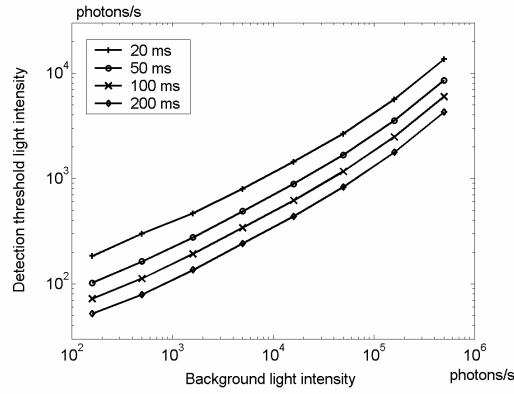
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The following captions are in the same order as the proceeding figures.

Fig. 1. Communication channel model of the blowfly photoreceptor, showing the transformations corresponding to optics, rhodopsin, biochemical cascade, membrane channels, and membrane impedance and the noise sources corresponding to photon shot noise, rhodopsin thermal noise, stochastic channel noise, and membrane thermal noise.

Fig. 2. (a) Impulse response of the biochemical cascade. (b) Impulse response of the membrane impedance. Both responses are at background light level 5000 photons/s.

Fig. 3. Responses to flash stimuli of different intensities at background light level 5000 photons/s. The response amplitude increases with increasing flash intensity, 2-10% of the background in increments of 2%. (a) Stimulus duration 20ms. (b) Stimulus duration 100ms.

Fig. 4. a) Performance of the ideal observer at the 2-AFC detection task under different background light intensities and different noise components in the photoreceptor system. b) Fraction of noise components under different background light intensities.

Fig. 5. Performance of the ideal observer at the 2-AFC detection task under different background light intensities and different flash durations in the photoreceptor system.