

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 optimal observer and a model of blowfly phototransduction to compute the threshold for 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, ideal observer, 2-AFC, detection threshold, biophysical model

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 extrapolates to performance on specific

tasks that are directly related to survival of the organism. In this work we present a framework for analysis of task specific information in the blowfly photoreceptor.

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 task (2-AFC) [2, 3], we determine the optimal detection performance for a detailed biophysical model of blowfly phototransduction [4]. We compute the response of the photoreceptor to incident stimuli that are intensity flashes of varying strength. We compute detection error of the ideal observer under the assumptions that noise is normally distributed and the covariance is 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 for 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 changes in the signal and with the introduction of noise. This begins even before transduction, as the arrival times of the photons are randomly distributed. Other sources of noise include the thermal activation of rhodopsin, the stochastic nature of channel transitions, and thermal noise resulting from the membrane impedance.

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 [5], their linear properties are well documented [6]. 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. This requirement is satisfied for the white noise stimuli commonly used for system identification [6] and is a reasonable model for many visual

tasks [7, 8]. We assume that each noise source contributes independent, additive noise at the location where it appears in Fig. 1.

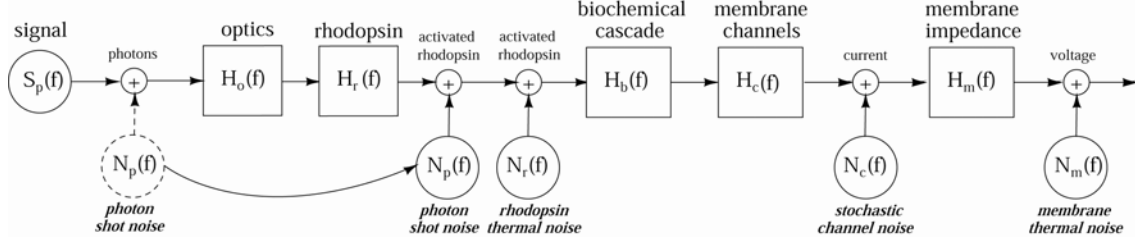


Fig. 1: Communication channel model of the blowfly photoreceptor, showing the transformations corresponding to optics, rhodopsin, biochemical cascade, membrane channels, and membrane impedance and the noise sources corresponding to photon shot noise, rhodopsin thermal noise, stochastic channel noise,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

The magnitude transfer functions and noise components of this model were described in [4]. Parameters of the model are estimated using data from [6, 9-12] as described in [4].

In the present work the model is extended into the time domain in order to apply ideal observer analysis, i.e. the *phase* of each linear filter must be specified in addition to the magnitude. At each background intensity, the transfer functions corresponding to optics, rhodopsin, and membrane channels are scaling factors with no frequency dependence.

The transfer functions corresponding to the biochemical cascade and the membrane impedance are frequency dependent, so we must specify the phase response of these components. The biochemical cascade is modeled as a gamma function [13]. The membrane impedance is modeled according to cable theory as a photoreceptor cell loaded at its synaptic terminal through gap junctions to five other photoreceptors looking into the same direction in space [10]. Phase responses of the biochemical cascade and the membrane impedance are computed from the gamma function and the complex impedance respectively. The entire model comprises the cascade of components shown in

Fig. 1, and allows us to compute responses 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 information and constraints. The performance of an ideal observer on a task can be used to quantify the information within the system as it relates to that task. We can apply ideal observer analysis to different stages of a system in order to reveal how the system transforms and transmits task-specific information. It can also be used as a benchmark to evaluate the performance of a system in comparison with other biological and artificial systems. We apply ideal observer analysis to the photoreceptor model described above in a 2-AFC detection task. The 2-AFC task presents one of two stimuli in an interval and requires the subject, in this case the ideal observer, to select one of the two choices based on its observations during the interval. In the present work the two stimuli consist of background light alone and a light flash superimposed on the background light, and the observation is the membrane voltage at the synaptic terminal of the photoreceptor over the interval. During each interval of the 2-AFC 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 as [3]:

$$K = E((X - E(X))(X - E(X))^T)$$

where E is the expectation operator. The test statistic d is given by [3]:

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

where m_0, m_1 are mean observation vectors for the background and flash stimuli 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 our assumption that the operating point for the system remains fixed, i.e. the noise is a wide sense stationary (WWS) signal, K may be computed as the inverse Fourier transform of the power spectral density (PSD) of the membrane voltage noise. Under our assumption that the noise is normally distributed and equal for both stimuli, the detection error can be computed by [3]:

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

where N is the cumulative distribution function (cdf) of a standard normal variable.

We adjust the intensity of the flash stimulus to find the threshold intensity, defined as the smallest light flash with detection error less than or equal to 25%.

4. Results

We use ideal observer analysis to find detection thresholds at different background light levels. The stimulus and observation intervals for the 2AFC task are 10ms. We expect the system to behave linearly for short intervals and small flashes, in order to minimize the effects of adaptation. The sample period is 10 μ s, so the observation vector X has 1000 samples. The mean observation vector for the flash light stimulus is computed using the model described above. The time course of the response is determined by the biochemical cascade and the membrane impedance, represented by the impulse responses from the photoreceptor model. The 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.

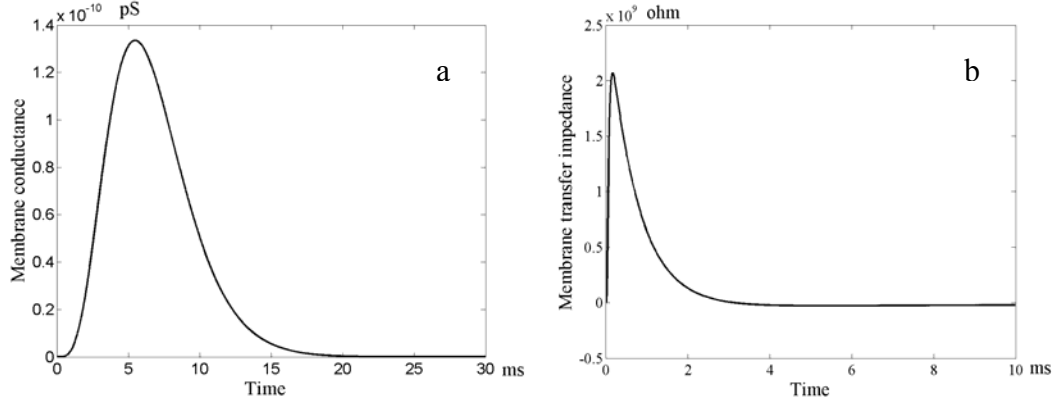


Fig. 2. (a) Impulse response of the biochemical cascade. (b) Impulse response of the membrane impedance. Both responses are at background light level 5000 photons/s.

The total impulse response of the system is determined by convolving the impulse responses of the biochemical cascade and the membrane impedance and scaling by the responses from other components in the system. The amplitude of the flash stimulus is given in terms of photon arrival rate (photons/s). It is converted to a discrete representation of the stimulus waveform, which is sampled in time and scaled by the sample period so that the photon arrival rate over each sample interval matches the original photon arrival rate of the stimulus. This discretized stimulus is convolved with the impulse response of the system to obtain the response observed by the ideal detector. Fig. 3 shows the system response to flash stimuli at the background level 5000 photons/s for flashes of 10 and 20 ms duration.

Under the assumption of equal noise covariance for background and flashes, we compute the noise PSD at each background light level using the noise sources and transfer functions of the photoreceptor model. The covariance function $C_r(t)$ is computed from

the inverse Fourier transform of the noise PSD, and is used to generate the covariance matrix K , where $K_{i,j} = C_\tau(|i-j|\Delta t)$ and Δt is the sample interval. K is a symmetric

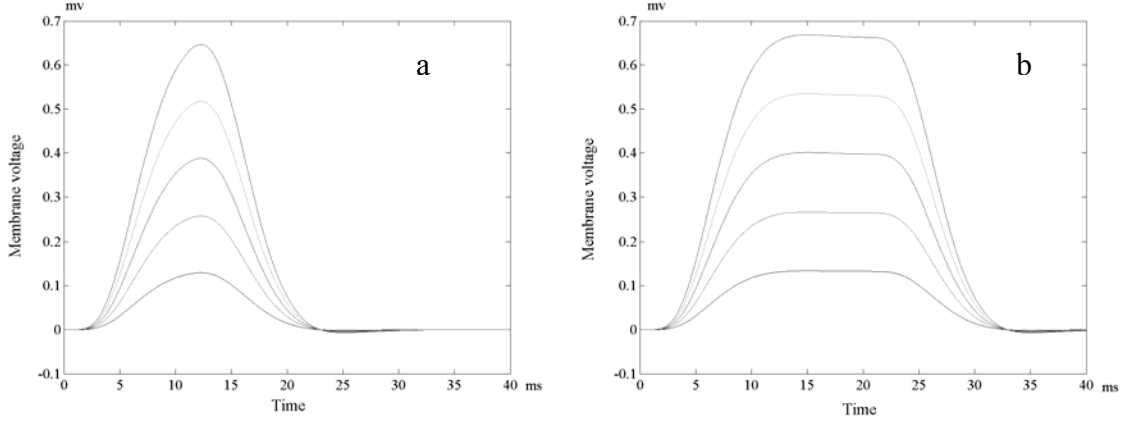


Fig. 3. Responses to flash stimuli of different intensities at background light level 5000 photons/s. The response amplitude increases with increasing flash intensity, from 2-10% of the background in increments of 2%. (a) Stimulus duration 10ms. (b) Stimulus duration 20ms.

matrix because the covariance of the noise at two sample points depends only on their time difference. Fig. 4 shows the noise covariance function at the background level 5000 photons/s for three cases: total noise, which comprises all noise sources of the photoreceptor model described above; photon noise, which uses only the photon shot

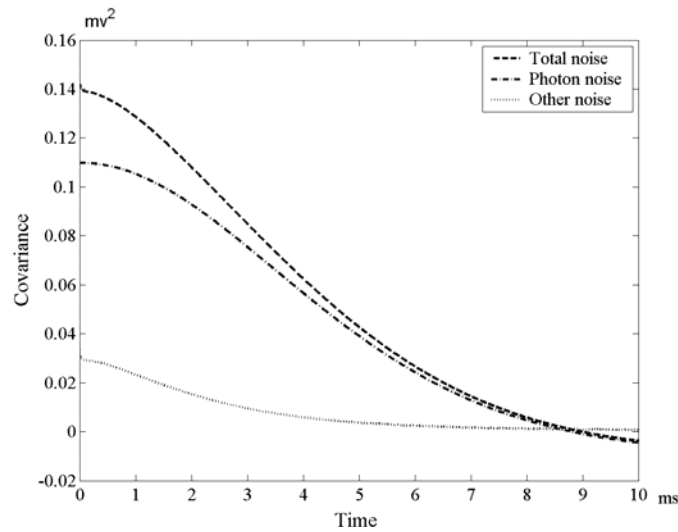


Fig. 4. Noise covariance at background light level 5000 photons/s for total noise photon noise only and other noise only.

noise; and other noise, which uses only the noise contributed by transduction components within the photoreceptor.

Fig. 5 shows the detection thresholds as a function of background light intensity for the same three cases as Fig. 4. Detection threshold increases with background light intensity according to a power function. This result is consistent with previous work in a vertebrate visual system [3]. 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 channel noise.

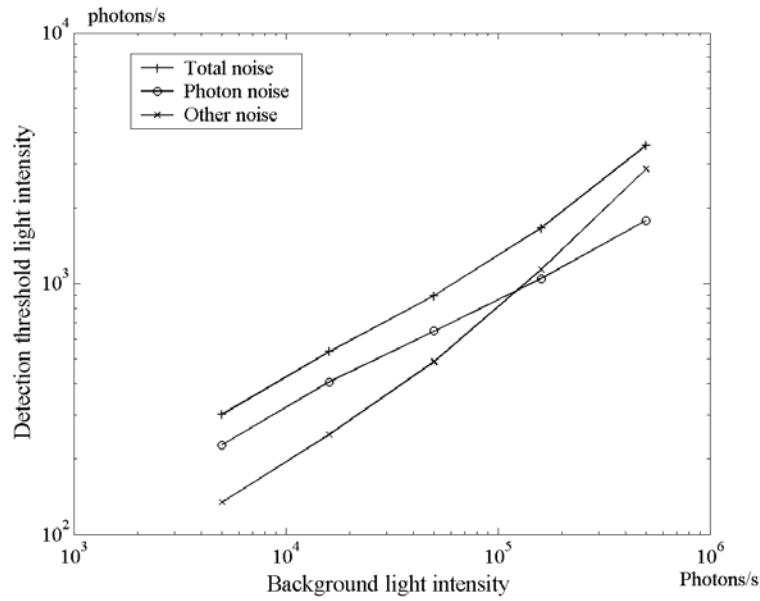


Fig. 5. Performance of the ideal observer at the 2-AFC detection task under different background light intensities and different noise components in the photoreceptor system.

5. Conclusion

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 system noise respectively.

In prior work [4] we have 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 parametric estimation and detection. In future work we expect that this model system will allow a direct comparison between parametric information and transmitted information, specifically between Fisher information with channel capacity, the maximum mutual information. This work establishes the basis for direct comparison between maximum information and task-specific information in a neural system.

Acknowledgements

We thank the National Science Foundation for support of this work through CAREER award 0225489.

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