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Relating information capacity to a biophysical model for blowfly photoreceptors

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Abstract

Photoreceptors measure and communicate information about visual stimuli to other neurons. In this process, the visual signal is converted between many different physical states. We present a communication channel model that describes transmission and degradation of the visual signal in the blowfly photoreceptor cell. The model is a cascade of linear systems and noise sources; these elements are derived from fundamental principles when possible, and parameters of the model are estimated from physiological data. We compute capacity and bit-energy using the model. Our results indicate that photon shot noise and channel noise are the dominant noise sources in blowfly phototransduction. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Information theory; Channel capacity; Blowfly; Photoreceptor; Bit energy

1. Introduction

We seek to gain better understanding of sensory information processing in physical systems both natural and engineered. To do so we must understand how to relate function to structure for these systems. We must also understand the tradeoffs between system performance and associated costs such as size, reliability and energy requirements. We utilize basic information theory to quantify function and physically motivated models to quantify costs. An information theoretic framework for quantifying these tradeoffs in VLSI was presented in [4] for a variety of delay circuits; we use the same approach to investigate photoreceptors of the blowfly *Calliphora vicina*.

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We describe a communication channel model that incorporates all physical transformations from photons entering the compound eye to voltage of the photoreceptor membrane at the synaptic terminal. This model allows us to investigate tradeoffs between cost and performance and provides a starting point for investigation into the efficiency of biological information processing.

2. The visual system of the fly

The visual system of the fly has been extensively studied by physiologists. Vision in the blowfly *Calliphora* begins with two compound eyes each of which are 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. Electrical signals from the photoreceptor cells project to cells in the lamina and the medulla. In this investigation we focus on the photoreceptors R1-6 which project to large monopolar cells in the lamina.

The fly receives behaviorally relevant information as light reflected or emitted from objects in the environment. Photons are guided through the optics of the compound eye to the photoreceptors. Absorption of photons activates photo-sensitive pigments in the photoreceptor cells. The activated pigments trigger a cascade of biochemical reactions which produce “messenger” molecules. These messengers cause ion channels in the photoreceptor membrane to open. The open channels provide a membrane conductance, which allows an ionic current to flow that changes the membrane voltage. This voltage change propagates down a short axon to the synaptic terminal in the lamina. In the discussion that follows, we investigate the signals transduced through photoreceptors which project onto a single large monopolar cell, ignoring any spatial aspects of information flow in the system.

3. A communication channel model

Information processing in the early visual system of the fly involves transformations between different physical degrees of freedom: photons, conformational state of proteins, concentrations of various chemical messengers, current, voltage. The goal of the above processes is to communicate information from one physical structure to another while preserving the message. We model these transformations as a cascade of communication channels that have band-width limitations.

Each of these transformations is associated with changes in the signal itself and with the inevitable 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 Johnson noise resulting from membrane impedence. We model each noise source as an independent, additive contribution to the channel. The structure of the model is shown in Fig. 1. Each transfer function is linear about an operating point, which is determined by the mean intensity of the incident light. Each noise source contributes

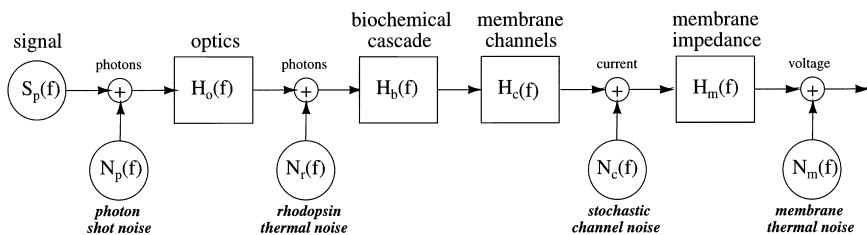


Fig. 1. A communication channel model of the blowfly photoreceptor.

Table 1
Summary of model equations

Signal	$S_p(f)$ determined by environment
Photon shot noise	$N_p(f) = 2I$
Optics	$H_o^2(f) = C_o(f)^2$
Rhodopsin thermal noise	$N_r(f) = 2 \times 10^{-3}$
Biochemical cascade	$H_b^2(f) = h_b^2/[1 + (2\pi f t_b)^2]^{m_b + 1}$
Membrane current	$H_c^2(f) = (V_m - E_{ch})^2$
Stochastic channel noise	$N_c(f) = 4N\gamma_c^2(V_m - E_{ch})^2 n_\infty(1 - n_\infty)\tau_c/[1 + (2\pi\tau_c f)^2]$
Transfer impedance	$ H_m(f) ^2 = V_{out}/I_{in} ^2$
Johnson noise	$N_m(f) = 4kT \text{Re}[Z_{out}(f)]$

independent, additive noise at the location in the system depicted. We determine the amplitude and power spectrum for each noise source, including photon shot noise, rhodopsin thermal noise, stochastic channel noise, and membrane thermal noise. The transfer functions and noise sources are modelled from first principles when possible and phenomenologically otherwise. While the cells under study exhibit nonlinearity at very low light levels or for large signals, they have been studied extensively as linear systems, and their linear properties are well documented in the literature [7]. Modelling the transfer functions as linear systems will be accurate when the variance of the signal is sufficiently small that the operating point remains fixed. This requirement is approximately satisfied for white noise stimulation protocols as in [5].

4. Model details

With a communication channel model and its relation to the structure established, we proceed to describe the components of the model. For the sake of brevity, detailed descriptions are omitted and the main equations are summarized in Table 1. More details about the model components and parameters can be found elsewhere [1–3]. The parameters of the optical attenuation, the biochemical transfer function, the membrane channels, and membrane impedance have been estimated from physiological data [6,8]; the procedure and parameters are summarized elsewhere [1].

5. Results

Our model allows us to determine the signal, noise, and overall capacity at each intermediate stage of the system, for various operating points, thereby gaining a better understanding of the limiting processes as the signal and noise are transformed and various noise sources are added. All parameters of the model are constrained using reported empirical data on blowfly physiology. A comparison between physiological data and the results of our model is shown in Fig. 2. On the left is data from [6] which represents noise power spectral density of the blowfly photoreceptor membrane. On the right is the result of our model for membrane voltage noise measured at the cell body.

5.1. Capacity

We calculate capacity according to Eq. (1).

$$C = \max_{S(f) : \sigma_s^2 \leq P} \int_0^\infty \log_2 \left(1 + \frac{S(f)}{N(f)} \right) df. \quad (1)$$

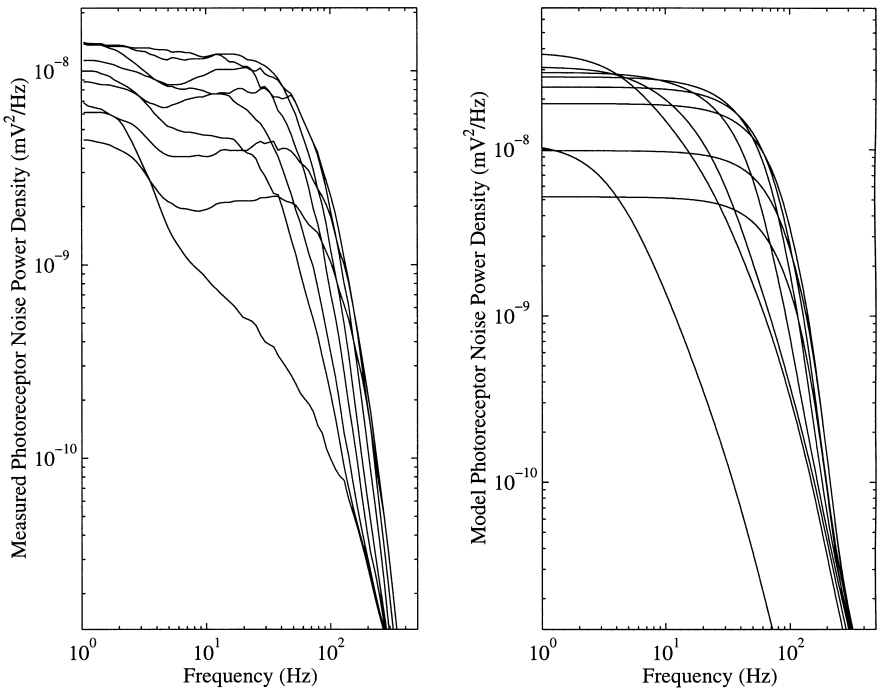


Fig. 2. Photoreceptor membrane voltage noise: On the left is data from [6], and on the right are results from the model.

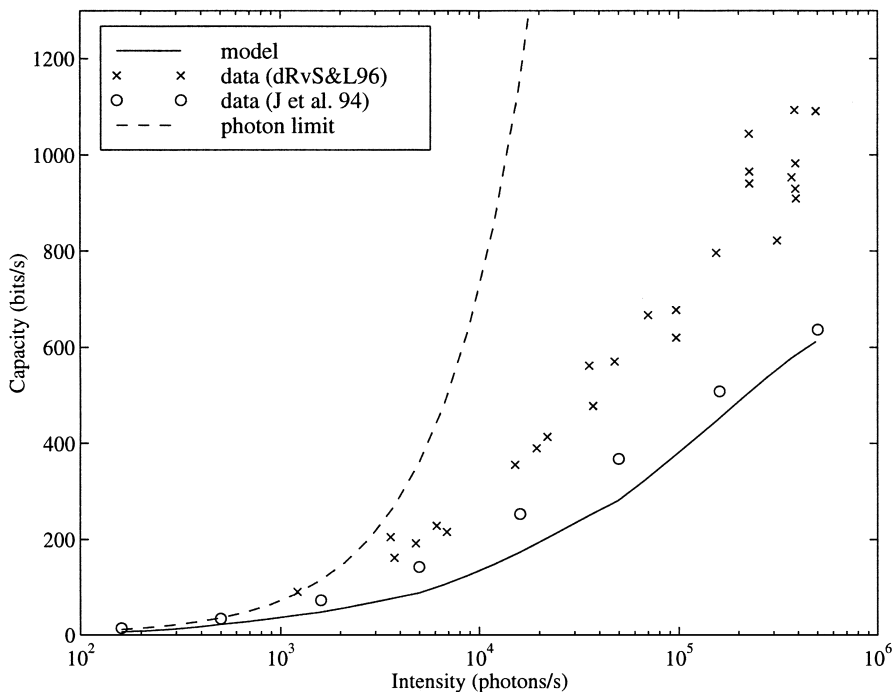


Fig. 3. Information capacity computed from our model and estimated from experimental data. 'x's are experimental estimates from [5], 'o's are estimated from data of [6], the solid line is the result from our model, and the dashed line is the photon shot noise limit.

The capacity is plotted in Fig. 3 as a function of incident light intensity. Empirical estimates from [5] and [6] are shown along with the results of the photoreceptor model and the photon shot noise limit.

5.2. Dominant noise sources

Our model also allows us to determine the dominant noise sources which limit the rates of information transmission. Fig. 4 shows the output-referred noise, i.e. voltage noise at the photoreceptor axon, for an incident intensity of 16 000 effective photons/s. Over the frequency range of physiological interest the dominant noise sources are photon shot noise and stochastic channel noise.

5.3. Bit-energy

We calculate the power dissipation due to signal flow as the free energy lost in transducing the signals. At this time we consider only the dissipation due to current

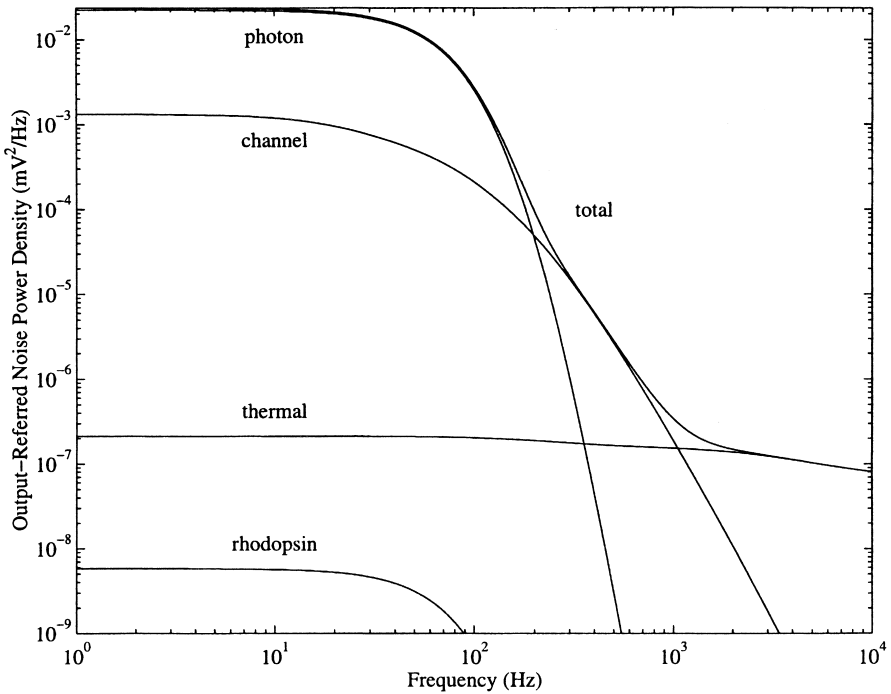


Fig. 4. Individual contributions of independent noise sources to output noise.

flow across the membrane; we do not model dissipation due to the biochemical cascade, synaptic transmission, or support processes such as protein synthesis. Our resulting model for power dissipation is simply the membrane current times the potential difference between the membrane voltage and the reversal potential, integrated over the surface area of the cell. We can obtain an approximation of this dissipation by considering the photoreceptor to be isopotential. This power dissipation is shown in the top panel of Fig. 5. Even in darkness, there is current flow across the membrane, so there is power dissipation with no signal present. It increases with background light intensity, but not very steeply. Because of the remarkable adaptation of the biochemical cascade, the power dissipation increases only one decade, when the background increases by more than three decades.

The bit-energy provides a metric for comparing the efficiency of communication among different technologies. This is defined as the ratio between the power dissipated and the information capacity, and it is the minimum energy required to transmit one bit of information. Our model provides bit-energy for the blowfly photoreceptor, as shown in the bottom panel of Fig. 5. Using the dissipation calculated from free energy as in the top panel of the figure, the bit-energy starts at ≈ 10 pJ/bit for low intensities, but quickly decreases to ≈ 1 pJ/bit at higher intensities.

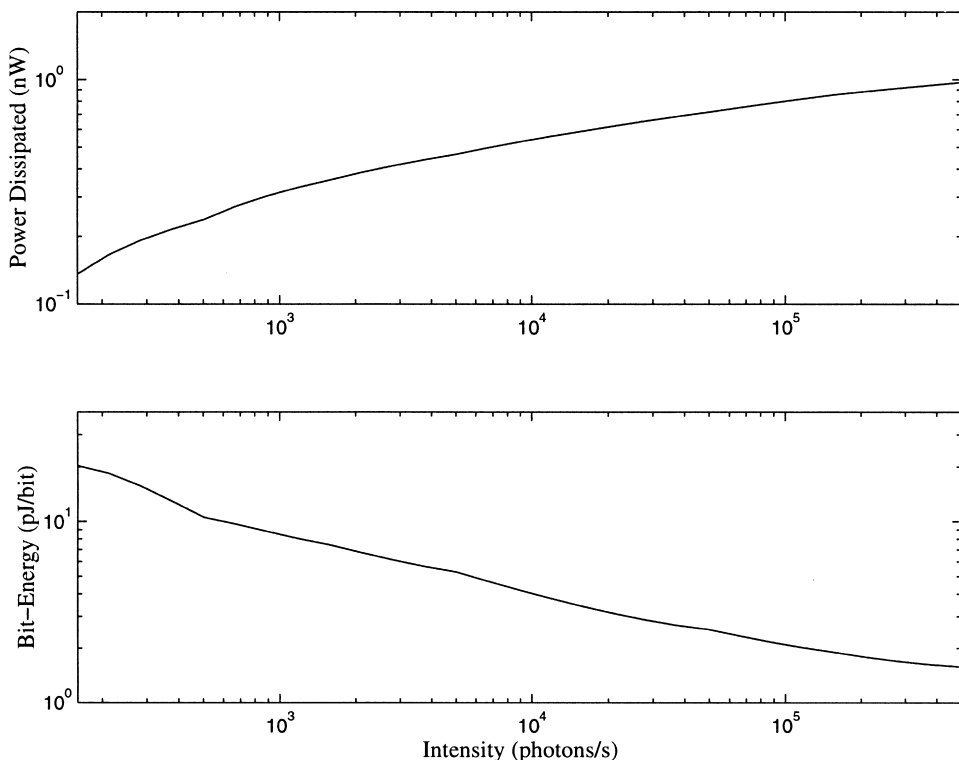


Fig. 5. Photoreceptor power (top panel) and bit-energy (bottom panel).

6. Discussion

We analyze information processing in a communication system constrained by the physical components from which it is constructed, from photons to rhodopsin to biochemistry to membrane currents to membrane voltage. The physical instantiation of the channel determines the noise, the signal constraints and the channel capacity. Such detailed analysis relates function to structure in a quantitative manner.

Information theoretic analyses typically consider communication between input and output for black box systems, but provide no insight into the mechanisms hidden within the box. We feel that it is important to understand neurobiology in terms of its fundamental and practical noise limitations. The models derived in the course of this work, furthermore, can be utilized to analyze tradeoffs between the various parameters of a biological system, and to understand which noise sources can be neglected under which operating conditions.

Once a quantitative measure of performance is established, i.e. capacity, its relation to costs such as power and constraints such as energy dissipation can be investigated. Biological systems are dissipative physical structures; signals are communicated by

the flow of ions or other chemical substances, and some driving force must power this flow. Therefore communication and computation requires the dissipation of energy. The energetic cost of information processing in the blowfly retina has been reported to be as high as 10^7 ATP per bit [9], and our work reported here predicts similar costs. We seek to understand how that energy expenditure is distributed across resources, and how different technologies and different ways of signal encoding are more or less energy-efficient.

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