

A COMPARATIVE STUDY OF INFORMATION CAPACITY FOR BIOPHYSICAL AND SILICON PHOTORECEPTORS

Pamela Abshire and Andreas G. Andreou

Electrical and Computer Engineering, The Johns Hopkins University
 3400 N. Charles St. / 105 Barton Hall
 Baltimore, MD 21218
pamela@olympus.ece.jhu.edu, andreou@jhunix.hcf.jhu.edu

ABSTRACT

We employ communication theory to analyze information processing in a silicon photoreceptor and in a biophysical model of the blowfly photoreceptor. We take channel capacity to be a quantitative measure of performance which is independent of any particular task. The physical instantiation of any channel determines the noise, the signal constraints and the channel capacity.

The channel model for each of the two systems is a cascade of linear bandlimiting sections followed by additive noise. Filters and noise are modelled from first principles when possible. Parameters for the blowfly model are determined from biophysical data available in the literature.

Such a comparative study is a first step towards understanding the performance, and the tradeoffs between system performance and associated costs such as size, reliability and energy requirements for natural and engineered sensory systems.

1. SENSORY INFORMATION PROCESSING IN PHYSICAL SYSTEMS

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. We must also understand the tradeoffs between system performance and associated costs such as size, reliability and energy requirements. An information theoretic framework for quantifying those tradeoffs in VLSI was presented in [4] for a variety of delay circuits; we utilize the same basic ideas to investigate two photoreceptors.

In this work we compare the functional properties and performance of a biological photoreceptor and an engineered photoreceptor. For both systems we construct a communication channel model that incorporates physical transformations between input and output, as well as degradation by noise. This model allows us to investigate tradeoffs between cost and performance and provides a starting point for investigation into the efficiency of information processing.

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2. COMMUNICATION CHANNEL MODEL

Information processing often involves transformations between different physical degrees of freedom, as information is communicated from one physical structure to another: photons, conformational state of proteins, concentrations of various chemicals, current, voltage. We model these transformations as a cascade of communication channels that have bandwidth limitations. We model each noise source as an independent, additive contribution to the channel.

In each model the signal power $S_n(f)$ at any stage n is the result of a cascade of linear filters $H_i(f)$, and the noise power $N_n(f)$ is the summed power of m independent, additive noise sources $N_j(f)$ which are also transformed by the cascade of linear filters. Explicitly, the signal and noise at stage n are given by:

$$S_n(f) = \prod_{i=1}^n |H_i(f)|^2 S_p(f) \quad (1)$$

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

where $S_p(f)$ is the power spectral density of the input signal and the noise from independent source j enters at stage k_j . The input to the system is the light reaching the photoreceptor as a function of time.

3. CHANNEL CAPACITY

The channel capacity of a system corrupted by Gaussian noise, in bits/sec, is given by [11]:

$$C = W \log_2 \left(1 + \frac{P}{N} \right) \quad (3)$$

when the noise variance is N , and the signal has bandwidth W and average power limitation P . This capacity is provided by a signal of Gaussian amplitude distribution and flat frequency spectrum. By extension for colored noise, the capacity is

$$C = \max_{S(f): \sigma_S^2 \leq P} \int_0^\infty \log_2 \left(1 + \frac{S(f)}{N(f)} \right) df \quad (4)$$

where the signal which maximizes the capacity can be found using the water-filling analogy. For further details see [5]. The channel capacity is an upper bound to the rate of information transmission, given by Equation 4 when the signal is limited only in average power and the noise is normally distributed. Although these assumptions are not strictly true for these systems, Equation 4 provides a close approximation to the actual capacity.

4. BLOWFLY PHOTORECEPTOR

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 photosensitive 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 lamina. In the discussion that follows, we investigate the signals transduced through photoreceptors onto a single LMC, ignoring spatial aspects of information flow in the system.

We explicitly model the filter characteristics and independent noise sources shown in Figure 1. The biochemical steps of invertebrate phototransduction aren’t characterized well enough for a first principles description, so the transfer function due to the biochemical cascade is phenomenological. It is modelled as an adapting bump function, with impulse response given by a gamma function [13]. The transfer function due to membrane impedance is modelled from first principles, according to the cable properties of the membrane [12]. The membrane model includes the light-gated conductance, a leakage conductance, and a weakly active potassium conductance. The transfer functions due to optics and membrane channels are frequency-independent gain terms. The noise sources due to photons, rhodopsin, stochastic channels, and membrane impedance are modelled from first principles. Details about the model components and parameters can be found elsewhere [1, 3, 2].

While the cells under study exhibit nonlinearity at very low light levels or for large signals [8], they have been studied extensively as linear systems, and their linear properties are well established in the literature [9]. 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 satisfied for stimulation protocols with average signal contrast as in [6].

5. ADAPTIVE SILICON PHOTORECEPTOR

We consider the Delbrück adaptive photoreceptor [7], shown in Figure 2. This circuit provides an analog output which has low gain for static signals and high gain for transient signals about an operating point. This adaptational strategy allows the output to represent a large dynamic range while retaining sensitivity to small inputs. We study the linearized

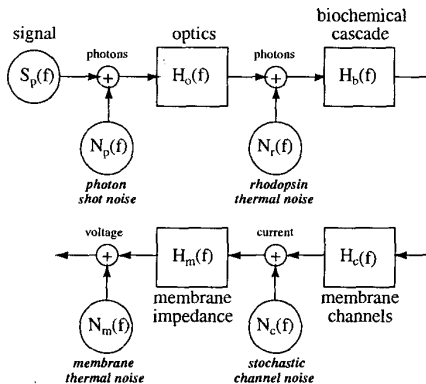


Figure 1: A communication channel model of the blowfly photoreceptor.

behavior about an operating point, as we did for the blowfly photoreceptor.

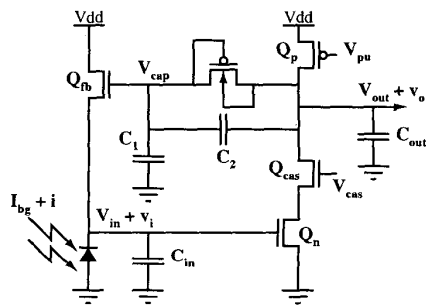


Figure 2: Adaptive photoreceptor circuit of Delbrück and Mead

This circuit has been considered in detail in [7]; the results will be given briefly here. The transfer function H_{tot} of the feedback circuit, from input current i to output voltage v_o , will be given by

$$H_{tot} = \frac{A/G}{(\tau_i s + 1)(\tau_o s + 1) + \frac{A g_{mn}}{G} \frac{g + s C_2}{g + s(C_1 + C_2)}} \quad (5)$$

where A is the gain of the output amplifier, G is the conductance at the input node, τ_i is the time constant at the input node, τ_o is the time constant of the output amplifier, g_{mn} is the transconductance of transistor Q_n , and g is the conductance of the adaptive element. The transfer function from current to voltage v_o at the output node is given by

$$H_{out} = \frac{B}{\tau_o s + 1} \quad (6)$$

where $1/B$ is the conductance at the output node. The parameters of these transfer functions will depend on the bias conditions and device and circuit parameters.

In this work we use a minimal model for the noise of a MOS transistor which includes just the shot noise. This component of the noise will be independent of device parameters or specifics of the fabrication process. Each MOS transistor and diode will contribute current shot noise $N(f) = 2qI$ where q is the elementary charge, and I is the current through the transistor. At the input node there will be photon shot noise and current shot noise contributed by the bias transistor, for a total of $4qI_{bg}$. At the output node, noise will be contributed by all three transistors of the feedback amplifier, for a total of $6qI_b$. The noise contributed by the adaptive element is neglected, since the current will be small. The total input-referred noise from these sources will be

$$N_{in,tot}(f) = 4qI_{bg} + \left| \frac{H_{out}}{H_{tot}} \right|^2 6qI_b. \quad (7)$$

6. RESULTS

Our models allow us to determine the signal, noise, and overall capacity at each intermediate stage of the systems described, 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. The capacity for the blowfly photoreceptor is plotted as the solid line in the upper panel of Figure 3, as a function of incident light intensity. Empirical estimates from [6] are shown along with the results of the model.

The capacity of the adaptive silicon photoreceptor is also shown in Figure 3. The three curves are for different bias conditions: the dotted line shows the maximum capacity (obtained as the bias current increases without bound), the dashed line shows the capacity when the silicon photoreceptor uses the same power as the blowfly photoreceptor, and the dash-dotted line shows the capacity when the silicon photoreceptor is biased for minimum bit energy, as discussed in the next section. Interestingly, the capacity of the blowfly photoreceptor is higher for lower light levels but there is a cross-over point beyond which the silicon photoreceptor can achieve higher capacity. As indicated in Figure 3 this cross-over is about 10^4 photons per second, or approximately as bright as a dimly lit room.

Our model also allows us to determine the dominant noise sources which limit the rates of information transmission. Over the frequency range of physiological interest, from DC to a few hundred Hz, the dominant noise sources for the blowfly photoreceptor are photon shot noise and stochastic channel noise. At this time the only sources modelled for the silicon photoreceptor are photon shot noise and current shot noise. When the adaptive silicon photoreceptor is biased with high current, the noise sources at the input node dominate; otherwise current shot noise of the transistors in the feedback amplifier plays a significant role.

7. EFFICIENCY

Having developed a measure for performance (i.e. capacity), we must specify cost in order to quantify the efficiency and understand the tradeoff between performance and cost. We take the cost to be the power dissipated in transducing

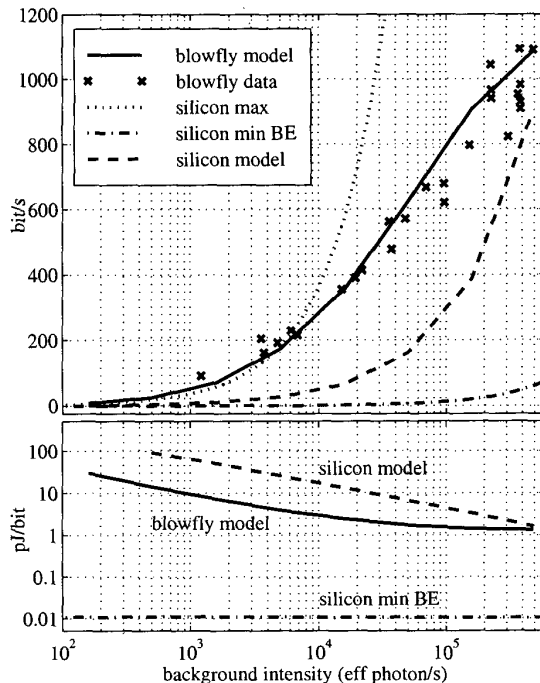


Figure 3: Top, information capacity as a function of incident intensity for blowfly photoreceptor computed from our model (solid) and estimated from experimental data (x's) [6], and for the silicon photoreceptor under three bias conditions: at arbitrarily high current (dot), using the same power as the blowfly (dash), and when biased for minimum bit-energy (dash-dot). Bottom, bit energy as a function of incident intensity for the blowfly photoreceptor (solid) and for the silicon photoreceptor at minimum bit energy (dash-dot) and when biased to use the same power as the blowfly (dash).

signals. In general, biological and VLSI 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 require the dissipation of energy.

We calculate the power dissipation for the blowfly photoreceptor as the free energy lost in transducing the signals. At this time we consider only the dissipation due to current 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 the membrane current times the potential difference between the membrane voltage and the reversal potential, integrated over the surface area of the cell. We approximate this by considering the photoreceptor to be isopotential. There is current flow across the membrane even in darkness, which results in power consumption without signal transduction. This membrane current increases

with background light intensity, but not much because of the adaptation of the biochemical cascade. The cost of information processing in the blowfly retina has been reported to be as high as 10^7 ATP per bit [10], and our work predicts similar costs. We calculate the power dissipation of the adaptive silicon photoreceptor as the bias and signal current which must be sourced from the power supply, multiplied by the power supply voltage.

Our measure of performance, the capacity, and our measure of cost, the power, allow us to define a measure for efficiency, the bit-energy, which is simply the ratio between the power dissipated and the information capacity. The bit-energy gives the minimum power required to transmit a single bit of information through the system; it provides a standard for comparing the efficiency of communication among different technologies [4].

$$BE = \frac{P}{C} \quad (8)$$

The bit energy for the blowfly photoreceptor and the adaptive silicon photoreceptor are shown in the lower panel of Figure 3. The bit-energy for the blowfly photoreceptor varies from ≈ 10 pJ/bit for low intensities to ≈ 1 pJ/bit for high intensities. As discussed above, the bit energy for the silicon photoreceptor depends on the bias of the feedback amplifier. The two curves correspond to curves in the upper panel: the dash-dotted curve is the minimum bit energy, and the dash-dotted curve in the upper panel shows the capacity at this bias. The dashed line is the bit energy when the silicon photoreceptor is biased to consume the same power as the blowfly photoreceptor, which corresponds to the capacity given by the dashed line in the upper panel. The bit energy for the maximum capacity, denoted by the dotted line in the upper panel, occurs for an arbitrarily large bias current and an arbitrarily large bit-energy; it is not shown.

8. DISCUSSION

In the preceding we have quantitatively related function to structure, for a biophysical model of the blowfly photoreceptor and for an adaptive silicon photoreceptor. The models developed in the course of this work can be utilized to analyze tradeoffs between the system parameters and to understand which noise sources can be neglected under which operating conditions.

The capacity of the blowfly photoreceptor is higher for lower light levels but there is a cross-over point beyond which the silicon photoreceptor has higher capacity. The bit energy of the silicon photoreceptor depends on the bias current: it can be made arbitrarily high by increasing the bias current, but when it is restricted to use as much power as the blowfly photoreceptor, the silicon photoreceptor provides a lower capacity (and a higher bit energy). It is interesting to note that the silicon photoreceptor can obtain a lower bit energy than the blowfly photoreceptor. The bias current which provides minimum bit energy is approximately half the photocurrent. At this bias condition, the capacity is very low in comparison to the blowfly photoreceptor, as shown in Figure 3.

Traditional engineering philosophy might suggest biasing the feedback amplifier of the silicon photoreceptor with as

high a current as possible, to maximize the capacity and provide the highest gain. Our work suggests that this is not the most efficient approach when power consumption is a design constraint.

9. REFERENCES

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