

Fisher Information Quantifies Task-Specific Performance 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 formulate the response of the photoreceptor to incident flashes and determine the optimal detection performance using ideal observer analysis. Furthermore, we derive Fisher information contained in the output of the photoreceptor, and show how Fisher information is related to the detection performance. In addition we use Fisher information to show the connections between detection performance, signal-noise ratio, and discriminability. Our detailed biophysical model of the blowfly photoreceptor provides a rich framework for information-theoretic study of neural systems.

I. 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 [1]. 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 [2]. Relying on their visual input, flies can chase mates at turning velocities of more than $3000^\circ s^{-1}$ with delay time of less than $30 ms$ [3].

The marvelous 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. It is crucial to quantify information processing in neural systems for both purposes. Developed in the 1940s [4], 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 [5], [6], [7]. Information transmission rate has been measured in many neural systems [8], and information channel capacity has been estimated in fly photoreceptors [7]. 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 of the system 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 measurement of communication channel, we quantified the effect of individual components on information capacity in the blowfly photoreceptor [9].

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, which are determined using the detailed biophysical model of blowfly phototransduction. We formulate the response of the photoreceptor to incident flashes and compute the optimal detection performance using ideal observer analysis. Furthermore, we derive Fisher information contained in the output of the photoreceptor, and show that Fisher information is directly related to the detection performance. Therefore it quantifies task specific information.

The remainder of the paper is organized as follows, in Section II we briefly describe our blowfly photoreceptor model; in Section III we compute the information capacity using the model; in Section IV, we analyze flash detection using ideal observer analysis; in Section V we relate Fisher information to the optimal detection performance; in Section VI we discuss and summarize our work.

II. 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

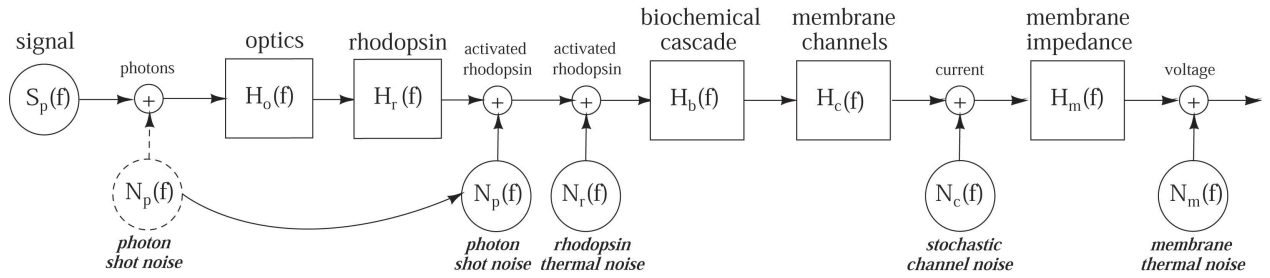


Fig. 1. Communication channel model of the blowfly photoreceptor.

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 [10]. In this investigation, we focus on the 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 by flies as incident light on their 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 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 photo-transduction 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 [11]. 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. 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. So it appears 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 [9]. Parameters of the model were estimated using experimental data as described in [9]. The extension of the model into the time domain was described in [12]. The entire model allows us to compute the response of the system to stimuli in the linear operating range.

III. MUTUAL INFORMATION AND INFORMATION CAPACITY

The use of entropy as a measure of information was first developed by Shannon [4]. Entropy is a measure of uncertainty of a random variable defined as $H(X) = E_{P(x)}[\log_2 1/P(X)]$, where $E[\cdot]$ is the expectation operator, and $P(x)$ is the probability mass function for a discrete random variable X or probability density function for a continuous random variable X . For each value x that X takes, it provides $\log_2 1/P(x)$ information in bits. The average uncertainty $H(X)$ specifies the required bits to perfectly encode the variable. Whereas entropy quantifies the uncertainty associated with one random variable, in many cases we are interested in how two or more random variables are related. Mutual information $I(X, Y)$ measures the amount of information one variable contains about the other, $I(X, Y) = E_{P(x,y)} \left[\log_2 \frac{P(X,Y)}{P(X)P(Y)} \right]$. $I(X, Y)$ can be written as

$$I(X, Y) = H(X) - H(X|Y) = H(Y) - H(Y|X), \quad (1)$$

thus the mutual information is the reduction in the uncertainty of one variable provided the other is known.

A discrete channel is defined as a system consisting of an input random variable X , an output random variable Y , and a probability function $P(y|x)$ that expresses the probability of observing the output y given the input x . The channel is said to be memoryless if the probability distribution of the output depends only on the current input and is conditionally independent of previous channel inputs or outputs given the current input. The information channel capacity of a discrete memoryless channel is defined as the maximum of the mutual information between the input and output over all possible input distributions.

$$C = \max_{P(x)} I(X, Y). \quad (2)$$

For an additive Gaussian noise channel, if there is no constraint on the input, the capacity of the channel is infinite. However, unconstrained inputs are physically implausible. The

most common limitation on the input is an energy or power constraint. We assume an average power constraint $E[X^2] \leq P$. The information capacity is therefore defined as

$$C = \max_{P(x): E[X^2] \leq P} I(X, Y). \quad (3)$$

The capacity of an additive Gaussian noise channel with a noise power spectrum $N(f)$ and a power constraint P can be determined according to the water-filling procedure [13]:

$$C = \int \frac{1}{2} \log_2 \left[1 + \frac{(\nu - N(f))^+}{N(f)} \right] df, \quad (4)$$

where ν is the total power spectrum of signal and noise. ν satisfies

$$\int (\nu - N(f))^+ df = P, \quad (5)$$

where $(x)^+ = x$ if $x \geq 0$, otherwise, $(x)^+ = 0$.

The biophysical model of phototransduction of Fig. 1 can be viewed as an additive Gaussian communication channel. We compute input-referred noise using the transfer function and noise sources introduced at each stage. We then apply (4) to compute the information capacity of the blowfly photoreceptor. This computation was performed at various incident light intensities, and the capacity is plotted as a function of incident light intensity in Fig. 2. In Fig. 2, the estimate of the information capacity computed directly from physiological measurements of transfer characteristics and noise is also shown as 'x's [7]. The dash 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.

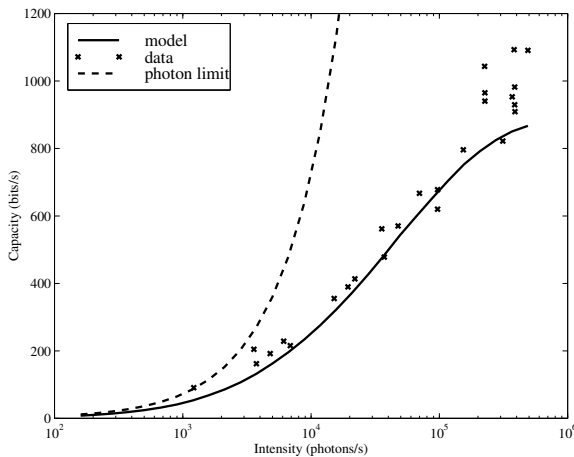


Fig. 2. Information capacity computed from our model and estimated from experimental data.

IV. FLASH DETECTION

The channel capacity given by (4) 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 does not inform us about 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 (i.e. the task is a two-alternative forced choice (2-AFC) task). We apply ideal observer analysis to quantify the optimal performance from the output of the system and later relate Fisher information to the detection performance.

A. 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. Photon arrival rate defines the background light intensity Λ 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 $n = \lambda \cdot T$. 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:

$$f(t) = \sum_{i=1}^n B(t - t_i), \quad (6)$$

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 [14]. We compute the mean system response as the expected system response to photons arriving during a flash:

$$E[f(t)] = E \left[\sum_{i=1}^n B(t - t_i) \right] = \sum_{i=1}^n E[B(t - t_i)]. \quad (7)$$

Photon arrival is a Poisson process. For this 2-AFC visual detection task the order of photon arrivals is irrelevant, so for a uniform flash with n photons in an interval, each arrival time is uniformly distributed in that period. Therefore each arrival time t_i , $i = 1, \dots, n$, satisfies:

$$P(t_i) = 1/T, \quad t_i \in [0, T]. \quad (8)$$

We compute the mean response to a single photon arrival as:

$$E[B(t - t_i)] = \int_0^t B(t - t_i) P(t_i) dt_i \quad (9)$$

$$= \int_0^t B(t - t_i) \cdot 1/T dt_i. \quad (10)$$

Then we compute the mean response to the photon stream as:

$$\begin{aligned} \bar{m}(\lambda, t) = E[f(t)] &= \lambda T \int_0^t B(t - t_i) \cdot 1/T dt_i \quad (11) \\ &= \lambda m'(t, T) \quad (12) \end{aligned}$$

where

$$m'(t, T) = \begin{cases} 0 & \text{if } t \leq 0 \\ \int_0^t B(t - t_i) dt_i & \text{if } 0 < t \leq T \\ \int_0^T B(t - t_i) dt_i & \text{if } t > T \end{cases} \quad (13)$$

Thus we see that the mean response is a linear function of the flash intensity λ because $m'(t, T)$ is determined by the background light level and flash duration. This agrees with our linear model.

B. Ideal observer analysis on 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 can be used to quantify the best possible performance of the system as it relates to that task. Therefore, ideal observer analysis applied to 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 [15], [16].

We apply ideal observer analysis to the photoreceptor model described above in the 2-AFC detection of flashes. 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 a vector $\vec{v} \in \mathbb{R}^k$, $\vec{v} = [v_0, v_1, \dots, v_{k-1}]$, from the uniformly sampled membrane voltage at the synaptic terminal of the photoreceptor over the interval. The ideal observer determines the presence or absence of the flash stimulus in the test interval optimally by minimizing detection error given the observation vector.

A test statistic d is computed according to [17]:

$$d^2 = \vec{m}(\lambda)^T \Sigma^{-1} \vec{m}(\lambda) \quad (14)$$

where $\vec{m}(\lambda)$ is the mean observation vector for a flash stimulus with duration T and intensity λ and Σ is the covariance matrix of the observation. $\vec{m}(\lambda)$ is obtained by uniformly sampling the mean response $\bar{m}(\lambda, t)$ over the interval $[0, T]$. From (12) we compute

$$\vec{m}(\lambda) = \lambda \vec{m}' \quad (15)$$

where \vec{m}' is a vector from the sampled function of $m'(t, T)$ in $[0, T]$ 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 $\vec{m}(\lambda)$ 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 (WSS) 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 [17]:

$$\Pr(\text{error}) = 1 - \Phi(d/2) \quad (16)$$

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 [12].

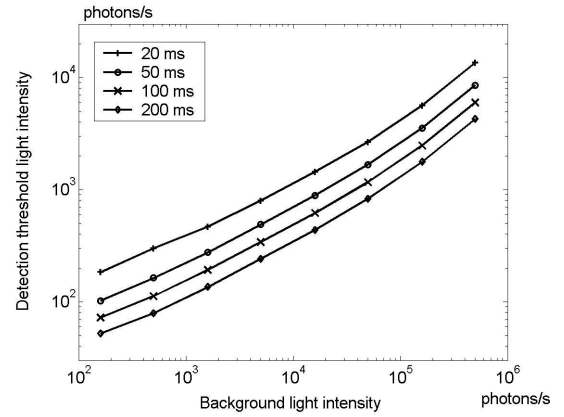


Fig. 3. Performance of the ideal observer on the 2-AFC flash detection task under different background light intensities and for different flash durations in the photoreceptor system.

The optimal performance is specified by the test statistic d , which directly quantifies the detection threshold and provides a comparison for the detection performance of different systems or a system at different operating points.

V. 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 which the probability distribution of X depends. It has been shown that Fisher information limits the accuracy of signal estimation according to Cramér-Rao bound [17],

$$\text{Var}_\theta[\hat{\theta}(X)] \geq \frac{\left\{ \frac{\partial}{\partial \theta} E[\hat{\theta}(X)] \right\}^2}{I_F(\theta)}, \quad (17)$$

where

$$I_F(\theta) \triangleq E \left[\left(\frac{\partial}{\partial \theta} \log P_\theta(X) \right)^2 \right]. \quad (18)$$

$\hat{\theta}(X)$ is the estimate of parameter θ from observations of the random variable X . $P_\theta(X)$ is the probability density function of X conditioned on θ .

At a given background light level Λ , the photoreceptor system can be modeled as a linear system with responses varying around the operating point set by the background

light level. The background light 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 as described in section II, the observation vector follows the multidimensional Gaussian distribution:

$$P(\vec{v}|\lambda) = \frac{1}{(2\pi)^{\frac{k}{2}}|\Sigma|^{\frac{1}{2}}} \exp \left[-\frac{1}{2}(\vec{v} - \vec{m}(\lambda))^T \Sigma^{-1}(\vec{v} - \vec{m}(\lambda)) \right] \quad (19)$$

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 solely determined by λ for a given background light and flash duration. This allow us to compute the Fisher information at the synaptic terminal using the distribution of the membrane voltage vector.

$$\frac{\partial \ln P(\vec{v}|\lambda)}{\partial \lambda} = \frac{\partial}{\partial \lambda} \left[-\frac{1}{2}(\vec{v} - \lambda \vec{m}')^T \Sigma^{-1}(\vec{v} - \lambda \vec{m}') \right] \quad (20)$$

$$= -\frac{1}{2} \left[-\vec{v}^T \Sigma^{-1} \vec{m}' - \vec{m}'^T \Sigma^{-1} \vec{v} \right] - \vec{m}'^T \Sigma^{-1} \vec{m}' \quad (21)$$

$$= \vec{v}^T \Sigma^{-1} \vec{m}' - \vec{m}'^T \Sigma^{-1} \vec{m}' \quad (22)$$

$$= (\vec{v} - \lambda \vec{m}')^T \Sigma^{-1} \vec{m}' \quad (23)$$

$$= (\vec{v} - \vec{m}(\lambda))^T \Sigma^{-1} \vec{m}' \quad (24)$$

$$I_F(\lambda) = \int_{\mathbb{R}^k} P(\vec{v}|\lambda) \left(\frac{\partial \ln P(\vec{v}|\lambda)}{\partial \lambda} \right)^2 d\vec{v} \quad (25)$$

$$= \vec{m}'^T (\Sigma^{-1})^T \left[\int_{\mathbb{R}^k} P(\vec{v}|\lambda) (\vec{v} - \vec{m}(\lambda)) (\vec{v} - \vec{m}(\lambda))^T dt \right] \Sigma^{-1} \vec{m}' \quad (26)$$

$$= \vec{m}'^T (\Sigma^{-1})^T \Sigma \Sigma^{-1} \vec{m}' \quad (27)$$

$$= \vec{m}'^T \Sigma^{-1} \vec{m}' \quad (28)$$

$$= \frac{1}{\lambda^2} \vec{m}(\lambda)^T \Sigma^{-1} \vec{m}(\lambda) \quad (29)$$

$$= \frac{d^2}{\lambda^2} \quad (30)$$

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

$$\Pr(\text{error}) = 1 - \Phi \left(\frac{1}{2} \lambda \sqrt{I_F(\lambda)} \right). \quad (31)$$

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 detection task.

From (28) we see that Fisher information can be computed by \vec{m}' and Σ which are functions of background light level and flash duration T . \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 Λ , and remains the same for different flash intensities λ ; we will write it as $I_F(\Lambda)$ 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

$$\lambda_{min} = \frac{d_{25\%}}{\sqrt{I_F(\Lambda)}}, \quad (32)$$

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.

VI. DISCUSSION

In the preceding section we have shown that Fisher information relates directly to detection performance. It is also related to basic characteristics of signal and noise. One fundamental property of Fisher information can be elucidated by considering the simple case where the noise at each sampling point is independent and identically distributed (i.i.d.) Gaussian $N(0, \sigma^2)$ of zero mean and variance σ^2 . Here the covariance matrix Σ of noise is $\sigma^2 I$ where I denotes the $k \times k$ identity matrix. In this case,

$$\lambda^2 I_F(\Lambda) = \vec{m}(\lambda)^T \Sigma^{-1} \vec{m}(\lambda) = \frac{\vec{m}(\lambda)^T \vec{m}(\lambda)}{\sigma^2} = k \frac{\overline{m^2}}{\sigma^2}, \quad (33)$$

where $\overline{m^2}$ is the average signal power defined as $\frac{1}{k} \sum_{i=0}^{k-1} m_i^2$. Note that σ^2 is the average noise power, so that $\lambda^2 I_F(\Lambda)$ is equivalent to the signal-noise ratio (SNR) times the number of samples. For a given λ , the higher the SNR is, the higher the Fisher information.

Fisher information also serves as a link between optimal detection and optimal parameter estimation. The ideal observer performs optimal parameter estimation of λ in the sense that it minimizes the expected estimation error. Given the conditional distribution of the observation vector $P(\vec{v}|\lambda)$, the minimum estimation variance is obtained from the Cramér-Rao bound,

$$\sigma^2(\hat{\lambda}) = \frac{1}{I_F(\Lambda)}. \quad (34)$$

The discriminability of a signal depends on the separation between the signal and its absence and the spread of the signal. The bigger the separation is, the easier the discrimination; the smaller the spread is, the easier the discrimination. A common measure of discriminability is defined by the ratio of the separation to the spread. In the case of flash discrimination, it is written as:

$$d' = \frac{\lambda}{\sigma(\hat{\lambda})}. \quad (35)$$

Replacing $\sigma(\hat{\lambda})$ from (34) we see that d' is equal to the detection statistic d obtained for the optimal detection. Thus the detection performance and the signal characteristics are also connected through Fisher information.

In this paper, we have extended the information-theoretic investigation of neural systems using the framework provided by a detailed biophysical model of blowfly photoreceptors. Specifically, we perform ideal observer analysis of flash detection in the photoreceptor model. We demonstrate that Fisher information is an information measure that quantifies performance in a specific task. We also show how the detection performance is connected to signal characteristics such as SNR and discriminability through Fisher information. In our future work, we will investigate in further detail how the individual components in the photoreceptor model and their biophysical parameters contribute to the Fisher information.

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