WORKSHOP PAPER

Sensory coding in the vertebrate retina: towards an adaptive control of visual sensitivity*

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Abstract. We propose a theoretical framework for the adaptive control of visual sensitivity in the vertebrate retina. The photoreceptor transfer function is modelled with a Michaelis–Menten law instead of a logarithmic function. This more plausible function has a biophysical correlate, and it allows consideration of the photoreceptor as the main locus of retinal adaptation. The retinal model suggests that the function of photoreceptors might be to control visual sensitivity, defined as the optimal transcoding of non-stationary visual information. This is done by using an adaptive transfer function whose parameters are spatiotemporally and locally estimated by the subsequent retinal circuit and fed back to the photoreceptors. The proposed model also supports the functional architecture of the vertebrate retina.

1. Introduction

The vertebrate visual system must deal with a large range of light intensities, as many as 10 log units between the absolute visual threshold and the light intensity provided by a summer day. It is composed of numerous nonlinear neural units organized in several layers, and receives a large spatial array of temporal inputs from the environment. Both the nonlinearity of neural units and the unknown dynamic ranges of the input array require the presence of some locally adaptive mechanisms in the transfer function. Given a nonlinear input–output relation of the visual processing the general problem of optimal sensory coding is to find the laws for the adaptation of parameters which state the range of the input signals which are optimally coded. Expressing the control of sensitivity in these terms raises two questions: how to choose the neural function (and its parameters), and how to control the parameters for obtaining an optimal sensory coding? In this paper we specifically address the former question at the photoreceptor level, and we suggest a function of the subsequent retinal network for the latter.

Although it is known that visual adaptation is one of the prominent functions of the vertebrate retina [1], it still remains unclear exactly where and how it occurs [2]. The photoreceptor is thought to be the main retinal locus where adaptation is essentially done [3]. But despite the recent molecular understanding of the enzymatic cascade leading to phototransduction in vertebrate photoreceptors [4], we still have little understanding of how the photoreceptor is involved in visual adaptation. Like other neurons, photoreceptors are nonlinear: their response range is limited, and they exhibit linear characteristics only

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over a small part of their operating range (one or two log units). They must also deal with unknown and varying light conditions which cannot be adequately perceived with the restricted range of linear processing. Although the logarithm provides considerable advantages in the coding of visual information, it only performs a static compression and its output range is infinite. Therefore it is neither a physically plausible nor adequate model of phototransduction. Indeed, from a neurophysiological viewpoint the photoreceptor function is better described by the Fechner law, which has a sigmoidal shape on a log scale. In this case, the control of visual sensitivity can be realized by horizontally shifting the sigmoidal function according to the mean level of light intensity, and by adjusting the slope in its 'linear' part according to the variance in the intensities.
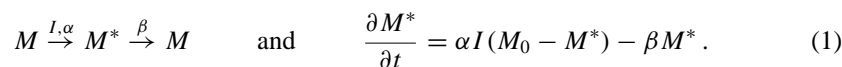
Consequently, in order to warrant an invariant perception in spite of continuous temporal and spatial changes in light conditions, photoreceptors should be strongly involved in optimally coding visual information; not only in morphological terms but also in functional terms: in other words, they must adapt according to statistical properties of the visual world which have to be estimated *locally* in order to take into account the temporal non-stationarity and the spatial inhomogeneity of the visual signal. This raises the question of how to actually estimate the statistical parameters of the input signal. In order to tackle these problems, we propose a photosensor model that is based on biophysical principles (section 2) and that shares important properties with vertebrate photoreceptors:

(i)   It compresses the input signal according to a Michaelis–Menten law (subsection 3.1).
(ii) It performs in a fast dynamics an adaptive spatiotemporal low-pass filtering which depends on the local signal-to-noise ratio (subsection 3.2).
(iii) It adapts to the changes of ambient light intensity in a slow dynamics by appropriate adjustments of the parameters of the Michaelis–Menten law (subsection 3.3).
(iv) It obeys the Weber and Fechner laws, and the shift property (subsections 3.4 and 3.5).
(v)   It works in synergy with the subsequent retinal network which it supplies with the neural signals necessary to adapt its nonlinear transfer function (section 4).

This engineering model demonstrates the advantages of these basic principles in visual adaptation. Finally it also lies within a spatiotemporal and structurally coherent model of the vertebrate retina whose function is the control of visual sensitivity.

2. A biophysical first-order model of phototransduction

Transduction in vertebrate photoreceptors includes detection, amplification and neural coding of the photonic signal. Most of the mechanisms involved are well known [4]: at a molecular level they can be described and modelled by a cascade of enzymatic reactions. As stated previously, phototranduction is a complex process, and we will therefore limit our scope to the membrane stage of transduction, that is to the action of a light-dependent messenger onto membrane channels which account for the generation of presynaptic potential. The law of mass action allows one to consider the following enzymatic reaction and its mathematical expression for modelling the binding of the internal messager onto a membrane channel:

$$M \overset{I,\alpha}{\to} M^* \overset{\beta}{\to} M \qquad \text{and} \qquad \frac{\partial M^*}{\partial t} = \alpha I (M_0 - M^*) - \beta M^* . \qquad (1)$$

These equations express the transformation of the molecule M (the receptor) into another M^* (e.g. an activated form) under the influence of a catalyst I (the ligand) at a rate α, and its free reformation at a rate β, assuming a constant total amount of the molecule (active and inactive forms), that is $[M] + [M^*] = [M_0]$. This enzymatic reaction can be mapped
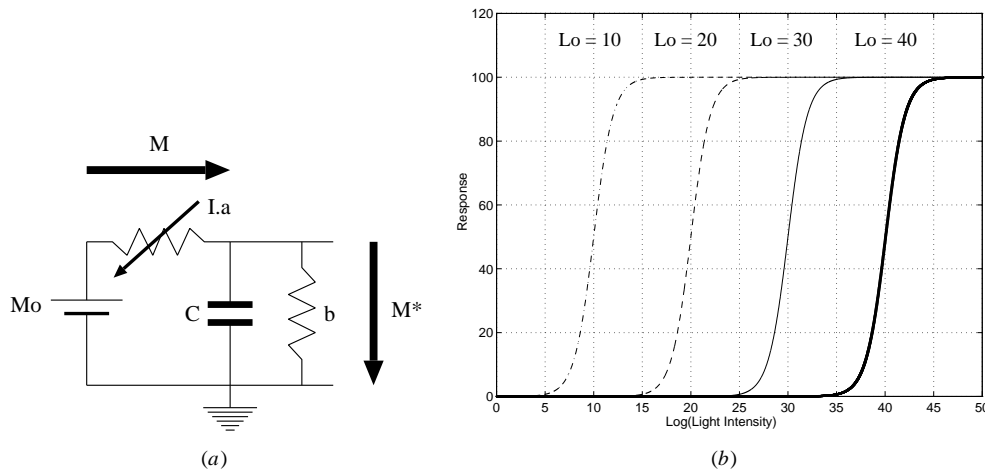
Figure 1. (*a*) Electrical model of the photoreceptor (see text for explanation). (*b*) The shift property of the Fechner law $V = f(\log I)$ for four values of $L_0 = \log(I_0)$.

onto an electrical circuit in which M, M^* and M_0 denote voltages (figure 1(*a*)): if β is related to the ratio b/C where b is a leakage conductance, C to a membrane capacity, M_0 to a potential generator, and α to the ratio a/C where a is a conductance modulated by the input signal I, equations (1) express the dynamics of our photosensor in which M^* takes the place of the receptor potential V. Despite its simplicity, this model can account for several properties well suited for adaptation to a varying visual environment.

3. Some basic properties

3.1. The Michaelis–Menten law

This model expresses an overall property of photoreceptors: their nonlinear and compressive transfer function. Particularly when stimulated with a constant light intensity I, equation (1) shows two basic properties: (i) its fast dynamics exhibits a temporal low-pass filtering of the input signal with a time constant (up to several tens of milliseconds) being inversely proportional to light intensity I, and (ii) the response at steady state follows a Michaelis–Menten law:

$$V(I) = \frac{I V_{\text{max}}}{I + \sigma} \qquad \text{with } \sigma = \frac{\beta}{\alpha} \tag{2}$$

where V_{max} is the saturation value of the potential equal to M_0, and σ is a dissociation constant which acts on the compression effect. This relation becomes quasi-linear with a slope V_{max}/σ when $I \ll \sigma$, and converges towards V_{max} when $\sigma \ll I$. Such an intensity–response relation has been observed in direct photocurrent measurement as well as in voltage recording in cone outer segments of salamander and turtle [5].

3.2. Local adaptive spatiotemporal regularization

A photoreceptor is actually always surrounded by other photoreceptors, and there exists in some vertebrate species an electrical coupling between neighbouring cones [7]. This coupling takes place at the level of the basal terminal of photoreceptors where the membrane
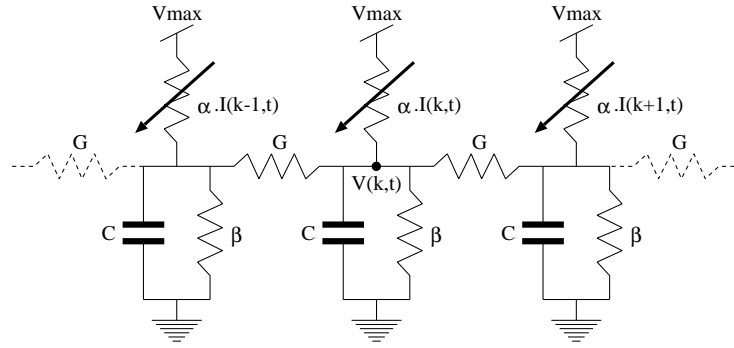
Figure 2. Resistive and capacitive network provided by the coupling between neighbouring cones through a conductance G. Due to the intensity dependence of the input conductance, this network is nonlinear: the time and space constants depend locally on the input signal.

potential V appears. The effect of this coupling simply is a connection of nodes V of neighbouring photoreceptors with a conductance G, leading to a resistive and capacitive network driven by a nonlinear input conductance αI (figure 2). Beyond the compressive nonlinearity, the multiplicative effect of the input signal I on the conductance α (figure 1(a)) implies that the spatiotemporal low-pass filtering performed by the resulting photoreceptor layer is modulated in a coherent way by light intensity: indeed, derivation of the nonlinear transfer function of this network shows that its space and time constants are given by $G/(\alpha I)$ and $C/(\alpha I)$, respectively. The input signal is then integrated within a spatiotemporal window whose size is inversely proportional to the light intensity. When one recalls that the signal-to-noise ratio decreases with light intensity, the advantage of such a solution becomes clearer: the dependence of space and time constants with light intensity is such that it allows the system to thwart the influence of spatiotemporal noise whatever the light conditions, as suggested in [8, 9]. In that way, as early as the first neural layer of the retina, the notion of *local adaptive spatiotemporal regularization* appears naturally.

3.3. Optimal sensory coding

Optimal sensory coding must occur as early as at the photoreceptor level. This implies an optimal representation of the input range of light intensity onto the response range of the photoreceptor: in order to achieve this optimization we use the simpler criterion of maximizing the sensitivity S of the system, defined as the slope of equation (2) between $I_0 - \Delta I$ and $I_0 + \Delta I$ where I_0 and ΔI denote the mean and standard deviation of the input signal, respectively. Maximizing S according to σ leads to its optimal value:

$$\sigma_{\text{opt}} = \sqrt{I_0^2 - \Delta I^2} \qquad \text{and} \qquad \sigma_{\text{opt}} \simeq I_0 \qquad \text{when } \Delta I \ll I_0. \tag{3}$$

Thus, optimal sensory coding can be achieved by adjusting with a slow dynamics (with time constants up to the order of several minutes) the parameter σ of the photoreceptor transfer function according to the mean I_0 and the standard deviation ΔI of light intensity.

3.4. The Weber law

Let us now consider that the photoreceptor temporally adapts but slowly compared to its temporal low-pass behaviour to a background stimulus I_0 according to equation (3)

when $\Delta I \ll I_0$. After visual adaptation which produces at first a transient response, its response tends to converge towards $\frac{1}{2} V_{\max}$ and this independently of the stimulus I_0. Then, detectability of an increment ΔI is achieved if $V(I_0 + \Delta I)$ exceeds a threshold Γ larger than $V_{\max}/2$. We can show that for these conditions the model obeys the Weber law [6], one of the basic psychophysical laws of light adaptation which expresses the constancy of the ratio $\Delta I / I_0$.

3.5. The Fechner law and the shift property

If we assume a Michaelis–Menten law which satisfies the Weber law (i.e. $\sigma_{\mathrm{opt}} \simeq I_0$), we can also express it as a function of the logarithm L of the light intensity I:

$$V(L) = V_{\max}/(1 + \exp(L_0 - L)).\tag{4}$$

This expression describes a sigmoid curve which shares some properties with another well known psychophysical law, the Fechner law: there exists a medium range of intensities, above the very small values and below the very large values, for which the response curve can be approximated by $V(L) = A \log L$ (figure 1(*b*)). In accordance with the criterion of maximization of the sensitivity and for $\Delta I \ll I_0$, we finally obtain a horizontal translation of this sigmoid according to L_0 (figure 1(*b*)). Thus, adaptation of σ with respect to the mean intensity provides the shift property in agreement with measurements of cone intracellular responses and in a more general way with sensory responses [1].

4. The photoreceptors in the retinal circuit

The first-order photoreceptor model we propose shows some basic properties for light adaptation. But in order to achieve this function the model requires a strong relation (see equation (3)) between some parameters of the photoreceptor transfer function and some statistical properties of the input signal. The electrical analogue of the Michaelis–Menten law (figure 1(*a*)) which could be considered as a membrane model for generating receptor potentials suggests a neurobiologically plausible mechanism to perform such a modulation of the photoreceptor transfer function: the leakage conductance β of the membrane might be modulated by a signal related to the mean and standard deviation of light intensity. These statistical parameters need to be estimated since they are not spatiotemporally constant in non-stationary environments. This raises the question of how these statistical parameters could be estimated. Since there is no linear measure of intensity available, the statistics cannot be derived directly and can only be based on the nonlinear photoreceptor output. A smarter and more natural solution is nonlinear feedback: the statistical parameters can be estimated from the photoreceptor output (i.e. the compressed signal) and fed back after expansion in terms of a modulation of essential photoreceptor parameters. A block diagram of the suggested structure is shown in figure 3, which in the following is compared to the typical neural structure of the vertebrate retina:

(i) the photoreceptor transduces light and compresses the resulting signal according to the estimates of the spatiotemporal mean $\hat{I}$ and the standard deviation $\Delta \hat{I}$;

(ii) the horizontal cells layer performs a spatiotemporal low-pass filtering of the photoreceptor output I, thus providing an estimate of the mean $\hat{I}$ through an inhibitory synaptic feedback by modulating the photoreceptor membrane conductance β;

(iii) bipolar cells receive the linear difference between photoreceptors and horizontal cells outputs, that is the instantaneous deviation $I - \hat{I}$;
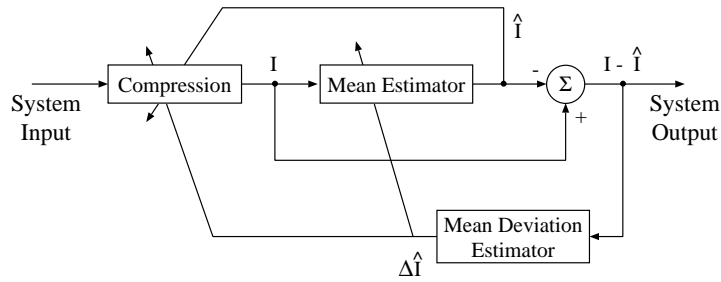
Figure 3. Structure provided by information theory in which estimation of the statistical parameters is made downstream of the photoreceptive compression. The modulation of the photoreceptor transfer function is realized through expansive feedbacks.

(iv) this signal is then rectified and spatiotemporally integrated by sustained amacrine cells which provide a signal related to the standard deviation $\Delta \hat{I}$ to dopaminergic cells; and finally

(v) these last cells release a neuromodulatory substance, dopamine, which reaches several sites [10] (e.g. photoreceptors and horizontal cells) where it modulates compression and mean estimation stages.

There are several theoretical reasons for the modulation of the mean estimator with a feedback signal: firstly, the theory of optimal filtering suggests, in order to obtain the best 'prediction', that the window size of the mean estimation should depend on the signal-to-noise ratio [11]. Thus the measurement of the prediction error by the bipolar cell could provide a means of adjusting the mean estimation. Secondly, optimal transcoding at the level of bipolar cells could also occur due to their nonlinear responses. But in this case, it can be performed by modulating the horizontal cell signal with the mean of the rectified bipolar output corresponding to the standard deviation estimation $\Delta \hat{I}$ [6].

It must also be noted that the precise nature of feedbacks in the model cannot be specified further without explicitly describing the relations between input and output statistics including some knowledge about the nature of the input signal (e.g. its probability density).

5. Conclusion

In summary the control of the visual sensitivity could be performed by an adaptive photoreceptor whose parameters should be spatiotemporally and locally estimated by the subsequent retinal circuit: we have proposed a model of the photoreceptor which links the Michaelis–Menten, Weber and Fechner laws, and which provides an optimal sensory coding according to the statistical properties of the input signal. These statistical characteristics are estimated by the subsequent retinal network and fed back onto the photoreceptor in order to adjust its nonlinear transfer function. Moreover, its nonlinearity also induces a spatiotemporal filtering, locally adapted to the characteristics of light signals. This biologically plausible model clarifies the role of the retina in visual adaptation and points out some of the neural strategies involved in this mechanism [6]: fast local synaptic feedbacks to adjust the photoreceptor response around the local spatiotemporal mean, and slow neurohormonal feedbacks to enhance the sensitivity of bipolar cells response according to the slow (light/dark) change from a non-stationary environment. Consequently, as claimed in [2], rather than functioning independently, each photoreceptor is an integral part of an

elaborate synaptic network. However, the possibility that these mechanisms are also present inside a single photoreceptor should not be excluded, since single photoreceptors already show temporal adaptation [3].

Acknowledgments

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