ADAPTIVE SPATIOTEMPORAL FILTERING BY A NEUROMORPHIC MODEL OF THE VERTEBRATE RETINA

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ABSTRACT

We propose a theoretical framework of the adaptive control of visual sensitivity performed by the vertebrate retina. Instead of a logarithmic function, the photoreceptor transfer function is modelled with a *Michaelis-Menten* law which has a more plausible biophysical correlate. We show that the neural and functional architecture of the retina supports the requirements for an optimal transcoding of non-stationary visual information: This control of visual sensitivity is done by using an adaptive transfer function whose parameters are spatiotemporally and locally estimated by the subsequent retinal circuit and fed back at the level of photoreceptors. Although the use of the resulting model remains limited in the context of digital image processing, it provides a good structural framework for an analog VLSI implementation of an adaptive spatiotemporal neuromorphic retina.

1. INTRODUCTION

In digital image processing, the visual signal is first of all sampled in space and time and quantized through an analog-to-digital conversion. This conversion requires to define the number of quantizing levels of the luminance, and the type of quantization (linear or nonlinear). However these parameters should depend on some characteristics of the input signal, more particularly its dynamic range and signal-to-noise ratio which are spatiotemporally fluctuating due to the non-stationarity of a real image. But in practice, these parameters are fixed globally for a given image, introduce quantization errors which can have some bad consequences on further digital filtering, and limit the performance of the system.

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. The limited operating range (one or two log units) of its processing units, the neurons, and the unknown dynamic ranges of the visual input compel some local and adaptive mechanisms in the image processing performed by the visual system. There are a lot of evidence for the basic role of photoreceptors in such a performance [1], but it still remains unclear where and how exactly the visual adaptation occurs [2]. Due to their limited response range, photoreceptors are linear over a very narrow part of their operating range. They must 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. The photoreceptor function must be more "natural", that is able to adapt according to some 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.

We suggest in this paper a non-linear extension at the photoreceptor level of the linear neuromorphic model of the spatiotemporal processing performed by the vertebrate retina we already proposed so as to perform a time-continuous enhancement of spatiotemporal contrasts [3]. This last model assumed no particular hypothesis on the photoreceptor, whereas this new model shares important properties with the vertebrate photoreceptors [4]: It compresses the input signal according to a Michaelis-Menten law (section 2); It performs in a fast dynamics an adaptive spatiotemporal low-pass filtering which depends on the local signal-

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to-noise ratio (section 3); It adapts to the changes of ambient light intensity in a slow dynamics by appropriate adjustments of the parameters of the Michaelis-Menten law (section 4); It achieves the Weber-Fechner law and the shift property (section 5); It works in synergy with the subsequent retinal network which supplies it with the neural signals necessary to adapt its non-linear transfer function (section 6).

This spatiotemporal and structurally coherent model demonstrates the advantages of the principles for the control of visual sensitivity found in the biological retina, and provide a theoretical and practical framework for adaptation in spatiotemporal image processing.

2. THE MICHAELIS-MENTEN LAW

By considering the biophysics of phototransduction [5], we can show that the last stage of the transduction, the neural coding of the photonic signal, consists in a compression with the electrical analogue shown in figure 1 [4]. The building-block of this circuit stands for the membrane of the photoreceptor cell where $V(k,t)$ denotes the neural response of photoreceptor k at time t, V_{max} its maximum response, β the membrane leakage conductance, C membrane capacitance, $\alpha \cdot I(k,t)$ the input conductance driven by the input signal $I(k,t)$ related to the visual signal.

Despite its simplicity, this model can account for several properties well suited to adapt to a varying visual environment. Firstly, it expresses an overall property of the photoreceptor: its non-linear and compressive transfer function. Particularly when stimulated with a constant light intensity I, its response shows two basic properties [4]: (i) its fast dynamics exhibits a temporal low-pass filtering of input signal with a time constant inversely proportional to light intensity I, and (ii) the response at steady state follows a Michaelis-Menten law:

$$V(I) = \frac{I \cdot V_{max}}{I + \sigma} \quad \text{with} \quad \sigma = \frac{\beta}{\alpha} \qquad (1)$$

where 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 photo-current measurement as well as in voltage recording in cone outer segments of salamander and turtle.

3. LOCAL ADAPTIVE SPATIOTEMPORAL REGULARIZATION

A photoreceptor is actually always surrounded by other photoreceptors, and in most vertebrate species there exists an electrical coupling between neighboring cones [6]. This coupling takes place at the output stage of photoreceptors where the membrane potential V appears (figure 1), and it connects nodes V of neighboring photoreceptors with a conductance G, leading to a resistive and capacitive network driven by a non-linear input conductance $\alpha.I$. Beyond the compressive non-linearity presented in section 2, the multiplicative effect of the input signal I onto the conductance α implies a direct modulation by light intensity of the spatiotemporal low-pass filtering performed by the photoreceptor layer: indeed, derivation of the non-linear transfer function of this network shows that its space and time constants are given by $G/(\alpha I)$ and $C/(\alpha I)$, respectively.

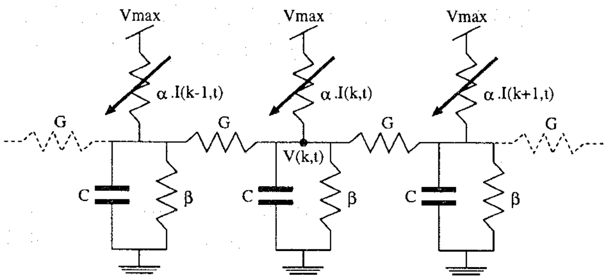

Figure 1: Electrical model of photoreceptors passively coupled: The coupling between neighboring cones through a conductance G provides a resistive and capacitive network. Due to the intensity-dependence of the input conductance, this network is non-linear: time and space constants depend locally on the input signal.

The advantages of such a non-linearity is not clearly obvious, but it means that the input signal is integrated within a spatiotemporal window whose size is inversely proportional to light intensity. It has a sense since the photonic absorption by the photoreceptors follows a *Poisson* law, so the signal-to-noise ratio increases proportionally with the light intensity. The presence of spatiotemporal noise in the visual input requires some filtering: In the case of a spatiotemporal low-pass filter provided by such a resistive and capacitive network, the theory of optimal filtering according to the Wiener-Hopf formula states that the regularization parameters, the time and space constants of this filter, should be inversely proportional to the signal-to-noise ratio. Taken together, these theoretical considerations suggest a particular dependence of the regularization parameters on the light intensity [4]. We can now understand the advantage of the non-linear filtering performed by the photoreceptor layer of the model: the dependence of space and time constants with light intensity allows the system to thwart the influence of spatiotemporal noise whatever the light conditions, as suggested in [7, 8]. In that way, as early as the first neural layer of the retina, a *local adaptive spatiotemporal regularization* naturally appears.

4. AN OPTIMAL SENSORY CODING

Since an optimal sensory coding must occur as early as at the photoreceptor level, the input range of light intensity must be optimally represented in 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 (1) between $I_o - \Delta I$ and $I_o + \Delta I$ where I_o and ΔI denote the mean and standard deviation of the input signal, respectively. Maximizing S according to σ leads to its optimal value:

$$\sigma_{opt} = \sqrt{I_o^2 - \Delta I^2} \qquad (2)$$

Thus, an optimal sensory coding can be achieved with a slow dynamics by adjusting the parameter σ of the photoreceptor transfer function according to the mean I_o and the standard deviation ΔI of light intensity. Section 6 suggests how these statistical parameters could be estimated.

5. WEBER-FECHNER LAW & CURVE SHIFTING

After visual adaptation which produces at first a transient response, the photoreceptor response to a background stimulus I_o tends to converge towards $V_{max}/2$ when $\Delta I \ll I_o$ according to Equations (1) and (2). Detectability of an increment ΔI is achieved if $V(I_o + \Delta I)$ exceeds a threshold Γ larger than $V_{max}/2$. We can show that for these conditions the model obeys the Weber law [4], one of the basic psychophysical laws of light adaptation which expresses the constancy of the ratio $\Delta I / I_o$.

If we assume a Michaelis-Menten law which satisfies the Weber law (i.e. $\sigma_{opt} \simeq I_o$), we can also express the steady-state response of the photoreceptor as a function of the logarithm L of the light intensity I:

$$V(L) = V_{max}/(1 + \exp(L_o - L)). \qquad (3)$$

This expression denotes 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 $V(L) = A \cdot \log L$. In accordance with the criterion of maximization of the sensitivity and for $\Delta I \ll I_o$, we finally obtain a horizontal translation of this sigmoid according to L_o (figure 2). Thus, adaptation of σ with respect to the mean intensity provides the shift property which is in agreement with measurements of cone intracellular responses and in a more general way with sensory responses [1]. Weber-Fechner law and shift property bring together a solution to the problem of the control of visual sensitivity – or optimal transcoding.

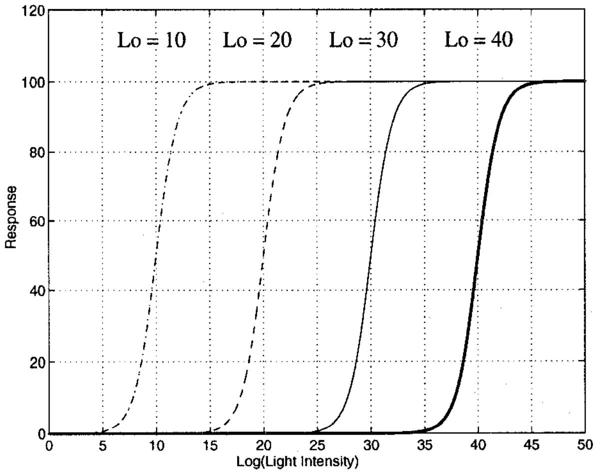

Figure 2: The shift property of the Fechner law $V = f(\log I)$ for 4 values of $L_o = \log(I_o)$.

6. FUNCTION OF THE RETINAL CIRCUIT

We previously stressed the need of a strong relation (see Equation (2)) between some parameters of the photoreceptor transfer function and some statistical properties of the input signal so as the photoreceptor model achieves its function in light adaptation. The electrical analogue of Michaelis-Menten law (figure 1) 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 non-linear photoreceptor output. An opportunist solution would use non-linear feedbacks: the statistical parameters could be indeed estimated from the compressed output of photoreceptors and fed back after expansion in terms of a modu-

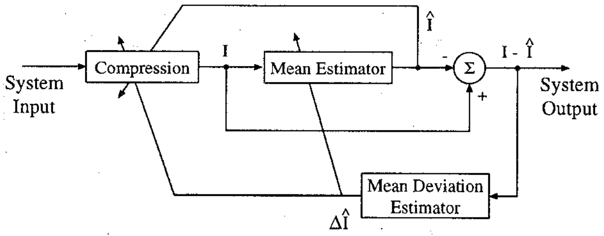

Figure 3: Structure provided by the information theory in which estimation of the statistical parameters is made downstream the photoreceptive compression. The modulation of the photoreceptor transfer function is realized through expansive feedbacks.

lation of essential photoreceptor parameters. A block diagram of the suggested structure is shown figure 3. This structure lies on the linear retinal model already proposed in [3] but with the addition of some feedbacks which are biologically strongly plausible [4]:

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

(ii) a second stage performs a spatiotemporal lowpass filtering of the photoreceptor output I, providing an estimate of the mean $\hat{I}$ through a feedback modulating the photoreceptor membrane conductance β;

(iii) a third stage receives the linear difference between photoreceptors and horizontal cells outputs, that is the instantaneous deviation $I - \hat{I}$;

(iv) this signal is then rectified and spatiotemporally integrated by a fourth stage which provides a signal related to the standard deviation $\Delta\hat{I}$, which modulates the compression and mean estimation stages.

The modulation of the mean estimator with the standard deviation estimation can be theoretically motivated according to a criterion of optimal filtering so as to estimate the best mean [9] or to match the limited bandwidth of the system output [4]. 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 input signal (e.g., its probability density).

7. 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 proposed a model of the photoreceptor which links Michaelis-Menten and Weber-Fechner laws, and 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 non-linear transfer function. Moreover, its non-linearity also induces a spatiotemporal filtering, locally adapted to the characteristics of light signals.

This theoretical framework of visual adaptation is particularly well suited for an analog VLSI implementation in which the building-blocks are intrinsically non-linear. Such a neuromorphic system was already designed and is patent pending.

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