

On the function of the retinal bipolar cell in early vision

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Abstract: The retinal bipolar cell is the most distal neuron which exhibits a center-surround receptive field in the vertebrate visual systems. The function of the bipolar cell was revealed in terms of an equivalent electric circuit model derived from previous physiological observations and the standard regularization problem, which is known as a computational framework of early vision. The response of bipolar cell was found to minimize a cost function consisting of two terms which relate to the second derivative and the smoothing of images.

1 Introduction

The retina plays important role in early vision. Previous physiological and morphological studies have revealed that the visual information processing is carried out by synaptic interactions between neural syncytia in the lower vertebrate retina. Thus, it is important to elucidate the spatio-temporal properties of the interacting multiple layers of syncytium. To date, the interaction between red cone and H1 horizontal cell syncytia has been described with analytical solutions by distributed models ^{[1][2]}, and discrete model ^[3]. Here, we propose the discrete model consisting of the red cone, the H1 horizontal cell and the bipolar cell. The discrete model has an advantage when we study the electrical properties of the response in relation to cell dimensions and cell spacings, which are critical parameters to determine a spatial resolution. The retinal bipolar cell is the most distal neuron which exhibits a center-surround receptive field in the vertebrate visual systems. We elucidate the function of the bipolar cell in terms of an equivalent electric circuit model derived from previous physiological observations and the standard regularization problem, which is known as a computational framework of early vision.

2 Modeling of distal retina circuit

In the distal part of the lower vertebrate retina, photoreceptors, horizontal cells and bipolar cells constitute the first network of visual information processing. Some of neurons are frequently coupled electrically and constitute a continual structure, syncytium. A typical example of such structure is seen in

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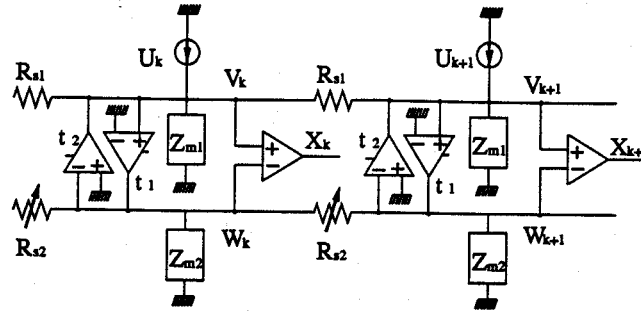


Fig. 1 An equivalent electric circuit model of the outer retina.

the network consisting of the red cone and the H1 horizontal cell. We propose an equivalent electrical circuit model of such network ^[3] (Fig. 1). Impedances $Z_{m1}(s)$, $Z_{m2}(s)$ and $Z_{m3}(s)$ represent membranes of the red cone, the H1 horizontal cell and bipolar cells, respectively. The coupling resistance connecting neighbouring cells of the red cone is represented by R_{s1} and that of the H1 horizontal cell by R_{s2} . A strength of synaptic input from the red cone to the H1 horizontal cell is expressed by t_1 and that from the H1 horizontal cell to the red cone t_2 . t_2 takes a negative value, since it is negative feedback ^[4]

A strength of synaptic input from the red cone to the bipolar cell is expressed by t_3 and that from the H1 horizontal cell to the bipolar cell t_4 . $t_3 \times t_4$ takes a negative value ^[5].

We calculate dynamical properties of electrical signals of the network in which neurons are arranged in an one-dimensional array, for simplicity. The one-dimensional model describes the voltage response to an image which is homologous in one direction, *e.g.*, a long narrow slit (Lamb, 1976).

We will consider n neurons which are numbered $1, \dots, n$ for each layer. Let us denote light-induced current and voltage distributions of the red cone, the H1 horizontal cell and the bipolar cells by vectors \mathbf{u} , \mathbf{v} , \mathbf{w} and \mathbf{x} which are

$$\mathbf{u} = \begin{pmatrix} U_1(s) \\ U_2(s) \\ \vdots \\ U_n(s) \end{pmatrix}, \quad \mathbf{v} = \begin{pmatrix} V_1(s) \\ V_2(s) \\ \vdots \\ V_n(s) \end{pmatrix}, \quad \mathbf{w} = \begin{pmatrix} W_1(s) \\ W_2(s) \\ \vdots \\ W_n(s) \end{pmatrix}, \quad \mathbf{x} = \begin{pmatrix} X_1(s) \\ X_2(s) \\ \vdots \\ X_n(s) \end{pmatrix}.$$

Applying Kirchoff's Current Law at each node of the red cone and the H1 horizontal cell of Fig 1, we obtain a set of equations,

$$(\mathbf{C}_2 \mathbf{C}_1 - t_1 t_2 R_{s1} R_{s2} \mathbf{E}) \mathbf{v} = -R_{s1} \mathbf{C}_2 \mathbf{u}, \quad (1)$$

$$(\mathbf{C}_1 \mathbf{C}_2 - t_1 t_2 R_{s1} R_{s2} \mathbf{E}) \mathbf{w} = t_1 R_{s2} R_{s1} \mathbf{u}. \quad (2)$$

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Here, C_1 and C_2 are

$$C_1 = \begin{pmatrix} c_1 & 2 & & & 0 \\ 1 & c_1 & 1 & & \\ & \ddots & \ddots & \ddots & \\ & & 1 & c_1 & 1 \\ 0 & & & 1 & c_1 + 1 \end{pmatrix}, C_2 = \begin{pmatrix} c_2 & 2 & & & 0 \\ 1 & c_2 & 1 & & \\ & \ddots & \ddots & \ddots & \\ & & 1 & c_2 & 1 \\ 0 & & & 1 & c_2 + 1 \end{pmatrix},$$

$$c_1 = -(2 + \frac{R_{s1}}{Z_{m1}(s)}), \quad c_2 = -(2 + \frac{R_{s2}}{Z_{m2}(s)}).$$

and E is the identity matrix.

The response of the bipolar cell \mathbf{x} , is expressed as

$$X_k = t_3 Z_{m3} V_k + t_4 Z_{m3} W_k. \quad (3)$$

On combining (1),(2) and (3) , we obtain the following equation from which the voltage response of the bipolar cell are calculated.

$$(C_1 C_2 - t_1 t_2 R_{s1} R_{s2} E) \mathbf{x} = R_{s1} Z_{m3} (t_1 t_4 R_{s2} E - t_3 C_2) \mathbf{u}. \quad (4)$$

We will elucidate the functional significance of the response in the following section.

3 Standard regularization

Some of early vision problems are formalized by standard regularization methods [7], [6]. The standard regularization problem usually refers to the minimization of a cost function. Since neural circuits consist of discrete elements , neuron, it is convenient to formulate on a finite dimensional space [8], [9]. Thus, under the present assumptions, the regularization problem for the finite dimensional case is formalized by the minimization of

$$J(\mathbf{x}, \mathbf{d}, \lambda) = \|\mathbf{x} - \mathbf{d}\|^2 + \sum_{r=1}^P \begin{cases} \lambda_r \|\mathbf{L}^{\frac{r}{2}} \mathbf{x}\|^2 & r : \text{even} \\ \lambda_r \|\mathbf{DL}^{\frac{r-1}{2}} \mathbf{x}\|^2 & r : \text{odd} \end{cases} \quad (5)$$

$$\mathbf{D} = \begin{pmatrix} 1 & & & & 0 \\ -1 & 1 & & & \\ & \ddots & \ddots & \ddots & \\ & & -1 & 1 & \\ 0 & & & -1 & 1 \end{pmatrix}, \mathbf{L} = \begin{pmatrix} -2 & 1 & & & 0 \\ 1 & -2 & 1 & & \\ & \ddots & \ddots & \ddots & \\ & & 1 & -2 & 1 \\ 0 & & & 1 & -2 \end{pmatrix},$$

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which is referred to as p -th order regularization problem ^{[6], [9]}. The unique solution is obtained by the following Euler-Lagrange equation,

$$\mathbf{x} - \mathbf{d} + \sum_{r=1}^P (-1)^r \lambda_r \mathbf{L}^r \mathbf{x} = 0. \quad (6)$$

4 Function of the bipolar cell circuit

Now, let us compare equations (4) to (6). To calculate spatial distributions of the steady state response, membranes of red cone, H1 horizontal cell and bipolar cell are represented by pure resistances R_{m1} , R_{m2} and R_{m3} , respectively. Eliminating "boundary effects", we can rewrite C_1 and C_2 of equation (4) as

$$C_1 = L - \frac{g_{m1}}{g_{s1}} E, \quad C_2 = L - \frac{g_{m2}}{g_{s2}} E$$

where $g_{m1} = 1/R_{m1}$, $g_{m2} = 1/R_{m2}$, $g_{m3} = 1/R_{m3}$, $g_{s1} = 1/R_{s1}$ and $g_{s2} = 1/R_{s2}$. Accordingly, equation (4) can be rewritten to the form of (6). Namely, equation (4) is expressed as

$$\mathbf{x} - \mathbf{d} - \lambda_1 \mathbf{L} \mathbf{x} + \lambda_2 \mathbf{L}^2 \mathbf{x} = 0 \quad (7)$$

where

$$\lambda_1 = \frac{g_{m1}g_{s2} + g_{m2}g_{s1}}{g_{m1}g_{m2} - t_1t_2}, \quad \lambda_2 = \frac{g_{s1}g_{s2}}{g_{m1}g_{m2} - t_1t_2} \quad (8)$$

$$\mathbf{d} = R_0(-\mathbf{L} + \nu \mathbf{E})\mathbf{u} \quad (9)$$

$$R_0 = \frac{g_{s2}}{g_{m1}g_{m2} - t_1t_2} \frac{t_3}{g_{m3}}, \quad \nu = \frac{1}{g_{s2}} \left(g_{m2} + \frac{t_4}{t_3} t_1 \right) \quad (10)$$

Thus, the voltage distribution of bipolar cell corresponds to the 2nd order regularization problem with regularization parameters shown above. Since these regularization parameters are expressed as functions of physiological parameters, *i.e.*, membrane conductance, coupling conductance and synaptic strength, we can deduce the functions of these parameters in distal retina with regard to the standard regularization formulation. In the previous study of the cone and horizontal cell ^{[6], [9]}, however, the data, \mathbf{d} , is not directly relevant to the spatial distribution of light intensity.

The equation (7) means that the response of bipolar cell provides a solution which minimizes the following cost function,

$$J = \sum_k [x_k - R_0(-u_{k-1} + 2u_k - u_{k+1}) - \nu R_0 u_k]^2 + \lambda_1 \sum_k (x_k - x_{k-1})^2 + \lambda_2 \sum_k (x_{k-1} - 2x_k + x_{k+1})^2 \quad (11)$$

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The first term of (11) requires \mathbf{x} to be close to the second derivative of \mathbf{u} and to $\nu R_0 \mathbf{u}$. Consider the *DC* input $U_k \equiv U(\text{constant})$ for all k or the *Trend* input $U_k \equiv ak + b, (a, b : \text{constant})$ for all k . If $\nu = 0$, i.e.,

$$g_{m2} + \frac{t_4}{t_3} t_1 = 0 \quad (12)$$

then $X_k \equiv 0$ for all k . This means that if eqn (12) holds, then the bipolar cell X_k does not respond to the *DC* component and the *Trend* component, namely, the bipolar cell X_k responds only to intensity differences and is insensitive to absolute values. On the other hand, the second and the third term of (11) requires \mathbf{x} to be smooth. Therefore, the bipolar cell X_k enhances contrasts after smoothing. Regularization parameters λ_1 and λ_2 specify how much weight should be put on the smoothing.

5 Adaptation mechanism

Several lines of evidence indicate that the electrical coupling between horizontal cells is controlled by dopamine ^{[10][11]}. Dopamine changes the receptive field of horizontal cell so that the response amplitude to a small spot of light increases and that to an annulus decreases. This change of receptive field is thought to be due to a conductance decrease of the gap-junction connecting neighbouring horizontal cells.

The effect of dopamine on the horizontal cell was mimicked by exposing the retina in the light-adapted state ^[12]. This suggests that the decrease of coupling conductance of H1 horizontal cell is somehow linked with light-adaptation mechanism. The most likely function of the dopamine is to adjust the receptive field size in accordance with the signal to noise ratio of the image, which is usually different in the light- and the dark-adapted states. The retina is confronted with several types of noises, e.g., the quantum noise of photon, the spontaneous thermal isomerization of photo-pigment and synaptic noises. The relative magnitude of these noises to the signal is thought to be small in the light-adapted state since the light intensity of the signal is high. Both λ_1 and λ_2 is to be decreased by decreasing of coupling conductance of H1 horizontal cell (g_{s2}) in the light-adapted state. This means that when the environment is light, the emphasis of the network on the smoothing decreases to gain the spatial resolution. When the mean intensity of the image becomes weak, the relative magnitude of the noises becomes large. In such a case, the network puts more emphasis on the smoothing by increasing λ_1 and λ_2 which are increased by g_{s2} . Namely, g_{s2} is not included (12).

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6 Conclusion

The retinal bipolar cell is the most distal neuron which exhibits a center-surround receptive field in the vertebrate visual systems. The function of the bipolar cell was revealed in terms of an equivalent electric circuit model derived from previous physiological observations and the standard regularization problem, which is known as a computational framework of early vision. The response of bipolar cell was found to minimize a cost function consisting of two terms which relate to the second derivative and the smoothing of images.

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