Electronic Circuit Model of Color Sensitive Retinal Cell Network

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Abstract. An equivalent electronic circuit model is developed to analyze the response of color sensitive retinal cell network. Gap junction between adjacent cells is reduced by bi-directional conductance, and chemical synaptic junction between layers is reduced to uni-directional trans-admittance with time lag of first order. On the basis of the previous physiological studies, we estimate parameter values in the electronic circuit model. It is appreciated for the model to perform adequately the properties of spectral response and spatio-temporal response. Frequency response of the network are also calculated.

1 Introduction

Retina performs sensing and pre-processing of chromatic signals in biological vision. Especially in lower vertebrate, retinal cell networks have been studied physiologically and morphologically. In both layers of cone and horizontal cell, adjacent cells of the same type are coupled electrically through gap junction, while the cells are not coupled to the other types [1] [2]. Interconnections between layers have been observed in cone pedicle morphologically and the model for cone-horizontal cell organization has been proposed [3]. Properties of receptive field and spectral response have been recorded and classified [4] [5].

Computational approaches have been developed. The ill-posed problems of early vision have been solved in the framework of regularization theory [6]. Two layered architectures have been proposed and implemented for solving problems of image processing [7] [8]. These chips are intelligent sensors of monochromatic signal.

The purpose of this paper is to develop three-layered network model of color sensitive retinal network. In the electronic circuit model, gap junction is reduced by conductance, and chemical synaptic junction by trans-admittance with time lag of first order. Circuit parameter values should be estimated to match the response of cells. We simulate to appreciate the properties of spectral response and dynamic response, and calculate frequency response of the network.

2 Electronic Circuit Model

Network of outer retinal cells consists of three layers: photoreceptor, horizontal cell and bipolar cell layer. In the present model, three types of cones, namely

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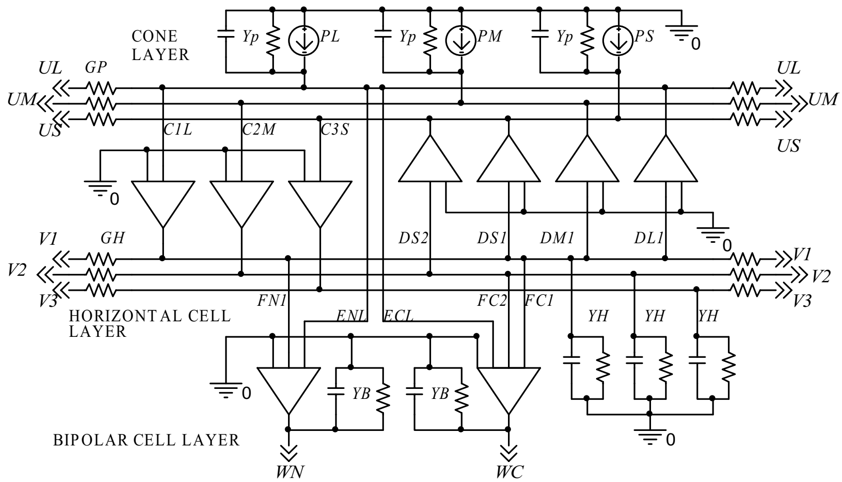


Fig. 1. Equivalent Electronic Circuit of Retina.

L-, M- and S-cone [9] are only taken into account in the photoreceptor layer. Horizontal cells are classified: mono-phasic L type, bi-phasic R-G type, bi-phasic Y-B type and triphasic type [10]. In bipolar cell layer ,two types are taken into account : opponent color cell and cell without color cording [4] [5].

It has been studied that mono-phasic L horizontal cell receives directly from only L-cones. Similarly, bi-phasic R-G cell receives directly from M-cones, Y-B type and triphasic type directly from S-cones. There are feedback pathways from monophasic L type to L-cones, M-cones and S-cones, in addition from bi-phasic R-G type to S-cones [3]. It has been deduced that specific types of bipolar cells receive signals from specific types of cones and horizontal cells [5].

On the basis of these previous works, an equivalent electronic circuit of retina is developed as shown in Fig.1. Main feature of the model is the following;

1) Gap junction between same types of adjacent cells is reduced by bi-directional coupling conductance.

2) Chemical synaptic junction between cone layer and horizontal layer is reduced by uni-directional trans-admittance with time lag of first order. Feed forward and feedback pathways coincide with the previous work on the retinal network organization [3].

3) Pathways from cone layer and horizontal cell layer to bipolar cell layer are reduced also by the same type of trans-admittance stated above.

Applying Kirchhoff's law, we derive the following equations presented in the form of Laplace transform. Where notation is the following ; P's: input photo induced current of the cones, U's: voltage of the cones, V's: voltage of the horizontal cells, W's: voltage of the bipolar cells, G's: equivalent conductance of the gap junctions, Y's: membrane admittance of the cells, C's,D's,E's,F's: equivalent trans-admittance of chemical synaptic junctions, $[\boldsymbol{I}]$: unit matrix.

Membrane conductance and capacitance have been measured in situ and in vitro, and estimated roughly 1[nS] and 50[pF]. Coupling conductance has been estimated roughly 50[nS] in cone layer, and 10^3[nS] in horizontal cell compartment. It has been appreciated that these estimations result the consistent properties of spatial response in the sense of half-decay [11]. Synaptic junction is described by trans-admittance with first order low pass filter, in which time constant has been estimated 16[msec] in the previous work [12].

Gain of each junction should be estimated to give consistent spectral response of the cells with the previous physiological studies. From the point of views, we estimate here typical values of parameters as shown in Table 1. To appreciate equivalency to biological retina, properties of spectral response to stationary light and dynamic response to flash light will be simulated with the model and compared with the previous physiological works in the following two sections.

$$G_P[\boldsymbol{A}]U_L + D_{L1}[\boldsymbol{I}]V_1 + [\boldsymbol{I}]P_L = 0 \tag{1}$$

$$G_P[\boldsymbol{A}]U_M + D_{M1}[\boldsymbol{I}]V_1 + [\boldsymbol{I}]P_M = 0 \tag{2}$$

$$G_P[\boldsymbol{A}]U_S + D_{S1}[\boldsymbol{I}]V_1 + D_{S2}[\boldsymbol{I}]V_2 + [\boldsymbol{I}]P_S = 0 \tag{3}$$

$$G_H[\boldsymbol{B}]V_1 + C_{1L}[\boldsymbol{I}]U_L = 0 \tag{4}$$

$$G_H[\boldsymbol{B}]V_2 + C_{2M}[\boldsymbol{I}]U_M = 0 \tag{5}$$

$$G_H[\boldsymbol{B}]V_3 + C_{3S}[\boldsymbol{I}]U_S = 0 \tag{6}$$

$$W_N = \pm(E_{NL}U_L + F_{N1}V_1)/Y_B \tag{7}$$

$$W_C = \pm(E_{CL}U_L + F_{C1}V_1 + F_{C2}V_2)/Y_B \tag{8}$$

where,

$$[\boldsymbol{A}] = \begin{bmatrix} a+1 & -1 & 0 & 0 & 0 \\ -1 & -a & -1 & 0 & 0 \\ & & \ddots & & \\ 0 & 0 & -1 & a & -1 \\ 0 & 0 & 0 & -1 & a+1 \end{bmatrix} \tag{9}$$

$$[\boldsymbol{B}] = \begin{bmatrix} b+1 & -1 & 0 & 0 & 0 \\ -1 & -b & -1 & 0 & 0 \\ & & \ddots & & \\ 0 & 0 & -1 & b & -1 \\ 0 & 0 & 0 & -1 & b+1 \end{bmatrix} \tag{10}$$

$$a = -(Y_P/G_P + 2), \quad b = -(Y_H/G_H + 2) \tag{11}$$

Table 1. Typical Value of Parameters [nS]

G_P	50	G_H	1×10^3
Y_P	$1 + 50 \times 10^{-3}s$	Y_H	$1 + 50 \times 10^{-3}s$
Y_B	$1 + 50 \times 10^{-3}s$	C_{1L}	$1/(1 + 16 \times 10^{-3}s)$
C_{2M}	$1/(1 + 16 \times 10^{-3}s)$	C_{3S}	$1/(1 + 16 \times 10^{-3}s)$
D_{C1}	$-1/(1 + 16 \times 10^{-3}s)$	D_{M1}	$-1/(1 + 16 \times 10^{-3}s)$
D_{S1}	$-0.3/(1 + 16 \times 10^{-3}s)$	D_{S2}	$-0.7/(1 + 16 \times 10^{-3}s)$
E_{NL}	$-1/(1 + 16 \times 10^{-3}s)$	E_{CL}	$-1/(1 + 16 \times 10^{-3}s)$
F_{N1}	$1/(1 + 16 \times 10^{-3}s)$	F_{C1}	$-0.7/(1 + 16 \times 10^{-3}s)$
F_{C2}	$-0.3/(1 + 16 \times 10^{-3}s)$		

3 Spectral Response of the Network

On the basis of the previous work [9], assume that normalized spectral response curves of photo currents in L-, M- and S-cone are represented as shown in Fig.2. Simulated response curves of horizontal cells are shown in Fig.3(a). Response curves of V_1 and V_2 coincide with these of mono-phasic L and bi-phasic R-G horizontal cell respectively, compared with the S-potentials which have measured in carp retina by Mitarai et al.[10]. Both response curves of Y-B and tri-phasic type are gained in V_3 for different values of trans-admittance ratio D_{1S}/D_{2S}. The increase of the ratio D_{1S}/D_{2S} shifts the neutral point to the right in abscissa. Critical ratio is $-0.45/-0.55$. It should be appreciated that only the three feed forward pathways and the four feed back pathways are essential to perform the well-known function of retina which converts tri-chromatic image to opponent color image, though there could be nine possible feed forward pathways and also nine feed back ones.

Spectral response curves of bipolar cells are shown in Fig.3 (b), in which response curves of bipolar cells W_C are drawn with triangles and voltages of bipolar cells W_N are drawn with circles.

The open symbol and the close one represent the response voltage value of the cells which are illuminated at the center and surround of the receptive field respectively. The response voltage curves of W_N and W_C coincide with these of the bipolar cell without color cording and the opponent color cell, which have been measured in goldfish retina by Kaneko [4] [5].

4 Dynamic Response of the Network

To simulate dynamic response of the network, the following empirical equations are applied for time course of photo induced currents which have been deduced by Baylor et al.[13], for step input illumination,

$$P_S = AI\{1 - \exp(-t/\tau)\}^n, \tag{12}$$

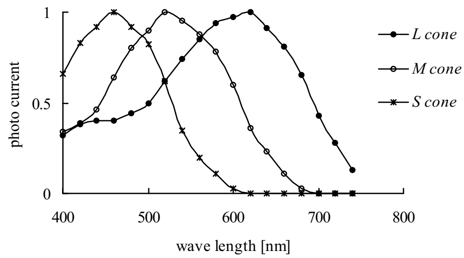


Fig. 2. Spectral Response Curves of Photo Induced Currents.

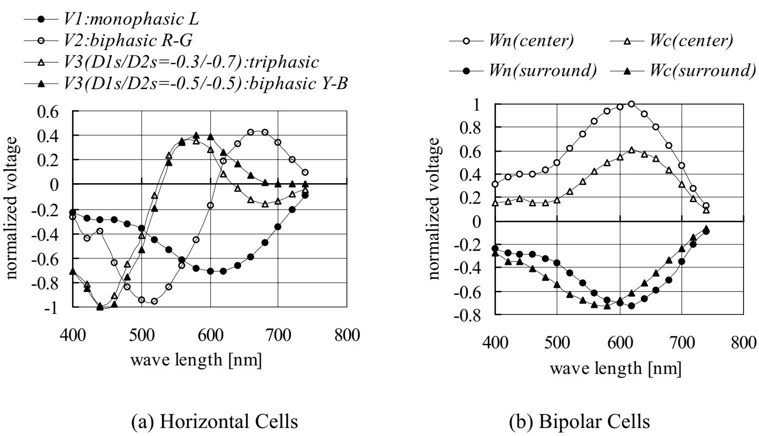


Fig. 3. Spectral Response Curves of Horizontal Cells and Bipolar cells.

for 5[msec] flash of light,

$$P_F = A'I \exp(-t/\tau)\{1 - \exp(-t/\tau)\}^{n-1} \tag{13}$$

where A, A', τ and n are empirical constants, I is strength of input light. The value of n has been deduced as 6 or 7, and value of τ should be deduced for each input light.

4.1 Dynamic Response to Diffuse Light

At first, we simulate the network property of dynamic response to the step input of diffused light, wave length of the light is 540[nm] . The values of τ and n in (12) are set to 10[msec] and 6 respectively. Time courses of the simulated photo current and voltage of cones are shown in Fig.4 (a) and (b) respectively.

The negative feed back pathways from horizontal cell layer to cone layer result the damped oscillation. It takes roughly 350[msec] to reach steady state after the step input has applied. Steady state voltage values of U_L and U_M are negative, whereas the value of U_S is positive, because of the negative feed back

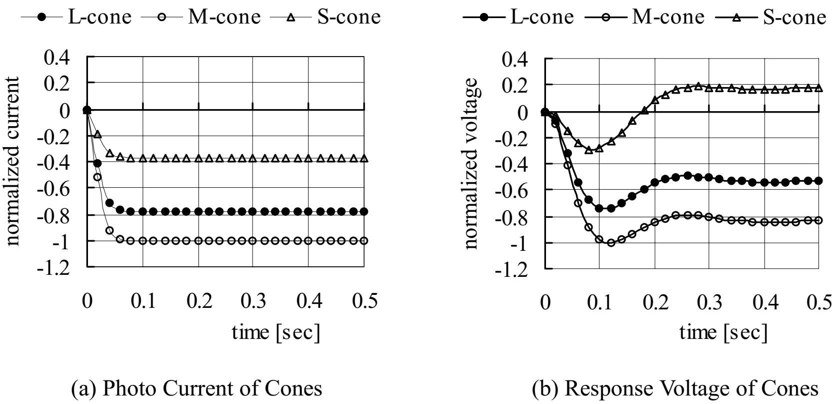


Fig. 4. Dynamic Response Curves to Step Input of Diffused Light,540[nm].

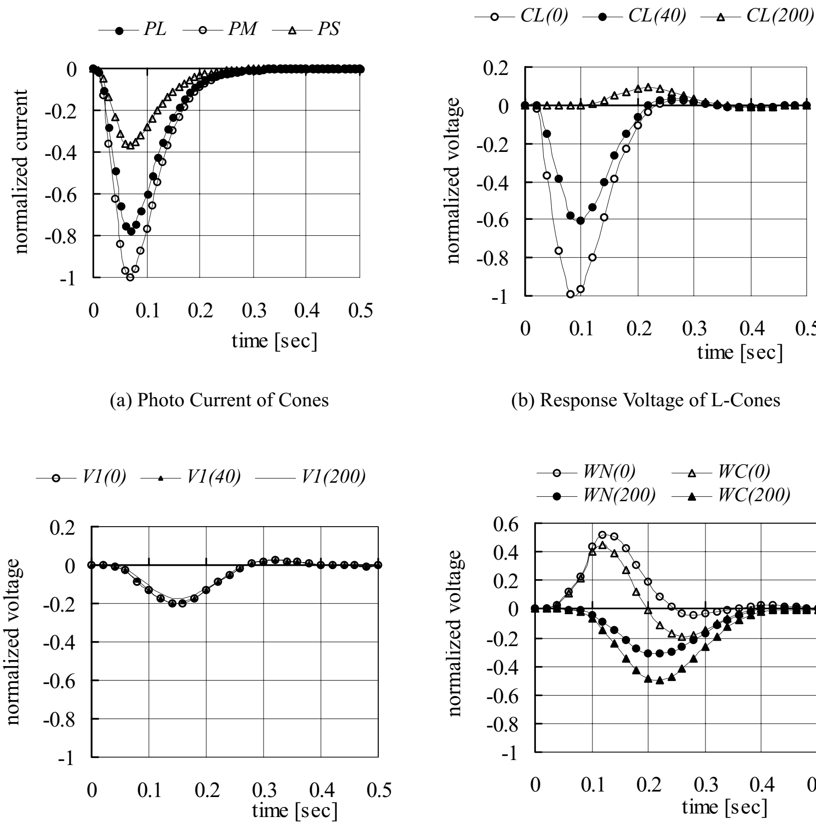
from horizontal cell layer to cone layer. The steady state values coincide with spectral response at 540[nm] in Fig.3 (a) in the preceding section. Delay of cone voltage depends dominantly on the time constant of membrane admittance.

4.2 Dynamic Response to Slit of Light

Consider that a displaced slit of light illuminates the sequence of cones. Width of slit is assumed 20[μ m], and the period of flash is 5[msec]. Time course of photo currents is given by (13) above mentioned, in which the values of τ and n are set to 40[msec] and 6 respectively. Estimating the spacing of cones, horizontal cell compartments and bipolar cell compartments to be 10[μ m], we simulate the dynamic response of the cells located at the center of the slit, 40[μ m] and 200[μ m] apart from the center. All of the voltage amplitudes are normalized by the peak value of L-cone at the center of slit.

As cones are electrically coupled weakly to adjacent ones, the amplitudes of response voltage decay in a short distance. Moreover the small amplitudes of contradict voltage begin to appear at the peripheral cells after roughly 100[msec], because of negative feed back from horizontal cell layer. The amplitudes of voltage in horizontal calls are less than those of cones but decay little, therefor horizontal cells have much wider receptive fields, because of roughly 20-fold stronger coupling conductance.

Bipolar cells receive signals from cone and horizontal cell layer through negative and positive trans-admittance with delay of first order. At the center of the slit, the signal from L-cone gives dominant effect through the negative junction. At periphery of receptive fields, as the signal from horizontal cell is dominant and the sign of cone voltage is contradict , so the contradict sign of voltage appears at peripheral cells. Delay of response is dependant on the time constant of trans-admittance between layers. Results of simulations are shown in Fig.5.



(a) Photo Current of Cones

(b) Response Voltage of L-Cones

(c) Response Voltage of Horizontal Cell *V1*

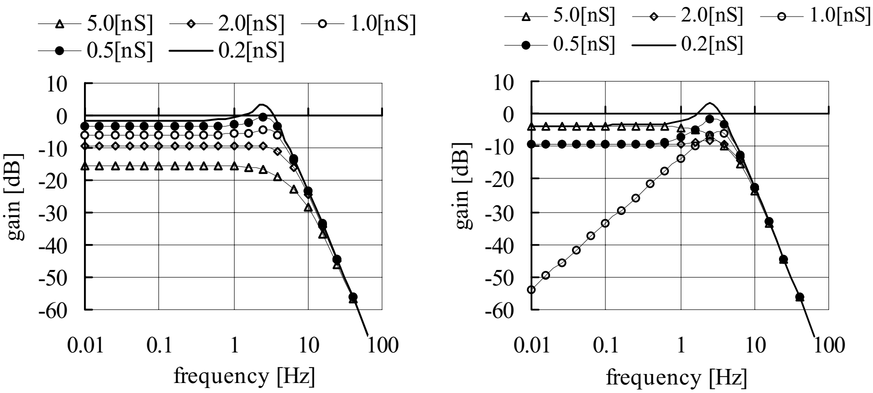
(d) Response Voltage of Bipolar Cells

Fig. 5. Dynamic Response Curves to Slit of Flash Light, 20[μ m], 5[msec] .

5 Frequency Response of Gain

The frequency response of the network is simulated to appreciate the effect of parameters. The gains in horizontal cell layer and bipolar cell layer depend little on the coupling conductance between adjacent cells, though it has been revealed that the value of the conductance in horizontal layer G_H depends on the level of input light [14] [15]. The effect of coupling conductance is dominant on space-frequency response [16] rather than time-frequency response.

The frequency response curves of horizontal cells are shown in Fig.6 (a) for various values of membrane conductance: real part of Y_H which has typical value 1[nS]. The network has low pass filter property and the knee points are roughly at 3 [Hz] in all cases, being estimated the values of the other parameters as shown in Table 1. Overshoot of gain is prominent with decrease of membrane conductance, if it should vary with environmental conditions. In the high frequency region,



(a)Gain of Horizontal Cell

(b) Gain of Bipolar Cell

Fig. 6. Frequency Response Curves of Horizontal Cell and Bipolar Cell.

gains have -60[dB/decade] for various values of membrane conductance. In low frequency region, gain is lowered with increase of membrane conductance.

The frequency response curves of bipolar cells are shown in Fig.6 (b). It has the narrow band pass filter characteristic when the value of membrane conductance is 1[nS]. The peak of gain is given roughly at 3[Hz], and -20[dB/decade] in the low frequency region, -60[dB/decade] in the high frequency region. The property depends critically on membrane conductance of horizontal cells, if it should be varied with environmental conditions. Either increase or decrease of membrane conductance result the low pass filter characteristic, which have knee point frequency roughly at 3[Hz], -60[dB/decade] in high frequency region. Decrease of membrane conductance results also prominent overshoot, which is similar to the frequency response of horizontal cells.

6 Conclusion

We developed the three layered electronic circuit to perform equivalent response to the color sensitive retinal network of lower vertebrate. From this study, we conclude the followings.

1. Gap junction should be reduced by bi-directional conductance, chemical synaptic junction by uni-directional trans-admittance with time lag of first order. Only the three feed forward and four feedback pathways are essential to perform the consistent response with the retinal cell network which has been studied biologically. Values of the circuit parameters can be estimated adequately.

2. The model developed here performs the well-known function of retina; Conversion of tri-chromatic image in cone layer to opponent color image in horizontal layer, and contrary response of center/surround receptive field in both cone layer and especially bipolar layer.

3. Behavior of the network should be low path filter, and the frequency response of horizontal cell has the knee point at roughly 3[Hz] when parameters take the typical values shown in Table 1. Gain in low frequency region depends on membrane conductance, whereas it depends little on coupling conductance in horizontal layer. It has been founded the fact that dopamine is released from interplexiform cells to lower the conductance in horizontal layer at high level of input light[14][15]. We have appreciated in the preceding study [16] that the increase of conductance should enhance the low pass filtering characteristics in space-frequency response. It should be preferable that the space-frequency low pass filtering enhances to eliminate random noises at low level of inputs and high space-frequency signals should be passed to enhance the spatial sensitivity at high level of inputs.

4. The frequency response of bipolar cell is sensitive on membrane conductance of horizontal cell, if it should be varied. In the present simulations, the network has narrow band pass filtering characteristics having maximum gain roughly at frequency 3[Hz], when the parameters take the typical values. It belongs to future works to discuss the biological meaning of it.

The approach presented here combines the biological organization and computational analysis. It should contribute numerical analysis and synthetic neurobiology of early color vision.

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