A unified mathematical model for the non-classical receptive field of ganglion cells in the retina

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Abstract

A mathematical model for receptive field of retinal ganglion cell is proposed. This model includes the effect of the non-classical receptive field, which is resulted from the cross-inhabitation between the amacrine cells. This model also concerns the nonlinear effect of the photoreceptors so that unifies the X and Y ganglion cells. The null-test response of the X cell, the on-off response of the Y cell, spot-area response curves and spatial frequency tuning curves of the X and Y cells are all simulated successfully. These results show that the non-classical receptive field is important on the spatial frequency response of the retinal ganglion cell.

1. Introduction

Ever since the pioneering work by Hartline and Ratliff [1][2], mathematical modeling of receptive fields has been common practice among neuroscientists working on the visual system. Rodieck introduced the difference of two circularly symmetric and concentric Gaussians as a model for the receptive field of retinal ganglion cells, which was known as the DOG model [3]. This choice is mathematically convenient, and Rodieck was able to derive an analytical solution for the response to moving bars with this type of receptive field. Later, Enroth-Cugell and Robson gave a solution to the spatial-frequency response for the same model [4]. This solution is the basis for the spatial-frequency analysis method, which has been widely, applied in the study of receptive fields the last 25 years [5]. Meanwhile, Enroth-Cugell and Robson gave a description of two previously unrecognized classes of ganglion cells that they called for X and Y cells. Hochstein and Shapley presented a modified DOG model for Y cell, which contains many nonlinear subunits independently of the center and surround [6][7]. Gaudiano proposed a unified DOG model for X and Y cells, in which Y cell obtains obviously nonlinearity from the receptors on the basis of a larger size of receptive field than X cell [8]. Other extensions of the DOG model have included temporal delays between the center and surround Gaussians [9] as well as nonconcentric [10] and elliptical Gaussians [11].

In recent years, many observations have been presented that there is a surrounding region outside the region of visual space in which stimuli evoke spike discharges (the so called ‘classical receptive field’). Stimuli in this region, although not capable of driving responses, can exert robust suppressive effects on the response to the presentation of stimuli in the classical receptive field (the so-called nonclassical receptive field) [12][13][14][15]. The nonclassical receptive field of ganglion cell is mainly determined by the neuronal network within the retina, possibly the serial amacrine-
amacrine amacrine-ganglion cell synapses [16].

Li et al has proposed a mechanic model for nonclassical receptive field of X cell, which is result from the cross-inhabitation between the pixels of the stimuli [17] [18].

Here we propose a unified model for nonclassical receptive field of ganglion cell. After simulation, we investigate the possible function of nonclassical receptive field in processing progress.

2 Model

The model we presented has four layers: photoreceptor layer, bipolar cell layer, amacrine cell layer and ganglion cell layer.

For the photoreceptor layer, the similar equations in Gaudiano’s model are used as followed [equation 1 and 2 in 8]:

\[
r(t) = l(t)z(t)
\]

\[
\frac{dz(t)}{dt} = F(G - z(t)) - Hl(t)z(t)
\]

where \(l(t)\) presents the incoming luminance signal, \(r(t)\) is the photoreceptor response, \(z(t)\) is the available quantity of the transmitter, and \(G\) is the saturation level of the transmitter, \(F\) and \(H\) are proportional coefficients.

For the bipolar cell layer, we also use the equations in Gaudiano’s model as followed [equation 4 in 8]:

\[
b^+(t) = r(t)
\]

\[
b^-(t) = M - r(t)
\]

where \(b^+(t)\) is the response of an ON-bipolar cell and \(b^-(t)\) OFF-bipolar cell. \(M\) is the saturation level of the cell.

For the amacrine cell inside the center of the receptive field of ganglion cell, its response is

\[
a^+(t) = b^+(t) - b^-(t)
\]

For the amacrine cell outside the center of the receptive field ganglion cell, equations are:

\[
a^-_i(t) = b^-(t) - b^+(t)
\]

\[
a^-_o(t) = a^-_i(t) - s(t)
\]

\[
s(t) = \int \int a^-_i(t,x,y)a^-_i(t,x+m,y+n)f(m,n)dmdn
\]

where \(a^-_i(t)\) is its original input, \(a^-_o(t)\) its final response to the ON-ganglion cell, \(s(t)\) the linear summary of inhibition of all other amacrine cells to this amacrine cell, and \(f(m,n)\) is the function of the cross-inhibition between the amacrine cell in \((x,y)\) and another one in \((x+m,y+n)\), which is a Gussian function of distance \((m,n)\) described as followed:

\[
f(m,n) = k_ie^{-(m^2+n^2)/r_i^2}
\]

where \(k_i\) and \(r_i\) are parameters in Gaussian function of cross-inhibition. These equations are similar to the equations in [17][18], but we use different cross-inhibition function.

For the ganglion cell, we concerns only one ON-ganglion cell, whose response is given by DOG model in two dimension as followed:

\[
g(t) = \int \int a^+(t)k_ce^{-(x^2+y^2)/r_c^2}dxdy
- \int \int a^-_o(t)k_se^{-(x^2+y^2)/r_s^2}dxdy
\]

where \(k_c\) and \(r_c\) are parameters in Gaussian function of the center of receptive field, and \(k_s\) and \(r_s\) are parameters in surround.

In our model, the photoreceptor density is 100 per degree square and the photoreceptors spread 10°*10° in visual field.
3 Simulation results

3.1 the null response of X cell and the on-off response of Y cell

Use the parameter given by Gaudiano [Appendix B in 8], we also simulate the null response of X cell and small on-off response of Y cell. These results are similar to the Gaudiano’s model [figure 3 and 4 in 8], we don’t present them here. It seems that nonclassical receptive field contribute little to these response in this model.

3.2 the area response curves

The area response curve is the main experimental evidence for the nonclassical receptive field of the retinal ganglion cell [figure 1 in 16]. Our simulation results are shown in figure 1. These results agree with the experimental results quite well.

3.3 the spatial frequency response curves

The spatial frequency response curves of X cell is shown in figure 2, in which \(f_d\) is the spatial response curve of the receptive field described by the DOG model (concerning center and surround part), \(f_c\) is the spatial response curve of the center part of the receptive field, and \(f_i\) is the spatial response curve of the whole receptive field including nonclassical receptive filed. As we see from figure 2, the existence of nonclassical receptive field increases the response of whole receptive field in low spatial frequency. This result shows that nonclassical receptive field is important in processing slow variations in luminance in visual field.

4 Summary and conclusion

This mechanical model for receptive field of retinal ganglion cell has two different points with the previous models. First, according to Gaudiano’s propose, we concern the nonlinear response of photoreceptor to unifies the X and Y ganglion cells. Second, we concern the effect of the cross-inhabitation between the amacrine cells, which result in the non-classical receptive field.

So that, the null-test response of the X cell, the on-off response of the Y cell, spot-area response curves and spatial frequency tuning curves of the X and Y cells are all simulated successfully with our model. These

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Figure 1. area response curves of X and Y cells

Figure 2 spatial frequency response curve
results show that the non-classical receptive field is important on the spatial frequency response of the retinal ganglion cell.

**Reference**


