A simulation model for analyzing the spatiotemporal receptive field of retinal ganglion cells in the presence of fixational eye movements

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Abstract

Understanding the receptive field dynamics of vertebrate retinal ganglion cells in the presence of fixational eye movements is considered to provide insights into information processing/encoding optimized behaviors in animals and autonomous robots in the future. Previous studies have proposed computational models that account for fixational eye movements, suggesting that the long-range spatial inhibitions provided by wide field amacrine cells to some subtypes of bipolar cells and ganglion cells dynamically shape the responses of ganglion cells. In the present study, we constructed a simulation model of a retinal circuit based on recent physiological findings and computational elements that are feasible for digital hardware implementation. The model validity was tested through computer simulation experiments and by analyzing the time series of spike outputs from the ganglion cell unit. As a preliminary result, we were able to quantify the spatiotemporal receptive field by applying a simple white-noise movie stimulus.

Keywords: Simulation, retina, spike, fixed eye movement, receptive field

1. Introduction

The vertebrate retinal system undertakes energy-saving and robust encoding of visual information in diverse and unpredictable visual environments, and under non-stationary body-eye movement conditions prior to cognitive processing in the brain. Therefore, understanding the principles and mechanisms of this information processing provides useful insights, not only into the visual system of vertebrates but also, in the future, into visual information processing optimized for autonomous robots.

Previous physiological and anatomical experiments have shown the basic response properties of major intraretinal neurons and the synaptic connections between them [1]. To elucidate how real-world visual information is processed, compressed, and encoded in neural circuits, it is necessary to determine the electrical activity of many neurons under natural conditions, where animal body and eye movements are constantly present.

However, it is not easy to conduct this using only ordinary physiological experiments due to technical limitations.

The "in silico" approach simulates the response of neuronal populations on a general-purpose computer that is complementary to physiological experiments. In recent years, hardware tools have been developed to emulate neural images of the neuronal layer in the retina in real time [2]. Robotic systems with gaze control characteristics similar to vertebrate eye movements have also been developed [3], which can simulate the spatiotemporal frequency modulation of the input light to the retina by fixation eye movement.

Recent retinal studies have proposed computational models that consider neuronal responses in the presence of fixational eye movements, suggesting that wide field amacrine cells provide relatively long-range inhibitory inputs to several subtypes of bipolar and ganglion cells, dynamically shaping the receptive field properties of these cells [4][5]. Based on these recent physiological findings, this study proposes a retinal neural circuit model for future hardware implementations. The basic circuit structure was implemented using software, and the receptive field dynamics of the ganglion cell units were quantified by simulation experiments and Spike-Triggered Average (STA) analysis [6] using this model.

2. Proposed Simulation Model

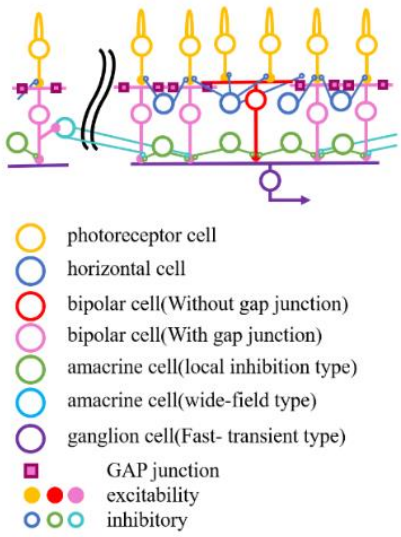

Fig. 1 Simulation model of retinal neural circuits in the presence of fixating eye movements.

Fig. 1 shows a simulation model of retinal neural circuits taking into account fixational eye movements, proposed with reference to previous studies [4][5]. This model includes photoreceptor cells (PCs), horizontal cells (HCs), bipolar cells (BCs), amacrine cells (ACs), ganglion cells (GCs) and the neural connections between these cells.

First, PCs detect light converting it into an electrical signal. The electrical signals were electrically coupled by gap junctions between the PCs, which propagate the signals faster in the horizontal direction. Electrical signals from PCs also reach the HCs with a delay. Gap junctions also exist between HCs, which propagate signals more widely than PCs. BCs form a center-surround antagonistic receptive field by subtracting the excitatory input from the PCs and inhibitory input from HCs.

A unique feature of this model is the neural circuitry of the inner retina after BCs. The BCs in the model are of the on-transient type, electrically coupled between neighboring bipolar cells (ECBCs) and electrically uncoupled (conventional bipolar cells; CBCs). There are also two types of ACs: local inhibition and wide field.

The output cells in the retinal model were fast-transient-type ganglion cells (FTGCs). From the location of the GCs, CBSs are located near the center, whereas EC BCs are located in the peripheral region. Each BC receives inhibitory signals from local inhibitory ACs. Inhibitory signals from wide field ACs have a larger amplitude and faster response than the local inhibition type and are excited by inputs from ECBCs. ECBCs receive inhibitory signals from distant, wide field ACs. In the presence of eye movements, excitatory signals from ECBCs increase the size of the receptive field of FTGCs, while inhibitory signals from wide field ACs decrease the size of the receptive field of FTGCs. The FTGCs integrate excitatory inputs from these BCs and output spike signals.

The spatial signal propagation properties through gap junctions present in photoreceptor, horizontal, and BCs, which are simulated by spatially convolving the Gaussian kernel in Equation (1).

$$g(x, y, \sigma) = \frac{1}{\sqrt{2\pi\sigma}} \exp\left(\frac{-x^2 + y^2}{2\sigma^2}\right) \qquad (1)$$

where σ is the scale parameter that determines the degree of spatial signal transmission spreading, and the scale

parameters for PC, HC, and ECBC are σ_{pc}, σ_{hc} and σ_{ecbc} respectively.

The delayed response of HCs to PCs, and the temporal characteristics of bipolar and ACs were simulated by a linear sum of first-order Infinite impulse response (IIR) filters, as expressed in the following equation:

$$J_m[x, y, n] = \alpha_m J_m[x, y, n-1] + (1-\alpha_m) I_{in}[x, y, n] \quad (2)$$

$$I_{out} = \sum_{i=1}^{3} k_i J_i \quad (3)$$

where m= {1,2,3}, α1=αhc for HCs, k1=1, k2= k3=0, $(\alpha_1, \alpha_2, \alpha_3) = (\alpha_{bc1}, \alpha_{bc2}, \alpha_{bc3})$, k_1=-1, k_2=2, k_3=-1 for BCs and $(\alpha_1, \alpha_2, \alpha_3) = (\alpha_{bc1}, \alpha_{bc2}, \alpha_{bc3})$, k_1= 2, k_2=-1, k_3=0.

The Izhikevich model [7] was employed to simulate the spike generation process using FTGC. The parameters of the model used in the experiments are summarized in Table 1. Note that this model was proposed for future implementations in operational circuits.

Table 1. Parameter list.

	Parameters	Values
PC	σ_{pc}	1
HC	σ_{hc}	3
	α_h	0.953
BC	σ_{ecbc}	1
	$(\alpha_{bc1}, \alpha_{bc2}, \alpha_{bc3})$	(0.875, 0.75, 0.625)
AC	$(\alpha_{ac1}, \alpha_{ac})$	(0.8, 0.6)
GC	(A, B, C, D)	(0.02, 0.2, -60, 8)
	v_{peek}	30

3. Experiments and results

STA was performed to quantify the receptive field dynamics of the FTGC units in the proposed model. The STA of a visual stimulus is widely employed in physiological experiments to localize the receptive field of the retinal ganglion cell[7].

The visual input to the model was a white noise movie stimulus, an example is shown in Fig. 2(a). The number of cells in each layer from the PC layer to the AC cell layer was set to 100 × 100, and the number of cells corresponded one-to-one to the number of pixels. Visual stimulus updates and various filter operations were performed every 5 ms, and numerical calculations of the Izhikevich model were performed with a resolution of 0.5 ms, considering the maximum frequency of spike output by actual GCs, and the speed and accuracy of the calculations. The simulation period was 500 s. The simulation code was implemented using Python programming language.

The spike response of the centrally located ganglion cell unit was recorded, resulting in a spike count of 11532 spikes during the entire simulation period. An STA was obtained by extracting the stimulus image stream in a time window from -150 ms before to 50 ms after the time of each spike and averaging the extracted image stream for all spikes, as shown in Fig. 2. In this spatiotemporal STA, yellow indicates a positive response, and dark blue indicates a negative response.

Fig. 2(c) shows the time profile on the horizontal dotted line in Fig. 2(b), showing a biphasic feature. At the central position, the STA intensity increased from 0 s and reached a positive peak at -10 ms before decaying and reaching a negative peak at -40 ms. The contrast in the time profile decreased further away from the central position. Fig. 2(d) shows the spatial profile of the vertical dotted line in Fig. 2(b). From the spatial profile at -10 ms, which is the positive peak, the ON region was approximately 10 pixels (see '4' in Fig. 2(d)). From the negative peak spatial profile was -40 ms, its OFF region was approximately 10 pixels (see '2' in Fig. 2(d)).

4. Conclusion

The receptive fields of the FTGC units were measured by performing STA analysis on the proposed model. The temporal and spatial structures of the receptive field, as observed physiologically, were visible in the receptive field of the FTGC unit.

A simulation time of approximately 22 h is required to obtain 11532 spikes. Therefore, it is necessary to implement the model in dedicated hardware to reduce the simulation time and the time required for data analysis. In addition, we plan to adjust the parameters of the spatial and temporal scales to obtain physiologically valid spatiotemporal characteristics of the receptive field.

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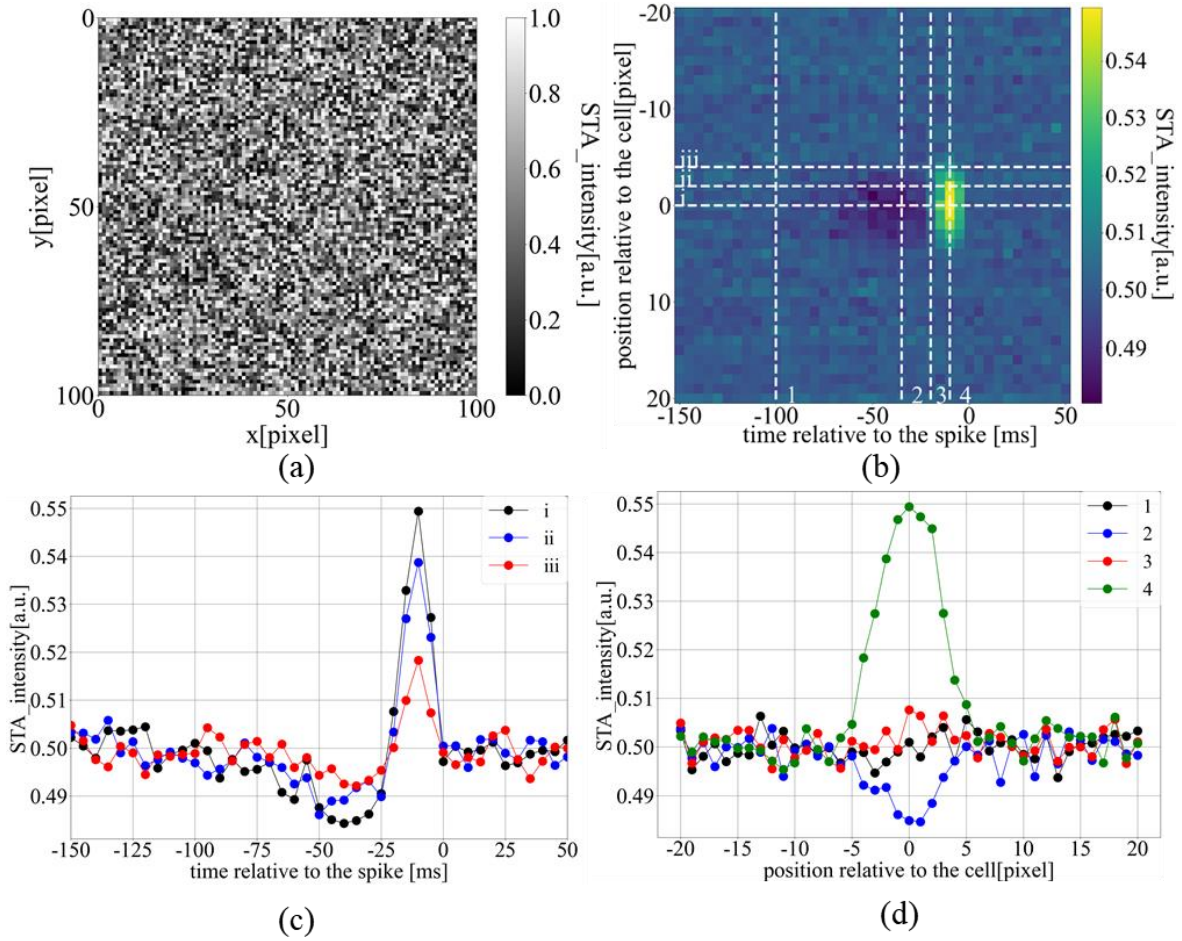

Fig. 2 Simulation experiment to characterize the spatiotemporal receptive field of the ganglion cell using STA analysis. (a) Examples of visual input. (b)Space-time STA plot of the fast-transient type ganglion cell (c) Temporal profile of the STA sliced at three positions labeled “i”, “ii”, “iii” in (b), (d) Spatial profile of the STA sliced at four time points labeled “1”, “2”, “3”, “4”, in (b).

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