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Letters

Recurrent network simulations of two types of non-concentric retinal ganglion cells

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Abstract

Recurrent network models are widely used to characterize the behaviors of neurons in the visual cortex. However, they are seldom used to simulate neurons in the retina. In this study, two slightly different recurrent network models are introduced to describe two types of non-concentric ganglion cells, i.e., the impressed-by-contrast cell and the suppressed-by-contrast cell in the cat retina. By simulations, it is found that the additive recurrent network is able to describe qualitatively the behavior of the impressed-by-contrast cell, while the other additive recurrent network with saturation rectification is able to describe qualitatively the behavior of the suppressed-by-contrast cell.

Keywords: Recurrent network; Retinal ganglion cell; W cell; Local edge detector; Uniformity detector

1. Introduction

Since extensive synaptic connectivity is a prominent feature of neural circuitry, recurrent network models are widely used to characterize the behaviors of neurons in the visual cortex [1,4]. They are rarely used to model ganglion cells in the retina because retinal ganglion cells are regarded to function in feedforward mode [8,9].

The impressed-by-contrast cell and the suppressed-by-contrast cell belong to W cells in the cat retina [13]. The impressed-by-contrast cell is also known as the local edge detector [5], and its morphological type is the zeta or theta cell [2,10,14]. The suppressed-by-contrast cell is also known as the uniformity detector [5], and its morphological form is still unknown [13,14].

The impressed-by-contrast cell and the suppressed-by-contrast cell have three possible pathways to communicate with local neighbors (Fig. 1). These pathways are direct electrical coupling, the path by short-range amacrine cells, and the path by long-range amacrine cells. The first pathway is direct electrical coupling (Fig. 1A). Homologous tracer coupling occurs between narrow field ganglion cells, as shown in rabbit [16]. Since the cat's impressed-by-contrast cell has a narrow dendritic field [2,10], it is possible that these ganglion cells are also directly electrically coupled. The second pathway is formed by short-range amacrine cells (Fig. 1B). The rabbit narrow field ganglion cells have heterologous tracer coupling with amacrine cells [16], and it is possible that the cat's impressed-by-contrast cell which also has a narrow dendritic field is tracer coupling with amacrine cells. The amacrine cells usually have electrical and chemical synapses with ganglion cells [11,16]. The local edge detector (or impressed-by-contrast cell) has a silent inhibitory surround with a diameter of 9° and its anatomical base is probably the second pathway [5]. The third pathway involves long-range amacrine cells (Fig. 1C). One candidate is the rabbit polyaxonal amacrine cell which has homologous and heterologous tracer coupling with many amacrine cells [15,16]. The uniformity detector

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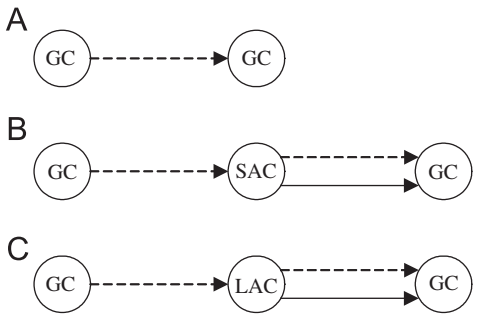

Fig. 1. Three pathways of the interaction between ganglion cells (GC). For simplicity, only one direction is plotted. (A) the direction path; (B) the path by short-range amacrine cells (SAC); and (C) the path by long-range amacrine cells (LAC). The dash and solid lines indicate the electrical and chemical synapses, respectively.

(or suppressed-by-contrast cell) shows a periphery effect [5], and the structural base of this periphery effect is believed to be the wide field, spiking and axon-bearing amacrine cells [7,12].

The behaviors of the impressed-by-contrast cell and the suppressed-by-contrast cell are conventionally described by feedforward summation models that neglect the recurrent connections between ganglion cells [13]. Recently, Kenyon et al. used feedback kinetics from axon-bearing amacrine cells to explain the high-frequency oscillatory potentials in cat alpha ganglion cells [11]. In this study, similar to Kenyon et al., the lateral influence from neighboring ganglion cells is taken into account. An additive recurrent network is used to characterize the impressed-by-contrast cell, and the other additive recurrent network with saturation rectification is used to characterize the suppressed-by-contrast cell. Through simulations, it is found that recurrent networks are able to reproduce qualitatively the behaviors of both types of non-concentric ganglion cells in the cat retina.

2. Models

2.1. The model for the impressed-by-contrast cell

2.1.1. The recurrent model

Each cell in the additive recurrent network model receives feedforward and recurrent inputs. The behavior of cell i, characterized by a firing rate r_i, is described by the standard rate model equation [1,4]:

$$\tau \frac{\mathrm{d}r_i}{\mathrm{d}t} = I_i + \sum_{j=1}^{N} W_{ij} r_j - r_i, \tag{1}$$

where I_i represents the feedforward input to cell i, W_{ij} is the weight of the influence from cell j to cell i, $\tau(=1\,\mathrm{ms})$ is a time constant, and N is the number of the cells in the network.

The feedforward input describes the response of a bipolar cell:

$$I_i = \left[\int \mathrm{d}x G_i(x) \int_0^{\infty} \mathrm{d}t' H(t') s(x, t - t') \right]_+, \tag{2}$$

where $s(x,t)$ represents the light stimulus and the notation $[]_+$ indicates rectification. The temporal kernel is a difference of Gamma functions [3]:

$$H(t) = \alpha^2 t \mathrm{e}^{-\alpha t} - \beta^2 t \mathrm{e}^{-\beta t}, \tag{3}$$

where $\alpha^{-1} = 22\,\mathrm{ms}$ and $\beta^{-1} = 302\,\mathrm{ms}$ as the best fit (see the last paragraph of this section). The spatial filter is a difference of Gaussians [6]:

$$G_i(x) = C\mathrm{e}^{-(x-\varphi_i)^2/\sigma_c^2} - S\mathrm{e}^{-(x-\varphi_i)^2/\sigma_s^2}, \tag{4}$$

where φ_i denotes the spatial position of cell i; C and S are the amplitude of the center and the surround Gaussians, respectively; σ_c and σ_s are corresponding radii; $\sigma_c = 0.12^\circ$, $\sigma_s = 0.32^\circ$, $S\sigma_s^2/C\sigma_c^2 = 1.03$. In the simulation, the distance between two cells is set to 50 μm by assuming a cell density of 378 cells/mm^2 [2]. The PA1 amacrine cell in the rabbit central retina has an axonal field of 3.1 mm^2 and it can influence 1172 (378×3.1) ganglion cells [15]. In the one-dimensional simulation, a PA1 cell can influence 34 (the square root of 1172) ganglion cells. Further, the PA1 cells have homologous tracer coupling [15]; it is possible that a PA1 cell can influence several local neighbors, therefore, N is chosen as 128 ($\approx 34 \times 3.8$). The drifting sinusoidal grating visual stimulus is [4]

$$s(x,t) = \cos 2\pi(Kx - ft), \tag{5}$$

with K the spatial frequency and f the temporal frequency. The influence on a cell from three lateral pathways is simplified to a Gaussian function. The recurrent weight matrix is

$$W_{ij} = \begin{cases} \frac{g}{N-1}\mathrm{e}^{-(\varphi_i-\varphi_j)^2/\sigma_w^2}, & i \neq j, \\ 0, & i = j, \end{cases} \tag{6}$$

where g equals to $0.9g_{\max}$, and $g_{\max}$ is the maximum of g at which the recurrent network remains stable. The Gaussian radius σ_w is chosen as 2° because it is assumed that the impressed-by-contrast cell has 16 influential neighbors when the sensitivity decreases by a factor of $1/e$ from its peak. The spatial properties of the model, i.e., the matrix W, do not account for interactions at any single pathway (Fig. 1); it is a concise representation of the contributions from all lateral pathways.

The steady-state solution of Eq. (1) is $r_i = I_i + \sum_{j=1}^{N} W_{ij} r_j$. Let the eigenvalues and eigenvectors of the recurrent matrix W be λ_i and ξ_i for $i = 1, 2, \ldots, N$, respectively. The solution is then

$$r_i = \sum_{\mu=1}^{N} \left(\frac{\xi_\mu^i}{1 - \lambda_\mu} \sum_{j=1}^{N} I_j \xi_\mu^j \right),$$

where ξ_μ^i is the ith element of the vector ξ_μ. When g is near zero, which means the recurrent connections are very weak,