

Research report

A two pathway model for tonic suppressed-by-contrast cells in the cat retina

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Abstract

A two pathway spatiotemporal model is proposed to describe the function of tonic suppressed-by-contrast cells of the cat retina. The model is able to describe the experimentally determined responses of such neurons to drifting sinusoidal gratings. It is also able to predict their responses to alternating sinusoidal gratings and flashing or moving spots of light, and these predictions resemble experimental observations, at least qualitatively. The model is physiologically plausible, it can be used to summarize the dynamic responses of the tonic suppressed-by-contrast cells of the cat and potentially to account for the responses of the suppressed-by-contrast cells of other species.

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Keywords: Suppressed-by-contrast cells; Uniformity detectors; Edge inhibitory off-center cells; G17 cells; Cat retina; Spatiotemporal model**1. Introduction**

Suppressed-by-contrast cells are a famous subgroup of W cells in the cat retina. They were first named by Rodieck in 1967 because their high maintained discharges [30–50 impulses per second (ips)] are suppressed or reduced when visual stimuli are present in their receptive fields [47]. It is generally believed that suppressed-by-contrast cells in the cat retina have two distinct types [35,54]. One type is suppressed transiently, introduced by Cleland and Levick (1974) as the uniformity detector [10]; the other type is suppressed tonically, introduced by Cleland and Levick (1974) as the edge inhibitory off-center cell.

Suppressed-by-contrast cells play an essential role in the visual system. W cells project to a variety of cortical targets such as the C-laminae of the lateral geniculate nucleus (LGN), the medial interlaminar nucleus, the superior colliculus, the pulvinar, and the nuclei of the accessory optic system [48,55]. These nuclei further relay the signals to cortical areas 17, 18, and 19. Moreover, these three cortical areas are presumably involved in eye movement, pupillary control, and motion perception [48]. In addition, Troy et al. (1989) proposed that suppressed-by-contrast

cells may be responsible for the neural measurement of contrast of a visual stimulus [57], thus participating in the contrast gain control of cortical cells [54]. Furthermore, suppressed-by-contrast cells might provide the driving signal to recruit the midbrain 'Hunting Servo' required to control the focusing power of the crystalline lens [53]. It is known that cats have substantial accommodative responses [40] to stimulation of the efferent path (the afferent path remains undetermined) [this mid-brain role is suggested by one of the reviewers of this paper]. Therefore, a computational model of suppressed-by-contrast cells will be beneficial in providing a better understanding of the functions of W cells, the retina, and the visual system.

Multi-subunit models, which are closely related to cells' anatomical structures, are widely used to model cells in early visual pathways. Rodieck (1965) used a two-subunit model [46], difference of Gaussians, to describe successfully the spatial structure of X cells in the cat retina. Hochstein and Shapley (1976) adopted multi-subunit models to explain the frequency double characteristics of Y cells [23]. Bonin et al. (2005) also employed such models to describe the suppressive field of LGN neurons [7], while Garcia-Perez (2004) used them to depict the nonlinear behaviors of simple cells in the visual cortex [21].

Although suppressed-by-contrast cells play a critical role in the visual system, in the literature, little attention has been given to explain how these cells work. In this study, a multi-subunit

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model composed of two pathways, an edge pathway and a linear pathway, is introduced to describe the behaviors of tonic suppressed-by-contrast (TS) cells in the cat retina. The edge pathway maps the TS cells' edge inhibitory behaviors, and the linear pathway maps their off-center concentric behaviors. The model qualitatively summarizes TS cells' responses to sinusoidal gratings and flashing or moving spots. The organizations of the model map well the anatomical retinal circuitry of the cat, and the model may be useful in explaining the responses of the suppressed-by-contrast cells of other species.

2. Methods

The two pathway organization of the model for TS cells is shown in Fig. 1. The light stimulus is processed simultaneously by the edge pathway and the linear pathway. The outputs of these two pathways are added, combined with the maintained discharge of the cell, truncated by the output rectifier, and then converted to the firing rate of the cell.

Both pathways are multi-subunit organizations. The edge pathway has a number of subunits and a pool mechanism. Each subunit consists of a spatial kernel, a temporal kernel, and a rectifier, while the pool mechanism has a spatial kernel. The linear pathway only has a single subunit which consists of a spatial kernel and a temporal kernel.

In the edge pathway, the output from a subunit located at (x_0, y_0) is

$$R_{ES}(x_0, y_0, t) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \int_0^{+\infty} G_{ES}(x_0 - x, y_0 - y) H(t') S(x, y, t - t') dx dy dt'. \quad (1)$$

The spatial kernel of a subunit is a difference of Gaussians [18,46]:

$$G_{ES}(x, y) = G(x, y, A_{ESC}, r_{ESC}) - G(x, y, A_{ESS}, r_{ESS}), \quad (2)$$

where $G(x, y, A, r)$ is a two-dimensional Gaussian function:

$$G(x, y, A, r) = A e^{-(x^2+y^2)/r^2}, \quad (3)$$

where A is the amplitude and r is the radius. A_{ESC} , r_{ESC} and A_{ESS} , r_{ESS} are the subunit center and surround parameters, respectively.

The temporal kernel of a subunit is a difference of Gamma functions [9,21,39,60]:

$$H(t) = \frac{\alpha(\alpha t)^n}{n!} e^{-\alpha t} - \gamma \frac{\beta(\beta t)^n}{n!} e^{-\beta t}, \quad (4)$$

where α , β , γ , and n are temporal parameters. γ , the transience factor [60], is usually in the range of 0–1. When γ is 0, the temporal property is totally tonic. When γ is 1, the temporal property is totally phasic.

$S(x, y, t)$ is the visual stimulus, and it is a spot or a sinusoidal grating.

The output of the edge pathway is

$$R_E(t) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} |R_{ES}(x_0, y_0, t)| G_P(x_0, y_0) dx_0 dy_0, \quad (5)$$

where $G_P(x, y)$ is the pool kernel, $G_P(x, y) = G(x, y, A_P, r_P)$. $||$ the subunit full wave rectifier, and $|x|$ is the absolute value of x .

The output of the linear pathway is

$$R_L(t) = \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \int_0^{+\infty} G_L(x, y) H(t') S(x, y, t - t') dx dy dt', \quad (6)$$

where $G_L(x, y)$ is the spatial kernel, $G_L(x, y) = G(x, y, A_{LC}, r_{LC}) - G(x, y, A_{LS}, r_{LS})$. The temporal kernel, $H(t)$, is the same as the subunit temporal kernel in the edge pathway (Eq. (4)).

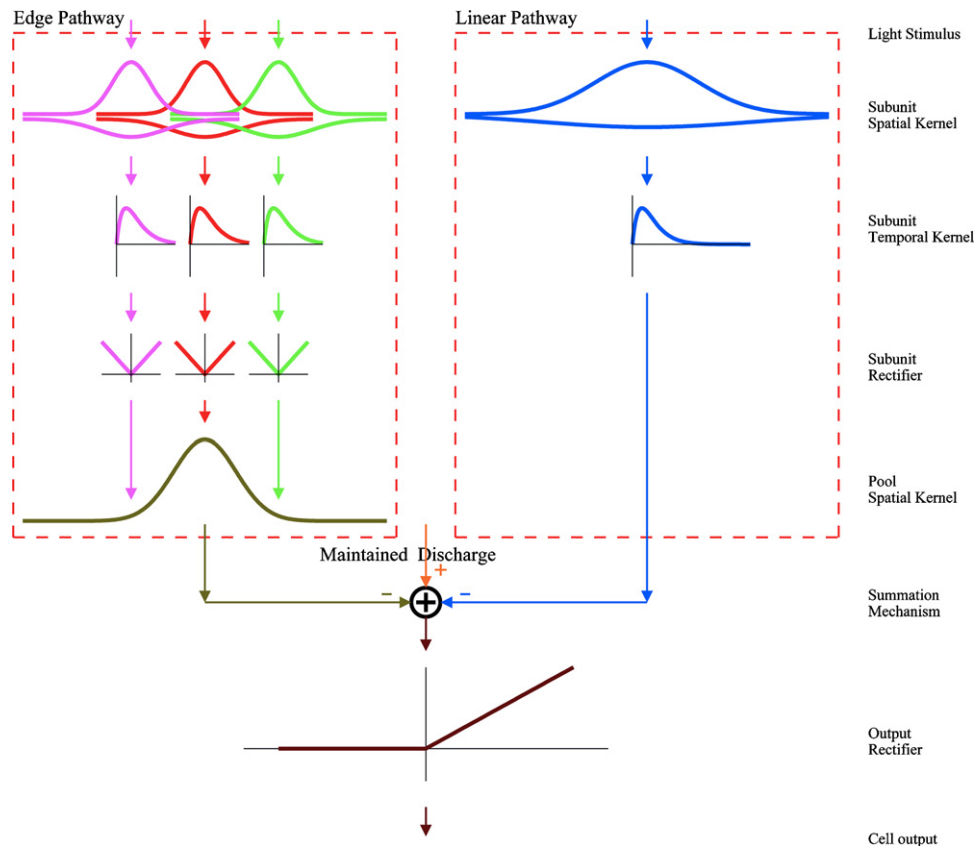


Fig. 1. The two pathway structure of the TS cell's model.

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