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Contrast saturation in a neuronally-based model of elementary motion detection

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Abstract

The Hassenstein–Reichardt (HR) correlation model is commonly used to model elementary motion detection in the fly. Recently, a neuronally-based computational model was proposed which, unlike the HR model, is based on identified neurons. The response of both models increases as the square of contrast, although the response of insect neurons saturates at high contrasts. We introduce a saturating nonlinearity into the neuronally-based model in order to produce contrast saturation and discuss the neuronal implications of these elements. Furthermore, we show that features of the contrast sensitivity of movement-detecting neurons are predicted by the modified model.

Keywords: Elementary motion detection; Neuronally-based model; Contrast sensitivity functions; Contrast saturation; Fly; Vision

1. Introduction

The detection of visual motion by insects is a long studied process in computational neuroscience. Motion detection models have been devised to describe the response of biological motion detectors [6], but the way such computation takes place at the cellular level remains an active research area [1]. Understanding how

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cells process motion from the changes in brightness in the visual input is not only an important task in itself, but could also provide clues for the understanding of more complicated processes, such as the prey pursuit system, which receives inputs from cells implicated in motion detection [5].

Tangential cells are directionally selective, movement-detecting neurons in the lobula plate of flies, which are involved in the optomotor response [7]. The Hassenstein–Reichardt (HR) correlational model [6], shown in Fig. 1a, has been used extensively to explain the response of tangential cells and of the elementary motion detectors (EMDs) these cells are thought to integrate [3]. Although predictive and widely used, the HR model has one major disadvantage: while it produces an output that closely matches the electrophysiological data, it does not provide any information regarding the computations performed by specific cells and synapses that allowed the biological system to arrive at such a result.

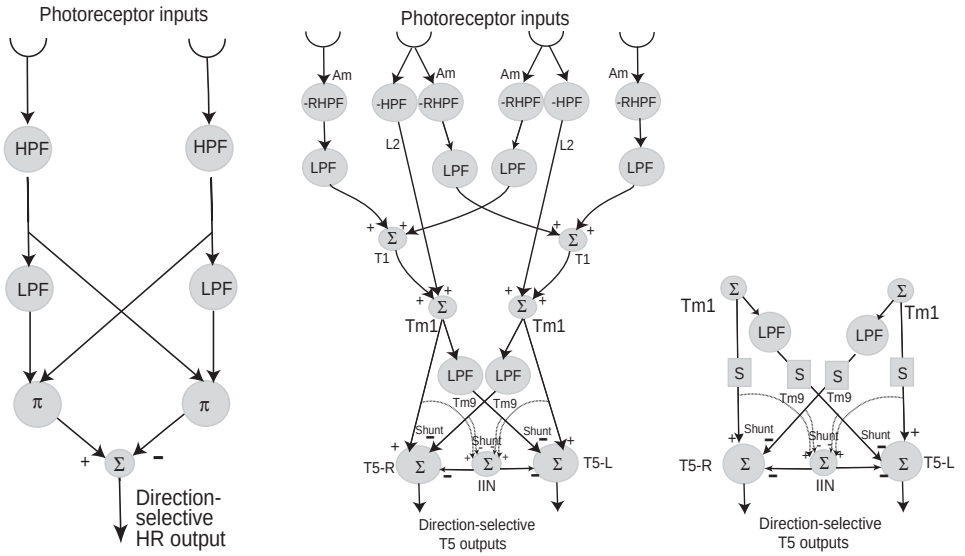

Fig. 1. Models of motion detection. (a) The Hassenstein–Reichardt model. The input from a photoreceptor is multiplied by the delayed (low-pass filtered) signal from the neighboring input unit. The computation of the difference between the two multiplications results in a directionally-selective output. HPF and LPF are high-pass and low-pass filters respectively, whereas $\sum$ and $\prod$ represent sum and multiplication, (b) the neuronally-based elementary motion detector model incorporating amacrine cells (Am), lamina monopolar cells (L2), basket T-cells (T1), two types of transmedullary cells (Tm1 and Tm9), T5 bushy T-cells (T5-R and T5-L) and an inhibitory interneuron (IIN). Excitatory and inhibitory inputs are represented by arrows with positive and negative signs, respectively. RHPF (relaxed high-pass filter) represents a HPF with a small low-pass component. A filter preceded by a negative sign indicates that the output of the filter was sign-inverted. Inhibitory inputs from the Tm9 cell are implemented as shunting, and (c) bottom portion of the neuronally-based EMD model showing the location where the saturation element (S) was inserted.

A neuronally-based EMD model has been proposed that incorporates anatomical and electrophysiological data accumulated throughout years of research [8]. The model, shown in Fig. 1b, uses mathematical expressions to represent the relationships between the responses of the cells implicated in the motion detection system of dipterous insects. The neuronally-based EMD model is distinguished from the HR model not only in that it is derived from the functional organization of identified cells, but also by the fact that it computes motion in two stages. First, responses to motion without regard to stimulus direction are computed at the Tm1 level by comparing the local signal from L2 with delayed surrounding signals from neighboring optic cartridges. Second, directional motion is computed at the T5 output through the integration of a subset of neighboring Tm signals with a specific alignment. The model incorporates shunting inhibition at the T5 level to achieve the essential nonlinearity. Model simulation results are consistent with electrophysiological recordings from T5 and Tm cells. In addition, despite not being mathematically equivalent to the HR model, the neuronally-based EMD model produces qualitatively similar results to those from the traditional HR model. This model serves as a basis for the understanding of the neural basis of motion detection and can be used, as in this study, to derive testable hypotheses about the network of cells and synapses that it represents.

In 1979 Dvorak et al. [2] derived contrast sensitivity functions (CSFs, see Methods) for type IIa1 tangential cells from female blowflies. Ten years later Egelhaaf et al. [3] showed that both the transient and the steady-state responses of HS tangential cells saturate at high contrasts. The authors modeled this behavior by inserting a saturating nonlinearity into a simple HR model. In this paper, we introduce a saturating element into the neuronally-based EMD model and present results that show that the modified model closely predicts the electrophysiological data. Furthermore, we present CSFs for the neuronally-based and HR models with saturation elements and show that the response of both models predicts features of the contrast sensitivity of tangential cells. However, unlike the HR model, the location of the saturating element in the neuronally-based EMD model can be identified with a specific synapse.

2. Methods

Simulations with the neuronally-based EMD model were run using the Matlab software (The Mathworks, Natick, MA). The two-dimensional simulations incorporated a 100×10 pixel image viewed by a 50×5 hexagonal array of photoreceptors and an equal number of EMD models. The filters used in the model were implemented as first order with time constants of 50 ms for the first low-pass and high-pass filters and 100 ms for the final low-pass filters. The time-step used for all simulations was 10 ms. Shunting inhibition was modeled as a ''dirty

multiplication" [9]:

$$F(I_e, I_s) = \text{pos}(I_e)\left(1 - \frac{\text{pos}(I_s)}{I_{s\,\max}}\right), \tag{1}$$

where the function pos() indicates that negative quantities are set to zero, I_e and I_s represent excitatory and shunting inputs, respectively, and $I_{s\,\max}$ is the maximum possible value of I_s. The input to all simulations was a two-dimensional sinusoidal grating moving in the horizontal direction with initial phase chosen randomly. The results of five simulations were averaged to obtain the model response, which was computed as the sum of the outputs of all functional units.

A saturating element was inserted in the neuronally-based EMD model similar to that used by Egelhaaf et al. [3]. The saturating element was implemented as a sigmoid function:

$$S(x) = A + B \cdot \frac{1}{1 + e^{-C \cdot x}}, \tag{2}$$

with parameters $A = -.085$, $B = .17$ and $C = 38$ set to match the electrophysiological data (see Fig. 2a) at transient and steady-state conditions. Fig. 1c shows the location of the saturating element in both the Tm1 and Tm9 pathways of the neuronally-based EMD model.

CSFs were computed as the inverse of the minimum contrast required for the model's response to reach a particular percentage of the maximum amplitude

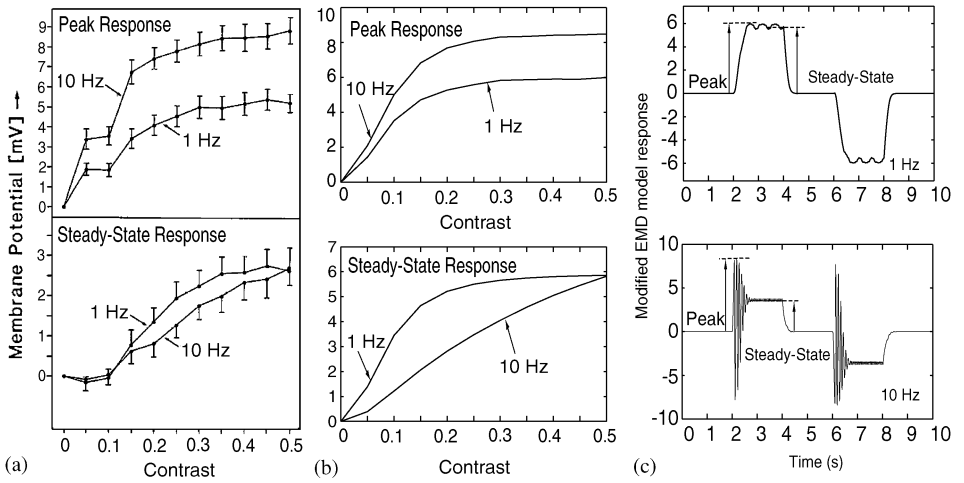

Fig. 2. Contrast saturation data. (a) Peak and steady-state responses from HS tangential cells for two temporal frequencies: 1 and 10 Hz, (b) neuronally-based EMD model (with saturation elements) responses to comparable inputs, and (c) sample transient responses of the modified model to sinusoidal stimuli at 1 and 10 Hz and a contrast of 0.25. The stimuli was stationary for 2 s, moved to the left 2 s, was stationary again for the next 2 s and moved to the right 2 s. The peak and steady-state responses are marked in the plots. The steady-state value was computed as the mean response amplitude after the response had become relatively stable. Panel **a** reproduced without permission from [3].

response (criterion response) to sinusoidal stimulus. To convert the spatial frequency units of cycles/optic cartridge (derived from the model implementation) to units of cycles/degree, as reported in [2], a conversion factor of 1.5 degrees/optic cartridge was used. This is in accordance with interommatidial angles for the fly *Lucilia sericata*, which vary from one to about two degrees depending on the region of the eye being examined [10].

3. Results

3.1. Modeling saturation at high contrasts

The measured responses of HS tangential cells to sinusoidal gratings which were initially stationary and then began moving suddenly are shown in Fig. 2a. The contrast of these stimuli was varied at two temporal frequencies (1 and 10 Hz) [3]. Both the peak value of the transient response and the steady-state response value is plotted. The peak response amplitudes at both frequencies reach saturation faster than the steady-state responses. The peak responses for both frequencies seem to saturate at about the same contrast, while the steady-state response at the 1 Hz frequency saturates faster than the response at 10 Hz. Furthermore, the peak responses are higher at the higher temporal frequency, whereas the steady-state responses are smaller. As shown in Fig. 2b, these features, as well as the crossing point between the two steady-state curves at a contrast of 0.5, are all predicted by the modified neuronally-based EMD model. Sample responses of this model to sinusoidal stimuli at temporal frequencies of 1 and 10 Hz and a contrast of 0.25 are shown in Fig. 2c.

Simulations with the saturating element inserted at different locations in the EMD model revealed that the results of the model predict these electrophysiological features only if the nonlinearities are placed as shown in Fig. 1c. For instance, inserting the nonlinearity before the low-pass filters in the Tm9 pathways produced nearly equal peak response amplitudes for both simulated frequencies at all contrasts (data not shown).

3.2. Measuring contrast sensitivity functions

Contrast sensitivity functions were computed for the neuronally-based and HR models with saturating nonlinearities and compared to the functions obtained by Dvorak et al. [2]. for type IIa1 tangential cells. Fig. 3a shows the CSFs from tangential cell recordings and from the neuronally-based and HR models with saturating nonlinearities (Figs. 3b and c). The results from both models share several features with the electrophysiological data. The sensitivity of both models peaks at the same range of intermediate spatial frequencies as the CSFs of tangential cells, while showing similar degrees of attenuation at low and high frequencies. Like the electrophysiological data, the CSFs of both models show flat regions at intermediate frequencies. However, unlike the CSFs of tangential cells, the CSFs of the models do

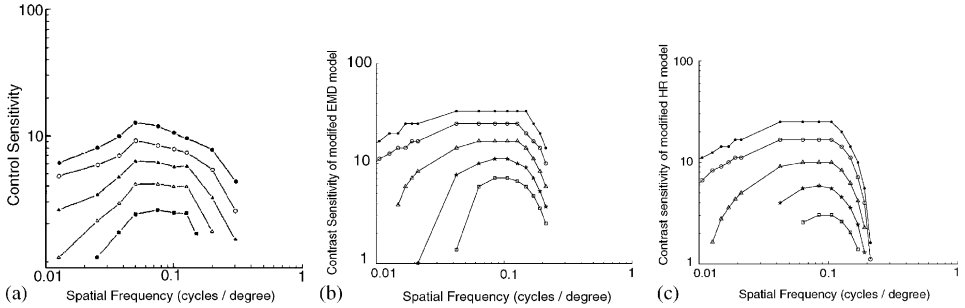

Fig. 3. Contrast sensitivity functions for criterion response amplitudes (top to bottom lines) of 5%, 10%, 25%, 50% and 75% of maximum amplitude response for: (a) type IIa1 tangential cells, (b) the neuronally-based model with saturation nonlinearities and (c) the HR model with saturation nonlinearities. Panel **a** reproduced without permission from [2].

not become flatter as the criterion response amplitudes become larger (criterion response amplitudes increase from top to bottom CSFs in Fig. 3).

4. Discussion

A saturating nonlinearity was inserted in a neuronally-based model of elementary motion detection with parameters tuned to match electrophysiology from HS tangential cells (see Fig. 2). The model was found to produce results which looked very similar to the biological data, accurately predicting the shape of the curves and their temporal frequency dependence. CSFs of the model were computed and found to predict several features of the CSFs of tangential cells (see Fig. 3). While the sensitivity amplitudes, rates of attenuation at low and high frequencies and spatial frequency tuning of the neuronally-based CSFs were similar to the electrophysiology, the CSFs of the model do not become flatter at high contrasts (higher criterion response amplitudes). This feature of the electrophysiological data is likely due to a neuronal mechanism that holds sensitivity constant at high contrasts to compensate for attenuation that results from the optical filtering of the visual stimulus [7]. Evidence of such mechanism has been found in humans and is termed "contrast constancy" [4]. This compensatory mechanism is not incorporated in the HR or the neuronally-based EMD models.

While the HR and neuronally-based EMD models were found to produce similar results in both experiments, the results from the neuronally-based model have implications for the physiology of the insect. The simulations showed that there is only one location for the saturation element in the EMD model that produces results that match the electrophysiology from [5] at both transient and steady-state conditions. This implies that if the neuronally-based EMD model is correct in the relationships between the cells it incorporates, this saturation may arise in the synapses of the transmedullary cells (both Tm1 and Tm9) onto T5.

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