

Contrast Saturation in a Neuronally-Based Model of Elementary Motion Detection

Zuley Rivera-Alvidrez and Charles M. Higgins

*Electrical and Computer Engineering / ARL Division of Neurobiology
University of Arizona, Tucson*

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.

Key words: 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

Corresponding author: Zuley Rivera-Alvidrez, zuley@ece.arizona.edu.

response of different stages of the motion detection system [1,2], but the way such computation takes place at the cellular level remains an active research area. Understanding how 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 [3].

Tangential cells are directionally selective, movement-detecting neurons in the lobula plate of flies, which are involved in the optomotor response [4]. The Hassenstein-Reichardt (HR) correlational model [1], shown in Figure 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 [5]. 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.

A neuronally-based EMD model has been proposed that incorporates anatomical and electrophysiological data accumulated throughout years of research [2]. The model, shown in Figure 1b, uses mathematical expressions to represent the relationships between the responses of the cells implicated in the motion detection system of dipterous insects. Simulations have been performed showing that the neuronally-based EMD model is as successful as the well established HR model in predicting the responses of EMDs and tangential cells for a number of complex visual stimuli [2]. Furthermore, the neuronally-based model may serve as a working model for the understanding of the neural basis of motion detection.

In 1979 Dvorak *et al.* [6] derived contrast sensitivity functions (CSFs) for type IIa1 tangential cells from female blowflies. Ten years later Egelhaaf *et al.* [5] 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 nonlin-

earity in a simple HR model. In this paper, we introduce a saturating element into the neuronally-based 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.

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 100x10 pixel image viewed by a 50x5 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” [7].

The input to all simulations was a two-dimensional sinusoidal grating moving in the horizontal direction with initial phase computed 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 (some EMD model units at or near the edges of the array were not fully functional due to the absence of photoreceptor inputs).

A saturating element was inserted in the neuronally based EMD model similar to that used by Egelhaaf *et al.* [5]. The saturating element was implemented as a sigmoid function:

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

with parameters A=-8, B=16 and C=37 set to match the electrophysiological data (see Fig. 2a) at transient and steady state conditions. Figure 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 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 [6], 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 [8].

3 Results

A. Modeling saturation at high contrasts. The response amplitudes of the HS tangential cells are shown in Figure 2a for sinusoidal visual stimuli at two temporal frequencies (1 Hz and 10 Hz) [5]. The figure illustrates some important features of the peak (transient) and steady-state responses. The peak response amplitudes at both frequencies reach saturation faster and at higher amplitudes than the steady-state responses. The peak responses for both frequencies seem to grow at the same rate, while the steady-state response at the 1 Hz frequency saturates faster than the response at 10 Hz. Furthermore, the final amplitudes of the peak responses depend on the temporal frequency of the stimuli, with lower frequencies saturating at lower amplitudes than higher frequencies. 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 as shown in Figure 2b. Simulations with the saturating element inserted in 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 Figure 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).

The saturation characteristics of tangential cells can also be modeled by an HR model if saturation nonlinearities are inserted in all inputs to the multiplication stages (after the filters), as demonstrated by Egelhaaf et al [5].

B. 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* [6]. for type IIa1 tangential cells. Figure 3a shows the CSFs from tangential cell recordings and from the neuronally-based and HR models with saturating non-linearities (Fig. 3b and 3c). 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 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 [6]. Evidence of such mechanism has been found in humans and is termed “contrast constancy” [9]. 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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Figure captions

Figure 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 Σ and Π 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. (c) Bottom portion of the neuronally-based EMD model showing the location where the saturation element (S) was inserted.

Figure 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 element) responses to comparable inputs. Panel a reproduced without permission from [5].

Figure 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 [6].

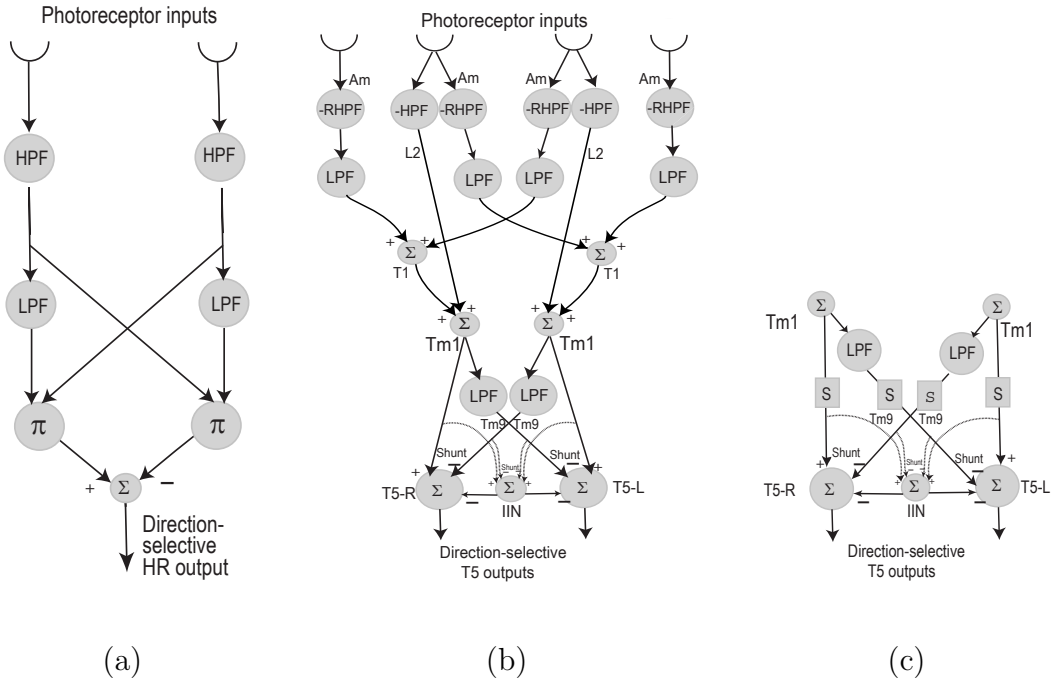


Fig. 1.

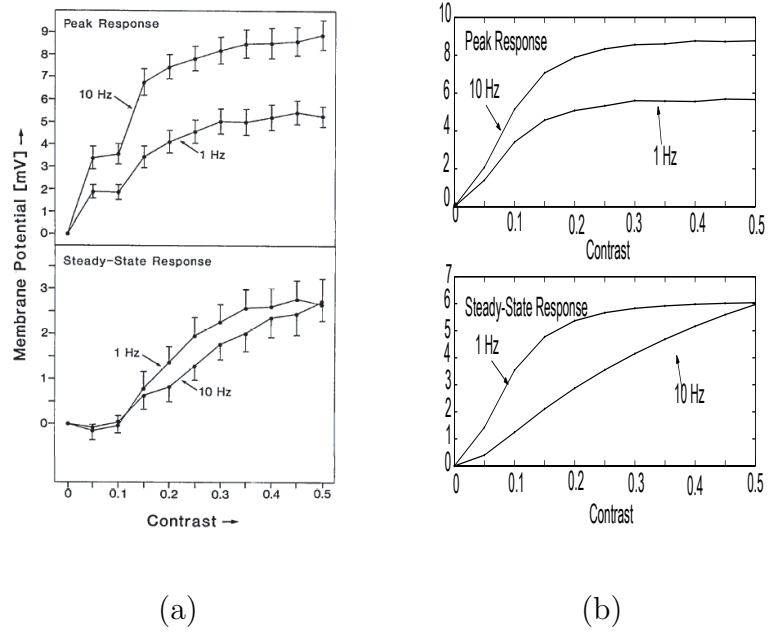


Fig. 2.

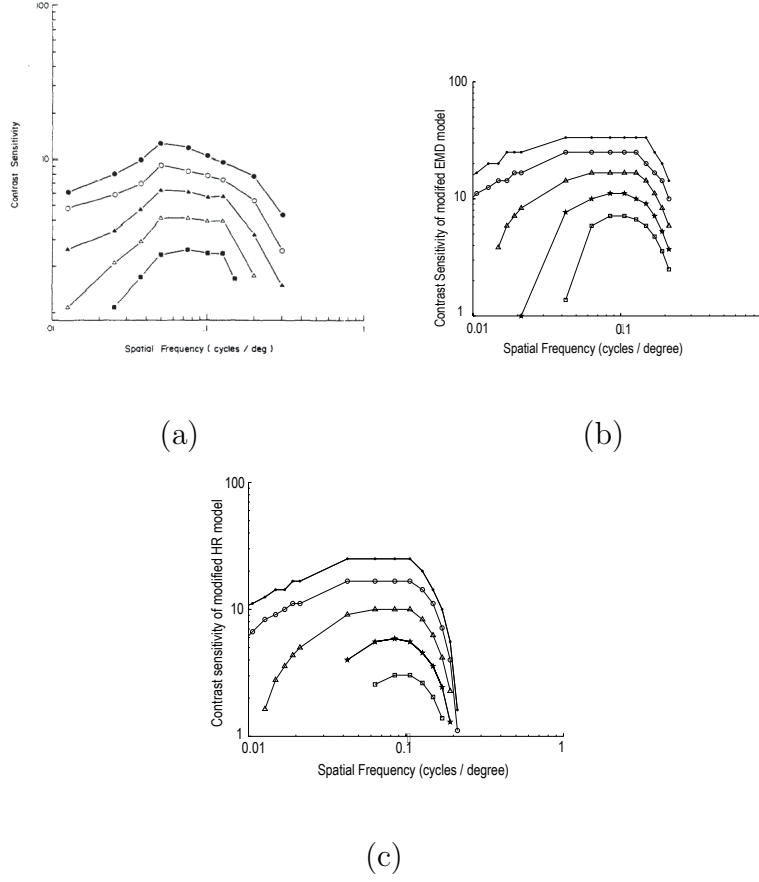


Fig. 3.



Zuley Rivera-Alvidrez received a B.S. degree in Computer Engineering from the University of Arizona in 2002. She is presently pursuing an M.S.E.E. degree from the same university. Her research interests include computational neuroscience and bio-robotics.



Charles M. Higgins received the Ph.D. in Electrical Engineering from the California Institute of Technology in 1993. He holds joint appointments in Electrical/Computer Engineering and Neurobiology at the University of Arizona, where his research focuses on investigation of neurobiological computational and control architectures.