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A model of the illusory contour formation based on dendritic computation

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Abstract

We proposed a new model of illusory contour formation based on the properties of dendritic computation. The basic elements of the network are a single-excitatory cell with two dendritic branches and an inhibitory cell. Both dendritic branches behave as an independent linear unit with a threshold. They sum all excitatory input from the nearby collinear cells, and the inhibition from one collateral of the corresponding inhibitory cell. Furthermore, the output of dendritic branches multiplicatively interacts before it is sent to the soma. The multiplication allows the excitatory cell to be active only if both of its branches receive enough excitation to reach the threshold. Computer simulations showed that the presented model of the illusory contour formation is able to perform perceptual grouping of nonadjacent collinear elements. It shows a linear response relationship with the input magnitude because dendritic inhibition counteracts recurrent excitation. The model can explain why illusory contours are stronger with irregular placement of inducing elements rather than regular placement and why top-down influences may prevent the illusory contour formation.

Keywords: Contour integration; Dendritic computation; Illusory contours; Recurrent excitation; Top-down processing

1. Introduction

Illusory (or subjective) contours are vivid percepts of lines between the inducing elements that do not have support in physical stimulation. They give rise to even more complex illusory figures such as Kanizsa square (Fig. 1a) or Ehrenstein figure (Fig. 1b) [1]. Neurophysiological investigations showed that many neurons in a monkey V2 cortex are sensitive to illusory contours. That is, neurons respond as if the real contour is presented in their receptive field. These neurons respond to real contours as well and they show similar orientation tuning curves for real and for illusory contours. Therefore, they could not distinguish between real and illusory contours. Later it was found that the strength of their response depends linearly on the size of the illusory line or the number of inducing elements up to a saturation point [2]. Psychophysical investigations with humans also revealed graded strength or clarity of illusory contours with the relative size of inducing elements [3].

How is sensitivity to the illusory contour formed in the neural tissue? Grossberg and Mingolla [4] proposed a model of boundary contour system (BCS), which is able to perform perceptual grouping. BCS is a two-dimensional network that simulates properties of neurons observed in the primary visual cortex including simple, complex, and hyper complex neurons. In order to explain illusory contour formation, they introduce a bipole cell that forms the illusory contour. The bipole cell is modelled as a recurrent excitatory network that computes the logical AND function between two collinear but spatially separated parts (or poles) of their receptive field. Bipole cells receive input from a network of complex cells that compete with each other in order to achieve a sharp contour detection. However, the model was not able to simulate the finding that the strength of illusory contour varies with input amplitude or number of inducing elements. The model also does not account for the fact that strength of the illusory contour depends on the placement of inducing elements. Irregular lines produce stronger impression of the

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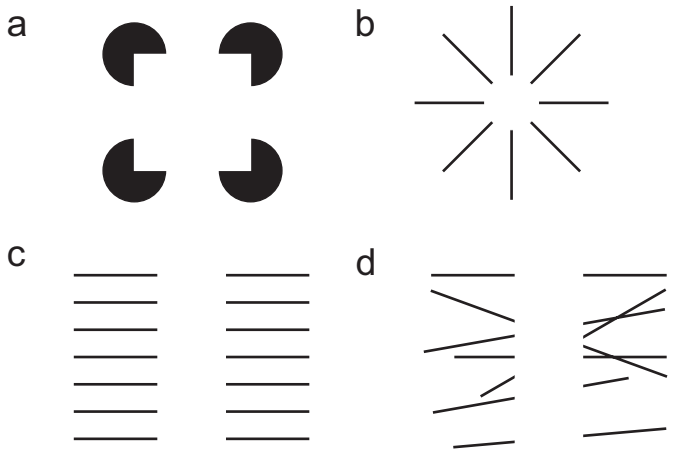

Fig. 1. Illusory figures: (a) Kanizsa square, (b) Ehrenstein figure; illusory contours formed by (c) regular inducers or (d) irregular inducers.

illusory contour (Fig. 1d) than regular inducing lines (Fig. 1c) [5]. Furthermore, illusory contour formation is not an obligatory process and it could be prevented by cognitive or top-down influences [1]. Moreover, attention may prevent collinear interaction between neighbouring line segments [6].

2. Model description

In this paper, we propose a new model of bipole cells and show how is illusory contour formed based on the properties of dendritic computation [7]. We suggest that the bipole cells use dendritic inhibition in order to achieve analogue sensitivity to the input magnitude [8]. First, bipole cells sum inputs along its dendritic branches. Outputs from dendritic branches multiplicatively interact (logical AND computation) before they reach cell's body. Therefore, bipole cell will become active only if both dendritic branches receive enough stimulation. When it is active, bipole cell sends inhibition to its dendritic branches in order to reduce the effect of recurrent excitation. In this way, the proposed model is able to group collinear elements into the illusory contour with analogue sensitivity to input magnitude.

The basic elements of the network are an excitatory cell with two dendritic branches and an inhibitory cell (Fig. 2). The excitatory cell (empty circle in Fig. 2) receives recurrent input from other excitatory cells, whose receptive fields are collinear with it and, therefore, forming a recurrent excitatory network (horizontal arrows at the top of the Fig. 2). Also it sends signal to other excitatory cells and to the inhibitory cell (filled circle in Fig. 2). Excitatory and inhibitory cells are modelled as continuous-time linear units with a threshold. The inhibitory cell has two collaterals which contacts dendritic branches of the excitatory cell. Both dendritic branches behave as an independent linear unit with a threshold. They summed all excitatory input from nearby collinear cells, and the

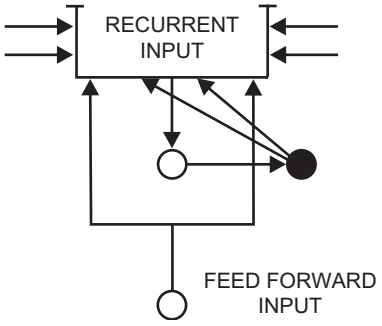

Fig. 2. A model of the illusory contour formation based on the properties of dendritic computation.

inhibition from one collateral of the corresponding inhibitory cell. The branches also receive direct input from a complex cell at corresponding locations. Furthermore, the output of dendritic branches multiplicatively interacts before it is sent to the soma. The multiplication allows excitatory cell to be active only if both of its branches receive enough excitation to reach the threshold. The excitatory cell must receive suprathreshold activation from both sides because illusory contours are possible only if at least two inducing elements are present. Therefore, basic property of the bipole cell is achieved using the dendritic multiplication.

We also introduced two different spatial scales in order to achieve smooth contour representation. The large-scale bipole cells detect the presence of the illusory contour. Their output is sent to the small-scale cells that smooth the contour by local recurrent interactions. Formally, the network is described as

$$\frac{\mathrm{d}xL_i}{\mathrm{d}t} = -A_1 xL_i + f\left[\sum_p g(xL_p)w_{1ip} + I_i w_{1ii} - h(yL_i)\right] \times f\left[\sum_q g(xL_q)w_{1iq} + I_i w_{1ii} - h(yL_i)\right], \quad (1)$$

$$\frac{\mathrm{d}yL_i}{\mathrm{d}t} = -yL_i + W_{1ii}g(xL_i) + TD_i. \quad (2)$$

Term xL_i denotes activity of the large-scale bipole cell at the spatial location i and yL_i is activity of the corresponding inhibitory cell. The parameter A describes passive decay that drives the cell toward the zero when no input is presented. Function $f()$ describes output of the computation from a single dendritic branch. In the simplest case it is given by

$$f[a] = \max[a - Tr, 0]^n, \quad (3)$$

where Tr is a threshold, and n could be smaller, larger or equal to 1. We also studied model behaviour with a more complex and biologically more realistic sigmoid function

$$f[a] = \frac{1}{1 + \mathrm{e}^{-B(a-C)}}. \quad (4)$$

Functions $g()$ and $h()$ describe an output from the excitatory and the inhibitory cells, respectively. They are defined as linear above threshold as shown in Eq. (3) with

$n = 1$. Feedforward input is denoted with I_i and the recurrent excitatory input is denoted with x_p and x_q, where indices p and q describes the left and the right pole of the bipole cell. Indices are given by $p = \{j: 1, \ldots, j<i\}$ and $q = \{j: j>i, \ldots, N\}$ and N is a network dimension. Term, w_{ij}, denotes strength of excitatory feedback and, w_{ii}, denote strength of feedforward excitatory connections. Recurrent connections are described with Gaussian fall-off from the centre of the receptive field

$$w_{1ir} = \frac{D}{2\pi\sigma^2}\exp\left[-\frac{(r-i)^2}{2\pi\sigma^2}\right], \tag{5}$$

where r is either p or q, D is amplitude and σ is a spatial spread of the Gauss kernel. W_{ii} denotes strength of excitatory to the inhibitory connection. The multiplication between two dendritic branches is denoted with $\times$ sign. In Eq. (2), term TD_i describes top-down influences on inhibitory cells which could prevent collinear contour grouping.

The small-scale bipole cells xS_i are given by

$$\frac{\mathrm{d}x\,S_i}{\mathrm{d}t} = -A_2 xS_i + f\left[\sum_p g(xS_p)w_{2ip} + g(xL_i)w_{2ii} - h(yS_i)\right] \times f\left[\sum_q g(xS_q)w_{2iq} + g(xL_i)w_{2ii} - h(yS_i)\right], \tag{6}$$

and their corresponding inhibitory cells yS_i are given by

$$\frac{\mathrm{d}y\,S_i}{\mathrm{d}t} = -yS_i + W_{2ii}g(xS_i) + TD_i. \tag{7}$$

The small-scale bipole cells receive input from the large-scale bipole cells. Their lateral connections are restricted to the nearest neighbours. Therefore, $p = i-1$ and $q = i+1$.

3. Results

In order to test properties of the proposed network, we performed computer simulations by solving a set of nonlinear differential equations (Fig. 3). For simplicity, we ignored the second spatial dimension. Also, we ignored computations in the retina and the primary visual cortex. Instead, we focused on the properties of recurrent excitatory network and its ability to connect nonadjacent input signals into a unique perceptual group. The model parameters were set to: $N = 30$; $A_1 = .1$; $A_2 = .001$; $D = 150$; $\sigma = 10$; $W_{1ii} = W_{2ii} = 1$; $w_{1ii} = .8$; $w_{2ii} = .2$; $w_{2ip} = w_{2iq} = 1$ for all i. Output functions $f()$, $g()$ and $h()$ are described as threshold linear (Eq. (3)) with $Tr = 0$ and $n = 1$. First, we showed that the model cells indeed behave as the bipole cells because they do not respond when one of its poles do not receive stimulation (Fig. 3a, dotted line). Furthermore, computer simulations revealed that proposed network is sensitive to the input magnitude as shown by

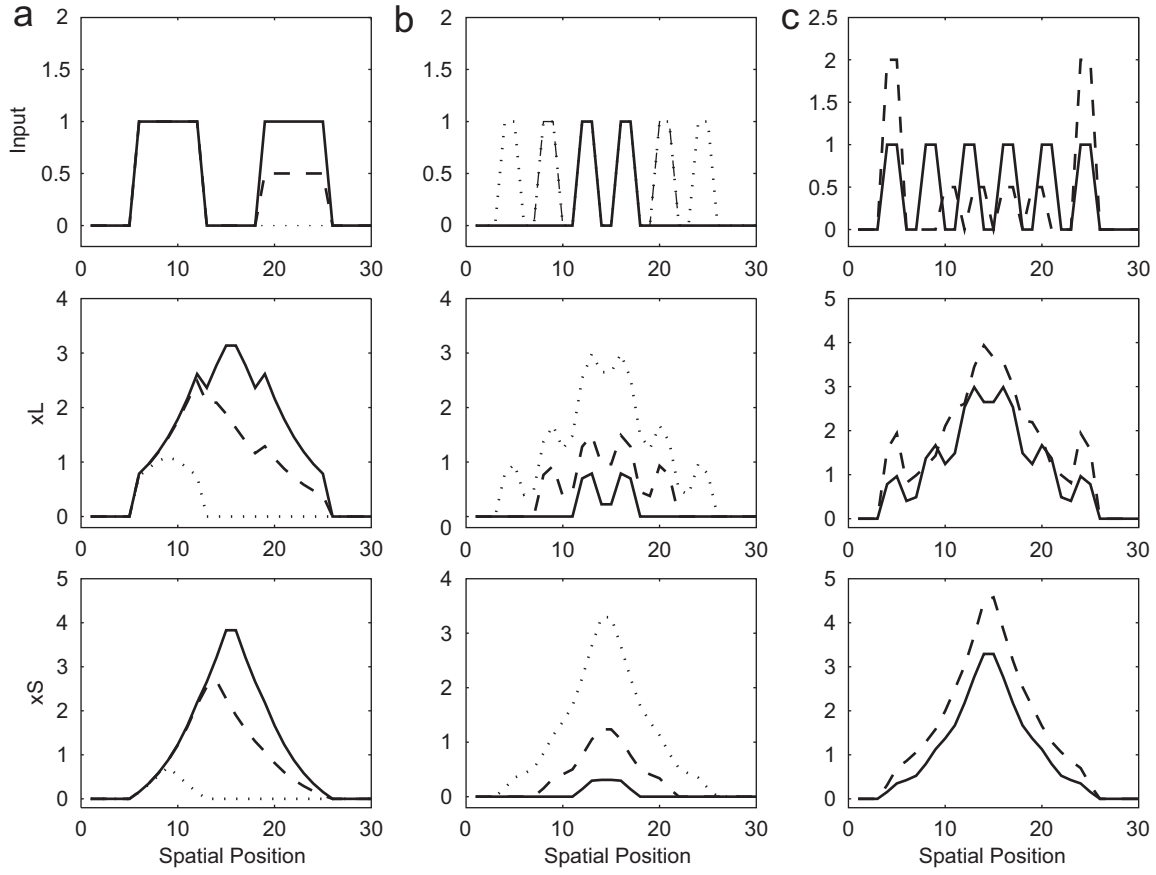

Fig. 3. Computer simulations illustrating the network behaviour.

different responses to different input magnitude of the right inducer (Fig. 3a, solid and dashed lines). Fig. 3b shows a linear relationship between the number of inducing elements and excitatory cell response. In this simulation, inducers are added from the middle two toward ends. In this way, we simulate the neurophysiological experiment described in [2] showing increase in cell's response with increase in the number of inducing elements. These simulations illustrate that the input magnitude could be defined either as a strength of individual contour elements or as a number of contour elements within the same dendritic branch. In both cases, cell response increases with input magnitude.

We also simulated the difference in strength or clarity of the illusory contour for regular or irregular placement of the inducing elements described by Gillam [5] (Fig. 3c). With irregular placement of the inducing elements some of the bipole cells will receive stronger input because the competition between the complex cells is distance dependent. Consider a case in which certain inducing element is isolated or placed far apart from other elements. The complex cell positioned over it will receive less inhibition compared to other complex cells. This situation is illustrated in the input vector of Fig. 3c (dashed line). On the other hand, with regular placement of the inducing elements, all complex cells will receive the same amount of inhibition (Fig. 3c, solid line). Due to the fact that the distance between regularly spaced elements is smaller than the distance between the most isolated elements in irregular arrangement, the total amount of inhibition will be greater with regular placement of elements. A strong inhibition between complex cells will provide weaker input to the bipole cells and consequently lead to weaker illusory contour when stimulus is a regular set of inducing elements.

According to Grossberg and Mingolla [4], illusory contour formation is an obligatory process that always produces strong contour. However, Albert [9] showed examples where illusory contours are weak or absent despite the existence of collinear inducers (e.g., when crosses are used as inducers in Fig. 1a). We suggest that the top-down influences (attending to or recognizing certain perceptual groupings) may reduce the strength of the illusory contour. This may happen because inducers could be recognized as independent figures (e.g., crosses) or they could draw attention to itself due to their symmetry or parallelism. The top-down influence on illusory contour formation and on collinear facilitation is explained in the presented framework by the operation of the inhibitory cells. We may assume that inhibitory cell receives excitation from higher visual centres when attention is directed in the part of the visual scene where its receptive field is located. This is described by the term *TD* in Eq. (2). The inhibitory cell will distribute this top-down signal to the dendritic branches of the corresponding excitatory cell and effectively raise their threshold for activation. If top-down signal is sufficiently strong it will completely prevent formation of the illusory contour and cells show no response although both parts of its receptive fields are stimulated. This may occur when a stronger perceptual grouping overrides the illusory figure [1,9]. The same mechanism also helps to explain why attention prevents collinear contour facilitation as observed by Ito and Gilbert [6].

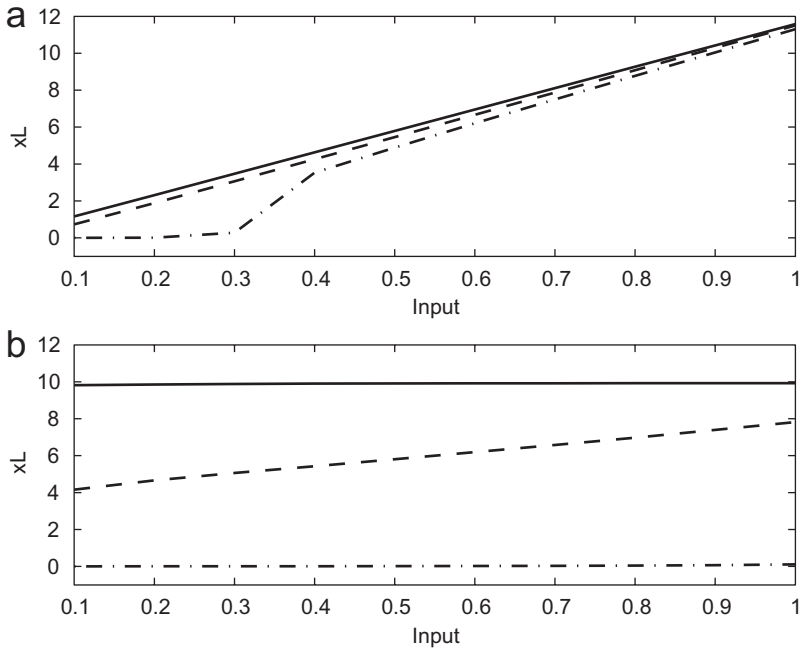

Fig. 4. Parametric simulations with different dendritic output functions $f()$. (a) Power function with exponent $n = .5$ (solid line), 1 (dashed line), or 2 (dash-dotted line). (b) Sigmoid output function with $C = .5$ (solid line), 1 (dashed line), or 2 (dash-dotted line).

We checked the robustness of the model in parametric simulations shown in Fig. 4. First, we studied how the network behaves with a different setting of exponent n in Eq. (3), which describes the output function $f()$ of the dendritic branches. Fig. 4a showed cell responses of a large-scale bipole cell, xL_i, as a function of the input strength for $n = .5$ (solid line), 1 (dashed line), and 2 (dash-dotted line). In these simulations, the input vector represents real contour which has the same value at all spatial locations i. All other parameters are set to the same values as in the simulations shown in Fig. 3. As can be seen, the model shows the linear response to the input magnitude when the dendritic output function is linear or slower then linear. For the faster then linear output function, response becomes linear at higher input magnitudes. In Fig. 4b we showed that the analogue sensitivity is not preserved for the sigmoid output function (Eq. (4)) with $B = 2$ and $C = .5$ (solid line), 1 (dashed line), or 2 (dash-dotted line).

Furthermore, we studied the model behaviour when the strength of synaptic weights between excitatory cells (w_{ij}) or excitatory and inhibitory cells (W_{ii}) are systematically varied (not shown). For simplicity, we set all w_{ij} to be of equal strength. The basic finding is that the model achieves analogue sensitivity as long as the synaptic weights between the excitatory cells are kept weaker than the weights between the excitatory and the inhibitory cells. When W_{ii} is set to 0, an unbounded growth of excitatory activity is observed. We also showed that the network behaviour is not altered when the excitatory and the inhibitory cells have nonlinear output functions or when a more complex neuron model is used instead of a simple linear threshold unit (i.e., nonlinear shunting model). Also, the introduction of direct inhibition between bipole cells through a separate population of inhibitory cells does not disrupt analogue sensitivity. It is interesting to note that in all simulations the network converges to a fixed point, and it does not engage in oscillatory behaviour as in the models of contour integration proposed by Li [10], and Yen and Finkel [11]. This result suggests that the dendritic computation increases the dynamic stability of the recurrent excitatory–inhibitory networks.

4. Discussion

The proposed model of bipole cells is based on properties of the dendritic computation. Recent neurophysiological and theoretical investigations showed that dendrites are not passive neuron's elements. Rather, they actively integrate incoming signals and behave as independent computational units with their own input–output functions [12]. Based on these findings, London and Häusser [7] proposed a dendritic toolkit; a set of computational mechanisms that dendrites could perform. Among them is multiplication or coincidence detection between different dendritic branches. Here, we proposed that the dendritic multiplication is responsible for a generation of the illusory contour. We also used local interaction between excitation and inhibition on isolated dendritic branches in order to achieve the MAX function computation. In [13], it is shown that feedforward dendritic inhibition allows computation of MAX function on cell's input. Here, a recurrent extension of the network with dendritic inhibition is used. A disadvantage of the proposed model is that a desirable behaviour is achieved when the output of a single dendritic branch is linear above threshold. On the other hand, theoretical analysis of the detailed model of the pyramidal neuron suggests sigmoid output function as a better description for dendrites [7].

In conclusion, the presented model of the illusory contour formation is able to perform perceptual grouping of nonadjacent collinear segments. It shows a linear response relationship with input magnitude because the dendritic inhibition regulates the signal flow and prevents unbounded growth of activity in the recurrent excitatory network [8]. Analogue sensitivity is achieved under a wide variety of parameter settings and input–output functions as shown in parametric simulations. The model can explain why illusory contours are stronger with irregular placement of inducing elements rather than regular placement and why the attention or other top-down signals may prevent the illusory contour formation. These findings could not be modelled with a recent extension of the BCS proposed by Grossberg and Raizada [14] and with the model of V1–V2 interaction proposed by Neumann and Sepp [15].

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