

# Neural circuit models for computations in early visual cortex

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## Abstract:

Some cortical circuit models study the mechanisms of the transforms from visual inputs to neural responses. They model neural properties such as feature tunings, pattern sensitivities, and how they depend on intra-cortical connections and contextual inputs. Other cortical circuit models are more concerned with computational goals of the transform from visual inputs to neural responses, or the roles of the neural responses in the visual behavior. The appropriate complexity of a cortical circuit model depends on the question asked. Modeling neural circuits of many interacting hypercolumns is a necessary challenge, which is providing insights to cortical computations, such as visual saliency computation, and linking physiology with global visual cognitive behavior such as bottom-up attentional selection.

## Introduction

A full computational understanding of the visual cortex requires understanding both of the following computations: (A) from visual inputs to neural responses, and (B) from neural responses to visual behavior. Physiological and anatomical data[1, 2, 3, 4, 5] suggest that neural interactions in intra-cortical circuits play a main role in shaping neural responses. Hence, understanding the neural circuit is essential for insights into the cortical computation. The computational issues of interest include, for example, how neural circuits enable the invariance of orientation tuning width of a neuron to input contrast, and whether the cortical circuits transform visual inputs to signals for guiding bottom-up attentional selection, and/or other goals. This review aims to understand computation by interacting neurons in early visual cortex. It omits phenomenological models of contextual influences, e.g., the divisive normalization model of cortical responses[6]), feedforward models of hierarchical processing across multiple visual areas for, e.g., object recognition[7, 8], circuit models of higher visual areas (e.g., frontal eye field[9]), and does not emphasize models which are purely on mapping visual inputs to neural responses (e.g., [10, 11, 12]).

Neural circuit models may be categorized into three levels of complexity, giving model classes referred to as reduced columnar models, hypercolumn models, and interacting hypercolumn models. The reduced columnar models[13••]) have all neurons sharing the same receptive field position and preferred feature (e.g., orientation, Fig. (1a)). They are often used to study response gain control by direct and contextual visual inputs, and their behavior can be linked to visual contrast sensitivity in behavior. The hypercolumn models contain interacting neurons tuned to different feature values in a single feature dimension, typically orientation (Fig. (1b))[14, 15••, 16•]. When this feature dimension is space[17, 18•], the neurons are no longer within a single cortical hypercolumn, however, the complexity of such models are similar to the hypercolumn model. They can be used to study feature tuning or response selectivity to feature patterns, and their behavior can be linked to feature discrimination behavior. The interacting hypercolumn models contain neurons tuned to both space (by their receptive field locations) and another feature such as orientation, color, motion direction, or depth (or even combinations of them) (Fig. (1c)). For example, when different model neurons have different receptive field locations and different preferred orientations spanning the

whole range of locations and orientations, a model can simulate neural responses to meaningful object contours and surface textures[19•, 20, 21••], and be linked to global visual behavior.

## The representative circuit models and their computations

For better overview, the reviewed models are presented by paraphrasing their main features (while citing the original references) using a common set of mathematical notations. Model parameters to reproduce all the simulation results (in Fig.2) are provided for interested readers.

### A reduced columnar model of an excitatory-inhibitory (E-I) cell pair for input gain control

This[13••, 15••] models a local circuit of a principal, pyramidal, excitatory (E) cell connected with an inhibitory(I) interneuron, each modeling a local group of similar cortical cells. With only one principal neuron, the preferred feedforward (direct) input feature is fixed, and hence this circuit cannot exhibit any input feature selectivity. However, it has been used to shed light on computations from visual inputs to neural responses to behavior. In particular, it demonstrated the mechanism for input gain control in the mapping (the contrast response function) from visual input to E neuron's response[13••] observed physiologically. Furthermore, this gain control by contextual inputs (via intra-cortical connections from other E-I pairs outside the model) was even suggested to play a role in the behavior of contour completion and pop out[15••], even though this suggestion can not be demonstrated in this reduced columnar model.

Let membrane potentials of the E and I neurons be  $x$  and  $y$  respectively, with their neural responses  $g_x(x)$  and  $g_y(y)$  as nonlinear, sigmoid-like, functions of  $x$  and  $y$ , then

$$\dot{x} = -\alpha_x x + J_{ee}g_x(x) - J_{ei}g_y(y) + I_e, \quad (1)$$

$$\dot{y} = -\alpha_y y + J_{ie}g_x(x) - J_{ii}g_y(y) + I_i, \quad (2)$$

where  $J_{ee}$ ,  $J_{ie}$ ,  $J_{ei}$ , and  $J_{ii}$  model the synaptic connection strengths between the neurons,  $\alpha_x$  and  $\alpha_y$  are constants modeling the inverses of membrane time constants of the E and I neurons respectively, while

$$I_e = T_e I_t + C_e I_c \quad (3)$$

$$I_i = T_i I_t + C_i I_c \quad (4)$$

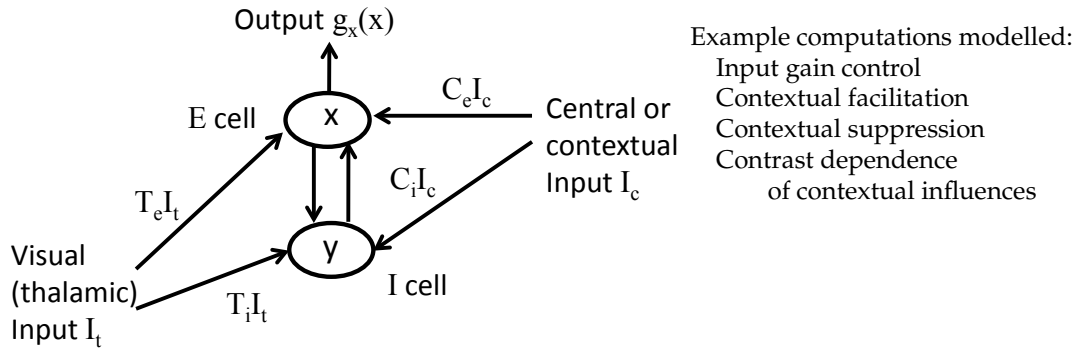
are inputs converged from the thalamic inputs  $I_t$ , via feedforward connection weights ( $T_e, T_i$ ), and contextual or central inputs  $I_c$ , via lateral or feedback connection weights ( $C_e, C_i$ ). The fixed point  $(\bar{x}, \bar{y})$ , where  $\dot{x} = \dot{y} = 0$ , typically approximates the temporal averages of neural activities  $x$  and  $y$  under static inputs ( $I_t, I_c$ ). To see how this circuit exhibits gain control, as in [13••], first examine the sensitivity of the response  $g_x(\bar{x})$  to thalamic input  $I_t$  (see[22•] for a proof in a simplified case)

$$\frac{\delta g_x(\bar{x})}{\delta I_t} = g'_x(\bar{x}) \frac{(\alpha_y + J_{ii}g'_y(\bar{y}))T_e - J_{ei}g'_y(\bar{y})T_i}{(\alpha_x - J_{ee}g'_x(\bar{x}))(\alpha_y + J_{ii}g'_y(\bar{y})) + J_{ei}J_{ie}g'_x(\bar{x})g'_y(\bar{y})} \quad (5)$$

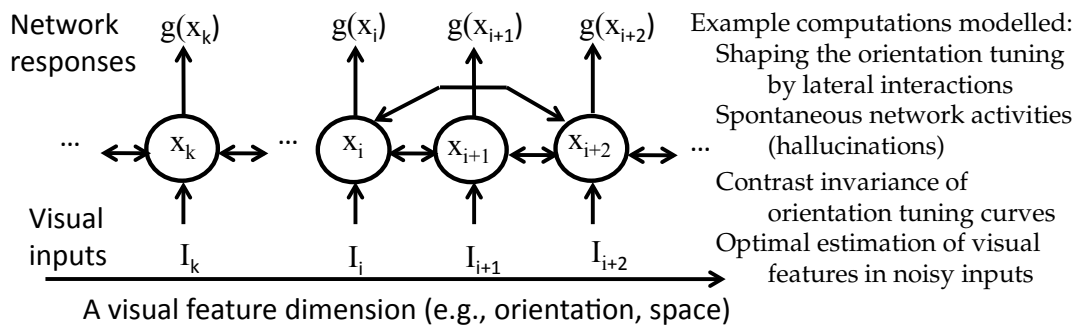
It increases with E cell's gain  $g'_x(\bar{x})$  but decreasing with I cell's gain  $g'_y(\bar{y})$  at the average activity  $(\bar{x}, \bar{y})$ . It is highest when thalamic and contextual/central inputs  $I_t$  and  $I_c$  are weak such that the I cell is not activated, i.e.,  $g'_y(\bar{y}) = 0$ , giving input sensitivity

$$\frac{\delta g_x(\bar{x})}{\delta I_t} = \frac{g'_x(\bar{x})T_e}{\alpha_x - J_{ee}g'_x(\bar{x})} \quad (6)$$

(a) a reduced columnar model, an excitatory-inhibitory (E-I) pair, for a given visual feature



(b) a hypercolumn model for input pattern selectivity in a single feature dimension



(c) a model of interacting hypercolumns for global spatial vision

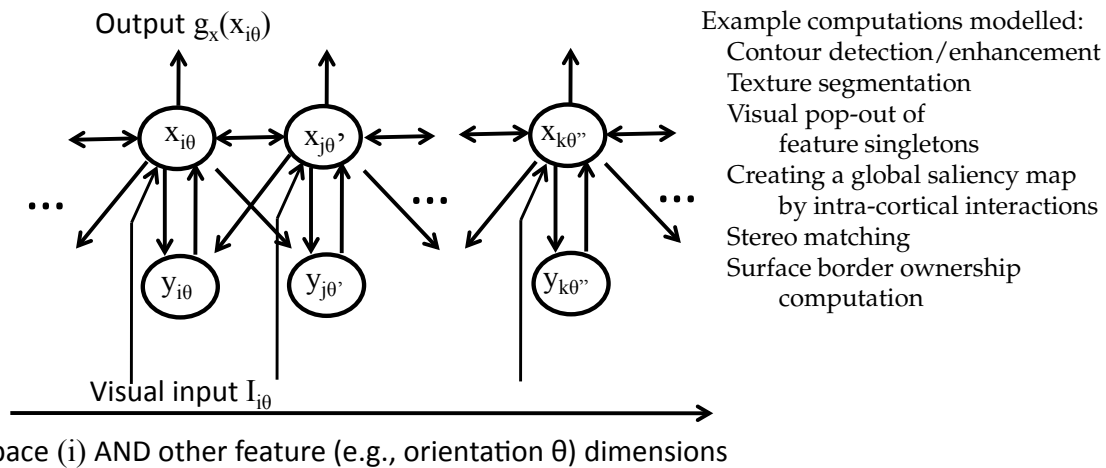


Figure 1: Three levels of complexity to model visual cortical circuits. A: an E-I network preferring a single visual feature, e.g., a particular orientation  $\theta$  at a particular location  $i$ , in response to feed-forward visual inputs, and contextual recurrent inputs or central feedback inputs. B: a network for a single feature dimension, e.g., a model of neurons tuned to various orientations  $\theta$  spanning  $0 < \theta \leq 180^\circ$ , or a model of neurons whose receptive fields  $i$  collectively span the visual field. C: a network of neurons for processing two feature dimensions, space (indexed by  $i$ ) and another dimension (indexed by  $\theta$ ) such as orientation. Different E-I pairs are tuned to different  $(i, \theta)$ . When  $\theta$  is orientation, input  $\{I_{i\theta}\}$  can include object contours and surface textures. Each computational issue is best addressed by a model of a suitable complexity.

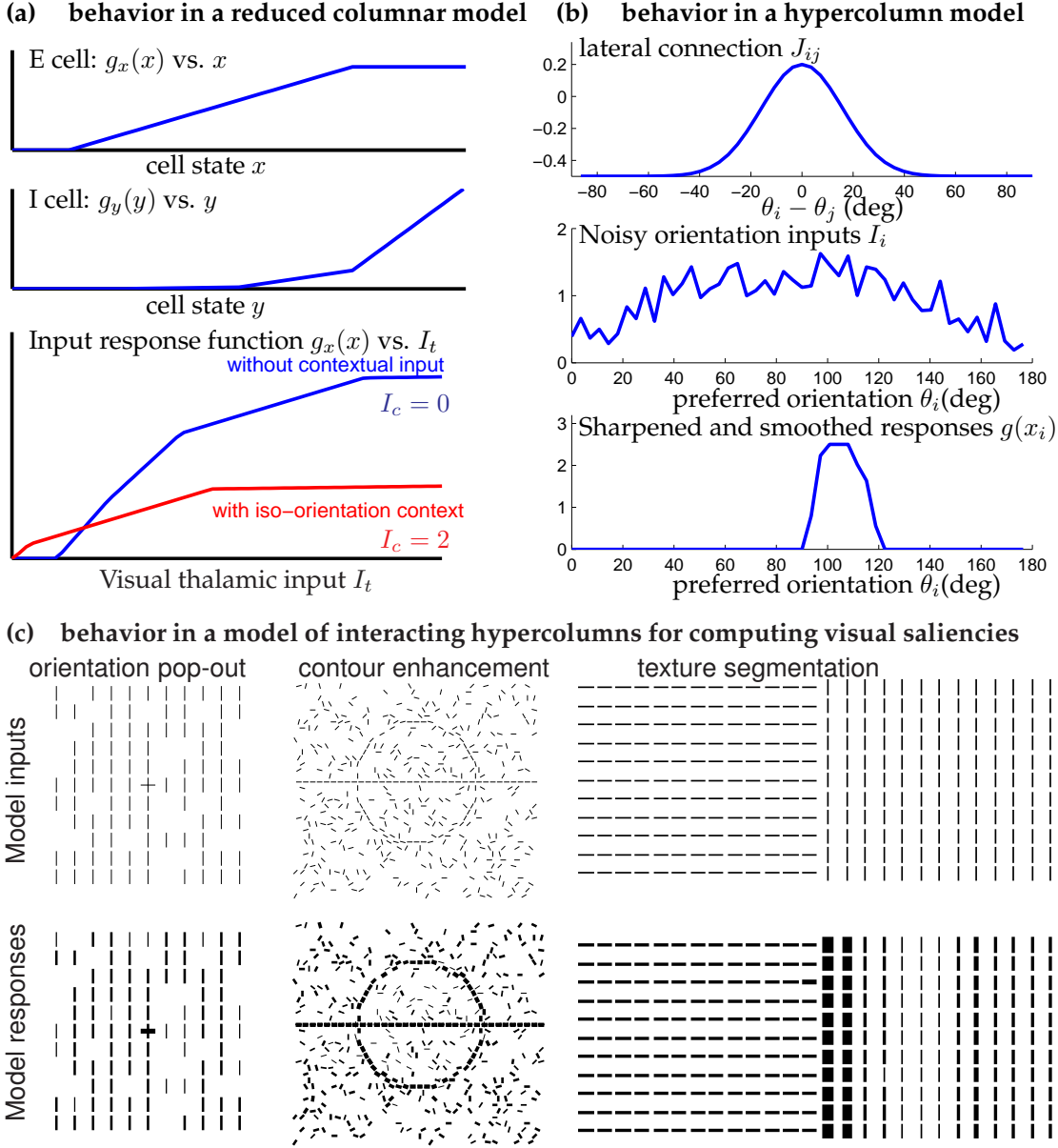


Figure 2: Example performances of models at the three levels of complexity in Fig. (1). A: an E-I pair model as in equations (1-4), with its piece-wise linear firing rates  $g_x(x)$  and  $g_y(y)$ , and its input response function  $g_x(x)$  vs.  $I_t$  under different contextual conditions.  $\alpha_x = \alpha_y = 1$ ,  $g_x(x) = 0, x-0.5$ , and  $2.5$  for  $x < 0.5, 0.5 \leq x \leq 3$ , and  $x > 3$  respectively;  $g_y(y) = 0, 0.1y - 0.1, y - 1.9$ , and  $5y - 13.9$  for  $y < 1, 1 \leq y \leq 2, 2 \leq y \leq 3$ , and  $y > 3$  respectively;  $(T_e, T_i) = (0.8, 0.2)$ ;  $(C_e, C_i) = (0.3, 0.9)$ ,  $(J_{ee}, J_{ei}, J_{ie}, J_{ii}) = (0.2, 1.5, 1, 0.2)$ . B: a hypercolumn circuit model of interacting neurons tuned to orientation, as in equation (9),  $N = 50$  model neurons are used for a model hypercolumn,  $g(x) = g_x(x)$  in A,  $J_{ij} = 0.7 \exp[-(i - j)^2 / (N/8)^2] - 0.5$ . Lateral connections helps to smooth, amplify and sharpen orientation input patterns. C: a model of interactions between E-I pairs in various hypercolumns and tuned to different orientations, as in equations (10-11), model parameters are as in [39\*\*]. Input and output strengths are visualized by the thicknesses of the bars plotted, each image is a part of a much larger image. The model gives relatively higher responses to conspicuous image locations.

in which the negative feedback from the I cell is non-existent. Meanwhile, this sensitivity is zero before the E cell's state  $\bar{x}$  is above the threshold to give a non-zero  $g'_x(\bar{x})$ , and is amplified by E cell's self-excitation  $J_{ee}$  (modeling mutual excitation within the group of pyramidal cells modelled by this single E model cell). Increasing thalamic input  $I_t$  raises I cell's  $\bar{y}$ , either directly via  $T_i I_t$  or indirectly via excitation from E to I, making  $g'_y(\bar{y}) > 0$  and thereby reducing the input sensitivity  $\delta g_x(\bar{x})/\delta I_t$ . When the I cell is activated sufficiently, E cell's response to  $I_t$  saturates or super-saturates, i.e.,  $\delta g_x(\bar{x})/\delta I_t \leq 0$ , when  $(\alpha_y + J_{ii}g'_y(\bar{y}))T_e \leq J_{ei}g'_y(\bar{y})T_i$ , even before the E cell saturates by itself when  $g'_x(\bar{x}) = 0$ . Such threshold, saturation, and super-saturation behavior (Fig. (2a)) are as physiologically observed[23, 24], and the behavior without the super-saturation has been well fitted by the phenomenological contrast response function  $R = R_{max}C^\gamma/(C_{50}^\gamma + C^\gamma)$  relating response  $R$  to input contrast  $C$  with model fitting parameters  $R_{max}$ ,  $C_{50}$  and  $\gamma$ [23].

Meanwhile, contextual visual inputs  $I_c$  outside the receptive field of the E-I pair typically cause lateral input  $(\delta I_e, \delta I_i) = (C_e I_c, C_i I_c)$  to the E-I pair, more so when they are oriented parallel to the inputs within the receptive fields[3, 4, 2, 25]. The sensitivity  $\delta g_x(\bar{x})/\delta I_c$  is obtained by simply replacing  $\delta g_x(\bar{x})/\delta I_t$  and  $(T_e, T_i)$  in equation (5) by  $\delta g_x(\bar{x})/\delta I_c$  and  $(C_e, C_i)$ , respectively. The change in  $g_x(\bar{x})$  caused by the lateral inputs  $(\delta I_e, \delta I_i) = (C_e I_c, C_i I_c)$  is then

$$\delta g_x(\bar{x}) = g'_x(\bar{x})I_c \frac{(\alpha_y + J_{ii}g'_y(\bar{y}))C_e - J_{ei}g'_y(\bar{y})C_i}{(\alpha_x - J_{ee}g'_x(\bar{x}))(\alpha_y + J_{ii}g'_y(\bar{y})) + J_{ei}J_{ie}g'_x(\bar{x})g'_y(\bar{y})} \quad (7)$$

Hence,  $I_c$  is facilitatory when

$$(\alpha_y + J_{ii}g'_y(\bar{y}))C_e > J_{ei}g'_y(\bar{y})C_i \quad (8)$$

and suppressive otherwise. Hence, the contextual influence depends on the I cell's state  $\bar{y}$ . Under weak feedforward input  $I_t$  when the I cell is inactivated and  $g'_y(\bar{y}) \approx 0$ , contextual influences are facilitatory[26, 27]. Stronger input  $I_t$  activates the I cell and increases  $g'_y(\bar{y})$ , and can switch the contextual influences to suppression, as physiologically observed[28, 27, 29, 30, 31]. Note that this switch in the effect of contextual influence is mainly caused by the low activation of the I cell by weak input, and by the stronger inhibition from the I cell when it is activated and more sensitive to inputs[13••]. When the contextual inputs are perpendicular to the (optimal) input within the receptive field of the modelled E-I pair,  $(C_e, C_i)$  are much smaller. This reduces the lateral inputs  $(\delta I_e, \delta I_i) = (C_e I_c, C_i I_c)$ , making the E cell's contrast response function  $g_x(\bar{x})$  vs.  $I_t$  similar to that without the contextual inputs (Fig. 2a). This switch of the contextual effect and its orientation sensitivity has been suggested[15••] to underlie contour completion in weak input, when the iso-orientation context enhances the response of the E-I pair, and orientation pop out in stronger inputs, when the E-I pair is less suppressed by the cross-orientation background whose evoked responses are more mutually suppressed within themselves.

This circuit with its nonlinear interactions between the E and I neurons has also been used to understand other phenomena such as context enabled learning[32] and faster responses to inputs while having positive feedback amplifications[33].

## “Hypercolumn” models for feature selectivity

To model response to input patterns and their impact on behavior, we need multiple principal cells preferring different feature values spanning a sufficient range at least in a single feature dimension. For example, one could model a hypercolumn by  $N$  interacting model neurons  $i$ , with their respective preferred orientations  $\theta_i$  spanning the whole orientation range. To an input pattern  $\mathbf{I} = (I_1, I_2, \dots, I_N)$ , its response pattern is  $g(\mathbf{x}) = (g(x_1), g(x_2), \dots, g(x_N))$ . Alternatively, the feature

dimension can be spatial locations, generalizing the concept of the “hypercolumn” model, so that  $I_i$  models feedforward input at location  $i$ , and  $g(x)$  is a spatial pattern of responses. The computational goals of the recurrent processing in such models have included [17, 18<sup>•</sup>, 14, 16<sup>•</sup>, 34<sup>•</sup>, 35] sharpening the neural feature tuning, denoising responses to noisy inputs, amplifying responses to certain weak input patterns, and maintaining or generating responses in the absence of inputs as in sensory hallucination.

Many hypercolumn models [17, 14, 16<sup>•</sup>, 34<sup>•</sup>] assume for simplicity that a neuron can be excitatory to some and inhibitory to other post-synaptic cells (see [13<sup>••</sup>, 11, 12, 18<sup>•</sup>] for exceptions), such that the model equation is like

$$\dot{x}_i = -x_i + \sum_j J_{ij} g(x_j) + I_i \quad (9)$$

where  $J_{ij}$ 's are elements of matrix  $J$  modeling the intra-cortical connections. Due to translation invariance,  $J_{ij}$  depends only on the difference  $|i - j|$  or  $|\theta_i - \theta_j|$ , and  $J_{ij} = J_{ji}$ . In the orientation dimension, if a raw input is oriented at  $\hat{\theta}$ , it may generate feedforward input  $I_i = A + C \cdot \cos(\theta_i - \hat{\theta})$  as the result of the orientation tuning curves (with constants  $A$  and  $C$ ). Under static inputs, such networks with symmetric connections between any two neurons (e.g., the Hopfield model [36]) are known to converge to stable (static) states  $\bar{x}$ , such that  $\bar{x}_i = \sum_j J_{ij} g(\bar{x}_j) + I_i$ . Zero  $J$  makes state  $\bar{x} = \mathbf{I}$ , but stronger  $J$  makes  $\bar{x}$  a distorted (e.g., more sharply tuned) version of  $\mathbf{I}$ . When  $J$  is strong enough the network could even have non-zero state  $\bar{x}$  under zero input  $\mathbf{I}$  [14, 16<sup>•</sup>]. For example, if  $J_{ij} = 1.1$  for  $|i - j| \leq 1$  and  $J_{ij} = -1$  otherwise, and if  $g(x)$  is a step function with  $g(x) = 1$  for  $x \geq 1$  and  $g(x) = 0$  otherwise, then a broadly tuned input  $\mathbf{I} = (\dots, 0, 0, 0.2, 0.3, 0.4, 0.5, 0.4, 0.3, 0.2, 0, 0, \dots)$  can lead to a more narrowly tuned response  $g(\bar{x}) = (\dots, 0, 0, 1, 1, 1, 0, 0, \dots)$ . If a transient input  $\mathbf{I}$  brings the network near this state  $\bar{x}$ , the network is likely to settle and remain in it as if it is a memory. A non-zero  $J$  also increases input response gain, as mutual excitation between nearby neurons amplifies input. An initially noisy orientation input biased to orientation  $\theta_i$  could evoke response  $g(\bar{x})$  as if the input is noise free and oriented near  $\theta_i$ , see Fig. (2b). As  $J$  becomes stronger,  $\bar{x}$  and the orientation tuning width of neurons become less sensitive to the shape and strength of  $\mathbf{I}$ . This helps to optimally estimate the visual input orientation  $\hat{\theta}$  from a noisy  $\mathbf{I}$ , by locating the peak position  $i$  in the population activity pattern  $g(\bar{x})$  and assigning  $\hat{\theta} = \theta_i$  [34<sup>•</sup>]. However, insensitivity of response shape  $g(\bar{x})$  to the input pattern  $\mathbf{I}$  makes the network unfaithful to input features. For example, the network could hallucinate an oriented input by a unimodal response pattern  $g(\bar{x})$  even when the actual input is non-oriented or have a bimodal pattern caused by two input orientations [37]. Avoiding hallucination requires decreasing  $J$ , at the expense of input sensitivity. However, in a network of orientation tuned E-I pairs [38<sup>•</sup>], sensitivity to oriented inputs and avoidance of hallucination can be achieved simultaneously.

## Models of interacting hypercolumns for spatial vision

To study spatial patterns of input features such as orientation, models should include visual features in at least two dimensions: space, indexed by  $i$ , and the interested feature dimension such as orientation, color, motion direction, depth, or other features, indexed by  $\theta$ . When  $\theta$  denotes orientation, visual patterns like object contours and surface textures can be represented as spatial configurations of oriented elements  $(i, \theta)$ . High complexity of such models makes them very difficult to harness. Therefore, in order to properly investigate the cortical roles, it is essential that the models are designed to have its responses resemble the physiological responses, particularly the responses under contextual influences which are sensitive to network interactions [29, 27, 30, 31]. One such model [22<sup>•</sup>, 39<sup>••</sup>] is a spatial array of interacting hypercolumns  $i$ , each composed of E-I

pairs ( $i\theta$ ) tuned to different features  $\theta$

$$\begin{aligned} \dot{x}_{i\theta} = & -\alpha_x x_{i\theta} - g_y(y_{i,\theta}) - \sum_{\Delta\theta \neq 0} \psi(\Delta\theta) g_y(y_{i,\theta+\Delta\theta}) \\ & + J_o g_x(x_{i\theta}) + \sum_{j \neq i, \theta'} J_{i\theta, j\theta'} g_x(x_{j\theta'}) + I_{i\theta} + I_o \end{aligned} \quad (10)$$

$$\dot{y}_{i\theta} = -\alpha_y y_{i\theta} + g_x(x_{i\theta}) + \sum_{j \neq i, \theta'} W_{i\theta, j\theta'} g_x(x_{j\theta'}) + I_c \quad (11)$$

where  $I_{i\theta}$ ,  $x_{i\theta}$ ,  $y_{i\theta}$ ,  $g_x(x_{i\theta})$ ,  $g_y(y_{i\theta})$  are analogous to the corresponding variables in equations (1-2),  $J_o$  is the self-excitation factor of E neurons,  $I_c$  and  $I_o$  model background inputs, including noise, feature unspecific surround suppression, and central feedbacks,  $\psi(\Delta\theta)$  models connection strength for intra-hypercolumn interactions,  $J_{i\theta, j\theta'}$  and  $W_{i\theta, j\theta'}$  are synaptic connection strengths between hypercolumns from the E neurons to other E and I neurons respectively. Suitable neural interactions make response patterns  $g(\mathbf{x}) = (\dots g(x_{i\theta}), \dots, g(x_{j\theta'}), \dots)$  enhance some visual inputs  $\mathbf{I} = (\dots I_{i\theta}, \dots, I_{j\theta'}, \dots)$  relative to others. For example, when the dominant interaction between colinearly aligned elements ( $i\theta$ ) and ( $j\theta'$ ) is mutual excitation via  $J_{i\theta, j\theta'}$  and that between near-parallel and non-aligned elements is mutual disinaptic inhibition via  $W_{i\theta, j\theta'}$ , and when between E neurons di-synaptic inhibition via  $W_{i\theta, j\theta'}$ 's dominates mono-synaptic excitation via  $J_{i\theta, j\theta'}$ 's, responses to smooth contours, to orientation pop-outs (e.g., a vertical bar among horizontal bars), or to texture borders can be relatively higher than those to homogeneous textures or noisy backgrounds (see Fig. (2c)). It can be shown[38\*, 21\*\*] that, in order to achieve sensitive amplification of conspicuous input elements relative to other inputs without sensory hallucinations, it is necessary to model the cortical circuit as an E-I network, whose oscillatory tendency[40] has non-intuitive computational benefits, instead of a simplified Hopfield-like network[20, 41\*] (like that described by equation (9)) in which connection strengths between neurons are symmetric.

This V1 model was instrumental to developing a theory — the V1 saliency hypothesis. In particular, due to contextual influences leading to iso-feature suppression (e.g., iso-orientation suppression[27]), the V1 response to a pop-out feature singleton in a background of uniformly featured elements (e.g., a horizontal bar among vertical bars) is higher than its responses to the background elements. The model showed that, even in images (like those used in many visual search studies) where saliency differences between input items are subtler, the model responses to more salient locations are consistently higher than its responses to less salient locations[42\*, 22\*, 39\*\*]. These findings inspired the hypothesis that V1 computes saliency from its inputs via its intra-cortical mechanisms, such that the most salient location in the visual field to guide attention in a bottom-up or goal independent manner is the receptive field location of the V1 cell most activated by the visual scene[42\*, 43, 44\*]. Since contextual suppression of V1 responses to a center stimulus is stronger when the context is presented to the same, rather than a different, eye as the center stimulus[45], the theory thus predicts surprisingly that visual attention can be captured by an eye-of-origin singleton, e.g., a vertical bar presented to the left eye among many identical vertical bars to the right eye, even though this singleton is perceptually so non-distinctive that observers typically can not distinguish it from background elements[46]. This prediction was nevertheless confirmed — this eye-of-origin singleton even out-competes a very salient and distinctive orientation singleton to capture attention and gaze, prolonging the reaction time to find this orientation singleton as a target in a visual search task[47, 48]. Several other non-trivial predictions from the theory have also been confirmed[49, 50].

Other E-I circuit models of comparable complexity have been used to demonstrate that neural tuning to surface border ownership in V2[51] could in principle emerge from intra-cortical

interactions[52], and that a single network[53] for stereo matching in random dot stereograms could also enhance responses to depth singletons and borders of depth surfaces as observed in V2 cells[54], while a Hopfield-like network for stereo matching could not[19•]. There are other complex cortical circuit models involving space and other visual features, with added complexity including interactions between multiple visual areas or cortical layers[20, 55•]. Proposed functions of these model circuits include visual segmentation, boundary completion, and feature filling-in. However, an insufficient understanding of these complex models has so far made it difficult to make the proposed functions precise and convincing.

## Concluding remarks

We have limited intuitions of the neural circuit models of more than two interacting neurons, except of those with special properties such as translation symmetry. It is important to find a minimal model which has all the necessary complexity, but no more, to address the problem of interest, whether to test the feasibility of a hypothesized behavioral role or to understand the mechanisms underlying neural responses. Meanwhile, a complex model, such as the one of interacting hypercolumns of E-I pairs in equations (10-11) should also be first understood at the level of their simpler components, a single E-I pair or a hypercolumn of them. It remains an exciting challenge to model neural circuits appropriately to discover and understand their computational roles[56, 57], particularly when modeling the recurrent interactions both within and between different visual cortical areas. Computational understanding of the computations in cortical circuits can then inspire phenomenological models for engineering applications[58, 59].

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A model with spiking neurons tuned to orientation only. The model neurons are for a cortical patch containing a few hypercolumns, so that intra-cortical connections can be short or longer range, within or between hypercolumns. It shows by simulation contextual influences which switches from facilitation to suppression as direct input to the E-I pair increases, the effect analyzed by Somers et al 1998. Although the model neurons are not tuned to spatial locations, the work suggested that facilitation may be used for contour completion and suppression for orientation pop out.

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