Self-organization of color opponent receptive fields and laterally connected orientation maps

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Abstract

Long-range lateral connections in the primary visual cortex (V1) are known to link neurons with similar orientation preferences, but it is not yet known how color-selective cells are connected. Using a self-organizing model of V1 with natural color image input, we show that realistic color-selective receptive fields, color maps, and orientation maps develop. Connections between orientation-selective cells match previous experimental results, and the model predicts that color-selective cells will primarily connect to other cells with similar chromatic preferences. These findings suggest that a single self-organizing system may underlie the development of orientation selectivity, color selectivity, and lateral connectivity.

Key words: Color maps, Orientation maps, Color blobs, Red-green receptive fields, Opponent cells

1 Introduction

Most simple cells in the primary visual cortex (V1) are selective for the orientation of a stimulus, but many are also selective for particular colors [12]. Recent experimental results have shown for the first time how these color-selective cells are organized at the map level, and how they relate to other visual maps such as orientation or ocular dominance [11].

In addition to their afferent input from the LGN, the neurons in these maps are connected intracortically through specific long-range lateral connections [10]. The lateral connections have been found to link cells with similar orientation preferences [6, 10], which allows suppressing redundancy in the input and improves the cells' ability to detect changes in a stimulus [4, 14]. However, the role of these connections in the development and adult function of color selectivity is not yet clear. The model presented here suggests that color blobs found in V1 connect

laterally to other color selective regions.

Although a number of computational models have shown that orientation maps can develop through activity-dependent self-organization (reviewed in [15]), to our knowledge only one previous model has shown how color-selective blobs can develop [1]. In that model, lateral connections were treated as fixed, isotropic interaction functions. Thus previous modeling work has not yet been able to make predictions about how the color-selective cells will be connected laterally, and what roles these connections could play in color and object perception.

In prior work with the LISSOM self-organizing model (Laterally Interconnected Synergetically Self-Organizing Map), we have shown how a Hebbian learning process can develop topographic maps, ocular dominance, orientation, and motion direction columns, and patterned lateral connections between them [3, 13, 14]. The model suggests that these self-organized maps and lateral connections function in adult visual perception to segment and bind coherent objects and reduce redundancy in the input, and that visual illusions and aftereffects arise through this process [4, 7, 14]. In this paper the model is extended further to develop dichromatic color preferences through the self-organization of red-green opponent cell receptive fields. Together, these results show that activity-dependent self-organization can explain many of the anatomical and functional characteristics of the cortex.
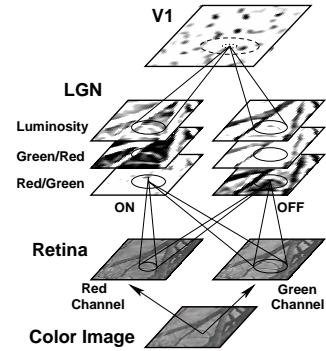
2   HLISSOM model

These simulations are based on the HLISSOM model [2], which extends LISSOM to include the ON and OFF channels of the LGN. HLISSOM is extended further to include dichromatic (red and green) color processing in the retina and LGN, showing V1 will develop blobs of laterally connected color-selective cells within the orientation map. The architecture for the HLISSOM model is shown in figure 1, and will be briefly reviewed below (See [2] for more details.)

The model consists of two-dimensional sheets of neural units modeling different areas of the visual system: two sheets of retinal photoreceptors representing different cone types, several paired sheets of ON-center/OFF-surround and OFF-center/ON-surround LGN units (each with a different color channel combination described below), and a sheet of cortical units ("neurons") representing V1. Because the focus is on the two-dimensional organization of V1, each cortical

Fig. 1. **HLISSOM model of orientation and red-green color selectivity.** The model is a hierarchy of sheets of neural units, modeling the visual pathway from the retinal photoreceptors to V1. For training and activation, color natural images are first separated into red and green channels, which become the bitmap activation patterns of the red and green photoreceptor sheets. Each LGN unit receives input from photoreceptor units in circular receptive fields (RFs). Connections to photoreceptor RFs are plotted for two example Red/Green LGN units. All units at the same position in the other four LGN sheets also receive input from the same location on the photoreceptors. Units in each LGN sheet have difference-of-Gaussian (DoG) shaped connections to the photoreceptors, with a small central region and a larger surround. ON units receive excitation in the center of the RF, and inhibition in the surround. OFF units receive inhibition in the center, and excitation in the surround. For Red/Green units, the center input comes from the Red channel, and the surround from the Green channel, and vice versa for Green/Red units. Neurons in V1 have circular RFs on all six LGN sheets; connections to two of the RFs are shown. V1 neurons also have lateral excitatory (small dotted circle) and lateral inhibitory (large dashed circle) connections to their neighbors. Once all LGN cells have been activated, initial V1 activity is computed from the LGN responses, and the activity then spreads laterally within V1. Both afferent and lateral V1 weights are adapted when the activity settles and eventually organizes into a map of regular orientation and color preferences with patchy lateral connections. (Natural image from Visual Delights, all rights reserved, www.visualdelights.net.)

neuron corresponds to a vertical column of cells through the six anatomical layers of the cortex.

The input to the model is a series of color bitmap images separated into red, green, and blue color channels. In the retina, the majority of photoreceptor cones are sensitive to medium (analogous to the green channel) or long (red) wavelengths [12], and so for simplicity the short-wavelength (blue) channel was omitted from this version of the model. The model simulates three common types of ganglion cell receptive fields: luminosity, red-center/green-surround, and green-center/red-surround.

For each image, the activity levels of all LGN cells are calculated. Each cell (i, j) computes its response η_{ij} as a scalar product of a fixed weight vector and its RFs on the photoreceptor sheets:

$$\eta_{ij} = \sigma \left(\sum_\rho \gamma_\rho \sum_{ab} X_{\rho ab} w_{ij,\rho ab} \right), \tag{1}$$

where ρ identifies the input sheet (either the red or green photoreceptors in the retina), σ is a piecewise linear sigmoid activation function, γ_ρ is a constant scaling factor, $X_{\rho ab}$ is the activation of input unit (a, b) on sheet ρ, and $w_{ij,\rho ab}$ is the corresponding weight value. Each V1 neuron computes its initial response like an LGN cell, then the V1 activity then settles through short-range excitatory and long-range inhibitory lateral interaction:

$$\eta_{ij}(t) = \sigma \left(\sum_\rho \gamma_\rho \sum_{ab} X_{\rho ab}(t-1) w_{ij,\rho ab} \right), \tag{2}$$

where ρ identifies one of the six LGN sheets or the lateral excitatory or lateral inhibitory weights to V1, γ_ρ is a constant scaling factor for each ρ (negative for inhibitory lateral weights), and $X_{\rho ab}(t-1)$ is the activation of input unit (a, b) during the previous settling step. The V1 activity pattern starts out diffuse, but within a few iterations of equation 2, converges into a small number of stable focused patches of activity, or activity bubbles.

After the activity has settled, the connection weights of each V1 neuron are modified. All V1 weights adapt according to the Hebb rule, normalized so that the sum of the weights from each sheet ρ is constant for each neuron (i, j):

$$w'_{ij,\rho ab} = \frac{w_{ij,\rho ab} + \alpha_\rho \eta_{ij} X_{\rho ab}}{\sum_{ab} \left[w_{ij,\rho ab} + \alpha_\rho \eta_{ij} X_{\rho ab} \right]}, \tag{3}$$

where η_{ij} stands for the activity of neuron (i, j) in the final activity bubble, $w'_{ij,\rho ab}$ is the new connection weight, and $w_{ij,\rho ab}$ the current connection weight, α is the learning rate for each type of connection, and $X_{\rho ab}$ is the presynaptic activity. The larger the product of the pre- and post-synaptic activity $\eta_{ij} X_{\rho ab}$, the larger the weight change. At long distances, few neurons have correlated activity and most long-range connections eventually become weak. The weakest connections are eliminated periodically, resulting in patchy lateral connectivity similar to that observed in the visual cortex.

For the experiments reported in this paper, three 36×36 ON-center/OFF-surround and three 36×36 OFF-center/ON-surround cell sheets received input from two 110×110 photoreceptor

sheets. Each ON/OFF cell had fixed Difference of Gaussians receptive fields (RF) within the photoreceptor arrays. Initially, the afferent weights of the 64×64 V1 neurons were random, and the lateral weights had a smooth circular Gaussian profile. The learning parameters were similar to those in our earlier V1 orientation model [4], scaled for this cortex size using the model scaling methodology presented in [2].

3 Results

Figure 2 shows the self-organized afferent weights for three representative neurons after 20,000 image fixations. Nearly all neurons developed receptive fields selective for orientation or for color, while some neurons were partially selective for both. These RFs are similar to those found experimentally in the cortex [8, 9, 11].

Figure 3 shows that the self-organized global orientation and color maps are also similar to those found in animals [5, 11]. Most neurons are selective for orientation, while neurons selective for color and not orientation group into regularly spaced blobs within the orientation map. Neurons surrounding the color-selective blobs tend to be selective for both color and orientation.

Long-range lateral connections between neurons follow the global organization of the orientation and color maps, connecting neurons with similar color or orientation preference (figure 2). For instance, as shown in biological experiments vertical-preferring cells tend to connect to other vertical-preferring cells [5], while the computational model predicts that experiments will show green-preferring cells tend to connect to other green-preferring cells. These connection patterns represent the correlations between units over the course of self-organization. As will be described below, the self-organized lateral weight patterns are likely to play a crucial role in adult visual perception as well as development.

4 Discussion and Future Work

The results demonstrate that a single Hebbian learning algorithm can explain how topographic maps, color sensitive receptive fields, and lateral connections self-organize together from color image stimuli. The model predicts that long-range lateral connections in V1 will be found to connect neurons with similar color preference as well as orientation preference.

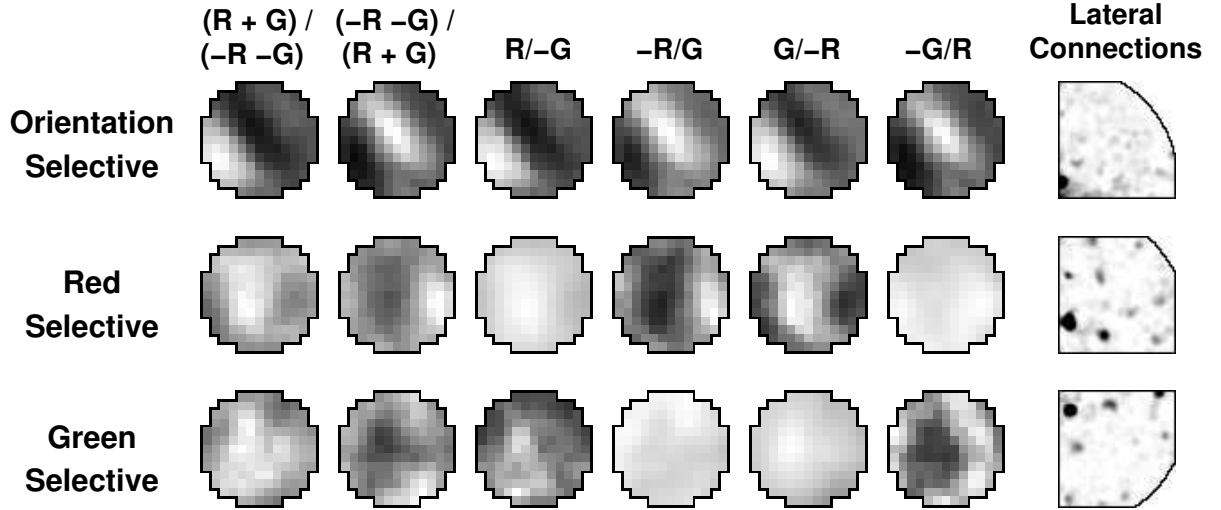|	(R + G) / (−R −G)	(−R −G) / (R + G)	R/−G	−R/G	G/−R	−G/R	Lateral Connections
Orientation Selective							
Red Selective							
Green Selective							

Fig. 2. **Self-organized color- and orientation-selective receptive fields.** These images show the afferent weights for typical orientation selective, red selective, and green selective neurons. White indicates a net ON subregion of the RF, i.e. an area that will excite the neuron if it is brighter than its surround. Black indicates OFF subregions. The top row of afferent weight plots shows that the most effective stimulus for this orientation-selective neuron would be a diagonal bar or grating that is angled from upper-left to lower-right. Either monochrome or color stimuli would be effective, because the neuron has similar-strength connections to ON or OFF LGN sheet of each color. The middle row of weights show a neuron that is selective to red colors. Response is strongest when there is activity from the ON red-center/green-surround LGN sheet (R/-G) and OFF green-center/red-surround LGN sheet (-G/R). It is less responsive to the LGN sheets that respond to green light (-R/G and G/-R), or to monochromatic stimuli. The color preferences are reversed for the green-selective neuron (bottom row), which is activated most strongly when its OFF red-center/green-surround (-R/G) and ON green-center/red-surround (G/-R) RFs are activated. The dark regions in the far right column represent the self-organized lateral weights to each neuron from other neurons in the V1 sheet. The darkest blob consists of short-range connections from nearby neurons that have a variety of preferences. The lighter blobs consist of long-range connections from distant patches of neurons with similar orientation and color preferences. Orientation selective neurons contact many other patches of orientation-selective neurons, while color-selective neurons contact a few, larger blobs of green or red-selective neurons. Such lateral color blob connections have not been measured experimentally in animals but constitute predictions of the model.

In future work the model will be extended to include tri-chromatic receptive fields, with an additional sheet of blue photoreceptors and additional LGN sheets of blue-yellow opponent units.

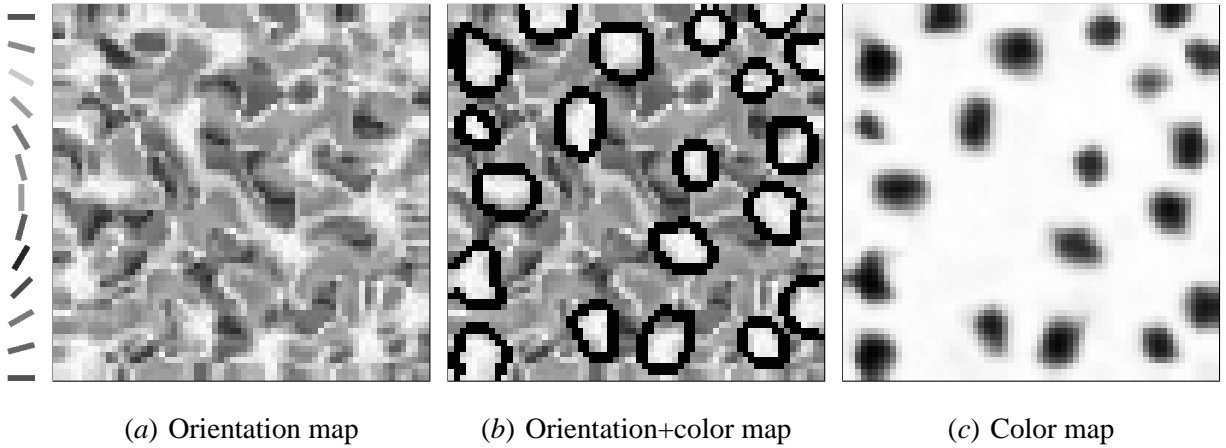(*a*) Orientation map   (*b*) Orientation+color map   (*c*) Color map

Fig. 3. **Self-organized orientation and color maps.** Through self-organization, smoothly varying maps of orientation and color preferences emerged in V1. Each of the 64×64 neurons is colored with its preferred orientation, according to the key at left. The orientation map (*a*) is similar to those found experimentally in animals, containing features such as pinwheels, linear zones, and fractures [5]. There are small regions of unselective neurons scattered through the map that are colored white in the plot. These non–orientation-selective regions match the color selective regions shown as black blobs in (*c*). Plot (*b*) outlines the color sensitive regions on the orientation map to make this relationship clear. These orientation and color maps are similar to those found experimentally in the macaque monkey[11].

It will also include input from two eyes, so that the interaction between color blobs and ocular dominance columns can be analyzed. In addition, we will calibrate the RGB color channel separations based on the response properties of the macaque S, M, and L cones. This model can then be validated against experimental results from particular species.

Other future studies will investigate how the color map and its connections operate in the adult. The self-organized connection patterns should improve object discrimination based upon color, which would help the visual system quickly separate salient objects in an otherwise uniform visual field. The connections may also be important for detecting color borders and achieving color constancy, i.e. recognizing colors as similar in different visual contexts. These studies will help clarify how the visual system develops to process color stimuli.

5   Conclusion

Hebbian learning of color images of natural scenes can explain how orientation selectivity, color selectivity, and lateral connectivity develop in V1. The model provides specific predictions for

the role of the lateral connections in the development and function of the color and orientation maps. This work helps strengthen our understanding of the developing and the adult visual cortex as a continuously adaptive input-driven system.

References

[1] Barrow, H. G., Bray, A. J., and Budd, J. M. L. (1996). A self-organizing model of 'color blob' formation. *Neural Comp.*, 8:1427–1448.

[2] Bednar, J. A. (2002). *Learning to See: Genetic and Environmental Influences on Visual Development*. PhD thesis, Department of Comp Sci, The Univ of TX at Austin. Tech Report AI-TR-02-294.

[3] Bednar, J. A., Kelkar, A., and Miikkulainen, R. (2002). Modeling large cortical networks with growing self-organizing maps. *Neurocomp*, 44–46:315–321.

[4] Bednar, J. A., and Miikkulainen, R. (2000). Tilt aftereffects in a self-organizing model of the primary visual cortex. *Neural Comp*, 12(7):1721–1740.

[5] Blasdel, G. G. (1992). Orientation selectivity, preference, and continuity in monkey striate cortex. *J Neurosci*, 12:3139–3161.

[6] Bosking, W. H., Zhang, Y., Schofield, B., and Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. *J Neurosci*, 17(6):2112–2127.

[7] Choe, Y., and Miikkulainen, R. (1998). Self-organization and segmentation in a laterally connected orientation map of spiking neurons. *Neurocomp*, 21:139–157.

[8] Conway, B. R. (2001). Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (v-1). *J Neurosci*, 21(8):2768–2783.

[9] DeAngelis, G. C., Ohzawa, I., and Freeman, R. D. (1995). Receptive-field dynamics in the central visual pathways. *Trends Neurosci*, 18:451–458.

[10] Gilbert, C. D., and Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and cortico-cortical connections in cat visual cortex. *J Neurosci*, 9:2432–2442.

[11] Landisman, C. E., and Ts'o, D. Y. (2002). Color processing in macaque striate cortex: Relationships to ocular dominance, cytochrome oxidase, and orientation. *J Neurophysi*, 87(6):3126–3137.

[12] Rowe, M. H. (2002). Trichromatic color vision in primates. *News Physiol Sci*, 17(3):93–98.

[13] Sirosh, J., and Miikkulainen, R. (1994). Cooperative self-organization of afferent and lateral connections in cortical maps. *Biol Cybernet*, 71:66–78.

[14] Sirosh, J., Miikkulainen, R., and Bednar, J. A. (1996). Self-organization of orientation maps, lateral connections, and dynamic receptive fields in the primary visual cortex. In Sirosh, et al., editors, *Lateral Interactions in the Cortex: Structure and Function*. Austin, TX: The UTCS NN Research Group. Electronic book, ISBN 0-9647060-0-8, http://nn.cs.utexas.edu/web-pubs/htmlbook96.

[15] Swindale, N. V. (1996). The development of topography in the visual cortex: A review of models. *Network – Comput Neural Sys*, 7:161–247.