Self-organization of spatiotemporal receptive fields and laterally connected direction and orientation maps

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Abstract

Studies of orientation maps in primary visual cortex (V1) suggest that lateral connections mediate competition and cooperation between orientation-selective units, but their role in motion perception has not been established. Using a self-organizing model of V1 with moving oriented patterns, we show that (1) afferent weights of each neuron organize into Gabor-like spatiotemporal receptive fields with ON and OFF lobes, (2) these receptive fields form realistic joint direction and orientation maps, and (3) lateral connections develop between regions with similar orientation and direction preferences. The model shows that a simple self-organizing algorithm can explain how orientation selectivity, direction selectivity, and lateral connectivity develops in V1. The model provides specific predictions for the patterns the lateral connections will form in the direction map, as well as suggesting roles for the connections in adult vision.

Key words: Self-organization, Cortical modeling, Vision, Orientation maps, Direction maps, Spatiotemporal receptive fields, Direction selectivity, Lagged cells

1 Introduction

Most simple cells in the primary visual cortex (V1) are selective for the direction and orientation of a moving stimulus. Recent measurement techniques have made it possible to plot the neurons' full spatiotemporal receptive fields, which include specific excitatory (ON) and inhibitory (OFF) subregions that vary over time [5]. The functional properties of these cells form a mosaic across V1, with patches of nearby neurons preferring similar directions and orientations [14].

In addition to their afferent input from the LGN, the neurons in these maps are connected intra-cortically through specific long-range lateral connections [7]. The lateral connections have been found to link cells with similar orientation preferences [3, 7], which can allow the connections to suppress redundancy in the input and improve the cells' ability to detect changes in a stimulus [2, 9, 13]. However, the role of these connections in the development and adult function of directional selectivity is not yet clear.

Several computational models have shown that directional selectivity and interleaved orientation and direction maps can develop through activity-dependent self-organization [6, 11, 15]. However, these simulations have included afferent connections only. 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 size preference columns, and patterned lateral connections between them [9, 12, 13].

Fig. 1. **CRF-LISSOM model of orientation and direction selectivity.** The model is a hierarchy of sheets of neural units, modeling the early visual pathway. In this implementation, there are eight sheets of LGN units. The LGN units receive input from their circular receptive fields (RFs) on the photoreceptors. Connections to a sample photoreceptor RF are plotted for two LGN units; all units at the same position in the other six LGN sheets also connect to the same RF. Each LGN sheet contains a homogenous group of units, with either ON- or OFF-center organization and a lag of 0, 1, 2, or 3 timesteps. Similarly, neurons in V1 have circular RFs on all eight 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. Moving input patterns are drawn on the photoreceptor sheet in discrete timesteps, like frames of a movie. At the first timestep, the ON and OFF LGN cells with time lag 3 compute their activity. At each subsequent timestep, the input pattern is moved slightly and LGN cells with lags 2, 1, and 0 compute their activity in turn. 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.
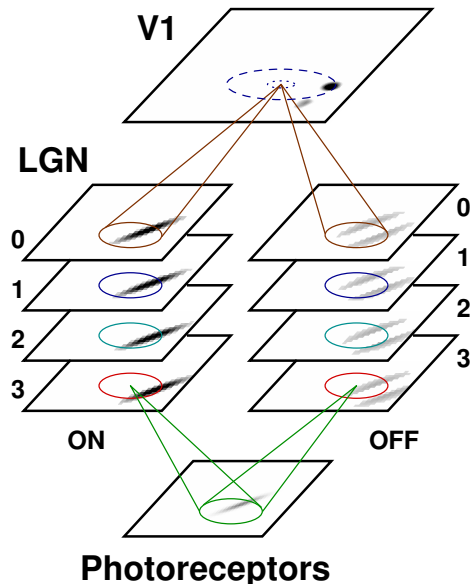
We have also shown that these self-organized maps and lateral connections can function in adult visual perception to segment and bind coherent objects, reduce redundancy in the input, and produce visual illusions [2, 4, 13]. In this paper we extend the model to develop motion and direction preferences through the self-organization of spatiotemporal receptive fields. Together, these results show that activity-dependent self-organization can explain many of the anatomical and functional characteristics of the cortex.

2 CRF-LISSOM model

These simulations are based on the CRF-LISSOM model [1], which extends LISSOM to include the ON and OFF channels of the LGN. The main idea is that directional selectivity can develop from LGN cells whose output arrives at the cortex after a delay. In the LGN, many cells fire soon after a retinal stimulus. However, other *lagged* cells have recently been found in cat LGN that respond only after a fixed delay [10]. The delay time in these lagged cells varies over a continuous range up to hundreds of milliseconds [16]. We will show below that V1 neurons can use these timing differences to develop spatiotemporal receptive fields.

The architecture for the CRF-LISSOM model is shown in figure 1, and will be briefly reviewed below. (For more details, see [2].) The model consists of a hierarchy of two-dimensional sheets of neural units modeling different areas of the visual system: a sheet of retinal photoreceptors, several paired sheets of ON-center and OFF-center LGN units (with a different lag for each pair), and a sheet of cortical units ("neurons") representing V1. Because the focus is on the two-dimensional organization of V1, each neuron corresponds to a vertical column of cells through the six anatomical layers of the cortex.

The model simulates behaviour at three different timescales, denoted by variables f, t, and s

in the equations below. Variable f represents a single fixation out of a sequence of thousands presented to the model. At each fixation, objects in the environment move in several discrete timesteps t. At each time t, lateral interactions are computed for several timesteps s within the cortex.

The input to the model is a series of activity patterns on the sheet of photoreceptors, such as two-dimensional oriented Gaussians. A sample input is drawn in the photoreceptor layer of figure 1. For a given moving input, the photoreceptor activity is drawn at multiple discrete timesteps. At each time step t, the activity levels of all LGN cells with lag t are calculated. Each cell (i, j) with lag t computes its response η_{ij} as a scalar product of a fixed weight vector and its receptive fields on the photoreceptor sheet at time t:

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

where ρ identifies the input sheet (the photoreceptors, in this case), 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 at timestep t, and $w_{ij,\rho ab}$ is the corresponding weight value. Each V1 neuron computes its initial response like that of an LGN cell, except that ρ identifies one of the ON and OFF LGN layers. After the initial response, the V1 activity settles through short-range excitatory and long-range inhibitory lateral interaction:

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

where ρ identifies either an LGN layer or the lateral excitatory or inhibitory weights to V1, γ_ρ is a constant scaling factor for each ρ (negative for inhibitory lateral weights), and $X_{\rho ab}(s-1)$ is the activation of target 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 to each sheet ρ is constant for each neuron (i, j):

$$w_{ij,\rho ab}(f+1) = \frac{w_{ij,\rho ab}(f) + \alpha_\rho \eta_{ij} X_{\rho ab}}{\sum_{ab} \left[w_{ij,\rho ab}(f) + \alpha_\rho \eta_{ij} X_{\rho ab} \right]}, \tag{3}$$

where η_{ij} stands for the activity of neuron (i, j) in the final activity bubble, $w_{ij,\rho ab}(f)$ is the connection weight from the previous fixation, 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 therefore 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, four 36×36 ON-center and four 36×36 OFF-center cell layers received input from a 54×54 photoreceptor sheet. Each ON/OFF cell had a fixed Difference of Gaussians receptive field (RF) within the photoreceptor array. Initially, the afferent weights of the 142×142 V1 neurons were random, and the lateral weights had a smooth circular Gaussian profile. The learning parameters were the same as in our earlier V1 orientation model [2], scaled for this cortex size using the model scaling methodology presented in [8].
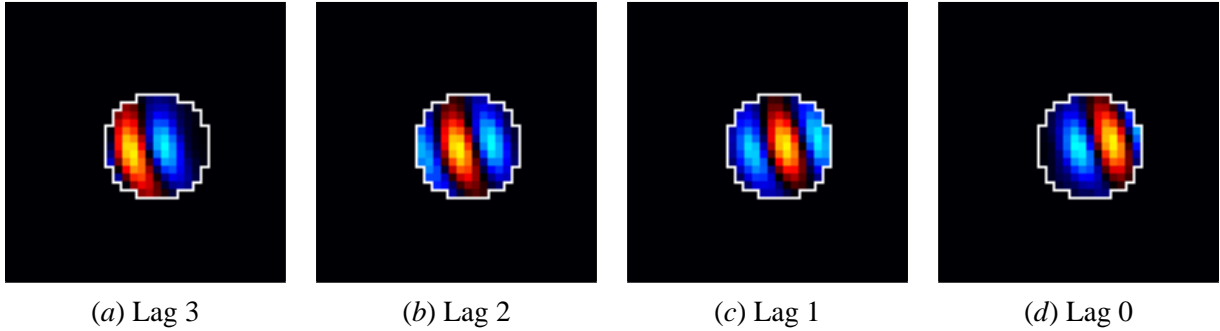
(*a*) Lag 3   (*b*) Lag 2   (*c*) Lag 1   (*d*) Lag 0

Fig. 2. **Self-organized spatiotemporal receptive field (*color figure*).** These images show the afferent weights for a typical neuron, plotted on the retina. As a visualization of the preferred stimulus of this neuron, the OFF weights were subtracted from the ON for each lag. In the resulting plots, red and yellow indicate net ON subregions of the retina, i.e. areas that will excite the neuron if they are brighter than their surround. Blue and cyan indicate OFF subregions. The white outline shows the extent of the RF before self-organization began. Together, the afferent weight plots show that the most effective stimulus for this neuron would be a bar or grating oriented at $110°$ (11 o'clock), moving from left to right. More specifically, this neuron will be highly active at time t if there was a bright bar aligned with the ON subregion in (*a*) at time $t - 3$, a bright bar aligned with the ON subregion of (*b*) at time $t - 2$, and so on until the present time t, where the bar will be aligned with the ON subregion of (*d*). These preferences form a spatiotemporal receptive field that cannot be expressed as a function of a fixed spatial RF and a time-dependent scaling factor. The RF is thus *space-time inseparable*, as found for most V1 cells [5].

3 Results

Figure 2 shows the self-organized afferent weights for a representative neuron after 20,000 image fixations. Nearly all neurons developed spatiotemporal receptive fields strongly selective for both direction and orientation. These receptive fields are similar to those found experimentally in the cortex [5]. As in the cortex, orientation and direction preferences were perpendicular for each neuron.

Figure 3 shows that the self-organized global orientation and direction maps are also similar to those found in animals [14]. For instance, a patch of neurons selective for one orientation and direction of motion will usually have an adjacent or contiguous patch selective for the same orientation, but the opposite direction. Lateral connections within the map follow this global organization, connecting neurons similar in both orientation and direction preference. 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, spatiotemporal receptive fields, and lateral connections synergetically self-organize from moving stimuli. The model predicts that lateral connections in V1 will connect neurons with similar direction preference as well as orientation preference, and will primarily extend along the orientation axis of the neuron. In future work we will further validate the model against experimental results, and will study how the orientation, direction preference, and lateral connectivity interact with other stimulus dimensions, such as spatial frequency preference.
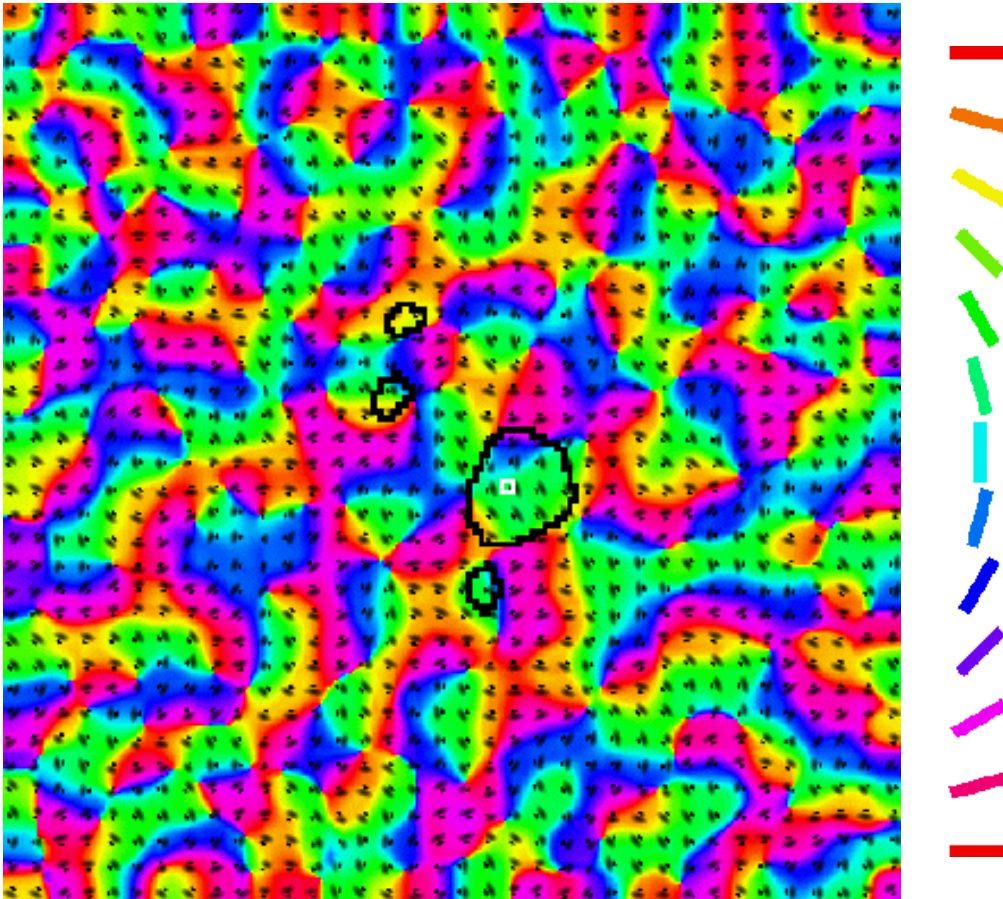
Fig. 3. **Self-organized orientation and direction map (*color figure*).** Through self-organization, a smoothly varying map of orientation and direction preferences emerged. Each of the 142×142 neurons is colored with its preferred orientation, according to the color key at right. The orientation map is similar to those found experimentally in animals, containing features such as pinwheels, linear zones, and fractures [14]. The direction preferences for every fourth neuron are plotted as black "T"s overlaid on the orientation map. Each T is formed from a bar representing the orientation preference of the neuron, plus an adjacent dot representing the direction of motion. As an example, the neuron from figure 2 is marked with a white square in the center of the plot. The neurons in that region of the map are plotted in green, representing an orientation preference of $110°$, and prefer motion from the bottom left to the upper right. Neurons in the green patch just up and to the left of the marked neuron prefer lines of the same orientation but moving in the opposite direction. Similar paired patches can be seen throughout the map, as found experimentally [14]. The black outline shows the extent of the self-organized long-range lateral weights for the marked neuron. The connections target other neurons that are aligned coaxially along the preferred orientation, and similar in both orientation and direction preference. Connections avoid neurons with the opposite direction preference. An animation of this plot is available at http://www.cs.utexas.edu/users/jbednar/dir_map.html.

Other studies will investigate how the direction map and its connections operate in the adult. The self-organized connection patterns should allow coherent moving objects to be bound together and segmented from other objects, as we have previously shown for static patterns [4]. Short-term direction-specific adaptation of the lateral connections should replicate the motion aftereffect, also known as the waterfall illusion, as we found for the tilt aftereffect [2]. This work will help unify explanations of development and adult visual function into a coherent theory of the visual cortex.

5 Conclusion

Hebbian learning of moving, oriented patterns in a self-organizing model can explain how orientation selectivity, direction selectivity, and lateral connectivity develop synergetically in V1. The model provides specific predictions for the role of the lateral connections in the development and function of the direction map. This work will help strengthen our understanding of the visual cortex as a continuously adaptive, self-organizing system.

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