

# Joint maps for orientation, eye, and direction preference in a self-organizing model of V1

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## Abstract

Primary visual cortex (V1) contains overlaid feature maps for orientation (OR), motion direction selectivity (DR), and ocular dominance (OD). Neurons in these maps are connected laterally in patchy, long-range patterns that follow the feature preferences. Using the LISSOM model, we show for the first time how realistic laterally connected joint OR/OD/DR maps can self-organize from Hebbian learning of moving natural images. The model predicts that lateral connections will link neurons of either eye preference and with similar DR and OR preferences. These results suggest that a single self-organizing system may underlie the development of spatiotemporal feature preferences and lateral connectivity.

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## 1. Introduction

Most simple cells in the primary visual cortex (V1) in mammals are selective for the direction (DR) and orientation (OR) of a moving stimulus, and respond to inputs at corresponding locations in each eye. 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 cells preferring the left or right eye (or both), and similar DRs and ORs [3,6,9].

In addition to their afferent input from the LGN, neurons in these maps are connected intra-cortically through specific long-range lateral connections. The lateral connections have been found to link cells with similar OR preferences [4], which can allow the connections to suppress redundancy in the input and improve the cells' ability to detect changes in a stimulus [7]. However, the role

of these connections in the development and adult function of DR selectivity is not yet clear.

Several computational models have demonstrated that DR and interleaved OR and DR maps can develop through activity-dependent self-organization [8,11]. However, these simulations have only modeled afferent connection learning, and have treated lateral connections as fixed. Also, although ocular dominance (OD) has been modeled in conjunction with OR, joint OR/OD/DR models have not yet been published. Including OD is potentially crucial, because it is known to interact with the OR map [3]. Finally, most prior models are based on abstract input patterns, and it is difficult to extend such models to process realistic images.

In prior work with the LISSOM self-organizing model (laterally interconnected synergetically self-organizing map), we have demonstrated how a Hebbian learning process can develop OR and DR maps, with patterned lateral connections between them [2]. We have also shown separately how individual maps, including those for OD, can form from natural images or spontaneous neural activity [1,7]. The model suggests that self-organized maps and lateral connections function in adult visual perception to segment and bind coherent objects and reduce

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redundancy in the input, and that visual illusions and aftereffects arise through this process [7]. In this paper, we extend the combined OR/DR model to include two eyes, to model OD, and to use natural image stimuli as inputs. Together, these results show that activity-dependent self-organization can explain the development of much of the map-level organization of the V1.

## 2. The LISSOM model

The model architecture is shown in Fig. 1, and will be briefly reviewed below (see [1] or [7] for more details).

The model consists of a hierarchy of two-dimensional sheets of neural units modeling different areas of the visual system: two sheets of retinal photoreceptors representing the left and right eyes, several paired sheets of ON-center/OFF-surround and OFF-center/ON-surround LGN units, and a sheet of cortical units (“neurons”) representing V1. The ON/OFF units are also called LGN units for simplicity, although they represent the entire pathway between the retinal photoreceptors and V1, including the retinal ganglion cells and connection pathways. Because the focus is on the two-dimensional organization of V1, each cortical neuron corresponds to a vertical column of cells through the six anatomical layers of the cortex.

Compared to simpler OR-only LISSOM networks, the model introduced in this paper includes two eyes (to model OD) and multiple LGN sheets with different time-delayed

copies of previous input patterns. The time delays model the “lagged” cells recently found in cat LGN that respond to retinal inputs only after a fixed delay. The delay time in these lagged cells varies over a continuous range up to hundreds of milliseconds [12]. We will show below that V1 neurons can use these timing differences to develop spatiotemporal receptive fields. Similarly, neurons will develop eye preferences based on differences in the patterns presented to each eye. These extensions allow the model V1 to develop simultaneous maps for OR, OD, and DR. The extensions result in 16 LGN sheets in total, 1 ON-center and 1 OFF-center sheet at each of four different lags for each eye, compared to two (one ON and one OFF) sheets in the OR-only LISSOM model.

The training patterns consisted of randomly chosen patches of natural images, moving in random directions. A sample input is drawn in the photoreceptor sheets of Fig. 1. The strength of the image in each eye was chosen randomly, but the total strength of the two eyes was kept constant. For each image presentation, the activity level of each LGN unit is calculated from the activity level of its receptive fields. Specifically, each LGN unit  $(i,j)$  with lag  $t$  computes its response  $\eta_{ij}$  as a scalar product of a fixed Difference of Gaussians weight vector and the activity in its receptive fields on a photoreceptor sheet at time  $t$ :

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

where  $\rho$  iterates over all RFs of this unit (for LGN units in this simulation, a single RF on either the left or right retina),  $\sigma$  is a piecewise linear sigmoid activation function,  $\gamma_{\rho}$  is a constant scaling factor,  $X_{\rho ab}$  is the activation of input unit  $(a,b)$  on sheet  $\rho$  at timestep  $t$ , and  $w_{ij, \rho ab}$  is the corresponding weight value. Each V1 neuron computes its initial response like an LGN unit, except that  $\rho$  iterates over all of the 16 ON or OFF LGN sheets for which the V1 unit has RFs. After the initial V1 response, the LGN activity remains constant while V1 activity settles through short-range excitatory and long-range inhibitory lateral interaction

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

where  $\rho$  identifies either an RF on the LGN sheet, or the lateral excitatory or inhibitory weights to V1,  $\gamma_{\rho}$  is a constant scaling factor for each  $\rho$  (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 Eq. (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 RF of every V1 neuron are modified according to a normalized Hebb rule. For a given V1 unit  $(i,j)$  and connection to any unit  $(a,b)$  in a specific RF  $\rho$ , the new

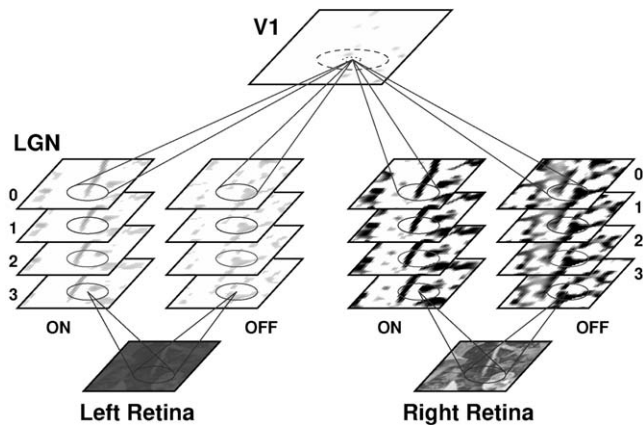


Fig. 1. LISSOM OR/OD/DR model. Each V1 unit receives inputs from RFs on 16 LGN sheets modeling different response types (ON- or OFF-center) and different connection lags (3, 2, 1, or 0). LGN RFs for one V1 unit are shown as solid circles; V1 units also have lateral excitatory (small dotted circle) and lateral inhibitory (large dashed circle) connections to their neighbors. Each LGN unit receives input from either the left or the right eye; sample RFs are shown for two LGN units for each eye. Moving input patterns are drawn on the retinal sheets in four discrete timesteps, like frames of a movie. Matching patterns are presented in each eye, with the relative brightness of each eye chosen randomly. At the first timestep, the ON and OFF LGN units with time lag 3 compute their activity. At each subsequent timestep, the input pattern is moved slightly and LGN units with lags 2, 1, and 0 compute their activity in turn. Once all LGN units have been activated, initial V1 activity is computed from the LGN responses, and the activity then spreads laterally within V1.

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