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Modeling Joint Development of Ocular Dominance and Orientation Maps in Primary Visual Cortex

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Abstract

We have combined earlier correlation-based models of striate ocular dominance and orientation preference map formation into a joint model. Cortical feature preferences are defined through patterns of synaptic connectivity to LGN cells which develop due to firing correlations of those LGN cells. Model parameters include spatial correlation patterns between ON- and OFF-center cells in separate eye layers of the LGN. A linear transformation yields correlation functions which predict whether orientation preferences, ocular dominance, or both, will develop. The model thus predicts the correlations between LGN cells which would be necessary to explain formation of visual maps by a linear process.

Introduction

We present a model for the joint development of simple-cell receptive fields (RFs), and orientation and ocular dominance (OD) maps due to correlations in the firing of LGN cells. The model combines elements of previously separate models [1]. This introduction reviews the main features of the model; fuller description may be found in [1].

Cortical cells, representing layer IV simple cells, are arranged in an array with coordinates given by letters $\vec{x}, \vec{y}$. Their receptive fields are determined by the patterns of input from neurons in the lateral geniculate nucleus (LGN).

The LGN contains four classes of cells each receiving input from either the (L) left or (R) right eye, and from either (N) ON- or (F) OFF-center retinal ganglion cells. LGN coordinates are expressed by greek letters $\vec{\alpha}, \vec{\beta}$.

Synaptic afferents to the cortex are grouped into four classes by the LGN input they receive: $I \in \{\mathrm{RN}, \mathrm{RF}, \mathrm{LN}, \mathrm{LF}\}$. These synaptic weight vectors, $S^I(\vec{z}, \vec{\alpha})$, are dynamical variables which code for the overall strength of connection between a neuron at cortical position $\vec{z}$ and the neuron at position $\vec{\alpha}$ in the indicated LGN layer. $S(\vec{z},\vec{\alpha})$ takes into account both the number of synapses between the two neurons (given by $A(\vec{z},\vec{\alpha})$) and the efficacy of those synapses.

The arbor function, $A(\vec{z},\vec{\alpha})$, is proportional to the number of synapses connecting a cortical cell at $\vec{z}$ with an LGN cell at $\vec{\alpha}$. It restricts the range of LGN locations from which a cortical cell can receive input to a radius, r_A, centered at an appropriate LGN position. Cortical and LGN locations are described in common, retinotopic units so the arbor function can be written as $A(|\vec{z}-\vec{\alpha}|)$.

A set of functions, $C(\vec{\alpha},\vec{\beta}) = C(|\vec{\alpha}-\vec{\beta}|)$, describe the average distance-dependant correlations between activities of pairs of LGN cells within or between classes. If the developmental dynamics are invariant under exchange of right and left eyes and of ON and OFF populations, then only four correlation functions are necessary: C^{ss} (same eye, same polarity), C^{so} (same eye, other polarity), C^{os} (other eye, same polarity), and C^{oo} (other eye, other polarity). We consider only time-invariant correlations, thus studying the most-restrictive case for joint OD and orientation map development.

An intracortical interaction function, $I(\vec{x},\vec{y}) = I(|\vec{x}-\vec{y}|)$ describes how activity at one cortical location encourages or discourages the development of correlated synaptic connections at nearby locations as a function of lateral distance.

Methods

The synaptic weights develop over time from initial small random strengths according to the influence of correlations in LGN activity. The unconstrained development of the synaptic weights is given by

$$\left.\frac{d}{dt}\right|_U \begin{pmatrix} S^{\mathrm{LN}}(\vec{x},\vec{\alpha}) \\ S^{\mathrm{LF}}(\vec{x},\vec{\alpha}) \\ S^{\mathrm{RN}}(\vec{x},\vec{\alpha}) \\ S^{\mathrm{RF}}(\vec{x},\vec{\alpha}) \end{pmatrix} = \eta A(\vec{x},\vec{\alpha}) \sum_{\vec{y}} I(\vec{x},\vec{y}) \begin{pmatrix} C^{ss} & C^{so} & C^{os} & C^{oo} \\ C^{so} & C^{ss} & C^{oo} & C^{os} \\ C^{os} & C^{oo} & C^{ss} & C^{so} \\ C^{oo} & C^{os} & C^{so} & C^{ss} \end{pmatrix} \begin{pmatrix} S^{\mathrm{LN}} \\ S^{\mathrm{LF}} \\ S^{\mathrm{RN}} \\ S^{\mathrm{RF}} \end{pmatrix} \tag{1}$$

where each $C^I S^J$ represents a spatial convolution $\sum_{\vec{\beta}} C^I(\vec{\alpha},\vec{\beta}) S^J(\vec{y},\vec{\beta})$. Synaptic development is constrained to occur within a limited range

$$\tfrac{d}{dt} S^I(\vec{x},\vec{\alpha}) = 0, \text{ except where } 0 \le S^I(\vec{x},\vec{\alpha}) \le 6A(\vec{x},\vec{\alpha}), \tag{2}$$

with $I \in \{\mathrm{RN},\mathrm{RF},\mathrm{LN},\mathrm{LF}\}$. Thus, any synaptic connection reaching zero or a maximum value is not allowed to develop further. Development is further constrained such that the total input onto any cortical cell remains constant:

$$\tfrac{d}{dt} S^I(\vec{x},\vec{\alpha}) = \left.\tfrac{d}{dt}\right|_U S^I(\vec{x},\vec{\alpha}) - A(\vec{x},\vec{\alpha})\epsilon(\vec{x}), \quad \text{where} \tag{3}$$

$$\epsilon(\vec{x}) = \textstyle\sum_{\vec{\beta},I} \left.\tfrac{d}{dt}\right|_U S^I(\vec{x},\vec{\beta}) \ / \ 4 \sum_{\vec{\beta}} A(\vec{\alpha},\vec{\beta}) \tag{4}$$

Due to the assumed symmetries between left and right eyes and between ON and OFF populations, the developmental equations may be re-written as

$$\left.\frac{d}{dt}\right|_U \begin{pmatrix} S^{\mathrm{SUM}} \\ S^{\mathrm{OD}} \\ S^{\mathrm{ORI+}} \\ S^{\mathrm{ORI-}} \end{pmatrix} = \eta A(\vec{x},\vec{\alpha}) \sum_{\vec{y}} I(\vec{x},\vec{y}) \begin{pmatrix} C^{\mathrm{SUM}} & 0 & 0 & 0 \\ 0 & C^{\mathrm{OD}} & 0 & 0 \\ 0 & 0 & C^{\mathrm{ORI+}} & 0 \\ 0 & 0 & 0 & C^{\mathrm{ORI-}} \end{pmatrix} \begin{pmatrix} S^{\mathrm{SUM}} \\ S^{\mathrm{OD}} \\ S^{\mathrm{ORI+}} \\ S^{\mathrm{ORI-}} \end{pmatrix} \tag{5}$$

The nomenclature is based on the receptive field properties which can be observed in the weight vectors: the total synaptic strength is coded in S^{SUM}, ocular dominance in S^{OD}, and preferred orientation in both $S^{\mathrm{ORI+}}$ and $S^{\mathrm{ORI-}}$:

$$\begin{array}{rl|rl} S^{\mathrm{SUM}} & \equiv S^{\mathrm{RN}} + S^{\mathrm{RF}} + S^{\mathrm{LN}} + S^{\mathrm{LF}} & C^{\mathrm{SUM}} & \equiv C^{ss} + C^{so} + C^{os} + C^{oo} \\ S^{\mathrm{OD}} & \equiv S^{\mathrm{RN}} + S^{\mathrm{RF}} - S^{\mathrm{LN}} - S^{\mathrm{LF}} & C^{\mathrm{OD}} & \equiv C^{ss} + C^{so} - C^{os} - C^{oo} \\ S^{\mathrm{ORI+}} & \equiv S^{\mathrm{RN}} - S^{\mathrm{RF}} + S^{\mathrm{LN}} - S^{\mathrm{LF}} & C^{\mathrm{ORI+}} & \equiv C^{ss} - C^{so} + C^{os} - C^{oo} \\ S^{\mathrm{ORI-}} & \equiv S^{\mathrm{RN}} - S^{\mathrm{RF}} - S^{\mathrm{LN}} + S^{\mathrm{LF}} & C^{\mathrm{ORI-}} & \equiv C^{ss} - C^{so} - C^{os} + C^{oo} \end{array} \tag{6}$$

Note that the unconstrained development of each of the composite weight vectors is independent of the other three. The constraints of (2) still apply to the raw weights: $S^{\mathrm{RN}}, S^{\mathrm{RF}}, S^{\mathrm{LN}}, S^{\mathrm{LF}}$. However, the subtractive constraint of (3) vanishes from all developmental equations other than for S^{SUM}:

$$\tfrac{d}{dt} S^{\mathrm{SUM}}(\vec{x},\vec{\alpha}) = \left.\tfrac{d}{dt}\right|_U S^{\mathrm{SUM}}(\vec{x},\vec{\alpha}) - 4A(\vec{x},\vec{\alpha})\epsilon(\vec{x}). \tag{7}$$

Each of the developmental equations may be seen as an eigenvalue problem:

$$\tfrac{d}{dt} S^{\mu} = \hat{E}^{\mu} S_i^{\mu} = \lambda_i^{\mu} S_i^{\mu}, \quad \text{where } \mu \in \{\text{OD, ORI+, ORI-, SUM}\} \tag{8}$$

The multiple eigenvectors S_i^{μ} of each operator $\hat{E}^{\mu}$ are numbered i by their eigenvalue, from largest to smallest: $\lambda_0^{\mu} \geq \lambda_1^{\mu} \geq \lambda_2^{\mu} \geq \cdots$.

Random initial fluctuations of synaptic weights in S^{μ} which resemble the shape of the principal eigenvectors S_i^{μ}, with i small, will grow exponentially faster than other patterns. Thus the pattern of weights in S^{μ} will grow to resemble one of these principal eigenvectors more and more closely. In this way, the principal eigenvectors of $\hat{E}^{\mu}$ determine the receptive field (RF) properties.

The principal eigenvectors of $\hat{E}^{\mu}$ depend on A, I and C^{μ}. To a first approximation, the RFs are determined by the shape of C^{μ} relative to A. Once A and C^{μ} have been set, I gives the cortical map (the variation of RFs across cortex).

For ocular dominance to develop, C^{OD} must satisfy the condition previously found in two-input models: the peak of its Fourier transform should be at frequency 0 (or at a wavelength long compared to the diameter of A.) In this case, the principal eigenvector S_0^{OD} of $\hat{E}^{\mathrm{OD}}$ consists of a set of monocular RFs, with a cortical OD pattern determined by I.

For the development of simple cells and orientation columns, one of $C^{\mathrm{ORI+}}$ or $C^{\mathrm{ORI-}}$ must satisfy the condition previously found in two-input models: the peak of its Fourier transform should correspond to two to three cycles per arbor diameter. For either case, the principal eigenvector of the corresponding operator, $\hat{E}^{\mathrm{ORI+}}$ or $\hat{E}^{\mathrm{ORI-}}$, leads to simple-cell-like RFs with alternating regions of ON- and OFF-center input, giving orientation preferences. In the RFs of

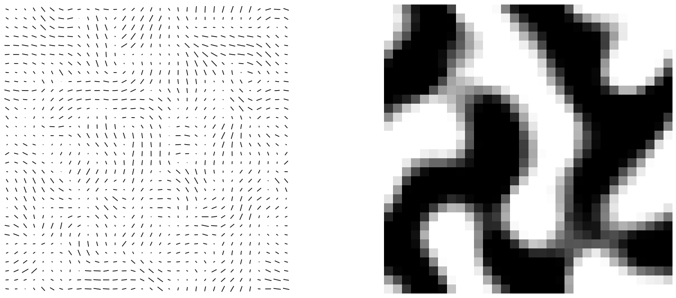

Figure 1: Model maps of orientation (left) and ocularity (right) for correlation functions given in the text with $r = 0.8$, $d = 0.09861$, thus $\lambda_0^{\text{ORI+}} = 0.8\lambda_0^{\text{OD}}$. Preferred orientation ϕ and specificity q are represented by orientation and length of line segments. Black and white represent left- and right-eye dominance.

$\hat{E}^{\text{ORI+}}$, ON subfields of the two eyes overlap, as do OFF subfields. In the RFs of $\hat{E}^{\text{ORI-}}$, ON subfields in one eye coincide with OFF subfields in the other eye. For both operators the two eyes have identical preferred orientations. The function I determines the variation in preferred orientation across cortex.

Results

OD and orientation preference maps can jointly develop from a fixed set of correlation functions if (1) the principal eigenvector of $\hat{E}^{\text{OD}}$ has monocular RFs, (2) the principal eigenvector of $\hat{E}^{\text{ORI+}}$ (or of $\hat{E}^{\text{ORI-}}$) has oriented RFs, and (3) the corresponding principal eigenvalues are of similar magnitude, e.g. $\lambda_0^{\text{OD}} \approx \lambda_0^{\text{ORI+}}$.

For example, consider a model with 32×32 positions in both cortex and LGN. Suppose the arbor A is positive over a radius $r_A = 6.5$ and zero outside. (Our arbor function $A(\vec{x}, \vec{\beta})$ is given by the overlap of two circles of radii r_A and $r_A/2$ with centers displaced by $|\vec{x} - \vec{\beta}|$, but results are similar with other functions [1].) Choose C^{OD} to be positive across the arbor to favor monocular RFs: $C^{\text{OD}}(\vec{\alpha}, \vec{\beta}) = de^{-(\vec{\alpha}-\vec{\beta})^2/r_A^2 r_d^2}$, $r_d = 0.8$. Choose $C^{\text{ORI+}}$ to oscillate within the arbor to favor oriented RFs: $C^{\text{ORI+}}(\vec{\alpha}, \vec{\beta}) = r(e^{-(\vec{\alpha}-\vec{\beta})^2/r_A^2 r_c^2} - \frac{1}{9}e^{-(\vec{\alpha}-\vec{\beta})^2/9r_A^2 r_c^2})$, $r_c = 0.24$. Let the other two correlation functions be negligible, $C^{\text{ORI-}} = 0$ and $C^{\text{SUM}} = 0$. Then choose an $I(\vec{x}, \vec{y})$ such that several cortical columns of RF variation will form: $I(\vec{x}, \vec{y}) = e^{-(\vec{x}-\vec{y})^2/r_A^2 r_I^2} - \frac{1}{9}e^{-(\vec{x}-\vec{y})^2/9r_A^2 r_I^2}$, $r_I = 0.33$.

Now, the principal eigenvector of $\hat{E}^{\text{OD}}$ has monocular RFs with $\lambda_0^{\text{OD}} = 197.95d$. The principal eigenvector of $\hat{E}^{\text{ORI+}}$ has oriented RFs with $\lambda_0^{\text{ORI+}} = 19.52r$. Both eigenvectors have spatial oscillation of RF across cortex. The ratio $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}} = 0.0986\frac{r}{d}$ determines whether ocular dominance, orientation preferences, or both, develop. Figure 1 shows a model map developed with $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}} = 0.8$.

To study the effect of variations in $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}}$, we must define measures of monocularity and orientation specificity. The monocularity of each cell is determined by the difference in connection strength between the right and left

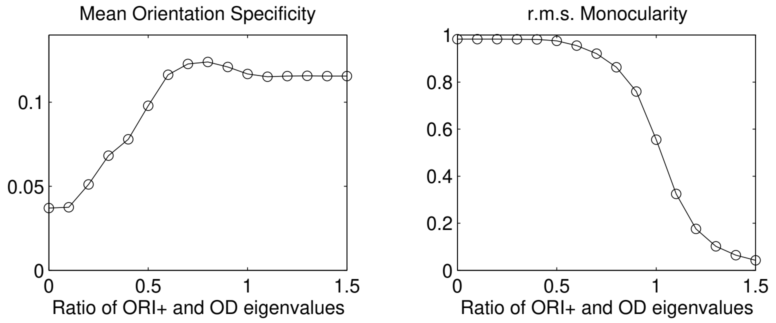

Figure 2: Variation in orientation specificity, Q, and monocularity M as a function of the ratio $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}}$. Correlation functions as in Fig. 1, with $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}}$ changed by varying r/d.

eyes. $m_{\vec{x}} = \sum_{\vec{\alpha}} S^{\text{OD}}(\vec{x},\vec{\alpha})/\sum_{\vec{\alpha}} S^{\text{SUM}}(\vec{x},\vec{\alpha})$. Right- or left-eye dominance give $m_{\vec{x}} = +1$ or -1. The r.m.s. average of $m_{\vec{x}}$ across all N cortical locations assesses the average cortical monocularity: $M = \frac{1}{N}(\sum_{\vec{x}} m_{\vec{x}}^2)^{1/2}$.

Preferred orientation, $\phi_{\vec{x}}^R$, or $\phi_{\vec{x}}^L$ is the orientation of a grating stimulus for which the cell at $\vec{x}$ gives a maximal response to R or L-eye stimuli. For simple cells, the preferred orientation is determined by the spatial arrangement of ON- and OFF-center inputs.

Orientation specificity, $q_{\vec{x}}^R$, or $q_{\vec{x}}^L$ measures the degree to which a cell responds preferentially to its preferred orientation. Our measure q (defined in [1]) can range from 0 (responds equally to all orientations) to 1 (responds to a single orientation), but generally $0 \le q_{\vec{x}} \le 0.27$. Mean specificity, Q, is computed by a weighted average of q across cortex: $Q = \frac{1}{N}\sum_{\vec{x}} \frac{1}{2}(q_{\vec{x}}^R(1+m_{\vec{x}}) + q_{\vec{x}}^L(1-m_{\vec{x}}))$.

Now consider the effect of $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}}$ by varying the ratio of r and d in $C^{\text{ORI+}}$ and C^{OD}. For $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}} \ll 1$, only an OD map develops (Fig. 2): most cells are completely monocular (high M) but ON and OFF regions overlap in the RFs (low Q). For $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}} \gg 1$, only an orientation map develops: ON and OFF regions are segregated into RF subregions, but most RFs are binocular. For an intermediate regime of $\lambda_0^{\text{ORI+}}/\lambda_0^{\text{OD}} \approx 1$, both OD and orientation maps develop: many cells are monocular, ON and OFF inputs are well segregated into RF subregions, and the orientation maps of the two eyes are aligned.

In the above, $\lambda_0^{\text{ORI-}} = 0$ and $\lambda_0^{\text{SUM}} = 0$. However, the results are altered very little for $\lambda_0^{\text{ORI-}}$ and λ^{SUM} small relative to $\max(\lambda_0^{\text{ORI+}}, \lambda_0^{\text{OD}})$. We have not studied development for $|\lambda_0^{\text{SUM}}| \gg 0$, but we have considered $C^{\text{ORI+}}$ and $C^{\text{ORI-}}$ each given by the equation above for $C^{\text{ORI+}}$ with independent magnitudes, r.

For $\lambda^{\text{ORI-}}$ less than about $(2/3)\lambda^{\text{ORI+}}$, maps develop essentially the same as for $\lambda^{\text{ORI-}} = 0$. For $\lambda^{\text{ORI+}}$ less than about $(2/3)\lambda^{\text{ORI-}}$, the principal eigenvectors of $\hat{E}^{\text{ORI-}}$ and $\hat{E}^{\text{OD}}$ dominate. Development is similar to the previous case except that (1) the requirement $\lambda^{\text{OD}} \approx \lambda^{\text{ORI+}}$ is replaced by $\lambda^{\text{OD}} \approx \lambda^{\text{ORI-}}$, (2) ON and

OFF subfields in one eye's RF align with subfields of the opposite type in the other eye (the preferred orientations of the eyes still match). When $\lambda_0^{\text{ORI+}}$ and $\lambda_0^{\text{ORI-}}$ are similar (when $|\lambda_0^{\text{ORI+}} - \lambda_0^{\text{ORI-}}|$ is less than about $\frac{1}{3}\max(\lambda_0^{\text{ORI+}}, \lambda_0^{\text{ORI-}})$), development of ON and OFF subfields in the right and left RFs occur independently and right- and left-eye preferred orientations can differ.

The developmental equations (5) for ocular dominance S^{OD} and orientation preference $S^{\text{ORI+}}$ (and $S^{\text{ORI-}}$) are independent when the synaptic weights are all unsaturated (i.e. $S^{\text{RN}}, S^{\text{RF}}, S^{\text{LN}}$, and S^{LF} are all non-zero and non-maximal.) The orientation and OD maps which develop in this condition are independent. However, once any synapse becomes saturated, its value is no longer allowed to change. This breaks the independence in the development of S^{OD} and $S^{\text{ORI+}}$ (as well as $S^{\text{ORI-}}$ and S^{SUM}) and relationships will develop between the feature maps. In simulations, we have observed that OD and orientation maps initially develop independently, but after synapses begin to saturate, the maps reorganize slightly so that the columns of OD and orientation tend to intersect perpendicularly, in a manner similar to the relationship seen in monkey primary visual cortex [3] and in abstract feature-map models (reviewed in [2]).

Summary and Conclusions

We have demonstrated that ocular dominance columns, simple cells, and orientation columns can jointly develop, with preferred orientations correlated between the two eyes, under a semi-linear correlation-based rule using time-invariant correlation functions. The necessary conditions are:

- The function C^{OD} must satisfy the condition previously found in two-input (two eye) models for the development of ocular dominance columns.
- One of the two correlation functions $C^{\text{ORI+}}$ or $C^{\text{ORI-}}$ must satisfy the condition previously found in two-input (ON and OFF input) models for the development of simple cells and orientation columns.
- The other of the two functions must be smaller; e.g. if $C^{\text{ORI+}}$ is the larger function, then $\lambda_0^{\text{ORI-}}$ should be less than about $2/3\lambda_0^{\text{ORI+}}$.
- The magnitudes of λ_0^{OD} and $\max(\lambda_0^{\text{ORI+}}, \lambda_0^{\text{ORI-}})$ should be comparable.
- The correlation function C^{SUM} should be sufficiently small that the constrained development of S^{SUM} does not interfere via synaptic saturation.

We have recently learned that Piepenbrock, Ritter and Obermayer have independently derived the diagonalization of (5). We gratefully acknowledge support by NIH (NS07067, EY11001-01), and grants from the Searle Scholars' Program and the Lucille P. Markey Charitable Trust.

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