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# A COMPARISON OF MODELS OF VISUAL CORTICAL MAP FORMATION

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## ABSTRACT

Several classes of models of visual cortical map characterization and development are compared. Characteristics and predictions of the models are compared to one another and to cortical maps observed in animals. Several models are found to predict incorrect map structure. Certain observed patterns of visual maps imply constraints on the processes which could be involved in their morphogenesis.

## 1 FEATURE MAPS IN VISUAL CORTEX

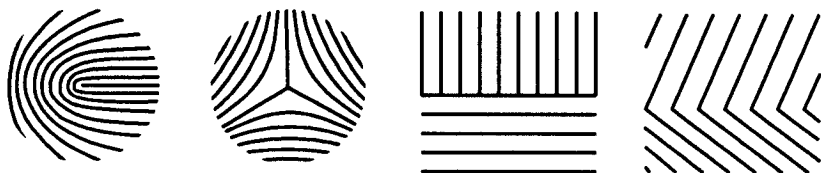
Individual cells in the mammalian primary visual cortex, or *striate cortex*, respond differently to features in visual input, with feature preferences determined in part by the pattern of connection between retinal light receptors and cortex. *Striate cortical receptive fields*, descriptions of features to which each cell responds, are often localized in the visual field, may be dominated by input from either eye, and usually show a preference for stimuli with a particular orientation. Several receptive field properties of neurons are arranged in the cortex in a complicated two-dimensional map such that nearby columns of neurons tend to have similar receptive fields. Due to the ordered projections from the eyes, a roughly topographic map of visual space is formed on the cortical surface. An optical imaging technique [1, 2, 4] reveals the embedded maps of ocular dominance and orientation preference over small patches of the cortex.

The details of the cortical maps vary greatly between individual animals, but certain organizing principles appear invariant. Depending on the species, ocular

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**Figure 1** Tangent curves illustrating local orientation preferences near (a),(b) vortex and (c),(d) fracture singularities. (Adapted from [13].)

dominance patterns consist of bands or patches of left- and right-eye dominance. Orientation preference changes smoothly over most of the map surface, including linear regions where *slabs* of cells with a common preferred orientation are aligned alongside one another. Regions of rapid change are primarily confined to one-dimensional *fractures* (Fig. 1c,d), across which orientation preference changes by up to  $90^\circ$  and *vortices* where orientation preference rotates through a complete cycle of  $180^\circ$  around a point [1, 2]. Loop vortices (Fig. 1a) where orientation preference rotates in the same direction as motion around a central point and tri-radius vortices (Fig. 1b) where orientation preference rotates in contrary motion exist in equal numbers. These structures correspond to the simplest singularities which are possible in a ridge-type pattern (Fig. 1) [13]. Fourier power spectra of the ocular dominance and orientation preference maps have a ring, or bi-lobed distribution, for species with isotropic or anisotropic map patterns. Map patterns are correlated such that vortices tend to lie at the centers of ocular dominance bands where receptive fields are primarily monocular, and linear regions tend to lie in binocular regions with the slab borders orthogonal to the ocular dominance column borders. A successful model of striate cortical map formation must be capable of explaining the development of these patterns and the correlations between them. Further details of the spatial patterns of orientation preference and ocular dominance may be found in [1, 12].

## 2 VISUAL CORTICAL MAP MODELS

Although often based on different developmental principles and degree of biological detail, many models are successful at predicting or describing the structure of striate cortical maps. We attempt to find the common features of successful models, as well as unique insights from individual models. Rather than discussing the details of a series of models, which are more fully described in the original references, we have organized a discussion of the most common modelling approaches around three classes of models based on similar principles: (1) *feature map models*, (2) *correlation-based learning models*, and (3) *pattern models*. Feature map models and correlation-based learning algorithms both

explain the development of feature selectivities based on the Hebbian learning hypothesis for synaptic change, but differ in the manner in which this principle is expressed. Pattern models, may also suggest developmental principles and processes, but the emphasis is on finding a concise description of the observed map patterns. A careful study of the structure of cortical maps reveals organizing principles which constrain the types of processes which could form the maps.

### 3 FEATURE MAP MODELS

The feature map models, which include the self-organizing feature map algorithm [6, 7, 12, 11], the elastic-net algorithm [3], and related models [16], comprise one class of developmental models. Although the details of the algorithms differ, these models share many features. They each assume a set of cortical units — either single cells, or local groups of cells — arranged in a two-dimensional lattice. The receptive field of each cortical unit is described as a feature vector, which encodes the strengths of connections to retinal receptors, either directly, or in an abstract representation. For example, a five-dimensional feature vector  $\vec{w} = \{x, y, q \sin(2\theta), q \cos(2\theta), z\}$  can describe the location of a receptive field in visual space  $x$  and  $y$ , the orientation preference  $\theta$  and orientation specificity  $q$ , and the ocularity  $z$  of a cortical unit. Feature map models have been used to provide a rationale for cortical map patterns, by suggesting that the maps are organized to map a high-dimensional visual feature space as completely as possible while maximizing continuity of feature preferences [3].

Feature map algorithms consider the development of cortical maps to be governed by neural activity driven either by images viewed by a young animal, or by the spontaneous firing of retinal cells, which can occur even before birth. Map formation proceeds through repetitive presentations of stimuli and modification of the receptive fields of the cells in response. The rule for receptive field modification requires that a distance measure, which must be computable by a single cortical unit, be defined between the input pattern vectors and the synaptic weight vectors. This distance determines the amount each neural unit is stimulated by an input pattern, and its form crucially affects the organization of the feature maps. Changes in the feature vectors are proportional to this distance. However, in the self-organizing feature map algorithm, competition for activity allows only units in a neighborhood around the unit with the smallest distance to modify their receptive fields, which generates the smooth map structure. Smoothness is maintained in the elastic-net model maps by a type of averaging of the receptive field properties of nearby neurons. Since the receptive fields are only adapted to more resemble the stimuli, if the stimuli show pronounced features, the specificity of the receptive fields will be high with regard to these features.

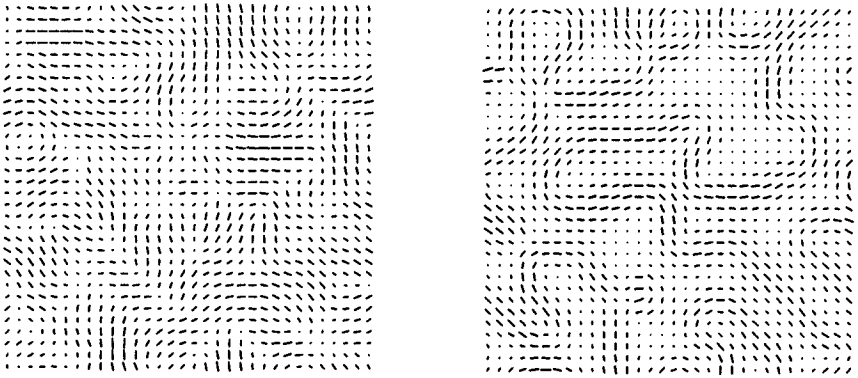
Maps produced by the feature map models closely resemble observed cortical maps in structure [3, 12], even though only the most basic properties of the maps are specified in advance. For example, ocularity varies across the cortical surface in blob- or band-like patterns. Orientation preferences vary smoothly and gradually across most areas of the cortex, except near the fractures and the loop and tri-radius vortices, and these are correlated with regions of gradual change in receptive field location. Feature specificity is high in most map areas, with the exact distribution of specificities being tunable through algorithm parameters. Power spectra of orientation and ocular dominance patterns can have a ring-like or bi-lobed distribution, and the orientation and ocularity map patterns may repeat on different length scales.

## 4 CORRELATION-BASED LEARNING

Correlation-based learning algorithms [8, 9, 10] comprise a second class of developmental models, which share many features with the feature map algorithms, but differ in the way the effect of retinal activity is implemented. Whereas feature-map models assume a competitive network where receptive fields change through a non-linear function of retinal input, correlation-based learning models assume a linear relationship. Thus patterns of correlation in the input will be represented in the receptive field properties of cortical cells.

In one such model of ocular dominance development [10], ocularity of each cortical cell is determined by the difference in total connection strength to receptors in each eye. Assuming that the activity in nearby cells in one retina is correlated, and that activity at greater distances or in opposite eyes is non- or anti-correlated, and taking a Gaussian or “Mexican-hat” function of intra-cortical influence, this model produces cortical patterns of ocular dominance resembling those seen experimentally. Miller [9] adapted this algorithm to study the development of orientation-selective cells and orientation preference maps. In his model a spatial “Mexican-hat” correlation function in the firing of retinal cells in the same population of ON- or OFF-center cells, with a weaker, inverted “Mexican-hat” correlation function for cells in different classes, leads to banded patterns of connection to ON- and OFF-center retinal cells, giving cortical cells an orientation preference.

When “Mexican-hat” intra-cortical interactions are included, receptive field properties become arranged in a repetitive map across the cortical surface. Maps of orientation preference show high orientation specificity and smooth variation in preferred orientation at most cortical locations, and the maps contain loop and tri-radius vortices in equal numbers. However, the organization of the maps seems to differ from the organization of cortical maps in some finer details. The difference in organization between the model and cortical maps is not immediately apparent in the maps developed with the best set of



**Figure 2** Maps of orientation preference from the correlation-based learning algorithm with (a) standard parameters, (b) one parameter altered. (See text)

model parameters, Fig. 2a. However, varying just one parameter in the model makes the organizing principles behind the model maps more clear. The model map in Fig. 2b was developed with the parameter determining the length-scale for correlations in the firing pattern of retinal cells set 27 percent longer than its preferred value. This map contains many cells which are unspecific to orientation, and the cells with high orientation specificity are mainly located in one of several “streams” which run through the map with their receptive field orientations aligned with the “streamlines”. As the parameters of the model are slowly returned to normal, the streams widen and grow together producing loop and tri-radius vortices. Nearby parallel streams grow together seamlessly, seldom producing one-dimensional fractures along which orientation preference changes abruptly. The “streamlines” in Fig. 2b suggest contour lines of a surface, whereas the curves in a general ridge system [13] and the experimental orientation preference maps cannot be associated with contour lines. If the model maps for normal parameter values are governed by the same principles, then the model may be rejected by this topological reasoning.

## 5 PATTERN MODELS

Pattern models attempt to find the most concise description of feature map structure, using an algorithm or formula with as few parameters as possible. The hypothesis is that studying the structure of cortical maps can help characterize types of processes which either are or are not capable of generating the observed patterns.

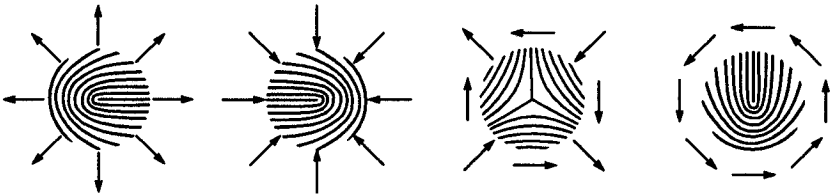
Several distinct pattern models have been successful at reproducing the patterns of ocular dominance [5, 14]. In one of the simplest, Rojer and Schwartz [14] demonstrated that the global patterns of ocular dominance in several species

can be reproduced by convolving a two-dimensional array of random real numbers with an appropriate filter and associating the positive and negative values in the resulting array with left- and right-eye dominances. A circularly-symmetric, decaying sinusoidal filter, or a "Mexican-hat" filter gives an isotropic ocular dominance pattern with a ring-like power spectrum similar to the pattern seen in cat striate cortex, whereas a similar anisotropic filter gives a pattern of mostly parallel, branching columns with a bi-lobed power spectrum as seen in macaque cortex. A few parameters in the shape of the filter can be tuned to give ocular dominance columns with any orientation, width and degree of branching. Although convolution with a filter is sufficient to give the global patterns, tuning the distribution of ocular dominance values requires applying some local operations, such as a threshold function associating each cortical unit wholly with either the right or left eye, or a more realistic sigmoidal function.

Since the power spectrum of typical orientation column systems has a ring or bi-lobed distribution similar to the ocular dominance column spectra, a similar algorithm should be able to generate orientation column patterns. The simplest such algorithm was proposed by Rojer and Schwartz [14]. A two-dimensional array of random real numbers is convolved with a circular sinusoidal filter and the local gradient vector of the resulting pattern is computed for each array unit. Dividing the angle of each gradient vector by two gives angles  $0^\circ \leq \theta < 180^\circ$  which may be taken as preferred orientations for cortical cells. The length of the gradient vectors gives the orientation specificity of the model cells, either directly or after being subjected to a local function, such as a sigmoid, to give the desired distribution of orientation specificities.

The pattern of orientation preferences given by this simple formula resembles in many ways the observed patterns of orientation columns. Cells with similar orientation preference are clustered together, and there are both loop and tri-radius vortices, and one-dimensional fractures. However, closer observation reveals a deficiency in the patterns. The orientation column pattern was derived from a vector field under the rather restrictive assumption that this vector field must be conservative. The properties of conservative vector fields then dictate that for any closed circuit through one of the model maps, the line integral  $\oint q \cos(2\theta)dx + q \sin(2\theta)dy$  always vanishes, where  $q(x, y)$  is the orientation specificity, and where the orientation preference angles  $\theta(x, y)$  are measured from the x-axis. Experimental maps, and other model maps are not similarly restricted<sup>3</sup>. The failure of this model illustrates the value of pattern models since it reveals that *any* model which relates the lines in an orientation column map to a conservative gradient field must fail for purely topographic reasons [13], regardless of the form of the physiological implementation.

<sup>3</sup>The integral can only be approximated in maps defined only at discrete points.



**Figure 3** (a)-(d) Vortices in orientation maps and the associated vector fields. The vector field in (d) is non-conservative.

Although maps generated by this model differ from experimental maps in all regions, the difference is most easily demonstrated at the vortices. The inserts in Fig. 3 show four types of vortices, all of which occur in orientation column maps. Also shown are the vector fields associated with each vortex with directions given by multiplying the orientation preference angles, measured from the x-axis, by two. The loop vortices in Fig. 3a,b are associated with gradient vector fields around a local maximum or minimum in a surface, and the tri-radius vortex of Fig. 3c is associated with the gradient vector field of a saddle point. Although the loop vortex in Fig. 3d is simply a rotated version of the vortices in Fig. 3a,b, such a vortex could not appear in a map from Rojer and Schwartz' model, since the associated vector field could not be derived from the gradient of any surface. All rotated version of the tri-radius vortex, Fig. 3c, are allowed.

It is possible to predict orientation map patterns based on their power spectra, without imposing the unnecessary constraint in Rojer and Schwartz' model. Taking a ring spectrum in a two-dimensional Fourier space, with some noise in the amplitudes and with random phases of the modes, and transforming to a real space generates a two-dimensional array of complex numbers which may be taken to represent orientation preference (phase) and specificity (magnitude) [17]. An optional local function can also be applied to give the desired distribution of orientation specificities. This method produces arrays of orientation preferences that resemble experimentally observed maps, and which aren't subject to the constraint of Rojer and Schwartz' model maps. Yet the algorithm remains simple enough to be implemented by many different biological processes.

Swindale [15] has presented a model for the combined development of orientation and ocular dominance columns, which follows an algorithm similar to those used in pattern models. A vector representing local feature preference is associated with each location in a cortical lattice. Feature preferences grow from initially small, random values through an iterative process of separately convolving the orientation and ocular dominance components of the feature vectors with "Mexican-hat" filters on different length scales. The column systems are coupled by making growth of orientation preference more rapid in

monocular regions of cortex. Maps developed from this simple model have linear regions, vortices and fractures in the orientation column map, and the ocular dominance pattern consists of blobs or branching parallel columns. The patterns are correlated such that vortices occur more often near the centers of the ocular dominance bands, and as a natural consequence the linear regions tend to intersect the ocular dominance bands at right angles. Like the pattern models, this algorithm is general enough to allow several physiological implementations.

## 6 CONCLUSIONS

Careful characterization of the structure of cortical map patterns is the first step toward understanding the rationale behind the maps and the processes responsible for creating them. The lines in cortical maps of orientation preference are organized in such a way which reveals that they could not, for example, be given by the lines in a force field or by surface contour lines. Some proposed models of cortical map formation may be rejected through such topological arguments, even before consideration of the validity of the suggested physiological mechanism.<sup>4</sup>

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