

BCM Network develops Orientation Selectivity and Ocular Dominance in Natural Scene Environment.

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Abstract

A two-eye visual environment is used in training a network of BCM neurons. We study the effect of misalignment between the synaptic density functions from the two eyes, on the formation of orientation selectivity and ocular dominance in a lateral inhibition network. The visual environment we use is composed of natural images. We show that for the BCM rule a natural image environment with binocular cortical misalignment is sufficient for producing networks with orientation selective cells and ocular dominance columns. This work is an extension of our previous single cell misalignment model (Shouval et al., 1996).

1 Introduction

It is generally accepted that both orientation selectivity and ocular dominance of receptive fields in the visual cortex of cats are dramatically influenced by the visual environment (for a comprehensive review see, Frégnac and Imbert, 1984). Organization of the different properties of receptive fields such as ocular dominance and orientation selectivity across the visual cortex is best observed by optical imaging techniques (Bonhoeffer and Grinvald, 1991; Blasdel, 1992). It has been shown that various plasticity models that use a simplified visual environment, have different effects on the structure of receptive field organization in the visual cortex (Erwin et al., 1995). Different models attempting to explain how cortical receptive fields evolve have been proposed over the years (von der Malsburg, 1973; Nass and Cooper, 1975; Perez et al., 1975; Sejnowski, 1977; Bienenstock et al., 1982; Linsker, 1986; Miller, 1994). Such models are composed of several components: the exact nature of the learning rule, the representation of the visual environment and the architecture of the network. Most of these models assume a simplified representation of the visual environment (e.g. von der Malsburg, 1973), or replace the visual environment by a second order correlation function (Miller, 1994).

Realistic representations of the visual environment have only recently been considered (Hancock et al., 1992; Law and Cooper, 1994; Shouval et al., 1996; Olshausen and Field, 1996), and only in

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recent years have the statistics of natural images been studied and used for predicting receptive field properties (Field, 1987; Field, 1989; Atick and Redlich, 1992; Bialek et al., 1991; Liu and Shouval, 1994; Shouval and Liu, 1996). Once actual visual scenes are used, it is possible to more realistically represent two-eye input, and account for the fact that the two eyes are not looking at exactly the same visual scene. For example, Li and Atick (1994) have used natural images to extract detailed two-eye power spectra from stereo images and used these results to predict properties of cortical receptive fields.

We have recently shown (Shouval et al., 1996) that single cell BCM neurons, trained in a binocular natural image environment can develop both orientation selectivity and varying degrees of ocular dominance. We have also shown in that study that PCA (Oja, 1982) neurons can not develop ocular dominance. This is a result of the invariance of the two-eye correlation function to a two-eye parity transformation.

In this paper we extend the single cell study to networks of interconnected neurons. The network interactions have two types of effects:

- (a) They can alter properties of single cell receptive fields.
- (b) They produce an organization of receptive fields across the cortex.

We study these two effects on BCM networks. The network setup does not alter the single cell results of a PCA learning rule (Oja, 1982), namely, the fact that cells remain binocular¹.

Sparse coding which has been advocated by Barlow for many years (Barlow, 1961) has recently been discussed in the context of visual cortical plasticity (Földiák, 1990; Fyfe and Baddeley, 1995; Olshausen and Field, 1996). Following theoretical predictions (Intrator and Cooper, 1992), we demonstrate that a network of BCM neurons achieves sparse coding without explicitly attempting to maximize the sparseness.

2 Methodology

The BCM theory (Bienenstock et al., 1982) was introduced to account for the dependence of orientation selectivity on the visual environment. We have used a variation, due to Intrator and Cooper (1992), of a nonlinear neuron with a non-symmetric sigmoidal transfer function. Using their notation, synaptic modification of a single linear neuron is given by:

$$\dot{m}_j(\mathbf{x}) = \eta \phi(c(\mathbf{x}), \Theta_M(\mathbf{x})) d_j, \quad (1)$$

where the neuronal activity is given by c , $\phi(c(\mathbf{x}), \Theta_M(\mathbf{x})) = c(\mathbf{x})(c(\mathbf{x}) - \Theta_M(\mathbf{x}))$, \mathbf{x} denotes the coordinates of the neuron within the network, m_j are the synaptic weights, d_j the inputs and Θ_M is the modification threshold. This modification threshold is a nonlinear function of some time averaged measure of cell activity. It can be replaced by the spatial average (under stationarity assumption) and is thus given by

$$\Theta_M(\mathbf{x}) = E[c^2(\mathbf{x})], \quad (2)$$

where E denotes the expectation over the visual environment.

¹This result can be shown to follow from an extension of the two-eye parity method to linear networks (Shouval et al., 1996).

Binocular Model

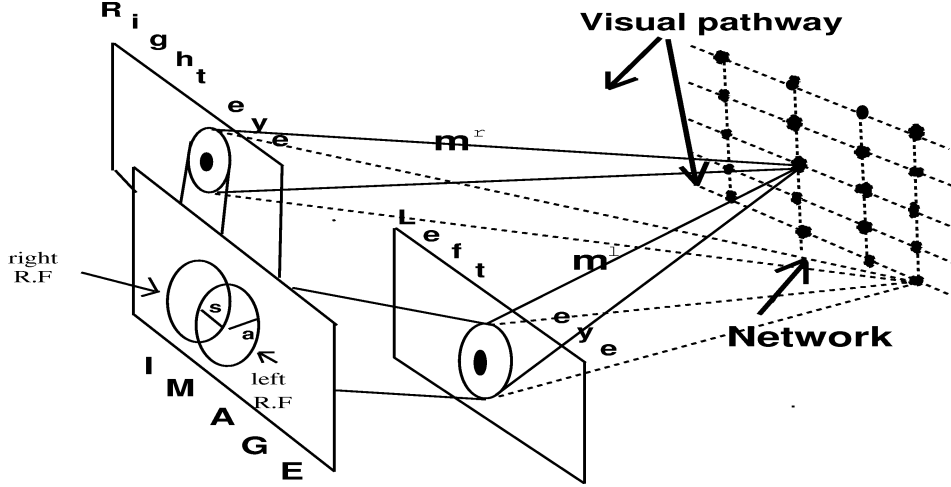


Figure 1: Schematic diagram of the two eye model, including the visual input preprocessing. Different cells in this network receive the same partially overlapping inputs. The receptive field radius is denoted by a and the shift between the receptive fields (of both eyes) is denoted by s .

In the lateral inhibition network c depends on the inputs, the synaptic weights and also on the activity of it's neighbors. The activity is given by²

$$c(x) = \sigma \left(\sum_{x'} I(\mathbf{x} - \mathbf{x}') \sigma(\mathbf{m}(x') \cdot \mathbf{d}) \right) \quad (3)$$

Where I is a lateral interaction matrix for which we used a balanced DOG and is given by

$$I(\mathbf{x}) = (1/2\pi\sigma_E^2) \exp\left(-\frac{1}{2} \left(\frac{x}{\sigma_E}\right)^2\right) - (1/2\pi\sigma_I^2) \exp\left(-\frac{1}{2} \left(\frac{x}{\sigma_I}\right)^2\right)$$

Where σ_E and σ_I are the length scales of the excitation and inhibition respectively. The transfer function σ is non symmetric around 0 to account for the fact that cortical neurons show a low spontaneous activity, and can thus fire at a much higher rate relative to the spontaneous rate, but can go only slightly below it³. In this work we have used a simplified version of the full gradient in which the lateral inhibition affects only the cell activity. Thus the network dynamics is given by Equations 1,2,3.

We have used the visual environment described in detail in our single cell study (Shouval et al., 1996). It is composed of a set of 24 natural images scanned at a 256 X 256 pixel resolution. We have avoided man-made objects, because they have many sharp edges, and straight lines, which make it easier to achieve oriented receptive fields. We have modeled the effect of the center surround retinal and LGN projections, by convolving the images with a difference of Gaussians (DOG) filter,

²We have also used the type of lateral network described in Intrator and Cooper (1992) with the same I and found no qualitative difference in the results.

³The actual sigma used in the simulations is $(e^x - e^{-x}) / (0.05e^x + 5e^{-x})$.

with a center radius of one pixel ($\sigma_1 = 1.0$) and a surround radius of three ($\sigma_2 = 3$). As illustrated in Figure 1, the input vectors from both eyes are chosen as small, partially overlapping, circular regions of the preprocessed natural images; these converge on the same cortical cell.

3 Results and discussion

We have extended our single cell results (Shouval et al., 1996) to networks of inter-connected neurons. The networks have been trained with a natural scene environment that was preprocessed with a DOG filter. The two eyes were exposed to small partially overlapping portions of these images. Figure 2 depicts results of a typical network. The resulting receptive fields (partially shown on the RHS of the top panel) are very similar to those obtained for single cells (Law and Cooper, 1994; Shouval et al., 1996). They are orientation selective and show various degrees of ocular dominance. The degree of ocular dominance depends on the overlap between the receptive fields of the two eyes – larger overlaps produce more binocular cells (Figure 3).

The activity histograms are displayed in the two panels at the bottom of Figure 2. The histogram on the left of the second panel represents the activity histogram composed of all the neurons in the network. The other histograms are of several single cells in the network. All histograms indicate sparse activity of the network as a whole and of each of the cells.

Sparse neuronal representation can be roughly characterized by neuronal activity which is inactive most of the time, namely has a distribution of activity which is highly peaked at zero and has heavy tails⁴. For this reason sparse activity is associated with a kurtotic activity distribution. We emphasize that in the BCM network case, sparse coding is an outcome of the dynamics of BCM learning and emerges despite the lack of an explicit "sparseness term" in the learning rule. It will be interesting to compare the resulting code with methods that maximize sparsity or kurtosis as a goal for neuronal coding and feature detection (Földiák, 1990; Fyfe and Baddeley, 1995; Olshausen and Field, 1996).

The entire network of BCM neurons shows an organization of Ocular Dominance bands and Orientation Selectivity bands in a form reminiscent to experimental results (Bonhoeffer and Grinvald, 1991). The relationship between these bands depends on the details of the lateral interaction term (I). As can be seen in Figure 3, it is possible to change the parameters of the lateral interaction in order to achieve cortical maps which exhibit a greater or a smaller resemblance to experimental cortical maps. We do not attempt to explore the full details of the lateral interaction here, since we believe that cortical maps are influenced by many other factors such as innate preferences to certain orientations, the more complex three dimensional anatomy of the cortex, the shape of the boundary of the cortical region and the details of the imaging techniques used to obtain the maps.

The organization of receptive fields across the cortex, presented above, includes many of the components required from a cortical map. It has both ocular dominance columns and varying orientation preferences. The orientation map has both linear regions and non-linear regions in which sharp transitions in orientation preference occur. This organization depends critically on the parameters of the lateral interaction term. As far as we know this is the first network model, trained in a natural image environment, which develops concurrently both ocular dominance and orientation selectivity. We do not know of any simplified environment that is appropriate for models which depend on statistics of higher order than two and thus, have chosen to study natural

⁴When the cell takes mostly positive values, the heavy tail is one-sided.

image environment. Recent models such as Olshausen and Field (1996) develop orientation selective neurons from a natural image environment, however do not attempt to model the binocular aspects of cortical cells or the organization of these receptive fields across the cortical sheet.

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Spatial organization of receptive fields: Orientation selectivity and ocular dominance

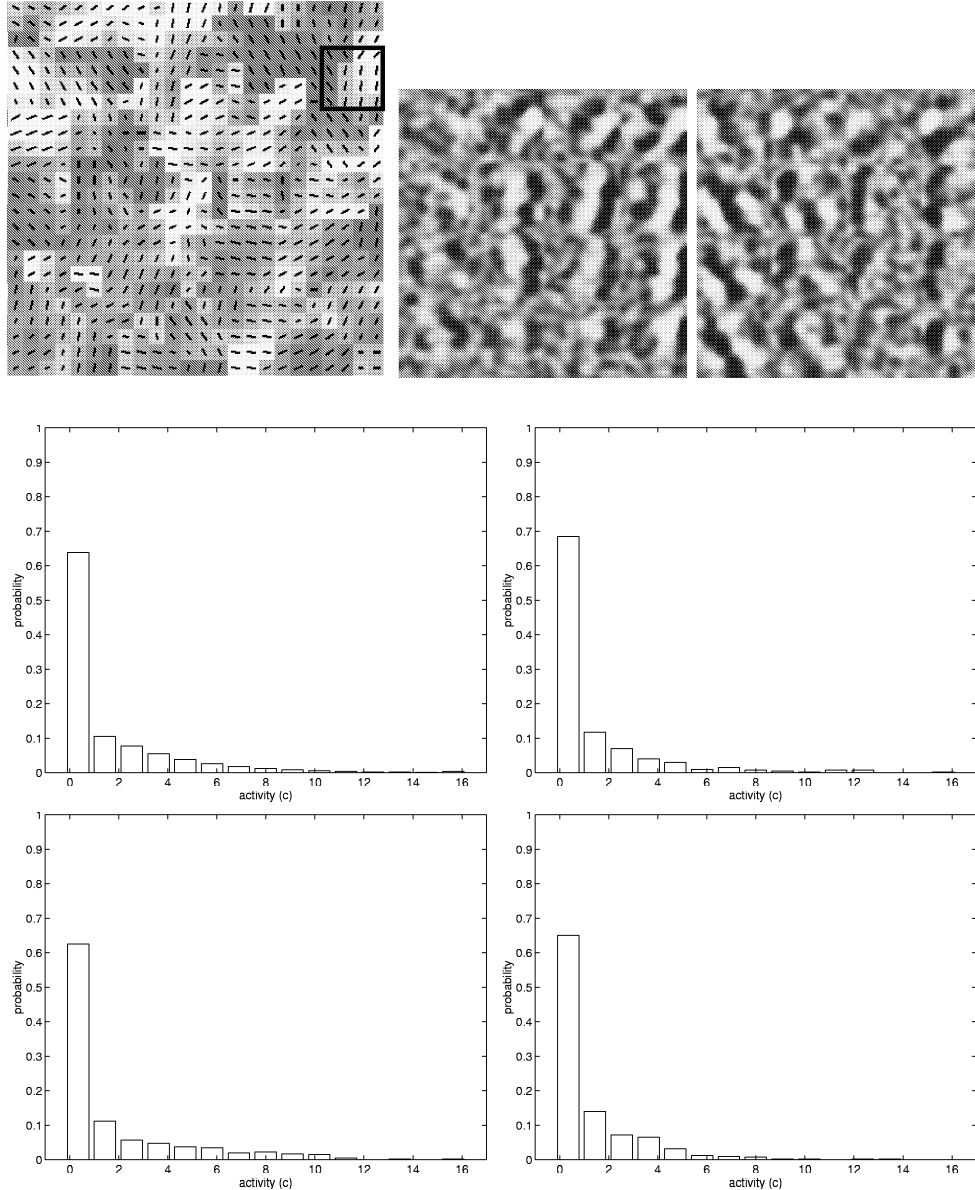


Figure 2: Top left panel represents combined Ocular Dominance and Orientation maps extracted by a network of 24 by 24 neurons with receptive fields of diameter 20 and a shift of 15 pixels between the two eyes. For this network $\sigma_E = 1$ and $\sigma_I = 5$. The orientation of the bars shows the preferred orientation of the cells, it's length represents the degree of orientation selectivity and the gray scale of the background represents Ocular Dominance. On the RHS of the top panel, receptive fields from the 4 by 4 region of the network that is enclosed in the black box, are displayed (left and right eye respectively). On the middle panel (left) a histogram of the activity of all neurons in the network is displayed. The three other histograms are of typical single cells in this network. It is evident that the response is sparse; most neurons have a large response only a small fraction of the time and small response most of the time.

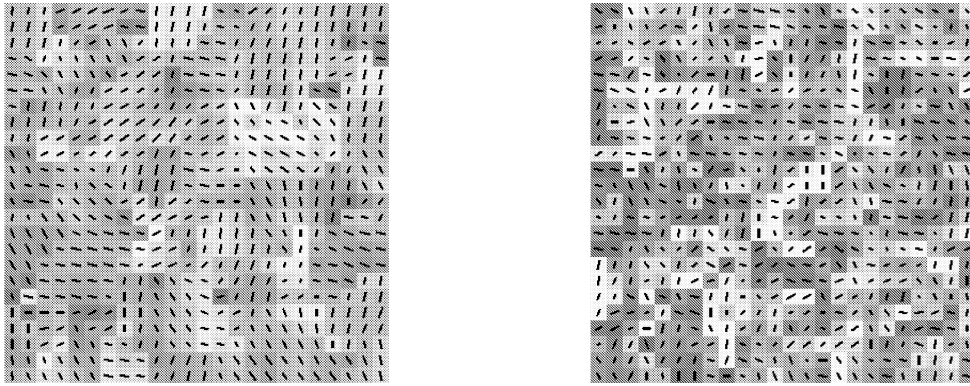


Figure 3: The effect of changing the parameters on network organization. On the left the effect of changing the overlap between the eyes is displayed. The displacement between the two eyes is 5 pixels, apart from that the parameters are identical to those in Figure 2. The Ocular Dominance bands become much weaker in this case. On the right the effect of changing the lateral interaction term I is displayed, here $\sigma_E = 0.7$ and $\sigma_I = 2$, apart from that the parameters are identical to the one in Figure 2. This has the effect of greatly reducing the continuity in the orientation and Ocular Dominance.