

Statistics of LGN activity determine the segregation of ON/OFF subfields for simple cells in cortex

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Abstract

Visual cortical simple cells show a strong preference for edges of a particular orientation [Hubel and Wiesel, 1962]. The receptive field of the cortical cell shows adjacent excitatory and inhibitory subfields, which are projections from ON-center and OFF-center LGN cells, respectively [Reid and Alonso, 1995]. Here we present a single cell model using ON and OFF channels, a natural scene environment, and the BCM [Bienenstock et al., 1982] learning rule. The results from the model imply that the input distribution from LGN to cortex should be almost symmetrical in order to develop the proper segregation of ON/OFF subfields; *There is a relation between the organization of simple cell receptive fields and the shape of the input distribution.*

1 Introduction

One of the important characteristics of the visual response of most neurons in cat striate cortex is that they show a strong preference for edges of a particular orientation [Hubel and Wiesel, 1962]. The receptive field of the cortical cell shows adjacent excitatory and inhibitory subfields. There is evidence that these subfields are projections from ON-center and OFF-center LGN cells, respectively [Reid and Alonso, 1995] and that the proper development of the cortical receptive fields requires activity (for review see Fregnac and Imbert, 1984).

In this paper we explore the segregation of the ON- and OFF-center LGN afferents, using a model of a single cortical cell with inputs from ON and OFF retinal and LGN cells. We use an environment composed of natural scenes and the BCM learning rule [Bienenstock et al., 1982, Intrator and Cooper, 1992], which has been shown to develop orientation selectivity in realistic visual environments [Law and Cooper, 1994, Shouval and Liu, 1994]. The results indicate that there may be a relation between the organization of simple receptive fields and the shape of the input distribution.

2 Methods

We use 13×13 circular patches from 12 preprocessed images of natural images as in [Law and Cooper, 1994, Blais et al., 1998]. The input consists of two channels, one representing ON center cells and the other OFF center cells, each receiving identical input. The two channels (ON and OFF) do not interact at the level of the LGN but converge in the cortex. We represent the total input to the BCM neuron by $\mathbf{d} = [\mathbf{d}^{\text{ON}}, \mathbf{d}^{\text{OFF}}]$, the synaptic weights by $\mathbf{m} = [\mathbf{m}^{\text{ON}}, \mathbf{m}^{\text{OFF}}]$. The response of the cortical cell is given by $c = \sigma_{\text{cortical}}(\mathbf{m} \cdot \mathbf{d})$ where $\sigma_{\text{cortical}}(\cdot)$ is a rectifying sigmoid, which sets the minimum and maximum values of the postsynaptic response.

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In the simulation, we have allowed the synaptic weights to change polarity during learning, so the final weights include both positive and negative weights. The weights should be interpreted as *effective* synapses in a mean-field approximation [Cooper and Scofield, 1988] of a network of BCM neurons, rather than single-cell synapses.

The vectors \mathbf{d}^{ON} and \mathbf{d}^{OFF} are related according to

$$\begin{cases} d_i^{\text{ON}} &= \sigma(D_i) + K \\ d_i^{\text{OFF}} &= \sigma(-D_i) + K \end{cases} \quad (1)$$

where the values D_i define the input pattern after retinal processing with an *excitatory*-center DOG filter, and the offset K is related to the level of LGN spontaneous activity. In previous work [Law and Cooper, 1994, Shouval and Liu, 1994], it was assumed that $K = 0$ so the value of $d_i^{\text{ON/OFF}}$ for spontaneous activity (LGN response to uniform activity) was zero. We find that the results do not depend strongly on K , so the level chosen for spontaneous activity is unimportant.

We define the LGN activation function σ as:

$$\sigma(D_i) = \begin{cases} D_i & \text{if } D_i \geq D_{\min} \\ D_{\min} & \text{if } D_i < D_{\min} \end{cases}, \quad (2)$$

where the lower cut-off D_{\min} is negative. For robustness in the simulations, Gaussian noise is added to each channel independently.

The variables \mathbf{d} , \mathbf{m} , and c obey the standard BCM equations;

$$\begin{cases} c = \sigma_{\text{cortical}}(\mathbf{m}^{\text{ON}} \cdot \mathbf{d}^{\text{ON}} + \mathbf{m}^{\text{OFF}} \cdot \mathbf{d}^{\text{OFF}}) \\ \dot{m}_i^{\text{ON}} = \mu \phi(c, \theta_M) d_i^{\text{ON}} \\ \dot{m}_i^{\text{OFF}} = \mu \phi(c, \theta_M) d_i^{\text{OFF}}, \end{cases} \quad (3)$$

where $\phi = c(c - \theta_M)/\theta_M$. The sliding threshold θ_M is defined as

$$\theta_M = E_t[c^2] = \frac{1}{\tau} \int_{-\infty}^t dt' c^2 e^{-[(t-t')/\tau]}. \quad (4)$$

Table 1 summarizes the BCM equations and parameters used in the simulations.

Learning rule	$\dot{\mathbf{m}} = \mu \phi \mathbf{d}$, $\phi = c(c - \theta_M)/\theta_M$ $\theta_M = \frac{1}{\tau}(c^2 - \theta_M)$
Cell response	$c = \sigma(\mathbf{m} \cdot \mathbf{d})$, $\begin{cases} \sigma(-\infty) = -1 \\ \sigma(+\infty) = 100 \end{cases}$
Retinal patch diameter	13 pixels
Retinal DOG ratio ¹	3:1
Initial synaptic weights	0.0 - 0.1
Initial threshold	$\theta_0 = 0.7$
Learning rate	$\mu = 10^{-6}$
Memory constant	$\tau = 300$

Table 1: Parameters of the model.

We explore the segregation of the ON and OFF channels into different subfields of the simple cell receptive field. Specifically, we look at two cases of the Equation 2; this allows us to determine the relation between some of the basic statistics of the LGN activity, and the segregation of the ON/OFF receptive fields. The two cases are

- **Symmetric LGN**

In this case, we assume that LGN cells operate in the linear region, where $-|D_{\min}| < D_i < |D_{\min}|$, and that LGN activities are measured relative to spontaneous activities, where $K = 0$. Since the results do not strongly depend on the value of K , we present the simplest case. Thus Equation 1 reduces

$$\begin{cases} d_i^{\text{ON}} &= D_i \\ d_i^{\text{OFF}} &= -D_i \end{cases}, \quad (5)$$

where D_i are the input values after retinal pre-processing with an ON-center DOG filter. Note that ON and OFF cells that see the same part of the retina display exactly opposite responses to light of *any* intensity, and that the input distribution is symmetric.

- **Non-Symmetric LGN**

The linear assumption cannot be valid for light of any intensity, since the *absolute* LGN cell activity must be positive. For example, assume that the absolute spontaneous activity is 14 Hz for all LGN cells. If an ON (OFF) cell fires with frequency 24 Hz, the OFF (ON) cell that sees the same part of the retina fires with frequency 4 Hz. However, light that leads to a response above 30 Hz of an ON (OFF) cell, will inhibit *all* activity of the corresponding OFF (ON) cell. LGN cells operate in the symmetric region when $-|D_{\min}| < D_i < |D_{\min}|$, and in the non-symmetric region when $D_i > |D_{\min}|$ or $D_i < -|D_{\min}|$. With the LGN activation function σ is defined by Equation 2, the magnitude of the lower cutoff D_{\min} can be interpreted as the difference between the spontaneous activity and the minimal activity of the LGN cells.

3 Results

Symmetric LGN

Simulation results for the two channel model, under the linear LGN assumption (activity in the symmetric region), is shown in Figure 1. The final configurations of the effective synapses \mathbf{m}^{ON} and \mathbf{m}^{OFF} display adjacent “excitatory” and “inhibitory” bands (cf. subregions of strong and weak thalamo-cortical connections). To see the relation between \mathbf{m}^{ON} and \mathbf{m}^{OFF} more clearly, we define the “sum” and “difference” configurations \mathbf{m}^+ and \mathbf{m}^- , shown in Figure 2. The summed configuration \mathbf{m}^+ lacks any significant structure and has a zero mean. This means that $m_i^{\text{ON}} \approx -m_i^{\text{OFF}}$, i.e. the effective synapses from ON and OFF cells that see the same part of the retina are of opposite type (“excitatory” versus “inhibitory”).

$$\begin{cases} \mathbf{m}^+ &= \frac{1}{\sqrt{2}} (\mathbf{m}^{\text{ON}} + \mathbf{m}^{\text{OFF}}) \\ \mathbf{m}^- &= \frac{1}{\sqrt{2}} (\mathbf{m}^{\text{ON}} - \mathbf{m}^{\text{OFF}}) . \end{cases} \quad (6)$$

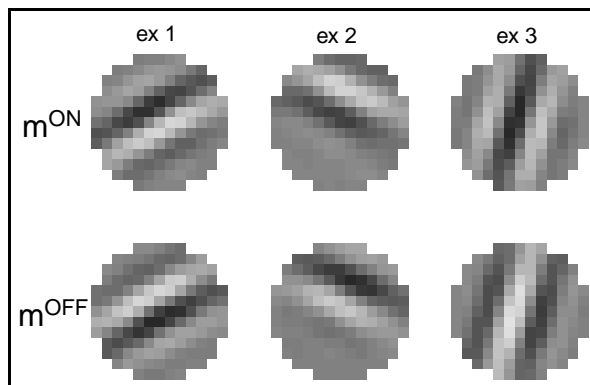


Figure 1: Weight configurations \mathbf{m}^{ON} (*top row*) and \mathbf{m}^{OFF} (*bottom row*) developed according to the ON/OFF channel model; each column represents an example. The brightness codes for the strengths of the synaptic weights.

We would like to point out that *restricting the weights to positive values* by, for example, imposing hard bounds on the weight values, has no noticeable effect on the receptive field arrangement. It is merely simpler to consider the case where the weights are allowed to be negative.

We make a variable substitution on the inputs in the BCM equation, defining the “sum” and “difference” input configurations \mathbf{d}^+ and \mathbf{d}^- , respectively, with the linearity constraint in Equation 5. It is straightforward to show that

$$\mathbf{m}^-(t) \propto \mathbf{m}^{\text{single}}(t) \quad (7)$$

$$\mathbf{m}^+(t) = \mathbf{m}^+(t=0) \quad (8)$$

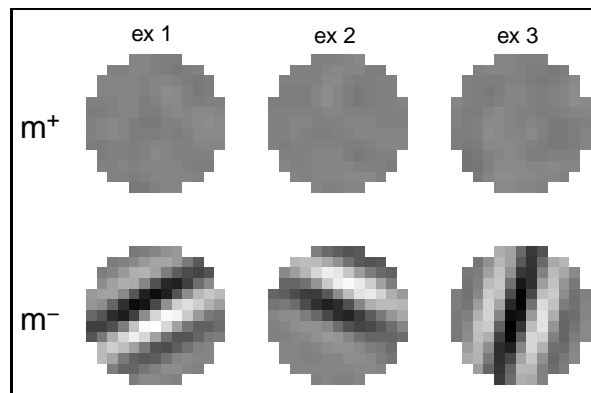


Figure 2: The “sum” and “difference” weight configurations \mathbf{m}^+ (top row) and \mathbf{m}^- (bottom row) for the examples in Figure 1.

where $\mathbf{m}^{\text{single}}$ is the weight configuration for a single channel model. The relation predicts that (1) the final ON and OFF receptive fields display the same type of elongated subregions of strong and weak connections as in previous single-channel models, and (2) subregions of strong ON synapses overlap subregions of weak OFF synapses and vice versa. This is consistent with the simulation results in Fig. 1 and Fig. 2.

Non-Symmetric LGN

To investigate the effect of the non-symmetric region, we perform simulations with a cut-off at D_{min} for different values. Note that whereas the input distributions are almost symmetrical around spontaneous activity for linear cells, they are *asymmetrical* with this cut-off. The results of simulations, for several values of the cut-off, are shown in Figure 3.

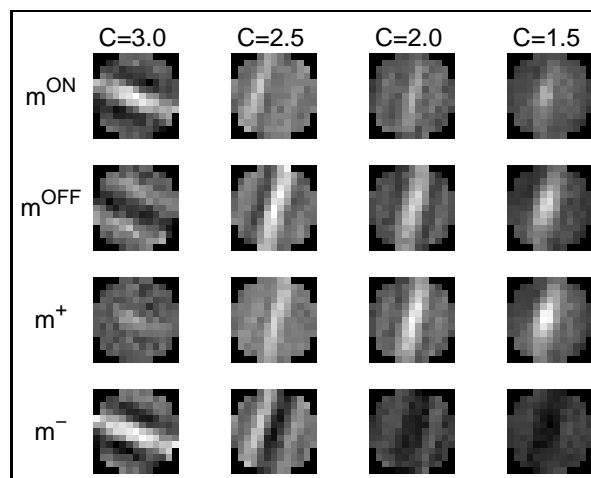


Figure 3: The ON and OFF channel weight configurations (first and second rows), and the corresponding “sum” and “difference” weight configurations (third and fourth rows) as a function of the LGN activity cut-off, D_{min} , (each column). The smaller the cut-off, the more non-symmetric the LGN cells are.

One observes that the stronger asymmetry yields a change in the results, from *reversed* weight configurations $\mathbf{m}^{\text{ON}} \approx -\mathbf{m}^{\text{OFF}}$ (or $\mathbf{m}^+ \approx \mathbf{0}$) to *equal* weight configurations $\mathbf{m}^{\text{ON}} \approx \mathbf{m}^{\text{OFF}}$ (or $\mathbf{m}^- \approx \mathbf{0}$).

4 Summary and Conclusions

The results from the ON/OFF channel model imply that, if the BCM learning rule is valid, and we accept the experimental evidence for the segregation of ON/OFF receptive fields [Reid and Alonso, 1995], then the input

distribution from LGN to cortex should be almost symmetrical. *There is a relation between the organization of simple cell receptive fields and the shape of the input distribution*; the mean of the input distribution, on the other hand, seems to be less important. If, however, the input distribution is very asymmetrical, we do not obtain the proper segregation of the ON/OFF receptive fields.

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