

Dynamics of Synaptic Plasticity: A Comparison between Models and Experimental Results in Visual Cortex

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Abstract

Receptive fields in the visual cortex can be altered by changing the visual environment, as has been shown many times in deprivation experiments. In this paper we simulate this set of experiments using two different models of cortical plasticity, BCM and PCA. The visual environment used is composed of natural images for open eye and of noise for closed eyes. We measure the response of the neurons to oriented stimuli, and use the time course information of the neuronal response to provide a preliminary quantitative comparison between the cortical models and experiment.

1 Introduction

Two important characteristics of the visual response of most neurons in cat striate cortex are that they are binocular and show a strong preference for contours of a particular orientation [7]. Although some orientation selectivity exists in striate cortex prior to visual experience, maturation to adult levels of specificity and responsiveness requires normal contour vision during the first 2 months of life (for review see Fregnac and Imbert, 1984).

Ocular dominance is a measure of how effectively the neuron can be driven through the left and right eyes, respectively. Up to the level of the LGN, visual information originating from the two eyes is segregated in separate pathways, striate cortex is thus the first site where individual cells receive afferent projections from both left and right eyes, and in normal kitten striate cortex most of the visually responsive cells are binocular.

One of the most dramatic examples of cortical plasticity is the alteration of ocular dominance in kitten striate cortex in monocular deprivation, a procedure in which, one eye is deprived of patterned stimuli (by either suturing the eyelid closed or using an eye patch). In such an imbalanced visual environment, cells in kitten's striate cortex change from mostly binocular to almost exclusively monocular: in less than 24 hours most cells lose their responsive to stimulation through the deprived eye and can only be driven through the eye that remains open [10, 13].

The change induced by monocular deprivation is reversible. In the rearing condition called reverse suture there is an initial period of monocular deprivation: after the cortical neurons have become monocular, the deprived eye is opened and the other eye closed. In this situation the cortical neurons lose responsiveness to the newly closed eye, and become responsive to the newly opened eye [2]. Acute studies indicate that, as the ocular dominance of cortical responsiveness shifts from one

eye to the other, there is rarely a period when cells can be strongly and equally activated by both eyes [10].

In this paper we model these experiments, looking specifically at the time course of neuronal response during visual deprivation. In this way we wish to directly compare two different learning rules with each other, and also with experiment. The visual environment to which open eyes are exposed is assumed to be composed of preprocessed natural images, whereas closed eyes receive noise as their inputs. The architecture assumed in these models is of single learning neurons, as a first step to understanding the behavior of networks.

We compare the two learning rules BCM [1, 8] and PCA [11]. Both of these rules have been shown to develop orientation selectivity in a realistic visual environment [9, 12]. Previous simulations of the deprivation experiments have been performed using simplified inputs for the BCM theory[3]. In this paper we use realistic inputs.

2 Methods

The visual environment used here is described in Law and Cooper, 1994. The exact time course of these simulations is dependent on the parameters chosen; we have therefore examined these over a large parameter regime. At each set of parameters we performed all of the deprivation simulations, and compared their timing ratios, in order to test the robustness of our predictions. Examples of the simulations for PCA and BCM are shown in Figure 1.

Table 2 shows the specific form of the BCM learning rule, as well as the range of parameters, which was used. The precise time course of the neuron activity is dependent on the choice of the functional form of both the modification function, ϕ , and the sigmoid. Variations of these are currently being investigated.

We measure the response $Y(t)$ of the neurons using oriented stimuli. Of particular interest is characteristic half-rise (half-fall) time for the growth (decay) of neuronal response, referred to as either $t_{1/2}$ or simply \mathcal{T} . The half-time measurement provides a direct comparison between the BCM and PCA models. It also provides a way to quantitatively translate between simulation cycles and real time, yielding a quantitative comparison with experiment.

3 Results

Summary of Experimental Results

Table 1 summarizes the experimental results to which we can compare the two models. Since the exact results depend on when in the critical period the experiments were done, we look at *ratios* of the experimentally determined development times, so we can make a reasonable comparison with the theory. The values of \mathcal{T} , either half-rise times, $\mathcal{T}_{\text{rise}}$, or half-fall times, $\mathcal{T}_{\text{fall}}$, from Table 1 give us the following ratios that we can then use in our comparison: ($\mathcal{T}_{\text{fall}}^{\text{RS}}/\mathcal{T}_{\text{fall}}^{\text{MD}} \approx 1$), ($2 < \mathcal{T}_{\text{rise}}^{\text{RS}}/\mathcal{T}_{\text{fall}}^{\text{MD}} < 16$), and ($0.33 < \mathcal{T}_{\text{rise}}^{\text{RS}}/\mathcal{T}_{\text{fall}}^{\text{BD}} < 16$).

PCA Results

We can use the full time-domain solution[14] of the PCA equations in order to explore the deprivation simulations analytically. Under the assumptions that natural scenes are dominated by the first eigenvector of the covariance matrix, \mathbf{v}_1 with eigenvalue λ_1 , and that closed eyes are presented with noise with variance σ^2 , we obtain the following equations for the time development of the weights

$$\mathbf{m}^{\text{MD}}(\mathbf{t}) = \left(e^{\lambda_1 t} \mathbf{v}_1 \quad e^{\sigma^2 t} \mathbf{v}_1 \right) / (e^{2\lambda_1 t} + e^{2\sigma^2 t})^{1/2} \quad (3.1)$$

$$\mathbf{m}^{\text{BD}}(\mathbf{t}) = (\mathbf{v}_1 \quad \mathbf{v}_1) / \sqrt{2} \quad (3.2)$$

$$\mathbf{m}^{\text{RS}}(\mathbf{t}) = \left(e^{\sigma^2 t} \mathbf{v}_1 \quad e^{\lambda_1 t} \epsilon \mathbf{v}_1 \right) / (e^{2\sigma^2 t} + \epsilon e^{2\lambda_1 t})^{1/2} \quad (3.3)$$

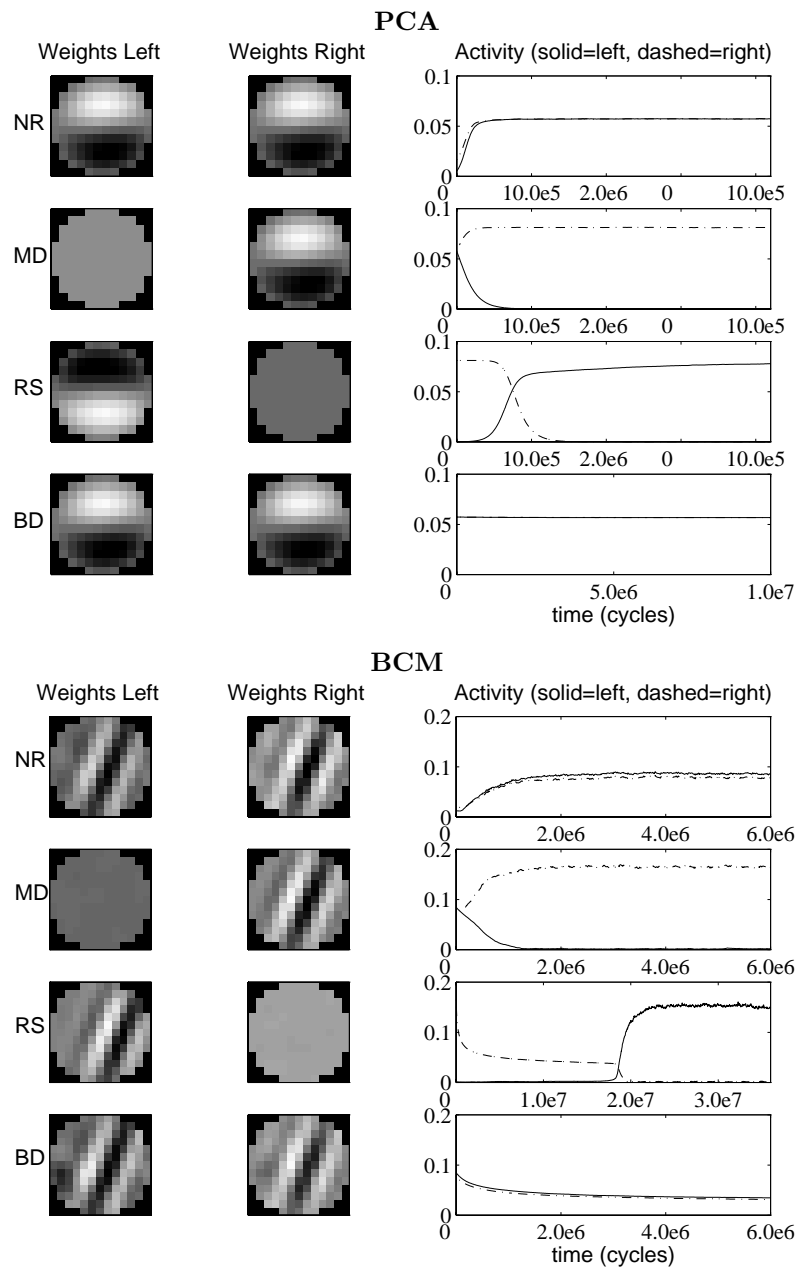


Figure 1: Example PCA (top) and BCM (bottom) Simulations. Left: Final weight configuration. Right: Maximum response to oriented stimuli, as a function of time. Simulations from top to bottom are as follows. Normal Rearing (NR): both eyes presented with patterned input. Monocular Deprivation (MD): following NR, one eye is presented with noisy input and the other with patterned input. Reverse Suture: following MD, the eye given noisy input is now given patterned input, and the other eye is given noisy input. Binocular Deprivation (BD): following NR, both eyes are given noisy input. **It is important to note that for BCM if Binocular Deprivation is run longer, selectivity will eventually be lost. This is not true for PCA**

Experiment	Reference	Half-Time \mathcal{T}
Monocular Deprivation	<ul style="list-style-type: none"> • OD changes were observed as early as 6 h[5, 10], complete loss of response to closed as early as 12 h[10] 	$\mathcal{T}_{\text{fall}}^{\text{MD}} \approx 6\text{-}12 \text{ h}$
Binocular Deprivation	<ul style="list-style-type: none"> • cortical response reduced within 3 d [4] 	$\mathcal{T}_{\text{fall}}^{\text{BD}} < 3 \text{ d}$
Reverse Suture	<ul style="list-style-type: none"> • the time course for the reduction of response to the newly deprived eye was similar to monocular deprivation[10] • At least 24 h of reverse suture is required before the responses to the deprived eye reappears[10] 	$\mathcal{T}_{\text{fall}}^{\text{RS}} \approx \mathcal{T}_{\text{fall}}^{\text{MD}}$ $\mathcal{T}_{\text{rise}}^{\text{RS}} \approx 1\text{-}4 \text{ d}$

Table 1: Summary of Experimental Results

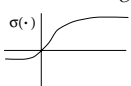
Learning Rule	$\dot{\mathbf{m}} = \eta c(c - \theta) \mathbf{d}$
Activation Rule	$\dot{\theta} = \frac{1}{\tau}(c^2 - \theta)$
cortical sigmoid	$c = \sigma(\mathbf{m} \cdot \mathbf{d})$  $\begin{cases} \sigma(-\infty) = -1 \\ \sigma(+\infty) = 50 \end{cases}$
Initial threshold	$\theta_o = 0.73$
Input mean	$\langle \mathbf{d} \rangle = -\mathbf{3.3} \cdot 10^{-5}$
Input variance	$\text{var}(\mathbf{d}) = \mathbf{1.0}$
RF Diameter	13 pixels
Retinal DOG ratio	3:1
Learning rate	$\eta = 5 \cdot 10^{-7}, \dots, 5 \cdot 10^{-5}$
Memory constant	$\tau = 10, \dots, 3510$
Noise Levels	uniform noise= [-.25:.25],...,[-2.5,2.5]

Table 2: Parameters for BCM

Comparing the MD and RS solutions (Equations 3.1 and 3.3) one sees that the times for the decay and recovery of neuronal activity must be identical for each regardless of noise levels and input statistics. Therefore the PCA model predicts correctly the time for the neuronal activity to fall in these deprivation situations, but fails to properly predict the time for the recovery of activity in RS compared to MD.

Equation 3.2 implies that a neuron following Oja's rule, experiencing binocular deprivation following normal rearing, performs a random walk about the normal reared state. Thus PCA is again inconsistent with the experiment results.

BCM Results

In order to determine the dependence of the response half-times on model and input parameters we need to perform simulations over a range of those parameters and measure the time \mathcal{T} for each of these. The parameter regime is initially chosen to give *stable* simulations, and then explored more finely to determine regions with consistent time ratios. Stability is lost if the learning rate is too large, or if the memory constant, τ , is too large causing BCM sliding threshold, θ , to move too slowly.

The two most important parameters are the noise level to the closed eye and the memory constant, τ . We see from Figure 2 that the noise level has a dramatic effect on the time course of the

neuronal response, and is different for each deprivation simulation. This allows us to possibly locate a range of noise levels for which the relative times are consistent with experiment. In the parameter regime tested we found surprisingly little effect from the memory constant on the time course. We are currently exploring possible reasons for this apparent difference between the natural scene environment and previous work done with abstract inputs[3], where the memory constant played a more important role in the timing.

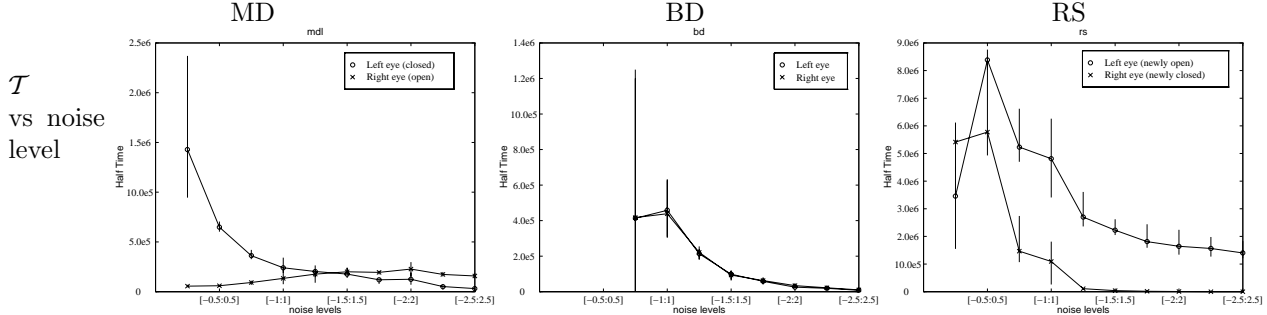


Figure 2: BCM Results: The effect of the noise level on the response half-times of deprivation simulations, Monocular Deprivation (MD), Binocular Deprivation (BD), and Reverse Suture (RS).

4 Summary and Conclusions

It has been demonstrated that the PCA rule fails to account for the time course of the deprivation experiments. Most dramatic is the result that binocular deprivation to a PCA neuron gives only a random walk response. BCM on the other hand can account for the time course, within a particular parameter regime. This parameter regime can be summarized by the range of 3 parameters: memory constant $\tau = 500, \dots, 3000$, learning rate $\eta = 4.5 \cdot 10^{-6}, \dots, 6 \cdot 10^{-6}$, and noise level $\sigma = 0.88, \dots, 1.4$ (or $[-1.1:1.1], \dots, [-1.45:1.45]$). Note that the valid parameter regime is *not* defined by a sharp boundary, but that near the edge the system is less robust.

One of the features of this approach is the direct calculation of the model parameters in terms of experimental quantities. Using the range of half-time values exhibited across the valid parameter regime for, say, monocular deprivation, and attributing that range to the known 6-12 hour range obtained from experiment, we can find a range for the possible values of τ in minutes. Doing this we find that τ ranges between 1-15 minutes. We are investigating how this time range might be affected by variations such as changes in the slope of the modification function, ϕ , at threshold and the form of the cortical sigmoid. A final determination of the allowed values of τ may give us clues to the cellular and molecular processes involved.

References

- [1] E. L. Bienenstock, L. N. Cooper, and P. W. Munro. Theory for the development of neuron selectivity: orientation specificity and binocular interaction in visual cortex. *Journal Neuroscience*, 2:32–48, 1982.
- [2] C. Blakemore and R. R. van Sluyters. Reversal of the physiological effects of monocular deprivation in kittens: further evidence for sensitive period. *J. Physiol. Lond.*, 248:663–716, 1974.
- [3] E. E. Clothiaux, L. N Cooper, and M. F. Bear. Synaptic plasticity in visual cortex: Comparison of theory with experiment. *Journal of Neurophysiology*, 66:1785–1804, 1991.
- [4] R. Freeman, R. Mallach, and S. Hartley. Responsivity of normal kitten striate cortex deteriorates after brief binocular deprivation. *Journal of Neurophysiology*, 45(6):1074–1084, 1981.

- [5] R. Freeman and C. Olson. Brief periods of monocular deprivation in kittens: Effects of delay prior to physiological study. *Journal of Neurophysiology*, 47(2):139–150, 1982.
- [6] Y. Frégnac and M. Imbert. Development of neuronal selectivity in the primary visual cortex of the cat. *Physiol. Rev.*, 64:325–434, 1984.
- [7] D. H. Hubel and T. N. Wiesel. Receptive fields, binocular interaction and functional architecture in the cat’s visual cortex. *J. Physiol*, 160:106–154, 1962.
- [8] N. Intrator and L. N. Cooper. Objective function formulation of the BCM theory of visual cortical plasticity: Statistical connections, stability conditions. *Neural Networks*, 5:3–17, 1992.
- [9] C. Law and L. Cooper. Formation of receptive fields according to the BCM theory in realistic visual environments. *Proceedings National Academy of Sciences*, 91:7797–7801, 1994.
- [10] L. Mioche and W. Singer. Chronic recording from single sites of kitten striate cortex during experience-dependent modification of synaptic receptive-field properties. *J. Neurophysiol.*, 62:185–197, 1989.
- [11] E. Oja. A simplified neuron model as a principal component analyzer. *Journal of Mathematical Biology*, 15:267–273, 1982.
- [12] H. Shouval and Y. Liu. How does retinal preprocessing affect the Receptive field of a stabilized hebbian neuron. In J. M. Bower, editor, *The Neurobiology of Computation: The Proceedings of the Third Annual Computation and Neural Systems conference*, pages 129–134. Kluwer, 1994.
- [13] T. N. Wiesel and D. H. Hubel. Single-cell responses in striate cortex of kittens deprived of vision in one eye. *Journal of Neurophysiology*, 26:1003–1017, 1963.
- [14] J. L. Wyatt and I. M. Elfadel. Time-domain solutions of Oja’s equations. *Neural Computation*, 7(5):915–922, 1995.