Appendix A: Robustness of Results

Since it is unlikely that BCM synaptic modification in its actual physiological realization exactly follows any of the mathematical forms used in our analysis and simulations, it is important to test the robustness of these results to modifications of our assumptions. These are described below.

Precise Overlap of ON/OFF Fields: Effect of Noise

In what follows, we investigate the robustness of our results (Linear Region) to noise in the ON and OFF channels — to what extent random noise affects the receptive field formation. The LGN inputs have the form:

$$
\begin{cases}
d_i^{\text{ON}} &= D_i + n_i^{\text{ON}}(t) \\
d_i^{\text{OFF}} &= -D_i + n_i^{\text{OFF}}(t) \,,
\end{cases}
\tag{11}
$$

where D_i represents the patterned input from retinal preprocessed images, and $n_i^{\text{ON}}(t)$ and $n_i^{\text{OFF}}(t)$ are independent but statistically equivalent noise terms. We choose Gaussian noise with mean zero, and standard deviation SD_n. The standard deviation of the patterned inputs is one. Thus, the signal-to-noise ratio (S/N) is the inverse of SD_n.

Fig. 8 shows the final weight configurations for simulations with different noise levels. For each noise level, we run three simulations (ex 1, ex 2, ex 3) with different initial conditions.

We see that *the ON/OFF channel model is very robust to noise*. Non-trivial receptive fields are obtained for $SD_n = 0.7$ ($S/N = 1.4$) as well as for such high noise levels as $SD_n = 4.0$ ($S/N = 0.25$). As a rule, there is less diversity in the receptive fields for higher

noise levels. This is also expected from a minimization problem with several local minima (In an objective function formulation of the BCM theory, the neuron minimizes an energy function). For low noise levels, there is a larger chance of being trapped in one of the many local minima while, for higher noise levels, the obtained weight configuration is more likely to be a global minimum.

There is, furthermore, a relation between the spatial frequency of the receptive fields and the noise level. As Fig. 8 shows, the spatial frequency of the bands decreases with increasing noise and vice versa.

Dependence on Spontaneous Activity or "Baseline Level"

It is known that spontaneous activity levels vary widely depending on a variety of external and internal factors (awakeness etc.). We have generally measured the LGN input d from the spontaneous activity level (d^s) — based on the possibly reasonable belief that spontaneous activity levels (those inputs relatively independent of external stimulation) should not result in modification of synapses. Thus, with the "baseline" at the level of spontaneous activity, the input

$$d = d^a - d^s \tag{12}$$

(where d^a is the actual firing frequency) so that the synaptic modification

$$\dot{m} = \phi \cdot d = 0 \tag{13}$$

when $d^a = d^s$. Although this seems to be a reasonable hypothesis, we have tested the dependence of our results on this assumption. It turns out that our results are relatively

independent of this hypothesis.

We address questions about the robustness of the ON/OFF model (Linear Region) to a shift in the input distribution: Is it necessary to use spontaneous firing rates as a "baseline" for the LGN-cortical activities, and, in particular, can we choose the reference level so that most inputs in the visual environment are positive? Note that, if an input d_i is *negative* $(d_i < 0)$, the relation $\dot{m}_i = \phi \cdot d_i$ requires potentiation of the i'th synapse $(\dot{m}_i < 0)$ whenever the post-synaptic response falls below the modification threshold $(c < \theta$ and $\phi < 0)$. There is, at present, no direct experimental evidence for this. Restricting d_i to values larger than zero, however, avoid potentiation of synapses for post-synaptic responses which are lower than the modification threshold.

As in the previous section, we assume that LGN cells operate in the linear region, where $-|D_{\min}| < D_i < |D_{\min}|$. However, we now choose a "baseline" for the LGN cell activities that is different from spontaneous; this is, as mentioned before, equivalent to *shifting the input distribution*. We write the inputs as

$$\begin{cases} d_i^{\mathrm{ON}} & = & D_i + K \\ d_i^{\mathrm{OFF}} & = & -D_i + K \, , \end{cases} \tag{14}$$

where K corresponds to the LGN spontaneous activity with respect to the *new* "baseline". Fig. 9 shows the distributions of d_i^{ON} and d_i^{OFF} for K=5 (inputs shifted 5 stds). As before, the distributions are almost symmetrical around spontaneous activity $(d_i = 5)$, but most inputs here are now positive.

Fig. 10 presents some examples of $\mathbf{m}^{\mathrm{ON}}$, $\mathbf{m}^{\mathrm{OFF}}$, $\mathbf{m}^+$ and $\mathbf{m}^-$ for simulations with $K = 5$. We compare the results to those in Fig. 4b, where $K = 0$. There are no qualitative differences. (It is straight-forward to show that the change in $m_i^+ = m_i^{\mathrm{ON}} + m_i^{\mathrm{OFF}}$ is

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independent of the synapse i, for any value of K. Thus, in the linear LGN case, $\mathbf{m}^{ON}$ and $-\mathbf{m}^{OFF}$ can only be different by a constant value.) In other words, the receptive field arrangement does not depend strongly on K: *The BCM model is robust to a change in the reference level for the LGN activities.* We use this result in Nonlinear Region, where $K = D_{\min}$.

Figure Captions

Figure 8

Receptive fields for simulations with varying noise levels and LGN cells in the linear region. The standard deviation of the patterned input is 1, and the standard deviation of the noise is given by SD_n. In (a): $SD_n = 0.7$. In (b): $SD_n = 4.0$. For each noise level, we run three simulations (ex 1, ex 2, ex 3) with different initial conditions and training input sequences. The figure shows that the ON/OFF channel model is very robust to noise. Non-trivial receptive fields are obtained for $SD_n = 0.7$ $(S/N = 1.4)$ as well as for such high noise levels as $SD_n = 4.0$ $(S/N = 0.25)$. However, the spatial frequency is lower and there is less diversity in the receptive fields for higher noise levels.

Figure 9

Shifted inputs: Input probability distributions (log-scale) from ON and OFF cells when $d_i^{ON} = D_i + 5$ and $d_i^{OFF} = -D_i + 5$. Note that the distributions are almost symmetrical around spontaneous activity $(d_i = 5)$, and that most inputs are positive.

Figure 10

Final weight configurations from simulations with $d_i^{ON} = D_i + 5$ and $d_i^{OFF} = -D_i + 5$ (linear region, shifted inputs). Note that there are no qualitative differences between these results and those in Fig. 4b, where $d_i^{ON} = D_i$ and $d_i^{OFF} = -D_i$ (linear region, $K = 0$). All results are illustrated for cells with different initial conditions and different training input sequences; each column represents one example.
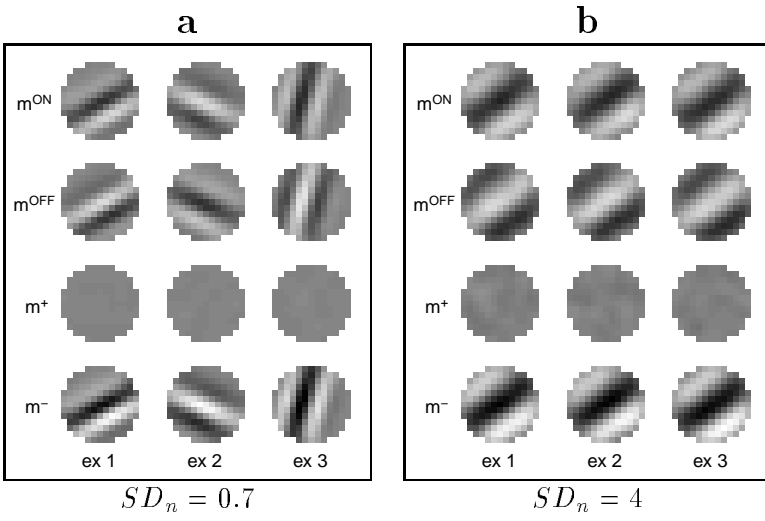
a **b**
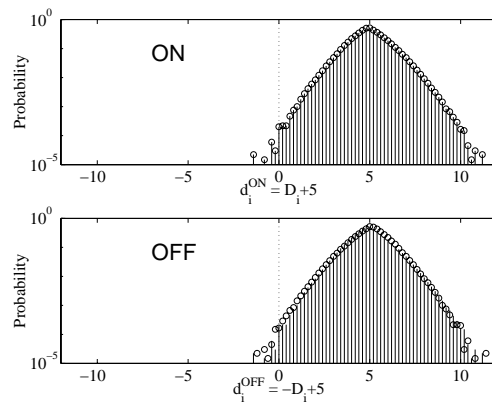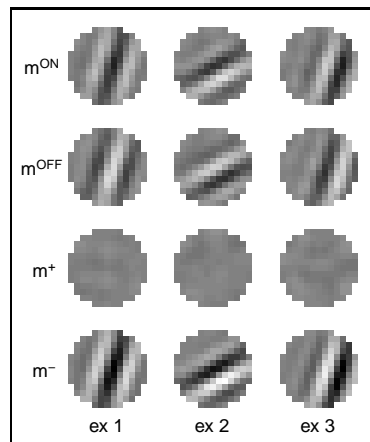
$SD_n = 0.7$ $SD_n = 4$

Figure 8:

Figure 9:

Figure 10: