

## Appendix B: Analysis of Subfield Segregation

In the following analysis, we show that the observed receptive field arrangement can be explained by the BCM equations. In fact, the relation  $\mathbf{m}^{\text{ON}} \approx -\mathbf{m}^{\text{OFF}}$  for the synapses follows directly from the property  $\mathbf{d}^{\text{ON}} = -\mathbf{d}^{\text{OFF}}$  of the LGN cells in the linear region. (A similar analysis can also be done for the shifted inputs in Eq. 3. We then get that  $\mathbf{m}^{\text{ON}} = -\mathbf{m}^{\text{OFF}} +$  a small constant.)

For convenience, we first make a variable substitution on the inputs, similar to Eq. 7 for the weights. We define the “sum” and “difference” input configurations  $\mathbf{d}^+$  and  $\mathbf{d}^-$ , respectively, by

$$\begin{cases} \mathbf{d}^+ &= \frac{1}{\sqrt{2}} (\mathbf{d}^{\text{ON}} + \mathbf{d}^{\text{OFF}}) \\ \mathbf{d}^- &= \frac{1}{\sqrt{2}} (\mathbf{d}^{\text{ON}} - \mathbf{d}^{\text{OFF}}) . \end{cases} \quad (15)$$

Then, we rewrite Eq. 4 in the transformed variables  $\mathbf{d}^+$ ,  $\mathbf{d}^-$ ,  $\mathbf{m}^+$  and  $\mathbf{m}^-$ . This gives

$$\begin{aligned} c &= \sigma_{\text{cort}} (\mathbf{m}^+ \cdot \mathbf{d}^+ + \mathbf{m}^- \cdot \mathbf{d}^-) \\ \begin{cases} \dot{m}_i^+ &= \mu \phi(c, \theta) d_i^+ \\ \dot{m}_i^- &= \mu \phi(c, \theta) d_i^- \end{cases} \end{aligned} \quad (16)$$

Eq. 6 is equivalent to

$$\begin{cases} d_i^+ &= 0 \\ d_i^- &= D_i \sqrt{2} . \end{cases} \quad (17)$$

which inserted into the “transformed” BCM equations gives

$$\begin{aligned}
c &= \sigma_{\text{cort}} \left( \mathbf{m}^- \cdot \mathbf{D} \sqrt{2} \right) \\
\begin{cases} \dot{m}_i^+ &= 0 \\ \dot{m}_i^- &= \mu \phi(c, \theta) D_i \sqrt{2} \end{cases}
\end{aligned} \tag{18}$$

Now compare Eq. 18 with the BCM equations

$$\begin{aligned}
c &= \sigma_{\text{cort}} \left( \mathbf{m}^{\text{single}} \cdot \mathbf{D} \right) \\
\begin{cases} \dot{m}_i^{\text{single}} &= \mu \phi(c, \theta) D_i \end{cases}
\end{aligned} \tag{19}$$

for synaptic modification of the weights  $m_i^{\text{single}}$  in a model where the *total* input is  $\mathbf{d} = \mathbf{d}^{\text{ON}} = \mathbf{D}$  (the “single-channel” model). First, we note that the weights  $m_i^-$  and  $m_i^{\text{single}}$  above obey the same equations for synaptic modification (except for a scaling factor), which means that

$$\mathbf{m}^-(t) \propto \mathbf{m}^{\text{single}}(t). \tag{20}$$

We know from earlier work that the synaptic weights  $m_i^{\text{single}}$  develop receptive fields with adjacent excitatory and inhibitory bands (see Fig. 3); this explains the structure of  $\mathbf{m}^-(t)$ . Secondly, we note that  $\dot{m}_i^+ = 0$  in Eq. 18, or equivalently (for all  $t > 0$ )

$$\mathbf{m}^+(t) = \mathbf{m}^+(t = 0), \tag{21}$$

where  $\mathbf{m}^+(t = 0)$  is the summed configuration before training. Because we start out with

small initial weight values, we have

$$\mathbf{m}^+ \approx \mathbf{0} . \tag{22}$$

Putting Eq. 20 and Eq. 22 together finally gives

$$\mathbf{m}^{\text{ON}} \approx -\mathbf{m}^{\text{OFF}} \propto \mathbf{m}^{\text{single}} . \tag{23}$$

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. 4b. The results also agree with experimental findings, for example Reid and Alonso 1995 , that both the subregion organization and the orientation of simple receptive fields are well established by converging thalamic inputs.