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

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OUTLINE

• Background

• ON/OFF channel model

• Simplest case: “linear LGN”
  · simulation and analysis

• Explore relevant variables:
  1. spontaneous activity
  2. zero firing level

• Conclusions
RESULTS FROM PREVIOUS BCM SIMULATIONS:

“SINGLE CHANNEL MODEL”

• Example of natural images:

  ![Image 1](image1.png) ![Image 2](image2.png) ![Image 3](image3.png)

• Receptive fields after training:

  ![Receptive Field 1](receptive_field1.png) ![Receptive Field 2](receptive_field2.png) ![Receptive Field 3](receptive_field3.png) ![Receptive Field 4](receptive_field4.png)
ON/OFF CHANNEL MODEL: ARCHITECTURE

\[ c = \sigma(m \cdot d) \]

- Image on the Retina
- ON Channel Ganglion Cells
- OFF Channel Ganglion Cells
- OFF Channel LGN
- ON Channel LGN
- Cortex (single cell)

**Formula:**

\[ c = \sigma(m \cdot d) \]
“LINEAR REGION” — SYMMETRIC RESPONSES

Stimulus

ON

OFF

time →
“NON-LINEAR REGION” – NON-SYMMETRIC RESPONSES

Stimulus

ON time → OFF

ON

OFF

time →
ON/OFF CHANNEL MODEL ("LINEAR LGN")

- Two channels of inputs:

\[
\begin{align*}
\mathbf{d}^{\text{ON}} &= [d_1^{\text{ON}}, \cdots, d_n^{\text{ON}}] \\
\mathbf{d}^{\text{OFF}} &= [d_1^{\text{OFF}}, \cdots, d_n^{\text{OFF}}]
\end{align*}
\]

- ON-cells and OFF-cells with overlapping receptive fields.

\[
\begin{align*}
d_i^{\text{ON}} &= D_i \\
d_i^{\text{OFF}} &= -D_i
\end{align*}
\]

ganglion/LGN responses
ON/OFF CHANNEL MODEL

• Inputs:

\[
\begin{align*}
d^{\text{ON}} &= [d_1^{\text{ON}}, \ldots, d_n^{\text{ON}}] \\
d^{\text{OFF}} &= [d_1^{\text{OFF}}, \ldots, d_n^{\text{OFF}}]
\end{align*}
\]

• Synaptic weights:

\[
\begin{align*}
m^{\text{ON}} &= [m_1^{\text{ON}}, \ldots, m_n^{\text{ON}}] \\
m^{\text{OFF}} &= [m_1^{\text{OFF}}, \ldots, m_n^{\text{OFF}}]
\end{align*}
\]

• Post-synaptic response:

\[
c = \sigma \left( m^{\text{ON}} \cdot d^{\text{ON}} + m^{\text{OFF}} \cdot d^{\text{OFF}} \right)
\]

• Learning rule:

\[
\begin{align*}
\dot{m}_i^{\text{ON}} &= \phi(c, \theta) d_i^{\text{ON}} \\
\dot{m}_i^{\text{OFF}} &= \phi(c, \theta) d_i^{\text{OFF}}
\end{align*}
\]
MODEL OF THE NEURON

\[ d_1 \quad d_2 \quad d_i \]

\[ m_1 \quad m_2 \quad m_i \]

- BCM learning rule:

\[
\begin{align*}
\dot{m}_i &= \phi(c, \theta)d_i \\
\theta &\sim E[c^2]
\end{align*}
\]

If \( d_i > 0 \):

\[
\begin{align*}
\dot{m}_i &> 0, \text{ when } c > \theta \\
\dot{m}_i &< 0, \text{ when } c < \theta
\end{align*}
\]
“LINEAR LGN”: SIMULATION RESULTS

Final weight configurations $\mathbf{m}^\text{ON}$ and $\mathbf{m}^\text{OFF}$:

$$
\begin{align*}
\mathbf{m}^+ &= \mathbf{m}^\text{ON} + \mathbf{m}^\text{OFF} \\
\mathbf{m}^- &= \mathbf{m}^\text{ON} - \mathbf{m}^\text{OFF} 
\end{align*}
$$

- Both $\mathbf{m}^\text{ON}$ and $\mathbf{m}^\text{OFF}$ display elongated subregions of strong ($m_i > 0$) and weak ($m_i < 0$) synapses.
- Inversion $\mathbf{m}^\text{ON} \approx -\mathbf{m}^\text{OFF}$:
  Implies that ON and OFF afferents segregate.
A SIMPLE EXPLANATION OF LINEAR LGN CASE.
(MAKE A CHANGE OF VARIABLES)

• Cortical Output:

\[
c = \sum m_i^{ON} d_i^{ON} + m_i^{OFF} d_i^{OFF}
\]

\[
= \sum (m_i^{ON} - m_i^{OFF}) D_i \equiv m^- \cdot D
\]

• Learning Rule:

\[
\left\{\begin{array}{l}
\frac{dm_i}{dt}^{ON} = \phi d_i^{ON} = \phi D_i \\
\frac{dm_i}{dt}^{OFF} = \phi d_i^{OFF} = \phi (-D_i)
\end{array}\right.
\]

\[
\Rightarrow \left\{\begin{array}{l}
\frac{dm_i}{dt}^{ON} + \frac{dm_i}{dt}^{OFF} \equiv \frac{dm_i}{dt}^+ = 0 \\
\frac{dm_i}{dt}^{ON} - \frac{dm_i}{dt}^{OFF} \equiv \frac{dm_i}{dt}^- = 2 \phi D_i
\end{array}\right.
\]
• ON/OFF channel model:

\[ c = \sigma (m^- \cdot D) \]
\[
\begin{align*}
\dot{m}_i^+ &= 0 \\
\dot{m}_i^- &= 2\phi(c, \theta) D_i
\end{align*}
\]

• Compare this with single channel model:

\[ c = \sigma (m^{\text{single}} \cdot D) \]
\[
\begin{align*}
\dot{m}_{i}^{\text{single}} &= \phi(c, \theta) D_i
\end{align*}
\]

Know: \( m^{\text{single}} \) develops oriented excitatory and inhibitory subregions.

The equations above imply

1. **ON/OFF inversion:**
\[
m^+(t) = m^+(t = 0) \approx 0 \implies m^{\text{ON}} \approx -m^{\text{OFF}}
\]

2. **Elongated subregions:**
\[
m^- \propto m^{\text{single}} \implies m^{\text{ON}} \approx -m^{\text{OFF}} \propto m^{\text{single}}
\]
RELEVANT VARIABLES

• Effect of the Level of Spontaneous Activity

• Effect of the Zero Firing Level
  · possible asymmetries in the LGN statistics
ACTIVITY HISTOGRAMS: “LINEAR REGION”

SYMMETRIC RESPONSES
**Activity Offset and Spontaneous**

\[
d_{i}^{\text{ON}} = D_i + K
\]
\[
d_{i}^{\text{OFF}} = -D_i + K
\]

- \(D\) is result of center-surround processing of retinal cells
- \(D = 0 \rightarrow\) response to uniform light patch \(\equiv\) spontaneous
- \(K\) (spontaneous) \(\leftrightarrow\) \(d\)
- Examples:

<table>
<thead>
<tr>
<th></th>
<th>spontaneous</th>
</tr>
</thead>
<tbody>
<tr>
<td>(K = 0)</td>
<td>(d = 0)</td>
</tr>
<tr>
<td>(K = 15)</td>
<td>(d = 15)</td>
</tr>
</tbody>
</table>
LGN Cell Activity Histograms:
Changing Spontaneous Activity

- Zero Spontaneous Activity ($K = 0$)

- Non-Zero Spontaneous Activity ($K = 5$)
ON/OFF CHANNEL MODEL RESULTS: Changing Spontaneous Activity

- Results are insensitive to level of spontaneous activity
**ACTIVITY:**

**OFFSETS AND SIGMOIDS**

\[ d_i = \sigma(D_i) + K \]

- \( D \) is result of center-surround processing of retinal cells
- \( D = 0 \rightarrow \text{response to uniform light patch} \equiv \text{spontaneous} \)

<table>
<thead>
<tr>
<th>( K )</th>
<th>(spontaneous) ( \leftrightarrow d )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( D_{\text{min}} + K )</td>
<td>(zero firing frequency) ( \leftrightarrow d )</td>
</tr>
</tbody>
</table>

- Examples:

<table>
<thead>
<tr>
<th>( K = 0, D_{\text{min}} = -1 )</th>
<th>spontaneous: ( d = 0 )</th>
<th>zero firing: ( d = -1 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K = 15, D_{\text{min}} = -15 )</td>
<td>spontaneous: ( d = 15 )</td>
<td>zero firing: ( d = 0 )</td>
</tr>
</tbody>
</table>
Activity Histograms: “Non-Linear Region”
Non-Symmetric Responses
ON/OFF ACTIVITY:
SYMMETRY AND NON-SYMMETRY

\[
\begin{align*}
    d_i^{ON} &= \sigma(D_i) + K \\
    d_i^{OFF} &= \sigma(-D_i) + K
\end{align*}
\]

Symmetric Statistics
\[
\begin{align*}
    d_i^{ON} &= D_i + K \\
    d_i^{OFF} &= -D_i + K
\end{align*}
\]

Non-Symmetric Statistics
\[
\begin{align*}
    d_i^{ON} &= D_i + K \\
    d_i^{OFF} &= D_{min} + K
\end{align*}
\]
or
\[
\begin{align*}
    d_i^{ON} &= D_{min} + K \\
    d_i^{OFF} &= D_i + K
\end{align*}
\]
LGN Cell Activity Histograms:

Changing Zero Firing Level

LGN activity:

\[
\begin{align*}
    d_{i}^{\text{ON}} &= \sigma(D_{i}) \\
    d_{i}^{\text{OFF}} &= \sigma(-D_{i})
\end{align*}
\]

- Histograms of $\sigma(D_{i})$ for different cut-offs $D_{\text{min}}$:

\[
\begin{align*}
    D_{\text{min}} = -4 &: 0.054 \% \text{ of the values cut off to } D_{\text{min}} \\
    D_{\text{min}} = -3 &: 0.43 \% \\
    D_{\text{min}} = -2 &: 2.7 \% \\
    D_{\text{min}} = -1 &: 13 \%
\end{align*}
\]
**ON/OFF Channel Model Results:**

**Changing Zero Firing Level**

<table>
<thead>
<tr>
<th>$D_{min}$</th>
<th>$m^{ON}$</th>
<th>$m^{OFF}$</th>
<th>$m^+$</th>
<th>$m^-$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$-3$</td>
<td>![Image]</td>
<td>![Image]</td>
<td>![Image]</td>
<td>![Image]</td>
</tr>
<tr>
<td>$-2.5$</td>
<td>![Image]</td>
<td>![Image]</td>
<td>![Image]</td>
<td>![Image]</td>
</tr>
<tr>
<td>$-2$</td>
<td>![Image]</td>
<td>![Image]</td>
<td>![Image]</td>
<td>![Image]</td>
</tr>
<tr>
<td>$-1.5$</td>
<td>![Image]</td>
<td>![Image]</td>
<td>![Image]</td>
<td>![Image]</td>
</tr>
</tbody>
</table>

- ON and OFF afferents fail to segregate when LGN responses are non-symmetric around spontaneous.
**ON/OFF CHANNEL MODEL RESULTS:**

**EFFECT OF ADDED NOISE**

<table>
<thead>
<tr>
<th>(D_{\text{min}} = -2.5)</th>
<th>(m^{\text{ON}})</th>
<th>(m^{\text{OFF}})</th>
<th>(m^{+})</th>
<th>(m^{-})</th>
</tr>
</thead>
<tbody>
<tr>
<td>std = 0</td>
<td><img src="image1.png" alt="Image" /></td>
<td><img src="image2.png" alt="Image" /></td>
<td><img src="image3.png" alt="Image" /></td>
<td><img src="image4.png" alt="Image" /></td>
</tr>
<tr>
<td>std = .2</td>
<td><img src="image5.png" alt="Image" /></td>
<td><img src="image6.png" alt="Image" /></td>
<td><img src="image7.png" alt="Image" /></td>
<td><img src="image8.png" alt="Image" /></td>
</tr>
<tr>
<td>std = .7</td>
<td><img src="image9.png" alt="Image" /></td>
<td><img src="image10.png" alt="Image" /></td>
<td><img src="image11.png" alt="Image" /></td>
<td><img src="image12.png" alt="Image" /></td>
</tr>
<tr>
<td>std = 1</td>
<td><img src="image13.png" alt="Image" /></td>
<td><img src="image14.png" alt="Image" /></td>
<td><img src="image15.png" alt="Image" /></td>
<td><img src="image16.png" alt="Image" /></td>
</tr>
<tr>
<td>std = 2</td>
<td><img src="image17.png" alt="Image" /></td>
<td><img src="image18.png" alt="Image" /></td>
<td><img src="image19.png" alt="Image" /></td>
<td><img src="image20.png" alt="Image" /></td>
</tr>
</tbody>
</table>

- BCM is *very* sensitive to asymmetry in LGN responses
- Added noise makes results more robust
**ON/OFF CHANNEL MODEL RESULTS:**

**ZERO FIRING LEVEL** \(\leftrightarrow d = 0\)

<table>
<thead>
<tr>
<th>(D_{\text{min}})</th>
<th>(m^{\text{ON}})</th>
<th>(m^{\text{OFF}})</th>
<th>(m^+)</th>
<th>(m^-)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(D_{\text{min}} = -3) 0.5%</td>
<td><img src="image1" alt="Image" /></td>
<td><img src="image2" alt="Image" /></td>
<td><img src="image3" alt="Image" /></td>
<td><img src="image4" alt="Image" /></td>
</tr>
<tr>
<td>(D_{\text{min}} = -2.5) 1%</td>
<td><img src="image5" alt="Image" /></td>
<td><img src="image6" alt="Image" /></td>
<td><img src="image7" alt="Image" /></td>
<td><img src="image8" alt="Image" /></td>
</tr>
<tr>
<td>(D_{\text{min}} = -2) 3%</td>
<td><img src="image9" alt="Image" /></td>
<td><img src="image10" alt="Image" /></td>
<td><img src="image11" alt="Image" /></td>
<td><img src="image12" alt="Image" /></td>
</tr>
<tr>
<td>(D_{\text{min}} = -1.5) 6.5%</td>
<td><img src="image13" alt="Image" /></td>
<td><img src="image14" alt="Image" /></td>
<td><img src="image15" alt="Image" /></td>
<td><img src="image16" alt="Image" /></td>
</tr>
</tbody>
</table>
CONCLUSIONS

- BCM learning rule, with ON/OFF model, leads to
  - elongated subregions of strong and weak synapses
  - segregation of ON and OFF subfields
- Results are insensitive to level of spontaneous
- ON and OFF afferents fail to segregate when LGN responses
  are significantly non-symmetric around spontaneous
- Added noise makes results more robust