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

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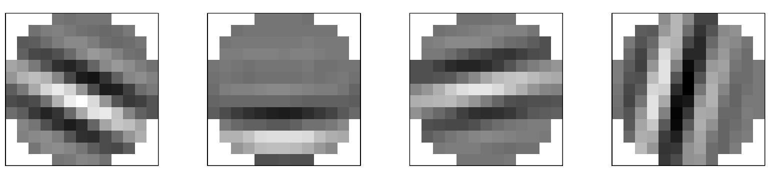
OUTLINE

- Background
- ON/OFF channel model
- Simplest case: “linear LGN”
  - simulation and analysis
- Explore relevant variables:
  1. spontaneous activity
  2. zero firing level
- Conclusions

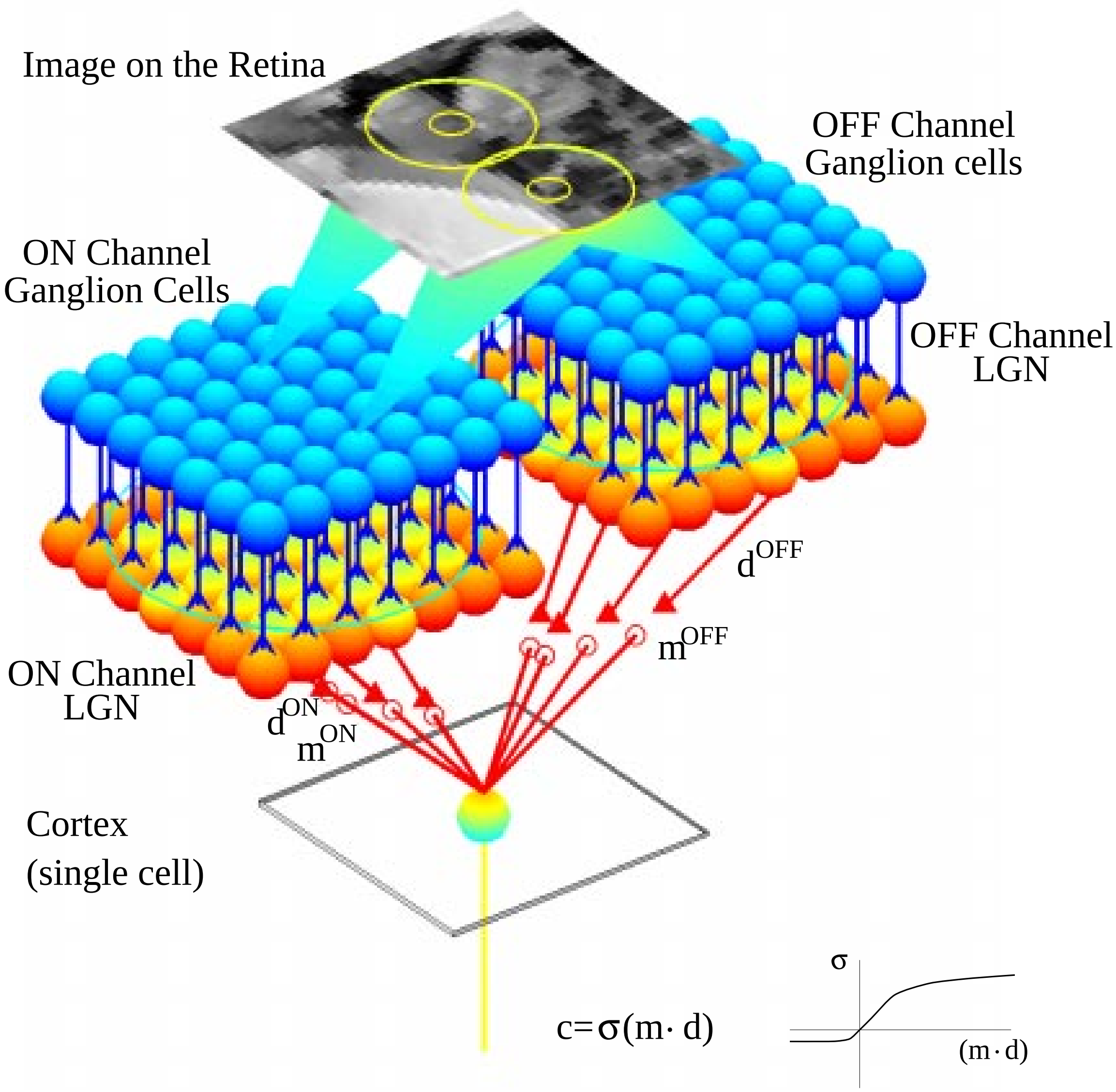
RESULTS FROM PREVIOUS BCM SIMULATIONS : "SINGLE CHANNEL MODEL"

- Example of natural images:

- Receptive fields after training:

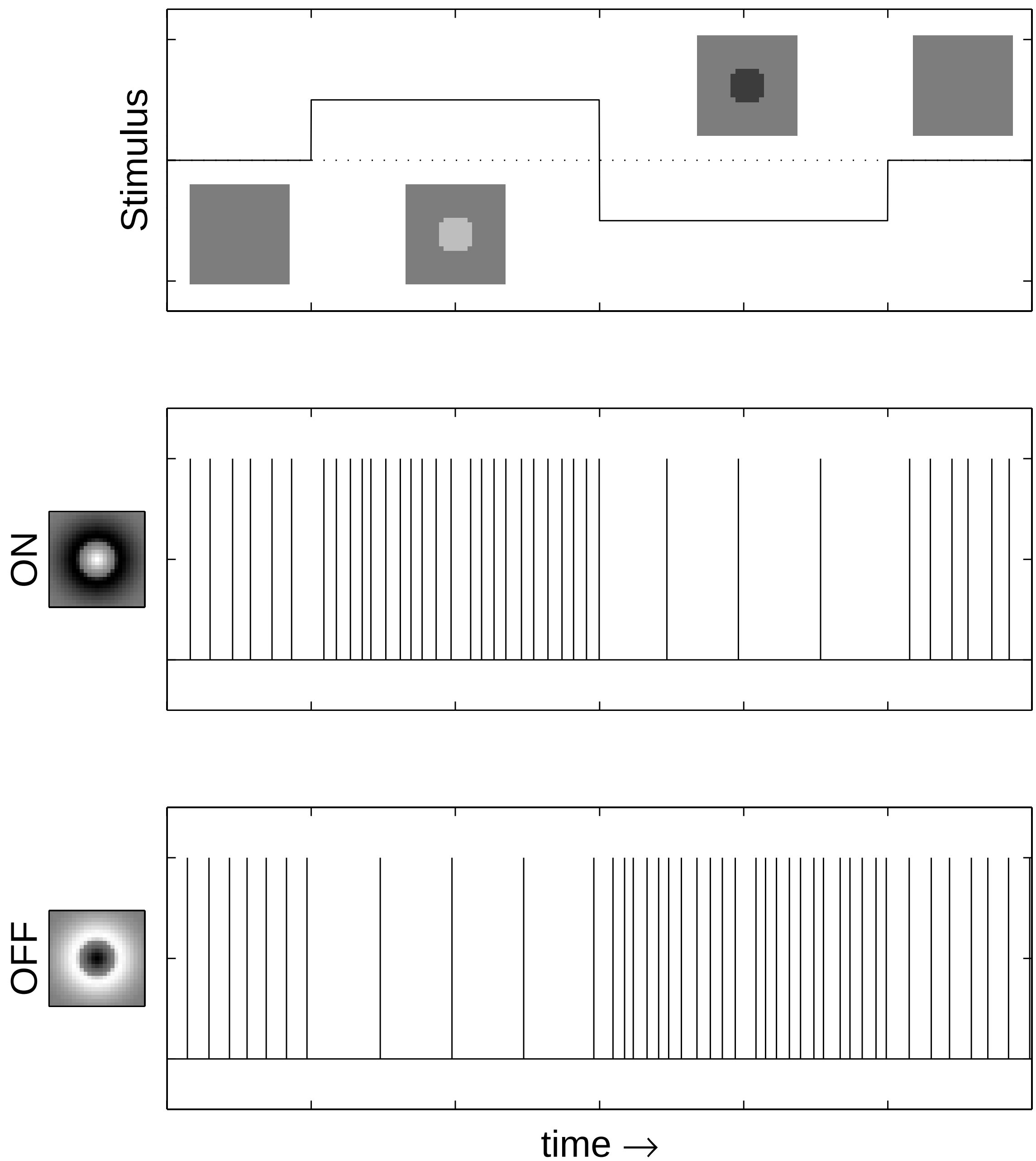


ON/OFF Channel Model: Architecture

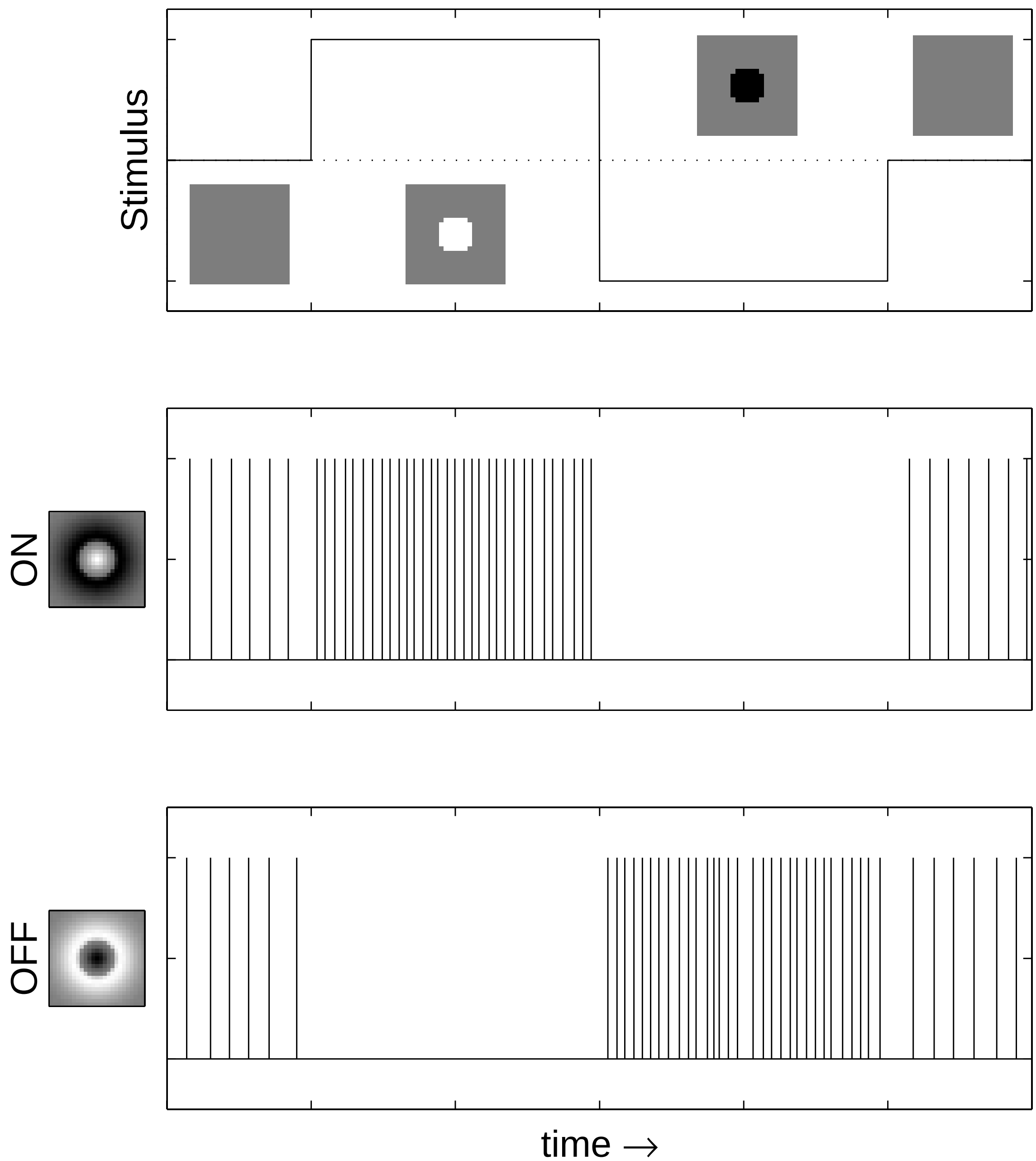


“Linear Region” –

Symmetric Responses



“NON-LINEAR REGION” – NON-SYMMETRIC RESPONSES



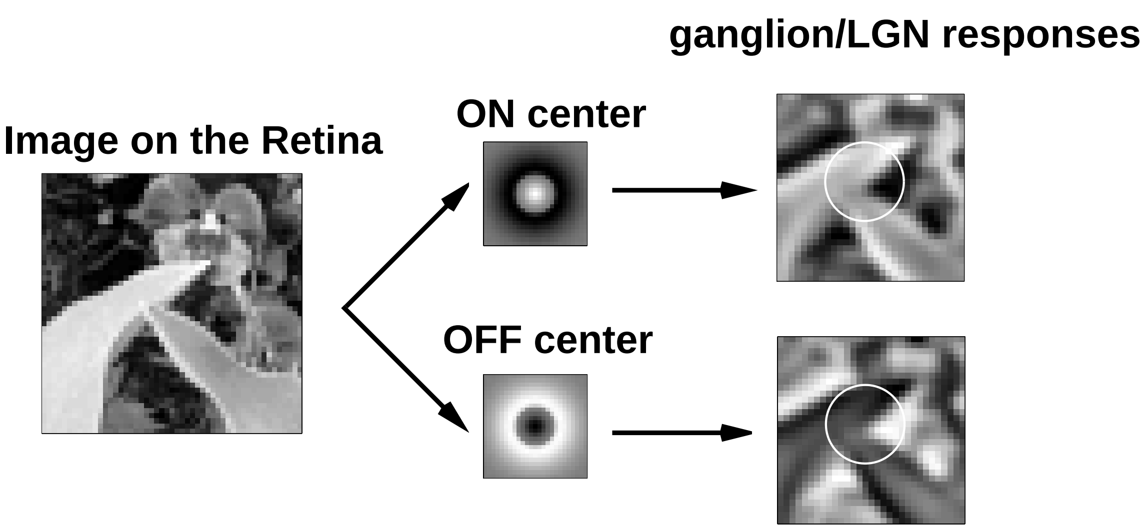
ON/OFF CHANNEL MODEL ("LINEAR LGN")

- Two channels of inputs:

$$\begin{cases} \mathbf{d}^{\mathrm{ON}} & = & [{d_1}^{\mathrm{ON}}, \cdots, {d_n}^{\mathrm{ON}}] \\ \mathbf{d}^{\mathrm{OFF}} & = & [{d_1}^{\mathrm{OFF}}, \cdots, {d_n}^{\mathrm{OFF}}] \end{cases}$$

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

$$\begin{cases} {d_i}^{\mathrm{ON}} & = & D_i \\ {d_i}^{\mathrm{OFF}} & = & -D_i \end{cases}$$



ON/OFF Channel Model

- Inputs:

$$\begin{cases} \mathbf{d}^{\mathrm{ON}} & = & [{d_1}^{\mathrm{ON}}, \cdots, {d_n}^{\mathrm{ON}}] \\ \mathbf{d}^{\mathrm{OFF}} & = & [{d_1}^{\mathrm{OFF}}, \cdots, {d_n}^{\mathrm{OFF}}] \end{cases}$$

- Synaptic weights:

$$\begin{cases} \mathbf{m}^{\mathrm{ON}} & = & [{m_1}^{\mathrm{ON}}, \cdots, {m_n}^{\mathrm{ON}}] \\ \mathbf{m}^{\mathrm{OFF}} & = & [{m_1}^{\mathrm{OFF}}, \cdots, {m_n}^{\mathrm{OFF}}] \end{cases}$$

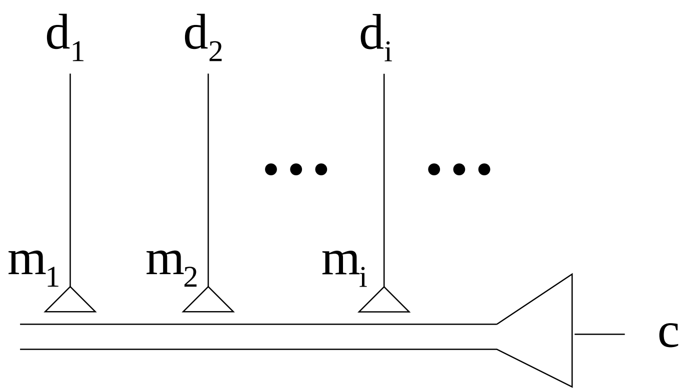
- Post-synaptic response:

$$c = \sigma\left(\mathbf{m}^{\mathrm{ON}} \cdot \mathbf{d}^{\mathrm{ON}} + \mathbf{m}^{\mathrm{OFF}} \cdot \mathbf{d}^{\mathrm{OFF}}\right)$$

- Learning rule:

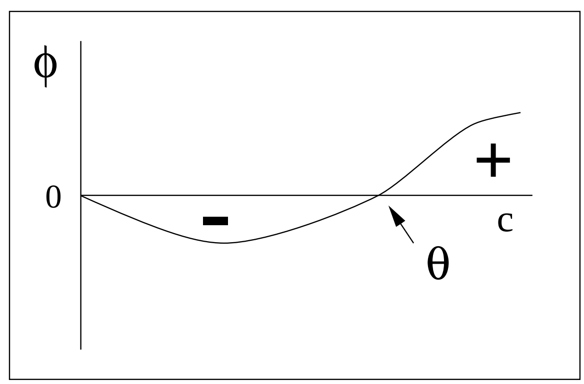
$$\begin{cases} \dot{m}_i^{\mathrm{ON}} & = & \phi(c,\theta)\, {d_i}^{\mathrm{ON}} \\ \dot{m}_i^{\mathrm{OFF}} & = & \phi(c,\theta)\, {d_i}^{\mathrm{OFF}} \end{cases}$$

Model of the Neuron



- BCM learning rule:

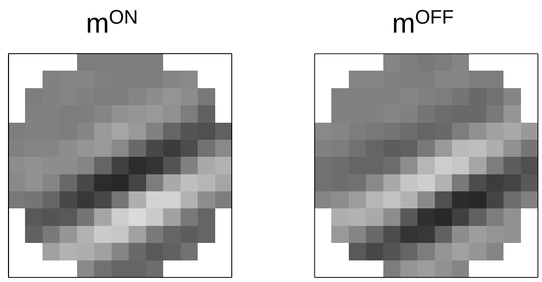
$$\begin{cases} \dot{m}_i & = & \phi(c,\theta) d_i \\ \theta & \sim & E[c^2] \end{cases}$$



If $d_i > 0$: $\begin{cases} \dot{m}_i & > & 0, & \text{when } c & > & \theta \\ \dot{m}_i & < & 0, & \text{when } c & < & \theta \end{cases}$

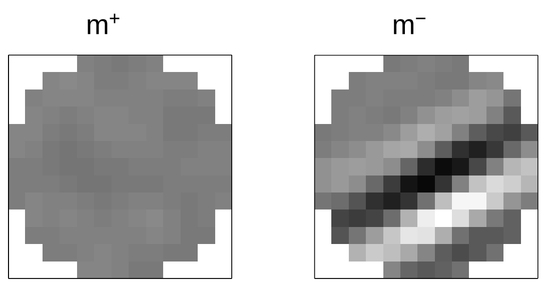
“LINEAR LGN”: SIMULATION RESULTS

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



Define

$$\begin{cases} \mathbf{m}^{+} & = & \mathbf{m}^{\mathrm{ON}} + \mathbf{m}^{\mathrm{OFF}} \\ \mathbf{m}^{-} & = & \mathbf{m}^{\mathrm{ON}} - \mathbf{m}^{\mathrm{OFF}} \ . \end{cases}$$



- Both $\mathbf{m}^{\mathrm{ON}}$ and $\mathbf{m}^{\mathrm{OFF}}$ display elongated subregions of strong ($m_i > 0$) and weak ($m_i < 0$) synapses.
- Inversion $\mathbf{m}^{\mathrm{ON}} \approx -\mathbf{m}^{\mathrm{OFF}}$:
  Implies that ON and OFF afferents segregate.

A Simple Explanation of Linear LGN Case.

(Make a Change of Variables)

- Cortical Output:

$$
\begin{aligned}
c &= \sum m_i^{\mathrm{ON}} d_i^{\mathrm{ON}} + m_i^{\mathrm{OFF}} d_i^{\mathrm{OFF}} \\
&= \sum \left(m_i^{\mathrm{ON}} - m_i^{\mathrm{OFF}}\right) D_i \equiv \mathbf{m}^{-} \cdot \mathbf{D}
\end{aligned}
$$

- Learning Rule:

$$
\begin{cases}
\frac{dm_i}{dt}^{\mathrm{ON}} = \phi\, d_i^{\mathrm{ON}} = \phi\, D_i \\
\frac{dm_i}{dt}^{\mathrm{OFF}} = \phi\, d_i^{\mathrm{OFF}} = \phi\,(-D_i)
\end{cases}
$$

$$
\Rightarrow
\begin{cases}
\frac{dm_i}{dt}^{\mathrm{ON}} + \frac{dm_i}{dt}^{\mathrm{OFF}} \equiv \frac{dm_i}{dt}^{+} = 0 \\
\frac{dm_i}{dt}^{\mathrm{ON}} - \frac{dm_i}{dt}^{\mathrm{OFF}} \equiv \frac{dm_i}{dt}^{-} = 2\,\phi\, D_i
\end{cases}
$$

- ON/OFF channel model:

$$c = \sigma\left(\mathbf{m}^- \cdot \mathbf{D}\right)$$
$$\begin{cases} \dot{m}_i^+ &= 0 \\ \dot{m}_i^- &= 2\,\phi(c,\theta)\,D_i \end{cases}$$

- Compare this with single channel model:

$$c = \sigma\left(\mathbf{m}^{\text{single}} \cdot \mathbf{D}\right)$$
$$\left\{ \dot{m}_i^{\text{single}} = \phi(c,\theta)\,D_i \right.$$

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

The equations above imply

1. ON/OFF inversion:
   $\mathbf{m}^+(t) = \mathbf{m}^+(t=0) \approx 0 \Longrightarrow$
   $\mathbf{m}^{\text{ON}} \approx -\mathbf{m}^{\text{OFF}}$

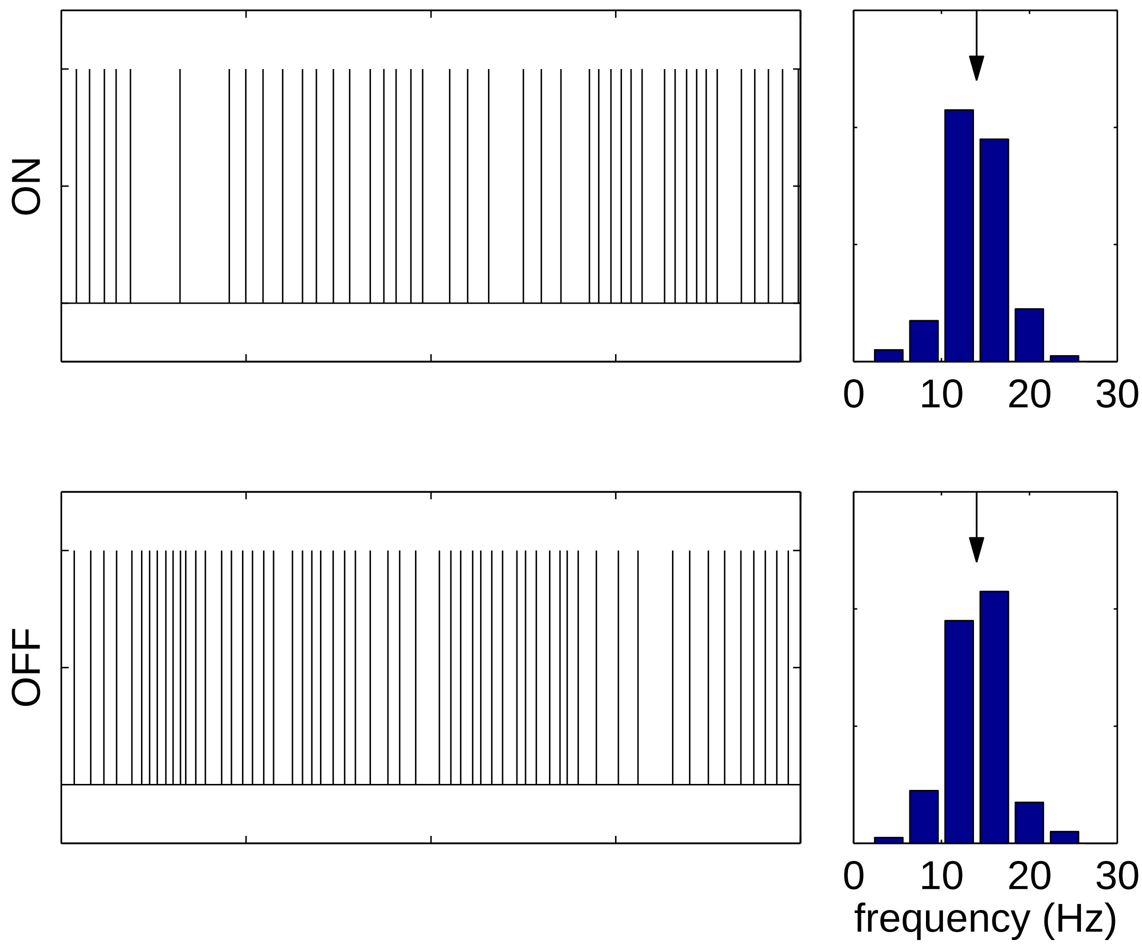
2. Elongated subregions:
   $\mathbf{m}^- \propto \mathbf{m}^{\text{single}} \Longrightarrow$
   $\mathbf{m}^{\text{ON}} \approx -\mathbf{m}^{\text{OFF}} \propto \mathbf{m}^{\text{single}}$

Relevant Variables

- Effect of the Level of Spontaneous Activity
- Effect of the Zero Firing Level
  - possible asymmetries in the LGN statistics

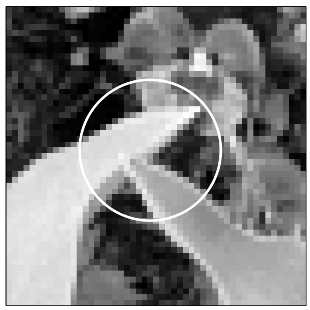
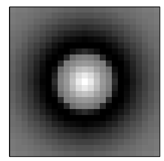
ACTIVITY HISTOGRAMS: "LINEAR REGION"

SYMMETRIC RESPONSES



Activity Offset and Spontaneous

$$d_i^{\mathrm{ON}} = D_i + K$$
$$d_i^{\mathrm{OFF}} = -D_i + K$$

 $*$  $= D_i$

- 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:

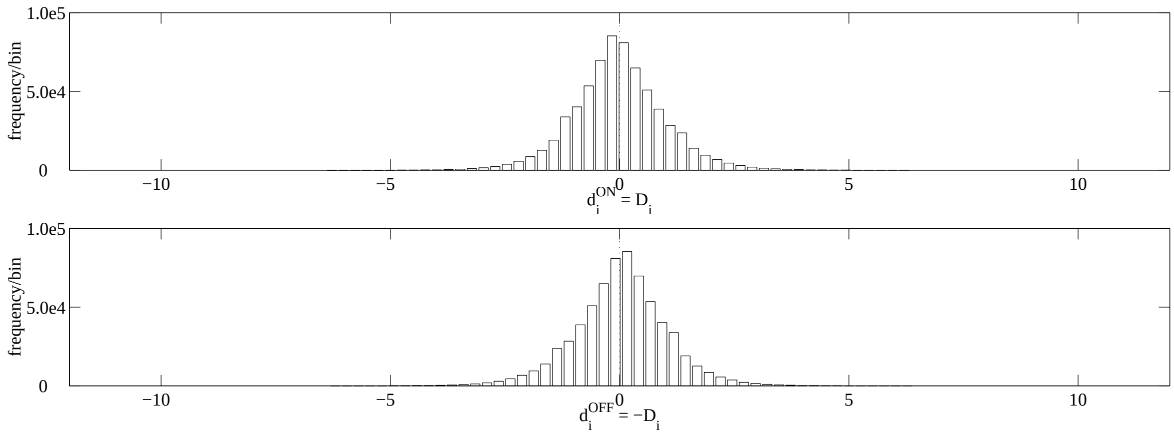
	spontaneous
$K = 0$	$d = 0$
$K = 15$	$d = 15$

LGN CELL ACTIVITY HISTOGRAMS: CHANGING SPONTANEOUS ACTIVITY

- Zero Spontaneous Activity ($K = 0$)

ON

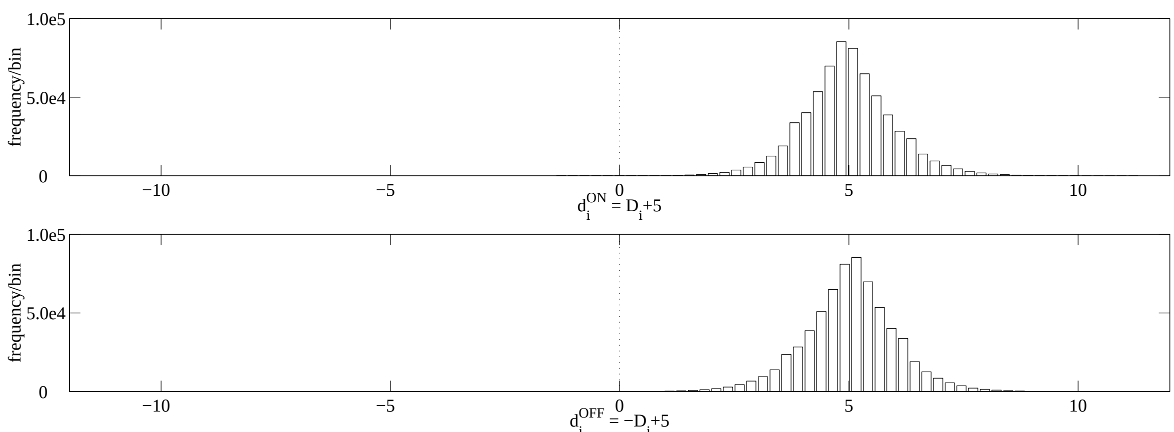
OFF



- Non-Zero Spontaneous Activity ($K = 5$)

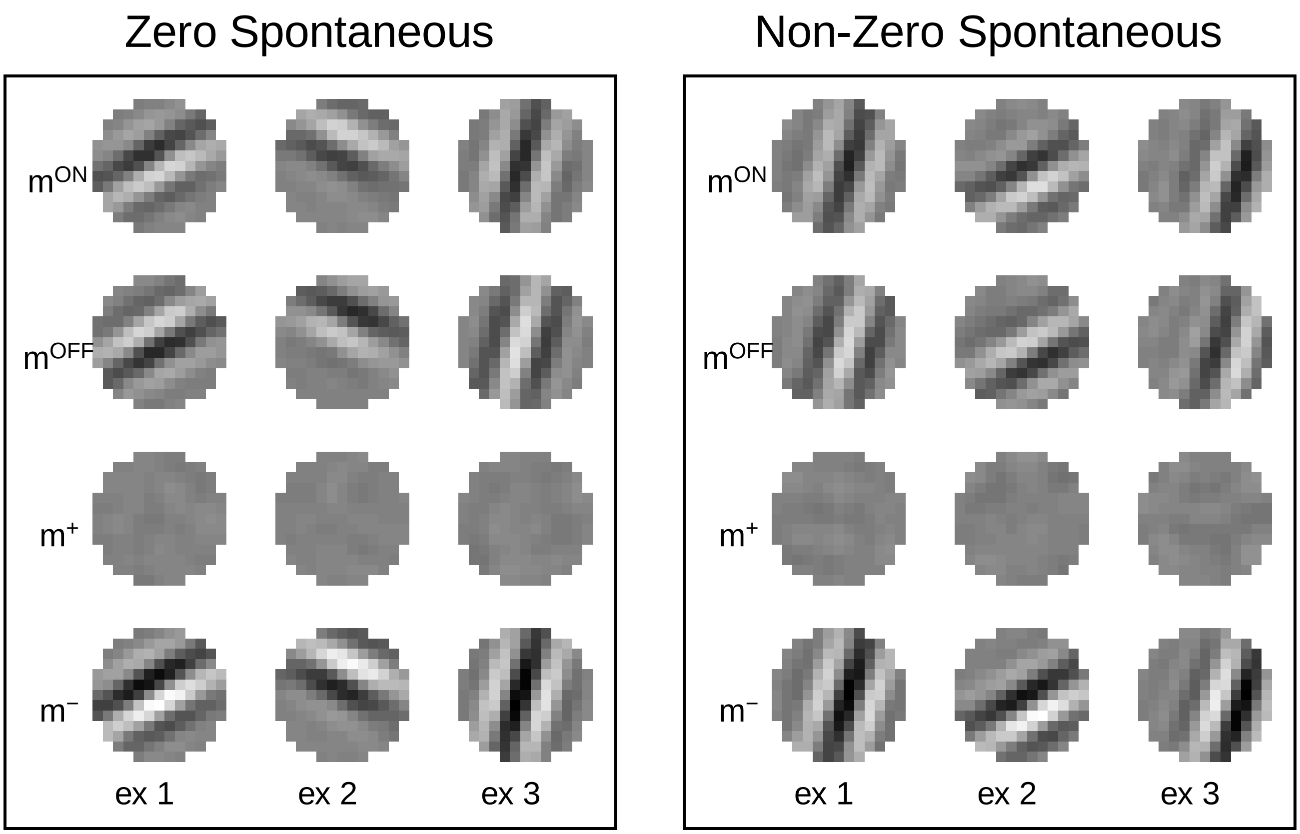
ON

OFF



ON/OFF Channel Model Results:

Changing Spontaneous Activity

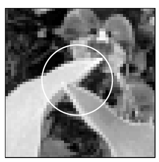
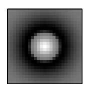


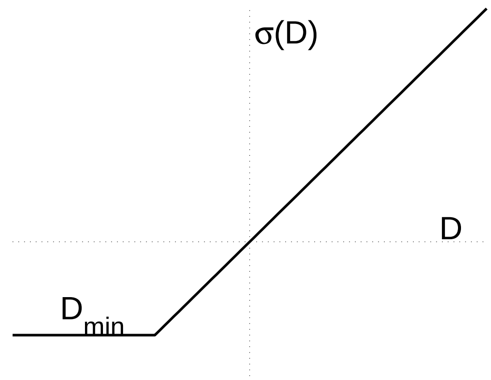
- Results are insensitive to level of spontaneous activity

Activity:

Offsets and Sigmoids

$$d_i \quad = \quad \sigma(D_i) + K$$

 $*$  $= D_i$



- D is result of center-surround processing of retinal cells
- $D = 0 \rightarrow$ response to uniform light patch $\equiv$ spontaneous
-

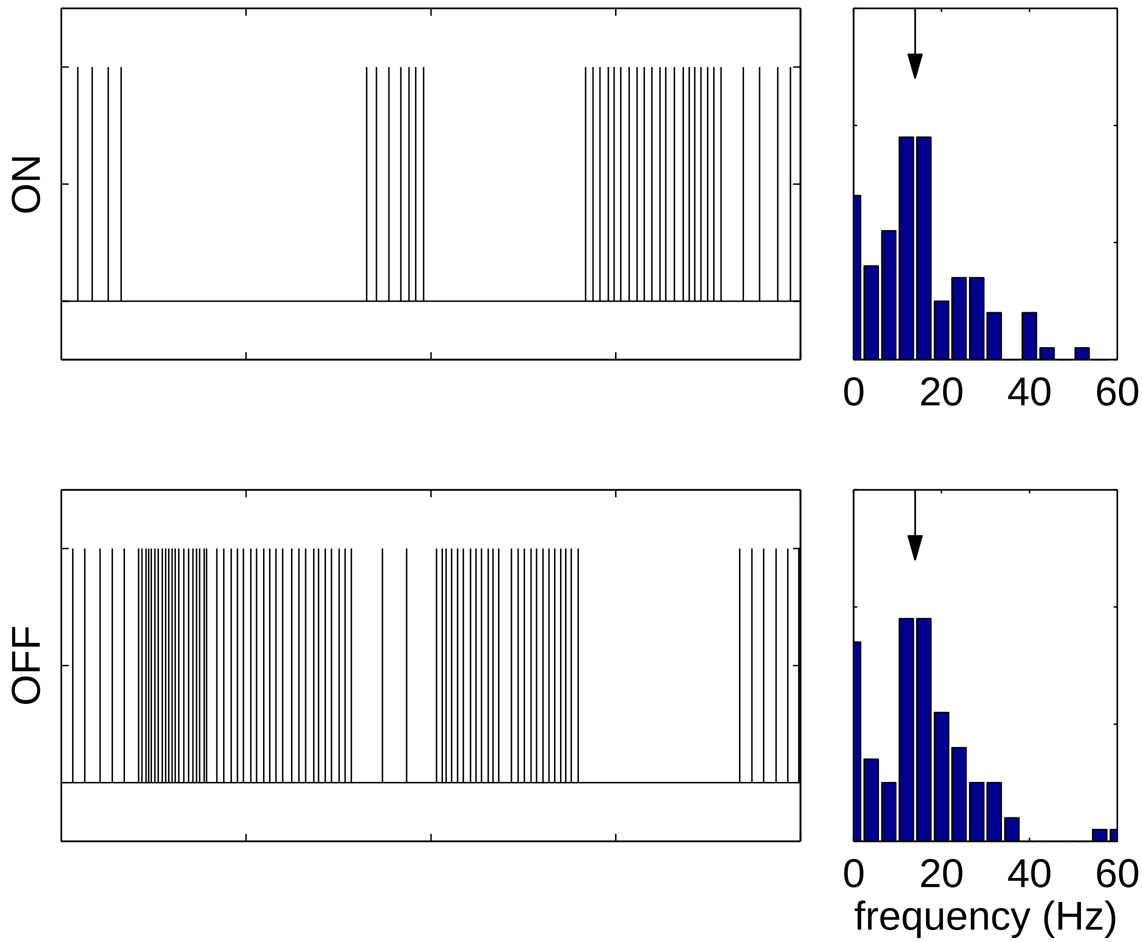
K	(spontaneous)$\leftrightarrow$ d
$D_{\min} + K$	(zero firing frequency)$\leftrightarrow$ d

- Examples:

	spontaneous	zero firing
$K = 0$, $D_{\min} = -1$	$d = 0$	$d = -1$
$K = 15$, $D_{\min} = -15$	$d = 15$	$d = 0$

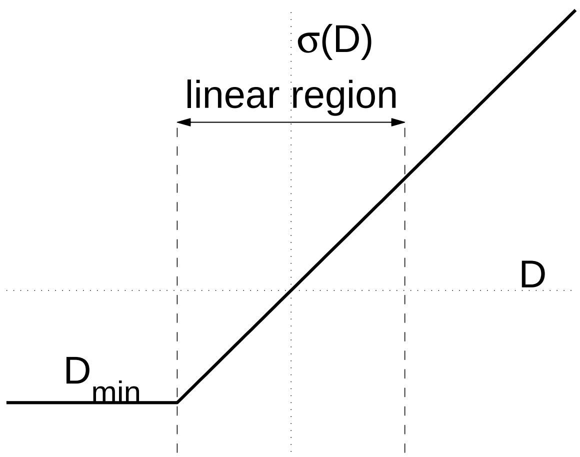
ACTIVITY HISTOGRAMS: "NON-LINEAR REGION"

NON-SYMMETRIC RESPONSES



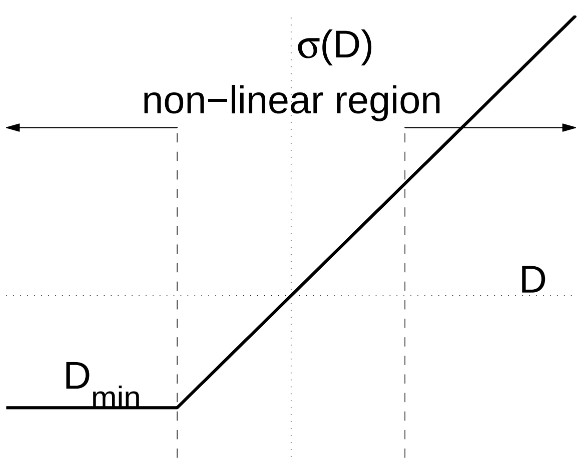
ON/OFF ACTIVITY: SYMMETRY AND NON-SYMMETRY

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



Symmetric Statistics

$$d_i^{\mathrm{ON}} = D_i + K$$
$$d_i^{\mathrm{OFF}} = -D_i + K$$



Non-Symmetric Statistics

$$d_i^{\mathrm{ON}} = D_i + K$$
$$d_i^{\mathrm{OFF}} = D_{\mathrm{min}} + K$$

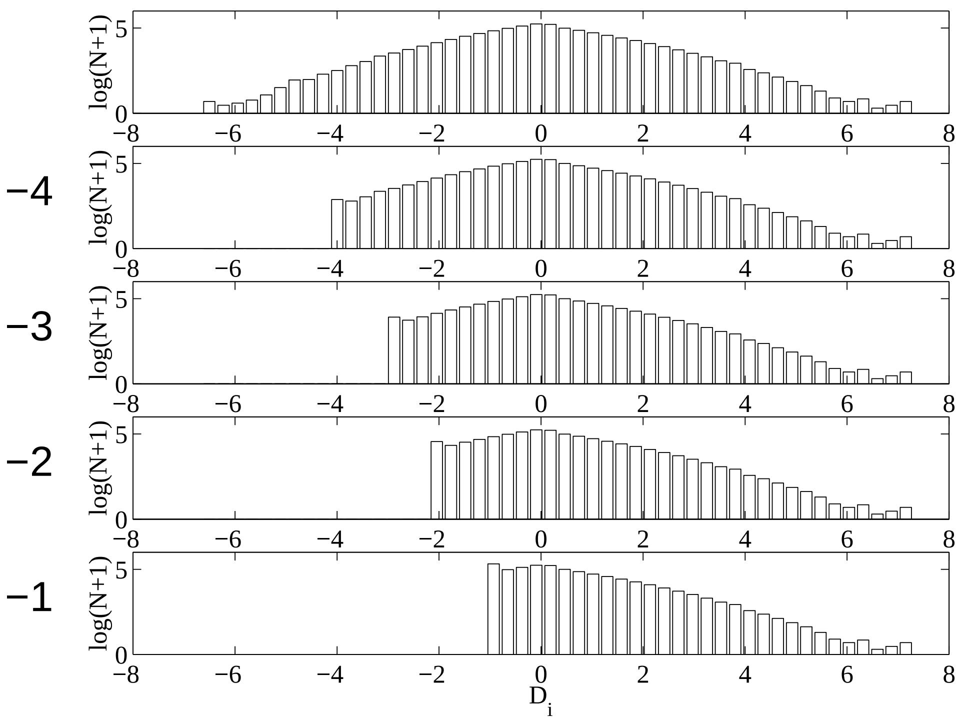
or

$$d_i^{\mathrm{ON}} = D_{\mathrm{min}} + K$$
$$d_i^{\mathrm{OFF}} = D_i + K$$

LGN Cell Activity Histograms: Changing Zero Firing Level

LGN activity: $$\begin{cases} {d_i}^{\mathrm{ON}} & = & \sigma(D_i) \\ {d_i}^{\mathrm{OFF}} & = & \sigma(-D_i) \end{cases}$$

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



· $D_{\min} = -4$: 0.054 % of the values cut off to $D_{\min}$

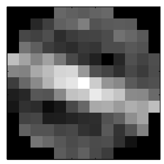
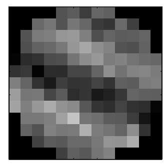
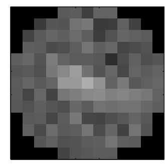
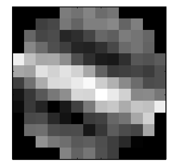
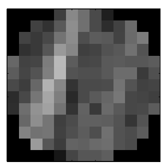
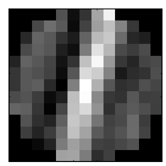
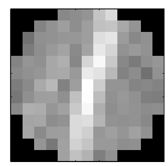
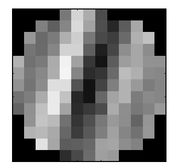
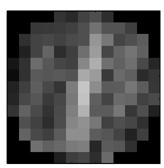
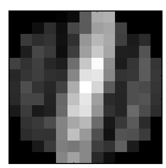
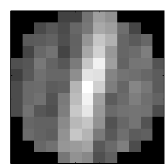
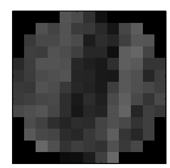
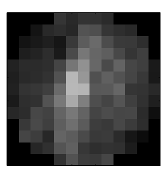
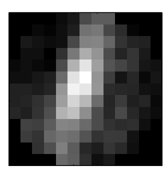
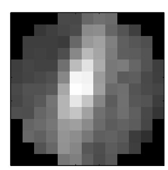
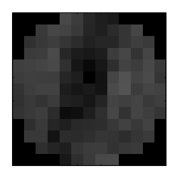
· $D_{\min} = -3$: 0.43 %

· $D_{\min} = -2$: 2.7 %

· $D_{\min} = -1$: 13 %

ON/OFF Channel Model Results:

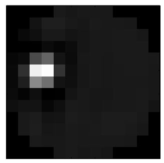
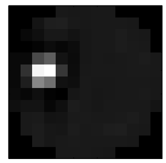
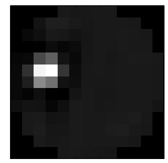
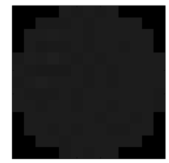
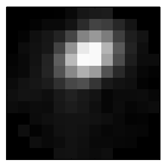
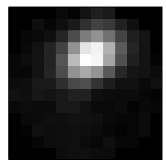
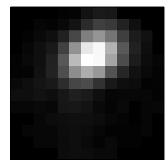
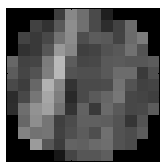
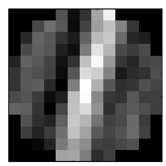
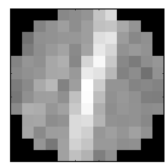
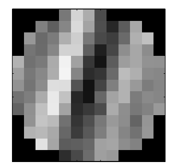
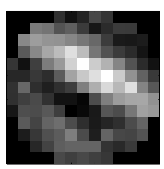
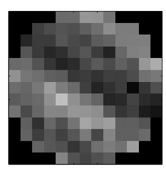
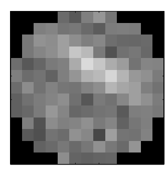
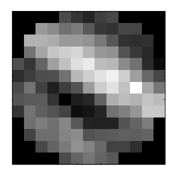
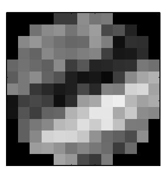
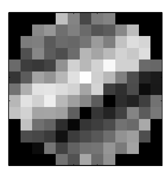
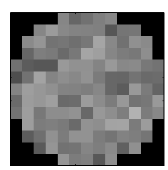
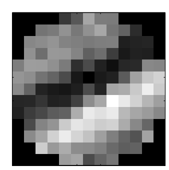
Changing Zero Firing Level

	m^{ON}	m^{OFF}	m^{+}	m^{-}
$D_{\min} = -3$ 0.5%				
$D_{\min} = -2.5$ 1%				
$D_{\min} = -2$ 3%				
$D_{\min} = -1.5$ 6.5%				

- ON and OFF afferents fail to segregate when LGN responses are non-symmetric around spontaneous

ON/OFF CHANNEL MODEL RESULTS:

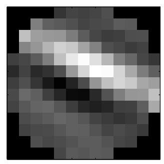
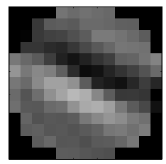
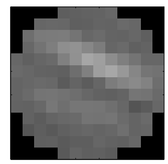
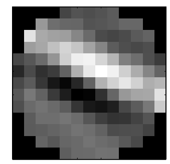
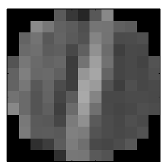
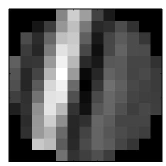
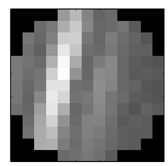
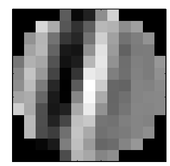
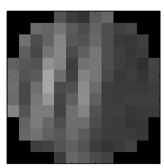
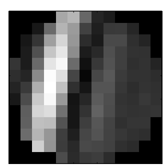
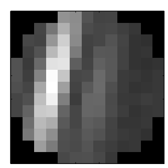
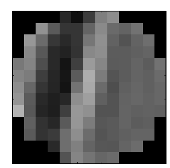
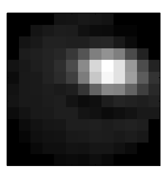
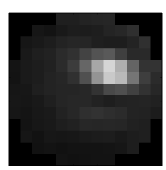
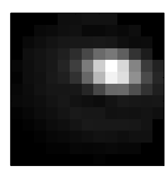
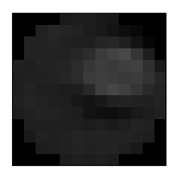
EFFECT OF ADDED NOISE

$(D_{\min} = -2.5)$	m^{ON}	m^{OFF}	m^{+}	m^{-}
std $= 0$				
std $= .2$				
std $= .7$				
std $= 1$				
std $= 2$				

- BCM is *very* sensitive to asymmetry in LGN responses
- Added noise makes results more robust

ON/OFF Channel Model Results:

Zero Firing Level $\leftrightarrow d = 0$

(std = .7)	m^{ON}	m^{OFF}	m^{+}	m^{-}
$D_{\min} = -3$ 0.5%				
$D_{\min} = -2.5$ 1%				
$D_{\min} = -2$ 3%				
$D_{\min} = -1.5$ 6.5%				

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