Balanced state and the primary visual cortex

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Main research interests

- Single neuron dynamics
  - Relation between coding properties and dynamics
  - Intrinsic conductances and dynamics of thalamic neurons
- Dynamics of large neural networks
  - Primary Visual Cortex: effects of plasticity and homeostatic processes
  - Prefrontal cortex: short term plasticity and working memory
  - Motor system: thalamo-cortical-basal ganglia loop and Parkinson's disease
- Medical imaging
  - Segmentation and registration
- Transfer of information in complex networks
  - Propagation of errors

Collaborators

- Single neuron dynamics
    - Inés Samengo (Bariloche)
    - Marcelo Montemurro (Manchester)
    - Marcela Nadal, Yimy Amarillo (Bariloche)
- Dynamics of large neural networks
    - Román Rossi (Bariloche, now in Mexico)
    - Soledad Gonzalo (Bariloche)
    - David Hansel, Carl van Vreeswijk (Paris)
    - Damián Dellavalle, Osvaldo Velarde (Bariloche)
- Medical imaging
    - Rodrigo Cárdenas (Bariloche)
    - Roberto Isoardi (FUESMEN, Mendoza)
    - Ariel Curiale (U. Cuyo, Mendoza)
- Transfer of information in complex networks
    - Marcelo Kuperman, Andrés Chacoma (Bariloche)

Outline

- Balanced state: motivation and properties
- Balanced state in systems with spatial structure
- Primary visual cortex: systems with and without orientation maps
- Plasticity in the primary visual cortex: analytical and numerical results
- Conclusions

Balanced state

- The firing patterns of cortical neurons in intact animals display a strong degree of temporal variability

- They can be approximated by a Poisson process with a small refractory period

(Softy and Koch, 1993)

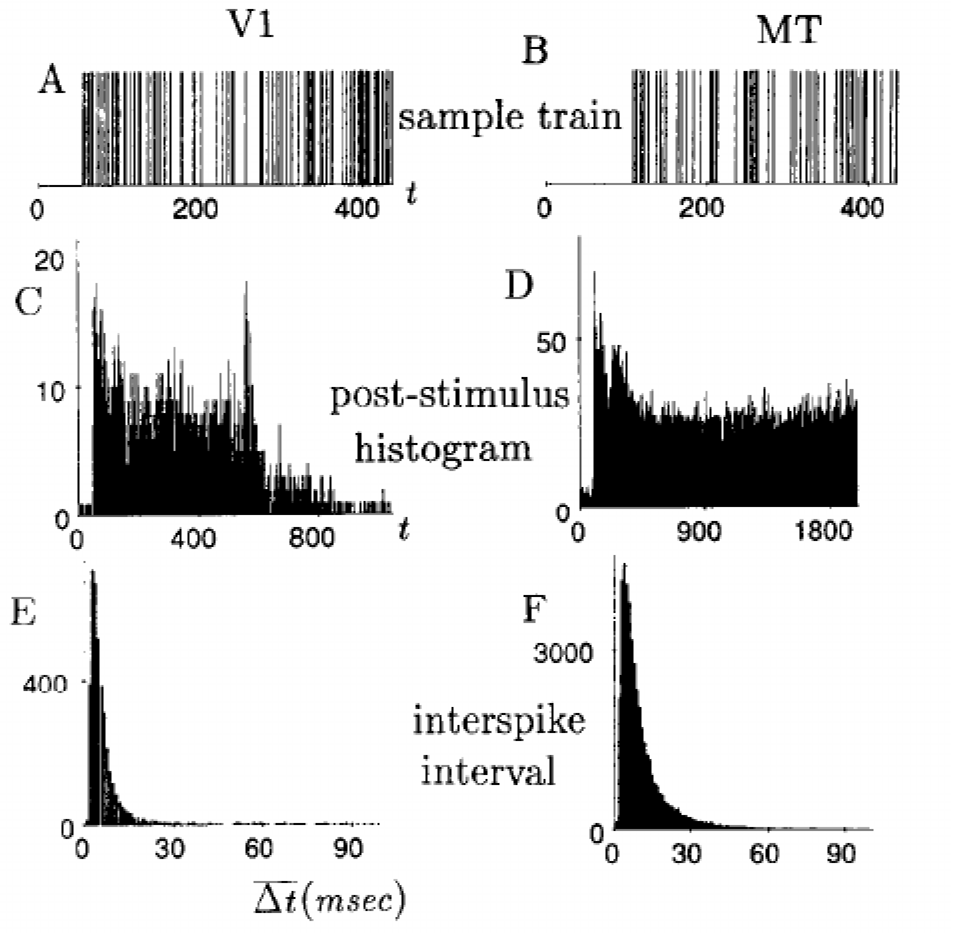
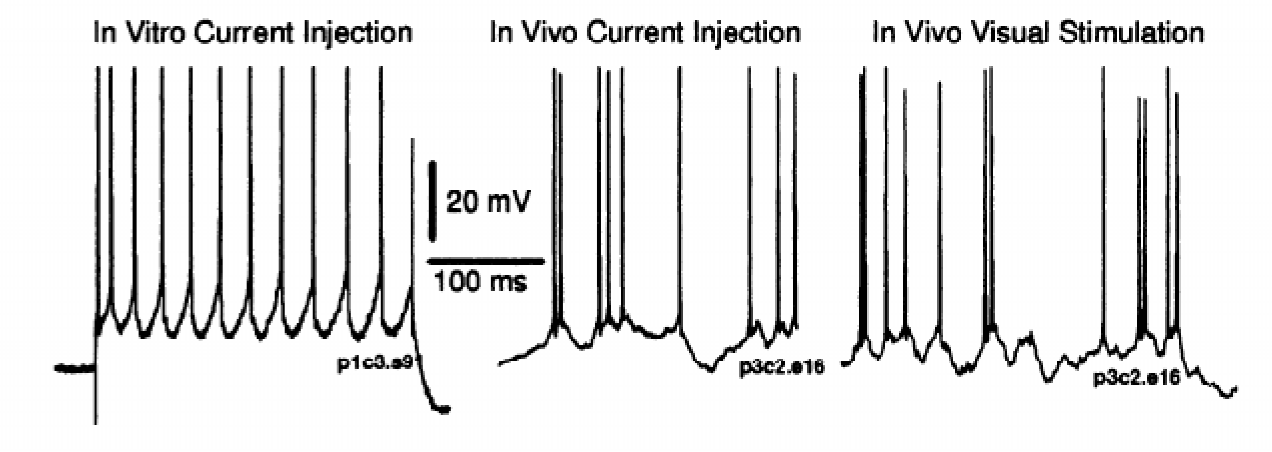


Figure 1. Firing statistics of neurons in areas V1 and MT. *A* and *B*, Sample spike trains from one of the fastest-firing nonbursting neurons recorded in each area. *C* and *D*, PSTHs from the same neuron. *E* and *F*, ISI histograms from the same neuron. These neurons are "typical" in that their firing times seem nearly random at all observed firing rates.

Balanced state

- On the other hand cortical neurons fire quite regularly when they receive a constant input (in vitro experiments)



- (Holt et al., 1996)

Balanced state

- Each cortical neuron receives hundreds or thousands of synaptic connections

- 3 x 10**8 synapses/mm**3
  10**5 neurons/mm**3

  (Beaulieu and Colonnier, 1985)

- Correlations between the activity of different cortical neurons are weak

  (Renart et al., 2010)

Balanced state

- In the limit of very large connectivity (K) each neuron should receive a net input order K + fluctuations order sqrt(K)
- How all this be compatible?
  - Very low firing rate?
  - Some degree of synchronization?
  - Additional sources of noise?
  - Cancellation of excitation and inhibition?

Balanced state

- Cancellation of excitation and inhibition

  (van Vreeswijk and Sompolinsky, 1996, 1998)

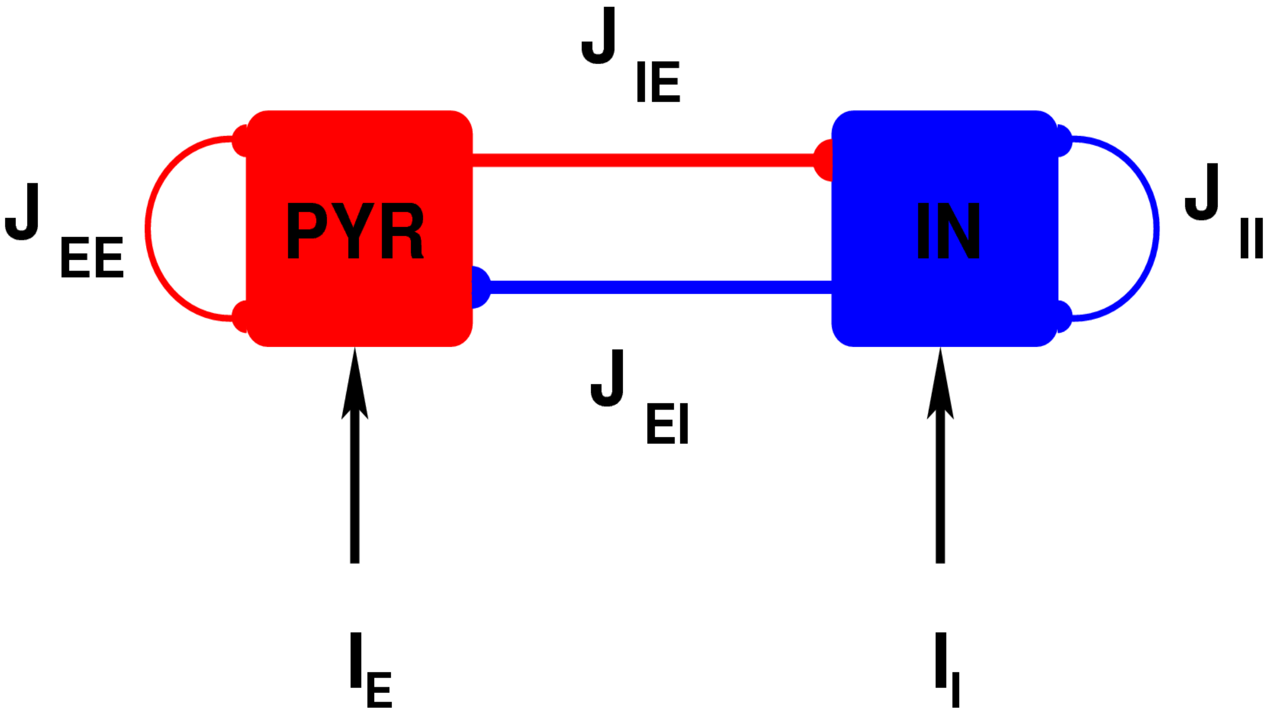
  - N_E, N_I excitatory and inhibitory neurons
  - K connections per neuron (average), no spatial structure
  - $1 << K << N_E, N_I$ (strongly diluted connectivity)
  - Synaptic efficacy O(1/sqrt(K)): “strong” synapses
- For binary neurons this system can be solved analytically

Balanced state

- The diluted connectivity guarantees there are no correlations.
- As K>>1 the distribution of inputs is Gaussian
- The distribution is characterized by fast and quenched terms whose correlations can be evaluated self-consistently
- In the limit of very large K it is easy to see why it leads to a highly variable state

Balanced state

- PYR: excitatory neurons
- IN: Inhibitory neurons



Balanced state

- $\nu_E = F(h_E)$, $\nu_I = F(h_I)$
- ν: firing rate; h: synaptic input; F: input-output transfer function

$h_E = \mathrm{sqrt}(K)\{J_{EE}\,\nu_E - J_{EI}\,\nu_I + I_E\}$
$h_I = \mathrm{sqrt}(K)\{J_{IE}\,\nu_E - J_{II}\,\nu_I + I_I\}$

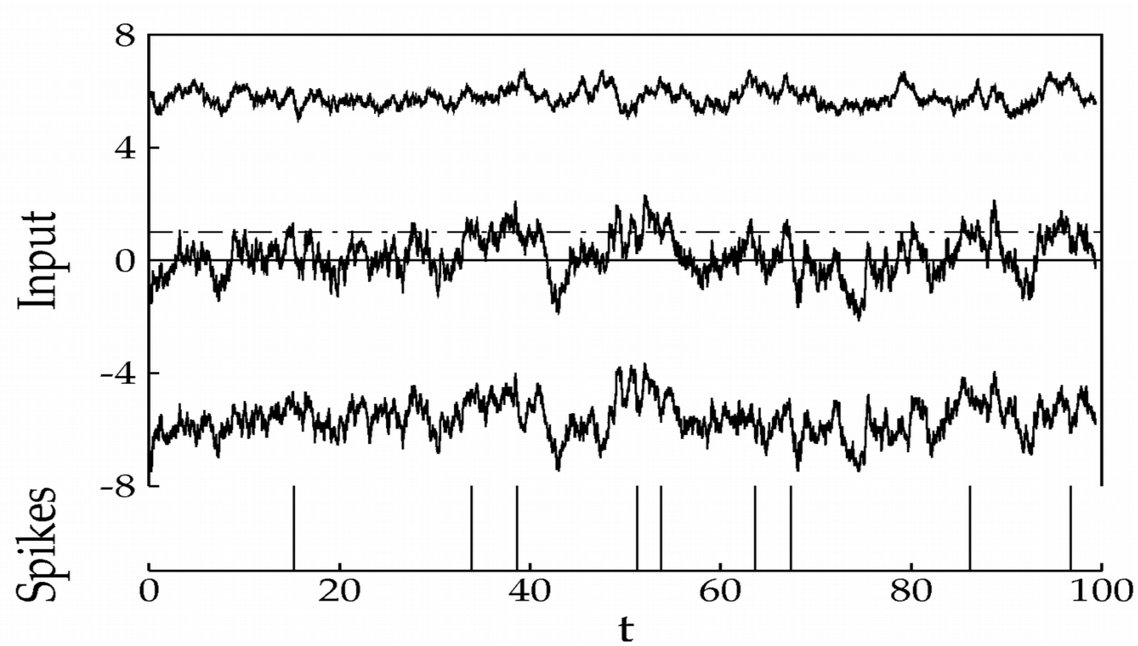
- In the limit of large K it must be

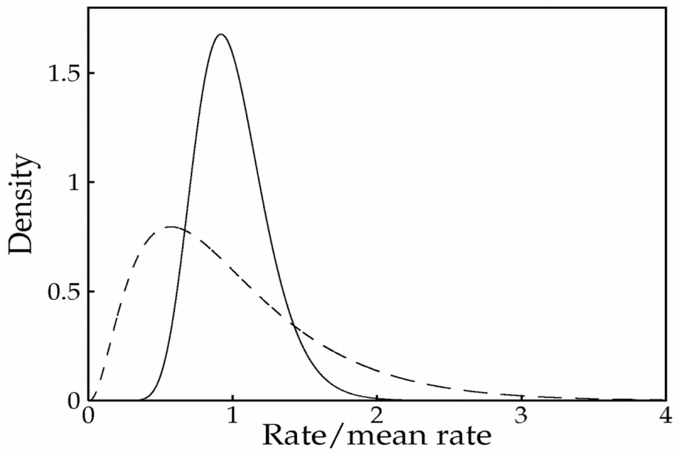
$J_{EE}\,\nu_E - J_{EI}\,\nu_I + I_E = O(1/\mathrm{sqrt}(K))$
$J_{IE}\,\nu_E - J_{II}\,\nu_I + I_i = O(1/\mathrm{sqrt}(K))$

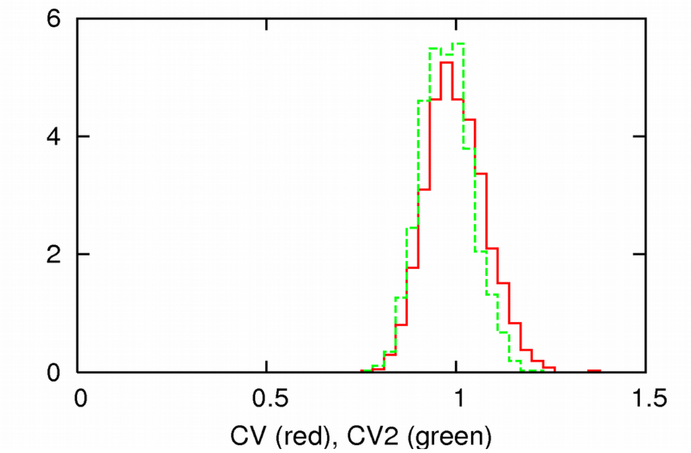
- The net inputs (h_E,h_I) must be order 1, otherwise the activity would be 0 or at saturation value
- But the fluctuations are proportional to ν_E^2 , ν_I^2
- The total fluctuation is order 1

Balanced state

- Numerical simulations







Balanced state

- Properties of the balanced state

- In the limit of very large K it must be

$$0 = J_{EE}\,\nu_E - J_{EI}\,\nu_I + I_E$$
$$0 = J_{IE}\,\nu_E - J_{II}\,\nu_I + I_I$$

Or

$$\nu_E = (J_{II}\,I_E - J_{EI}\,I_I)/(J_{EI}\,J_{IE} - J_{EE}\,J_{II})$$
$$\nu_I = (J_{IE}\,I_E - J_{EE}\,I_I)/(J_{EI}\,J_{IE} - J_{EE}\,J_{II})$$

- There is a LINEAR relation between the firing rates and the external inputs. Single neuron input-output transfer function (**F**) is irrelevant
- The firing rates become lower if all the couplings become stronger

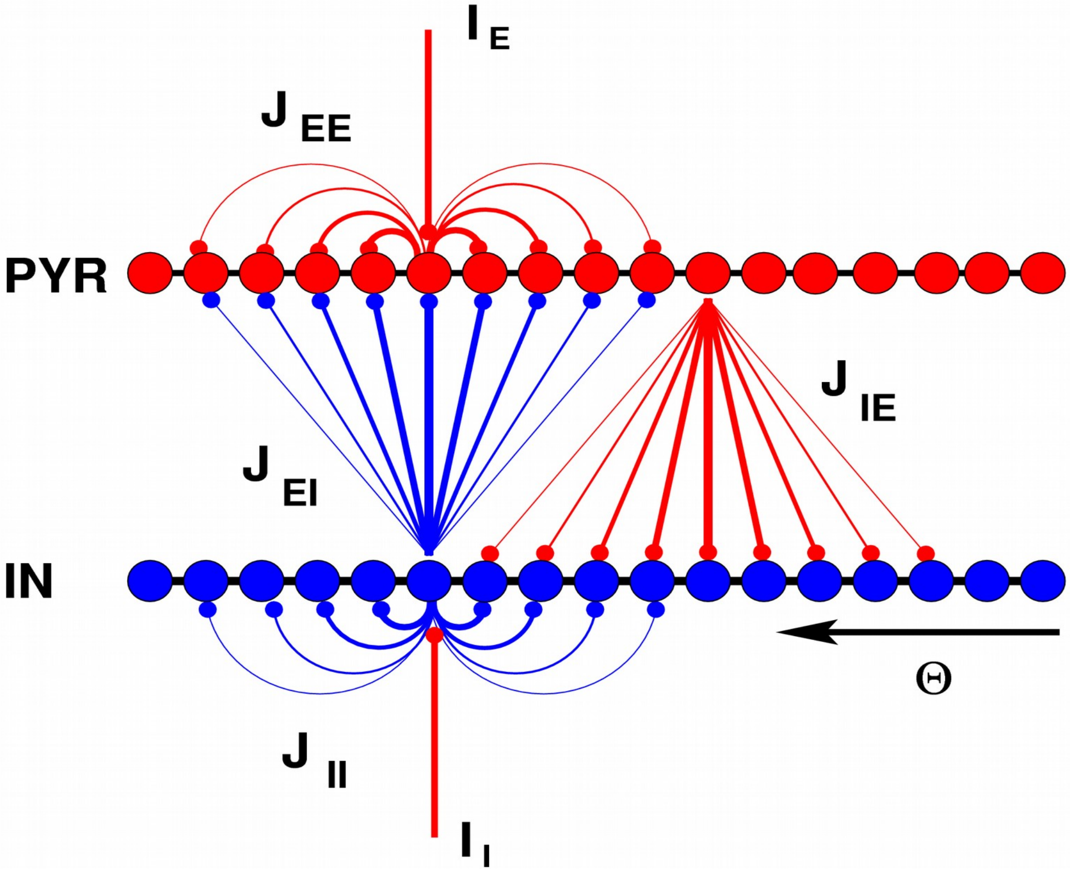
Balanced state

- Properties of the balanced state
- Conditions for stability
  - $J_{EI} J_{IE} - J_{EE} J_{II} > 0$
  - $J_{II} - J_{EE} > 0$
  - $\tau_I < \tau_E$ (fast inhibition)

Balanced state

- Systems with spatial structure

(Rosenbaum and Doiron, 2014)



Balanced state

- Systems with spatial structure

- Now the balance conditions have to be satisfied locally
  $J_{EE} * \nu_E(\theta) - J_{EI} * \nu_I(\theta) + I_E(\theta) = O(1/\mathrm{sqrt}(K))$
  $J_{IE} * \nu_E(\theta) - J_{II} * \nu_I(\theta) + I_i(\theta) = O(1/\mathrm{sqrt}(K))$

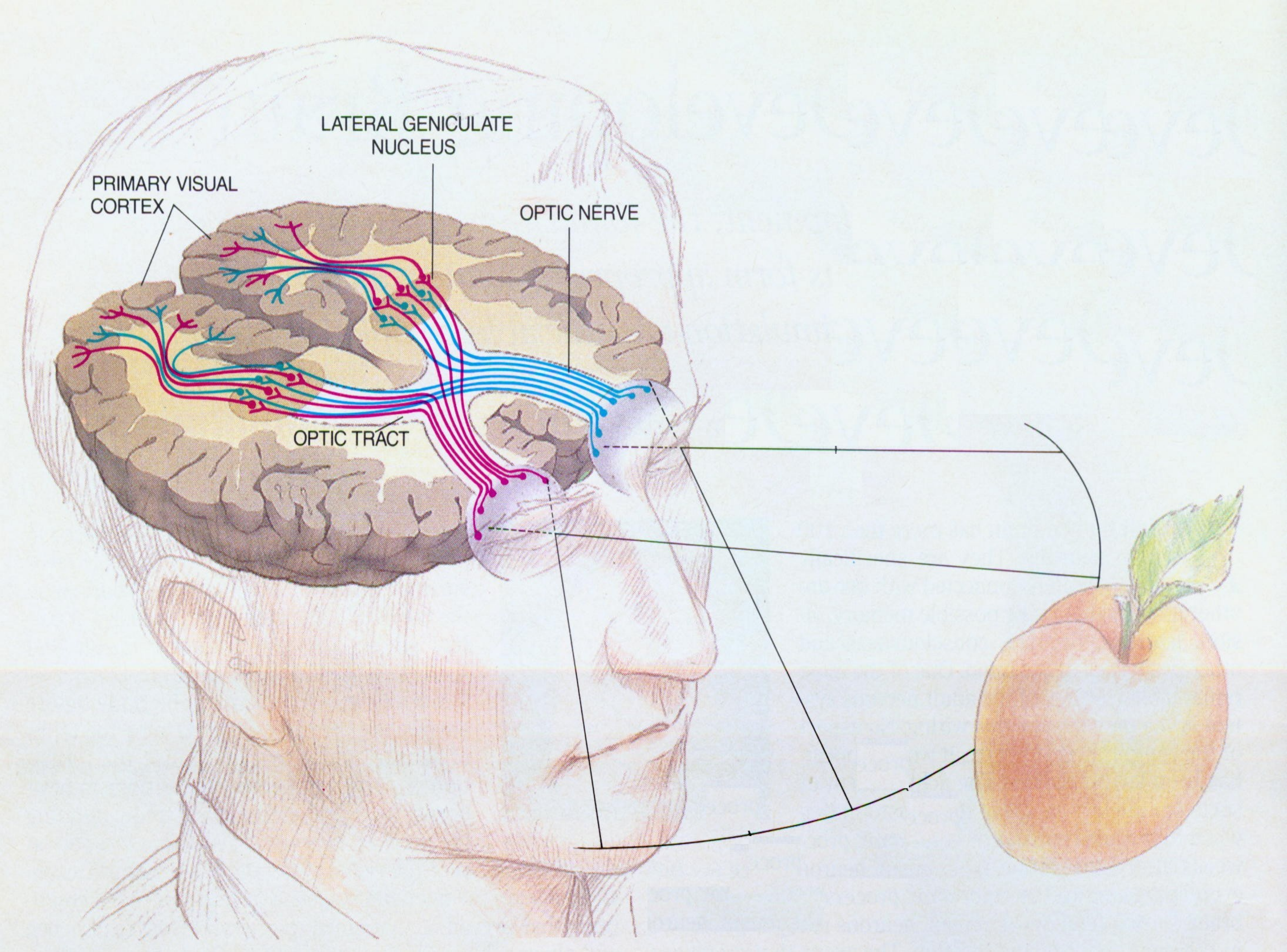
  where * is the convolution operator

- In Fourier space:
  $\tilde{J}_{EE}(n)\, \tilde{\nu}_E(n) - \tilde{J}_{EI}(n)\, \tilde{\nu}_I(n) + I_E(n) = O(1/\mathrm{sqrt}(K))$
  $\tilde{J}_{IE}(n)\, \tilde{\nu}_E(n) - \tilde{J}_{II}(n)\, \tilde{\nu}_I(n) + I_i(n) = O(1/\mathrm{sqrt}(K))$

- Taking the limit of very large K:
  $\tilde{\nu}_E(n) = (\tilde{J}_{II}(n)\, \tilde{I}_E(n) - \tilde{J}_{EI}(n)\, \tilde{I}_I(n))/(\tilde{J}_{EI}(n)\, \tilde{J}_{IE}(n) - \tilde{J}_{EE}(n)\tilde{J}_{II}(n))$

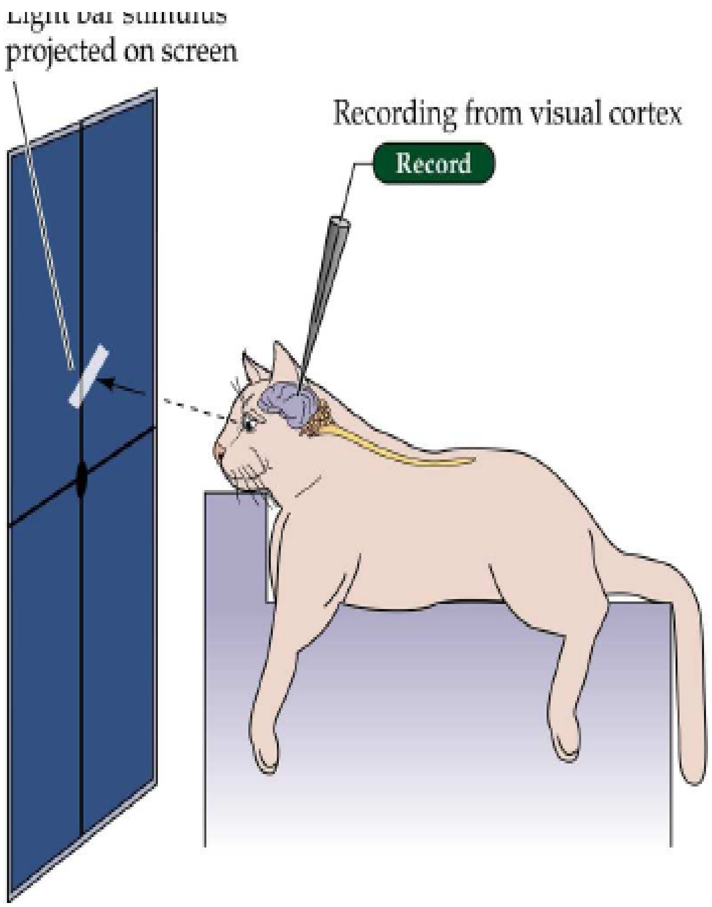
  $\tilde{\nu}_I(n) = (\tilde{J}_{IE}(n)\, \tilde{I}_E(n) - \tilde{J}_{EE}(n)\, \tilde{I}_I(n))/(\tilde{J}_{EI}(n)\, \tilde{J}_{IE}(n) - \tilde{J}_{EE}(n)\tilde{J}_{II}(n))$

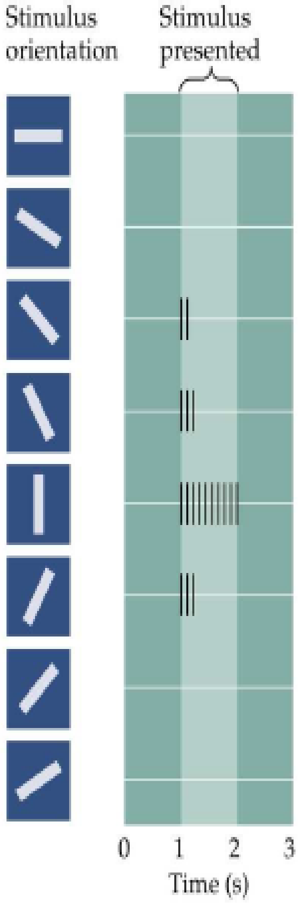
Primary visual cortex



Primary visual cortex

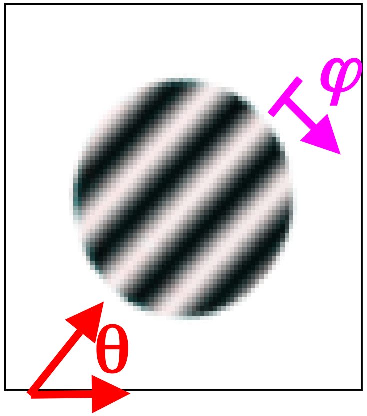
- Orientation selectivity

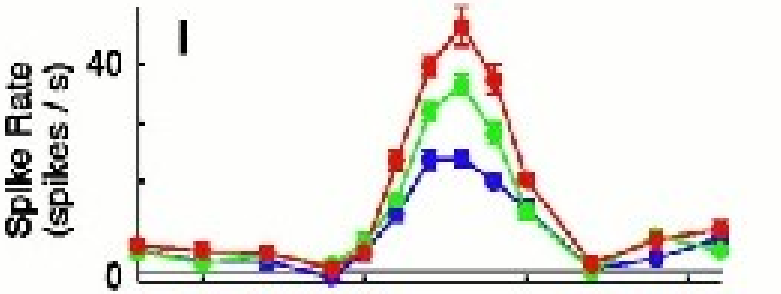


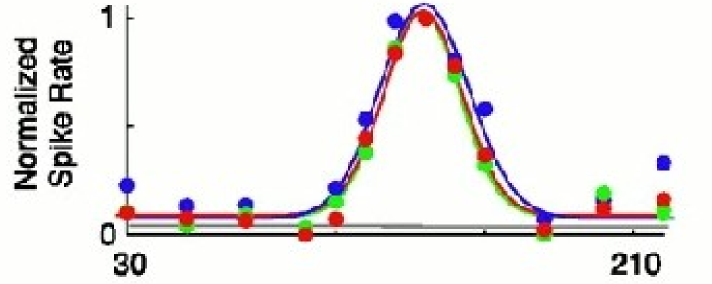


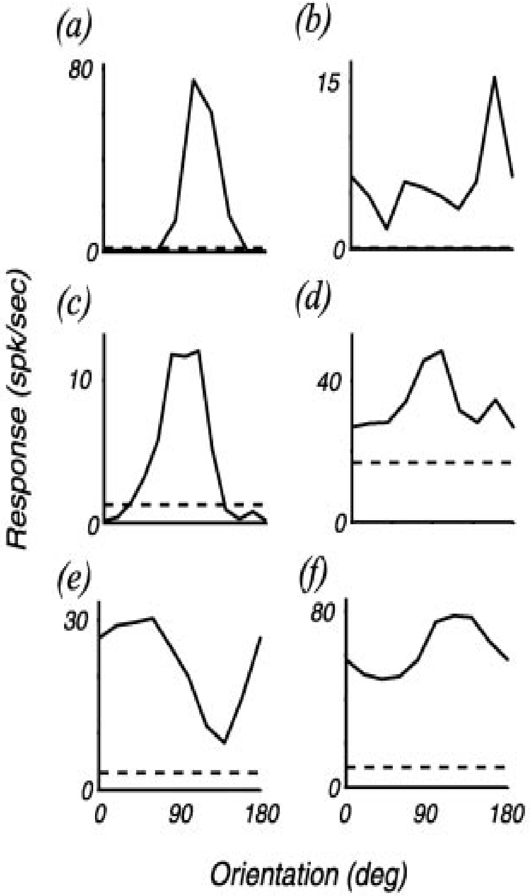
Primary visual cortex

- Orientation selectivity



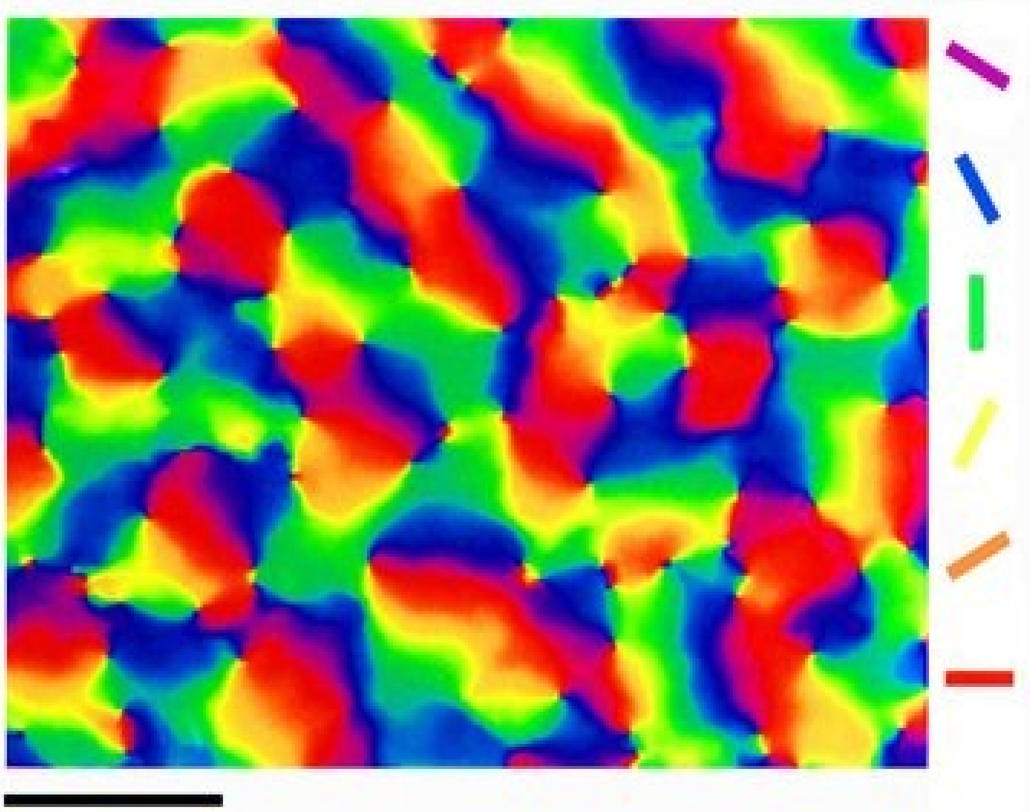






Primary visual cortex

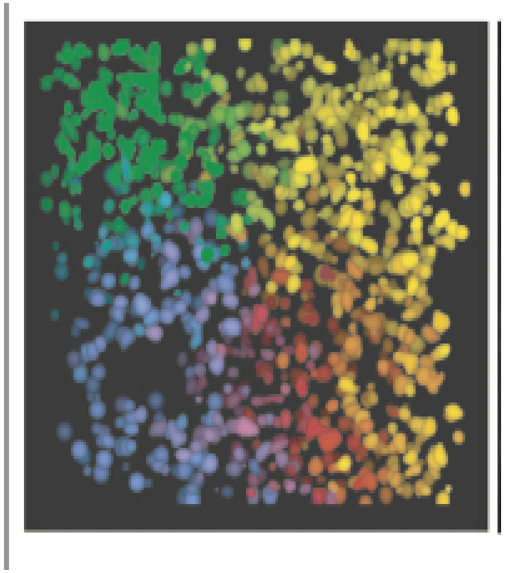
- Orientation maps

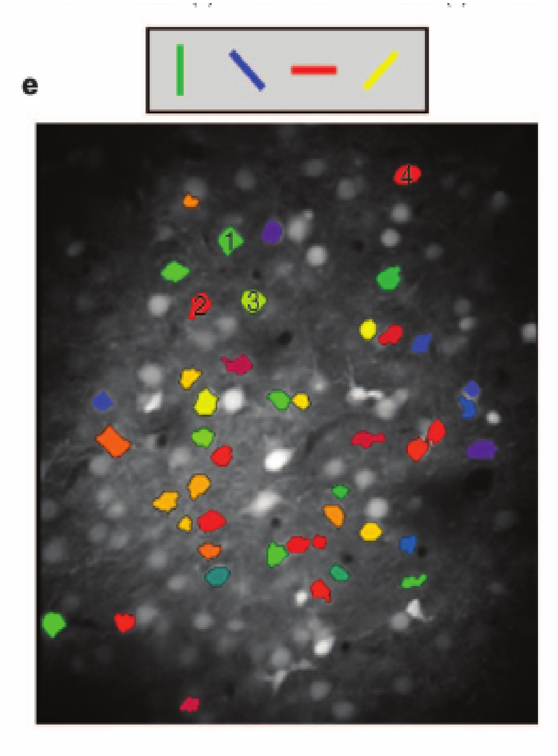


Modified from Blasdel G.G. and Salama G. *Voltage sensitive dyes reveal a modular organization in monkey striate cortex*, Natu
(1986)

Primary visual cortex

- Cat/monkey vs. rat/mouse





(Ohki and Reid, 2007)

Salt-and-pepper

Primary visual cortex

- Neurons in rodent V1 are orientation selective (Niell and Stryker, 2008)

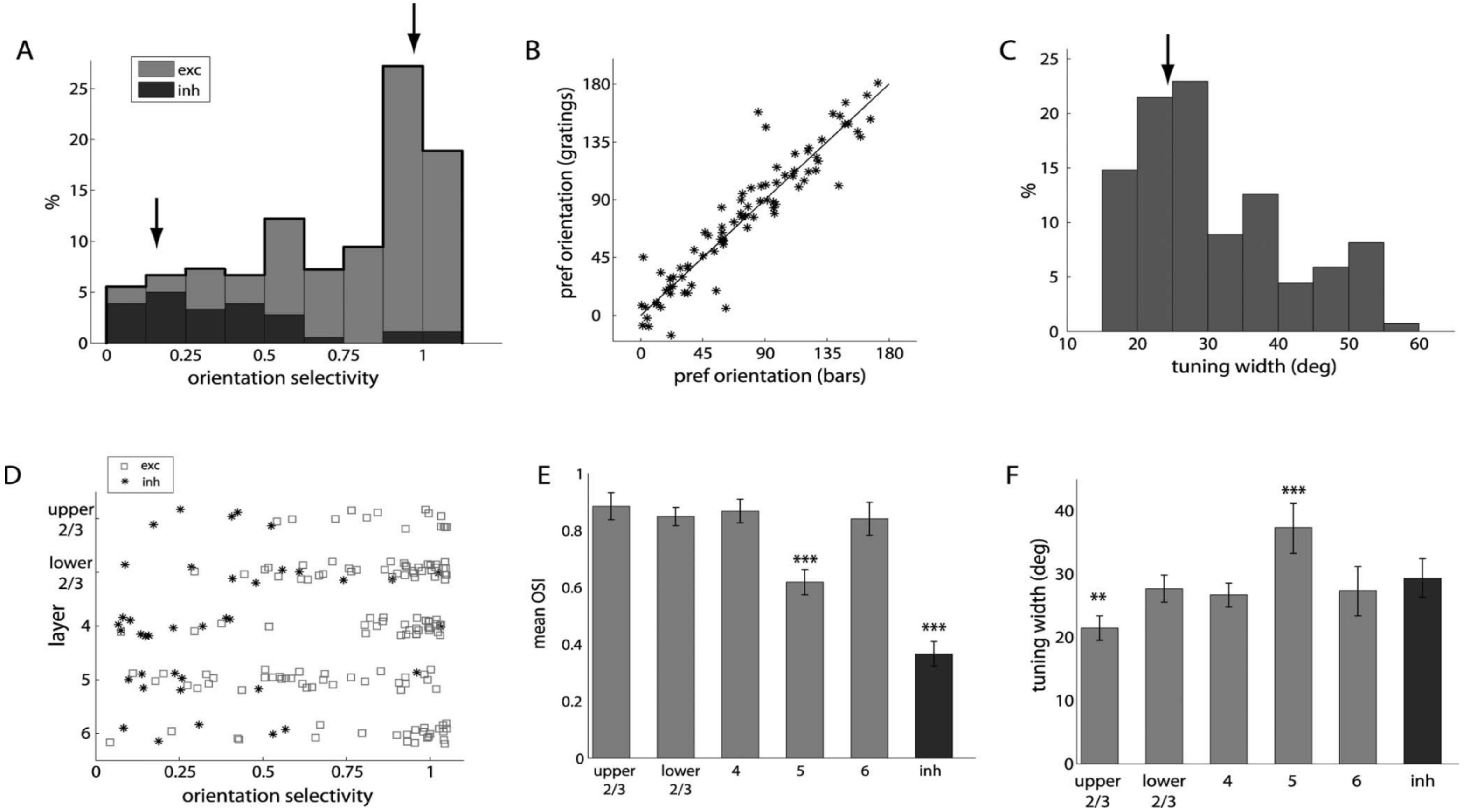


Figure 4. Orientation selectivity. ***A***, Histogram of OSI for all responsive units ($n = 182$), with gray and black representing proportion of putative excitatory (exc) and inhibitory (inh) units. Arrows show values for units in Figures 2 and 3. ***B***, Comparison of preferred orientation angle (degree) as measured with bars and gratings demonstrates consistency. ***C***, Histogram of mean tuning width for all orientation-selective units ($n = 135$). Arrow shows value for unit in Figure 2. ***D***, Orientation selectivity by layer and cell type. ***E***, Mean OSI for each layer and cell type. ***F***, Median width of orientation tuning for all oriented units by layer.

Primary visual cortex

- What are different mechanisms underlying the two cases?
- What is the contribution of the of the intracortical connections to selectivity?
- In rodents, are intracortical connections functionally organized and if this is so what is the effect on orientation selectivity?

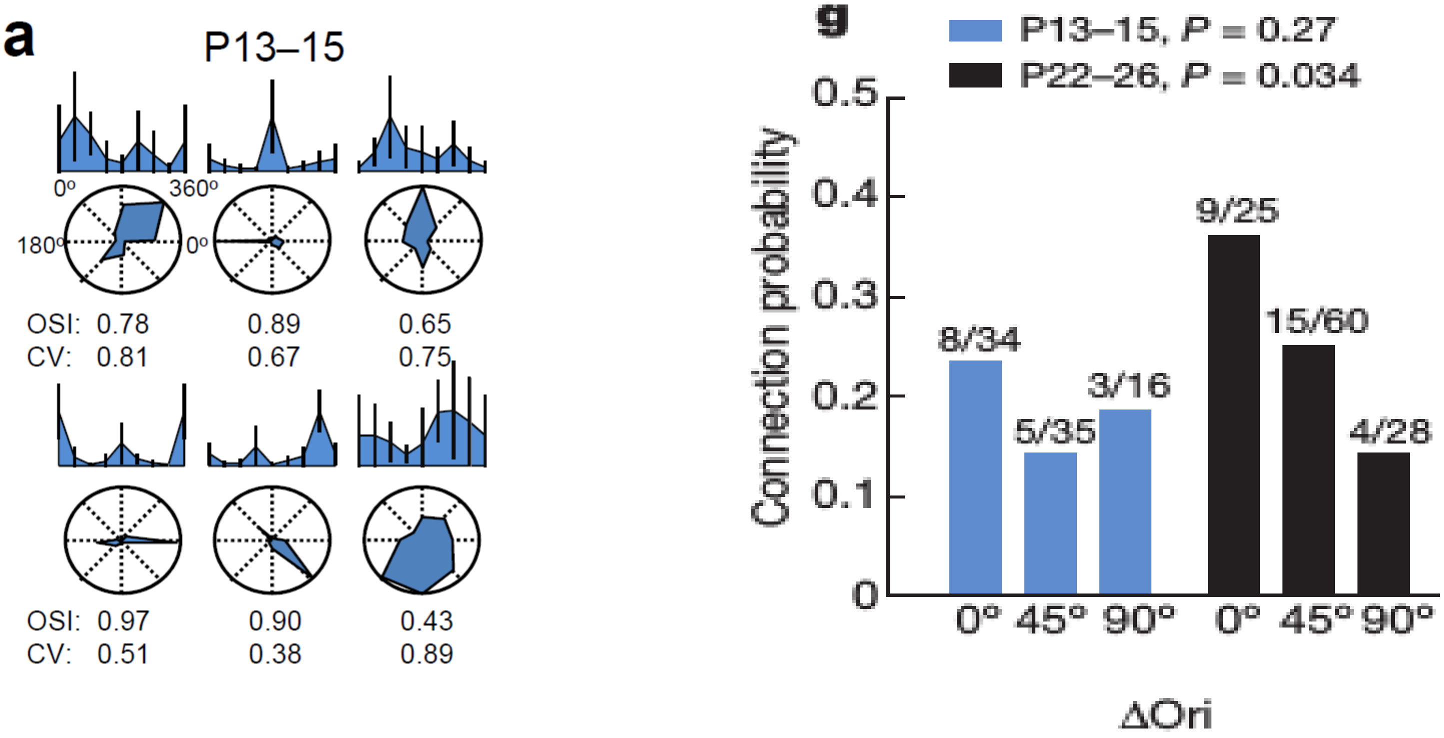
~~«The mixed salt-and-pepper organization of preferred orientation in rodents [...] argues for specific connectivity between neurons»~~

(Ohki and Reid, 2007)

Primary visual cortex

- Selectivity present in mouse at eye opening

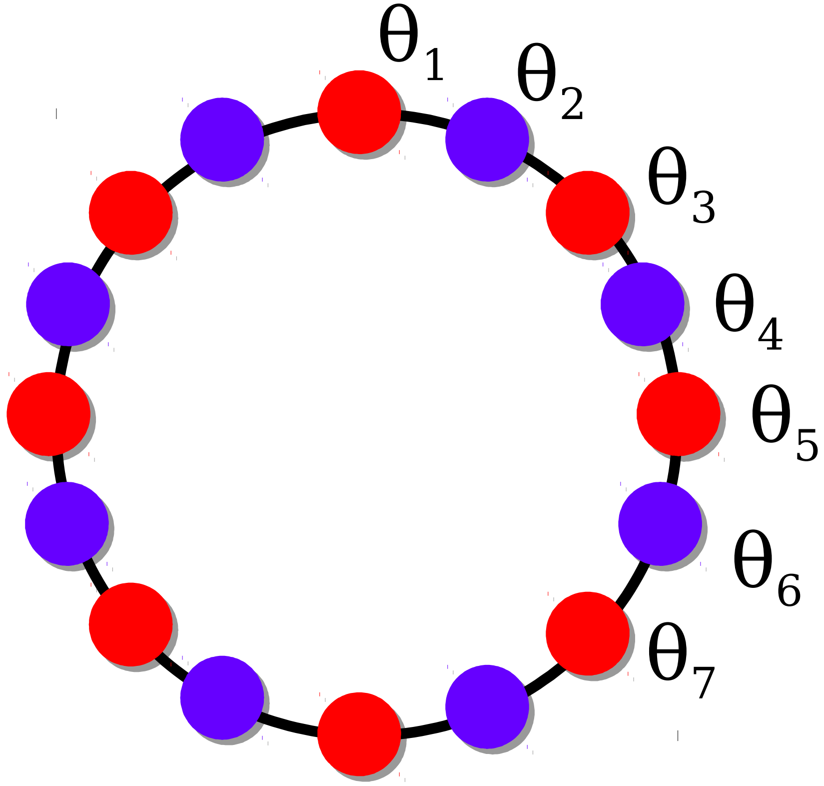
Ko et al, 2013



- At eye opening: Neurons are selective to orientation; EE connectivity is non specific.
- After critical period: Specificity in the EE connectivity

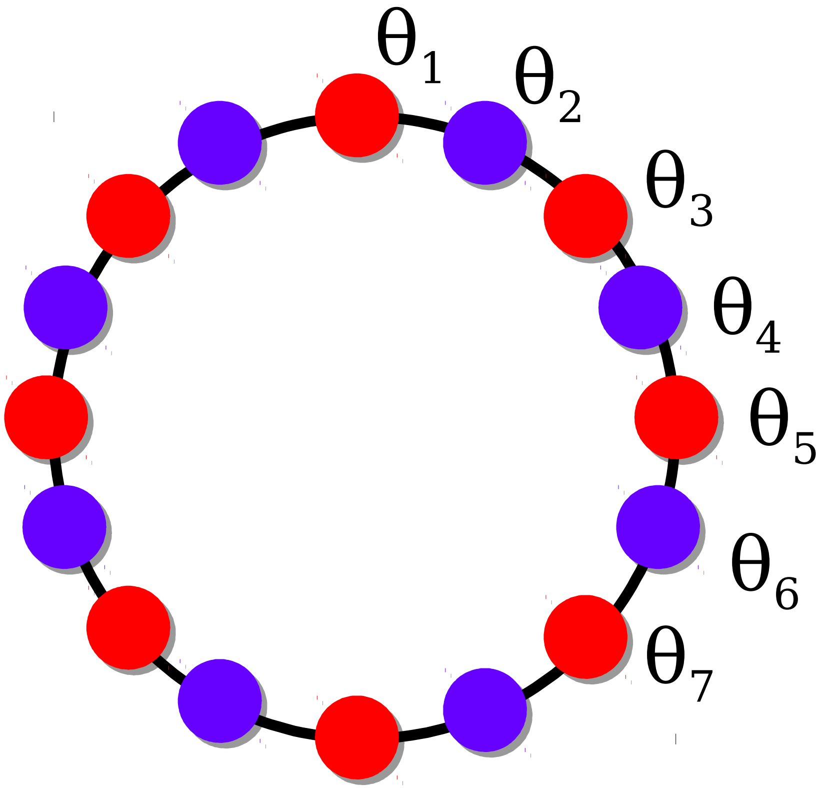
The Models

- Reduced model

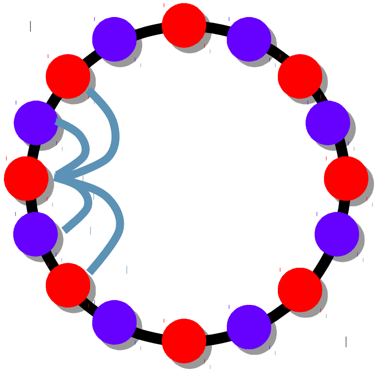


The Models

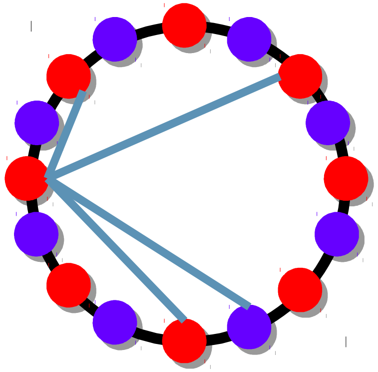
- Reduced model



Orientation Map

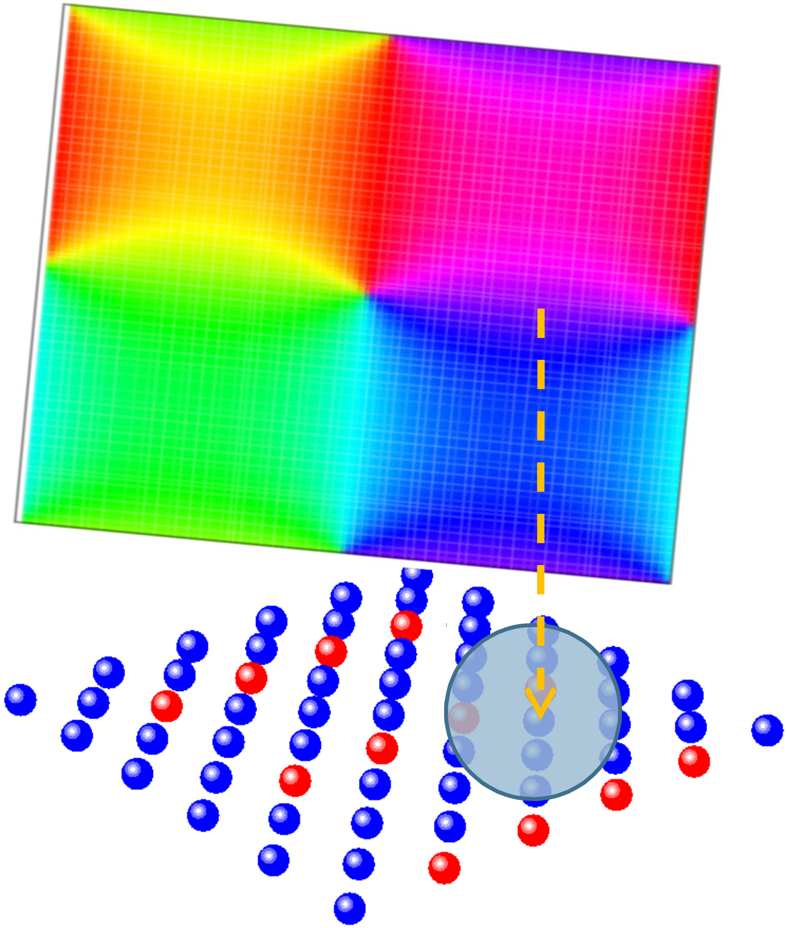


Salt and Pepper



The Models

- Computational Model



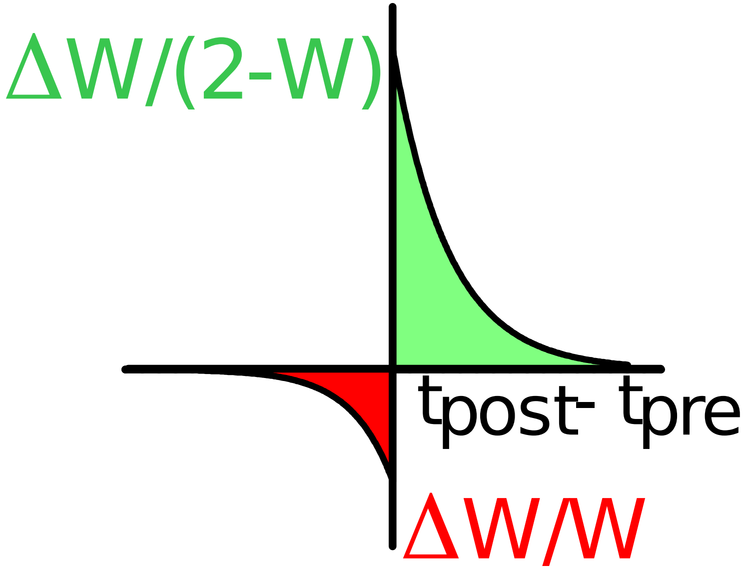
Preferred orientation

The Models

- Plasticity Rules

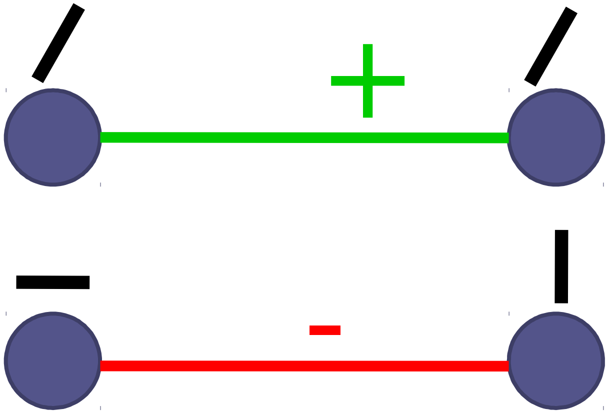
<u>STDP</u>

Spike-Timing
Dependent Plasticity



<u>Reconnection Rule:</u>

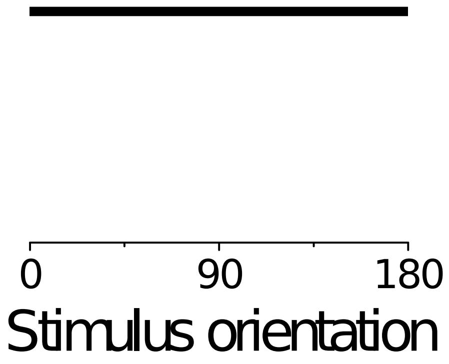
Connection probability of
neurons with similar
preferred orientation is
strengthened

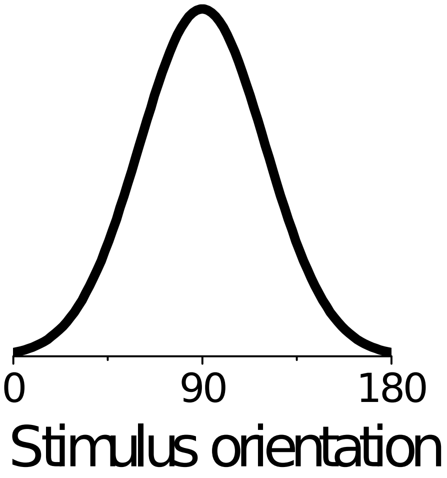


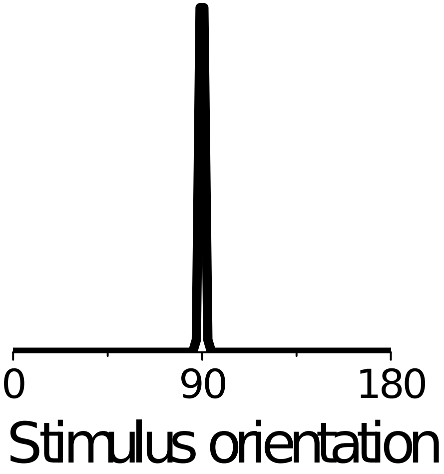
The Models

- Orientation Selectivity Index

$$OSI = \frac{\sqrt{\left(\sum_\theta f(\theta)\cos(2\theta)\right)^2 + \left(\sum_\theta f(\theta)\sin(2\theta)\right)^2}}{\sum_\theta f(\theta)}$$



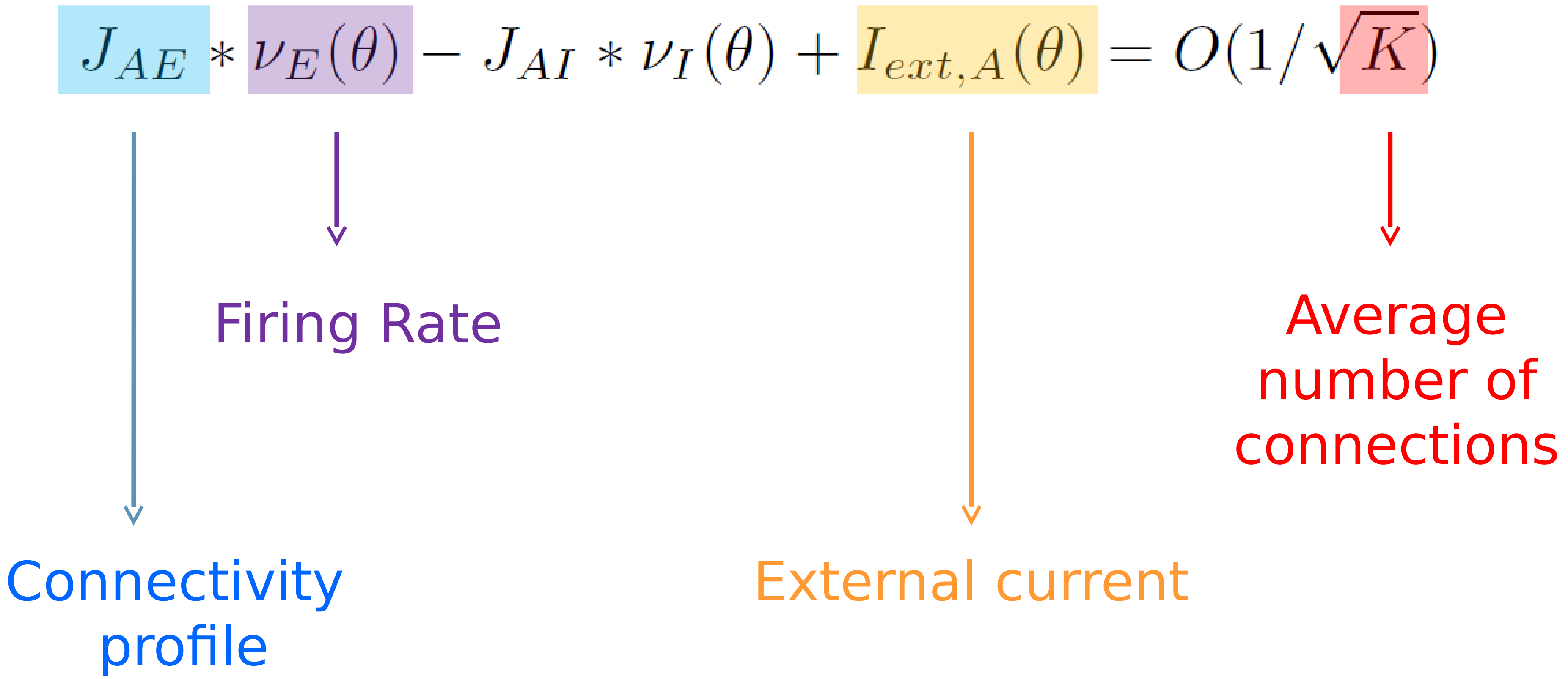




Reduced Model

Balance equations

$$A = E, I$$



$$J_{AE} * \nu_E(\theta) - J_{AI} * \nu_I(\theta) + I_{ext,A}(\theta) = O(1/\sqrt{K})$$

Firing Rate

Average number of connections

Connectivity profile

External current

Reduced Model

$$\tilde{J}_{AE}(n)\tilde{\nu}_E(n) - \tilde{J}_{AI}(n)\tilde{\nu}_I(n) + \tilde{I}_{ext,A}(n) = O(1/\sqrt{K})$$

Solutions

$$\begin{aligned}
\tilde{\nu}_E(n) &= \frac{\tilde{J}_{II}(n)\tilde{I}_{ext,E}(n) - \tilde{J}_{EI}(n)\tilde{I}_{ext,I}(n)}{\tilde{J}_{IE}(n)\tilde{J}_{EI}(n) - \tilde{J}_{EE}(n)\tilde{J}_{II}(n)} \\
\tilde{\nu}_I(n) &= \frac{\tilde{J}_{IE}(n)\tilde{I}_{ext,E}(n) - \tilde{J}_{EE}(n)\tilde{I}_{ext,I}(n)}{\tilde{J}_{IE}(n)\tilde{J}_{EI}(n) - \tilde{J}_{EE}(n)\tilde{J}_{II}(n)}
\end{aligned}$$

Stability of the balanced state

$$\begin{aligned}
\tilde{J}_{EE}(n) - \tilde{J}_{II}(n) &< 0 \\
\tilde{J}_{IE}(n)\tilde{J}_{EI}(n) - \tilde{J}_{EE}(n)\tilde{J}_{II}(n) &> 0
\end{aligned}$$

Reduced Model

1) If the spatial structure of the connectivity profile depends only on the presynaptic population

$$\tilde{J}_{AB}(n) = G_{AB}\tilde{J}_B(n) \quad \text{with:} \quad A, B = E, I$$

2) The external current is the same for both populations

$$\tilde{I}_{ext,E} = \tilde{I}_{ext,I} = \tilde{I}_{ext}$$

Reduced Model

1) If the spatial structure of the connectivity profile depends only on the presynaptic population

2) The external current is the same for both populations

$$\tilde{\nu}_E(n) = \frac{\tilde{J}_{II}(n)\tilde{I}_{ext,E}(n) - \tilde{J}_{EI}(n)\tilde{I}_{ext,I}(n)}{\tilde{J}_{IE}(n)\tilde{J}_{EI}(n) - \tilde{J}_{EE}(n)\tilde{J}_{II}(n)}$$

$$\tilde{\nu}_I(n) = \frac{\tilde{J}_{IE}(n)\tilde{I}_{ext,E}(n) - \tilde{J}_{EE}(n)\tilde{I}_{ext,I}(n)}{\tilde{J}_{IE}(n)\tilde{J}_{EI}(n) - \tilde{J}_{EE}(n)\tilde{J}_{II}(n)}$$

↓

$$\tilde{\nu}_E(n) = \frac{(G_{II}I_{ext,E} - G_{EI}I_{ext,I})\tilde{I}_{ext}(n)}{(G_{IE}G_{EI} - G_{EE}G_{II})\tilde{J}_E(n)}$$

$$\tilde{\nu}_I(n) = \frac{(G_{IE}I_{ext,E} - G_{EE}I_{ext,I})\tilde{I}_{ext}(n)}{(G_{IE}G_{EI} - G_{EE}G_{II})\tilde{J}_I(n)}$$

Reduced Model

External Current

$$I_{ext,A}(\theta, \theta_0) = (1 + 2\rho\cos(2(\theta - \theta_0)))\, I_{ext,A}$$

Orientation selectivity index of the external current

Reduced Model

External Current

$$I_{ext,A}(\theta,\theta_0) = (1 + 2\rho\cos(2(\theta - \theta_0)))\, I_{ext,A}$$

- $\tilde{I}_{ext}(0) = I_{ext,A}$
- $\tilde{I}_{ext}(1) = \rho I_{ext,A}$
- $\tilde{I}_{ext}(n) = 0 \quad \text{for all } n > 1$

Reduced Model

- $\tilde{I}_{ext}(0) = I_{ext,A}$
- $\tilde{I}_{ext}(1) = \rho I_{ext,A}$
- $\tilde{I}_{ext}(n) = 0 \quad \text{for all } n > 1$

$$\begin{aligned}
\tilde{\nu}_E(n) &= \frac{(G_{II} I_{ext,E} - G_{EI} I_{ext,I}) \tilde{I}_{ext}(n)}{(G_{IE} G_{EI} - G_{EE} G_{II}) \tilde{J}_E(n)} \\
\tilde{\nu}_I(n) &= \frac{(G_{IE} I_{ext,E} - G_{EE} I_{ext,I}) \tilde{I}_{ext}(n)}{(G_{IE} G_{EI} - G_{EE} G_{II}) \tilde{J}_I(n)}
\end{aligned}$$

Reduced Model

- $\tilde{I}_{ext}(0) = I_{ext,A}$
- $\tilde{I}_{ext}(1) = \rho I_{ext,A}$
- $\tilde{I}_{ext}(n) = 0 \quad \text{for all } n > 1$

➡

$$\begin{aligned}\tilde{\nu}_E(n) &= \frac{(G_{II}I_{ext,E} - G_{EI}I_{ext,I})\tilde{I}_{ext}(n)}{(G_{IE}G_{EI} - G_{EE}G_{II})\tilde{J}_E(n)}\\ \tilde{\nu}_I(n) &= \frac{(G_{IE}I_{ext,E} - G_{EE}I_{ext,I})\tilde{I}_{ext}(n)}{(G_{IE}G_{EI} - G_{EE}G_{II})\tilde{J}_I(n)}\end{aligned}$$

OSI

$$\boxed{\begin{matrix}\dfrac{\tilde{\nu}_E(1)}{\tilde{\nu}_E(0)}\\[2ex] \dfrac{\tilde{\nu}_I(1)}{\tilde{\nu}_I(0)}\end{matrix}}\quad\begin{matrix} = \rho\dfrac{\tilde{J}_E(0)}{\tilde{J}_E(1)}\\[2ex] = \rho\dfrac{\tilde{J}_I(0)}{\tilde{J}_I(1)}\end{matrix}$$

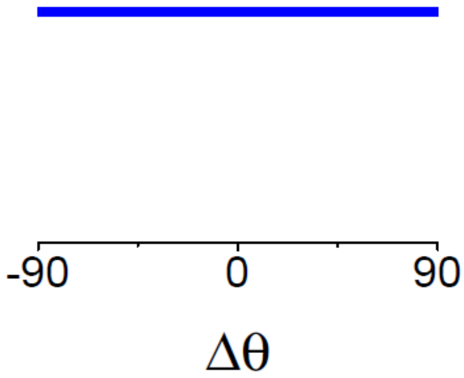
Reduced Model

$$\frac{\tilde{\nu}_E(1)}{\tilde{\nu}_E(0)} = \rho\frac{\tilde{J}_E(0)}{\tilde{J}_E(1)}$$

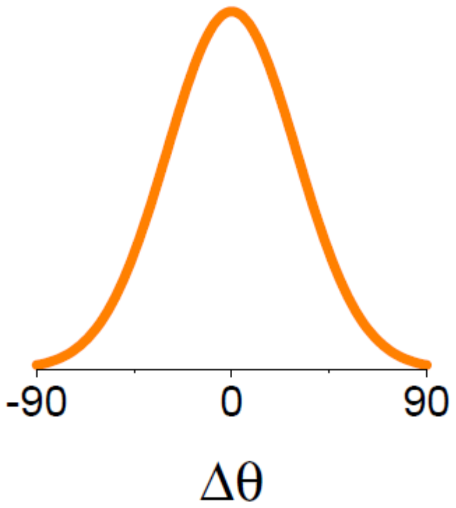
Mean value of the connectivity profile

Modulation of the connectivity profile

Salt and Pepper



Orientation Map



Reduced Model

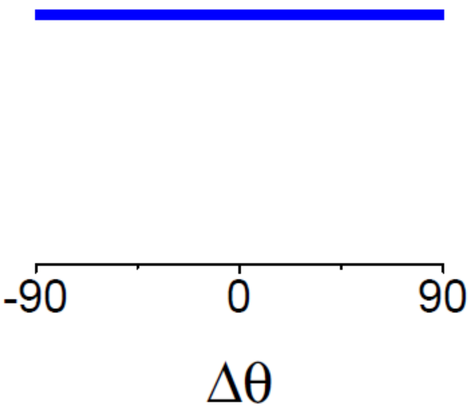
$$\frac{\tilde{\nu}_E(1)}{\tilde{\nu}_E(0)} = \rho \frac{\tilde{J}_E(0)}{\tilde{J}_E(1)}$$

Mean value of the connectivity profile

Modulation of the connectivity profile

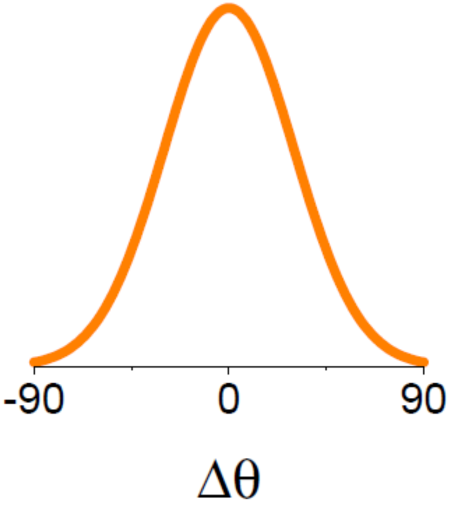
Salt and Pepper

$$\tilde{J}_E(1) \sim \frac{1}{\sqrt{K}}$$



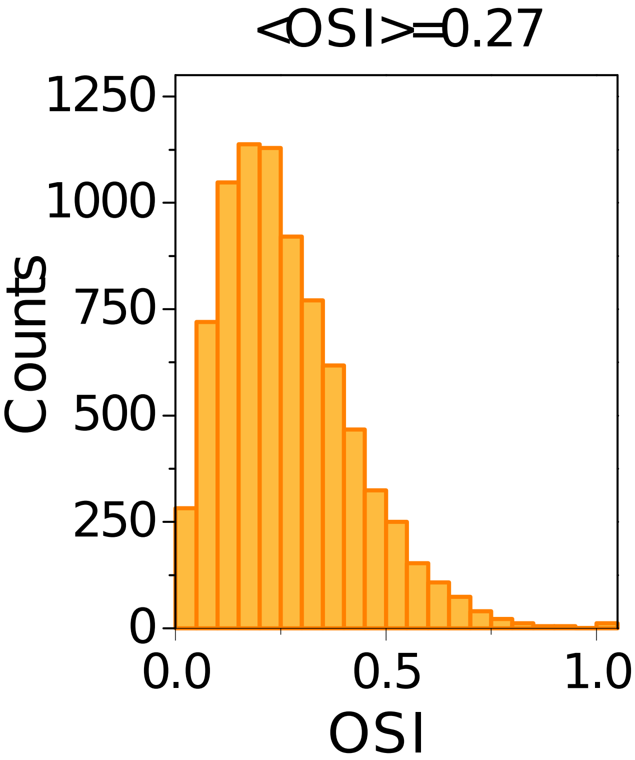
Orientation Map

$$\tilde{J}_E(1) \sim 1$$

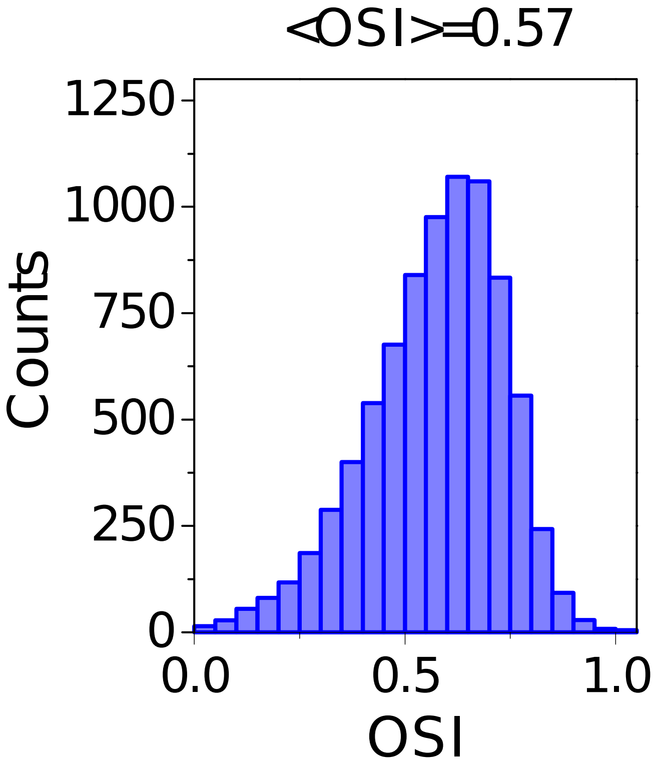


Simulation Results

Orientation Map



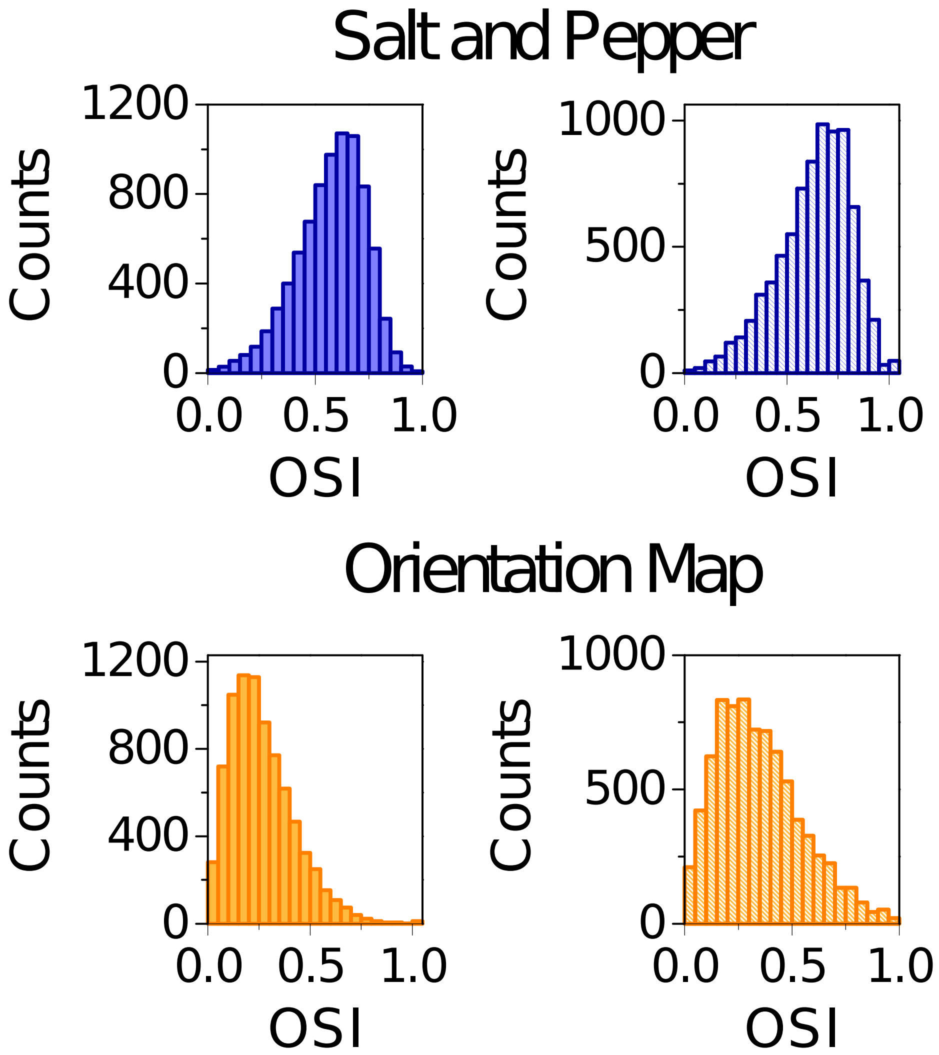
Salt and Pepper



As predicted by the model, keeping all the other parameters the same, orientation selectivity is larger for Salt and Pepper.

Simulation Results

Control STDP


Salt and Pepper

Orientation Map

Salt and Pepper

0.57 → 0.63

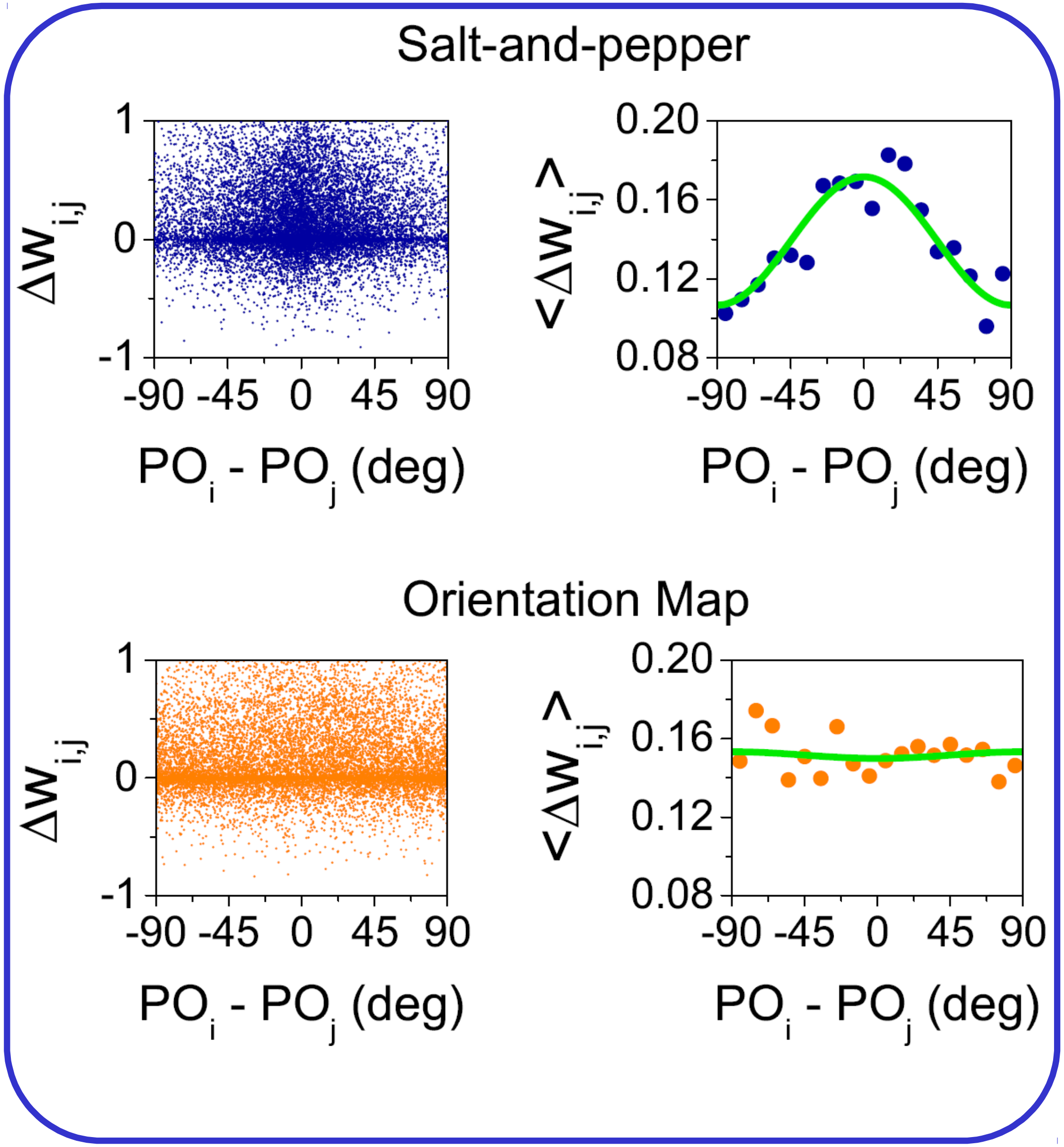
≈10%

Orientation Map

0.23 → 0.36

≈56%

Simulation Results



$\nu_i=\nu_i^0(1+2\,\rho\;\cos(\theta-\theta_i))$

$\nu_j=\nu_j^0(1+2\,\rho\;\cos(\theta-\theta_j))$

$<\Delta\;w_{ij}> \approx$

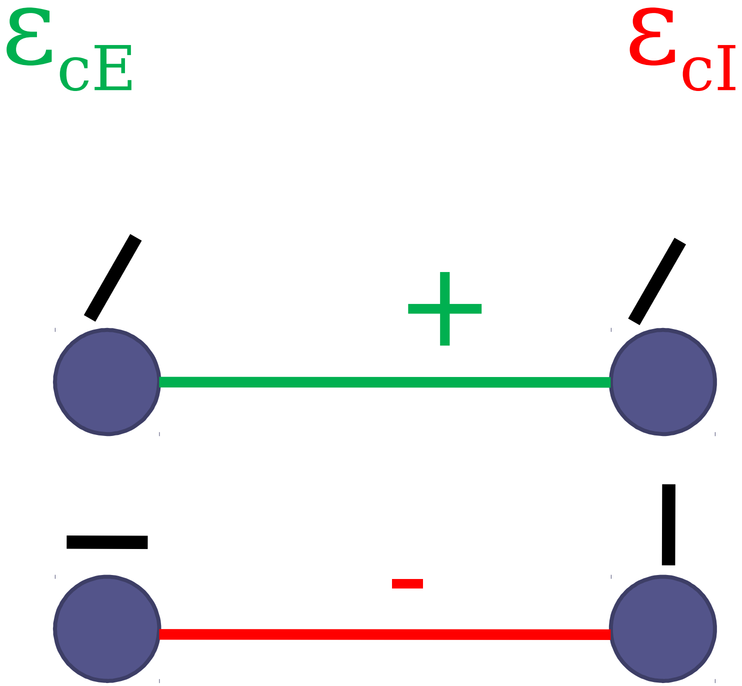
$\nu_i^0\nu_j^0(1+2\,\rho^2\cos(\theta_\iota-\theta_j))$

- More selective systems generate more modulate interactions, but this goes AGAINST an increase in selectivity

Simulation Results

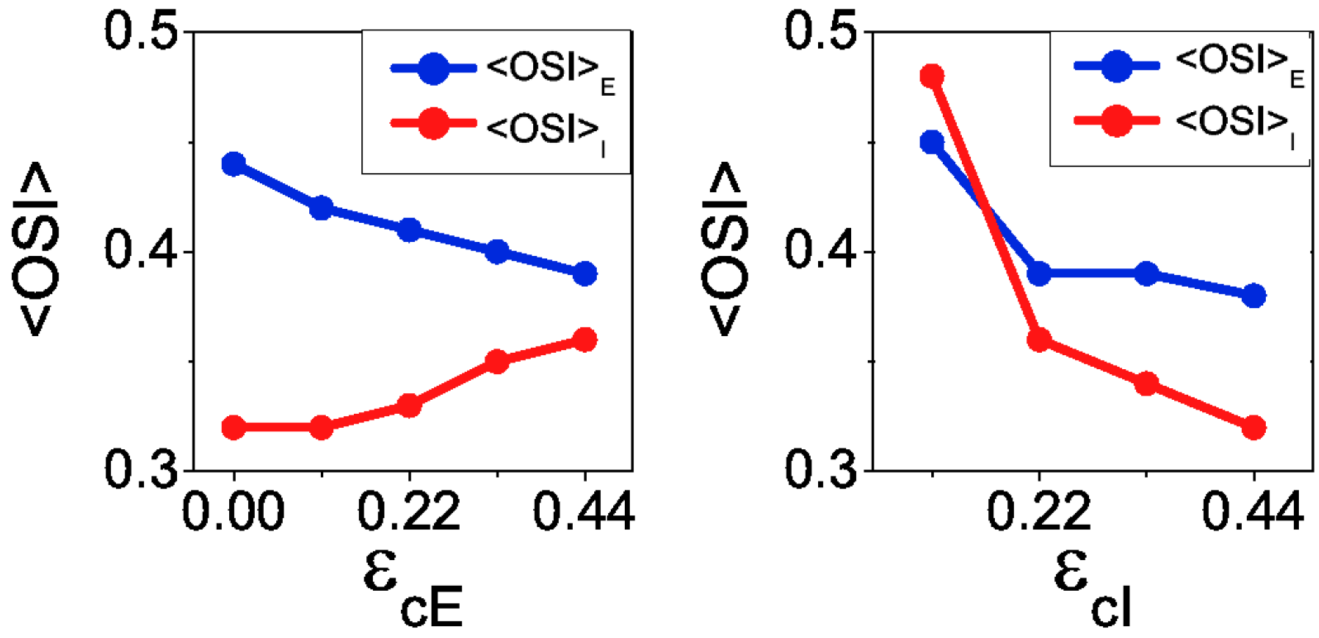
Reconnection Rule

ε: Reconnection probability between neurons



Simulation Results

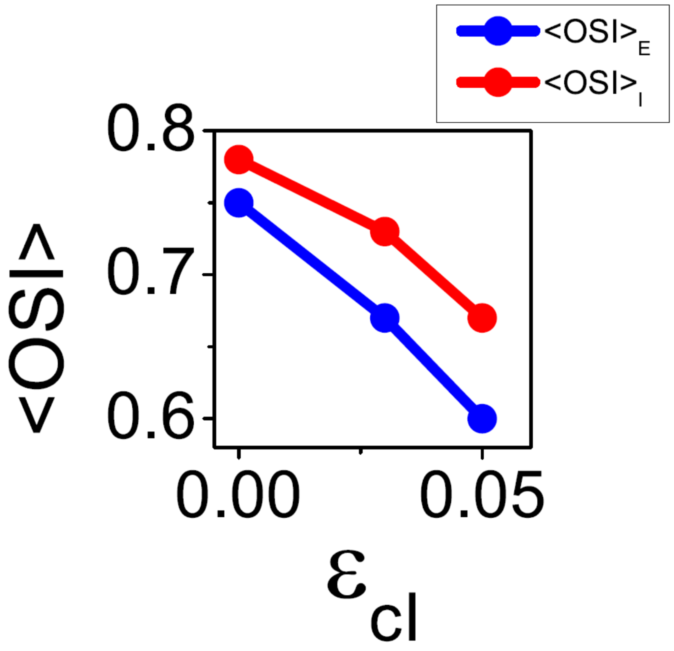
Reconnection Rule

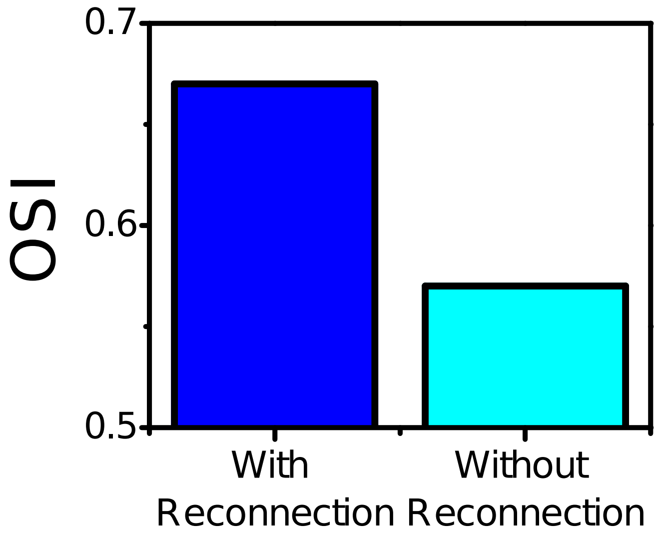


As predicted by the model, functional connectivity decreases orientation selectivity.

Simulation Results

Reconnection Rule





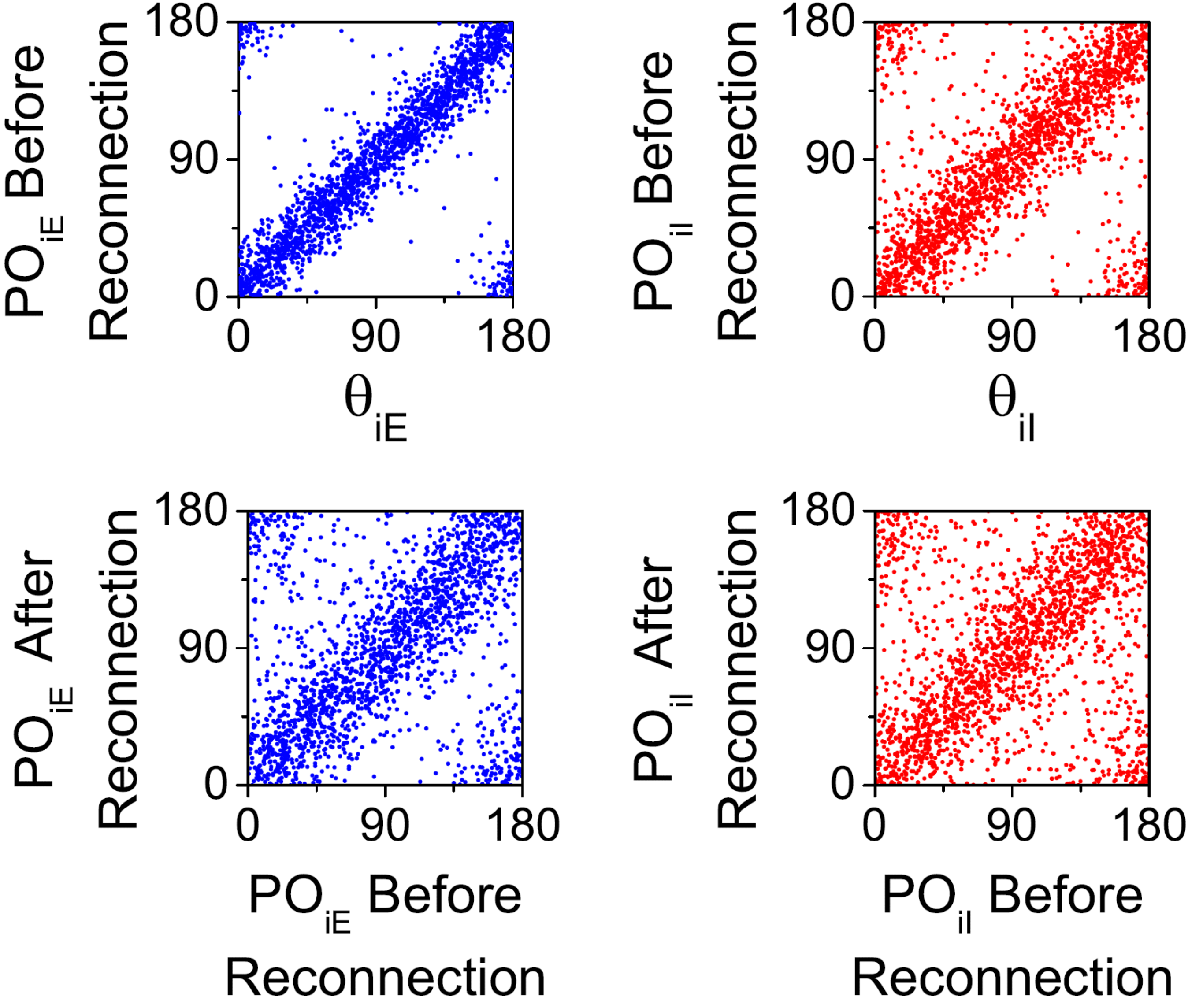
If the balanced state becomes unstable, selectivity can be increased by generating functional connectivity in the excitatory interactions.

Conclusions

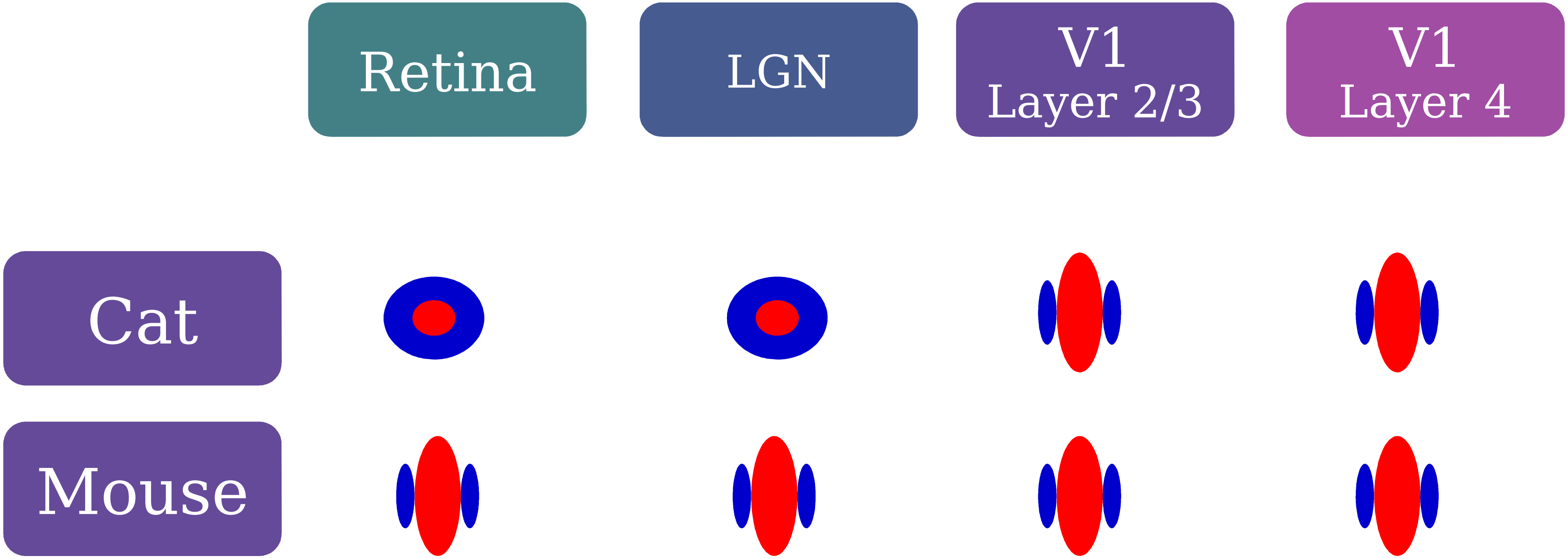
- Does functional connectivity improves orientation selectivity?
- It depends on the dynamical state!

- In the balanced state selectivity increases by decreasing the modulation of the connectivity profile.
- Salt and Pepper is more selective than Orientation Map for the same feed-forward input.
- Since STDP increases the mean value of the connectivity profile, it improves selectivity.
- It is necessary to get more information about functional connectivity of inhibitory interactions


CUEVA
DEL
CIELO



PO$_{iE}$ Before Reconnection
180
90
0
0
90
180
θ_{iE}
PO$_{iI}$ Before Reconnection
180
90
0
0
90
180
θ_{iI}
PO$_{iE}$ After Reconnection
180
90
0
0
90
180
PO$_{iE}$ Before Reconnection
PO$_{iI}$ After Reconnection
180
90
0
0
90
180
PO$_{iI}$ Before Reconnection



	Retina	LGN	V1 Layer 2/3	V1 Layer 4
Cat				
Mouse				

Scholl et al., 2013