



# Hold that thought: neural circuits supporting persistent percepts

Shaul Druckmann and Dmitri "Mitya" Chklovskii

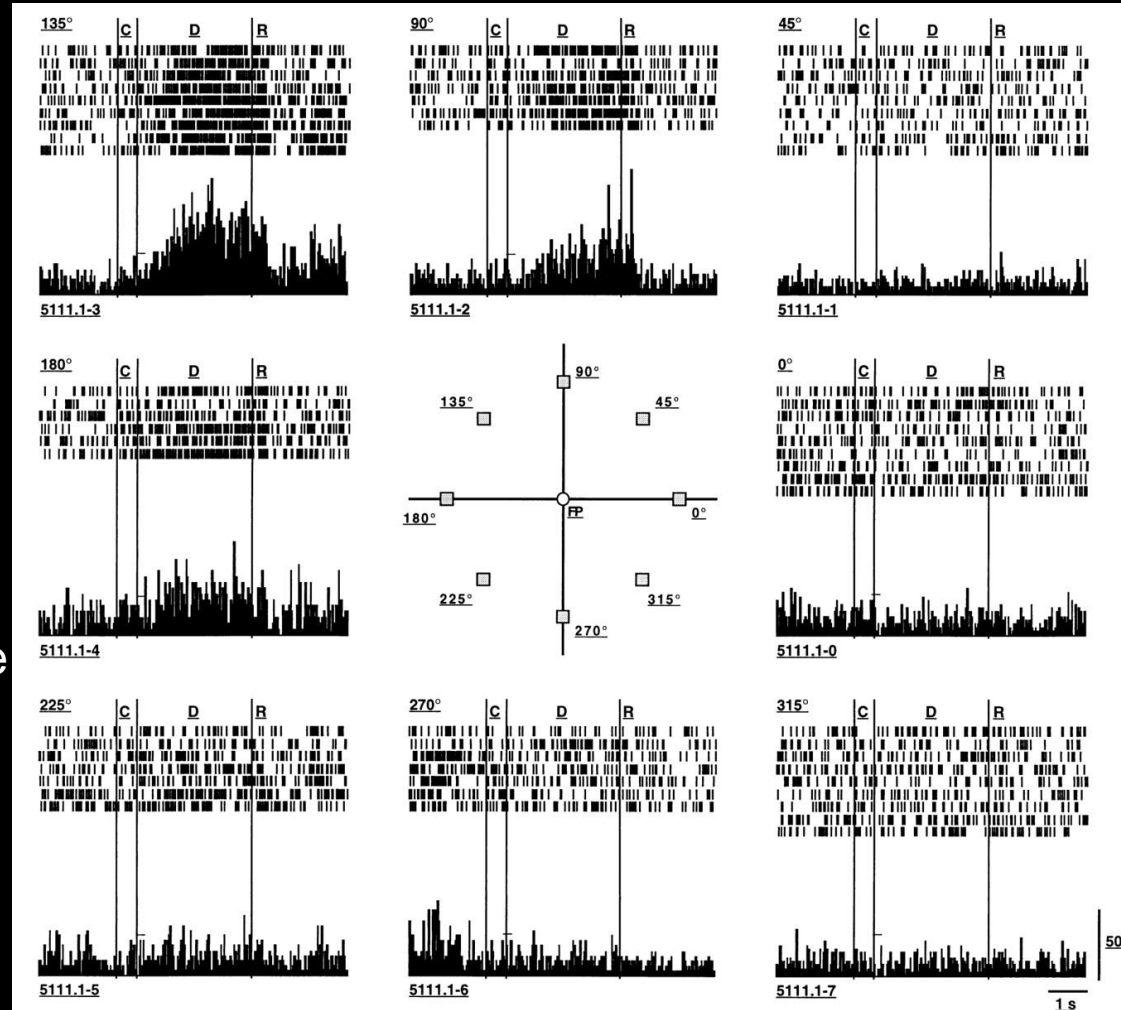
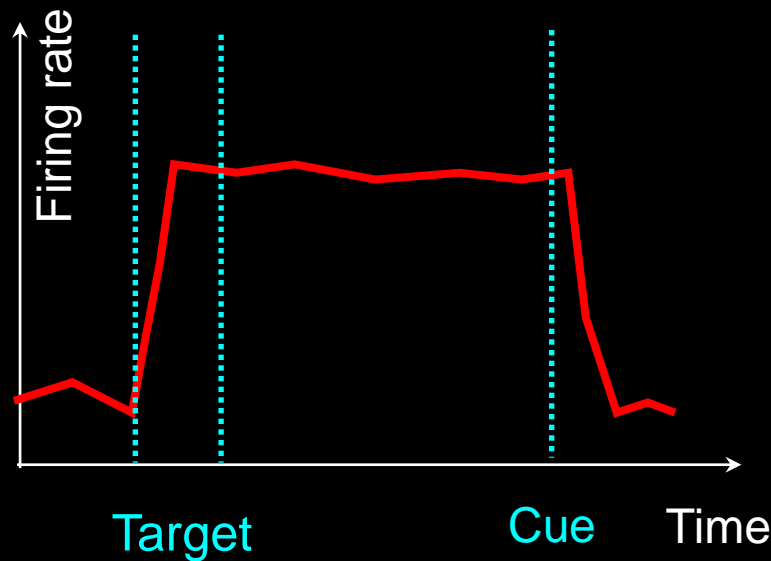
*Janelia Farm*

*Howard Hughes Medical Institute*

# Working memory task

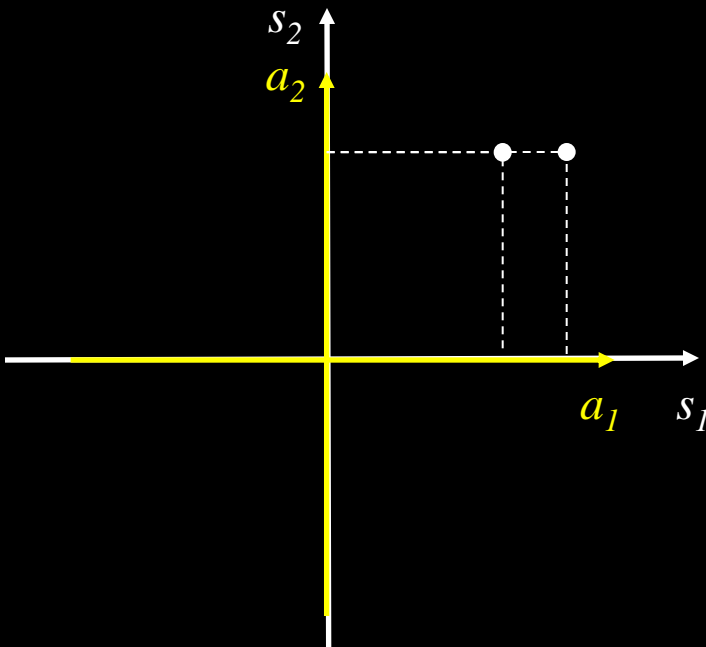


# Conventional explanation: stimulus memory, or percept, is maintained by persistent activity



Goldman-Rakic P PNAS 1996;93:13473-13480

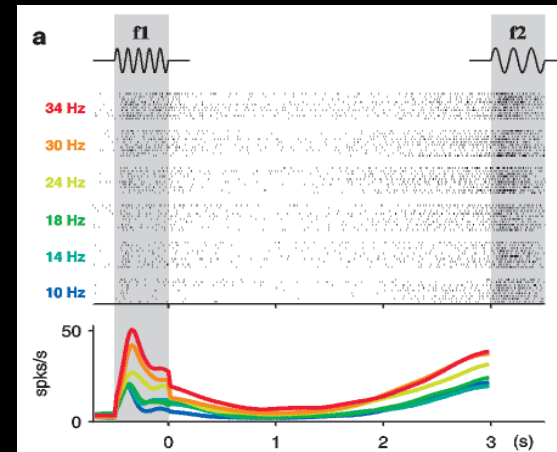
# Representation of a sensory percept with neuronal activity



Orthogonal representation

Sensory dimensions: 2

Number of neurons, or activity dimensions: 2



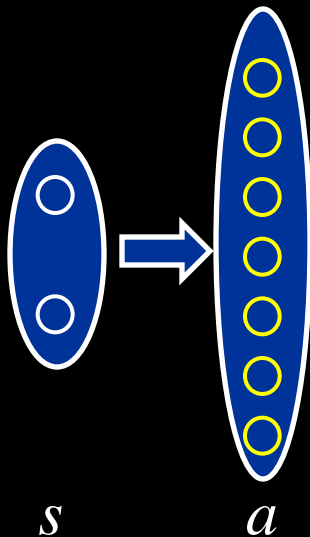
*Brody, Hernandez, Zainos, Romo (2003)*

How can time-varying neuronal activity  
support persistent percepts?

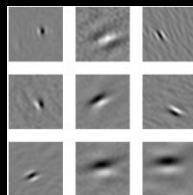
# Redundant neural representations

## Primary visual cortex

# thalamic  $\ll$  # cortical  
inputs neurons



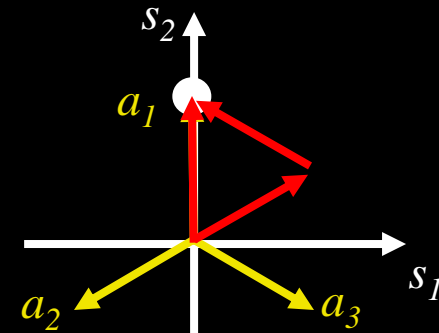
Non-orthogonal receptive fields  
in monkey V1 (*Ringach*):



## The Mercedes-Benz frame

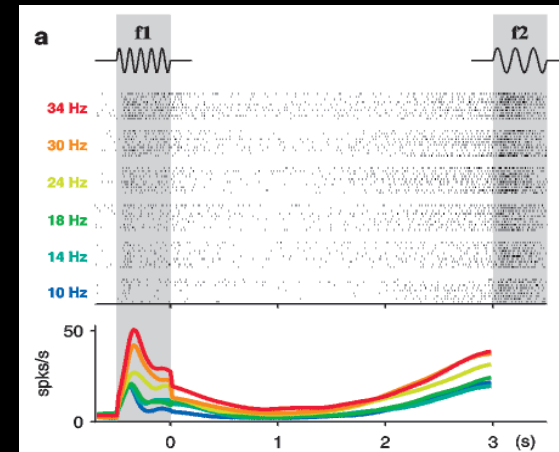
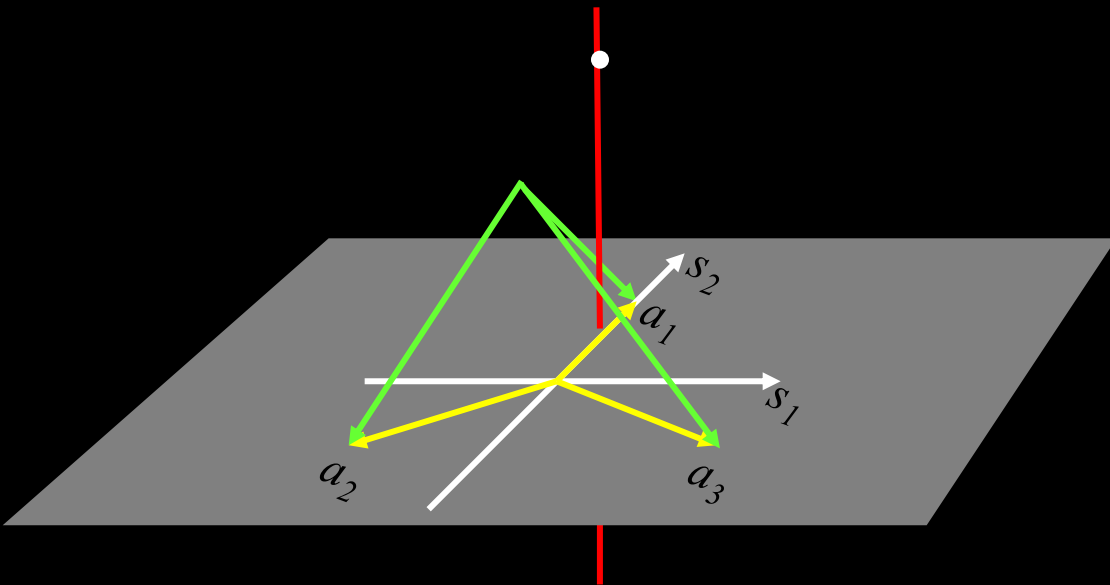
$s$  - sensory percept: 2 dimensions

$a$  - neural activity: 3 dimensions



$$\begin{aligned}
 \bullet &= a_1 \times \begin{array}{|c|} \hline \uparrow \\ \hline \end{array} + a_2 \times \begin{array}{|c|} \hline \swarrow \\ \hline \end{array} + a_3 \times \begin{array}{|c|} \hline \searrow \\ \hline \end{array} \\
 \uparrow &= 1 \times \begin{array}{|c|} \hline \uparrow \\ \hline \end{array} + 0 \times \begin{array}{|c|} \hline \swarrow \\ \hline \end{array} + 0 \times \begin{array}{|c|} \hline \searrow \\ \hline \end{array} \\
 \uparrow &= 0 \times \begin{array}{|c|} \hline \uparrow \\ \hline \end{array} - 1 \times \begin{array}{|c|} \hline \swarrow \\ \hline \end{array} - 1 \times \begin{array}{|c|} \hline \searrow \\ \hline \end{array}
 \end{aligned}$$

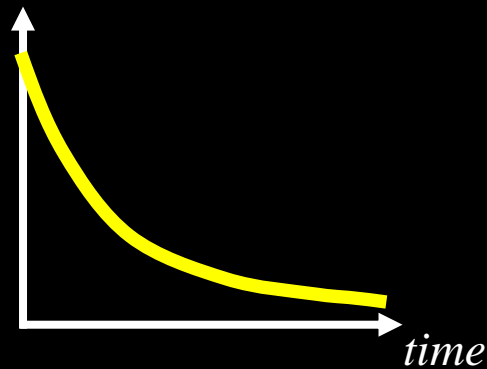
In a redundant representation, multiple neuronal activity patterns correspond to the same percept



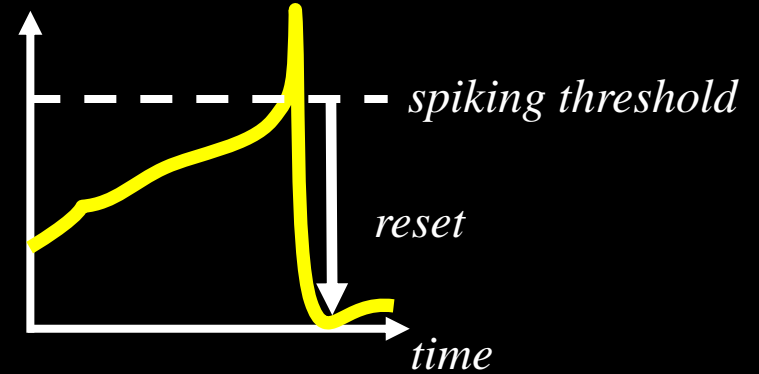
Brody, Hernandez, Zainos, Romo (2003)

How can percept-preserving dynamics be generated in neurons?

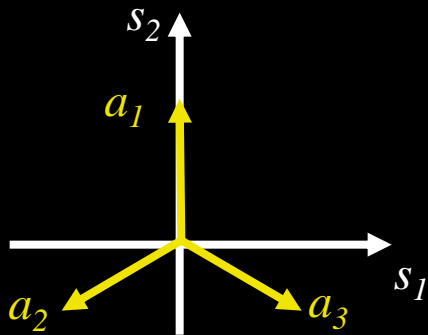
neuronal activity



membrane potential

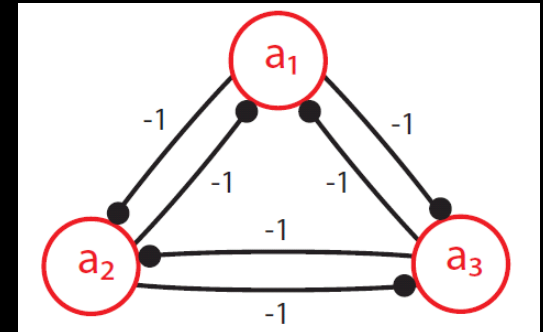


## A circuit supporting persistent percepts in the Mercedes-Benz frame

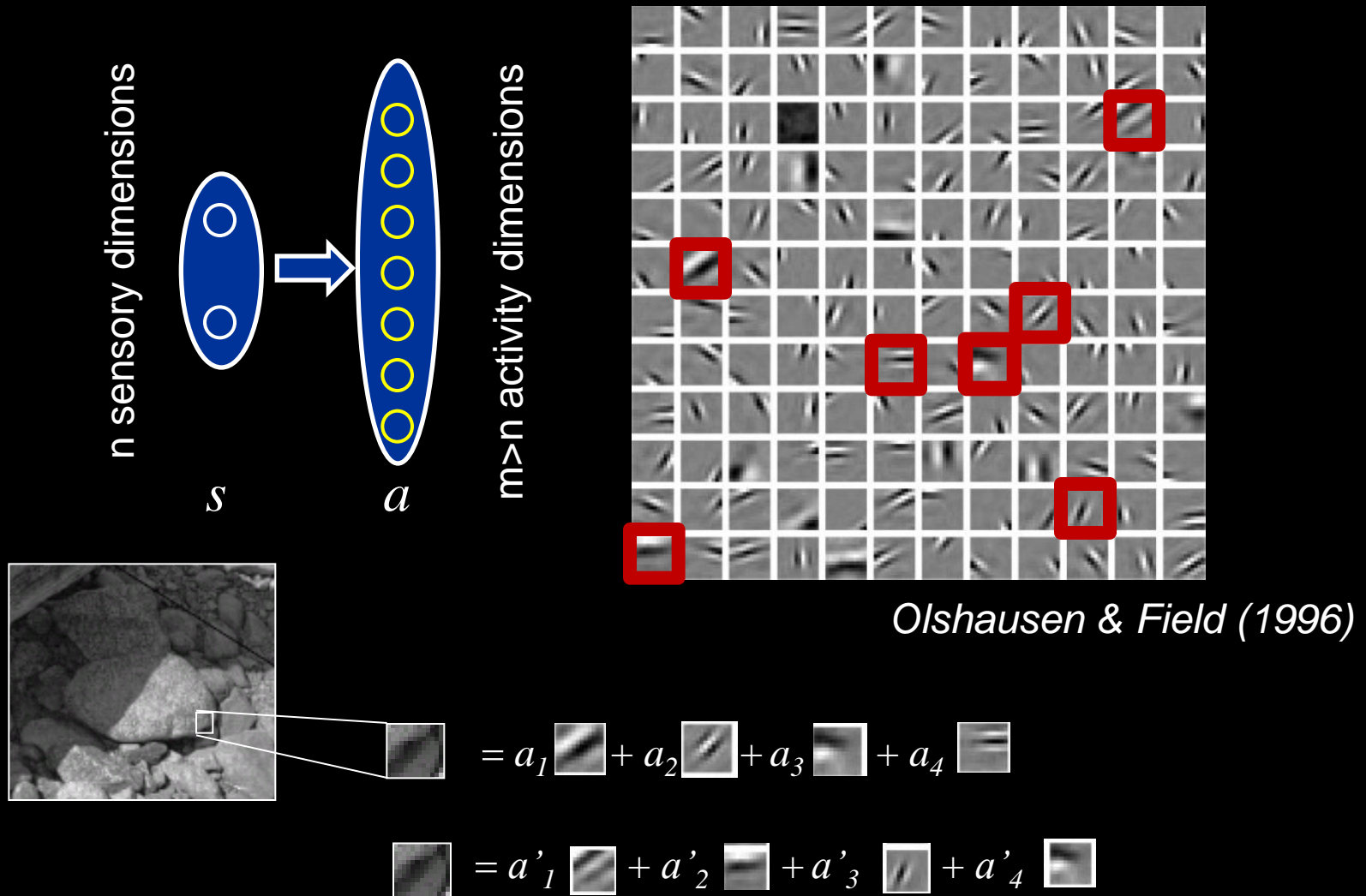


Vector re-expression

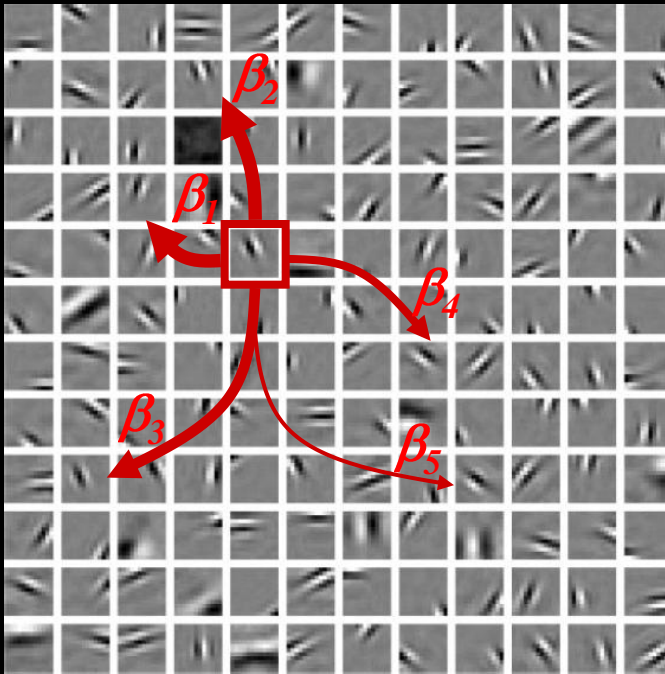
$$\uparrow = -1 \times \swarrow - 1 \times \searrow$$



# Representation of a visual percept as a linear combination of V1 feature vectors, or receptive fields



# Neural circuits supporting persistent percepts: REceptive Field REcombination (REFIRE) networks

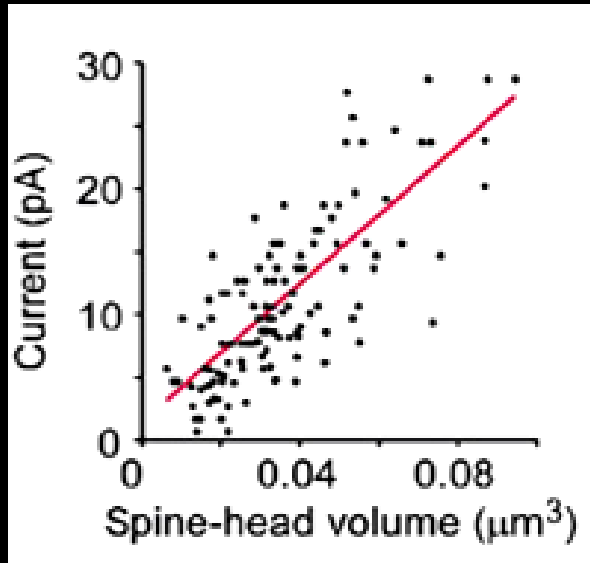


$$\boxed{\text{img}} = \beta_1 \boxed{\text{img}} + \beta_2 \boxed{\text{img}} + \beta_3 \boxed{\text{img}} + \beta_4 \boxed{\text{img}} + \beta_5 \boxed{\text{img}}$$

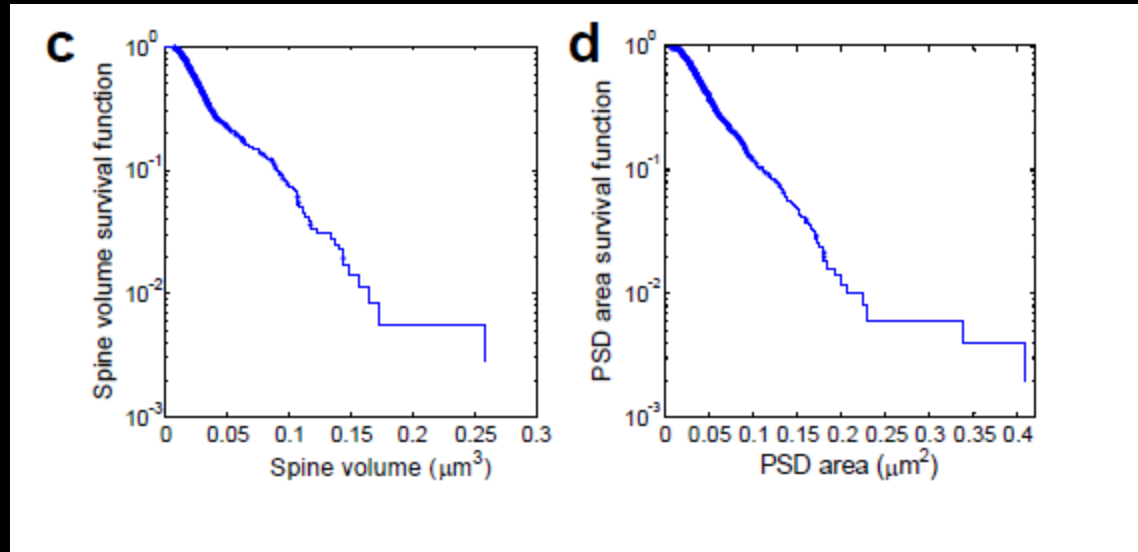
before reset of  $a_4$ :  $\boxed{\text{img}} = a_1 \boxed{\text{img}} + a_2 \boxed{\text{img}} + a_3 \boxed{\text{img}} + a_4 \boxed{\text{img}}$

after reset of  $a_4$ :  $\boxed{\text{img}} = a_1 \boxed{\text{img}} + a_2 \boxed{\text{img}} + a_3 \boxed{\text{img}} + a_4 ( \beta_1 \boxed{\text{img}} + \beta_2 \boxed{\text{img}} + \beta_3 \boxed{\text{img}} + \beta_4 \boxed{\text{img}} + \beta_5 \boxed{\text{img}} )$

# Choosing a particular REFIRE network: economy of synaptic volume/weight



Matsuzaki, Ellis-Davies, Nemoto, Miyashita, Iino & Kasai (2001)



Mischenko, Hu, Spacek, Mendenhall, Harris, Chklovskii (2010)

$$\vec{\beta} = \text{argmin} \{ \sum_i |\beta_i| \} \text{ such that } \begin{bmatrix} \text{img} \end{bmatrix} = \beta_1 \begin{bmatrix} \text{img} \end{bmatrix} + \beta_2 \begin{bmatrix} \text{img} \end{bmatrix} + \beta_3 \begin{bmatrix} \text{img} \end{bmatrix} + \beta_4 \begin{bmatrix} \text{img} \end{bmatrix} + \beta_5 \begin{bmatrix} \text{img} \end{bmatrix}$$

# Sparsest REFIRE network computed for V1 feature vectors

Choose a sparse decomposition of feature vectors that minimizes total synaptic weight, or volume cost:

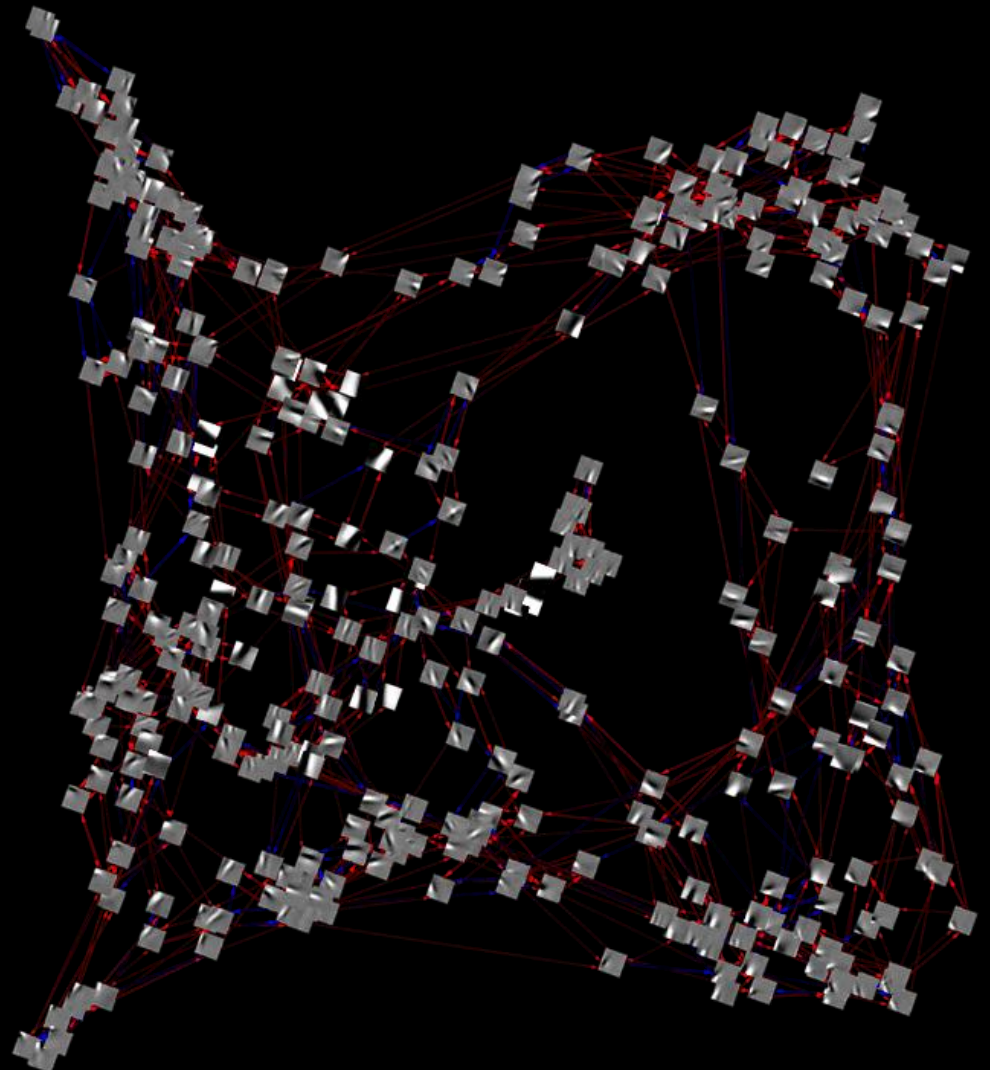
$$\mathbf{D}_j = \mathbf{d}_1, \mathbf{d}_2, \dots, \mathbf{d}_{j-1}, \mathbf{d}_{j+1} \dots \mathbf{d}_m$$

$$\beta_j^* = \min_{\beta_j \in \mathcal{R}^{m-1}} \|\mathbf{d}_j - \mathbf{D}_j \beta_j\|_2^2 + \lambda_1 \|\beta_j\|_1$$

$$\mathbf{L} = [\tilde{\beta}_1, \tilde{\beta}_2, \dots, \tilde{\beta}_m]$$

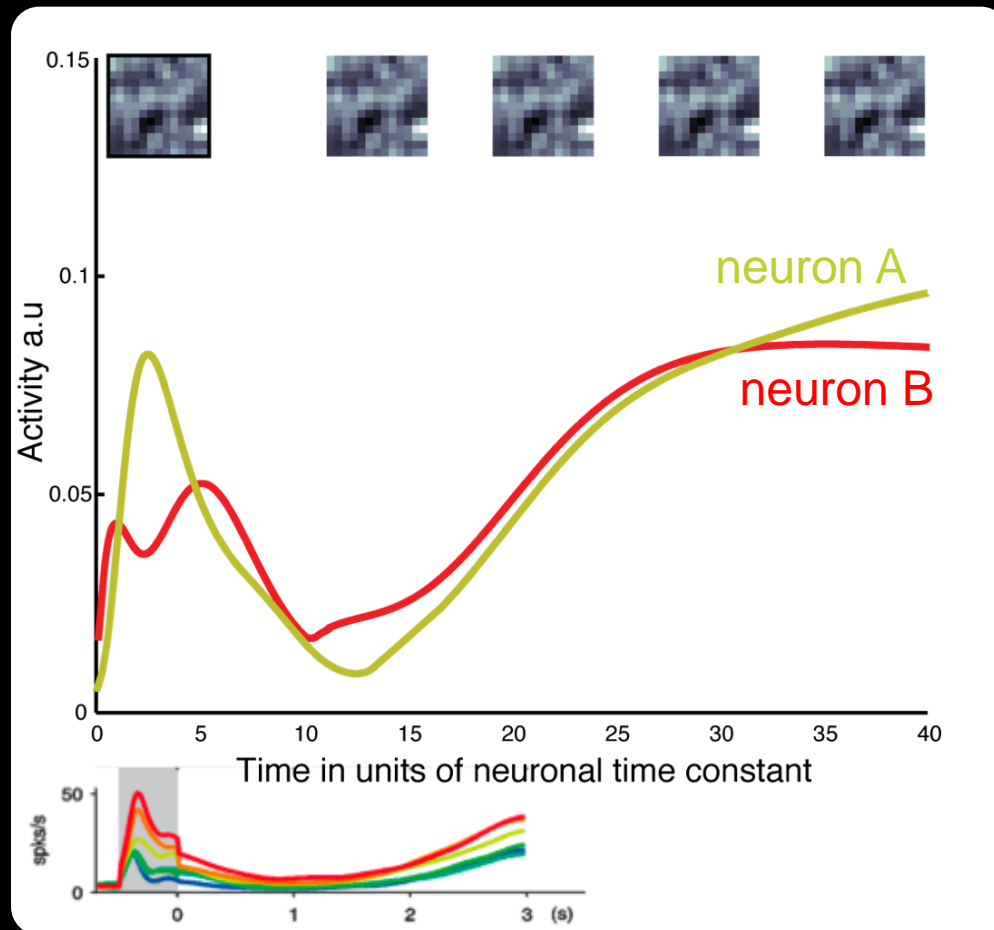
Weights computed using SPAMS package (*Mairal et al.*)

→  
excitatory  
→  
inhibitory

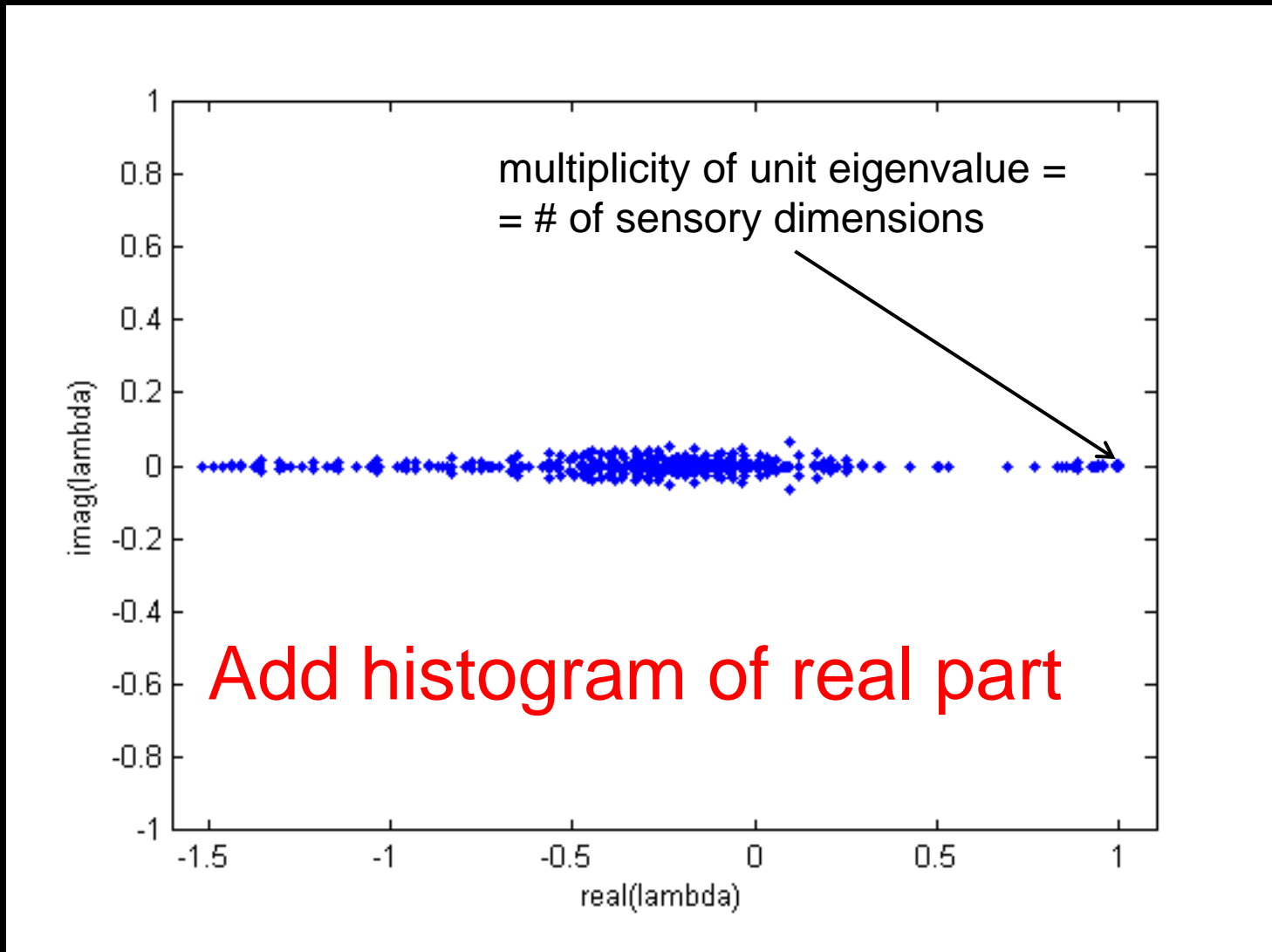


Only 10% of strongest connections are shown

# Computer simulations: despite varying activity, percepts persist



# Eigenspectrum of the sparsest REFIRE network



$\beta = \operatorname{argmin} \{ \sum_i |\beta_i| \}$  shrinks Gershgorin circles restricting eigenvalue moduli to 1

# Persistent percepts with non-linear dynamics

$$\begin{cases} s = D a \\ \dot{a} = (L - I) f \\ f = \text{spike}(a, 1) \end{cases}$$

$s$  - sensory inputs ( $n$ )  
 $D$  - over-complete dictionary  
 $a$  - sub-threshold voltage ( $m > n$ )  
 $L$  - lateral connectivity matrix  
 $f$  - supra-threshold voltage

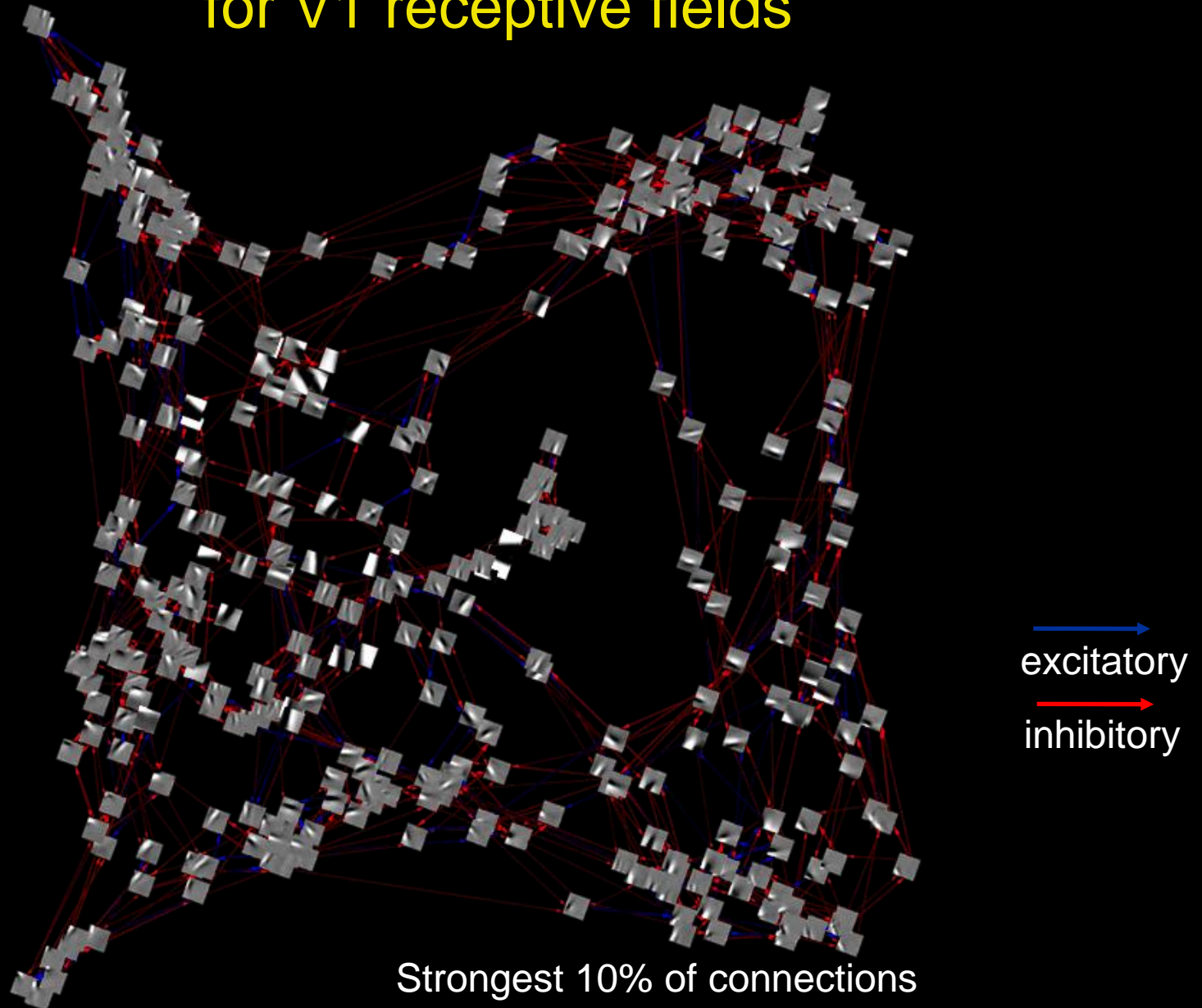
$$\text{spike}(a(\tau_0), 1) = \begin{cases} 0, & a(\tau_0) < 1 \\ \delta(\tau - \tau_0), & a(\tau_0) \geq 1 \end{cases}$$

$$\dot{s} = D \dot{a} = D(L - I) f = 0$$

## Dynamical properties of the sparsest REFIRE circuit may account for several poorly understood properties of cortical networks

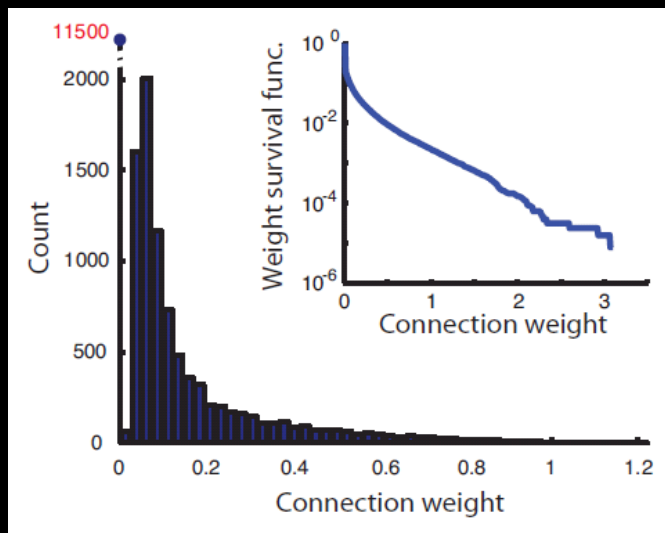
- Wide distribution of firing rates (*Koulakov, Hromadka & Zador, 2009*)
- Spike counts have high coefficient of variation (*Softky & Koch, 1993*)
- “Weak thalamic input” dominates neuronal responses despite much more numerous recurrent cortical connections (*Douglas, Koch, Machowald, Martin & Suarez, 1995*)

# Sparsest REFIRE circuit computed for V1 receptive fields

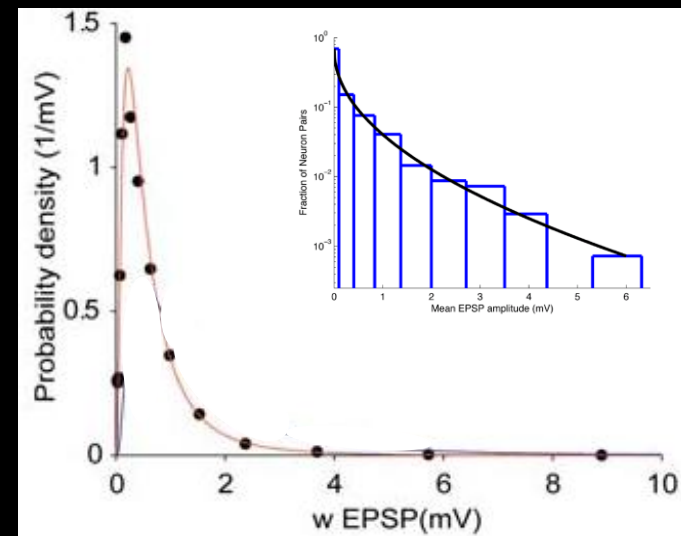


# Distribution of connection weights

Model network



Experiment: rat visual cortex



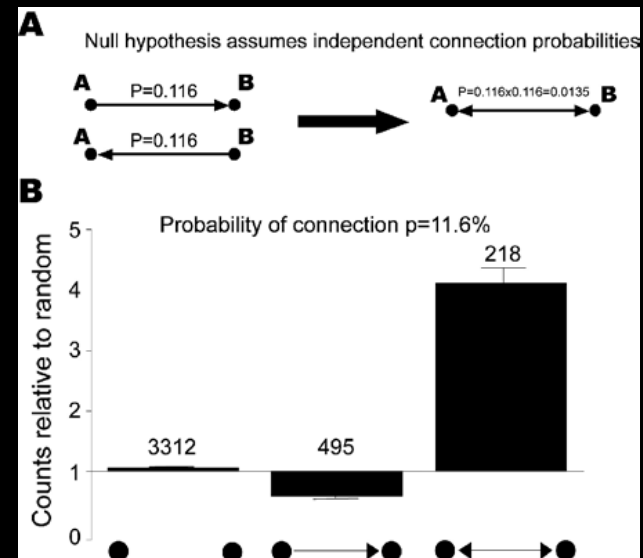
*Song, Sjostrom, Reigl, Nelson, Chklovskii (2005)*

# Frequency of reciprocal connections matches experiments

Model network

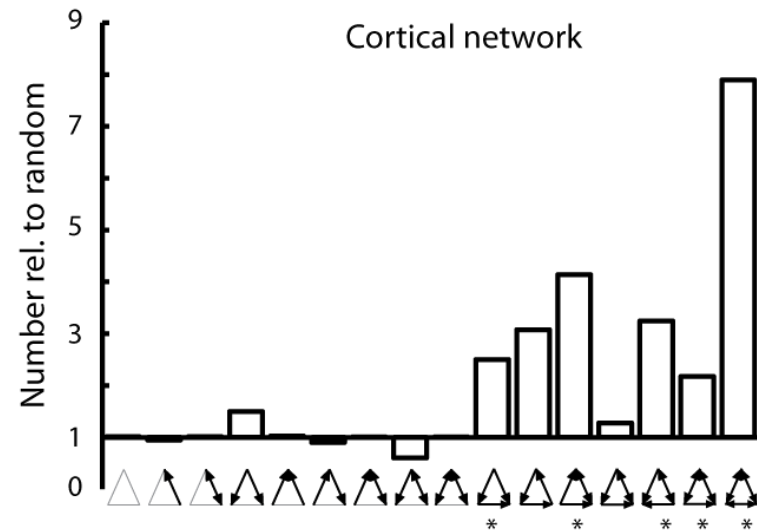
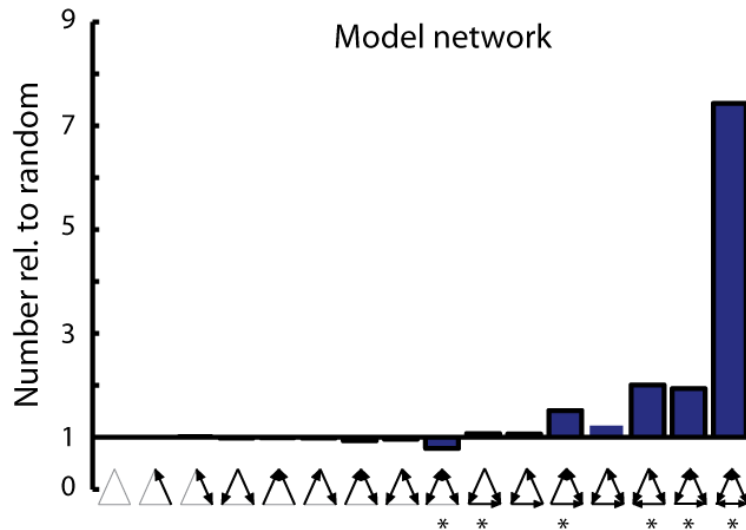
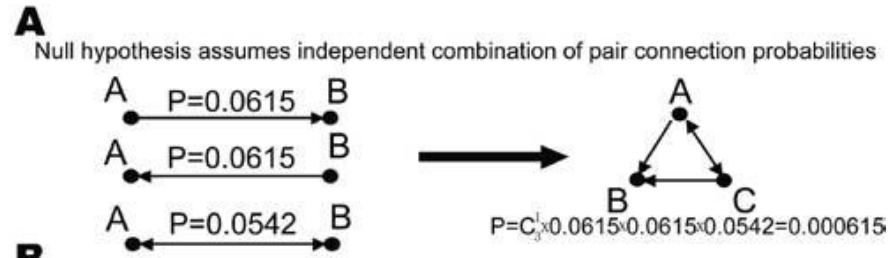
Experiment: rat visual cortex

$$P_{\Rightarrow} = 0.09 \quad P_{\Leftrightarrow} = 0.03$$



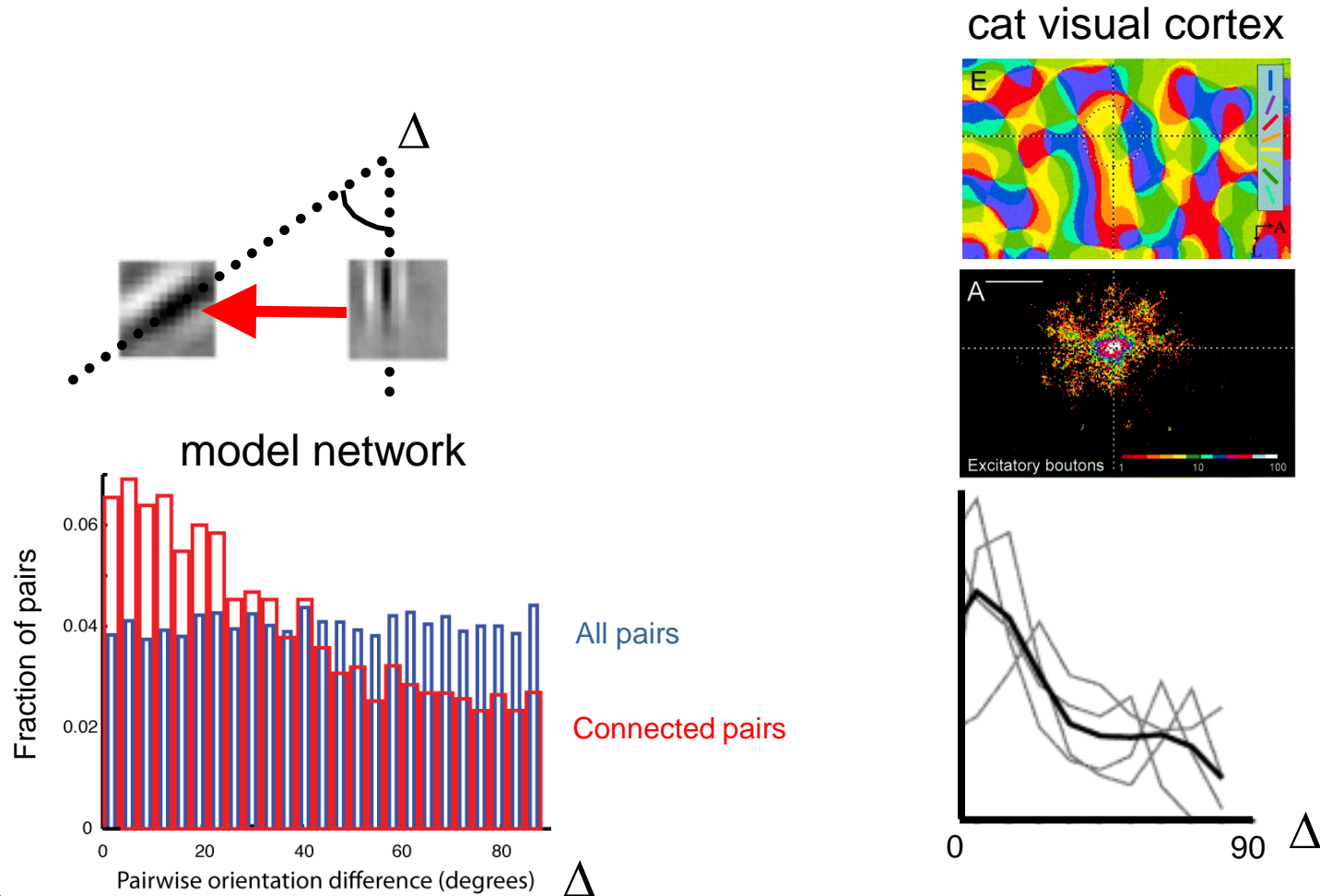
*Song, Sjöström, Reigl, Nelson, Chklovskii (2005)*

# Network motifs match experiments

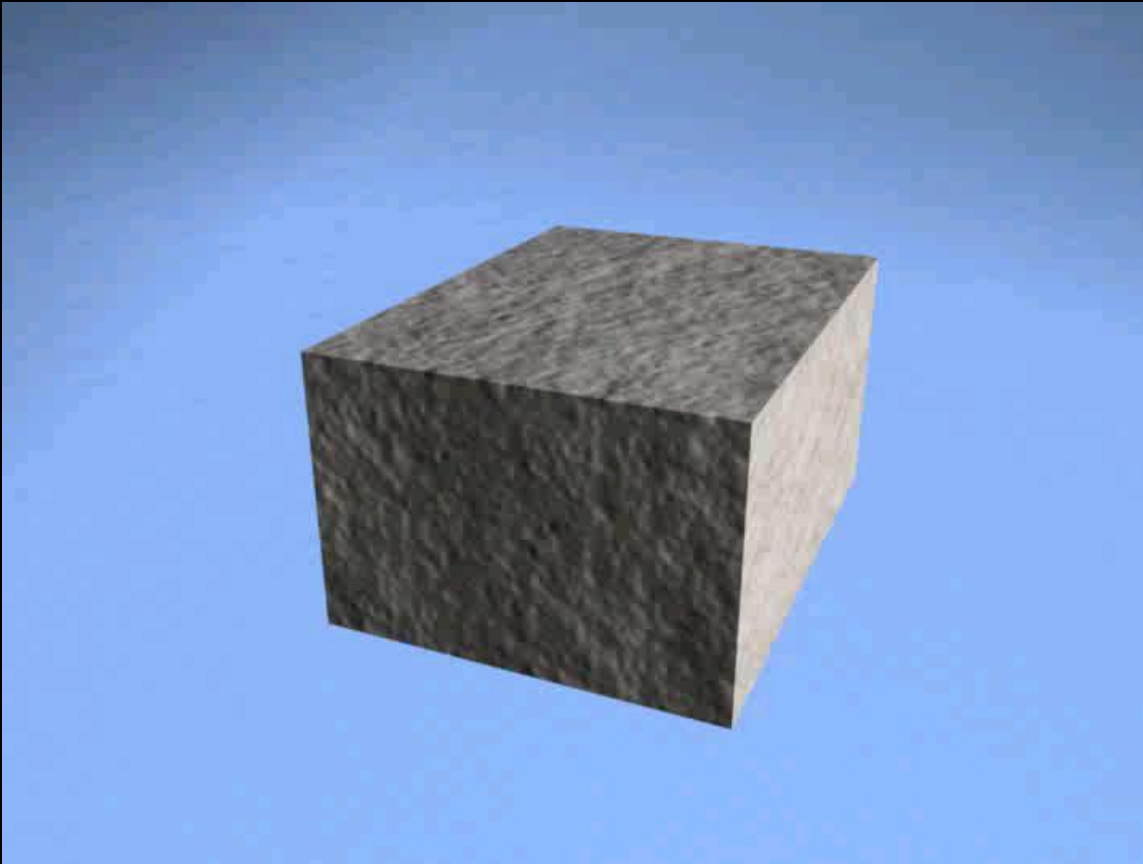


Song, Sjostrom, Reigl, Nelson, Chklovskii (2005)

# Orientation preference of lateral connections



# Reconstruction of neural circuits using electron microscopy (EM)

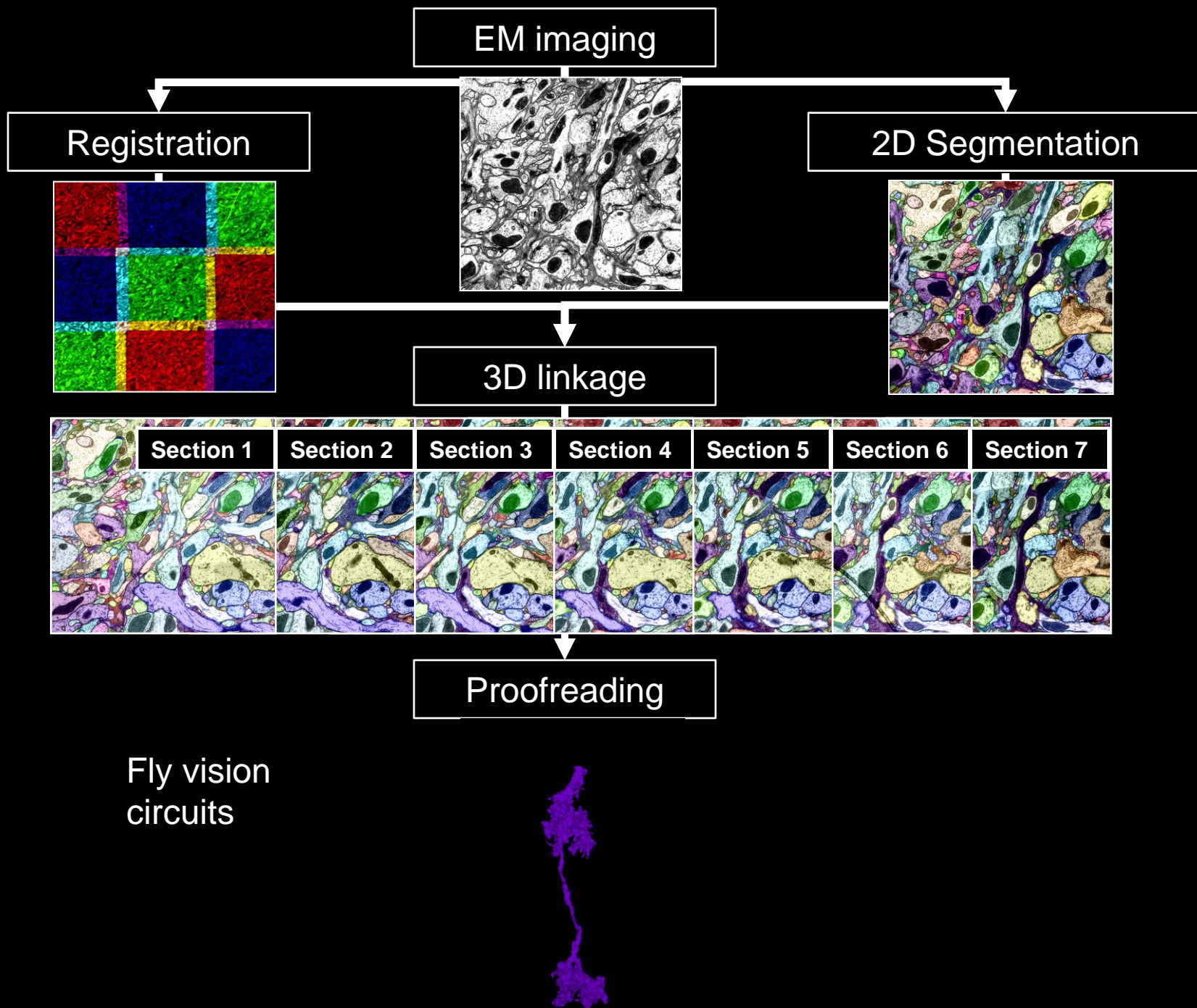


Volume  $10 \times 10 \times 10$  micron<sup>3</sup>

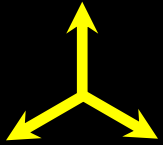
- Tissue preparation and sectioning ~ days
- Image acquisition ~ days
- Circuit reconstruction ~ year

Grand challenge for computer vision

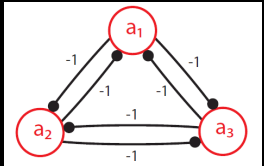
# *Janelia Farm reconstruction pipeline*



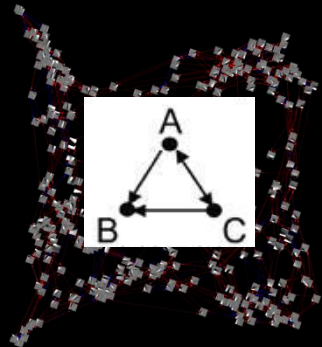
# Summary



In a redundant representation, some changes in activity do not change the percept. Such decoupling of representation and activity offers computational advantages



Contribution of a neuron to a representation lost to post-spiking reset, or leakiness, can be compensated by distributing activity to other neurons via appropriately weighted connections (REFIRE circuit)



Sparsest REFIRE circuit shares many anatomical and physiological properties with the cortical network in V1 and other cortical areas

Test the REFIRE hypothesis by large scale circuit reconstructions

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Stephan Saalfeld

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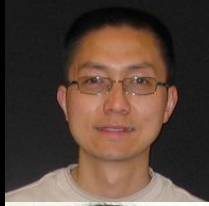
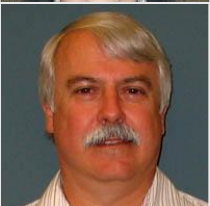
Pat Rivlin

Bruce Kimmel

Reed George

Victor Shapiro

Margaret Jefferies



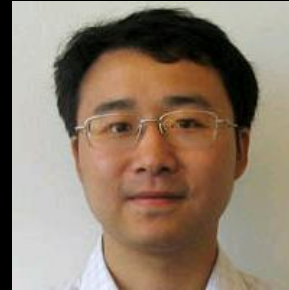
# The Chklovskii group



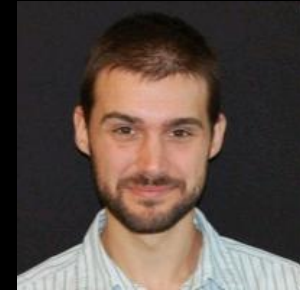
**Arjun  
Bharioke**



**Shaul  
Druckmann**



**Tao Hu**



**Juan Nunez-  
Iglesias**



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