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# The Quest for the Emergent Brain

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Keynote Address
19th Satellite Meeting on Dynamical Neuroscience
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"The whole is greater than the sum of its parts."

Aristotle

"The whole is greater than the sum of its parts."

Aristotle

## Emergent phenomena in complex systems:

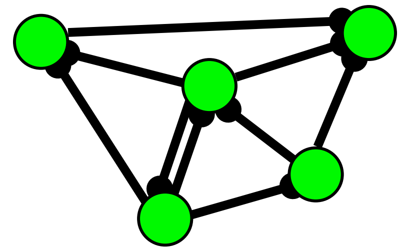
- Many strongly interacting degrees of freedom
- Multiple scales/levels
- Nonlinear
- Noisy
- Phase transition/bifurcation
- Surprising/unexpected
- Spontaneous, self-organized, pattern formation, adaptive,...

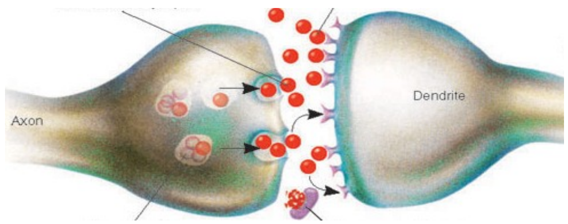
# Outline

1. Associative Memory in Attractor Networks
2. All-Or-None Rule Discovery
3. Emergence of Chaos in Large Scale Networks
4. Emergence of Excitation-Inhibition Balance
5. Emergence of Sensory Selectivity in Cortical Circuits

# 1. Associative Memory in Attractor Networks

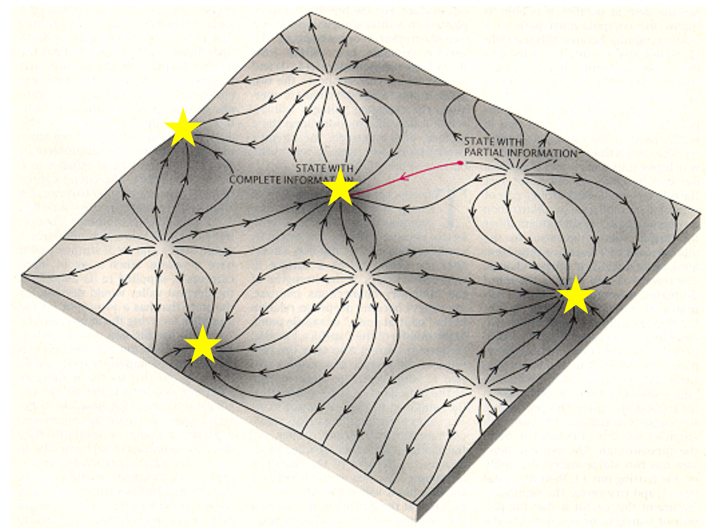
# Hopfield Model of Associative Memory






**Learning:**
Hebb Rule

When two cells fire together
the synapse between them strengthens

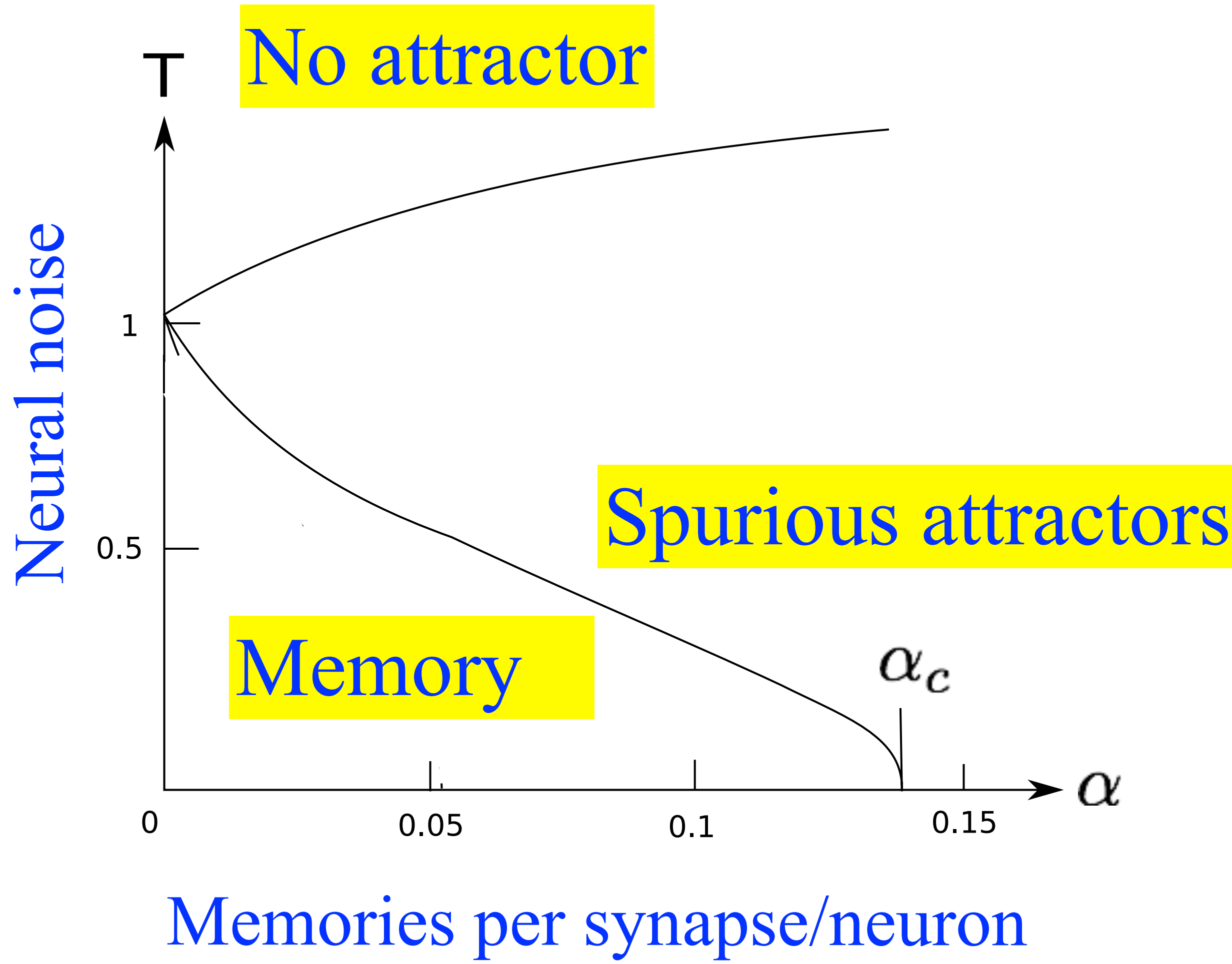



**Retrieval:**
Convergence to the memory attractor

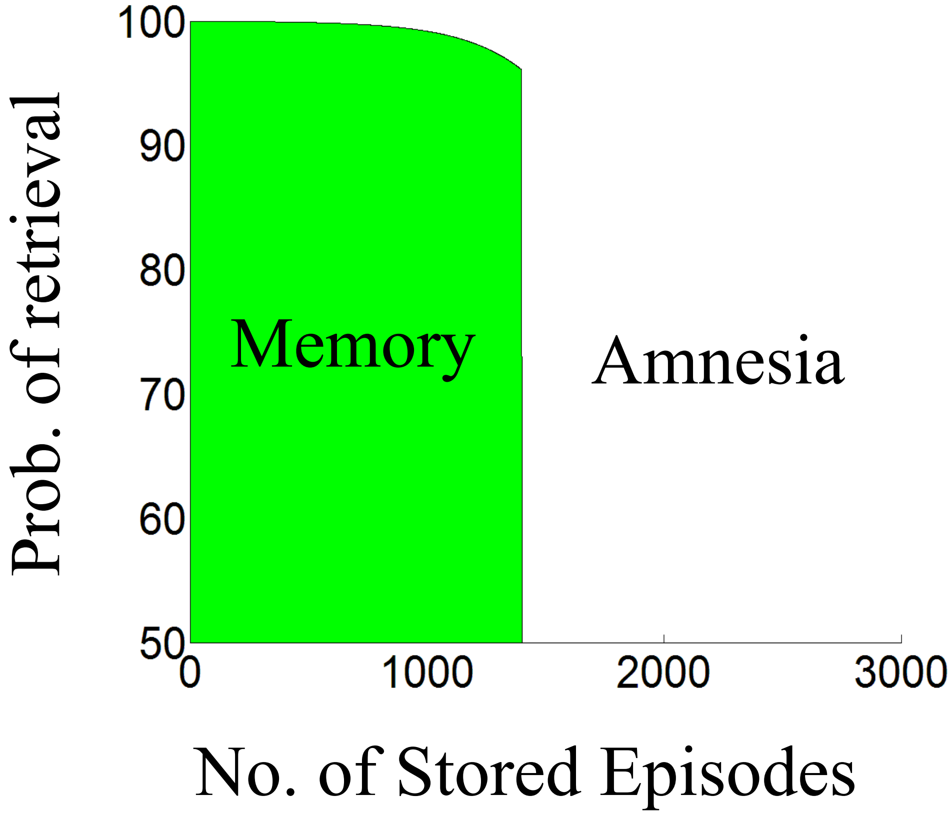
**Memory Capacity:**
Maximum Number of Stored Memories = 14% of the number of synaptic connections per neuron.

Amit, Gutfreund, HS , 1985

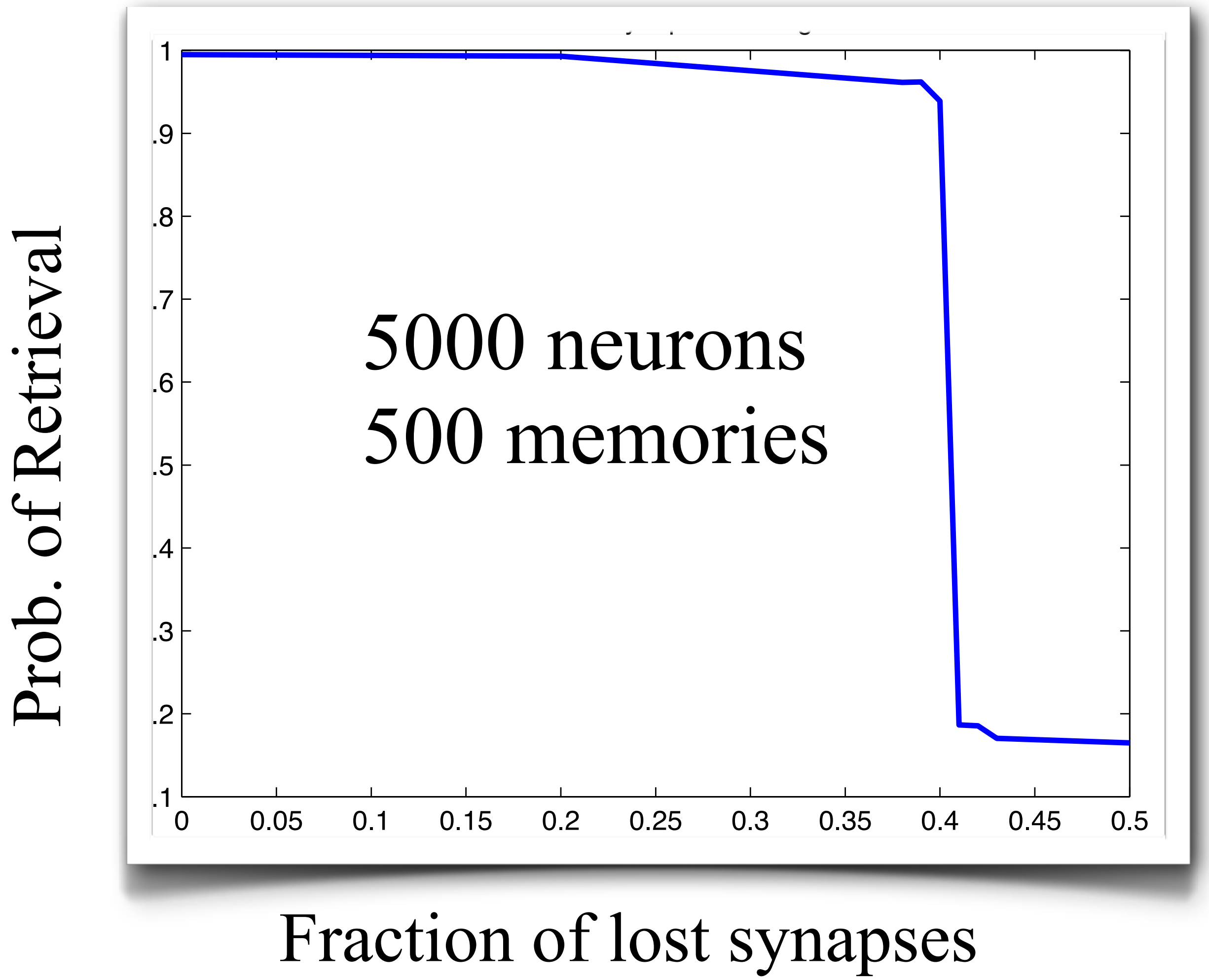
# Phase Diagram of Associative Memory Network



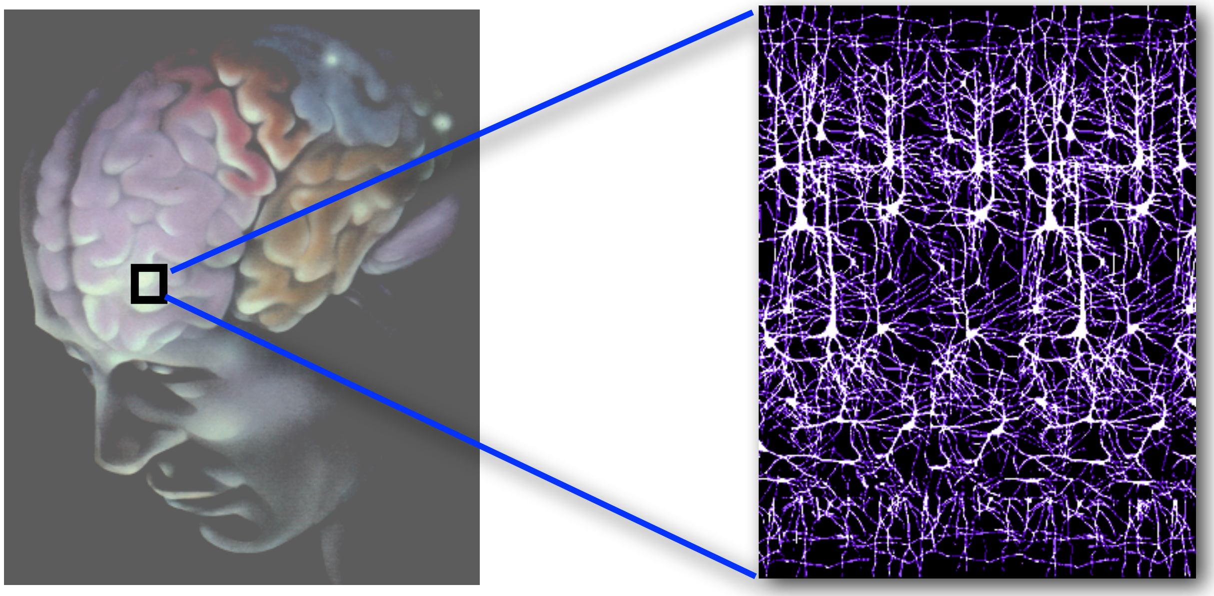
# Discontinuous Emergence of Memory Attractors



# Effect of Random Pruning of Cell/Synapses

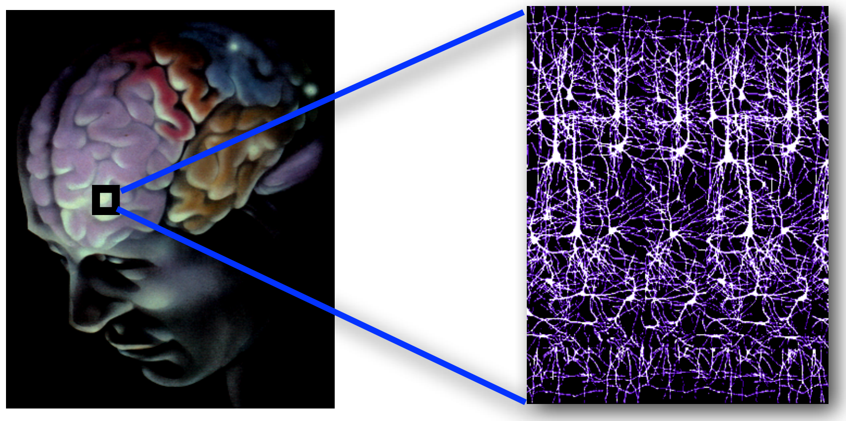


# Cortical Column in the Human Brain



- 100,000 neurons
- 10,000 synapses per neuron
- 4 km of wiring
- 1,400 memories
- 100,000 cells per memory

# Memory and the Human Brain

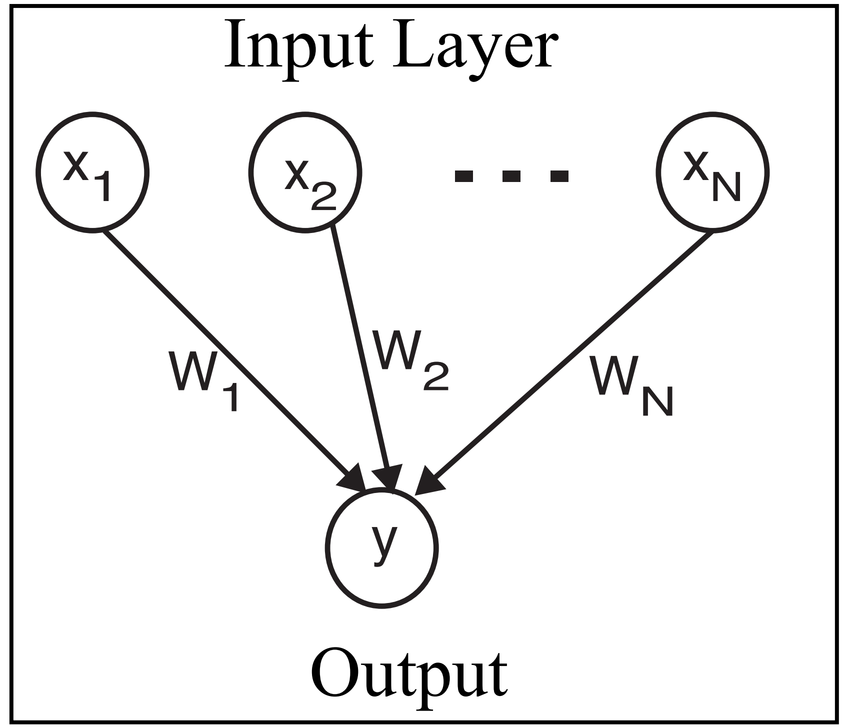


- 100 years = 36, 000 days
- 100 episodes per day
- 3,600,000 episodes=2,600 columns
- Human Cortex = 200,000 columns

# 2. All-Or-None Rule Discovery

# Sudden Rule Discovery

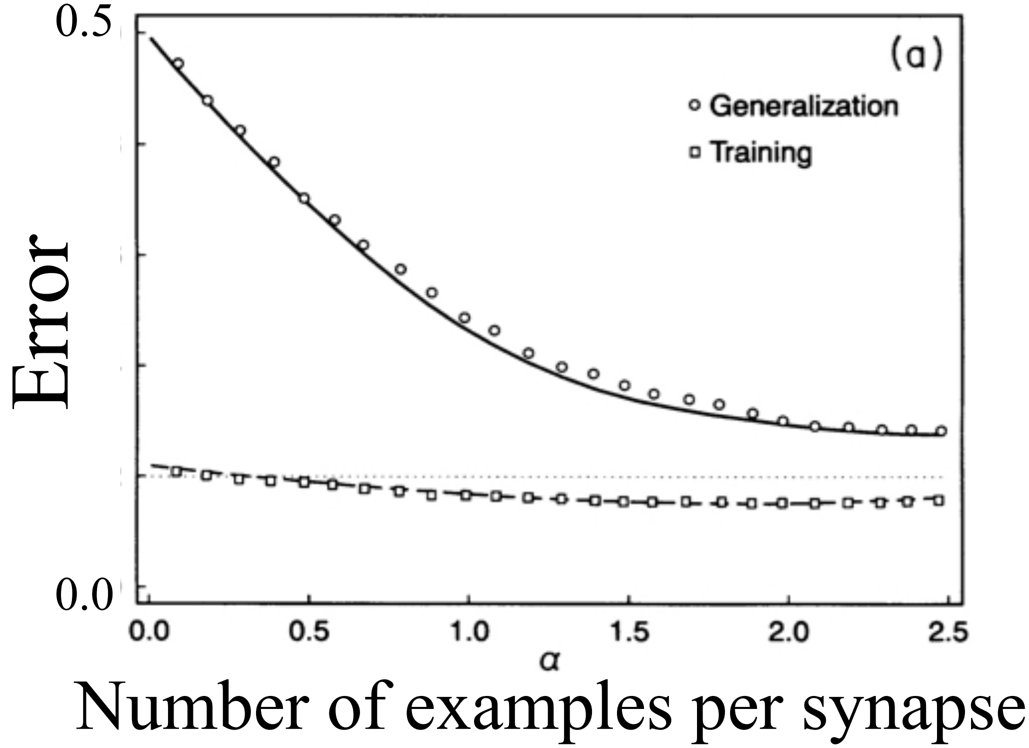
Binary Perceptron



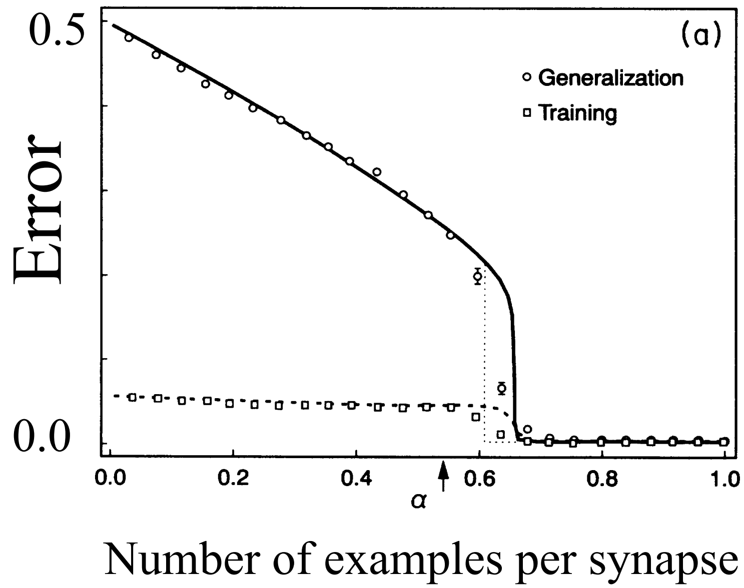

- Error-based noisy rule learning
- Rule is threshold linear
- Binary modifiable weights

Seung, Tishby, HS, 1990

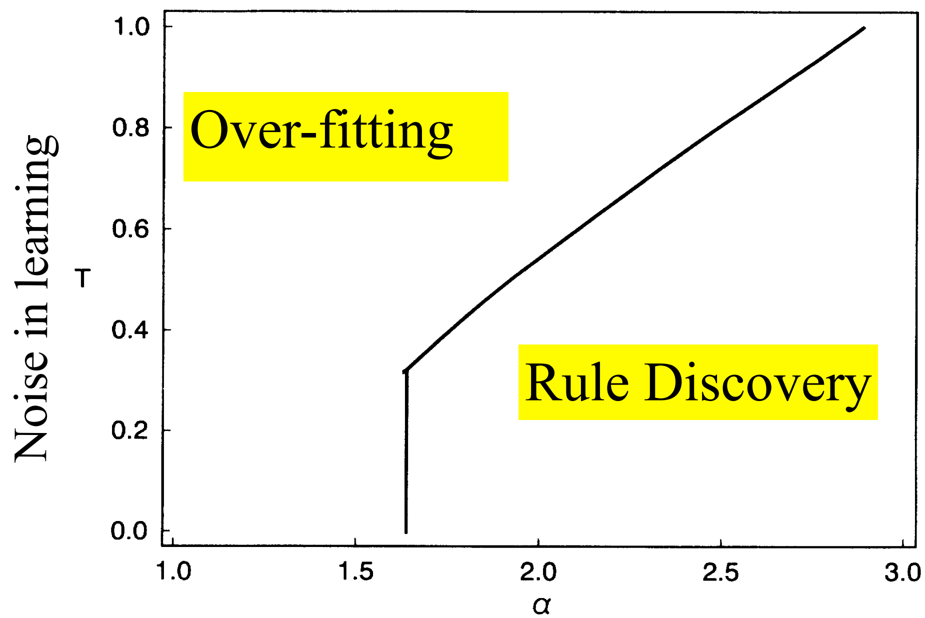
# Typical Learning Curve



# Binary Rule Learning-Phase Diagram

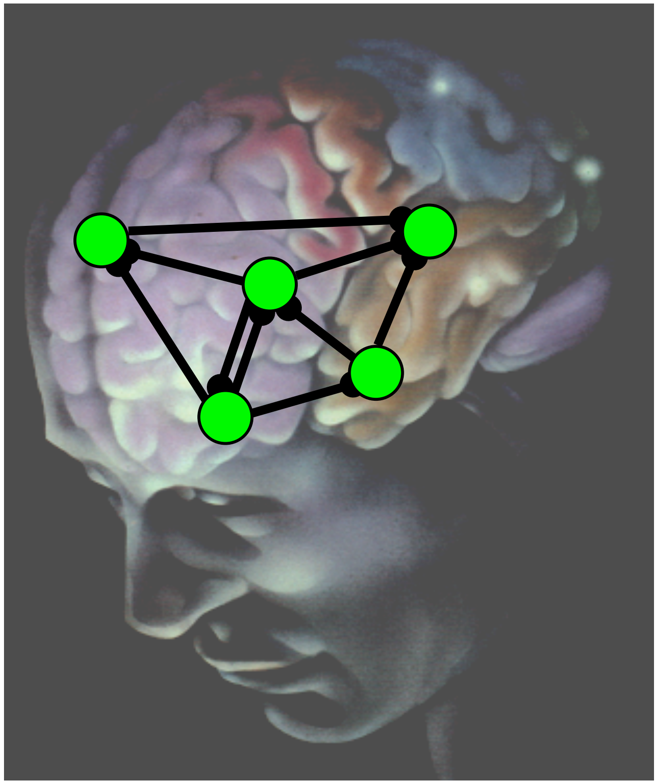



Nonlinear constraints on the weights give rise to a sudden transition to perfect generalization.



# 3. Emergence of Chaos in Large Scale Networks

# Emergence of Chaos in Large Scale Networks



$$\tau_0 \frac{dV_i}{dt} = -V_i + \sum_{j=1}^{N} W_{ij} g(V_j)$$

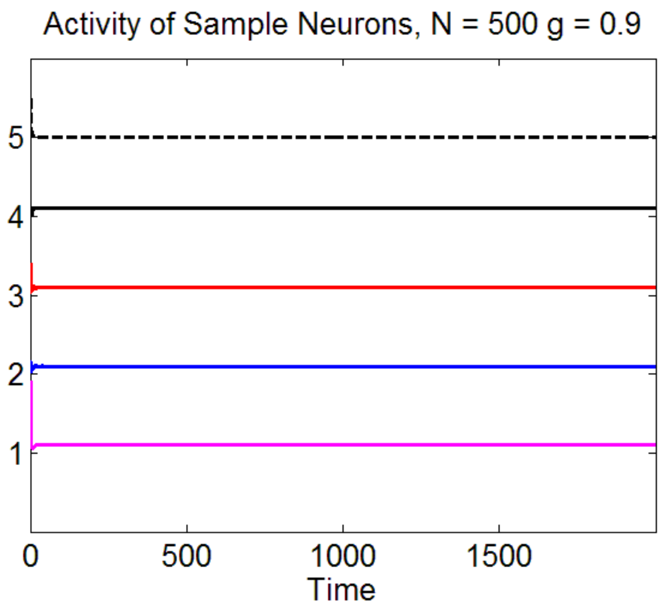
$V_i =$ Synaptic potential in a local column

Equal Strength of Excitatory and Inhibition $\sum_{j=1}^{N} W_{ij} \approx 0$

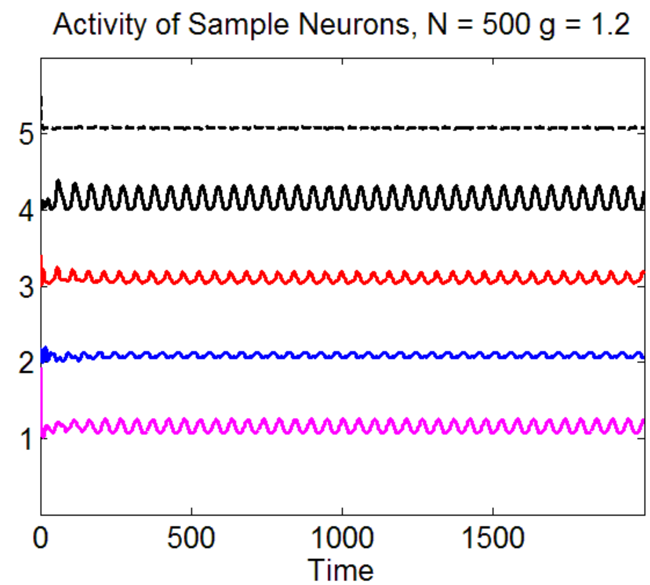
Synaptic Gain=g $\sum_{j=1}^{N} W_{ij}^2 = g^2$

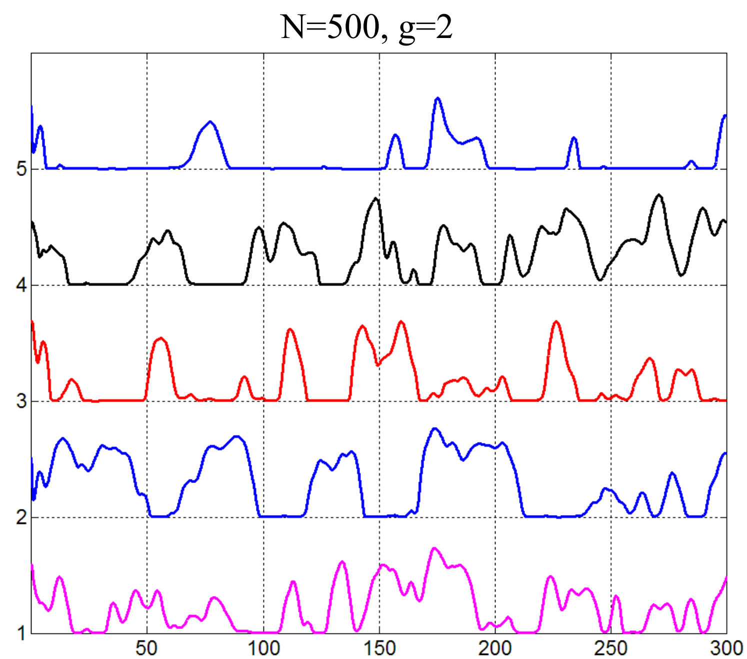
HS, Crisanti, Sommers, 1988

low gain, inactive

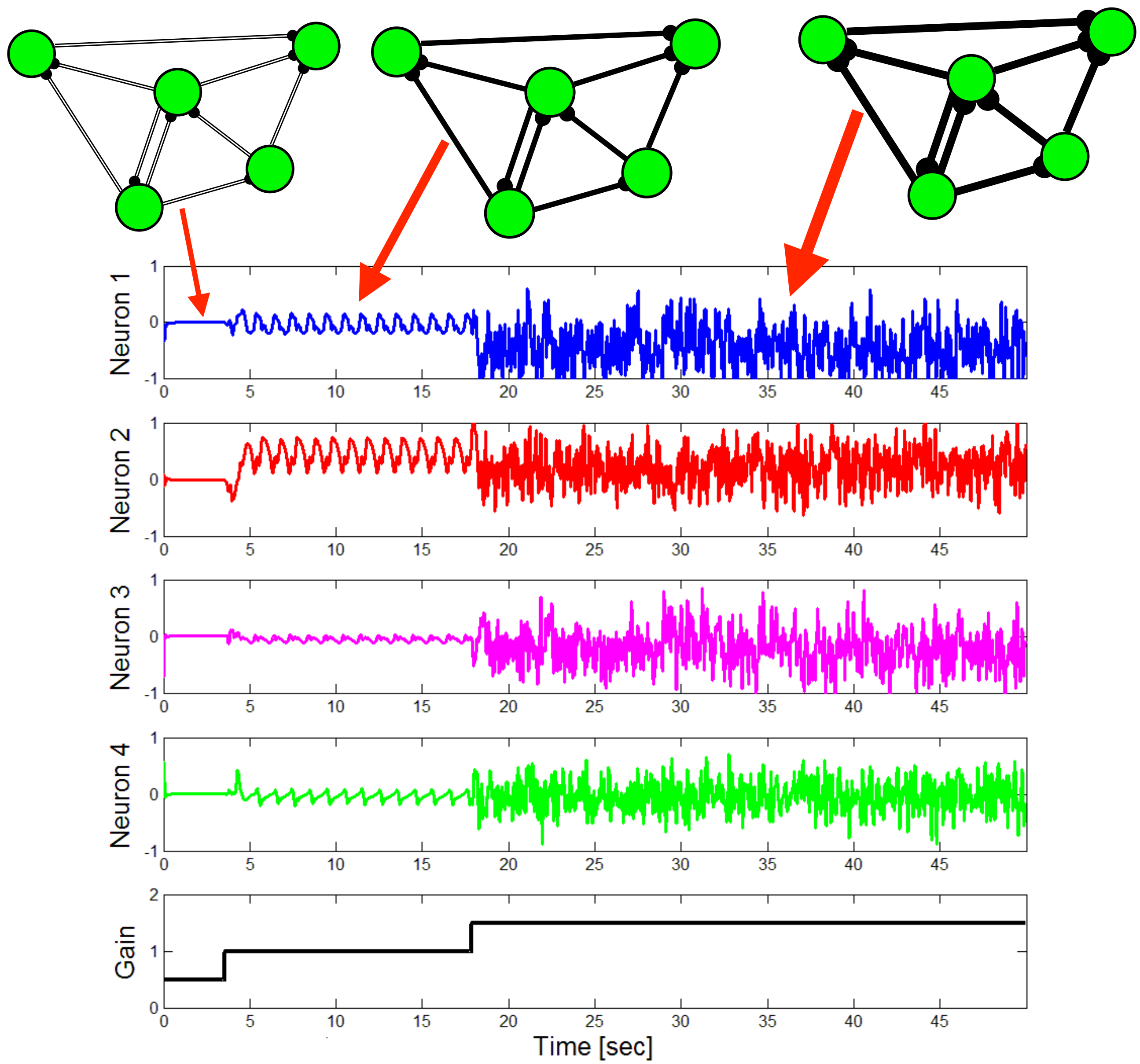



intermediate gain, oscillations



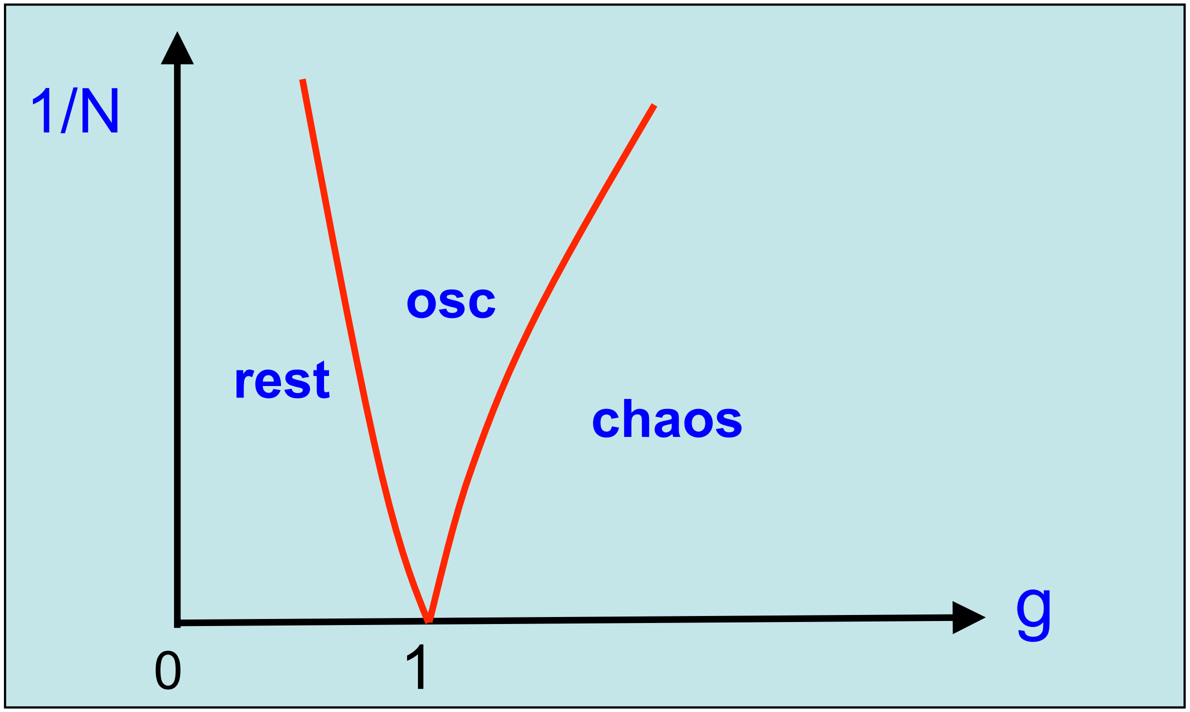

High gain, chaos


Neuron 1
Neuron 2
Neuron 3
Neuron 4
Gain
Time [sec]

## Phase Diagram of Onset of Chaos

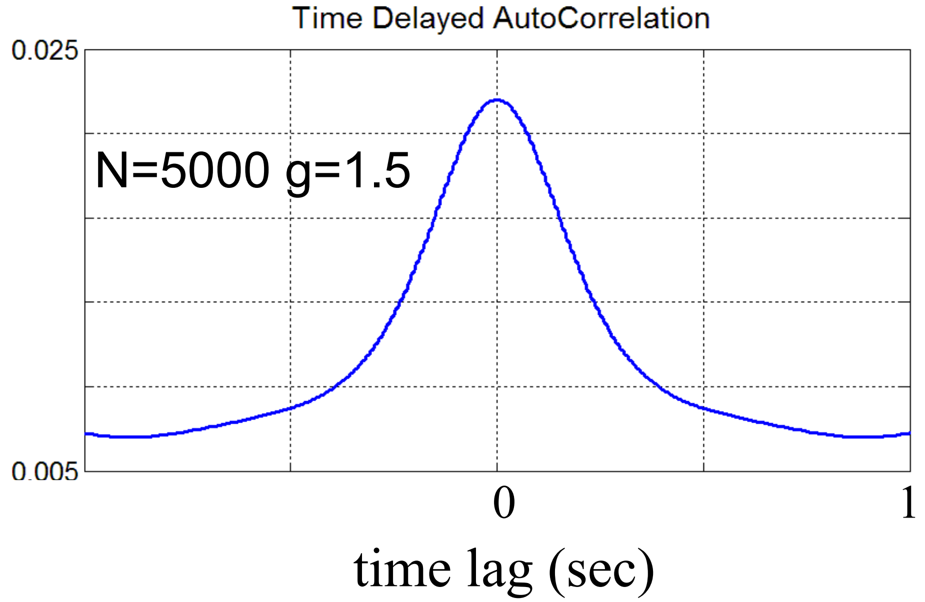
small networks

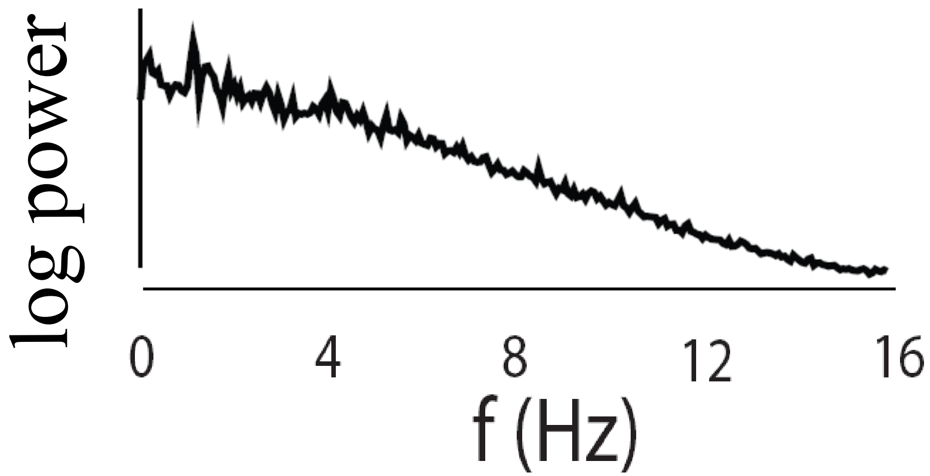
large networks




In the limit of large network size: a sharp transition from a ‘rest’ fixed point to chaos at g=1.

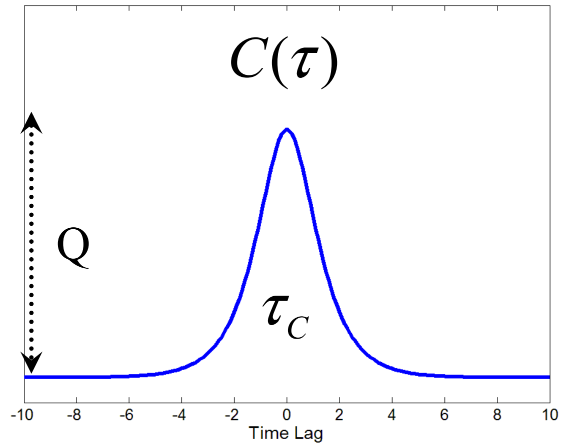
# Chaotic Fluctuations Are Slow



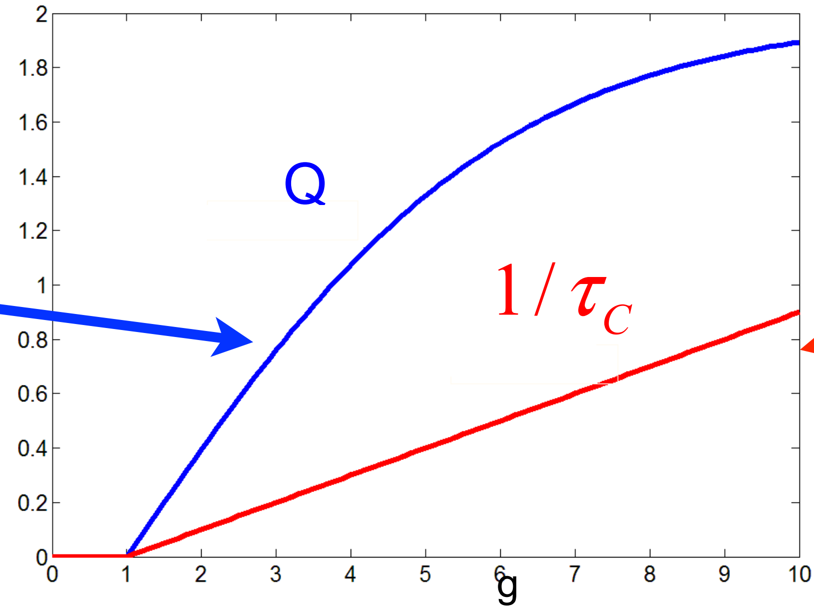



# Onset of Chaotic Fluctuations

Autocorrelations of local activities



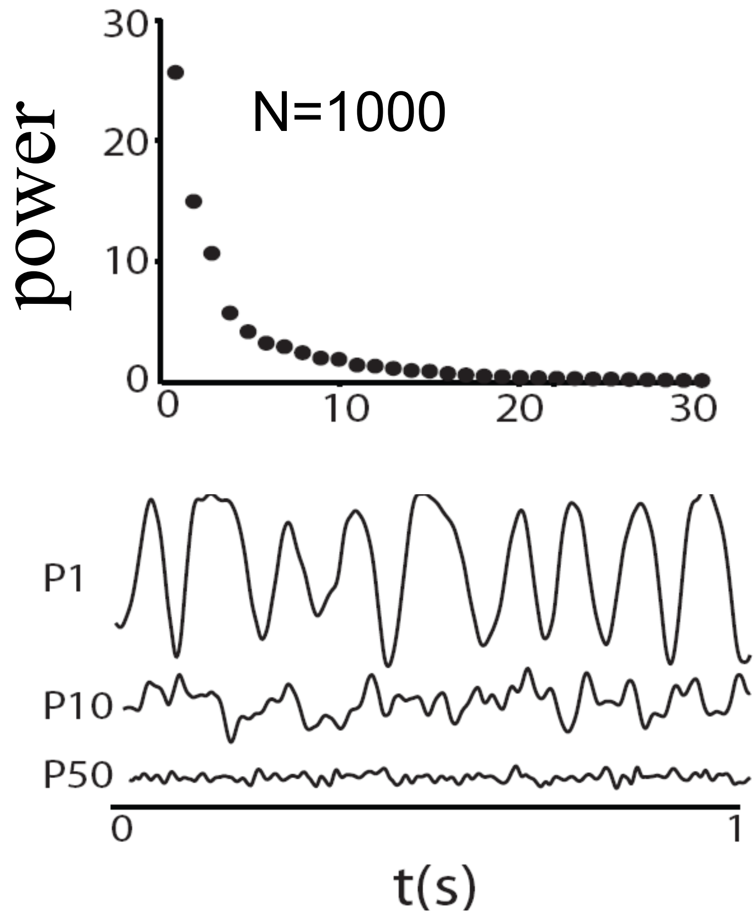

magnitude increases



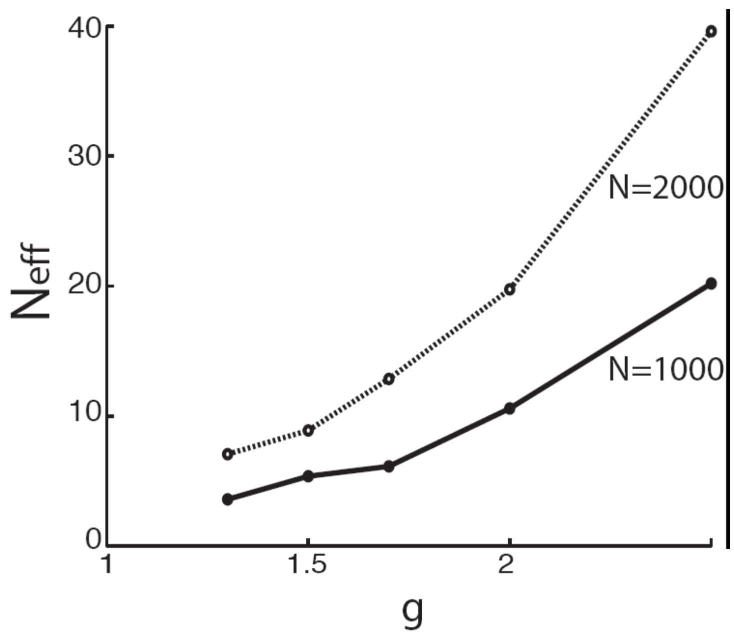

Speeds up

# Dimensionality of Chaotic Fluctuations

## Principal Component Analysis

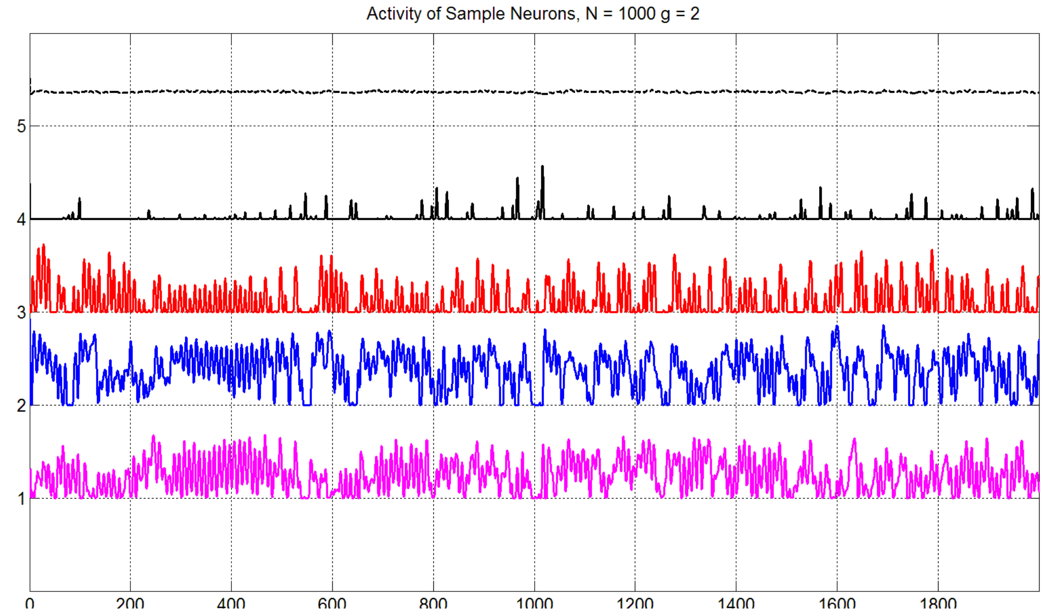



## number of dimensions

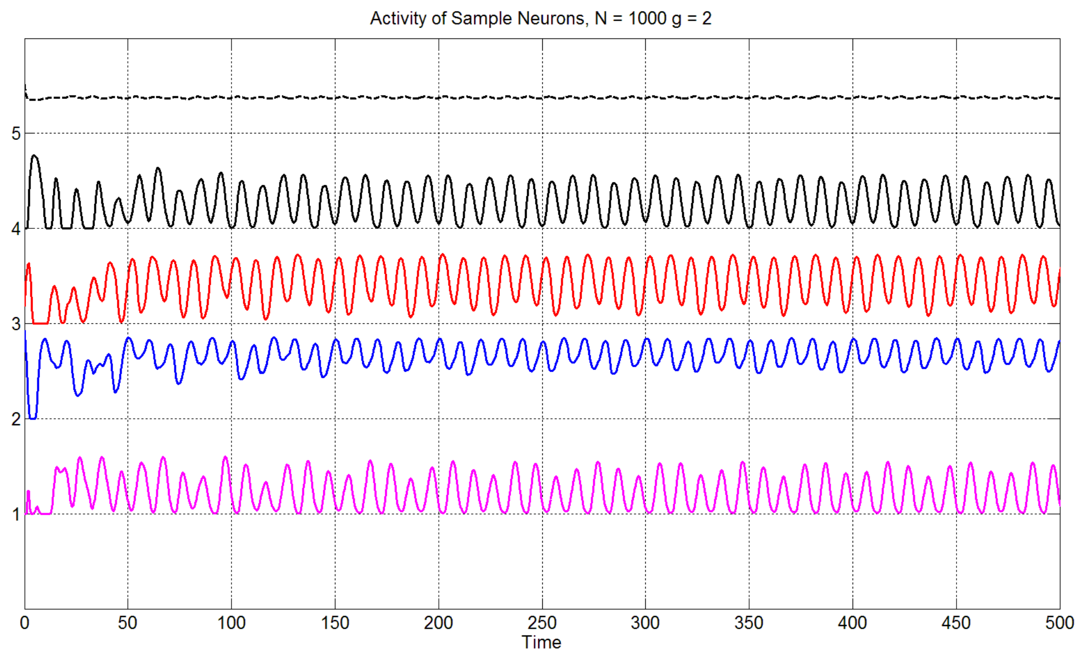



Rajan, Abbott, HS, 2010

# Entrainment by External Periodic Stimulation



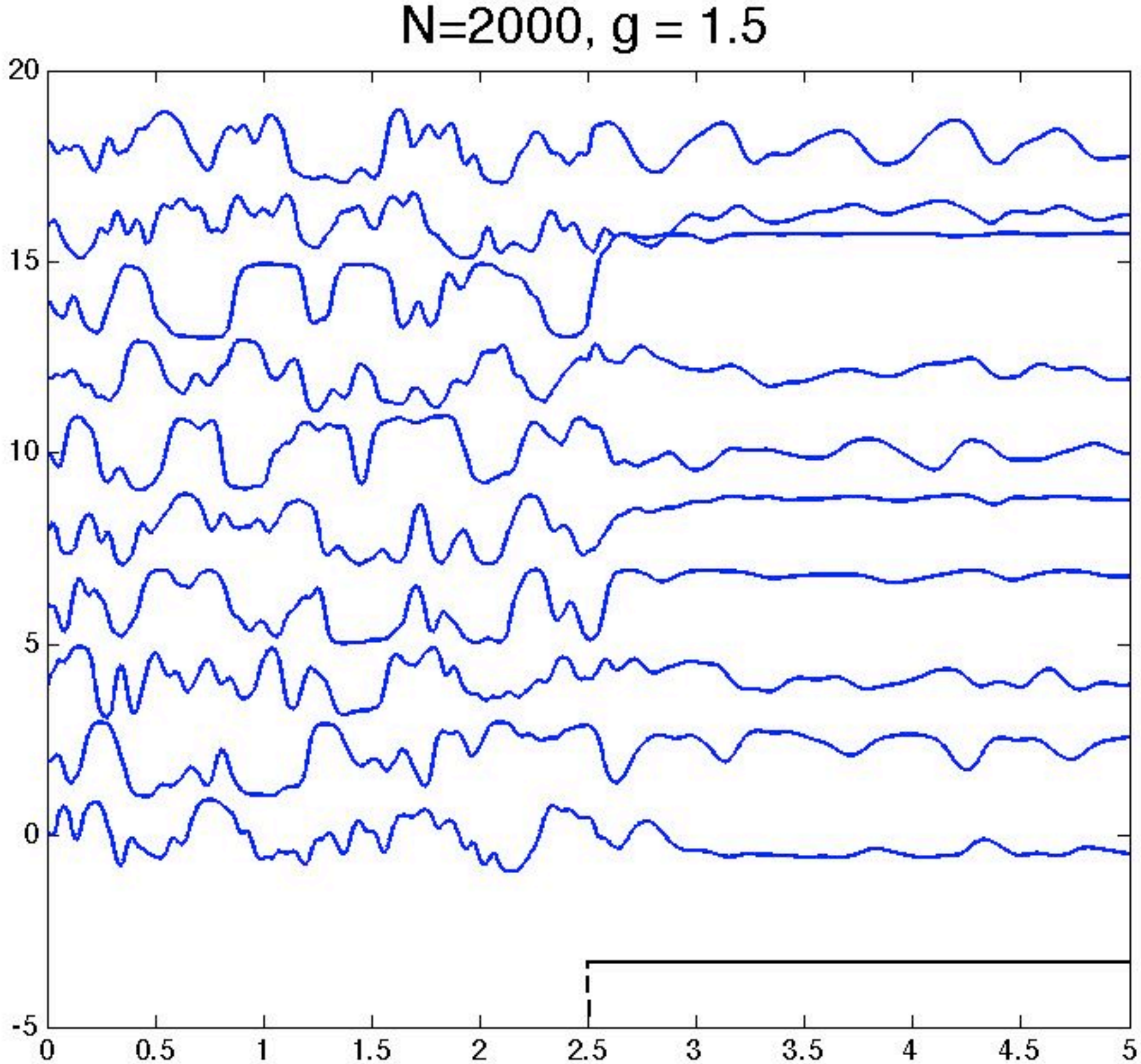

Partial entrainment, low amplitude




Complete entrainment, high amplitude

Rajan, Abbott, HS, 2010

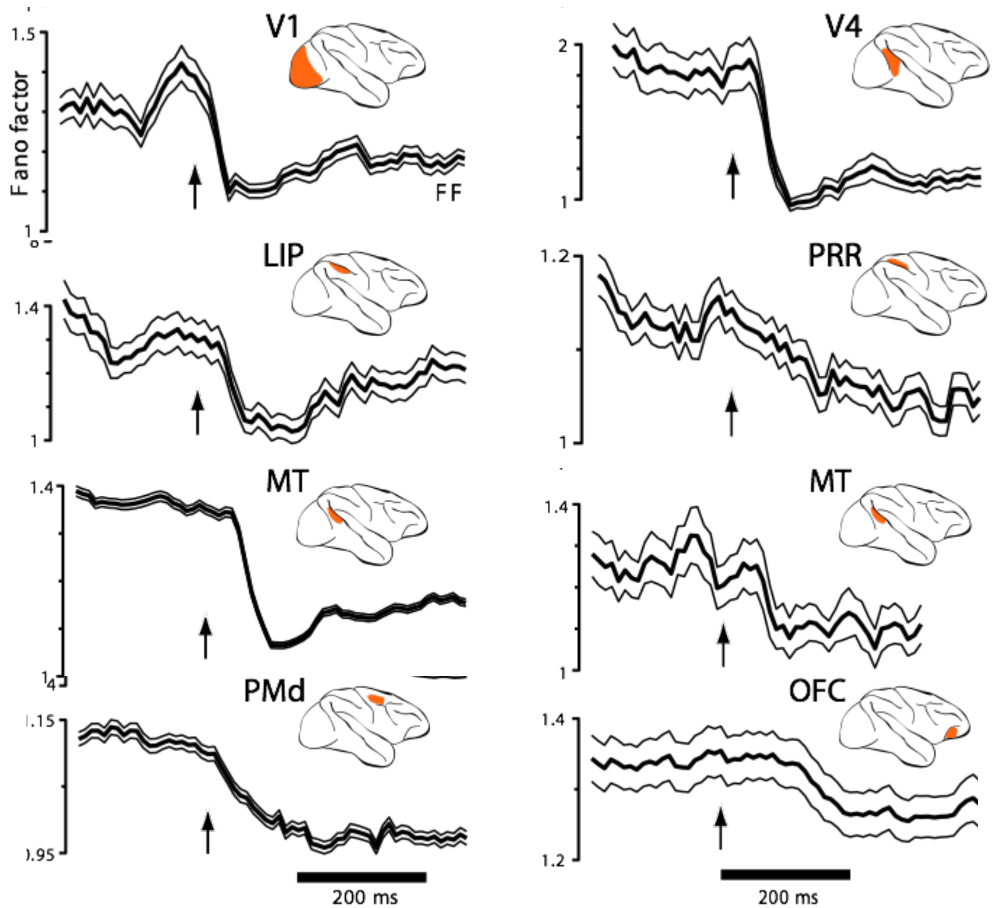
# Network Gain Suppression by External Sparse Tonic Stimulation




At time 2.5 s random external input is applied on 5% of the neurons.

HS, 2011

# Suppression of Fluctuations by External Stimulation

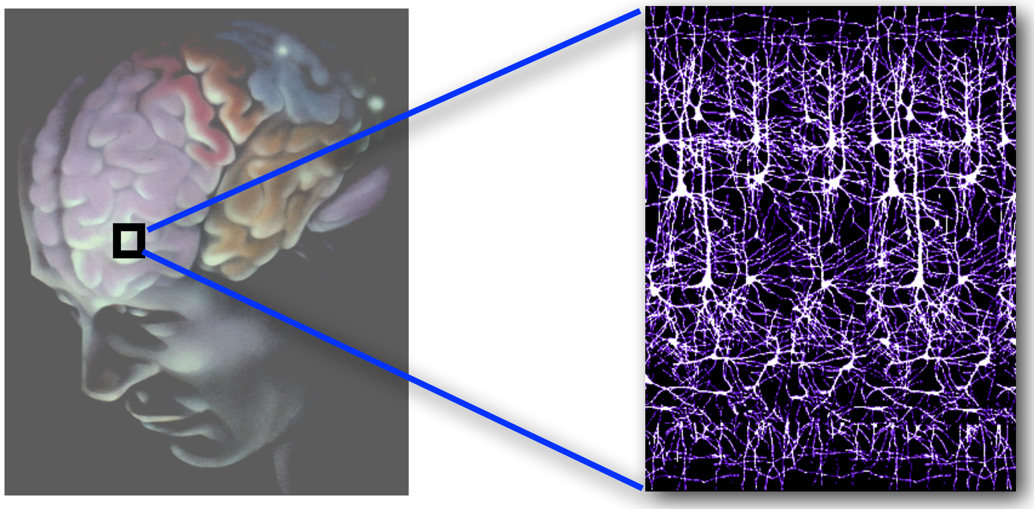



Churchland MM, Yu BM, Cunningham JP, Sugrue LP, Cohen MR, Corrado GS, Newsome WT, Clark AM, Hosseini P, Scott BB, Bradley DC, Smith MA, Kohn A, Movshon JA, Armstrong KM, Moore T, Chang SW, Snyder LH, Ryu, SI, Santhanam G, Sahani M, and Shenoy KV

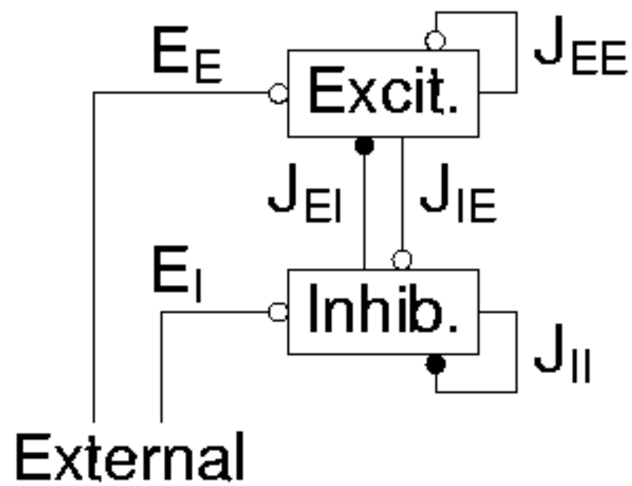
*Nature Neurosc. 2010*

## 4. Emergence of Excitation-Inhibition Balance in Local Cortical Circuits

# Emergence of Excitation - Inhibition Balance in Local Cortical Circuits

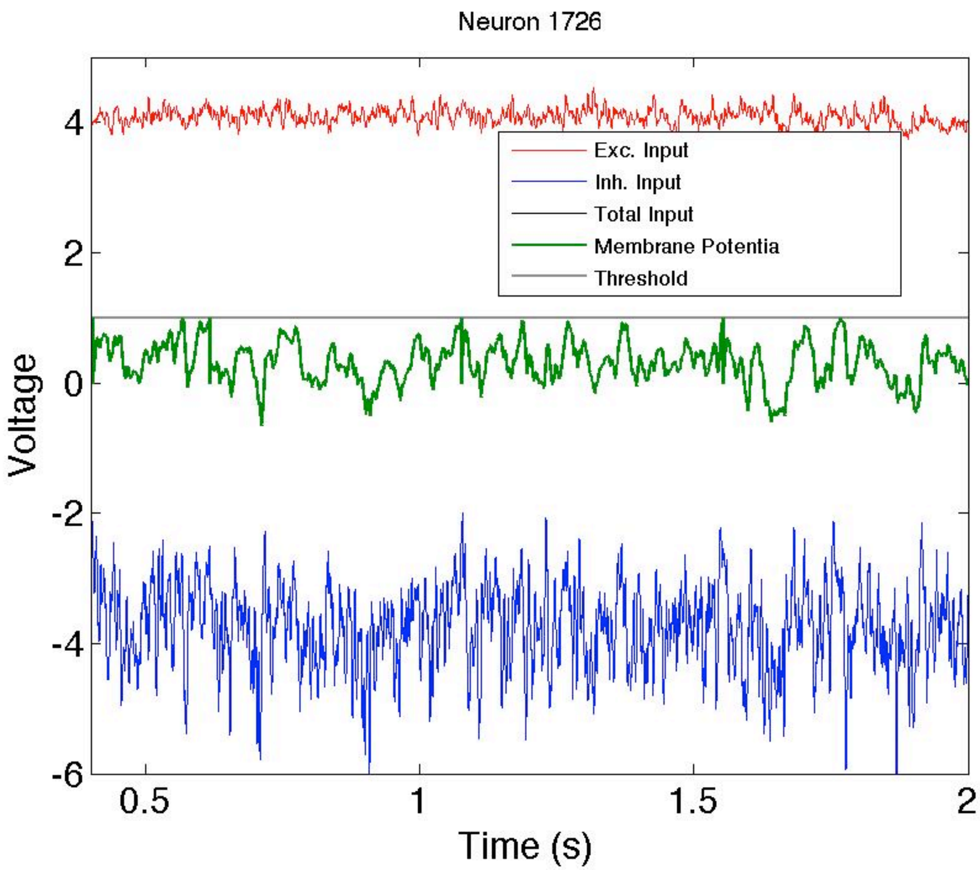


- A model column with strong sparse recurrent inhibition and excitation




van Vreeswijk and HS, 1996

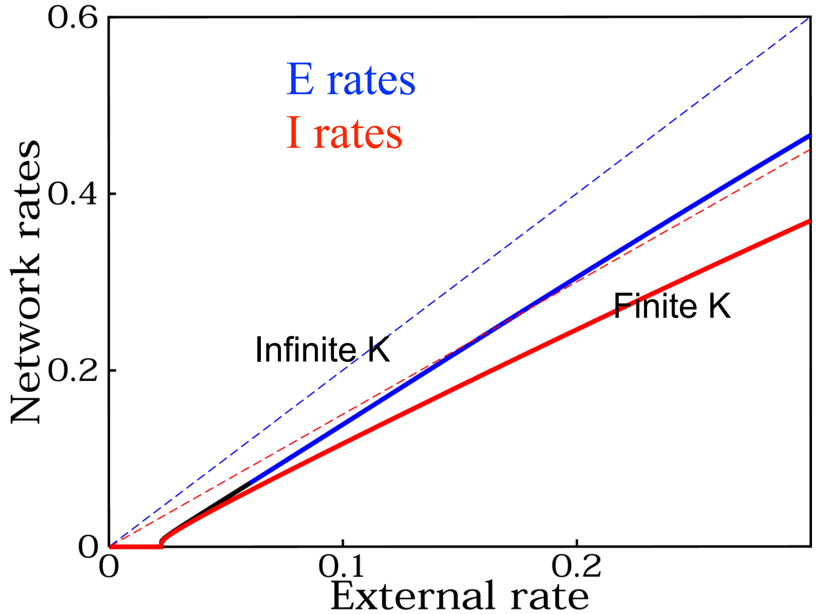
# Spontaneous Balancing of Excitation and Inhibition




The balance equations:

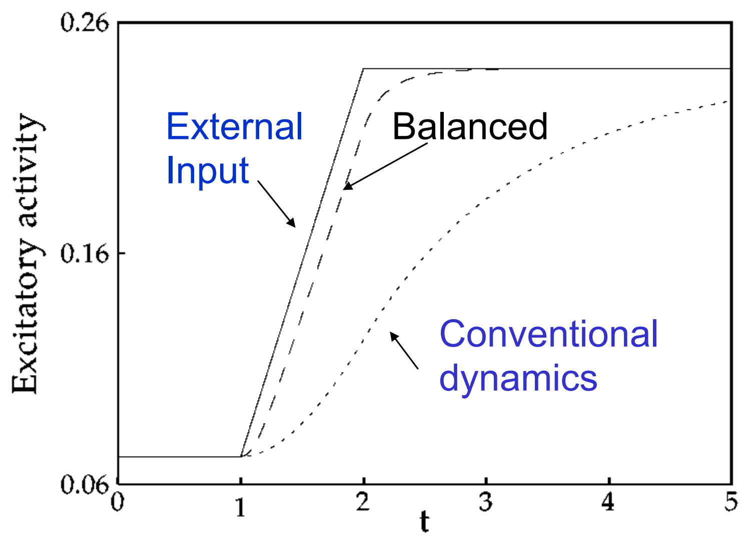
$$E_o + J_{EE} r_E - J_{EI} r_I \approx 0$$
$$I_o + J_{IE} r_E - J_{II} r_I \approx 0$$

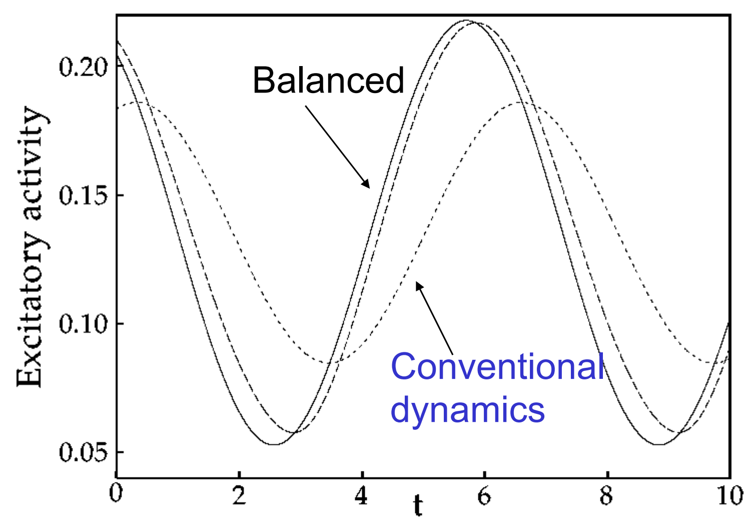
# Functional Advantages of Balanced Networks




Linearizing network response

Ultra fast response

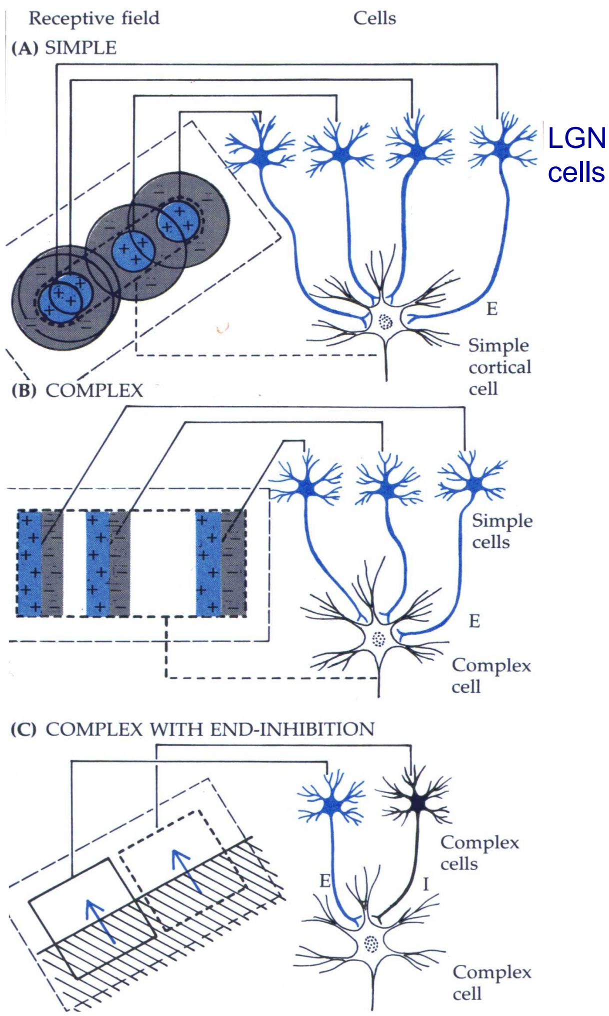


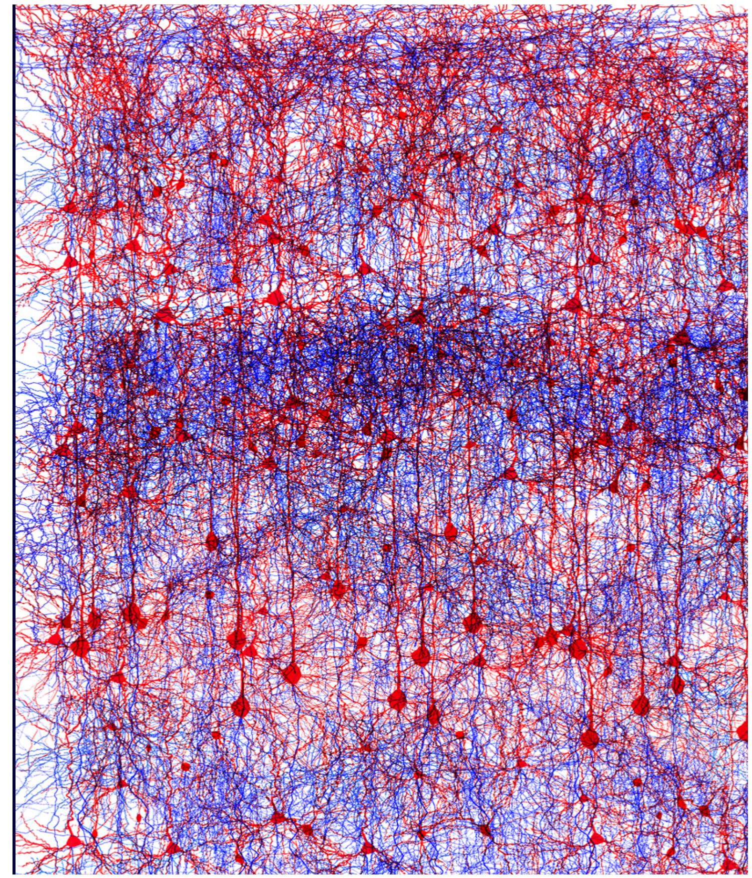
## 5. Emergence of Sensory Selectivity in Cortical Circuits:

### A. tuned connectivity

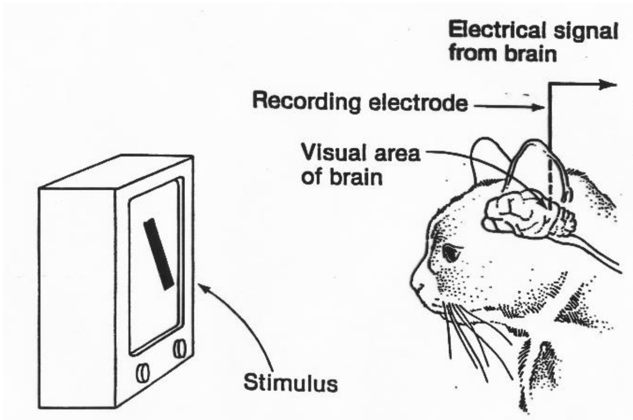
# Emergence of Sensory Selectivity in Cortical Circuits

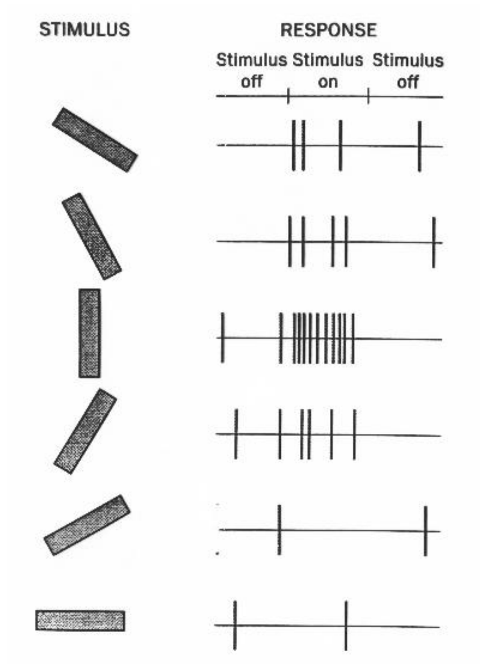



?

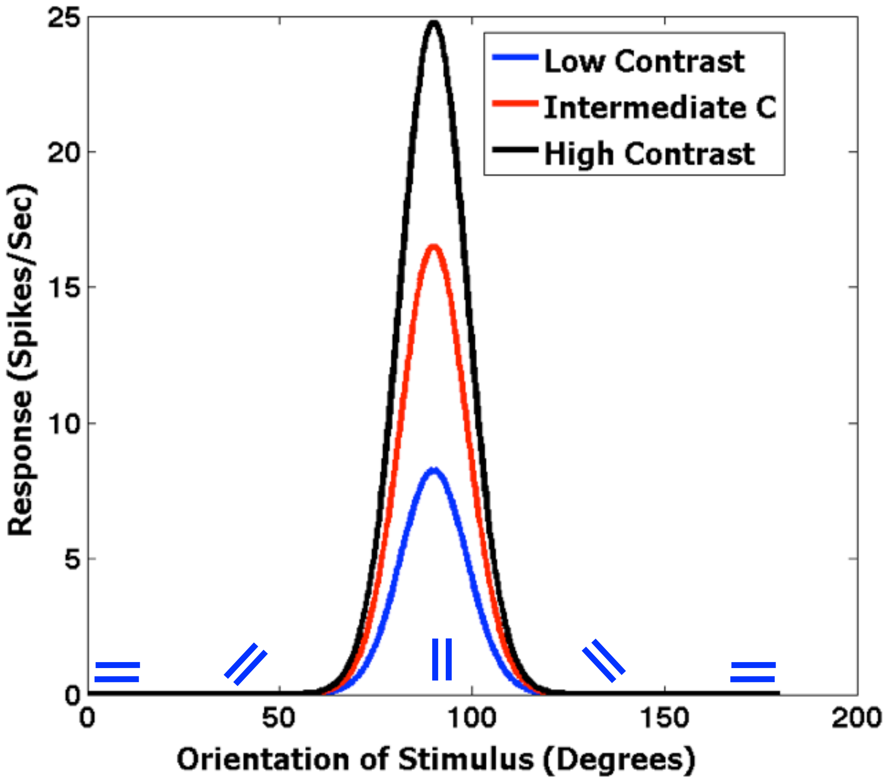


# Orientation Columns in Visual Cortex



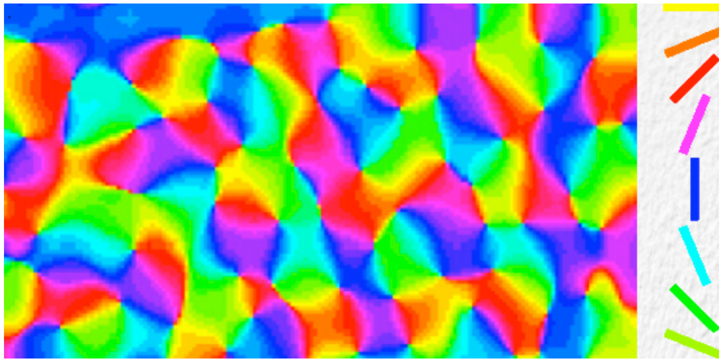

(Hubel and Wiesel, 19




Contrast Invariant
Orientation Selectivity
of Single Cortical Neurons

# Orientation Selectivity in Visual Cortex

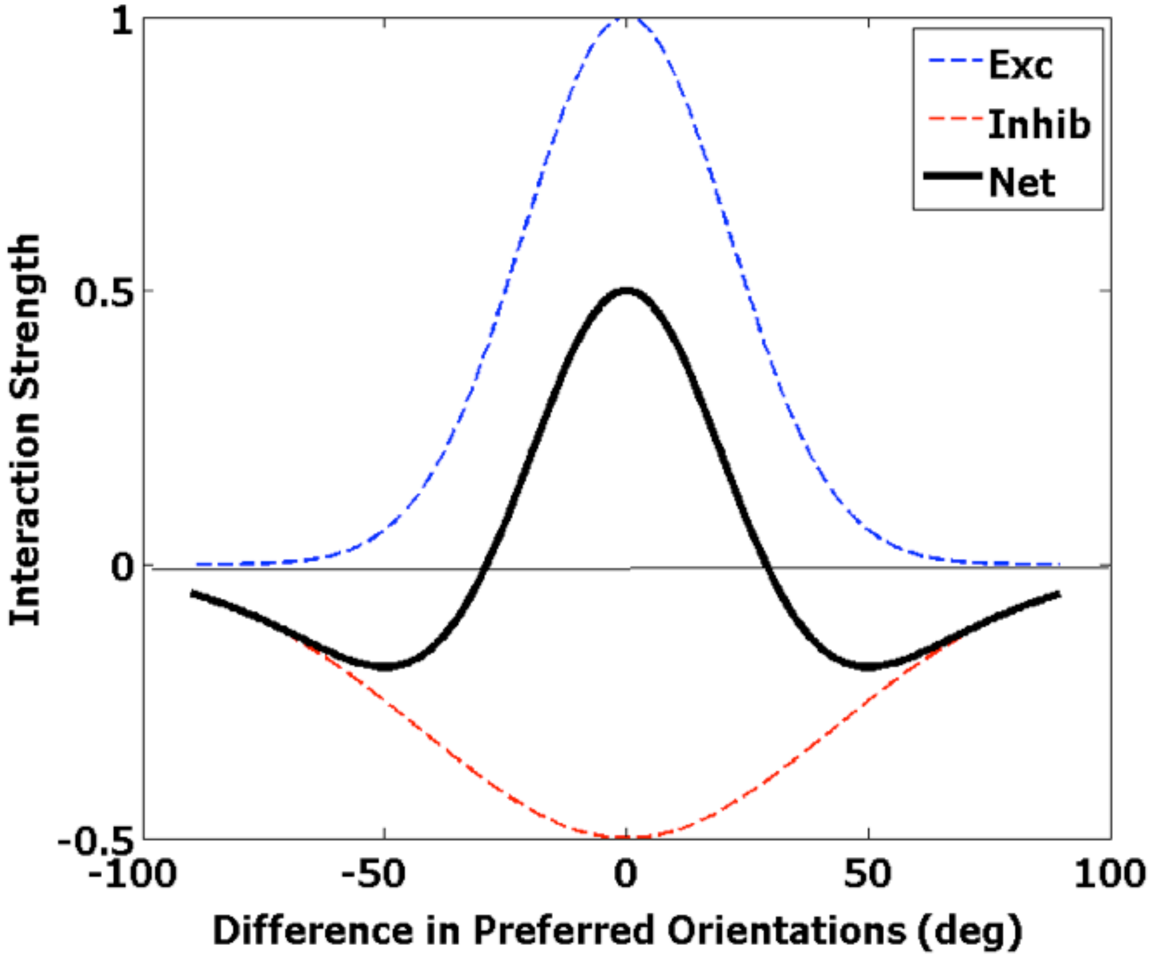
## Pinwheel Architecture of Orientation Tuning in V1 in Cats and Primates



- What is the relation between cortical maps and connectivity?

- What is the relation between orientation preference and connectivity?

# The Ring Model

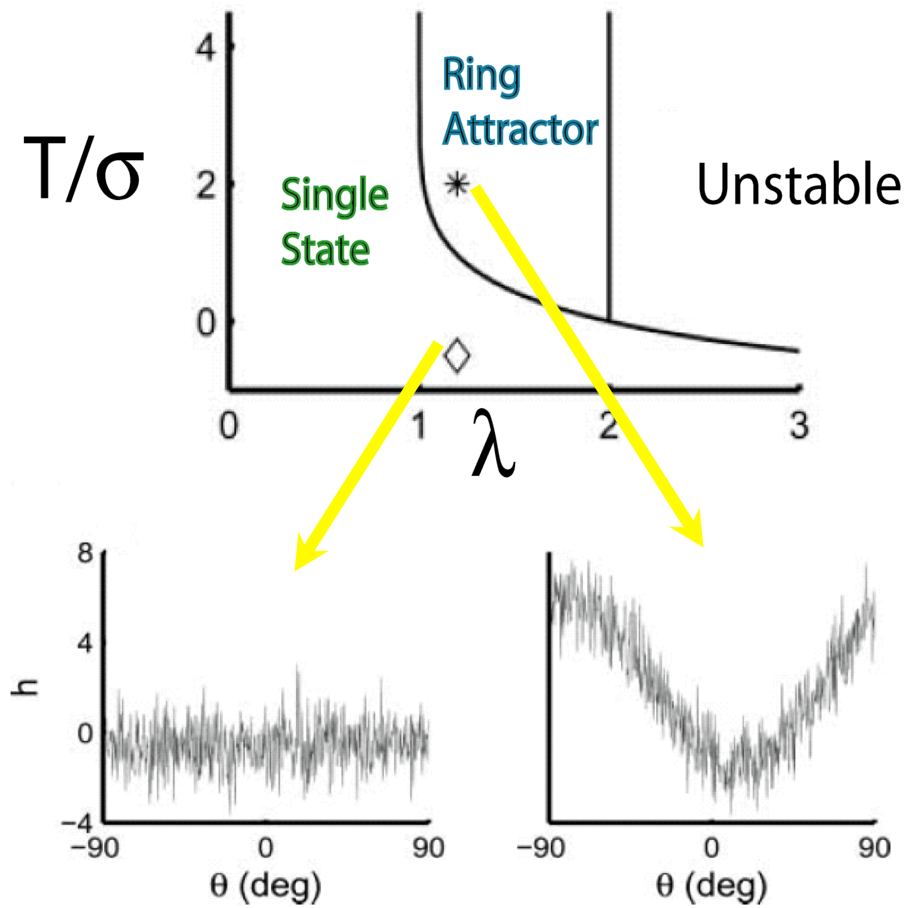



Ben Yishai, Lev Bar Or, SH, 1995

-Cortical Amplification

-Cortical Enhancement of Selectivity

# The Ring Attractor



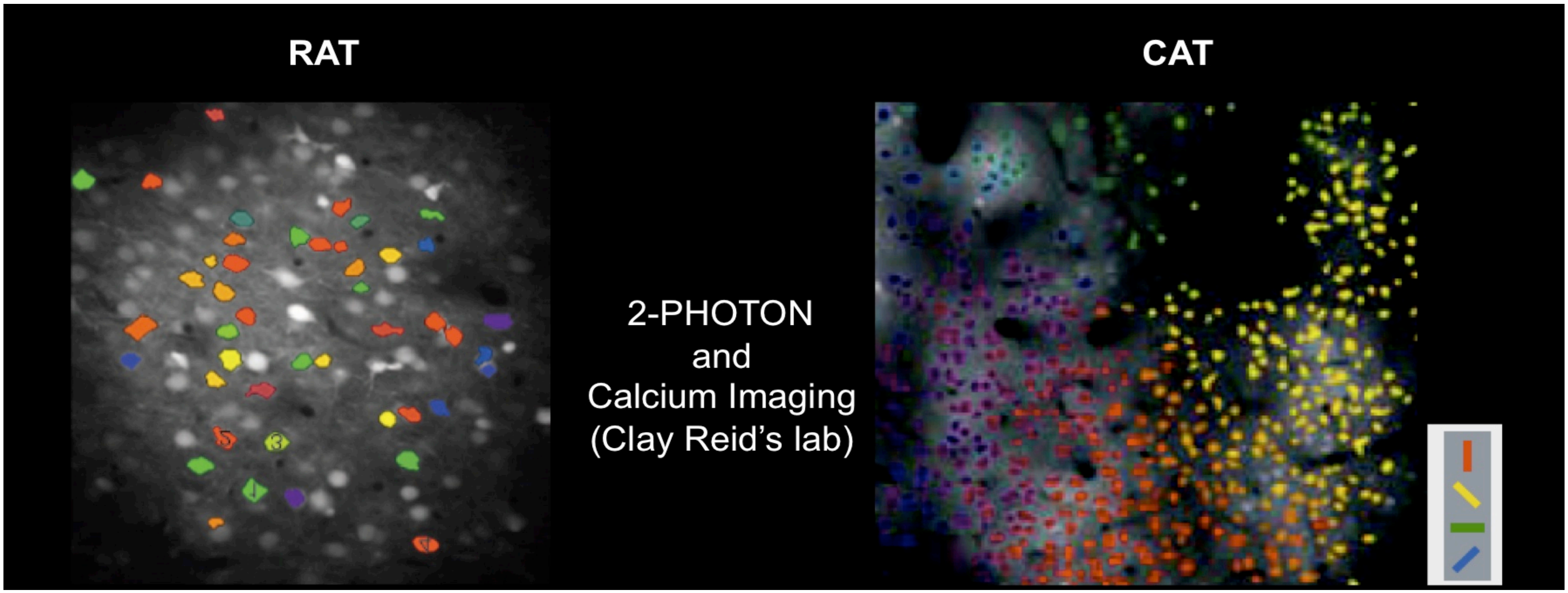

- Circuit develops a manifold of stable ‘bump’ states.
- Weakly tuned input selects the matched state

## 5. Emergence of Sensory Selectivity in Cortical Circuits:

### B. random connectivity

# Orientation Coding in V1

“Salt and Pepper” Orientation Columns

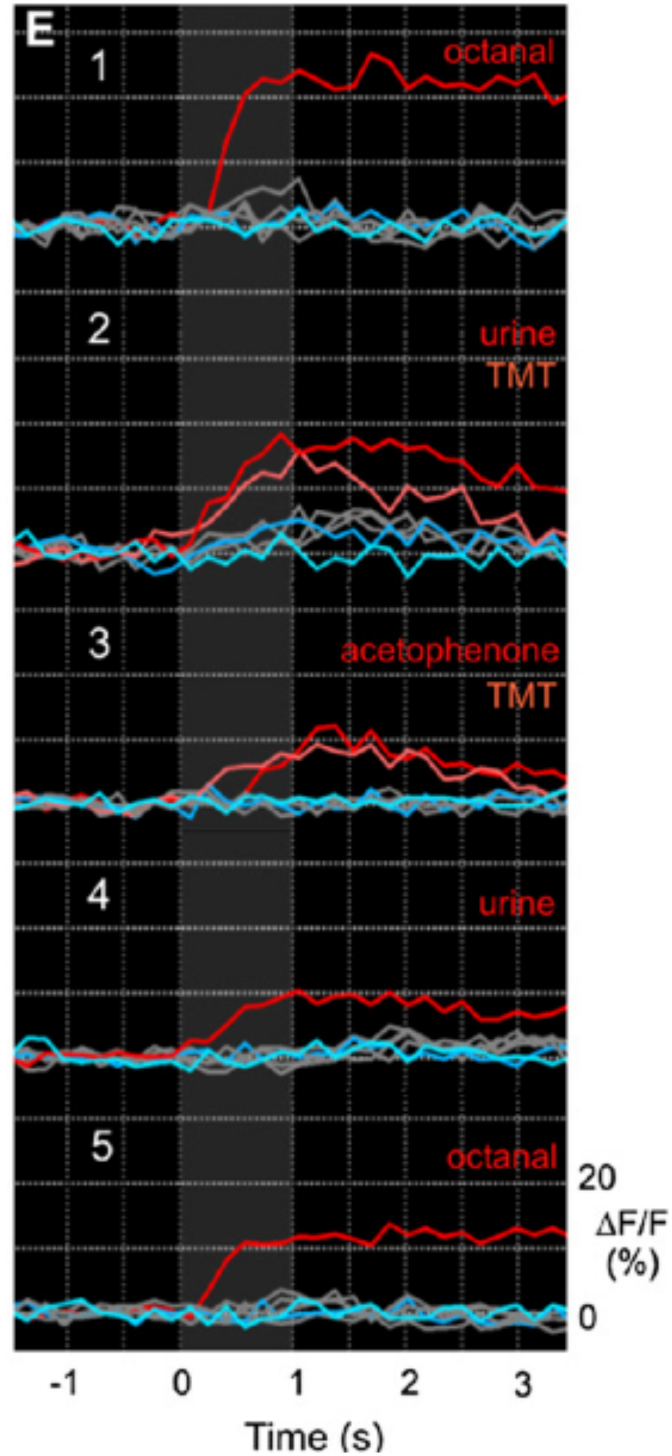



Architecture suggests that in rodents connectivity is less structured in orientation space

# Random Architecture in Olfactory Cortex

Cortical neurons appear to sample randomly the activities of the glomeruli in the olfactory bulb

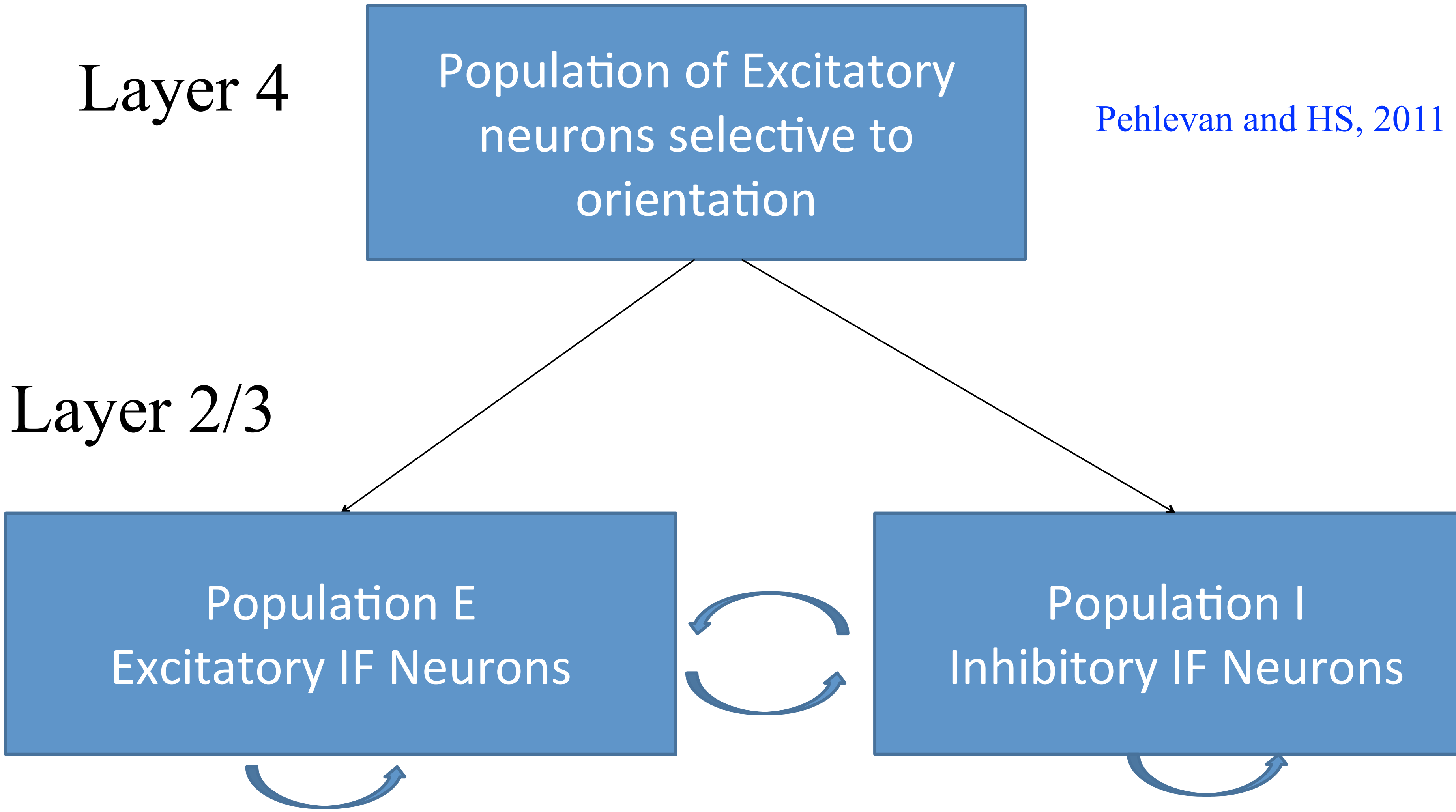
*Stettler and Axel, Neuron, 2009*



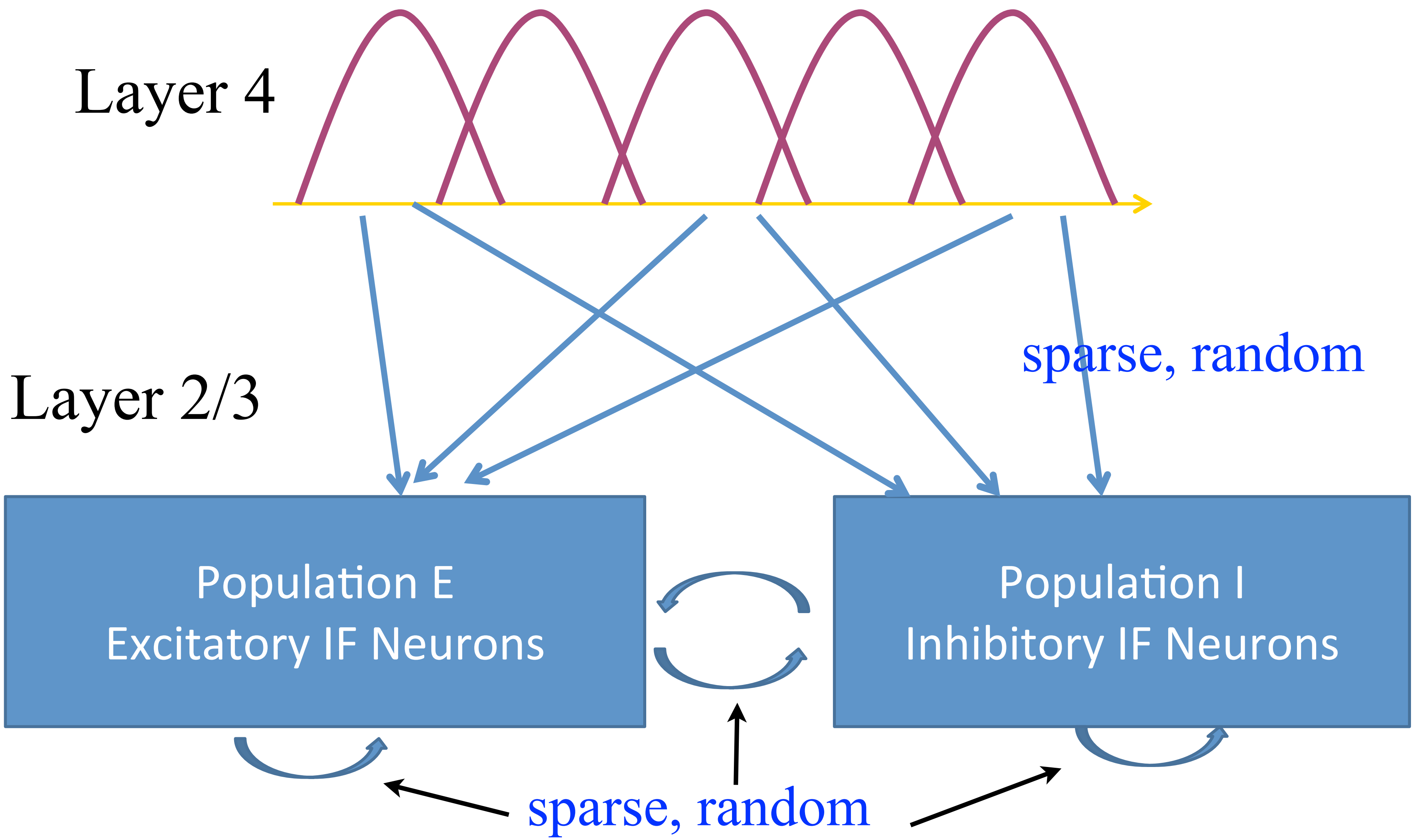
# Questions

- Is **“fire together wire together”** a necessary requirement for sensory selectivity?
- Can a network with random connectivity generate neurons with high, contrast invariant orientation selectivity?

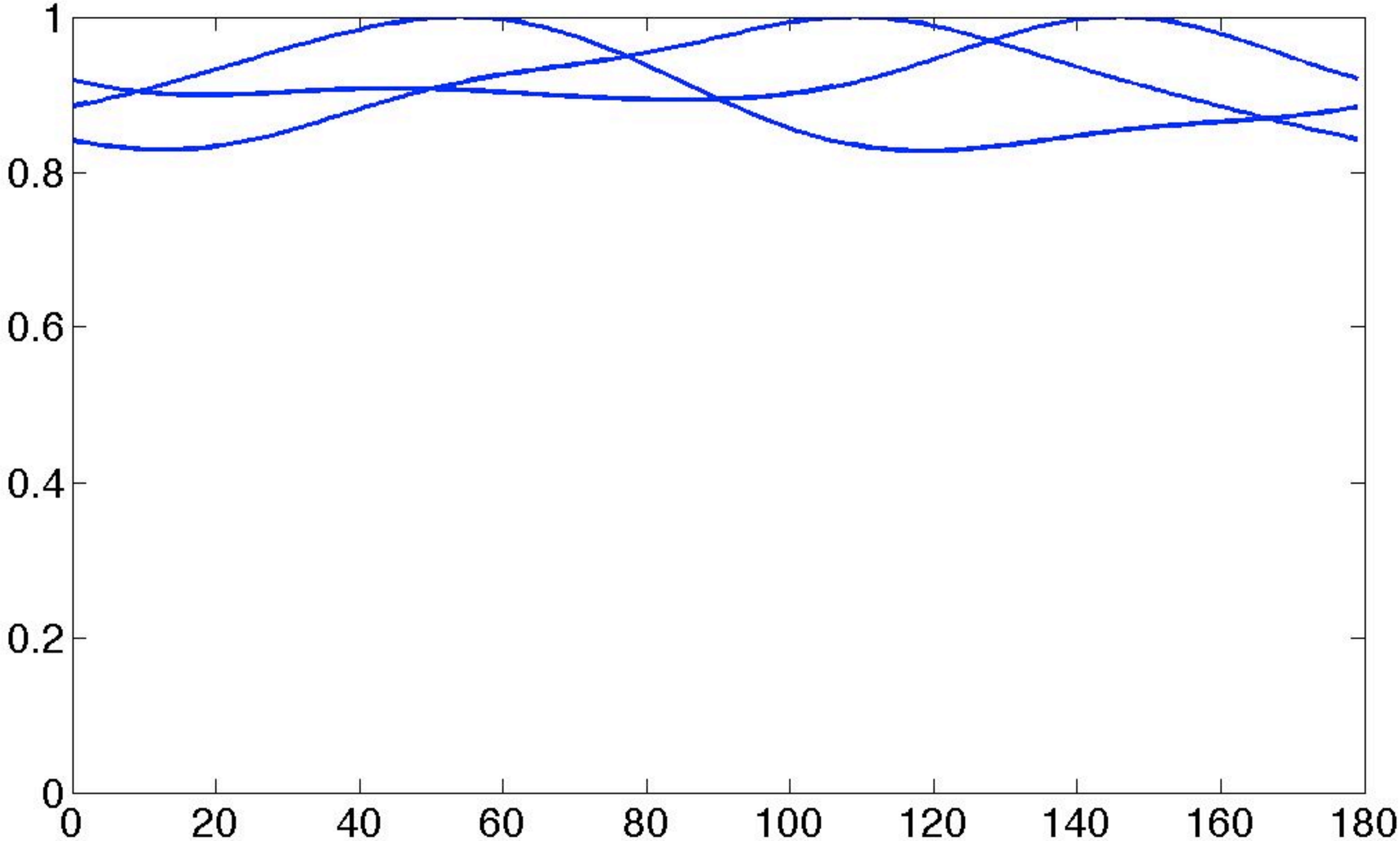
# Model of Sensory Selectivity in Randomly Connected Cortical Networks



# Each Layer 2/3 neuron samples a random subset of Layer 4 population



# Poorly Tuned Input to Sample 3 Neurons in Layer 2/3



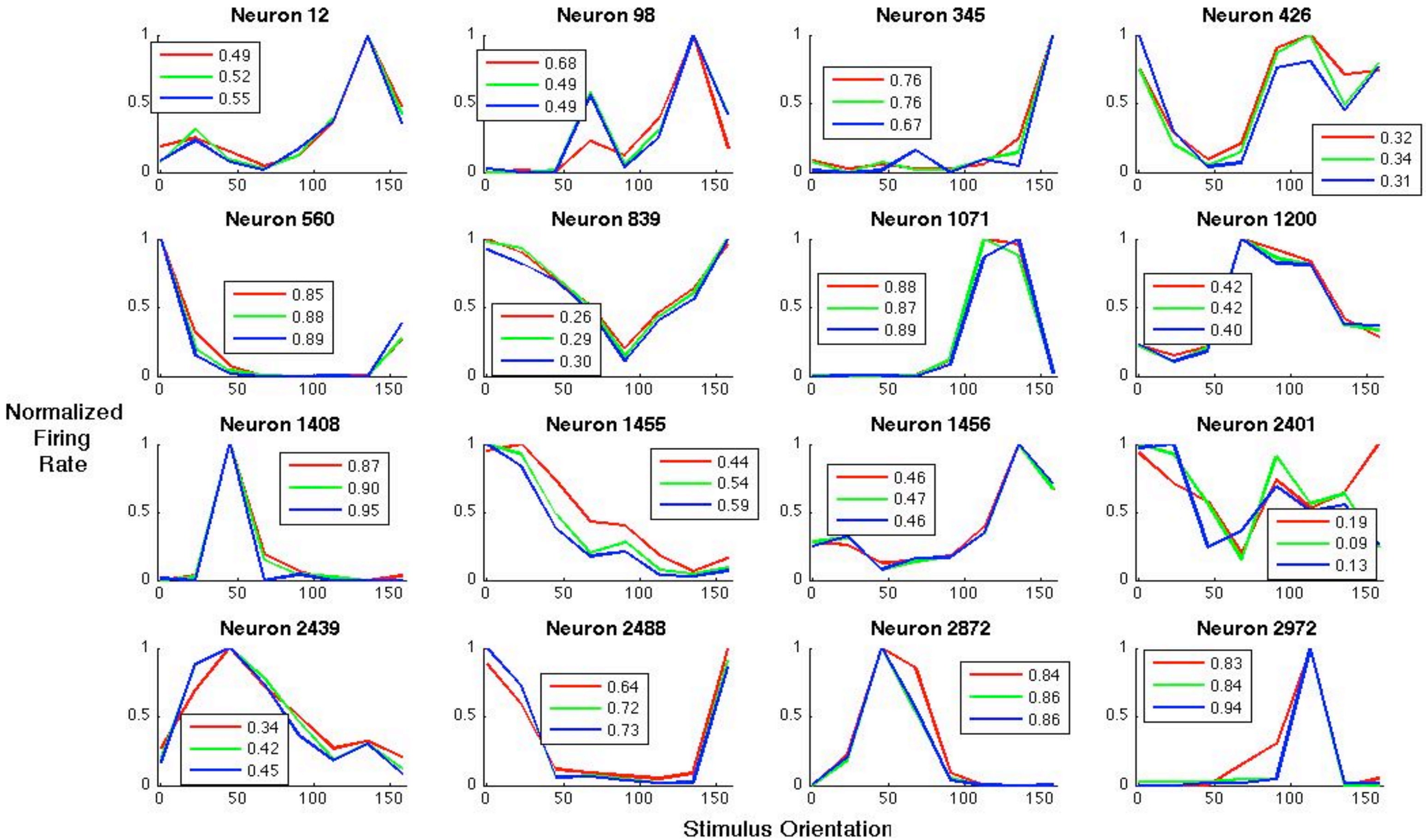

Stimulus Orientation

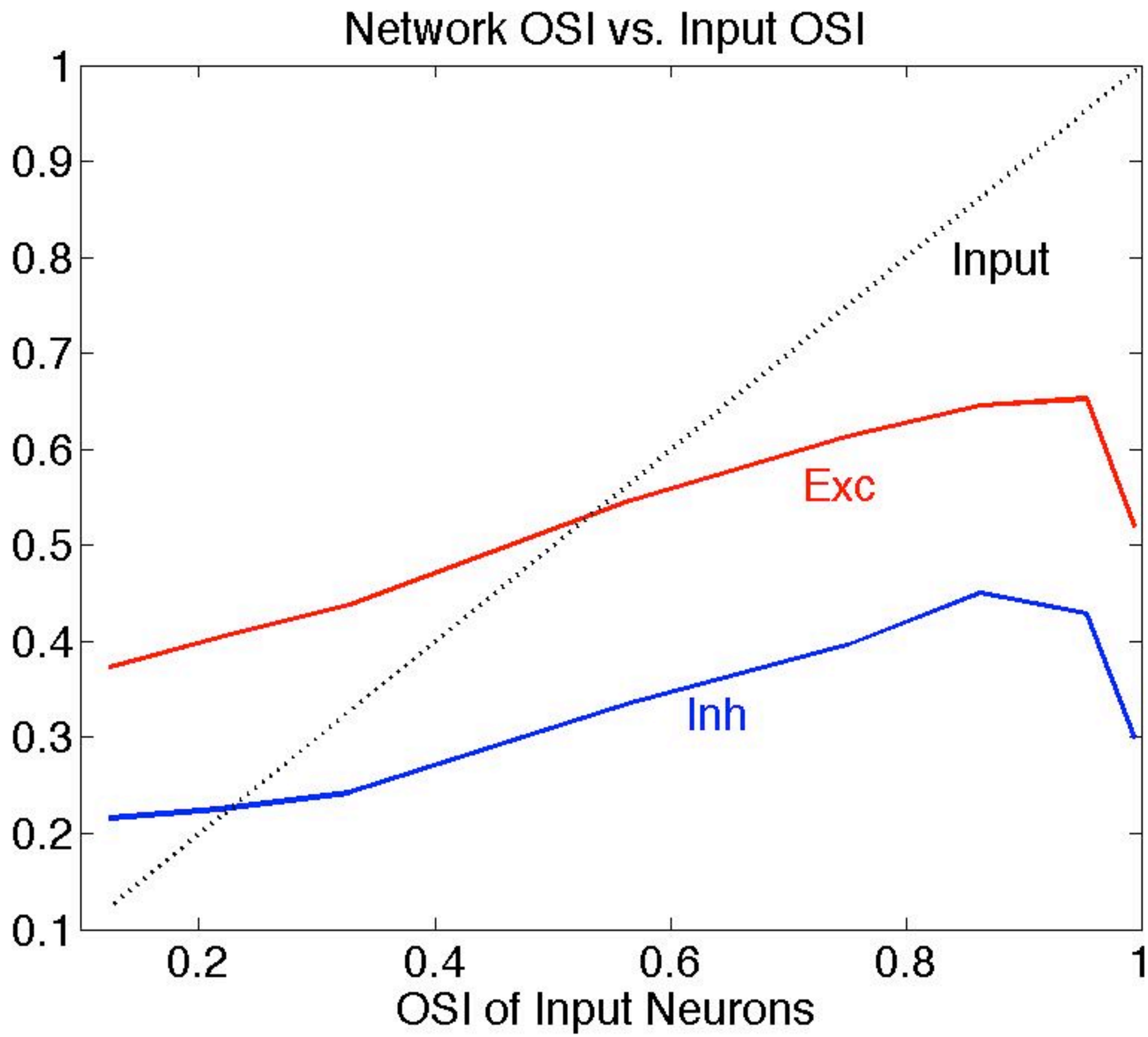
# Model

- Strong sparse random excitatory inputs
- Strong sparse random recurrent inhibition and excitation
- I&F neurons
- Input neurons are tuned to orientation
- Network in a balanced state:
  - irregular firing statistics
  - dynamic balancing between excitation and inhibition

# Contrast Invariant Orientation Selectivity of Neurons in the Random Balanced Network

## Balanced State Cancels the Large Untuned Component in the External Input






OSI=Orientation Selectivity Index

# Conclusion

Dynamical balance between E and I generates sensitive to small random biases in sensory inputs.

## Experimental Predictions

1. Poor stimulus specificity of cortical wiring
2. Neurons are selective to complex patterns.
3. Inhibition co-modulated with excitation

# Concluding remarks

- Exploring the cellular and molecular mechanisms is not sufficient. One needs to understand also the principles of organization and dynamics at the circuit level.
- Neuronal circuits can exhibit emergent properties, not simply deduced from their micro properties. Key factors are: nonlinearity, feedback, and randomness.
- Nonlinear synaptic plasticity dynamics can also give rise to emergent properties in learning.
- Collective circuit properties are robust to many microscopic details but may undergo dramatic phase transitions in the system's state induced by changes in certain critical 'control' parameters.
- The balance between excitation and inhibition is central to the functioning of cortical circuitry. However, E/I balance assumes different forms in different conditions (e.g., tuned balanced vs. spontaneous balance).
- Circuit instability can be induced either by an increase in the gain of both E and I or by disrupting the E/I ratio.
- External stimulation may control the network state either directly by 'enslaving' the neurons or indirectly by changing the circuit's gain.

"The ability to reduce everything to simple fundamental laws does not imply the ability to start from those laws and reconstruct the universe.The constructionist hypothesis breaks down when confronted with the twin difficulties of scale and complexity.

At each level of complexity entirely new properties appear. Psychology is not applied biology, nor is biology applied chemistry. We can now see that **the whole becomes not merely more, but very different from the sum of its parts**."

(Phil Anderson, 1972)

- Supported by:

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