Statistical properties of network connectivity optimizing storage of persistent activity patterns

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The Hebbian scenario: theory vs experiment

According to ‘Hebbian’ theories:

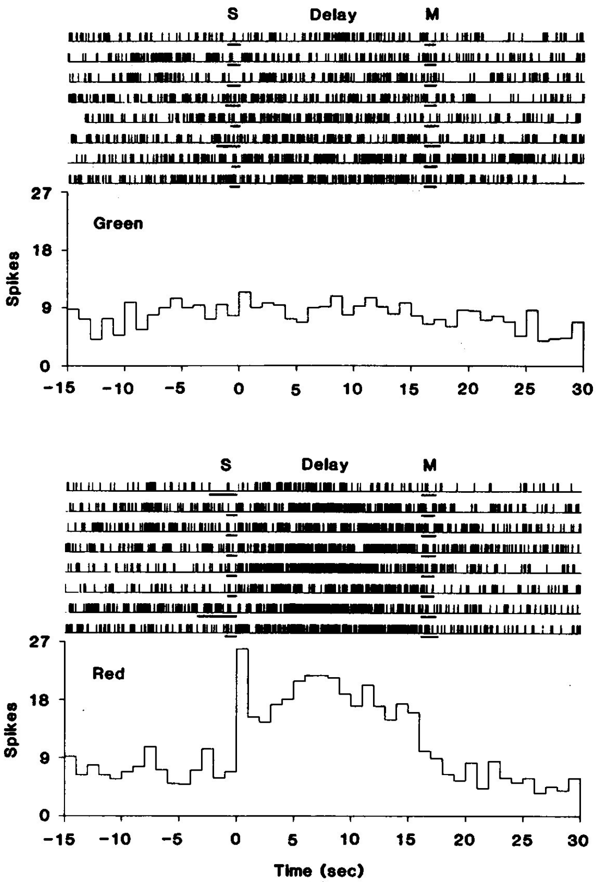
- External inputs impose specific patterns of activity in a network;
- These patterns induce synaptic modifications (long-term memory storage);
- These synaptic modifications allow the network to form attractors strongly correlated with the stored patterns - hence, activity correlated with a pattern is sustained in absence of the stimulus that elicited it (short-term/working memory storage)

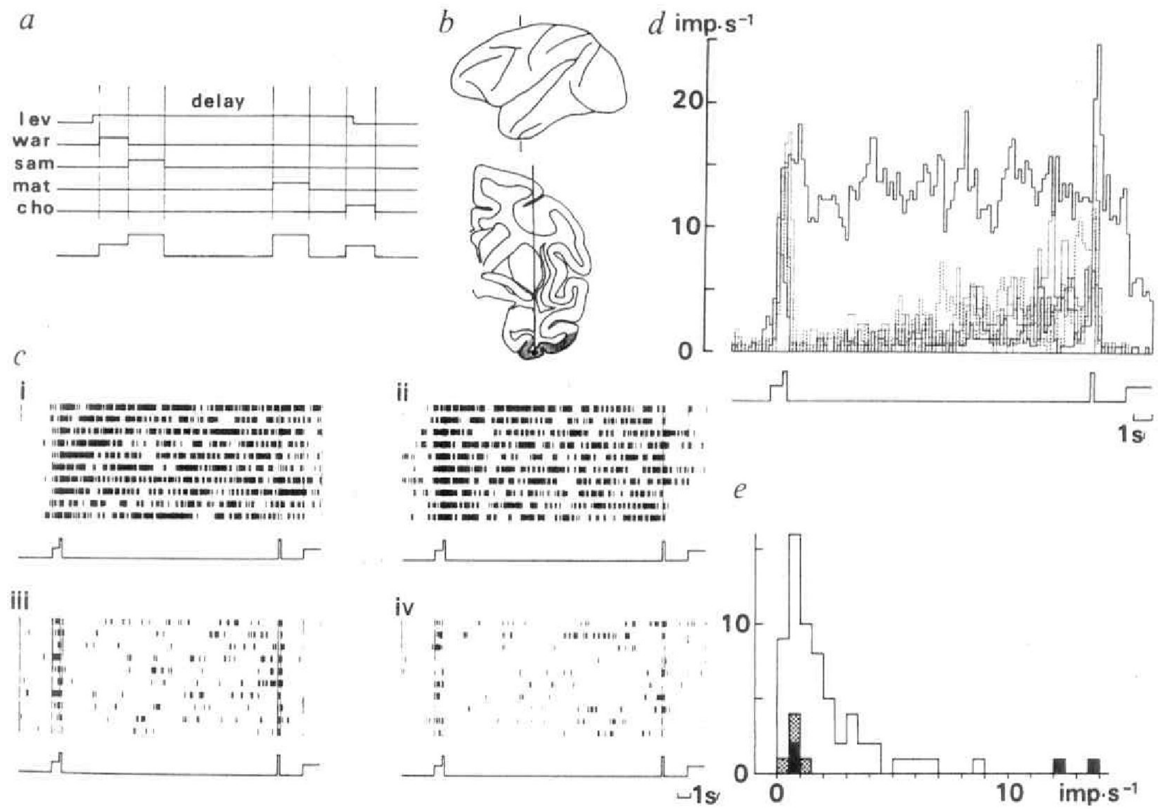
This leads to two questions:

1. Is neuronal activity in the brain consistent with this scenario?
2. Is synaptic connectivity in the brain consistent with this scenario?

‘Object’ working memory and persistent activity (IT)

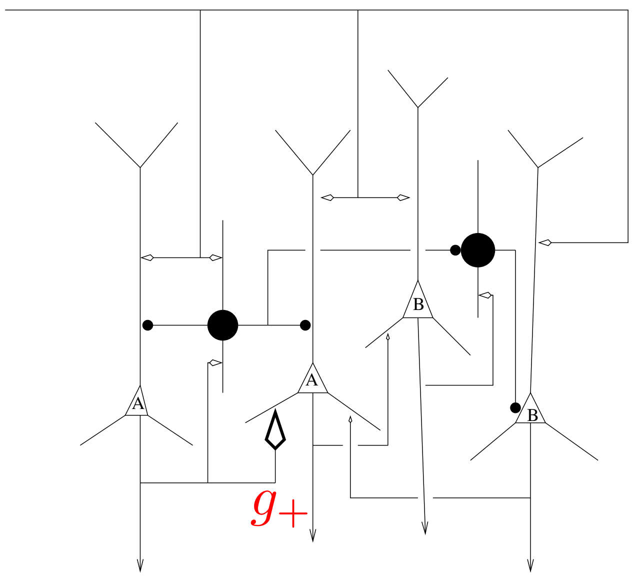
- Fuster and Jervey 1981
- Miyashita and Chang 1988



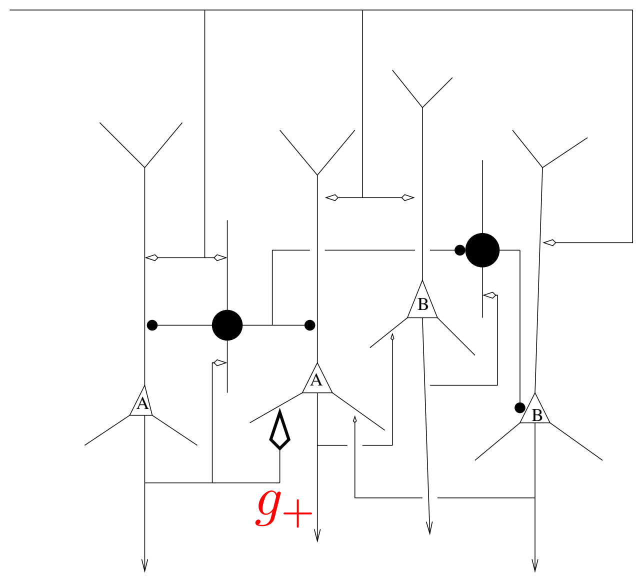


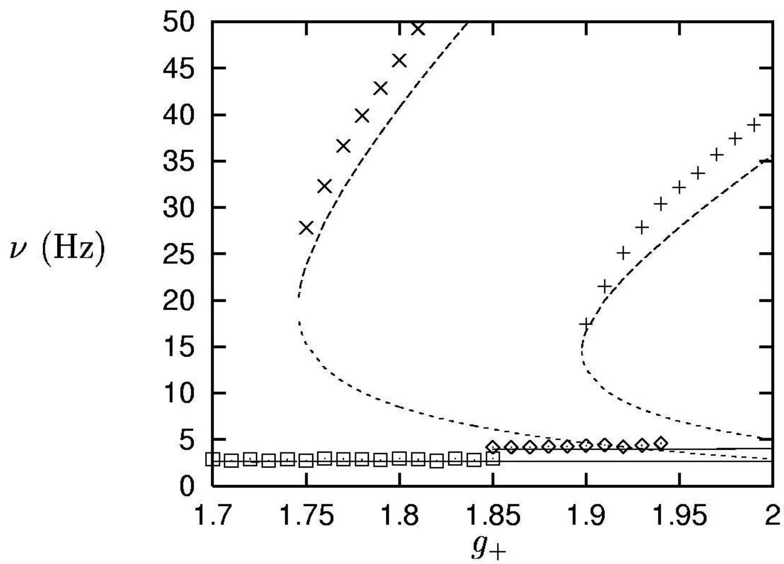
See also: visuo-spatial working memory (Goldman-Rakic), parametric working memory (Romo), decision-making (Shadlen), . . .

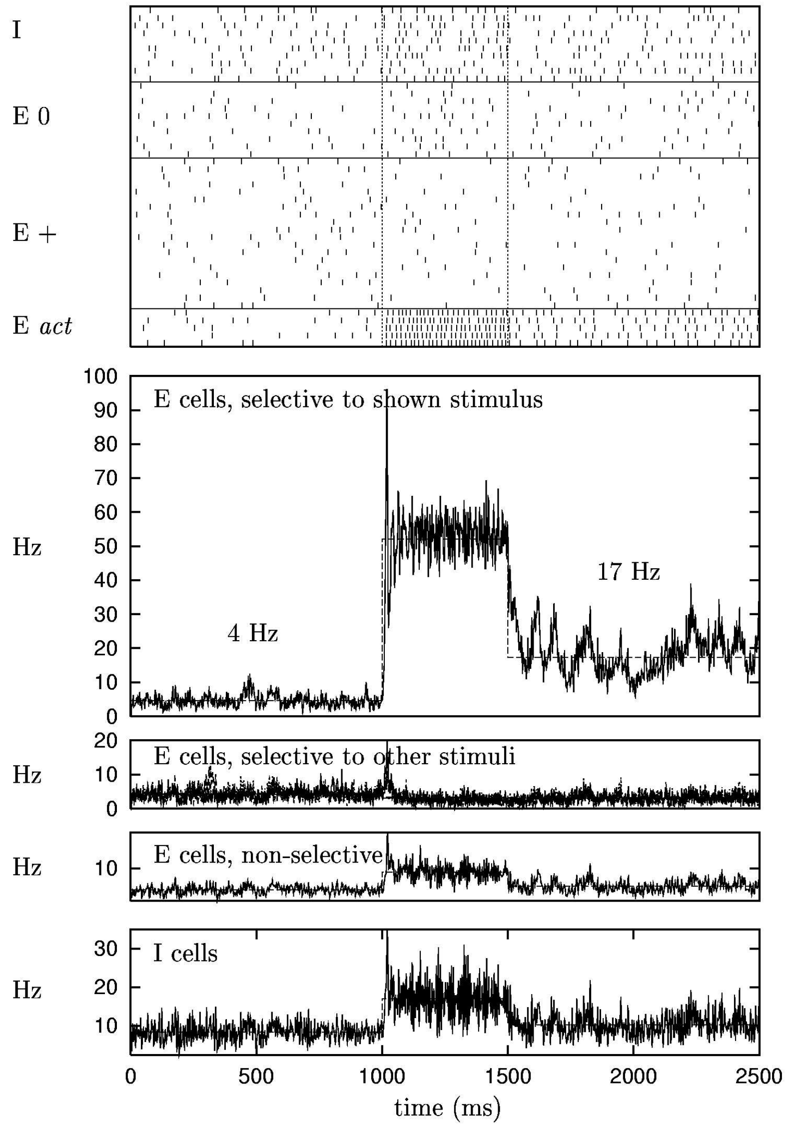
Persistent activity in spiking network models



Persistent activity in spiking network models







. . ., Amit and Brunel 1997, Brunel 2000, . . .

Synaptic connectivity in attactor networks

- Synaptic matrix should have some degree of symmetry (if neurons A and B are activated in a pattern, then both synapses connecting the two neurons should strengthen).
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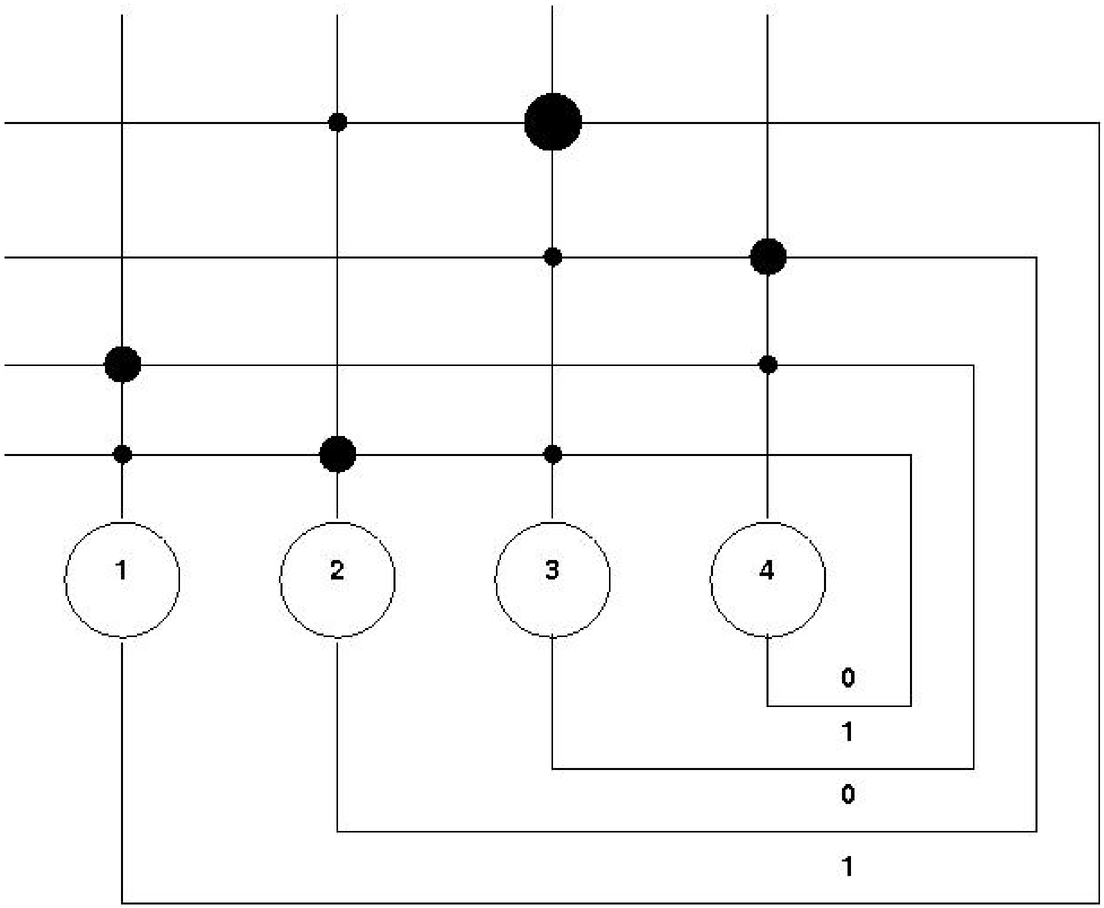
- Statistics of connectivity depends on the details of the 'learning rule'
- **Study optimality properties of attractor networks: Elizabeth Gardner (1988) approach**
  - Rather than focusing on a given learning rule, study space of coupling matrices satisfying a set of constraints imposed by learning.

$\Rightarrow$ For a given robustness level, compute maximal storage capacity;

$\Rightarrow$ For a given number of attractors, compute maximal robustness

$\Rightarrow$ Statistical properties of optimal synaptic connectivity

A simplified attractor neural network



- Fully connected network of $N \gg 1$ binary neurons;
- Stores a large number ($p \equiv \alpha N$) of fixed point attractor states (stable representations of external stimuli)
- Each attractor state: random binary pattern with coding level f
- Robustness level κ (measures size of basin of attraction of each attractor);

Questions

When the network stores many attractors (in particular when it is close to its maximal capacity):

- What is the distribution of synaptic weights

$$P(w_{ij})?$$

- What is the distribution of specific synaptic motifs (pairs, triplets, etc)

$$P(w_{ij}, w_{ji})?$$

$$P(w_{ij}, w_{ji}, w_{ik}, \ldots)?$$

Gardner approach

- Subspace of solutions to learning problem in w space:

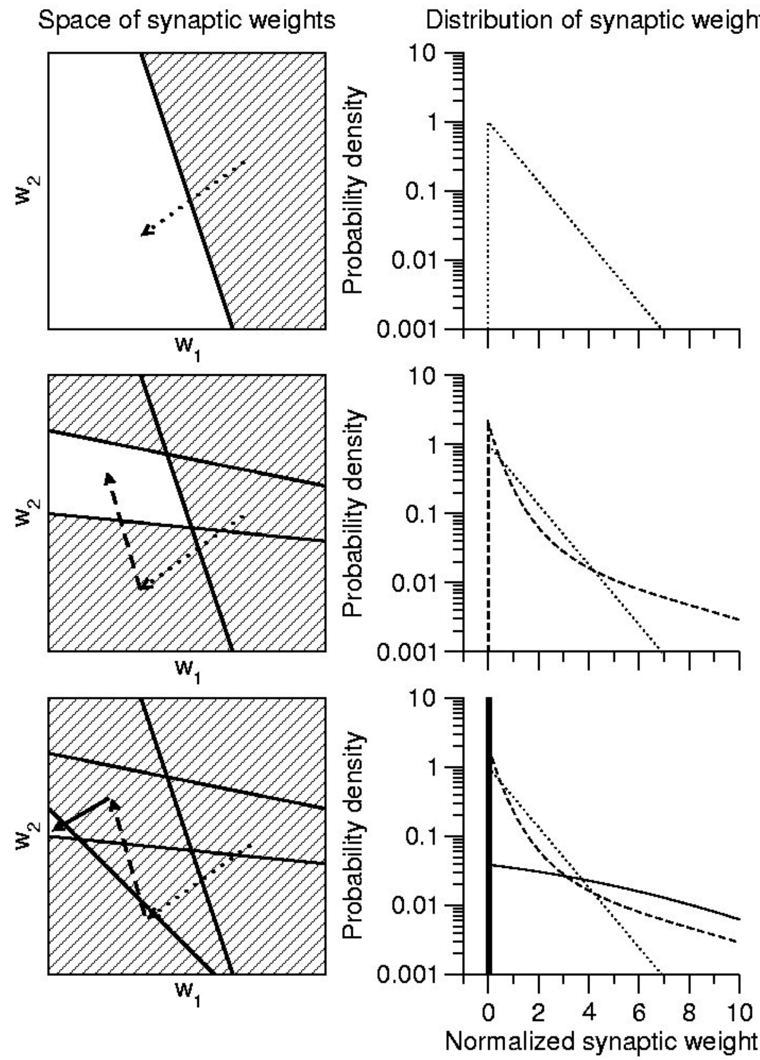
$$\vec{w}_i.\vec{\xi}^\mu > \theta + \kappa \quad \text{if } \xi_i^\mu = 1$$

$$\vec{w}_i.\vec{\xi}^\mu < \theta - \kappa \quad \text{if } \xi_i^\mu = 0$$

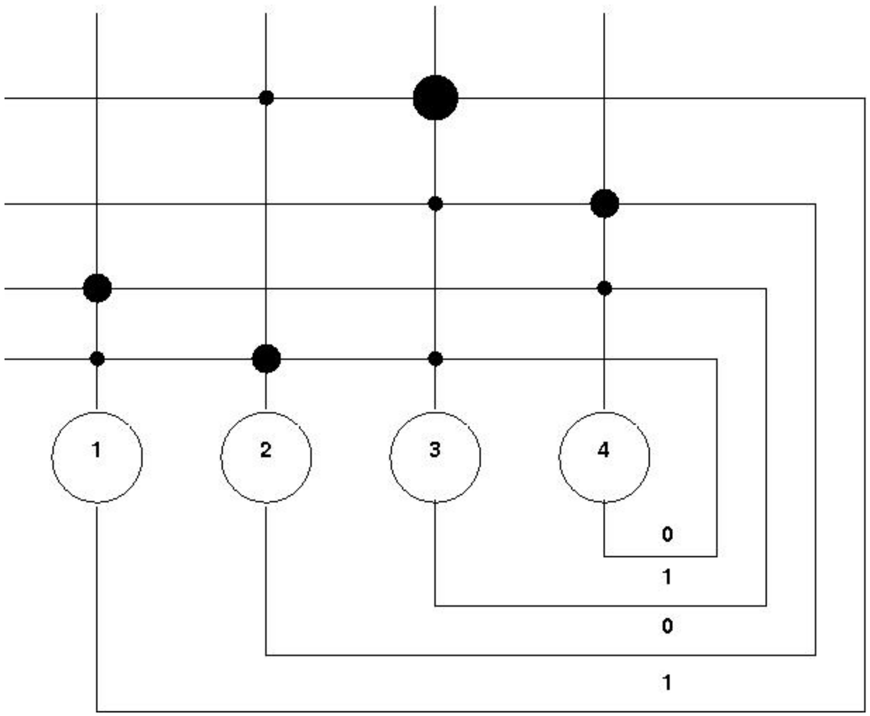
- The volume of this subspace is:

$$V = \int dr(\vec{w}_i) \prod_{\mu=1}^{p} \Theta\left[(2\xi_i^\mu - 1)\left(\vec{w}_i.\vec{\xi}^\mu - \theta\right) - \kappa\right]$$

- Compute 'typical' volume using replica method;
- Storage capacity obtained when volume goes to zero;
- Compute the distribution of weights in that volume.



Distribution of weights in an optimal attractor network

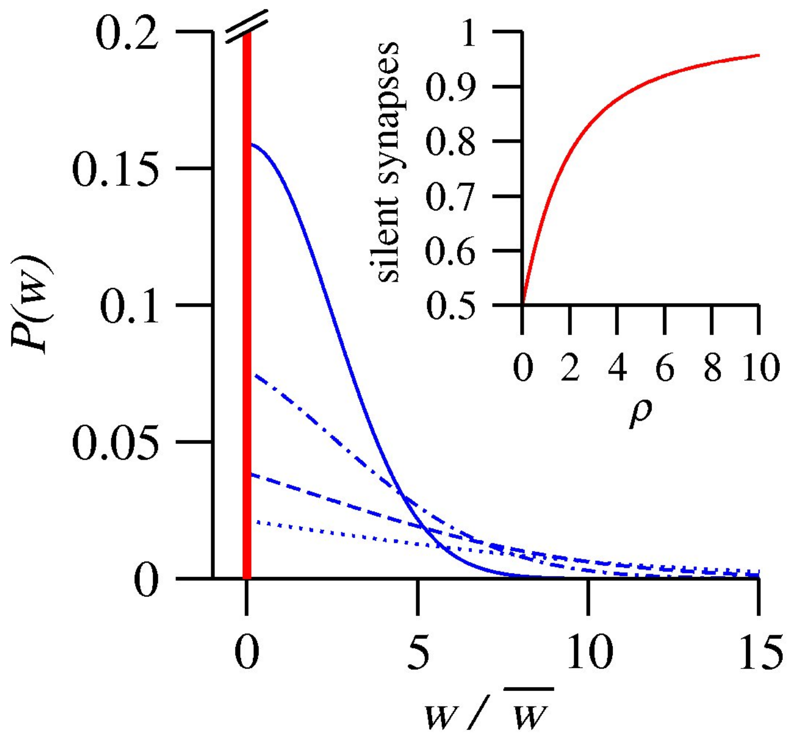


- For each neuron, finding synaptic weights consistent with stored attractors is equivalent to perceptron problem

The synaptic weight distribution at maximal capacity

At maximal capacity:

$$P(w_i = W) = S\delta(W) + \frac{1}{\sqrt{2\pi}\sigma_W} \exp\left[-\frac{1}{2}\left(\frac{W}{\sigma_W} + W_0(S)\right)^2\right]\Theta(W)$$



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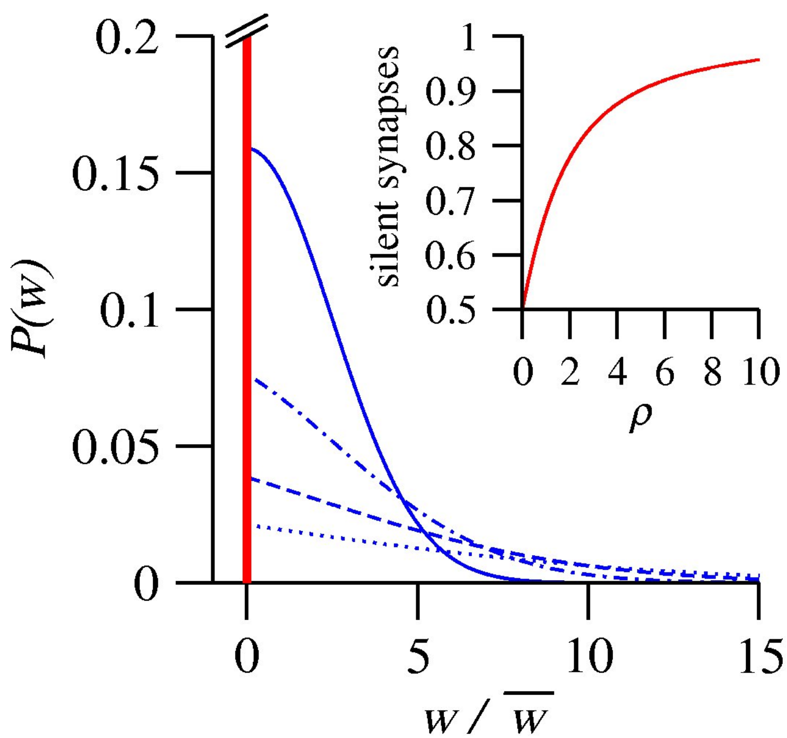


Distribution characterized by

- The fraction of zero weight synapses S depends on robustness parameter

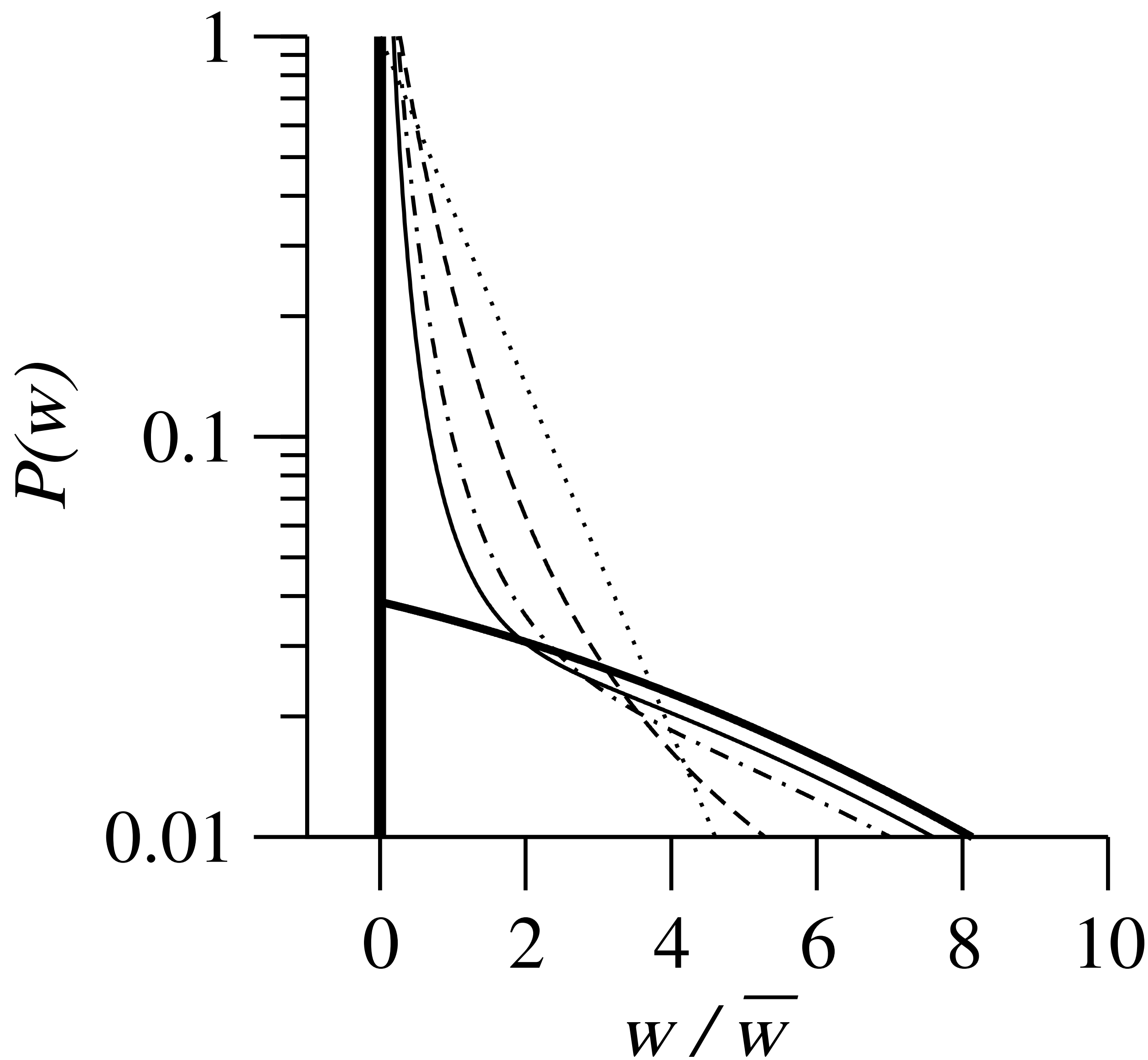
$$\rho = \frac{\kappa}{\overline{W}\sqrt{f(1-f)N}}$$

  where $\overline{W} \sim \theta/fN$ is the average synaptic weight

- The width of the truncated Gaussian σ_W depends on S and $\overline{W}$.

Brunel et al 2004

Distribution of weights below capacity



Distribution of weights: theory vs experiment

- Large fraction of zero weight synapses is consistent with data:
  - **Anatomy:** nearby pyramidal cells are locally potentially almost fully connected (Kalisman et al 2005)
  - **Electrophysiology:** nearby pyramidal cells have connection probability of $\sim 10\%$ (Mason et al 1991, Markram et al 1997, Sjostrom et al 2001, Holmgren et al 2003)

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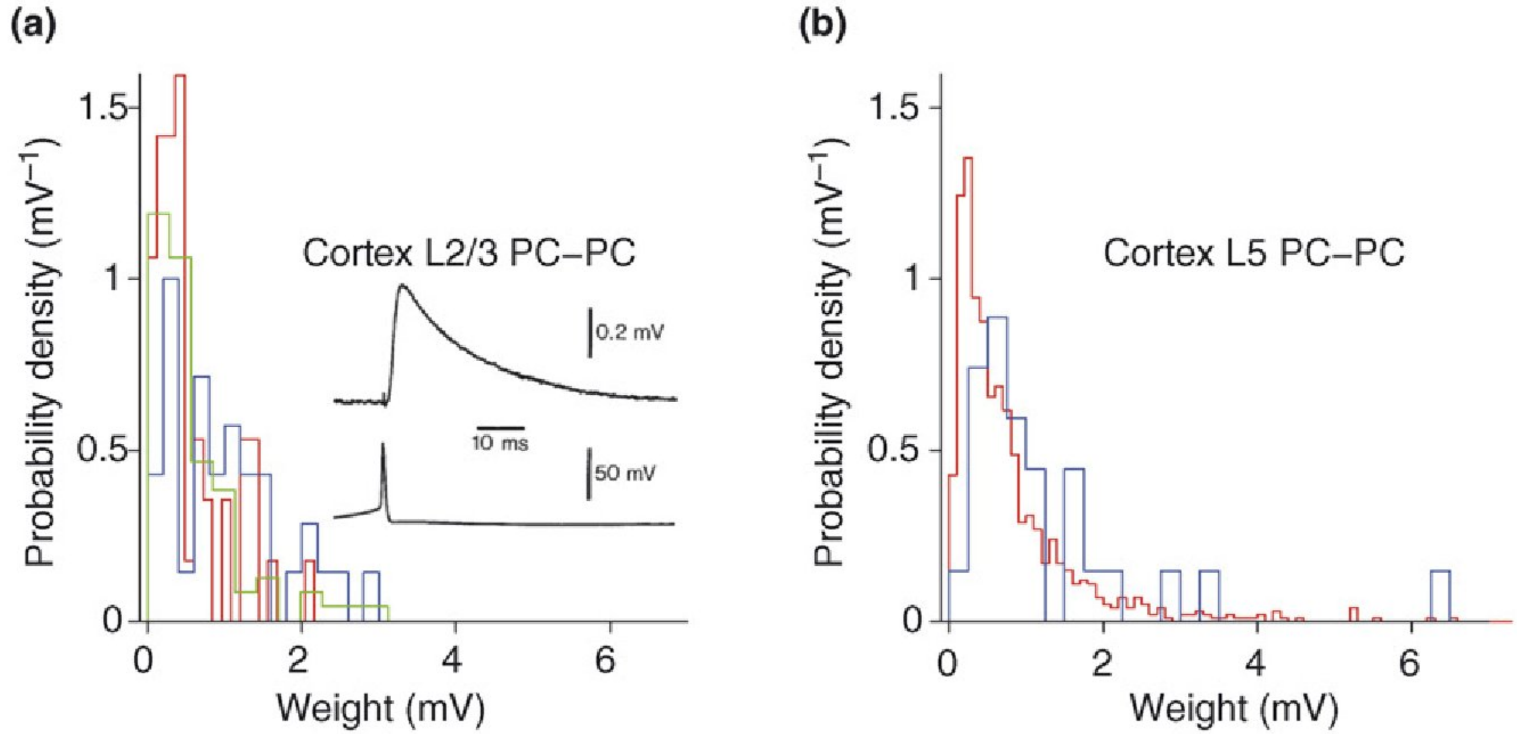
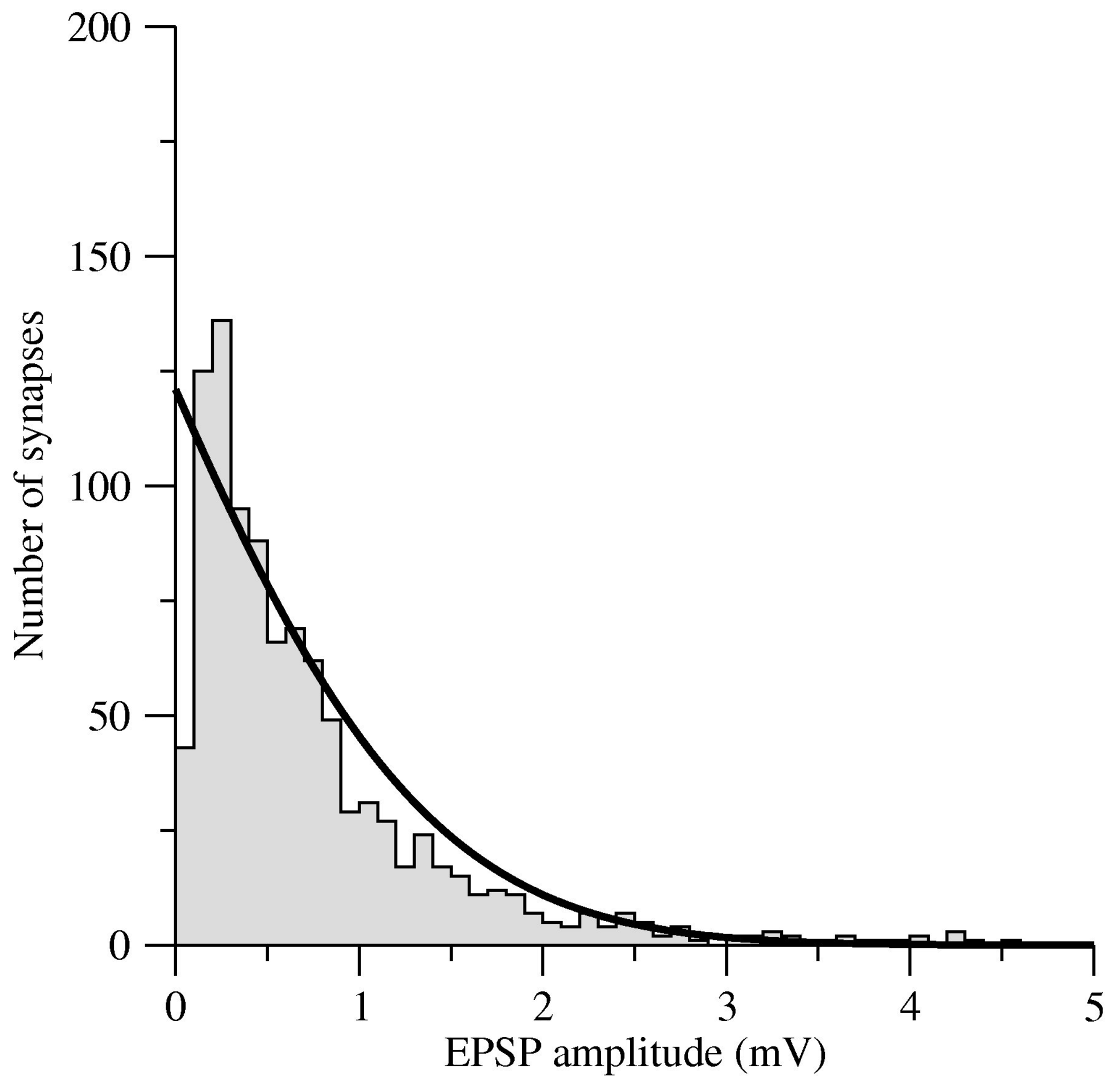
$\Rightarrow$ **Large fraction of 'potential' or 'silent' synapses.**

Distribution of synaptic weights in cortex



Mason et al 1991; Markram et al 1997; Sjostrom et al 2001; Holmgren et al 2003; Feldmeyer et al 2003; Frick et al 2007

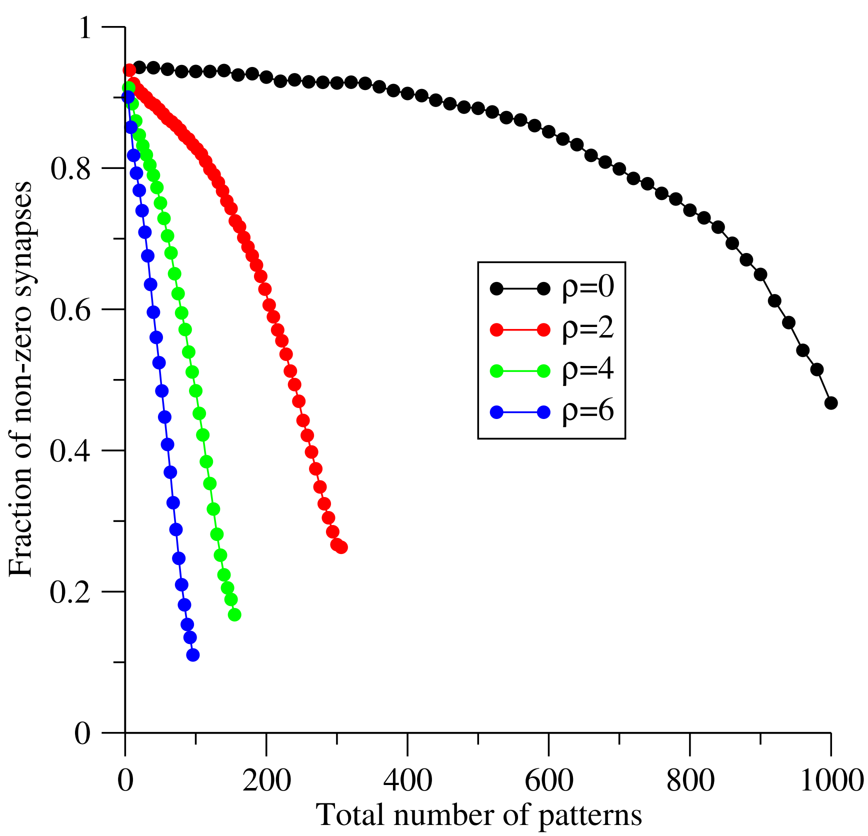
Sjostrom dataset vs theory

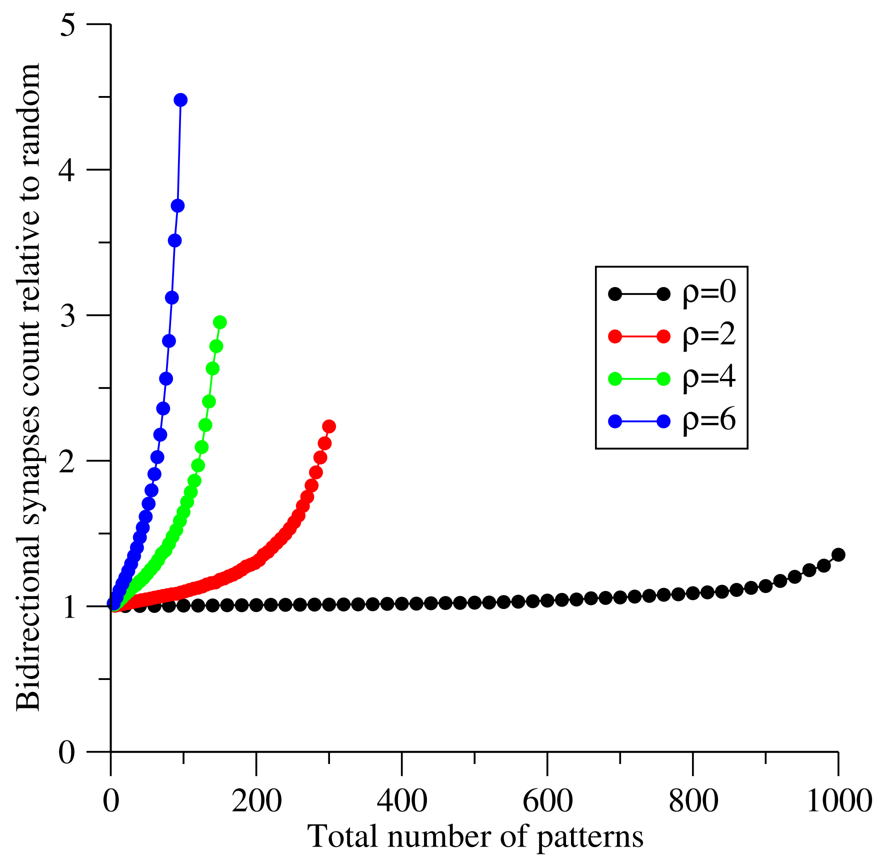


Sjostrom et al 2001; Song et al 2005

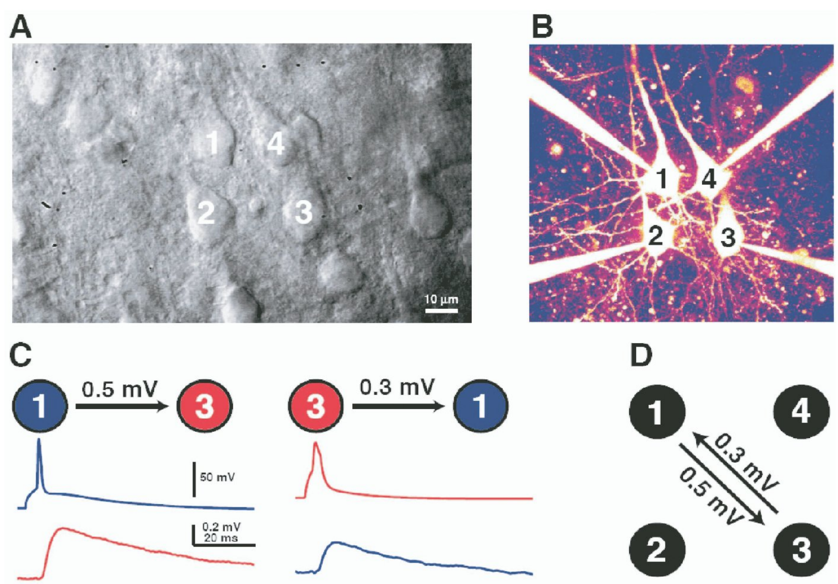
Two-neuron connectivity as a function of storage level

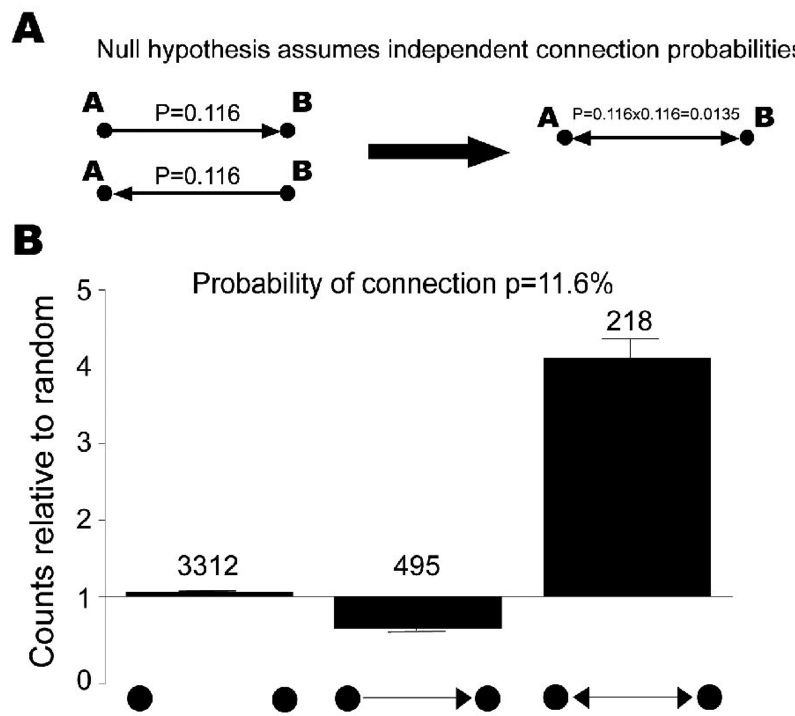
- Fully connected network of $N = 1000$ neurons;
- Storing random patterns, using perceptron learning algorithm independently for each neuron;





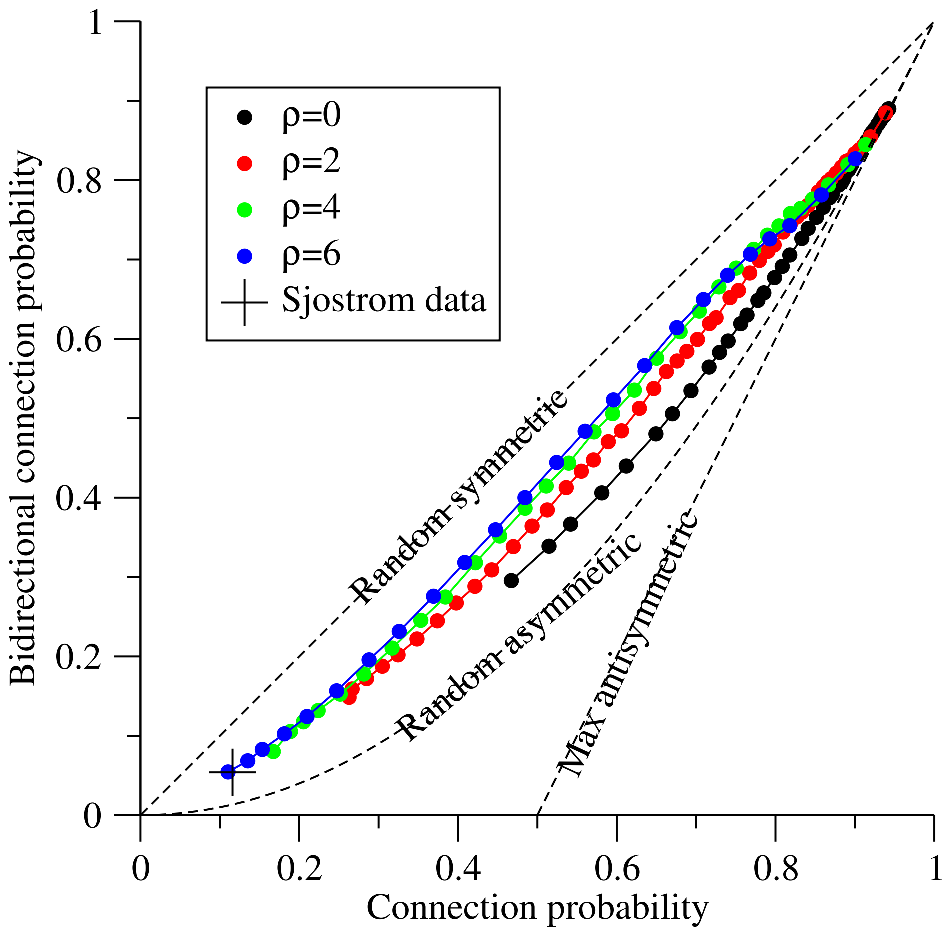
Two-neuron connectivity patterns in cortex





Song et al 2005

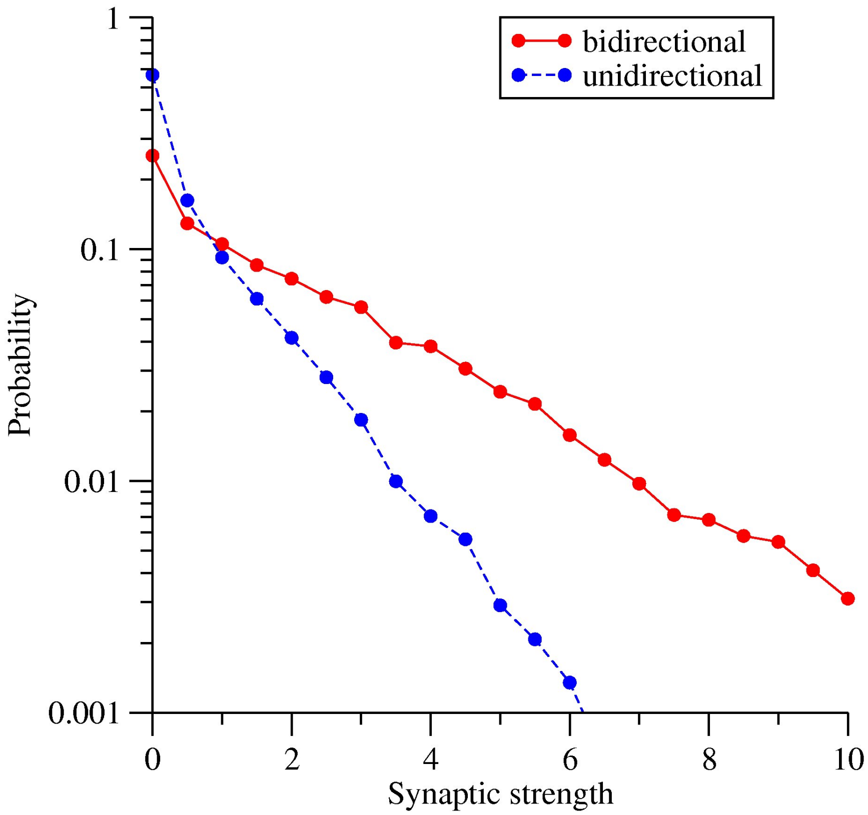
Two-neuron connectivity: theory vs experiment

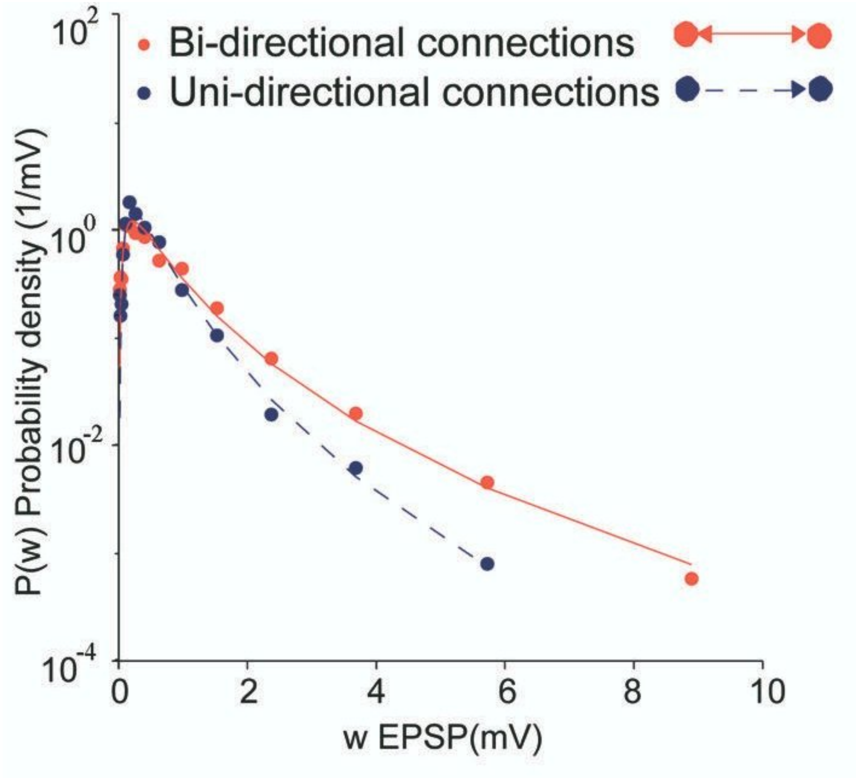


See also:

- Markram et al (1997) rat L5 somatosensory cortex: 3 times more than random;
- Song et al (2005) rat L5 visual cortex: 4 times more than random;
- Wang et al (2006)
  - rat PFC: 4 times more than random;
  - rat Visual cortex: 2 times more than random;
- Lefort et al (2009) mouse barrel cortex: $\sim$ random

Bidirectional vs unidirectional connections





Conclusions

- A network optimized to store a large number of attractors has
  - Sparse connectivity matrix;
  - The sparser the matrix, the more robust the network is;
  - Positive weights have broad distribution;
  - There is a strong overrepresentation of bidirectional connections
  - Optimal connectivity matrix approximately half-way between fully random and fully symmetric network
- All these features are consistent with the available statistics of connectivity in cortex

Collaborators

Perceptron/Cerebellum:

- Boris Barbour
- Philippe Isope
- Vincent Hakim
- Jean-Pierre Nadal