Statistical properties of network connectivity optimizing information storage

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Learning and memory: theoretical approaches

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  $\Rightarrow$ Study consequences of the learning rule at the network level;

- **Study optimality properties of specific networks** (Elizabeth Gardner 1988)

  Rather than focusing on a given learning rule, consider the space of all possible connectivity matrices.

  $\Rightarrow$ Average volume of subspace of weights that solve a particular learning task;

  $\Rightarrow$ Maximal storage capacity (Gardner 1988, etc);

  $\Rightarrow$ Statistics of synaptic connectivity in optimal networks

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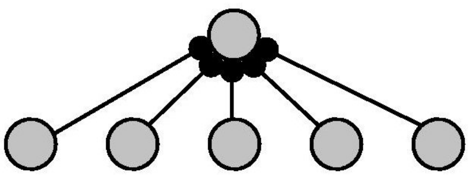

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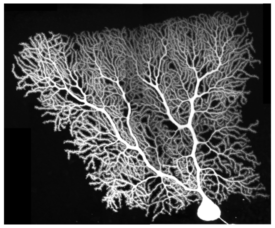
  - Cerebellum: GC $\longrightarrow$ PC network



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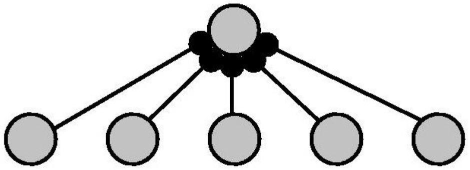
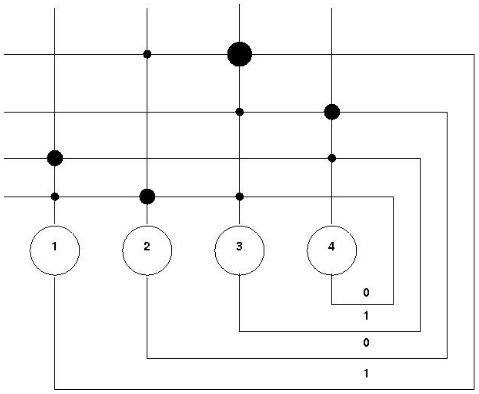


  - Recurrent network



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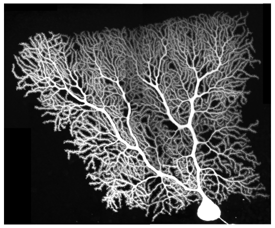
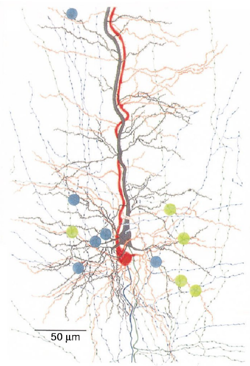
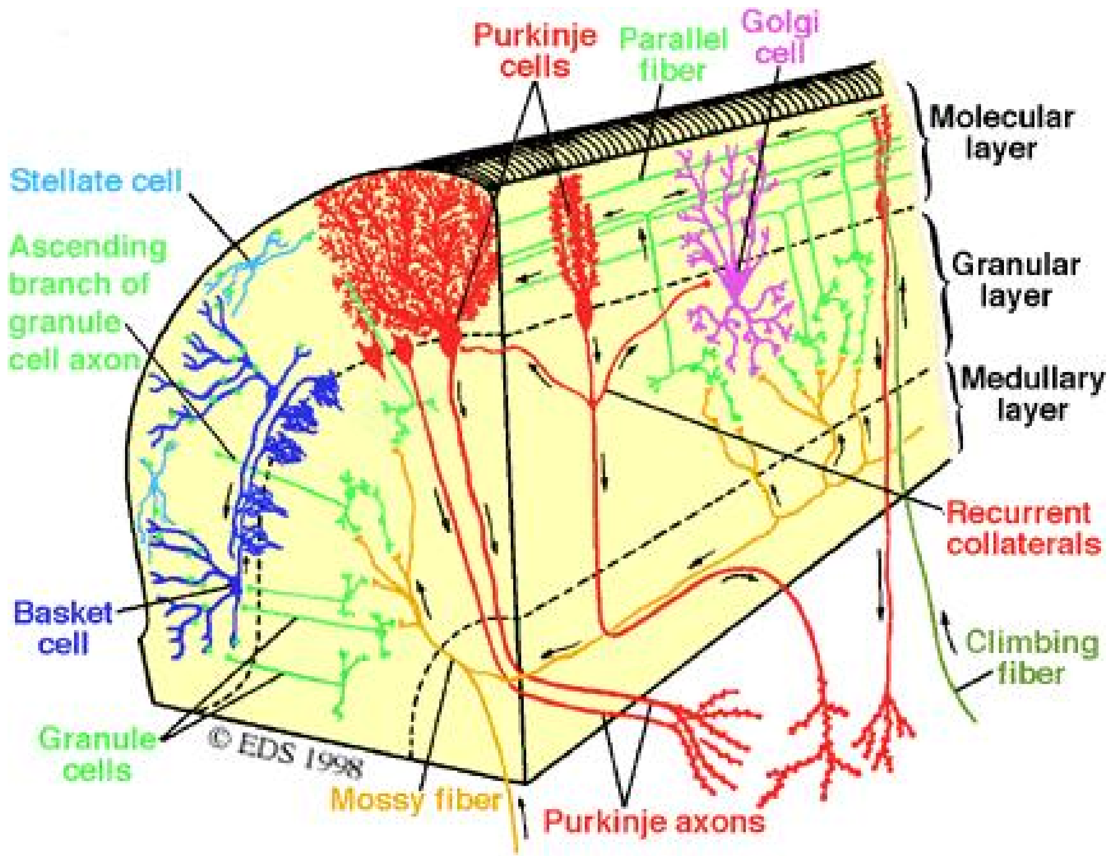


  - Neocortex: Pyr cell network

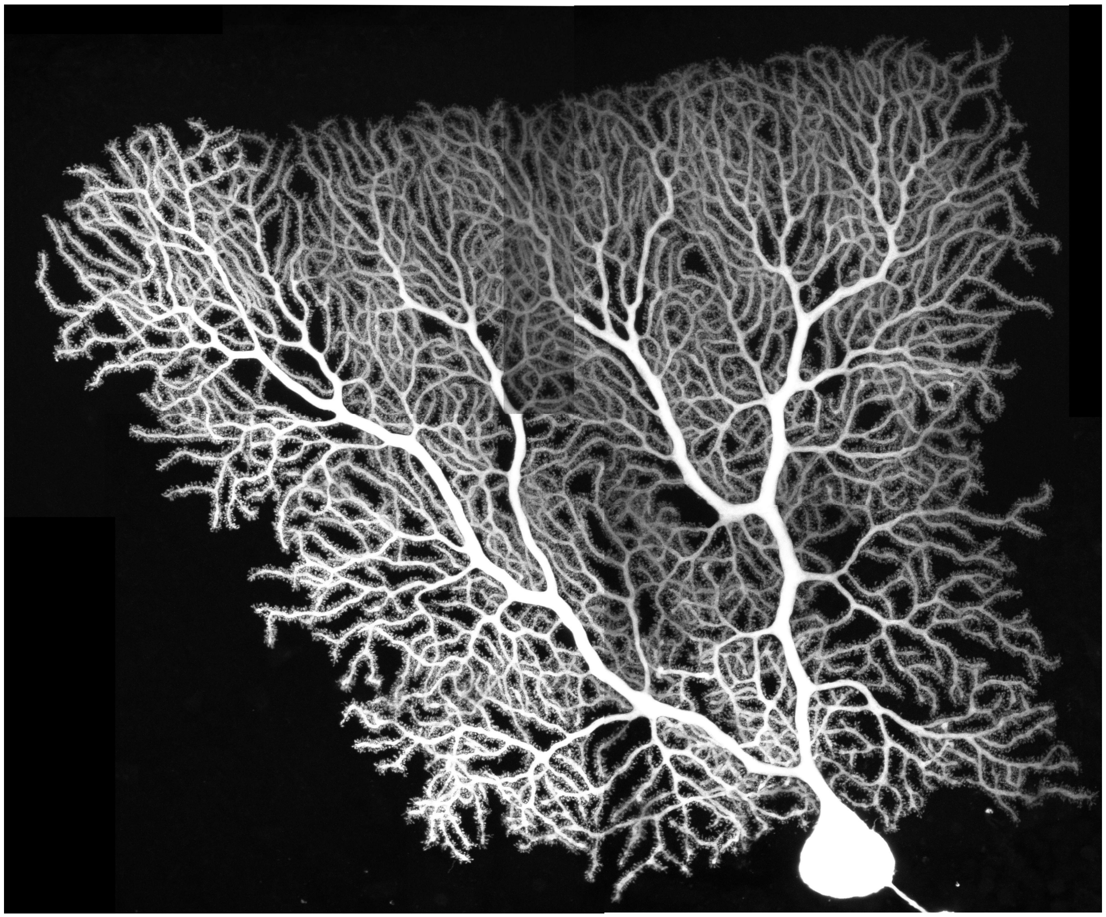


Cerebellar cortex

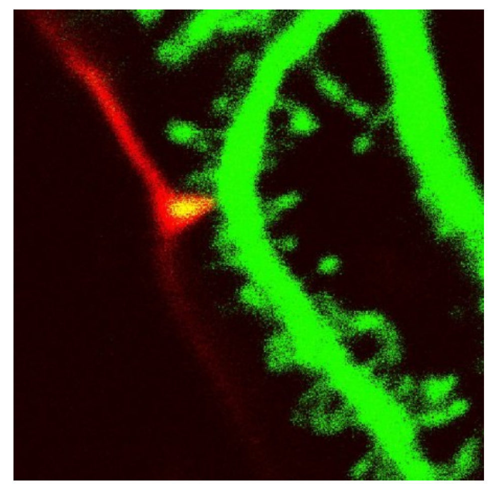
- Involved in motor learning;
- Often thought as a feedforward structure;
- Mossy fibers (sensory and contextual inputs) $\longrightarrow$ granule cells (GCs)
- GCs $\longrightarrow$ Purkinje cells (PC) through parallel fibers
- PC $\longrightarrow$ motor output (through deep cerebellar nuclei)



Purkinje cell

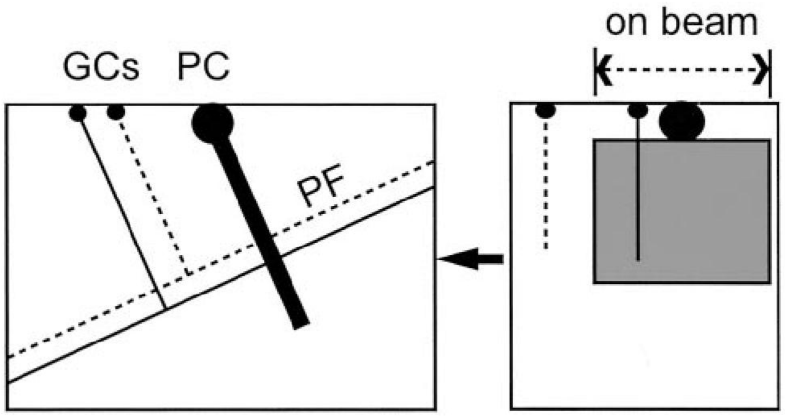


- 150,000 GC $\longrightarrow$ PC synapses per PC
- thought to be a major site of learning in cerebellum since Marr and Albus
- known to be plastic (LTD, LTP) since Ito



Statistics of GC-PC connectivity

(adult rats)



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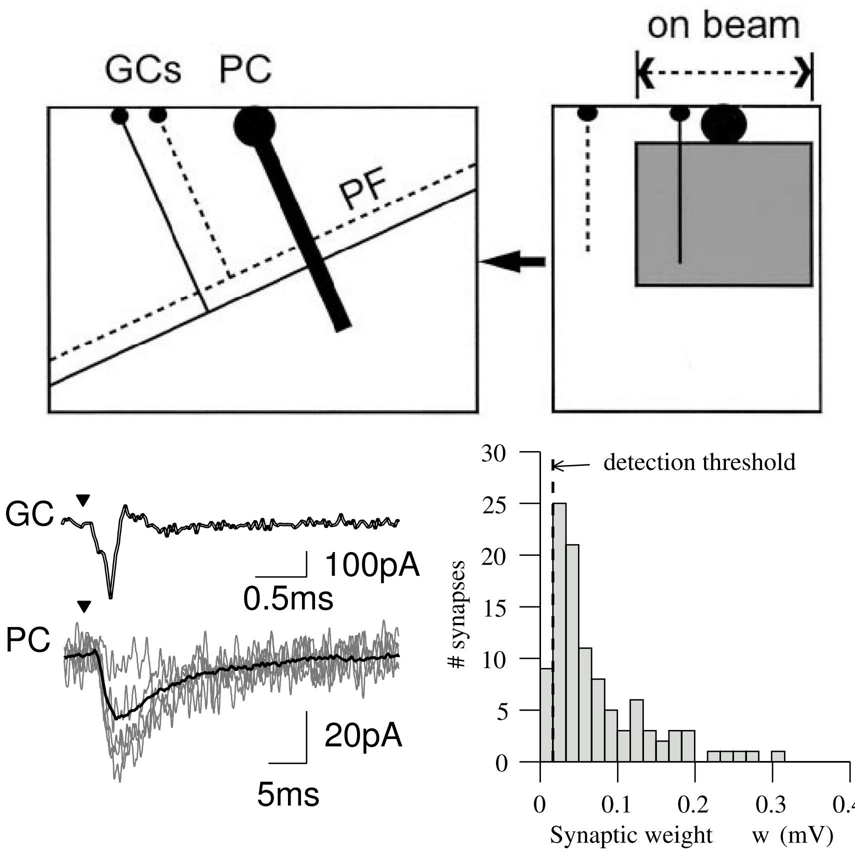

Isope and Barbour, J Neurosci 2002

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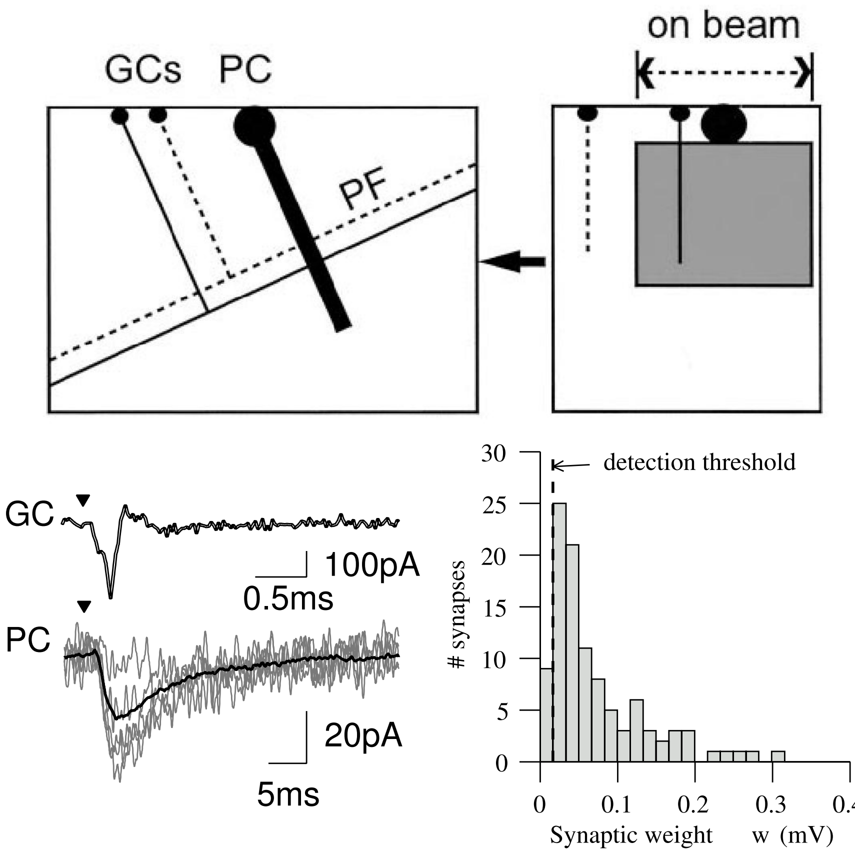

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- EM predicts $\sim 50\,\%$ connection probability

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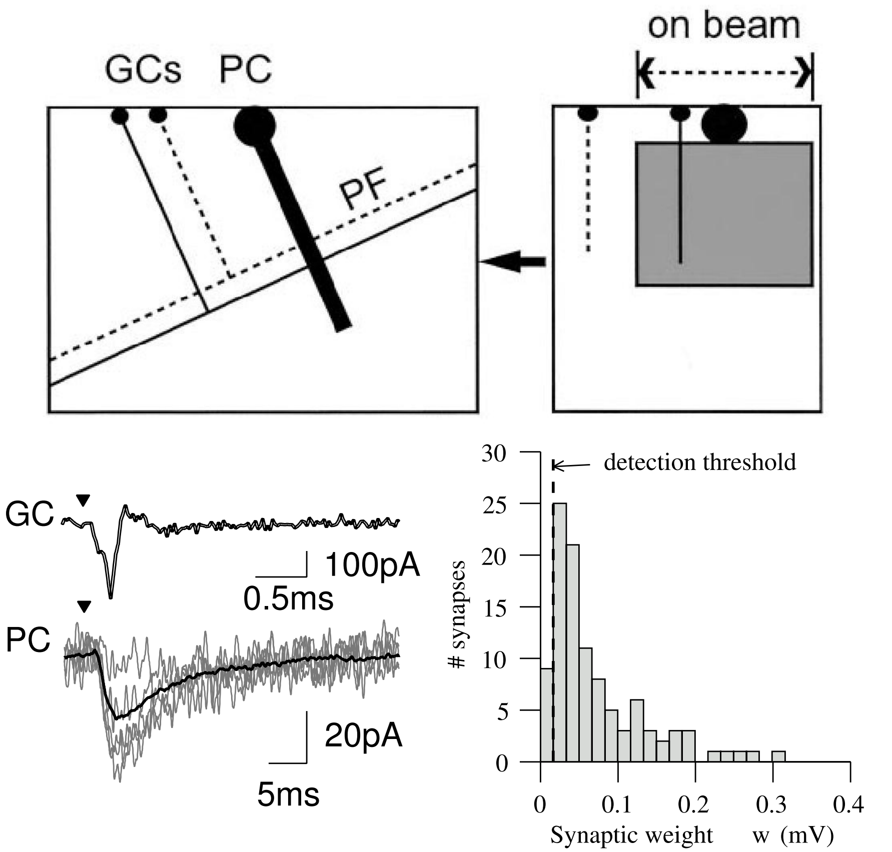

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- Electrophysiology gives less than 10 % of detectable responses

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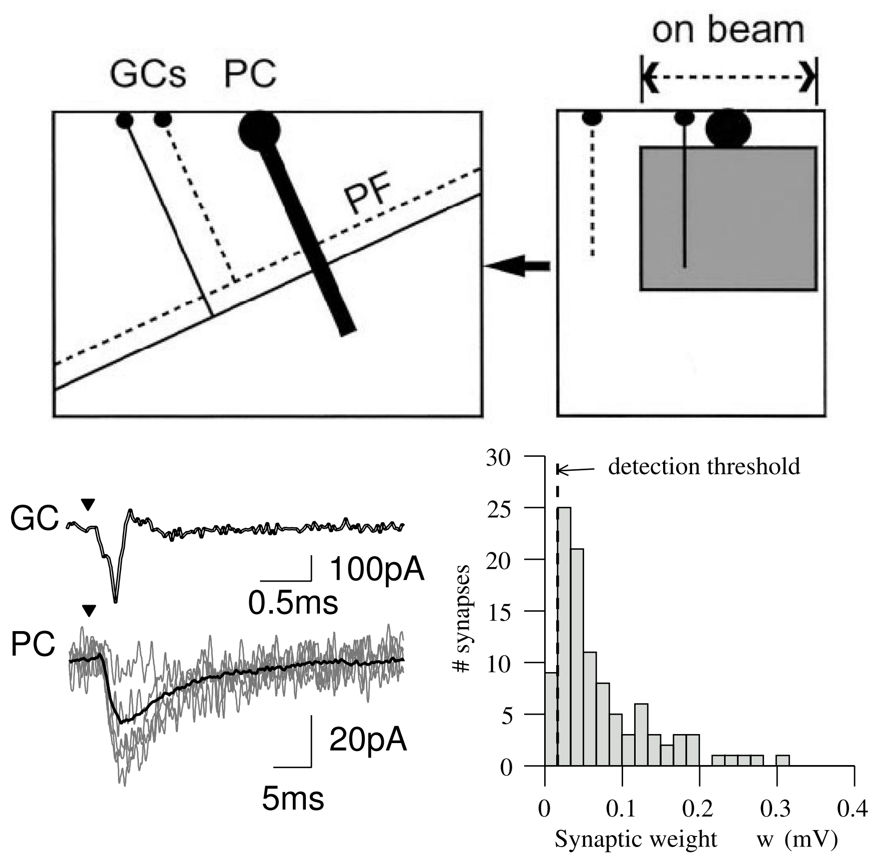

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- $\Rightarrow$ more than 80 % of synapses are electrically silent!

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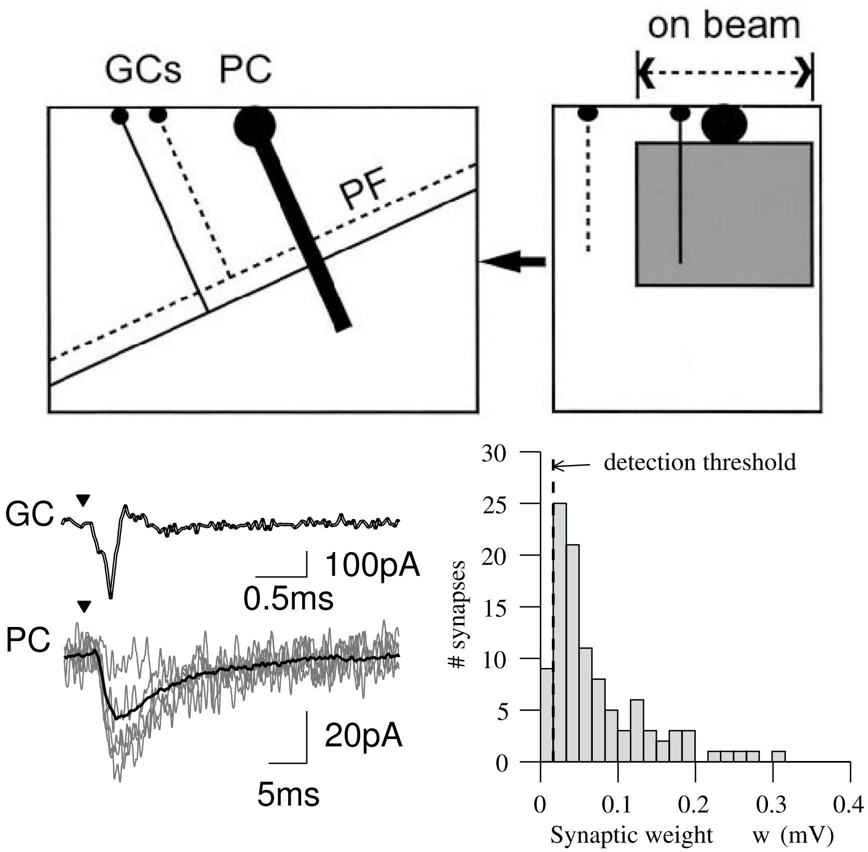

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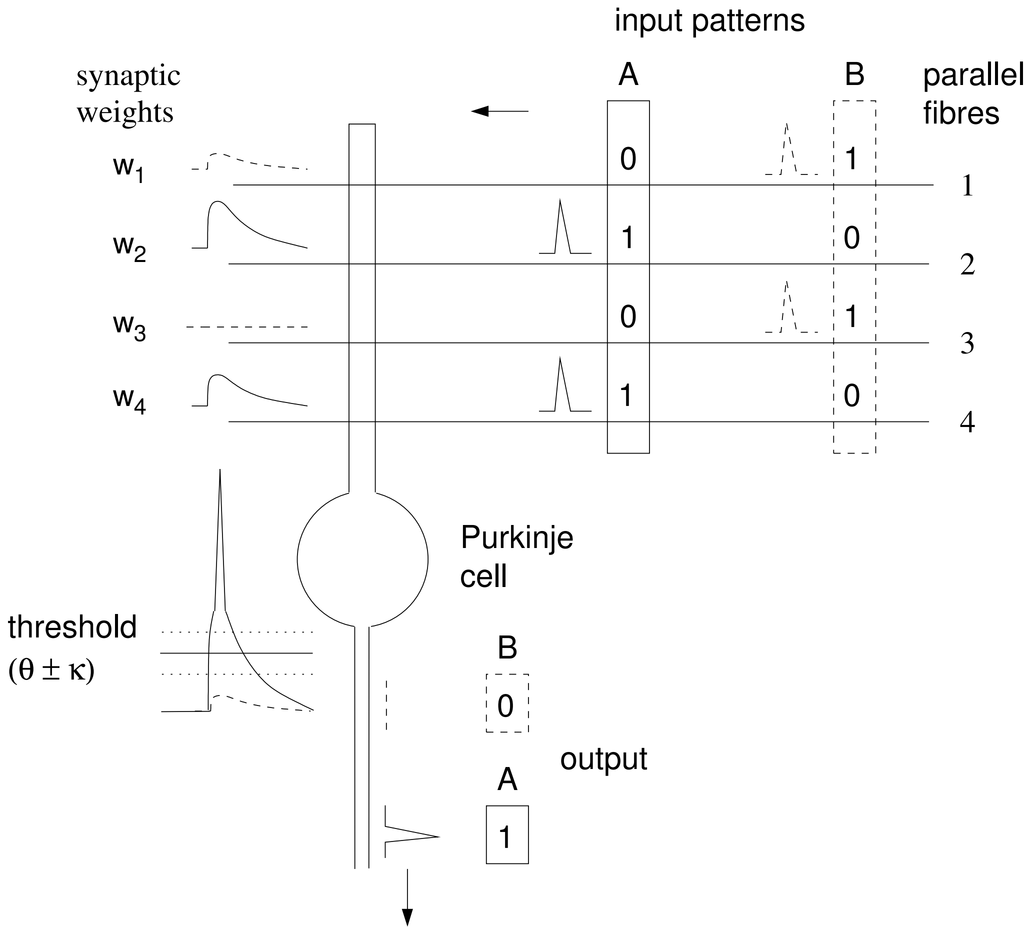
- EM predicts $\sim$ 50 % connection probability
- Electrophysiology gives less than 10 % of detectable responses
- $\Rightarrow$ more than 80 % of synapses are electrically silent!
- $\Rightarrow$ why so many ‘useless’ synapses?

Modeling PCs as a perceptron



Marr 1969, Albus 1971

- $N \sim 150,000$ synapses/GC inputs;
- sums linearly its inputs;
- emits a spike if inputs $> \theta \sim 10$ mV (threshold)
- has to learn a set of $p \equiv \alpha N$ random uncorrelated input/output associations, $G_i^\mu \rightarrow P^\mu$ with
  - f ('input coding level', fraction of active GCs in a pattern);
  - f' ('output coding level', fraction of patterns for which PC fires);
- by appropriate choice of its synaptic weights $w_i \geq 0$.
- in a robust way (as measured by κ);

Gardner approach

- Subspace of solutions to learning problem in w space:

$$\vec{w}.\vec{G}^{\mu} > \theta + \kappa \quad \text{if } P^{\mu} = 1$$

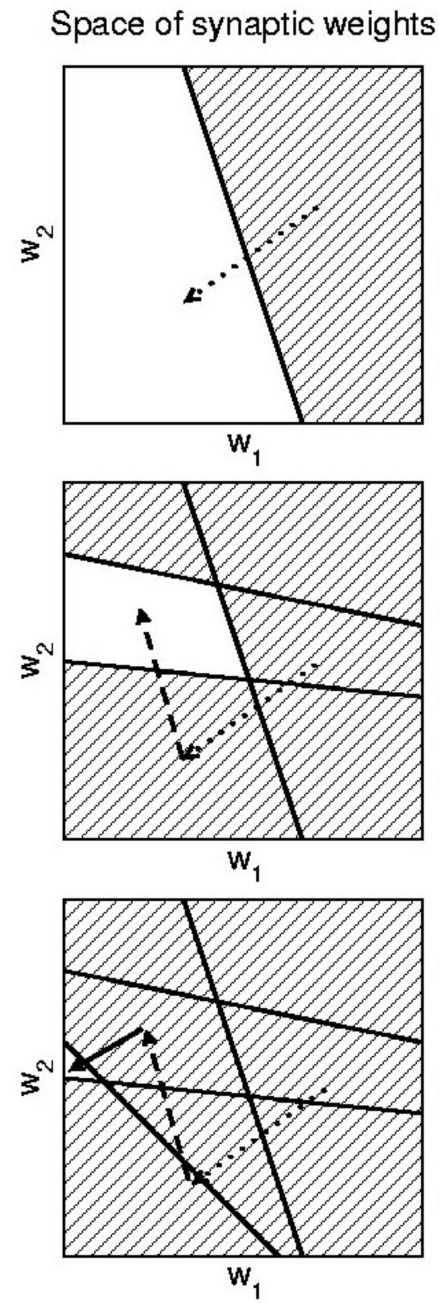
$$\vec{w}.\vec{G}^{\mu} < \theta - \kappa \quad \text{if } P^{\mu} = 0$$

- The volume of this subspace is:

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

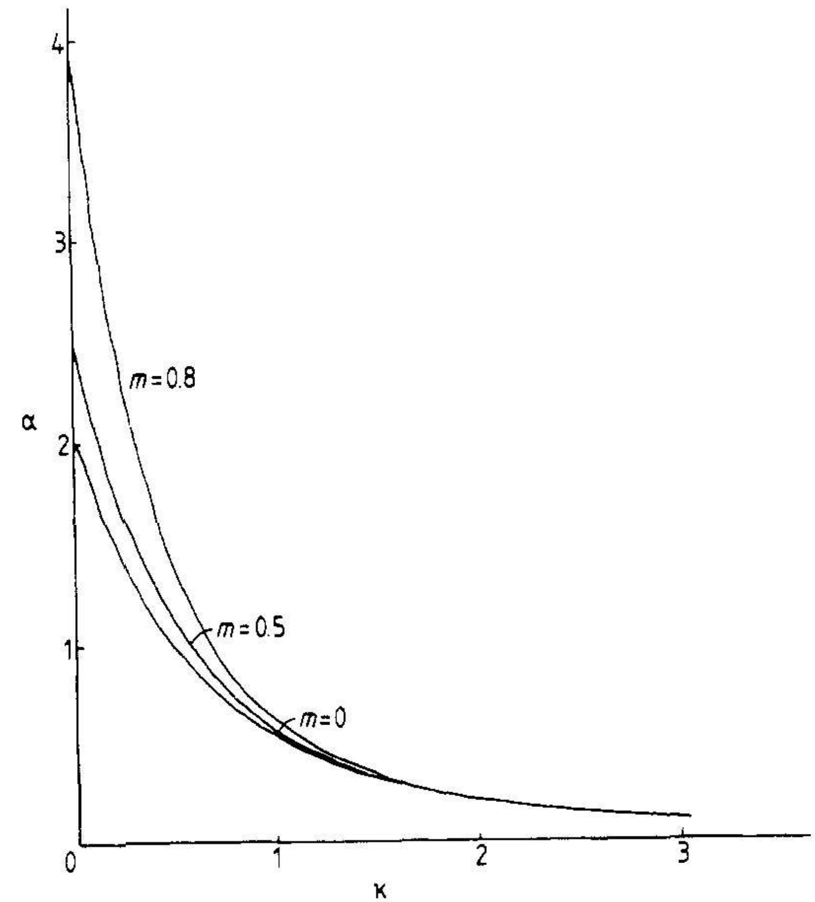
- Compute $\langle \log V \rangle / N$ to get typical volume using replica method;
- Storage capacity obtained when volume goes to zero;
- The distribution of weights is

$$P(w) = \frac{1}{V} \int dr(\vec{w})\, \delta(w - w_1) \prod_{\mu=1}^{p} \Theta \left[(2P^{\mu} - 1) \left(\vec{w}.\vec{G}^{\mu} - \theta \right) - \kappa \right]$$



Known results on the storage capacity of the perceptron

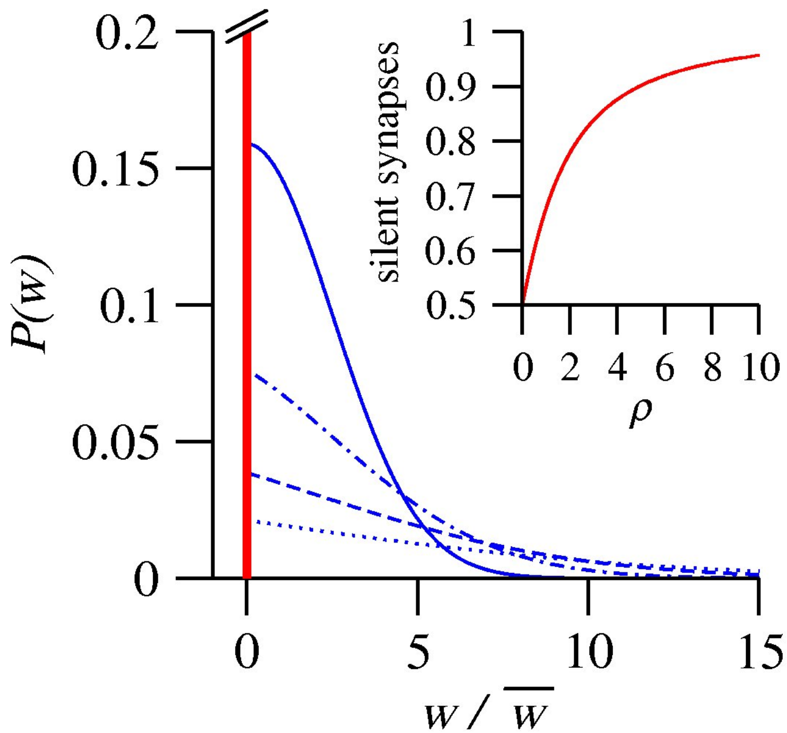
- Unconstrained weights, $f' = 0.5$, $\kappa = 0$
  $\Rightarrow \alpha_{max} = 2$ (Cover 1965, Gardner 1988)
- Tradeoff between capacity and robustness (Gardner 1988)
- Sign-constrained synapses:
  $\Rightarrow \alpha_{max} = 1$ (Amit et al 1989)



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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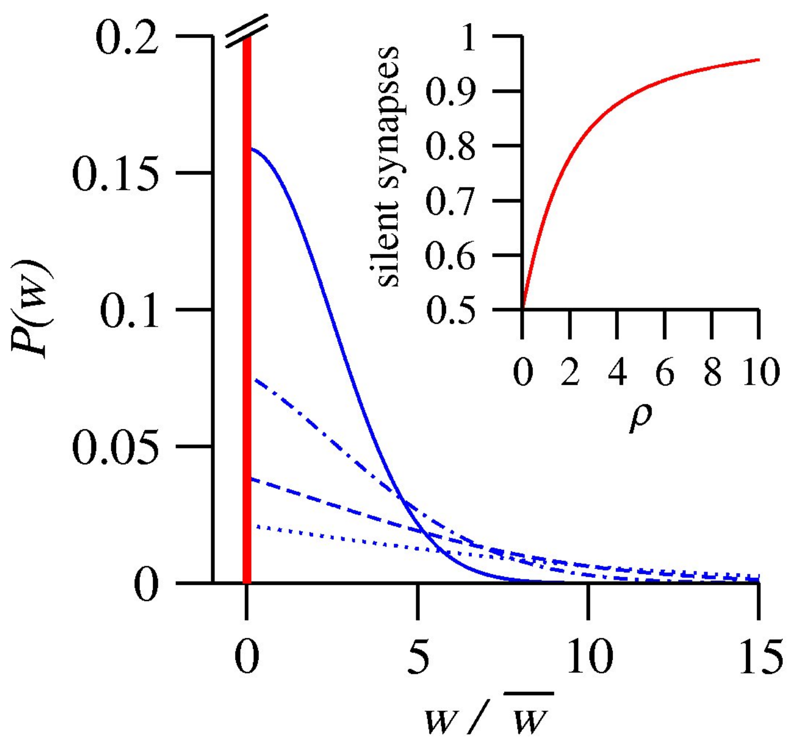


Distribution characterized by

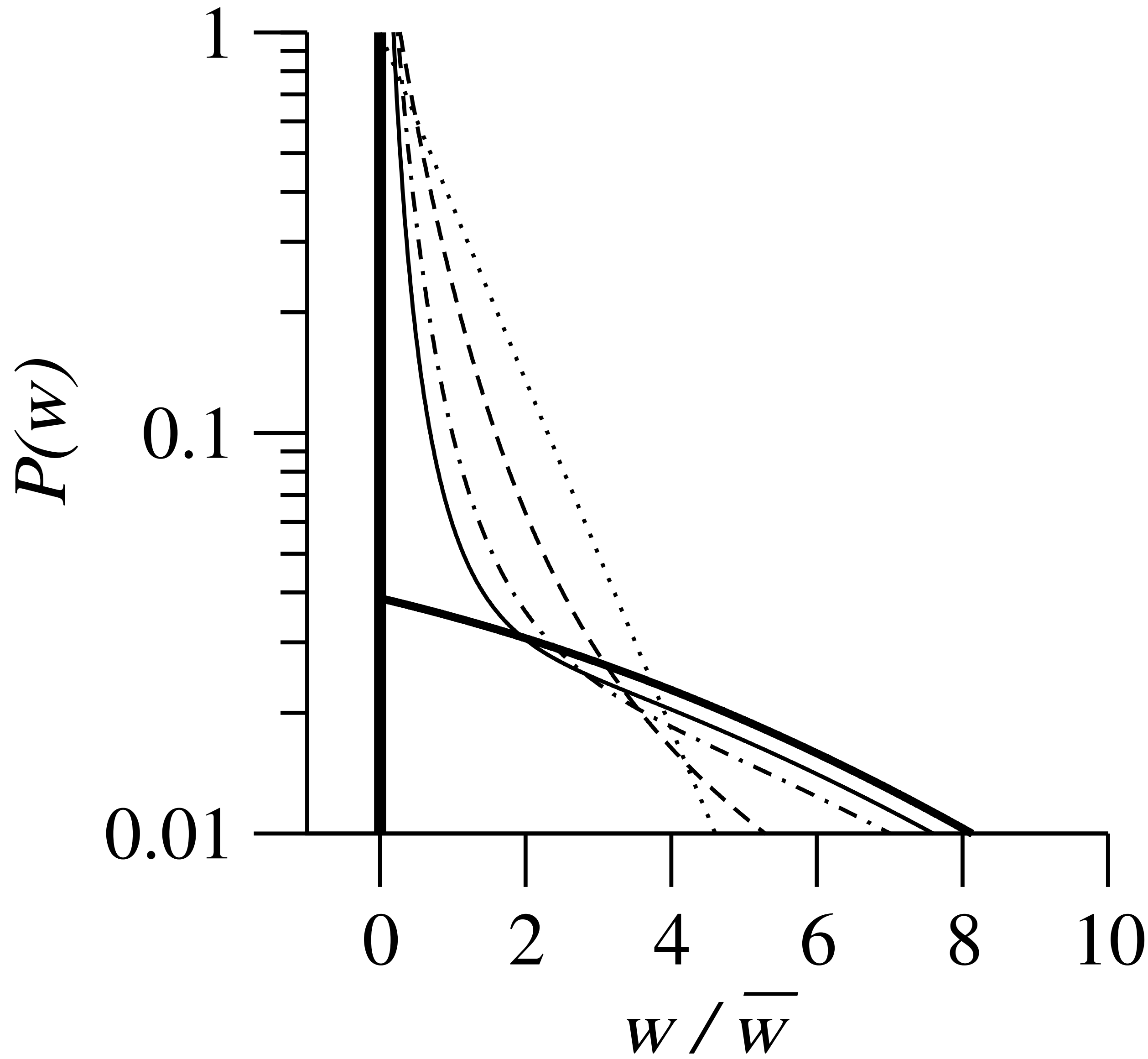
- The fraction of 'silent' synapses S depends on robustness parameter

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

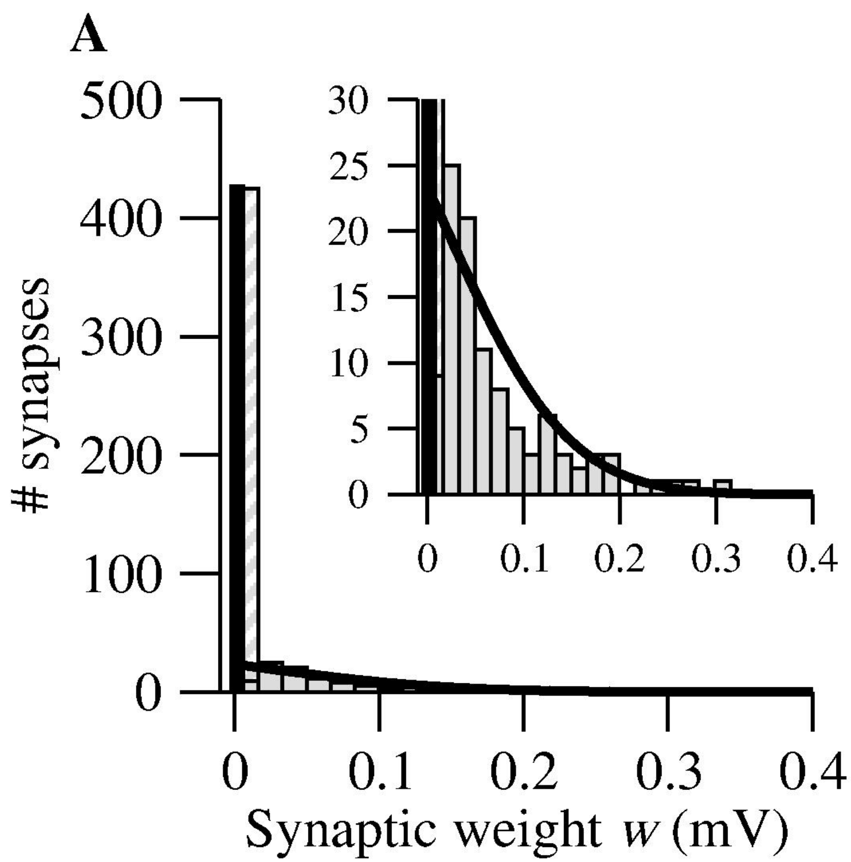
where $\overline{W} \sim \theta/fN$ is the average synaptic weight

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

Distribution of weights below capacity



Theory vs experiment



Best fit parameters:

- The Purkinje cell appears to operate near maximal capacity
  $\alpha = (0.97 \pm 0.03)\alpha_c$

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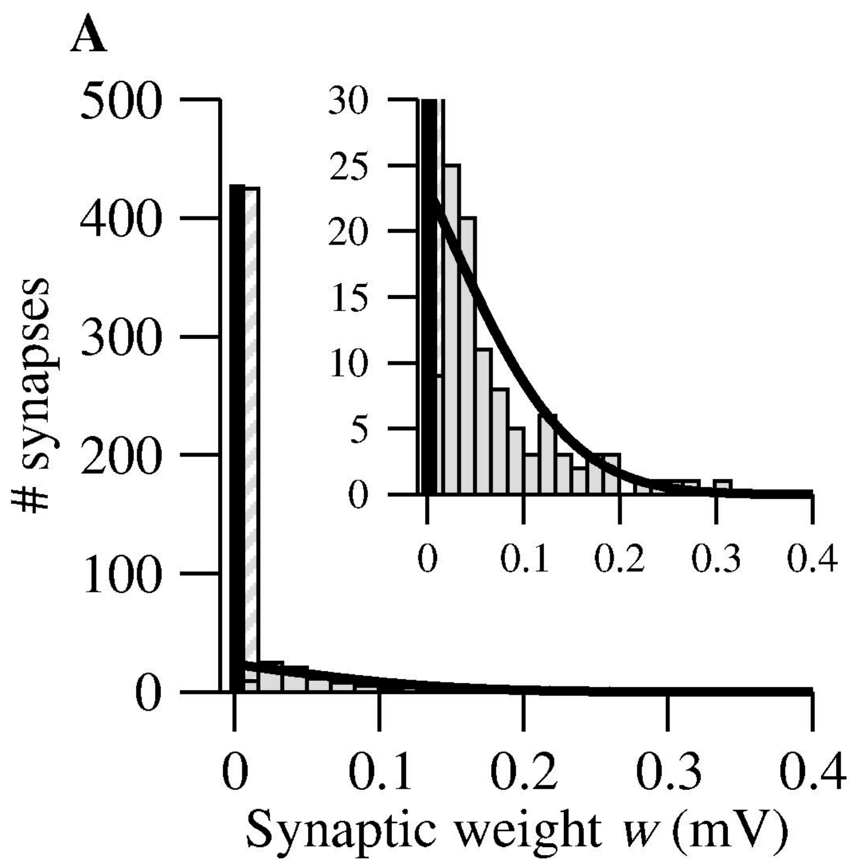

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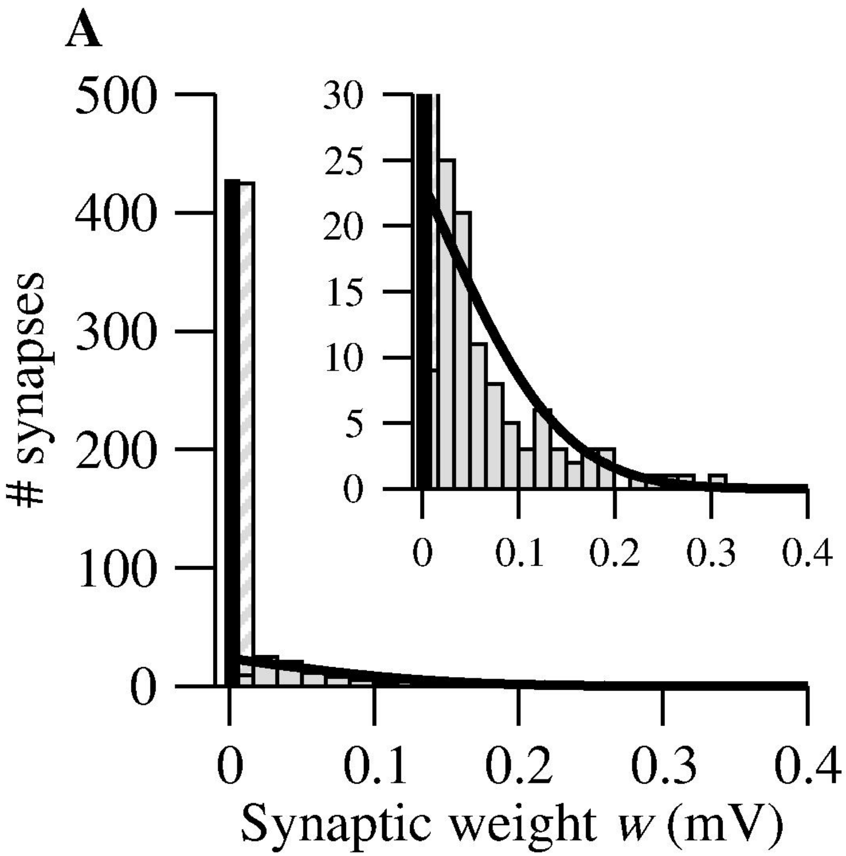

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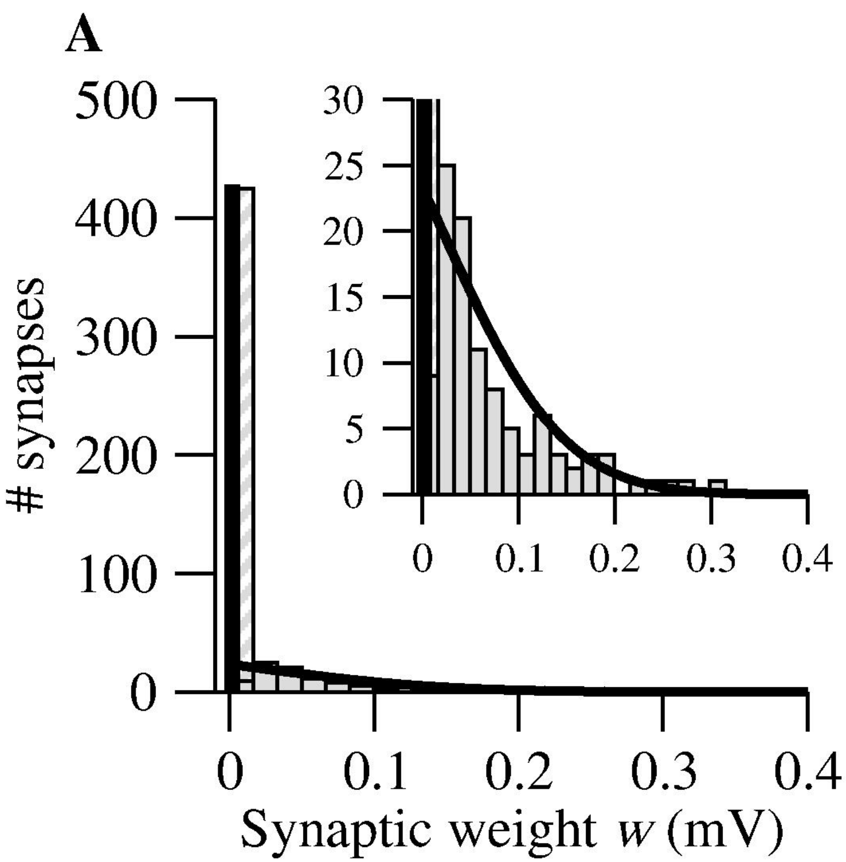

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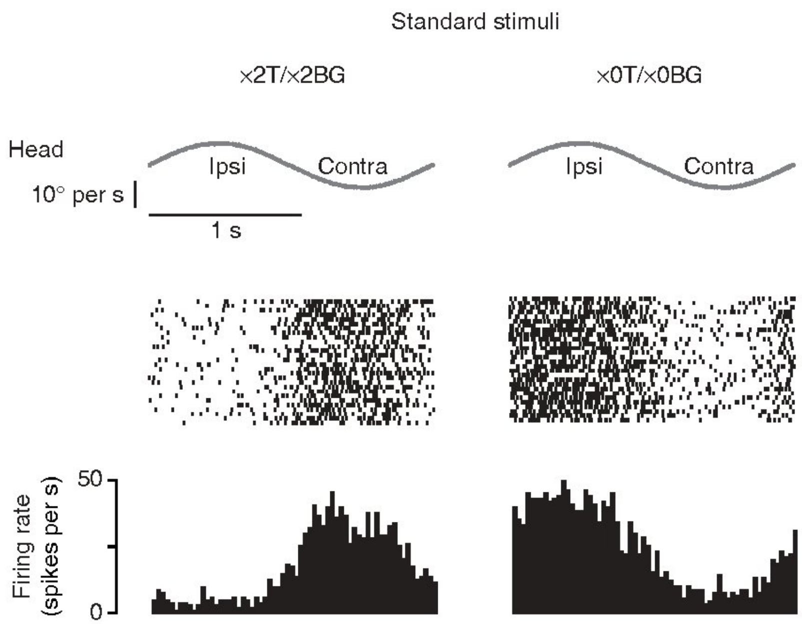
  f' = 37 %
  $\Rightarrow$ Sparse input and non-sparse output—ratio $\sim$100
- Robustness parameter
  κ = 0.8 mV

Towards more realistic models of Purkinje cells



Ke et al 2009

- Analog (instantaneous firing rate) inputs and outputs?
- Temporal correlations?

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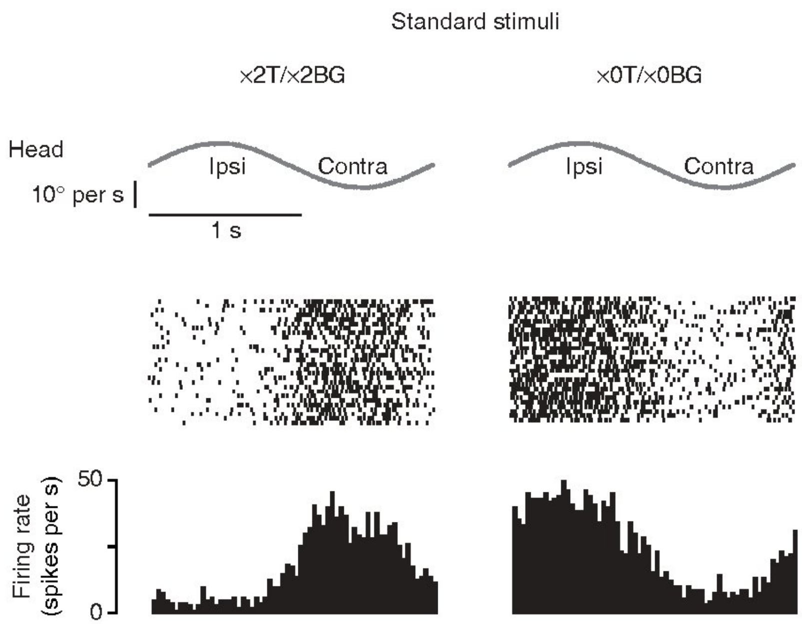

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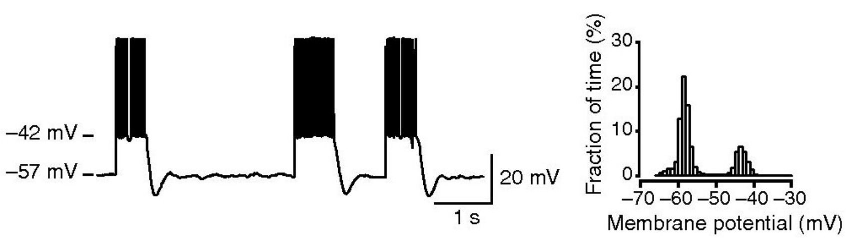


Loewenstein et al 2005

- Analog (instantaneous firing rate) inputs and outputs?

- Temporal correlations?

- Bistability of Purkinje cells?

Analog inputs/output

- Each granule cell has a firing rate drawn from a distribution with mean μ_G, variance σ_G^2;
- Purkinje cell has a required total input current drawn from a distribution with mean μ_P, variance σ_P^2;
- Firing rate of PC: monotonically increasing function oinput current
- Constraints imposed by learning are no longer inequalities, but rather equalities:

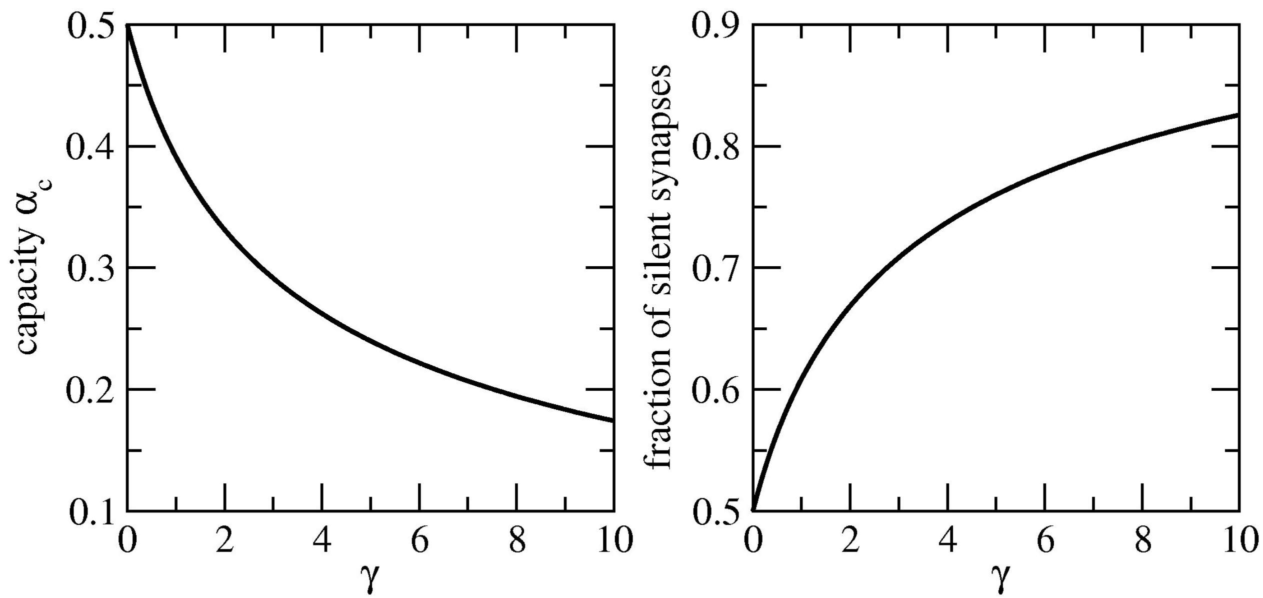
$$\vec{w}.\vec{G}^{\mu} = \theta + P^{\mu}$$

Capacity and distribution of weights

- Capacity depends on a single parameter

$$\gamma = \frac{\sigma_P^2 \mu_G^2}{\theta^2 \sigma_G^2}$$

- Distribution of weights identical to binary perceptron;
- Fraction of silent synapses $= 1-$ Capacity



Optimal statistics of inputs/outputs

- To optimize capacity, $\gamma = (\sigma_P^2 \mu_G^2)/(\theta^2 \sigma_G^2)$ should be as small as possible;
- Distribution of GC firing rate maximizing σ_G/μ_G is a binary sparse distribution, with cells silent most of the time, firing at maximal frequency with small probability.
- Fits with intracellular recordings of GCs in vivo (Chadderton et al 2004): GCs have very low spontaneous rates ($\ll 1$Hz) but occasionnally respond with brief high frequency bursts to external stimulation.
- Distribution of PC firing rate: σ_P should be small to minimize γ, but should be larger than intrinsic noise $\sigma \Rightarrow$ optimum at some finite value of σ_P, depending on σ.

Learning sequences with temporal correlations

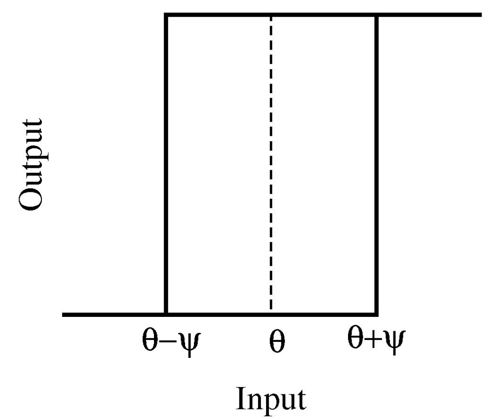
- Sequences$=$ Markov chains with temporal correlations c_{in}, c_{out}.

$$\text{Prob}(G_i(t+1)=1) \quad = \quad f + c_{in}(G_i(t) - f) \qquad (1)$$

$$\text{Prob}(P(t+1)=1) \quad = \quad f' + c_{out}(P(t) - f') \qquad (2)$$

- Correlations do not affect capacity/distribution of weights when $c_{in} = 0$ or $c_{out} = 0$
- Capacity increases with correlations when $c_{in} \sim c_{out}$

Impact of bistability on storage of correlated sequences



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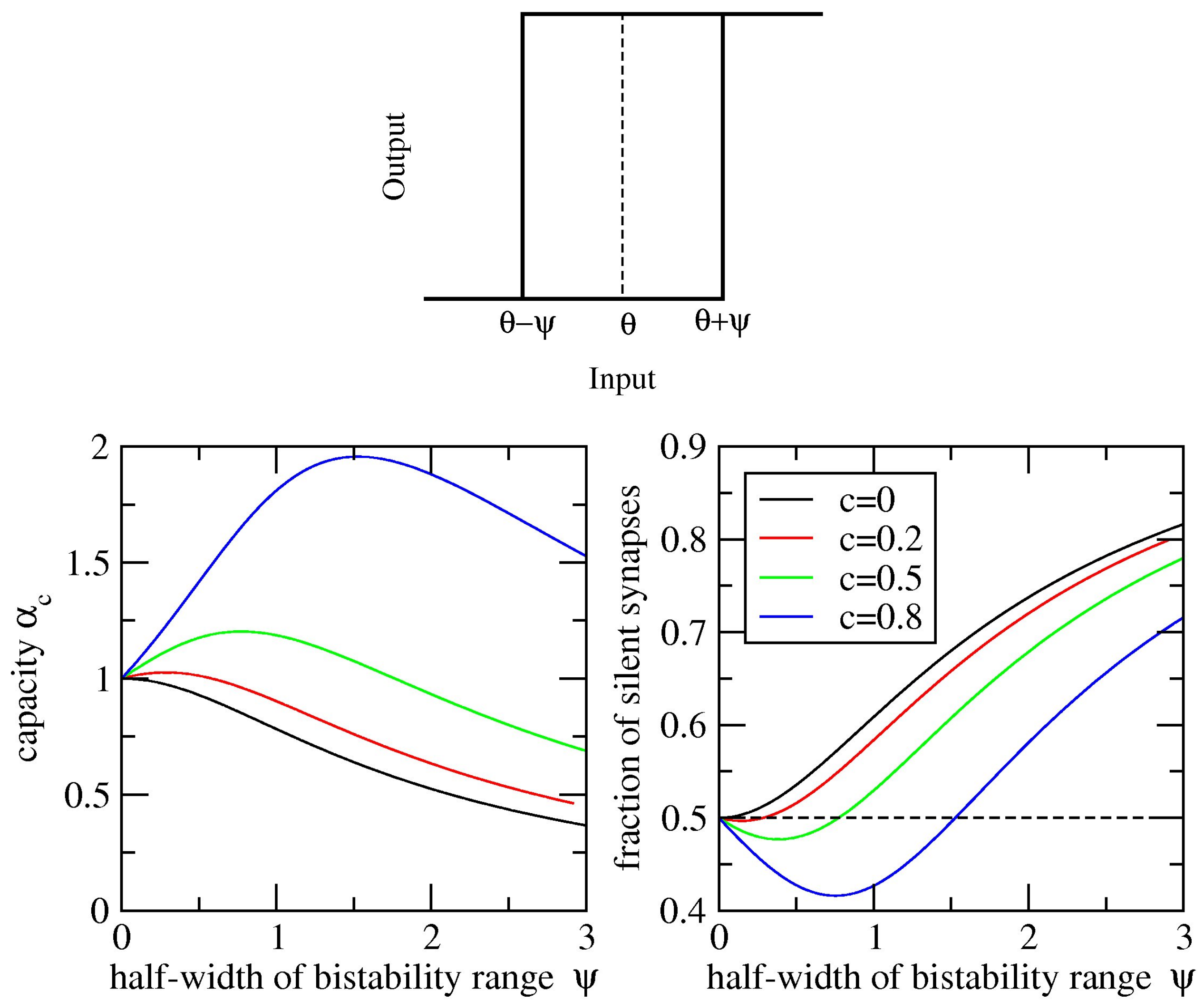

Conclusions 1

- Large fraction of silent synapses needed for optimizing information storage;
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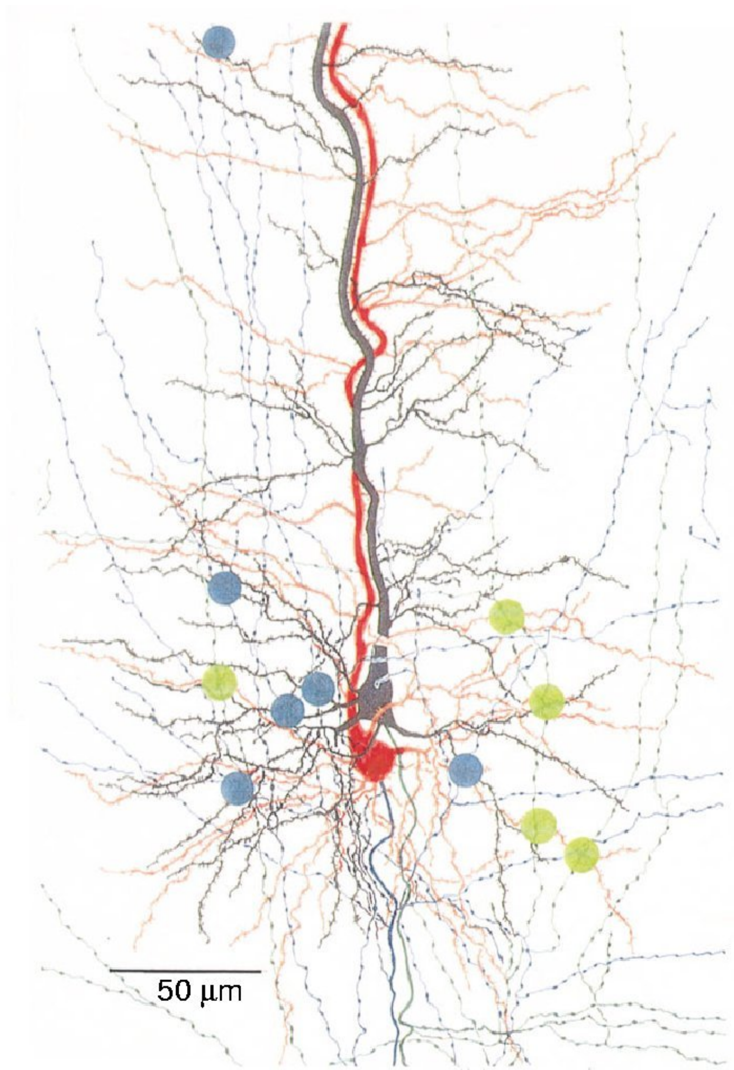
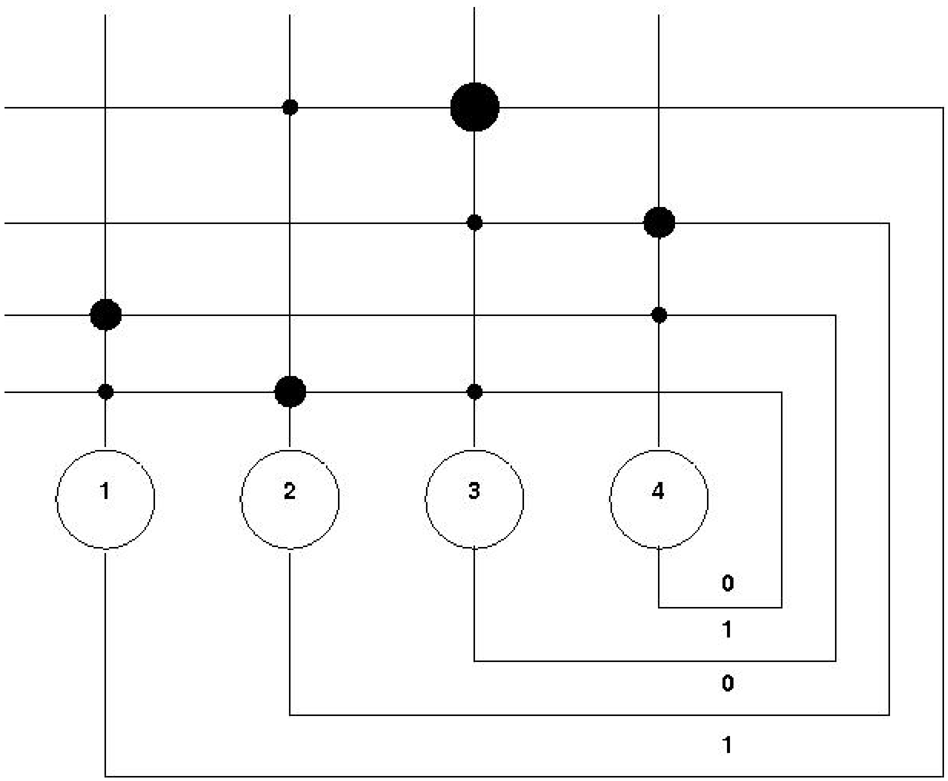
- Details of the model affect quantitatively storage capacity, and the fraction of silent synapses, but not the qualitative shape of the weights distribution;

Neocortex: pyramidal cell network



A simple attractor neural network model



- 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 (close to its maximal capacity, for a given robustness level):

- What is the distribution of synaptic weights

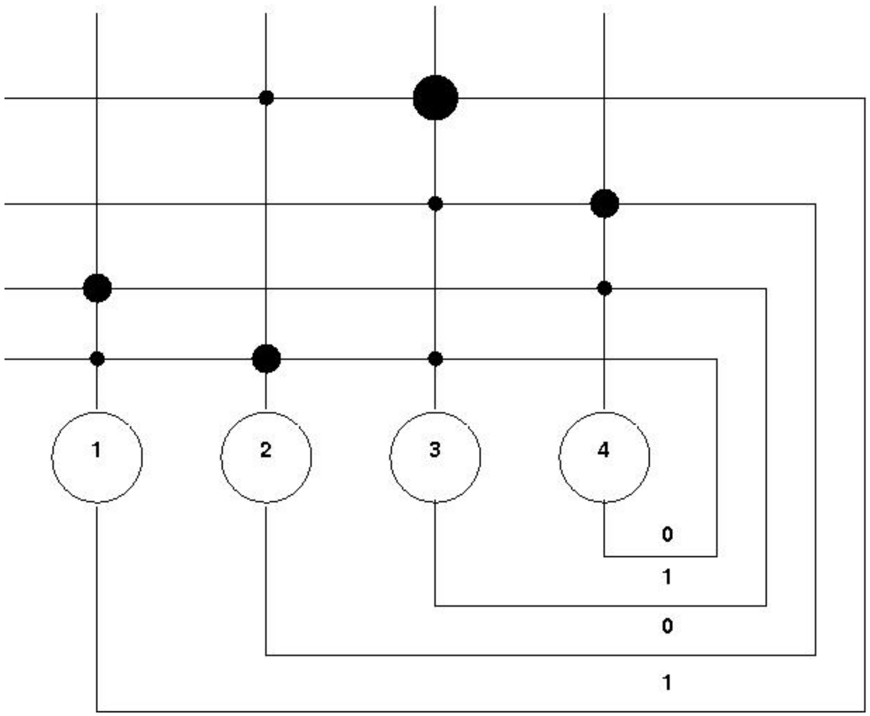
$$P(w_{ij})?$$

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

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

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

Distribution of weights



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

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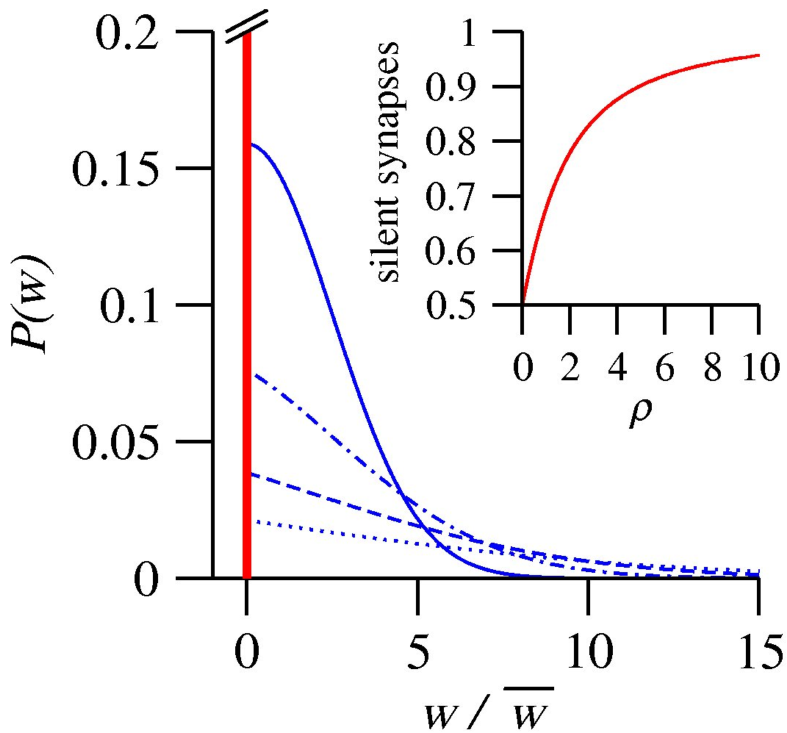

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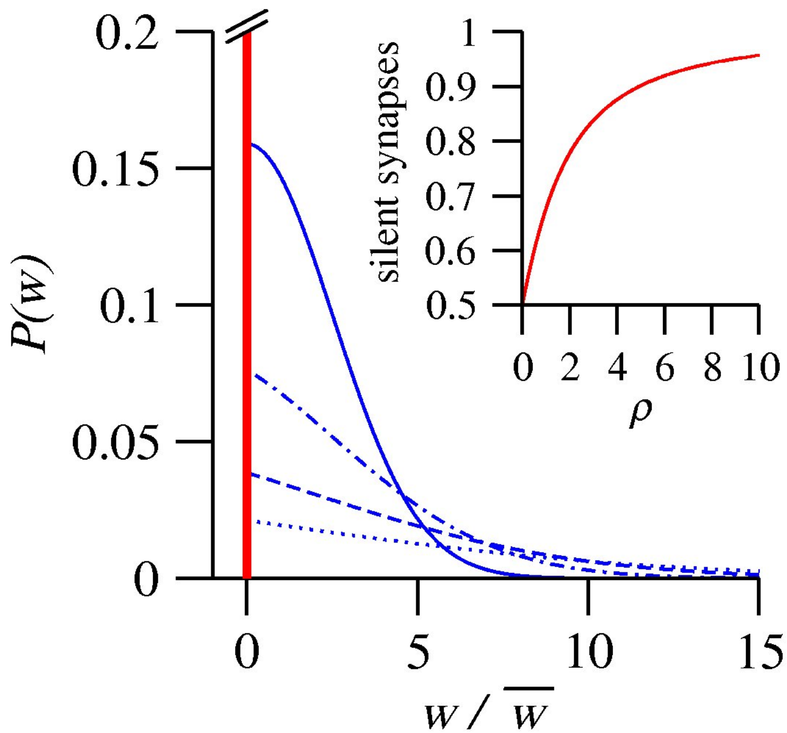

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Distribution of weights: theory vs experiment

- Large fraction of zero weight synapses is consistent with data:
  - **Anatomy:** nearby pyramidal cells are potentially 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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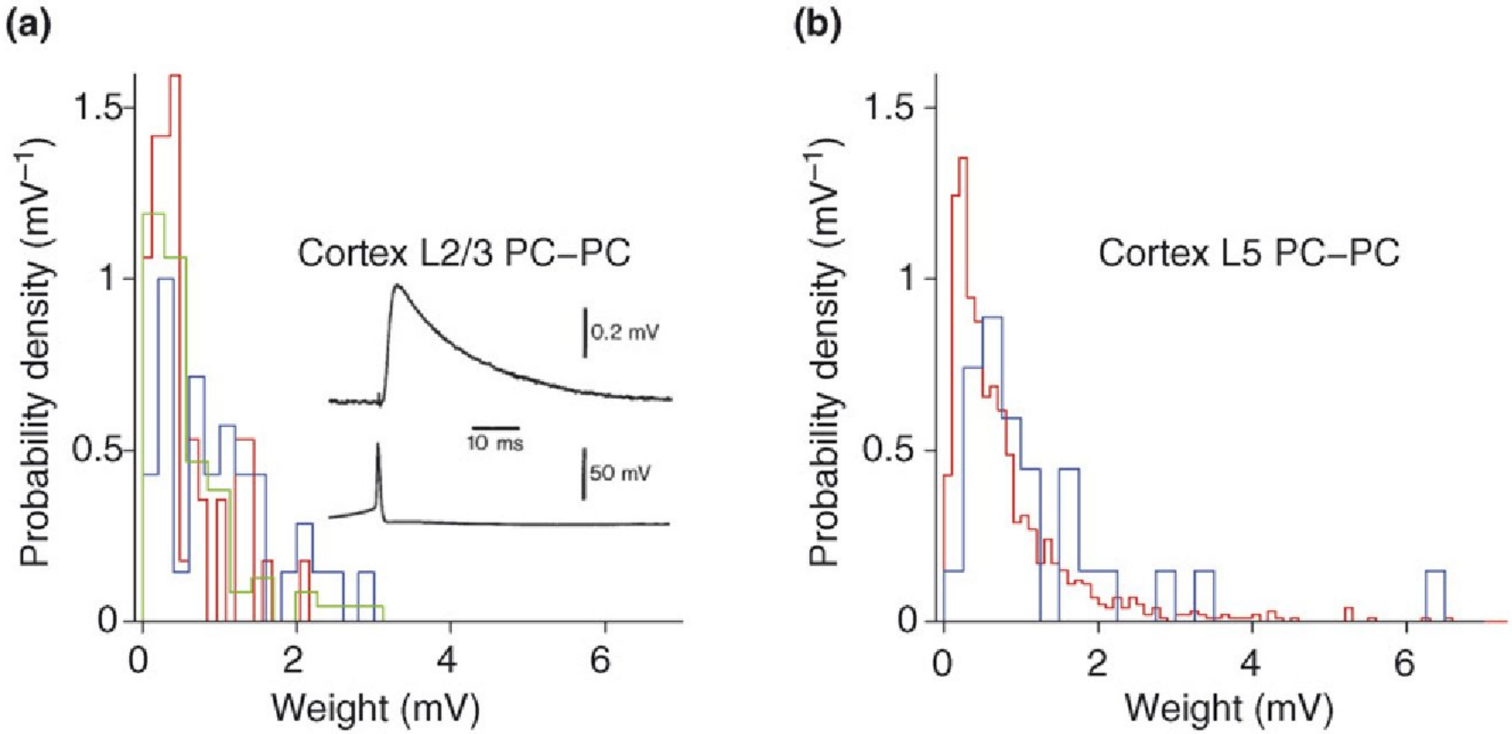
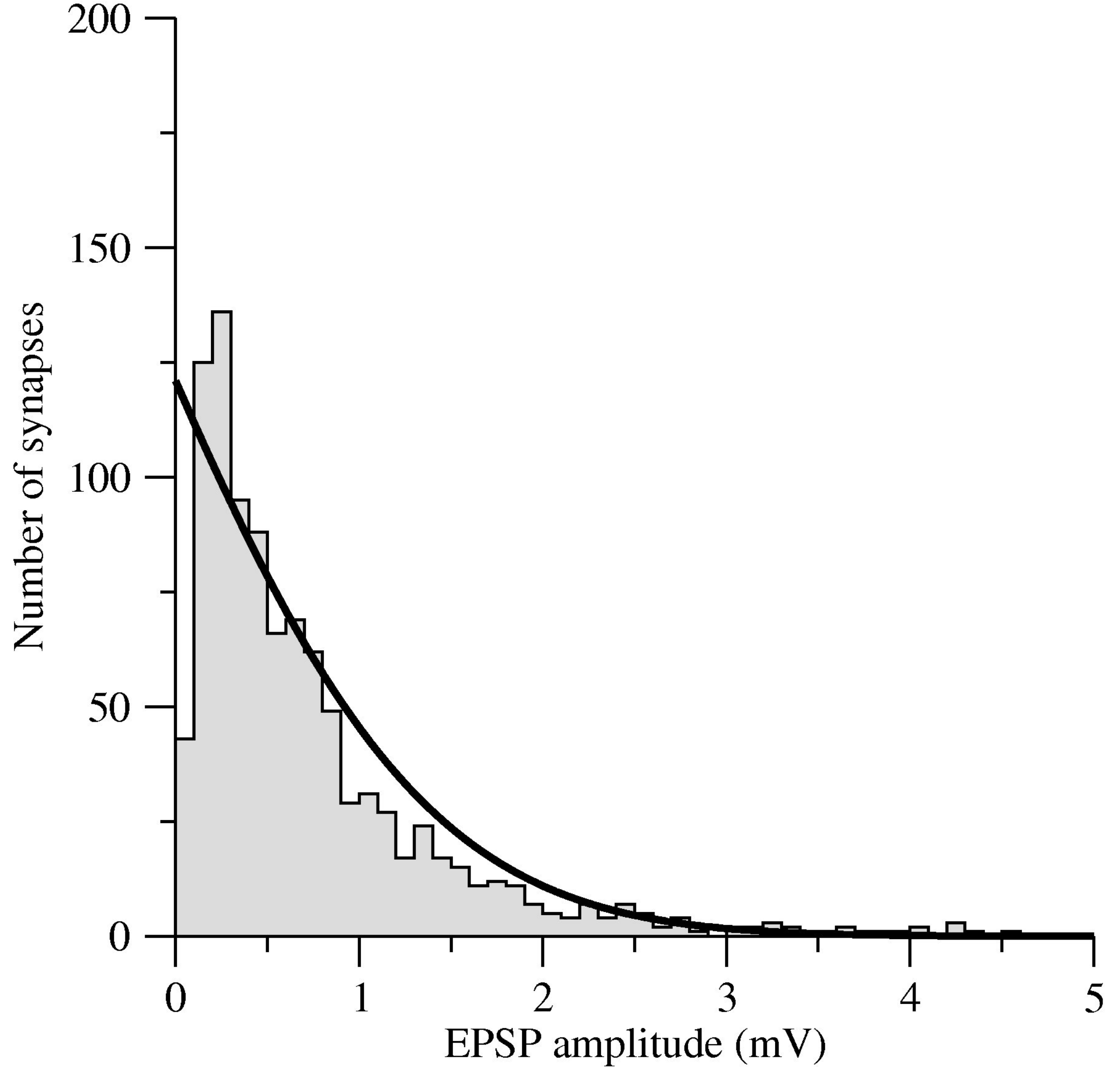
$\Rightarrow$ **Large fraction of zero-weight ('potential' or 'silent') synapses.**

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

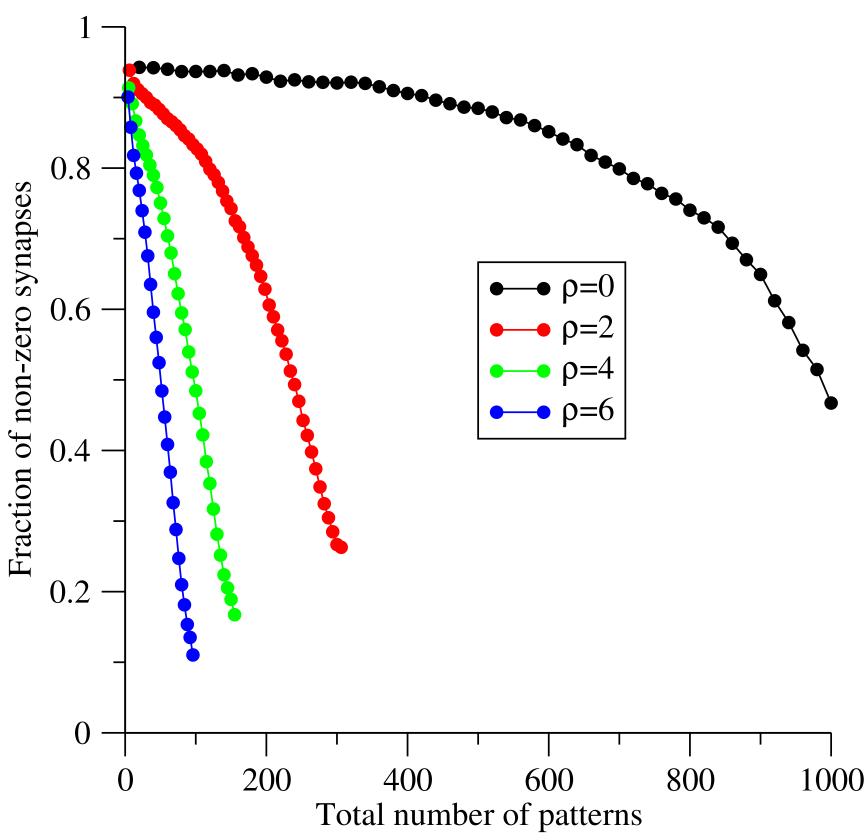
Sjostrom data vs theory

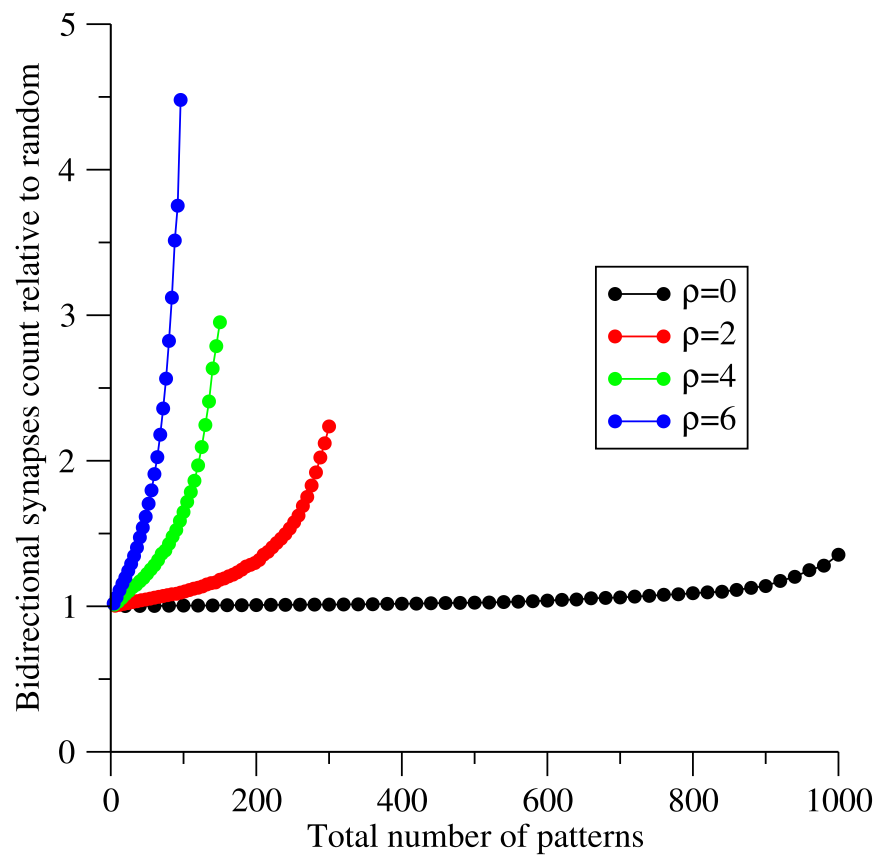


Sjostrom et al 2001; Song et al 2005

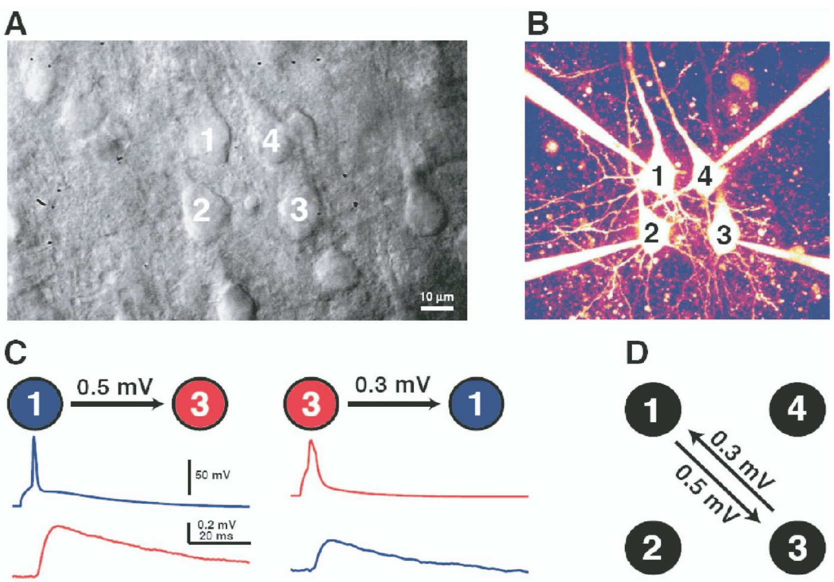
Two-neuron connectivity in an attractor network

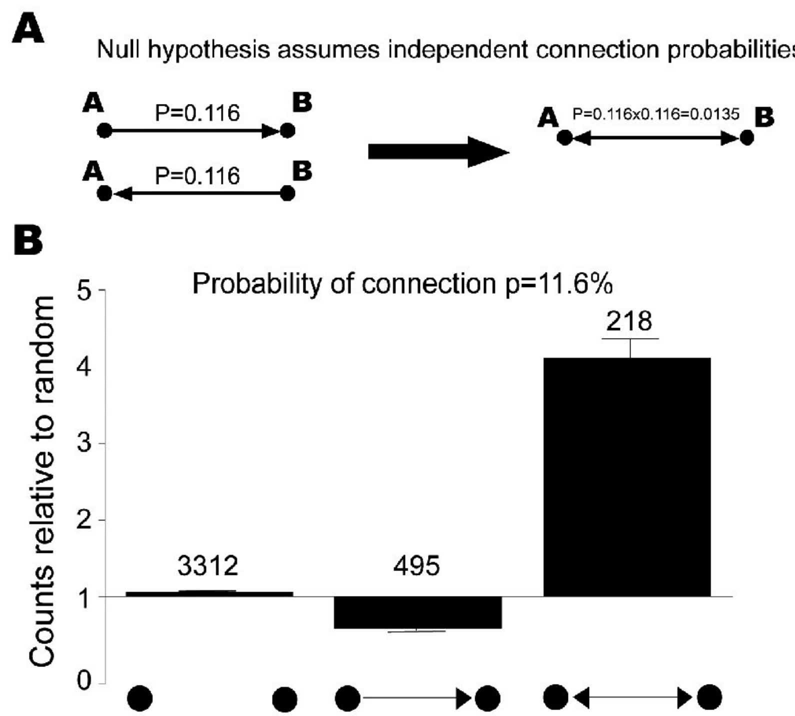
- Fully connected network of $N = 1000$ neurons;
- Storing random patterns, using perceptron learning algorithm independently for each neuron;





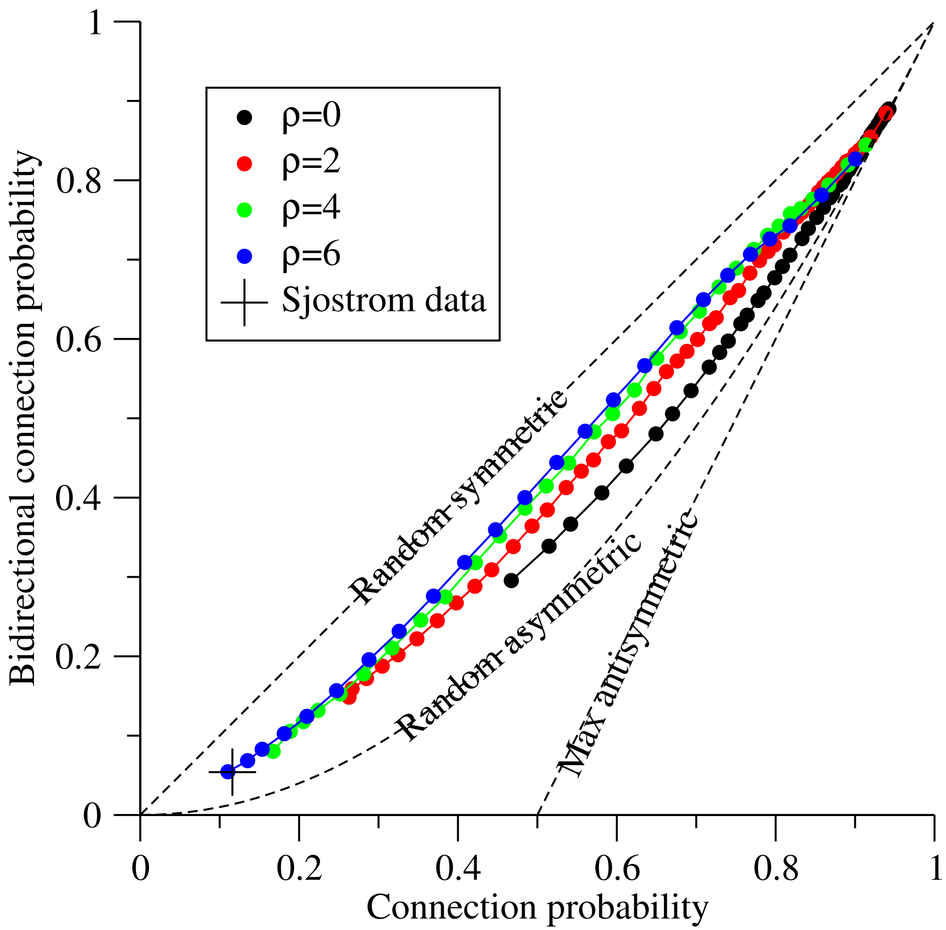
Two-neuron connectivity patterns in cortex





Song et al 2005

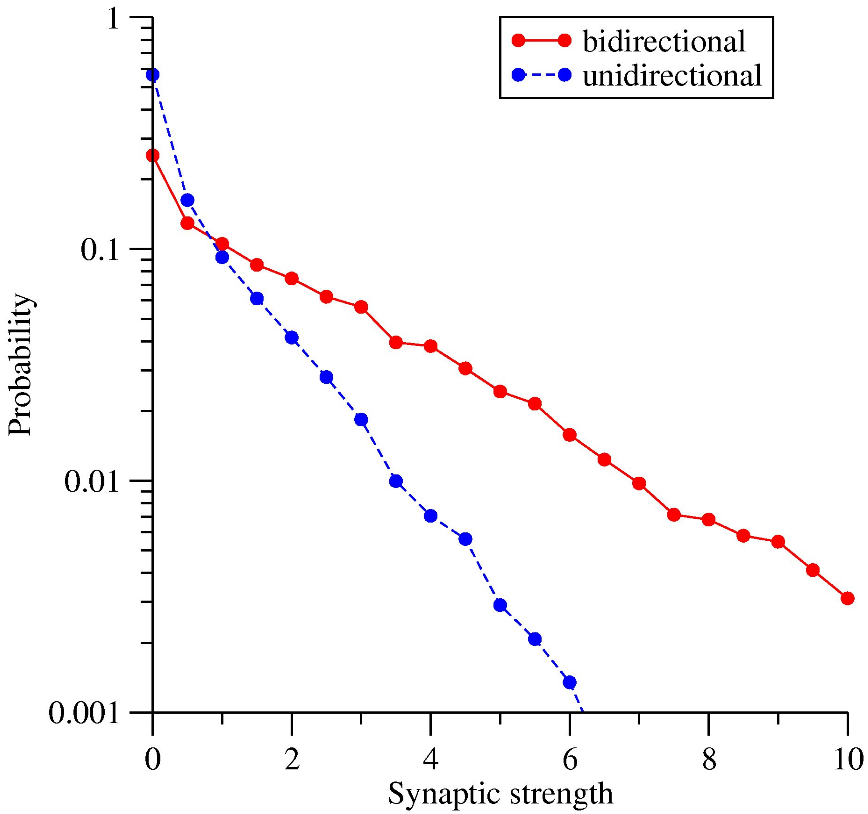
Two-neuron connectivity: theory vs experiment

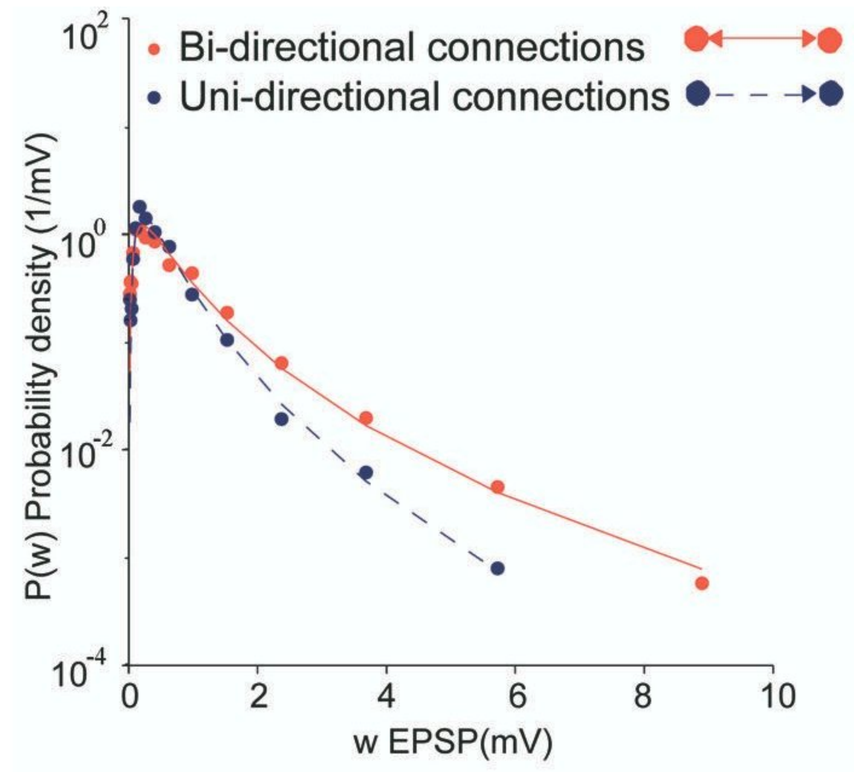


See also:

- Markram et al (1997) rat L5 somatosensory cortex: 3 x random;
- Wang et al (2006)
  - rat PFC: 4 x random;
  - rat visual cortex: 2 x 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;
  - Strong overrepresentation of bidirectional connections, compared to a random network
  - 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

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  - Sparse connectivity matrix;
  - The sparser the matrix, the more robust the network;
  - Strong overrepresentation of bidirectional connections, compared to a random network
  - 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
- A network optimized to store a large number of sequences have
  - Again a sparse connectivity matrix;
  - No overrepresentation of bidirectional connections

Collaborators

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