Robust performance of inhomogeneous forgetful associative memory networks

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School of Informatics
University of Edinburgh

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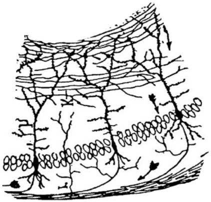
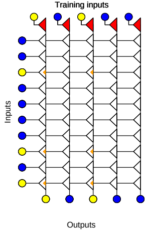
Motivation

Theoretical networks of *simple* neurons show how parts of the CNS with mutable synapses could store and retrieve memories



Cajal



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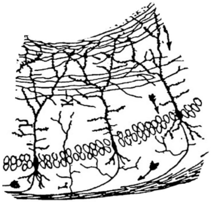

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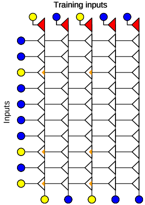

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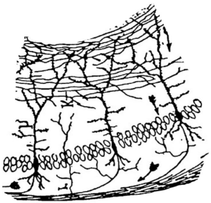

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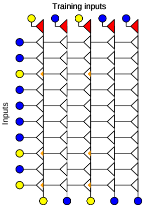

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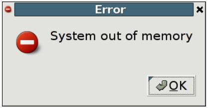

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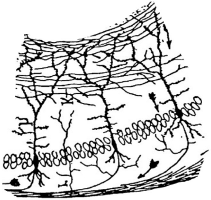

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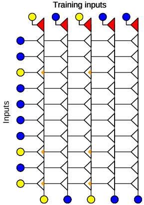

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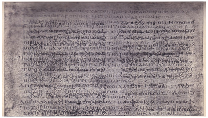

Memories need to be forgotten to make space for new ones: *Palimpsests*

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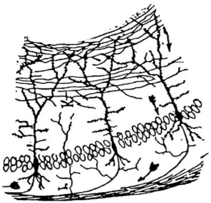

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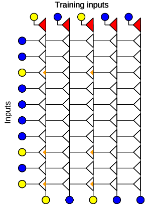

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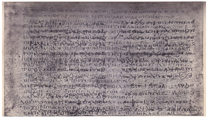

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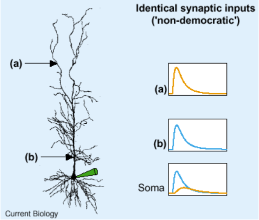

[Häusser, 2001]

Real neurons are not homogeneous: *differential attenuation*

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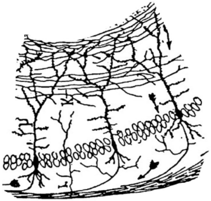

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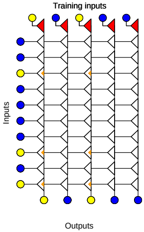

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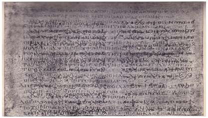

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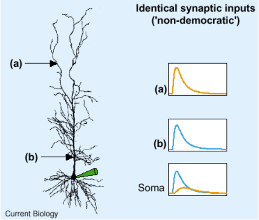

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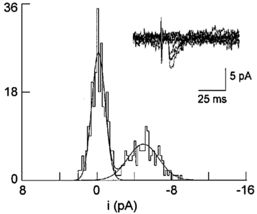

[Bolshakov et al., 1997]

Real synapses are not deterministic: *stochastic transmission*

Overview

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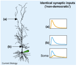

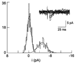

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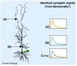
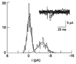
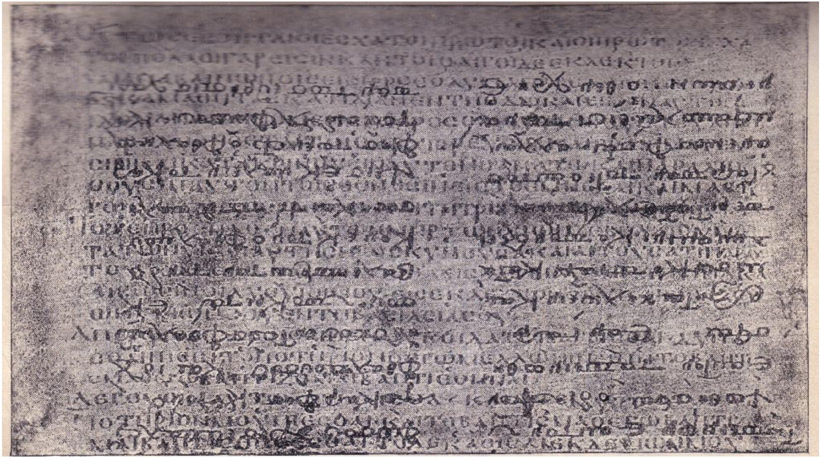




- Highlights
  - There is an optimal rate at which to forget
  - Optimal network capacity scales with size
  - Differential attenuation predicted to affect performance less than stochastic transmission

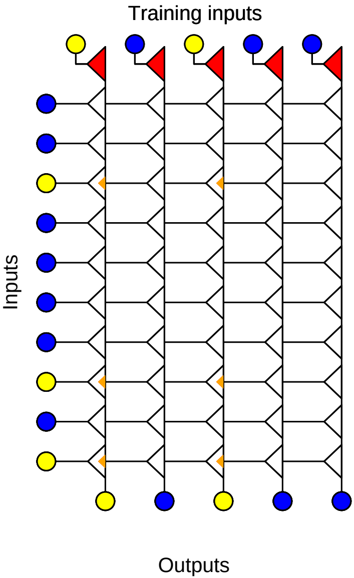
Inhomogeneity 1: Forgetting



Codex Ephraemi Rescriptus (5th century and 12th century)

- Newer memories have a stronger trace in the network

Learning and forgetting memories



- Random binary-valued patterns
  - Input sparsity p
  - Output sparsity r
- $w_{ij}(t) = e^{-1/\tau} w_{ij}(t-1) + \Delta_{ij}(t)$
- Learning rule, e.g. Hebbian
- τ is *forgetting time constant*
  - $\tau \to \infty$: “rememberful” memory
  - Here $\tau = 3.5$

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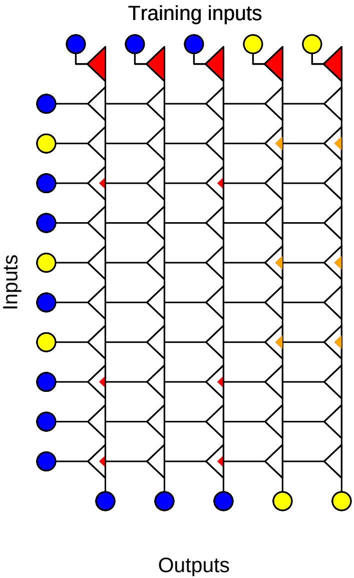

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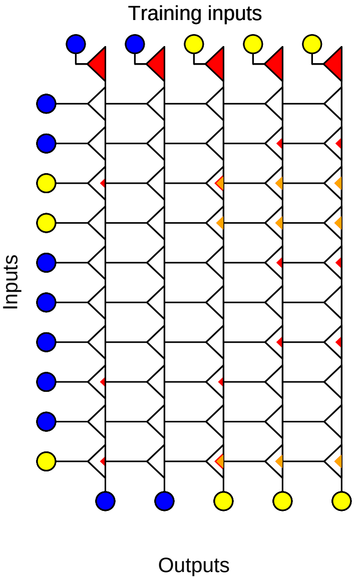

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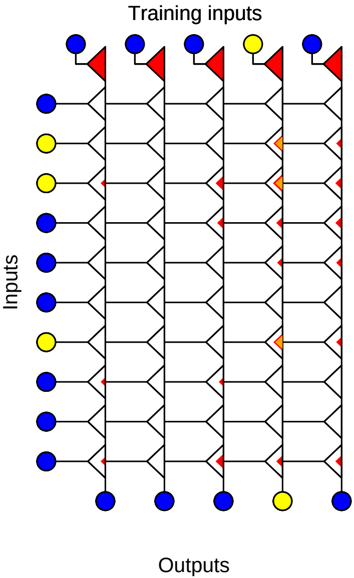

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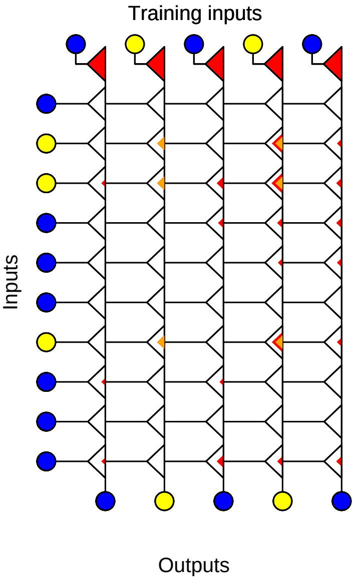

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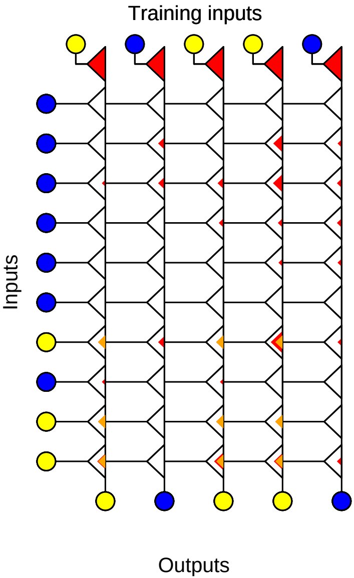

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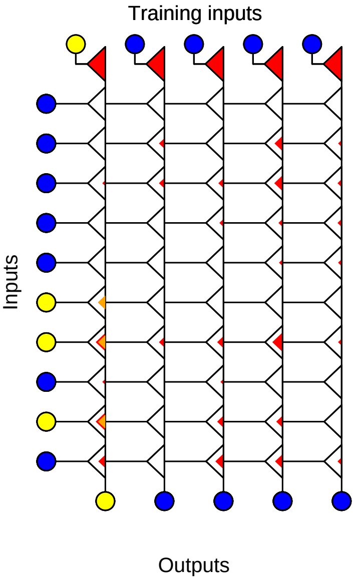

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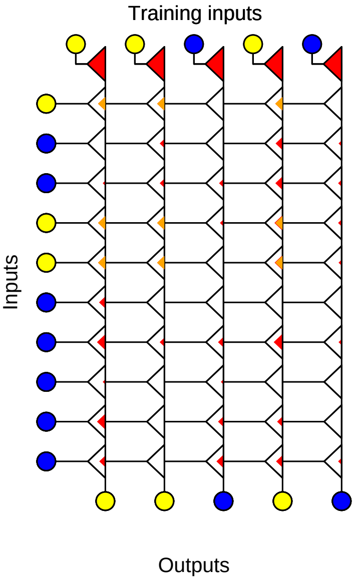

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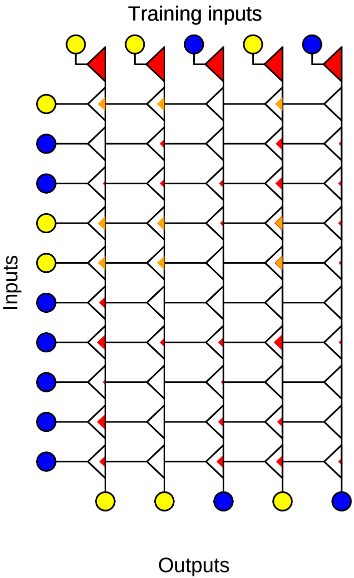

- General learning rule

		Post	
	$\Delta_{ij}(t)$	0	1
Pre	0	α	β
	1	γ	δ

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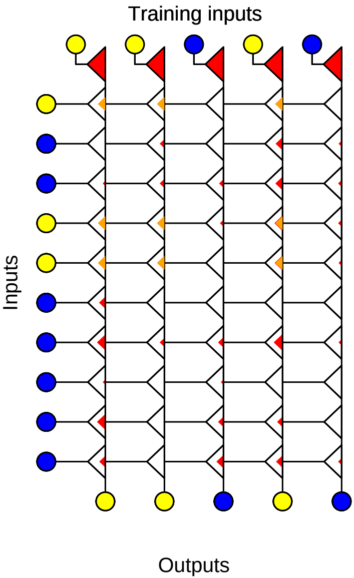

- e.g. Hebbian

Pre	$\Delta_{ij}(t)$	Post 0	Post 1
	0	0	0
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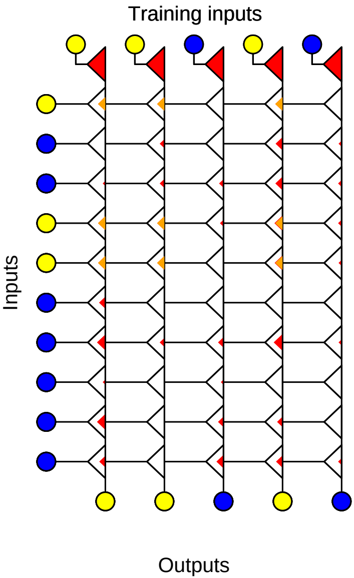

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$\Delta_{ij}(t)$		Post 0	Post 1
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- e.g. Heterosynaptic

$\Delta_{ij}(t)$		Post 0	Post 1
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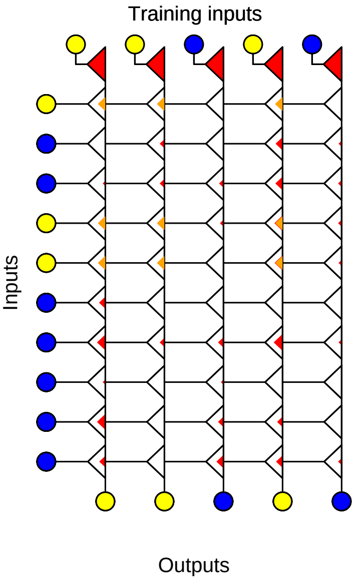

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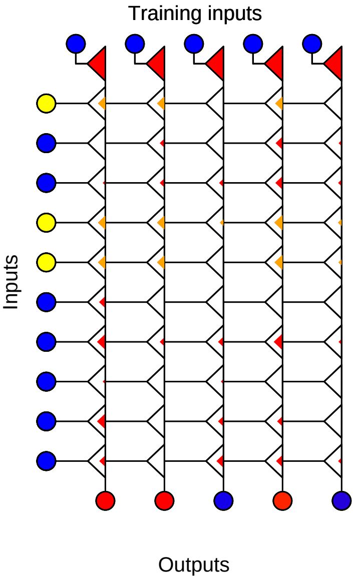
- A rule is *balanced* if the expected weight is zero
  - e.g. the Heterosynaptic rule

Recalling memories



- Dendritic sum (like membrane potential at soma)

$$d_j = \sum_i w_{ij} a_i$$

Most recent memory

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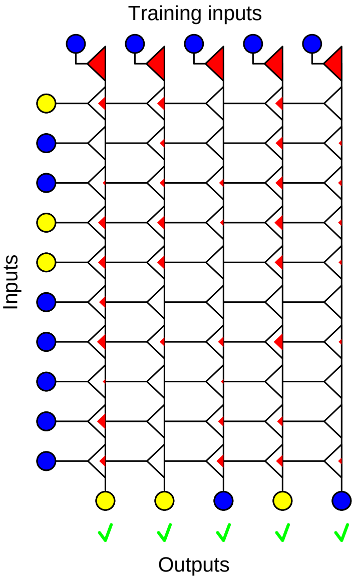

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- Output (like spike)

$$o_j = \begin{cases} 0 & \text{if } d_j < \theta_j \\ 1 & \text{if } d_j > \theta_j \end{cases}$$

where θ_j is the *per-unit* optimal threshold [Dayan and Willshaw, 1991]

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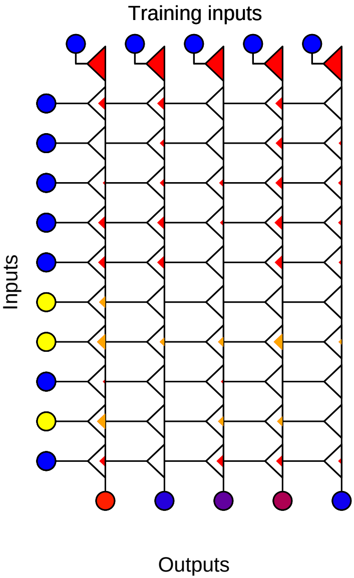

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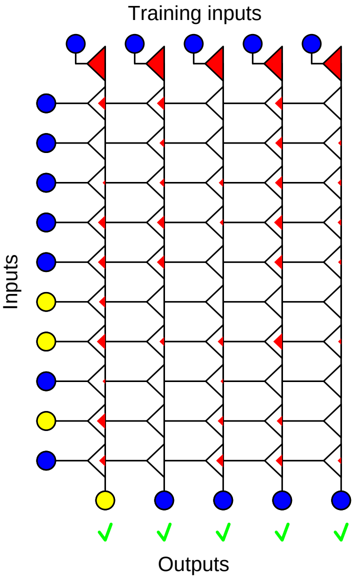

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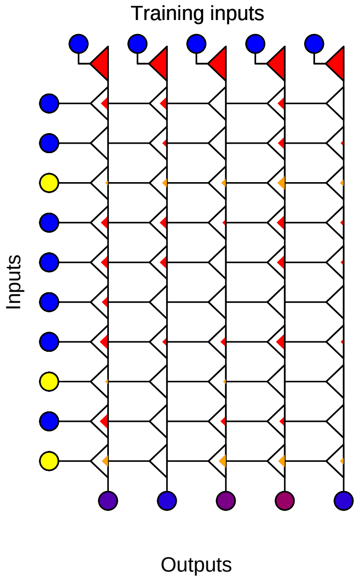

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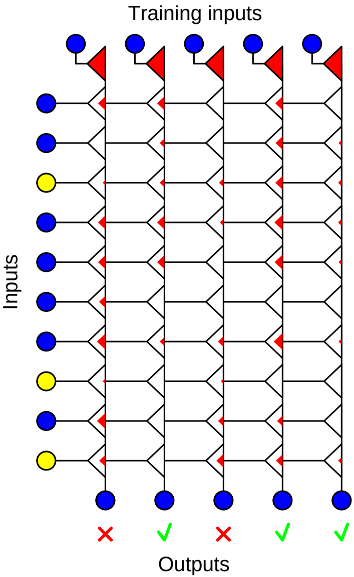

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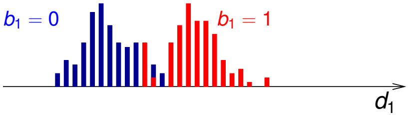

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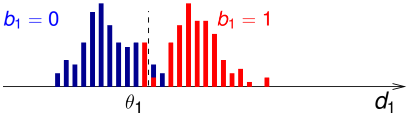

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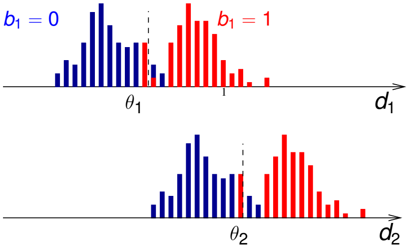

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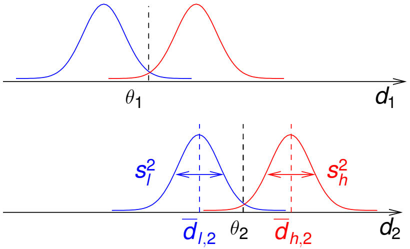

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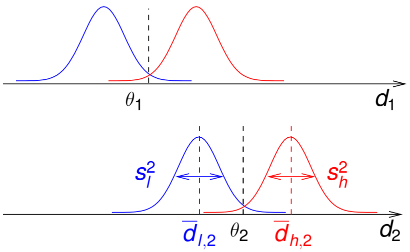

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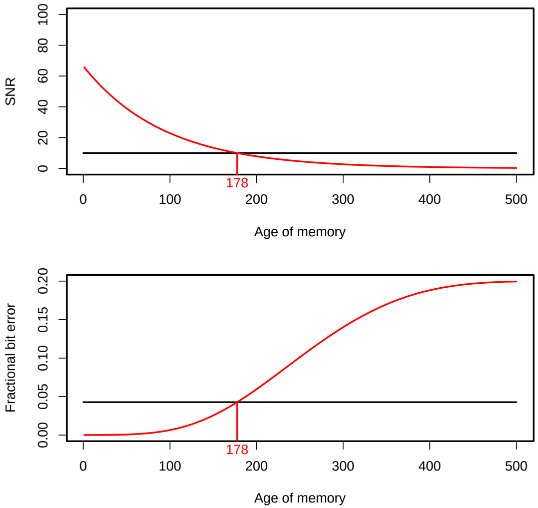
$$= f(p, r, N_{\text{units}}, \tau)$$

where $f(\cdot)$ is complicated

Palimpsest properties



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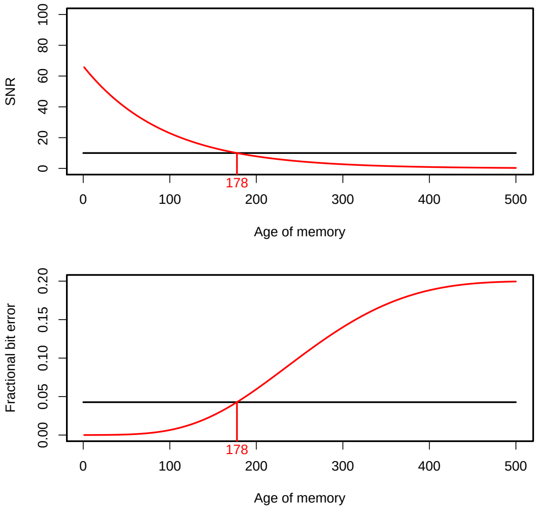
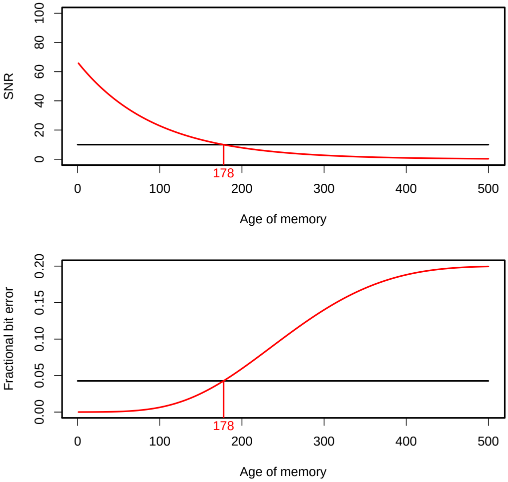


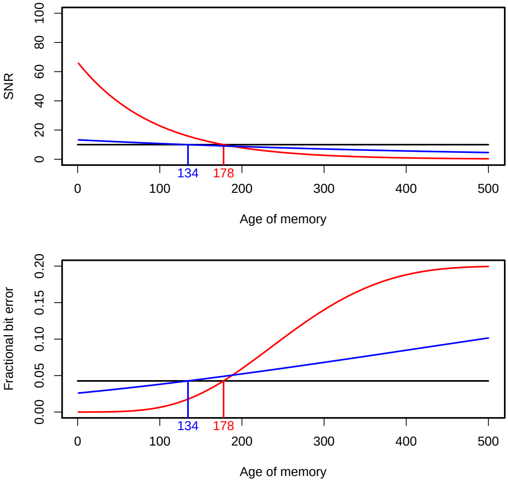
- Associative nets with general learning rules act as palimpsests
- Define *capacity* of network as age of memory whose error (or equivalently SNR) reaches an criterion value

How best to forget?



Quickly

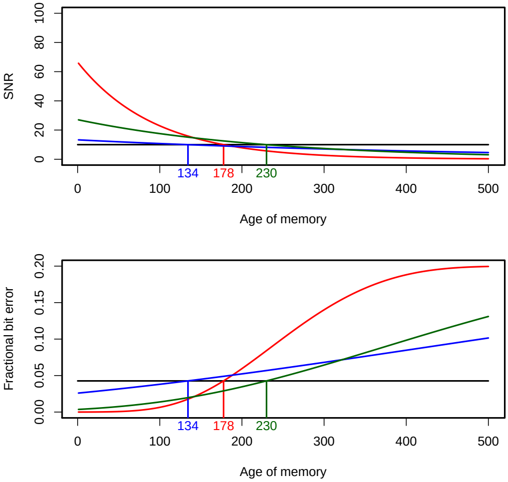
How best to forget?



Quickly

Slowly

How best to forget?



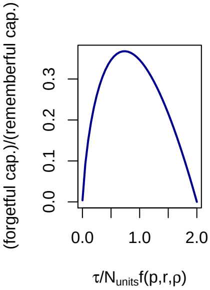
Quickly
Slowly
Optimally

How best to learn?

- Hebbian Learning Rule
  - Large number of input neurons (N_{units}):

$$\text{capacity} \approx \frac{\tau}{2}\left(\ln N_{\text{units}} - 2\ln\tau + \ln\frac{1-p}{pr^2\rho_c}\right)$$

where ρ_c is the SNR criterion.



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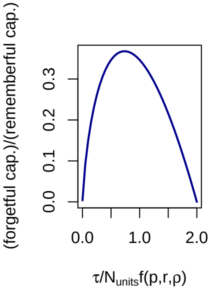

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  - For large N_{units}

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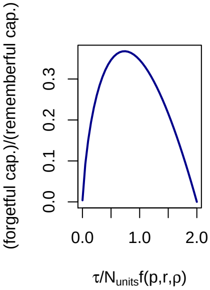

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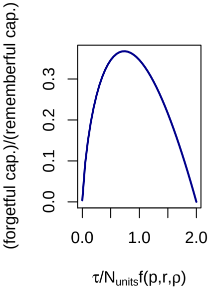

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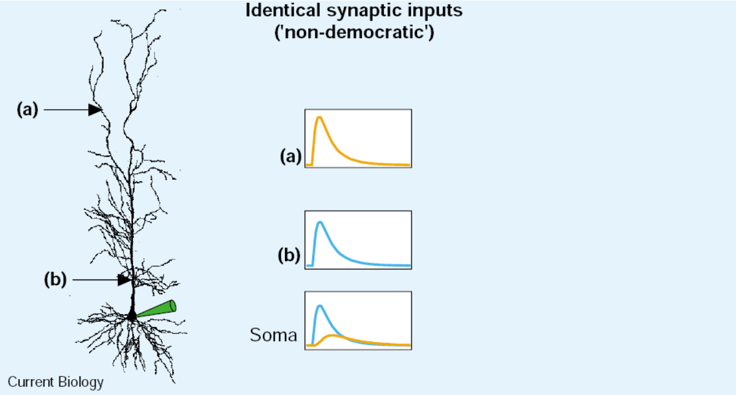
- Conclusion: **balanced rules scale best**
  - As in rememberful nets [Dayan and Willshaw, 1991]
  - Optimal capacity approximately a third ($1/e$) of "rememberful" net

Inhomogeneity 2: Differential Attenuation



[Häusser, 2001]

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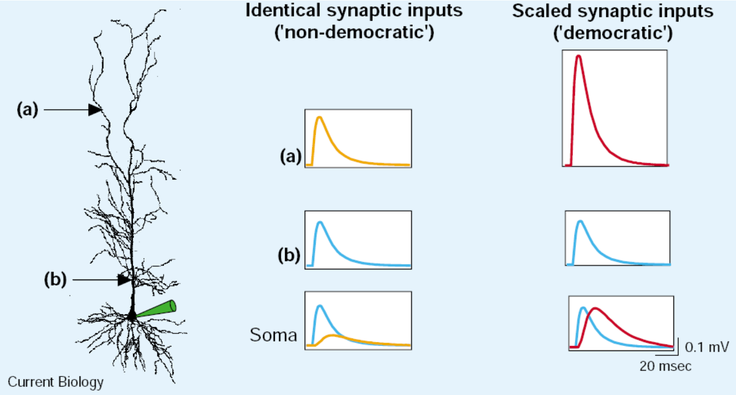

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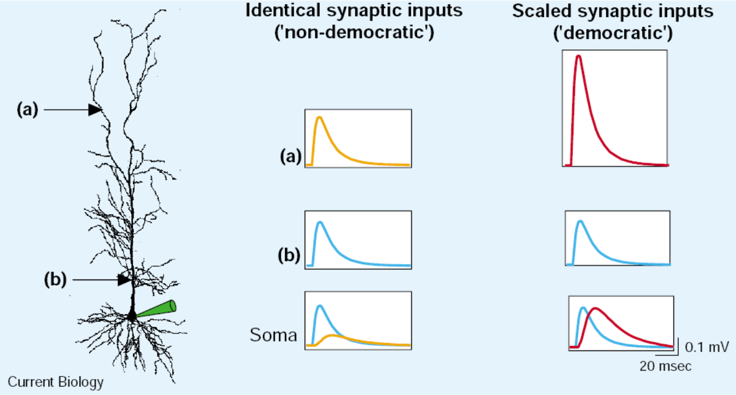
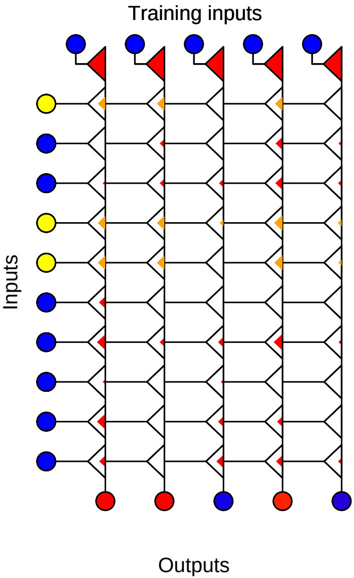


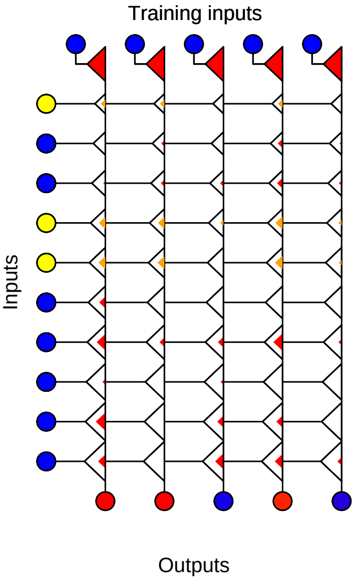
[Häusser, 2001]

- What effect does differential attenuation have on performance?

Modelling differential attenuation



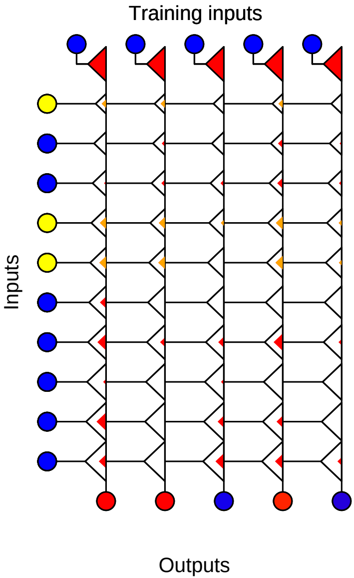
Modelling differential attenuation



- Input *attenuation factors* f_i

$$d_j = \sum_i f_i w_{ij} a_i$$

Modelling differential attenuation



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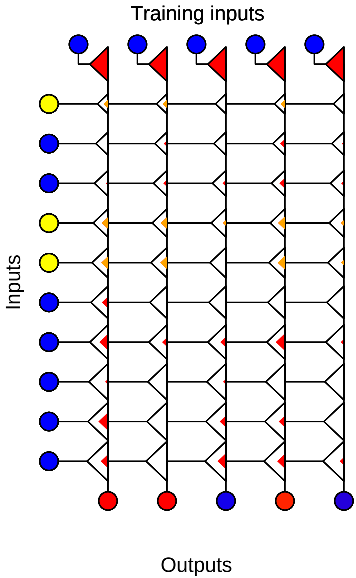
- Balanced capacity reduction

$$1 + (\mathrm{CV}(f))^2$$

$$\mathrm{CV}(f) = \frac{\mathrm{SD}(f)}{\mathrm{MEAN}(f)}$$

Modelling differential attenuation



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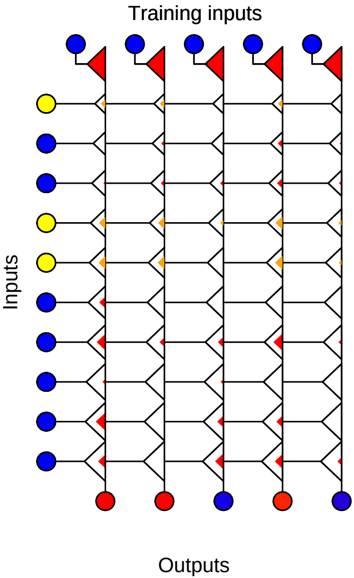

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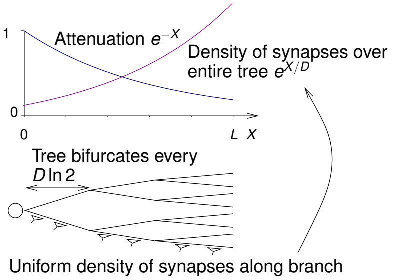
- $\sim$independent of forgetting

Example: a branching dendritic tree



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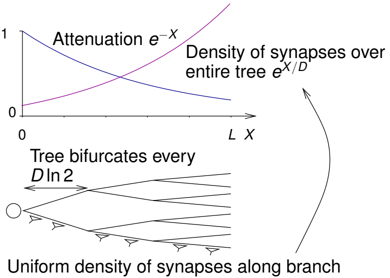
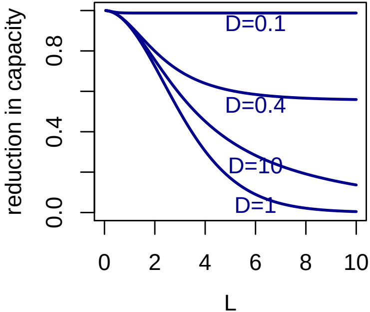
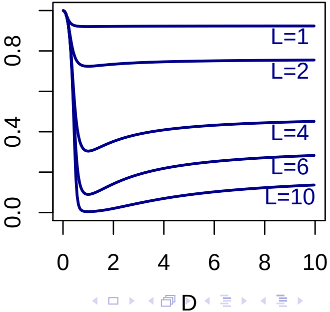


$$\frac{(1-2D)\left(e^{L(\frac{1}{D}-1)}-1\right)^2}{(D-1)^2(e^{\frac{L}{D}}-1)(e^{L(\frac{1}{D}-2)}-1)}$$





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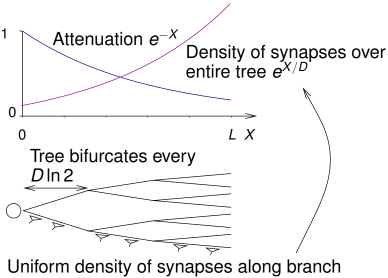
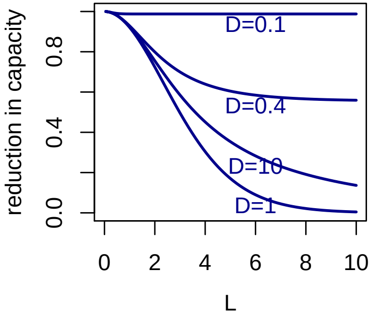
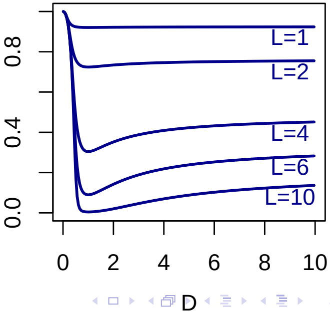


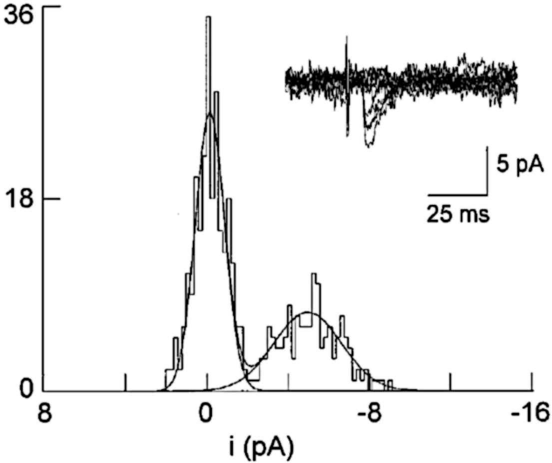
- Capacity is reduced at worst by factor of 1.4 for Schaffer Collaterals ($L = 2$)

$$\frac{(1-2D)\left(e^{L(\frac{1}{D}-1)}-1\right)^2}{(D-1)^2(e^{\frac{L}{D}}-1)(e^{L(\frac{1}{D}-2)}-1)}$$





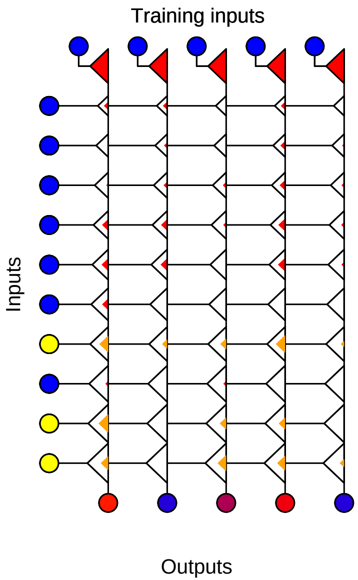
Inhomogeneity 3: Stochastic transmission



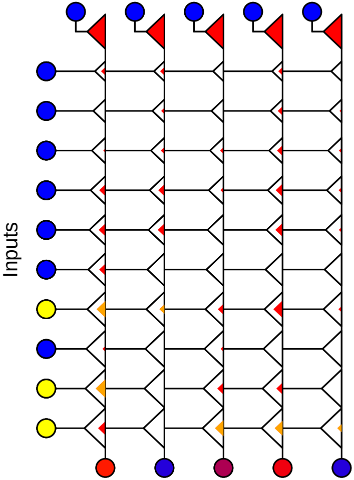
[Bolshakov et al., 1997]

- Quantal failure
- Fluctuations in quantal amplitude

Modelling stochastic transmission



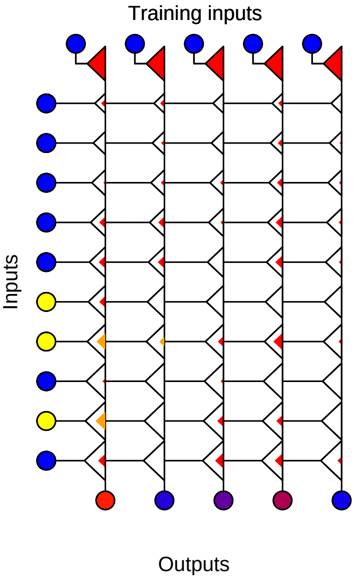
Modelling stochastic transmission



- *Stochastic transmission factors $g_{ij}(t)$*

$$d_j = \sum_i f_i g_{ij}(t) w_{ij} a_i$$

Modelling stochastic transmission



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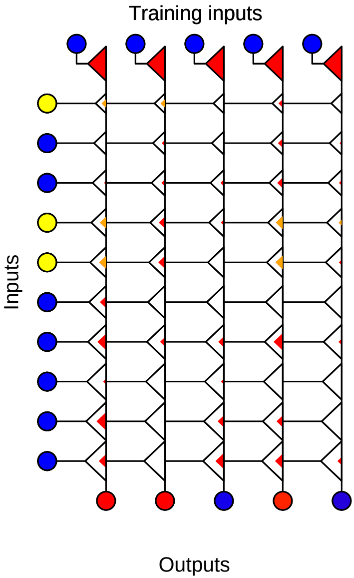

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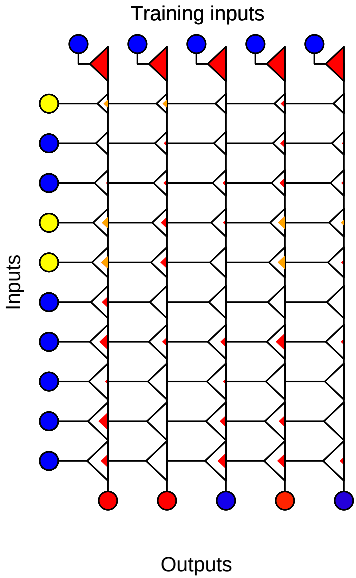
$$1 + (\mathrm{CV}(g))^2 / (1 - p)$$

Modelling stochastic transmission



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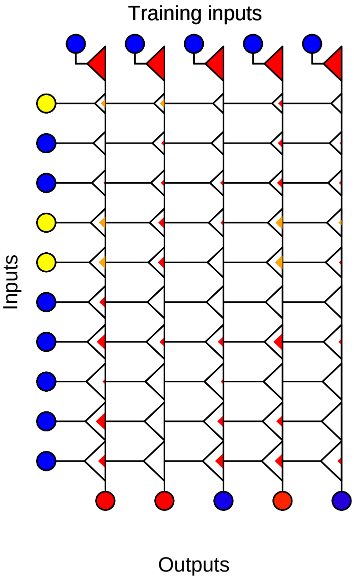
Modelling stochastic transmission



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- $\sim$independent of forgetting and differential attenuation

Effect of stochastic transmission in the hippocampus

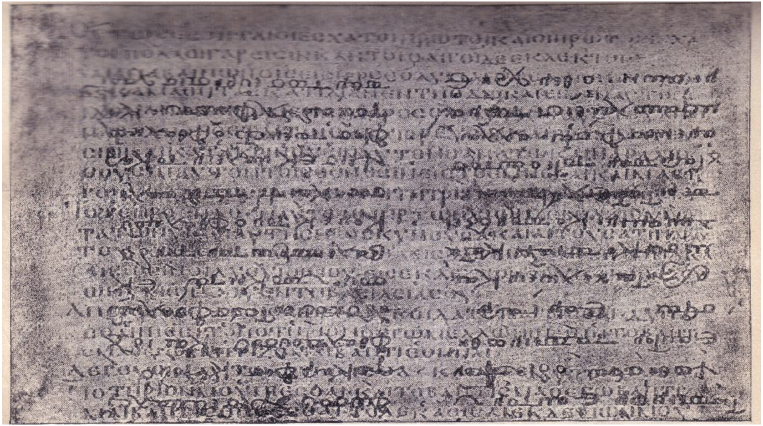
- **Factorial reduction of capacity is in range**
  - **2–15 (balanced)**
  - **1.4–4 (Hebbian)**
- CV(g) Estimated from quantal analysis:
  - Maximum value of $(\mathrm{CV}(g))^2 \approx 10$ [Stricker et al., 1996]
  - $(\mathrm{CV}(g))^2 \approx 0.5$ in a potentiated state [Bolshakov et al., 1997]
  - $(\mathrm{CV}(g))^2 \approx 2$ for unpotentiated synapses [Bolshakov et al., 1997]
- p in range 0.2–0.3 (*in vivo* recordings from CA3 [Leutgeb et al., 2004, Barnes et al., 1990]

Conclusions

- First unified analysis of the effects of differential attenuation and stochastic transmission on the performance of forgetful associative memories
- Different types of inhomogeneity are approximately independent from one another
- There is an optimal rate at which to forget
- Optimal network capacity scales with size
- Stochastic transmission is likely to have a more pronounced effect on the performance of memory networks in the hippocampus than differential attenuation
  - Surprising in the context of the findings that synaptic conductances are scaled according to distance from the soma
- Performance is robust

Palimpsests

- Forgetful (Hopfield) neural network [Nadal et al., 1986, Parisi, 1986] ...
- ... a document written on vellum over the incompletely-erased trace of an earlier document



Codex Ephraemi Rescriptus (5th century and 12th century)

Barnes, C. A., McNaughton, B. L., Mizumori, S. J. Y., Leonard, B. W., and Lin, L.-H. (1990).
Comparison of spatial and temporal characteristics of neuronal activity in sequential stages of hippocampal processing.
Progress in Brain Research, 83:287–300.

Bolshakov, V. Y., Golan, H., Kandel, E. R., and Siegelbaum, S. A. (1997).
Recruitment of new sites of synaptic transmission during the cAMP-dependent late phase of LTP at CA3–CA1 synapses in the hippocampus.
Neuron, 19:635–651.

Dayan, P. and Willshaw, D. J. (1991).
Optimising synaptic learning rules in linear associative memories.
Biological Cybernetics, 65:253–265.

Häusser, M. (2001).
Dendritic democracy.