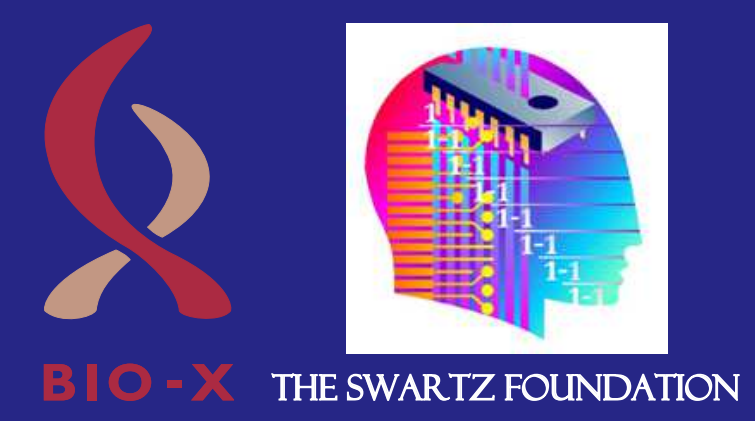


# Learning and memory with complex synapses

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## Background

### Storage capacity of synaptic memory

A classical perceptron, when used as a recognition memory device, has a memory capacity proportional to the number of synapses,  $N$ .

However, this requires synapses to have a dynamic range also  $\propto N$ . If synaptic efficacies are limited to a fixed dynamic range, this introduces a strong tradeoff between learning and forgetting due to new memories overwriting old. If we wish to store new memories rapidly, then memory capacity is  $\mathcal{O}(\log N)$ .

[Amit and Fusi (1992), Amit and Fusi (1994)]

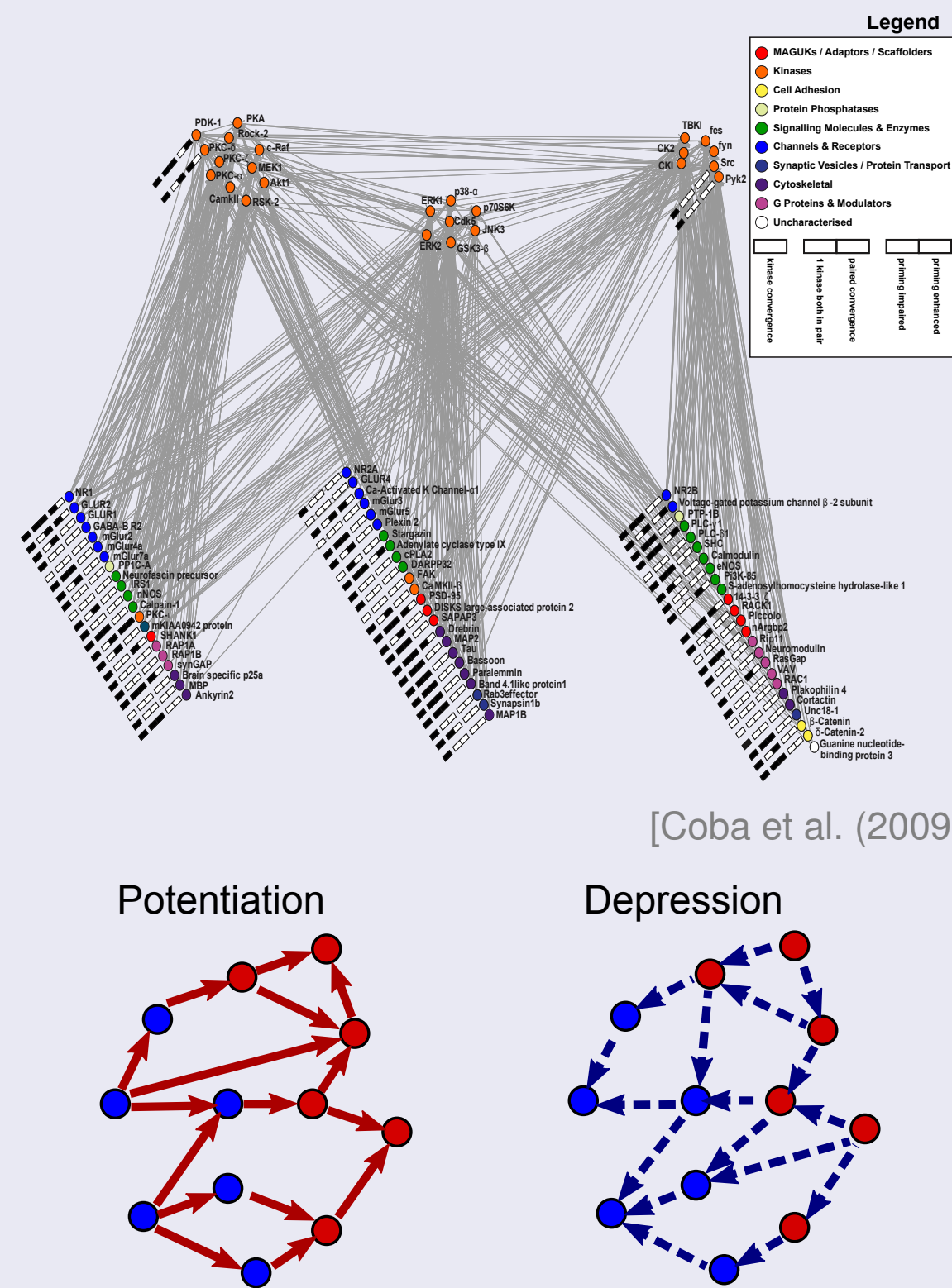
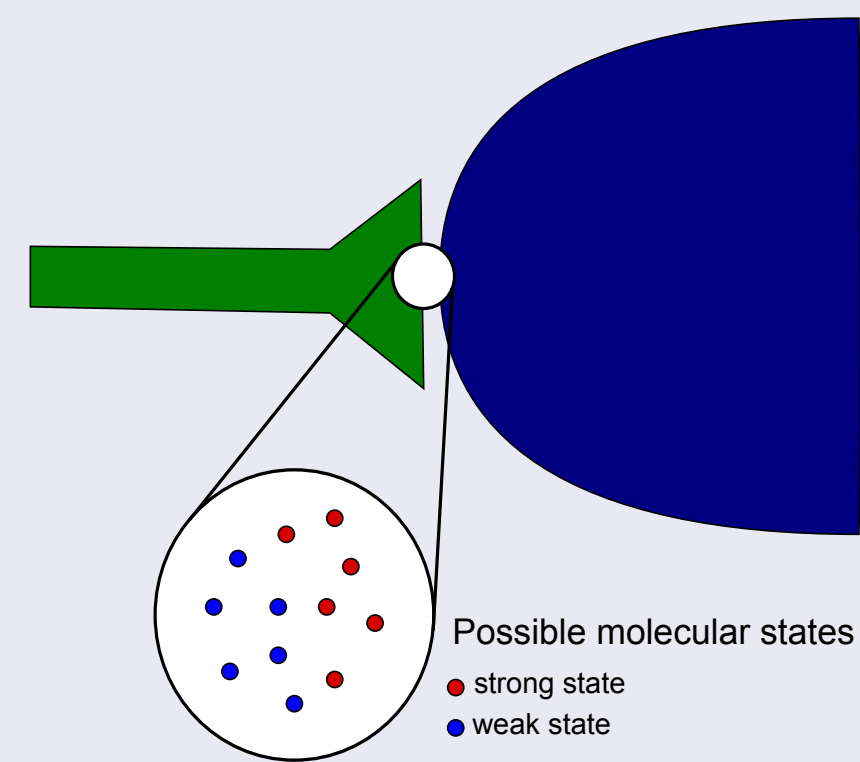
To circumvent this tradeoff, it is essential to enlarge our theoretical conception of a synapse as a single number.

### Complex synapses

In reality, a synapse is a complex dynamical system.

We will describe a synapse by stochastic processes on a finite number of states,  $M$ .

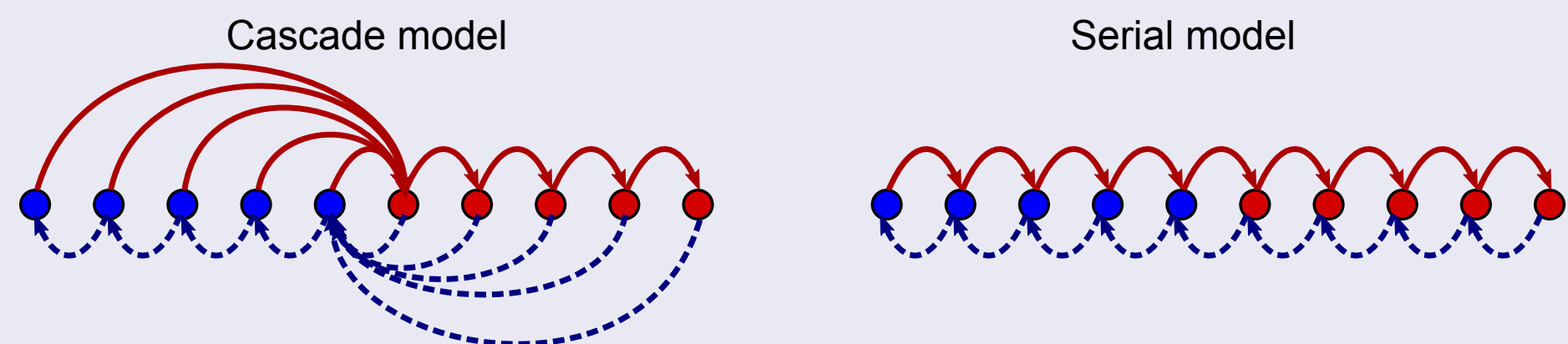
Potentiation and depression cause transitions between these states.



[Coba et al. (2009)]

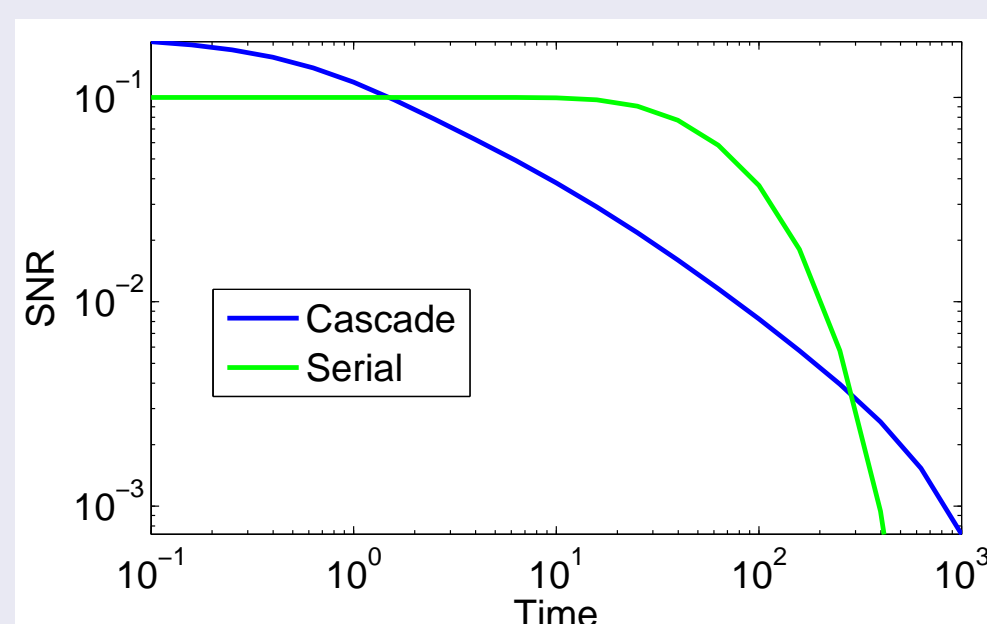
### Cascade and serial models

Two example models of complex synapses.



[Fusi et al. (2005), Leibold and Kempter (2008)]

These have different memory storage properties



### Questions

- Can we understand the space of *all possible* synaptic models?
- How does the structure (topology) of a synaptic model affect its function (memory curve)?
- How does synaptic complexity (number of states) extend the frontiers of possibility for memory?
- Which synaptic state transition topologies maximize measures of memory?

## Framework

### Synaptic state transition models

We have two Markov processes describing transition probabilities for potentiation,  $\mathbf{M}^{\text{pot}}$ , and depression,  $\mathbf{M}^{\text{dep}}$ .

Plasticity events are potentiating with probability  $f^{\text{pot}}$  and depressing with probability  $f^{\text{dep}}$ .

After the memory we are tracking, subsequent plasticity events occur at rate  $r$ , with transition probabilities

$$\mathbf{M}^{\text{forget}} = f^{\text{pot}}\mathbf{M}^{\text{pot}} + f^{\text{dep}}\mathbf{M}^{\text{dep}}.$$

This will eventually return it to the equilibrium distribution,  $\mathbf{p}^\infty$ .

[Fusi et al. (2005), Fusi and Abbott (2007), Barrett and van Rossum (2008)]

### Memory curve

We use the ideal observer approach: read synaptic weights directly. This is an upper bound on what could be read from network activity.

The reconstruction probability of a single synapse is:

$$s(t) = f^{\text{pot}}P(\text{strong}, t|\text{pot}, 0) + f^{\text{dep}}P(\text{weak}, t|\text{dep}, 0)$$

Alternatively, if  $\vec{w}$  is an  $N$ -element vector of synaptic strengths,

$$\text{Signal} = \langle \vec{w}_{\text{ideal}} \cdot \vec{w}(t) - \vec{w}_{\text{ideal}} \cdot \vec{w}(\infty) \rangle$$

$$\text{Noise} = \text{Var}(\vec{w}_{\text{ideal}} \cdot \vec{w}(\infty))$$

If we ignore correlations between different synapses, the signal-to-noise ratio is:

$$\text{SNR}(t) \sim \sqrt{N}(s(t) - s(\infty)).$$

## Upper bounds on performance

### Area bound

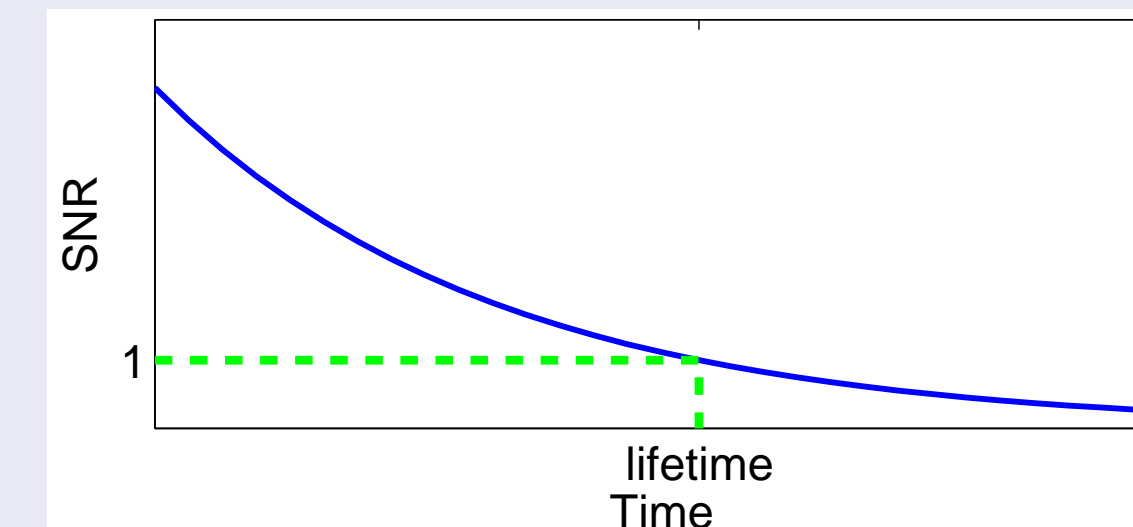
The memory lifetime is bounded by the area under the SNR curve:

$$\text{SNR}(\text{lifetime}) = 1 \implies \text{lifetime} < A.$$

We can show that this area has an upper bound:

$$A \leq \sqrt{N}(M-1)/r.$$

This is saturated by a transition diagram with a linear chain topology.



### Proof: Impose an ordering on the states

Let  $\mathbf{T}_{ij}$  be the mean first passage time from state  $i$  to state  $j$ . The following quantity

$$\eta = \sum_j \mathbf{T}_{ij} \mathbf{p}_j^\infty,$$

is independent of the initial state  $i$ . It is known as Kemeny's constant.

[Kemeny and Snell (1960)]

We define:

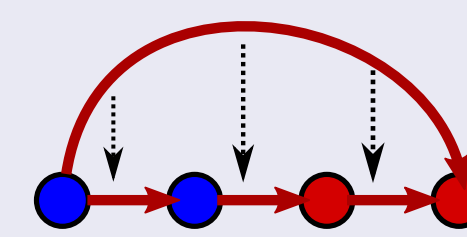
$$\eta_i^+ = \sum_{j \in \text{strong}} \mathbf{T}_{ij} \mathbf{p}_j^\infty, \quad \eta_i^- = \sum_{j \in \text{weak}} \mathbf{T}_{ij} \mathbf{p}_j^\infty.$$

These measure "distance" to the strong/weak states. They can be used to arrange the states in an order (increasing  $\eta^-$  or decreasing  $\eta^+$ ).

### Maximal area

Given any synaptic model, we can construct one with a linear chain topology that has

- the same state order,
- the same equilibrium distribution,
- a larger area.



Uses a deformation that reduces "shortcut" transition probabilities and increases the bypassed "direct" ones.

The area of this model is

$$A = \frac{2\sqrt{N}}{r} \sum_k \mathbf{p}_k^\infty |k - \langle k \rangle|.$$

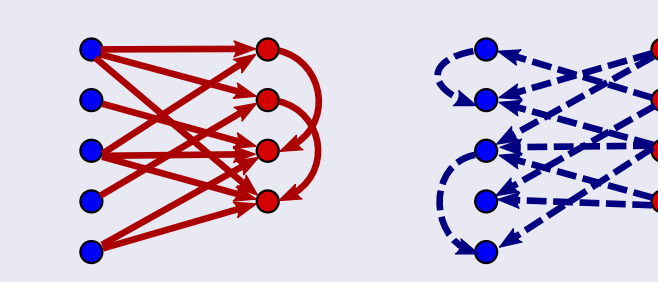
This is maximized when the equilibrium probability distribution is concentrated at both ends.

### Initial SNR bound

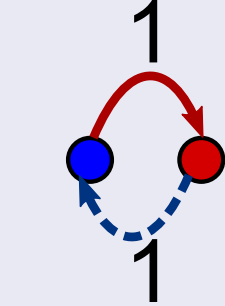
Initial SNR is closely related to equilibrium flux between strong & weak states

$$\text{SNR}(0) \leq \frac{4\sqrt{N}}{r} \Phi_{-+}.$$

Max when potentiation guarantees  $\mathbf{w} \rightarrow \text{strong}$ , depression guarantees  $\mathbf{w} \rightarrow \text{weak}$ .



→ Equivalent to:



$$\implies \text{SNR}(t) = \sqrt{N}(4f^{\text{pot}}f^{\text{dep}})e^{-rt}.$$

Maximal initial SNR:  $\text{SNR}(0) \leq \sqrt{N}$ .

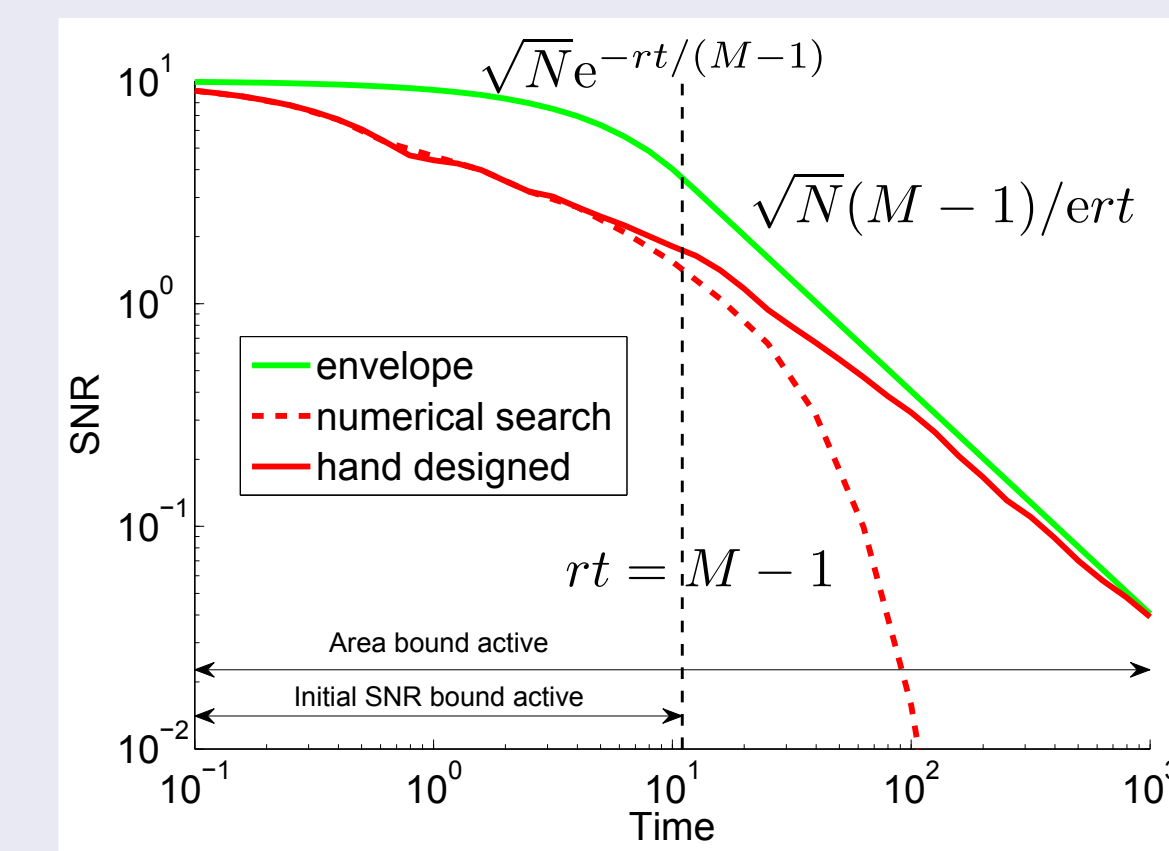
## The memory envelope

### The frontiers of possibility: a maximal SNR curve

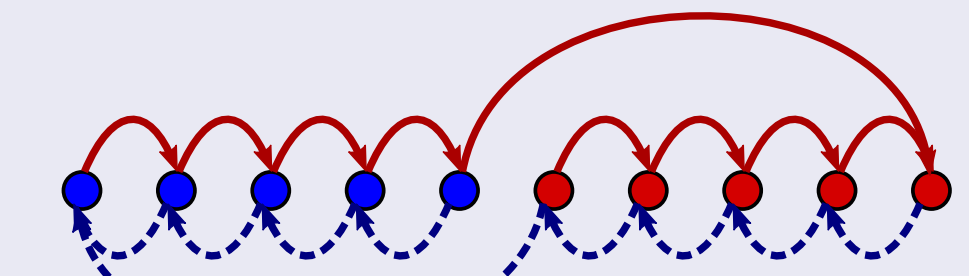
Markovian learning and forgetting  $\implies$  SNR is a sum of decaying exponentials.

Optimizing the SNR *at one time*,  $t_0$ , over the space of such curves, subject to upper bounds on initial SNR and area, yields an upper bound on SNR at  $t_0$  for *any* synaptic model. The resulting optimal memory curve is a single exponential (optimizing at two or more well separated times requires multiple exponentials).

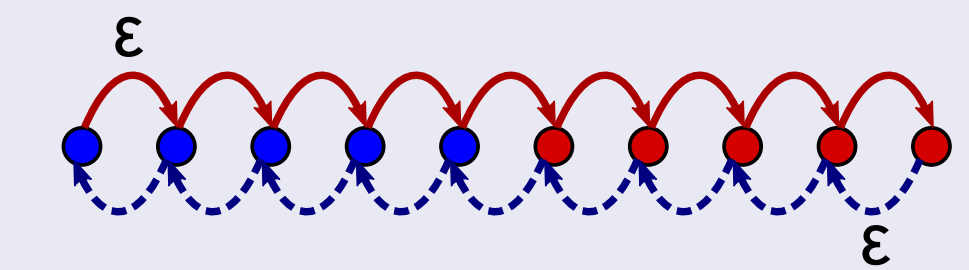
Varying  $t_0$  yields a memory envelope curve with a power law tail.



Early times: (varying  $M$ )



Late times: (varying  $\epsilon$ )



## Summary

- We have formulated a general theory of learning and memory with complex synapses.
- We can impose an order on the internal states of a synapse through the theory of first passage times.
- The area under the memory curve of any synaptic transition diagram cannot exceed that of a linear chain with the same equilibrium probability distribution.
- We find a memory envelope: a single curve that cannot be exceeded by the memory curve of *any* synaptic model. Synaptic complexity ( $M$  internal states) raises the memory envelope linearly in  $n$  for times  $> \mathcal{O}(M)$ .

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