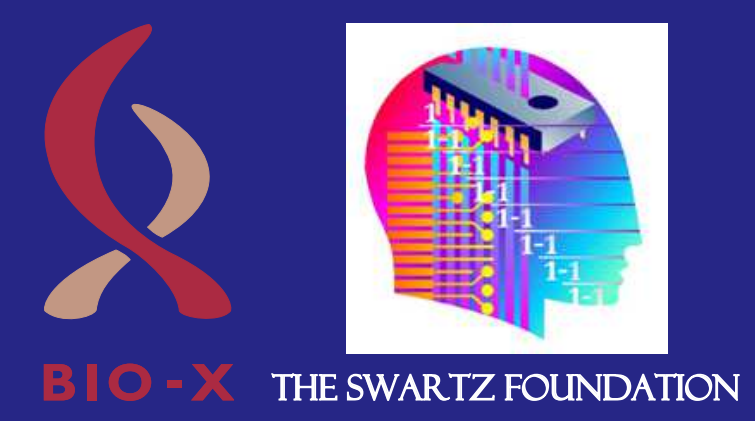# Learning and memory with complex synapses

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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 $\mathcal{O}(\log N)$.
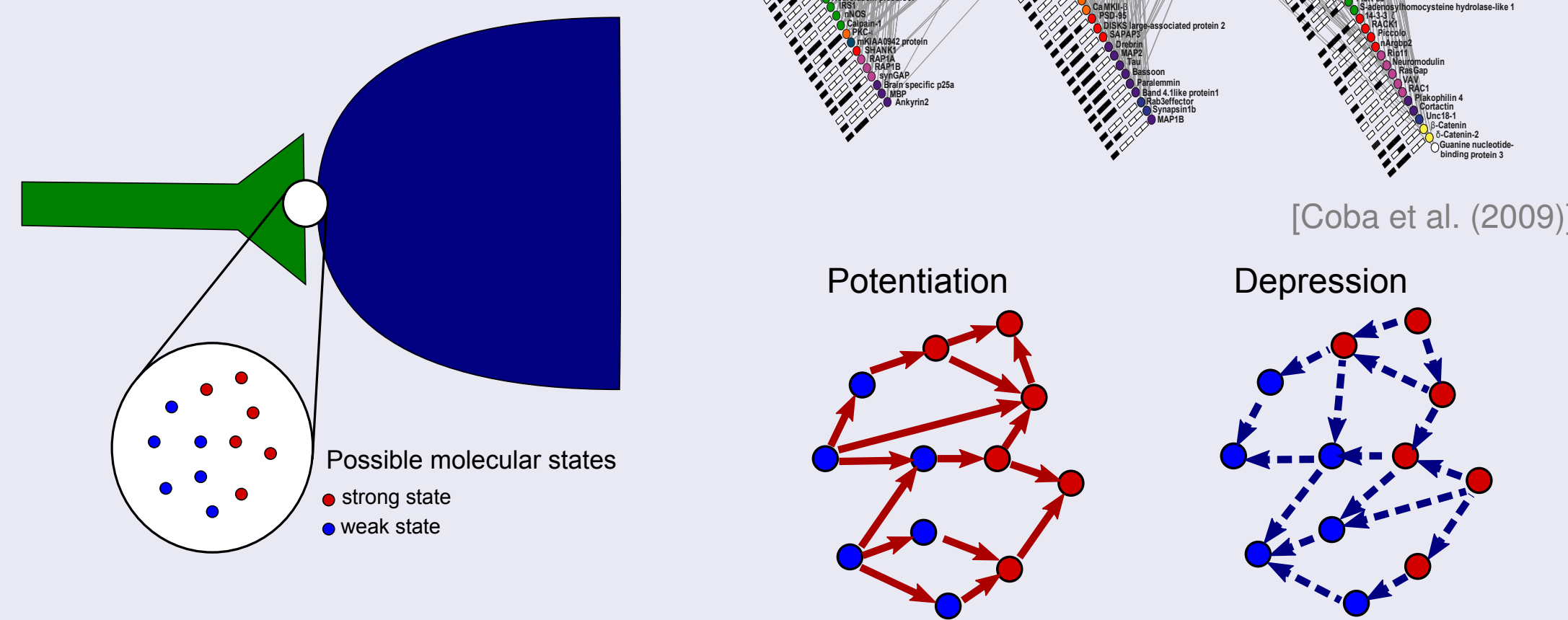
[Amit and Fusi (1992), Amit and Fusi (1994)]

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.

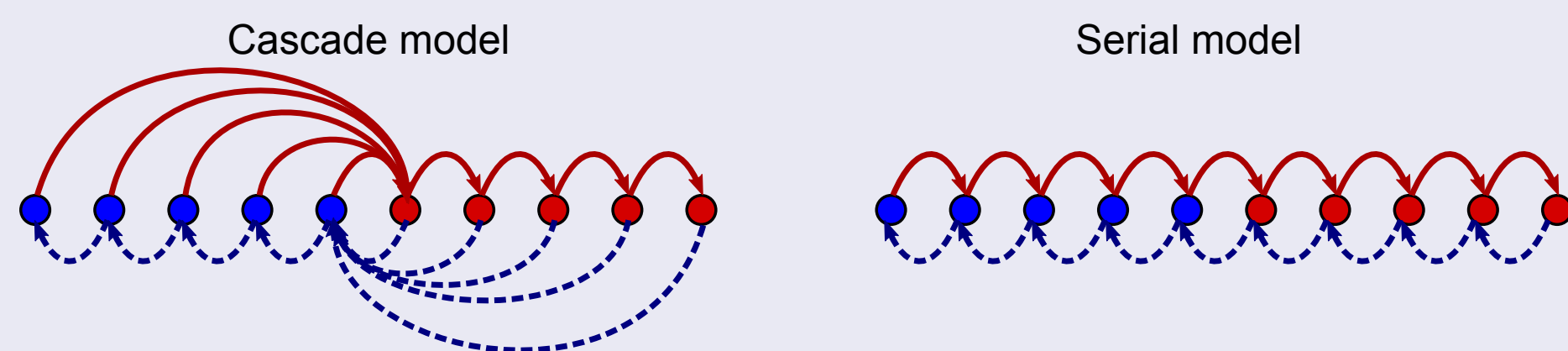We will describe a synapse by stochastic processes on a finite number of states, M.

Potentiation and depression cause transitions between these states.
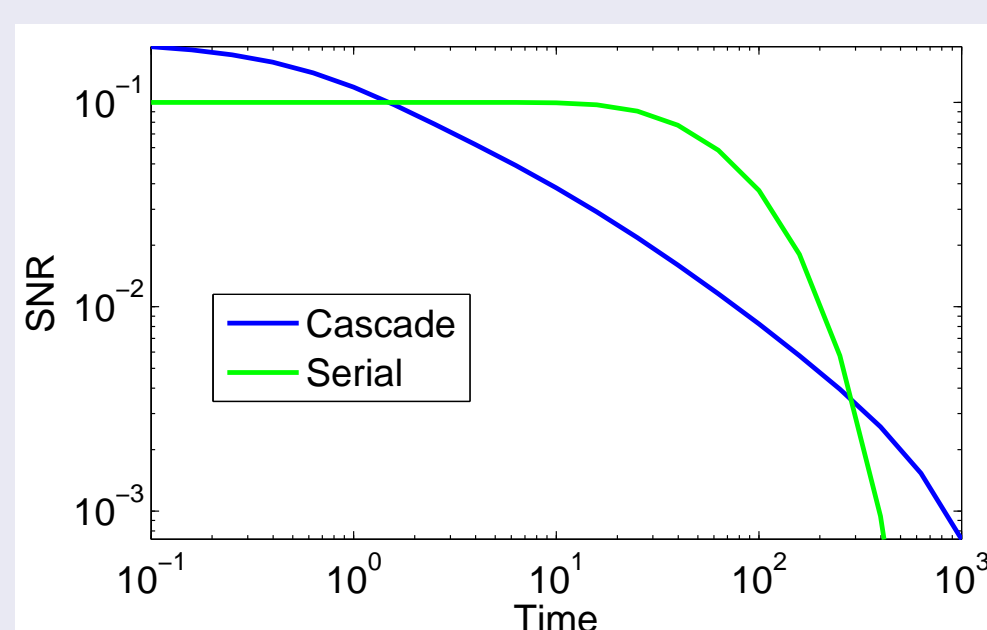

Legend

[Coba et al. (2009)]

Possible molecular states
- strong state
- weak state

Potentiation   Depression

Cascade and serial models

Two example models of complex synapses.

Cascade model   Serial model

[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^{pot} and depressing with probability f^{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:

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

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

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

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

If we assume there are no 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
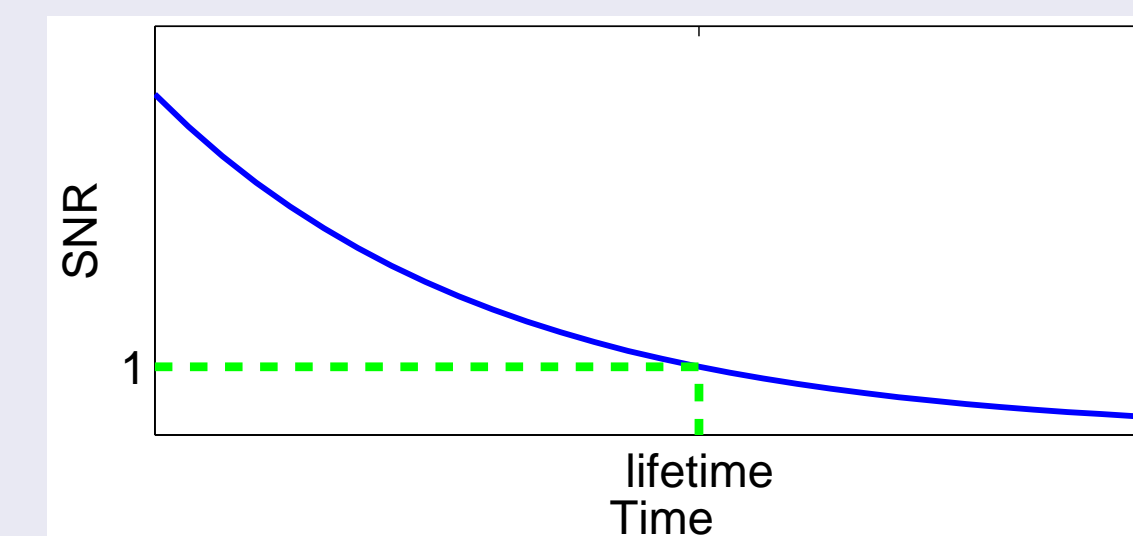
The memory lifetime is bounded by the area under the SNR curve:

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

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 Kemeney's constant. [Kemeny and Snell (1960)]

We define:

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

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

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

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

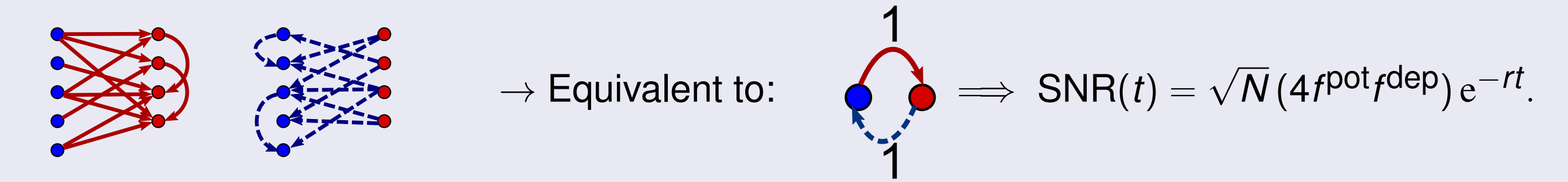This is maximized when the equilibrium probability distribution is concentrated at both ends.
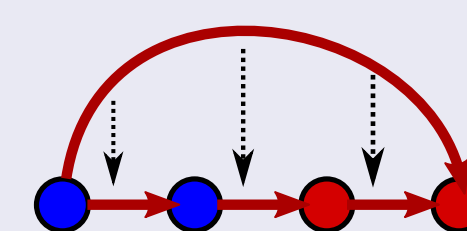
Initial SNR bound

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

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

Maximized when potentiation guarantees $\vec{w} \to$ strong, depression guarantees $\vec{w} \to$ weak.

$\to$ 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).
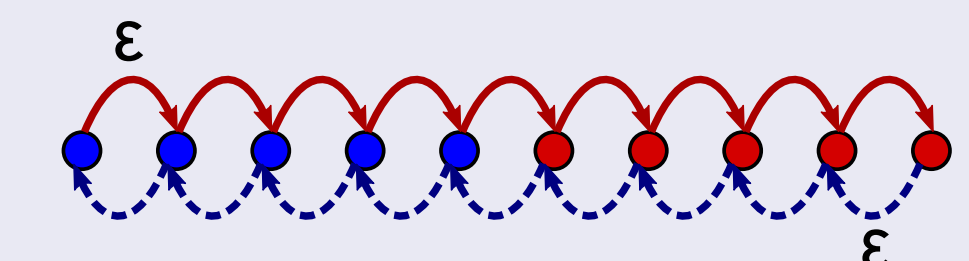
Varying t_0 yields a memory envelope curve with a power law tail.
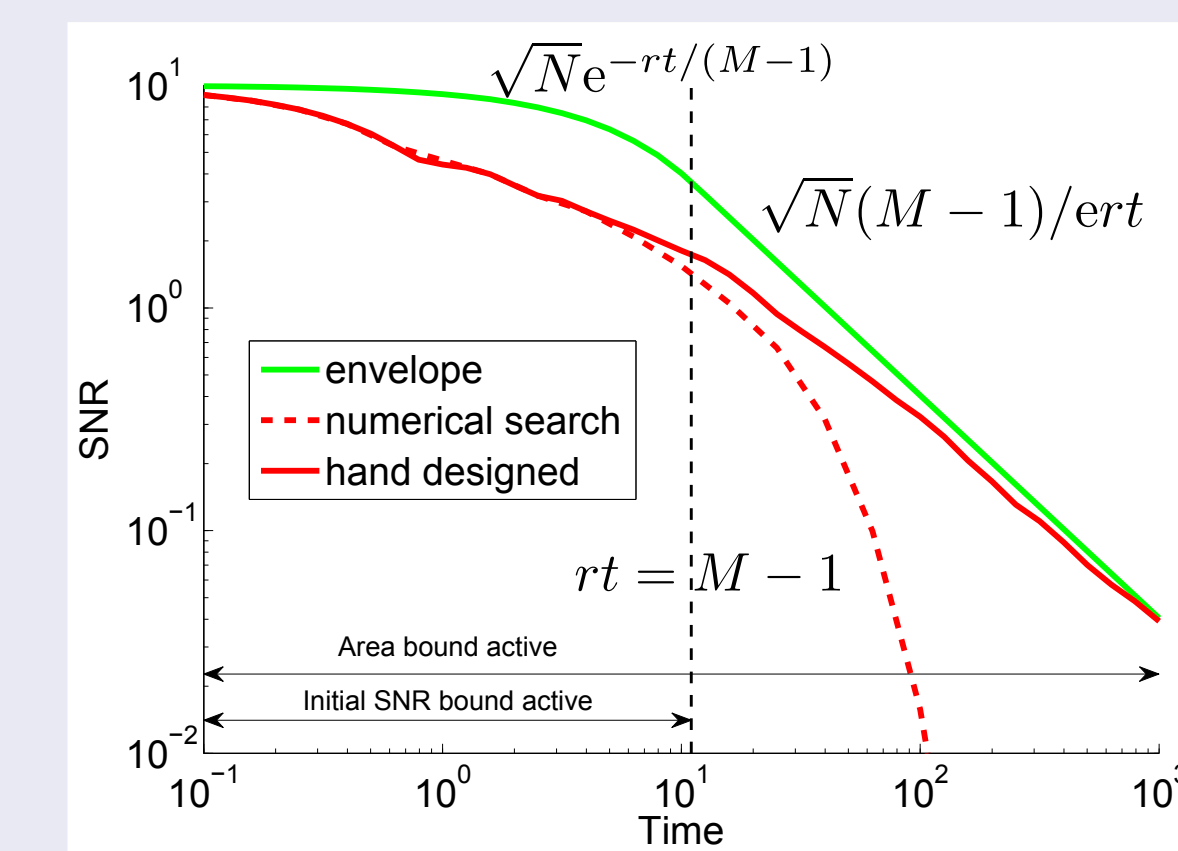
Early times: (varying M)
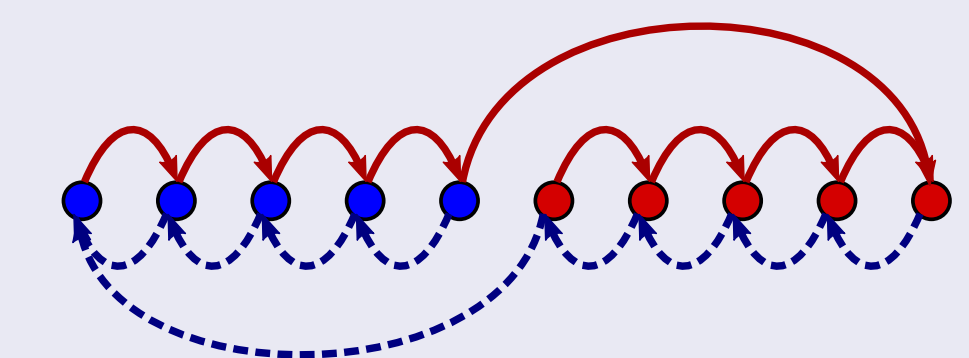
Late times: (varying ε)

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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