

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)]

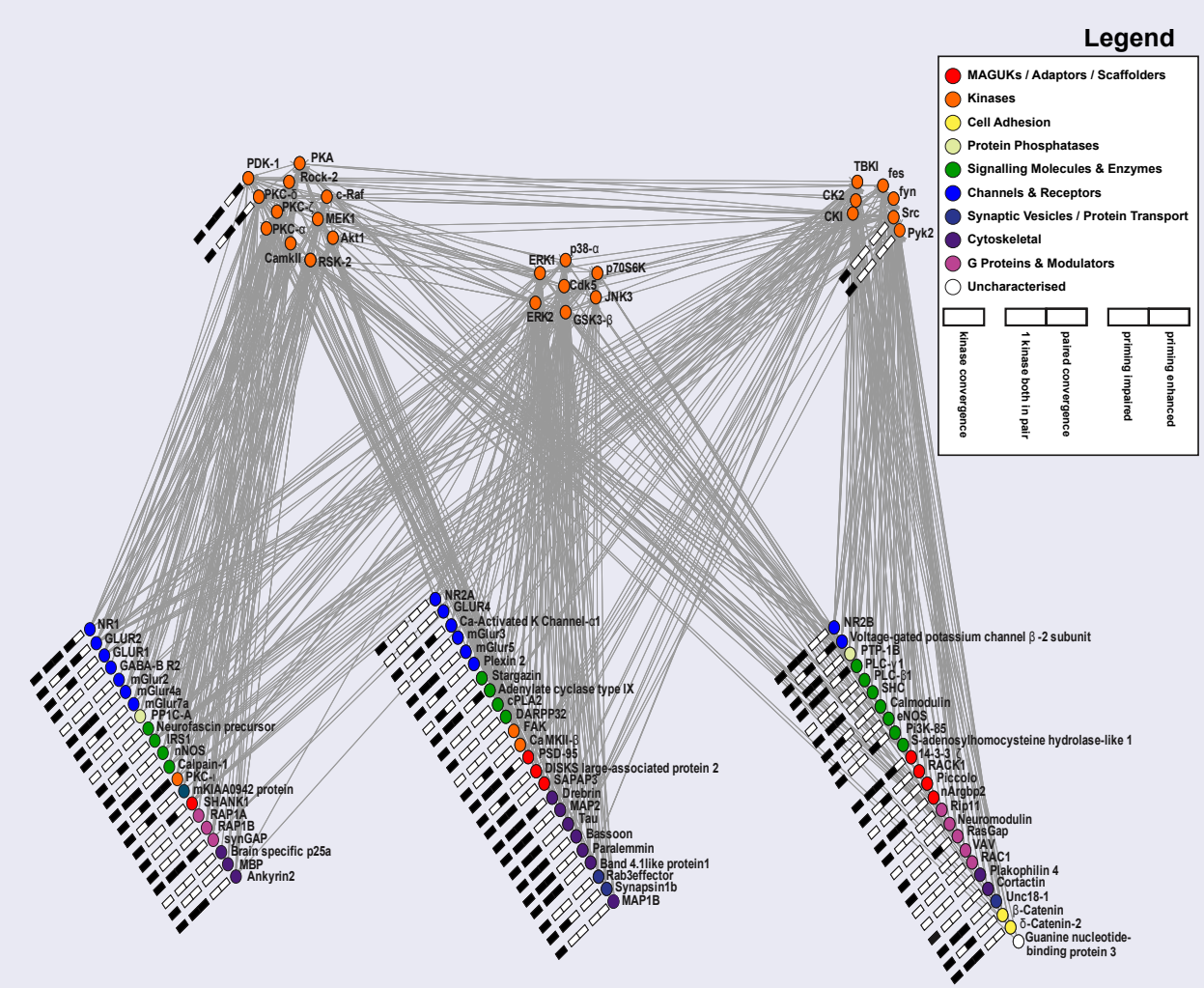
To circumvent this tradeoff, it is essential to enlarge our theoretical conception of a synapse as a single number.

Complex synapses

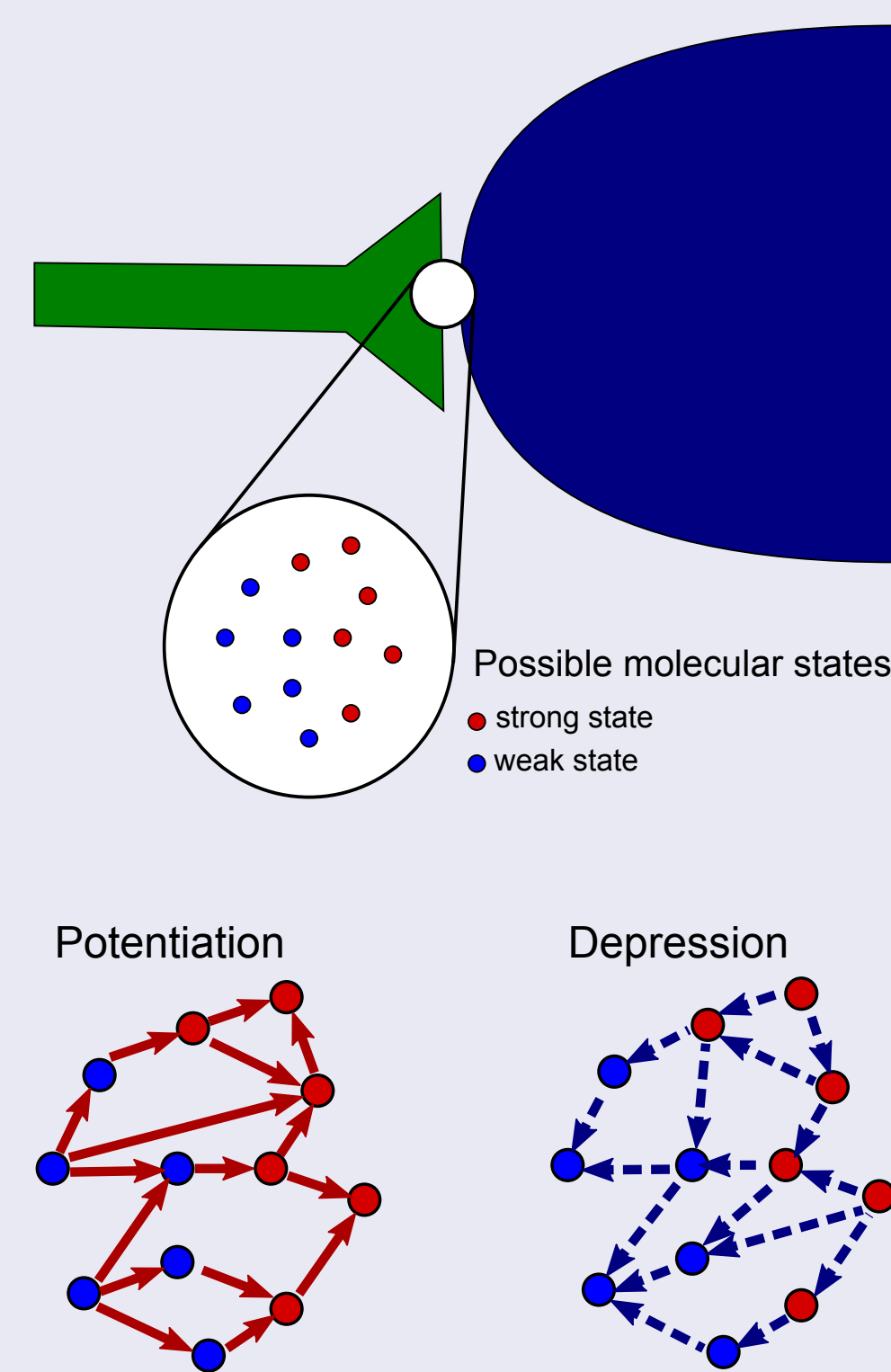
In reality, a synapse is a complex dynamical system.

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

Potentiation and depression cause transitions between these states.

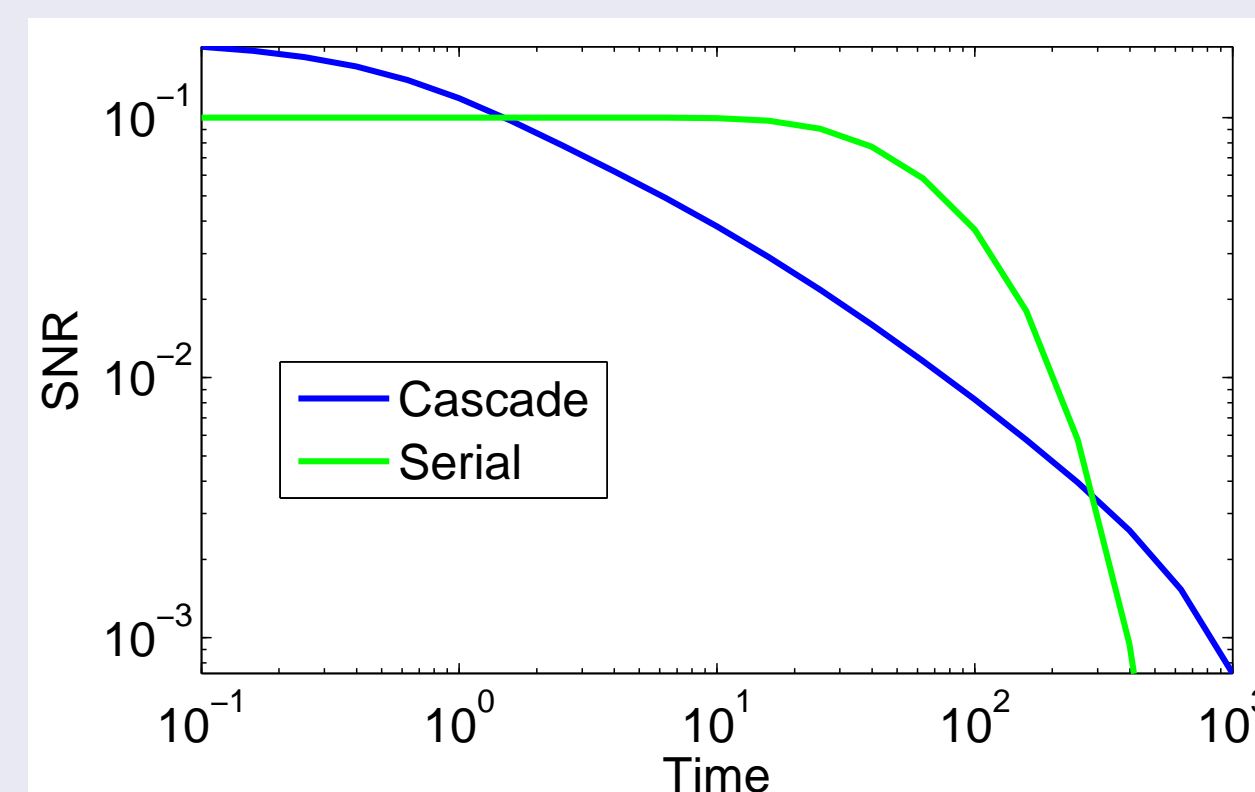
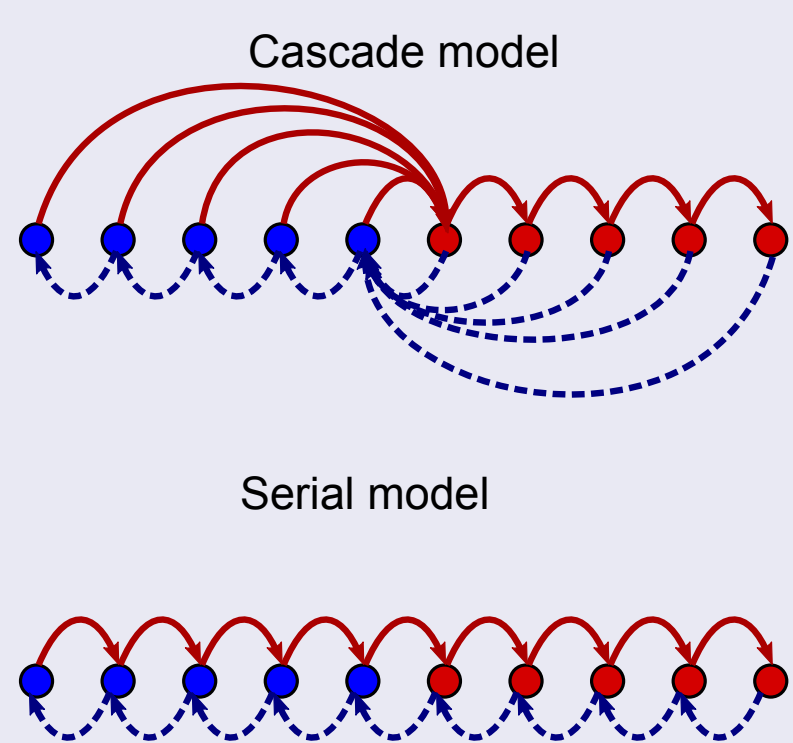


[Coba et al. (2009)]



Cascade and serial models

Two example models of complex synapses with different memory storage properties.



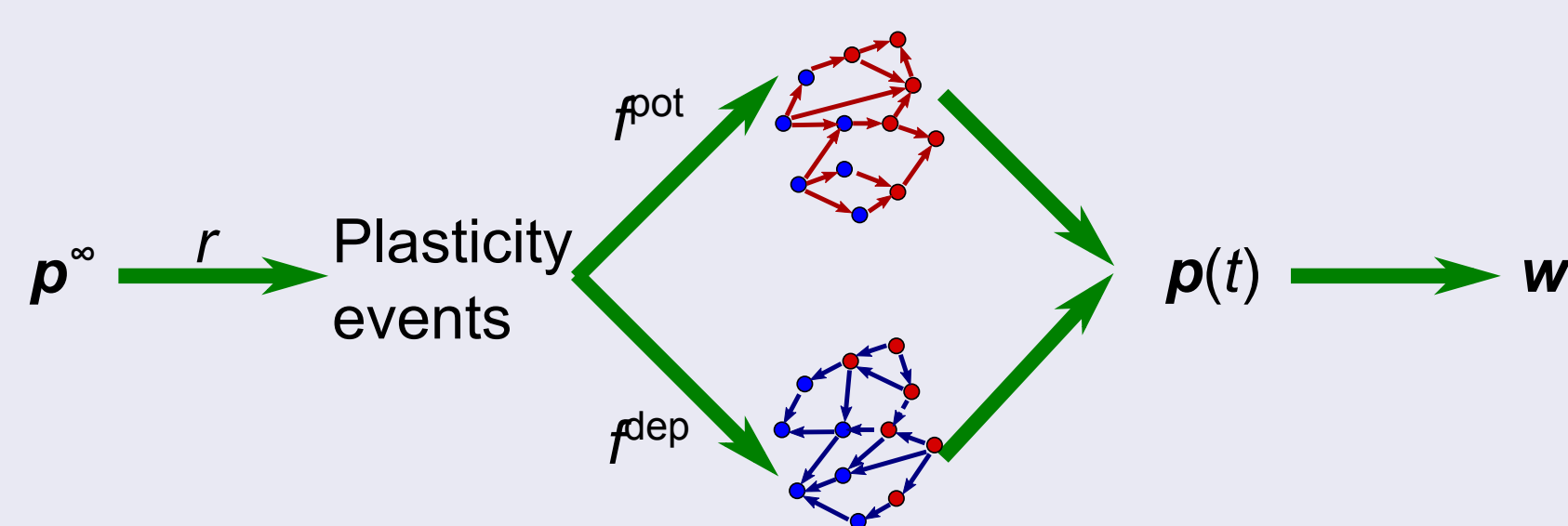
[Fusi et al. (2005), Leibold and Kempster (2008)]

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



Assumptions:

- Candidate plasticity events occur independently at each synapse,
- Each synapse responds with the same state-dependent rules,
- Synaptic weight takes only two values, ± 1 .

[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. To measure memory quality, let \vec{w} be an N -element vector of synaptic strengths,

$$\text{SNR}(t) = \frac{\langle \vec{w}_{\text{ideal}} \cdot \vec{w}(t) \rangle - \langle \vec{w}_{\text{ideal}} \cdot \vec{w}(\infty) \rangle}{\sqrt{\text{Var}(\vec{w}_{\text{ideal}} \cdot \vec{w}(\infty))}}$$

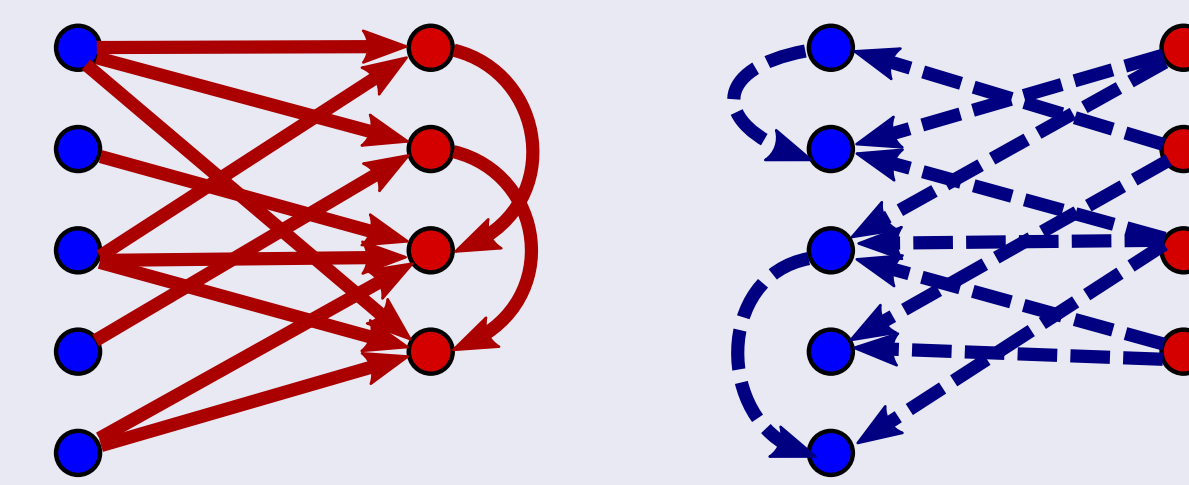
Upper bounds on performance

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 $\vec{w} \rightarrow \text{strong}$, depression guarantees $\vec{w} \rightarrow \text{weak}$.



→ Equivalent to two-state model



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

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

Area bound

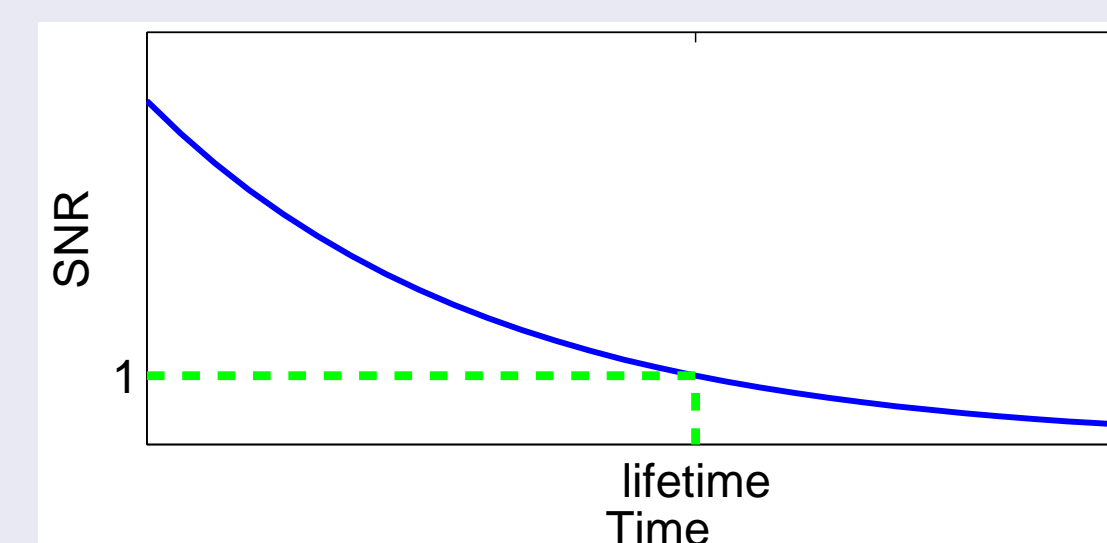
The memory lifetime is bounded by the area under the SNR curve:

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

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 the serial 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

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

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

[Kemeny and Snell (1960)]

We define:

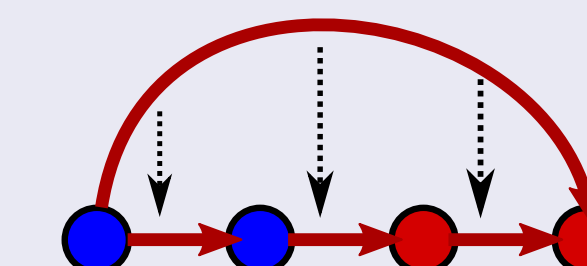
$$\eta_i^+ = \sum_{j \in \text{strong}} \mathbf{T}_{ij} \mathbf{p}_j^\infty, \quad \eta_i^- = \sum_{j \in \text{weak}} \mathbf{T}_{ij} \mathbf{p}_j^\infty.$$

These measure "distance" to the strong/weak states. They can be used to arrange the states in an order (increasing 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.

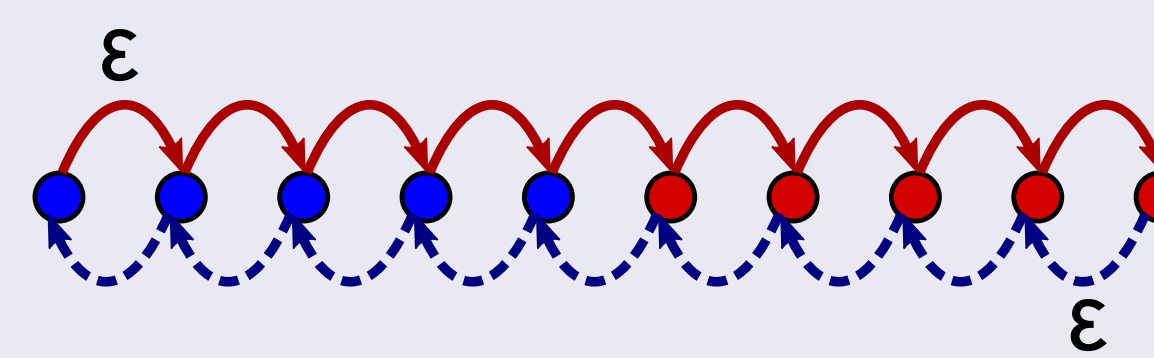


Uses a deformation that reduces "shortcut" transition probabilities and increases the bypassed "direct" ones.

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.



In the limit $\varepsilon \rightarrow 0$.

Eigenmode decomposition

We can split the system along eigenvectors of the stochastic forgetting process:

$$\text{SNR}(t) = \sqrt{N} \sum_a \mathcal{I}_a e^{-rt/\tau_a}.$$

The upper bounds on initial SNR and area tell us:

$$\sum_a \mathcal{I}_a \leq 1, \quad \sum_a \mathcal{I}_a \tau_a \leq M - 1.$$

- What are the implications for the full memory curve?
- Are there any other important constraints?

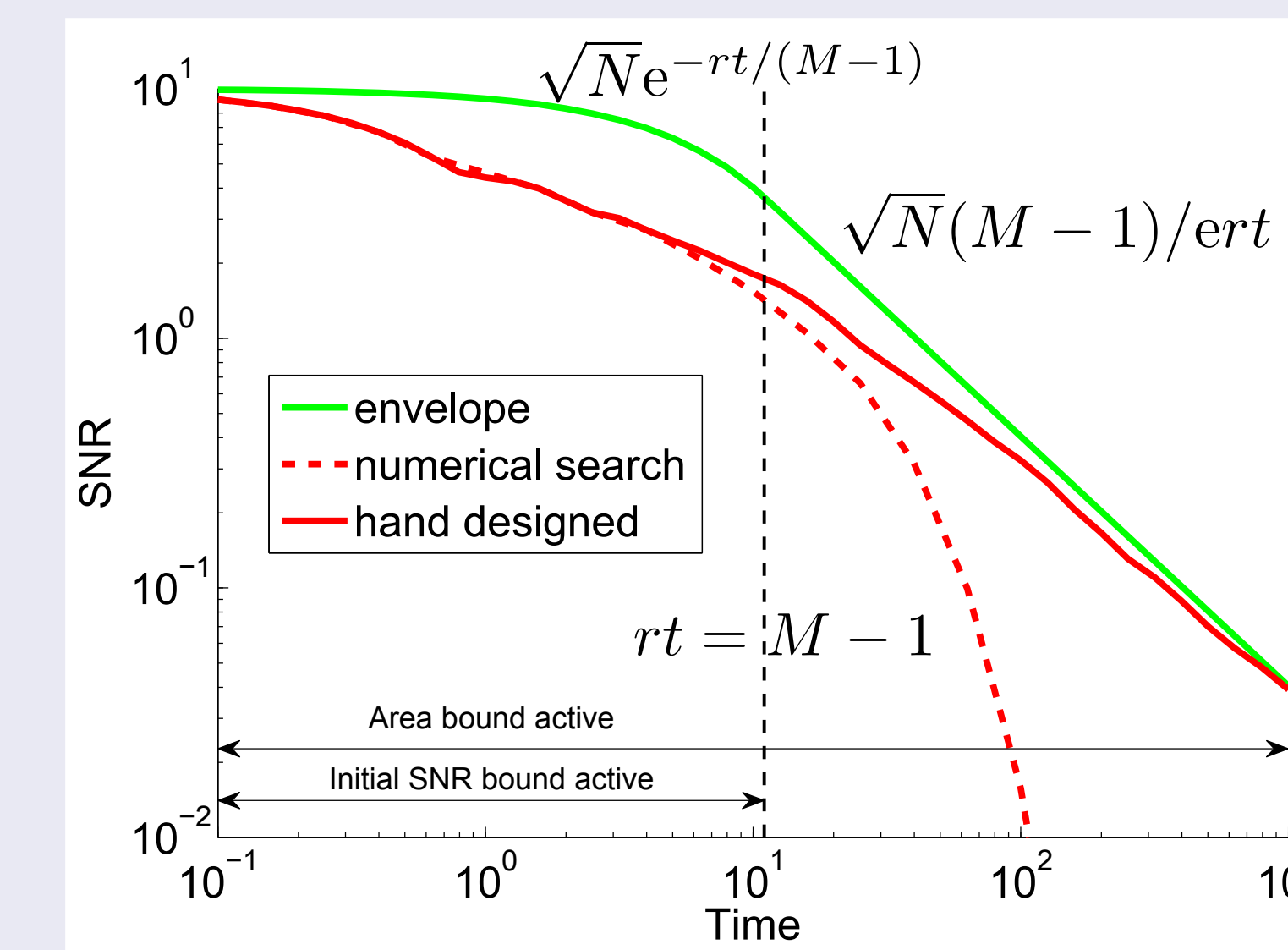
The memory envelope

The frontiers of possibility: a maximal SNR curve

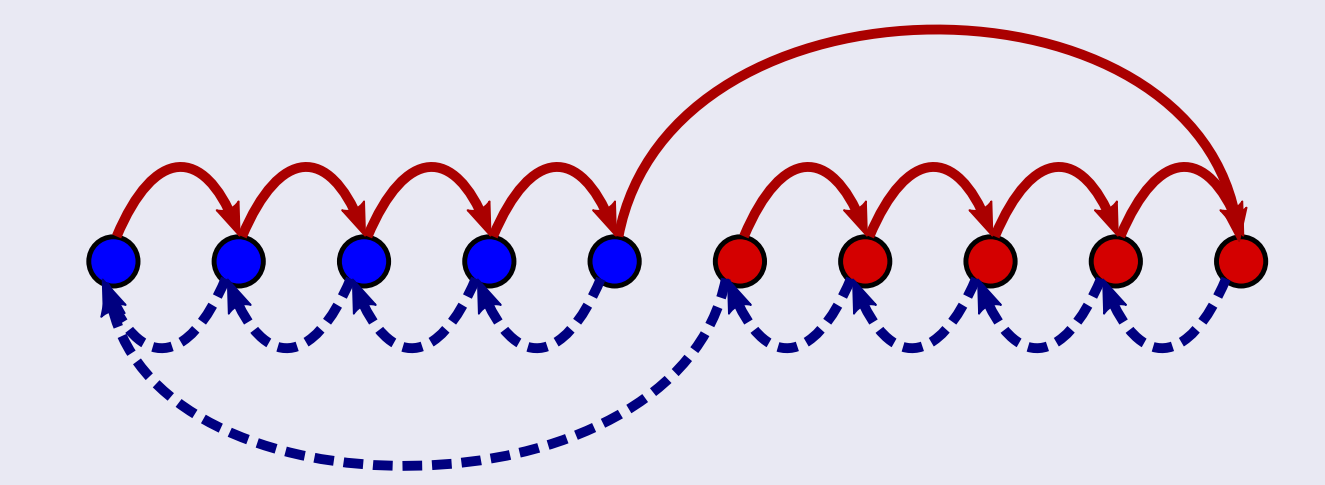
Markovian learning and forgetting \implies SNR is a sum of decaying exponentials.

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).

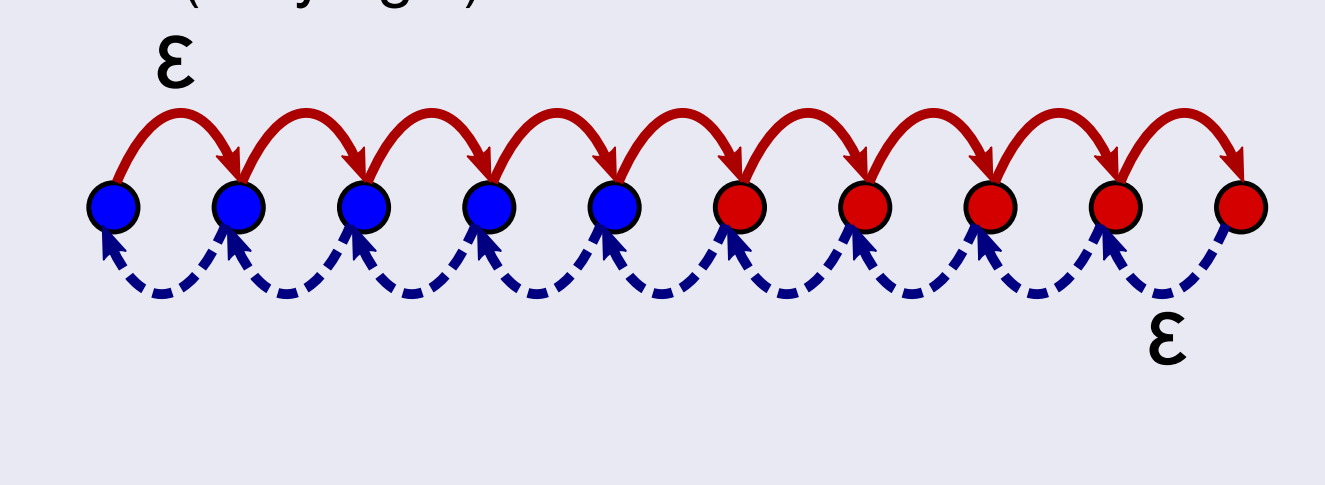
Varying t_0 yields a memory envelope curve with a power law tail.



Early times: (varying M)



Late times: (varying ε)

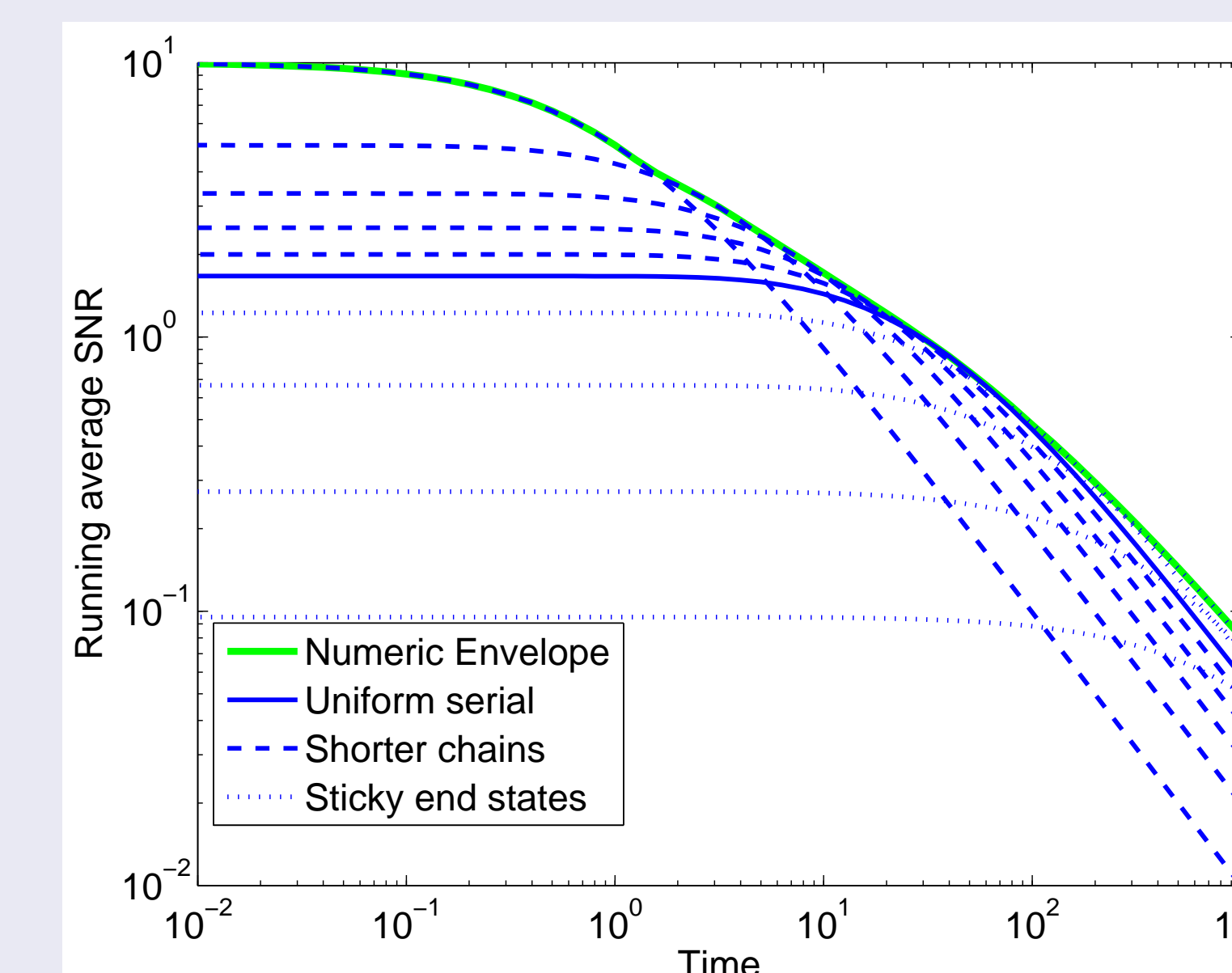


Envelope for running average memory curve

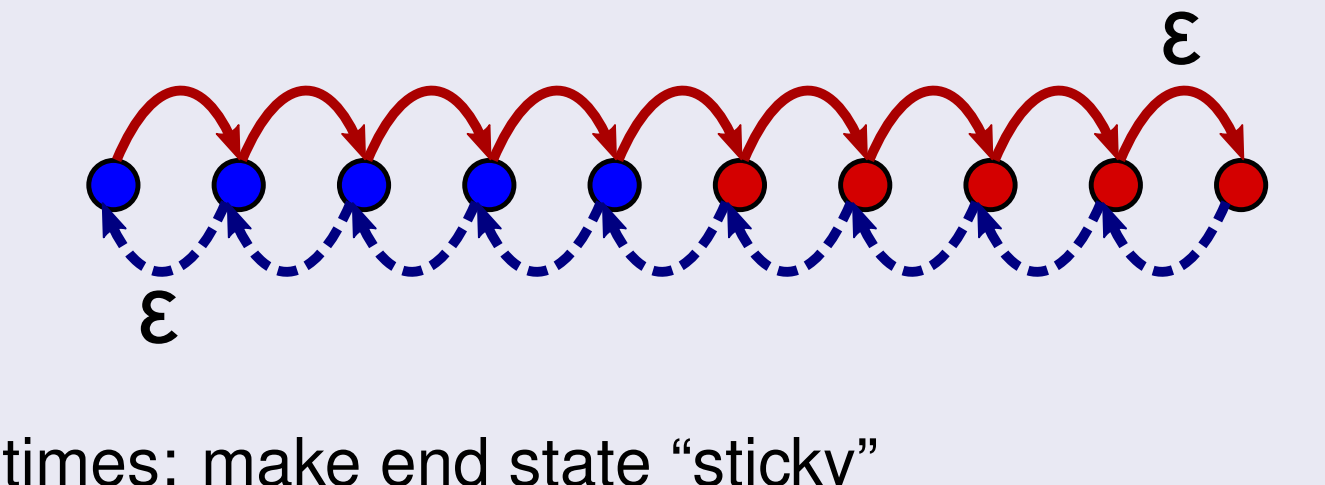
We define the running average SNR:

$$\widehat{\text{SNR}}(\tau) = \frac{1}{\tau} \int_0^\infty dt e^{-t/\tau} \text{SNR}(t) \sim \frac{1}{\tau} \int_0^\tau dt \text{SNR}(t)$$

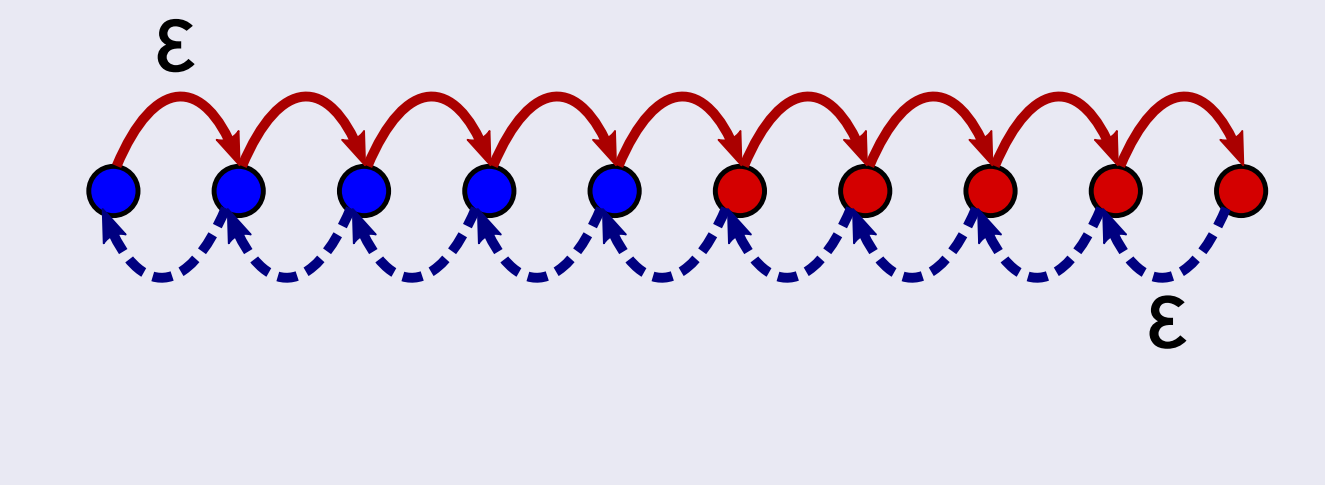
For any τ , this is maximized by a model with the serial topology.



Earlier times: shorten the chain



Later times: make end state "sticky"



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 M for times $> \mathcal{O}(M)$.

References

- D. J. Amit and S. Fusi, "Constraints on learning in dynamic synapses", *Network: Computation in Neural Systems*, 3(4):443–464, (1992) .
- D. J. Amit and S. Fusi, "Learning in neural networks with material synapses", *Neural Computation*, 6(5):957–982, (1994) .
- M. P. Coba, A. J. Pocklington, M. O. Collins, M. V. Kopanitsa, R. T. Uren, S. Swamy, M. D. Croning, J. S. Choudhary, and S. G. Grant, "Neurotransmitters drive combinatorial multistate postsynaptic density networks", *Sci Signal*, 2(68):ra19, (2009) .
- S. Fusi, P. J. Drew, and L. F. Abbott, "Cascade models of synaptically stored memories", *Neuron*, 45(4):599–611, (Feb, 2005) .
- Christian Leibold and Richard Kempster, "Sparseness Constrains the Prolongation of Memory Lifetime via Synaptic Metaplasticity", *Cerebral Cortex*, 18(1):67–77, (2008) .
- S. Fusi and L. F. Abbott, "Limits on the memory storage capacity of bounded synapses", *Nat. Neurosci.*, 10(4):485–493, (Apr, 2007) .
- A. B. Barrett and M. C. van Rossum, "Optimal learning rules for discrete synapses", *PLoS Comput. Biol.*, 4(11):e1000230, (Nov, 2008) .
- J.G. Kemeny and J.L. Snell, *Finite markov chains*. Springer, 1960.

Acknowledgements

SL and SG thank the Swartz Foundation, Burroughs Wellcome Foundation, Stanford Bio-X Neuroventures, Genentech and DARPA for funding, and Larry Abbott, Stefano Fusi, Marcus Benna, David Sussillo and Jascha Sohl-Dickstein for useful conversations.