Learning and memory with complex synaptic plasticity

based on work with Surya Ganguli

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Stanford University, Applied Physics

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Introduction

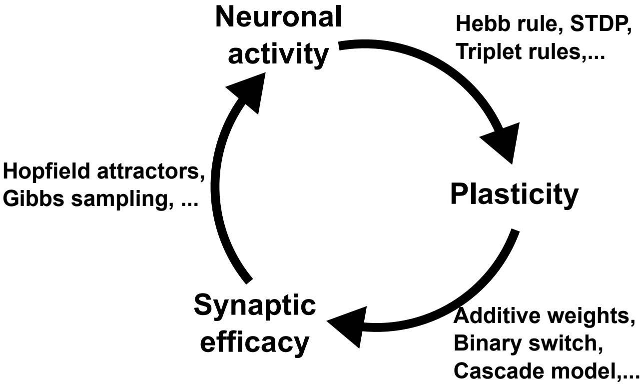
We often model synaptic plasticity as the change of a single number (synaptic weight). In reality, there is a complex dynamical system inside a synapse.

Semi-realistic models of synaptic plasticity have terrible memory without synaptic complexity.

We will study the entire space of a broad class of models of complex synapses to find upper bounds on their performance.

This leads to understanding of what structures are useful for storing memories for different timescales.

Synaptic learning and memory



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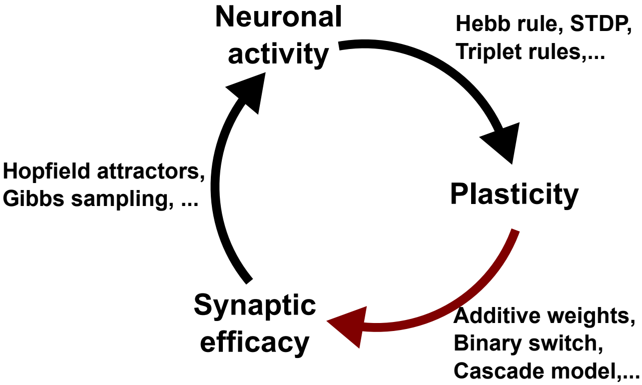
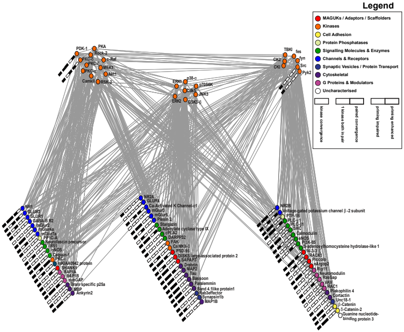
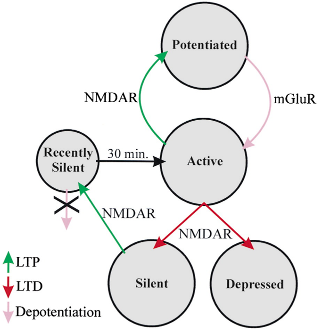


Synapses are complex



[Coba et al. (2009)]

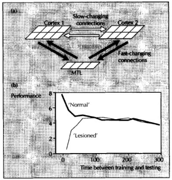


[Montgomery and Madison (2002)]

There is a complex, dynamic system underlying synaptic plasticity.

Timescales of memory

Memories stored in different places for different timescales

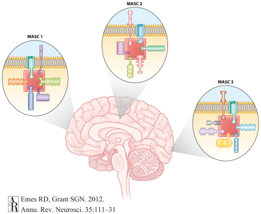


[Squire and Alvarez (1995)]

cf. Cerebellar cortex vs. cerebellar nuclei.

[Krakauer and Shadmehr (2006)]

Different synapses have different molecular structures.



[Emes and Grant (2012)]

Outline

1. Why complex synapses?
2. Modelling synaptic memory
3. Upper bounds
4. Envelope memory curve
5. Experimental tests?

Section 1

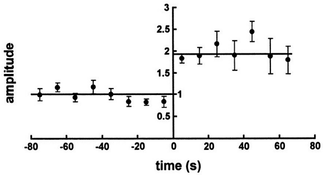
Why complex synapses?

Storage capacity of synaptic memory

A classical perceptron has a capacity $\propto N$, ($\#$ synapses).

Requires synapses' dynamic range also $\propto N$.

With discrete, finite synapses:
$\implies$ new memories overwrite old.



[Petersen et al. (1998), O'Connor et al. (2005)]

When we store new memories rapidly, memory capacity $\sim \mathcal{O}(\log N)$.

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

Trade-off between learning and remembering

	Learning	**Remembering**
Very plastic		

Trade-off between learning and remembering

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Trade-off between learning and remembering

	Learning	**Remembering**
Very plastic		
Very rigid		

Trade-off between learning and remembering

	Learning	**Remembering**
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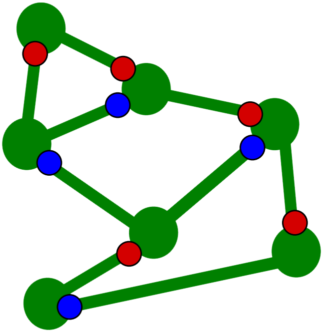
Circumvent tradeoff: go beyond model of synapse as single number.

Section 2

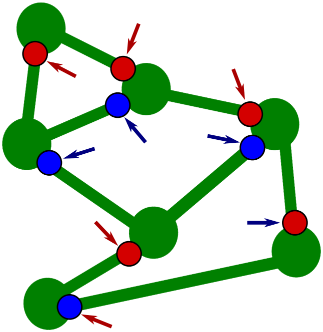
Modelling synaptic memory

Synapses given a sequence of patterns (pot & dep) to store



Recognition memory

Synapses given a sequence of patterns (pot & dep) to store



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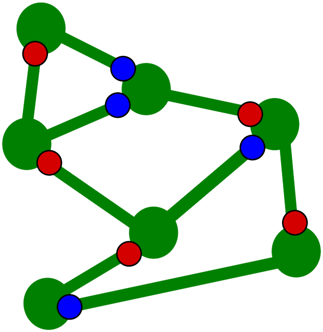

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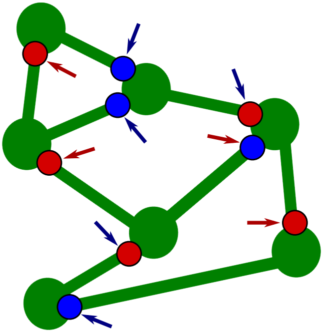

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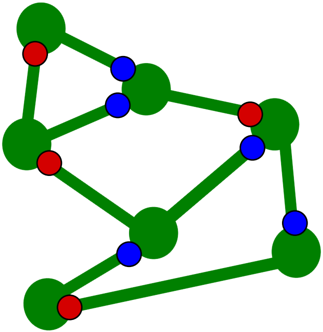

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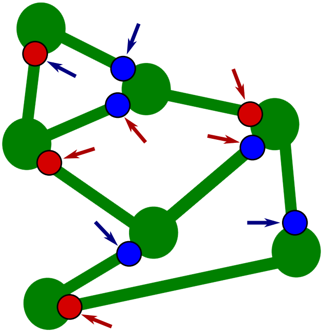

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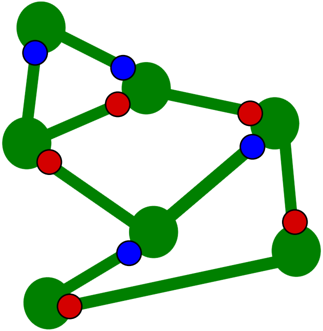

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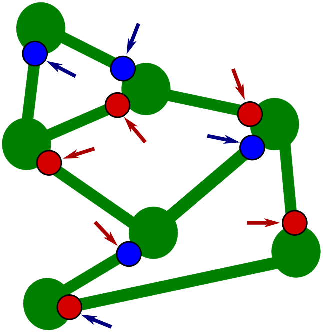
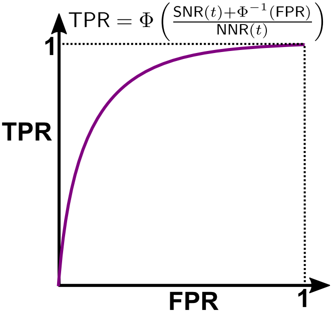


Later: presented with a pattern. Has it been seen before?

Quantifying memory quality

Have we seen pattern before? Test if $\vec{w}_{\text{ideal}} \cdot \vec{w}(t) \gtrless \theta$?
$\vec{w}_{\text{ideal}} \cdot \vec{w}(\infty) \sim$ null distribution $\implies$ ROC curve:



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

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

Averaging over recall times

Look at:

$$\overline{\mathsf{SNR}}(\tau) = \left\langle \mathsf{SNR}(t) \right\rangle_{P(t\,|\,\tau)}, \qquad P(t\,|\,\tau) = \frac{\mathrm{e}^{-t/\tau}}{\tau}.$$

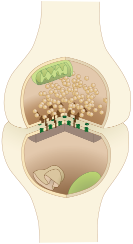
$\tau =$ mean recall time.

Like a "running average":

$$\widehat{\mathsf{SNR}}(\tau) = \frac{1}{\tau}\int_0^\infty \mathrm{d}t\, \mathrm{e}^{-t/\tau}\ \mathsf{SNR}(t) \sim \frac{1}{\tau}\int_0^\tau \mathrm{d}t\ \mathsf{SNR}(t)$$

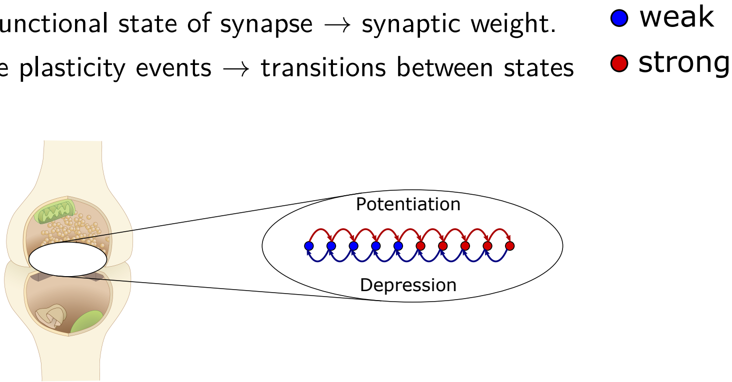
Different brain regions $\rightarrow$ different τ.

Models of complex synaptic dynamics



Models of complex synaptic dynamics

- Internal functional state of synapse → synaptic weight.
- Candidate plasticity events → transitions between states



States: #AMPAR, #NMDAR, NMDAR subunit composition,
CaMK II autophosphorylation, activating PKC, p38 MAPK,...

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

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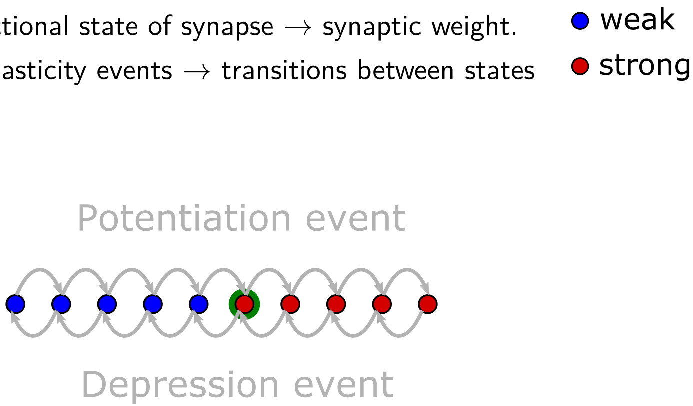

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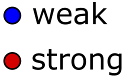

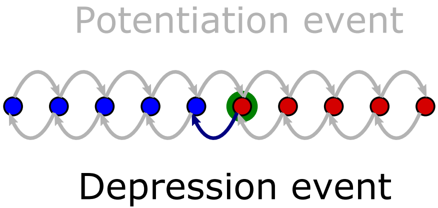

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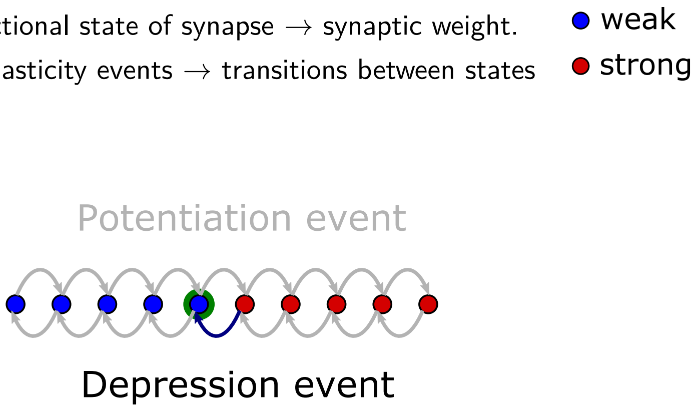

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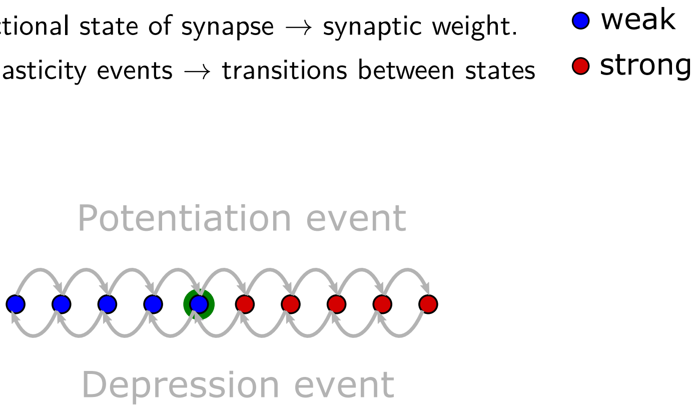

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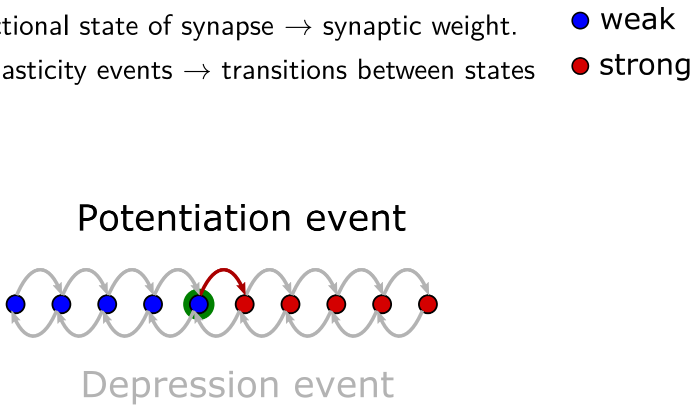

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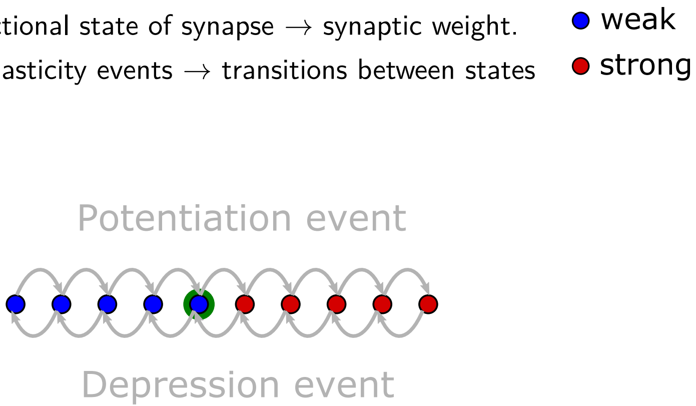

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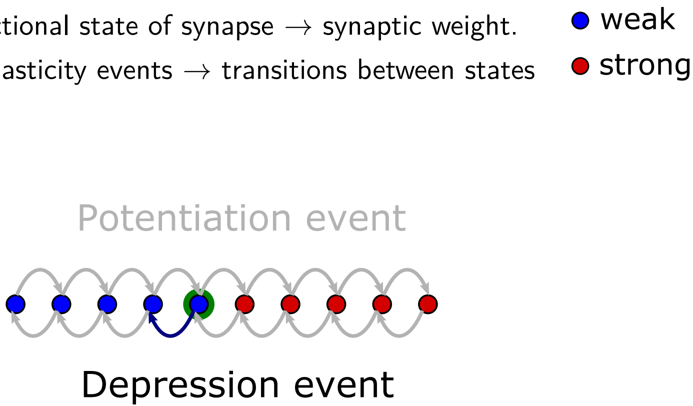

Metaplasticity: change propensity for plasticity
(independent of change in synaptic weight).

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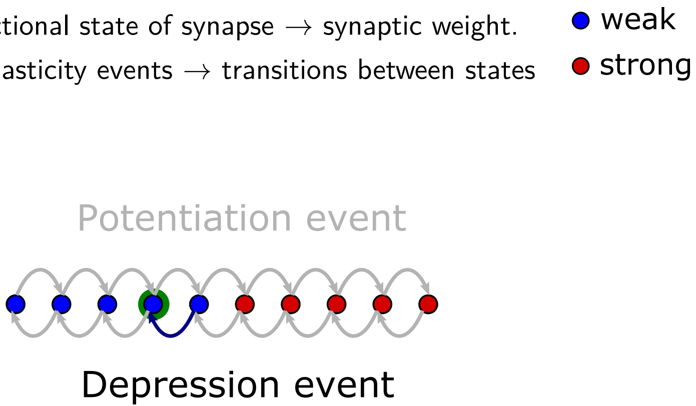

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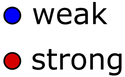

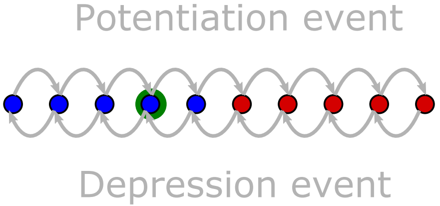

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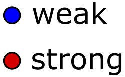

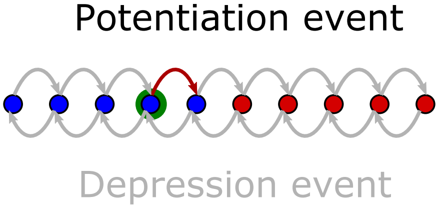

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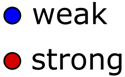

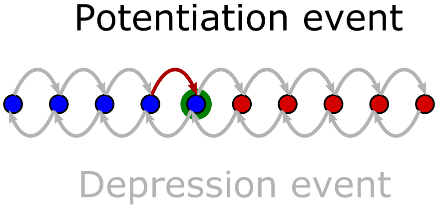

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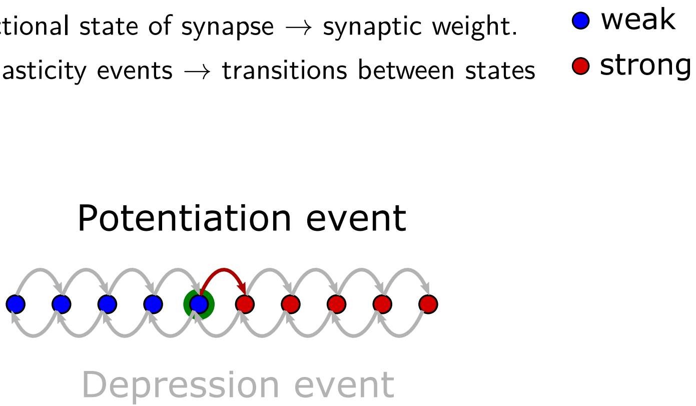

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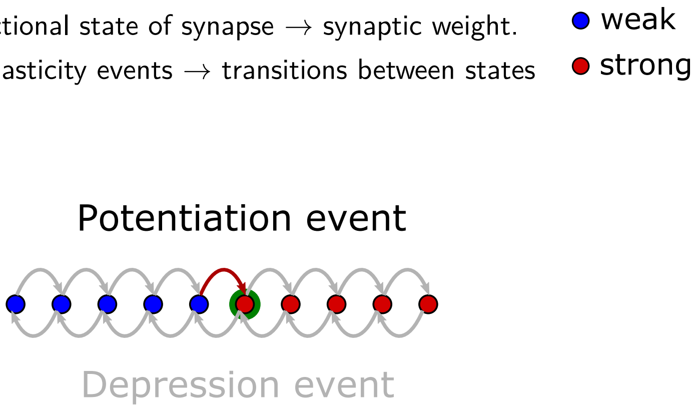

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Models of complex synaptic dynamics

- Internal functional state of synapse → synaptic weight.
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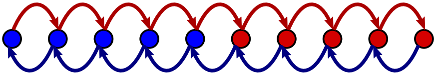
weak
strong

Potentiation



Depression

Metaplasticity: change propensity for plasticity
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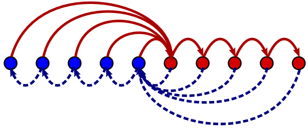
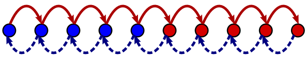
Example models

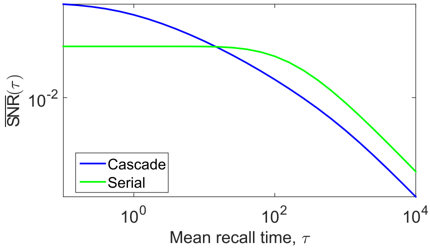
Two example models of complex synapses.





[Fusi et al. (2005), Leibold and Kempter (2008), Ben-Dayan Rubin and Fusi (2007)]

These have different memory storage properties

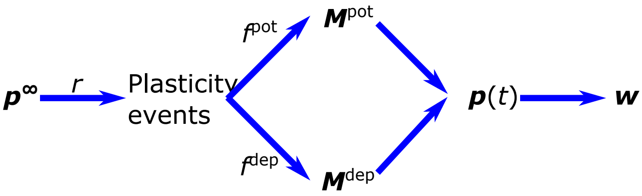


Questions

- Can we understand the space of *all possible* synaptic models?
- How does structure (topology) of model $\rightarrow$ function (memory curve)?
- What are the limits on what can be achieved?
- Which transition topologies saturate these limits?
- Can synaptic structure be tuned for different timescales of memory?

Parameters for synaptic dynamics

There are N identical synapses with M internal functional states.



$$\frac{\mathrm{d}\mathbf{p}(t)}{\mathrm{d}t} = r\mathbf{p}(t)\mathbf{W}^{\mathrm{F}}, \qquad \mathbf{W}^{\mathrm{F}} = f^{\text{pot}}\mathbf{M}^{\text{pot}} + f^{\text{dep}}\mathbf{M}^{\text{dep}} - \mathbf{I},$$

$$\mathbf{p}^\infty\mathbf{W}^{\mathrm{F}} = 0.$$

Constraints

Memory curve given by

$$\mathrm{SNR}(t) = \sqrt{N}(2f^{\text{pot}}f^{\text{dep}})\,\mathbf{p}^{\infty}\left(\mathbf{M}^{\text{pot}} - \mathbf{M}^{\text{dep}}\right)\exp\left(rt\mathbf{W}^{\mathrm{F}}\right)\mathbf{w},$$
$$\overline{\mathrm{SNR}}(\tau) = \sqrt{N}(2f^{\text{pot}}f^{\text{dep}})\,\mathbf{p}^{\infty}\left(\mathbf{M}^{\text{pot}} - \mathbf{M}^{\text{dep}}\right)\left[\mathbf{I} - r\tau\mathbf{W}^{\mathrm{F}}\right]^{-1}\mathbf{w}.$$

Constraints: $\mathbf{M}_{ij}^{\text{pot/dep}} \in [0,1], \qquad \sum_j \mathbf{M}_{ij}^{\text{pot/dep}} = 1.$

Eigenmode decomposition:

$$\mathrm{SNR}(t) = \sqrt{N}\sum_a \mathcal{I}_a\,\mathrm{e}^{-rt/\tau_a},$$
$$\overline{\mathrm{SNR}}(\tau) = \sqrt{N}\sum_a \frac{\mathcal{I}_a}{1 + r\tau/\tau_a},$$

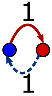
Section 3

Upper bounds

Upper bounds on measures of memory

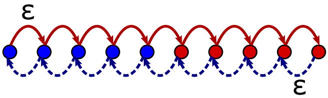
Initial SNR:

$$\mathrm{SNR}(0) = \overline{\mathrm{SNR}}(0) \leq \sqrt{N}.$$



Area under curve:

$$\mathcal{A} = \int_0^\infty \mathrm{d}t\ \mathrm{SNR}(t) = \lim_{\tau\to\infty} \tau\,\overline{\mathrm{SNR}}(\tau) \leq \sqrt{N}(M-1)/r.$$



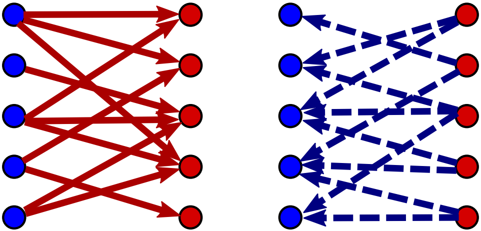
[Lahiri and Ganguli (2013)]

Initial SNR as flux

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

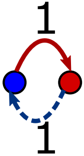
$$\mathrm{SNR}(0) \leq \frac{4\sqrt{N}}{r}\,\mathbf{\Phi}_{-+}.$$

Max when potentiation guarantees $\mathbf{w} \to +1$,
depression guarantees $\mathbf{w} \to -1$.



Two-state model

Two-state model equivalent to previous slide:

Transitions: 

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

Maximal initial SNR:

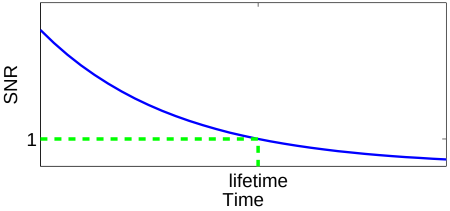
$$\mathrm{SNR}(0) \leq \sqrt{N}.$$

Area under memory curve

$$\mathcal{A} = \int_0^\infty \mathrm{d}t\ \mathsf{SNR}(t), \qquad \overline{\mathsf{SNR}}(\tau) \to \frac{\mathcal{A}}{\tau} \quad \text{as} \quad \tau \to \infty.$$

Area bounds memory lifetime:

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



This area has an upper bound:

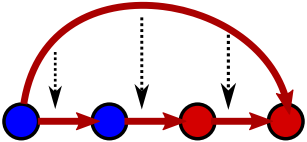
$$\mathcal{A} \leq \sqrt{N}(M-1)/r.$$

Saturated by a model with linear chain topology.

Proof of area bound

For any model, we can construct perturbations that

- preserve equilibrium distribution,
- increase area.



details

e.g. decrease "shortcut" transitions, increase bypassed "direct" ones.
Endpoint: linear chain

The area of this model is

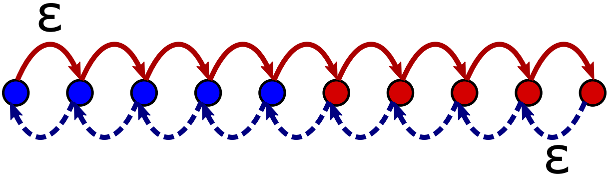
$$A = \frac{2\sqrt{N}}{r} \sum_k \mathbf{p}_k^\infty \left| k - \langle k \rangle \right| .$$

Max: equilibrium probability distribution concentrated at both ends.

[Barrett and van Rossum (2008)]

Saturating model

Make end states "sticky"



Has long decay time, but terrible initial SNR.

$$\lim_{\varepsilon \to 0} A = \sqrt{N}(M-1)/r.$$

Section 4

Envelope memory curve

Bounding finite time SNR

SNR curve:

$$\overline{\text{SNR}}(\tau) = \sqrt{N} \sum_a \frac{\mathcal{I}_a}{1 + r\tau/\tau_a},$$

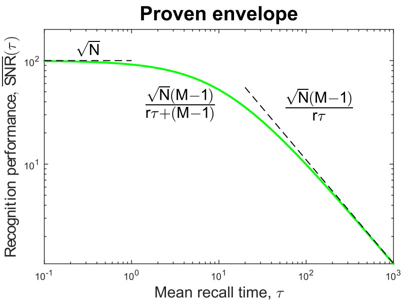
subject to constraints:

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

We can maximise wrt. $\mathcal{I}_a, \tau_a$.

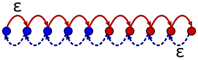
Proven envelope: memory frontier

Upper bound on memory curve at *any* time.



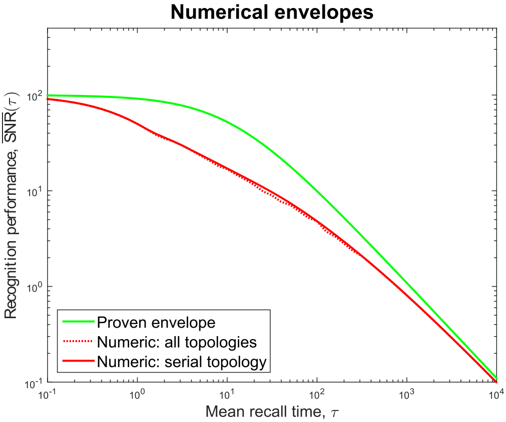
Initial SNR:

Late times:

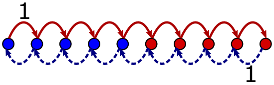


[Lahiri and Ganguli (2013)]

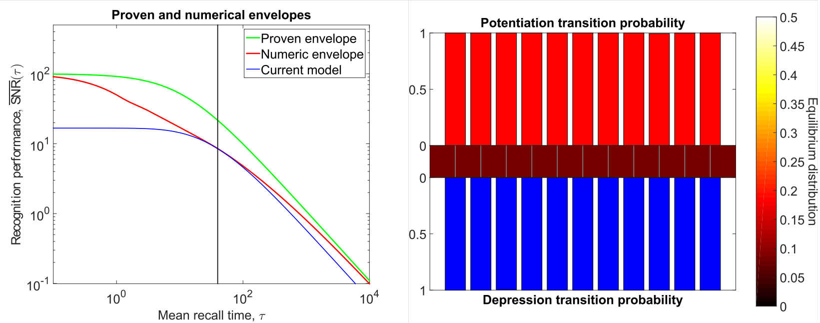
No model can ever go above this envelope. Is it achievable?



Serial topology:



Models that maximise memory for one timescale



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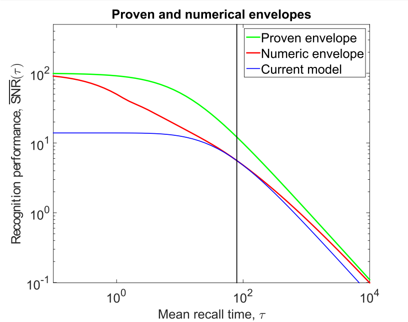

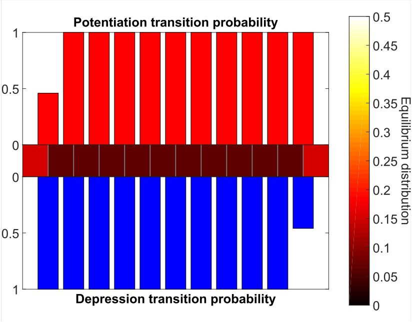

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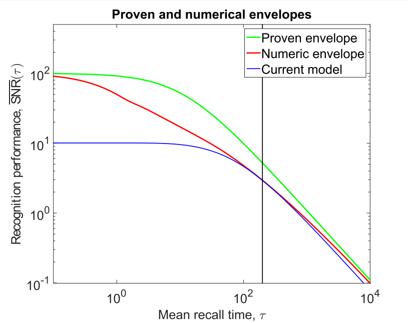

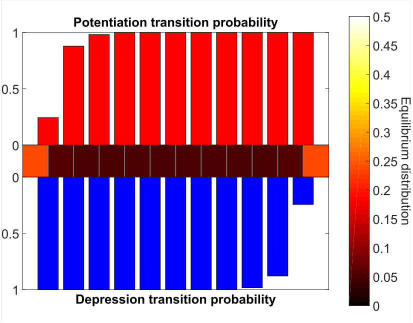

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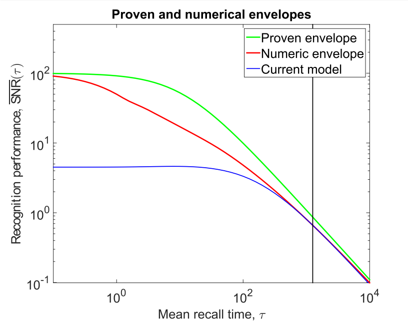

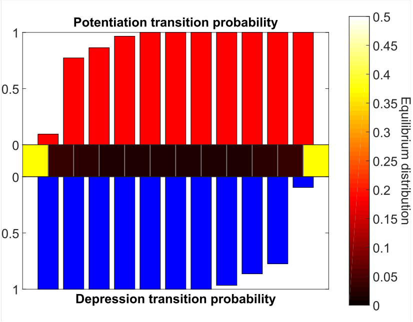

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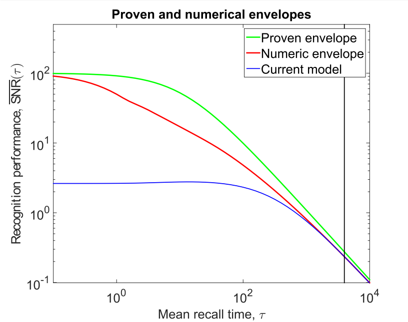

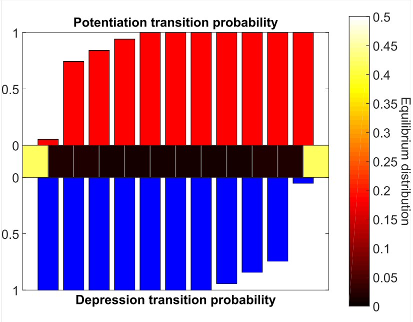

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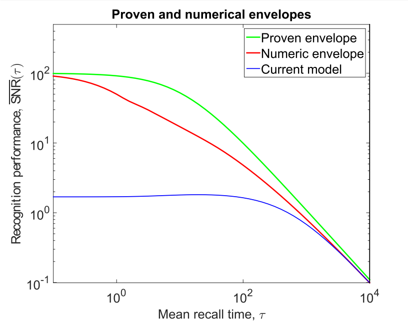

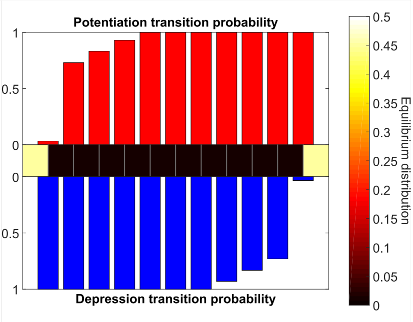

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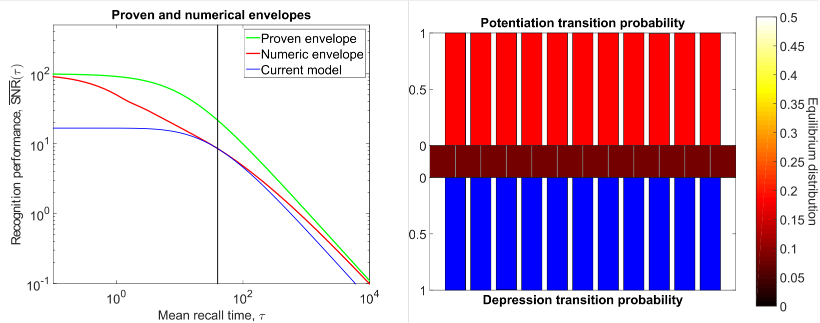

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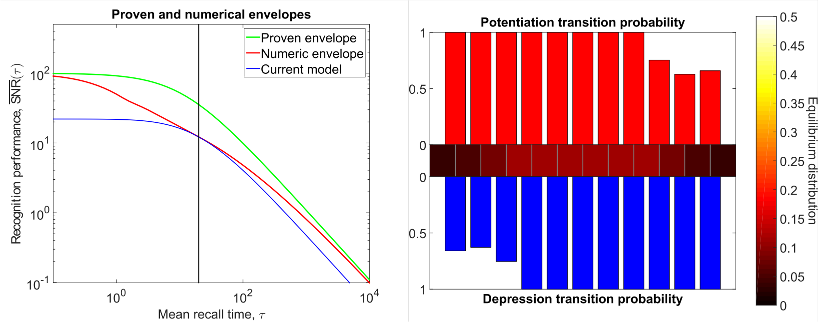

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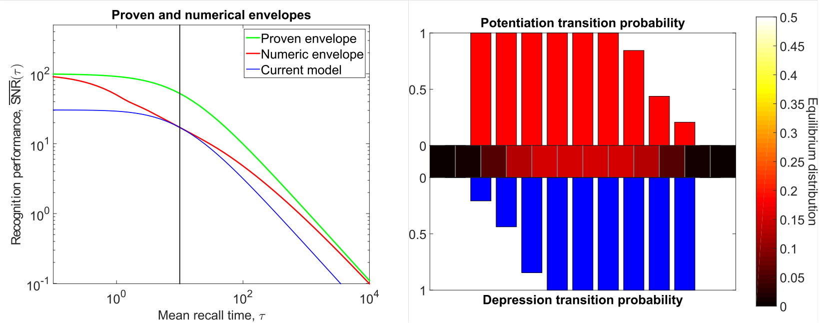

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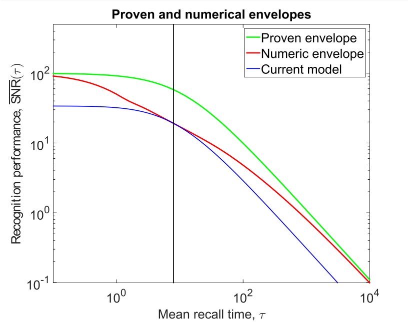

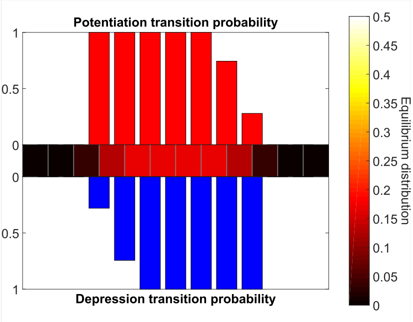

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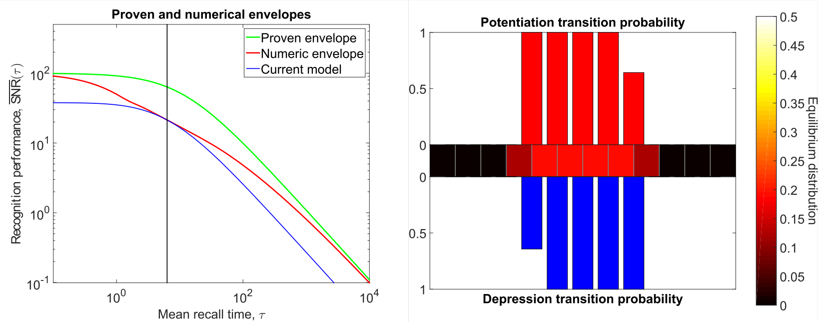

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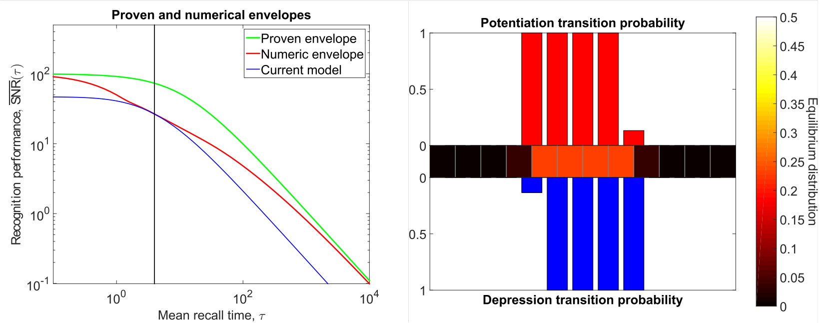

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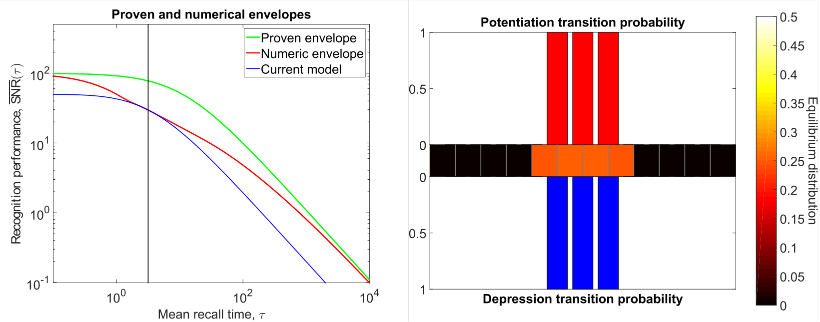

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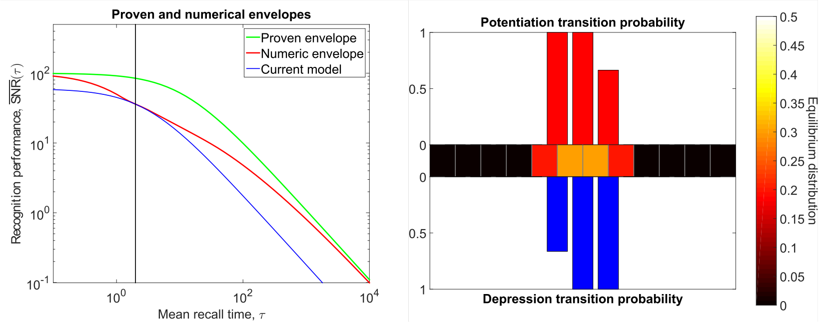

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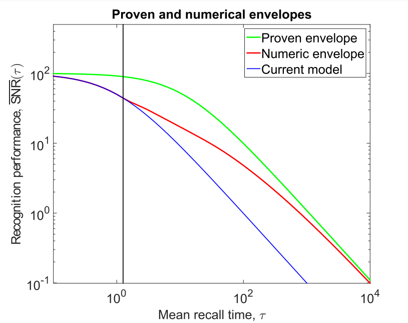

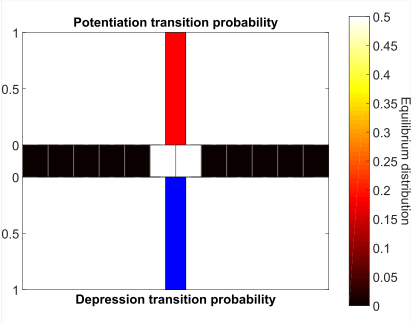

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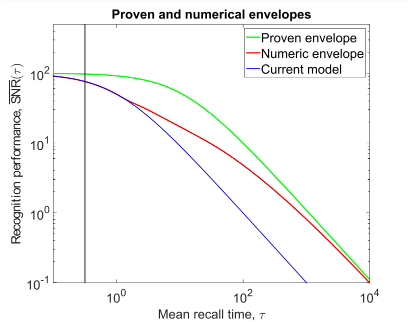

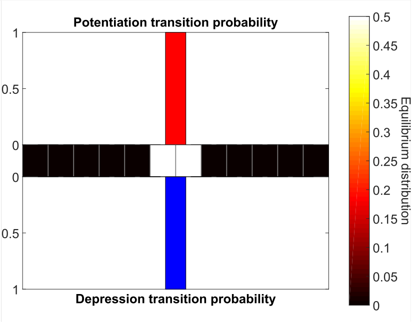

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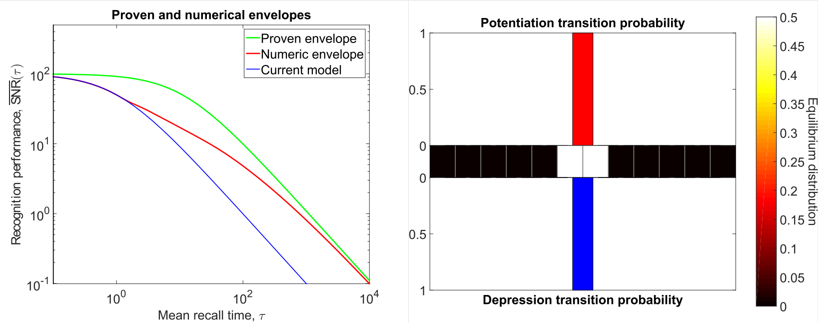
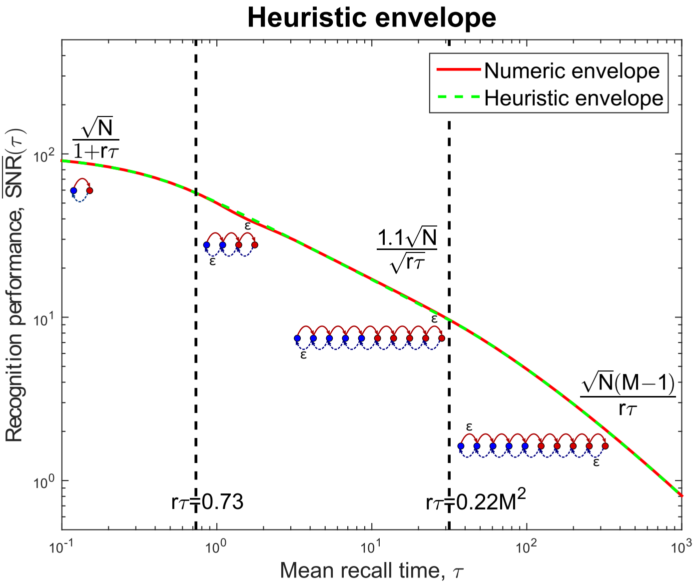


Heuristic envelope



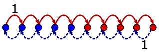
Synaptic structures for different timescales of memory

Real synapses limited by molecular building blocks.
Evolution had larger set of priorities.

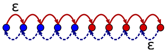
What can we conclude?

Short timescales $\longrightarrow$ Intermediate timescales $\longrightarrow$ Long timescales

$\longrightarrow$



$\longrightarrow$



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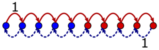
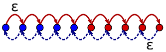


$\longrightarrow$

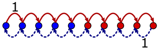
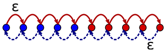


short & wide $\longrightarrow$ long & thin

Synaptic structures for different timescales of memory

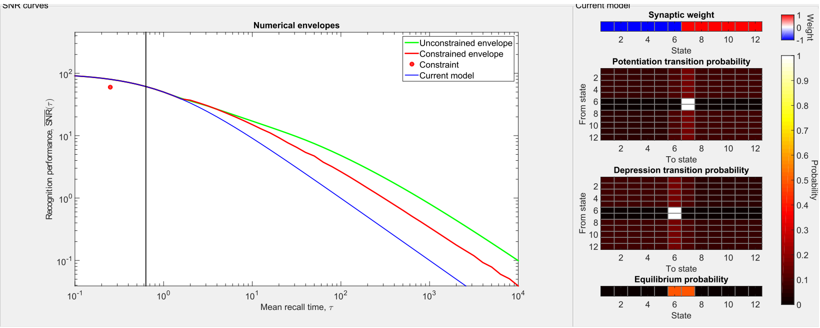
Real synapses limited by molecular building blocks.
Evolution had larger set of priorities.

What can we conclude?

Short timescales	$\longrightarrow$	Intermediate timescales	$\longrightarrow$	Long timescales
	$\longrightarrow$		$\longrightarrow$	
short & wide	$\longrightarrow$	long & thin		
		strong transitions	$\longrightarrow$	weak transitions

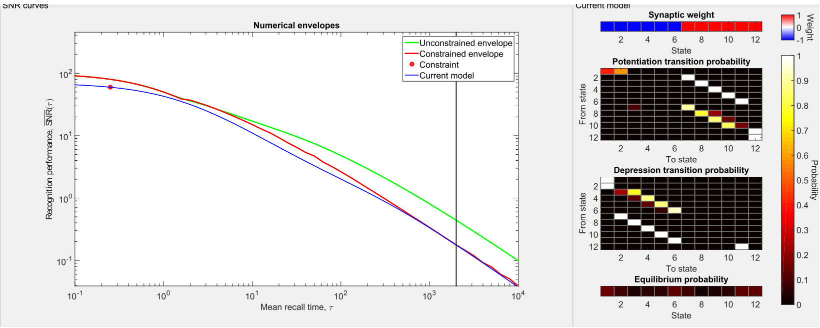
Two-time envelope: early constraint

Maximise $\overline{\mathrm{SNR}}(\tau_1)$ subject to $\overline{\mathrm{SNR}}(\tau_2) \geq S_2$.



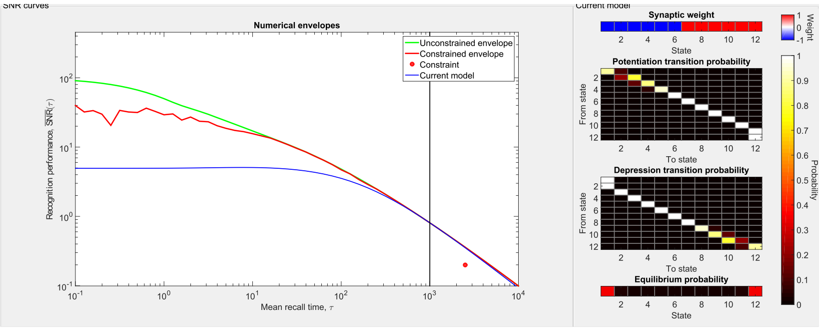
Two-time envelope: early constraint

Maximise $\overline{\text{SNR}}(\tau_1)$ subject to $\overline{\text{SNR}}(\tau_2) \geq S_2$.



Two-time envelope: late constraint

Maximise $\overline{\mathrm{SNR}}(\tau_1)$ subject to $\overline{\mathrm{SNR}}(\tau_2) \geq S_2$.



Two-time envelope: late constraint

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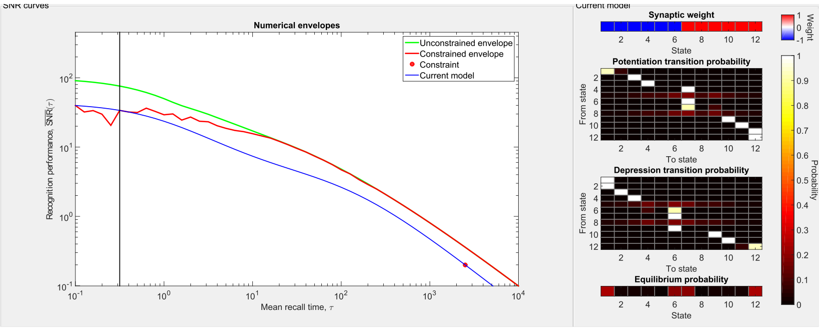


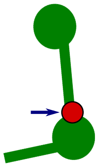
Section 5

Experimental tests?

Proposed Experimental design

Subject a synapse to a sequence of candidate plasticity events.

Observe the changes in synaptic efficacy.



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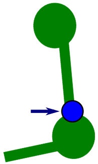

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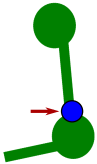

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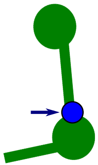

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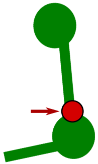

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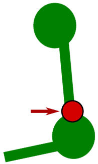

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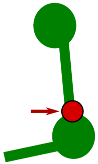


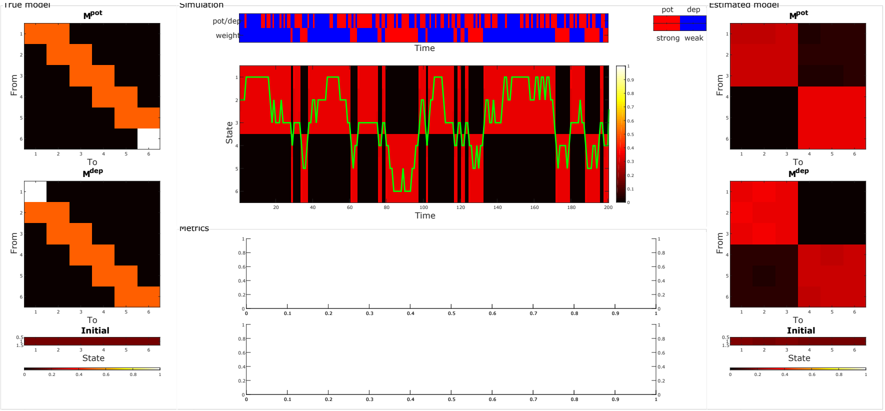
EM algorithms:
Sequence of hidden states → estimate transition probabilities
Transition probabilities → estimate sequence of hidden states

[Baum et al. (1970), Rabiner and Juang (1993), Dempster et al. (2007)]

Spectral algorithms:
Compute $P(w_1), P(w_1, w_2), P(w_1, w_2, w_3), \ldots$ from data,
from model.

[Hsu et al. (2008)]

Fitting algorithm



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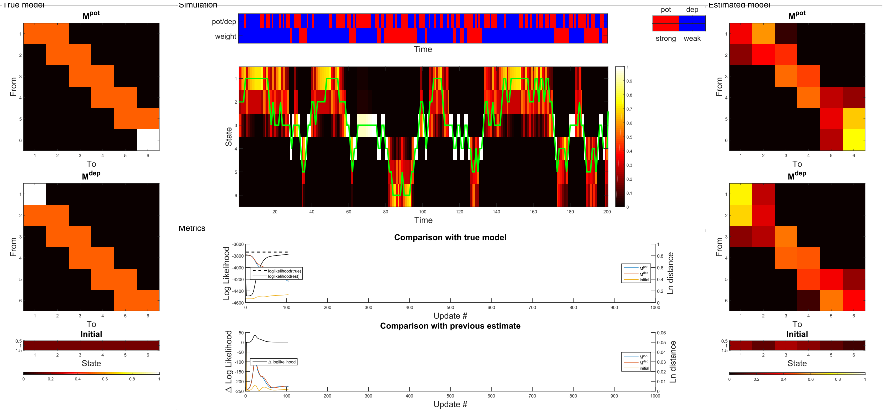

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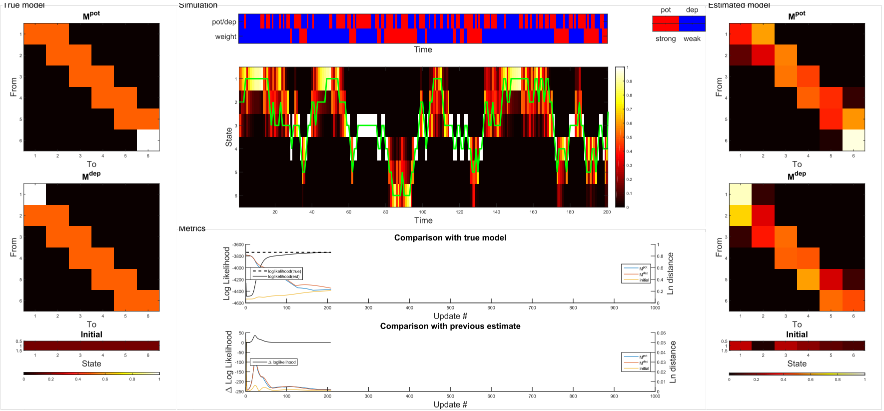

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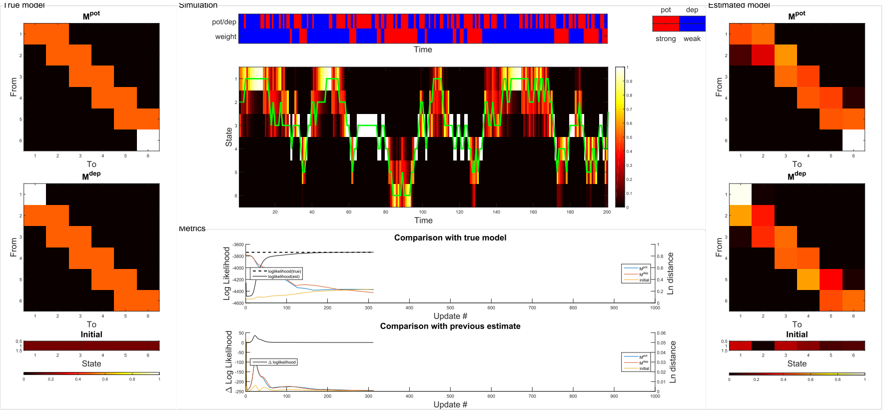

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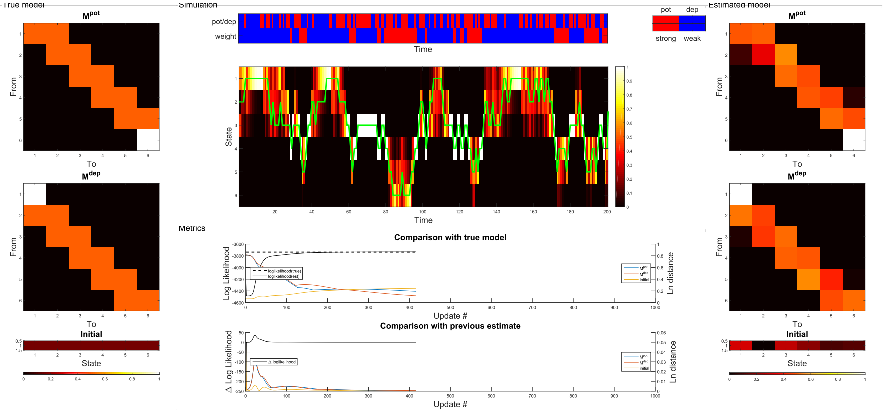

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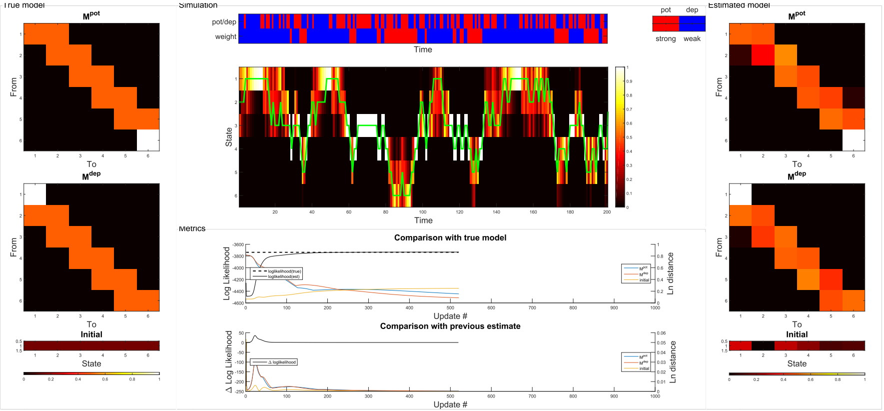

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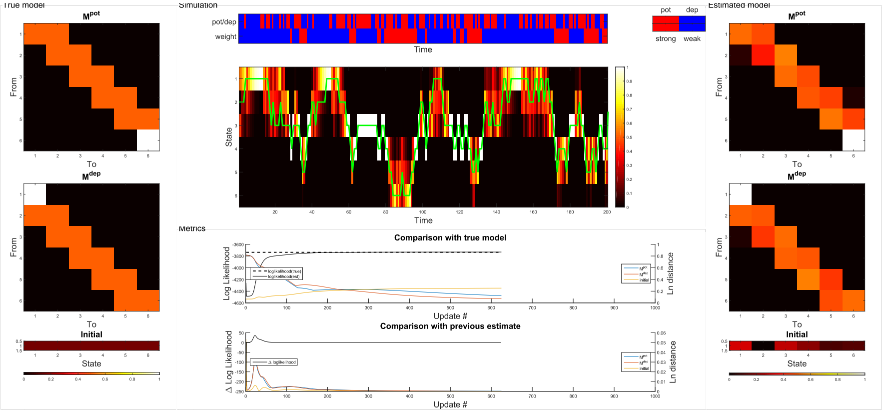

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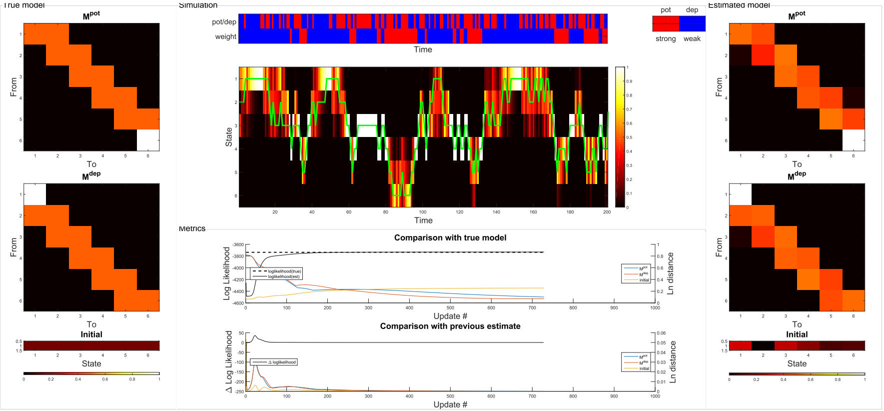

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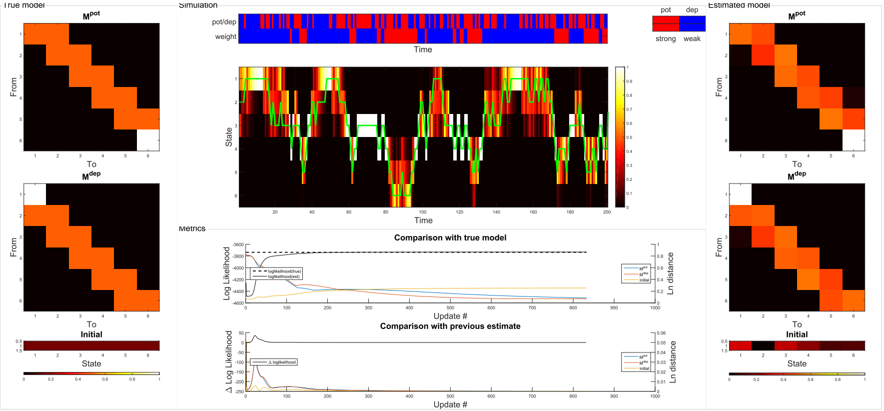

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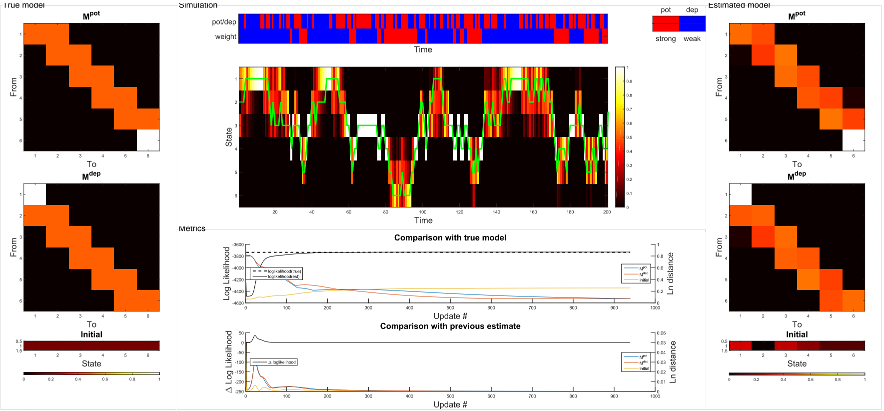

Experimental problems

- Need single synapses.
- Need long sequences of plasticity events.
- Need to control types of candidate plasticity events.
- Need to measure synaptic efficacies.

When we patch the postsynaptic neuron $\rightarrow$ Ca washout.

Summary

- We have formulated a general theory of learning and memory with complex synapses.
- The area under the memory curve of any model $<$ linear chain with same equilibrium 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 $> \mathcal{O}(M)$.
- We understood which types of synaptic structure are useful for storing memories for different timescales.
- Gap between envelope and what we can achieve at early times?
- Trade-off between SNR at different times?

Acknowledgements

Thanks to:

- Surya Ganguli
- Stefano Fusi
- Marcus Benna
- David Sussillo
- Jascha Sohl-Dickstein

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Techinical detail: ordering states

Let $\mathbf{T}_{ij}$ = mean first passage time from state i to state j. Then:

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

is independent of the initial state i (Kemeney's constant).

[Kemeny and Snell (1960)]

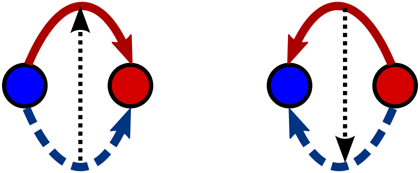
We define:

$$\eta^+_i = \sum_{j \in \text{strong}} \mathbf{T}_{ij} \mathbf{p}^\infty_j, \qquad \eta^-_i = \sum_{j \in \text{weak}} \mathbf{T}_{ij} \mathbf{p}^\infty_j.$$

They can be used to arrange the states in an order (increasing η^- or decreasing η^+). back

Technical detail: upper/lower triangular

With states in order:



Endpoint: potentiation goes right, depression goes left.

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