

Learning and memory with complex synaptic plasticity

based on work with Surya Ganguli

Subhaneil Lahiri

Stanford University, Applied Physics

November 11, 2015

Introduction

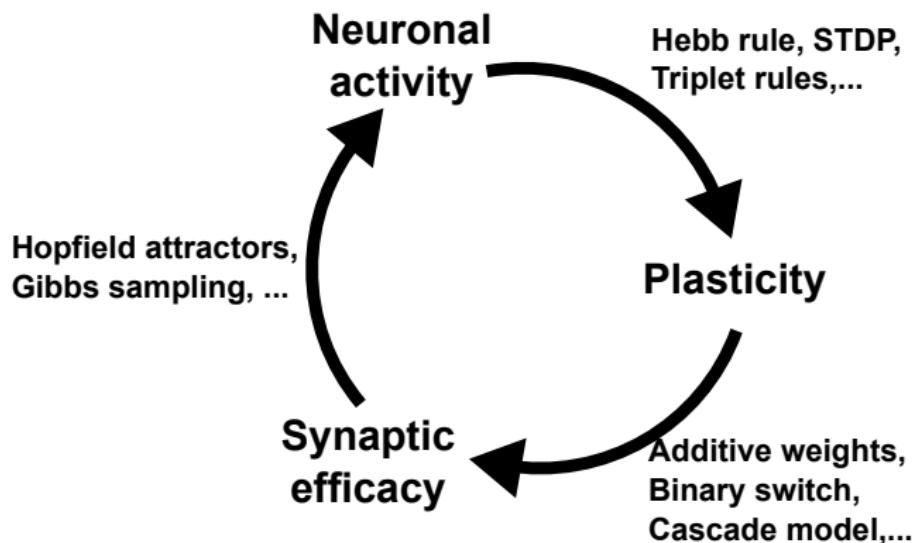
We often model synaptic plasticity as the change of a single number (synaptic weight). In reality, there is a complex dynamical system inside a synapse.

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

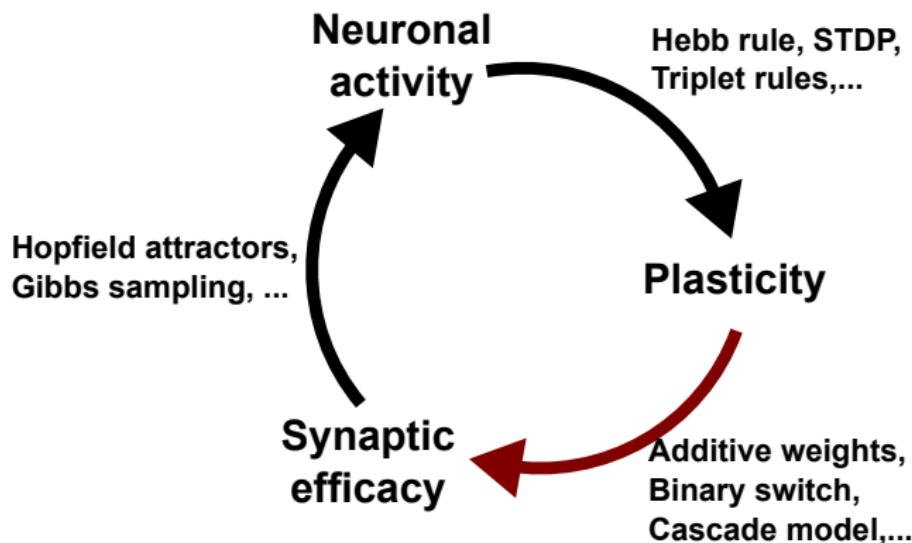
We will study the entire space of a broad class of models of complex synapses to find upper bounds on their performance.

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

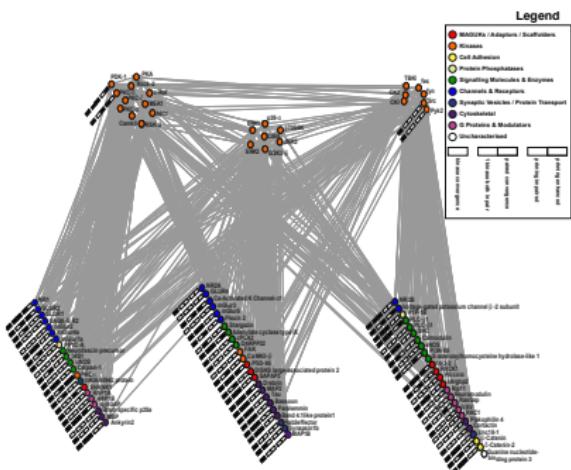
Synaptic learning and memory



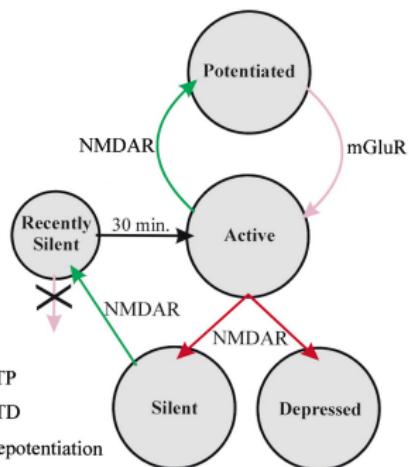
Synaptic learning and memory



Synapses are complex



[Coba et al. (2009)]

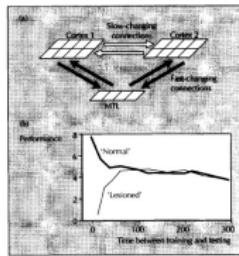


[Montgomery and Madison (2002)]

There is a complex, dynamic system underlying synaptic plasticity.

Timescales of memory

Memories stored in different places for different timescales

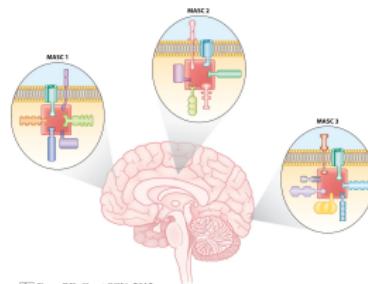


[Squire and Alvarez (1995)]

cf. Cerebellar cortex vs. cerebellar nuclei.

[Krakauer and Shadmehr (2006)]

Different synapses have different molecular structures.



Emes RD, Grant SGN. 2012.
Annu. Rev. Neurosci. 35:111–31

[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

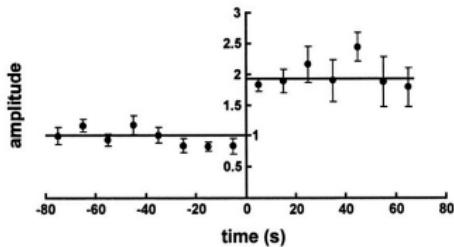
Why complex synapses?

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:
⇒ 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

Learning Remembering

Very plastic



Trade-off between learning and remembering

Learning Remembering

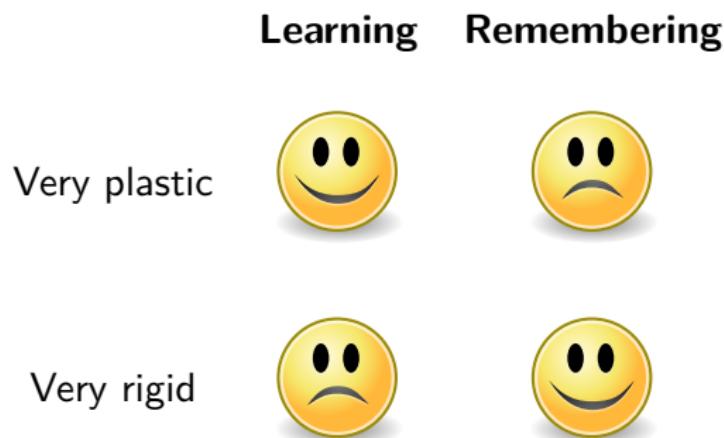
Very plastic



Very rigid



Trade-off between learning and remembering



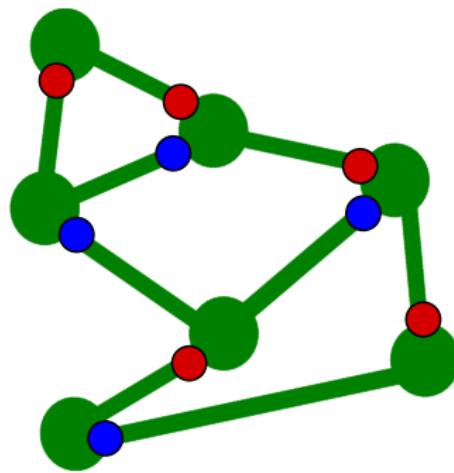
Circumvent tradeoff: go beyond model of synapse as single number.

Section 2

Modelling synaptic memory

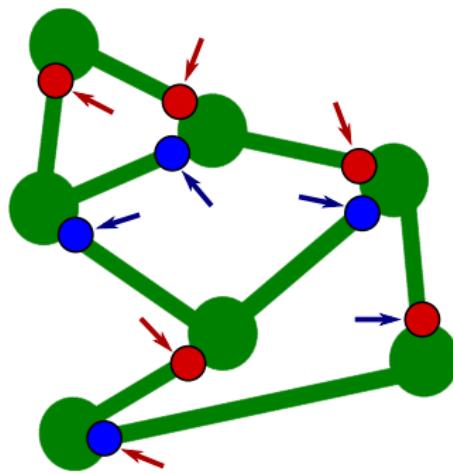
Recognition memory

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



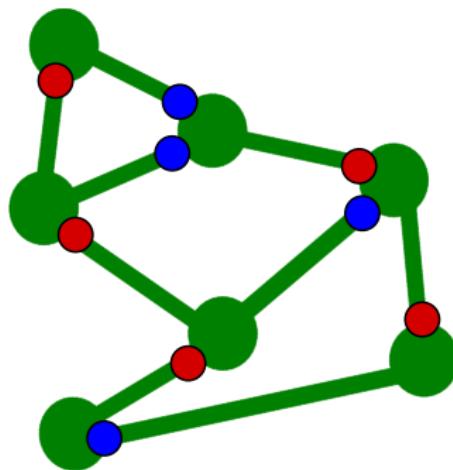
Recognition memory

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



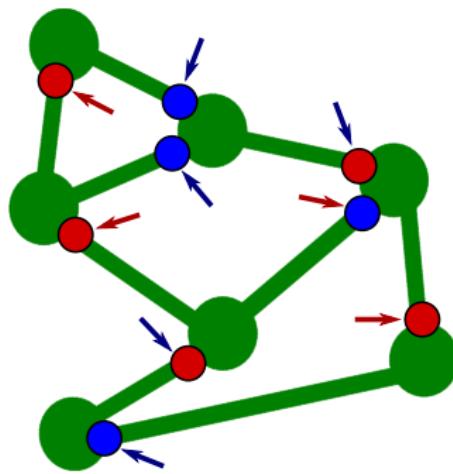
Recognition memory

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



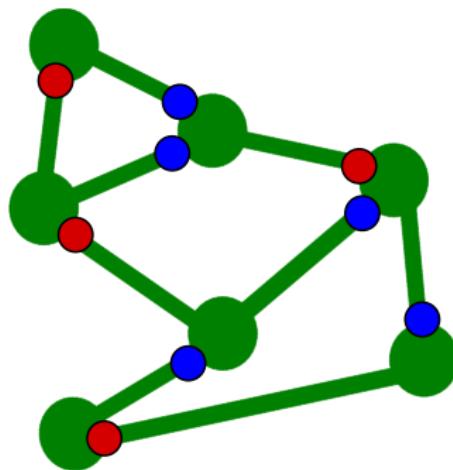
Recognition memory

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



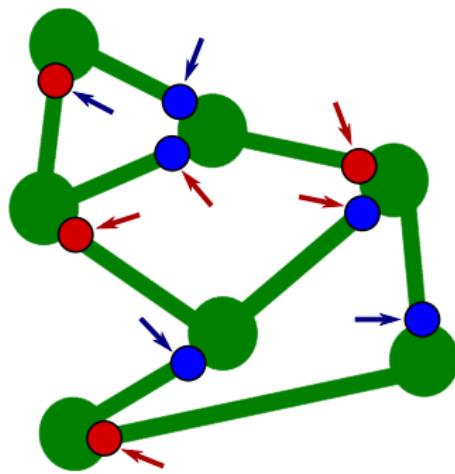
Recognition memory

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



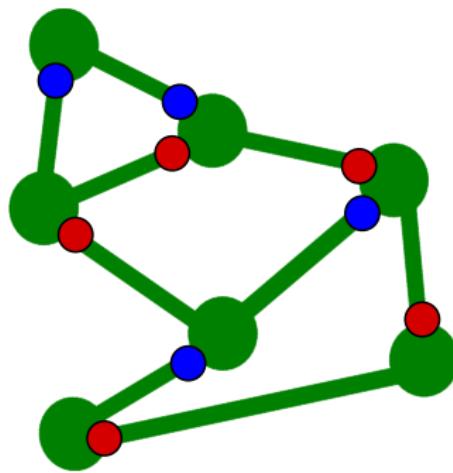
Recognition memory

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



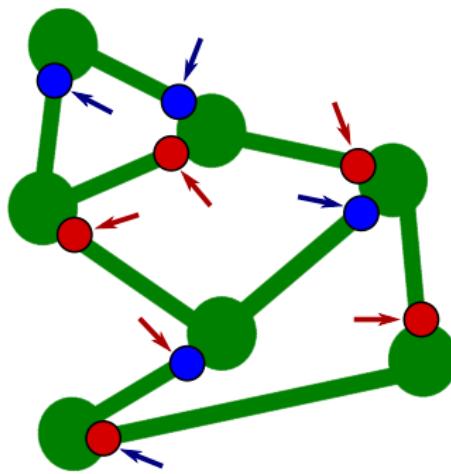
Recognition memory

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



Recognition memory

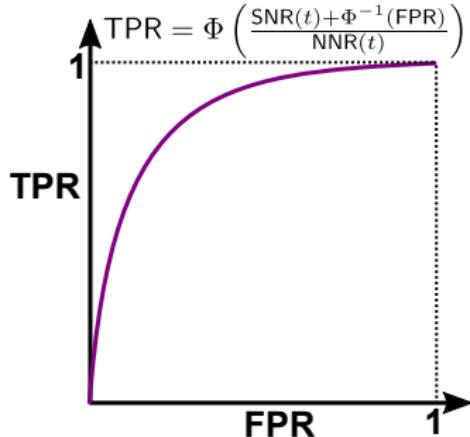
Synapses given a sequence of patterns (pot & dep) to store



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

Quantifying memory quality

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



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

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

Averaging over recall times

Look at:

$$\overline{\text{SNR}}(\tau) = \langle \text{SNR}(t) \rangle_{P(t|\tau)}, \quad P(t|\tau) = \frac{e^{-t/\tau}}{\tau}.$$

τ = mean recall time.

Like a “running average”:

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

Different brain regions \rightarrow different τ .

Models of complex synaptic dynamics

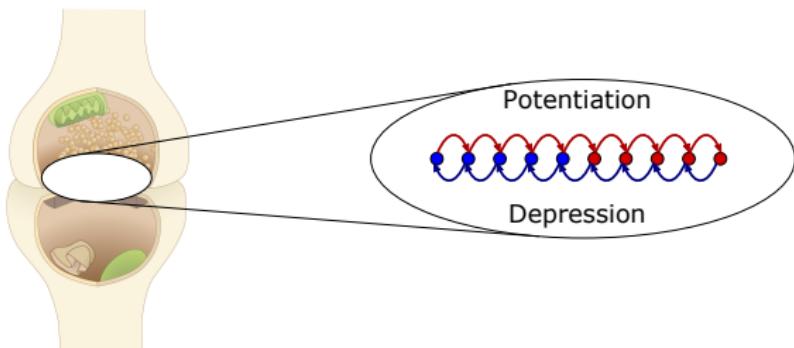


Models of complex synaptic dynamics

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

weak

strong



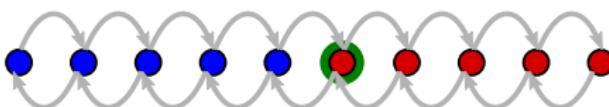
States: #AMPAR, #NMDAR, NMDAR subunit composition,
CaMK II autophosphorylation, activating PKC, p38 MAPK,...

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

Models of complex synaptic dynamics

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

Potentiation event

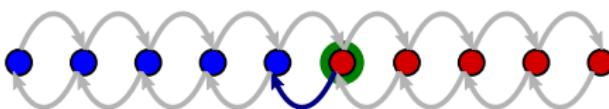


Depression event

Models of complex synaptic dynamics

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

Potentiation event

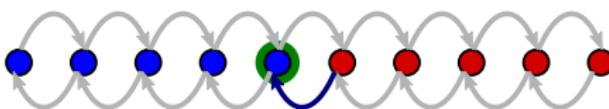


Depression event

Models of complex synaptic dynamics

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

Potentiation event

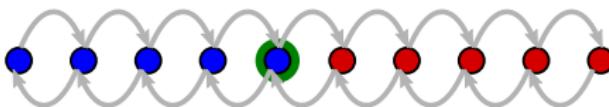


Depression event

Models of complex synaptic dynamics

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

Potentiation event

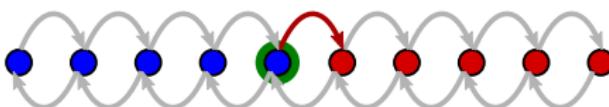


Depression event

Models of complex synaptic dynamics

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

Potentiation event

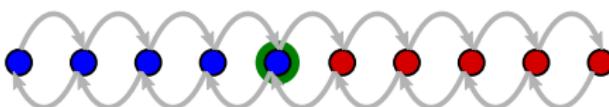


Depression event

Models of complex synaptic dynamics

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

Potentiation event

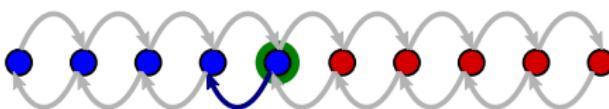


Depression event

Models of complex synaptic dynamics

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

Potentiation event



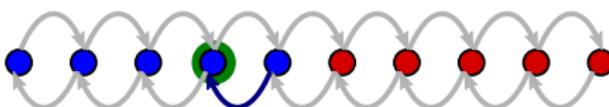
Depression event

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

Models of complex synaptic dynamics

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

Potentiation event



Depression event

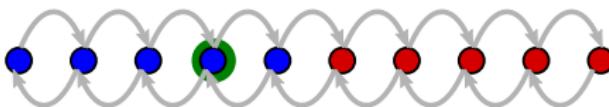
Metaplasticity: change propensity for plasticity
(independent of change in synaptic weight).

Models of complex synaptic dynamics

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

● weak
● strong

Potentiation event



Depression event

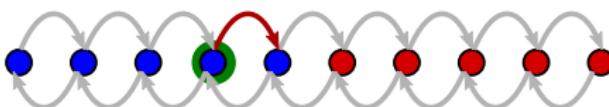
Metaplasticity: change propensity for plasticity
(independent of change in synaptic weight).

Models of complex synaptic dynamics

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

● weak
● strong

Potentiation event



Depression event

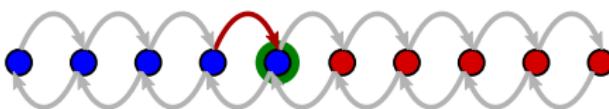
Metaplasticity: change propensity for plasticity
(independent of change in synaptic weight).

Models of complex synaptic dynamics

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

● weak
● strong

Potentiation event



Depression event

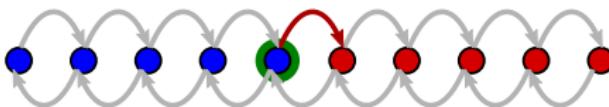
Metaplasticity: change propensity for plasticity
(independent of change in synaptic weight).

Models of complex synaptic dynamics

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

● weak
● strong

Potentiation event



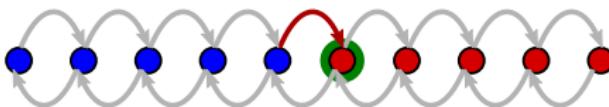
Depression event

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

Models of complex synaptic dynamics

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

Potentiation event



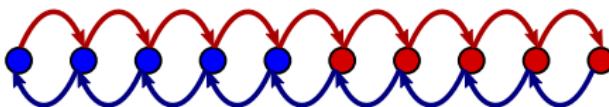
Depression event

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

Models of complex synaptic dynamics

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

Potentiation

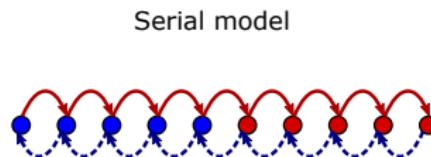
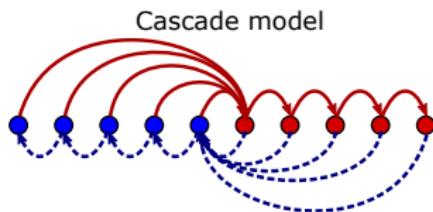


Depression

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

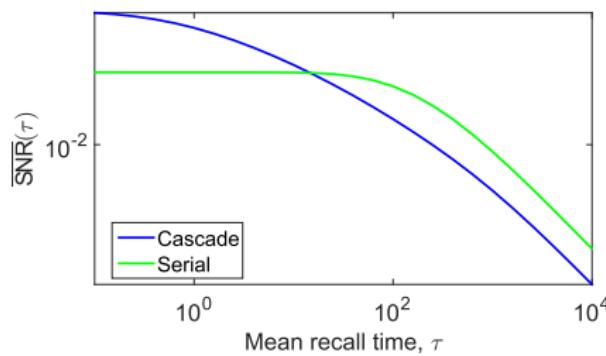
Example models

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

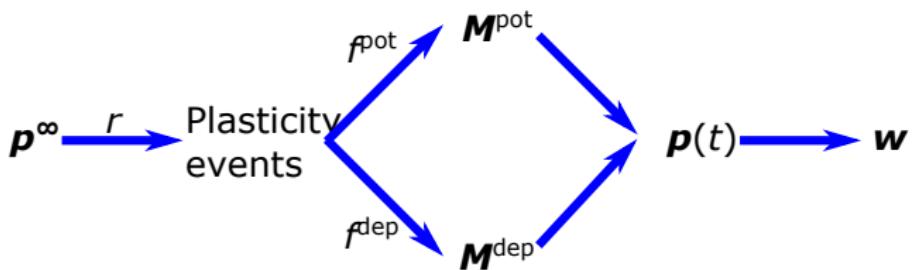


Questions

- Can we understand the space of *all possible* synaptic models?
- How does structure (topology) of model → 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.



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

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

Constraints

Memory curve given by

$$\text{SNR}(t) = \sqrt{N} (2f^{\text{pot}} f^{\text{dep}}) \mathbf{p}^\infty (\mathbf{M}^{\text{pot}} - \mathbf{M}^{\text{dep}}) \exp(rt\mathbf{W}^F) \mathbf{w},$$

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

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

Eigenmode decomposition:

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

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

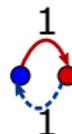
Section 3

Upper bounds

Upper bounds on measures of memory

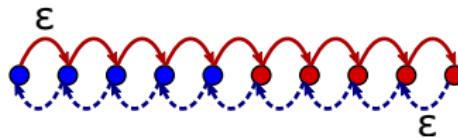
Initial SNR:

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



Area under curve:

$$\mathcal{A} = \int_0^\infty dt \text{ SNR}(t) = \lim_{\tau \rightarrow \infty} \tau \overline{\text{SNR}}(\tau) \leq \sqrt{N}(M - 1)/r.$$



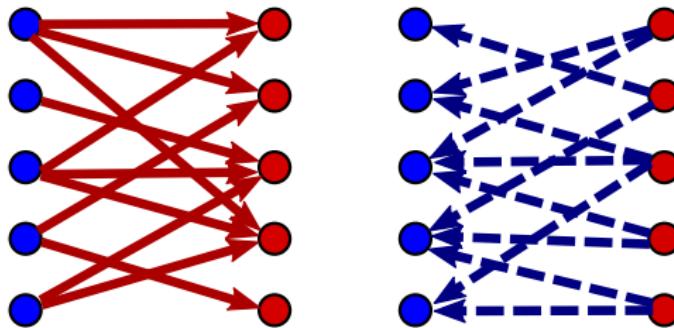
[Lahiri and Ganguli (2013)]

Initial SNR as flux

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

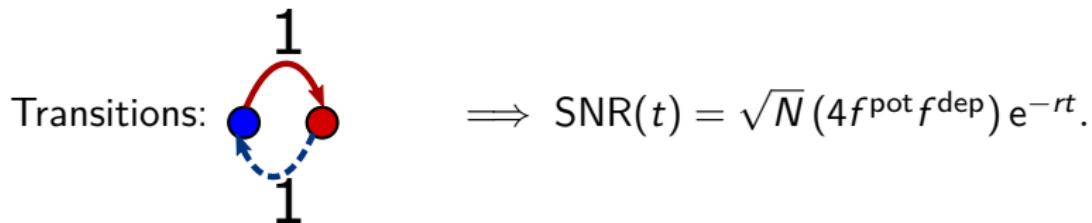
$$\text{SNR}(0) \leq \frac{4\sqrt{N}}{r} \Phi_{-+}.$$

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



Two-state model

Two-state model equivalent to previous slide:



Maximal initial SNR:

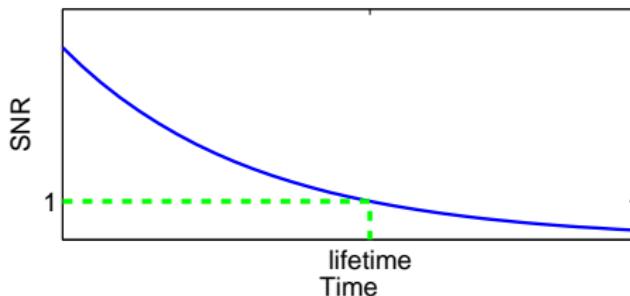
$$\text{SNR}(0) \leq \sqrt{N}.$$

Area under memory curve

$$\mathcal{A} = \int_0^\infty dt \text{ SNR}(t), \quad \overline{\text{SNR}}(\tau) \rightarrow \frac{\mathcal{A}}{\tau} \quad \text{as} \quad \tau \rightarrow \infty.$$

Area bounds memory lifetime:

$$\begin{aligned}\text{SNR(lifetime)} &= 1 \\ \implies \text{lifetime} &< \mathcal{A}.\end{aligned}$$



This area has an upper bound:

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

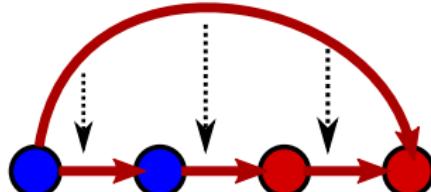
Saturated by a model with linear chain topology.

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

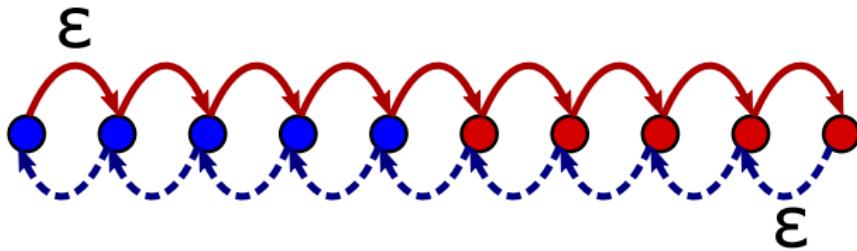
$$A = \frac{2\sqrt{N}}{r} \sum_k \mathbf{p}_k^\infty |k - \langle k \rangle|.$$

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.

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

Section 4

Envelope memory curve

Bounding finite time SNR

SNR curve:

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

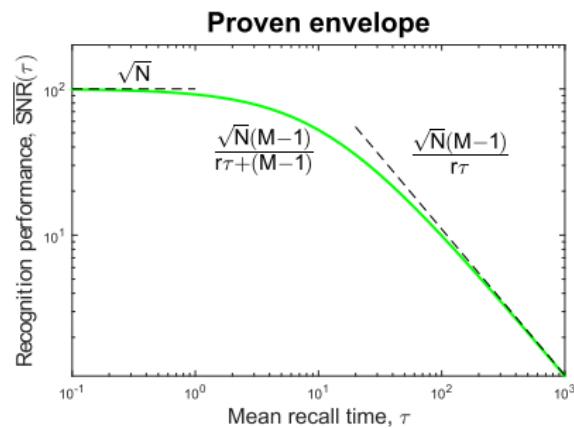
subject to constraints:

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

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

Proven envelope: memory frontier

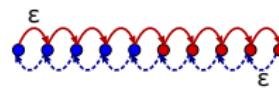
Upper bound on memory curve at *any* time.



Initial SNR:



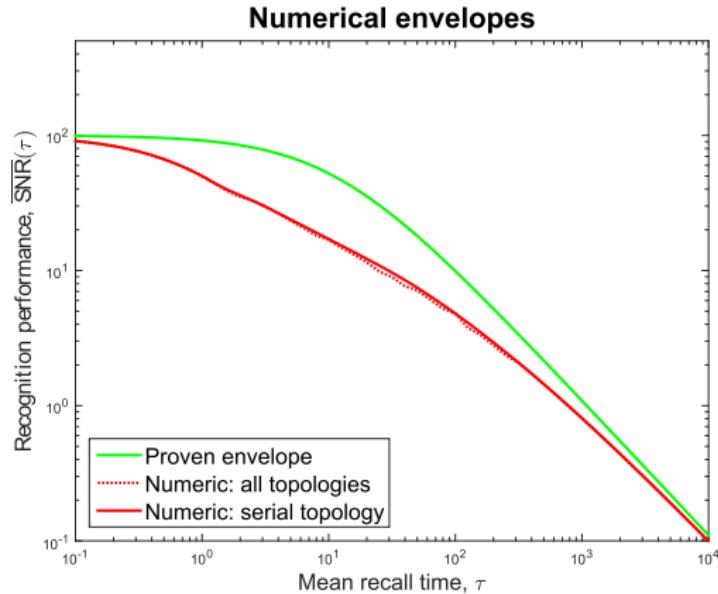
Late times:



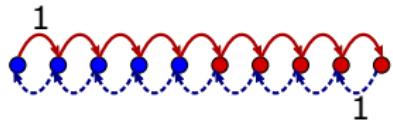
[Lahiri and Ganguli (2013)]

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

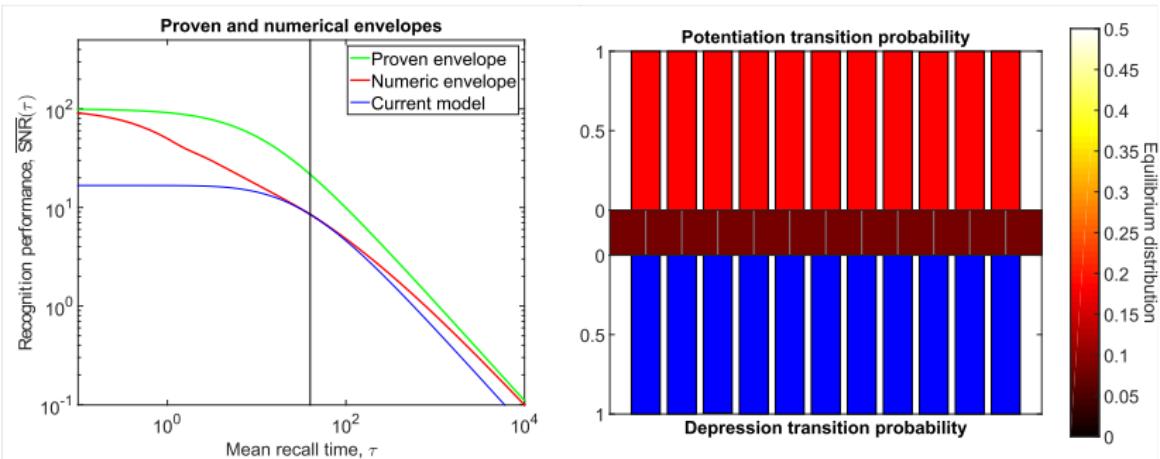
Achievable envelope



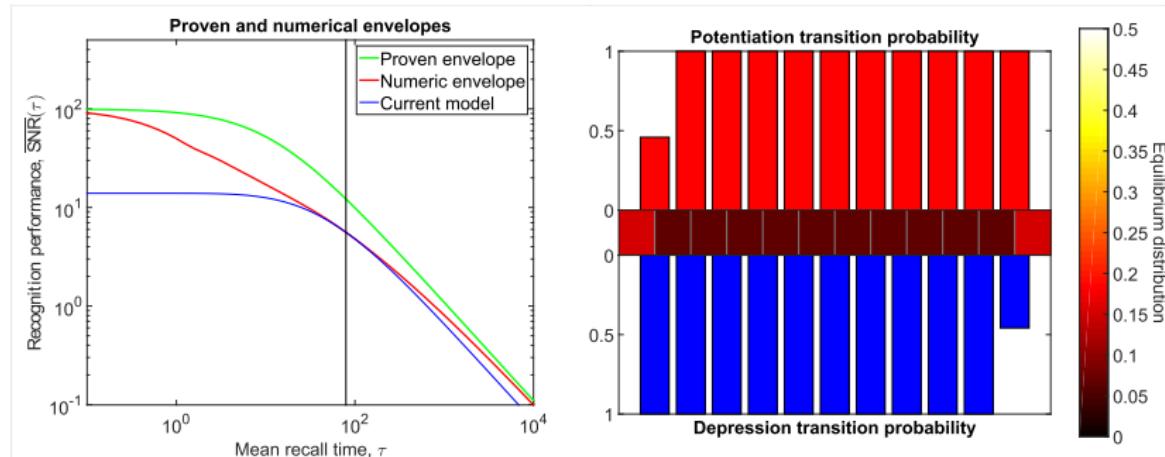
Serial topology:



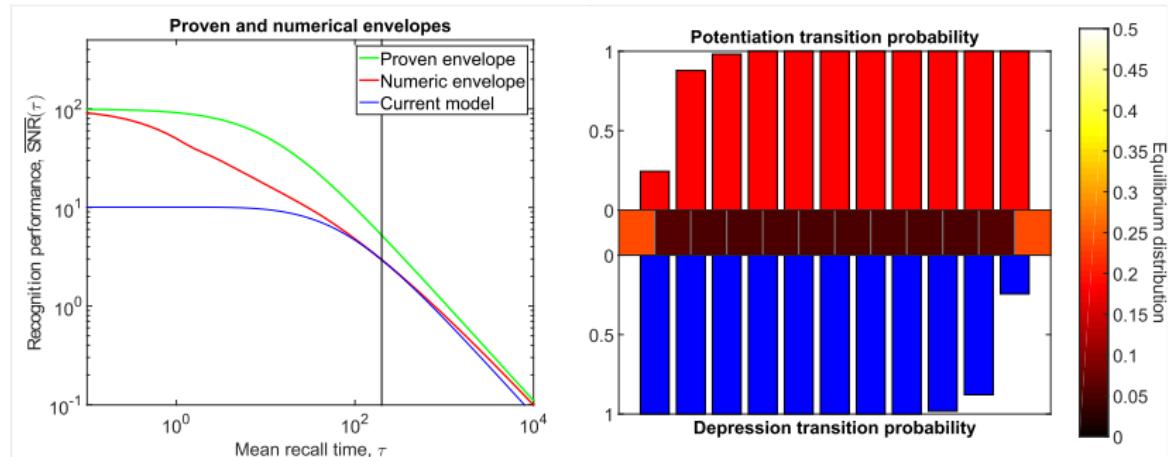
Models that maximise memory for one timescale



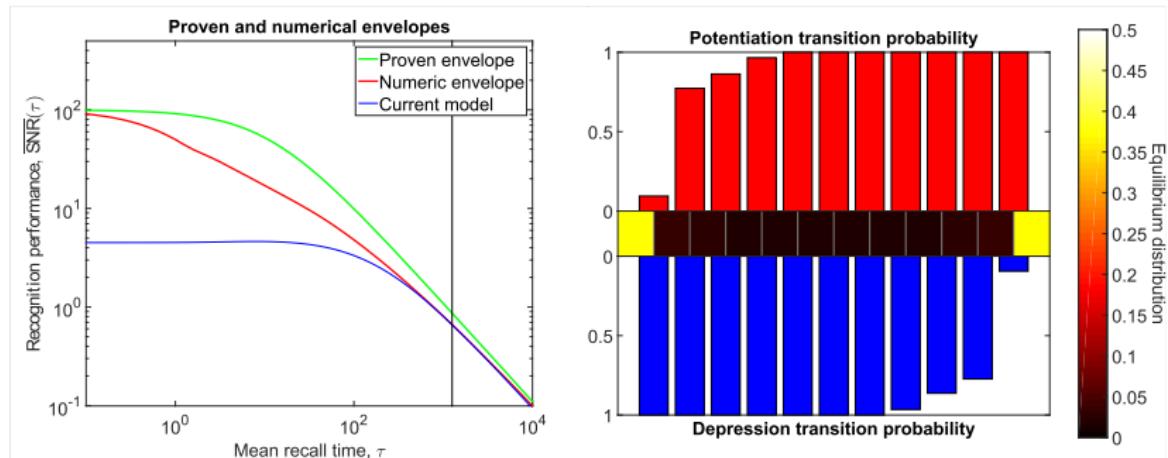
Models that maximise memory for one timescale



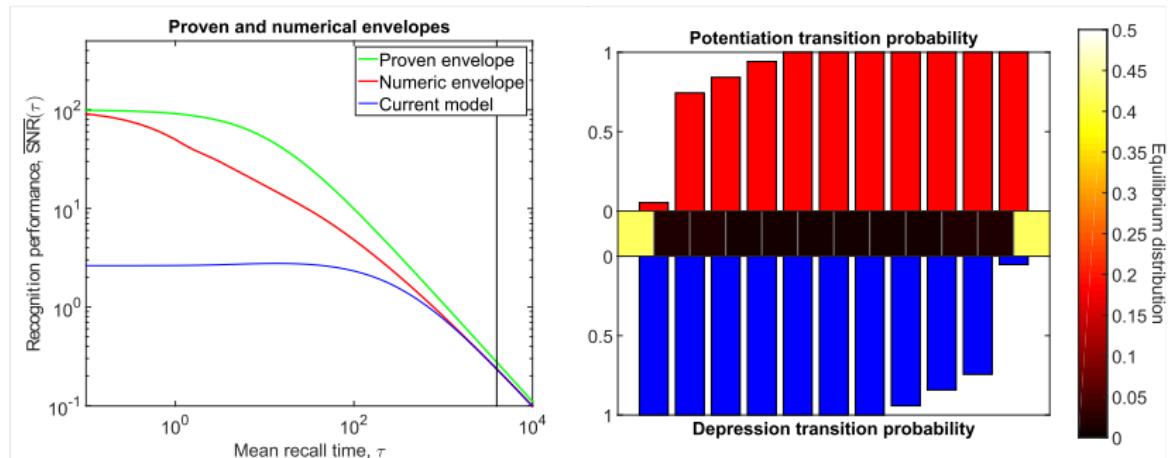
Models that maximise memory for one timescale



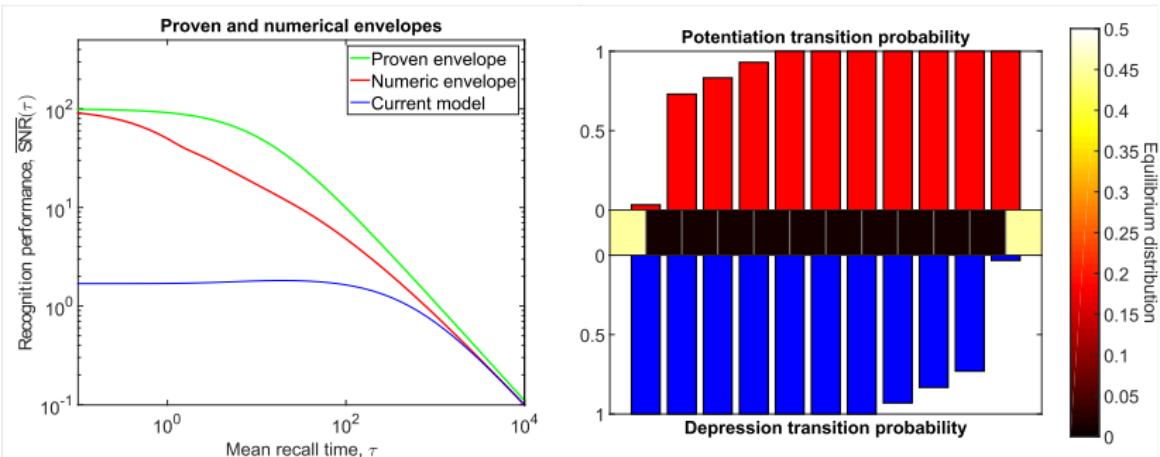
Models that maximise memory for one timescale



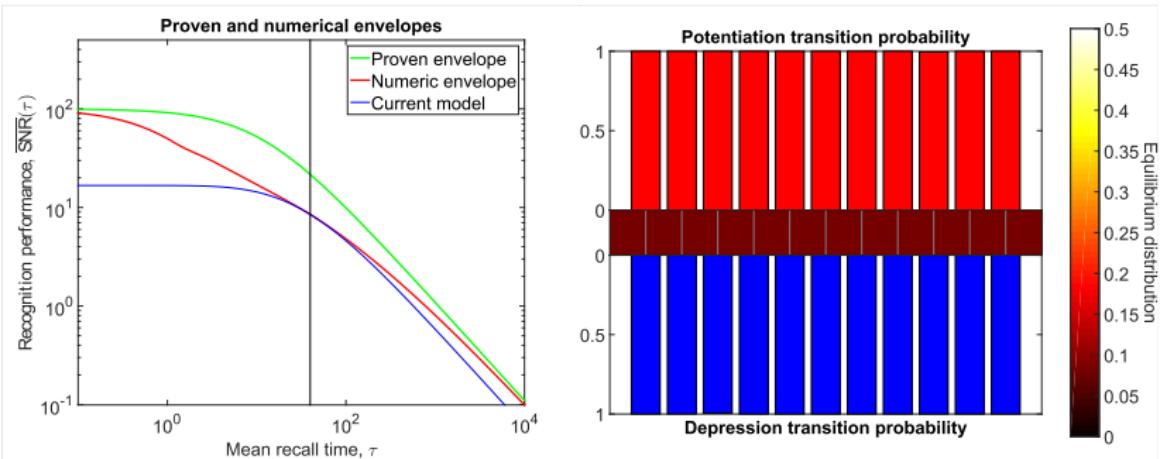
Models that maximise memory for one timescale



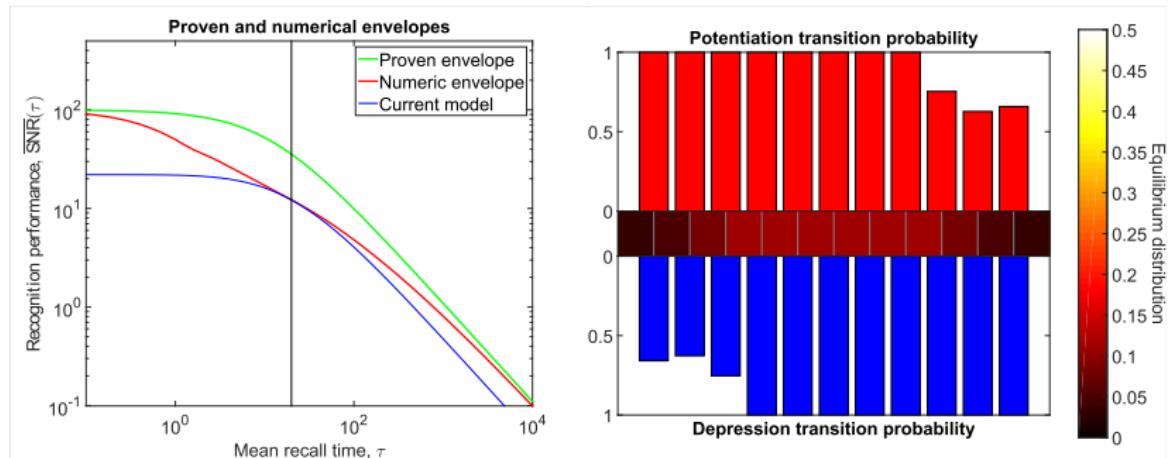
Models that maximise memory for one timescale



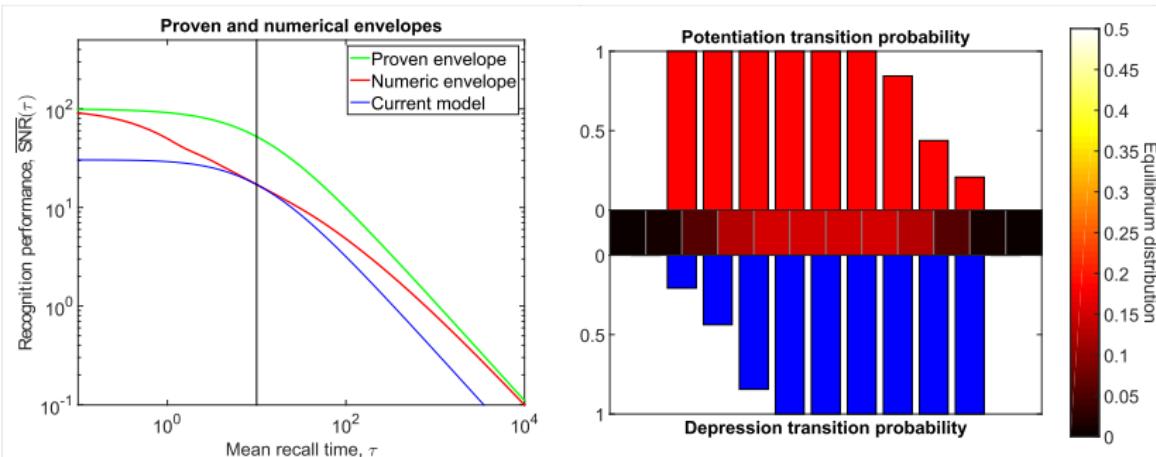
Models that maximise memory for one timescale



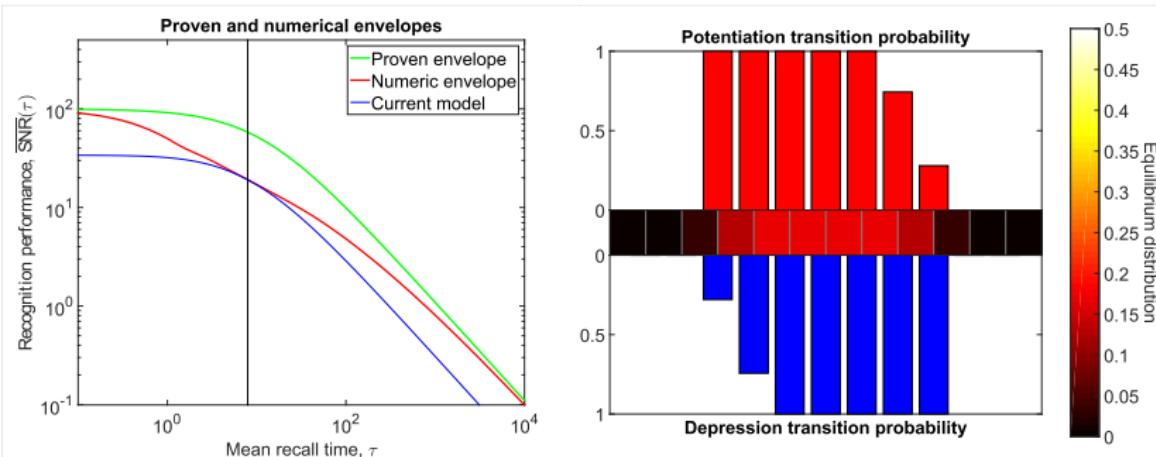
Models that maximise memory for one timescale



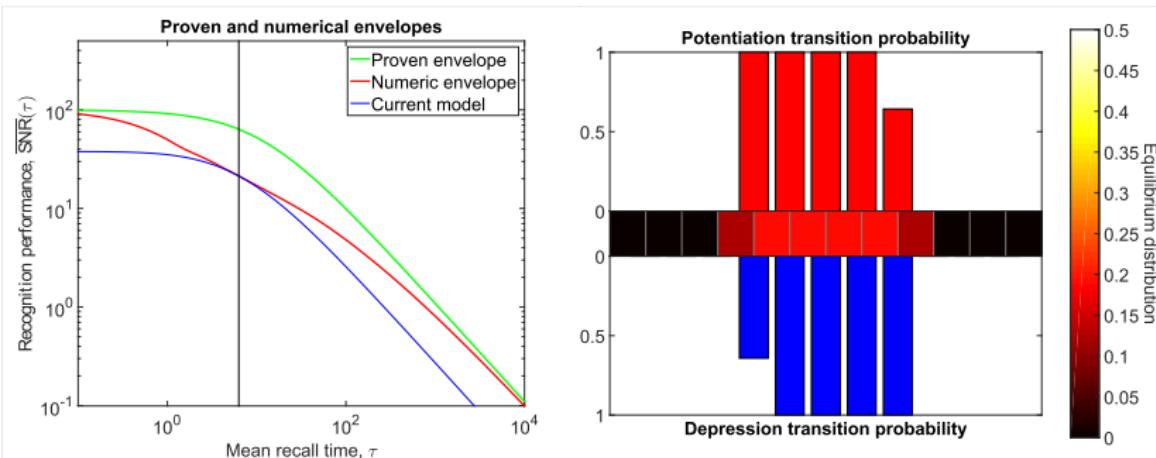
Models that maximise memory for one timescale



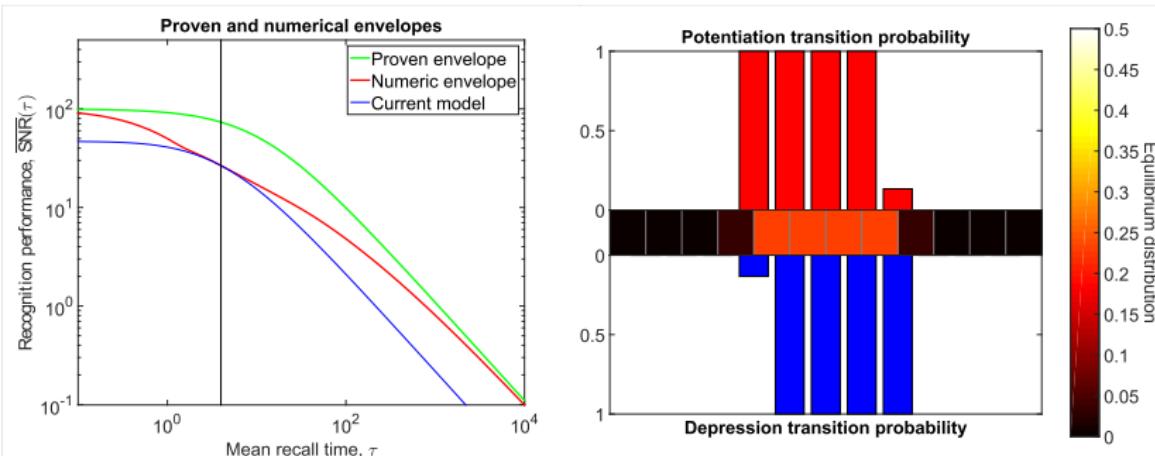
Models that maximise memory for one timescale



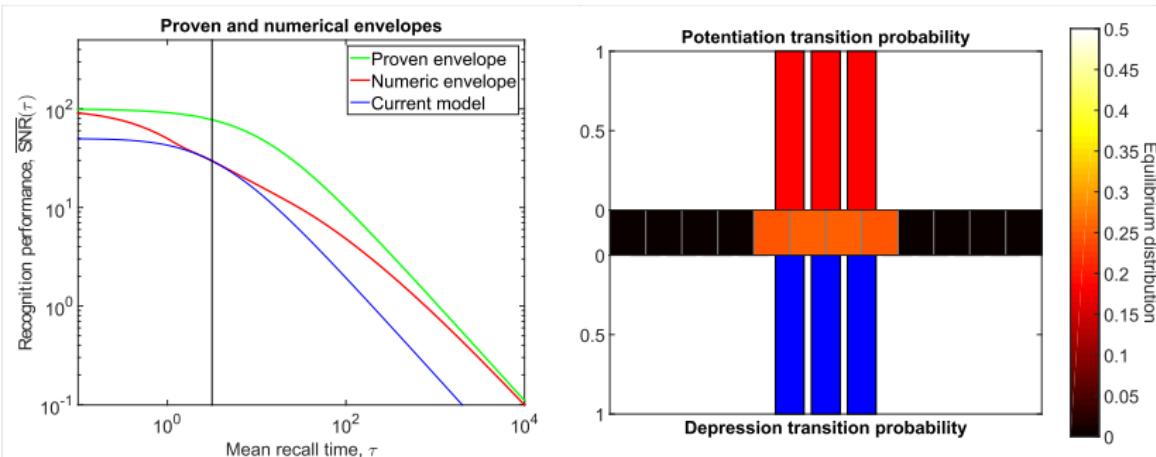
Models that maximise memory for one timescale



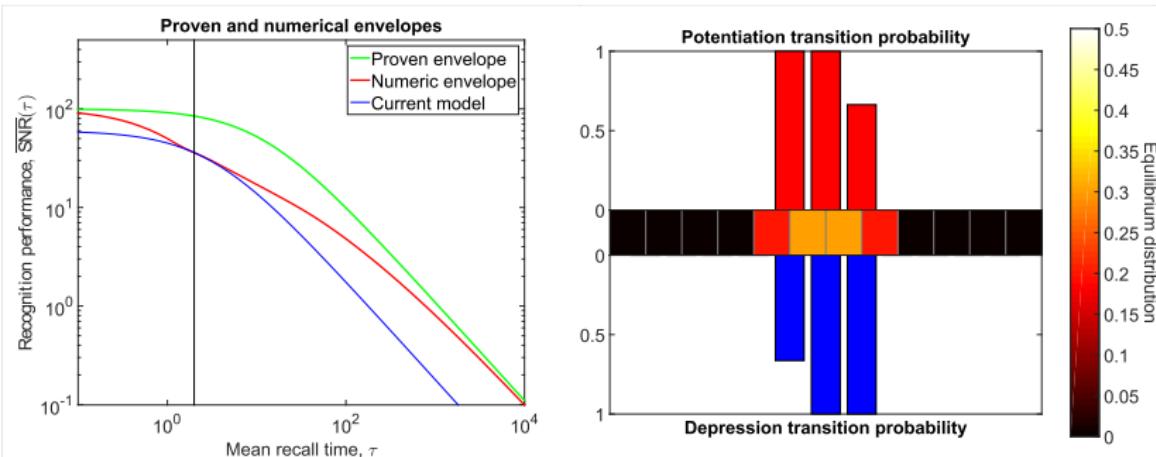
Models that maximise memory for one timescale



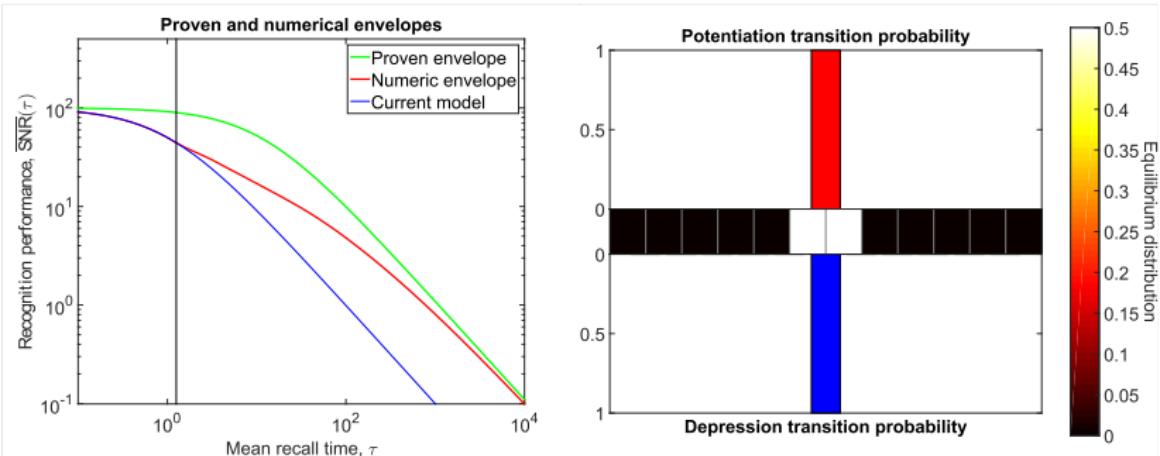
Models that maximise memory for one timescale



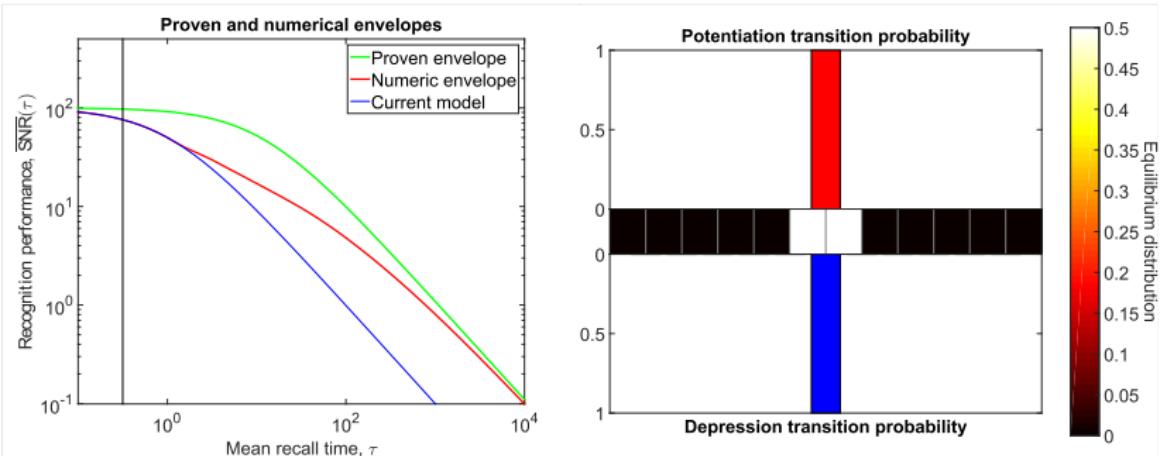
Models that maximise memory for one timescale



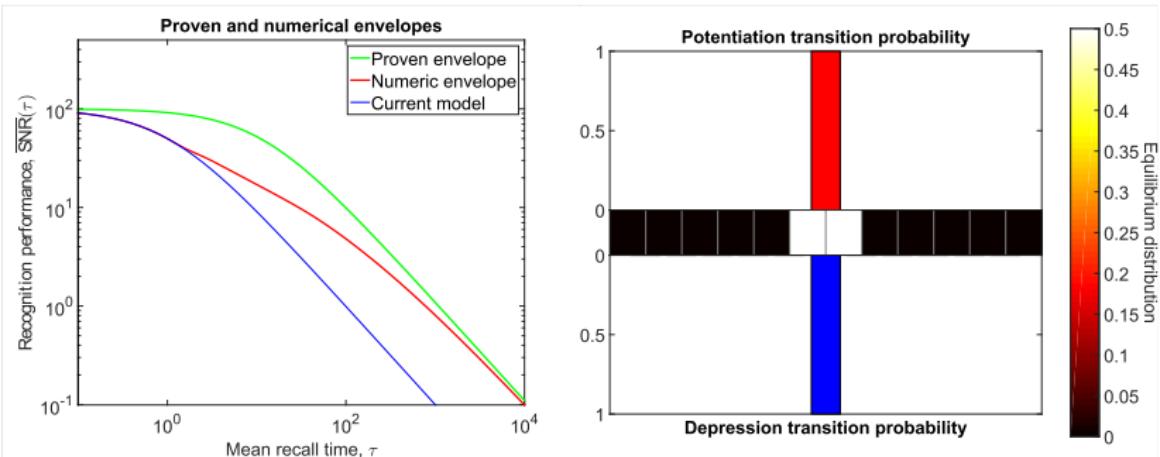
Models that maximise memory for one timescale



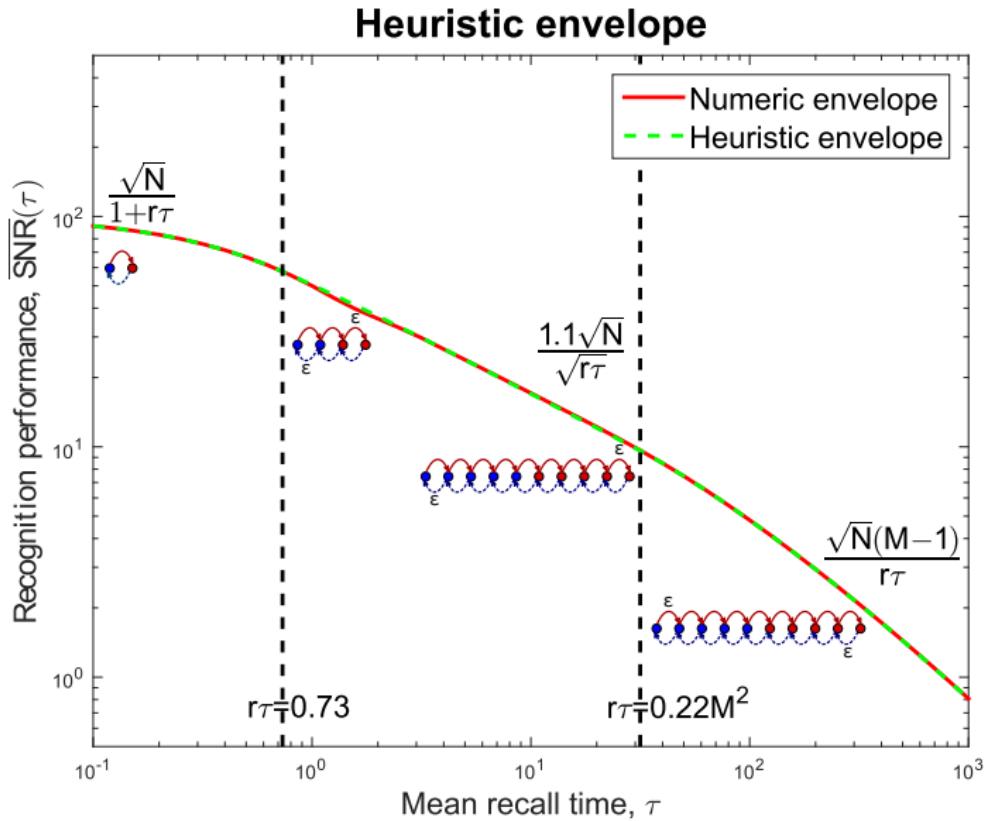
Models that maximise memory for one timescale



Models that maximise memory for one timescale



Heuristic envelope

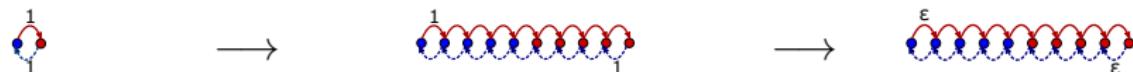


Synaptic structures for different timescales of memory

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

What can we conclude?

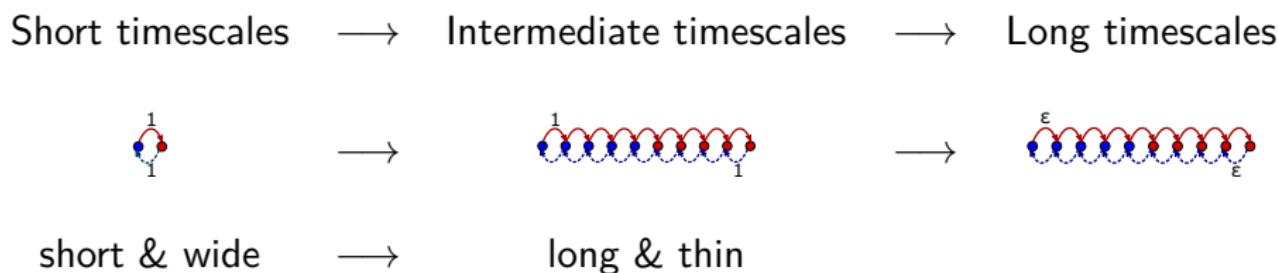
Short timescales → Intermediate timescales → Long timescales



Synaptic structures for different timescales of memory

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

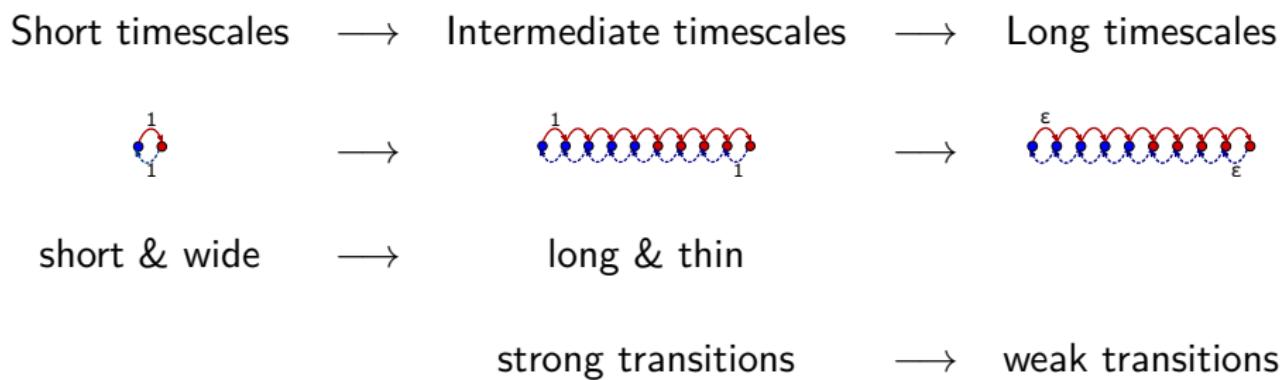
What can we conclude?



Synaptic structures for different timescales of memory

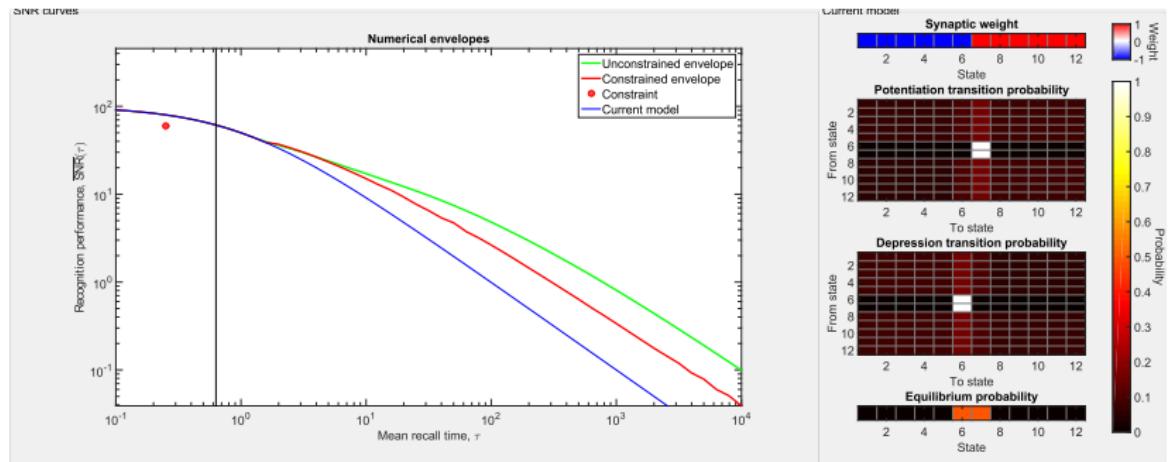
Real synapses limited by molecular building blocks.
Evolution had larger set of priorities.

What can we conclude?



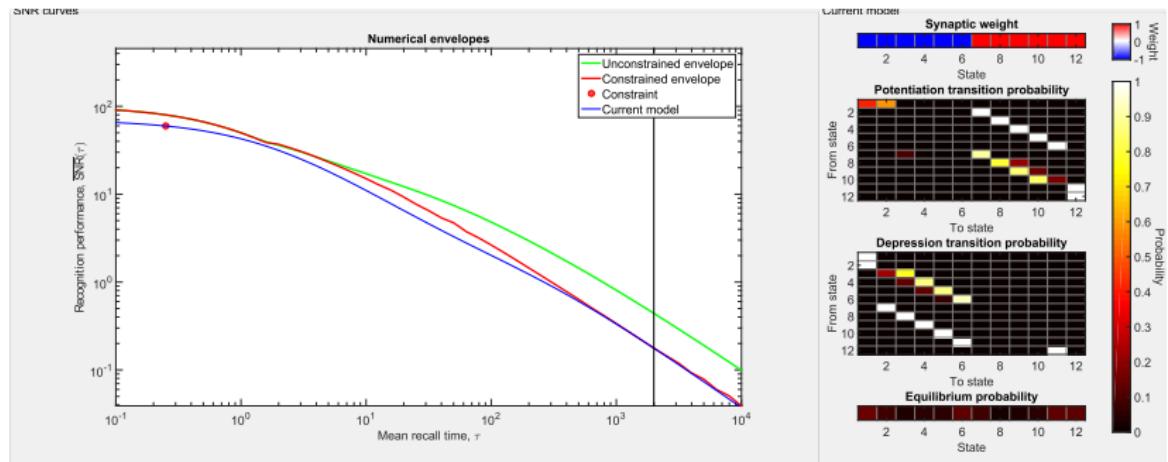
Two-time envelope: early constraint

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



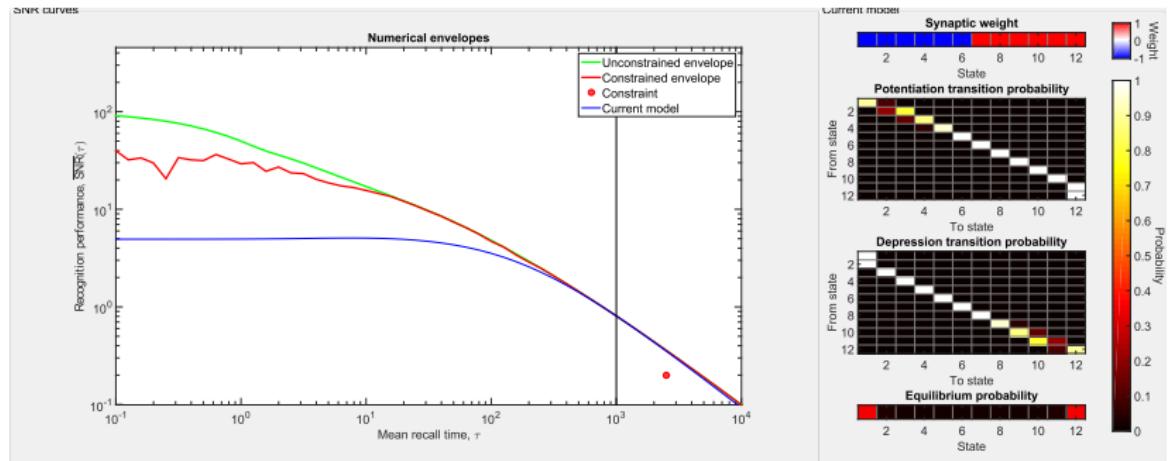
Two-time envelope: early constraint

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



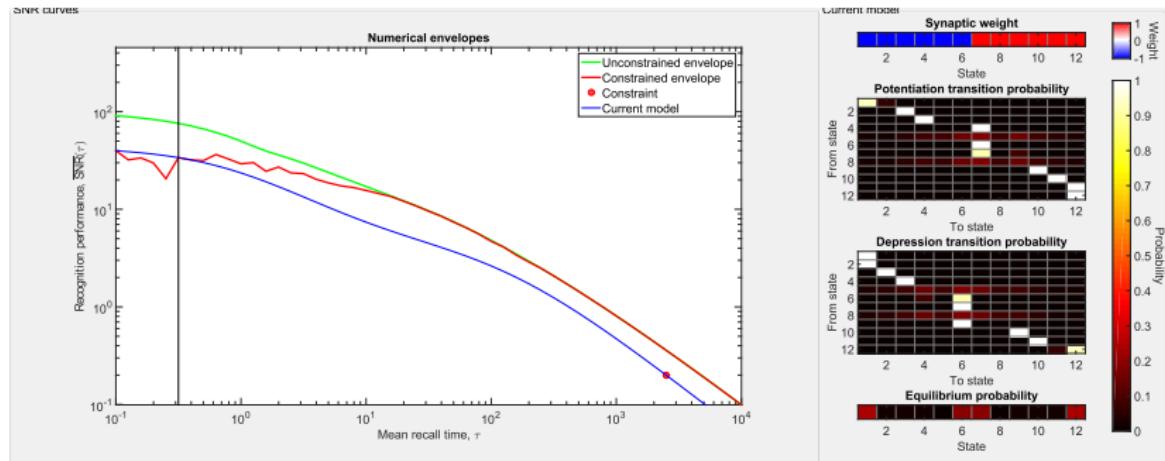
Two-time envelope: late constraint

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



Two-time envelope: late constraint

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

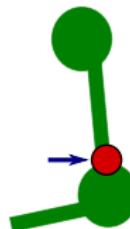


Section 5

Experimental tests?

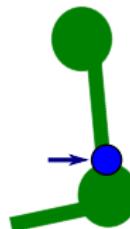
Proposed Experimental design

Subject a synapse to a sequence of candidate plasticity events.
Observe the changes in synaptic efficacy.



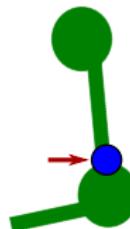
Proposed Experimental design

Subject a synapse to a sequence of candidate plasticity events.
Observe the changes in synaptic efficacy.



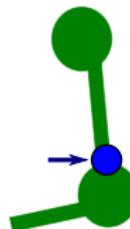
Proposed Experimental design

Subject a synapse to a sequence of candidate plasticity events.
Observe the changes in synaptic efficacy.



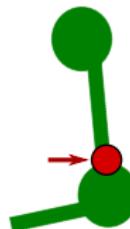
Proposed Experimental design

Subject a synapse to a sequence of candidate plasticity events.
Observe the changes in synaptic efficacy.



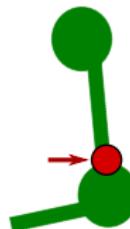
Proposed Experimental design

Subject a synapse to a sequence of candidate plasticity events.
Observe the changes in synaptic efficacy.



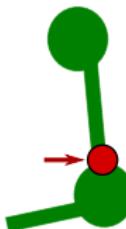
Proposed Experimental design

Subject a synapse to a sequence of candidate plasticity events.
Observe the changes in synaptic efficacy.



Proposed Experimental design

Subject a synapse to a sequence of candidate plasticity events.
Observe the changes in synaptic efficacy.



EM algorithms:

Sequence of hidden states → estimate transition probabilities

Transition probabilities → estimate sequence of hidden states

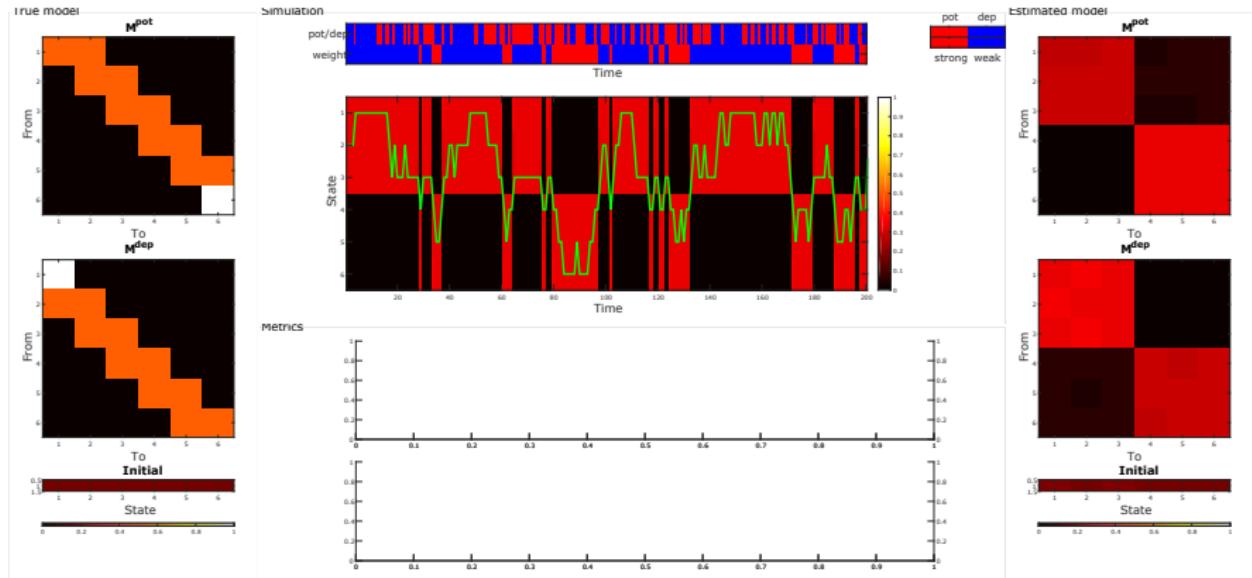
[Baum et al. (1970), Rabiner and Juang (1993), Dempster et al. (2007)]

Spectral algorithms:

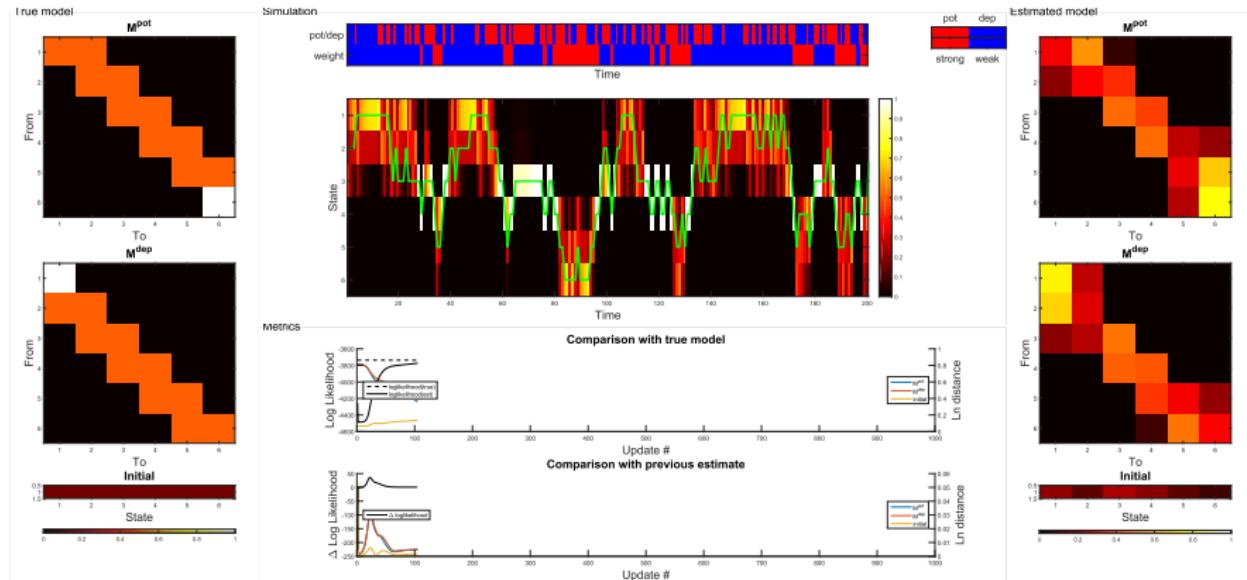
Compute $P(w_1)$, $P(w_1, w_2)$, $P(w_1, w_2, w_3), \dots$ from data,
from model.

[Hsu et al. (2008)]

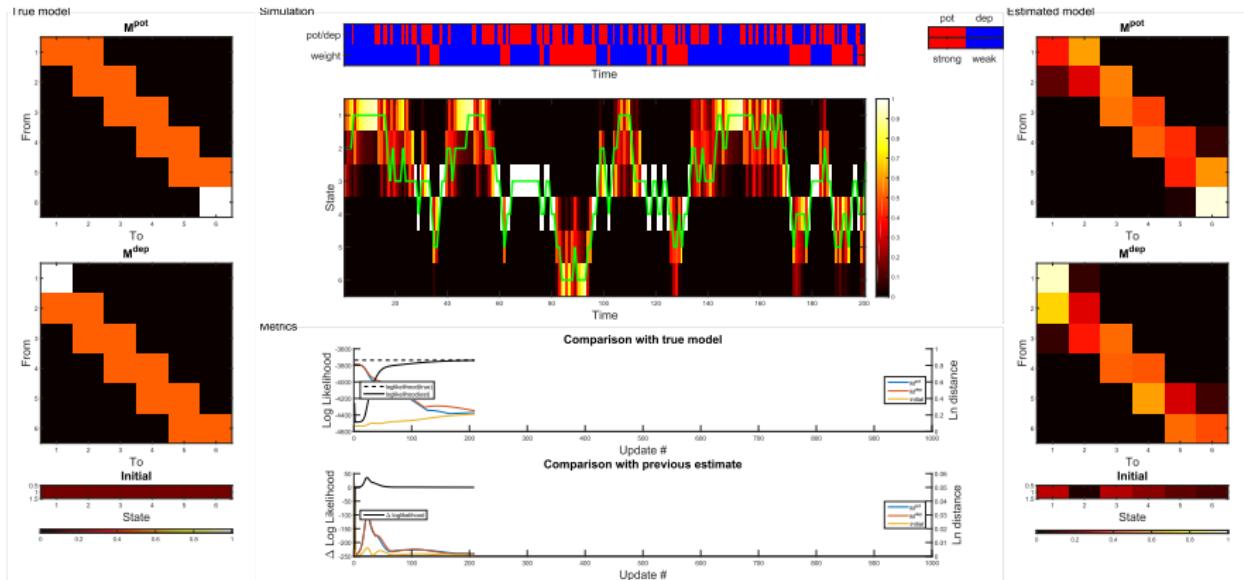
Fitting algorithm



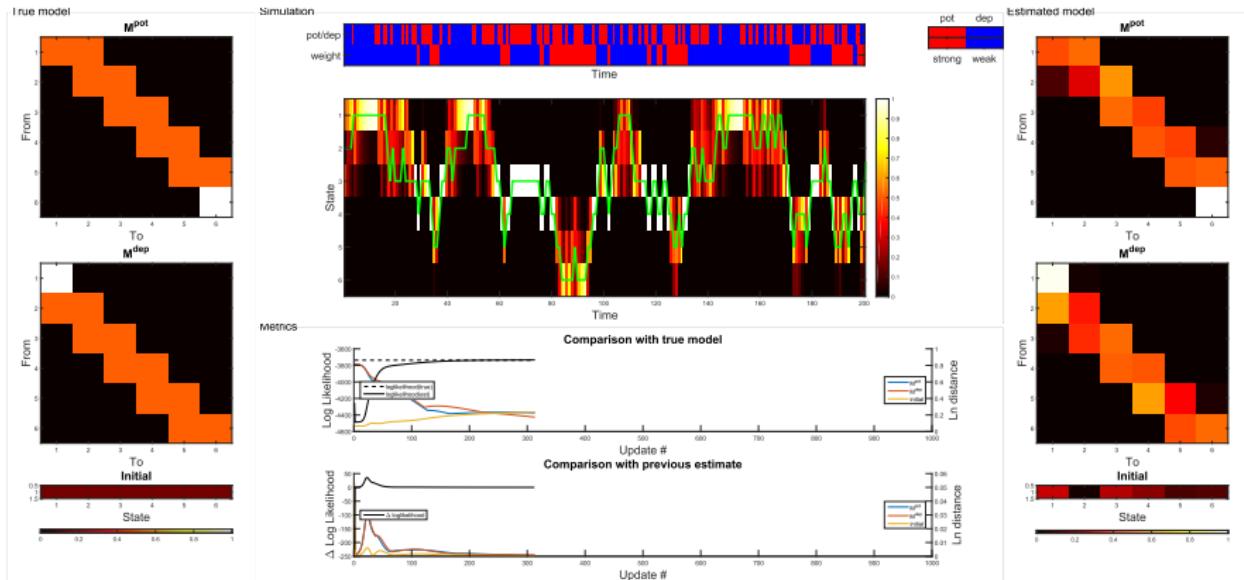
Fitting algorithm



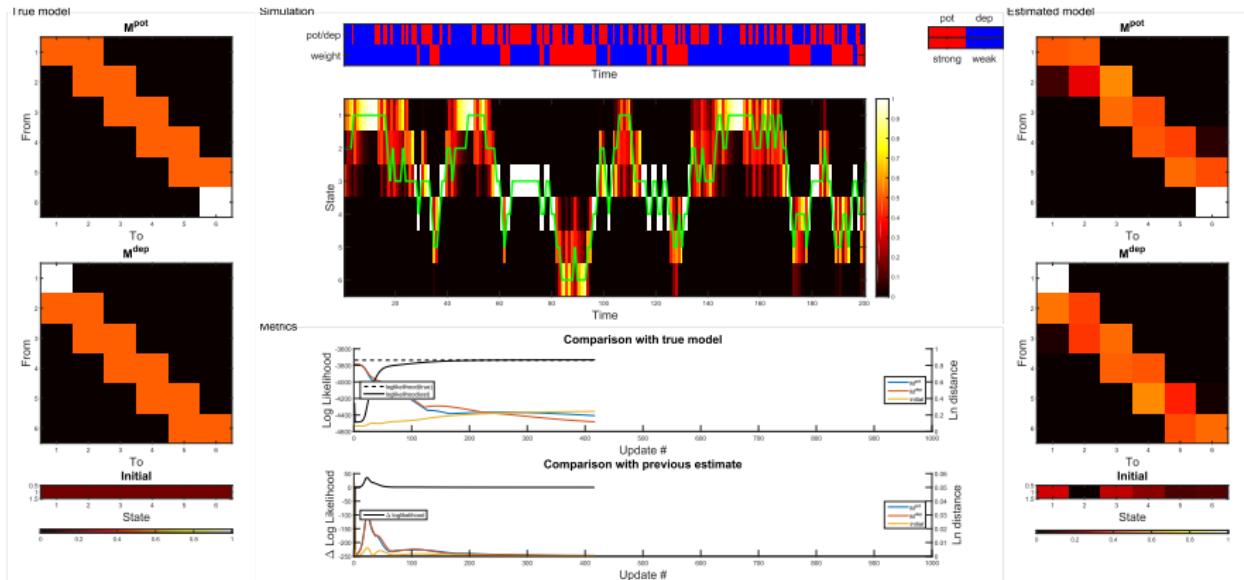
Fitting algorithm



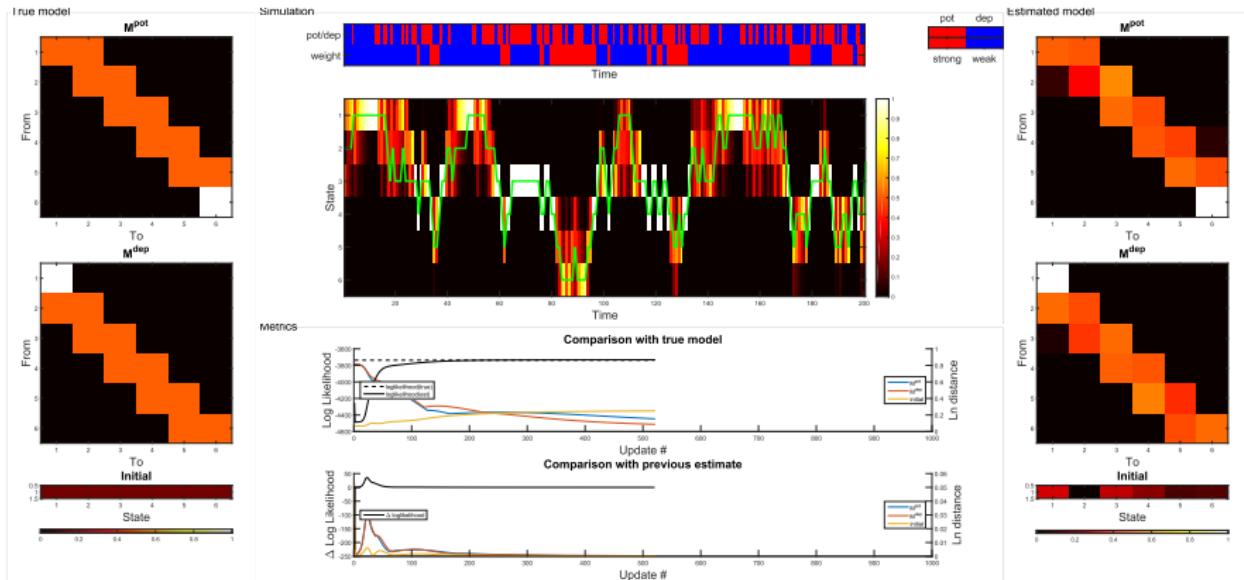
Fitting algorithm



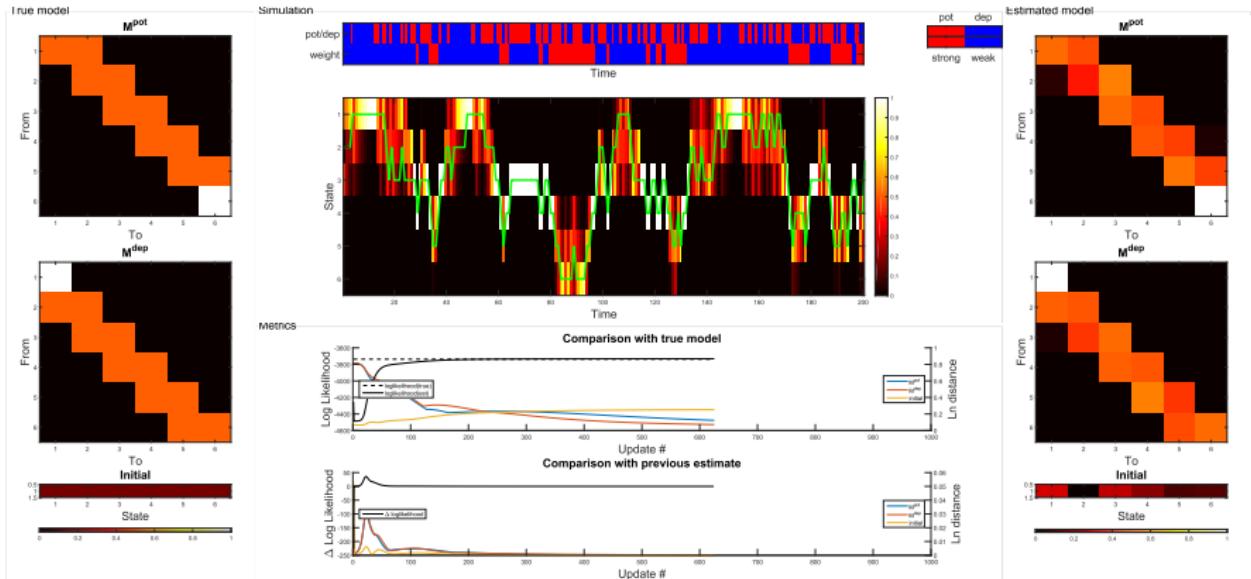
Fitting algorithm



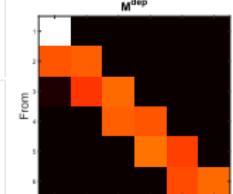
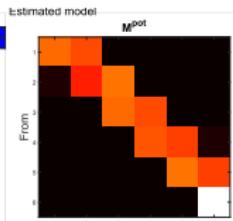
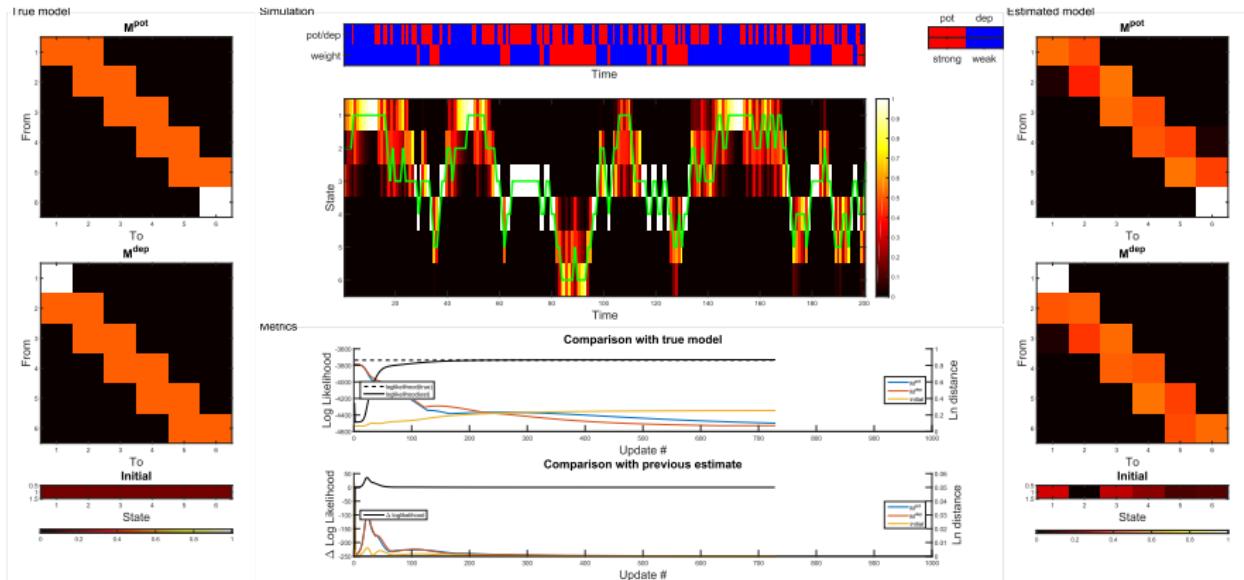
Fitting algorithm



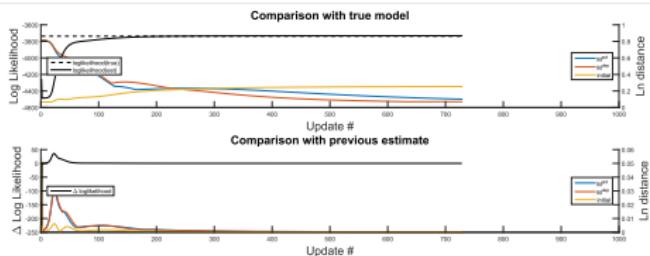
Fitting algorithm



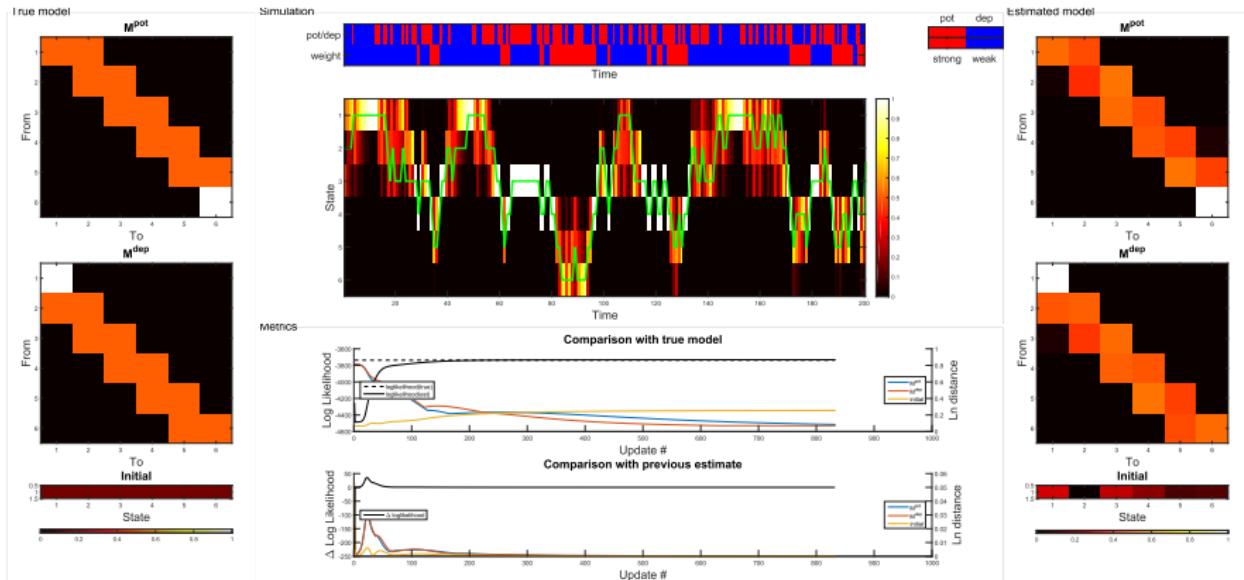
Fitting algorithm



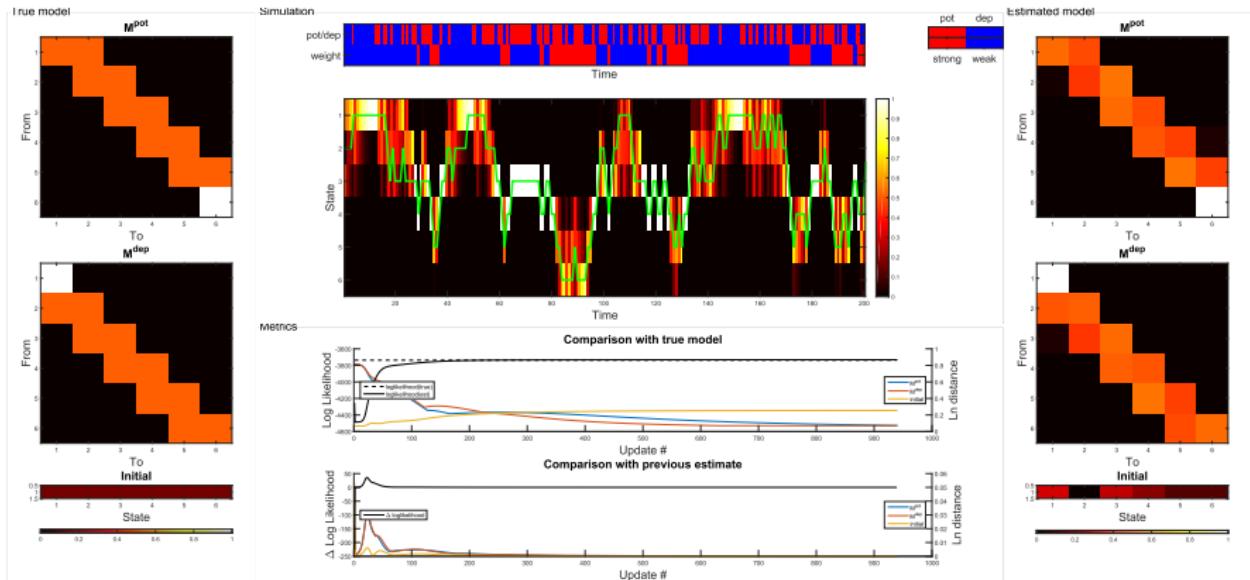
Metrics



Fitting algorithm



Fitting algorithm



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 → 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

References I



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) .

5



Johanna M. Montgomery and Daniel V. Madison.

“State-Dependent Heterogeneity in Synaptic Depression between Pyramidal Cell Pairs”.

Neuron, 33(5):765 – 777, (2002) .

5

References II



Larry R Squire and Pablo Alvarez.

“Retrograde amnesia and memory consolidation: a neurobiological perspective”.

Current Opinion in Neurobiology, 5(2):169–177, (April, 1995) .

6



John W Krakauer and Reza Shadmehr.

“Consolidation of motor memory.”.

Trends in neurosciences, 29(1):58–64, (January, 2006) .

6



Richard D. Emes and Seth G.N. Grant.

“Evolution of Synapse Complexity and Diversity”.

Annual Review of Neuroscience, 35(1):111–131, (2012) .

6

References III



Carl C. H. Petersen, Robert C. Malenka, Roger A. Nicoll, and John J. Hopfield.

“All-or-none potentiation at CA3-CA1 synapses”.

Proc. Natl. Acad. Sci. U.S.A., 95(8):4732–4737, (1998) .

9



Daniel H. O'Connor, Gayle M. Wittenberg, and Samuel S.-H. Wang.

“Graded bidirectional synaptic plasticity is composed of switch-like unitary events”.

Proc. Natl. Acad. Sci. U.S.A., 102(27):9679–9684, (2005) .

9



D. J. Amit and S. Fusi.

“Constraints on learning in dynamic synapses”.

Network: Computation in Neural Systems, 3(4):443–464, (1992) .

9

References IV



D. J. Amit and S. Fusi.

“Learning in neural networks with material synapses”.

Neural Computation, 6(5):957–982, (1994) .

9



S. Fusi, P. J. Drew, and L. F. Abbott.

“Cascade models of synaptically stored memories”.

Neuron, 45(4):599–611, (Feb, 2005) .

26

41



S. Fusi and L. F. Abbott.

“Limits on the memory storage capacity of bounded synapses”.

Nat. Neurosci., 10(4):485–493, (Apr, 2007) .

26

References V



A. B. Barrett and M. C. van Rossum.

“Optimal learning rules for discrete synapses”.

PLoS Comput. Biol., 4(11):e1000230, (Nov, 2008) .

26 50



Christian Leibold and Richard Kempter.

“Sparseness Constrains the Prolongation of Memory Lifetime via Synaptic Metaplasticity”.

Cerebral Cortex, 18(1):67–77, (2008) .

41



Daniel D Ben-Dayan Rubin and Stefano Fusi.

“Long memory lifetimes require complex synapses and limited sparseness”.

Frontiers in computational neuroscience, 1(November):1–14, (2007) .

41

References VI



Subhaneil Lahiri and Surya Ganguli.

“A memory frontier for complex synapses”.

In C.J.C. Burges, L. Bottou, M. Welling, Z. Ghahramani, and K.Q. Weinberger, editors, *Advances in Neural Information Processing Systems 26*, pages 1034–1042. NIPS, 2013.

46 54



LE Baum, T Petrie, George Soules, and Norman Weiss.

“A maximization technique occurring in the statistical analysis of probabilistic functions of Markov chains”.

The annals of mathematical statistics, 41(1):164–171, (1970) .

82 83 84 85 86 87 88

References VII



Lawrence R Rabiner and Biing-Hwang Juang.

Fundamentals of speech recognition, volume 14 of *Signal Processing*.

Prentice Hall, Inc., Upper Saddle River, NJ, USA, 1993.

ISBN 0-13-015157-2.

82 83 84 85 86 87 88



A. P. Dempster, N. M. Laird, and D. B. Rubin.

“Maximum Likelihood from Incomplete Data via the EM Algorithm”.

Journal of the Royal Statistical Society. Series B (Methodological), (October, 2007) .

82 83 84 85 86 87 88



Daniel Hsu, Sham M. Kakade, and Tong Zhang.

“A Spectral Algorithm for Learning Hidden Markov Models”.

pages 1460–1480, (nov, 2008) , arXiv:0811.4413.

82 83 84 85 86 87 88

References VIII



J.G. Kemeny and J.L. Snell.

Finite markov chains.

Springer, 1960.

110

Techinical detail: ordering states

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

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

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

[Kemeny and Snell (1960)]

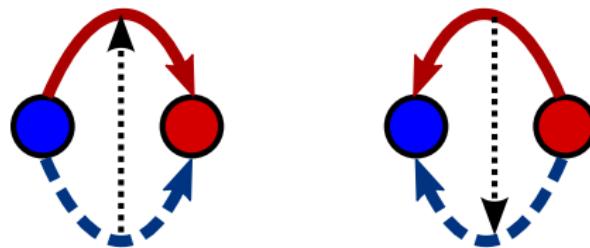
We define:

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

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.

[back](#)