A memory frontier for complex synapses

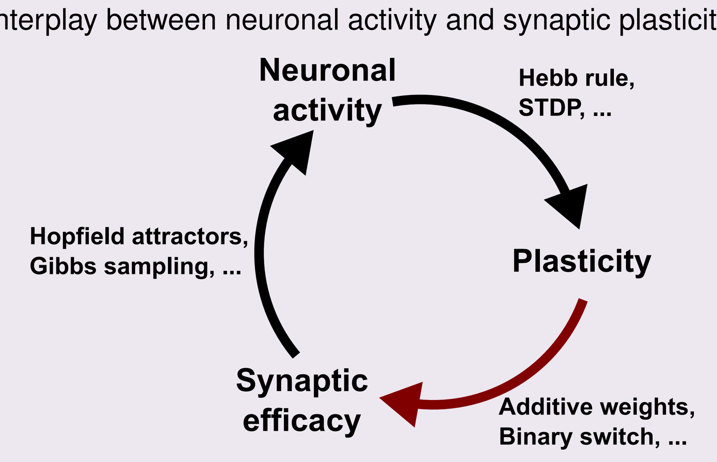
Subhaneil Lahiri and Surya Ganguli

Department of Applied Physics, Stanford University, Stanford CA

Background

Synaptic learning and memory

Learning and memory involve the interplay between neuronal activity and synaptic plasticity.



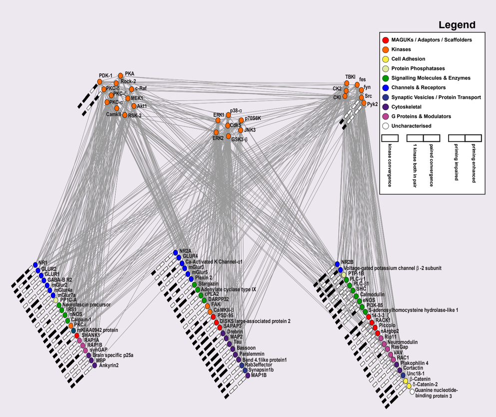
Theorists frequently neglect the question of how plasticity is implemented.
A synapse is often modeled as a single number: the synaptic weight.

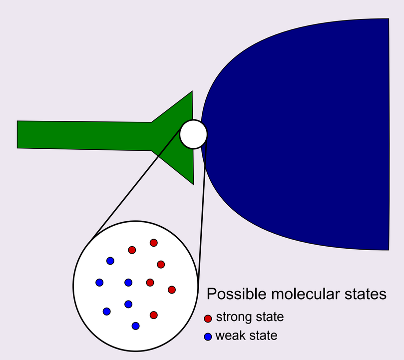
Complex synapses

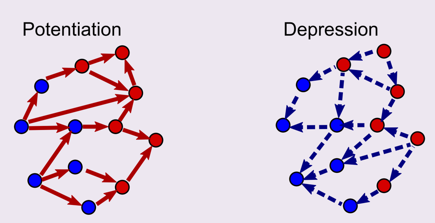
In reality, a synapse is a complex dynamical system.

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)]

Storage capacity of synaptic memory

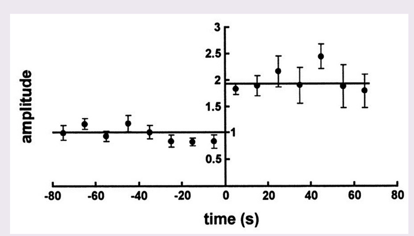
A classical perceptron, when used as a recognition memory device, has a memory capacity $\propto N$, the number of synapses.

However, this requires synapses' dynamic range to be also $\propto N$.

If synaptic efficacies are limited to a fixed dynamic range,
$\rightarrow$ strong tradeoff between learning and forgetting
– due to new memories overwriting old.

If we wish to store new memories rapidly, then memory capacity is $\propto \log N$.

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

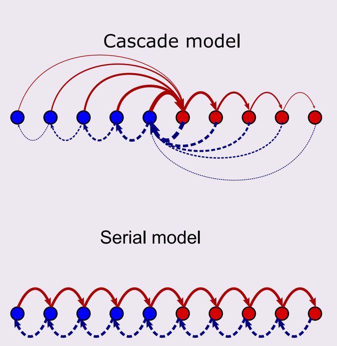


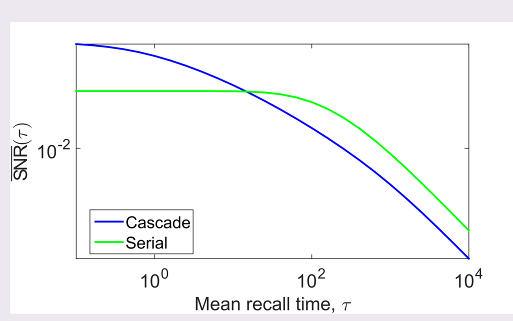
[Petersen et al. (1998), O'Connor et al. (2005)]

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

Cascade and serial models

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

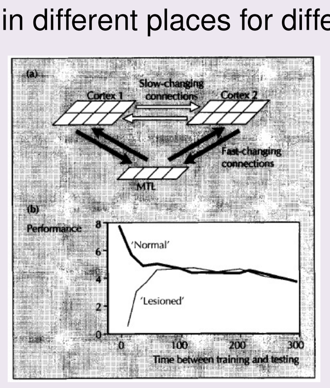




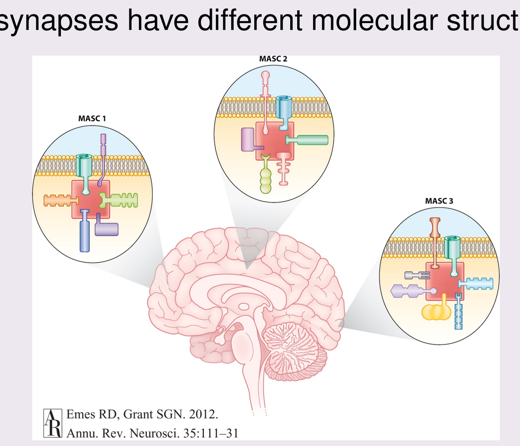
[Fusi et al. (2005), Leibold and Kempter (2008), Ben-Dayan Rubin and Fusi (2007)]

Timescales of memory

Memories stored in different places for different timescales



Different synapses have different molecular structures.



Also: Cerebellar cortex vs. cerebellar nuclei.

[Squire and Alvarez (1995), Krakauer and Shadmehr (2006)]

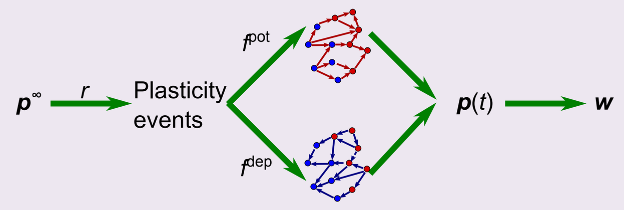
[Emes and Grant (2012)]

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)?
- Can synaptic structure be tuned to store memories over different timescales?
- 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

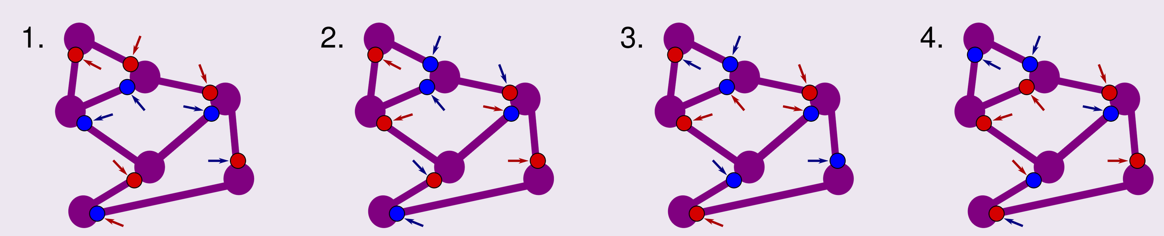


Assumptions:
- Candidate plasticity events occur independently at each synapse,
- Each synapse responds with the same state-dependent rules,
- Synaptic weight takes only two values, ± 1.

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

Recognition memory

The synapses are given a sequence of patterns (potentiation & depression) to store



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

Memory curve

Ideal observer approach: read synaptic weights directly $\rightarrow$ upper bound on what could be read from network activity.

Measure overlap between $\vec{w}(t)$, the N-element vector of synaptic strengths, and $\vec{w}_{\text{ideal}}$, the pattern we are testing.

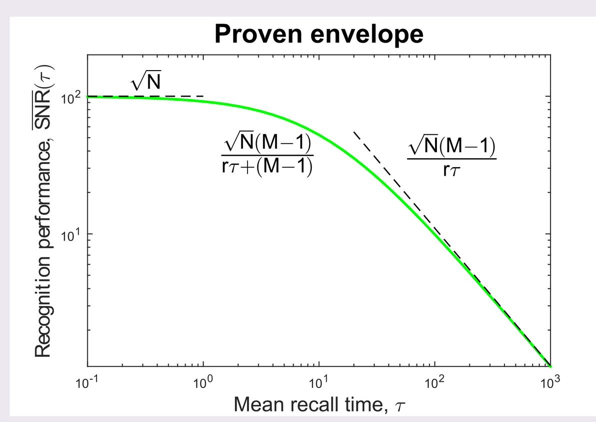
Performance measured by signal-to-noise ratio, with mean recall time: τ.

$$\overline{\text{SNR}}(\tau) = \frac{1}{\tau}\int_0^\infty \mathrm{d}t\, e^{-t/\tau}\, \frac{\langle \vec{w}_{\text{ideal}} \cdot \vec{w}(t)\rangle - \langle \vec{w}_{\text{ideal}} \cdot \vec{w}(\infty)\rangle}{\sqrt{\text{Var}(\vec{w}_{\text{ideal}} \cdot \vec{w}(\infty))}}.$$

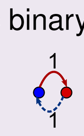
The memory envelope

Proven upper bounds

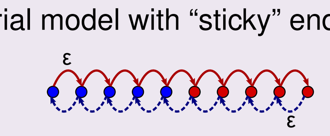
Proven upper bounds on initial SNR and late time tail $\rightarrow$ upper bound on memory curve at *any* time.



Initial SNR: deterministic binary synapse



Late times: serial model with "sticky" end states

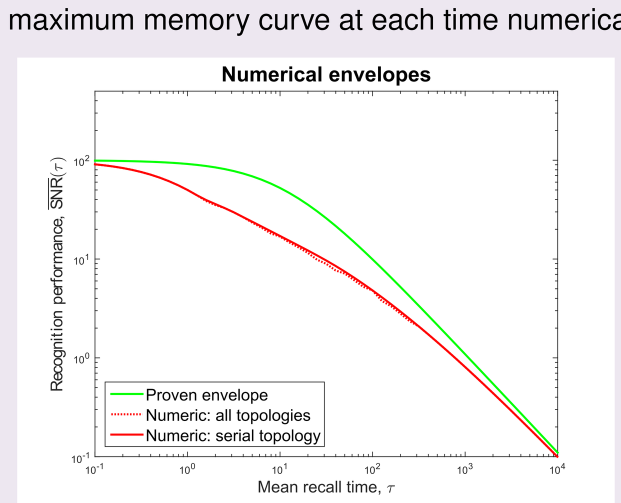


[Lahiri and Ganguli (2013)]

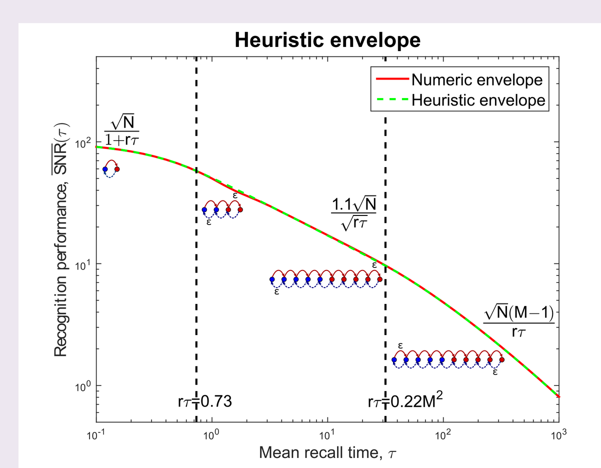
No model can ever go above this envelope. Is it achievable?

Numeric upper bounds

Find maximum memory curve at each time numerically:



At any single timescale: best model has serial topology.

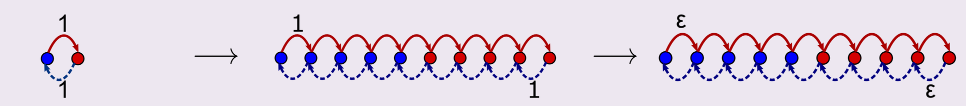


Earlier times: shorten the chain.
Later times: make end state "sticky".

Conclusions

Take-home message

Real synaptic structures are limited by the set of molecular building blocks, and they have a larger set of priorities.
What can we conclude?



short & wide $\longrightarrow$ long & thin

deterministic $\longrightarrow$ stochastic

Experimental tests?

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

Expectation-Maximization algorithms: Sequence of hidden states $\rightarrow$ estimate transition probabilities
Transition probabilities $\rightarrow$ estimate sequence of hidden states

Problems:
- Need a long sequence of plasticity events.
- Need to control candidate plasticity events.
- Need to measure synaptic efficacies.

Summary

- We have formulated a general theory of learning and memory with complex synapses.
- 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 what types of synaptic structure are useful for storing memories for different timescales.

References

- 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) .
- 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) .
- 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) .
- 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) .
- 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 Kempter, "Sparseness Constrains the Prolongation of Memory Lifetime via Synaptic Metaplasticity", *Cerebral Cortex*, 18 (1):67–77, (2008) .
- 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) .
- Larry R Squire and Pablo Alvarez, "Retrograde amnesia and memory consolidation: a neurobiological perspective", *Current Opinion in Neurobiology*, 5(2):169–177, (April, 1995) . ISSN 09594388.
- John W Krakauer and Reza Shadmehr, "Consolidation of motor memory.", *Trends in neurosciences*, 29(1):58–64, (January, 2006) . ISSN 0166-2236.
- Richard D. Emes and Seth G.N. Grant, "Evolution of Synapse Complexity and Diversity", *Annual Review of Neuroscience*, 35(1):111–131, (2012) .
- 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) .
- 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. URL http://papers.nips.cc/paper/4872-a-memory-frontier-for-complex-synapses.

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.