# A memory frontier for complex synapses

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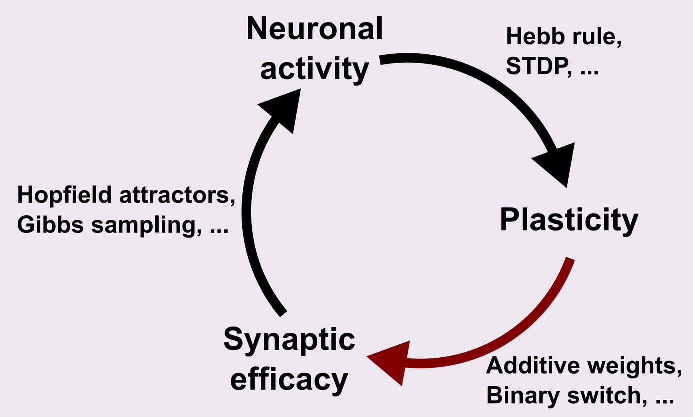
## Background

### Synaptic learning and memory

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



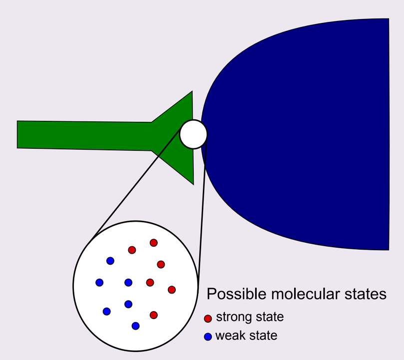

Theorists frequently neglect the question of how plasticity is implemented.
A synapse is often modeled as a single number: the synaptic weight.

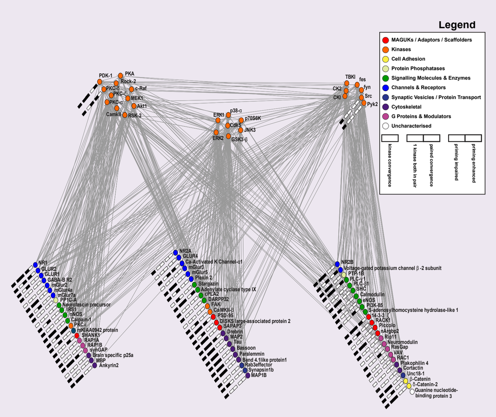
### Complex synapses

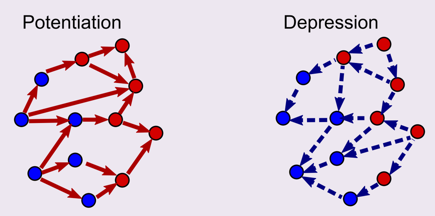
In reality, a synapse is a complex dynamical system.

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

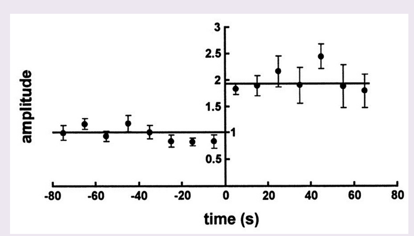
A classical perceptron, when used as a recognition memory device, has a memory capacity $\propto N$, the number of synapses.

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)]

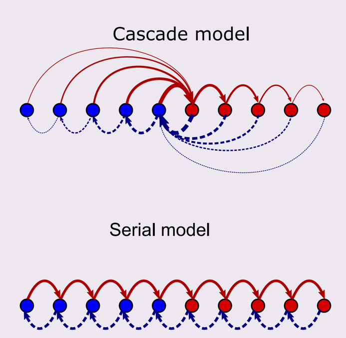


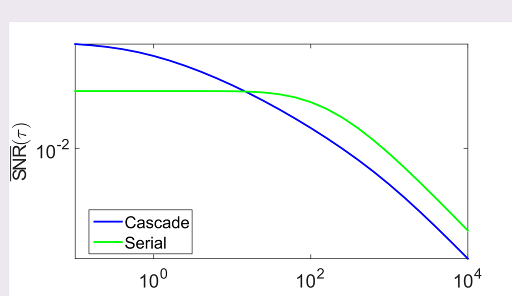

[Petersen et al. (1998), O'Connor et al. (2005)]

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.

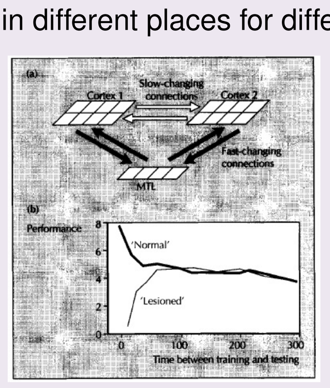



[Fusi et al. (2005), Leibold and Kempter (2008), Ben-Dayan Rubin and Fusi (2007)]

### Timescales of memory

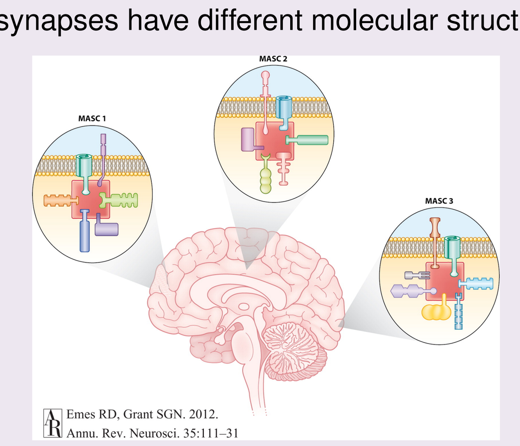
Memories stored in different places for different timescales



Also: Cerebellar cortex vs. cerebellar nuclei.

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

Different synapses have different molecular structures.



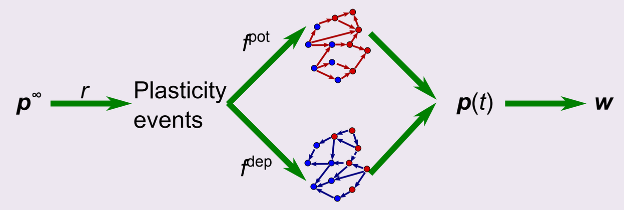
[Emes and Grant (2012)]

## 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



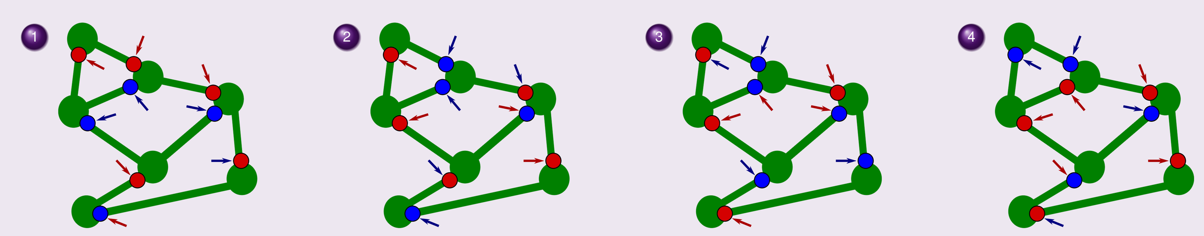

Assumptions:

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

[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.

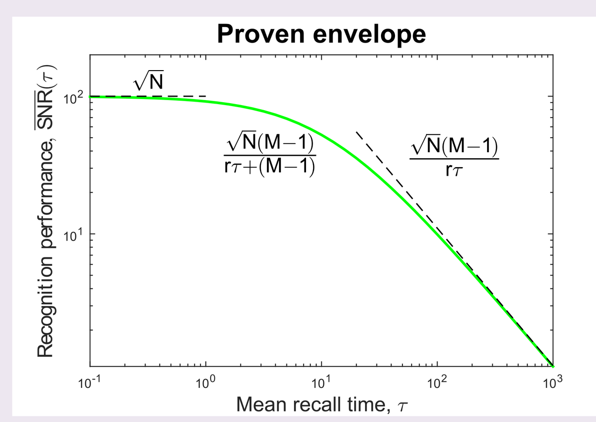
Performance measured by signal-to-noise ratio, with mean recall time: $\tau$.

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

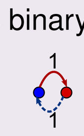
## The memory envelope

### Proven upper bounds

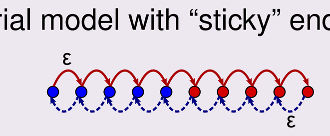
Proven upper bounds on initial SNR and late time tail $\rightarrow$ upper bound on memory curve at *any* time.




Initial SNR: deterministic binary synapse



Late times: serial model with "sticky" end states

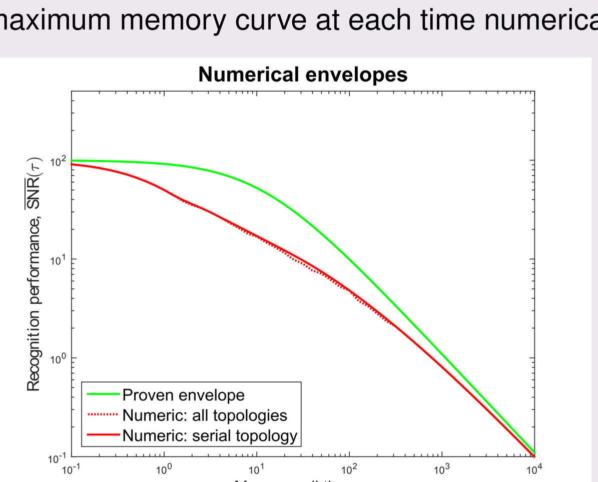


[Lahiri and Ganguli (2013)]

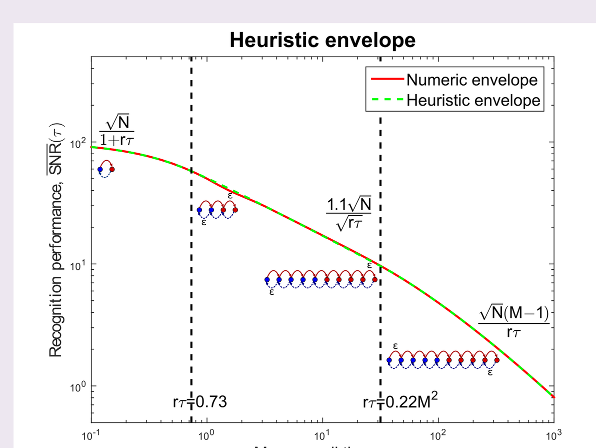
No model can ever go above this envelope. Is it achievable?

### Numeric envelope for memory curves

Find maximum memory curve at each time numerically:




At any single timescale: best model has serial topology.



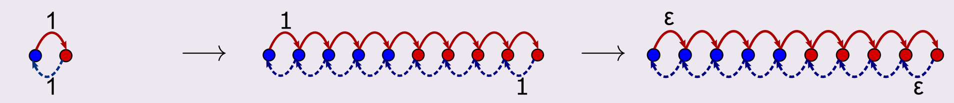

Earlier times: shorten the chain.
Later times: make end state "sticky".

## Conclusions

### Synaptic structures for different timescales of memory

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

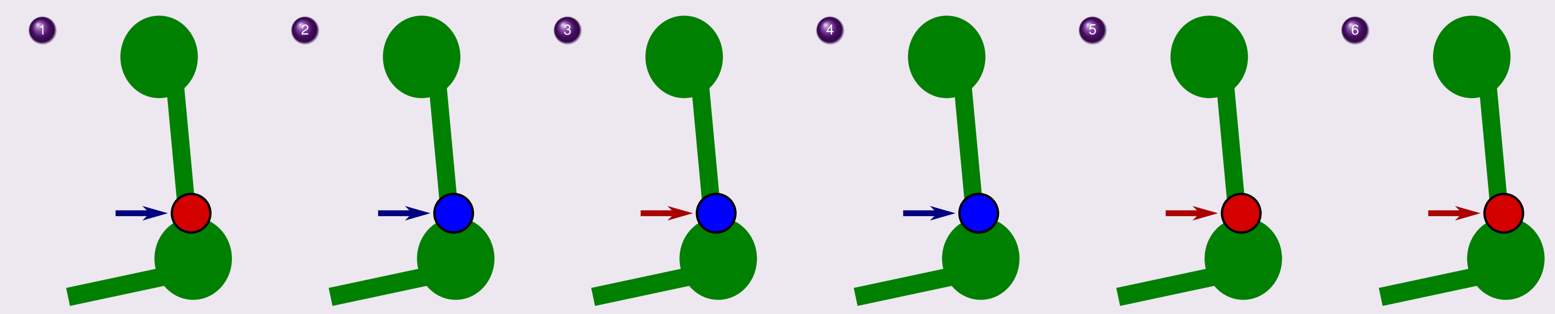


short & wide $\longrightarrow$ long & thin

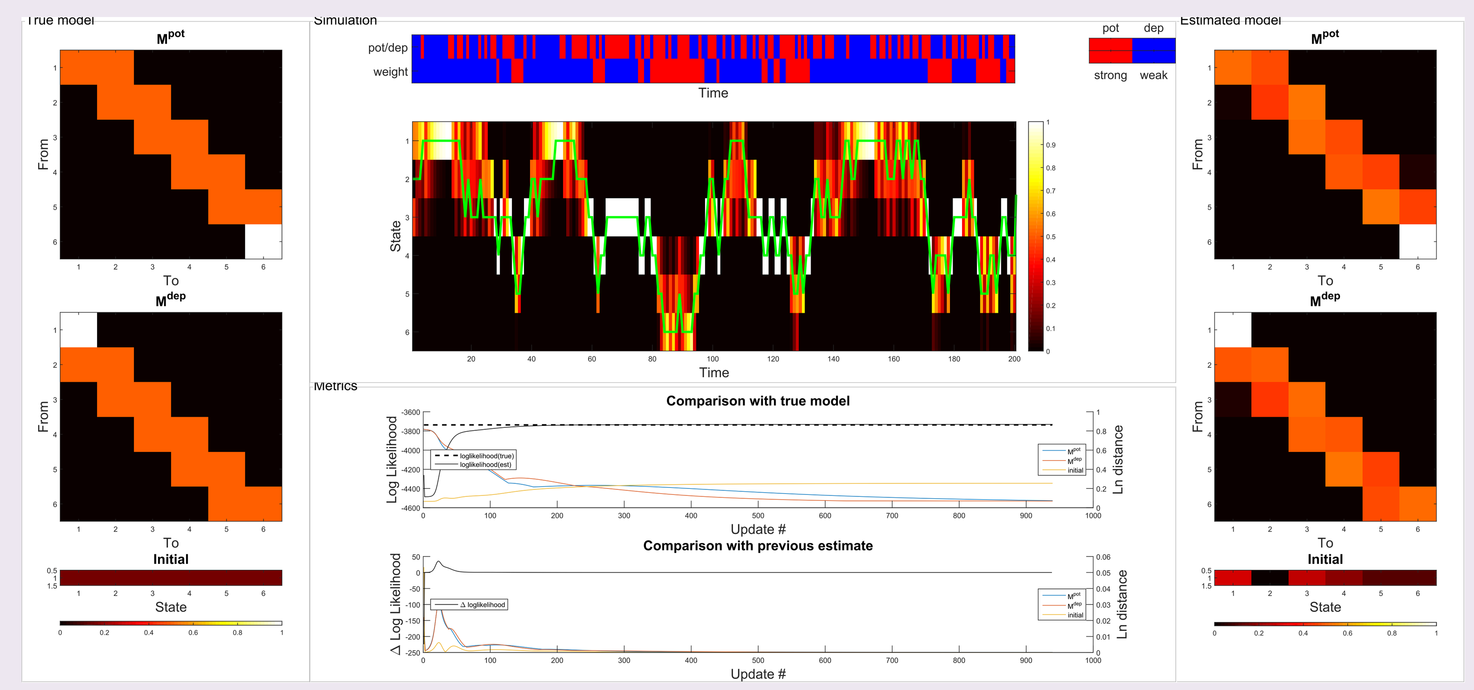
strong transitions $\longrightarrow$ weak transitions

### 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 single synapses.
- Need long sequences of plasticity events.
- Need to control types of 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 which types of synaptic structure are useful for storing memories for different timescales.

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