# The synaptic dynamics of learning and memory

Subhaneil Lahiri

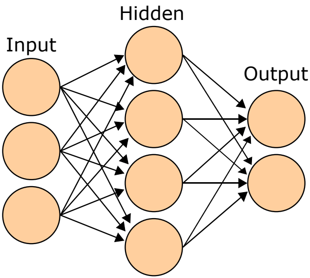
Stanford University, Applied Physics

May 13, 2019

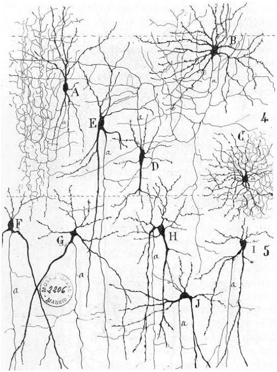
"A memory frontier for complex synapses", S Lahiri and S Ganguli.
*Adv. Neural Inf. Process. Syst. 26, pp. 1034–1042., (2013)*.

# What is a synapse?

Comp-neuro/deep-learning




Cellular biology



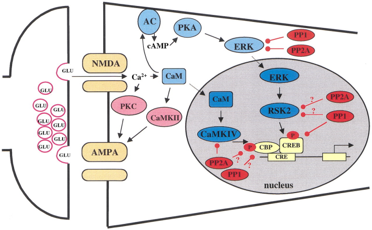

[Cajal (1899)]

# What is a synapse?

Comp-neuro/deep-learning

$$W_{ij}$$

Cellular biology



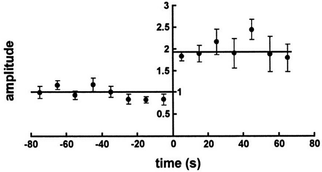

[Klann (2002)]

# Storage capacity of synaptic memory

Hopfield model, perceptron: capacity $\propto N$, (# synapses).

Assumes unbounded analogue synapses

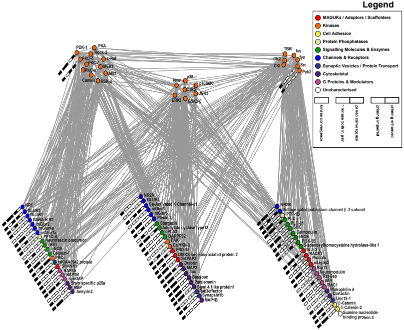
With discrete, finite synapses:
$\Longrightarrow$ memory capacity $\sim \mathcal{O}(\log N)$.
[Amit and Fusi (1992), Amit and Fusi (1994)]



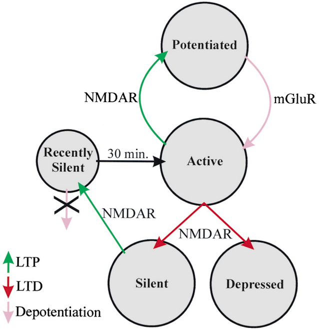

[Petersen et al. (1998), O'Connor et al. (2005)]

New memories overwrite old $\Longrightarrow$ stability-plasticity dilemma.

# Synapses are complex




[Coba et al. (2009)]




[Montgomery and Madison (2002)]

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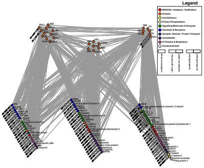

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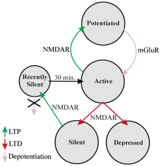
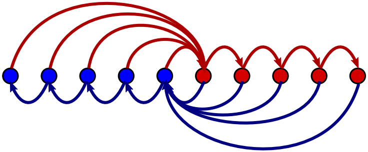



[Montgomery and Madison (2002)]

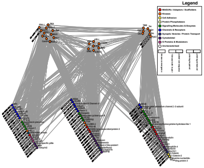
Cascade model



Capacity $\propto N^{2/3}$.

[Fusi et al. (2005)]

# Synapses are complex

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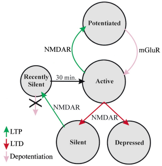


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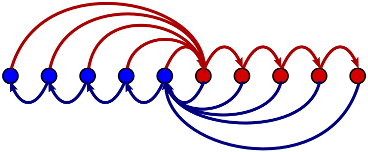


Capacity $\propto N^{2/3}$. [Fusi et al. (2005)]

Capacity $\propto N$. [Benna and Fusi (2016)]

# My approach

We want to study the structure-function relationship of biological processes.

Not trying to build a *single* model.

Instead, we build a broad framework of models to find:

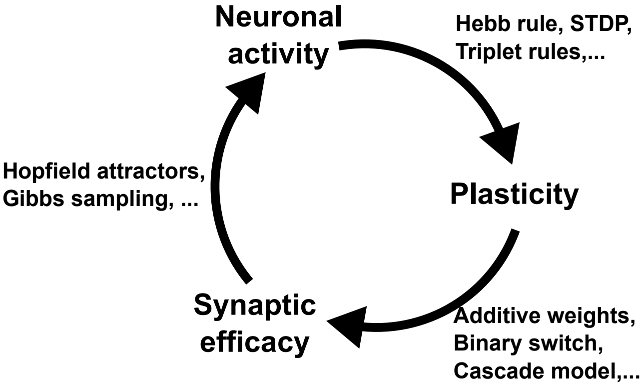
- $\rightarrow$ underlying mechanisms and principles.
- $\rightarrow$ trade-offs between aspects of performance (e.g. learning vs. memory).
- $\rightarrow$ properties of models that best manage these trade-offs.

# Outline

1. Timescales of memory
   - Quantifying memory quality
   - Frontiers of memory
   - Implications of memory limits

2. Designing experiments

# Synaptic learning and memory



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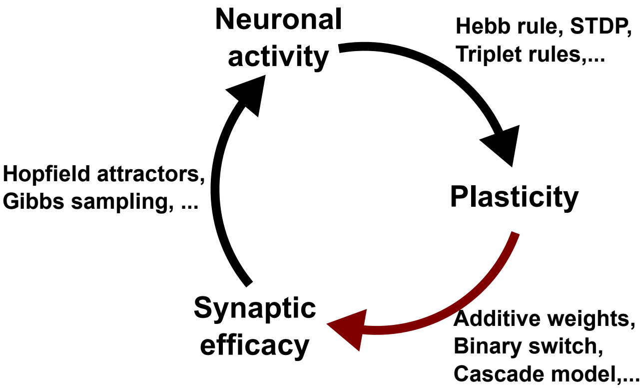
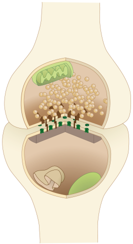
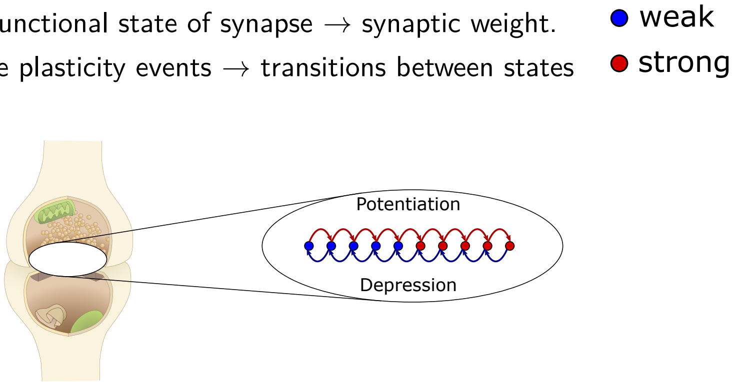


# Models of complex synaptic dynamics



# Models of complex synaptic dynamics

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




[Fusi et al. (2005), Fusi and Abbott (2007), Barrett and van Rossum (2008)]
[Smith et al. (2006), Lahiri and Ganguli (2013)]

# Models of complex synaptic dynamics

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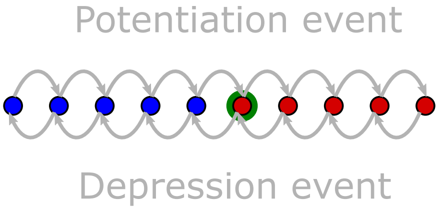
weak

strong



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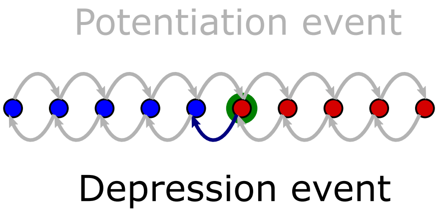

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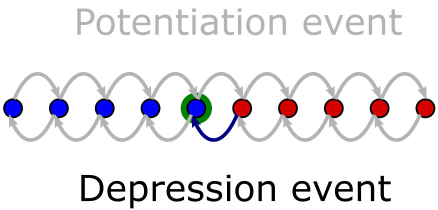

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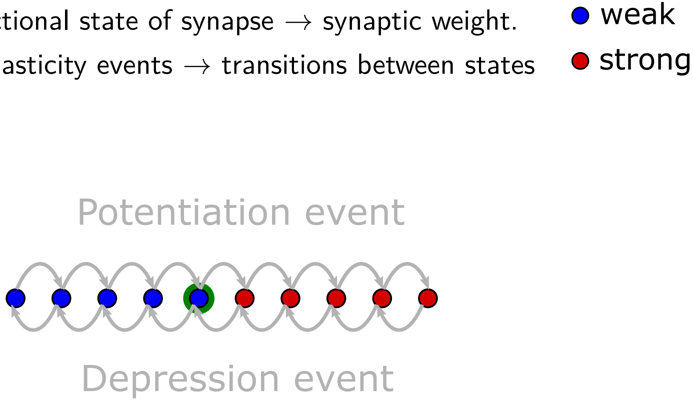

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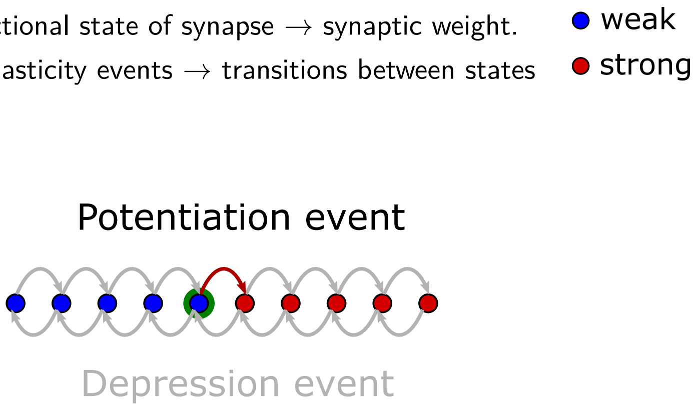

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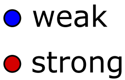


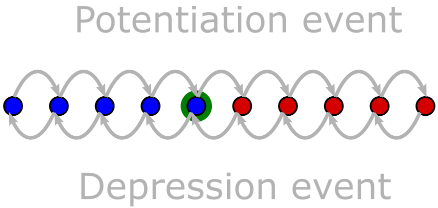

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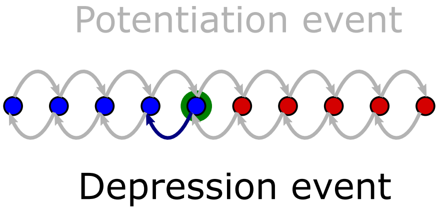


Metaplasticity: change propensity for plasticity
(independent of change in synaptic weight).

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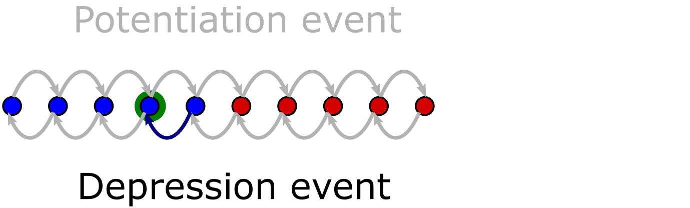


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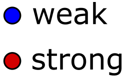


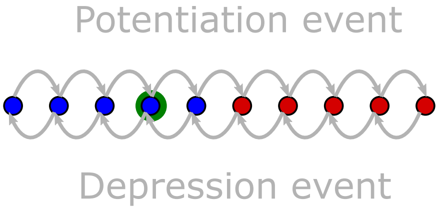


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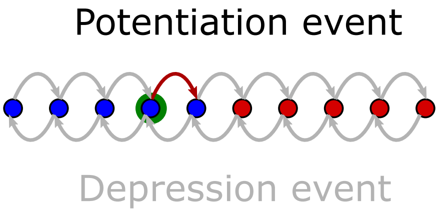


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- Candidate plasticity events $\rightarrow$ transitions between states

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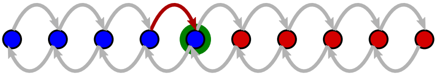
strong

Potentiation event



Depression event

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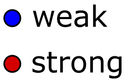


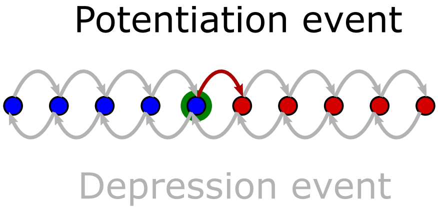


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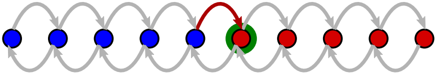

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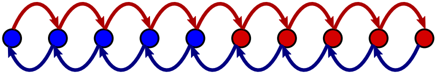

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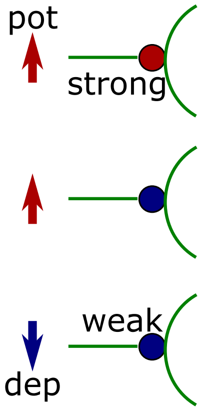
# Synaptic memory curves



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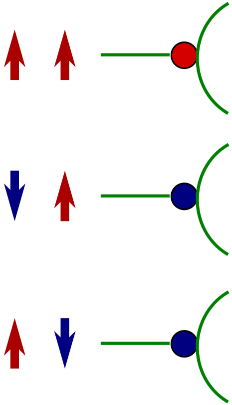

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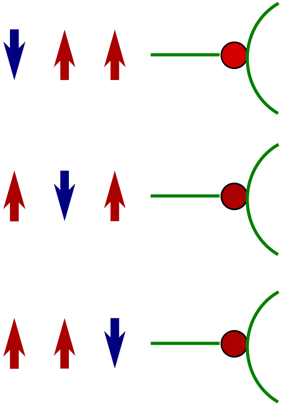

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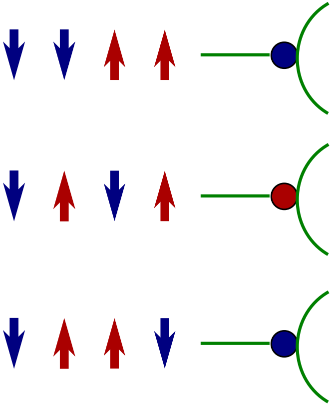

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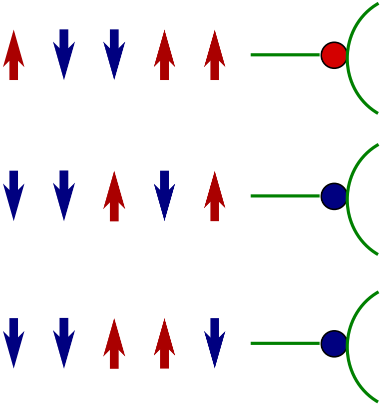

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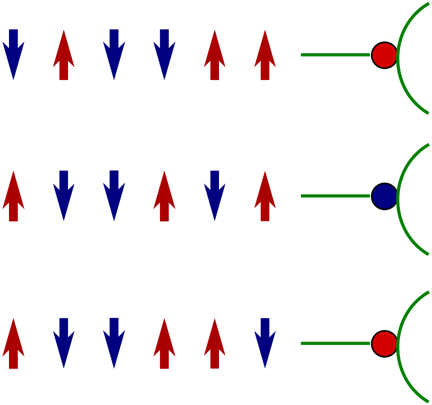

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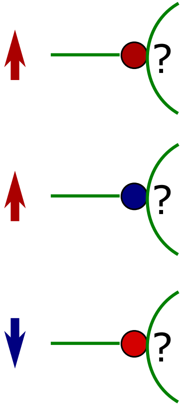



Recognition memory: has this pattern been seen before?

Hypothesis test statistic: $\vec{w}(t) \cdot \vec{w}_{\text{test}}$. [Sommer and Dayan (1998)]

# Quantifying memory quality

Test if $\vec{w}(t) \cdot \vec{w}_{\text{test}} \gtrless$ threshold? [Sommer and Dayan (1998)]

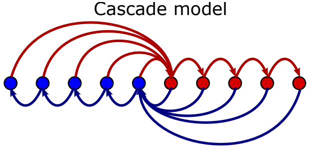
Compare with null-distribution: $P\left[\vec{w}_{\text{null}} \cdot \vec{w}_{\text{test}}\right]$

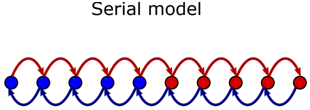
$$\text{SNR}(t) = \frac{\langle \vec{w}(t) \cdot \vec{w}_{\text{test}} \rangle - \langle \vec{w}_{\text{null}} \cdot \vec{w}_{\text{test}} \rangle}{\sqrt{\text{Var}(\vec{w}_{\text{null}} \cdot \vec{w}_{\text{test}})}},$$

$\Rightarrow$ discriminability: KL divergence, Chernoff distance, ROC curve, ...

# Specific models of complex synaptic dynamics

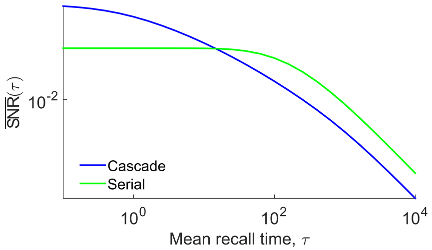
Two example models of complex synapses.



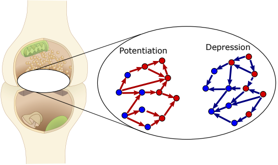

[Fusi et al. (2005), Leibold and Kempter (2008), Ben-Dayan Rubin and Fusi (2007)]

These have different memory storage properties

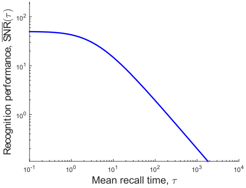


# General principles relating structure and function?

Synaptic structure




Synaptic function




- What are the fundamental limits of memory?
- Which models achieve these limits?
- What are the theoretical principles behind the optimal models?

# Parameters for synaptic dynamics

$$
\begin{aligned}
f^{\text{pot/dep}} &= \text{fraction of events that are pot/dep},\\
\text{pot. event: } \mathbf{M}^{\text{pot}}_{ij} &= \text{transition prob. } i \to j,\\
\text{dep. event: } \mathbf{M}^{\text{dep}}_{ij} &= \text{transition prob. } i \to j.
\end{aligned}
$$

Constraints:

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

# Eigenmodes are more convenient parameters

Eigenmodes:

$$\left(f^{\text{pot}}\mathbf{M}^{\text{pot}} + f^{\text{dep}}\mathbf{M}^{\text{dep}}\right)\mathbf{u}_a = \lambda_a \mathbf{u}_a.$$

Contribution to SNR:

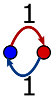
$$\text{SNR}(t) = \sum_a \mathcal{I}_a \, \mathrm{e}^{-t/\tau_a}.$$

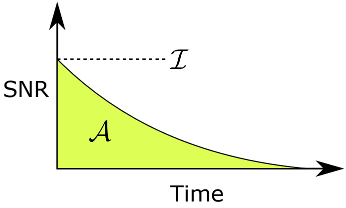
What are the constraints?

# Upper bounds on measures of memory

Initial SNR:

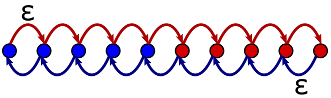
$$\mathcal{I} = \mathrm{SNR}(0) = \sum_a \mathcal{I}_a \le \sqrt{N}.$$




Area under curve:

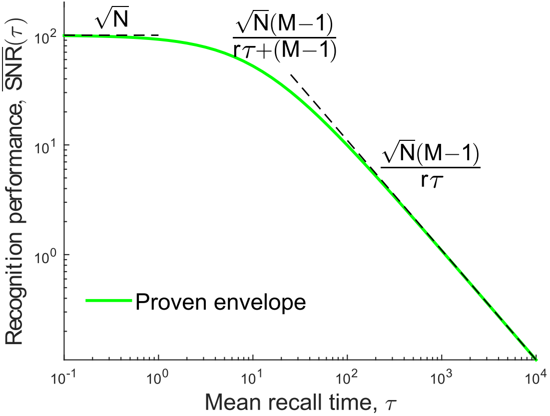
$$\mathcal{A} = \int_0^\infty \mathrm{SNR}(t)\,\mathrm{d}t = \sum_a \mathcal{I}_a \tau_a \le \sqrt{N}(M-1)/r.$$




[Lahiri and Ganguli (2013)]

# Proven envelope: memory frontier

Upper bound on memory curve at *any* timescale.



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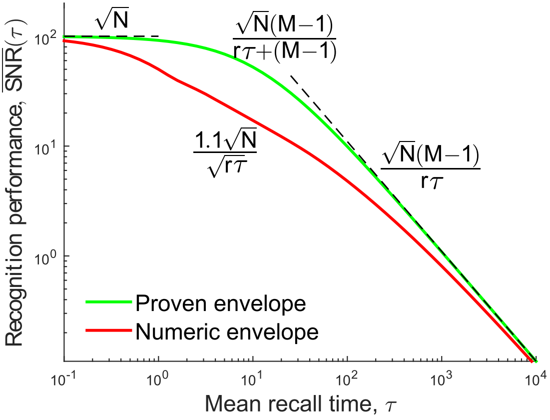
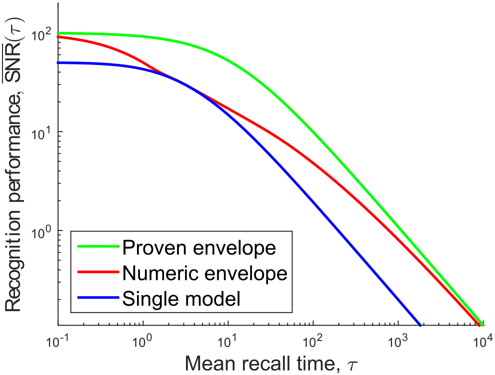
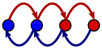


# Models that maximize memory for one timescale



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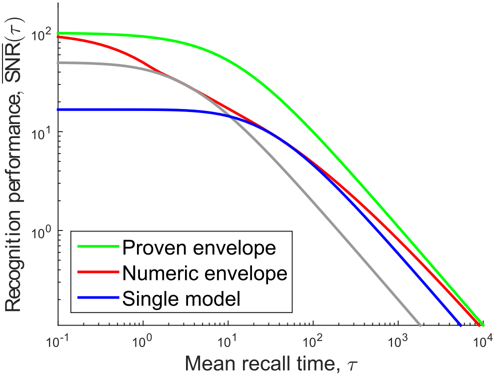


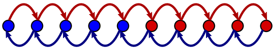

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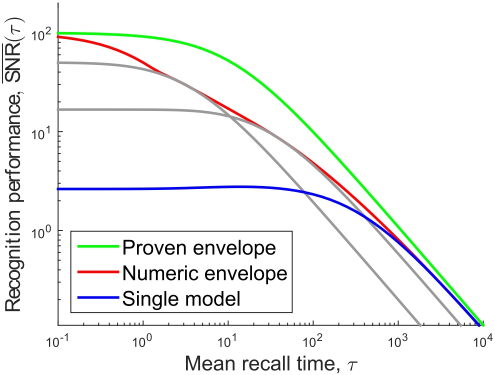
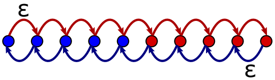
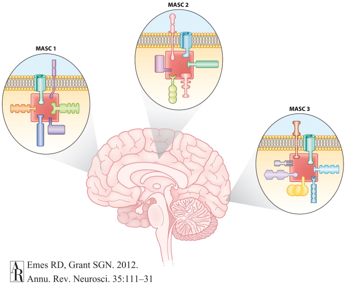


# Synaptic diversity and timescales of memory

Different synapses have different molecular structures.




[Emes and Grant (2012)]

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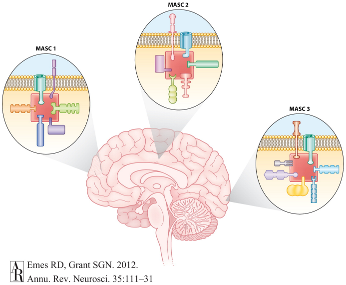
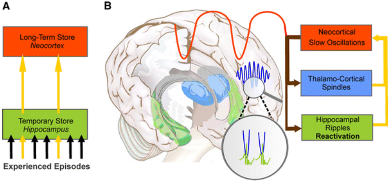



[Emes and Grant (2012)]

Memories stored in different places for different timescales

[Squire and Alvarez (1995)]

[McClelland et al. (1995)]




[Born and Wilhelm (2012)]

Also: Cerebellar cortex $\rightarrow$ nuclei.

[Attwell et al. (2002)]

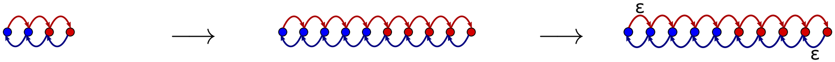
[Cooke et al. (2004)]

# Synaptic structure and function: general principles

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

What can we conclude?

Short timescale $\longrightarrow$ Moderate timescale $\longrightarrow$ Long timescale



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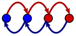
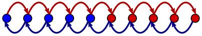
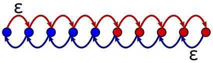
 $\longrightarrow$  $\longrightarrow$ 


short topology $\longrightarrow$ long topology

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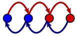
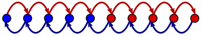
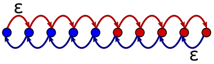
 $\longrightarrow$  $\longrightarrow$ 


short topology $\longrightarrow$ long topology

deterministic synapse $\longrightarrow$ stochastic synapse

# Experimental tests?

Traditional experiments:

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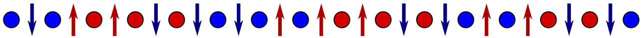
To fit a model: long sequence of small plasticity events.
Observe the changes in synaptic efficacy.



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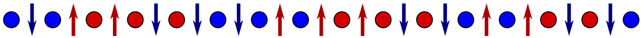
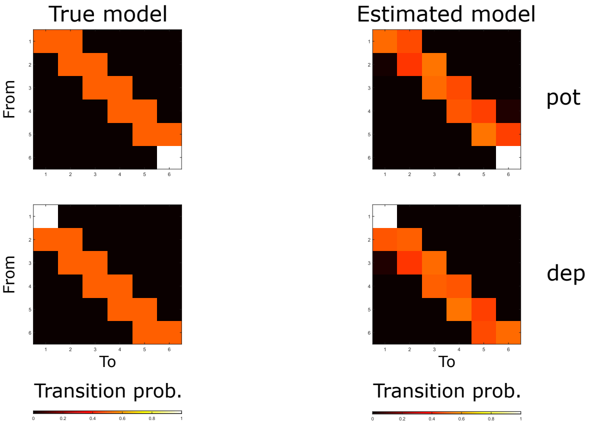


**EM algorithms:**
Sequence of hidden states $\rightarrow$ estimate transition probabilities
Transition probabilities $\rightarrow$ estimate sequence of hidden states

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

# Simulated experiment




Problem: need *long* sequences.
Whole cell patch of postsynaptic neuron → Ca washout.

# Conclusions

- 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.
- We understood which types of synaptic structure are useful for storing memories for different timescales.
- We studied more than a single model. We studied *all possible models*, to extract general principles relating synaptic structure to function

# Acknowledgements

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Rhea Kimpo

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Hanmi Lee

Marcus Benna

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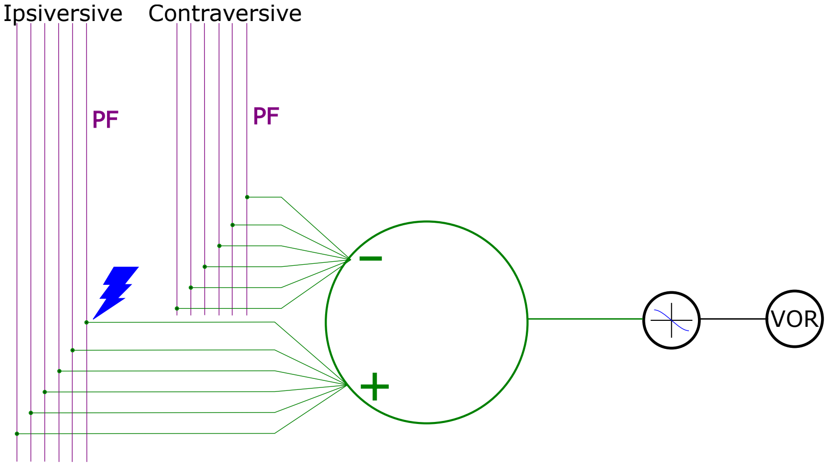
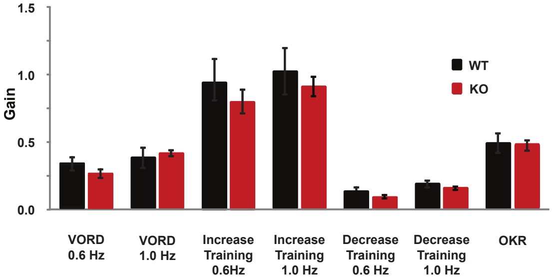
# Model of circuit

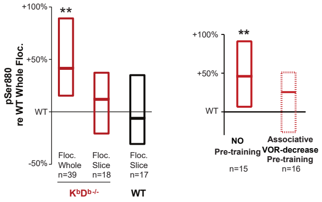


# Baseline



1.5
1.0
0.5
0.0
Gain
WT
KO
VORD 0.6 Hz
VORD 1.0 Hz
Increase Training 0.6Hz
Increase Training 1.0 Hz
Decrease Training 0.6 Hz
Decrease Training 1.0 Hz
OKR

# Evidence: level of depression



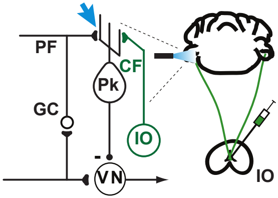

Basal level of GluR2 phosphorylation at serine 880 in AMPA receptor.

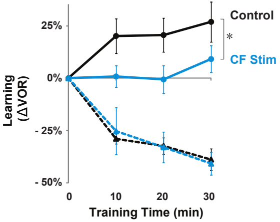
Biochemical signature of PF-Pk LTD.

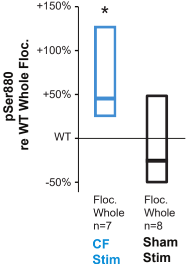
Shows that # depressed synapses in flocculus is larger in KO than WT.

# Evidence: saturation by CF stimulation

Use Channelrhodopsin to stimulate CF →increase LTD in PF-Pk synapses
→simulate saturation in WT.

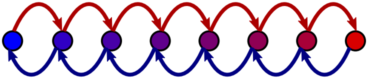


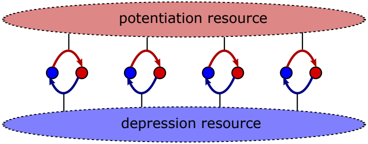



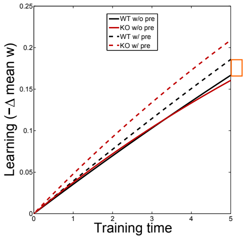
# Other models that fail

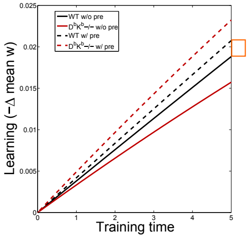
## Multistate synapse



Pooled resource model



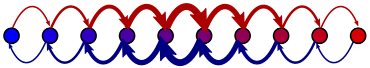



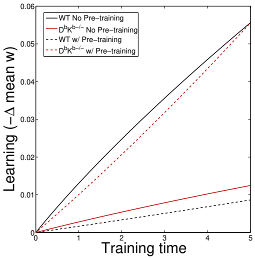




[Amit and Fusi (1994)]

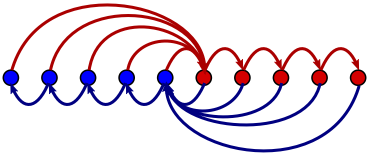
# Other models that work

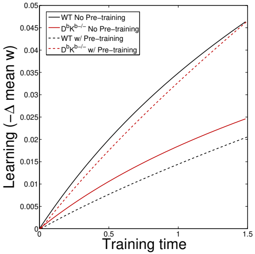
Non-uniform multistate model





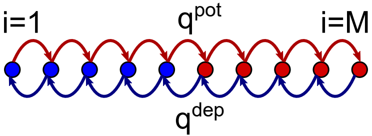

Cascade model






[Fusi et al. (2005)]

# Mathematical explanation




Serial synapse: $\boldsymbol{\pi}_i \sim \mathcal{N}\left(\frac{q^{\text{pot}}}{q^{\text{dep}}}\right)^i$.

Learning rate $\sim \boldsymbol{\pi}_{M/2}\left(\frac{q^{\text{dep}}}{q^{\text{pot}}}\right) = \mathcal{N}\left(\frac{q^{\text{pot}}}{q^{\text{dep}}}\right)^{\frac{M}{2}-1}$.

For $M > 2$: larger $q^{\text{dep}} \implies$ slower learning.

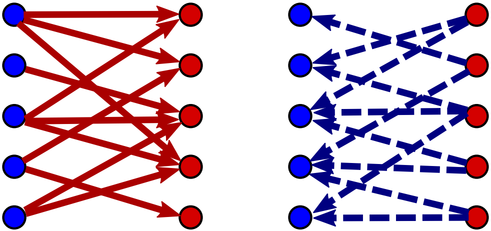
For $M = 2$: larger $q^{\text{dep}} \implies$ larger $\mathcal{N} \implies$ faster learning.

# Initial SNR as flux

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

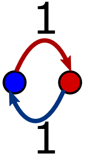
$$\mathrm{SNR}(0) \leq \frac{4\sqrt{N}}{r}\,\mathbf{\Phi}_{-+}.$$

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: 


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

Maximal initial SNR:

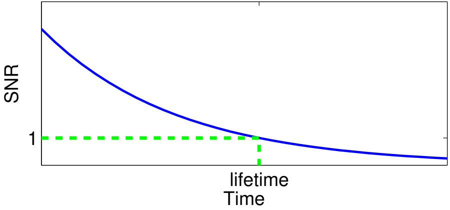
$$\mathrm{SNR}(0) \leq \sqrt{N}.$$

# Area under memory curve

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

Area bounds memory lifetime:

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




This area has an upper bound:

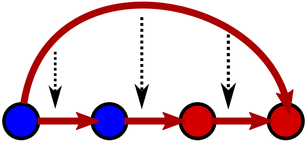
$$\mathcal{A} \leq \sqrt{N}(M-1)/r.$$

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

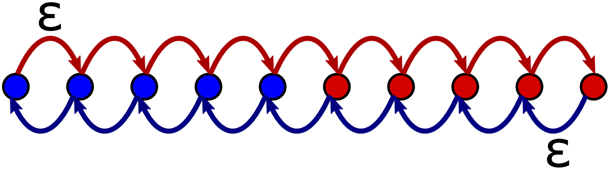
$$A = \frac{2\sqrt{N}}{r} \sum_k \pi_k \left| k - \langle k \rangle \right|.$$

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.

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

# Technical detail: ordering states

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

$$\eta = \sum_j \mathbf{T}_{ij} \boldsymbol{\pi}_j,$$

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

[Kemeny and Snell (1960)]

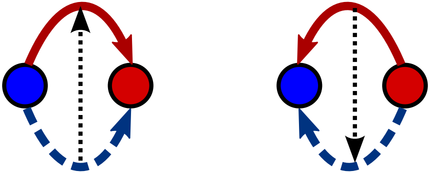
We define:

$$\eta_i^+ = \sum_{j \in \text{strong}} \mathbf{T}_{ij} \boldsymbol{\pi}_j, \qquad \eta_i^- = \sum_{j \in \text{weak}} \mathbf{T}_{ij} \boldsymbol{\pi}_j.$$

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

# Technical detail: upper/lower triangular

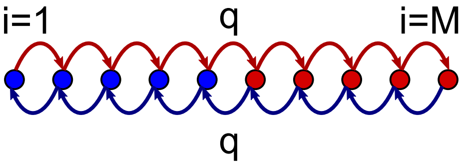
With states in order:



Endpoint: potentiation goes right, depression goes left.

back

# Intuition for using topology




$$\mathcal{I} \propto q, \qquad \max_a \tau_a \propto \frac{1}{q},$$

$$\mathcal{I} \propto \frac{1}{M}, \qquad \max_a \tau_a \propto M^2,$$

$$\Longrightarrow$$

Stochasticity: $\mathcal{I} \propto \dfrac{1}{\tau_{\max}}$,

Topology: $\mathcal{I} \propto \dfrac{1}{\sqrt{\tau_{\max}}}$.

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