Learning and memory with complex synaptic plasticity

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My research areas

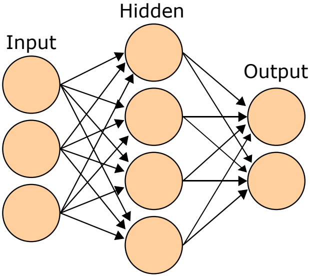
Learning and memory
Structure of synapses & function.
Learning v. remembering tradeoff.
Success & failure in trying to enhance learning.

Energy use in living systems
Energy cost of signalling/sensing.
Tradeoffs with accuracy & speed.
Thermodynamics $\leftrightarrow$ information geometry.

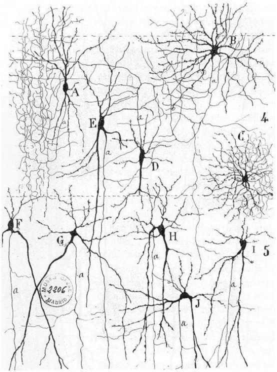
High dimensional statistics
Theory of random projections and the geometry of data.
Neural recordings as projections.

What is a synapse?

Comp-neuro/machine learning



Cellular biology



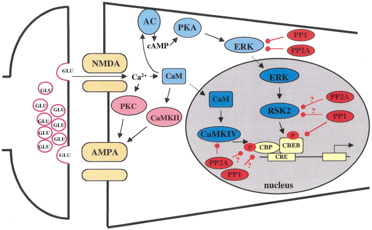
[Cajal (1899)]

What is a synapse?

Comp-neuro/machine learning

$$W_{ij}$$

Cellular biology



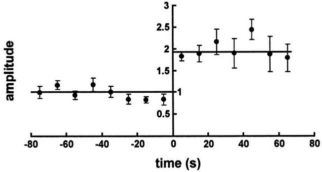
[Klann (2002)]

Storage capacity of synaptic memory

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

Assumes unbounded analogue synapses

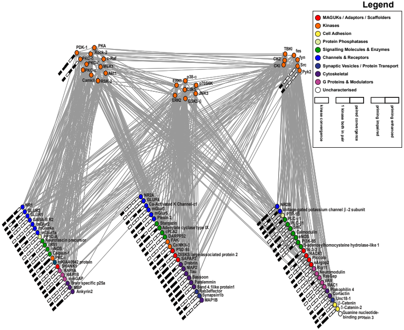
With discrete, finite synapses:
$\Longrightarrow$ memory capacity $\sim \mathcal{O}(\log N)$.
[Amit and Fusi (1992), Amit and Fusi (1994)]



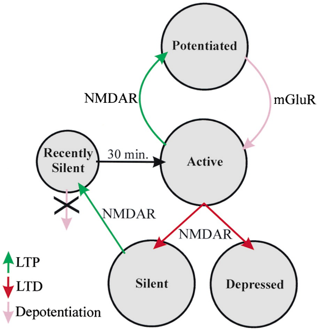
[Petersen et al. (1998), O'Connor et al. (2005)]

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

Synapses are complex

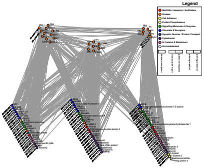


[Coba et al. (2009)]



[Montgomery and Madison (2002)]

Synapses are complex



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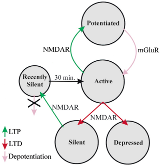
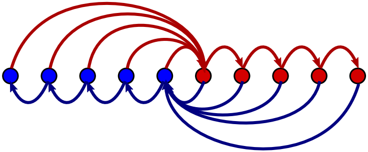


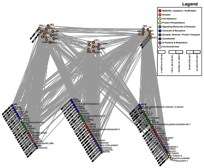
[Montgomery and Madison (2002)]

Cascade model



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

Synapses are complex



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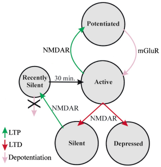

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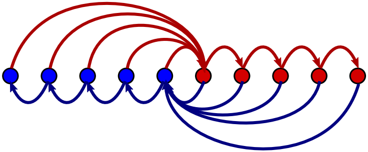


Capacity $\propto N^{2/3}$. [Fusi et al. (2005)]

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:

→ underlying mechanisms and principles.

→ trade-offs between aspects of performance (e.g. learning vs. memory).

→ properties of models that best manage these trade-offs.

Outline

1. Memory over different timescales
   - Quantifying memory quality
   - Frontiers of memory
   - Implications of memory limits

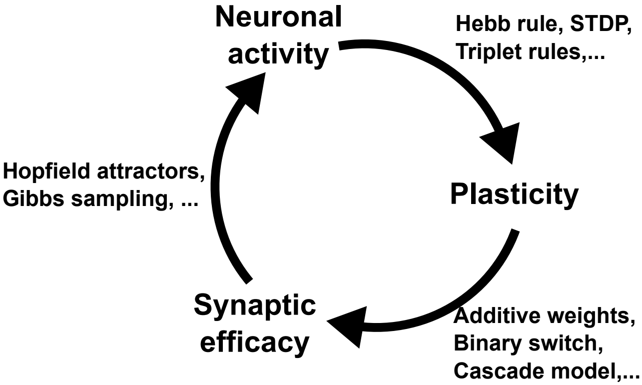
2. Designing experiments

Section 1

Memory over different timescales

“A memory frontier for complex synapses”, S Lahiri and S Ganguli.
Adv. Neural Inf. Process. Syst. 26, pp. 1034–1042., (2013).
NeurIPS 2013 Outstanding Paper Award.

Synaptic learning and memory



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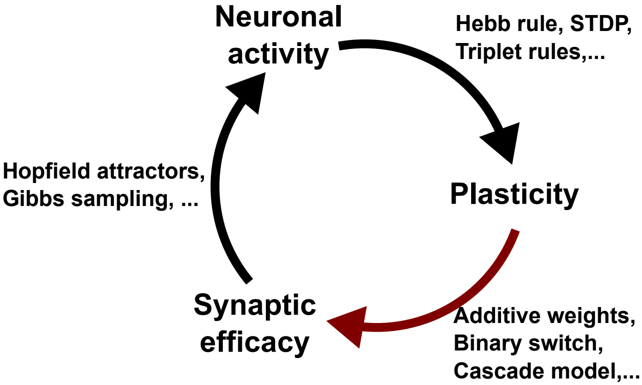
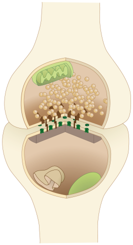


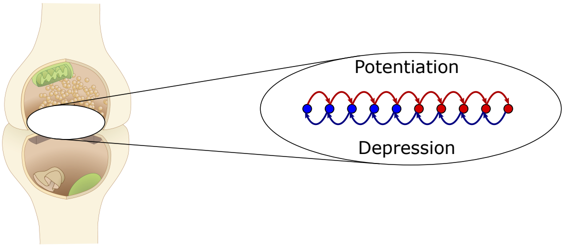
Models of complex synaptic dynamics



Models of complex synaptic dynamics

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

● 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)]
[Smith et al. (2006), Lahiri and Ganguli (2013)]

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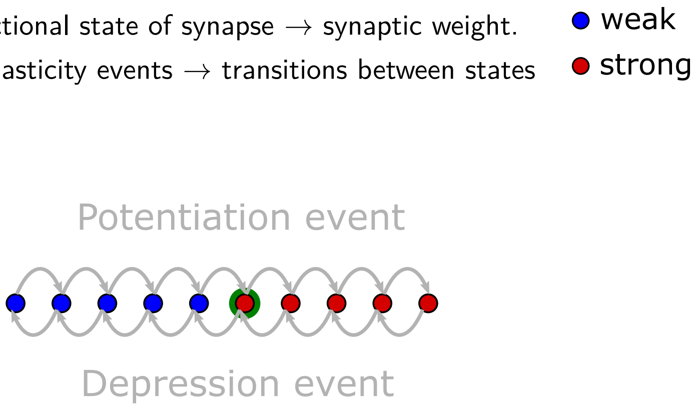

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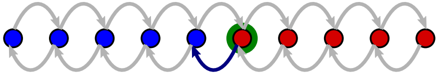
Potentiation event



Depression event

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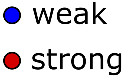

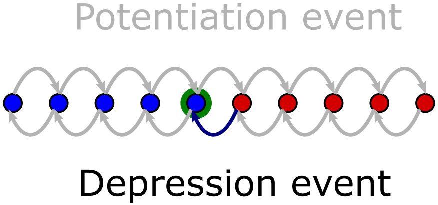

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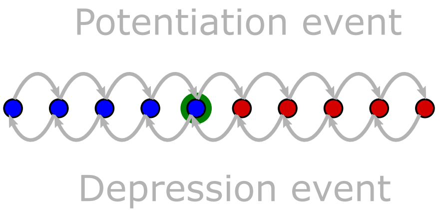

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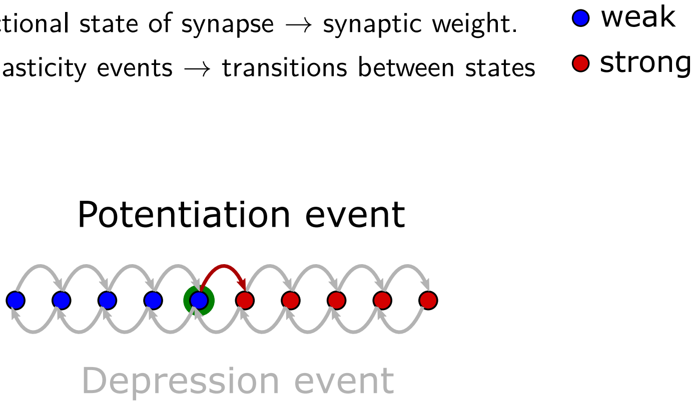

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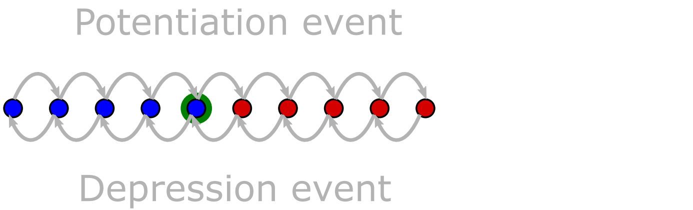

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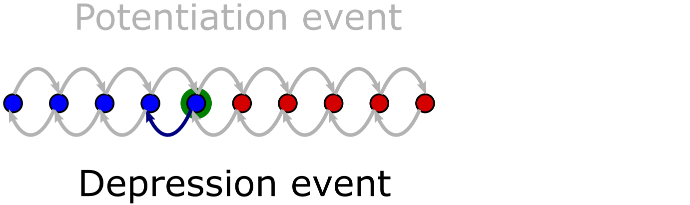

Metaplasticity: change propensity for plasticity
(independent of change in synaptic weight).

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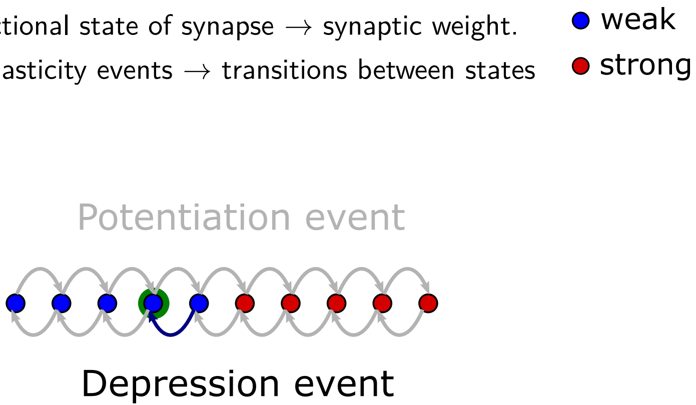

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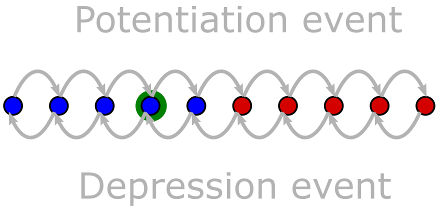

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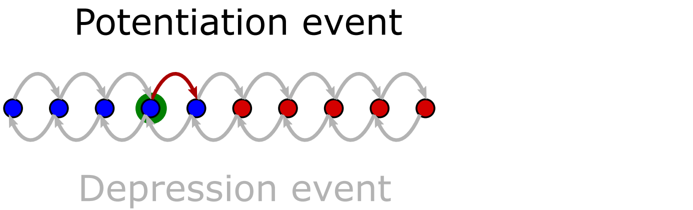

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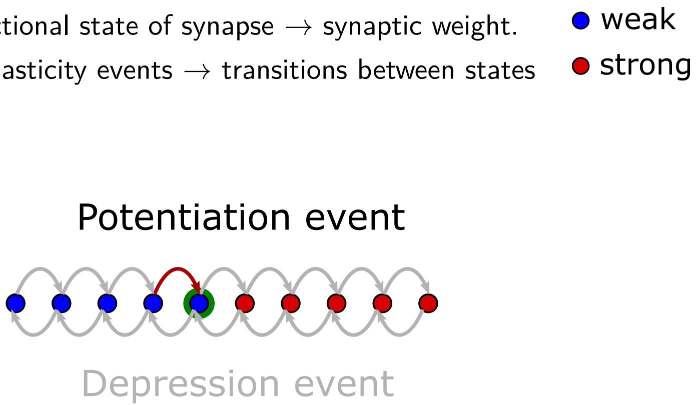

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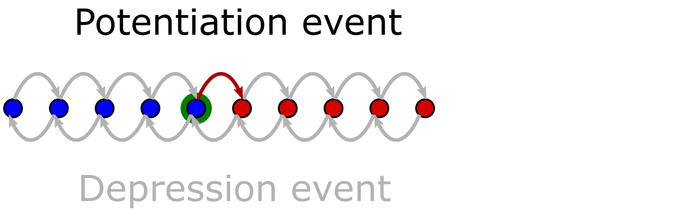

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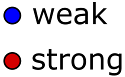

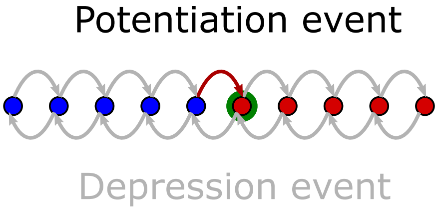

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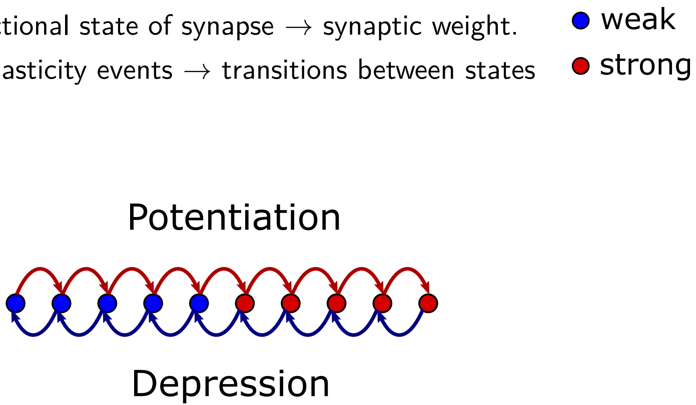

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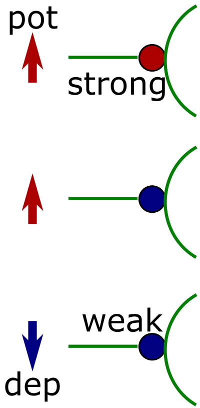
Synaptic memory curves



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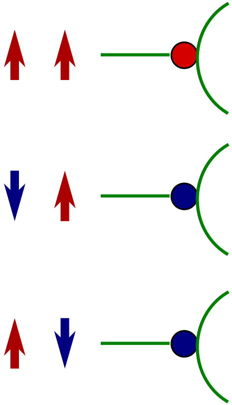

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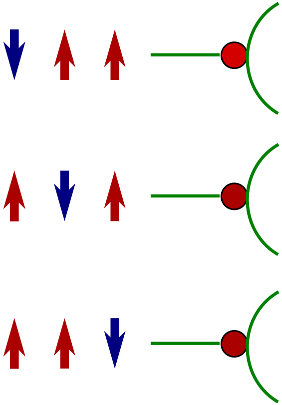

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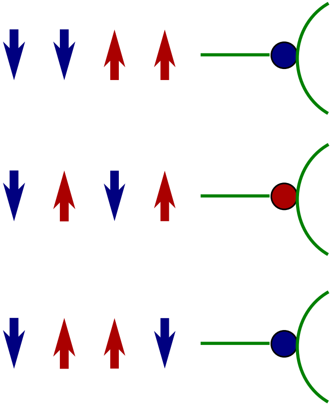

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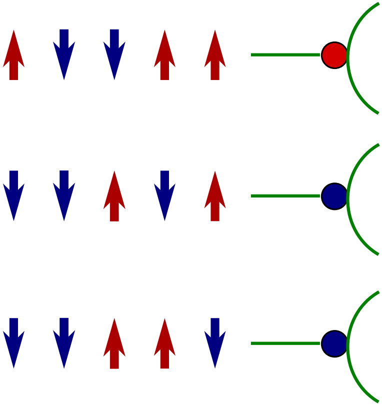

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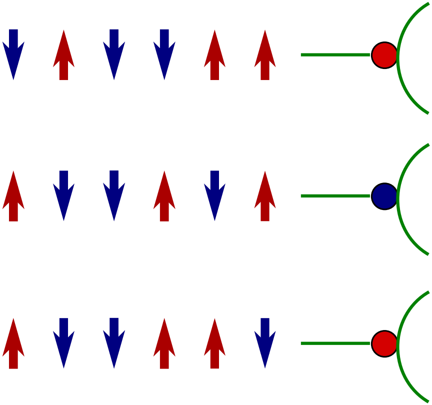

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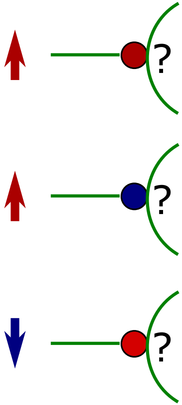

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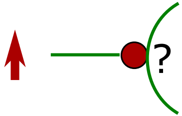
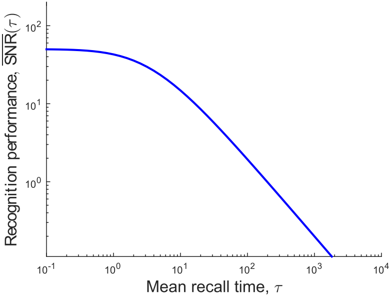
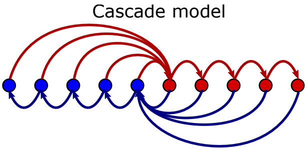


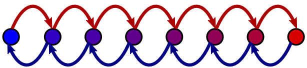
Recognition memory: has this pattern been seen before?
Performance described by SNR of $\vec{w}(t) \cdot \vec{w}_{\text{test}}$.



Specific models of complex synaptic dynamics

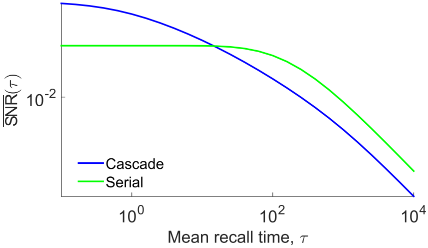
Two example models of complex synapses.





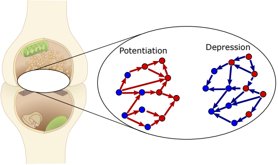
[Fusi et al. (2005), Leibold and Kempter (2008), Ben-Dayan Rubin and Fusi (2007)]

These have different memory storage properties

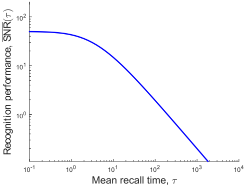


General principles relating structure and function?

Synaptic structure



Synaptic function

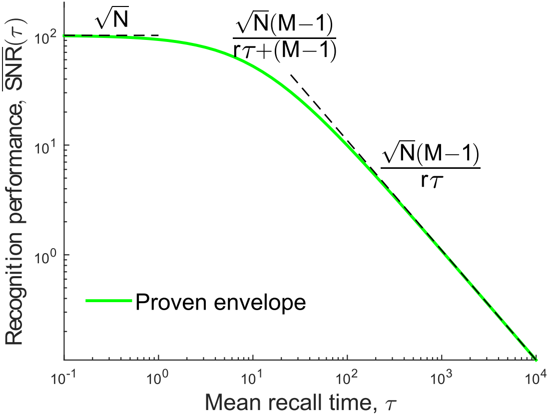


- What are the fundamental limits of memory?
- Which models achieve these limits?
- What are the theoretical principles behind the optimal models?

Proven envelope: memory frontier

Upper bound on memory curve at *any* timescale.

N: # synapses,
M: # states.



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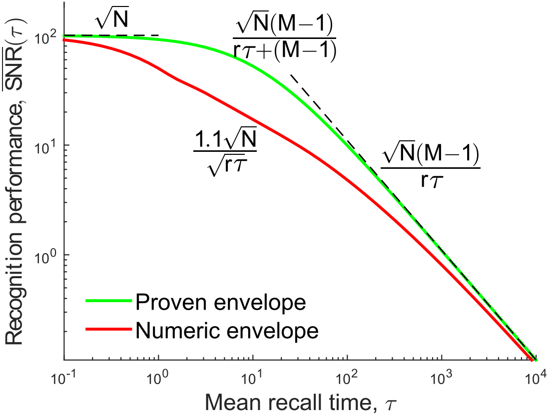
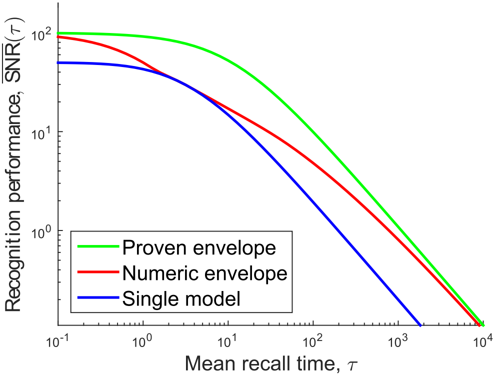
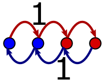


Models that maximize memory for one timescale





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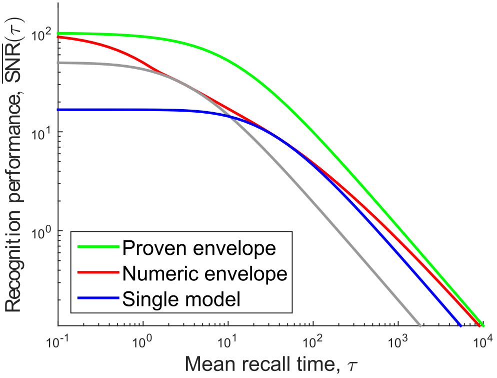

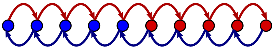

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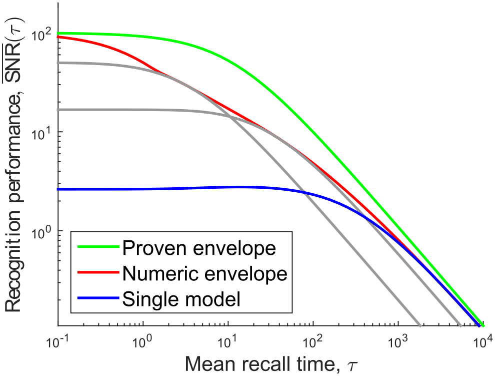
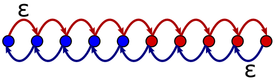
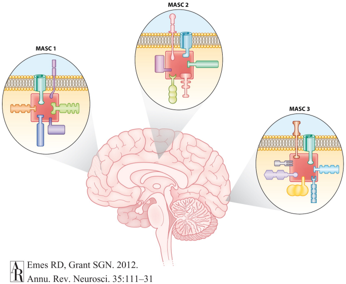




Synaptic diversity and timescales of memory

Different synapses have different molecular structures.



[Emes and Grant (2012)]

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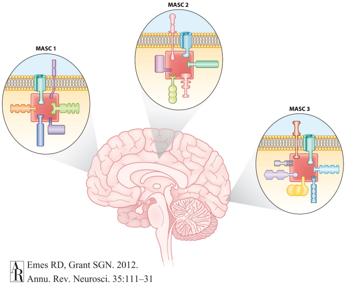
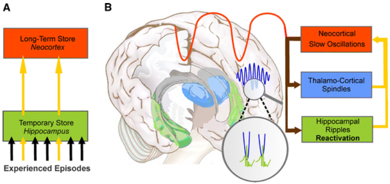


[Emes and Grant (2012)]

Memories stored in different places for different timescales

[Squire and Alvarez (1995)]

[McClelland et al. (1995)]



[Born and Wilhelm (2012)]

Also: Cerebellar cortex → nuclei.

[Attwell et al. (2002)]

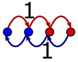
[Cooke et al. (2004)]

Synaptic structure and function: general principles

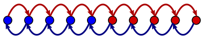
Real synapses limited by molecular building blocks.
Evolution had larger set of priorities.

What can we conclude?

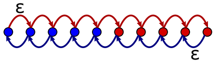
Short timescale $\longrightarrow$ Moderate timescale $\longrightarrow$ Long timescale



$\longrightarrow$



$\longrightarrow$

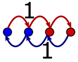


Synaptic structure and function: general principles

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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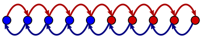

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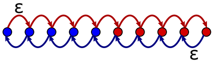

short topology $\longrightarrow$ long topology

Synaptic structure and function: general principles

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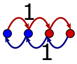
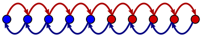
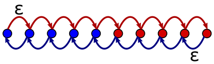
Short timescale	$\longrightarrow$	Moderate timescale	$\longrightarrow$	Long timescale
	$\longrightarrow$		$\longrightarrow$	
short topology	$\longrightarrow$	long topology		
		deterministic synapse	$\longrightarrow$	stochastic synapse

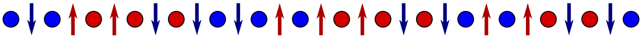
Experimental tests?

Traditional experiments:

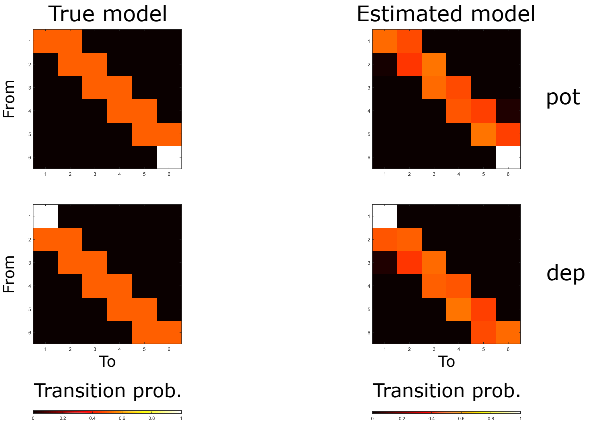
Experimental tests?

Traditional experiments:

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



Simulated experiment



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

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.
- 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

Future directions

Learning and memory

- Multiple presentations.
- Correlations.
- More realistic tasks.
- Relation to molecular structure?

Energy use in living systems

- Include space as well as time.
- Coarse graining: molecules $\to$ cells $\to$ systems.

High dimensional statistics

- Theory of noisy random projections.

Acknowledgements

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Funding: Swartz Foundation, Stanford Bio-X Genentech fellowship.

Summary

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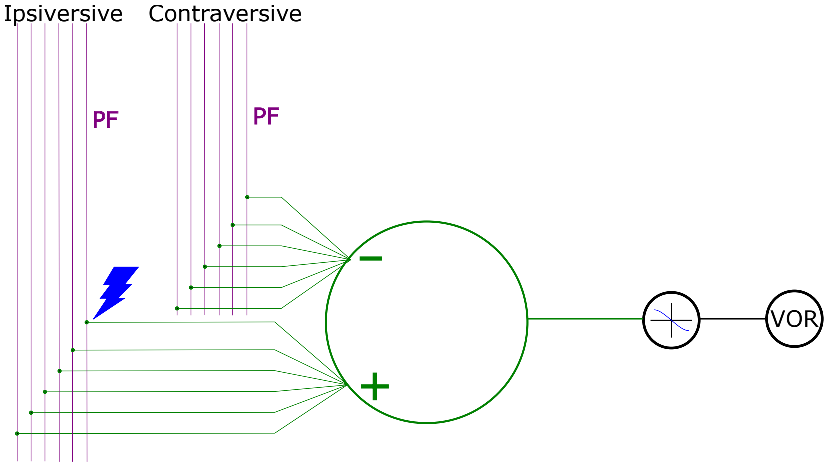
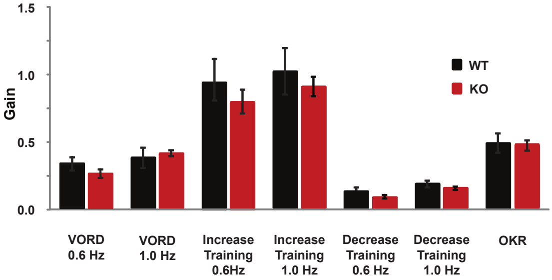
- We studied more than a single model. We studied *all possible models*, to extract general principles relating synaptic structure to function

Model of circuit

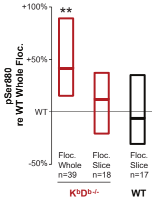


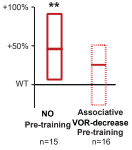
Baseline



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





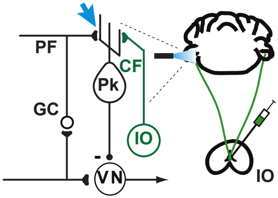
Basal level of GluR2 phosphorylation at serine 880 in AMPA receptor.

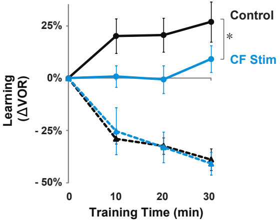
Biochemical signature of PF-Pk LTD.

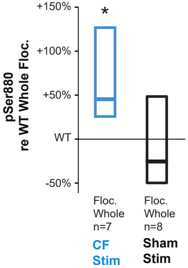
Shows that # depressed synapses in flocculus is larger in KO than WT.

Evidence: saturation by CF stimulation

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

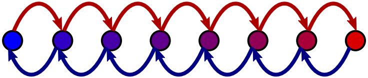




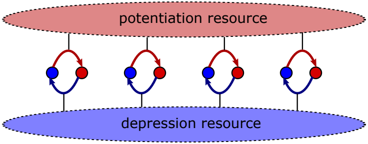


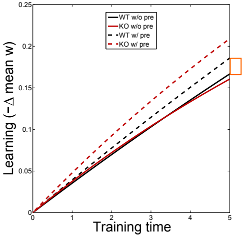
Other models that fail

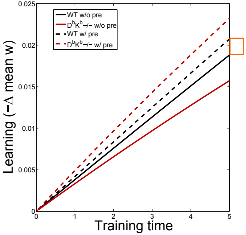
Multistate synapse



Pooled resource model



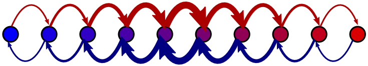


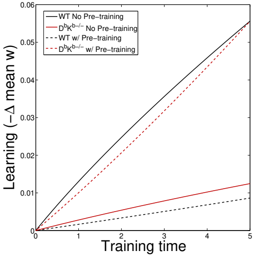


[Amit and Fusi (1994)]

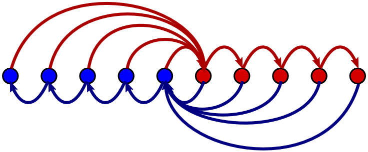
Other models that work

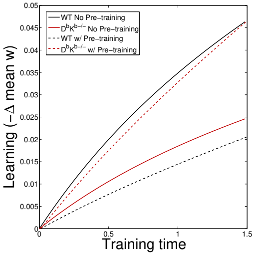
Non-uniform multistate model





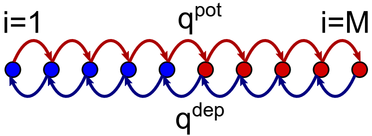
Cascade model





[Fusi et al. (2005)]

Mathematical explanation



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

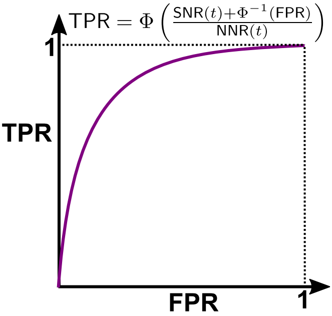
Learning rate $\sim \boldsymbol{\pi}_{M/2} \left(\frac{q^{\text{dep}}}{q^{\text{pot}}} \right) = \mathcal{N} \left(\frac{q^{\text{pot}}}{q^{\text{dep}}} \right)^{\frac{M}{2}-1}.$

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

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

Quantifying memory quality

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



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

$$\overline{\text{SNR}}(\tau) = \int \mathrm{d}\tau \, \frac{e^{-t/\tau}}{\tau} \, \text{SNR}(t).$$

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

Also: KL divergence, Chernoff distance, ...

Parameters for synaptic dynamics

$$f^{\text{pot/dep}} = \text{fraction of events that are pot/dep},$$

pot. event: $M_{ij}^{\text{pot}} = \text{transition prob. } i \to j,$ $\qquad \mathbf{W}^{\text{pot}} = f^{\text{pot}}(\mathbf{M}^{\text{pot}} - I),$

dep. event: $M_{ij}^{\text{dep}} = \text{transition prob. } i \to j,$ $\qquad \mathbf{W}^{\text{dep}} = f^{\text{dep}}\big(\mathbf{M}^{\text{dep}} - I\big).$

Constraints:

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

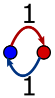
Memory curve given by

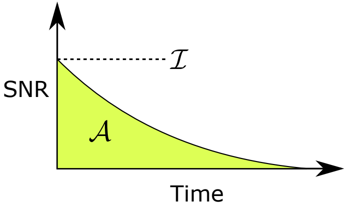
$$\begin{aligned}\overline{\text{SNR}}(\tau) &= \sqrt{N}\,\boldsymbol{\pi}\left(\mathbf{W}^{\text{pot}} - \mathbf{W}^{\text{dep}}\right)\left[\mathbf{I} - r\tau\left(\mathbf{W}^{\text{pot}} + \mathbf{W}^{\text{dep}}\right)\right]^{-1}\mathbf{w}.\\ &= \sqrt{N}\sum_a \frac{\mathcal{I}_a}{1 + r\tau/\tau_a}.\end{aligned}$$

Upper bounds on measures of memory

Initial SNR:

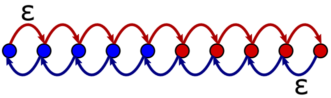
$$\mathcal{I} = \mathrm{SNR}(0) = \sum_a \mathcal{I}_a \leq \sqrt{N}.$$





Area under curve:

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



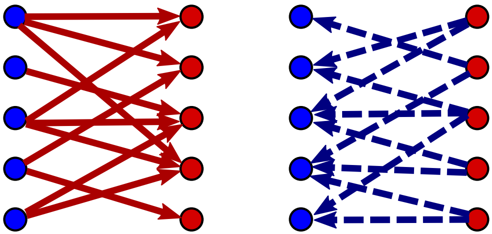
[Lahiri and Ganguli (2013)]

Initial SNR as flux

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

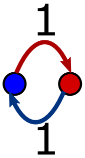
$$\mathrm{SNR}(0) \leq \frac{4\sqrt{N}}{r}\,\mathbf{\Phi}_{-+}.$$

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



Two-state model

Two-state model equivalent to previous slide:

Transitions: 

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

Maximal initial SNR:

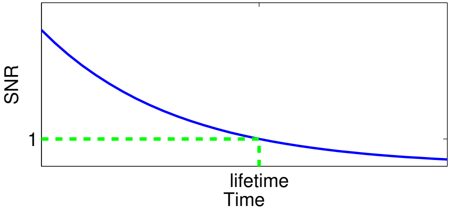
$$\mathrm{SNR}(0) \leq \sqrt{N}.$$

Area under memory curve

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

Area bounds memory lifetime:

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



This area has an upper bound:

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

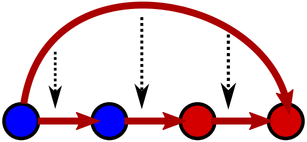
Saturated by a model with linear chain topology.

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

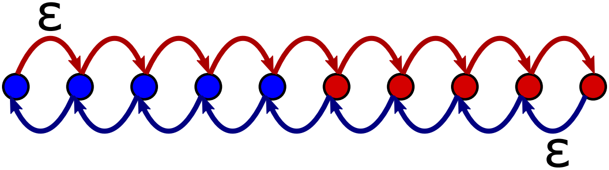
$$A = \frac{2\sqrt{N}}{r} \sum_k \pi_k \left| k - \langle k \rangle \right| .$$

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)]

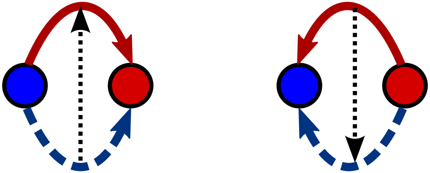
We define:

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

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

Technical detail: upper/lower triangular

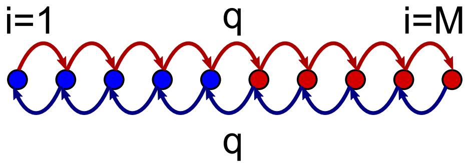
With states in order:



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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