

2013-04-15

Complex synapses

A general theory of learning and memory with Complex
Synapses
based on work with Surya Ganguli

Subhaneil Lahiri

Stanford University, Applied Physics

April 15, 2013

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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 memory have terrible storage 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.

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Complex synapses

└ Introduction

1. amplitude of psp.
2. finite number of values.

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 memory have terrible storage 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.

- 1 Why complex synapses?
- 2 Modelling synaptic complexity
- 3 Upper bounds
- 4 Envelope memory curve

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Complex synapses

└ Outline

1. review terrible properties of simple synapses.
2. mathematical formalism of model, quantify performance (memory decay over time)
3. upper bounds on single numbers that depend on whole memory curve (decay over time)
4. upper bounds at finite times

Outline

- 1 Why complex synapses?
- 2 Modelling synaptic complexity
- 3 Upper bounds
- 4 Envelope memory curve

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Complex synapses
└ Why complex synapses?

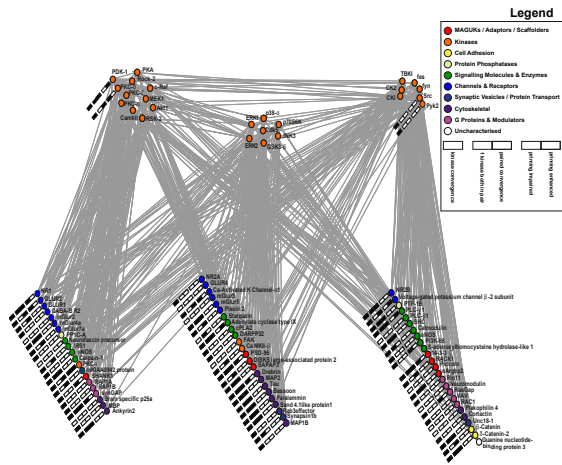
Section 1

Why complex synapses?

Section 1

Why complex synapses?

Complex synapse



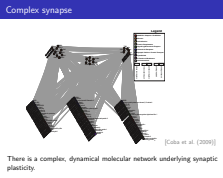
[Coba et al. (2009)]

There is a complex, dynamical molecular network underlying synaptic plasticity.

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Complex synapses

- Why complex synapses?
- Complex synapse



1. Molecular network, post-synaptic density, from Seth Grant
2. Does this matter?
3. Could just be the machinery for changing synaptic weight
4. link back to questions on "There"

Storage capacity of synaptic memory

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

Requires synapses' dynamic range also $\propto N$.

If we restrict synaptic weight to a fixed, finite set of values,
 \implies tradeoff between learning and forgetting:
new memories overwriting old.

If we wish to store new memories rapidly, memory capacity $\sim \mathcal{O}(\log N)$.
[Amit and Fusi (1992), Amit and Fusi (1994)]

To circumvent this tradeoff, need to go beyond model of a synapse as a single number.

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Complex synapses

└ Why complex synapses?

└ Storage capacity of synaptic memory

1. very plastic: learn easy, forget easy
2. little plasticity, remember better, learn harder
3. or sparse $\sim \log N/N$
4. one way around limit: complexity

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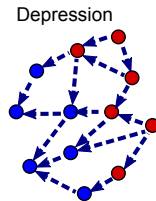
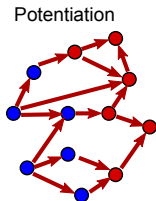
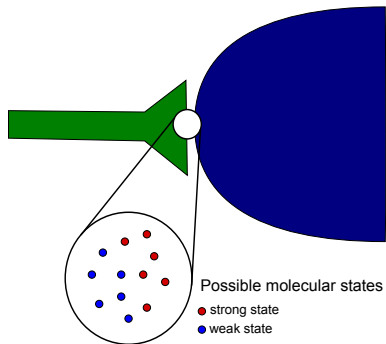
Complex synapses
└─ Modelling synaptic complexity

Section 2

Modelling synaptic complexity

Section 2

Modelling synaptic complexity

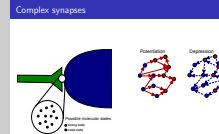


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Complex synapses

└ Modelling synaptic complexity

└ Complex synapses



1. functional states, not molecules
2. synaptic weight depends on state
3. many states can have same weight
4. stochastic transitions

Simplifying assumptions

- There are N identical synapses with M internal functional states.
- States of different synapses are independent of each other.
- Which synapses eligible for plasticity chosen randomly.
- Potentiating/depressing plasticity events \sim Poisson processes with rates $rf^{\text{pot/dep}}$, where $f^{\text{pot}} + f^{\text{dep}} = 1$.
- Potentiation and depression are described by Markov processes with transition probabilities $\mathbf{M}^{\text{pot/dep}}$.
- Synaptic weights of the internal states are given by vector \mathbf{w} .
Can only take values ± 1 .

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Complex synapses

└ Modelling synaptic complexity

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- Synaptic weights of the internal states are given by vector \mathbf{w} .
Can only take values ± 1 .

1. allows us to concentrate on synapse, not neuron/network
2. don't care if STDP...
3. r = total rate of plasticity events per synapse, $f^{\text{pot/dep}}$ = fraction of events that are potentiating/depressing.
4. matrix elements: transition prob from $i \rightarrow j$, given pot/dep
5. looks like binary synapse from outside. Inside...
6. ideal observer reads weights, not electrical activity: don't model neurons/network
7. upper bound on electrical activity readout

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

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

At $t = 0$, the memory is created by $\mathbf{M}^{\text{pot/dep}}$ with probability $f^{\text{pot/dep}}$.

Forgetting caused by subsequent memories, evolving as

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

Eventually, this will settle into the equilibrium distribution:

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

1. for this one, we keep track of pot/dep, look for inc/dec of \mathbf{w}
2. \mathbf{W}^F is forgetting matrix, \mathbf{I} = identity, don't keep track of pot/dep
3. In equilibrium prior to memory creation

\vec{w} is the N -element vector of synaptic weights.

$$\text{Signal} = \langle \vec{w}_{\text{ideal}} \cdot \vec{w}(t) - \vec{w}_{\text{ideal}} \cdot \vec{w}(\infty) \rangle$$

$$\text{Noise} = \text{Var}(\vec{w}_{\text{ideal}} \cdot \vec{w}(\infty))$$

Related to reconstruction probability of single synapses.

$$\text{SNR}(t) \sim \sqrt{N} P(\text{strong/weak}, t | \text{pot/dep}, t=0) - \dots (t=\infty).$$

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Complex synapses

└ Modelling synaptic complexity

└ Memory curve

1. of different synapses
2. ideal observer reads weights, not states
3. upper bound on electrical activity readout
4. ideal: pot→strong...
5. subtract baseline, some overlap even w/o encoding
6. if we ignore correlations...

\vec{w} is the N -element vector of synaptic weights.

$$\text{Signal} = \langle \vec{w}_{\text{ideal}} \cdot \vec{w}(t) - \vec{w}_{\text{ideal}} \cdot \vec{w}(\infty) \rangle$$

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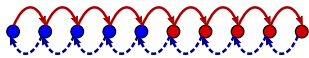
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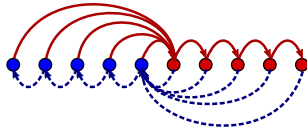
Example models

Two example models of complex synapses.

Multistate model

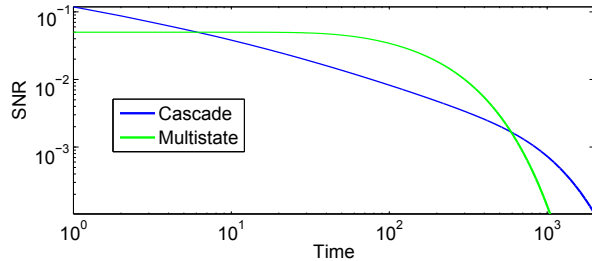


Cascade model



[Amit and Fusi (1994), Fusi and Abbott (2007), Fusi et al. (2005)]

These have different memory storage properties



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Complex synapses

└ Modelling synaptic complexity

└ Example models

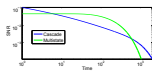
Example models

Two example models of complex synapses.



[Amit and Fusi (1994), Fusi and Abbott (2007), Fusi et al. (2005)]

These have different memory storage properties



1. previous work, also: Benna-Fusi
2. Multistate good at one time, bad at others,
3. Cascade, less well at that time, better over range of times.

- Can we understand the space of *all possible* synaptic models?
- How does structure (topology) of model \rightarrow function (memory curve)?
- What are the limits on what can be achieved?
- Which transition topologies saturate these limits?

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Complex synapses

└ Modelling synaptic complexity

└ Questions

Questions

- Can we understand the space of all possible synaptic models?
- How does structure (topology) of model \rightarrow function (memory curve)?
- What are the limits on what can be achieved?
- Which transition topologies saturate these limits?

1. not just individual models
2. understand net (link on topology)
3. avoid using word “optimal”. depends on what want to do.

Memory curve given by

$$\text{SNR}(t) = \frac{\sqrt{N}(2f^{\text{pot}}f^{\text{dep}})}{\sqrt{4\mathbf{p}_+^\infty\mathbf{p}_-^\infty}} \mathbf{p}^\infty \left(\mathbf{M}^{\text{pot}} - \mathbf{M}^{\text{dep}} \right) \exp(rt\mathbf{W}^F) \mathbf{w}.$$

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

Eigenmode decomposition:

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

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Complex synapses

└ Modelling synaptic complexity

└ Memory curve 2

1. prefactors don't do anything, ignore
2. prior state, encoding, forgetting, readout
3. difficult to to apply
4. what are constraints on these?

Memory curve given by

$$\text{SNR}(t) = \frac{\sqrt{N}(2f^{\text{pot}}f^{\text{dep}})}{\sqrt{4\mathbf{p}_+^\infty\mathbf{p}_-^\infty}} \mathbf{p}^\infty \left(\mathbf{M}^{\text{pot}} - \mathbf{M}^{\text{dep}} \right) \exp(rt\mathbf{W}^F) \mathbf{w}.$$

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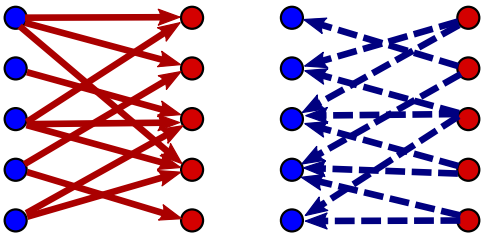
$$\text{SNR}(t) = \sqrt{N} \sum_a \mathcal{I}_a e^{-rt/\tau_a}.$$

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 $\mathbf{w} \rightarrow -1$.



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Complex synapses

└ Upper bounds

└ Initial SNR

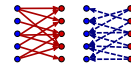
└ Initial SNR as flux

Initial SNR as flux

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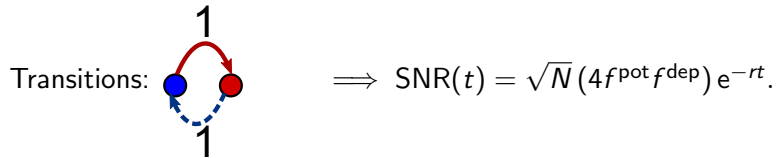
Max when potentiation guarantees $\mathbf{w} \rightarrow +1$,
depression guarantees $\mathbf{w} \rightarrow -1$.



1. flux = eq prob \times trans prob
2. usually saturated: pot never dec, dep never inc
3. transitions out of one node sum to 1
4. equivalent to two-state model: doesn't matter which strong/weak state, same prob of going to other set.

Two-state model

Two-state model equivalent to previous slide:



Maximal initial SNR:

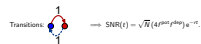
$$\text{SNR}(0) \leq \sqrt{N}.$$

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Complex synapses
└ Upper bounds
└ Initial SNR
└ Two-state model

Two-state model

Two-state model equivalent to previous slide:



Maximal initial SNR:

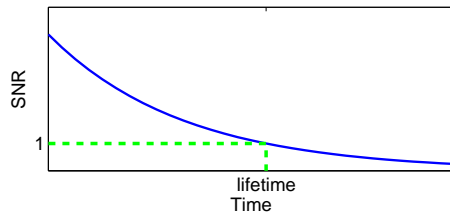
$$\text{SNR}(0) \leq \sqrt{N}.$$

1. decays very quickly
2. $f^{\text{pot}} = \frac{1}{2}$
3. Initial SNR not a good thing to optimise.

Area under memory curve

Memory lifetime bounded by area under SNR curve:

$$\text{SNR}(\text{lifetime}) = 1 \\ \Rightarrow \text{lifetime} < \mathcal{A}.$$



This area has an upper bound:

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

Saturated by a model with linear chain topology.

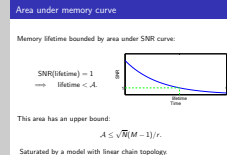
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Complex synapses

└ Upper bounds

└ Area under memory curve

└ Area under memory curve



1. lifetime = area under green j area under blue
2. capacity $\sim r$ lifetime, #new memories before we forget original.
3. reminder: $N = \# \text{synapses}$, $M = \# \text{states}$
4. proof next slide

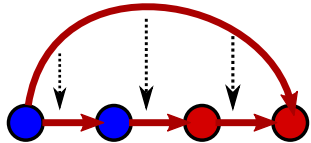
Proof of area bound

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)]



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Complex synapses

└ Upper bounds

└ Area under memory curve

└ Proof of area bound

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[Barrett and van Rossum (2008)]



1. relies on order & technical condition
2. max given \mathbf{p}^∞
3. now max wrt. \mathbf{p}^∞
4. keep c.o.m. in middle
5. similar result, slightly different conditions: linear weights, mutual info

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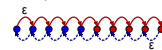
Complex synapses

└ Upper bounds

└ Area under memory curve

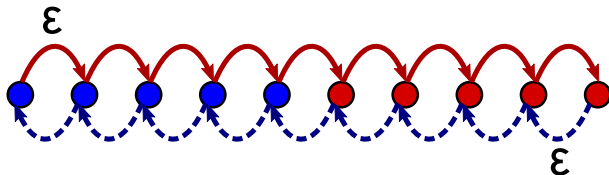
└ Saturating model

Make end states "sticky"



Has long decay time, but terrible initial SNR.

Make end states "sticky"



Has long decay time, but terrible initial SNR.

1. Difficult to get out of end state.
2. Area not a good thing to optimise

- Complex synapses
 - Envelope memory curve

Envelope memory curve

Envelope memory curve

SNR curve:

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

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 .

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Complex synapses

└ Envelope memory curve

└ Bounding finite time SNR

1. from eigenmode decomposition
2. from initial, area bounds

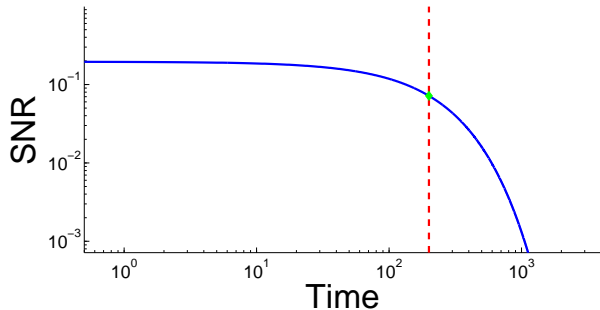
SNR curve: $\text{SNR}(t) = \sqrt{N} \sum_a \mathcal{I}_a e^{-rt/\tau_a}$.

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Constructing the envelope



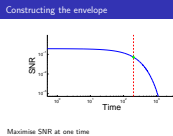
Maximise SNR at one time

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Complex synapses

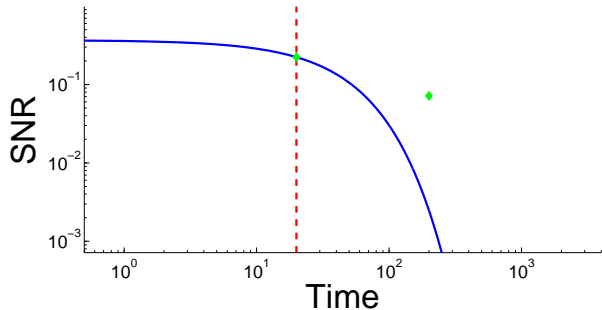
└ Envelope memory curve

└ Constructing the envelope



1. One exp. only constrains SNR at that time, not others

Constructing the envelope



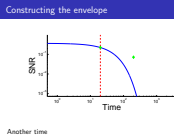
Another time

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Complex synapses

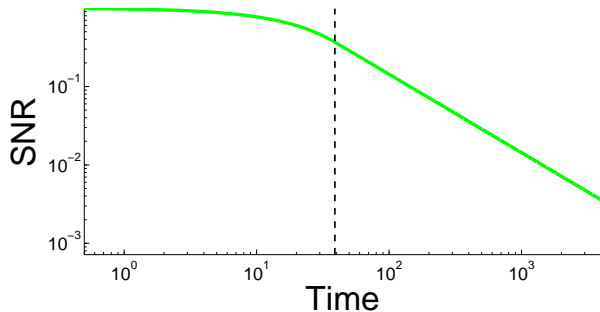
└ Envelope memory curve

└ Constructing the envelope



1. One exp. only constrains SNR at that time, not others
2. get another bound

Constructing the envelope



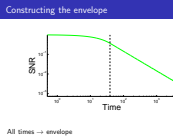
All times \rightarrow envelope

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Complex synapses

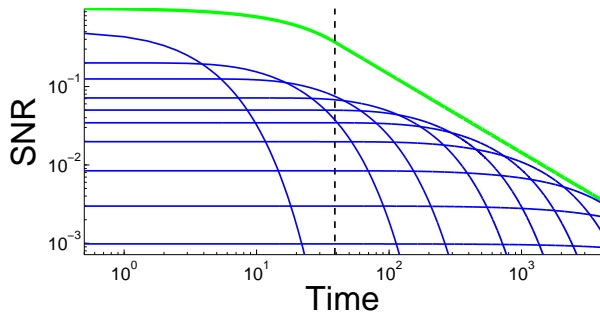
└ Envelope memory curve

└ Constructing the envelope



1. One exp. only constrains SNR at that time, not others
2. get another bound
3. vary time of max. no curve can cross this.
4. Regions: `init(1)`; `area(1,2)`
5. is it tight? can any constrained set of exps be achieved?

Constructing the envelope



Memory curves of example models.

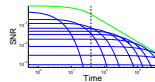
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Complex synapses

└ Envelope memory curve

└ Constructing the envelope

Constructing the envelope

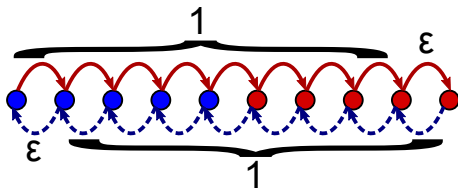


Memory curves of example models.

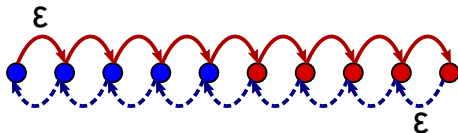
1. One exp. only constrains SNR at that time, not others
2. get another bound
3. vary time of max. no curve can cross this.
4. Regions: `init(1); area(1,2)`
5. is it tight? can any constrained set of exps be achieved?
6. no
7. One exp. discuss models next slide

Best models at single times

Early times:



Late times:



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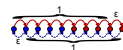
Complex synapses

└ Envelope memory curve

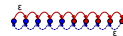
└ Best models at single times

Best models at single times

Early times:



Late times:



1. shorten length of chain, keeping deterministic
2. Area maximising.
3. two mechs for slowing forgetting: time (lower trans prob) and space (diffusion length)

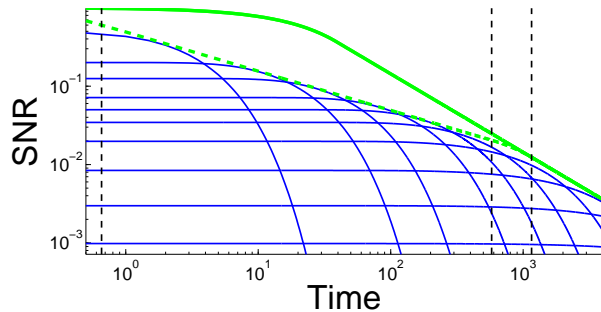
Conjecture: additional constraint

$$\mathcal{I}_a \sqrt{\tau_a} \leq \mathcal{O}(1).$$

Saturated by a diffusive chain:

$$\text{SNR}(0) \sim \frac{1}{M}, \quad \text{time-scale} \sim M^2.$$

1. Tested experimentally. Discuss later



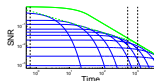
$$\begin{aligned}
 rt < \mathcal{O}(M^2), & \quad \text{envelope} \sim (rt)^{-1/2}, \\
 rt > \mathcal{O}(M^2), & \quad \text{envelope} \sim (rt)^{-1}.
 \end{aligned}$$

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Complex synapses

└ Envelope memory curve

└ Envelope 2



$$\begin{aligned}
 rt < \mathcal{O}(M^2), & \quad \text{envelope} \sim (rt)^{-1/2}, \\
 rt > \mathcal{O}(M^2), & \quad \text{envelope} \sim (rt)^{-1}.
 \end{aligned}$$

1. dashed: conjecture. tight.
2. earlier: diffusion limited. later: stochastic limited.
3. regions: init(1); sqrt(2,3); area(3,4)
4. Benna-Fusi hugs envelope? cascade $\sim t^{-3/4}$

Lifetime of a memory bounded by where envelope crosses 1

$$N > \mathcal{O}(M^2) \implies \text{lifetime} \leq \frac{\sqrt{N}(M-1)}{er},$$

$$N < \mathcal{O}(M^2) \implies \text{lifetime} \leq \frac{\gamma^2 N}{2er}.$$

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Complex synapses

└ Envelope memory curve

└ Lifetime bound

Lifetime of a memory bounded by where envelope crosses 1

$$\begin{aligned} N > \mathcal{O}(M^2) &\implies \text{lifetime} \leq \frac{\sqrt{N}(M-1)}{er}, \\ N < \mathcal{O}(M^2) &\implies \text{lifetime} \leq \frac{\gamma^2 N}{2er}. \end{aligned}$$

1. $\gamma \sim \mathcal{O}(1)$ constant in additional constant
2. First t^{-1} assumes M low. Second $t^{-1/2}$ applies to Benna-Fusi.
3. Independent synapses?

Additional constraint: other forms?

Involving eigenmodes:

$$\mathcal{I}_a \sqrt{\tau_a}, \quad \sum_a \mathcal{I}_a \sqrt{\tau_a}, \quad \sum_a \mathcal{I}_a^2 \tau_a.$$

Not involving eigenmodes

$$\mathcal{A} \times \text{SNR}(0), \quad \int dt \text{SNR}(t)^2.$$

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Complex synapses

└ Envelope memory curve

└ Additional constraint: other forms?

Involving eigenmodes:

$$\mathcal{I}_a \sqrt{\tau_a}, \quad \sum_a \mathcal{I}_a \sqrt{\tau_a}, \quad \sum_a \mathcal{I}_a^2 \tau_a.$$

Not involving eigenmodes

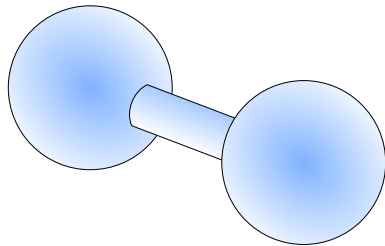
$$\mathcal{A} \times \text{SNR}(0), \quad \int dt \text{SNR}(t)^2.$$

1. as one-time max only involved one exp, would also work
2. right units
3. easier to work with?
4. L2 doesn't have nice expression in terms of matrices

Cheeger inequality

Cheeger constant:

$$\phi \equiv \min_S \left\{ \frac{\text{Perimeter}(\partial S)}{\text{Area}(S)} \right\}.$$



Timescale for diffusion to equilibrate

$$\frac{1}{D\tau_{\text{diffusion}}} > \mathcal{O}(1) \phi^2.$$

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Complex synapses

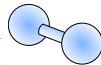
└ Envelope memory curve

└ Cheeger inequality

Cheeger inequality

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$$\phi = \min_S \left\{ \frac{\text{Perimeter}(\partial S)}{\text{Area}(S)} \right\}.$$



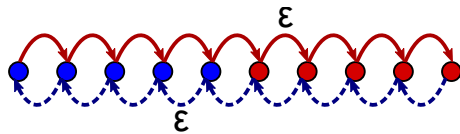
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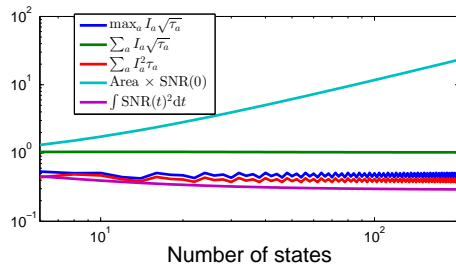
1. split into two pieces. pick smaller. higher dim.
2. bottleneck
3. if we want slow diffusion, need lhs small \rightarrow need bottleneck.
4. purely geometric
5. also inequality in other direction: want slow diffusion \rightarrow need bottleneck.
Not useful for us

Counter examples?

Put bottleneck somewhere else:



Set $\epsilon = 1/M$, see how putative constraints vary:



Also tried: random Markov chains.

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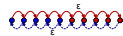
Complex synapses

└ Envelope memory curve

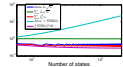
└ Counter examples?

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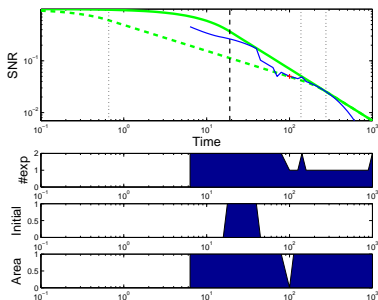
1. eq prob concentrated near middle. bottleneck at ϵ .
2. high initial snr and long timescale in different modes.
3. only eigenmode dependent constraints survive (and L2 - but difficult to work with).

Two-time envelope

Maximise $\text{SNR}(t_1)$ subject to constraint $\text{SNR}(t_2) = S_2$.

For t_1 close to t_2 , get single exponential. Far away, get two exponentials.

See tradeoff between $\text{SNR}(t_1)$ and $\text{SNR}(t_2)$.



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Complex synapses

└ Envelope memory curve

└ Two-time envelope

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See tradeoff between $\text{SNR}(t_1)$ and $\text{SNR}(t_2)$.



1. Max at multiple times, \rightarrow multiple timescales? cascade? Benna-Fusi?
2. only implemented first 2 constraints
3. numerics not working. 2 exp solution need to solve 2 transcendental equations.

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 $> \mathcal{O}(M^2)$.
- For times $< \mathcal{O}(M^2)$: conjecture that the model that reaches the envelope uses deterministic transitions \rightarrow diffusive forgetting.

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Complex synapses

— Envelope memory curve

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Thanks to:

- Surya Ganguli
- Stefano Fusi
- Marcus Benna

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Complex synapses

└ Envelope memory curve

└ Acknowledgements

Thanks to:
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• Stefano Fusi
• Marcus Benna

1. Last slide!

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└ Envelope memory curve

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- Complex synapses
 - Envelope memory curve
 - References

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Technical detail: ordering states

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

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

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](#)

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Complex synapses

└ Envelope memory curve

└ Technical detail: ordering states

1. Measure “distance” to the strong/weak states.
2. sum to constant, \implies two orders same

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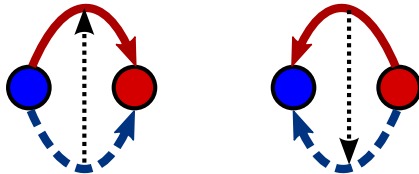
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Technical detail: upper/lower triangular

With states in order:



Endpoint: potentiation goes right, depression goes left.

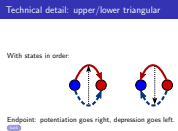
[back](#)

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Complex synapses

└ Envelope memory curve

└ Technical detail: upper/lower triangular



1. pot & dep with same initial & final state
2. pot/dep matrices are upper/lower triangular.
3. one other pert. too technical, even for bonus slide!