A general theory of learning and memory with Complex Synapses

based on work with Surya Ganguli

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Introduction

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.

Introduction

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.

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We will study the entire space of a broad class of models of complex synapses to find upper bounds on their performance.

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

Outline

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

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 describe performance at all times
4. upper bounds at finite times

Section 1

Why complex synapses?

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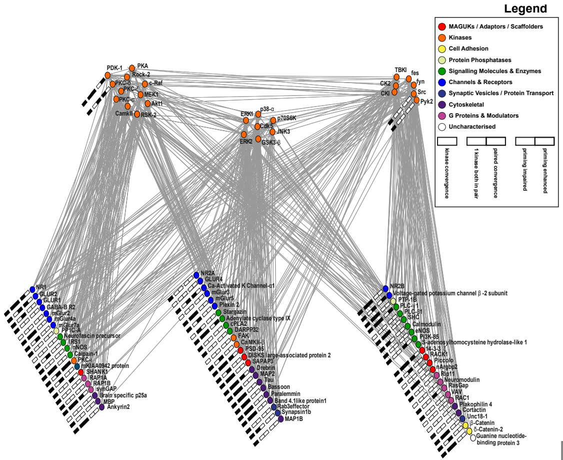
Complex synapses
└─Why complex synapses?

Section 1

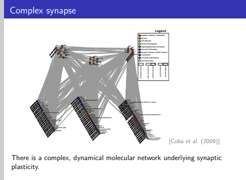
Why complex synapses?

Complex synapse



[Coba et al. (2009)]

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



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.

Storage capacity of synaptic memory

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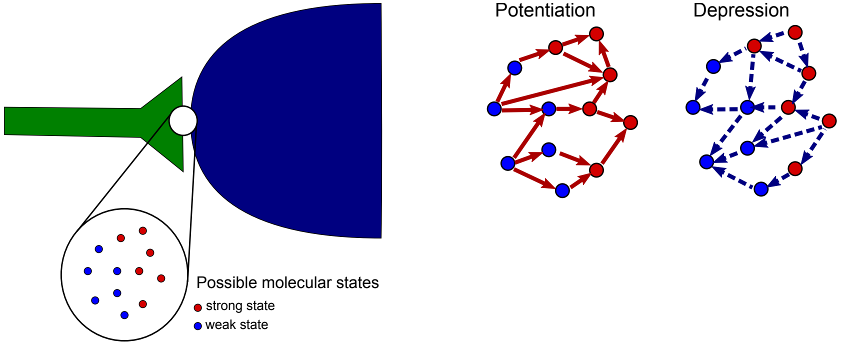
1. very plastic: learn easy, forget easy
2. little plasticity, remember better, learn harder
3. or sparse $\sim \log N/N$
4. one way around limit: complexity

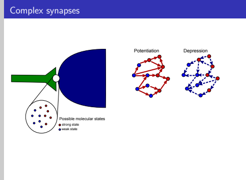
Section 2

Modelling synaptic complexity

Section 2
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 $\mathbf{M}^{\text{pot/dep}}$.
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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 $i \to j$, given pot/dep
5. looks like binary synapse from outside. Inside...

Dynamics

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

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

Eventually, this will settle into the equilibrium distribution:

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

Memory curve

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

$$\begin{aligned} \text{Signal} &= \langle \vec{w}_{\text{ideal}} \cdot \vec{w}(t) - \vec{w}_{\text{ideal}} \cdot \vec{w}(\infty) \rangle \\ \text{Noise} &= \text{Var}\left(\vec{w}_{\text{ideal}} \cdot \vec{w}(\infty) \right) \end{aligned}$$

Related to reconstruction probability of single synapses.

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

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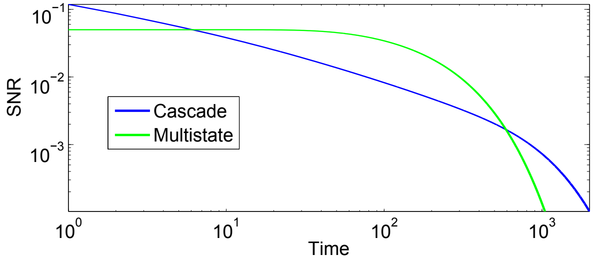
1. of different synapses
2. ideal observer reads weights, not states
3. upper bound on electrical activity readout
4. ideal: pot→strong...
5. subtract baseline, some overlap even w/o encoding
6. if we ignore correlations...

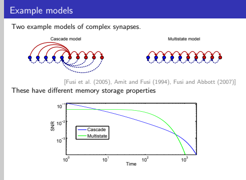
Example models

Two example models of complex synapses.

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

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.

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?

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- 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 2

Memory curve given by

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

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

Eigenmode decomposition:

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

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

Section 3

Upper bounds

Complex synapses
└─Upper bounds

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Section 3

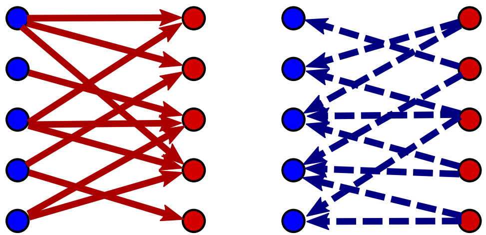
Upper bounds

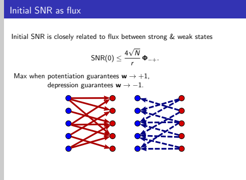
Initial SNR as flux

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

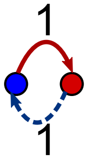




1. usually saturated: pot never dec, dep never inc
2. transitions out of one node sum to 1
3. equivalent to two-state model: doesn't matter which strong/weak state, same prob of going to other set.

Two-state model

Two-state model equivalent to previous slide:

Transitions: 

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

Maximal initial SNR:

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

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Two-state model

Two-state model equivalent to previous slide:

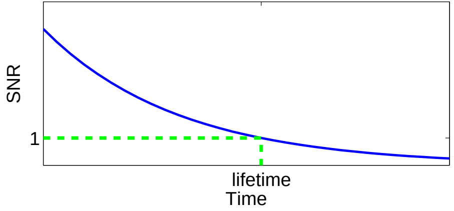
Transitions: $\implies \mathrm{SNR}(t) = \sqrt{N}\,(4 f^{\mathrm{pot}} f^{\mathrm{dep}})\,\mathrm{e}^{-rt}$.

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

1. decays very quickly
2. $f^{\mathrm{pot}} = \frac{1}{2}$

Memory lifetime bounded by area under SNR curve:

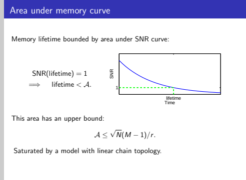
$$\text{SNR(lifetime)} = 1 \quad \implies \quad \text{lifetime} < \mathcal{A}.$$



This area has an upper bound:

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

Saturated by a model with linear chain topology.

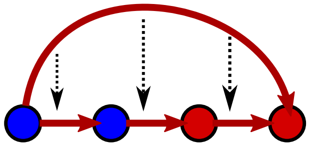


1. lifetime = area under green ¡ area under blue
2. capacity $\sim r$ lifetime, #new memories before we forget original.
3. reminder: N =#synapses, M =#states
4. proof next slide

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

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

Max: equilibrium probability distribution concentrated at both ends.

[Barrett and van Rossum (2008)]

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[Barrett and van Rossum (2008)]

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

Section 4

Envelope memory curve

Section 4
Envelope memory curve

Bounding finite time SNR

SNR curve:

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

subject to constraints:

$$\sum_a \mathcal{I}_a \leq 1, \qquad \sum_a \mathcal{I}_a \, \tau_a \leq M - 1.$$

We can maximise wrt. $\mathcal{I}_a, \tau_a$.

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

Acknowledgements

Thanks to:

- Surya Ganguli
- Stefano Fusi
- Marcus Benna

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1. Last slide!

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Complex synapses
└Envelope memory curve
└References

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Techinical detail: ordering states

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

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

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

[Kemeny and Snell (1960)]

We define:

$$\eta^+_i = \sum_{j\in\text{strong}} \mathbf{T}_{ij}\mathbf{p}^\infty_j, \qquad \eta^-_i = \sum_{j\in\text{weak}} \mathbf{T}_{ij}\mathbf{p}^\infty_j.$$

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

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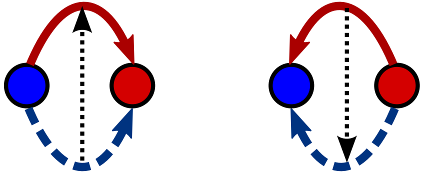
They can be used to arrange the states in an order (increasing η^- or decreasing η^+). back

1. Measure "distance" to the strong/weak states.
2. sum to constant, $\Longrightarrow$ two orders same

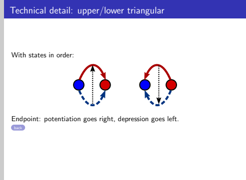
Technical detail: upper/lower triangular

With states in order:



Endpoint: potentiation goes right, depression goes left.

back



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!