# A general theory of learning and memory with Complex Synapses

based on work with Surya Ganguli

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April 11, 2013

Complex synapses

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

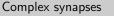
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#### Introduction

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.



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└─Introduction

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

# Outline

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

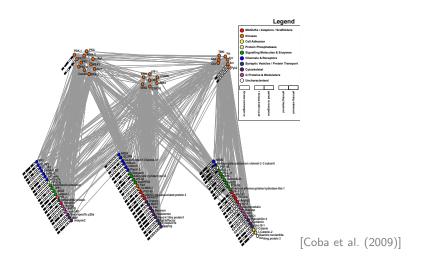


- 1. review terrible properties of simple synapses.
- 2. mathematical formalism of model, quantify performance (memory decay over time)
- 3. upper bounds on single numbers that describe performance at all times
- 4. upper bounds at finite times

# Section 1

Why complex synapses?

# Complex synapse



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"

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

- 1. very plastic: learn easy, forget easy
- 2. little plasticity, remember better, learn harder
- 3. or sparse  $\sim \log N/N$

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4. one way around limit: complexity

# Complex synapses

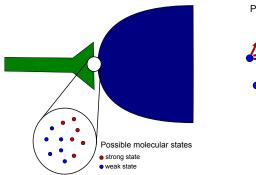
# -Modelling synaptic complexity

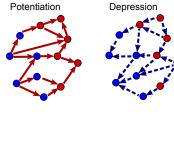
Section 2 Modelling synaptic complexity

Section 2

Modelling synaptic complexity

### Complex synapses





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 M<sup>pot/dep</sup>.
- Synaptic weights of the internal states are given by vector  $\mathbf{w}$ . Can only take values  $\pm 1$ .



Complex synapses

Modelling synaptic complexity

Simplifying assumptions

simplifying assumptions

- Which synapses elieible for plasticity chosen randomly
- Potentiating/depressing plasticity events ~ Poisson processes with rates rfpcc/dep, where fpcc + fdep = 1.
- Potentiation and depression are described by Markov processes with transition probabilities M<sup>pot/dep</sup>.
- Synaptic weights of the internal states are given by vector 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,  $f^{\text{pot/dep}} = \text{fraction of events}$  that are potentiating/depressing.
- 4. matrix elements: transition prob from  $i \rightarrow j$ , given pot/dep
- 5. looks like binary synapse from outside. Inside...

# **Dynamics**

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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

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

Eventually, this will settle into the equilibrium distribution:

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

Complex synapses



Modelling synaptic complexity └─Dynamics

- 1. for this one, we keep track of pot/dep, look for inc/dec of w
- 2. **W**<sup>F</sup> is forgetting matrix, **I** =identity, don't keep track of pot/dep
- 3. In equilibrium prior to memory creation

Complex synapses

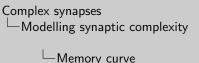
# Memory curve

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

$$\mathsf{Signal} = \langle ec{w}_\mathsf{ideal} \cdot ec{w}(t) - ec{w}_\mathsf{ideal} \cdot ec{w}(\infty) 
angle \ \mathsf{Noise} = \mathsf{Var} \left( ec{w}_\mathsf{ideal} \cdot ec{w}(\infty) 
ight)$$

Related to reconstruction probability of single synapses.

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





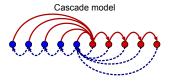
Memory curve

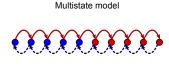
- 1. of different synapses
- 2. ideal observer reads weights, not states
- 3. upper bound on electrical activity readout
- 4. ideal: pot→strong...
- 5. subtract baseline, some overlap even w/o encoding
- 6. if we ignore correlations...

# Example models

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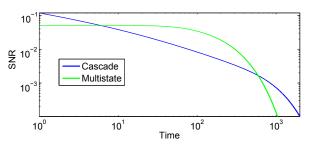
Two example models of complex synapses.





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

These have different memory storage properties



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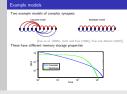
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Complex synapses

-Modelling synaptic complexity

Example models



- 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 → 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

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

Constraints:

$$\mathsf{M}^{\mathsf{pot}/\mathsf{dep}}_{ij} \in [0,1], \qquad \sum_{j} \mathsf{M}^{\mathsf{pot}/\mathsf{dep}}_{ij} = 1.$$

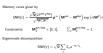
Eigenmode decomposition:

$$\mathsf{SNR}(t) = \sqrt{N} \sum_{a} \mathcal{I}_a \, \mathsf{e}^{-\mathit{rt}/ au_a}.$$

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 2

Section 3

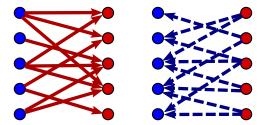
Upper bounds

#### Initial SNR as flux

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

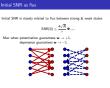
$$\mathsf{SNR}(0) \leq \frac{4\sqrt{N}}{r}\,\mathbf{\Phi}_{-+}.$$

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





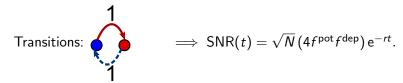
Complex synapses Upper bounds -Initial SNR ☐Initial SNR as flux



- 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.

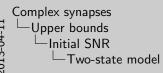
#### Two-state model

Two-state model equivalent to previous slide:



Maximal initial SNR:

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



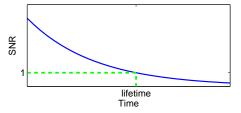


- 1. decays very quickly
- 2.  $f^{\text{pot}} = \frac{1}{2}$
- 3. Initial SNR not a good thing to optimise.

#### Area under memory curve

Memory lifetime bounded by area under SNR curve:

$$\mathsf{SNR}(\mathsf{lifetime}) = 1$$
  $\Longrightarrow \mathsf{lifetime} < \mathcal{A}.$ 



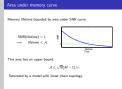
This area has an upper bound:

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

Saturated by a model with linear chain topology.

Complex synapses

Upper bounds
Area under memory curve
Area under memory curve



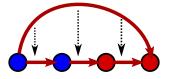
- 1. lifetime = area under green ; area under blue
- 2. capacity  $\sim r$  lifetime, #new memories before we forget original.
- 3. reminder: N = #synapses, M = #states
- 4. proof next slide

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#### Proof of area bound

For any model, we can construct perturbations that

- preserve equilibrium distribution,
- increase area.





e.g. decrease "shortcut" transitions, increase bypassed "direct" ones. Endpoint: linear chain

The area of this model is

$$A = \frac{2\sqrt{N}}{r} \sum_{k} \mathbf{p}_{k}^{\infty} |k - \langle k \rangle|.$$

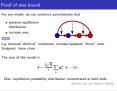
Max: equilibrium probability distribution concentrated at both ends.

[Barrett and van Rossum (2008)]

Complex synapses

Upper bounds

Area under memory curve
Proof of area bound

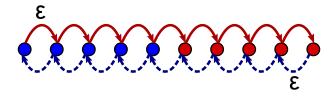


- 1. relies on order & technical condition
- 2. max given  $\mathbf{p}^{\infty}$
- 3. now max wrt.  $\mathbf{p}^{\infty}$
- 4. keep c.o.m. in middle
- 5. similar result, slightly different conditions: linear weights, mutual info

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# Saturating model

Make end states "sticky"



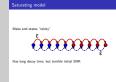
Has long decay time, but terrible initial SNR.

Complex synapses

Upper bounds

Area under memory curve

Saturating model



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

# Complex synapses Envelope memory curve

# Section 4

# Envelope memory curve

# Bounding finite time SNR

SNR curve:

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

subject to constraints:

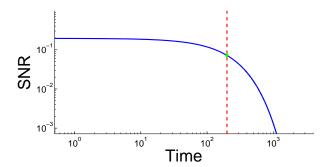
$$\sum_{a} \mathcal{I}_{a} \leq 1, \qquad \sum_{a} \mathcal{I}_{a} \tau_{a} \leq M - 1.$$

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

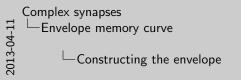
Complex synapses
Envelope memory curve
Bounding finite time SNR

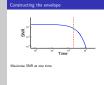


- 1. from eigenmode decomposition
- 2. from initial, area bounds

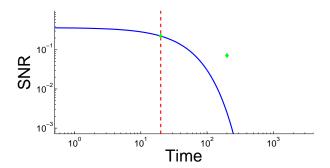


Maximise SNR at one time





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



Another time



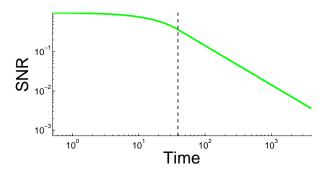
Complex synapses

Envelope memory curve



Constructing the envelope

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



All times  $\rightarrow$  envelope



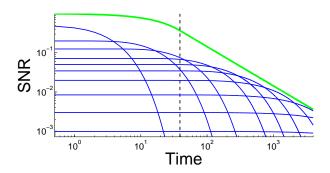
Complex synapses

Envelope memory curve





- 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 acheived?

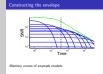


Memory curves of example models.



Complex synapses

Envelope memory curve

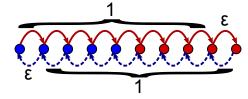


Constructing the envelope

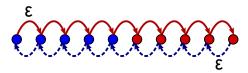
- 1. One exp. only constrains SNR at that time, not others
- 2. get another bound
- 3. vary time of max. no curve can cross this.
- 4. Regions: init(1); area(1,2)
- 5. is it tight? can any constrained set of exps be acheived?
- 6. no
- 7. One exp. discuss models later

# Best models at single times

Early times:



Late times:



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Envelope memory curve

Best models at single 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)

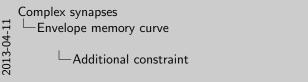
#### Additional constraint

Conjecture: additional constraint

$$\mathcal{I}_{a}\sqrt{\tau_{a}} \leq \mathcal{O}(1).$$

Saturated by a diffusive chain:

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

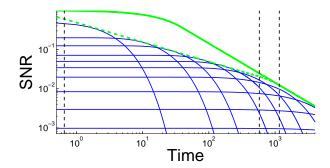


Conjecture: additional constraint Saturated by a diffusive chain:

Additional constraint

1. Tested experimentally. Discuss later

# Envelope 2



$$rt < \mathcal{O}(M^2)$$
 envelope  $\sim (rt)^{-1/2}$ ,  $rt > \mathcal{O}(M^2)$  envelope  $\sim (rt)^{-1}$ .

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Envelope memory curve

Envelope 2



- 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 bound

Lifetime of a memory bounded by where envelope crosses 1

$$N > \mathcal{O}(M^2) \implies \mathsf{lifetime} \leq rac{\sqrt{N}(M-1)}{\mathsf{e}r},$$
  $N > \mathcal{O}(M^2) \implies \mathsf{lifetime} \leq rac{\gamma^2 N}{2\mathsf{e}r}.$ 



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Envelope memory curve

Lifetime bound

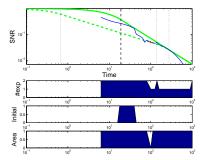
- 1.  $\gamma \sim \mathcal{O}(1)$  constant in additional constaint
- 2. First  $t^{-1}$  assumes M low. Second  $t^{-1/2}$  applies to Benna-Fusi.
- 3. Independent synapses?

### Two-time envelope

Maximise  $SNR(t_1)$  subject to constraint  $SNR(t_2) = S_2$ .

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

See tradeoff between  $SNR(t_1)$  and  $SNR(t_2)$ .





Complex synapses

Envelope memory curve

☐ Two-time envelope



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

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#### Additional constraint: other forms?

Involving eigenmodes:

$$\mathcal{I}_{a}\sqrt{ au_{a}}, \qquad \sum_{a}\mathcal{I}_{a}\sqrt{ au_{a}}, \qquad \sum_{a}\mathcal{I}_{a}^{2} au_{a}.$$

Not involving eigenmodes

$$\mathcal{A} \times \mathsf{SNR}(0), \qquad \int \! \mathrm{d}t \; \mathsf{SNR}(t)^2.$$

Complex synapses Envelope memory curve Additional constraint: other forms?



- 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:

heeger constant: 
$$\phi \equiv \min_{\mathcal{S}} \left\{ \frac{\mathsf{Perimeter}(\mathcal{S})}{\mathsf{Area}(\mathcal{S})} \right\}.$$

Timescale for diffusion to equilibriate

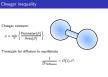
$$\frac{1}{D\tau_{
m diffusion}} < \mathcal{O}(1) \, \phi^2$$



Complex synapses

Envelope memory curve

-Cheeger inequality



- 1. split into two pieces. pick smaller. higher dim.
- 2. bottleneck
- 3. if we want fast diffusion, need lhs large  $\rightarrow$  no bottlenecks.
- 4. purely geometric
- 5. also inequality in other direction: want slow diffusion  $\rightarrow$  need bottleneck. Not useful for us

# Cheeger inequality: Markov chains

Cheeger constant:

$$\phi \equiv \min_{\mathcal{S}} \left\{ rac{oldsymbol{\Phi}_{\mathcal{S}\mathcal{S}^{\mathrm{c}}}}{oldsymbol{\mathsf{p}}^{\infty}(\mathcal{S})} 
ight\}.$$

Timescale to equilibriate:

$$\frac{1}{\max_a \tau_a} < \mathcal{O}(1) \, \phi^2.$$

Simple proof assuming detailed balance. More complicated proof for general case.

[Sinclair and Jerrum (1989)]

[Lawler and Sokal (1988)]



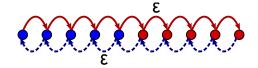
Complex synapses Envelope memory curve Cheeger inequality: Markov chains



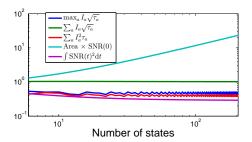
- 1. split states into two subsets. pick smaller.
- 2. again bottleneck
- denominator varies
- 4.  $\mathcal{O}(1)$  bit differs
- 5. bottleneck need not be between strong & weak.

# Counter examples?

Put bottleneck somewhere else:



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



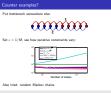
Also tried: random Markov chains.



Complex synapses

Envelope memory curve

-Counter examples?



- 1. eg prob concentrated near middle. bottleneck at  $\epsilon$ .
- 2. high inital snr and long timescale in different modes.
- 3. only eigenmode dependent constraints survive (and L2 but difficult to wor with).

# 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.

Complex synapses Envelope memory curve -Summary

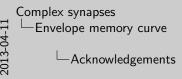
. We have formulated a general theory of learning and memory with The area under the memory curve of any model < linear chain with

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

# Acknowledgements

#### Thanks to:

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- Stefano Fusi
- Marcus Benna



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Marcia Benna

1. Last slide!

#### References I



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References IV

# Techinical detail: ordering states

Let  $T_{ii}$  = mean first passage time from state i to state j. Then:

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

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

[Kemeny and Snell (1960)]

We define:

Subhaneil Lahiri (Stanford)

$$\eta_i^+ = \sum_{j \in \mathsf{strong}} \mathbf{T}_{ij} \mathbf{p}_j^\infty, \qquad \eta_i^- = \sum_{j \in \mathsf{weak}} \mathbf{T}_{ij} \mathbf{p}_j^\infty.$$

Complex synapses

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



April 11, 2013

Fechinical detail: ordering states Complex synapses Envelope memory curve ☐ Techinical detail: ordering states

- They can be used to arrange the states in an order (increasing  $\eta^-$
- 1. Measure "distance" to the strong/weak states.
- 2. sum to constant,  $\implies$  two orders same

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

# Technical detail: upper/lower triangular

With states in order:





Endpoint: potentiation goes right, depression goes left.

back



Complex synapses

Envelope memory curve

☐ Technical detail: upper/lower triangular



Fechnical 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!