From Hebbian learning to spike-timing-dependent plasticity

A modeling viewpoint

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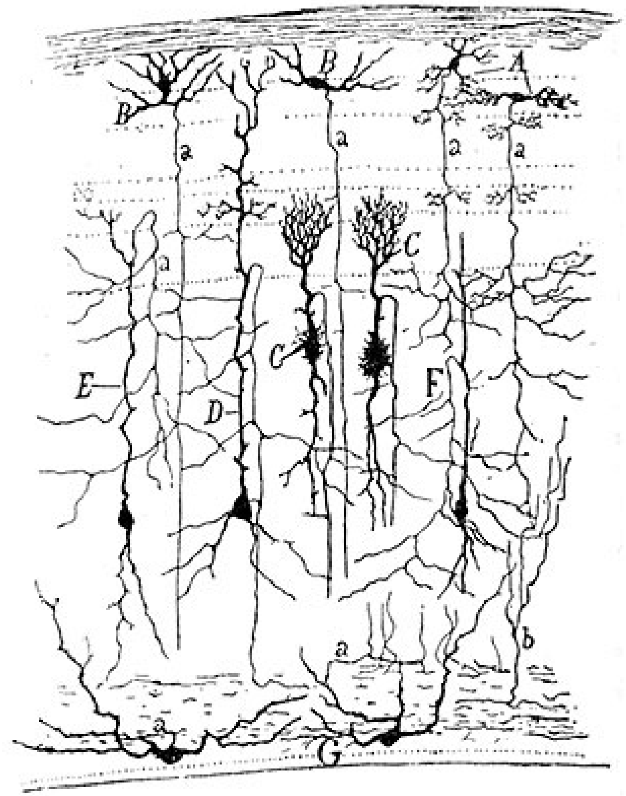
Outline

- **Historical perspective on learning in neuronal systems**
- From Hebbian learning to spike-timing-dependent plasticity
- Weight dynamics and “information” representations:
  - Principal component analysis (PCA)
  - Detection of spike patterns by STDP
  - Neuronal assemblies in recurrent networks
- From biological learning to machine learning:
  - Unsupervised vs supervised vs reinforcement learning

A bit of history

- Paul Broca (1796-1881): localization of function, for example language
- Karl Lashley (1890-1958): storage of memory in brain regions (engram)

- How are brain functions (psychology) implemented in the brain?
- How to learn functions?



Ramon y Cajal 1905

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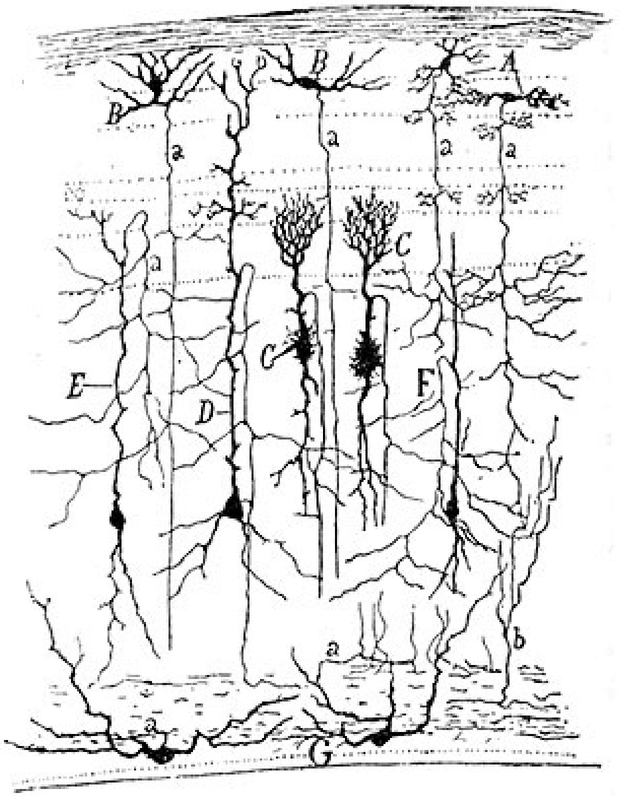

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Learning in neuronal systems: where and what?

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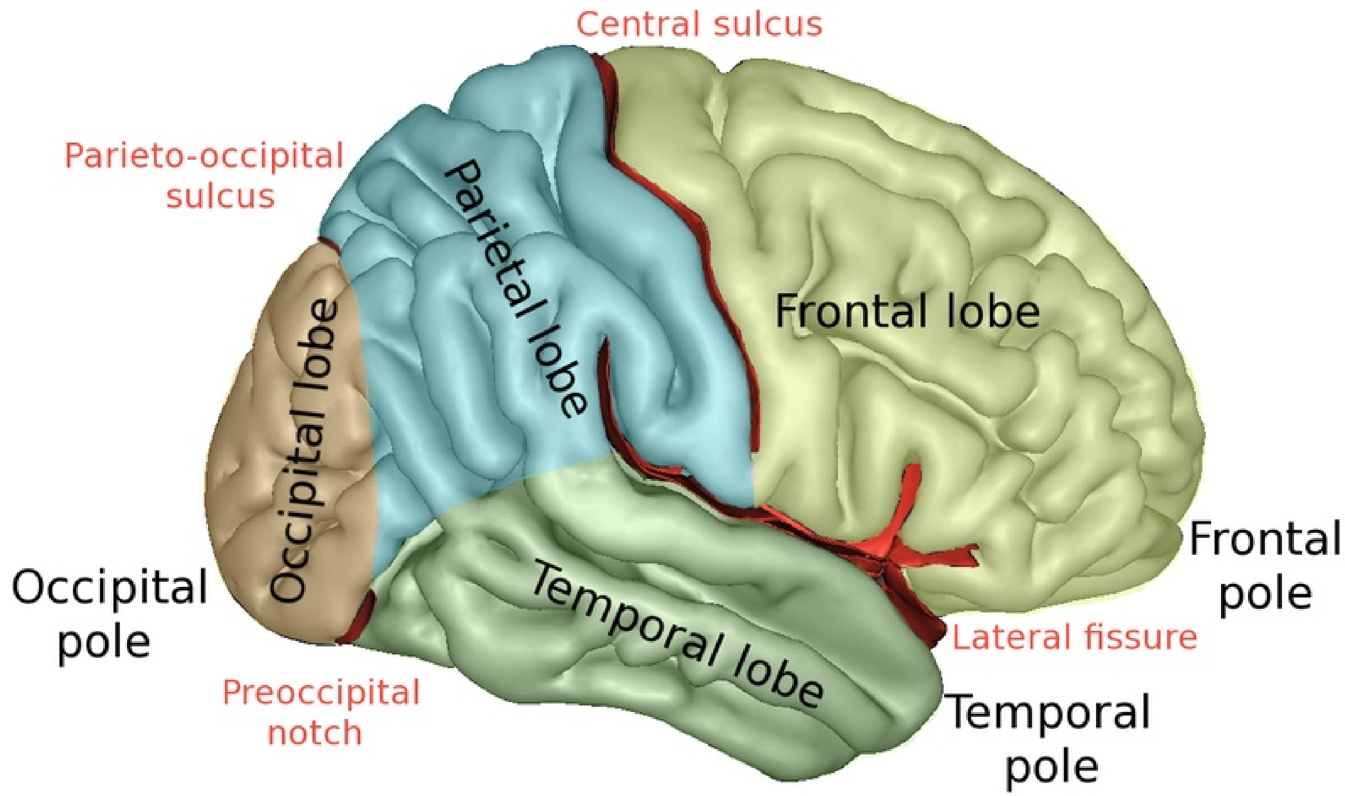

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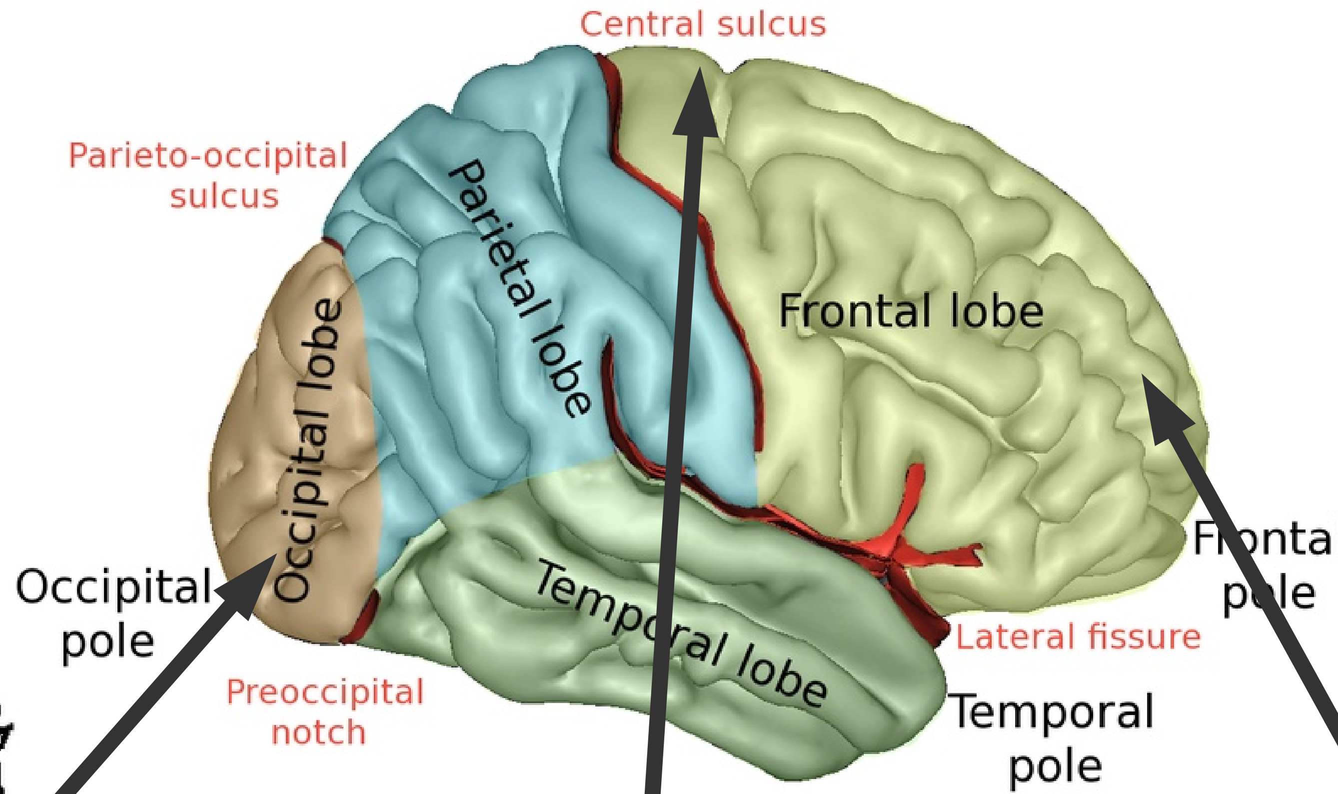
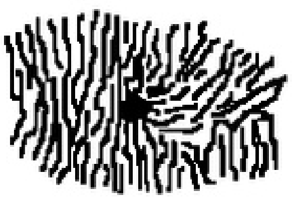


wikipedia

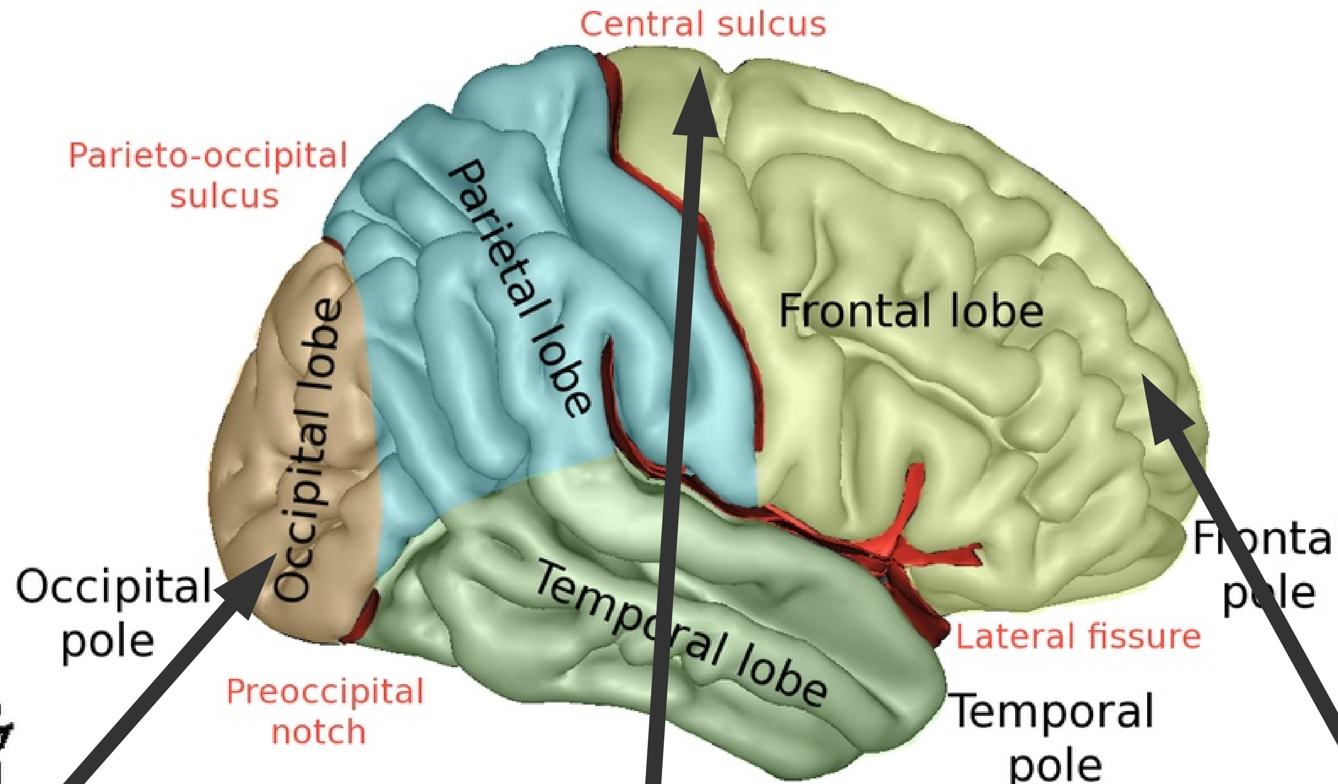


Orientation columns in primary visual cortex (V1)

Locomotion in motor cortex

Long-term memory in prefrontal cortex

Learning in neuronal systems: where and what?



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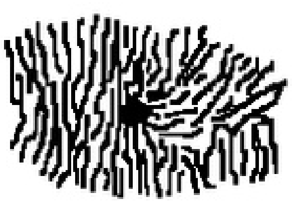

Orientation columns in
primary visual cortex (V1)

Unsupervised
learning

Locomotion in
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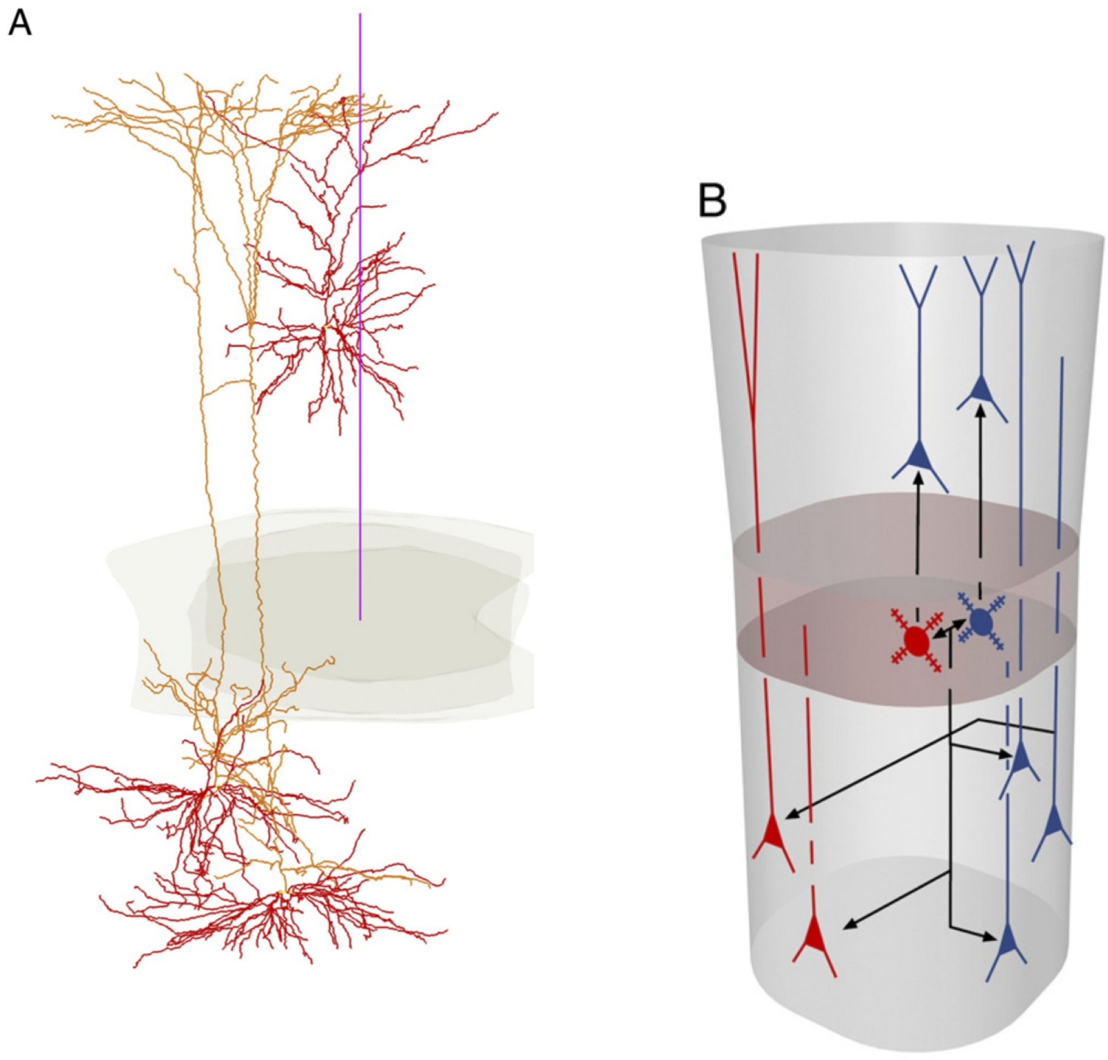
Reinforcement
learning

Long-term memory in
prefrontal cortex

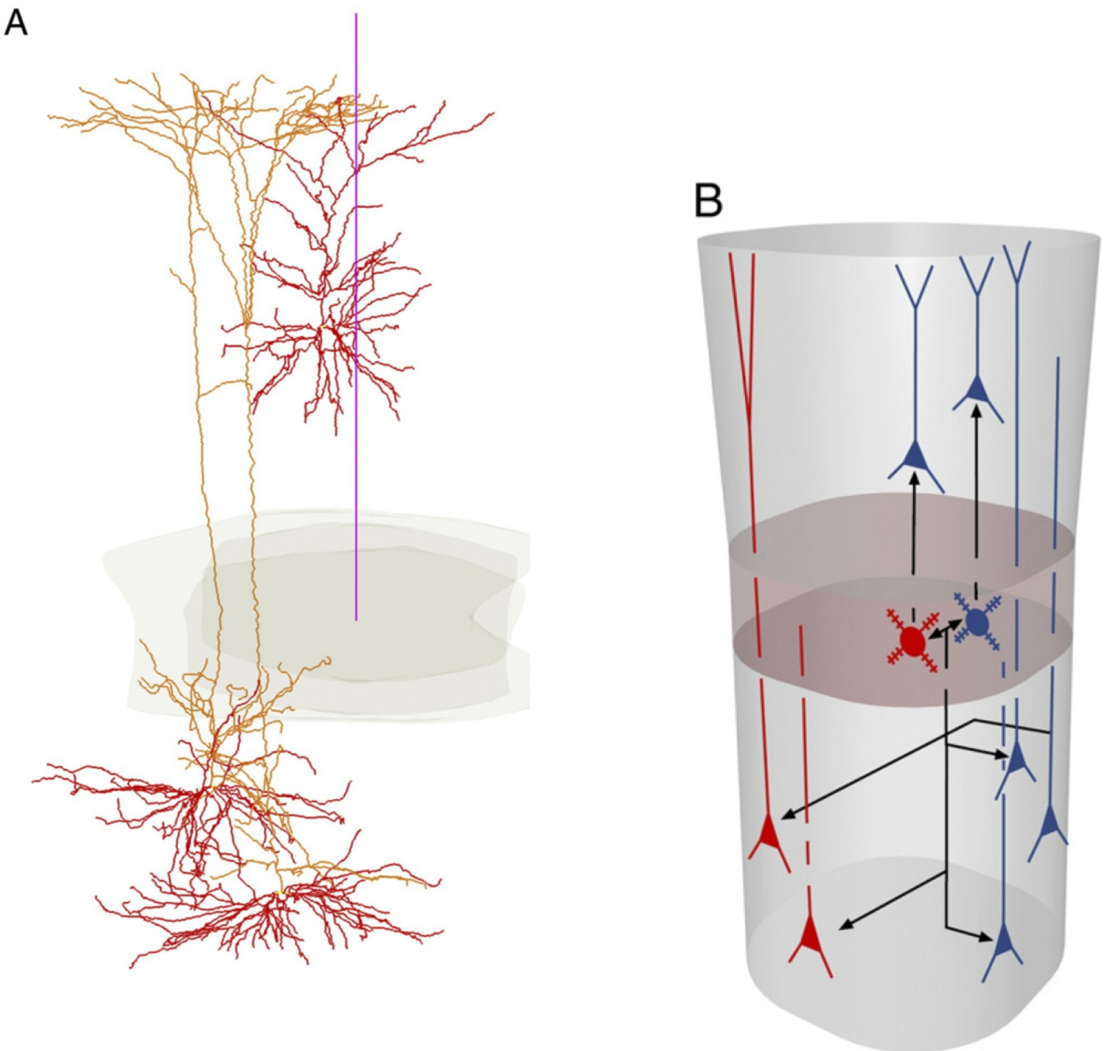
Supervised
learning

Formalizing experimental observations



Helmstaedter *BRR* 2007

Formalizing experimental observations



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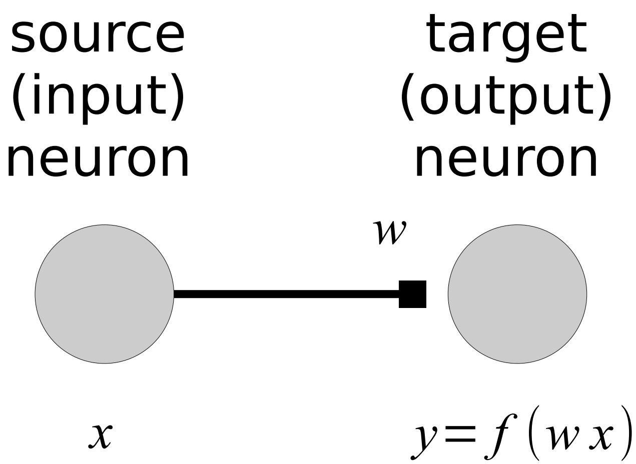
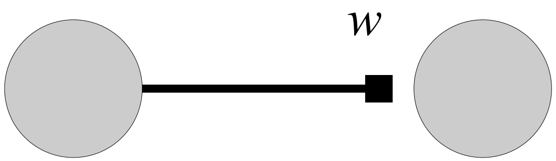


Models of neuronal learning

Synaptic plasticity



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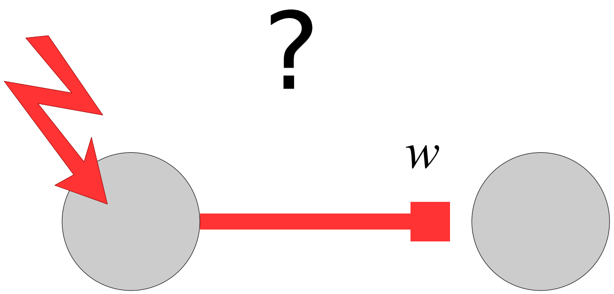

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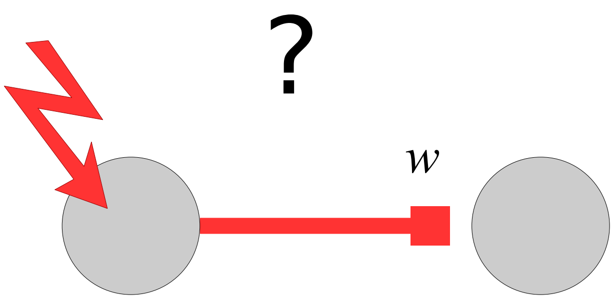
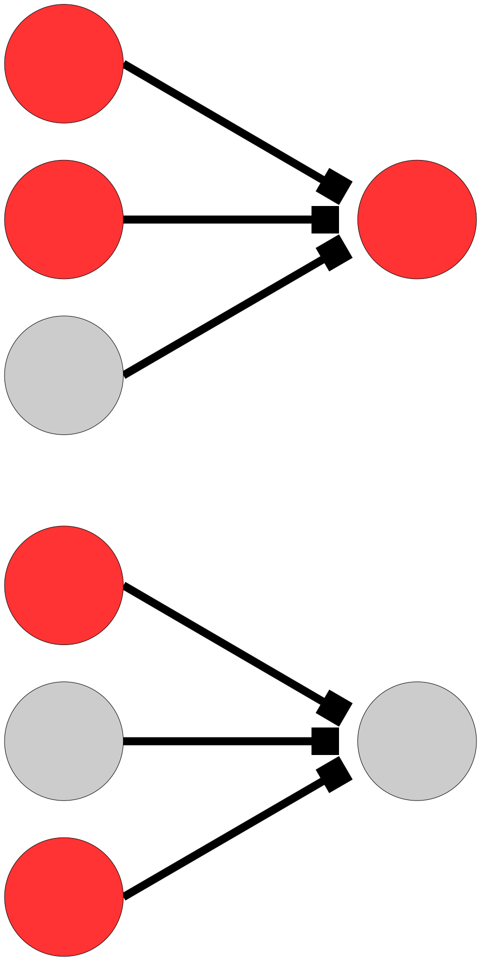


Tuning function
e.g. pattern
classification



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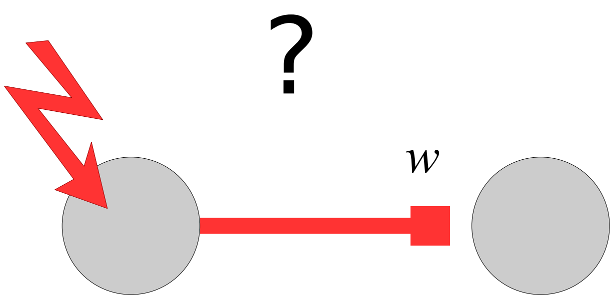

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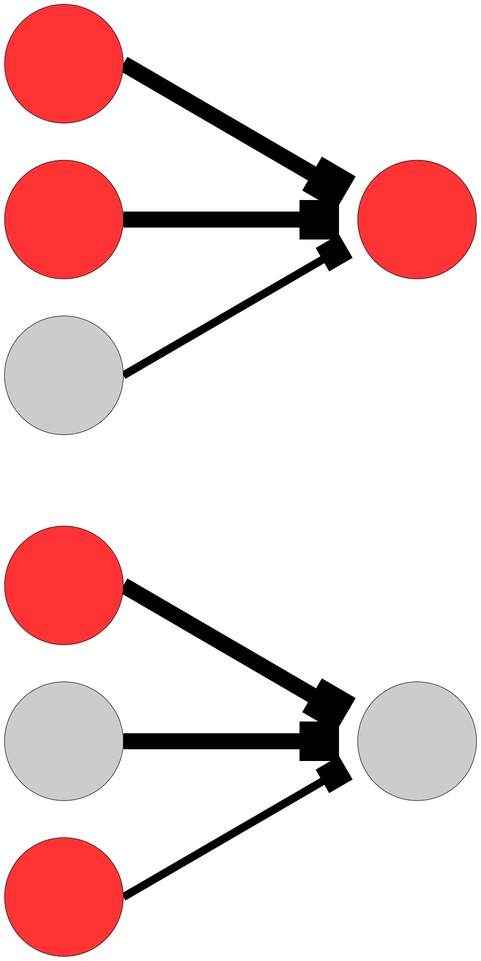

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- D Hebb *The Organization fo Behavior* 1949: how does environment and experience shape brain structure and function?

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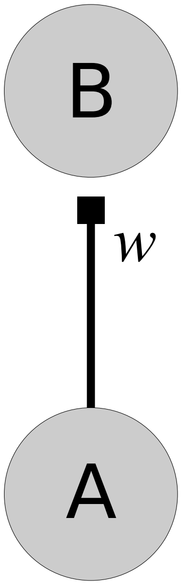

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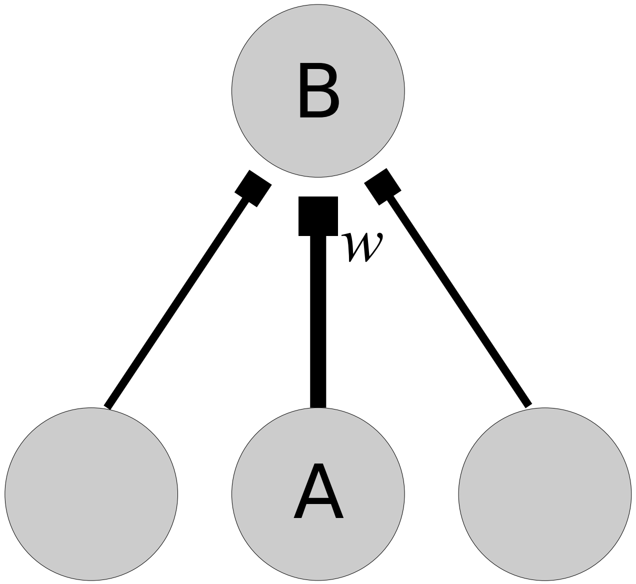

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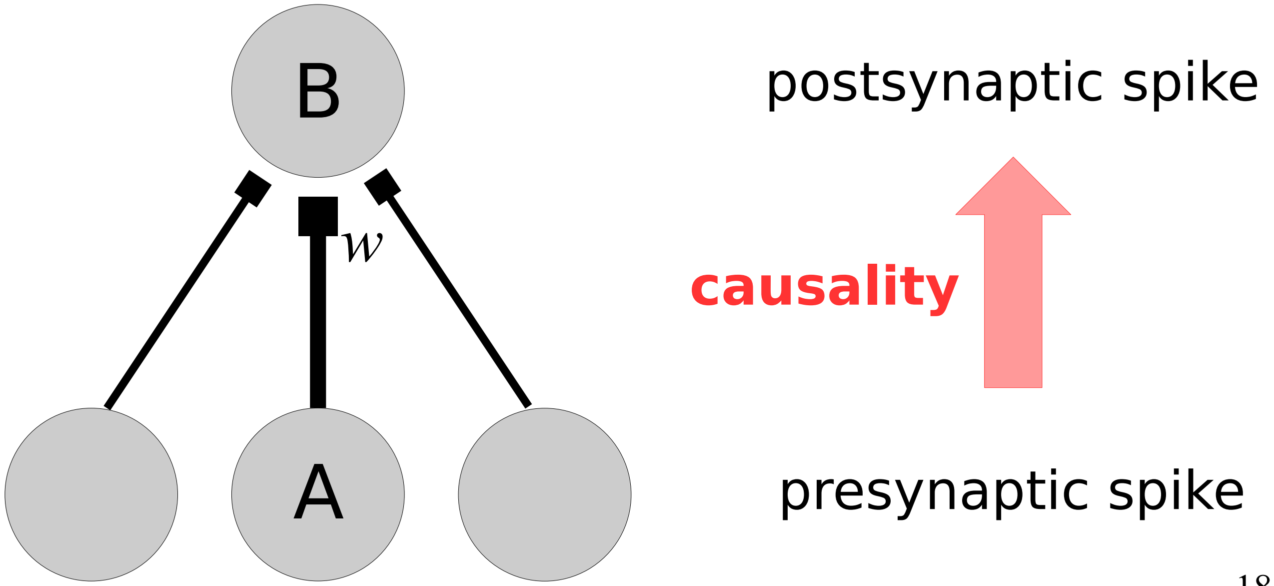

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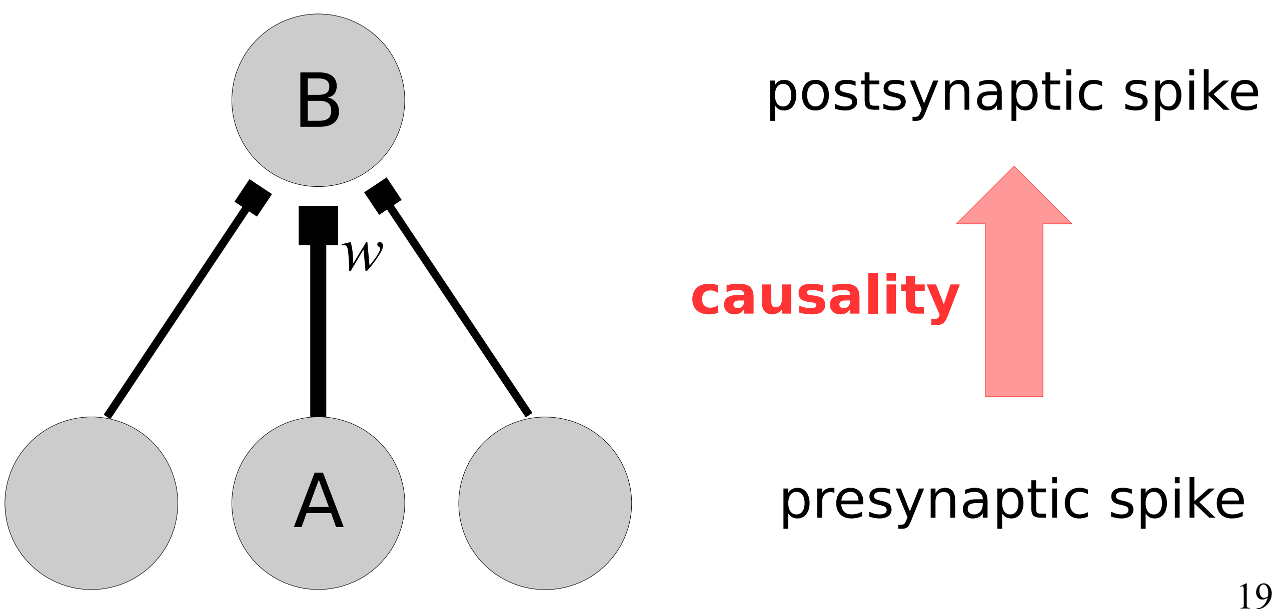
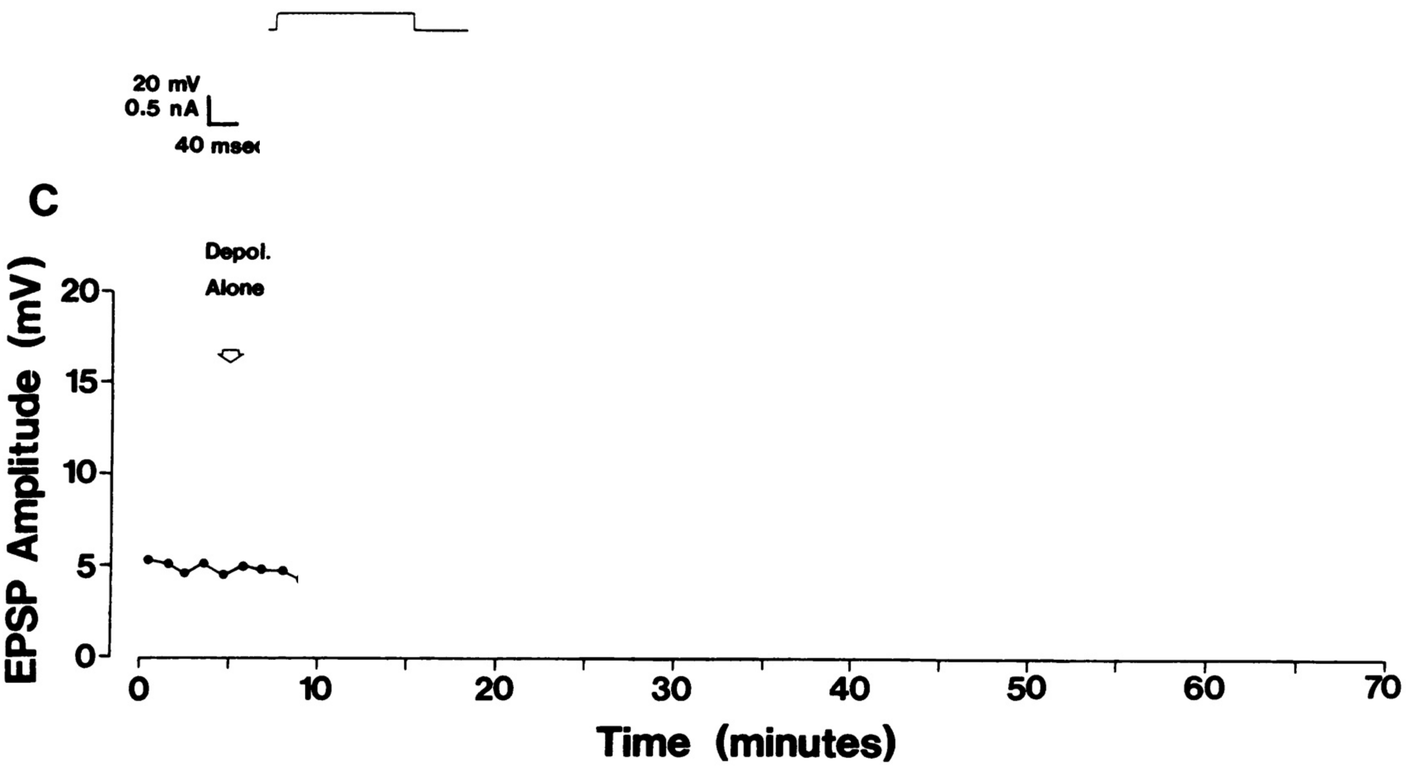
Unsupervised learning



Experimental evidence from rat hippocampus



Kelso *PNAS* 1986
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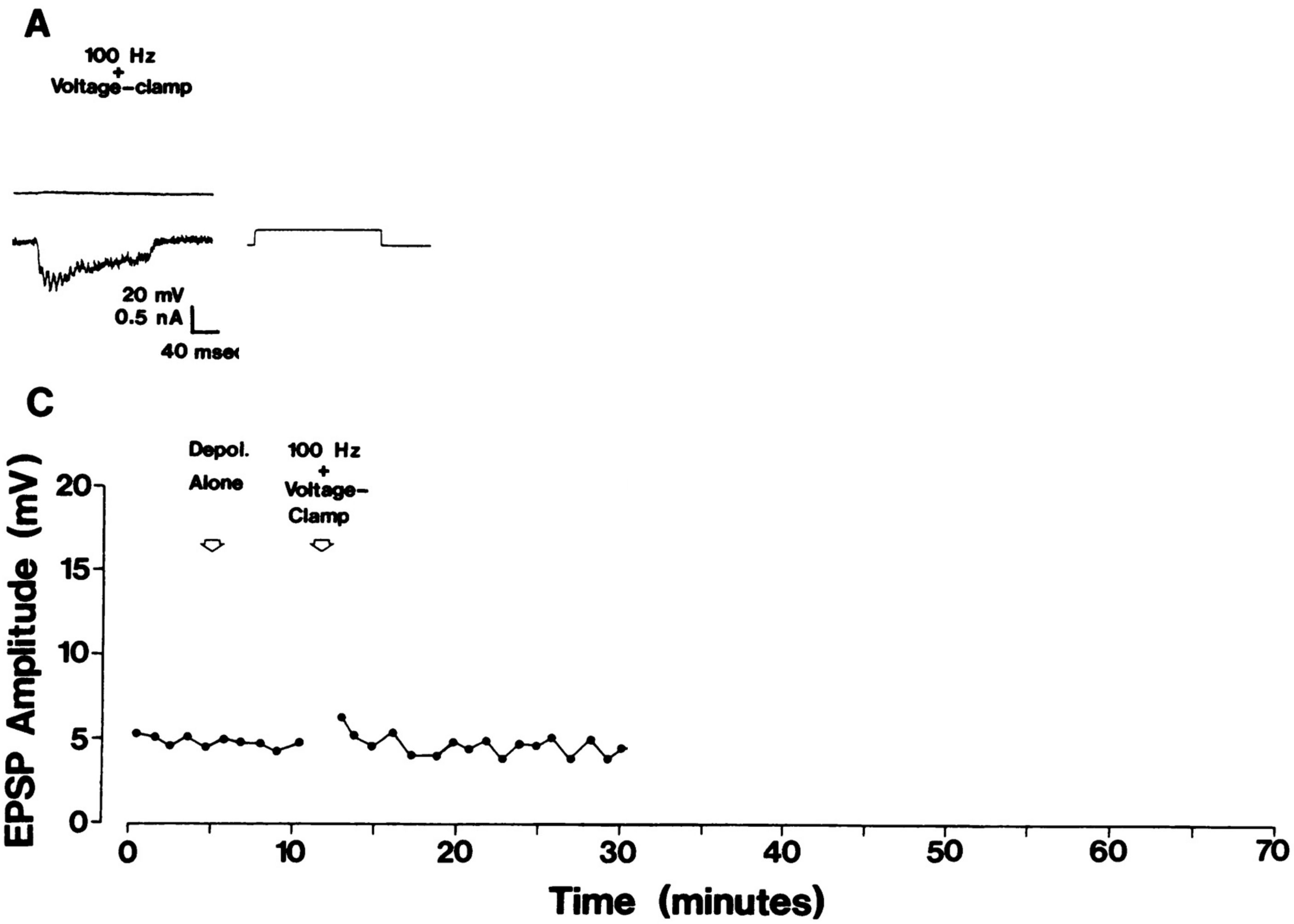

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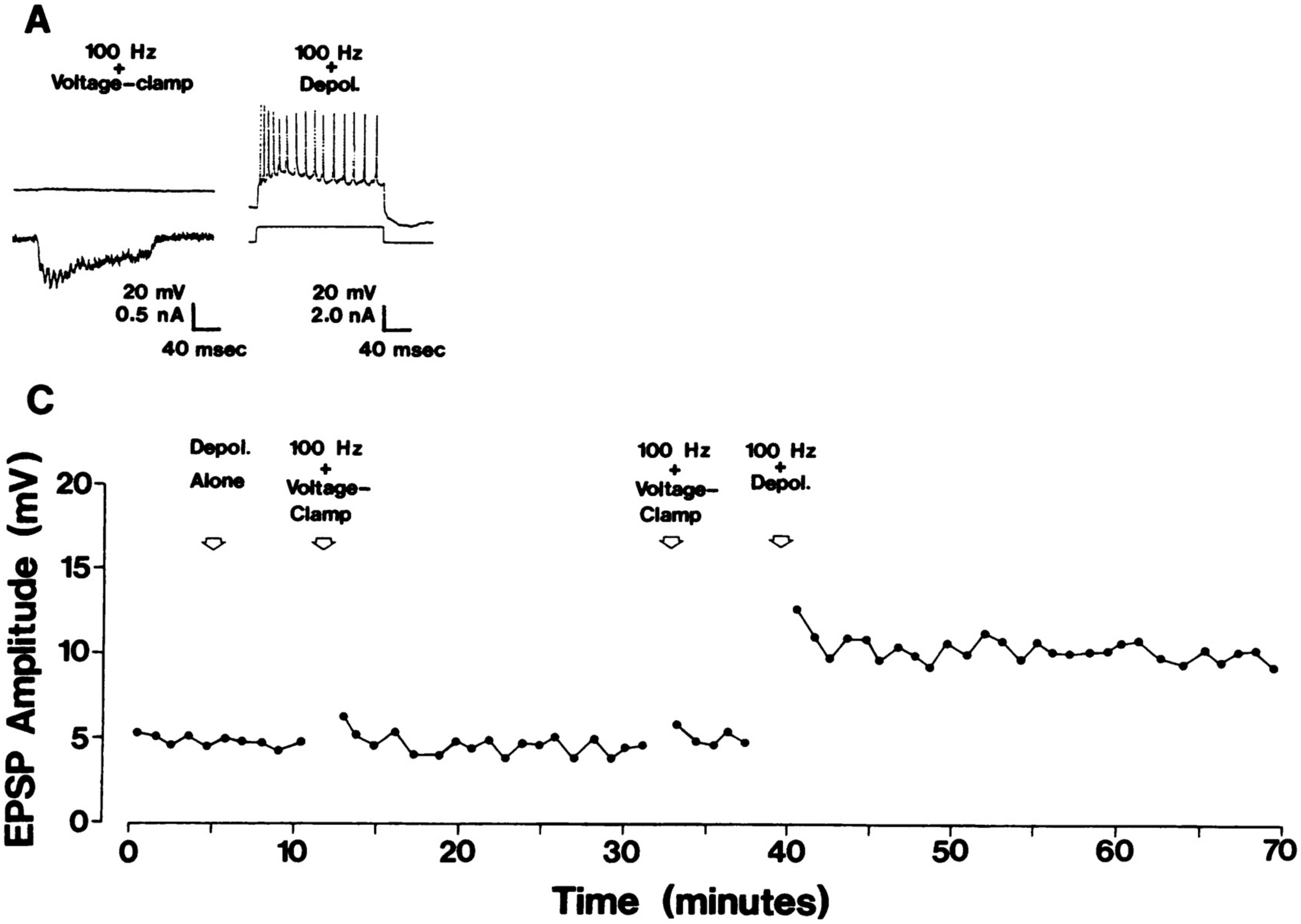

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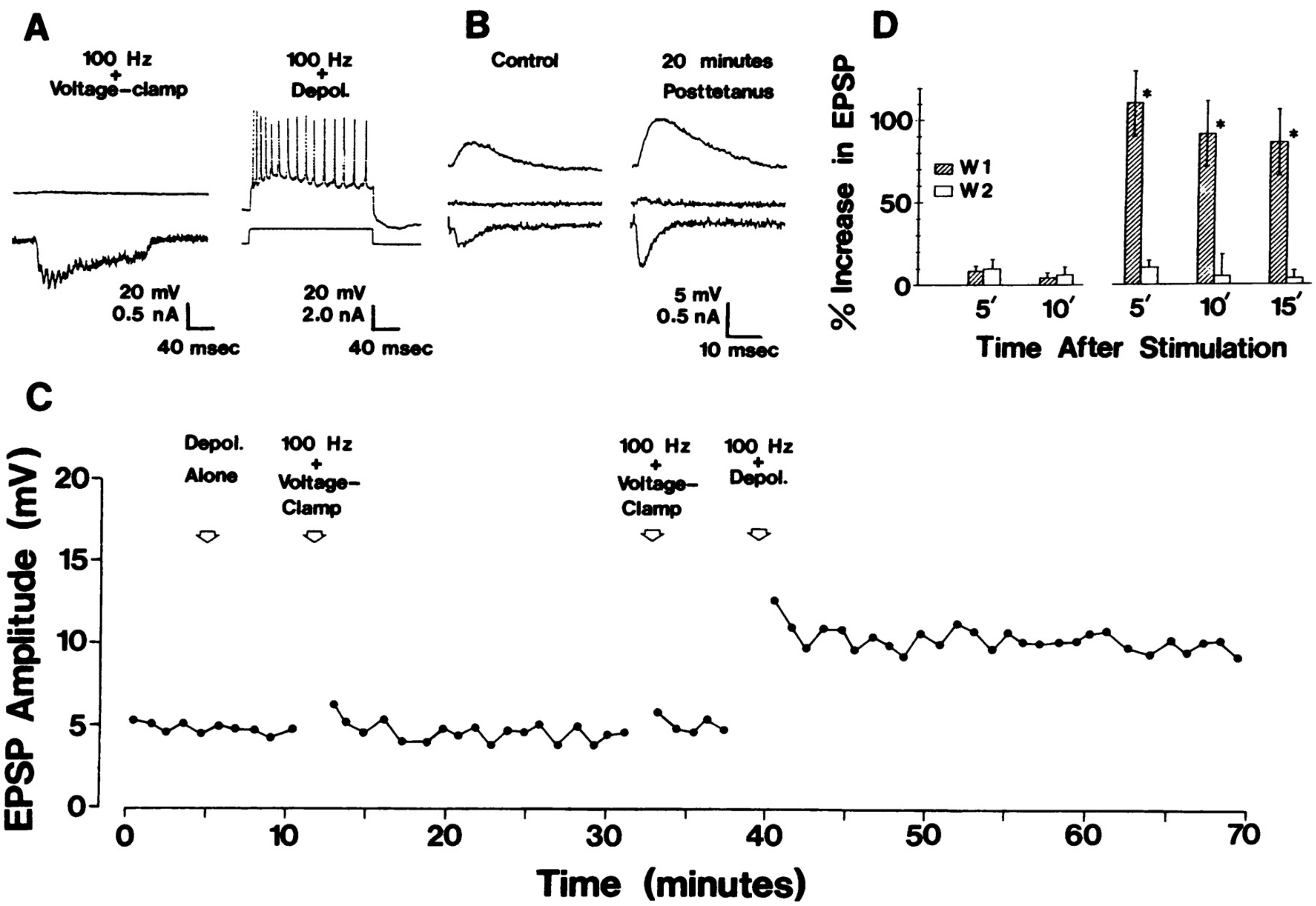

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Spike timing matters!

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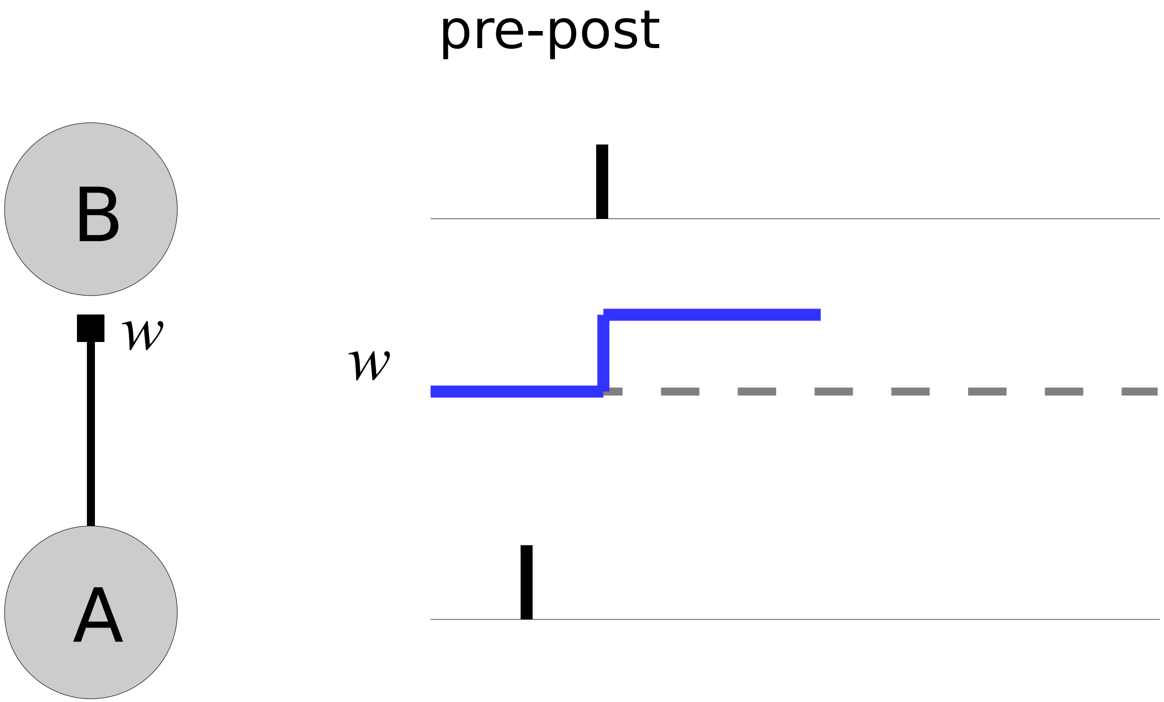
- Gerstner *Science* 1999



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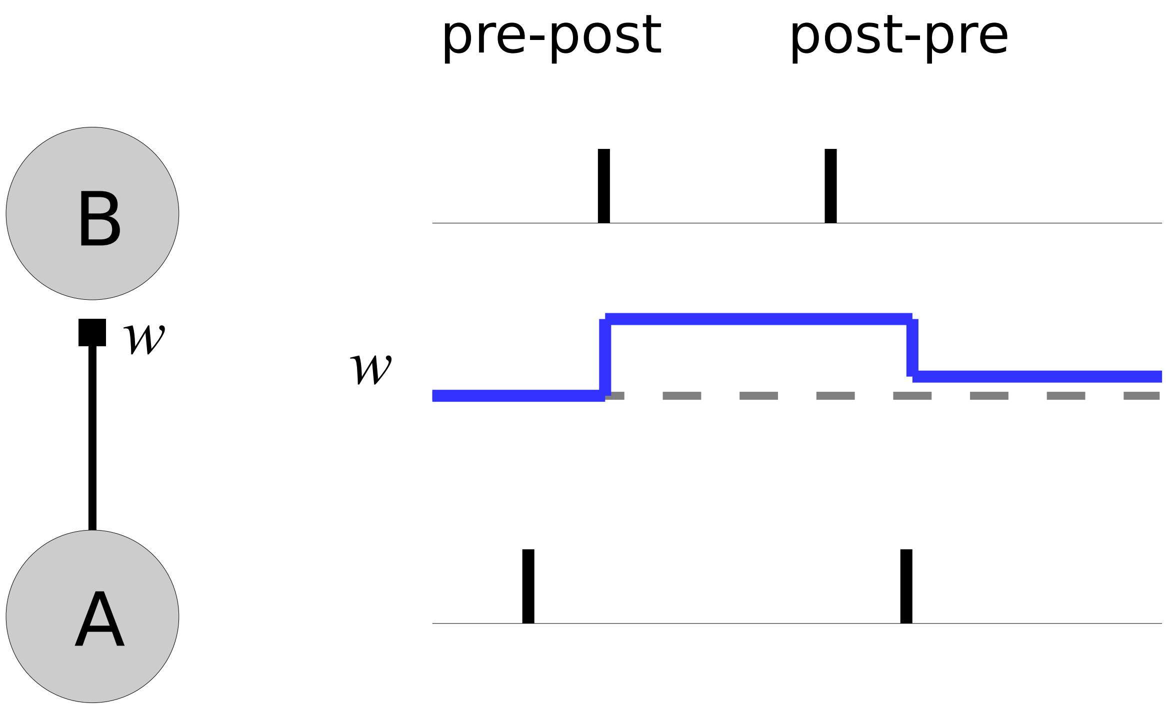

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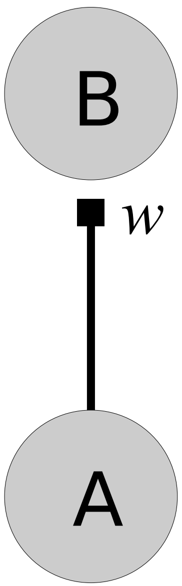
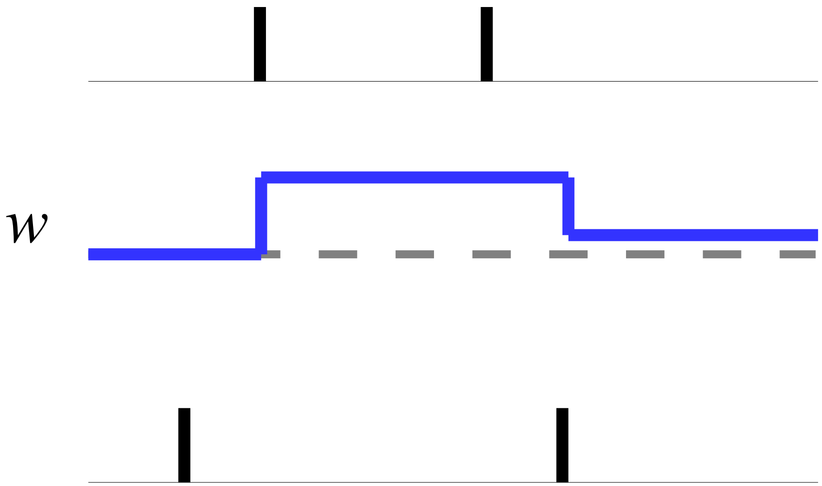
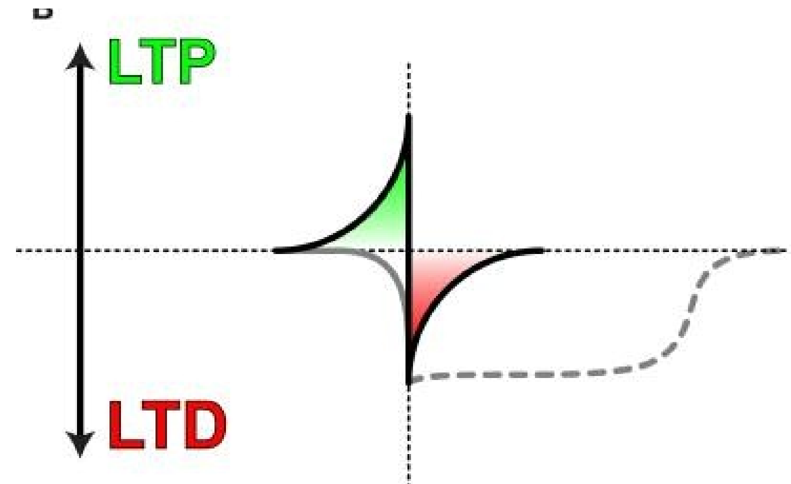


pre-post post-pre



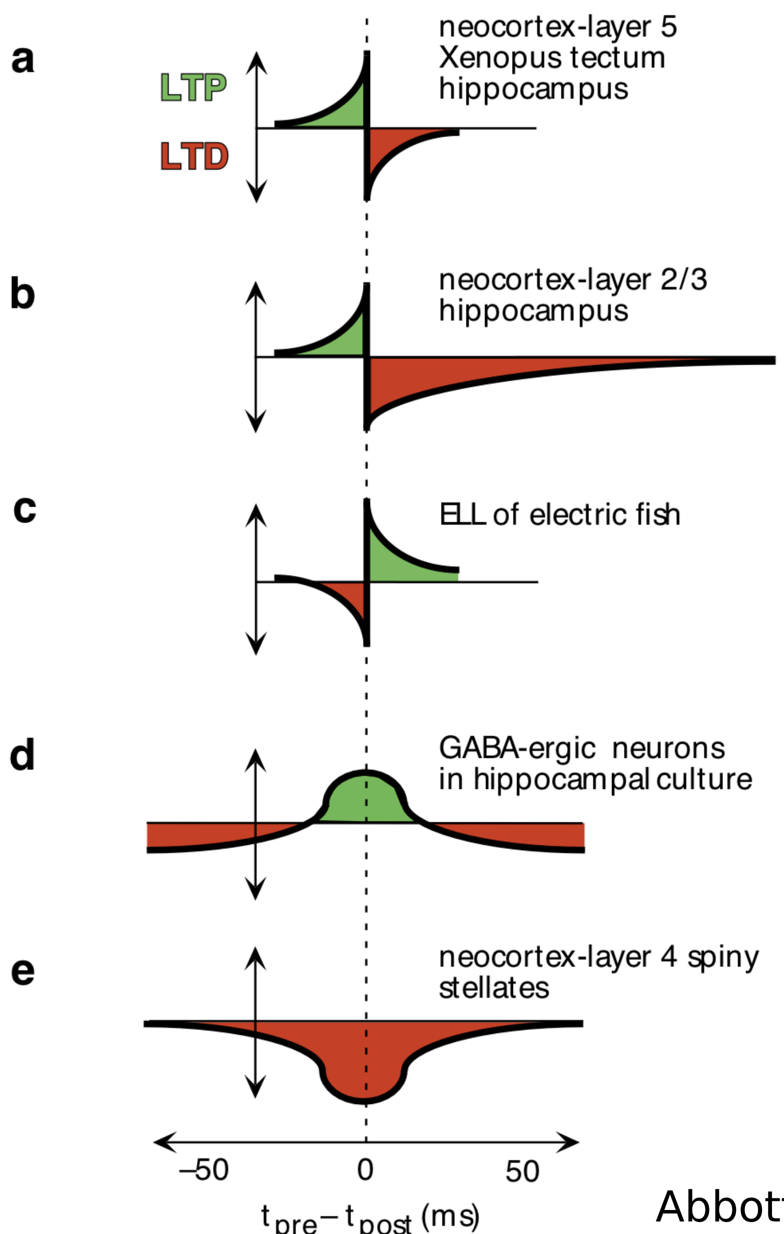


$$t_A - t_B = t_{pre} - t_{post}$$

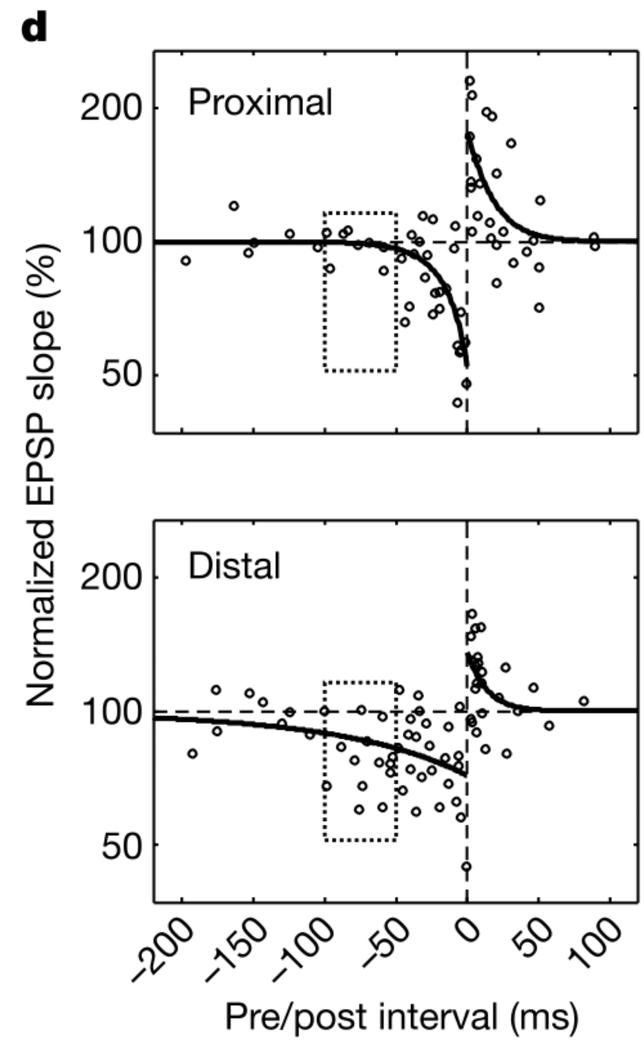
Markram *J Syn Neurosci* 2011

Spike-timing-dependent plasticity (STDP):
temporally Hebbian, “takes part in firing it”

Many STDP windows exist, yielding various timescales



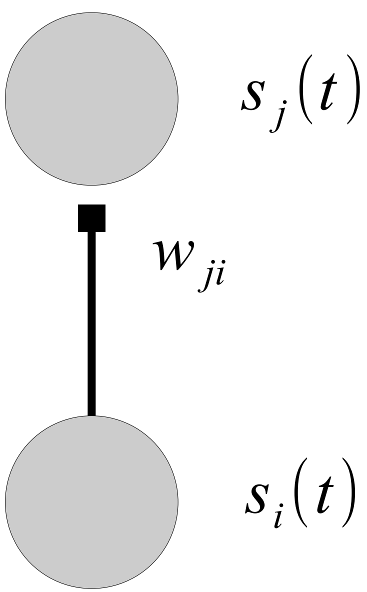
Abbott and Nelson, *Nat Neurosci* 2000

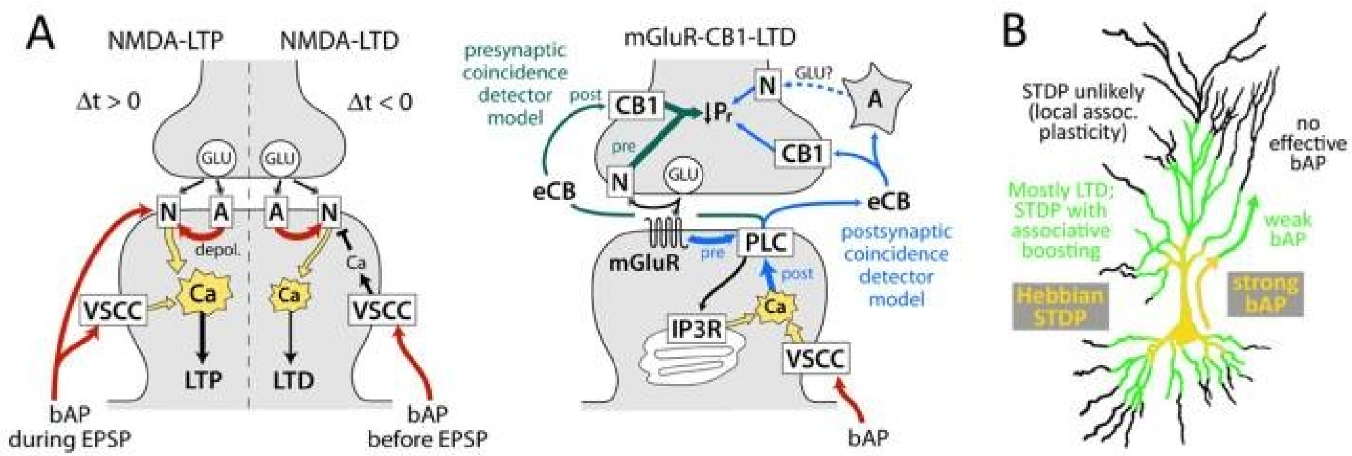


Froemke *Nature* 2005

Biophysical models and other mechanisms

- Weight dependence: van Rossum *J Neurosci* 2000, Morrison *Neural Comput* 2007
- Calcium-based: Shouval Biol Cybern 2002; Standage *PLoS ONE* 2014
- Post-synaptic voltage dependence: Clopath *Nat Neurosci* 2010
- Inhibitory plasticity: Vogels *Science* 2011
- Neuronal morphology: Froemke *Nature* 2005
- Neuromodulation: Brzosko *Neuron* 2019





Feldman *Neuron* (2012)

Summary for experimental evidence and modeling of synaptic plasticity

- Complex dependencies upon recent spike timing, ion concentrations, etc.
- But most experiments are in vitro! (see supplementary slides)
  - Many STDP protocols involve 60 repeated pairing to obtain observable weight change
  - Positive replications of results in-vivo still scarce…
- Monosynaptic plasticity is not the only mechanism at play

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- **Questions:**
  - What matters for neuronal function?
  - Effect in network?
  - Need to formalize plasticity update (i.e. simplified model) so we can build typology of functional effects

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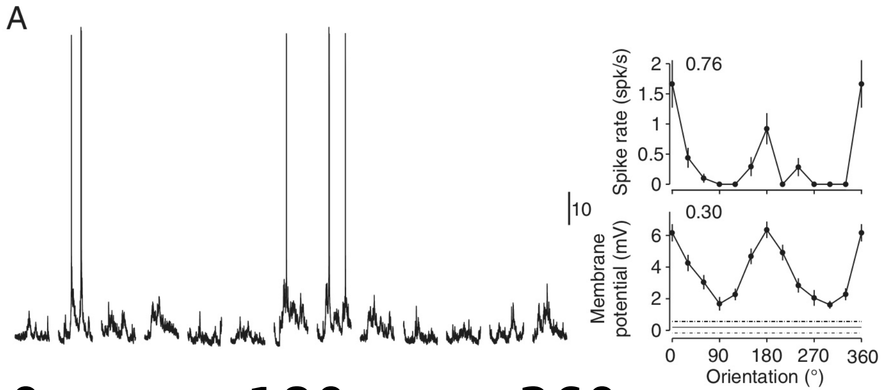
Stimulus represented in rate patterns



0 180 360

stimulus orientation

Orientation selectivity
of V1 neuron

Orientation selectivity
of its inputs (LGN)

Tan *J Neurosci* 2011

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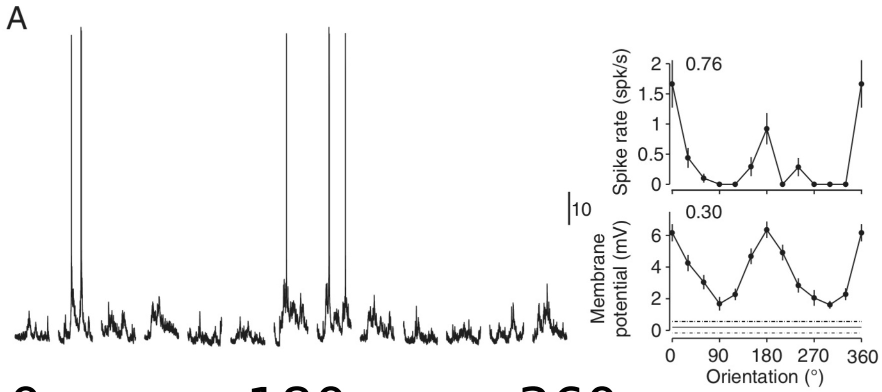

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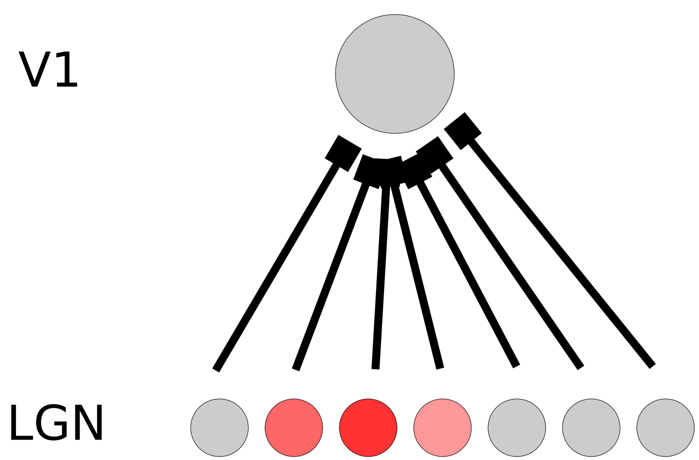

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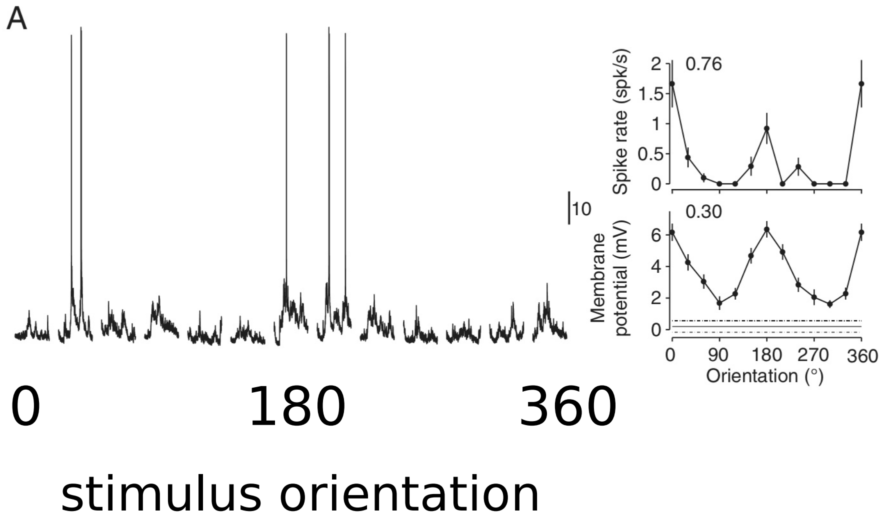

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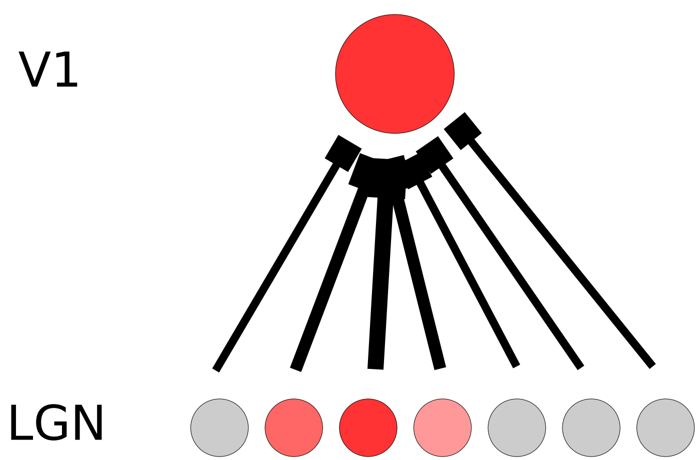
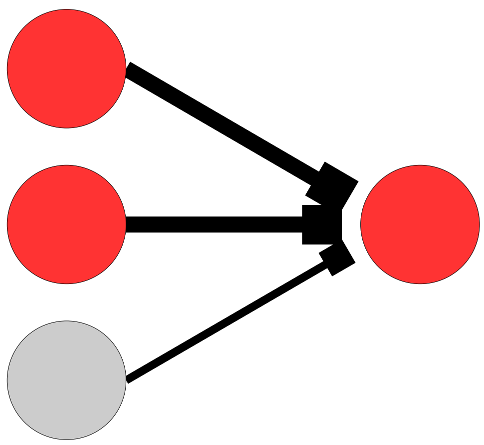


Tan *J Neurosci* 2011

On abstract level: rate-pattern recognition

most frequently
repeated pattern



less frequently
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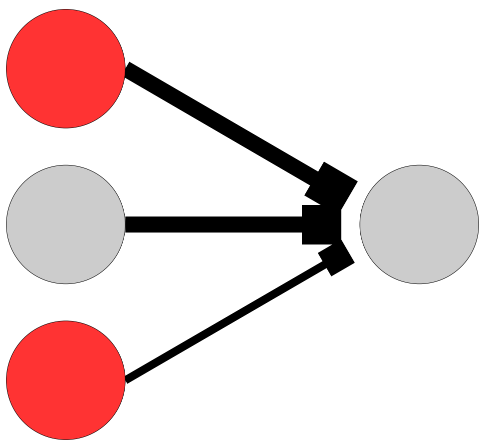
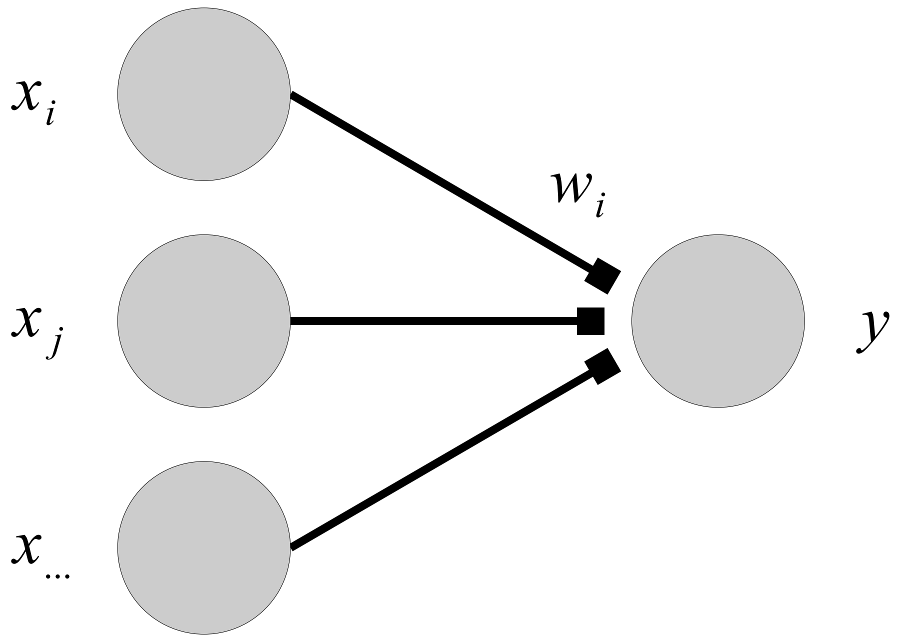
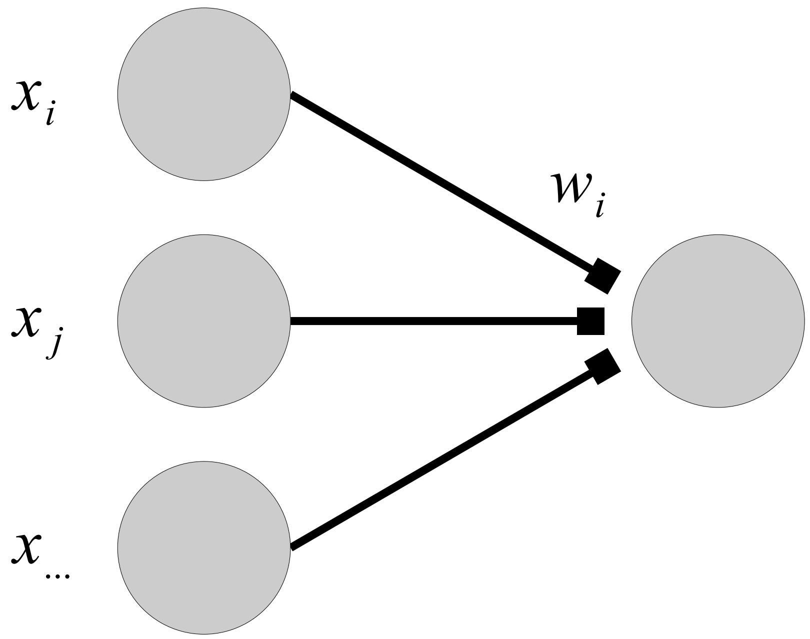


Weight dynamics for rate neuron



$$\dot{w}_i \propto x_i \, y$$

Weight dynamics for rate neuron



$$y=\sum_j w_j x_j$$

$$\dot{w}_i \propto x_i y = \sum_j x_i x_j w_j$$

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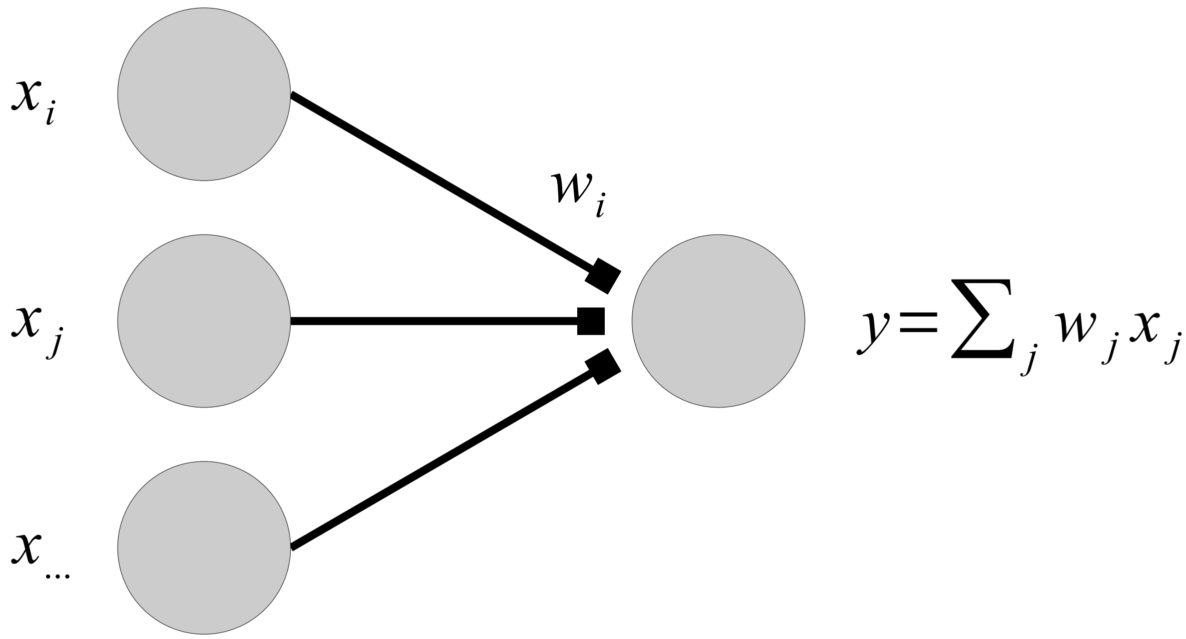

$$\dot{w}_i \propto x_i y = \sum_j x_i x_j w_j$$

$$\dot{w} = C w \quad \text{with} \quad C_{ij} = \langle x_i x_j \rangle$$

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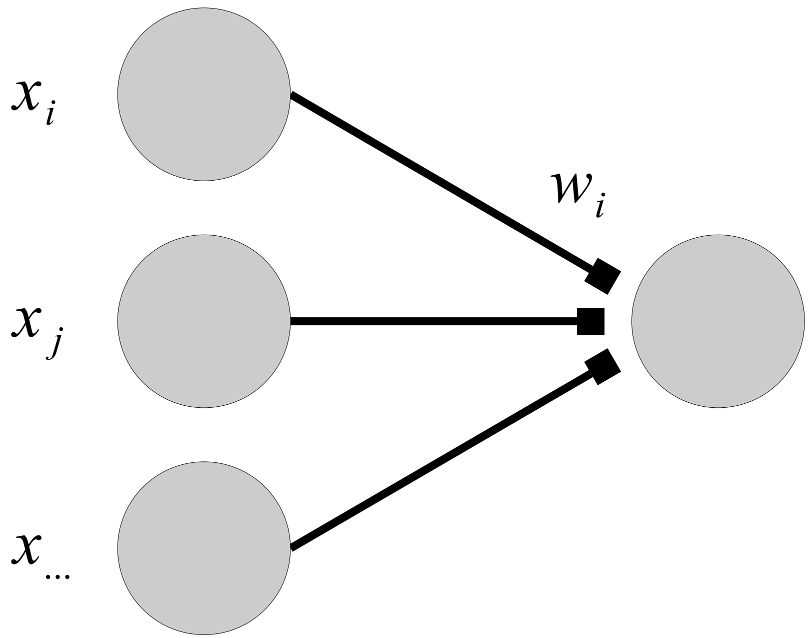

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Hebbian dynamics is intrinsically unstable!

$$\dot{w} = C w \quad \text{with} \quad C_{ij} = \langle x_i x_j \rangle$$

Main direction of growth

$$w \sim e^{\lambda_{max} t} [V_{max} . w(t=0)] V_{max}$$

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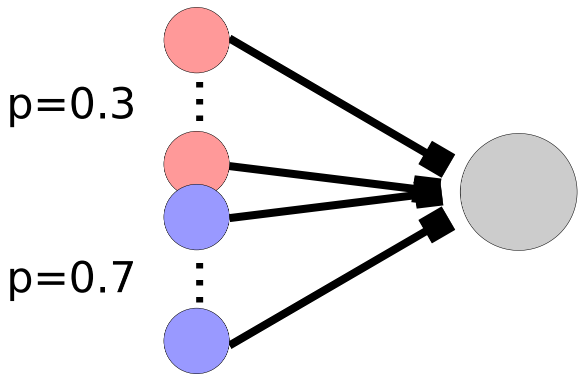

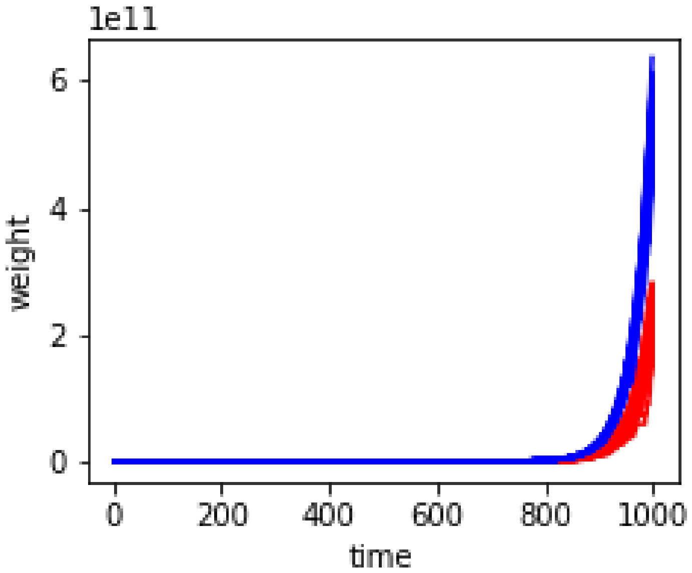

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Stabilization by synaptic competition: Oja's rule

$$\dot{w}_i = y\left(x_i - y\,w_i\right)$$

Oja *J Math Biol* 1982

Stabilization by synaptic competition: Oja's rule

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stabilization effect

$$\sum_j w_j \sim const$$

Oja *J Math Biol* 1982

Stabilization by synaptic competition: Oja's rule

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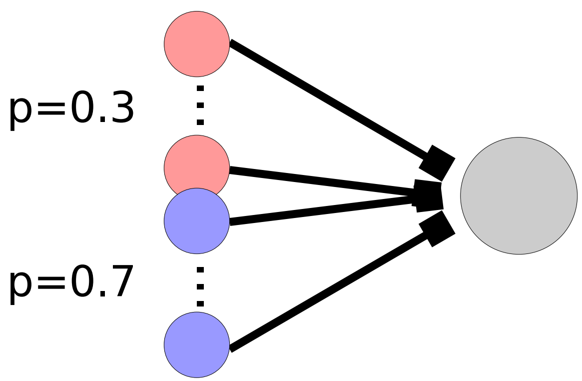
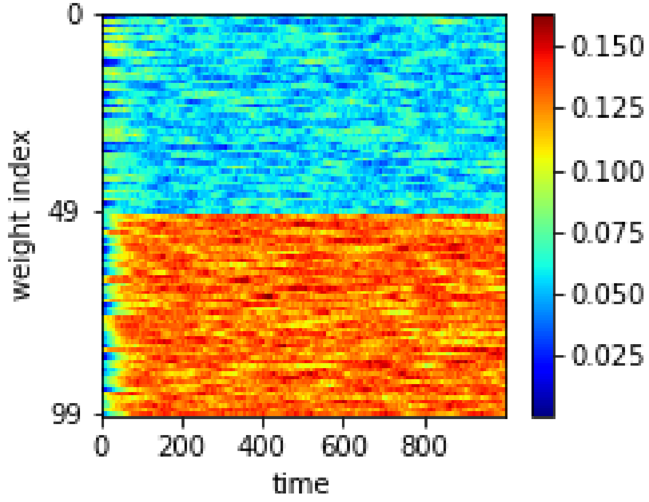
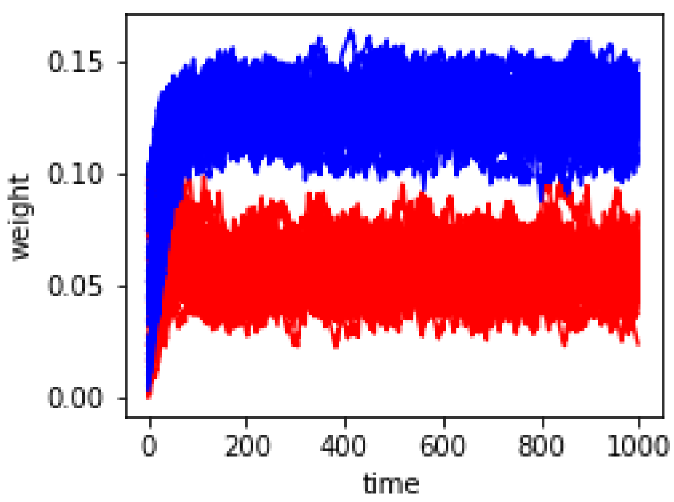
- Select dominating eigenvector of *C*
- Principal component analysis (PCA)







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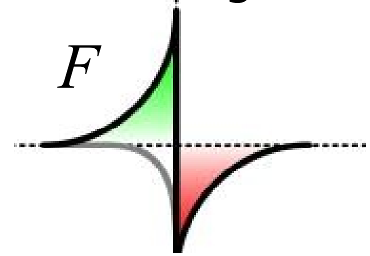
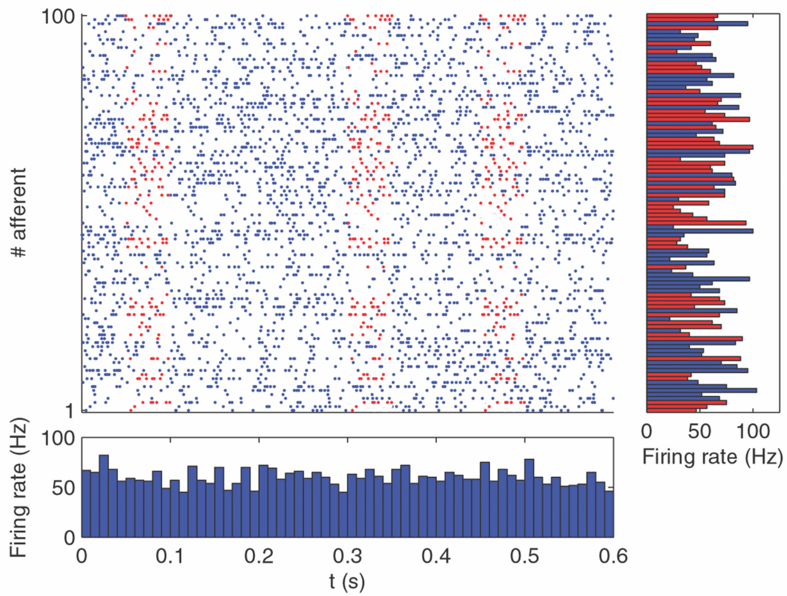
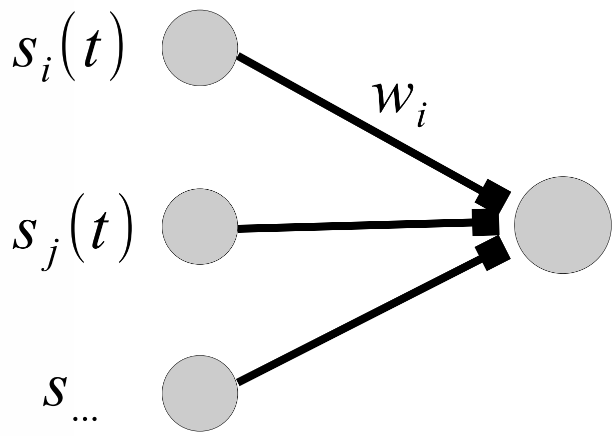
Unsupervised learning for detection of spike patterns

STDP learning window



frozen Poisson spike pattern





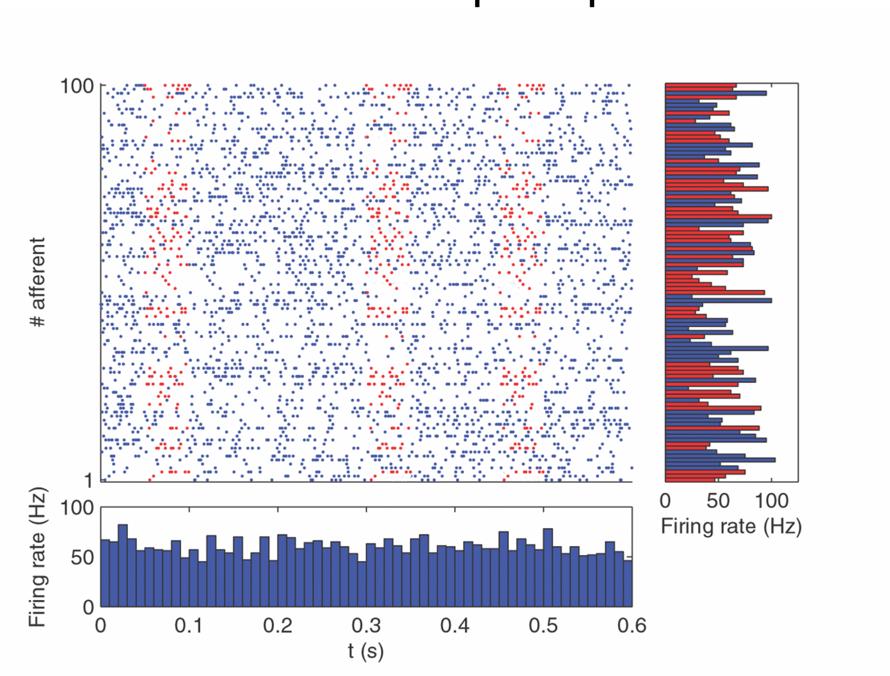
output neuron

$$\dot{w}_{...} = F(t_{pre} - t_{post}) - a_{pre}$$

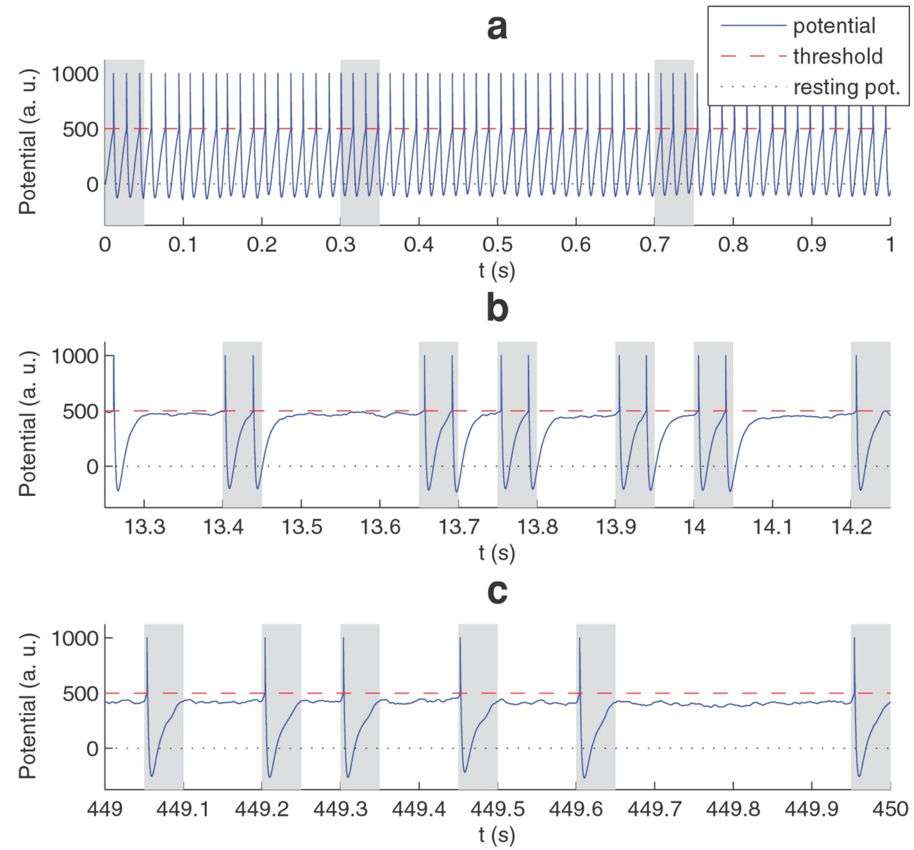
Masquelier *PLoS ONE* 2008

Unsupervised learning for detection of spike patterns

frozen Poisson spike pattern



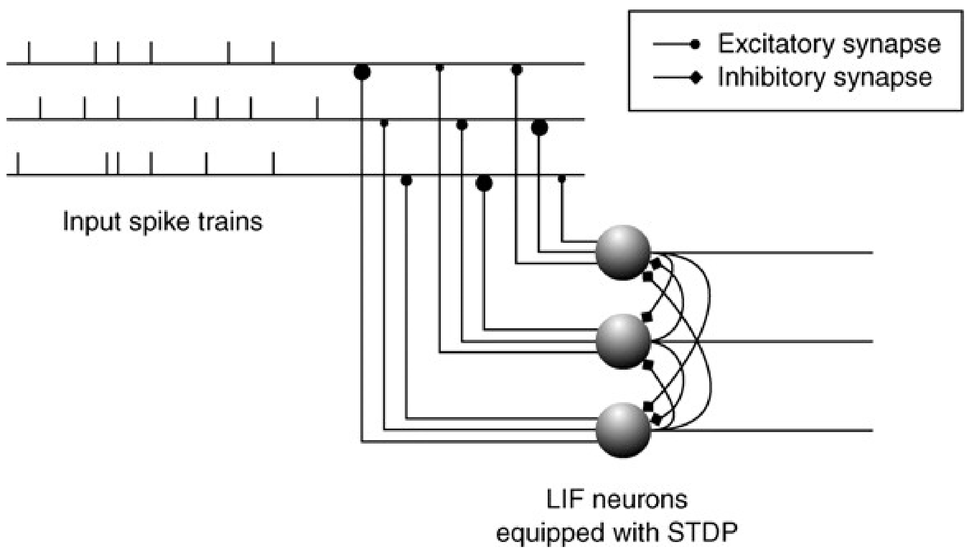
output neuron becomes selective
(LTP for synapses from early spikes)

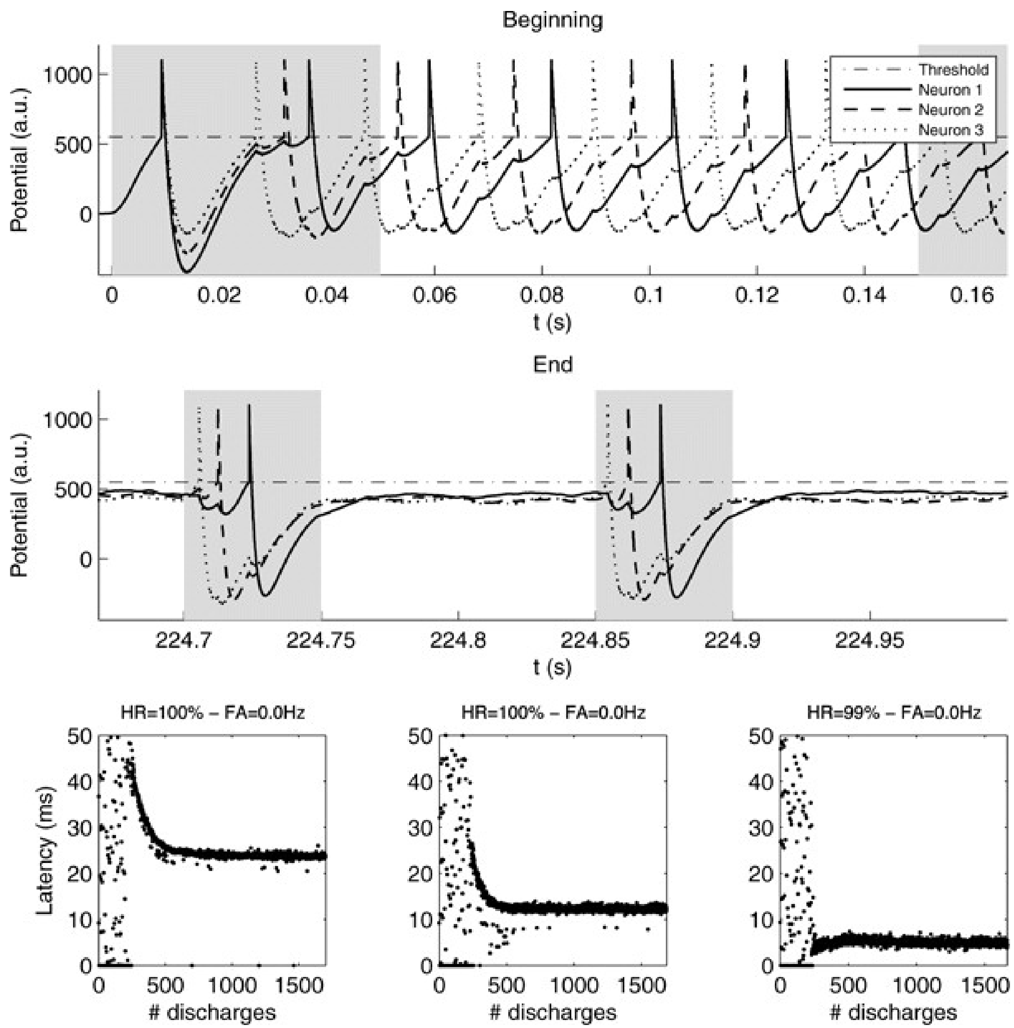


$$\dot{w}_{...} = F\left(t_{pre} - t_{post}\right) - a_{pre}$$

Masquelier *PLoS ONE* 2008

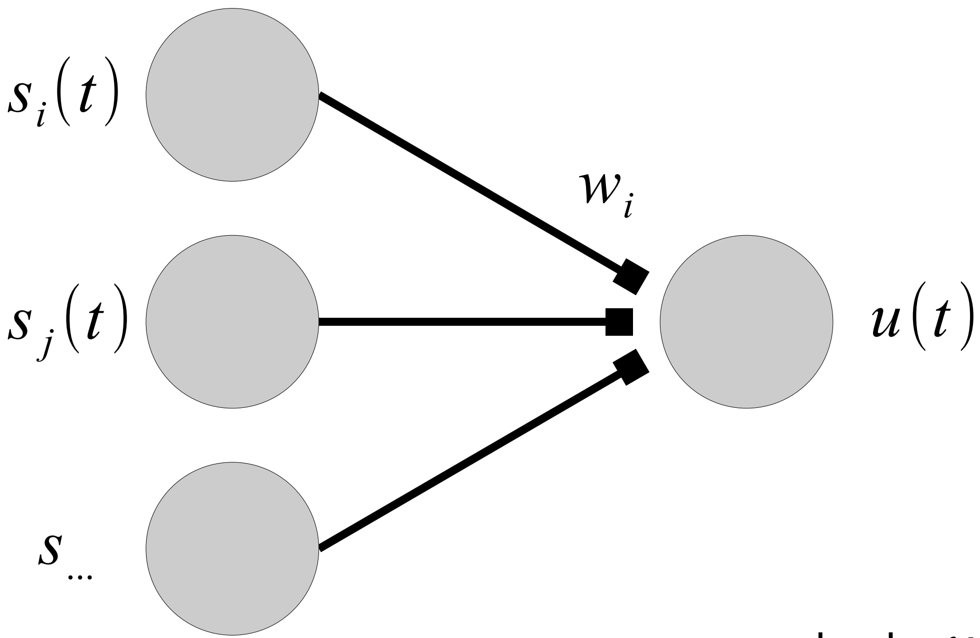
Learning the full pattern, not just the start





Masquelier *Neural Comput* 2009

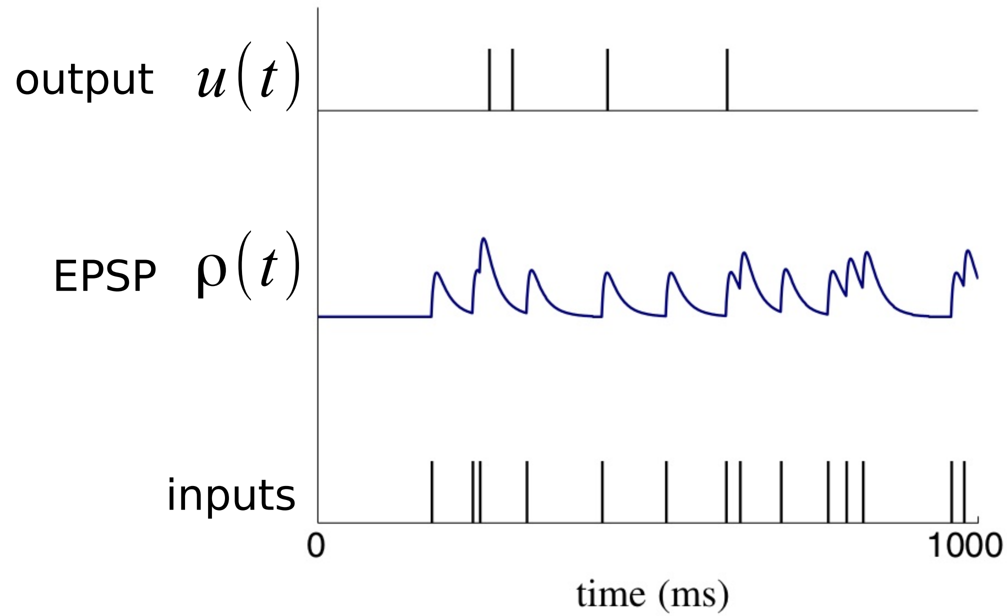
Maths for weight dynamics



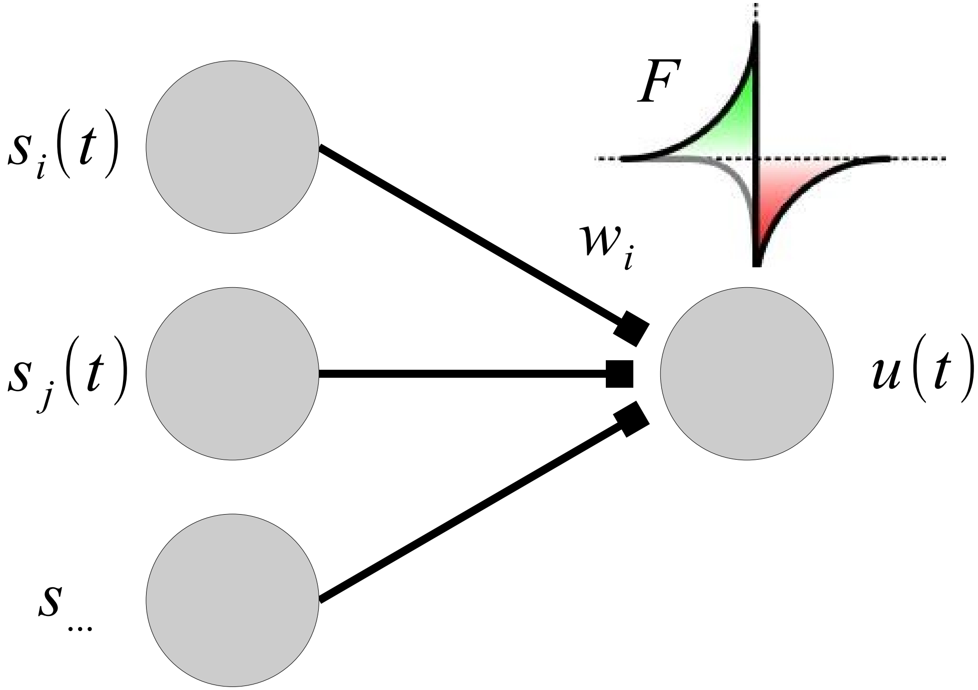
Hawkes process,
Poisson neuron

$$\rho(t) = \sum_j w_j [\epsilon * s_j](t)$$

$$P[u(t)=1] \propto \rho(t)$$



Maths for weight dynamics



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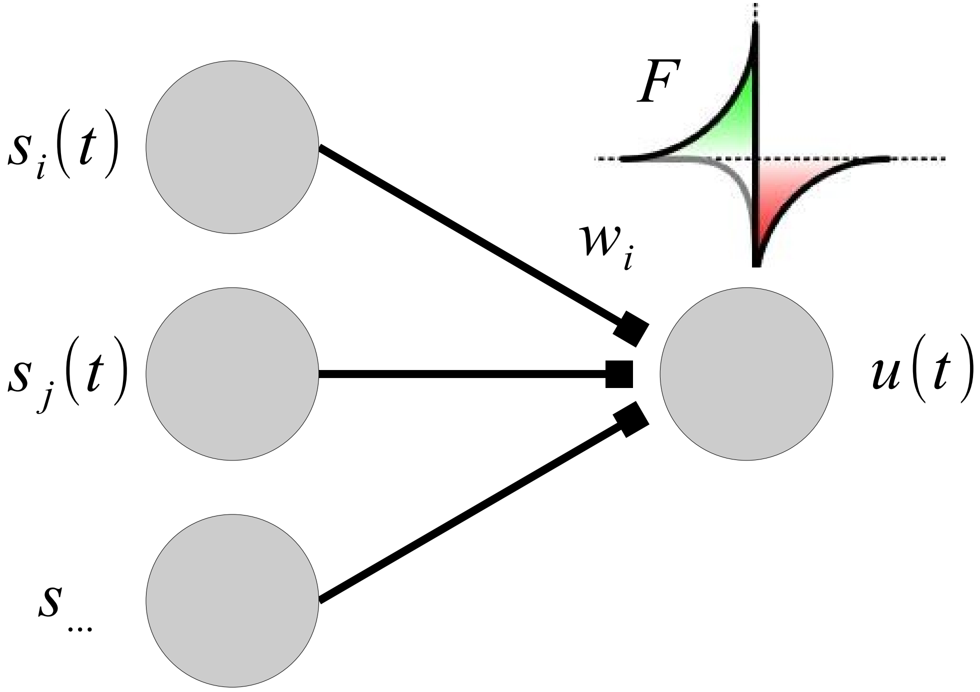

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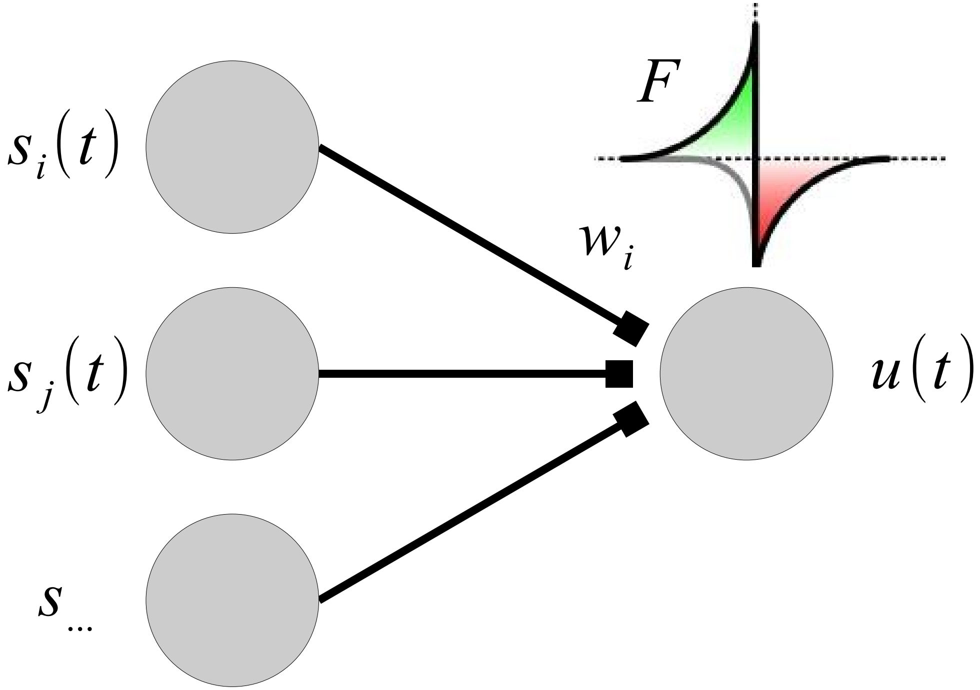
$$= \int_t \int_\tau F(\tau) s_i(t) u(t-\tau) \, d\tau \, dt$$

Maths for weight dynamics



Hawkes process,
Poisson neuron

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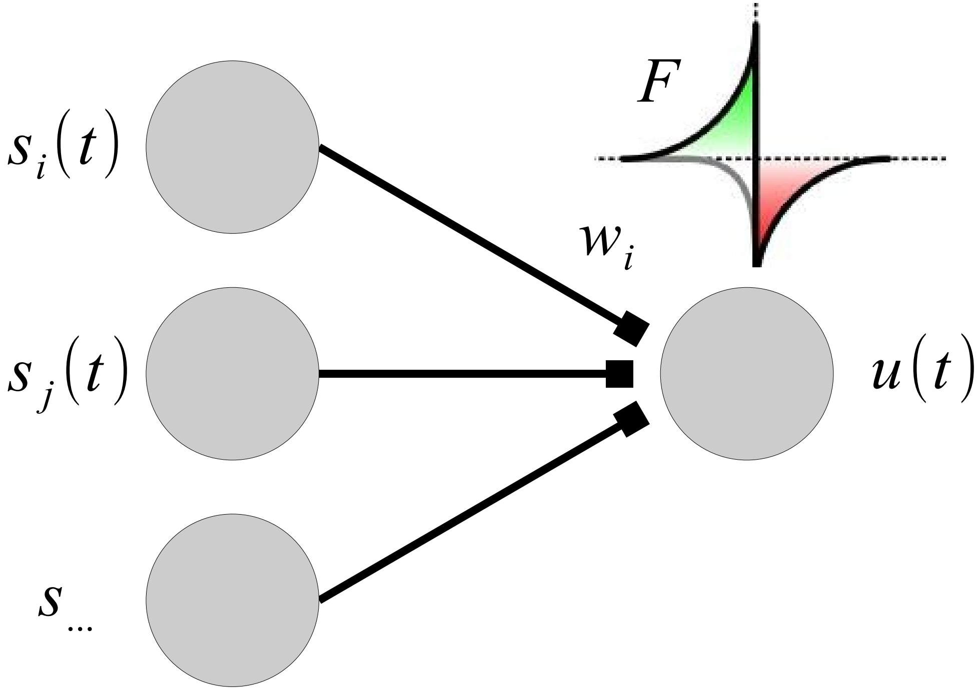
$$\begin{aligned}\dot{w}_i &= \sum_{t_i, t_{post}} F(t_i - t_{post}) \\ &= \int_t \int_\tau F(\tau) s_i(t) u(t-\tau) \, d\tau \, dt \\ &= \sum_j w_j \int_\tau [F * \epsilon](\tau) C_{ij}(\tau) \, d\tau\end{aligned}$$

spike-time correlogram

$$C_{ij}(\tau) = \langle s_i(t) s_j(t-\tau) \rangle$$

Maths for weight dynamics



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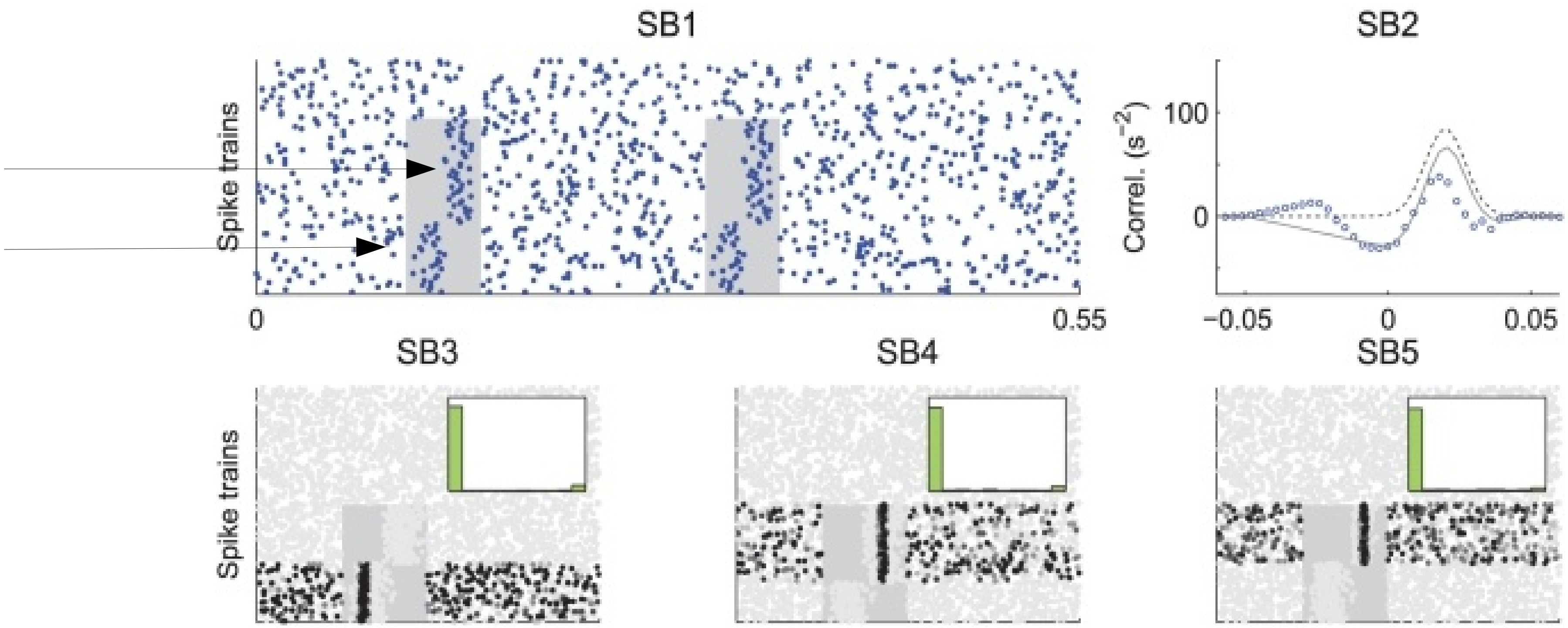
$$\dot{w} = \tilde{C} w$$

spike-time correlogram

$$C_{ij}(\tau) = \langle s_i(t) s_j(t-\tau) \rangle$$

STDP selects early, dense and sharp spike clusters

competition between spike clusters (PCA on correlation structure)



PCA becomes ICA with additional regularization:

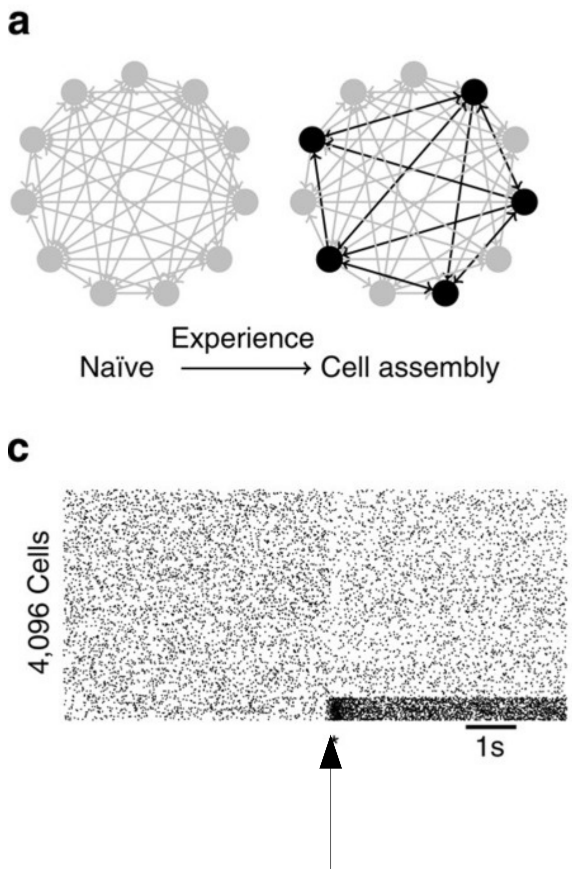
$$\dot{w} = \tilde{C}\, w - a_{pre}$$

Gilson *PLoS Comput Biol* 2011

Outline

- Historical perspective on learning in neuronal systems
- From Hebbian learning to spike-timing-dependent plasticity
- **Weight dynamics and “information” representations:**
  - Principal component analysis (PCA)
  - Detection of spike patterns by STDP
  - **Neuronal assemblies in recurrent networks**
- From biological learning to machine learning:
  - Unsupervised vs supervised vs reinforcement learning

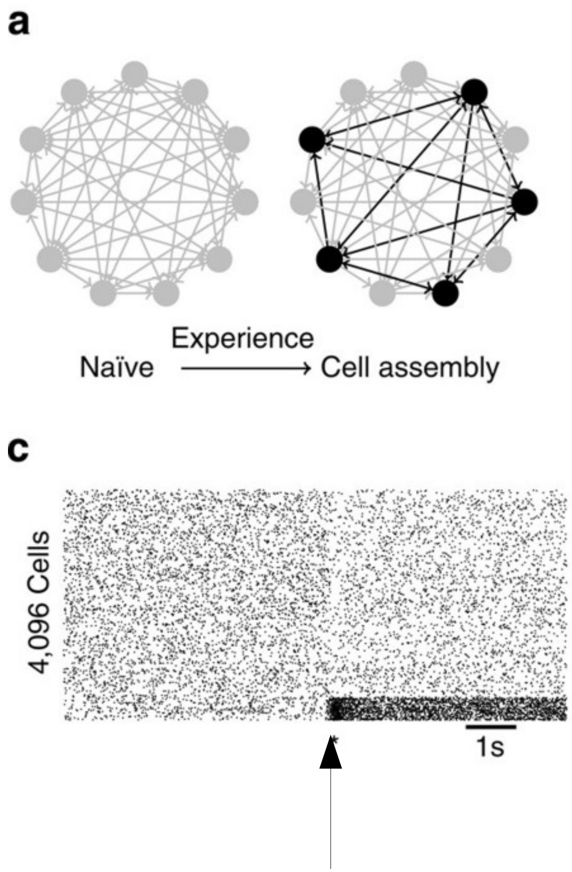
STDP and neuron assemblies



stimulus

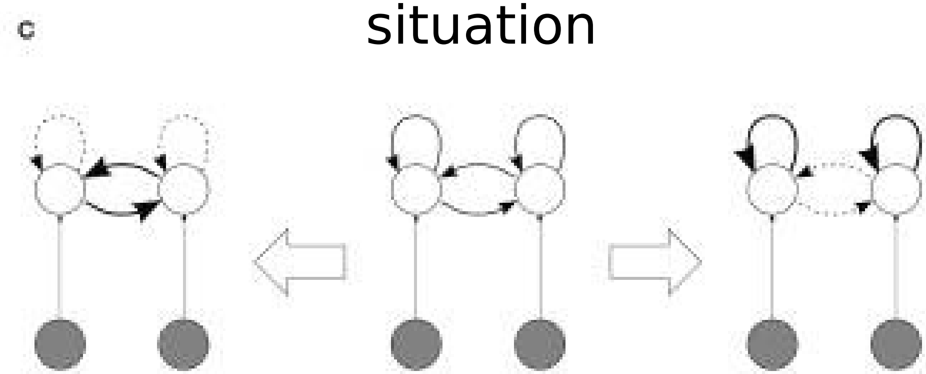
Zenke *Nat Comm* 2015

STDP and neuron assemblies



stimulus

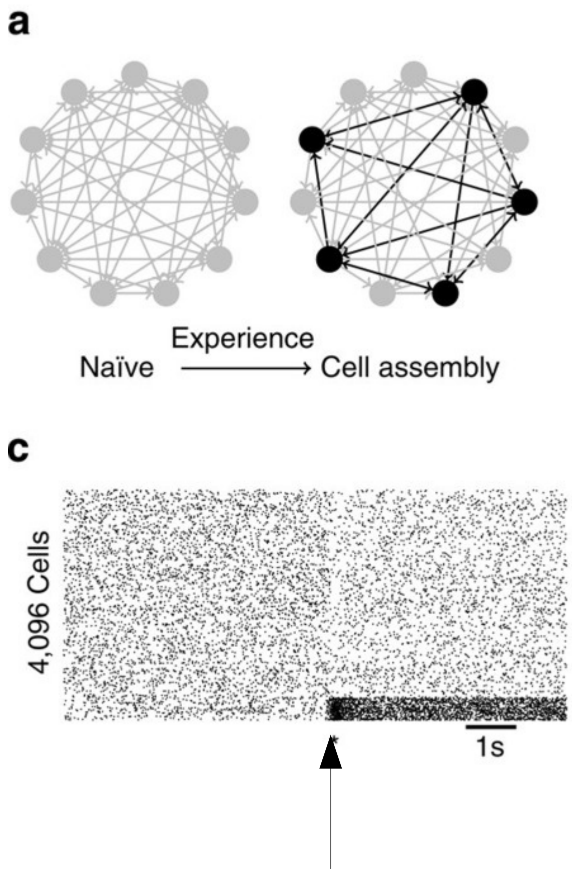
initial
situation



Zenke *Nat Comm* 2015

Gilson *Biol Cybern* 2009

STDP and neuron assemblies



stimulus

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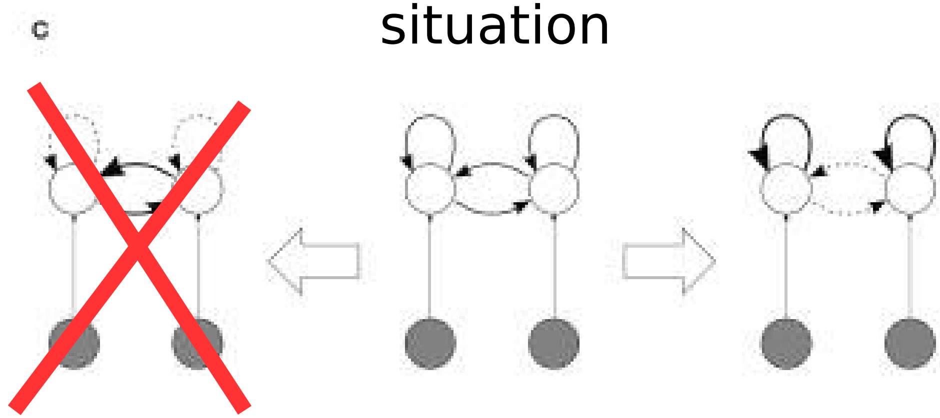
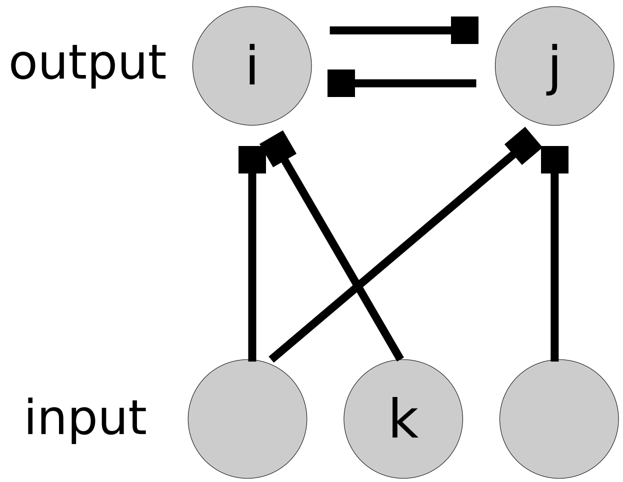


Zenke *Nat Comm* 2015

Gilson *Biol Cybern* 2009

Weight dynamics in recurrent networks



$$\dot{w}_{ij} = \int_{\tau} F(\tau) \langle s_j(t) s_i(t-\tau) \rangle d\tau$$

$$\rho_i(t) = \sum_j w_{ij} [\epsilon * s_j](t) + \sum_k w_{ik} [\epsilon * s_k](t)$$

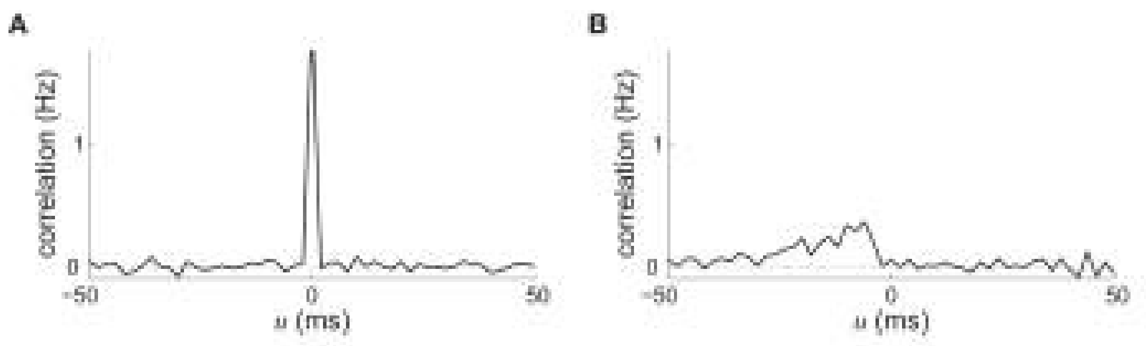
But $\boldsymbol{s_i}$ depends on $\boldsymbol{s_j}$ too!

Echos in networks due to recurrent connections

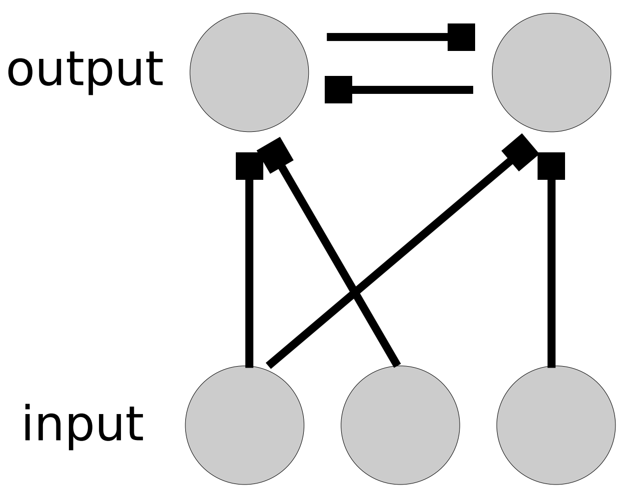
Gilson *Biol Cybern* 2009

Correlation structure in recurrent networks

input-input　　　　input-output



$$\tau = t_{input} - t_{output}$$



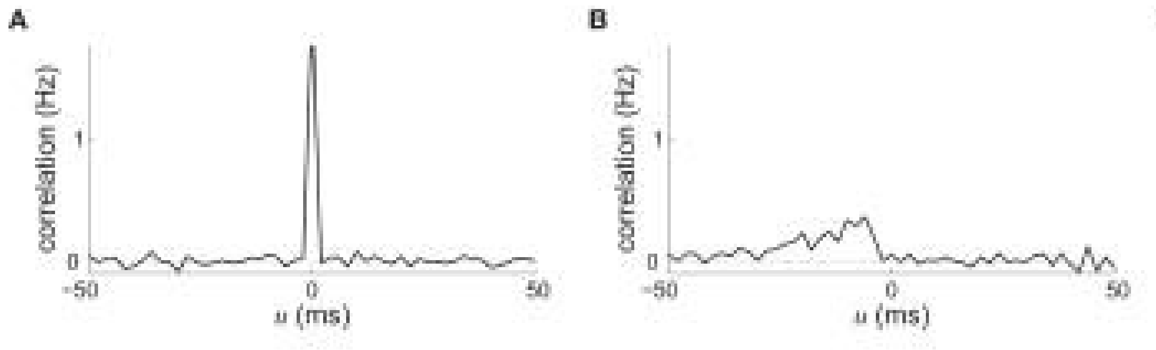
$$\dot{w}_{ij} = \int_{\tau} F(\tau)\, C(\tau)\, d\tau$$

Gilson *Biol Cybern* 2009

Correlation structure in recurrent networks

input-input

input-output



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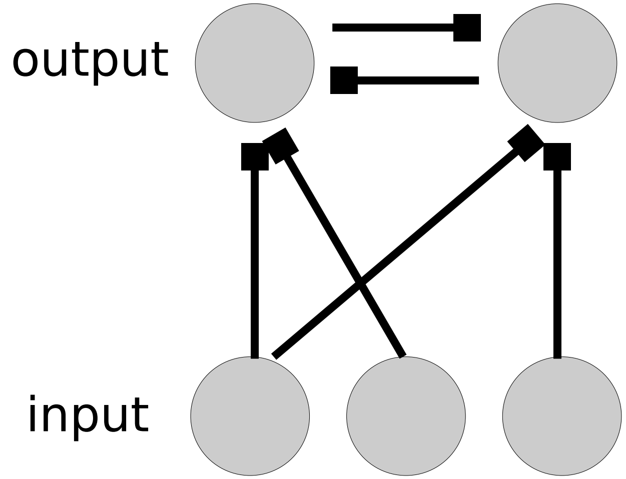
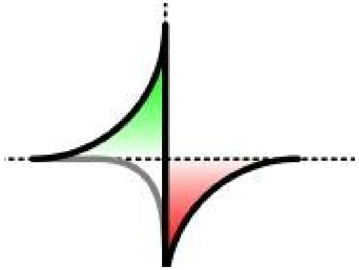


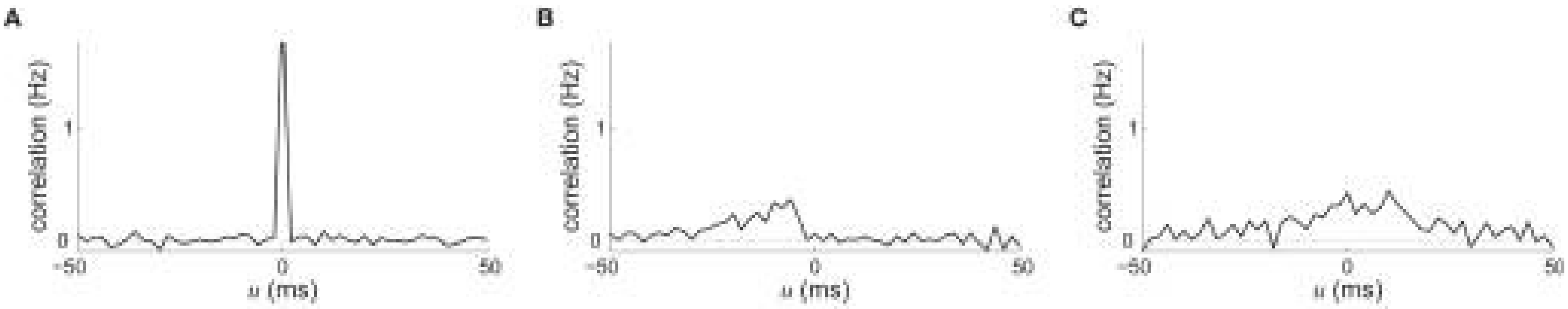


$$\dot{w}_{ij} = \int_{\tau} F(\tau)\, C(\tau)\, d\tau > 0$$

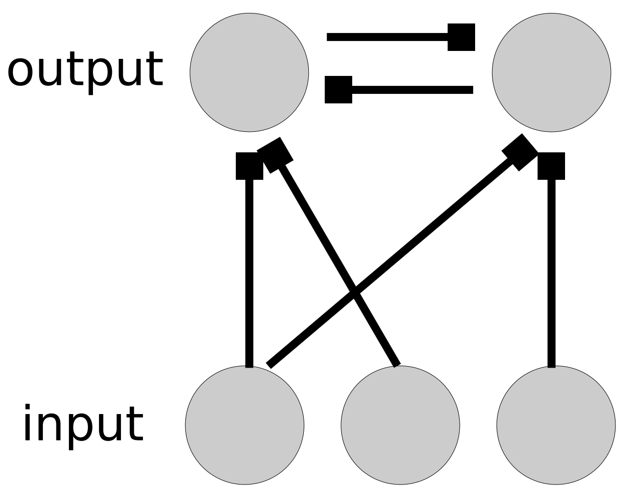
Gilson *Biol Cybern* 2009

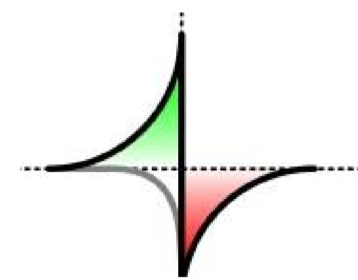
Correlation structure in recurrent networks

input-input　　input-output　　output-output



$$\tau = t_{input} - t_{output}$$





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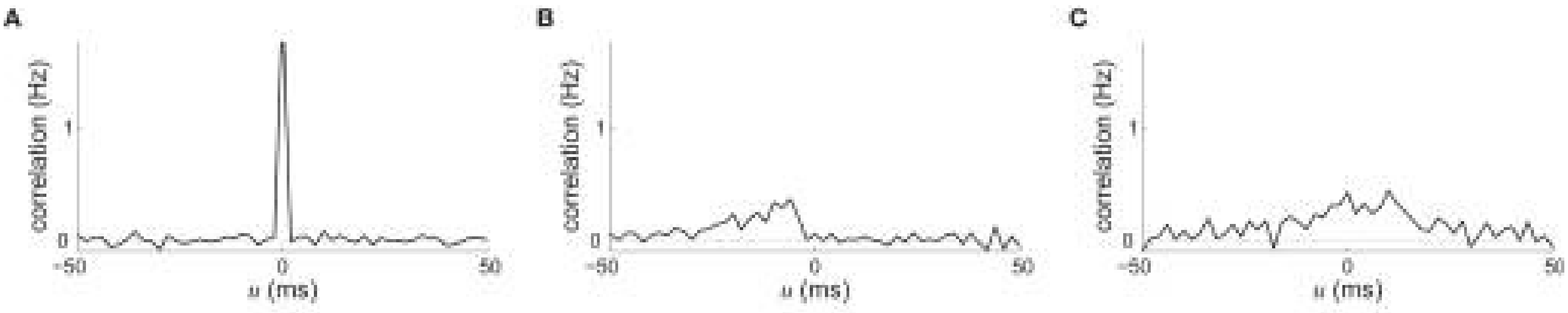
Gilson *Biol Cybern* 2009

Correlation structure in recurrent networks

input-input | input-output | output-output



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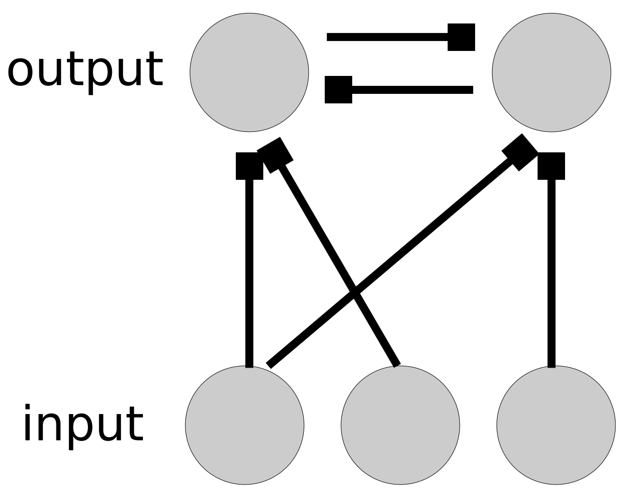
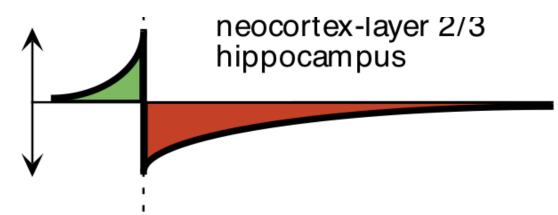


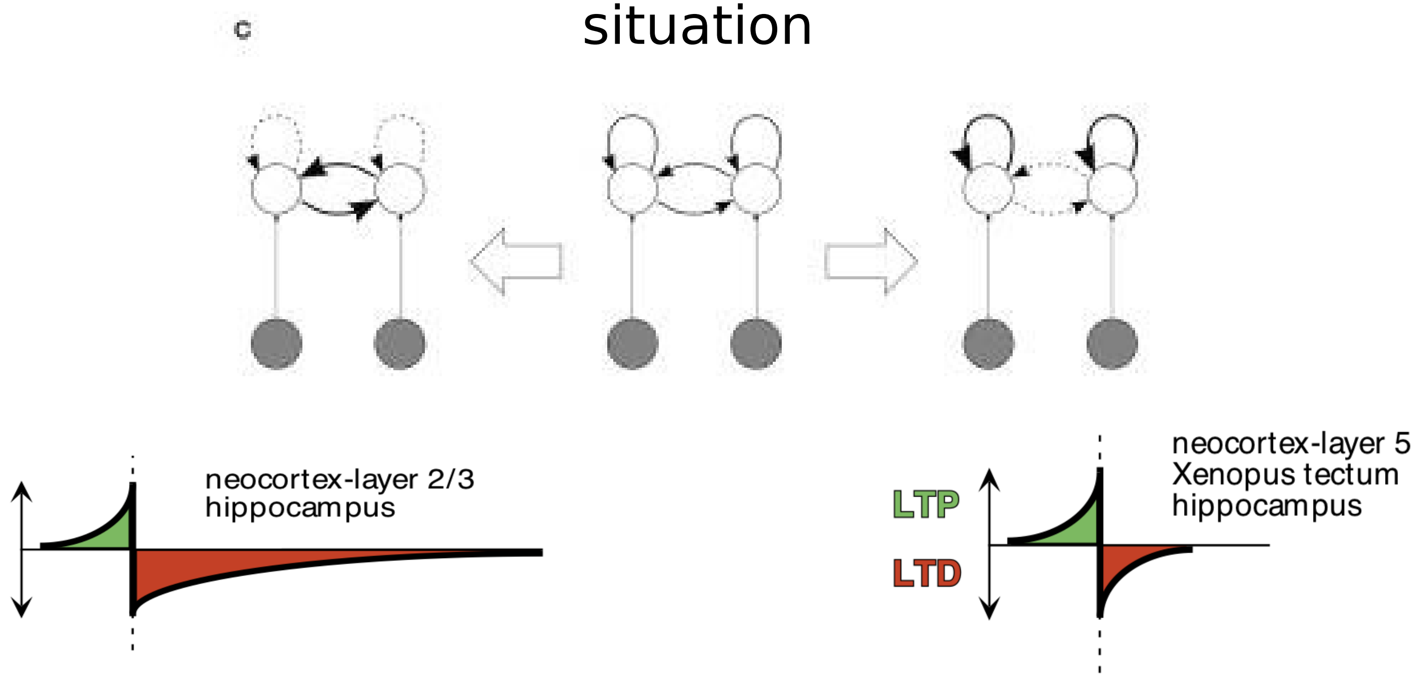


$$\dot{w}_{ij} = \int_{\tau} F(\tau) C(\tau) d\tau < 0$$

Gilson *Biol Cybern* 2009

STDP and neuron assemblies

initial
situation

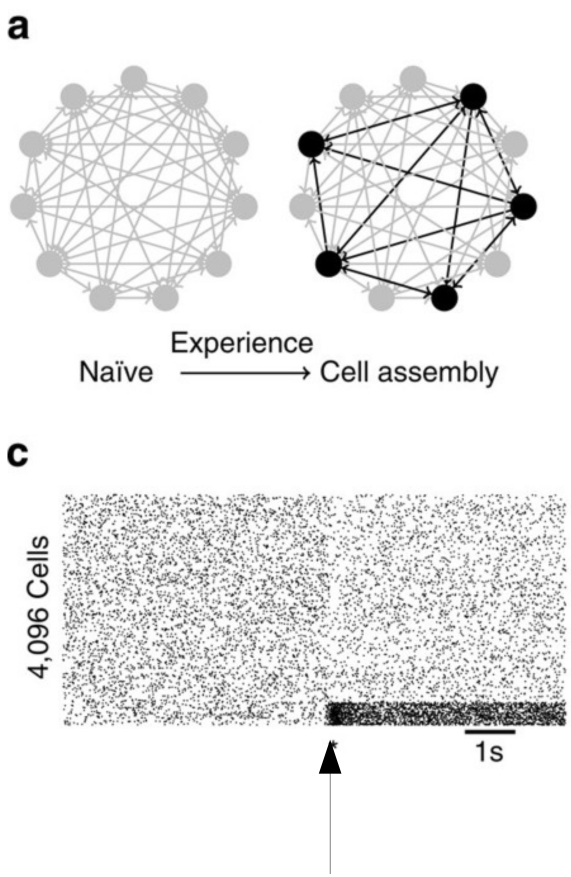


axonal delays

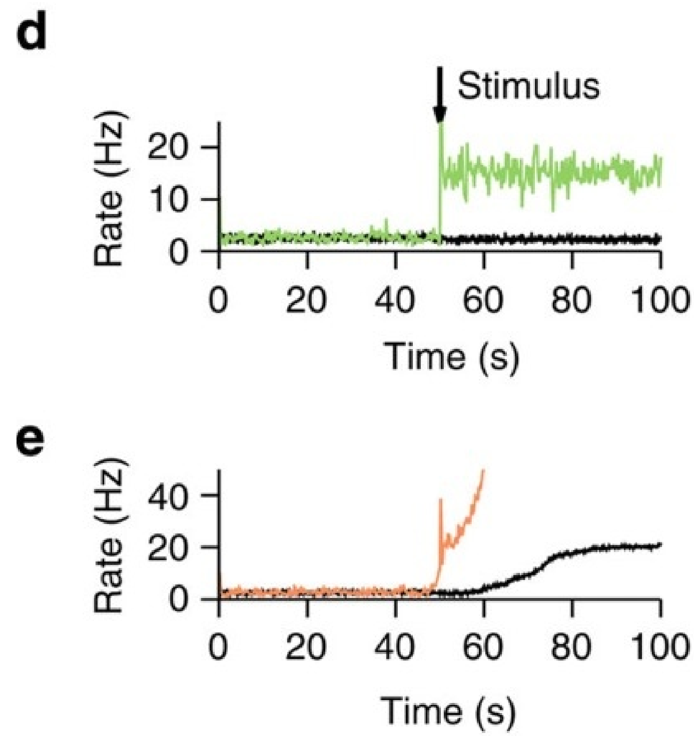
dendritic delays

Gilson *Biol Cybern* 2009

Stability in recurrent networks with ongoing plasticity



stimulus

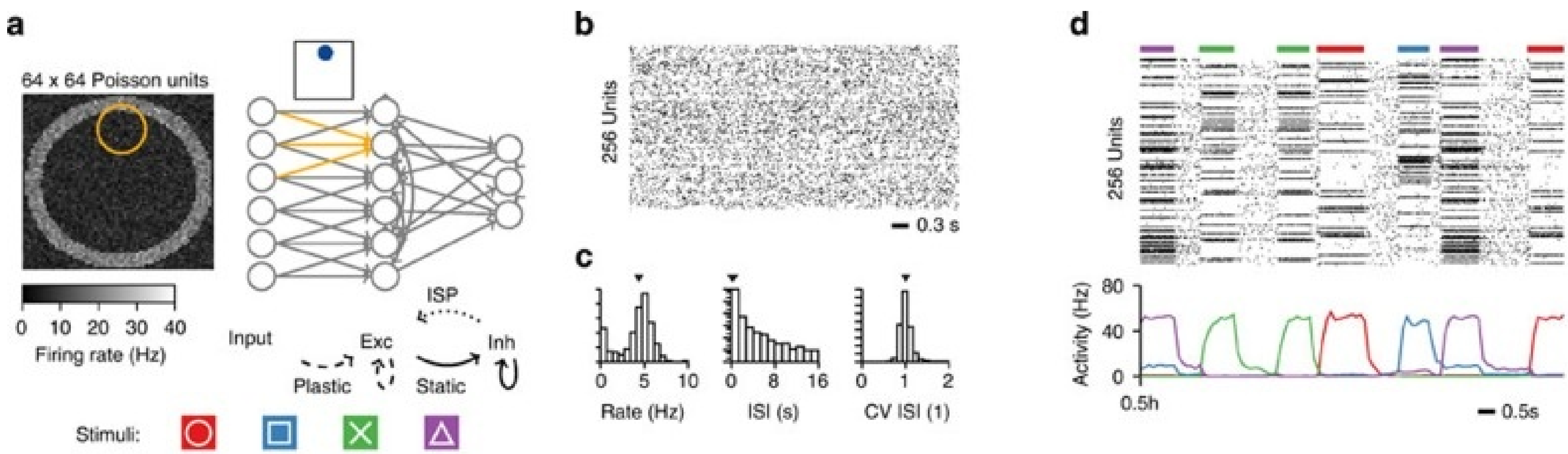


tSTDP off

tSTDP on

Zenke *Nat Comm* 2015

Stability in recurrent networks with ongoing plasticity



$$\dot{w} = F\left(\{t_{pre}\}, \{t_{post}\}\right) - \beta\left(w - w^{eq}\right) r_{post}^{4} + \alpha\, r_{pre}$$

Zenke *Nat Comm* 2015

Summary for plastic weight dynamics

- Learned weight structure represent the input statistics and shape the neuronal function (input-output mapping)
  - implement selectivity to pattern
  - create cell assemblies that receive correlated inputs
- Beware of weight instability!
  - other mechanisms are necessary to stabilize learning, like heterosynaptic plasticity that models resource limitation

Outline

- Historical perspective on learning in neuronal systems
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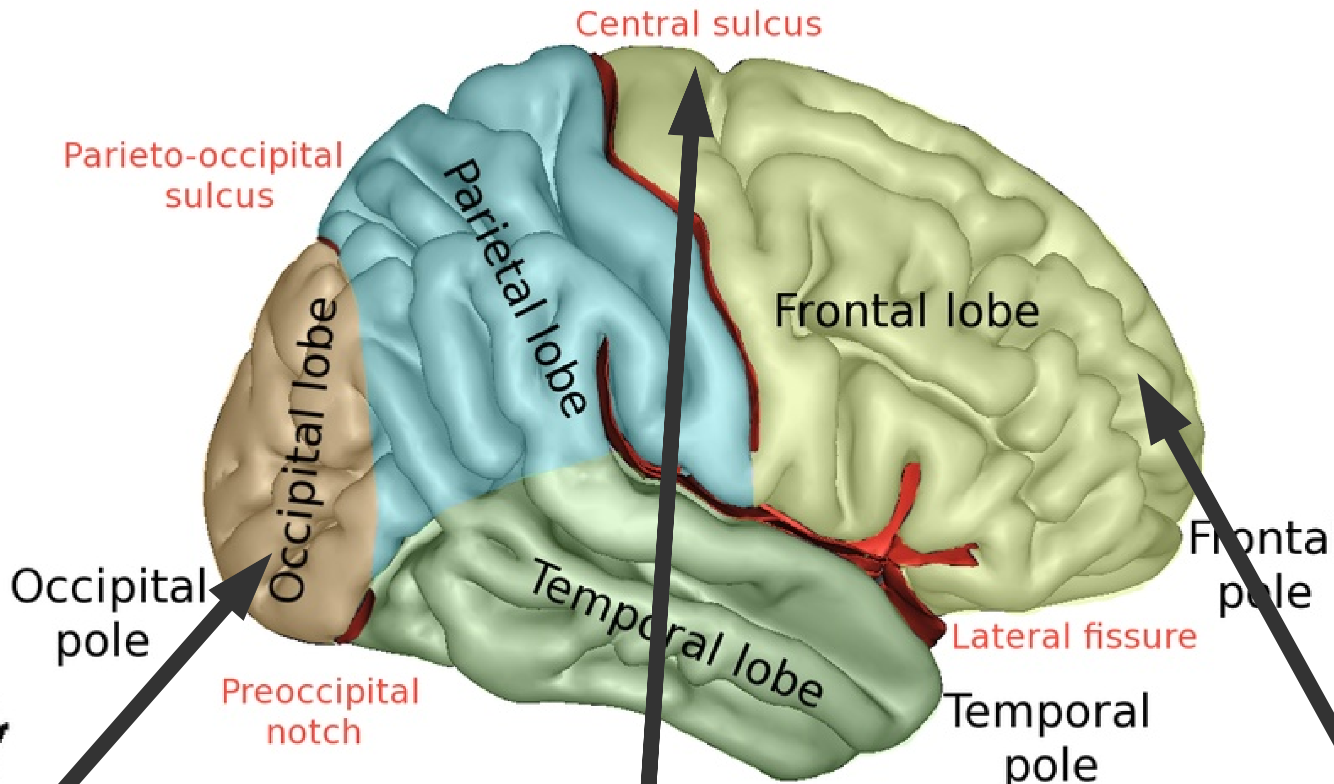
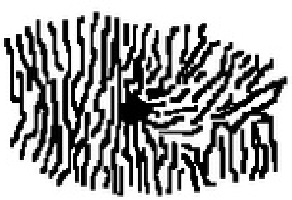
Learning in neuronal systems



wikipedia



Orientation columns in primary visual cortex (V1)

Unsupervised learning

Locomotion in motor cortex

Reinforcement learning

Long-term memory in prefrontal cortex

Supervised learning

Types of learning

unsupervised
(Hebbian, STDP)

$$\dot{w}_i = y\, x_i$$

supervised
(delta rule,
perceptron)

$$\dot{w}_i = \left(\bar{y}^{\,A} - y\right) x_i^A$$

$\bar{y}^{\,A}$ objective for input of class *A*

Types of learning

unsupervised
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$$\dot{w}_i = y\, x_i$$

supervised
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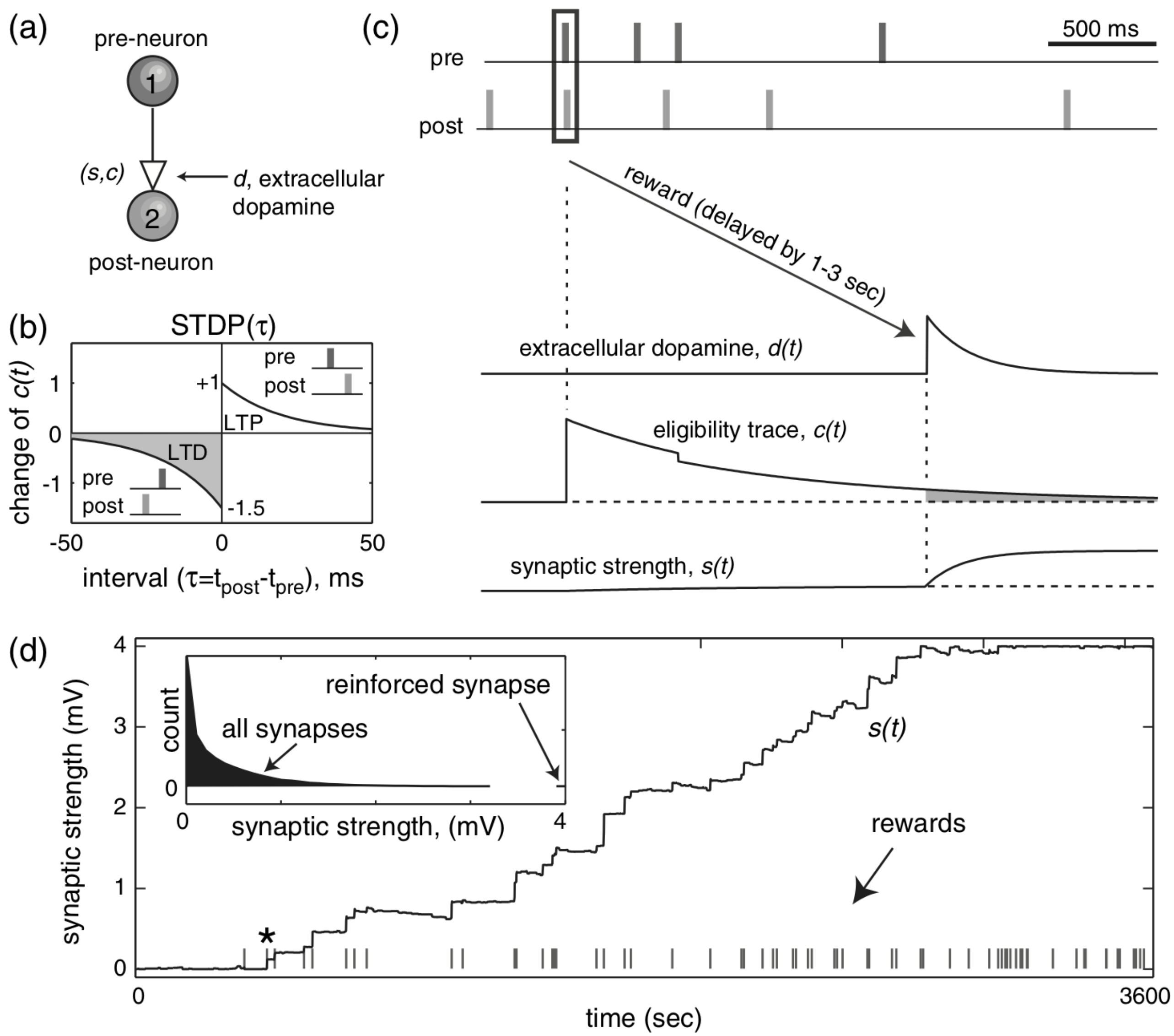
$\bar{y}^{A}$ objective for input of class A

reinforcement
learning

$$\dot{w}_i = \epsilon\, y\, x_i$$

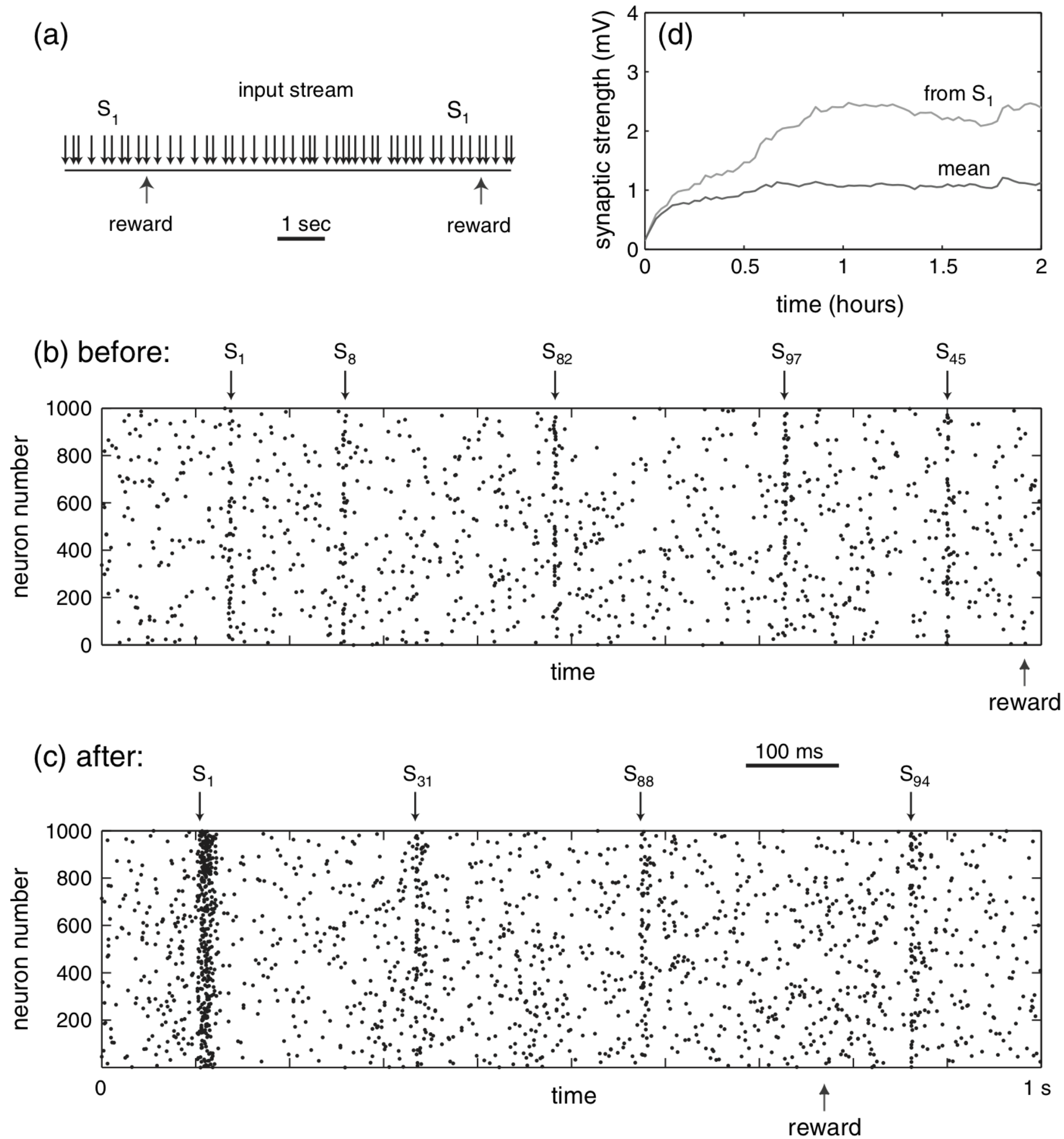
ϵ modulator (dopamine, acetylcholine)

Reward-modulated STDP



Izhikevich *Cereb Cortex* 2007

Reward-modulated STDP



Izhikevich *Cereb Cortex* 2007

Presentation available on
http://www.matthieugilson.eu

upf. Universitat Pompeu Fabra Barcelona

European Commission

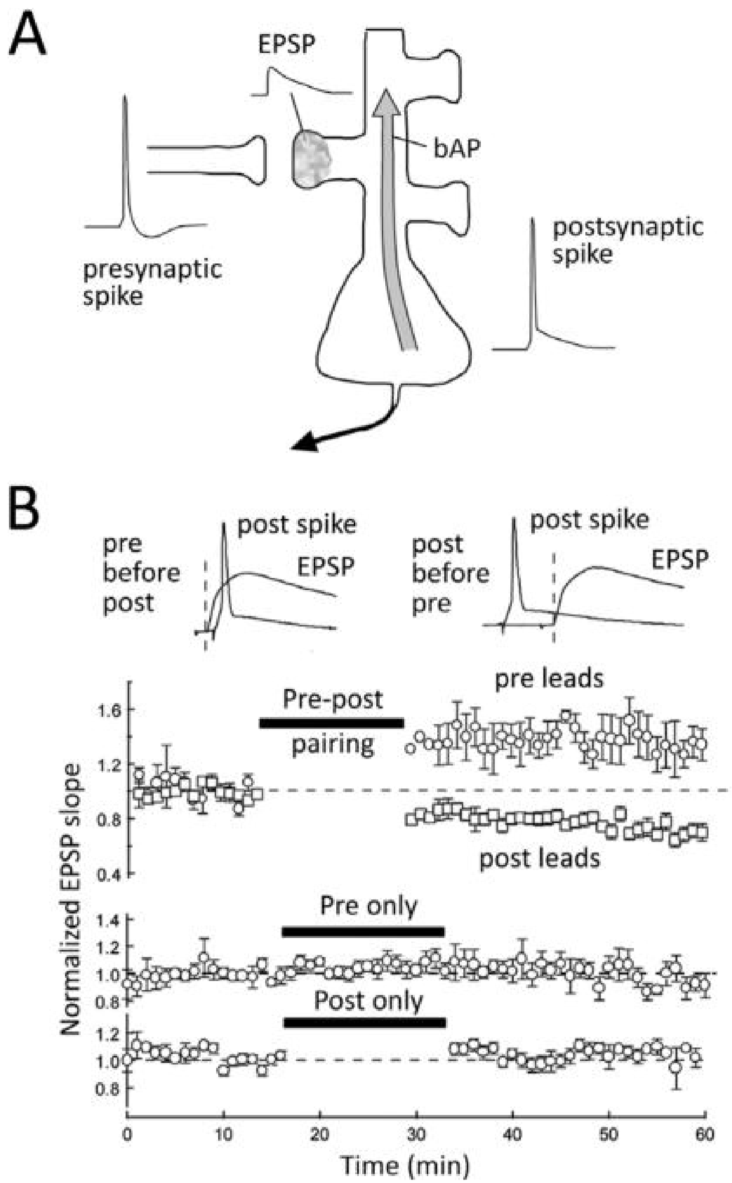
Human Brain Project

MARIE CURIE ACTIONS

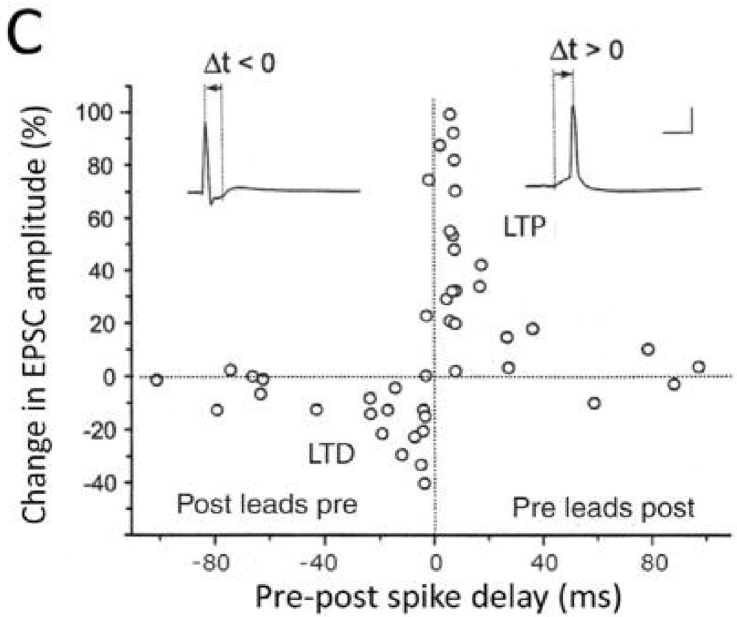
Supplementary material about STDP

- **Experimental evidence of STDP: how rich should the model be?**
- Weight dynamics and “information” representations:
  - Ocular dominance and symmetry breaking
- Future challenges:
  - Distributed information representations

STDP: what do experiments really say?



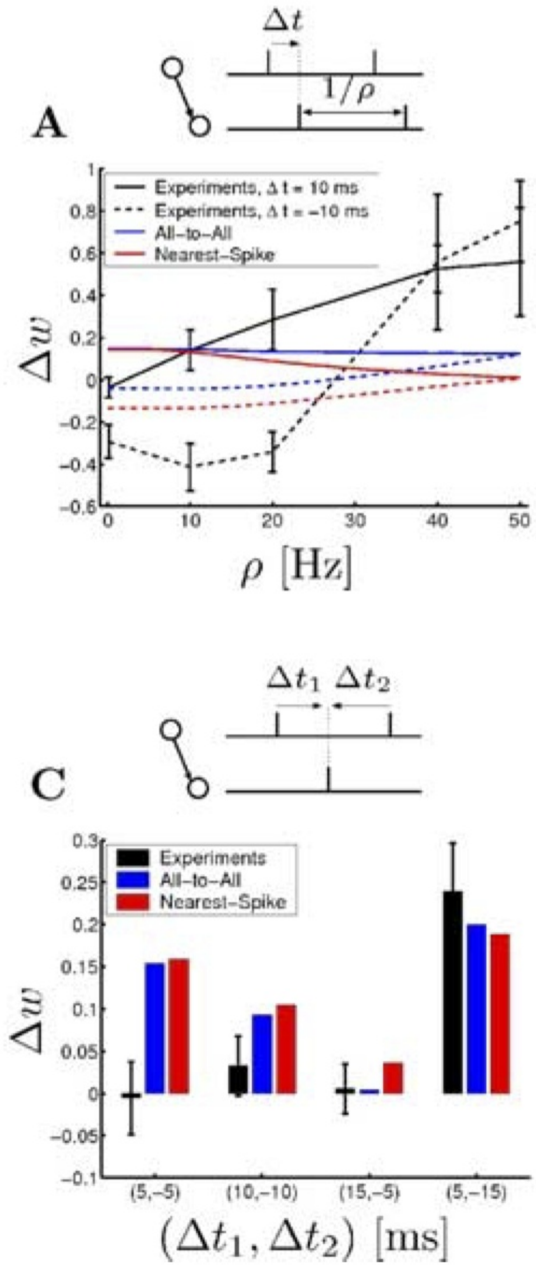
Weight change after 60 pre-post pairings!



$$t_{post} - t_{pre}$$

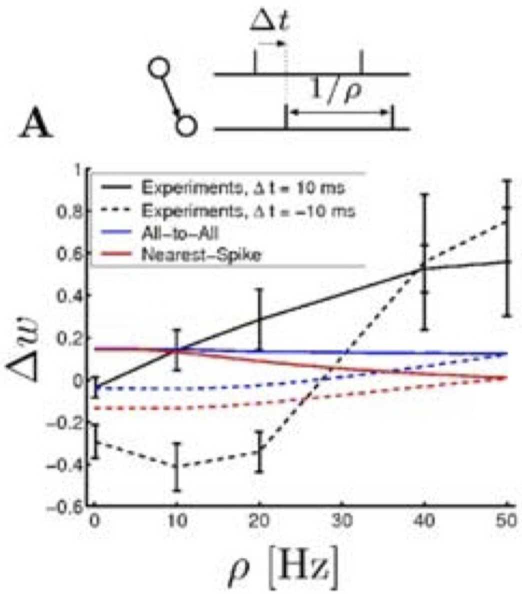
from review Feldman *Neuron* (2012)
data: Bi and Poo (1998), Feldman (2000)
stochastic STDP model: Elliott (2008)

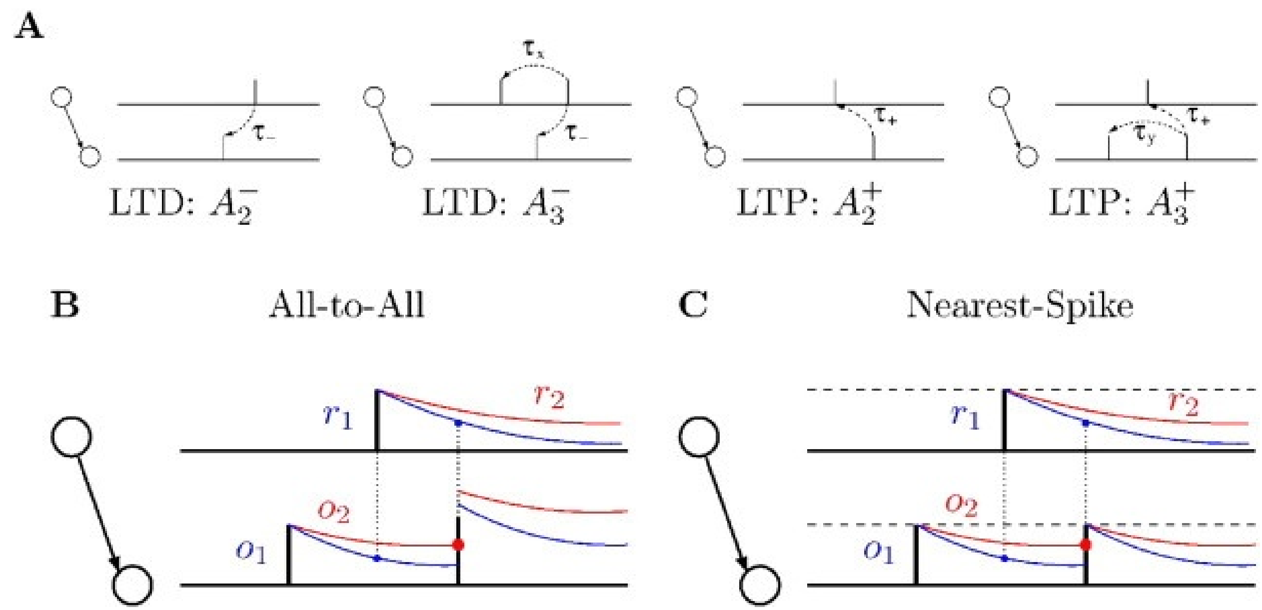
Beyond spike pairs



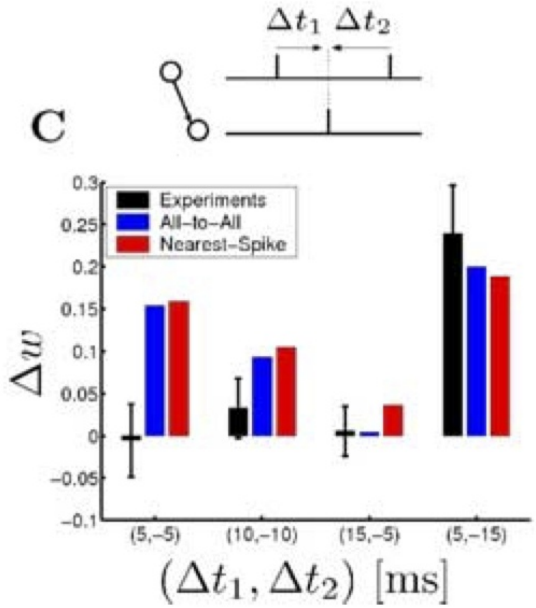
data: Sjostrom *Neuron* (2001)
model: Pfister *J Neurosci* (2006)

Beyond spike pairs





STDP based on triplet of spikes
in addition to spike pairs



data: Sjostrom *Neuron* (2001)
model: Pfister *J Neurosci* (2006)

Supplementary material about STDP

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- **Weight dynamics and “information” representations:**
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- Future challenges:
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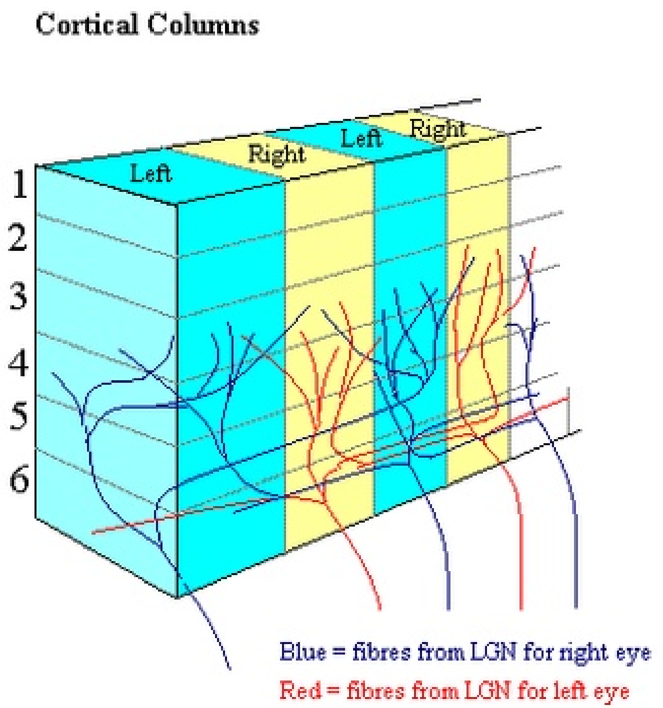
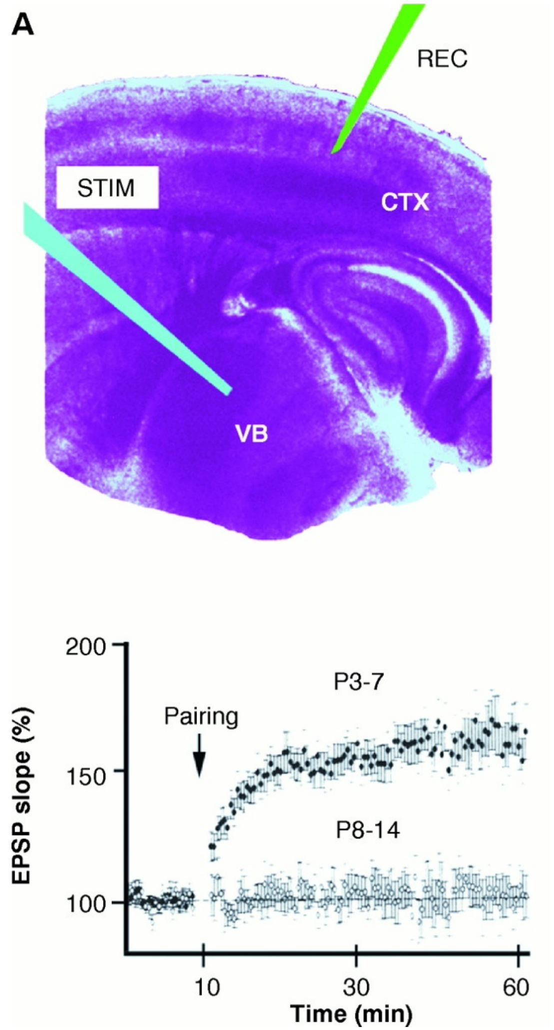
Ocular dominance

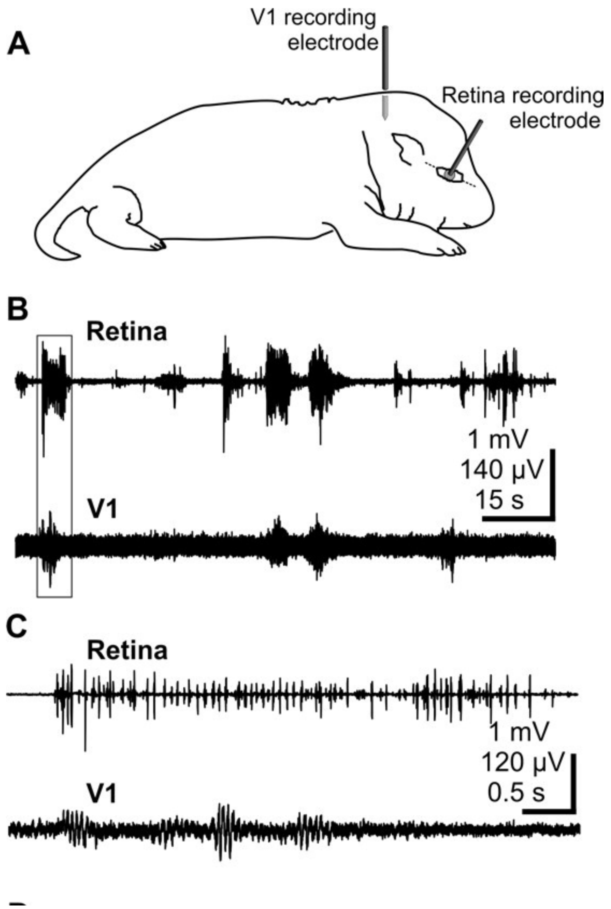
- Symmetric inputs from the two eyes
- How to specialize to one optical input only?



wikipedia



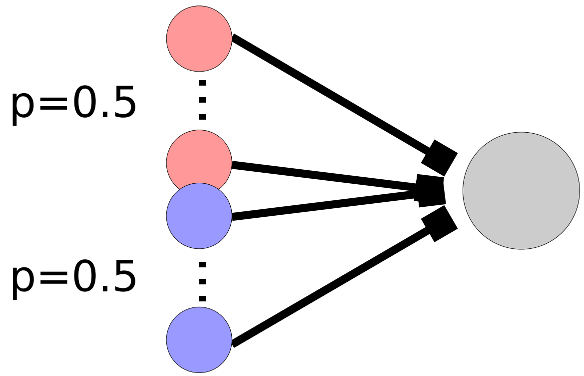
Katz *Science* 1996

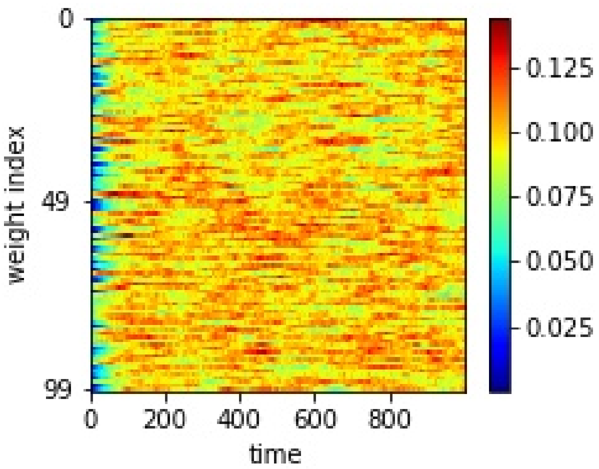


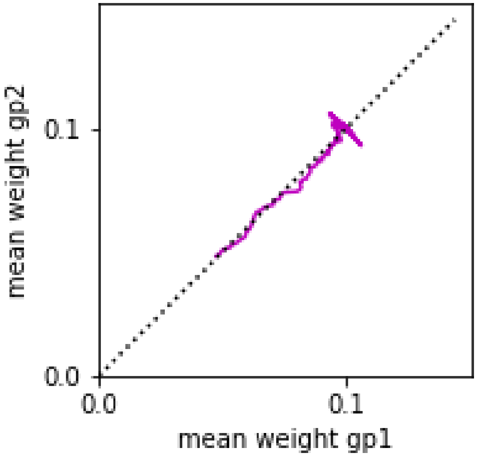
Hanganu *J Neurosci* 2006

Ocular dominance

- Symmetric inputs from the two eyes
- How to specialize to one optical input only?
- PCA cannot discriminate between the 2 dominating eigenvectors







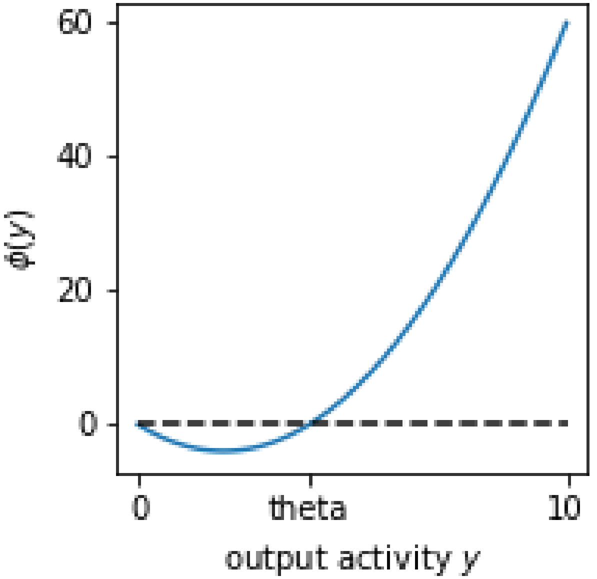
BCM rule

- Symmetric inputs from the two eyes
- How to specialize to one optical input only?
- PCA cannot discriminate between the 2 dominating eigenvectors

$$\dot{w}_i = \phi(y) x_i$$

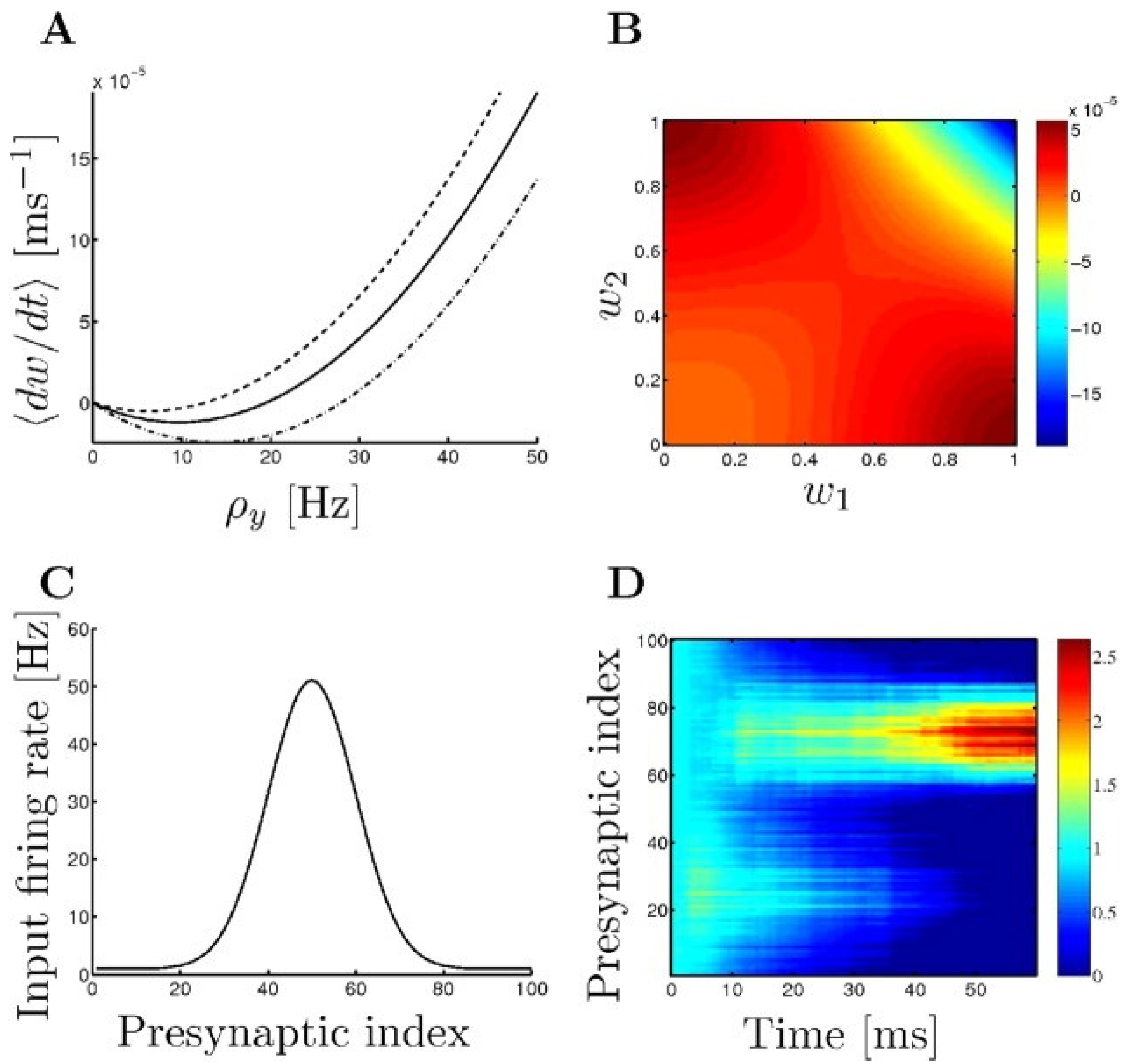
$$\phi(y) = y(y - \theta)$$

$$\theta = \langle y^2 \rangle = \int_{t-T<t'<t} [y(t')]^2 dt'$$



Bienenstock, Cooper, Munro
J Neurosci 1981

Triplet STDP and BCM



enforces winner-take-all behavior: strong specialization and symmetry breaking

Pfister *J Neurosci* 2006

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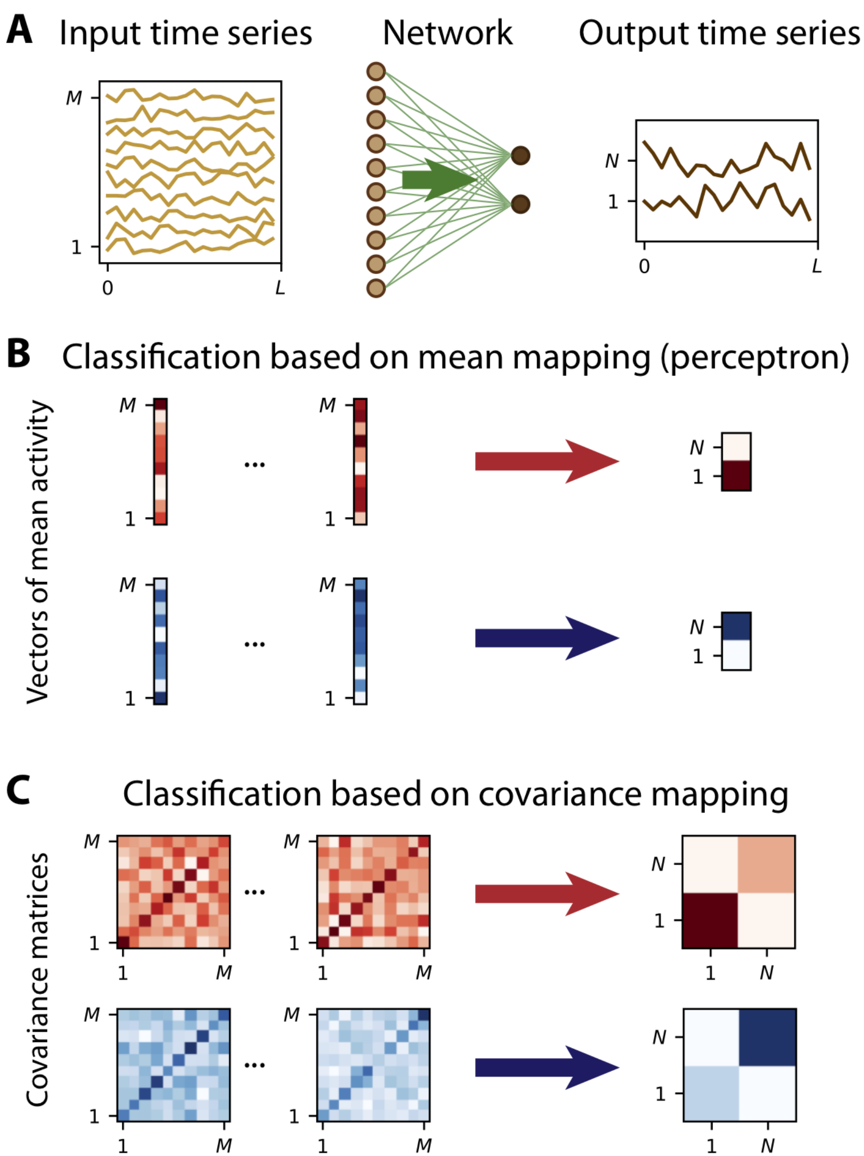
- **Future challenges:**
  - **Distributed information representations**

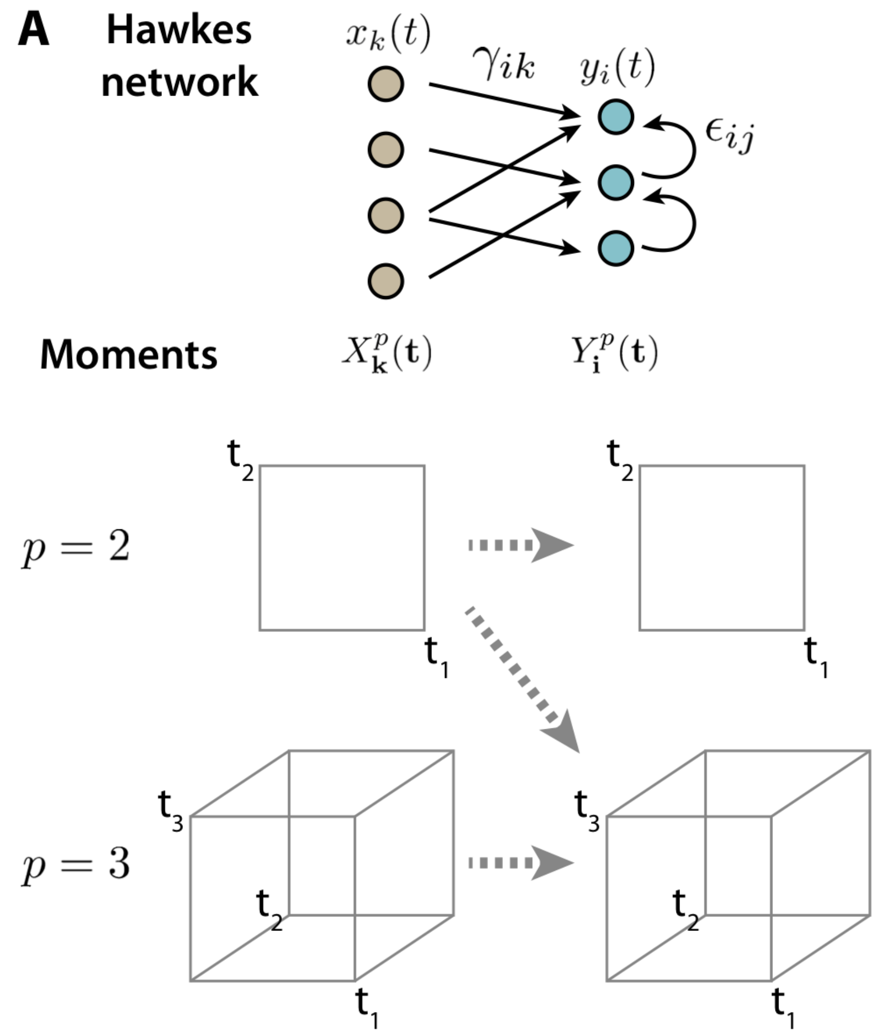
Towards theory for distributed computations

Dynamics level	Spiking statistics	Neuronal activation mechanisms	Synaptic plasticity
Functional level	Information representation	Input-output mapping	Learning

Neuronal information in high-order correlations



Gilson M, D Dahmen, Moreno-Bote R, Insabato A, Helias M
PLoS Comput Biol 2020



Gilson M, Pfister J-P (*arXiv*)

Further reading on link with information theory

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