From Hebbian learning to spike-timing-dependent plasticity

A modeling viewpoint

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Center for Brain and Cognition, Univ Pompeu Fabra, Barcelona (Spain)
Human Brain Project (SP4)

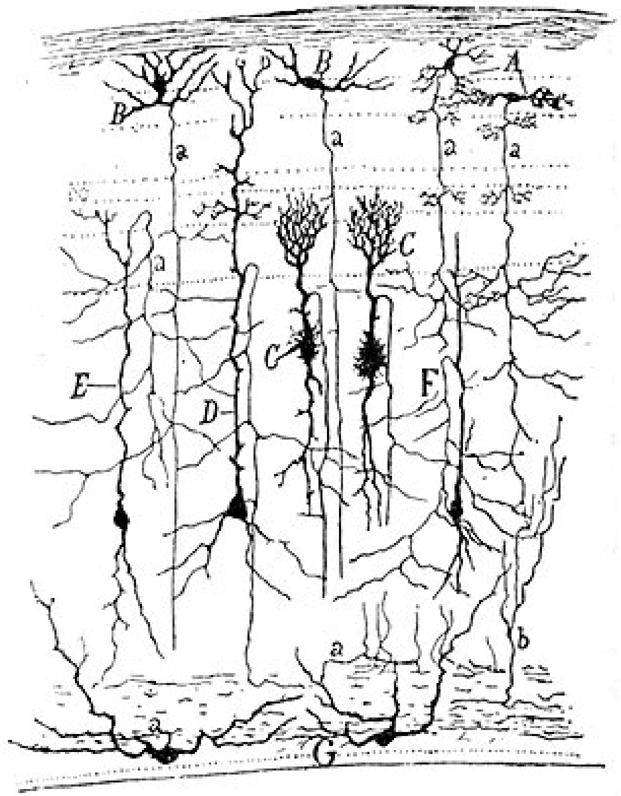
Outline

- Historical perspective on learning in neuronal systems
- From Hebbian learning to spike-timing-dependent plasticity
- Weight dynamics and “information” representations:
  - Principal component analysis (PCA)
  - Spatio-temporal filtering of spike trains
  - Ocular dominance and symmetry breaking
  - Neuronal assemblies in recurrent networks
- Future challenges
  - Unsupervised vs supervised vs reinforcement learning
  - Distributed information representations

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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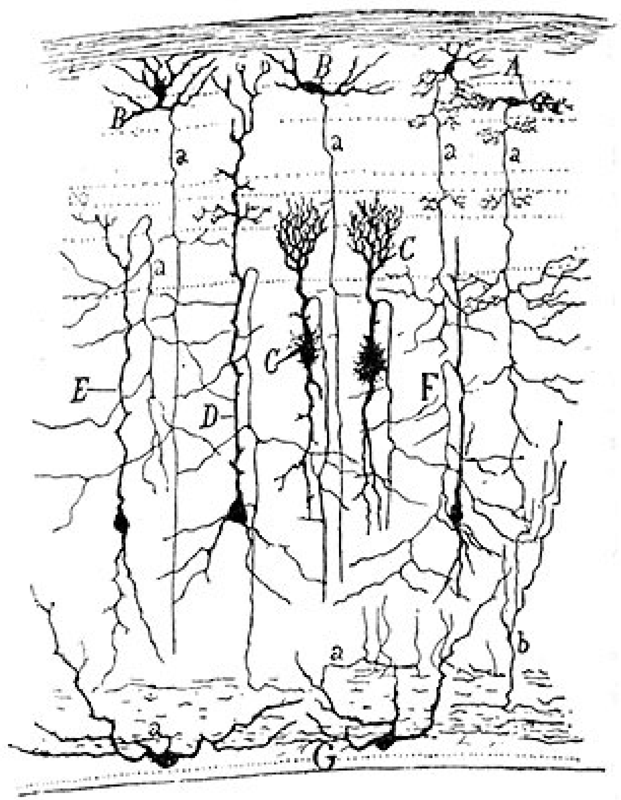

Ramon y Cajal 1905

Hebb (1949): “When an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased”

Learning in neuronal systems: where and what?

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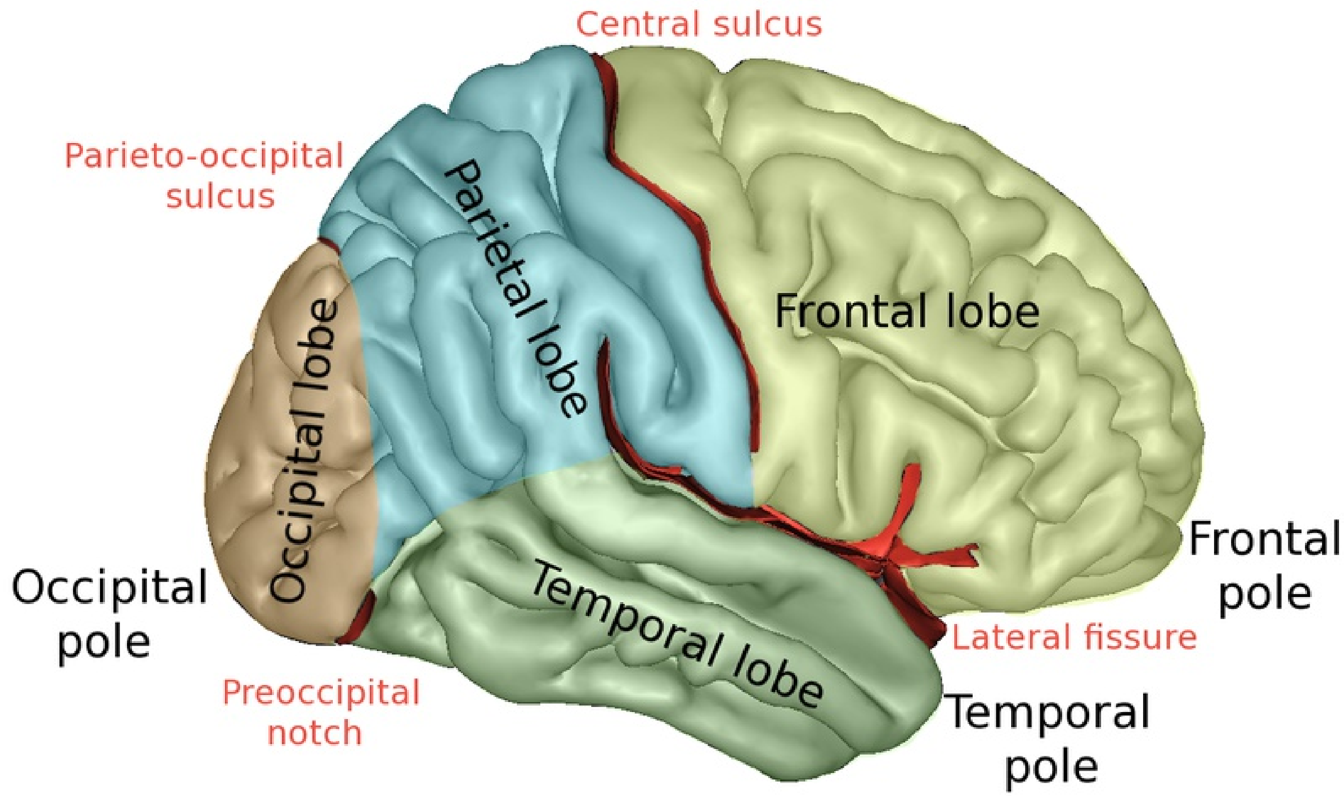

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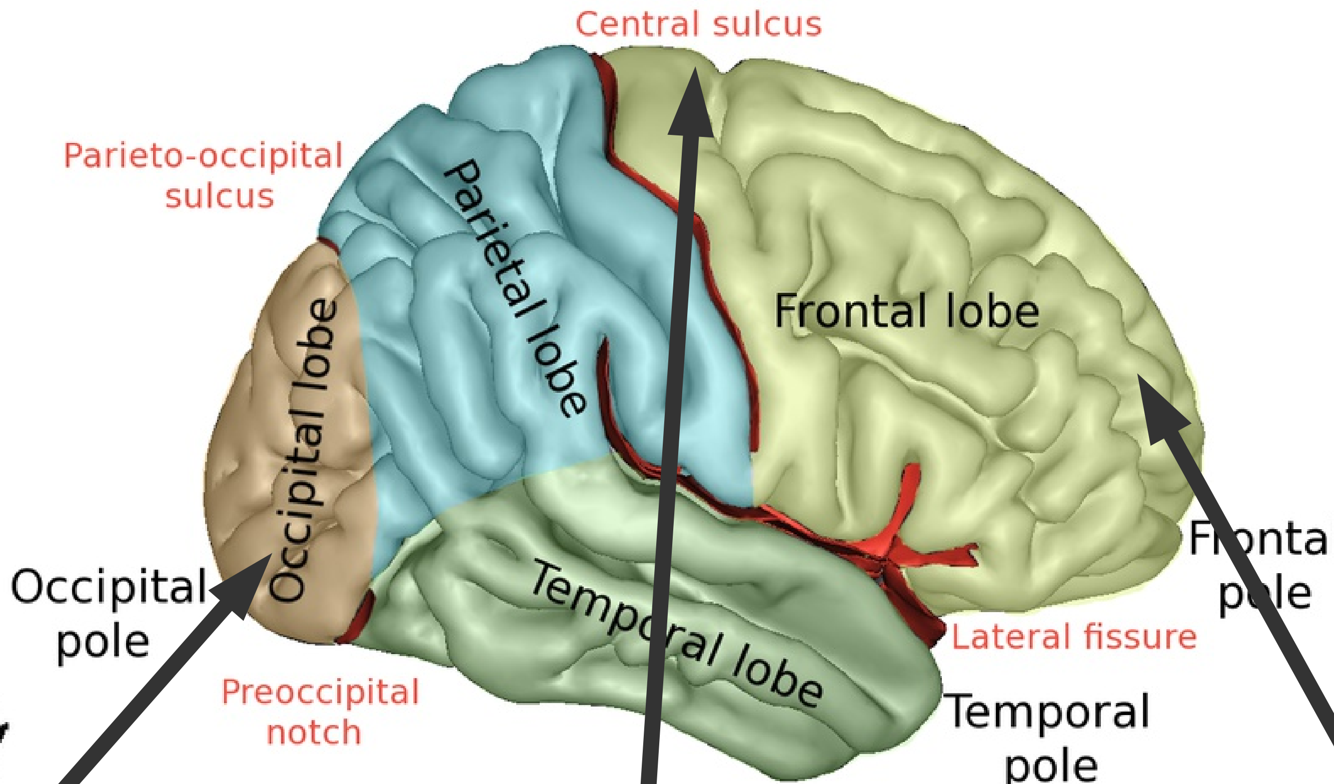

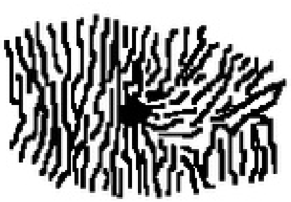

wikipedia

Orientation columns in primary visual cortex (V1)

Locomotion in motor cortex

Long-term memory in prefrontal cortex (like now, hopefully)

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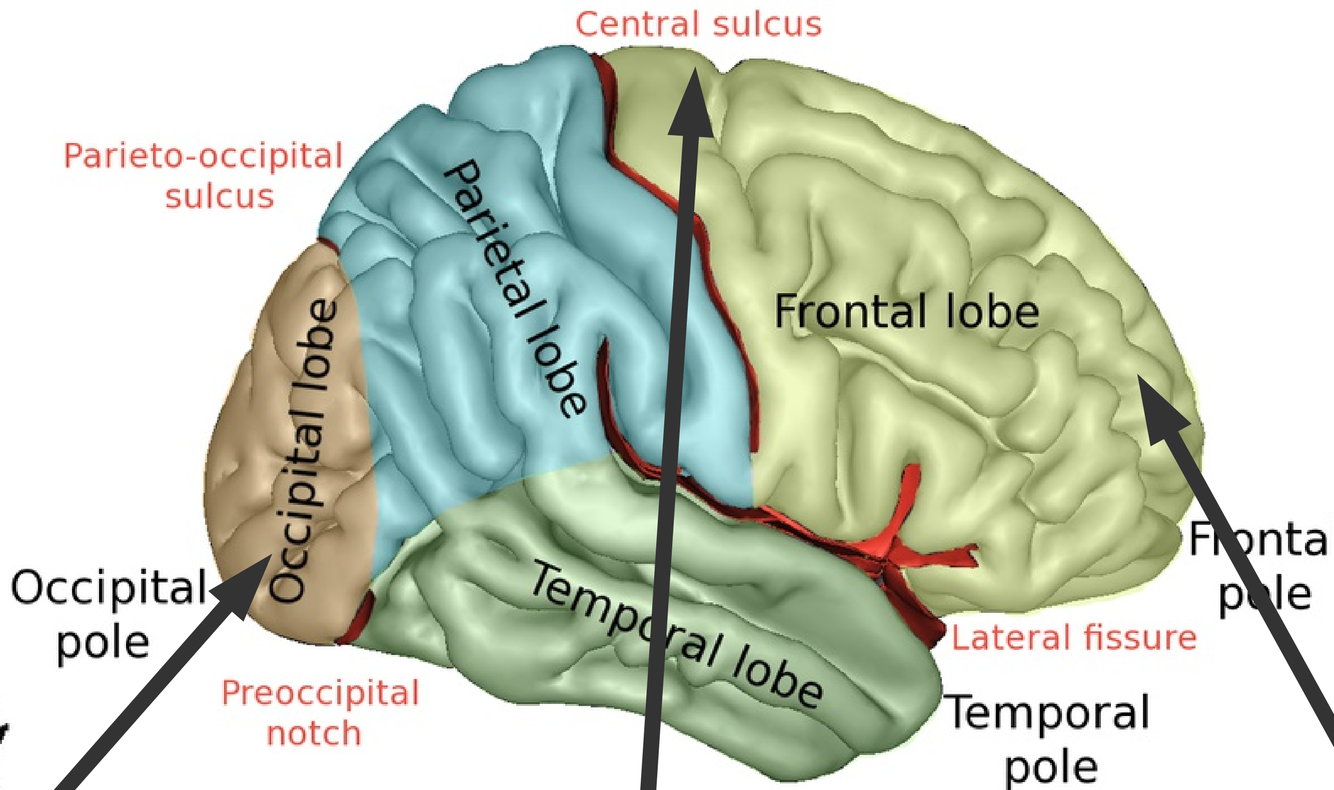

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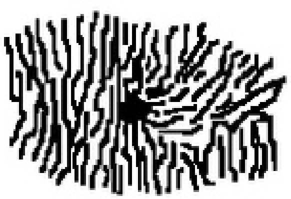


Orientation columns in primary visual cortex (V1)

Unsupervised learning

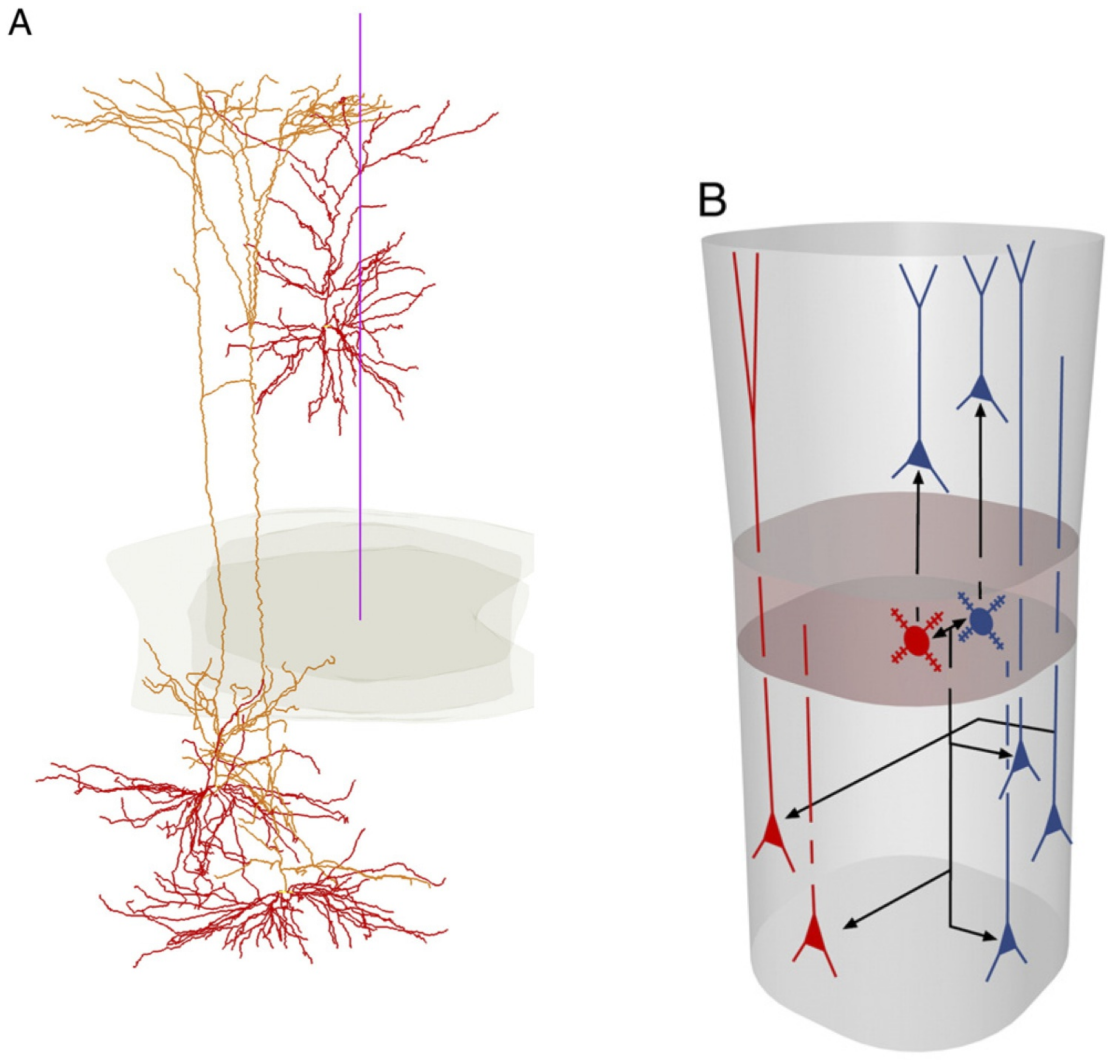
Locomotion in motor cortex

Reinforcement learning

Long-term memory in prefrontal cortex (like now, hopefully)

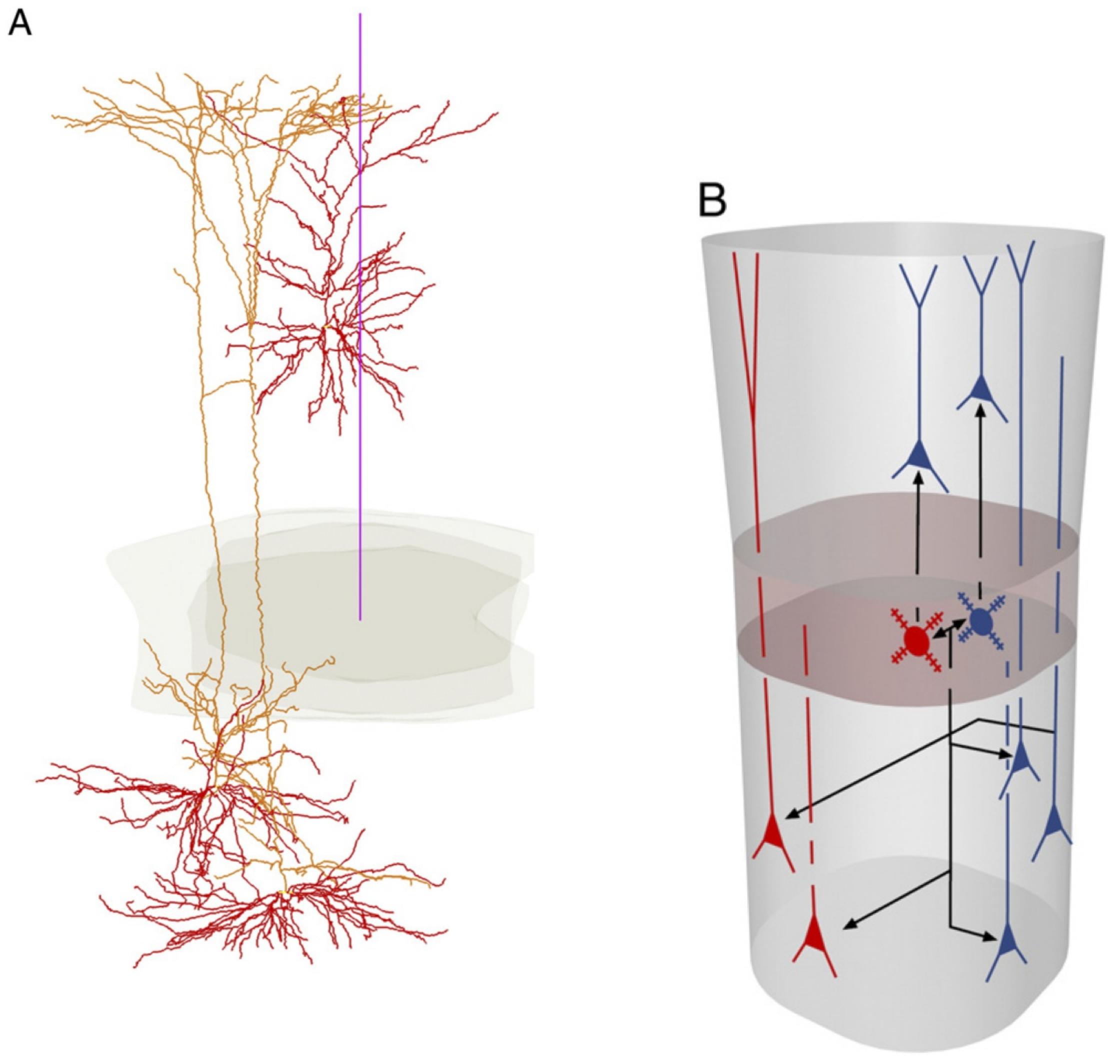
Supervised learning

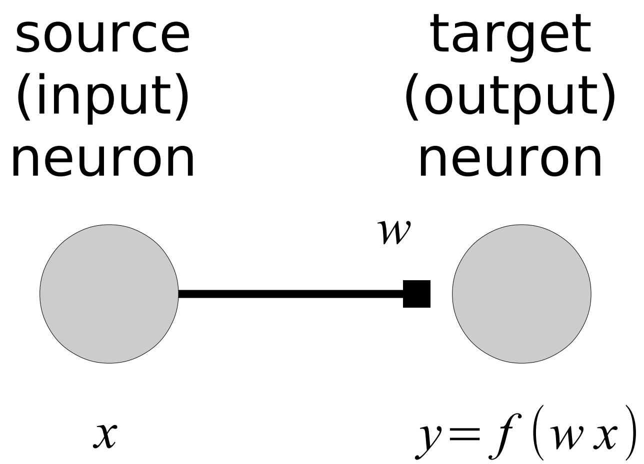
Formalizing experimental observations



Helmstaedter *BRR* 2007

Formalizing experimental observations

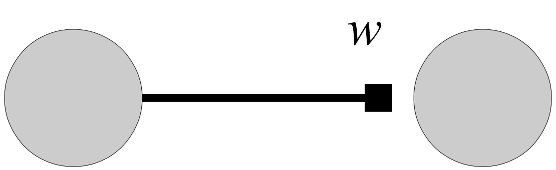




Helmstaedter *BRR* 2007

Models of neuronal learning

Synaptic plasticity



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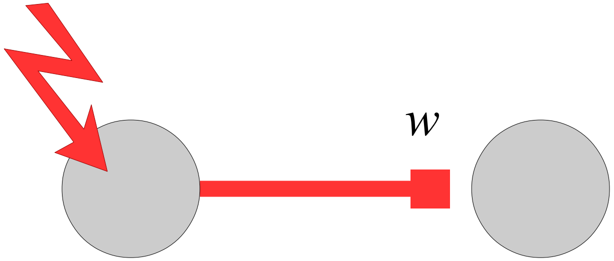

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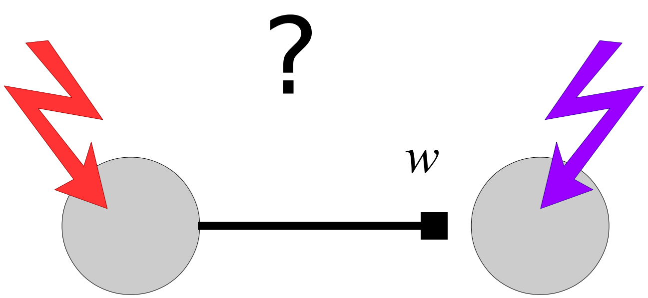

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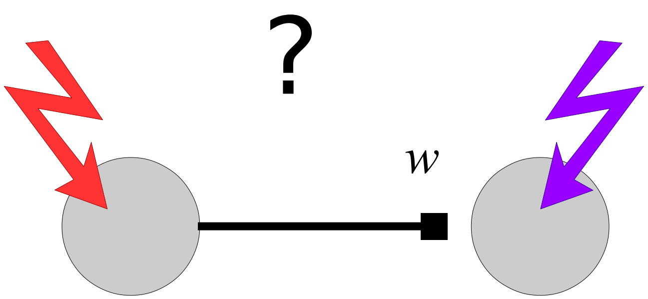
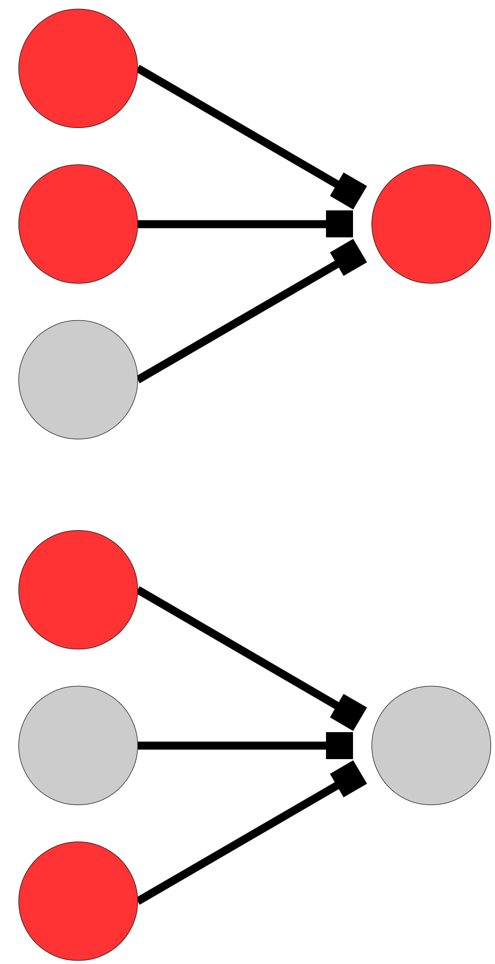


Tuning function
e.g. pattern
classification



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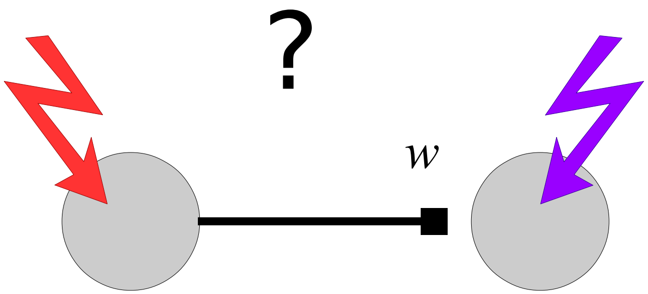

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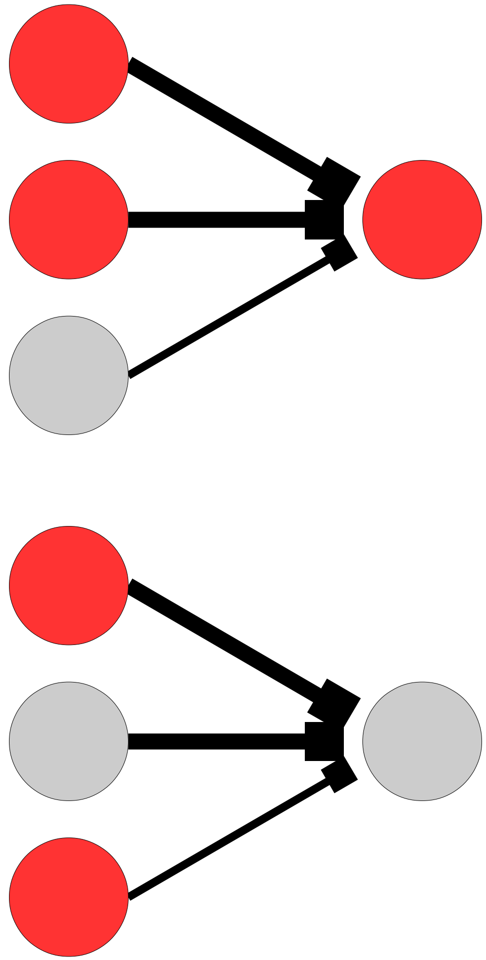

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Hebb's postulate or rule

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

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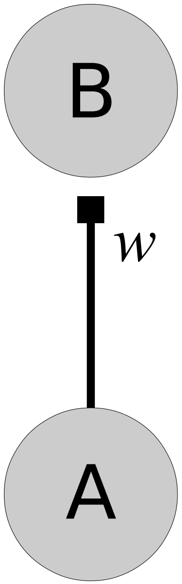

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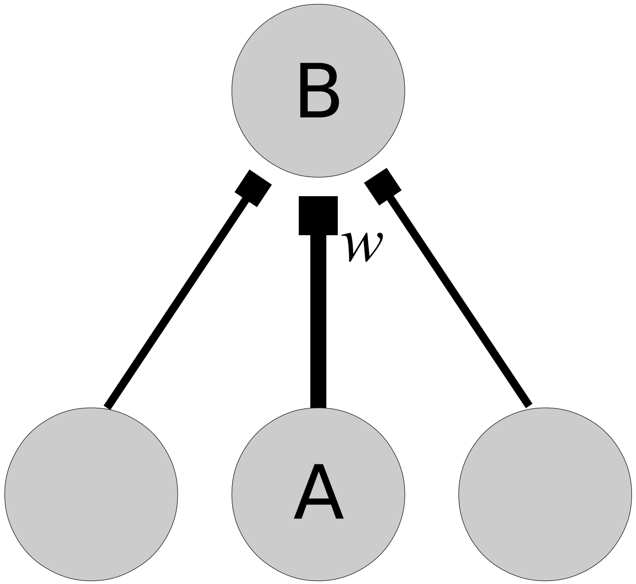

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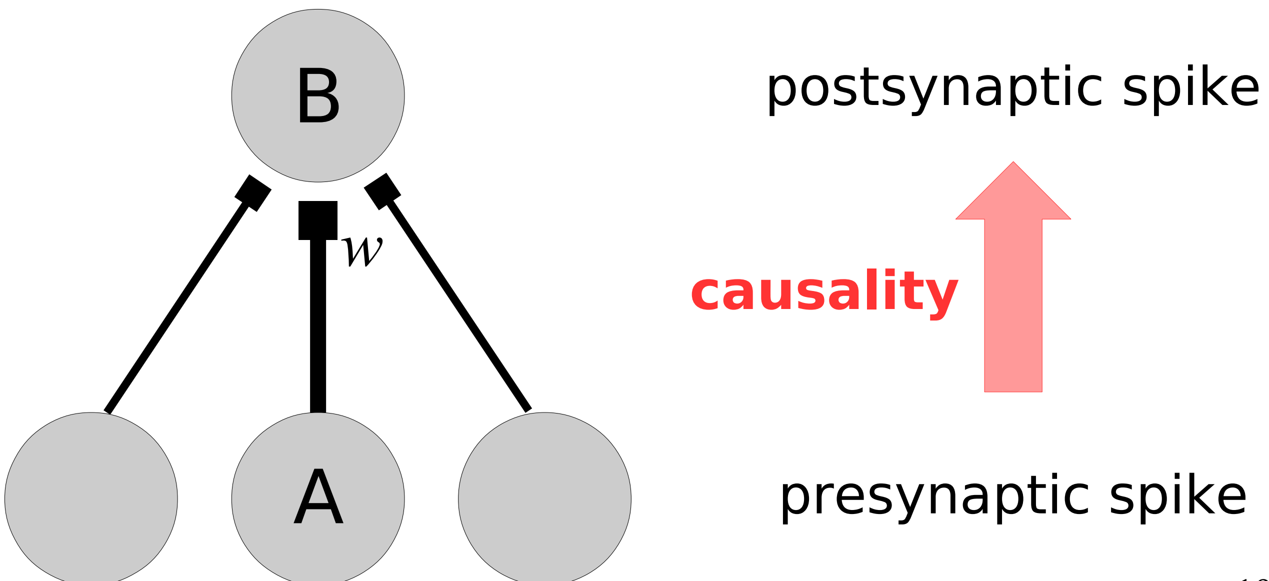

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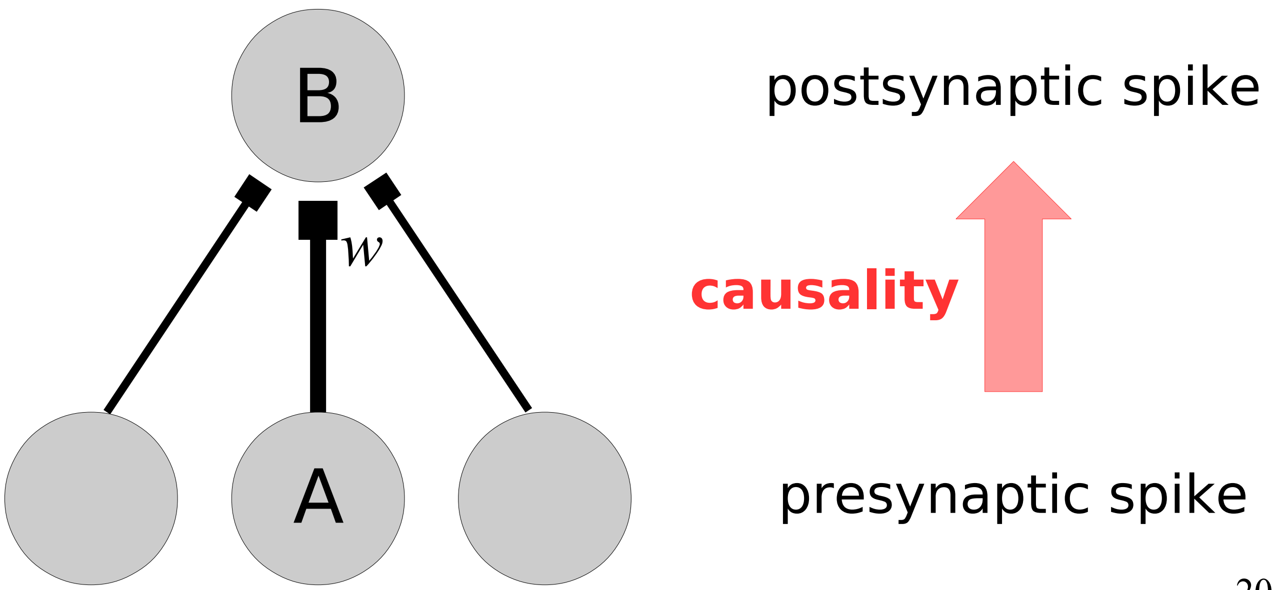
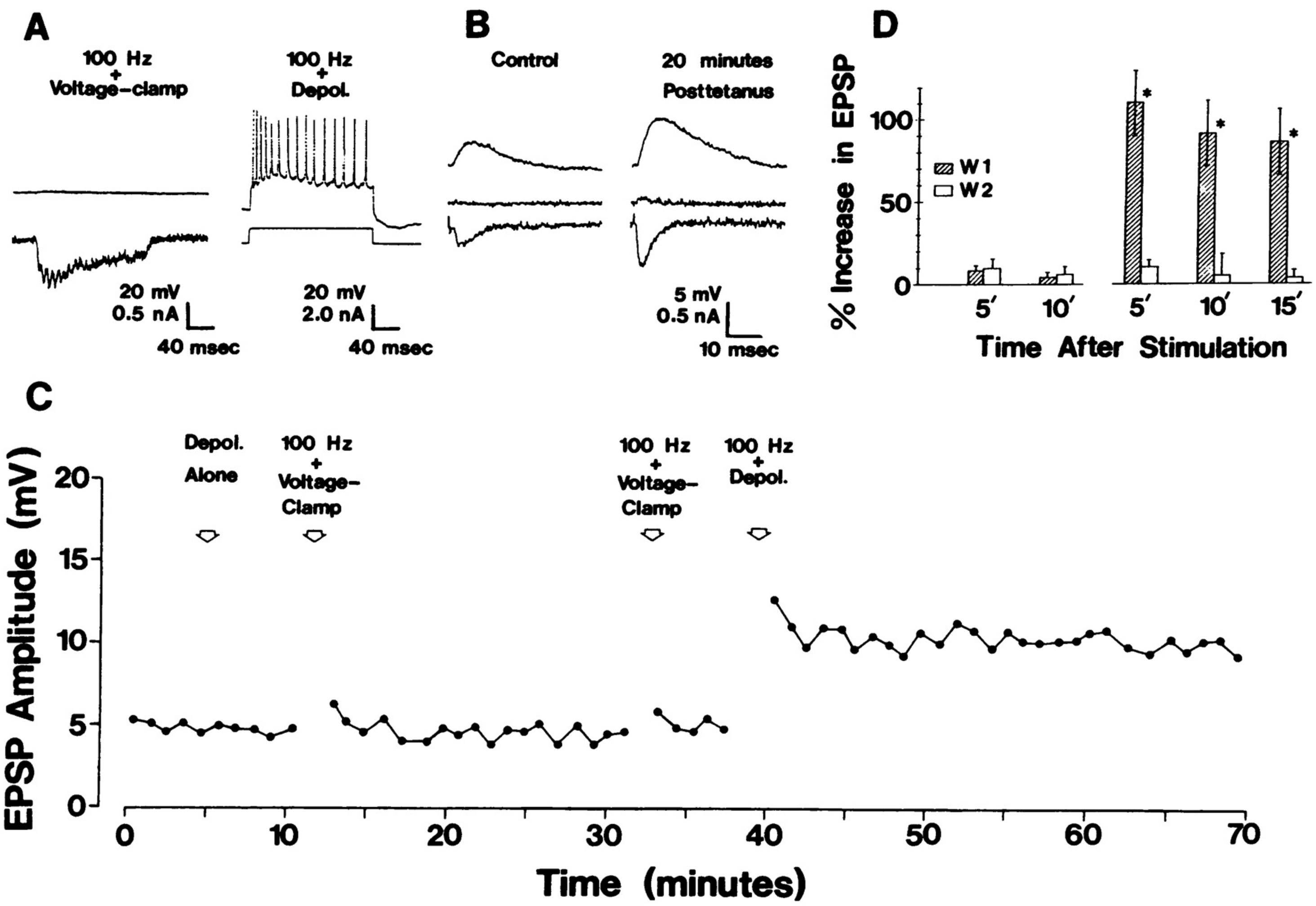
Unsupervised learning

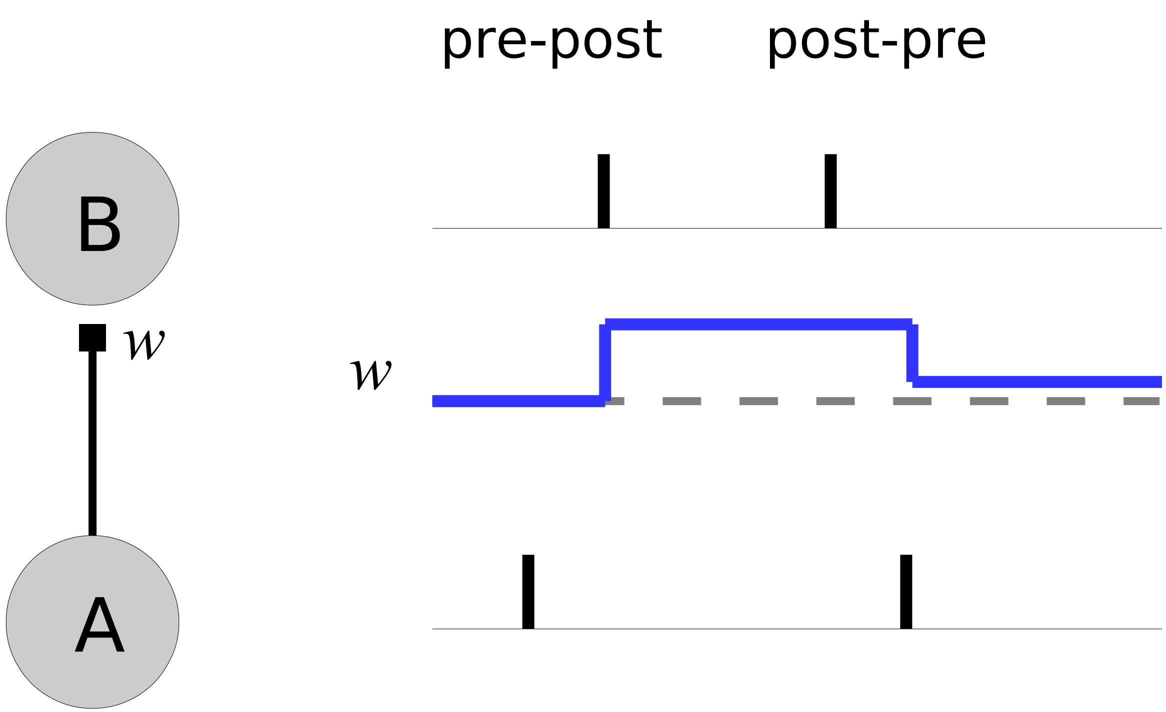


Experimental evidence from rat hippocampus



Kelso *PNAS* 1986
see also Jaffe *J Neurophysiol* 1990, Antonov *Neuron* 2003

Spike timing matters!



- Markram *Science* 1997
- Gerstner *Science* 1999

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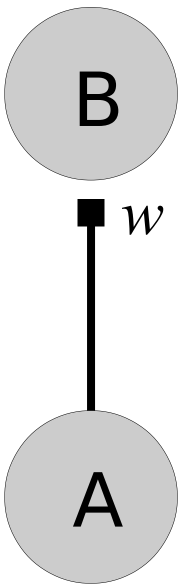
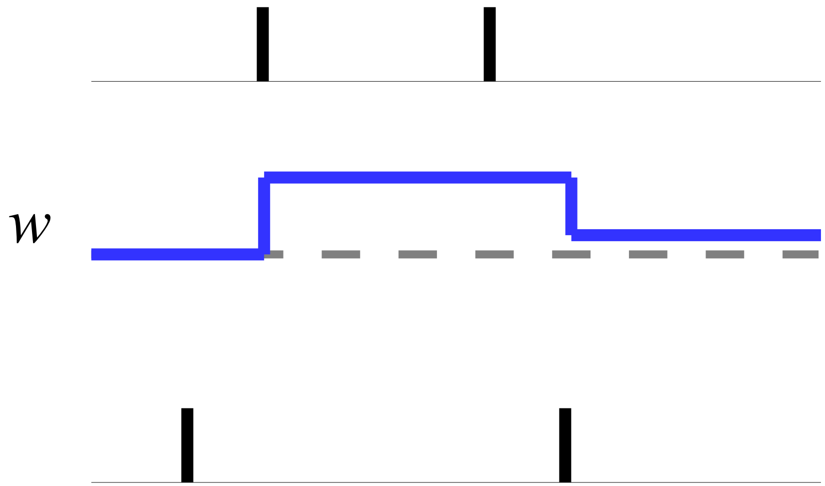
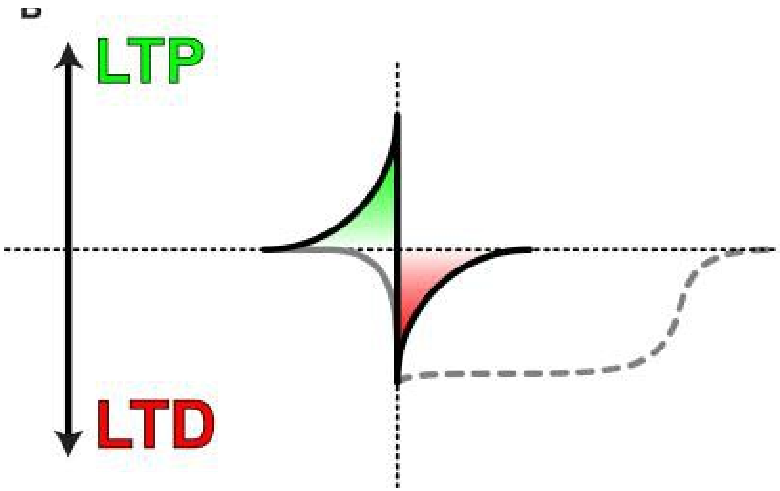


pre-post   post-pre



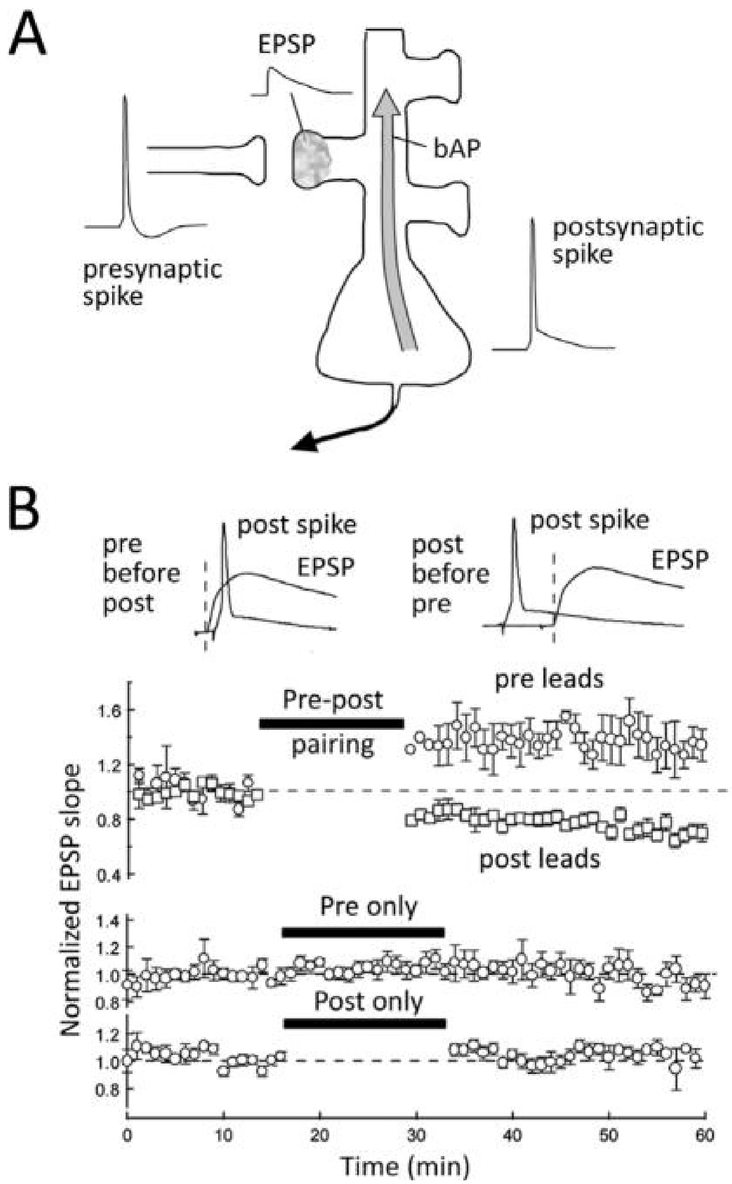


$$t_A - t_B = t_{pre} - t_{post}$$

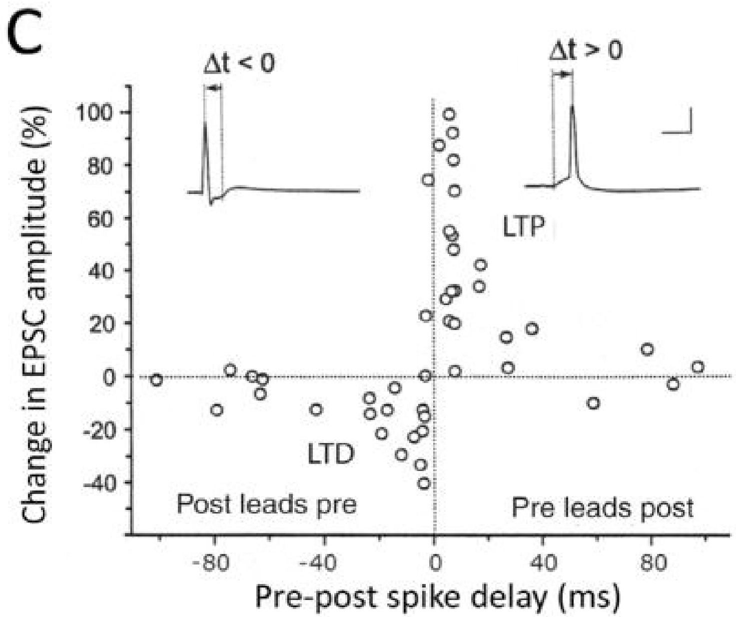
Markram *J Syn Neurosci* 2011

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

But what do experiments really say?



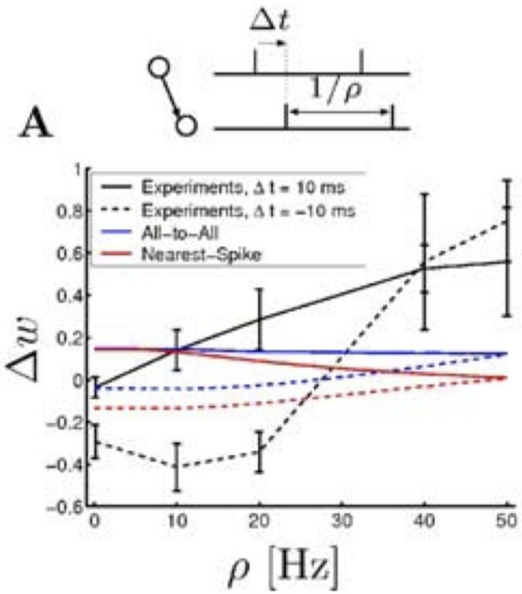
Weight change after 60 pre-post pairings!

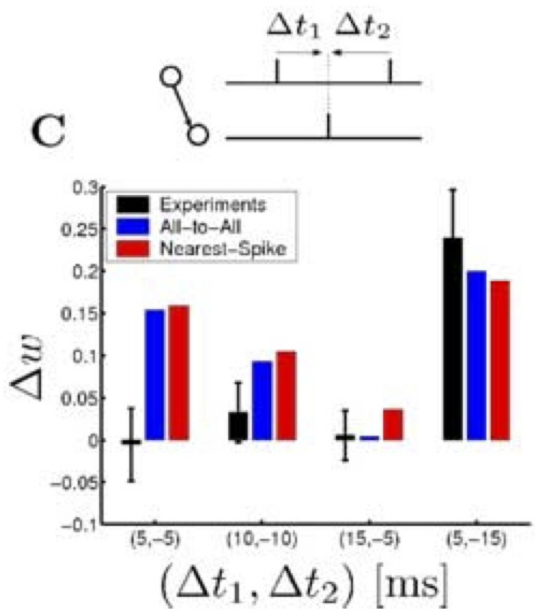


$$t_{post} - t_{pre}$$

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

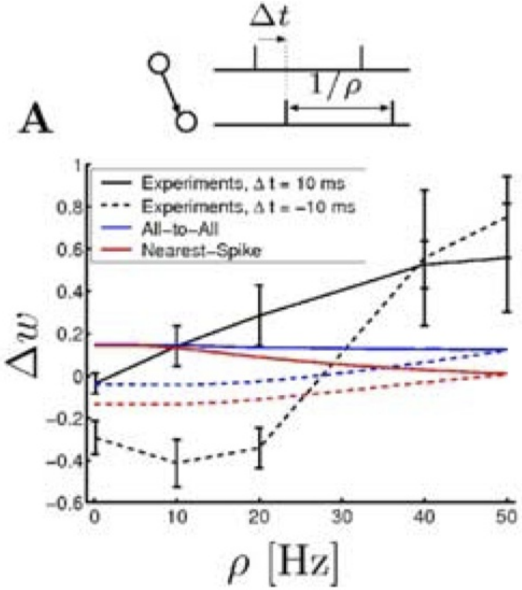
Beyond spike pairs

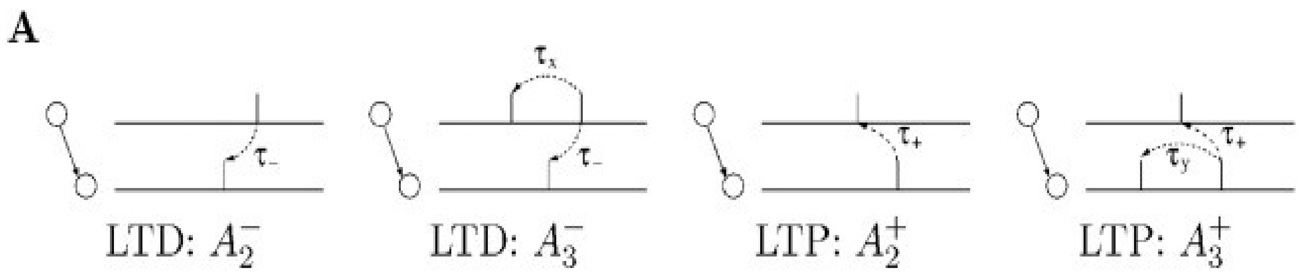


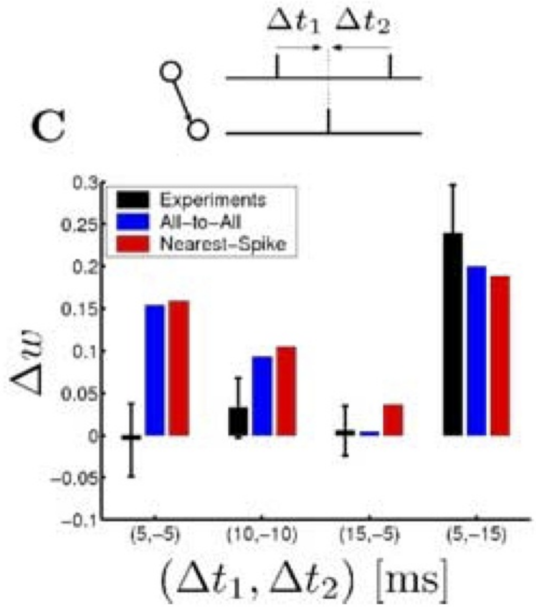


data: Sjostrom *Neuron* (2001)
model: Pfister *J Neurosci* (2006)

Beyond spike pairs



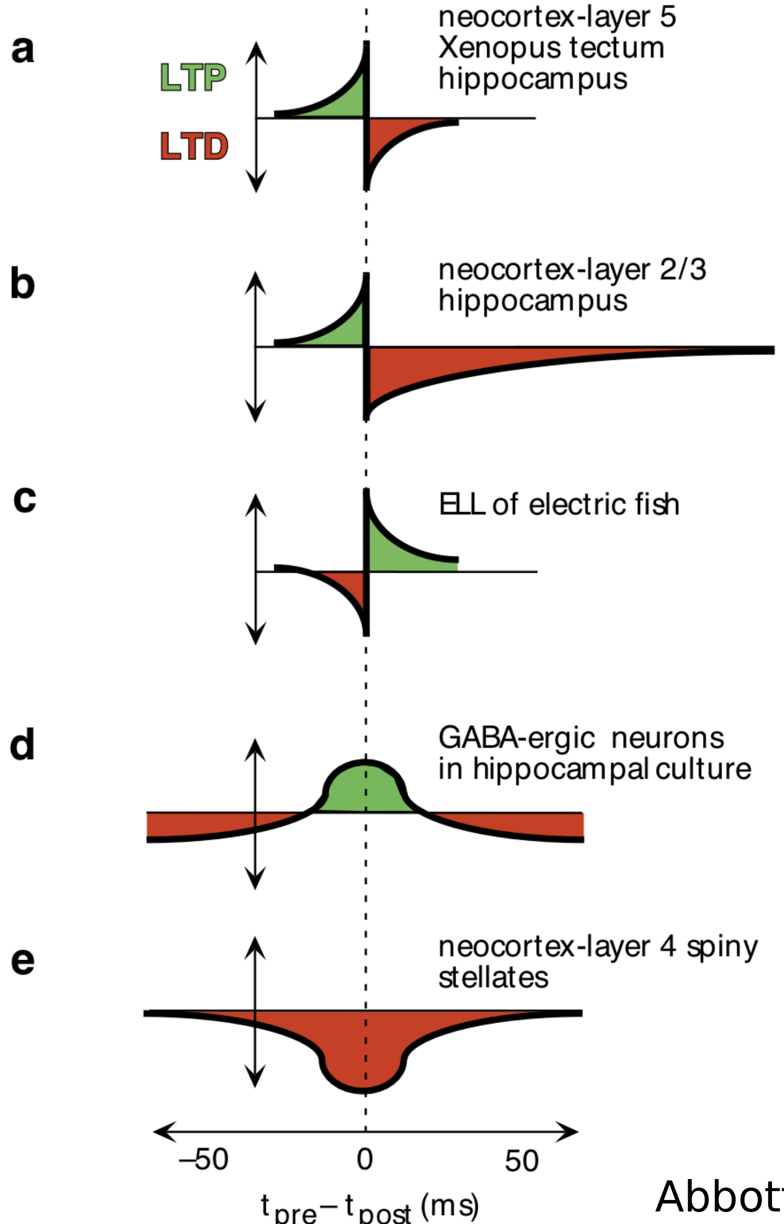




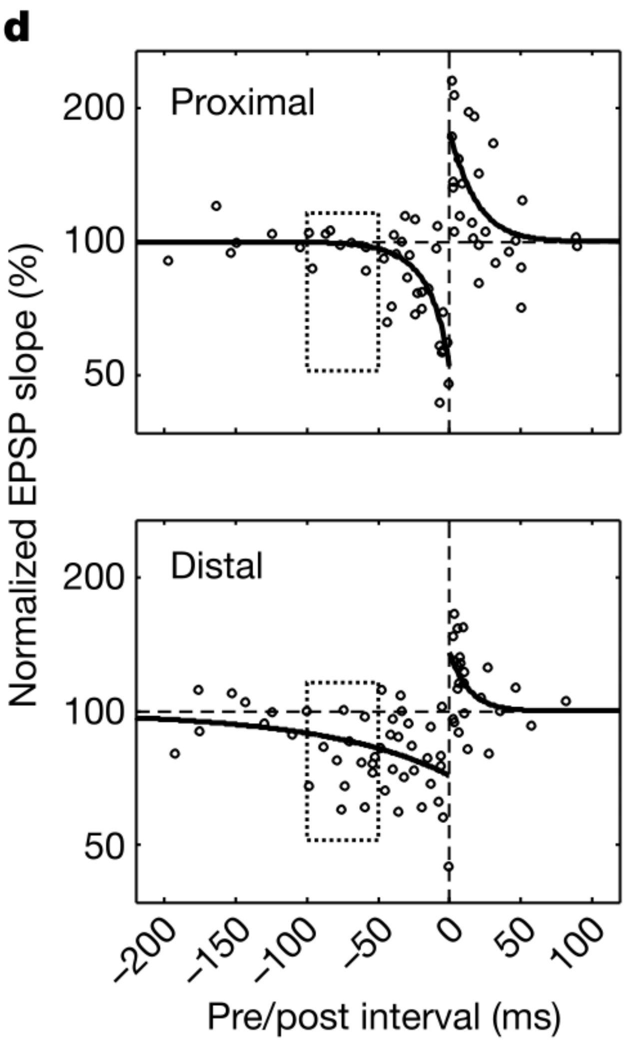
STDP based on triplet of spikes
in addition to spike pairs

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

Many STDP windows exist, yielding various timescales



Abbott and Nelson, *Nat Neurosci* 2000

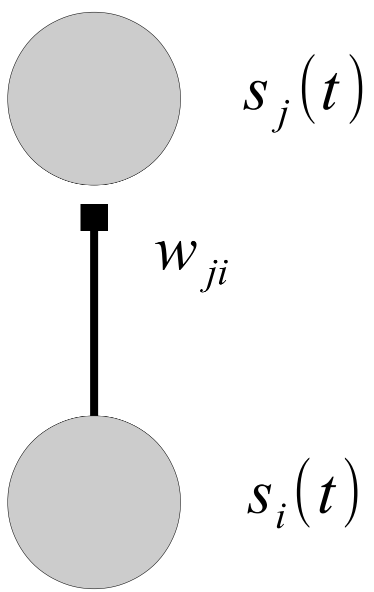


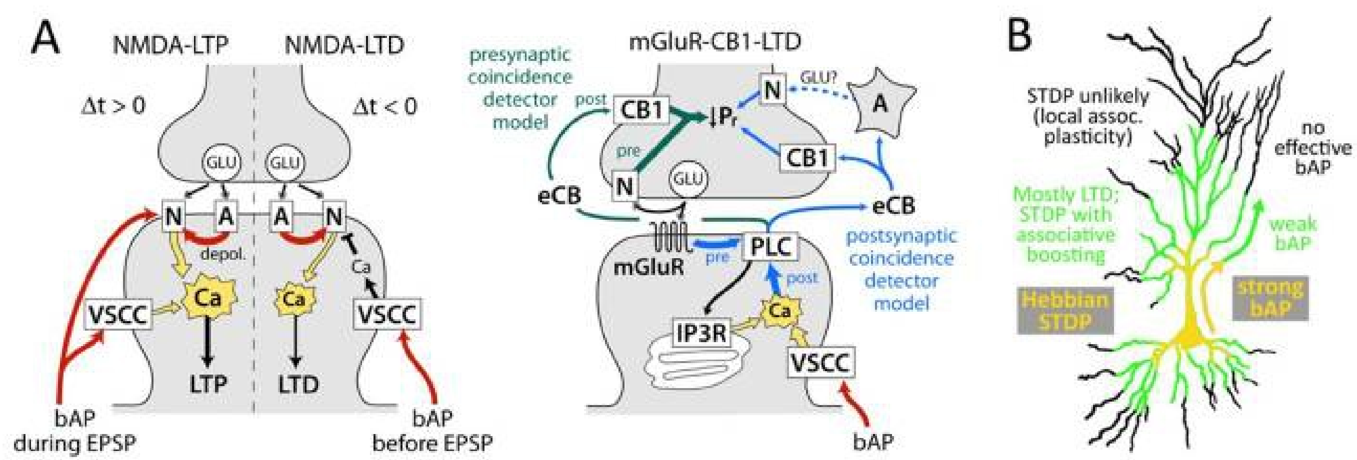
Froemke *Nature* 2005

Other dependencies and biophysical models

- 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

$$\dot{w}_{ji} = F[s_i(t), s_j(t'), w_{ji}, \ldots]$$





Feldman *Neuron* (2012)

Summary for experimental evidence and modeling of synaptic plasticity

- Complex dependencies upon spike timing, current value of weight, etc.
- Most experiments are in vitro!
  - Many STDP protocols involve 60 repeated pairing to obtain observable weight change
  - Positive replications of results in-vivo still scarce...
- Also short-term plasticity
- Monosynaptic plasticity is not the only mechanism at play

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- Monosynaptic plasticity is not the only mechanism at play
- **Questions:**
  - What matters for neuronal function?
  - Why the need for temporal resolution of spikes (a few ms)?
  - Effect in network?
  - Need to formalize plasticity update (i.e. simplified model) so we can build typology of functional effects

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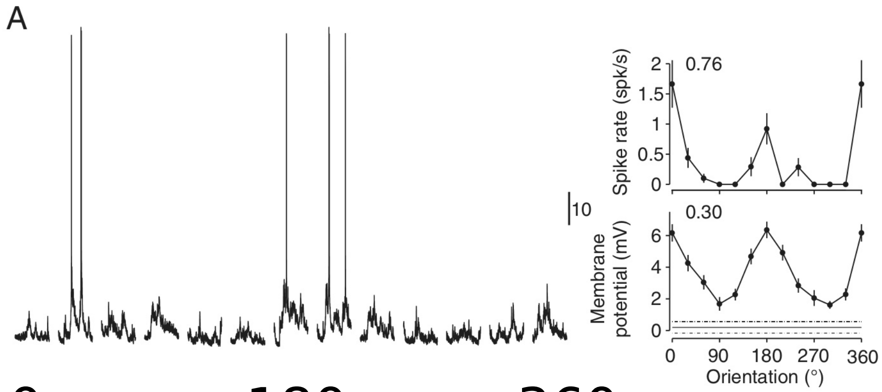
Stimulus represented in rate patterns



0 180 360

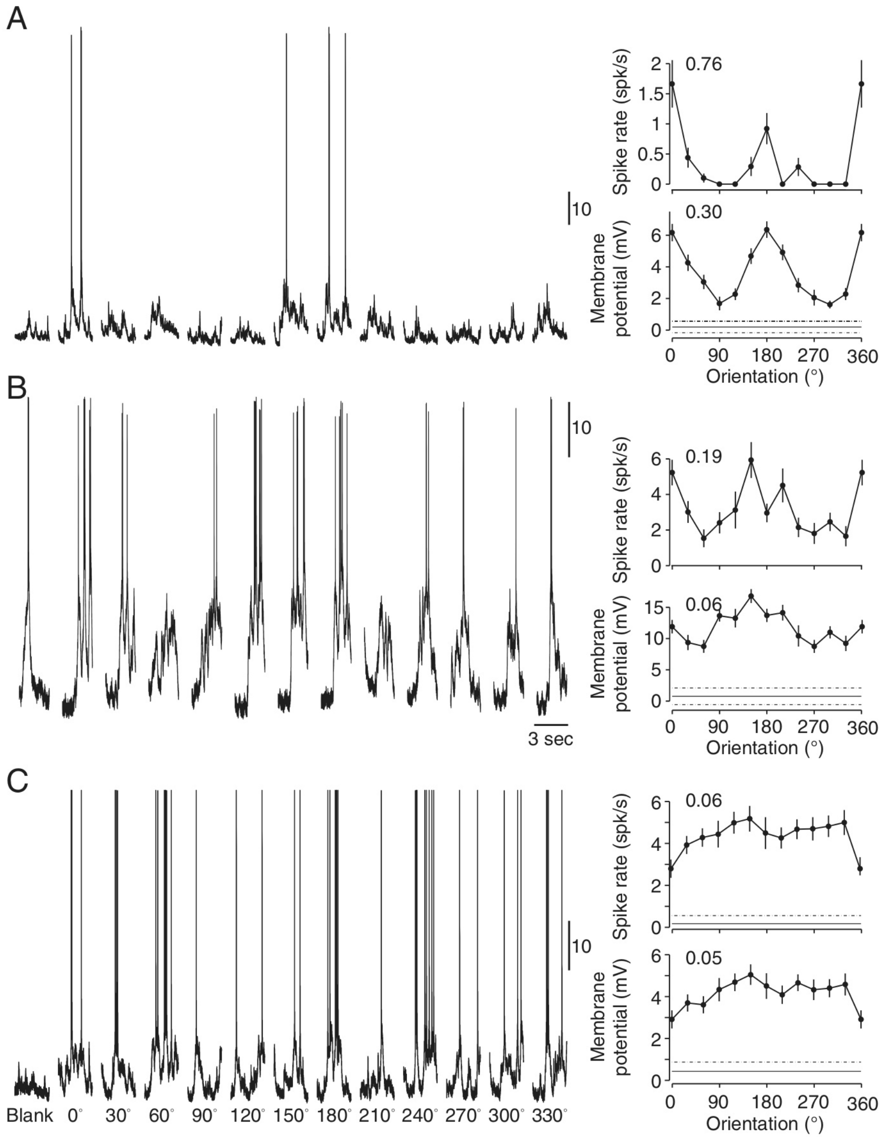
stimulus orientation

Orientation selectivity of V1 neuron

Orientation selectivity of its inputs (LGN)

Tan *J Neurosci* 2011

Stimulus represented in rate patterns



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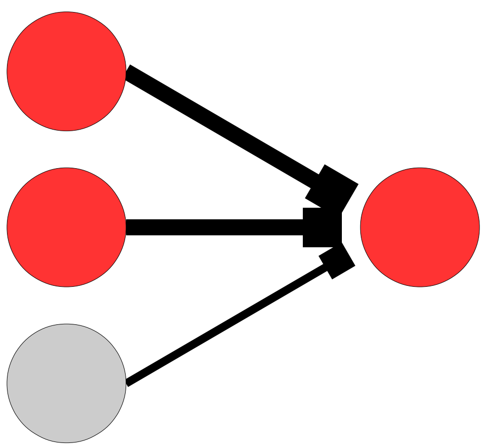
Rate-pattern recognition

most frequently
repeated pattern



less frequently
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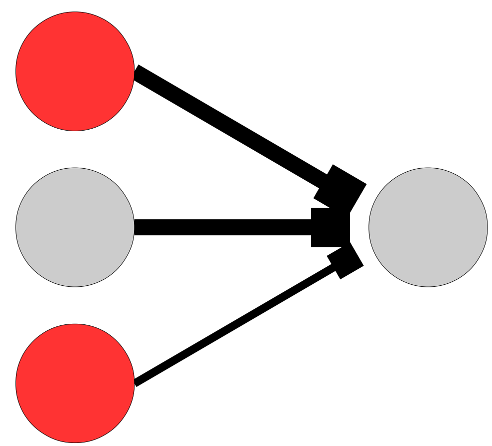
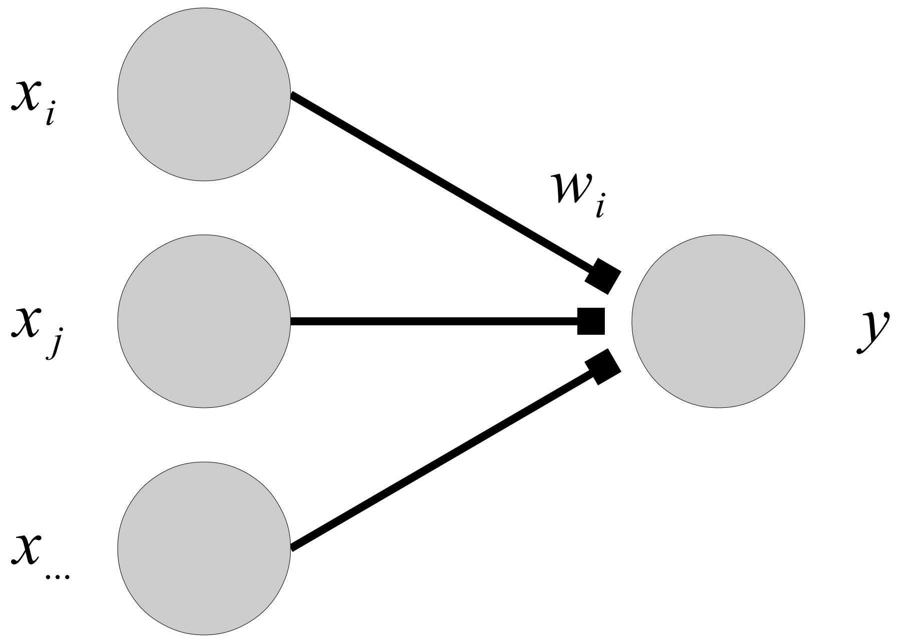
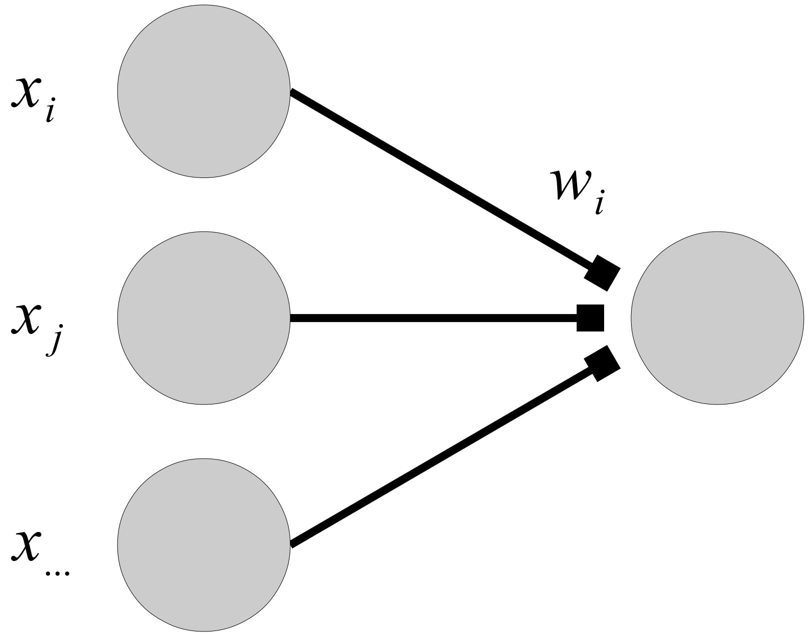


Weight dynamics for rate neuron



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

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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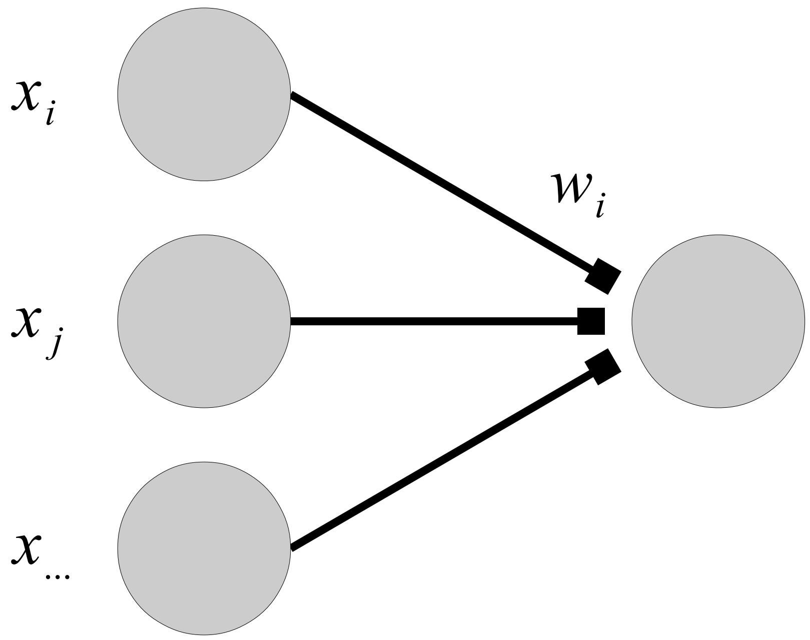

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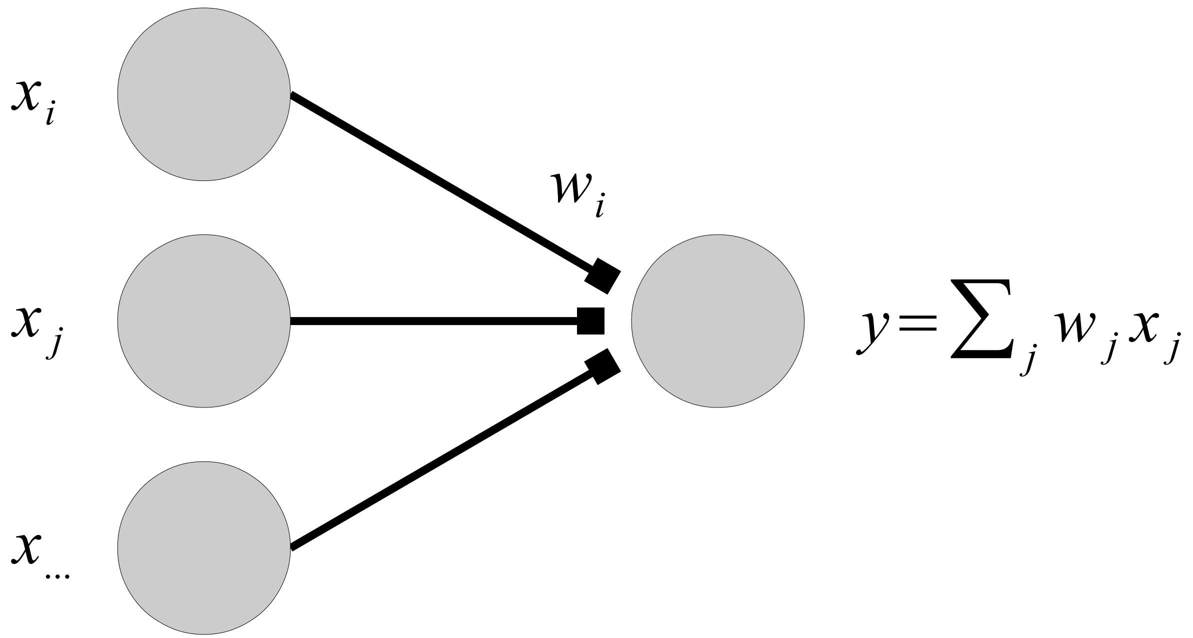

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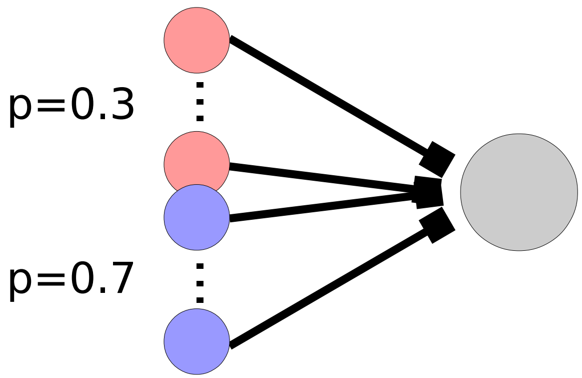
Hebbian dynamics is intrinsically unstable!

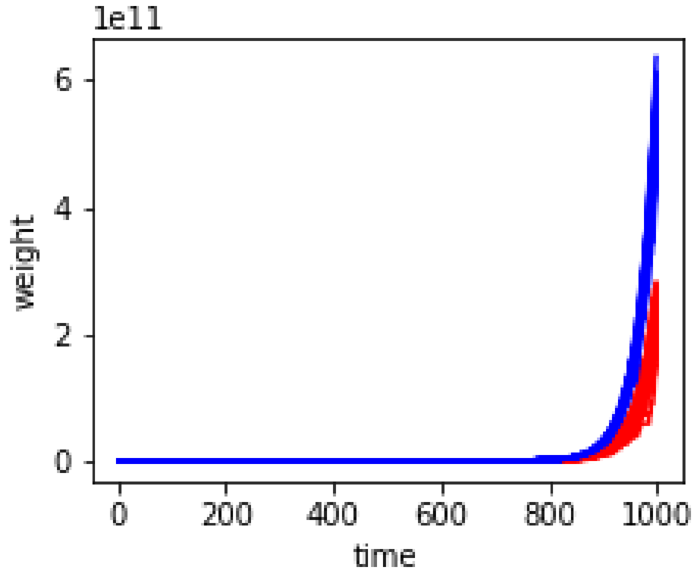
$$\dot{w} = C w \quad \text{with} \quad C_{ij} = \langle x_i x_j \rangle$$

Main direction of growth

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

Weight dynamics for rate neuron





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Stabilization by synaptic competition: Oja's rule

$$\dot{w}_i = y\left(x_i - y\sum_j w_j\right)$$

$$\sum_j w_j \sim const$$

Oja *J Math Biol* 1982

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heterosynaptic plasticity

Oja *J Math Biol* 1982

Stabilization by synaptic competition: Oja's rule

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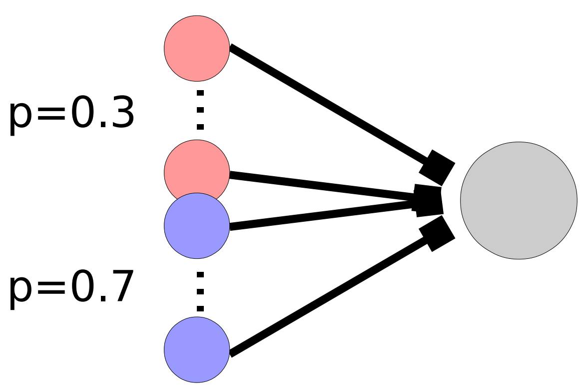
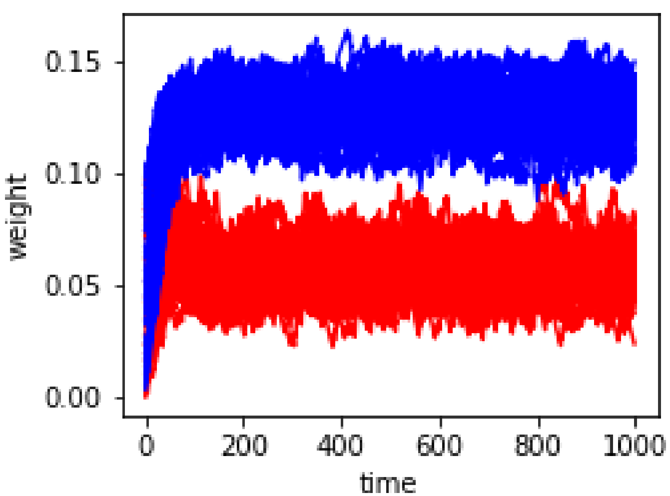
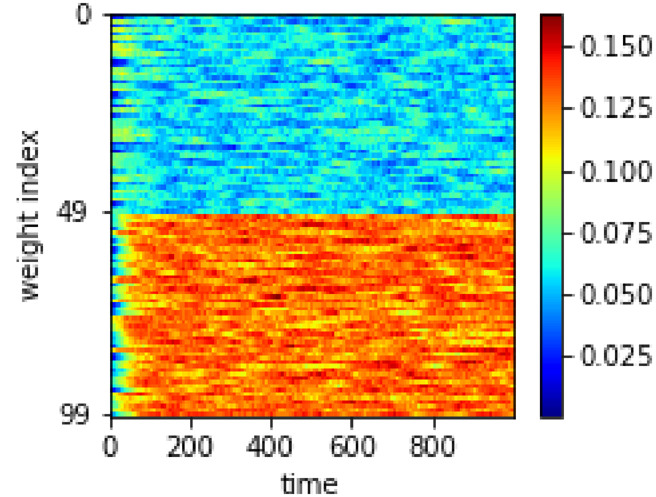
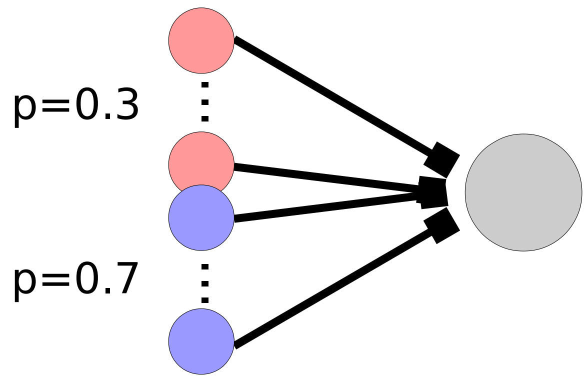
- Select dominating eigenvector of *C*
- Principal component analysis (PCA)

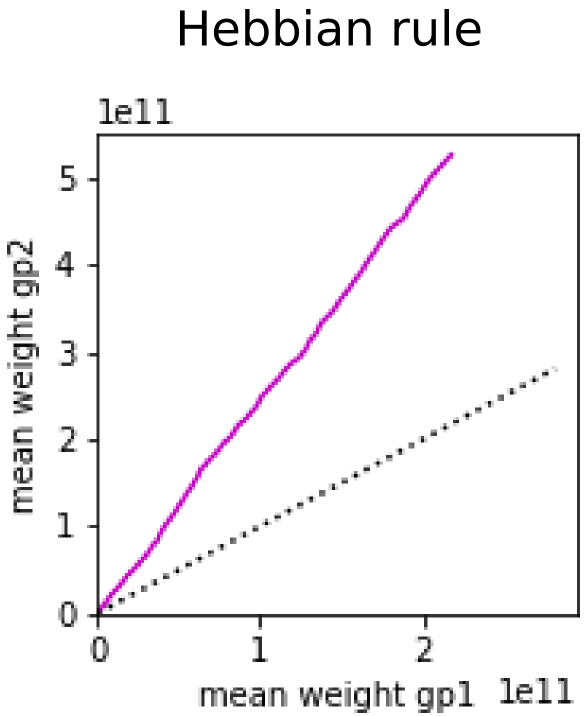


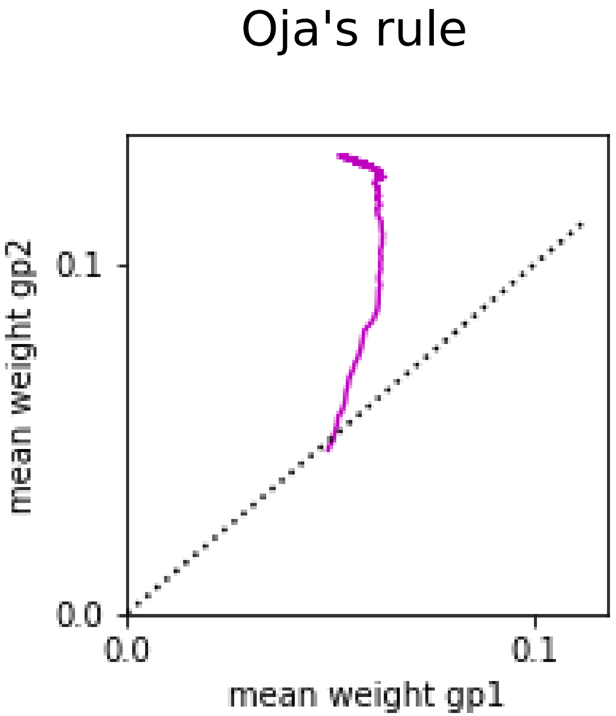




Phase space of group-average weights







Outline

- Historical perspective on learning in neuronal systems
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- **Weight dynamics and “information” representations:**
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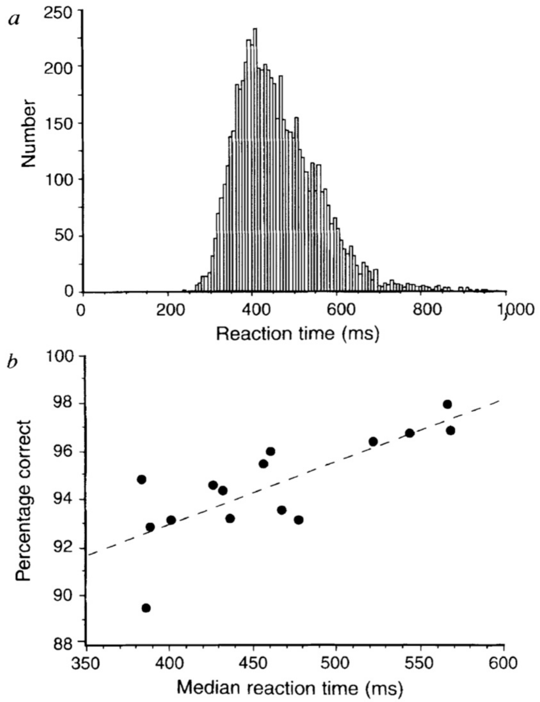
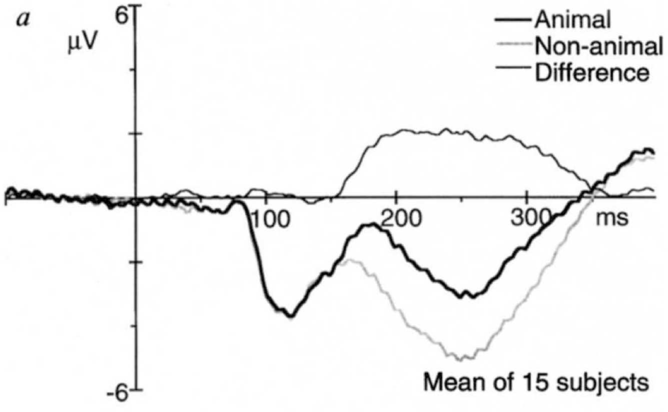
Rapid visual categorization

- Human subjects
- EEG recording
- Human vs non human images
- Only first spikes contribute to decision



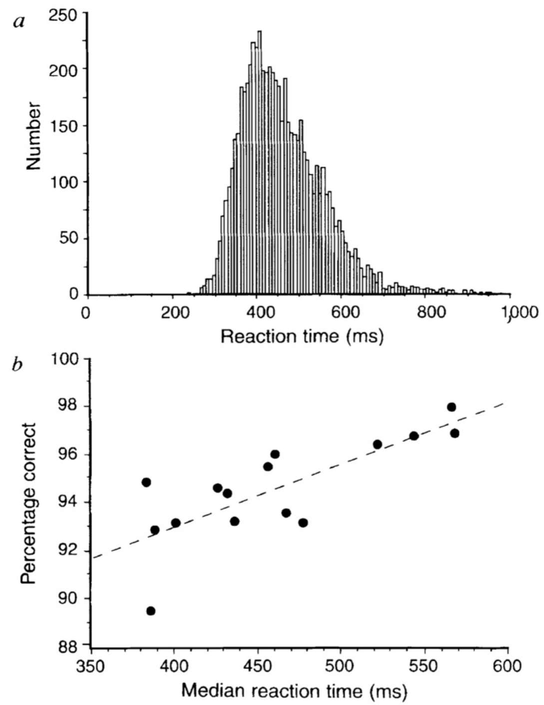


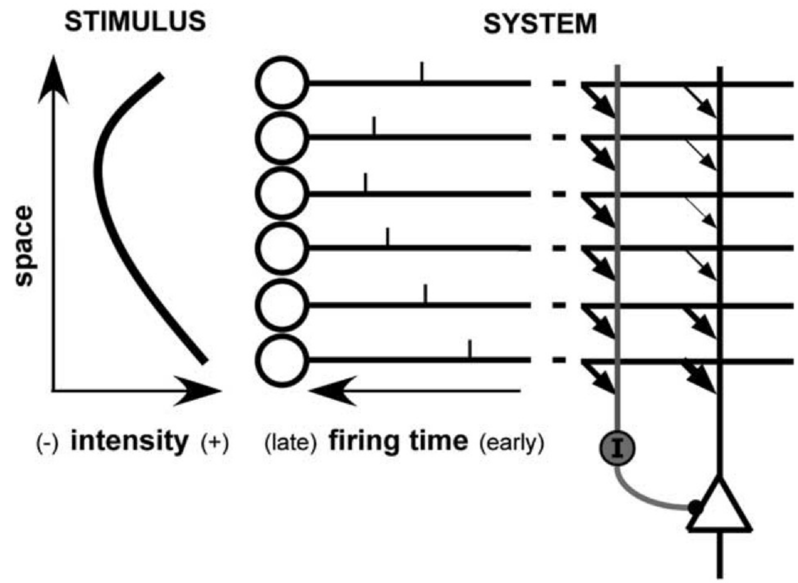
Thorpe *Nature* 1996,
Guyonneau *J Physiol Paris* 2004

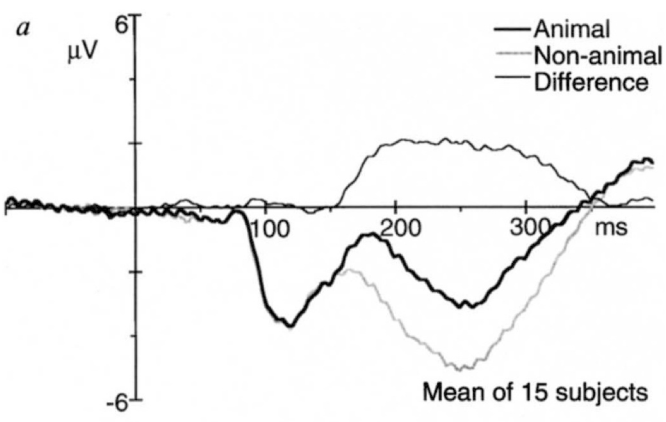
Rapid visual categorization

Xxxx more clear

- Human subjects
- EEG recording
- Human vs non human images
- Only first spikes contribute to decision

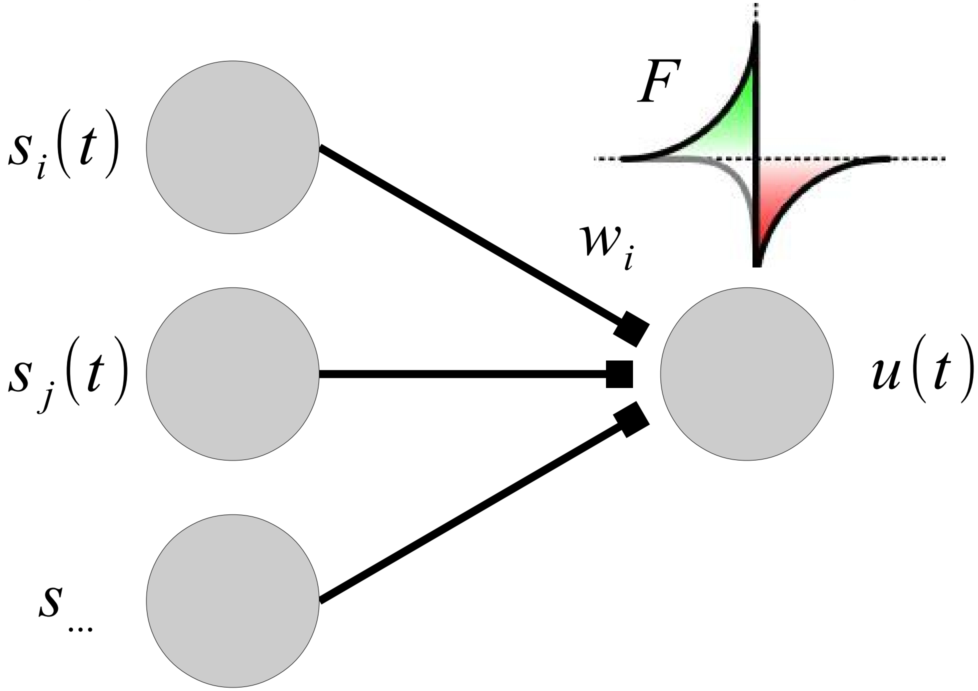






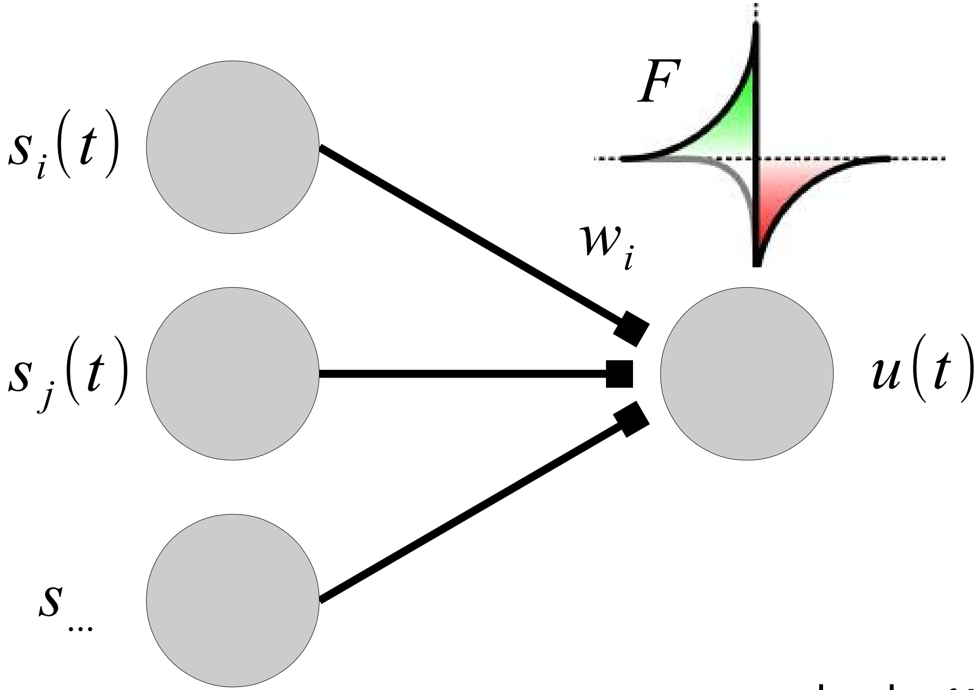
Thorpe *Nature* 1996,
Guyonneau *J Physiol Paris* 2004

Learning window and weight dynamics for STDP



$$\dot{w}_i = \sum_{t_i, t_{post}} F(t_i - t_{post})$$

Learning window and weight dynamics for STDP

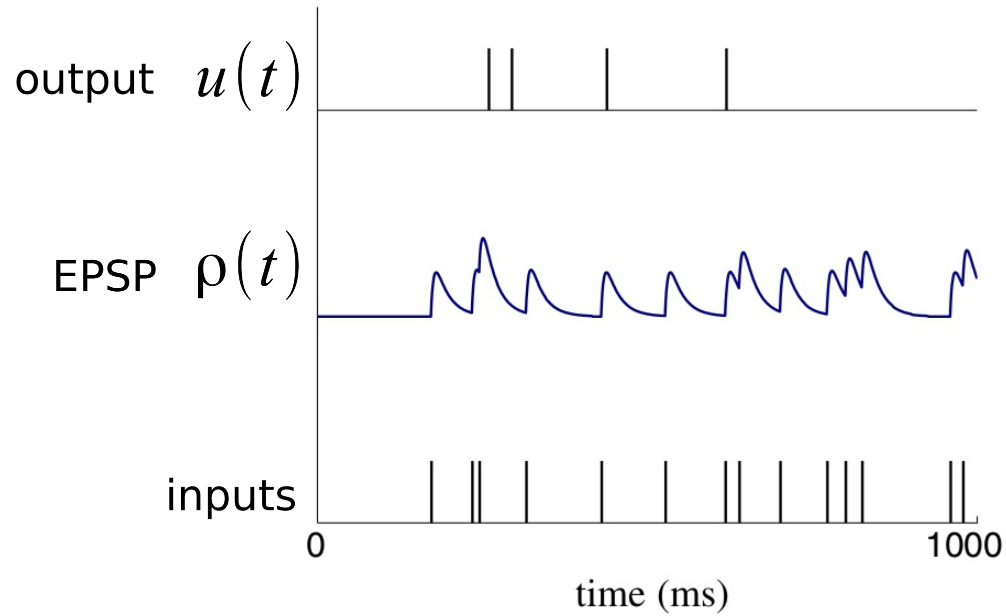


$$\dot{w}_i = \sum_{t_i, t_{post}} F(t_i - t_{post})$$

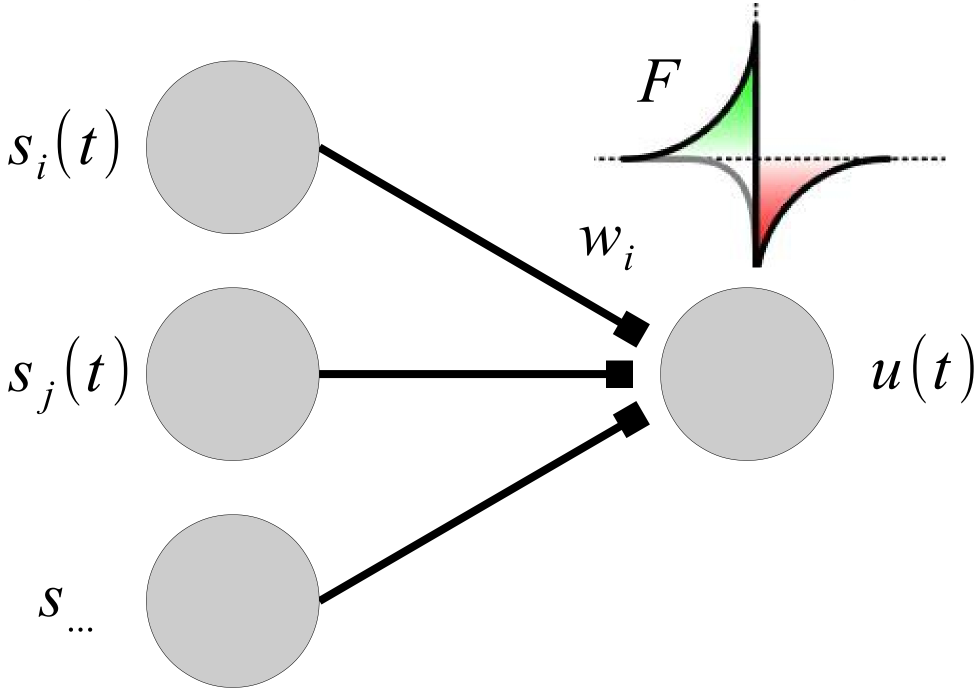
Hawkes process,
Poisson neuron

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

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



Learning window and weight dynamics for STDP



Hawkes process,
Poisson neuron

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

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

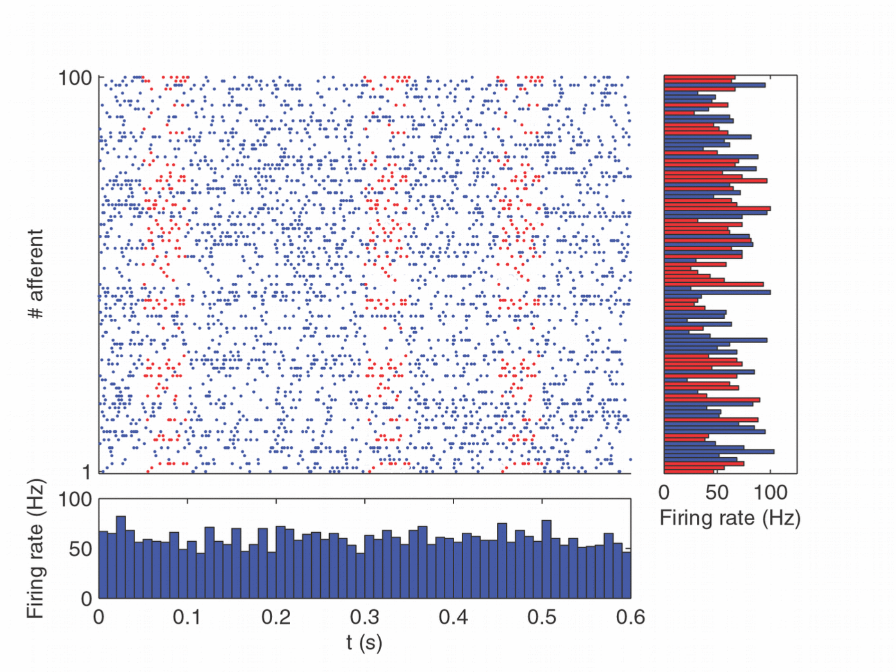
$$\dot{w}_i = \sum_{t_i, t_{post}} F(t_i - t_{post})$$
$$= \int_t \int_\tau F(\tau) s_i(t) u(t-\tau) \, d\tau \, dt$$
$$= \sum_j w_j \int_\tau [F * \epsilon](\tau) C_{ij}(\tau) \, d\tau$$

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

$$\dot{w} = \tilde{C} w \qquad \tilde{C} = \int [F * \epsilon](\tau) C(\tau) \, d\tau$$

Unsupervised learning for pattern detection

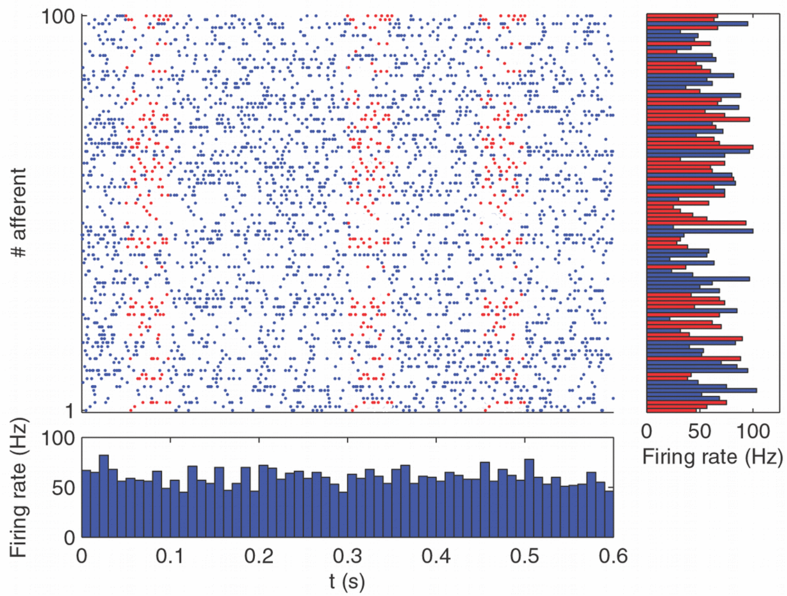
frozen Poisson spike pattern



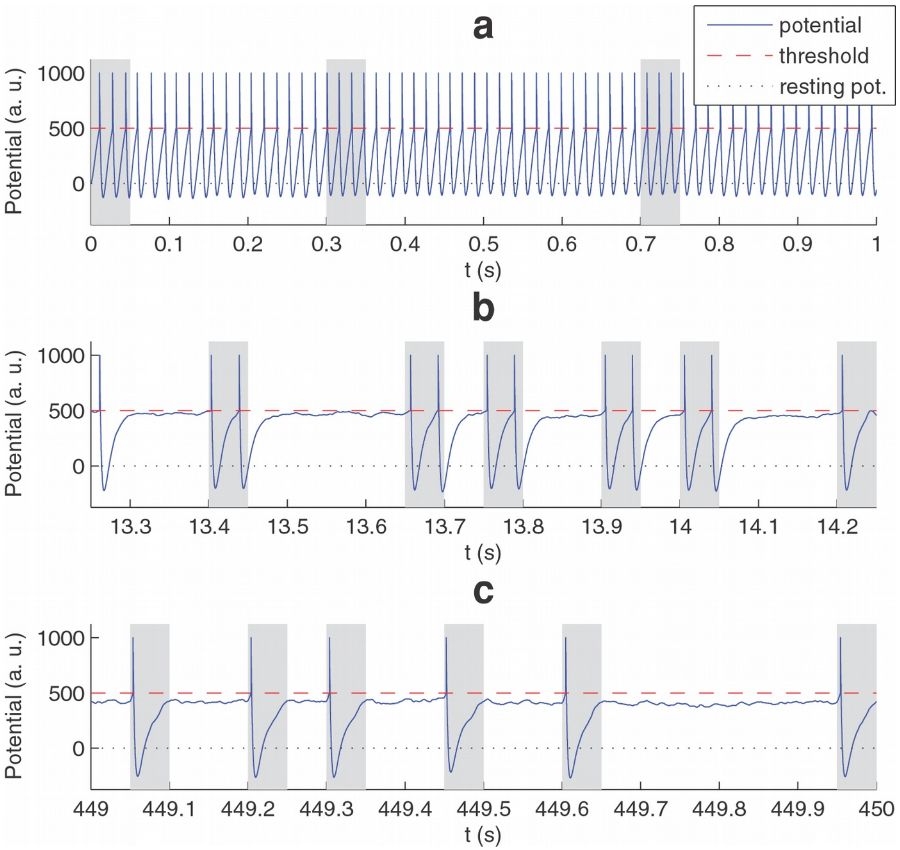
Masquelier *PLoS ONE* 2008

Unsupervised learning for pattern detection

frozen Poisson spike pattern



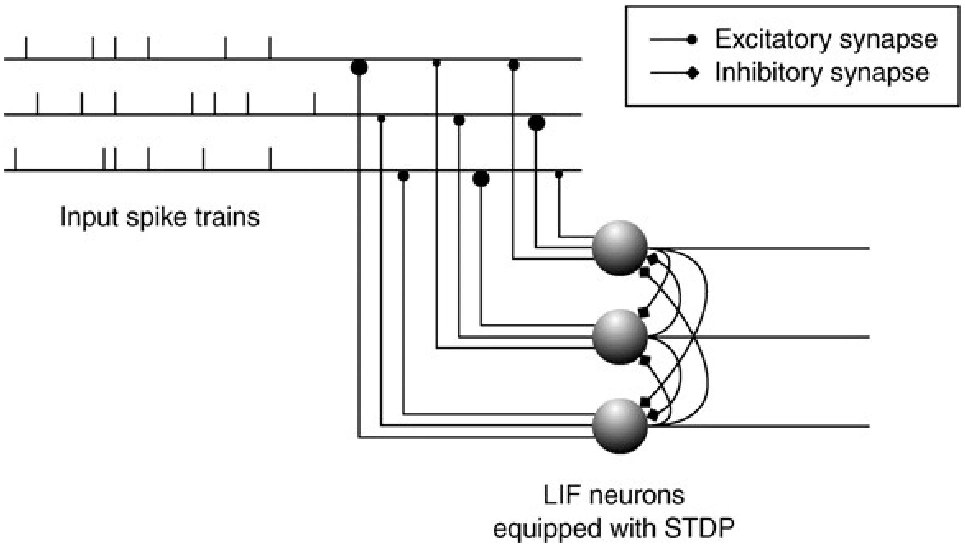
output neuron becomes selective
(LTP for synapses from early spikes)

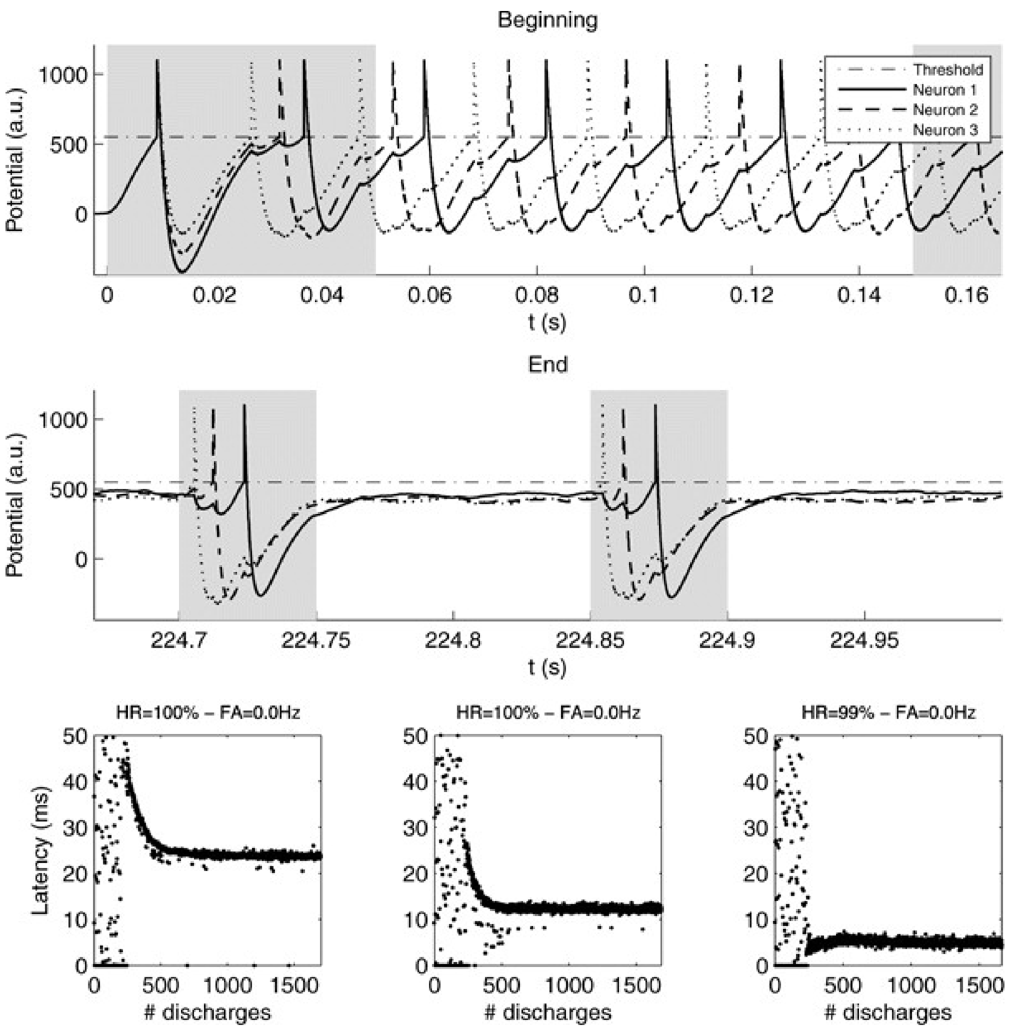


$$\dot{w} = F\left(t_{pre} - t_{post}\right) - a_{pre}$$

Masquelier *PLoS ONE* 2008

Learning the full pattern, not just the start

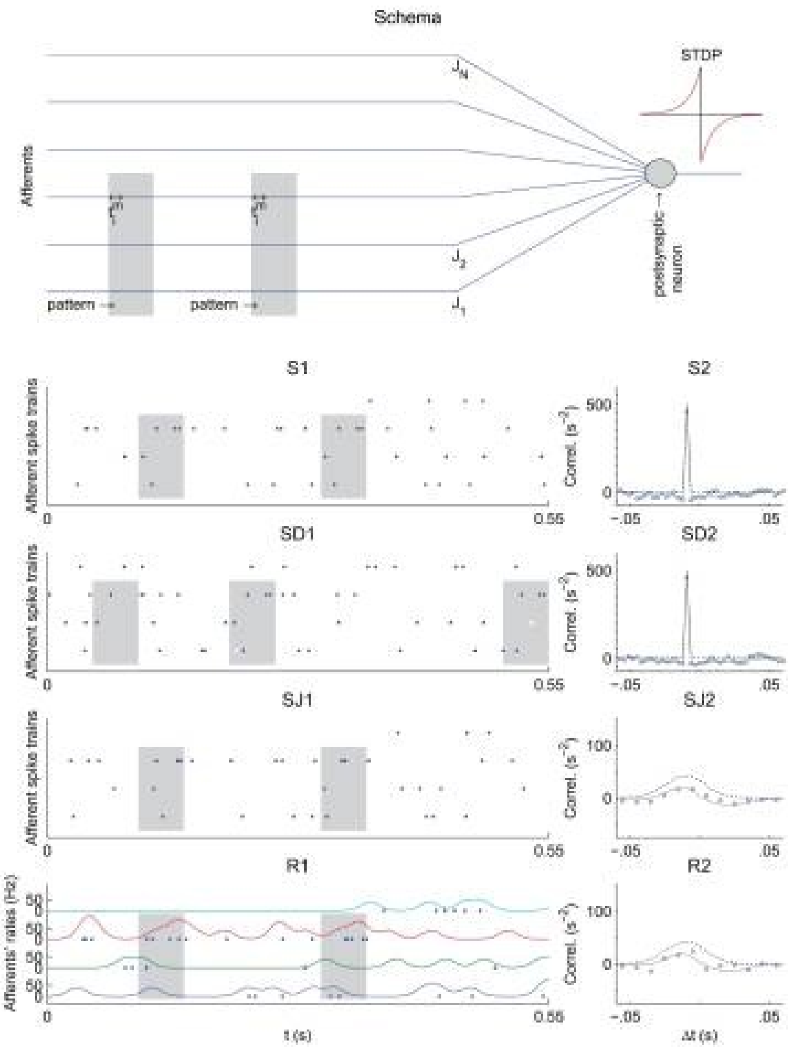




Masquelier *Neural Comput* 2009

Unsupervised learning for pattern detection

only spike correlations matter:
spike pattern, cofluctuating rates



Gilson *PLoS Comput Biol* 2011

Unsupervised learning for pattern detection

only spike correlations matter:
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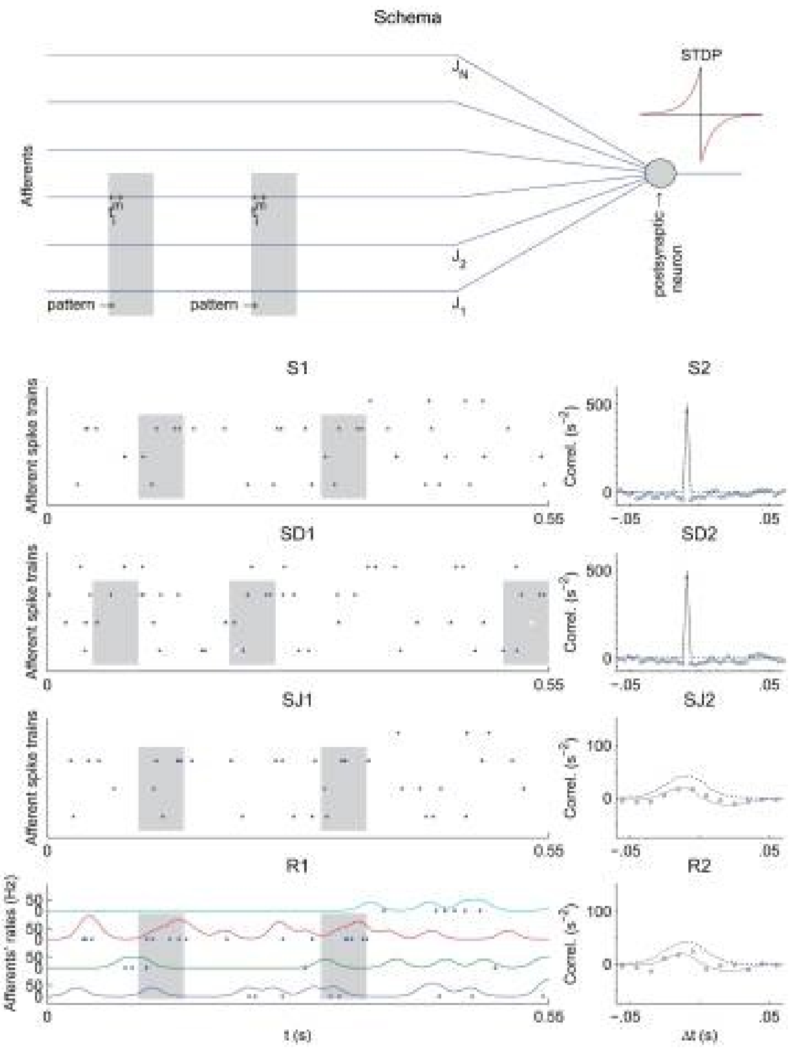
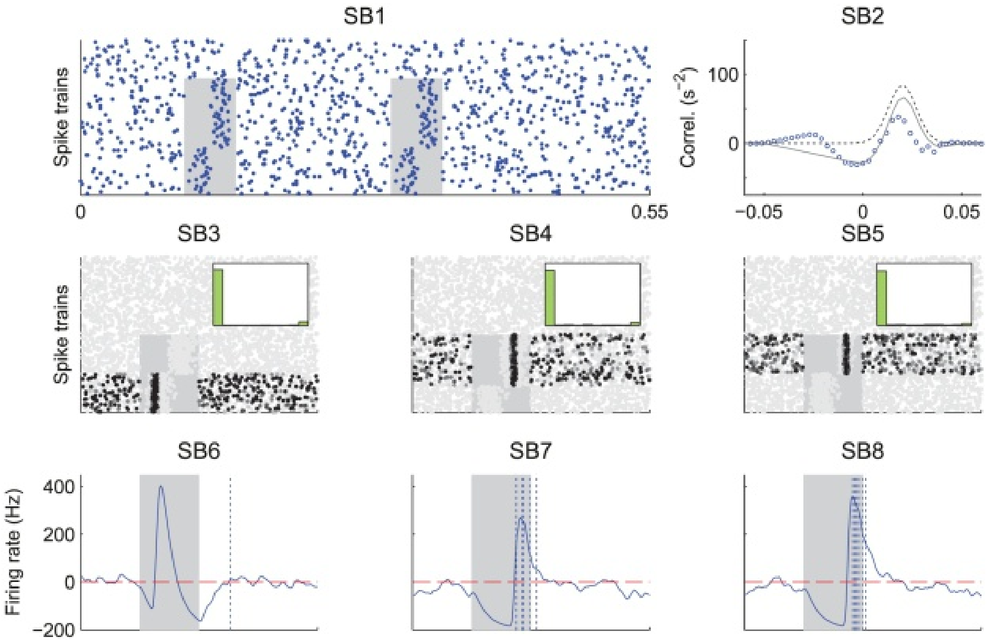


STDP spots early, dense
and sharp spike clusters



depends on $F * \epsilon$

Gilson *PLoS Comput Biol* 2011

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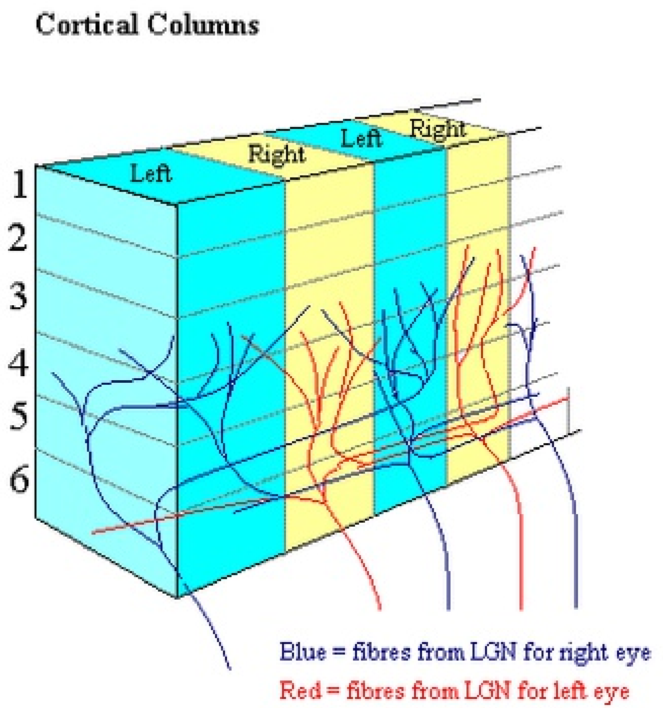
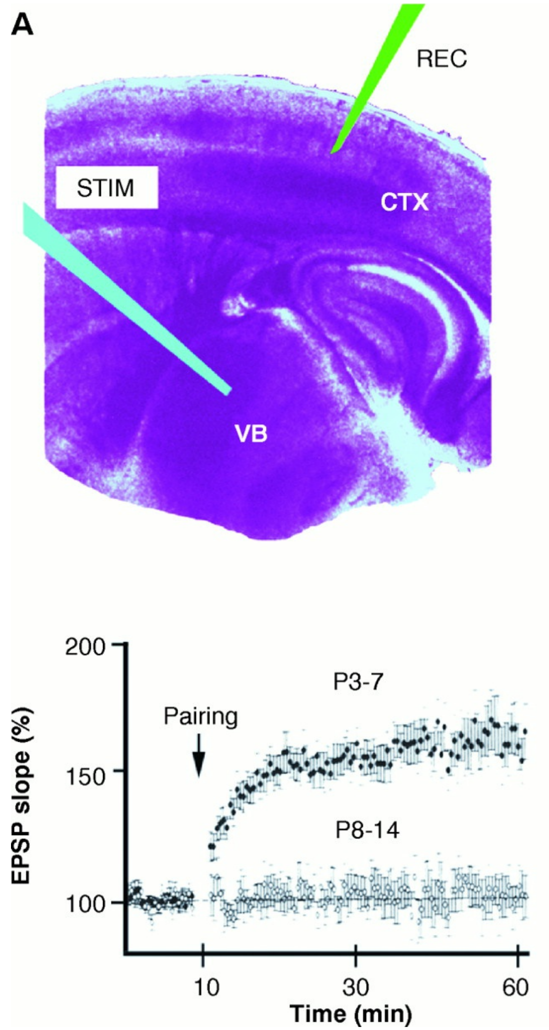
Ocular dominance

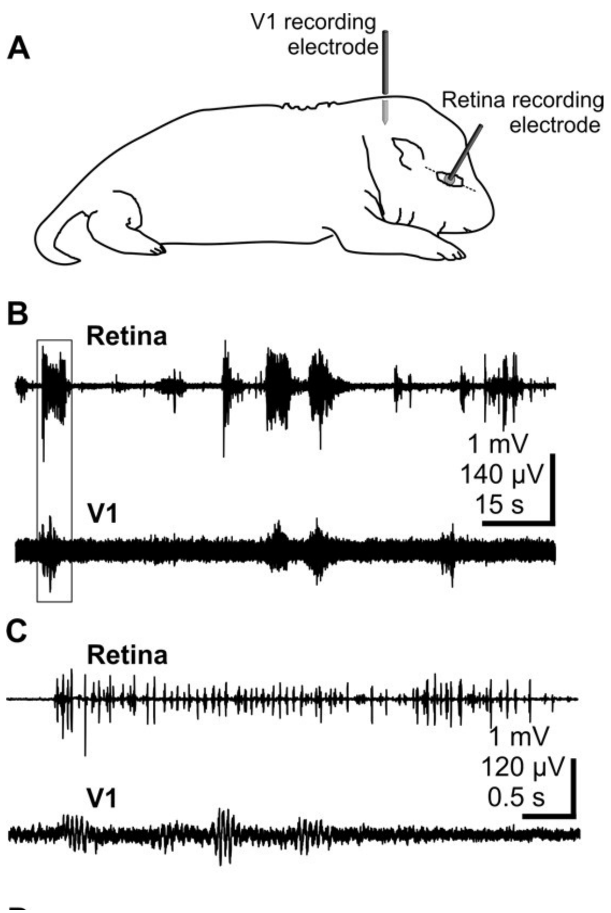
- Symmetric inputs from the two eyes
- How to specialize to one optical input only?



wikipedia



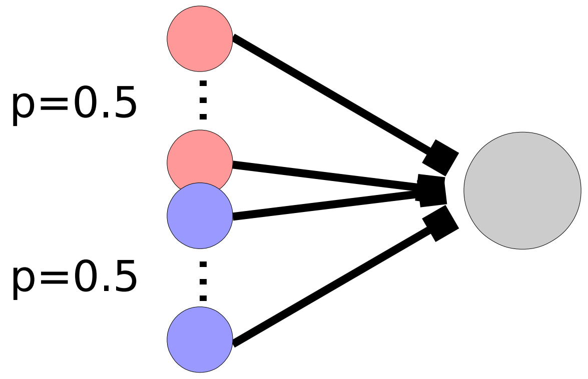
Katz *Science* 1996

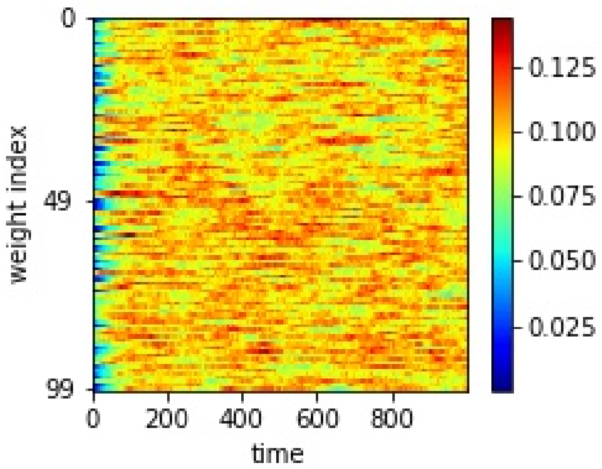


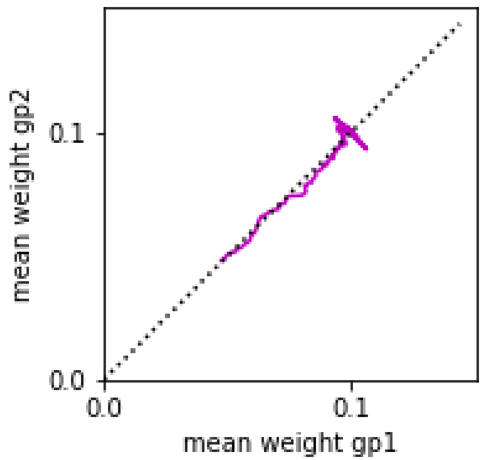
Hanganu *J Neurosci* 2006

Ocular dominance

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







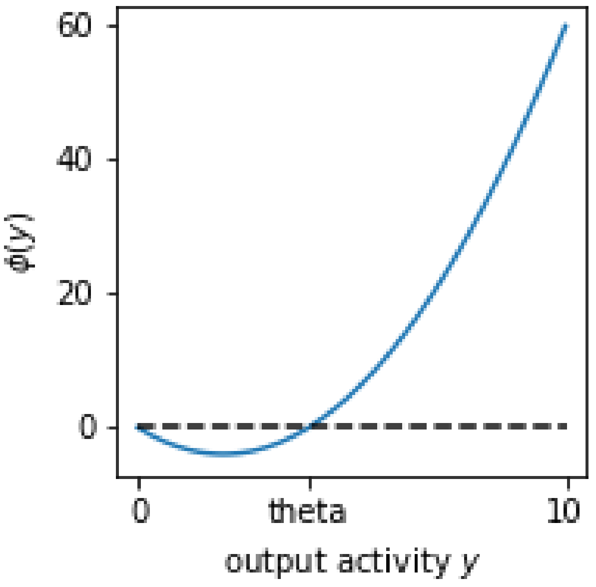
BCM rule

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

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

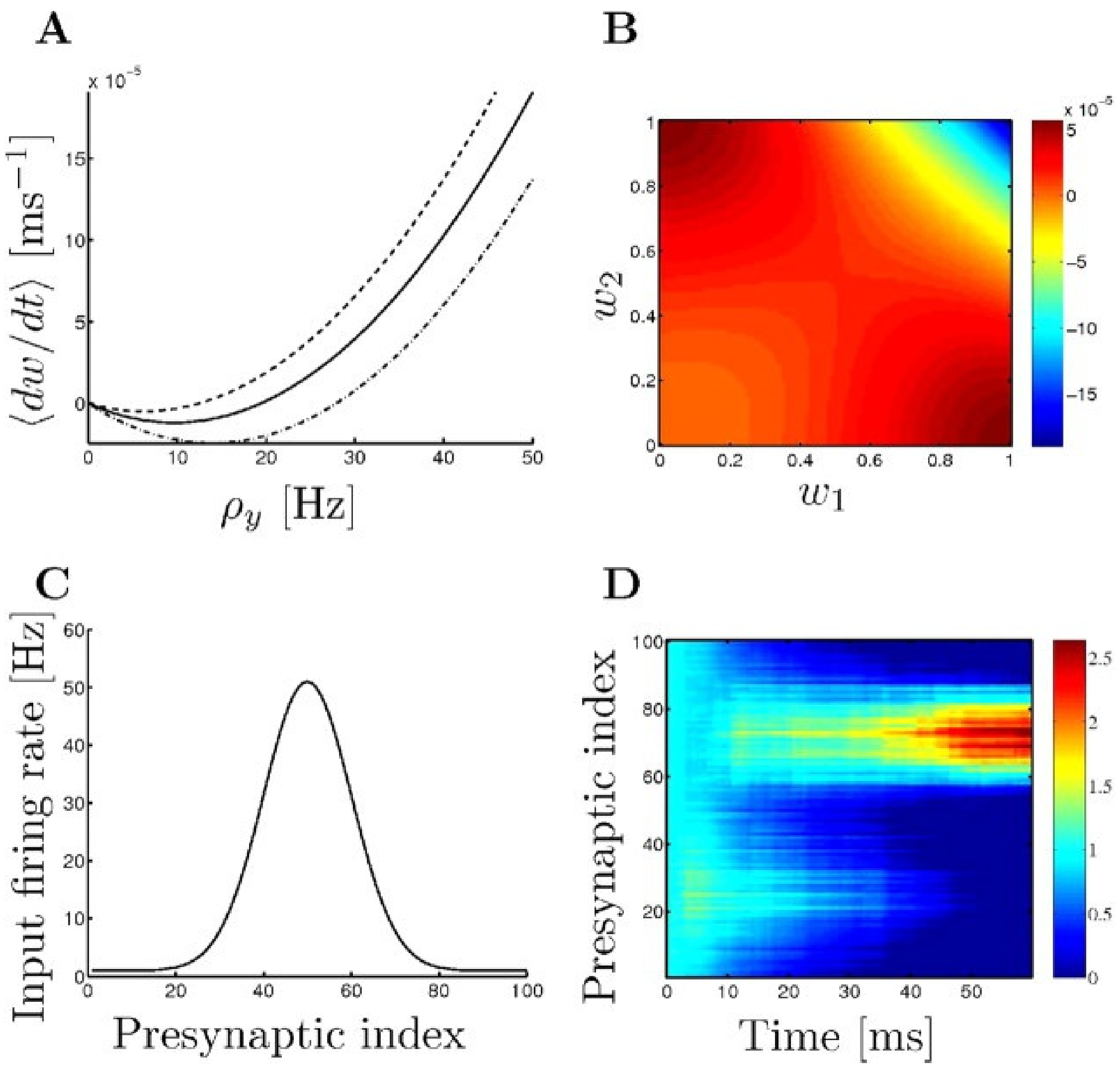
$$\phi(y) = y(y - \theta)$$

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



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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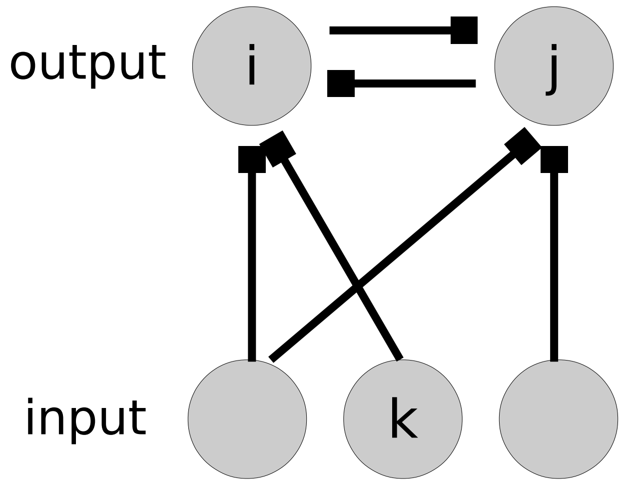
Maths for weight dynamics



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

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

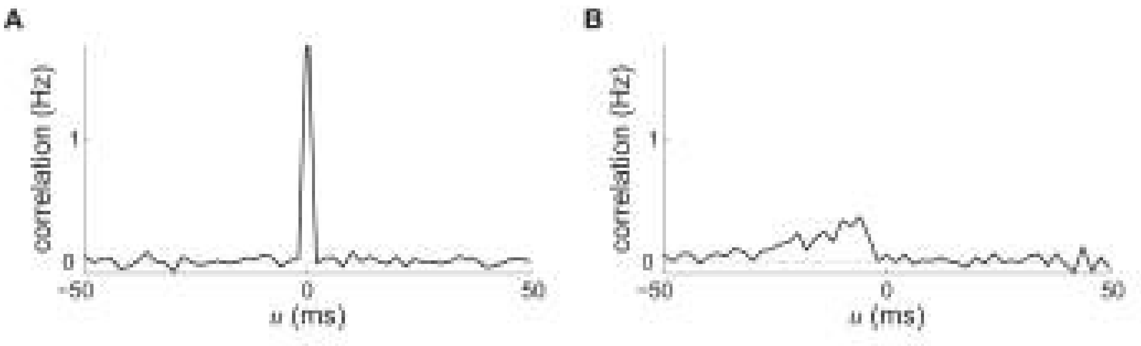
But s_j depends on s_i too!

Echos in networks due to
recurrent connections

Gilson *Biol Cybern* 2009

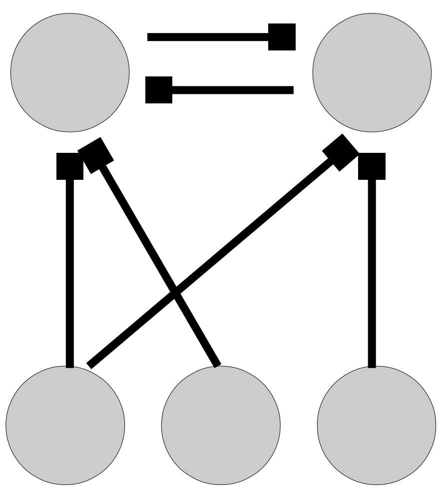
Correlation structure in recurrent networks

input-input   input-output



$t_{input} - t_{output}$

output

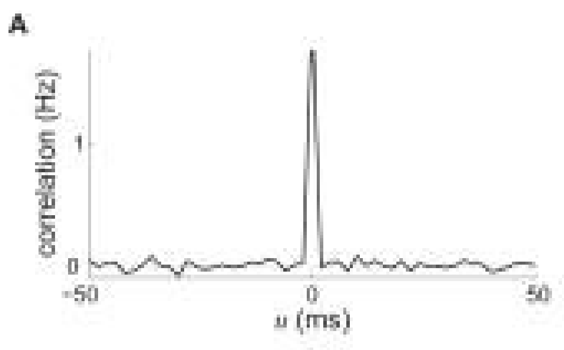


input

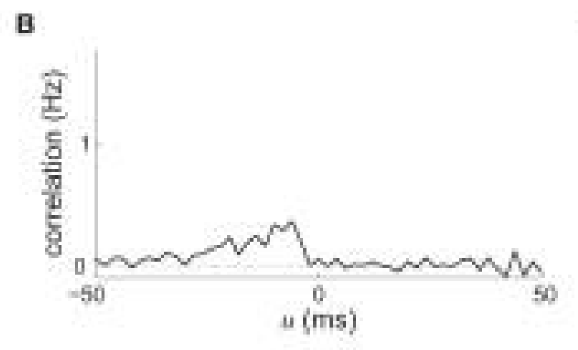
Gilson *Biol Cybern* 2009

Correlation structure in recurrent networks

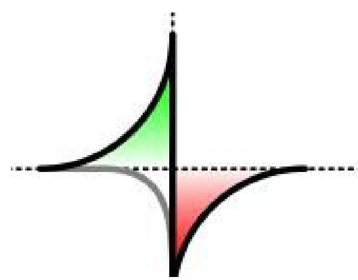
input-input

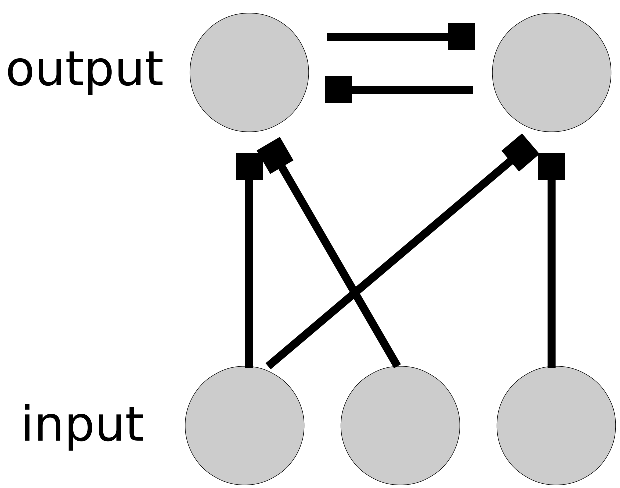


input-output



$t_{input} - t_{output}$

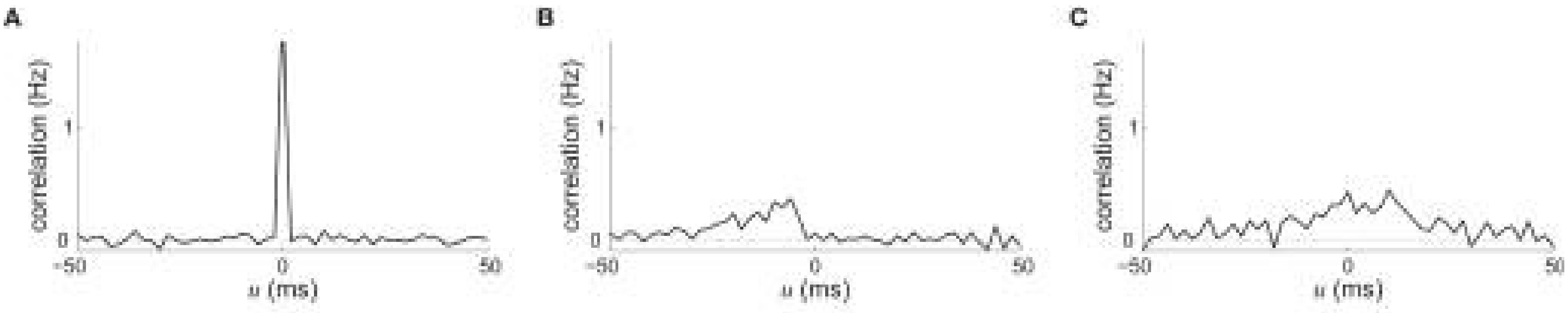




Gilson *Biol Cybern* 2009

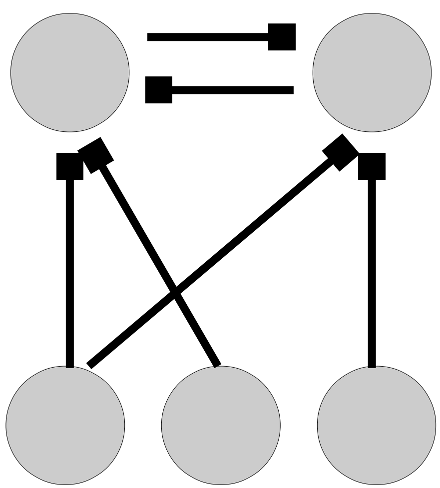
Correlation structure in recurrent networks

input-input | input-output | output-output

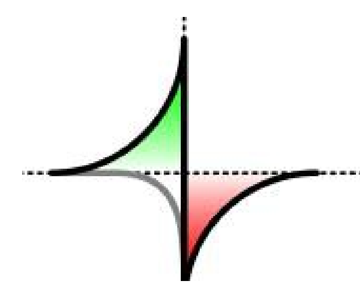


$t_{input} - t_{output}$

output

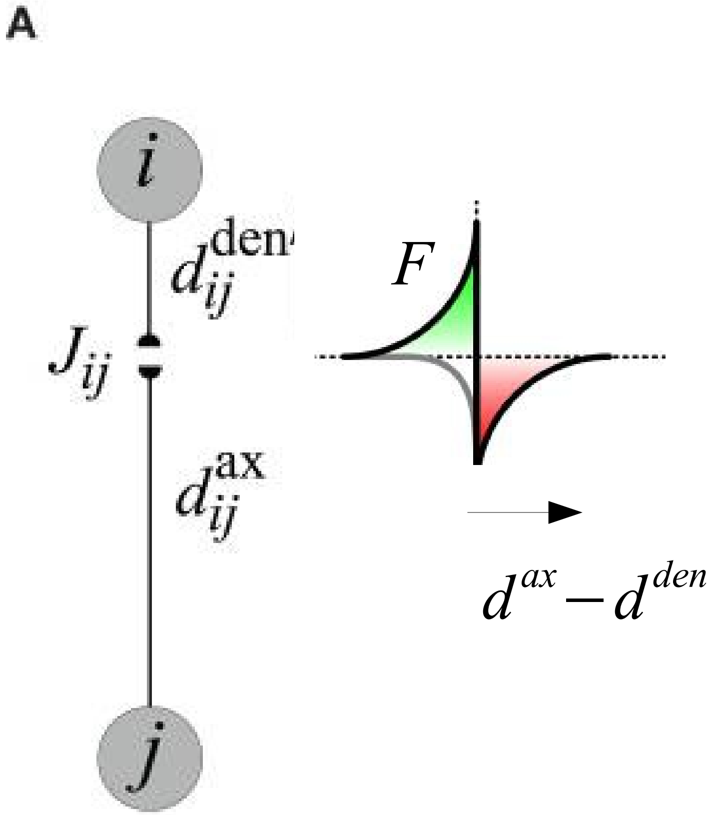


input



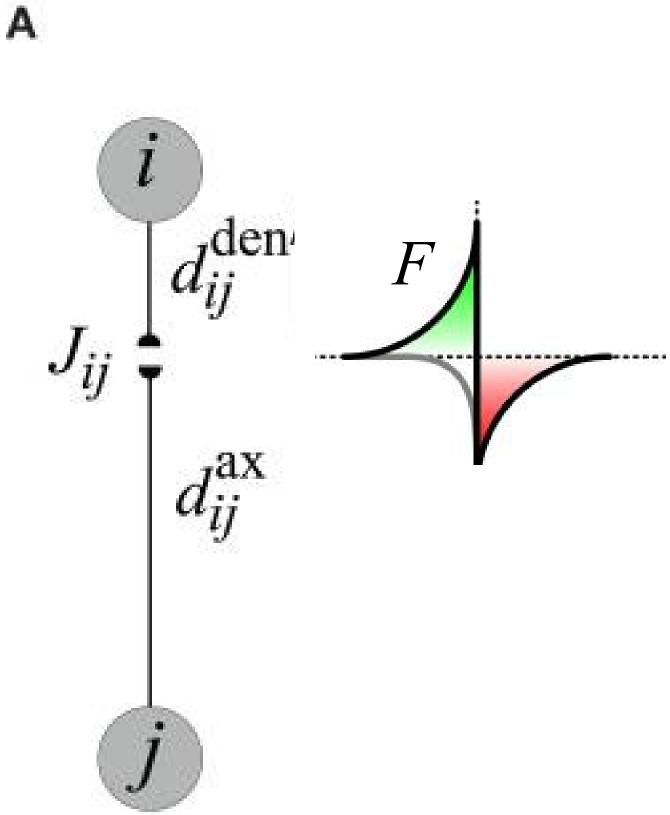
Gilson *Biol Cybern* 2009

Effect of synaptic delays

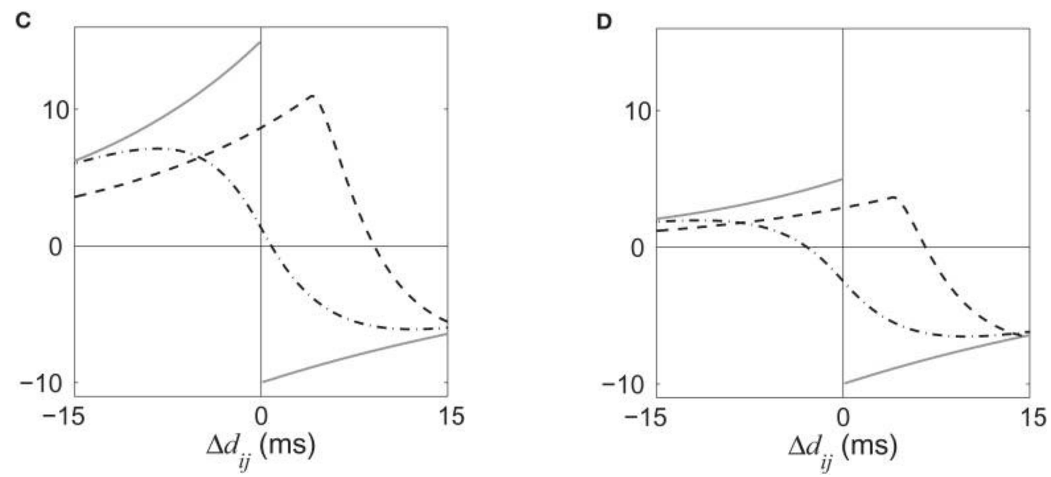


Gilson *Biol Cybern* 2009

Effect of synaptic delays



effective learning window $F * \epsilon$



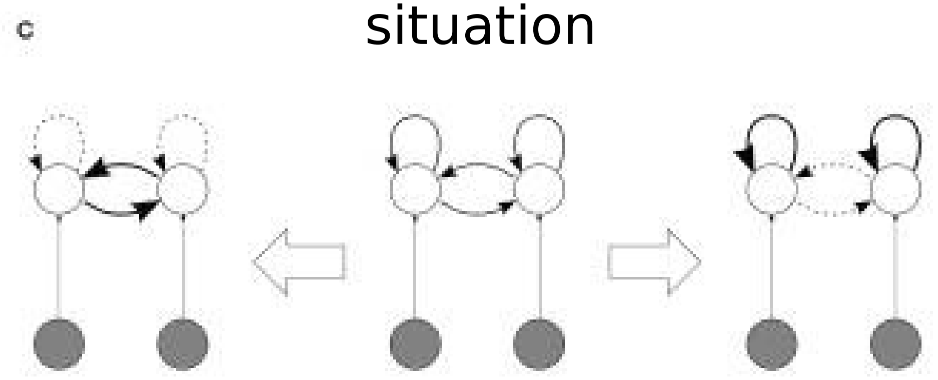
$d^{ax} - d^{den}$

dashed: feedforward
dashed-dotted: recurrent

Gilson *Biol Cybern* 2009

STDP and neuron assemblies

initial
situation



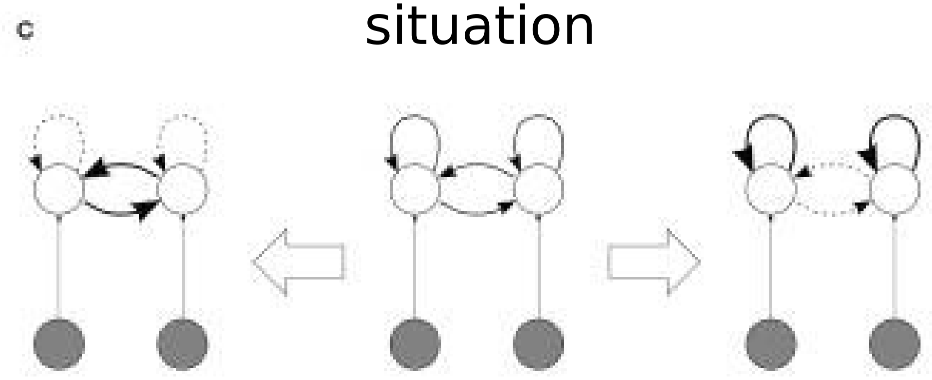
axonal delays

dendritic delays

Gilson *Biol Cybern* 2009

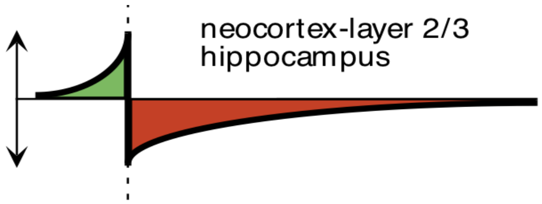
STDP and neuron assemblies

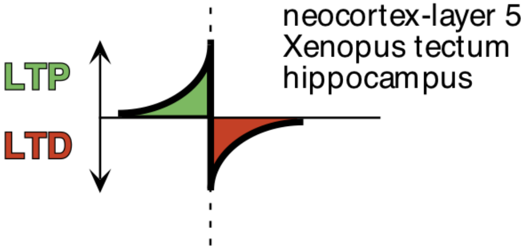
initial
situation



axonal delays

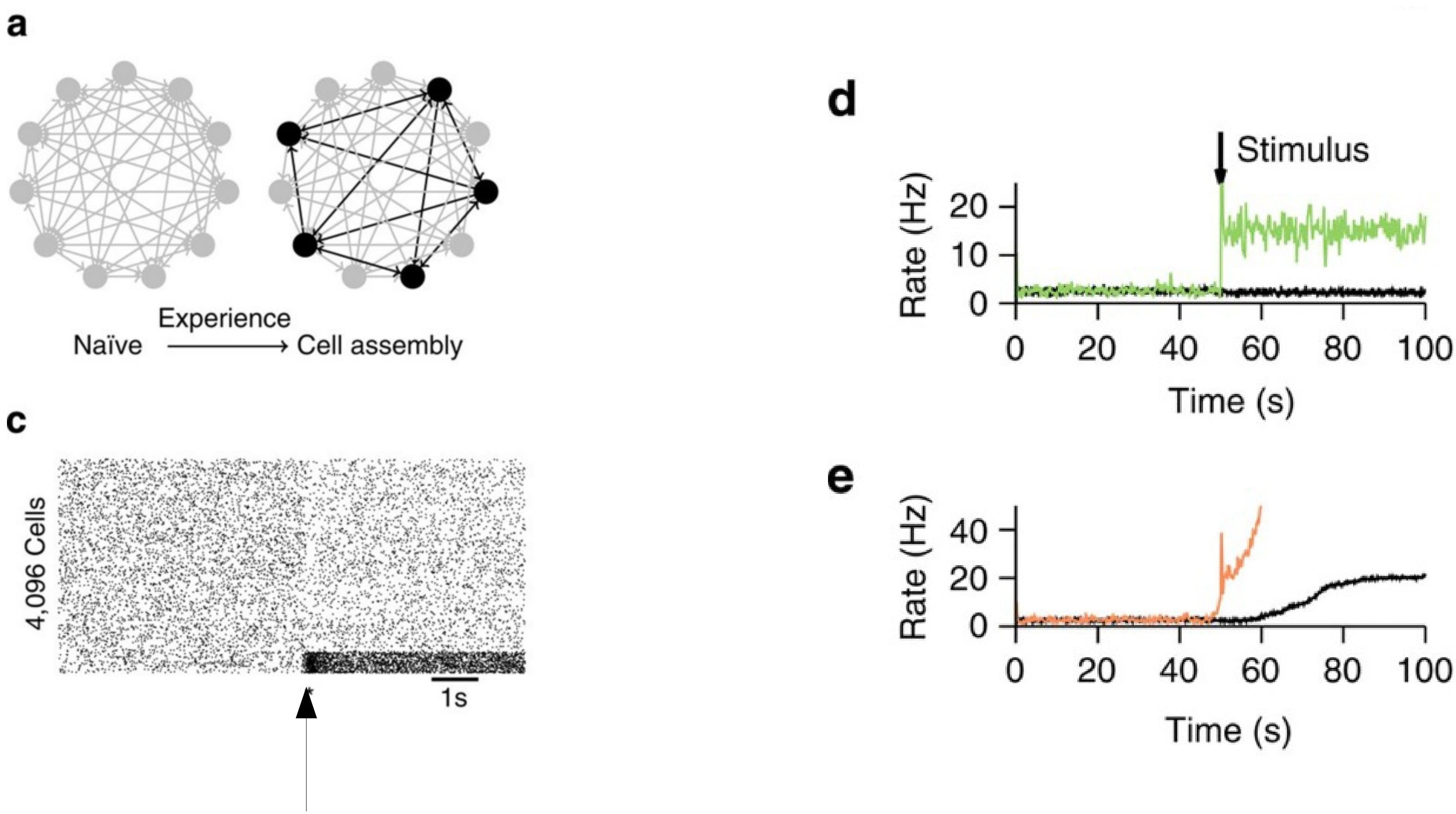
dendritic delays





Gilson *Biol Cybern* 2009

Stability in recurrent networks with ongoing plasticity



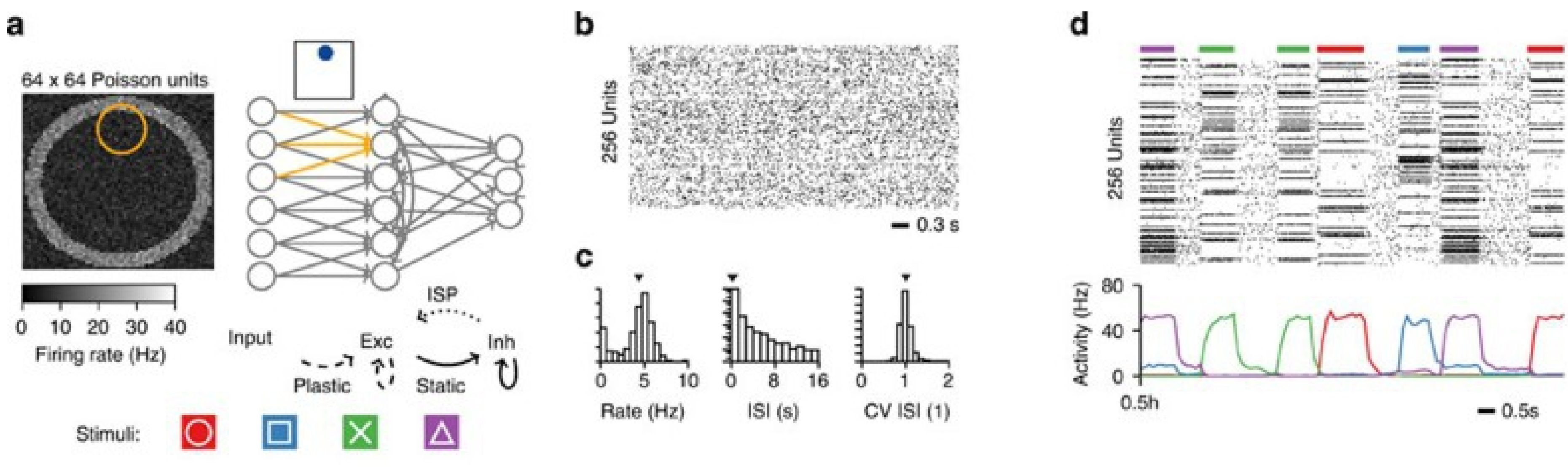
tSTDP off

tSTDP on

stimulus

Zenke *Nat Comm* 2015

Stability in recurrent networks with ongoing plasticity



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

Zenke *Nat Comm* 2015

Summary for plastic weight dynamics

- STDP can be Hebbian type (pairwise) or BCM type (triplet), so it has the same instability issue as rate-based rules

- 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

- Other mechanisms are necessary to stabilize learning, like heterosynaptic plasticity that models resource limitation (resulting in synaptic competition)

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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*

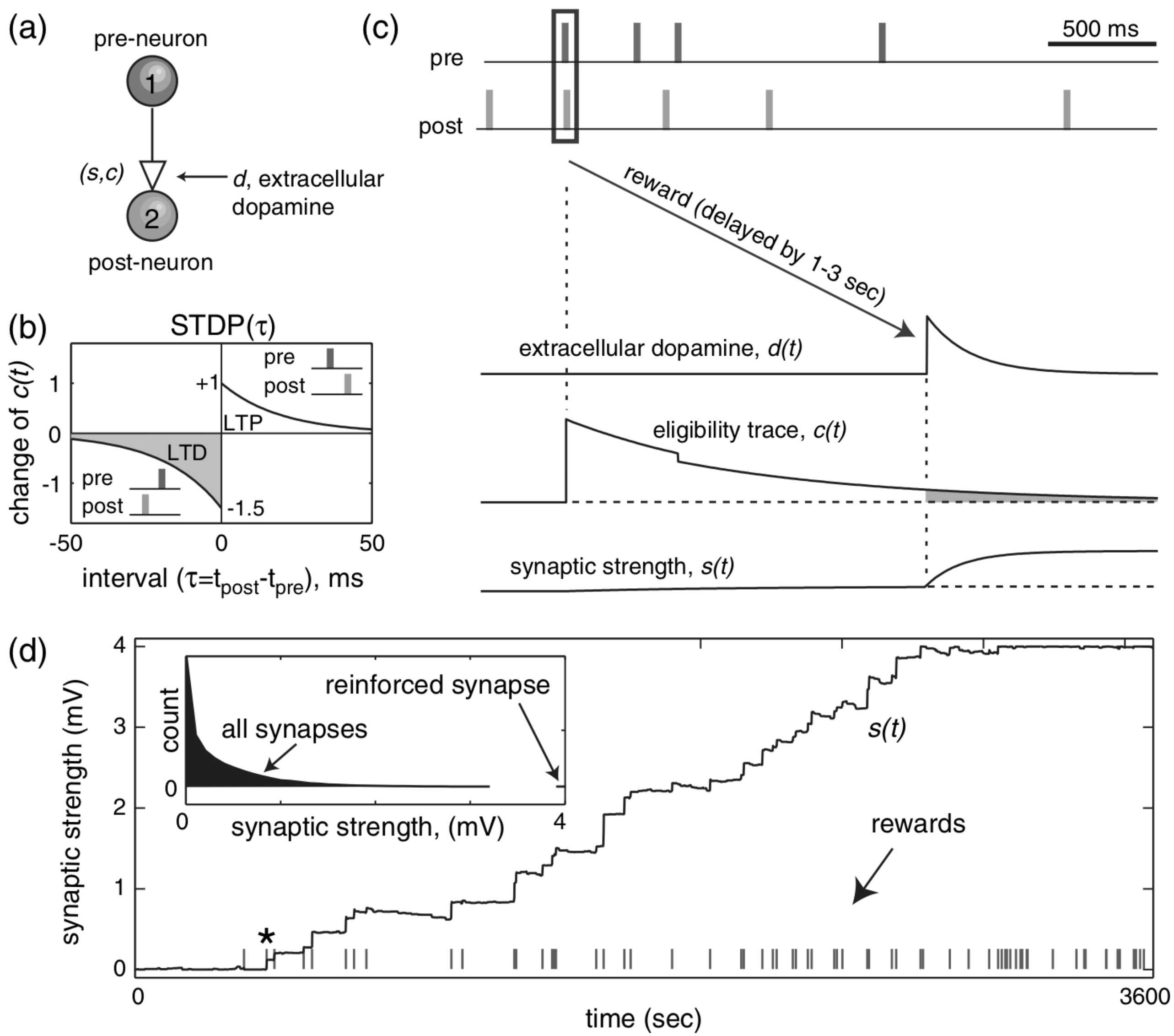
Types of learning

unsupervised (Hebbian, STDP) $\dot{w}_i = y\, x_i$

supervised (delta rule, perceptron) $\dot{w}_i = \left(\bar{y}^A - y\right) x_i^A$ $\quad \bar{y}^A$ objective for input of class *A*

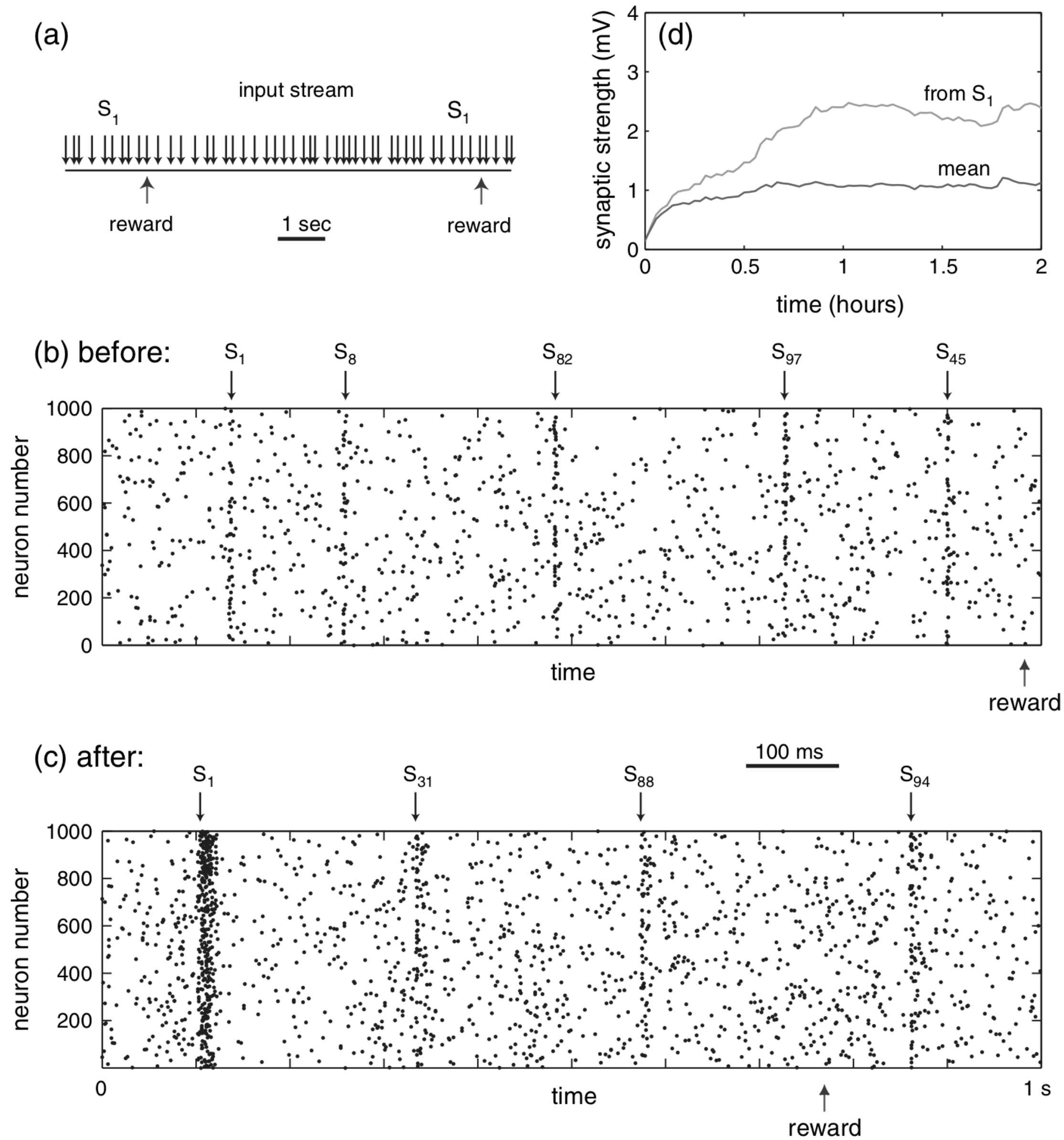
reinforcement learning $\dot{w}_i = \epsilon\, y\, x_i^A$ $\quad \epsilon$ modulator (dopamine, acetylcholine)

Reward-modulated STDP



Izhikevich *Cereb Cortex* 2007

Reward-modulated STDP



Izhikevich *Cereb Cortex* 2007

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Towards theory for distributed computations

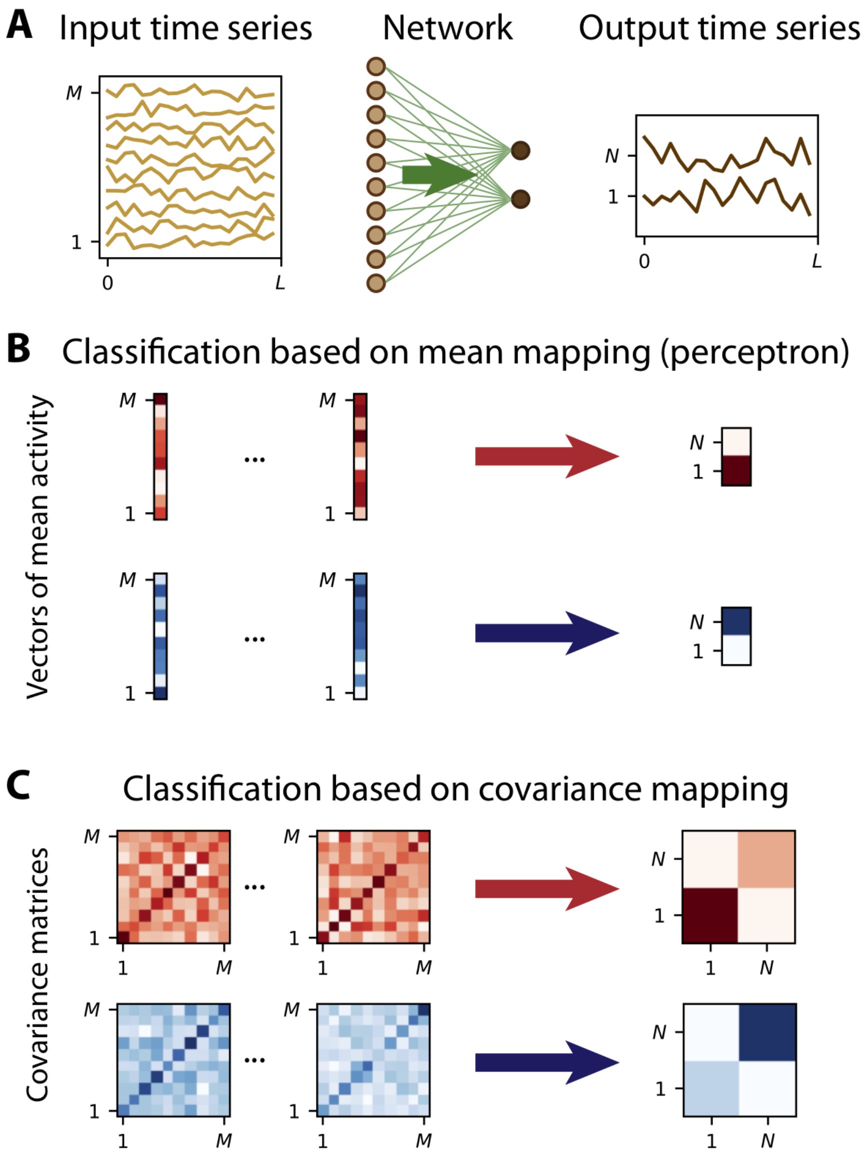
Dynamics level

Spiking statistics	Neuronal activation mechanisms	Synaptic plasticity

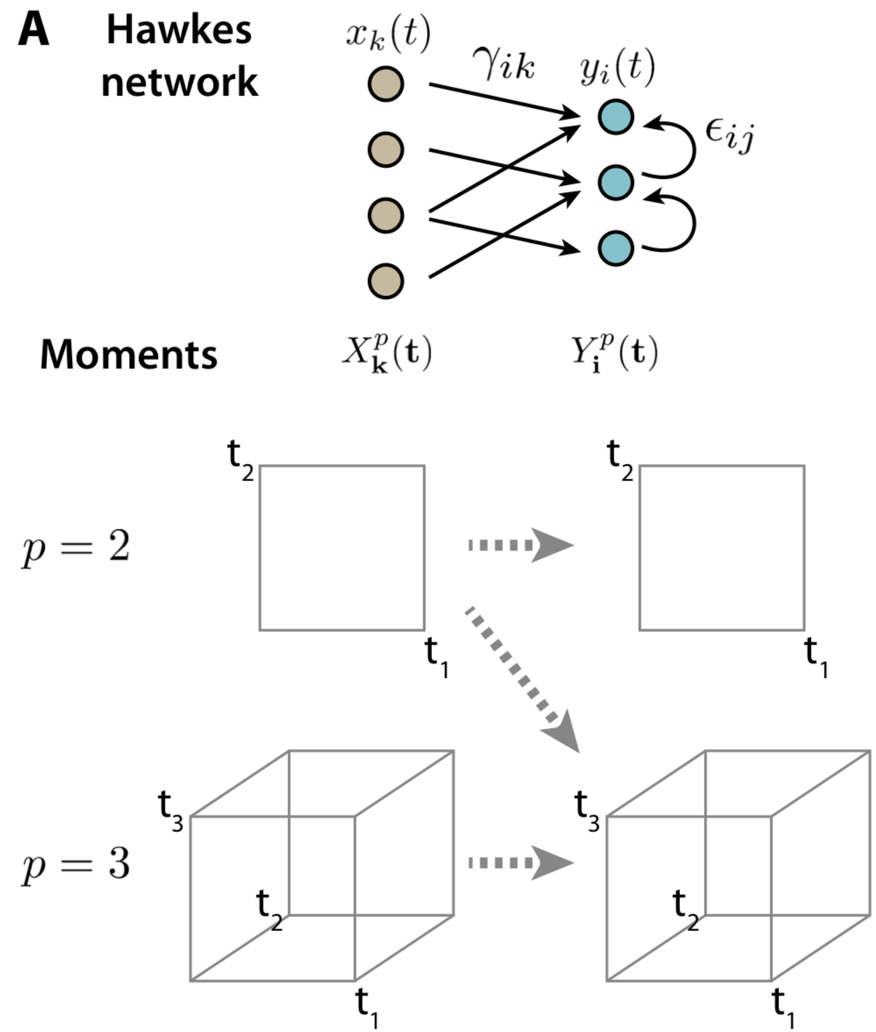
Towards theory for distributed computations

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 (*bioRxiv*)



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

Further reading on link with information theory

PLoS Comput Biol. 2013 Apr;9(4):e1003037. doi: 10.1371/journal.pcbi.1003037. Epub 2013 Apr 25.

Bayesian computation emerges in generic cortical microcircuits through spike-timing-dependent plasticity.

Nessler B[1], Pfeiffer M, **Buesing** L, **Maass** W.

Neural Comput. 2016 Sep;28(9):1859-88. doi: 10.1162/NECO_a_00862. Epub 2016 Jul 8.

Linking Neuromodulated Spike-Timing Dependent Plasticity with the Free-Energy Principle.

Isomura T[1], Sakai K[2], Kotani K[3], Jimbo Y[4].

Front Neural Circuits. 2018 Jul 31;12:53. doi: 10.3389/fncir.2018.00053. eCollection 2018.

Eligibility Traces and Plasticity on Behavioral Time Scales: Experimental Support of NeoHebbian Three-Factor Learning Rules.

Gerstner W[1], Lehmann M[1], Liakoni V[1], Corneil D[1], Brea J[1].

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

Universitat Pompeu Fabra Barcelona

European Commission

Human Brain Project

MARIE CURIE ACTIONS