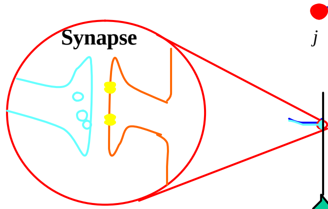
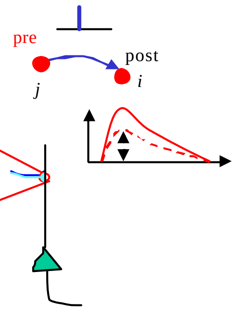
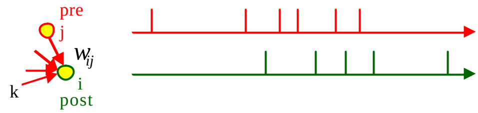
Models of synaptic Plasticity

Wulfram Gerstner
EPFL, Lausanne





Hebbian Learning

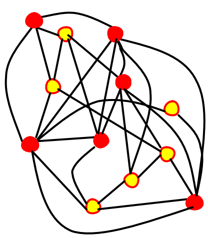


*When an axon of cell **j** repeatedly or persistently takes part in firing cell **i**, then j's efficiency as one of the cells firing i is increased*

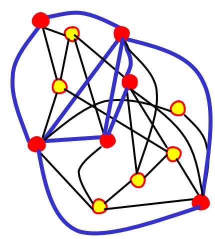
Hebb, 1949

- local rule
- simultaneously active (correlations)

Hebbian Learning



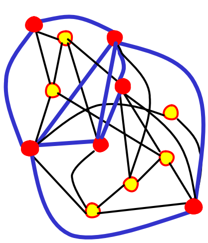
Hebbian Learning



item memorized

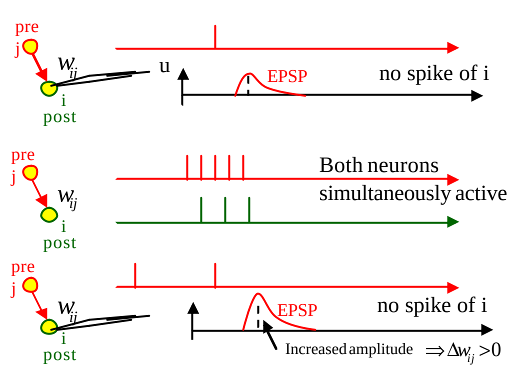
Hebbian Learning

Recall:
Partial info



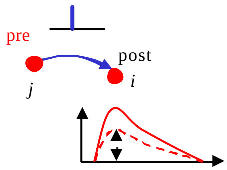
item recalled

Hebbian Learning in experiments (schematic)



Synaptic Dynamics

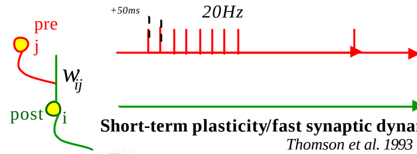
Induction of changes
- *fast (if stimulated appropriately)*
- *slow (homeostasis)*



Persistence of changes
- *long (LTP/LTD)*
- *short (short-term plasticity)*

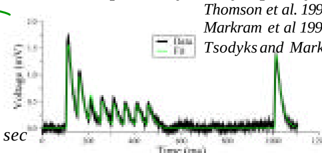
Functionality
- *useful for learning a new behavior*
- *useful for development (e.g., wiring for receptive field development)*
- *useful for activity control in network*
- *useful for coding*

Classification of plasticity: short-term vs. Long-term



Short-term plasticity/fast synaptic dynamics

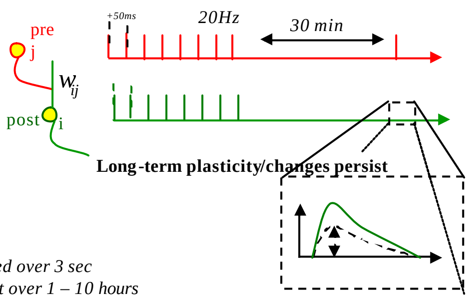
Thomson et al. 1993
Markram et al 1998
Tsodyks and Markram 1997



Changes
- *induced over 0.5 sec*
- *recover over 1 sec*

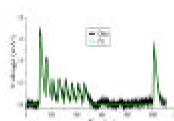
Data: Silberberg, Markram
Fit: Richardson (Tsodyks-Markram model)

Classification of plasticity: short-term vs. Long-term



Changes
- *induced over 3 sec*
- *persist over 1 – 10 hours*

Classification of plasticity: short-term vs. Long-term

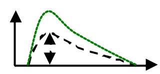


Changes
- *induced over 0.1-0.5 sec*
- *recover over 1 sec*

Protocol
- *presynaptic spikes*

Model
- *well established*
  (Tosdyks, Senn, Markram)

LTP/LTD/Hebb

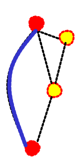


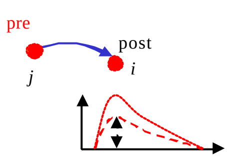
Changes
- *induced over 0.5-5sec*
- *remains over hours*

Protocol
- *presynaptic spikes + …*

Model
- *we will see*

Hebbian Learning = unsupervised learning

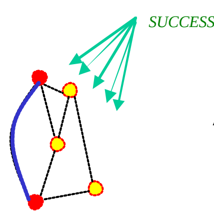




$$w_{ij}\, e\left(t - t_j^f\right)$$

$$\Delta w_{ij} \propto F(pre, post)$$

Reinforcement Learning = reward + Hebb



$$\Delta w_{ij} \propto F(pre, post, SUCCESS)$$

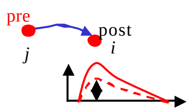
local global

Classification of plasticity: unsupervised vs reinforcement

LTP/LTD/Hebb

Theoretical concept

- *passive changes*
- *exploit statistical correlations*



Functionality

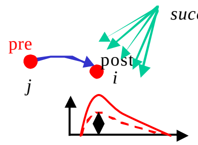
-useful for development

(wiring for receptive fields)

Reinforcement Learning

Theoretical concept

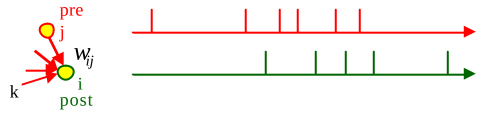
- *conditioned changes*
- *maximise reward*



Functionality

- *useful for learning a new behavior*

Hebbian Learning



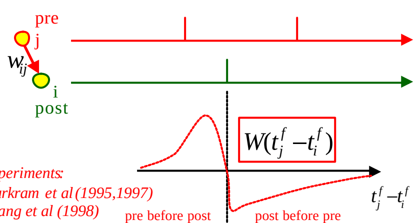
*When an axon of cell **j** repeatedly or persistently takes part in firing cell **i**, then j's efficiency as one of the cells firing i is increased*

Hebb, 1949

- local rule
- simultaneously active (correlations)

Rate model: active = high rate = many spikes per second

Spike Timing Dependent Plasticity and Hebbian Learning



Experiments:
Markram et al (1995,1997)
Zhang et al (1998)
Bi&Poo (2001)

$$\Delta w_{ij} = W(t_j^f - t_i^f)$$

Classification of plasticity standard LTP/LTD vs STDP

LTP/LTD/Hebb

exp. Protocol

- *extracell. stimulation + …*
  - *postsyn. depol*
  - *postsyn. activity*

Model

- *we will see*

$\Delta w_{ij} \propto pre * post$

STDP

exp. Protocol

- *presyn spike + …*
  - *postsyn. spike*

Model

- *we will see*

$\Delta w_{ij} \propto pre * post$

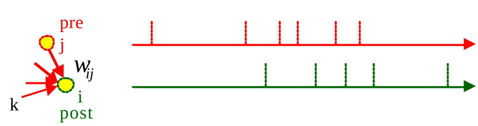
Models of synaptic Plasticity

√ 0. Introduction

I. Hebbian Learning (unsupervised): review of rate-based theory

II. Spike-Timing Dependent theory

Hebbian Learning (rate models)



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Hebb, 1949

- local rule
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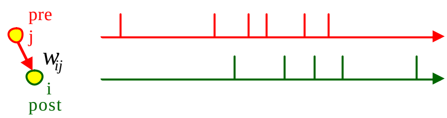
Rate model: active = high rate = many spikes per second

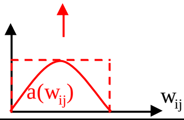
Rate-based Hebbian Learning



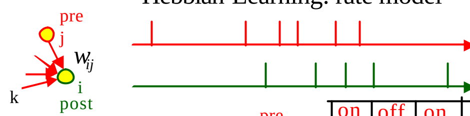
$$\frac{d}{dt} w_{ij} = F(w_{ij}; n_j^{pre}, n_i^{post})$$

$$\frac{d}{dt} w_{ij} = a_0 + a_1^{pre} n_j^{pre} + a_1^{post} n_i^{post} + a_2^{corr} n_j^{pre} n_i^{post} + \dots$$

a = a(w_{ij})

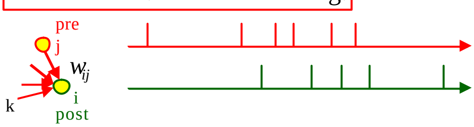


Hebbian Learning: rate model



pre	on	off	on	off
post	on	on	off	off
$\frac{d}{dt} w_{ij} = a_2^{corr} n_j^{pre} n_i^{post}$	+	**0**	**0**	**0**
$\frac{d}{dt} w_{ij} = a_2^{corr} n_j^{pre} n_i^{post} - c$	+	-	-	-
$\frac{d}{dt} w_{ij} = a_2^{corr} n_j^{pre} (n_i^{post} - J)$	+	**0**	-	**0**
$\frac{d}{dt} w_{ij} = a_2^{corr} (n_j^{pre} - J)(n_i^{post} - J)$	+	-	-	+

Exercise now: Hebbian Learning:



Show that

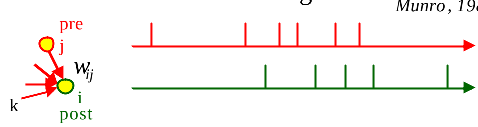
$$\frac{d}{dt} w_{ij} = a_2^{corr} (n_i^{post} - J) n_j^{pre}$$

Is a special case of

$$\frac{d}{dt} w_{ij} = a_0 + a_1^{pre} n_j^{pre} + a_1^{post} n_i^{post} + a_2^{corr} n_j^{pre} n_i^{post} + \dots$$

Rate-based Hebbian Learning: BCM

Bienenstock, Cooper Munro, 1982



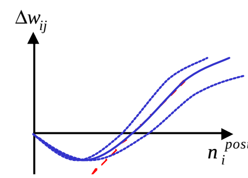
presynaptically gated

$$\frac{d}{dt} w_{ij} = a_2^{corr} (n_i^{post} - J) n_j^{pre}$$

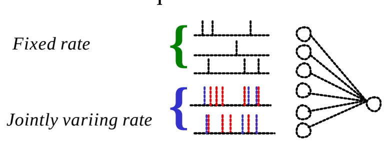
BCM

$$\frac{d}{dt} w_{ij} = a_2^{corr} \Phi(n_i^{post} - J) n_j^{pre}$$

$$J = f(\bar{n}_i^{post})$$

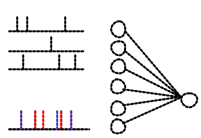


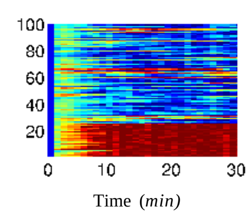
Functional consequences of Hebbian Learning



Detects correlations in the input

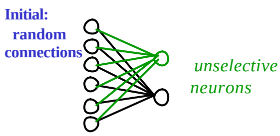
Example: BCM



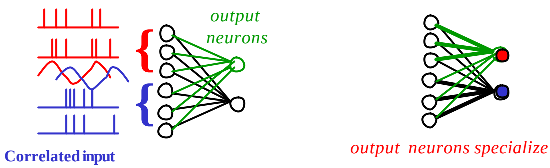


Plasticity rule detects where the 'interesting' input occurs
-- some synapses strengthened at the expense of others

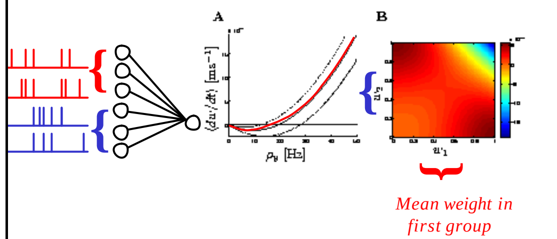
Synaptic changes for development



BCM leads to specialized Neurons (developmental learning); BUT: ***rate model***

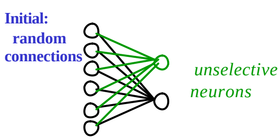


Functional properties: specialisation

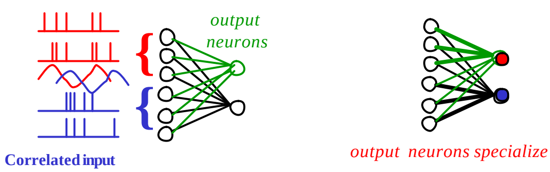


BCM leads to specialized Neurons (developmental learning); BUT: ***rate model***

Detour: Receptive field development



Hebbian learning leads to specialized Neurons (developmental learning);



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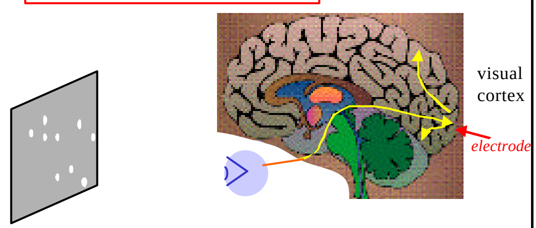

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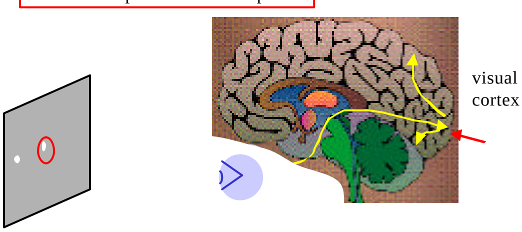
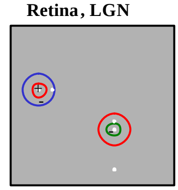


Detour: Receptive field development

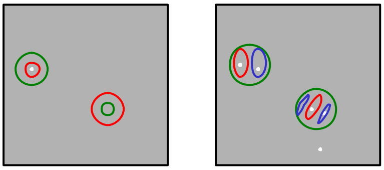
Receptive fields:
Retina, LGN



Detour: Receptive field development

Receptive fields: **Retina, LGN**

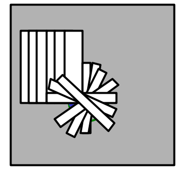
Receptive fields: **visual cortex V1**



Orientation selective

Detour: Receptive field development

Receptive fields: **visual cortex V1**



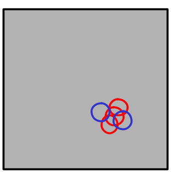
Orientation selective

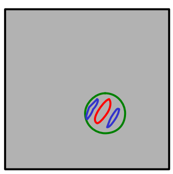
Detour: Receptive field development

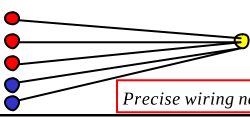
What makes cells Orientation selective? - wiring

Receptive fields: **in LGN**

Receptive fields: **visual cortex V1**



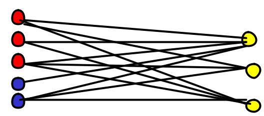




Precise wiring necessary – how done?

Detour: Receptive field development

Precise wiring necessary – how done?



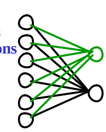
Make connetions plastic:

Hebbian (unsupervised) learning rule

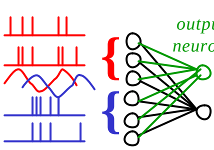
Detour: Receptive field development

Hebbian leanring leads to specialized Neurons (developmental learning);

Initial: random connections

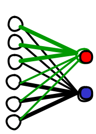


unselective neurons



output neurons

Correlated input

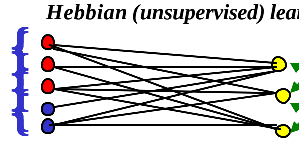


output neurons specialize

Detour: Receptive field development

Precise wiring necessary – how done?

Hebbian (unsupervised) learning rule



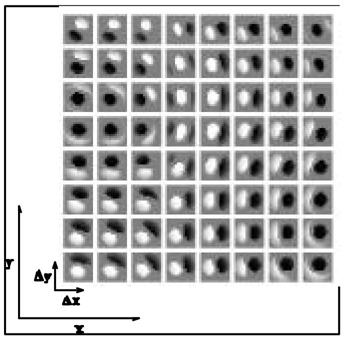
LGN neurons

cortical neurons

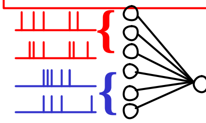
Stimulation with Locally correlated inputs

Wiring develops = receptive fields develop

Detour: Receptive field development - model results



Exercise now: Hebbian Learning:

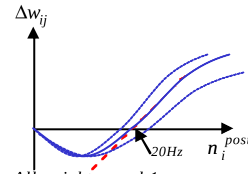


$$n_i^{post} = g(I_i) = \sum_j w_{ij} n_j^{pre}$$

BCM rule

$$\frac{d}{dt} w_{ij} = a_2^{corr} \Phi(n_i^{post} - J) n_j^{pre}$$

20Hz



Assume 2 groups of 10 neurons each. All weights equal 1.
a)Group 1 fires at 3 Hz, group 2 at 1 Hz. What happens?
b)Group 1 fires at 3 Hz, group 2 at 2.5 Hz. What happens?
c) As in b, but make theta a function of the averaged rate. What happens?

Models of synaptic Plasticity

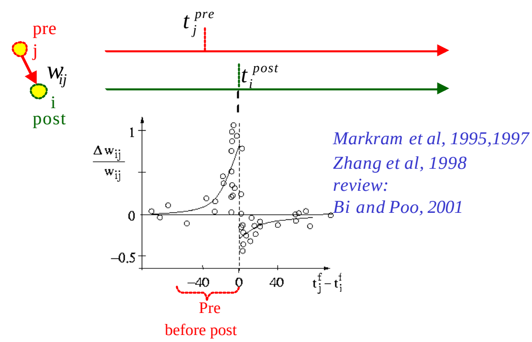
0. Introduction
   0.1 detour: short-term plasticity

√ I. Hebbian Learning (unsupervised): review of rate-based theory)

II. Spike-Timing Dependent theory

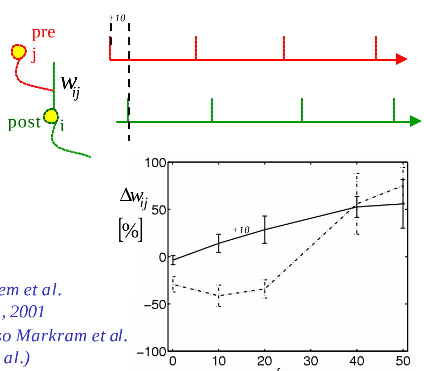
→ *-Experiments (basic)*
-Functional models
-Detailed models
-Minimal models
-Optimal models

Spike-time dependent learning window



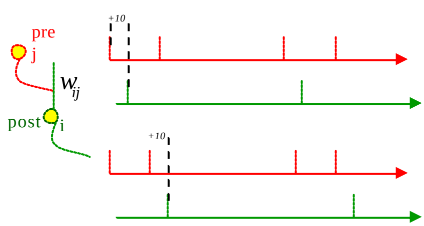
Markram et al, 1995,1997
Zhang et al, 1998
review:
Bi and Poo, 2001

Frequency dependence of STDP



Sjöstroem et al.
Neuron, 2001
(see also Markram et al.
Senn et al.)

Spike Triplets, quadruplets, …



Froemke and Dan, Nature, 2002
Wang, …, and Bi, Nat. Neuroscience, 2005

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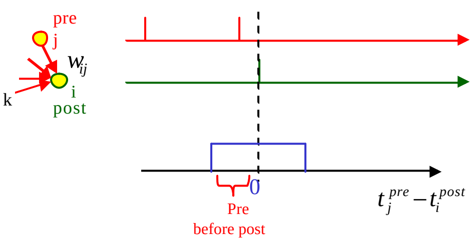
I. Hebbian Learning (unsupervised): review of rate-based theory)

II. Spike-Timing Dependent theory

- *-Experiments (basic)*
- *-Functional models*
- *-Detailed models*
- *-Minimal models*
- *-Optimal models*

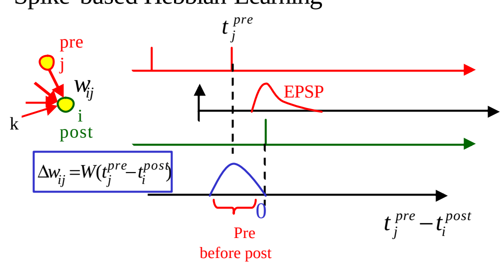
Spike based models

Spike-based Hebbian Learning



- local rule
- simultaneously active (correlations)

Spike-based Hebbian Learning

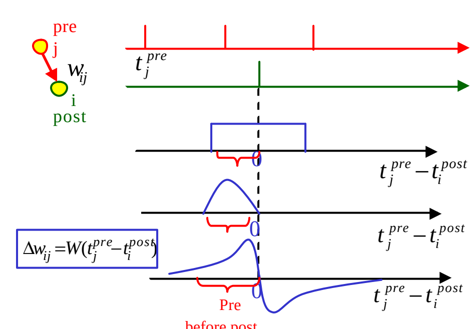


causal rule

'neuron j takes part in firing neuron'

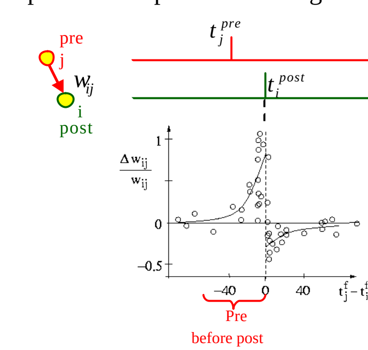
Hebb, 1949

Spike-time dependent learning window



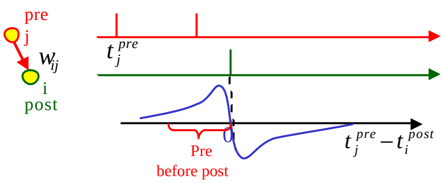
Temporal contrast filter (Gerstner et al. 1996)

Spike-time dependent learning window



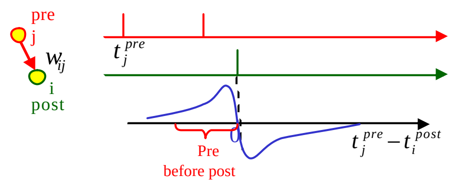
Markram et al, 1997
Zhang et al, 1998
review:
Bi and Poo, 2001

Spike-time dependent learning: phenomenol. model



$$\Delta w_{ij} = \sum_{t_j^{pre}, t_i^{post}} W(t_j^{pre} - t_i^{post}) + \sum_{t_j^{pre}} b^{pre} + \sum_{t_j^{pre}} b^{post} + b_o$$

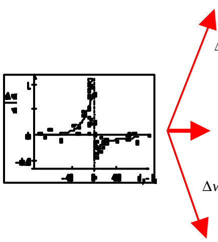
Spike-time dependent learning: voltage dependence



$$\Delta w_{ij} = \sum_{t_j^{pre}, t_i^{post}} W(t_j^{pre} - t_i^{post}) + \sum_{t_j^{pre}} b^{pre} + \sum_{t_j^{pre}} b^{post} + b_o$$

$$\Delta w_{ij} = \sum_{t_j^{pre}, t_i^{post}} W(u_i^{post}, t_j^{pre} - t_i^{post}) + \sum_{t_j^{pre}} b^{pre}(u_i^{post}) + \sum_{t_j^{pre}} b^{post}(u_i^{post}) + b_o(u_i^{post})$$

Which kind of model?



Descriptive Models

$$\Delta w = \begin{cases} A^{+} \exp\left(\frac{t_j - t_i}{\tau^{+}}\right), & \text{if } t_j < t_i \\ A^{-} \exp\left(-\frac{t_j - t_i}{\tau^{-}}\right), & \text{if } t_j > t_i \end{cases}$$

Gerstner et al. 1996
Song et al. 2000
Gütig et al. 2003

Mechanistic Models

Senn et al. 2000
Abarbanel et al. 2002
Shouval et al. 2000

$$\Delta w = g\left(a(t)\,\bar{b}(t) - a^{h}(t)\,b(t)\right)$$

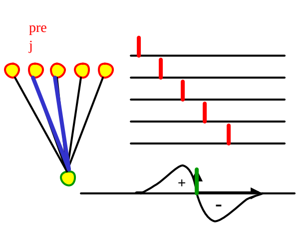
Optimal Models

Chechik, 2003
Hopfield/Brody, 2004
Dayan/London, 2004

Functional consequences of STDP

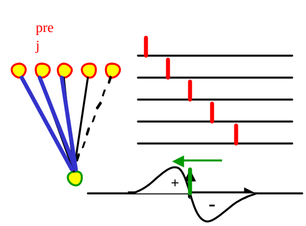
- **Learning to be fast**
- Learning spike patterns
- improving temporal precision

Derivative filter and prediction



Mehta et al. 2000,2002
Song et al. 2000

Derivative filter and prediction



Mehta et al. 2000,2002
Song et al. 2000

Postsynaptic firing shifts, becomes earlier

Models of synaptic Plasticity

0. Introduction
   0.1 detour: short-term plasticity

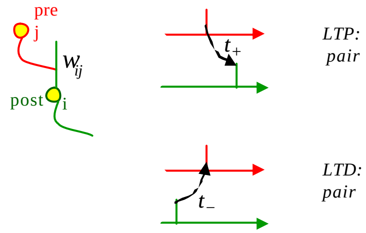
√ I. Hebbian Learning (unsupervised): review of rate-based theory)

II. Spike-Timing Dependent theory

- *-Experiments (basic)*
- *-Functional models*
- → *-Minimal models*
- *-Detailed models*
- *-Improved minimal model*

classical model of spike-based Hebbian Learning

Gerstner et al. 1996; Kempter et al. 1999

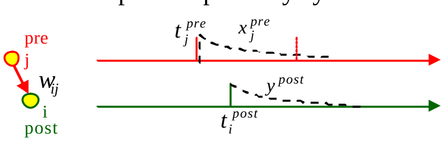


Minimal number of terms ? --- only 2 terms .

Voltage dependent? --- no voltage dependence.

weight dependent? --- possible.

Spike-time dependent plasticity by local variables

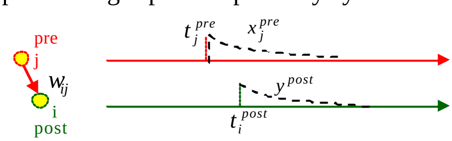


$$t_+ \frac{d}{dt} x_j^{pre} = -x_j^{pre} + d(t - t_j^{pre})$$ Update with pres. spike

$$t_- \frac{d}{dt} y^{post} = -y^{post} + d(t - t_i^{post})$$ Update with posts. spike

$$\frac{d}{dt} w_j = a(w_j) x_j^{pre} d(t - t_i^{post}) + a(w_j) y^{post} d(t - t_j^{pre})$$

Spike-timing dependent plasticity by local variables



$$t_+ \frac{d}{dt} x_j^{pre} = -x_j^{pre} + d(t - t_j^{pre})$$ Update with pres. spike

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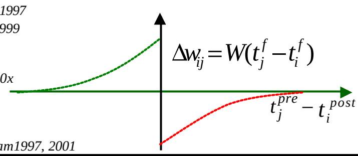
Gerstner et al. 1996; 1997
Kempter et al. 1998,1999
Abbott et al. 2000
Kistler et al. 2000
Van Rossum et al. 200x
Guetig et al 200x
Roberts 1999,2000
Karmarkar 200x
Senn Tsodyks Markram 1997, 2001



Which kind of model?

Descriptive Models

$$\Delta w = \begin{cases} A^+ \exp\left(\frac{t_j - t_i}{\tau^+}\right), \text{ if } t_j < t_i \\ A^- \exp\left(-\frac{t_j - t_i}{\tau^-}\right), \text{ if } t_j > t_i \end{cases}$$

Gerstner et al. 1996
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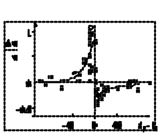

Mechanistic Models

Senn et al. 2000
Abarbanel et al. 2002
Shouval et al. 2000

$$\Delta w = g\left(a(t)\,\bar{b}(t) - a^h(t)\,b(t)\right)$$

Optimal Models

Chechik 2003
Hopfield/Brody 2004
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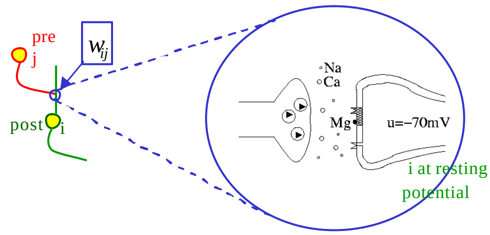
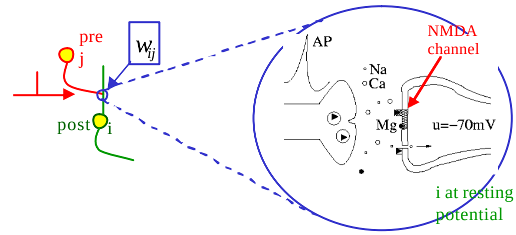
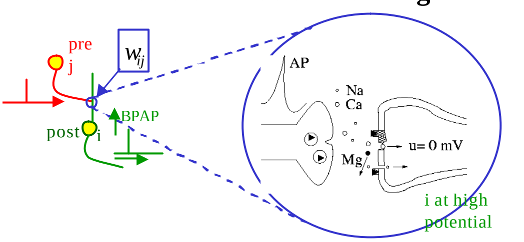
Detailed models of Hebbian learning



Detailed models of Hebbian learning



Detailed models of Hebbian learning

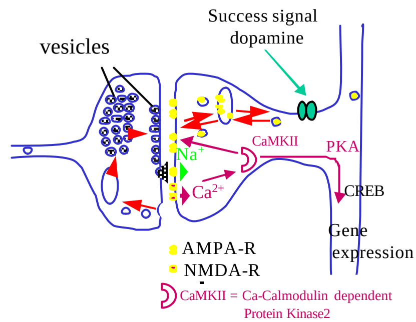


NMDA channel :

- glutamate binding after presynaptic spike
- unblocked after postsynaptic spike

→ **elementary correlation detector**

Changes in synaptic connections



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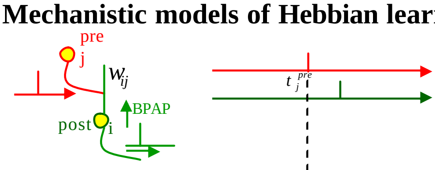
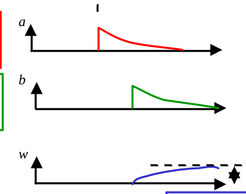
Mechanistic models of Hebbian learning



pre $$\frac{da}{dt} = -\frac{a}{t_a} + d(t - t_j^{pre})$$

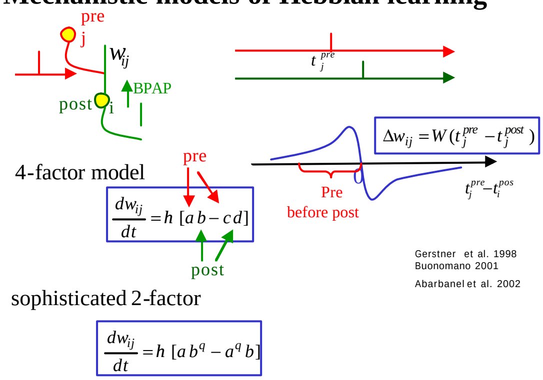
post $$\frac{db}{dt} = -\frac{b}{t_a} + d(t - t_i^{post})$$

$$\frac{dw_{ij}}{dt} = h\ a\ b$$

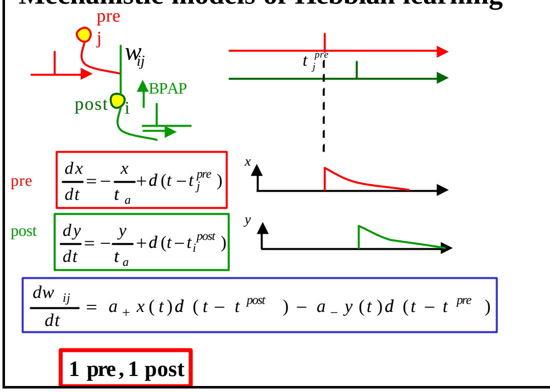


$$\Delta w_{ij} = W(t_j^{pre} - t_j^{post})$$

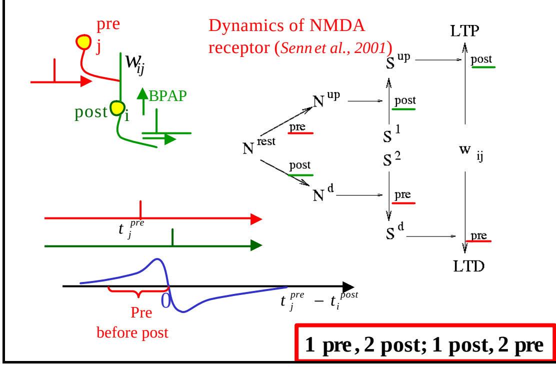
Mechanistic models of Hebbian learning



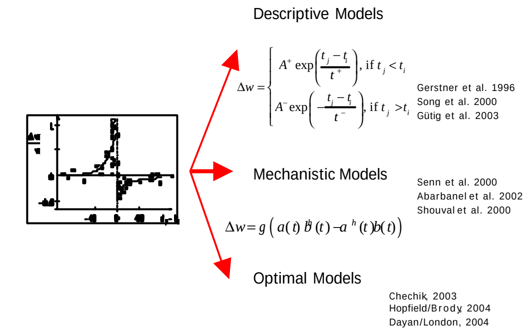
Mechanistic models of Hebbian learning



Mechanistic models of Hebbian learning



Which kind of model?



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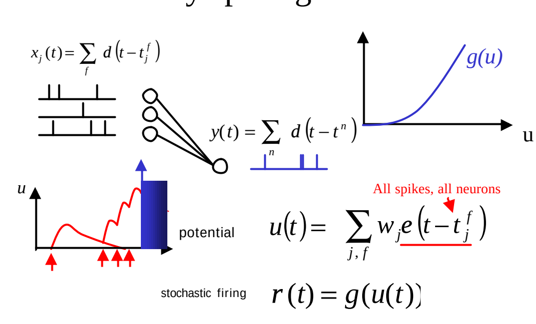
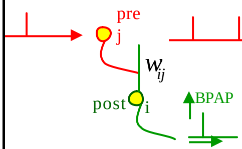
- *-Mechanistic models*
- → ***-A FRAMEWORK***
- *-Minimal model (2)*

Stochastically spiking neuron model



spike-based Hebbian Learning



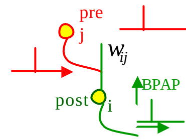
$u_j^{pre}(t)=\sum_f d(t-t_j^f)$

$u_i^{post}(t)=\begin{cases} u_i(t) & totalPSP \\ \sum_f d(t-t_i^f) & if\ BPAP \end{cases}$

$$\frac{d}{dt}w_{ij}=F(w_{ij};u_j^{pre},u_i^{post})$$

expand

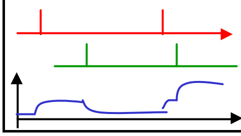
spike-based Hebbian Learning



$u_j^{pre}(t)=\sum_f d(t-t_j^f)$

$u_i^{post}(t)=\begin{cases} u_i(t) & totalPSP \\ \sum_f d(t-t_i^f) & if\ BPAP \end{cases}$

$$\frac{d}{dt}w_{ij}=b_0(w_{ij},u_i)+\sum_f b_1^{pre}(w_{ij},u_i,t-t_j^f)+\sum_f b_1^{post}(w_{ij},u_i,t-t_i^f)$$
$$+b_{ij}^{pair}(w_{ij},u_i,t-t_i^f,t-t_j^f)+triplets+...$$



Minimal number of terms ?

Voltage dependent?

weight dependent (saturation)?

Models of synaptic Plasticity

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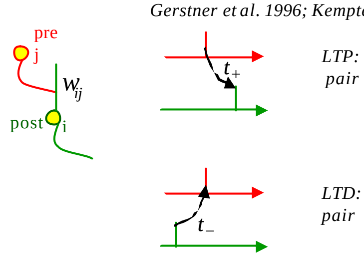
- ***-A FRAMEWORK***
- → *-A Minimal model*
- *-Optimal models*

classical model of spike-based Hebbian Learning

Gerstner et al. 1996; Kempter et al. 1999

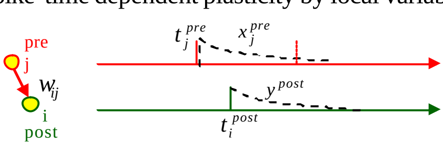


Minimal number of terms ? --- only 2 terms .

Voltage dependent? --- no voltage dependence.

weight dependent? --- possible.

Spike-time dependent plasticity by local variables

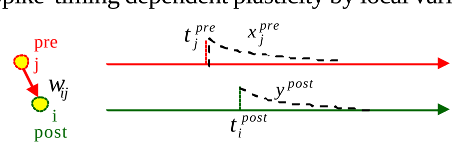


$t_+\frac{d}{dt}x_j^{pre}=-x_j^{pre}+d(t-t_j^{pre})$ Update with pres. spike

$t_-\frac{d}{dt}y^{post}=-y^{post}+d(t-t_i^{post})$ Update with posts. spike

$$\frac{d}{dt}w_j=a(w_j)x_j^{pre}d(t-t_i^{post})+a(w_j)y^{post}d(t-t_j^{pre})$$

Spike-timing dependent plasticity by local variables



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Gerstner et al. 1996; 1997
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Van Rossum et al. 200x
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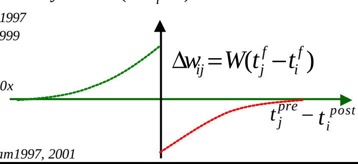
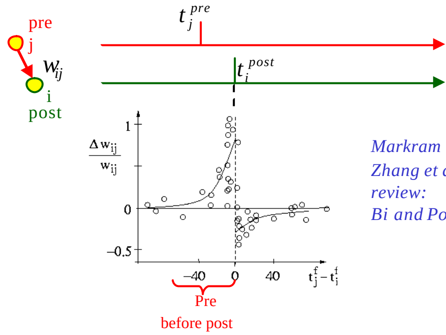
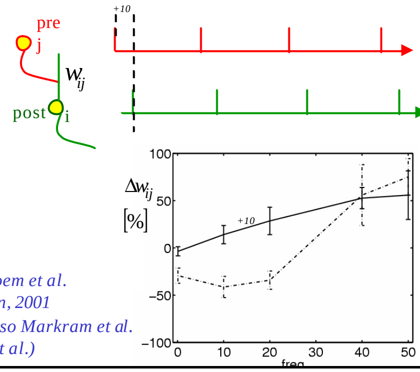


Spike-time dependent learning window



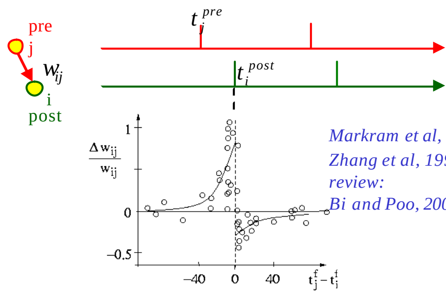
Markram et al, 1997
Zhang et al, 1998
review:
Bi and Poo, 2001

Frequency dependence of STDP



Sjöstroem et al.
Neuron, 2001
(see also Markram et al.
Senn et al.)

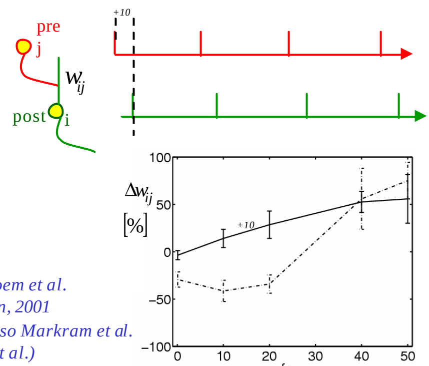
Spike-time dependent learning window



Markram et al, 1995,1997
Zhang et al, 1998
review:
Bi and Poo, 2001

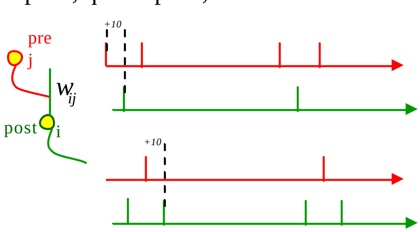
Pair-based STDP cannot account for frequency dependence

Pair-based STDP cannot account for frequency dependence



Sjöstroem et al.
Neuron, 2001
(see also Markram et al.
Senn et al.)

Spike Triplets, quadruplets, …



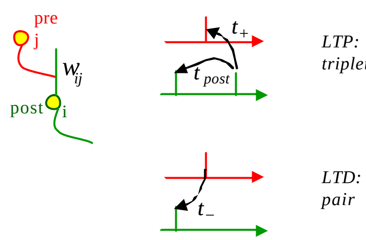
Experimental results show asymetry

Froemke and Dan, Nature, 2002
Wang, …, and Bi, Nat. Neuroscience, 2005

Pair-based STDP cannot account for asymetry

Minimal model of spike-based Hebbian Learning

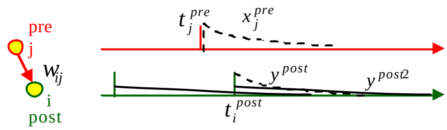
(Pfister and Gerstner, J. Neuroscience, 2006)



Minimal number of terms ? --- only 2 terms .

Voltage dependent? --- no voltage dependence.

Spike-time dependent plasticity by local variables



$$\tau_+ \frac{d}{dt} x_j^{pre} = -x_j^{pre} + d(t-t_j^{pre})$$ Update with pres. spike

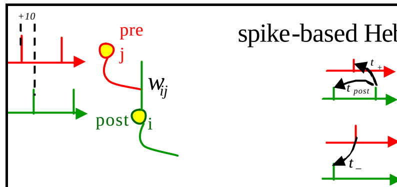
$$\tau_- \frac{d}{dt} y^{post} = -y^{post} + d(t-t_i^{post})$$ Update with posts. spike

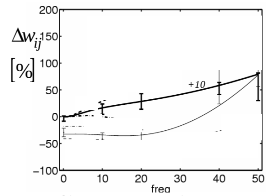
$$\tau^{post} \frac{d}{dt} y^{post2} = -y^{post2} + d(t-t_i^{post})$$

$$\frac{d}{dt} w_j = a_+(w_j) x_j^{pre} d(t-t_i^{post}) + a_-(w_j) y^{post} d(t-t_j^{pre})$$

$$+ a(w_j) x_j^{pre} y^{post2} d(t-t_i^{post})$$

spike-based Hebbian Learning





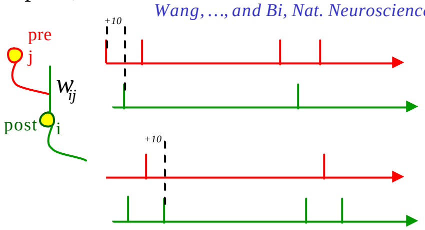
Sjöstroem experiment

Minimal model reproduces Frequency dependence of STDP

(Pfister and Gerstner, J. Neuroscience, 2006)

Spike Triplets, …

Wang, …, and Bi, Nat. Neuroscience, 2005

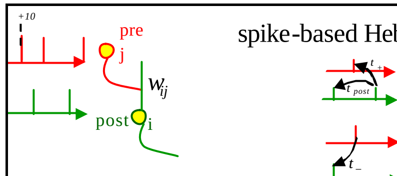


Our minimal models accounts for asymmetry

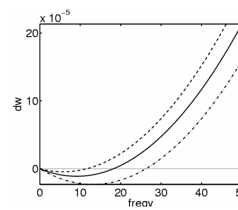
(Triplet experiment of Bi)

(Pfister and Gerstner, J. Neuroscience, 2006)

spike-based Hebbian Learning

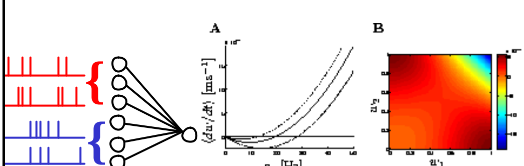


Poisson spike trains



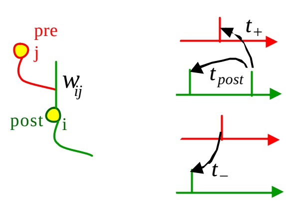
BCM property

Functional properties: receptive field development



(Pfister and Gerstner, J. Neuroscience, 2006)

Minimal model of spike-based Hebbian Learning



LTP: triplet

LTD: pair

With only 2 terms in expansion:
- BCM theory
- Sjöstroem experiment (frequency dependence of STDP)
- Bi's triplet experiment

(Pfister and Gerstner, J. Neuroscience, 2006)