



Neural Computation Theories of Learning

Brain-Inspired Computing



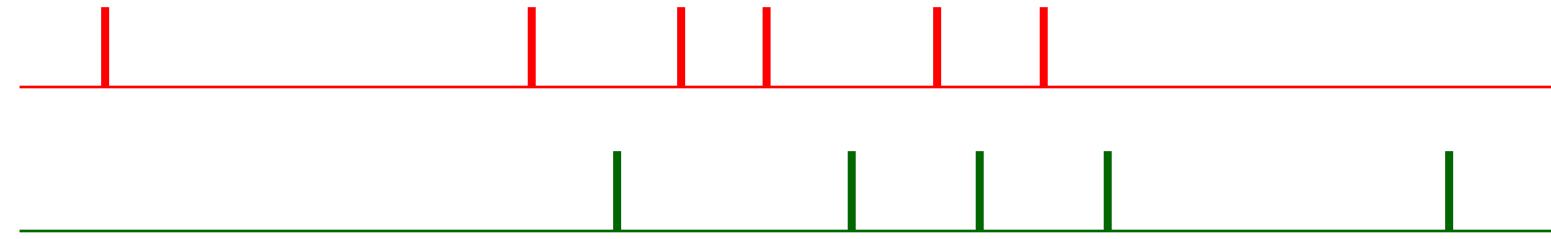
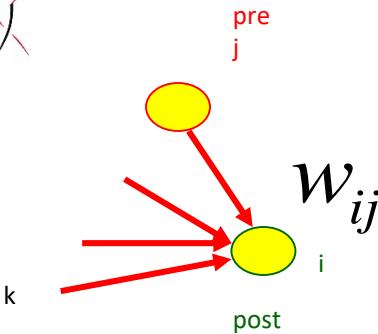
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Correlation-based learning in a firing rate formalism

- For the time being, we content ourselves with a description in terms of mean firing rates



Hebbian Learning: Rate Models



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



General formula for the change of the synaptic efficacy

2 important aspects of Hebb's plasticity

- **Locality**: the change of the synaptic efficacy can only depend on local variables, i.e., on information that is available at the site of the synapse, such as pre- and postsynaptic firing rate, and the actual value of the synaptic efficacy, but not on the activity of other neurons.

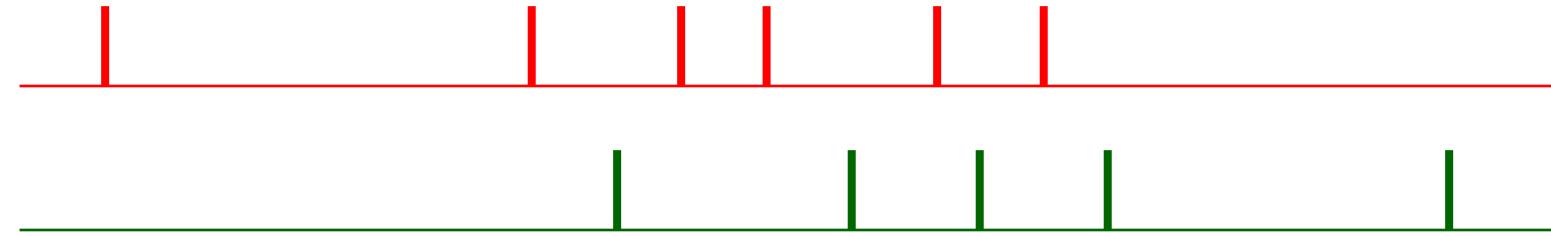
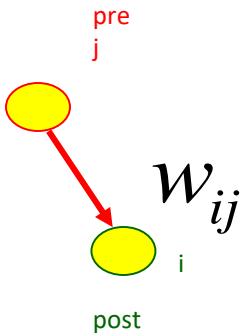
$$\frac{d}{dt} w_{ij} = F(w_{ij}; v_j^{\text{pre}}, v_i^{\text{post}})$$

A sufficiently “well-behaved” function, not yet determined

- **Joint activity**: implies that pre- and postsynaptic neurons have to be **active simultaneously** for a synaptic weight change to occur.
We can use this property to learn something about the function F



Rate based Hebbian Learning

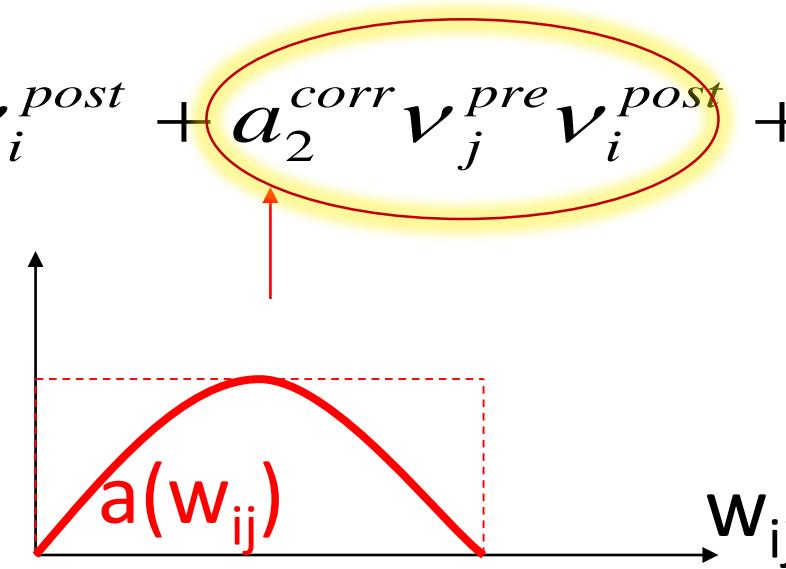


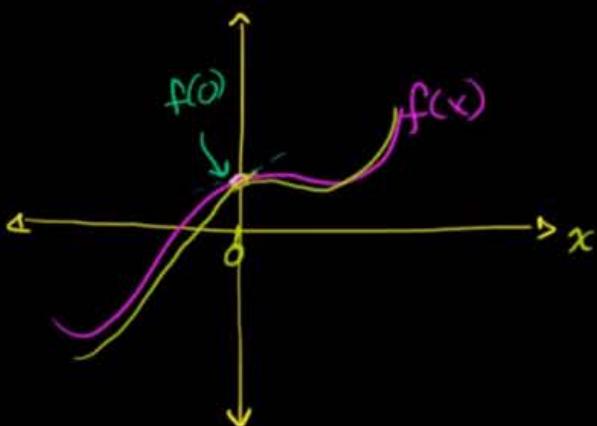
Blackboard

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

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

$$a = a(w_{ij})$$





$$f(0), f'(0), f''(0), f'''(0) \dots$$

$$P(0) = f(0) \quad P(x) = \underline{\underline{f(0)}} \quad (1)$$

$$P'(0) = f'(0) \quad * P(x) = \underline{\underline{f(0) + f'(0)x}} \quad (2)$$

$$P(0) = f(0) \checkmark$$

$$P'(x) = \underline{\underline{f'(0)}}$$

$$\underline{\underline{P'(0) = f'(0)}}$$

$$(3) P(x) = f(0) + f'(0)x + \frac{1}{2} f''(0)x^2$$

$$P(0) = f(0) \quad P'(x) = f'(0) + f''(0)x$$

$$P'(0) = f'(0) \quad P''(x) = f''(0)$$

$$P''(0) = f''(0)$$

$$P(x) = f(0) + f'(0)x + f''(0) \cdot \frac{1}{2!} x^2 + f'''(0) \cdot \frac{1}{3!} \frac{x^3}{2 \cdot 3 \cdot 1}$$

$$+ f''''(0) \cdot \frac{1}{4!} \frac{x^4}{3 \cdot 2 \cdot 1} + \dots + f^n(0) \cdot \frac{x^n}{n!}$$

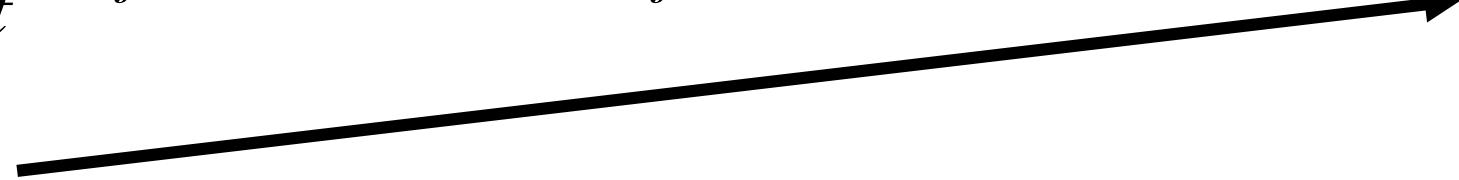
\uparrow
 $4! = 4 \cdot 3 \cdot 2 \cdot 1$

* MacLaurin Series



Hebbian Rule and Taylor series Expansion

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



This term implements the **AND** condition for joint activity.

- If the Taylor expansion had been stopped *before the bilinear term*, the learning rule would be called ‘**non-Hebbian**’, because pre- or postsynaptic activity alone induces a change of the synaptic efficacy and joint activity is irrelevant.

Therefore, a Hebbian learning rule needs either the **bilinear term**

$$a_2^{corr} v_j^{pre} v_i^{post}$$

or a **higher-order term** such as

$$a_3^{corr} v_j^2 v_i$$

that *involves the activity of both pre- and postsynaptic neurons.*



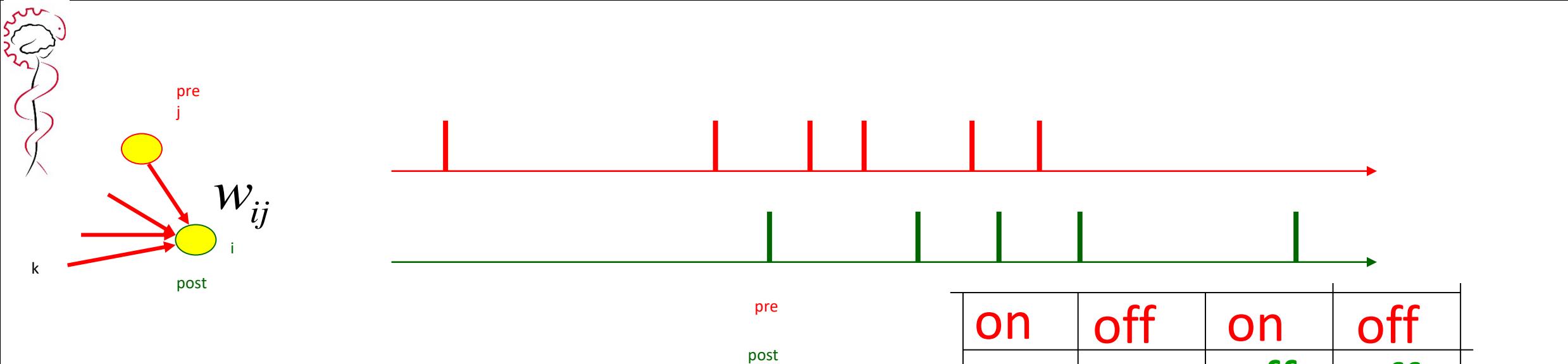
The simplest choice for a Hebbian learning rule
within the Taylor expansion

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

Fix $a_2^{corr} = c > 0$

And then set all other terms to zero

$$\frac{d}{dt} w_{ij} = a_2^{corr} v_j^{pre} v_i^{post} = c v_j^{pre} v_i^{post}$$



$$\frac{d}{dt} w_{ij} = a_2^{corr} v_j^{pre} v_i^{post}$$

pre
post

	on	off	on	off
on	on	off	off	
+	0	0	0	



The coefficient a_2^{corr} depends on w_{ij}

- This dependence can be used to limit the growth of weights at a maximum value w_{max}
- Two standard choices of weight-dependence

'hard bound'

$$a_2^{corr} = \gamma$$

$$0 < \gamma < w_{max}$$

weight growth stops abruptly if γ reaches the upper bound w_{max}

'soft bound'

$$a_2^{corr}(w_{ij}) = \gamma(w_{max} - w_{ij})^\beta$$

a change tends to zero as its w_{ij} approaches its maximum value

where γ and β are positive constants (typically $\beta=1$)



No possibility for a decrease of synaptic weights

In a system where synapses can only be strengthened, all efficacies will eventually saturate at their upper maximum value - **how do we solve this?**

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

IF $\left\{ \begin{array}{l} a_2^{corr}(w_{ij}) = \gamma(w_{\max} - w_{ij})^\beta \\ w_{\max} = \beta = 1 \\ a_0(w_{ij}) = -\gamma_0 w_{ij} \end{array} \right.$ *soft bound*

In the absence of stimulation, synapses spontaneously decay back to zero

$$\frac{d}{dt} w_{ij} = \gamma(1 - w_{ij})v_i v_j - \gamma_0 w_{ij}$$



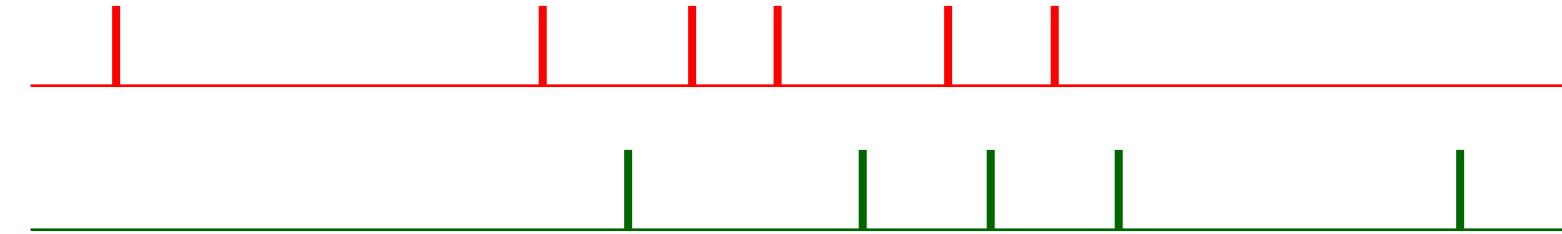
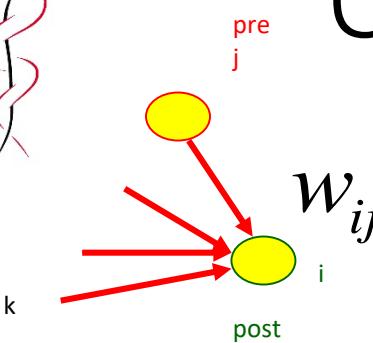
Covariance Rule (Sejnowksi, 1977)

$$\frac{d}{dt} w_{ij} = \gamma(v_i - \langle v_i \rangle)(v_j - \langle v_j \rangle)$$

- Where $\langle v \rangle$ is the average value of the firing rate
- This rule is based on the idea that the rates v_i and v_j fluctuate around mean values $\langle v_i \rangle, \langle v_j \rangle$ that are taken as running averages over the recent firing history



Other Rate based-Hebbian Learning Schemes



- 1) Standard Hebb rule
- 2) Hebb with decay
- 3) Hebb with postsynaptic LTP/LTD threshold
- 4) Covariance rule.

$$\frac{d}{dt} w_{ij} = a_2^{\text{corr}} v_j^{\text{pre}} v_i^{\text{post}}$$

$$\frac{d}{dt} w_{ij} = a_2^{\text{corr}} v_j^{\text{pre}} v_i^{\text{post}} - c$$

$$\boxed{\frac{d}{dt} w_{ij} = a_2^{\text{corr}} v_j^{\text{pre}} (v_i^{\text{post}} - \vartheta)}$$

$$\frac{d}{dt} w_{ij} = a_2^{\text{corr}} (v_j^{\text{pre}} - \vartheta)(v_i^{\text{post}} - \vartheta)$$

pre
post

on	off	on	off
on	on	off	off
+	0	0	0
+	-	-	-
+	0	-	0
+	-	-	+



Oja's rule (Oja, 1982)

$$\frac{d}{dt} w_{ij} = \gamma(v_i v_j - w_{ij} v_i^2)$$

Hebbian Term

Oja's rule converges asymptotically to synaptic weights that are normalized to

$$\sum_j w_{ij}^2 = 1$$

Why squaring
the weights?

The sum implies competition between the synapses that make connections to the same postsynaptic neuron, i.e., if some weights grow, others must decrease

Introducing a nonzero quadratic term
 $a_2^{post} = -\gamma w_{ij}$



BCM rule (Bienenstock-Cooper-Munro, 1982)

$$\frac{d}{dt} w_{ij} = \phi(v_i - v_\theta) v_j$$

- Nonlinear function φ (general)
- Reference rate v_θ

We allow $v_\theta = f(< v_i >)$

so as to be a function of the average firing rate of the postsynaptic neurons

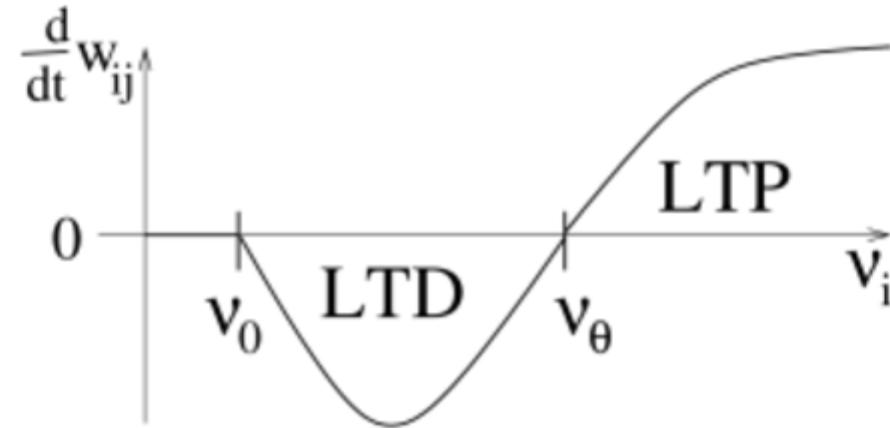
- The BCM rule leads to input selectivity and has been successfully used to describe the **development** of receptive fields

BCM rule: Schematics

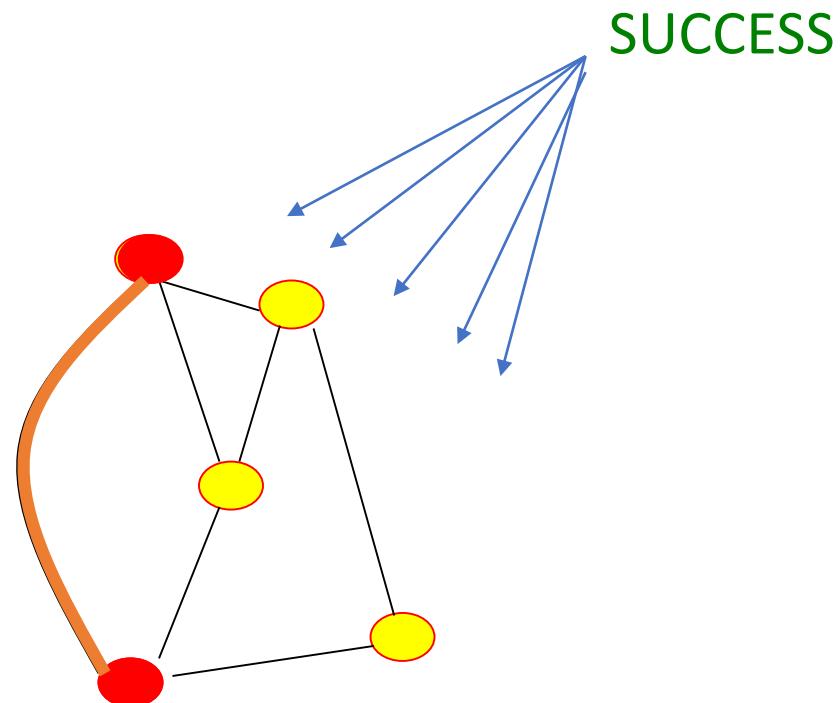
$$\frac{d}{dt} w_{ij} = \phi(v_i - v_\theta)v_j$$

$$\phi = \eta v_i$$

For stationary input, it can be shown that the postsynaptic rate v_i under the BCM-rule has a fixed point at v_θ which is unstable. To avoid that the postsynaptic firing rate blows up or decays to zero, it is necessary to turn v_θ into an **adaptive variable** which depends on the average rate $\langle v_i \rangle$



BCM rule. Synaptic plasticity is characterized by two thresholds for the postsynaptic activity. Below v_0 no synaptic modification occurs, between v_0 and v_θ synapses are depressed, and for postsynaptic firing rates beyond v_θ synaptic potentiation can be observed. Often v_0 is set to zero.



Reinforcement Learning = reward + Hebb

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

↑
local global

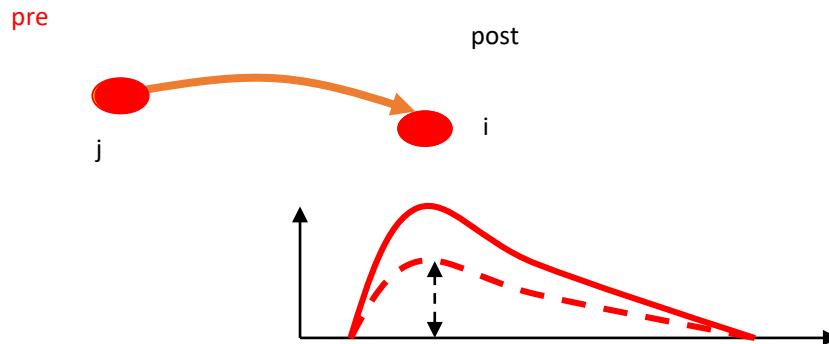


Unsupervised vs reinforcement Learning

LTP/LTD/Hebb

Theoretical concept

- passive changes
- exploit statistical correlations



Functionality

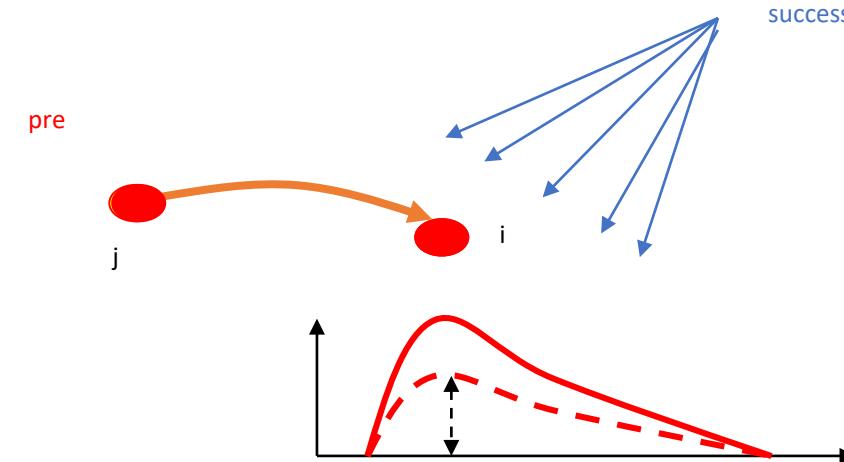
- useful for development

(wiring for receptive fields)

Reinforcement Learning

Theoretical concept

- conditioned changes
- maximize reward



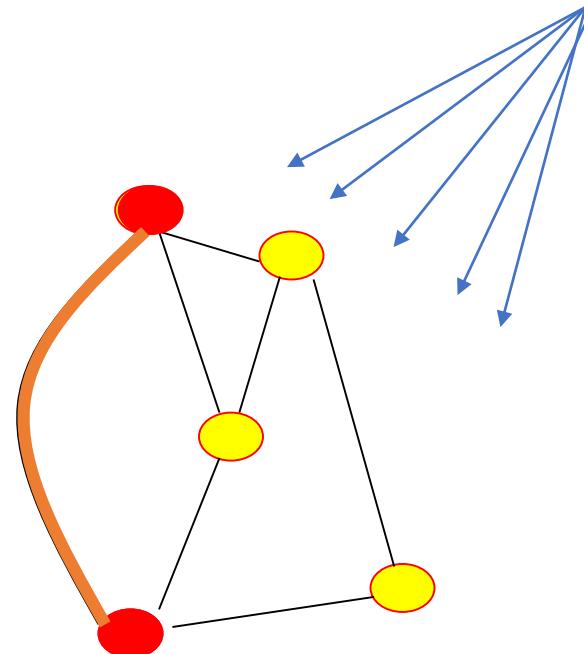
Functionality

- useful for learning a new behavior



Modulated Hebbian Learning

= neuromodulator + Hebb



Neuromodulator: Interestingness, surprise;
attention; novelty

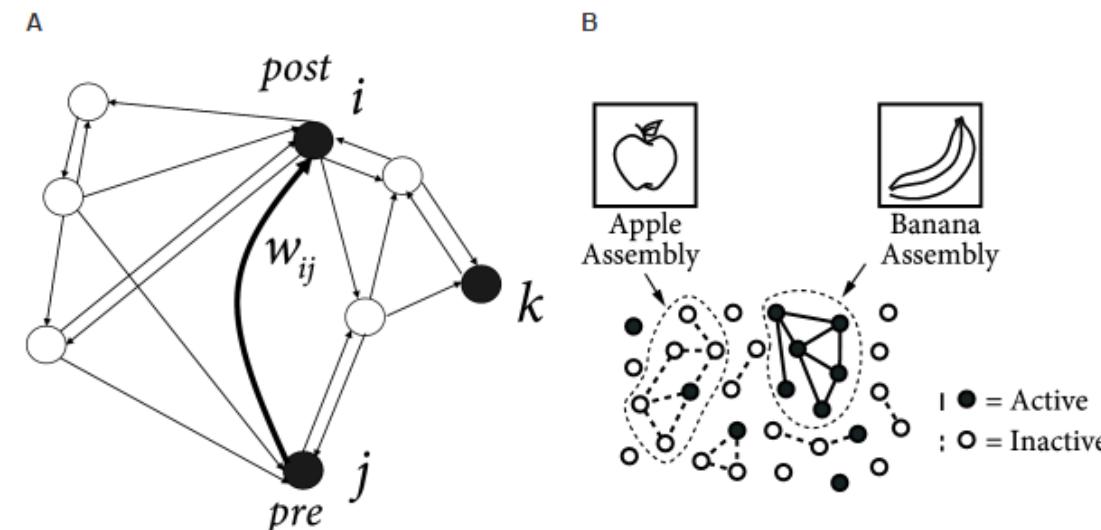
$$\Delta w_{ij} \propto F(\text{pre}, \text{post}, \text{MOD})$$





Hebb rule: Correlation based Learning

- Hebbian learning is **unsupervised**
 - There is no notion of ‘good’ or ‘bad’ changes of a synapse
- Synaptic changes happen **whenever there is joint activity of pre- and postsynaptic neurons**
 - Firing patterns may reflect sensory stimulation or ongoing brain activity
 - There is no feedback signal from a ‘supervisor’ or from the environment



Hebbian learning. A. The change of a synaptic weight w_{ij} depends on the state of the presynaptic neuron *j* and the postsynaptic neuron *i* and the present efficacy w_{ij} , but not on the state of other neurons *k*. B. Hebbian learning strengthens the connectivity within assemblies of neurons that fire together, e.g. during the perception of banana. Schematic figure.



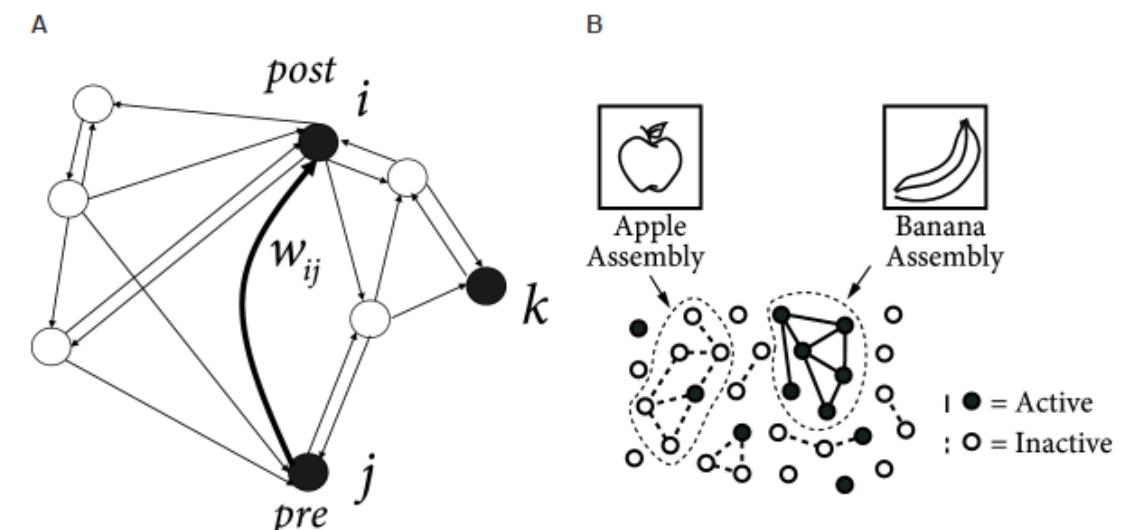
Hebb rule: Correlation based Learning

When an axon of cell A is near enough to excite 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.

Modifications of the synaptic transmission efficacy are driven by correlations in the firing activity of pre- and postsynaptic neurons

Neurons that 'fire together, wire together'

Correlation-based learning is now generally called *Hebbian learning*



Hebbian learning. A. The change of a synaptic weight w_{ij} depends on the state of the presynaptic neuron j and the postsynaptic neuron i and the present efficacy w_{ij} , but not on the state of other neurons k . B. Hebbian learning strengthens the connectivity within assemblies of neurons that fire together, e.g. during the perception of banana. Schematic figure.

2 types of Hebbian Learning Rules

- ~~Rate-based~~
 - ~~Correlation-based learning~~
- Spike-based



The Marshmallow test

A study on delayed gratification in the late **1960s** and early **1970s** (led by psychologist Walter Mischel, then a professor at Stanford University)

1988: "preschool children who delayed gratification longer in the self-imposed delay paradigm, were described more than 10 years later by their parents as adolescents who were significantly more competent"

1990: the ability to delay gratification also correlated with higher SAT scores

2006: The ability to delay in order to receive a cookie (at age 4) relates to the reaction time on a Go/no go task

2011: brain imaging study of a sample from the original Stanford participants when they reached mid-life showed key differences between those with high delay times and those with low delay times in two areas: the prefrontal cortex (more active in high delayers) and the ventral striatum (an area linked to addictions) when they were trying to control their responses to alluring temptations

Postsynaptic Neuron Activity

Arrival of a presynaptic spike at a synapse triggers an input signal $i(t)$ into the postsynaptic neuron

This signal corresponds to the synaptic electric current flowing into the biological neuron

In a simple model the time course of $i(t)$ can be described by the exponential function

$$i(t) = \int_0^{\infty} S_j(s-t) \exp(-s/\tau_s) \, ds$$

where τ_s is the synaptic time constant and $S_j(t)$ denotes a presynaptic spike train

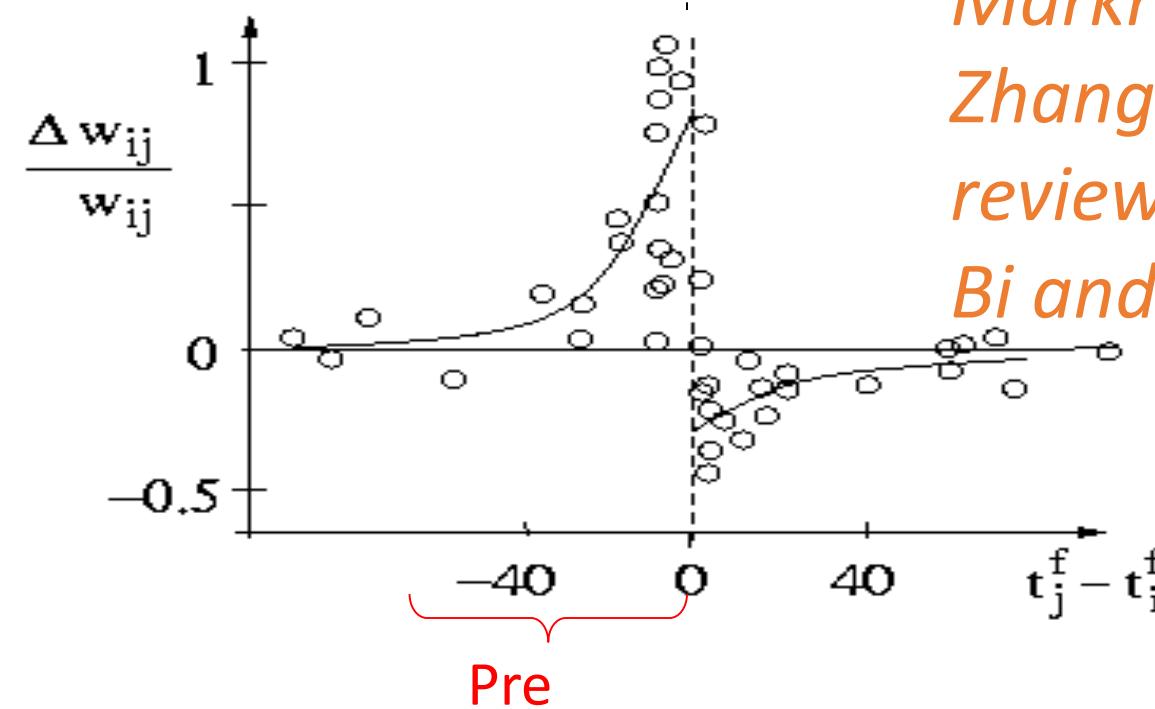
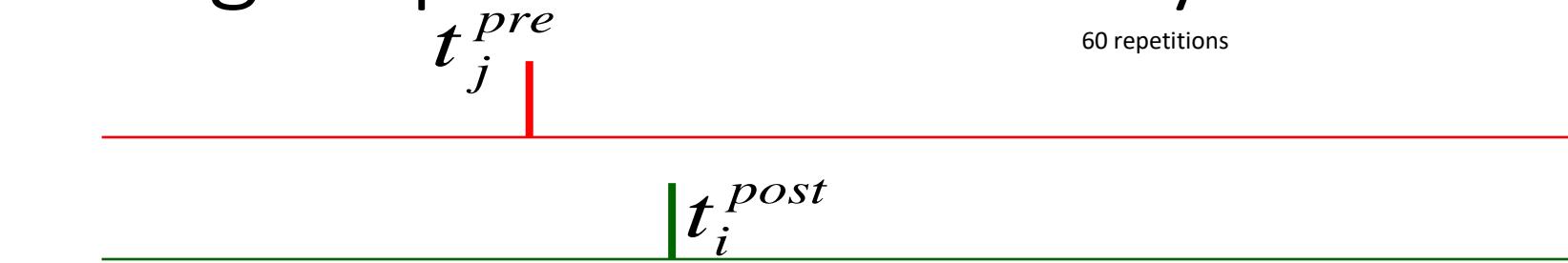
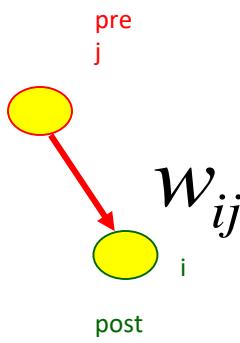
Spike-Timing-Dependent Plasticity (STDP)

- The resulting change in the synaptic efficacy Δw_{ij} after several repetitions of the experiment is a function of the **difference $t_j^f - t_i^f$** , between the firing times of pre- and postsynaptic neuron
- The direction of the change depends critically, on the **relative timing** of pre- and postsynaptic spikes on a millisecond time-scale
- The synapse is strengthened if the presynaptic spike occurs shortly before the postsynaptic neuron fires, but the synapse is weakened if the sequence of spikes is reversed

This observation is indeed in agreement with Hebb's postulate because presynaptic neurons that are active slightly before the postsynaptic neuron are those which 'take part in firing it' whereas those that fire later obviously did not contribute to the postsynaptic action potential



Spike Timing Dependent Plasticity



before post

Markram et al, 1995,1997

Zhang et al, 1998

review:

Bi and Poo, 2001

Mathematical Formalism of Spike-Timing Dependent Plasticity

$$\begin{aligned} \frac{d}{dt} w_{ij}(t) = & S_j(t) \left[a_1^{\text{pre}} + \int_0^\infty A_-(w_{ij}) W_-(s) S_i(t-s) ds \right] \\ & + S_i(t) \left[a_1^{\text{post}} + \int_0^\infty A_+(w_{ij}) W_+(s) S_j(t-s) ds \right] \end{aligned}$$



The main idea of STDP

- Each spike leaves a trace

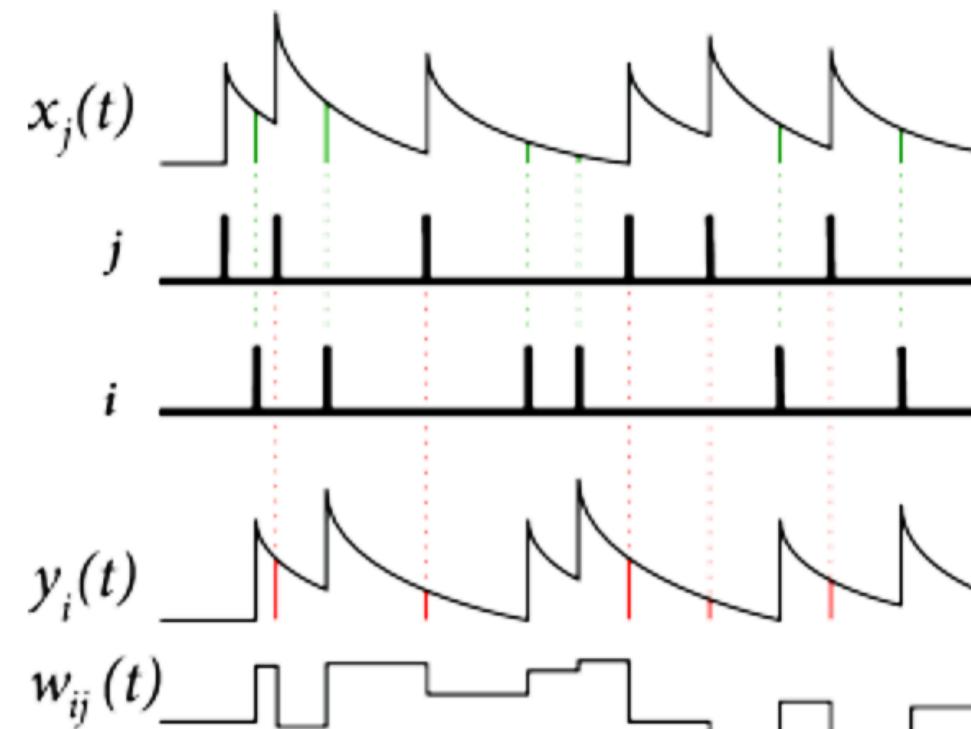
$$\frac{d}{dt} x_j = -\frac{x_j}{\tau_+} + \sum_f \delta(t - t_j^f)$$

$$\frac{d}{dt} y_i = -\frac{y_i}{\tau_-} + \sum_f \delta(t - t_i^f)$$

- The trace variable is increased by an amount of **one** at the moment of a presynaptic spike and **decreases exponentially** with time constant τ afterwards
- The traces x_j and y_i play an important role during the weight update
 - At the moment of a presynaptic spike, a decrease of the weight is induced proportional to the value of the postsynaptic trace y_i
 - Analogously, at the moment of a postsynaptic spike, potentiation of the weight occurs, which is proportional to the trace x_j left by a previous presynaptic spike



Pair-based STDP



Implementation of pair-based plasticity by local variables: The presynaptic spikes leave a trace $x_j(t)$, postsynaptic spikes a trace $y_i(t)$. The weight increases at the moment of a postsynaptic spike proportional to the momentary value of the trace $x_j(t)$ left by previous presynaptic spike arrivals. Analogously we get depression for post-before-pre pairings at the moment of a presynaptic spike (vertical dashed lines highlight moments of spike firing); from Morrison et al.

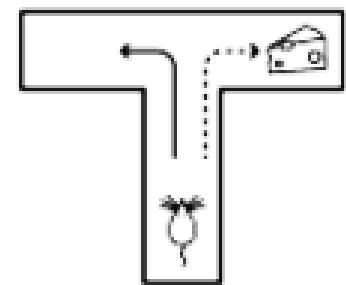
But

Unsupervised Hebbian learning
is of limited use for
behavioral learning
because
it makes no distinction between
actions that do and
those that do not lead to a successful outcome

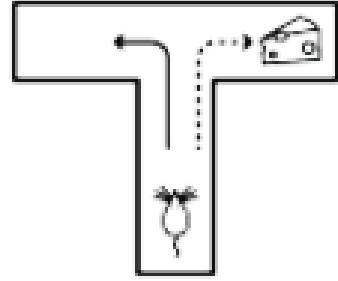


Reward-based Learning

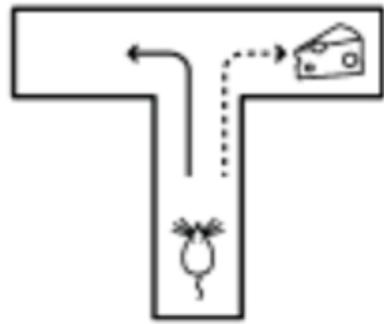
- Conditioning experiments: animals learn complex action sequences if the desired behavior is rewarded, e.g.,
 - In a simple T-maze an animal has to decide at the bifurcation point whether to turn left or right.
 - In each of several trials, the same arm of the maze is baited with a piece of cheese that is hidden in a hole in the floor and therefore neither visible nor smellable.
 - After a few trials the animal has learned to reliably turn into the baited arm of the maze.



How?



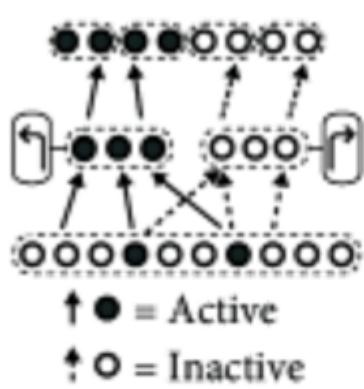
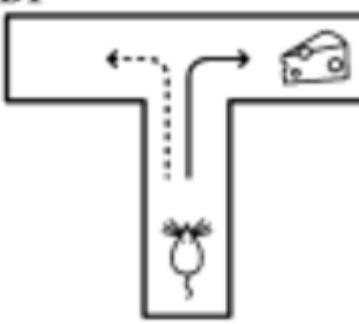
- The momentary sensory state at the bifurcation point is represented by activity in the sensory cortices and, possibly, in hippocampal place cells.
- The action plan (e.g., ‘turn left’) is represented by groups of cells in several brain areas likely to include striatum, whereas the final control of muscle activity involves areas in motor cortex.
- During the realization of the action plan ‘turn left’ several groups of neurons are jointly active
- Unsupervised Hebbian learning strengthens the connections between the jointly active cells so that, at the next trial, it becomes more likely that the animal takes the same decision again.
- However, turning left does not lead to success if the cheese is hidden in the other branch of the maze.

A**A1****A2**

Motor cortex

Striatum

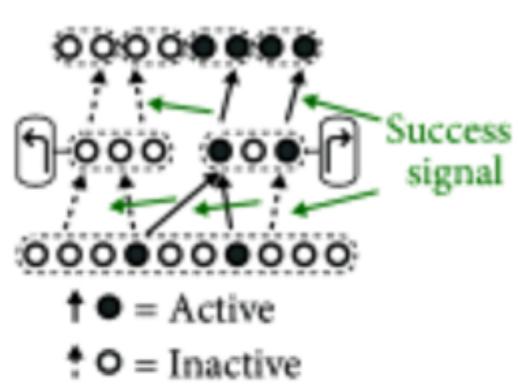
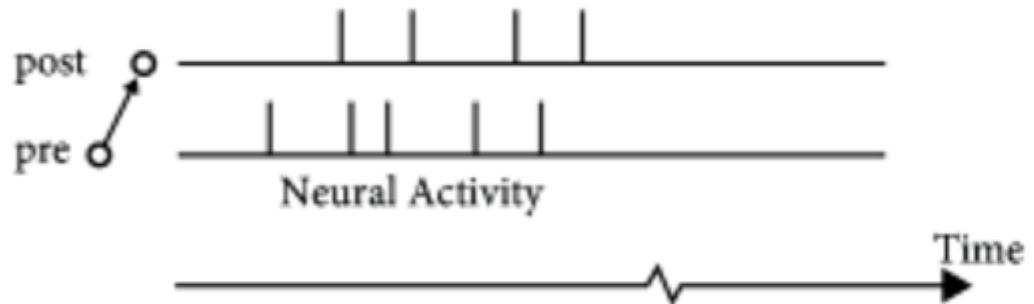
Sensory cortex

**B****B1****B2**

Motor cortex

Striatum

Sensory cortex

**A3****B3**

Hebbian learning versus reward-modulated Hebbian learning in a T-maze decision task (schematic).

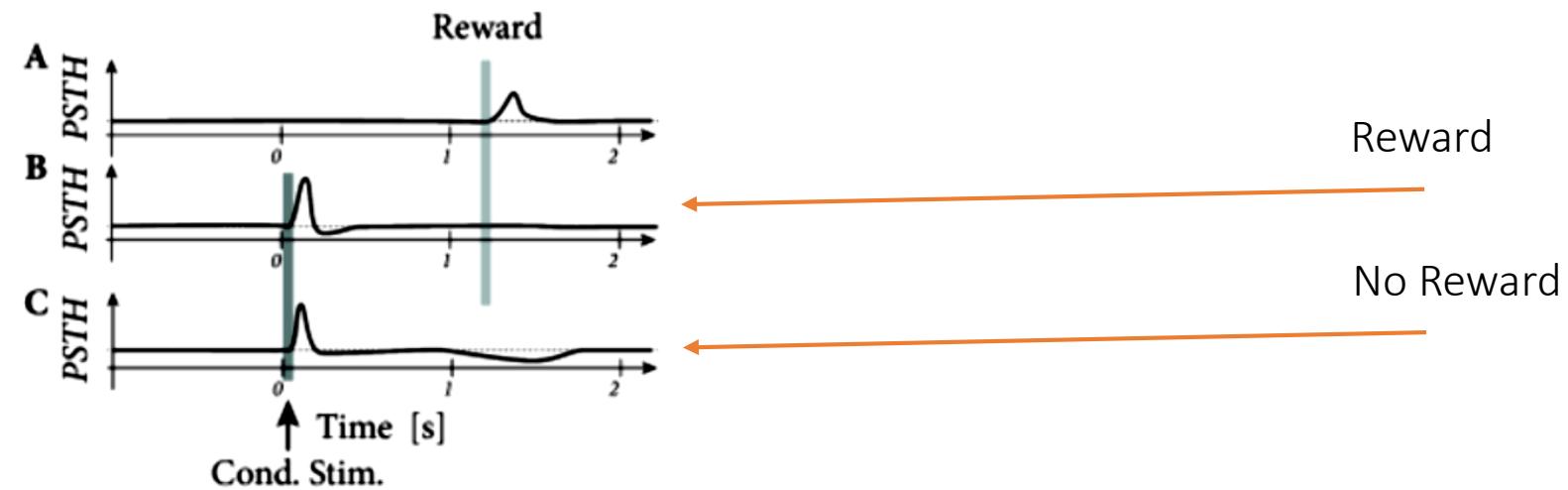
The momentary sensory state of the animal is encoded by the layer of sensory cortex neurons; the action plan by a set of striatal neurons; and the motor output by neurons in motor cortex. **A.** Hebbian learning. Joint activity of neurons in sensory, striatal, and motor areas strengthens the links between the active neurons, despite the fact that turning left does not lead to success. **B.** Reward-modulated Hebbian learning. Joint activity of pre-and postsynaptic neurons strengthens connections only if, within a delay of a few seconds, a success signal is broadcast in the brain.

Going beyond unsupervised Hebbian Learning rules

- Rules of synaptic plasticity have to take into account the success of an action.
 - Neuromodulators such as dopamine are ideal candidates to broadcast a success signal in the brain, where success can loosely be defined as '**reward minus expected reward**'.
- The success often comes with a delay of a few seconds after an action has been taken.
 - Thus, the brain needs to somehow store a short-term memory of past actions.
 - A suitable location for such a memory are the synapses themselves.

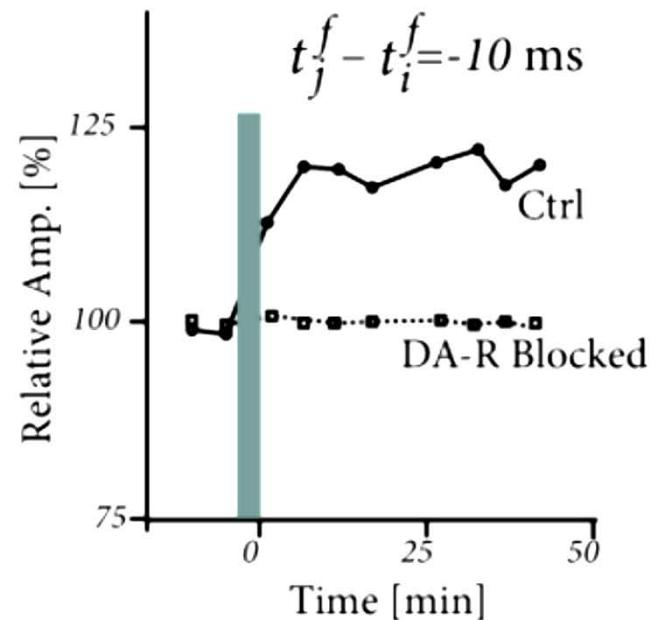


Reward-based Learning and dopaminergic neurons

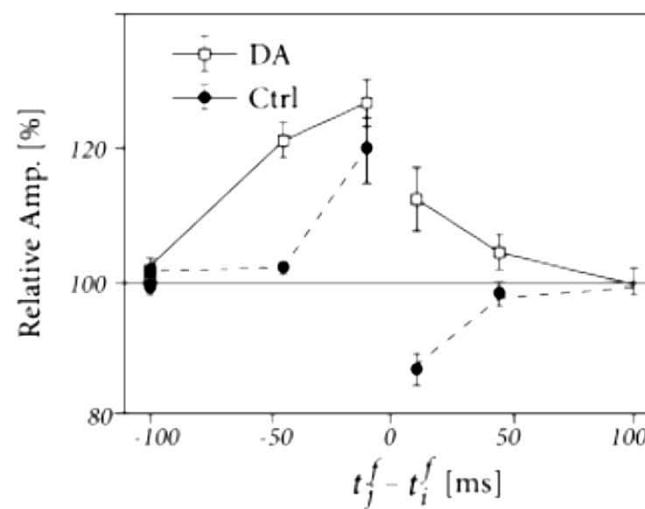


Dopamine encodes reward minus expected reward. **A.** The activity of dopaminergic neurons (PSTH) increases at the moment when a reward R occurs. **B.** If a conditioning stimulus such as a tone beep or a light reliably occurs one second before the reward, the same neurons no longer respond to the reward but after the CS that predicts the reward. **C** If the reward is predicted by the CS but not given, the PSTH exhibits a dip below the baseline (dashed lines) at the moment when the reward is expected. Schematic figure summarizing data from Schultz et al.

Dopamine-modulated Hebbian learning



An STDP protocol normally gives rise to long-term potentiation
However, if **dopamine receptors are blocked**, no change occurs



The STDP window in a control situation (dashed line and filled data points) changes if **additional extracellular dopamine is present** (solid lines, large open squares)

Math: Reward-modulated Hebbian learning

$$\tau_e \frac{d}{dt} e_{ij} = -e_{ij} + H(\text{pre}_j, \text{post}_i)$$

Synaptic eligibility trace

If the joint activity of pre- and postsynaptic neuron stops, the Hebbian term H vanishes and the eligibility trace decays back to zero with a time constant τ_e

$$\frac{d}{dt} w_{ij} = M \cdot H(\text{pre}_j, \text{post}_i) e_{ij}$$

Weight change

The update of synaptic weights requires a nonzero-elibility trace and a neuromodulatory success signal M

While in standard Hebbian learning synaptic plasticity depends on two factors (i.e. pre- and postsynaptic activity), weight changes now depend on three factors, i.e., the two Hebbian factors and the neuromodulator M

$$M(t) = R(t) - \langle R \rangle$$

Modulator signal $M =$
= reward – expected reward

About the Reward signal

- The expectation $\langle R \rangle$ is empirically estimated as a running average
- The time constant τ_e is typically chosen in the range of one second, so as to bridge the delay between action choice and final reward signal.



Learning with R-STDP



- Suppose a table tennis player plays a serve or a piano player a rapid scale
- In both cases the executed movements are
 - **extremely rapid** (A rapid scale on a piano means touching about 10 different keys per second; the complex gliding movement to give the ball its spin takes less than a second)
 - have been **practiced** many times, and
 - are often performed in '**open loop**' mode, i.e., without visual feedback during the movement.
- There is, however, **feedback** after some delay which signals the success (or failure) of the performed action, e.g. the ball went off the table or the scale contained a wrong note
- It is likely that for such fast movements **spike timing plays an important role**
- Motor cortex is involved in the control of limb movements
- Experimental data from the arm area of primary motor cortex indicates that **populations of neurons encode the direction of hand motion** during reaching movements in three-dimensional space
 - Each neuron i has a **preferred direction of motion** represented as a vector d_i .
 - The vectors of different neurons are added up with a **weighting function proportional to the cells firing rate**.
- For the rapid movements of less than one second, a single neuron is expected to emit at most a few spikes. Therefore a desired trajectory can be represented as a target **spatio-temporal spike pattern**

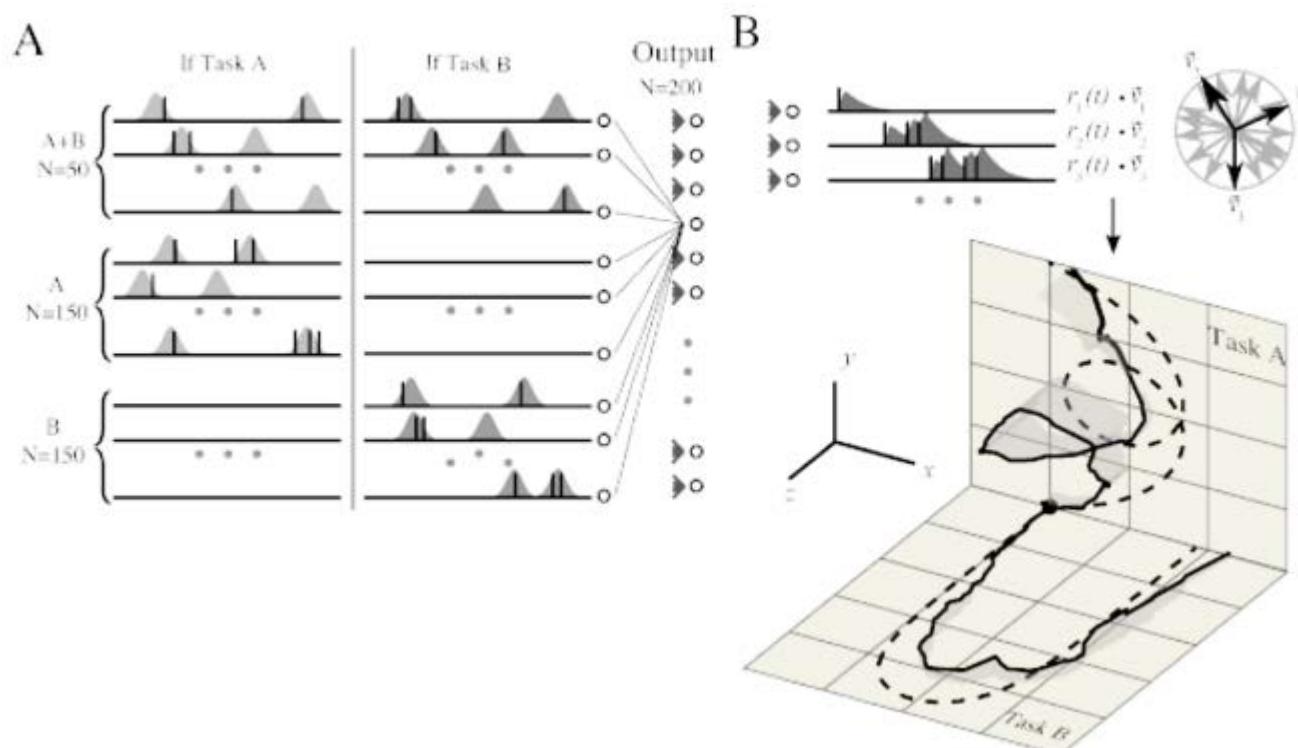
Learning with R-STDP

- Model neurons in motor cortex receive spike input from neurons in sensory areas that represent, e.g., the vertical movement of the ball that is launched at the beginning of the serve, as well as the intention of the player
- During practice sessions, the aim is to associate the spatio-temporal spike pattern in the input layer with the target spike pattern in the layer of motor cortex neurons while the only **feedback is the success signal available at the end of the movement**
- A two-layer network of spiking neurons can learn this task, if synaptic connections use a reward-modulated STDP rule

Reward

- It is important that the global neuromodulatory signal provided at the end of each trial, is not the raw reward, but success defined as ‘reward - expected’ reward
- If a single task has to be learned, the expected reward can be estimated from the running average over past trials
- However, if several trajectories (e.g., two different serves or two different scales) have to be learned in parallel, then the expected reward needs to be estimated separately for each trajectory

Learning with R-STDP



A. The input consists of 350 spike trains with a temporal precision of 20ms. 50 unspecific neurons fired for both tasks, whereas half of the other neurons fired only for task A or task B. The output consists of 200 spiking model neurons.

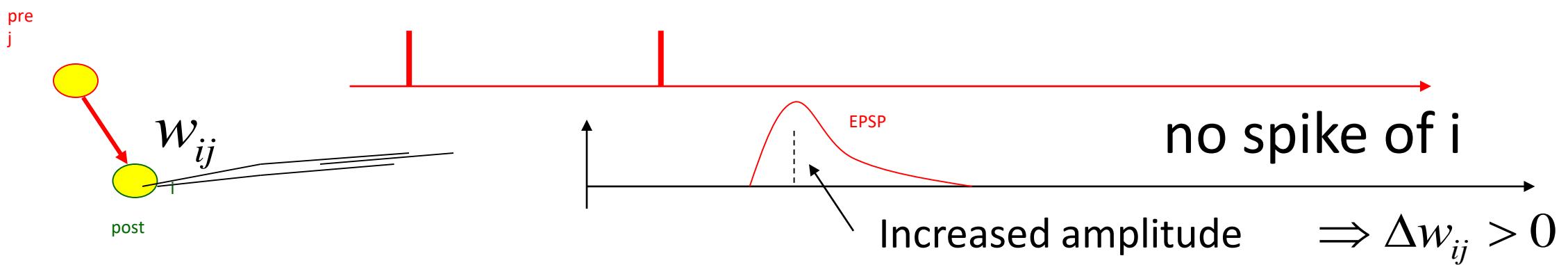
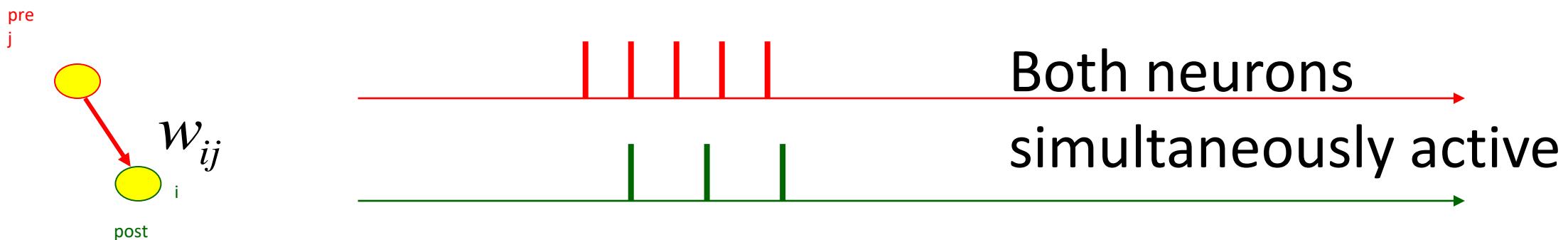
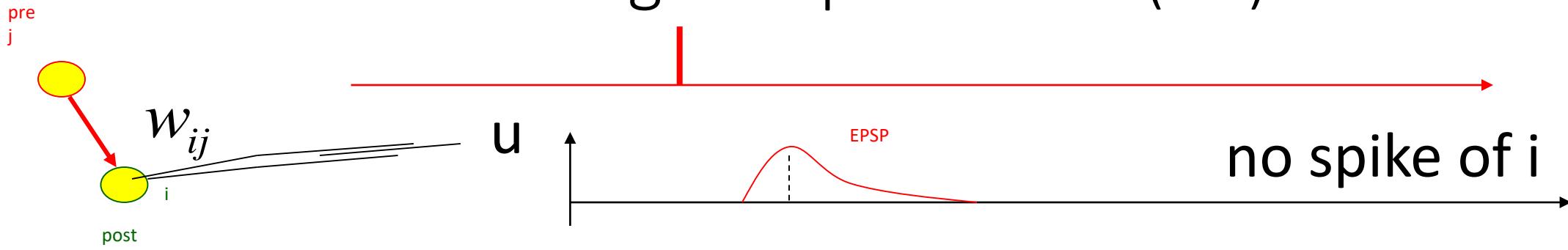
B. Output spike trains were convolved with a filter (top). The resulting continuous signal for neuron i is interpreted as speed of movement in direction d_i , where different neurons code for different directions.

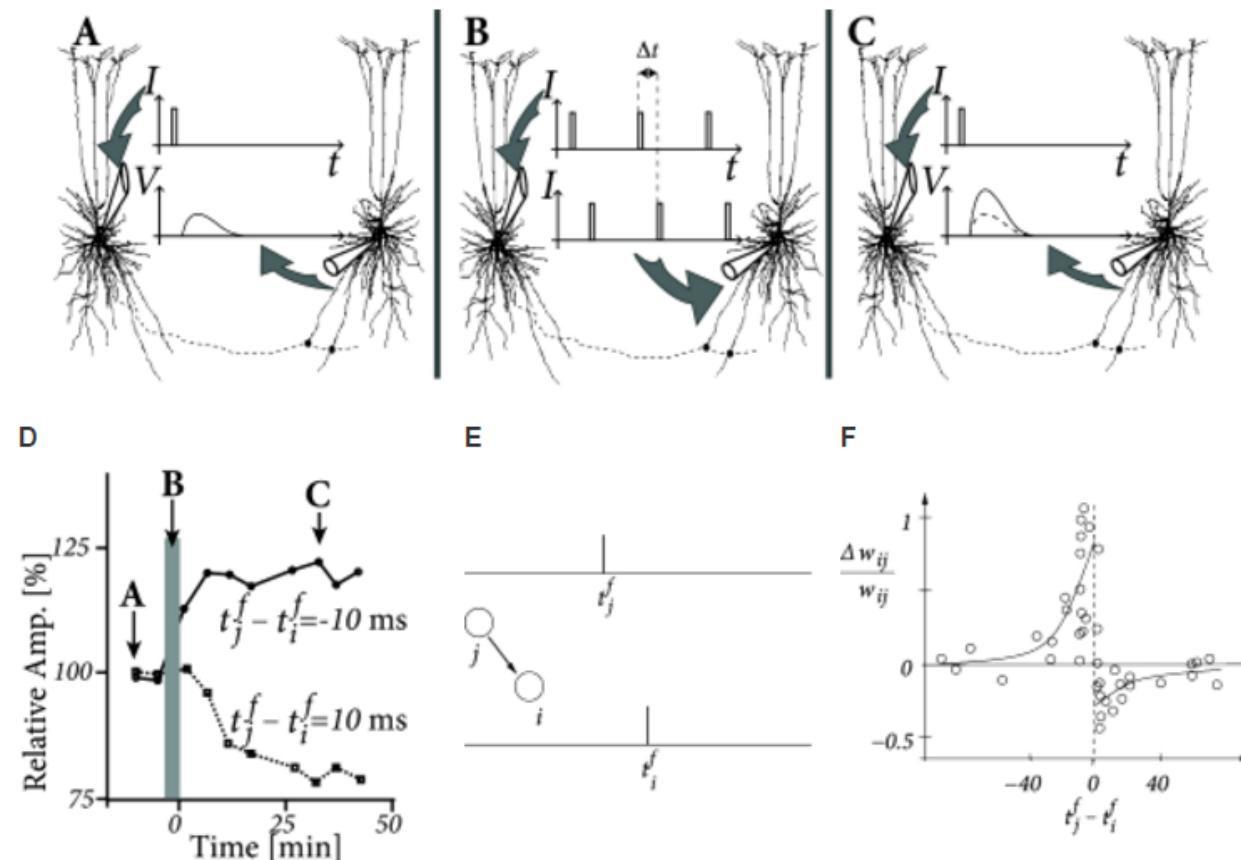
The two target trajectories (bottom, dashed lines) correspond to two different target spatio-temporal spike train patterns.

After a learning period of 10 000 trials, the network output generates a trajectory (full black lines) close to the target trajectories.

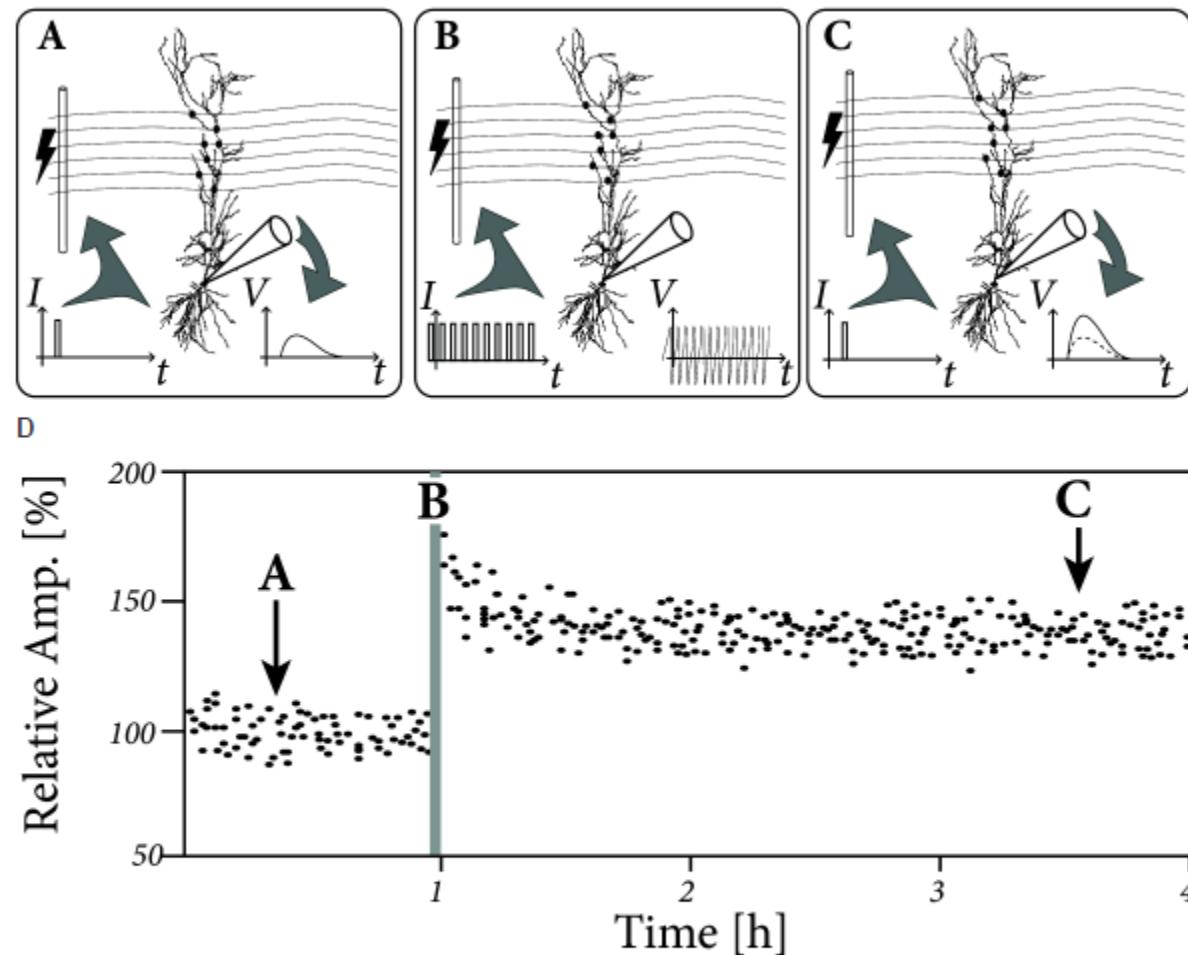


Hebbian Learning in experiments (schematic)





Spike-Timing-Dependent Plasticity. **A.** Intracellular electrodes are used to identify two synaptically coupled neurons (axons are shown as dashed lines). A test pulse (I) injected into the presynaptic neuron causes an EPSP in the postsynaptic neuron (V). **B.** During the plasticity induction protocol of a few seconds ('pairing'), both neurons are stimulated with current pulses forcing spikes at precise moments in time. **C.** After the pairing protocol, the presynaptic neuron is stimulated by another current pulse, testing the level of potentiation of the synapse (before pairing protocol, dashed line; after, full line). **D.** Amplitude of EPSP relative to initial amplitude as a function of time after the pairing protocol. If the presynaptic spike is 10 ms before the postsynaptic one, potentiation occurs (full line). If the order of the spikes is inverted, depression occurs (data points redrawn after Markram et al. (328)). **E.** Synaptic changes Δw_{ij} occur only if presynaptic firing at $t_j^{(f)}$ and postsynaptic activity at $t_i^{(f)}$ occur sufficiently close to each other. **F.** The STDP window summarizes the timing requirements between pre- and postsynaptic spikes. Experimentally measured weight changes (circles) as a function of $t_j^{(f)} - t_i^{(f)}$ in milliseconds overlayed on a schematic two-phase learning window (solid line). A positive change (LTP) occurs if the presynaptic spike precedes the postsynaptic one; for a reversed timing, synaptic weights are decreased (data points redrawn after the experiments of Bi and Poo (55)).



A. Small pulses are applied to the presynaptic fibers in order to measure the strength of the postsynaptic response

The amplitude of the test pulse is chosen such that the stimulation evokes a postsynaptic potential, **but no action potentials**

B. The input fibers are strongly stimulated by a sequence of high frequency pulses so as to evoke postsynaptic firing

C. The strength of the postsynaptic response to small pulses is tested again

A significantly increased amplitude of postsynaptic potentials is found

This change in the synaptic strength persists over many hours and is thus called **Long-Term Potentiation** or LTP

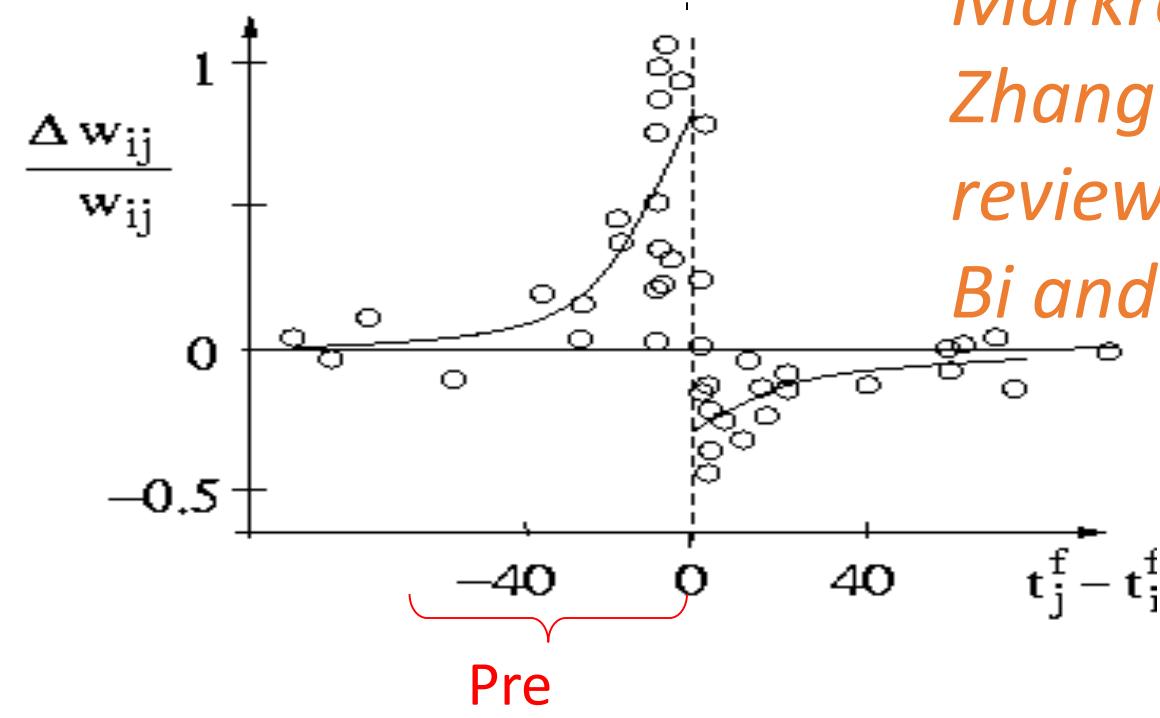
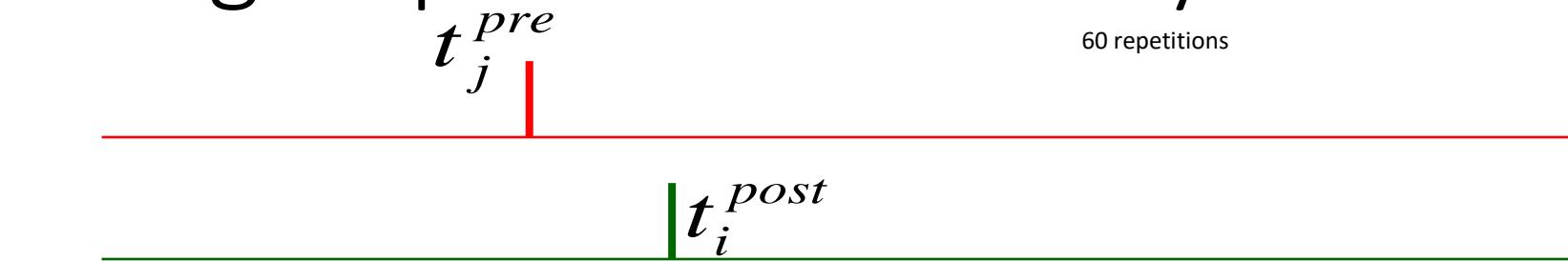
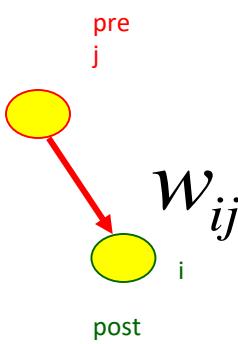
Schematic drawing of a paradigm of LTP induction. A. A weak test pulse (left) evokes the postsynaptic response sketched on the right-hand side of the figure. B. A strong stimulation sequence (left) triggers postsynaptic firing (right, the peak of the action potential is out of bounds). C. A test pulse applied some time later evokes a larger postsynaptic response (right; solid line) than the initial response. The dashed line is a copy of the initial response in A. D. The relative amplitude as measured with the test pulses illustrated in A and C is increased after the strong stimulation at $t = 1$ h. (Schematic figure.)

Spike-Timing-Dependent Plasticity (STDP)

- The resulting change in the synaptic efficacy Δw_{ij} after several repetitions of the experiment is a **function of the difference $t_j^f - t_i^f$ between the firing times of pre- and postsynaptic neuron**
- The direction of the change depends critically, on the **relative timing of pre- and postsynaptic spikes on a millisecond time-scale**
- The synapse is strengthened if the presynaptic spike occurs shortly before the postsynaptic neuron fires, but the synapse is weakened if the sequence of spikes is reversed
- This observation is indeed in agreement with Hebb's postulate because presynaptic neurons that are active slightly before the postsynaptic neuron are those which 'take part in firing it' whereas those that fire later obviously did not contribute to the postsynaptic action potential



Spike Timing Dependent Plasticity



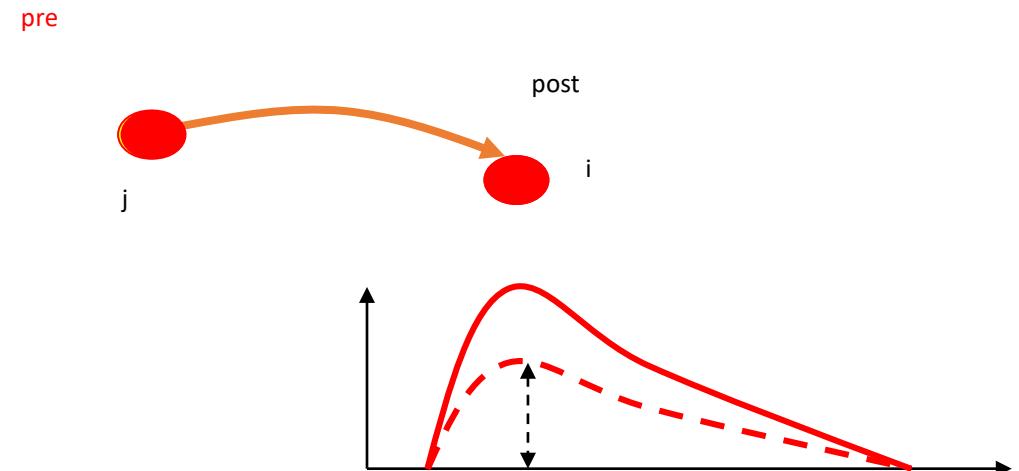
*Markram et al, 1995,1997
Zhang et al, 1998
review:
Bi and Poo, 2001*



Hebbian Learning

= unsupervised learning

$$\frac{dw_{ij}}{dt} = \alpha \cdot v_i \cdot u_j$$



where w_{ij} is the weight of a connection from an input unit j with activity u_j to an output unit i with activity v_i , and α is the learning rate.

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

What is the problem with Hebbian Learning?

If we apply a stimulus to the input units and allow the connections to develop according to the Hebbian learning rule, **then all connections will grow and eventually saturate**, and no selectivity will emerge.

To develop selectivity, some dependencies among weights are needed, so that **changes at one connection will influence the others**.



Models of Synaptic Plasticity

Hebbian Learning Rules

Where do you expect to find neuromorphic chips?

- Airports (e.g., analyzing odors)
- Tracking the source of a sound
- Neuroprosthetics
- Neuromodulation

