

4. Associators and Synaptic Plasticity

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Lecture Notes on Brain and Computation

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Outline

- 4.1 Associative memory and Hebbian learning
- 4.2 The physiology and biophysics of synaptic plasticity
- 4.3 Mathematical formulation of Hebbian plasticity
- 4.4 Synaptic scaling and weight distributions

4.1 Associative memory and Hebbian learning

- To find the general principles of brain development is one of the major scientific quests in neuroscience
- Not all characteristics of the brain can be specified by a genetic code
 - ◆ The number of genes would certainly be too small to specify all the detail of the brain networks
 - ◆ Advantageous that not all the brain functions are specified genetically
 - To adapt to particular circumstances in the environment
- An important adaptation mechanism that is thought to form the basis of building associations
- Adapting synaptic efficiencies (learning algorithm)

4.1.1 Hebbian learning

- Donald O. Hebb, *The Organization of Behavior*
- *“When an axon of a cell A is near enough to excite cell B or repeatedly or persistently takes part in firing it, some growth or metabolic change takes place in both cells such that A’s efficiency, as one of the cells firing B, is increased.”*
- Brain mechanisms and how they can be related to behavior
- Cell assemblies
- The details of synaptic plasticity
- Experimental result and evidence
- *Hebbian learning*

4.1.2 Associations (1)

- Computer memory
 - ◆ Information is stored in magnetic or other physical form
 - ◆ Using memory address for recalling
 - ◆ Natural systems cannot work with such demanding precision
- The human memory
 - ◆ Recall vivid memories of events from small details
 - ◆ Learn associations
 - Trigger memories based on related information
 - ◆ Only partial information can be sufficient to recall memories
 - ◆ Association memory
 - The basis for many cognitive functions

4.1.2 Associations (2)

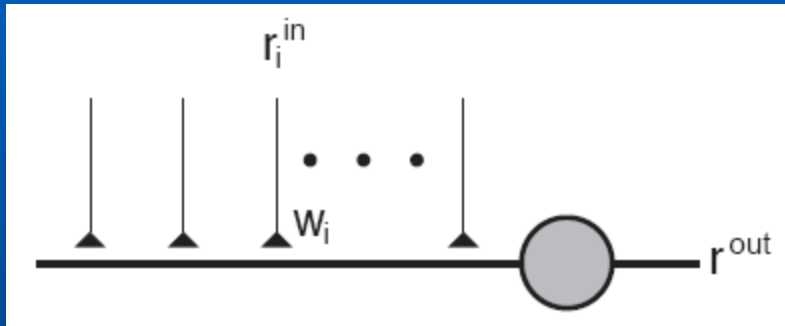


Fig. 4.1 A simplified neuron that receives a large number of inputs r_i^{in} .

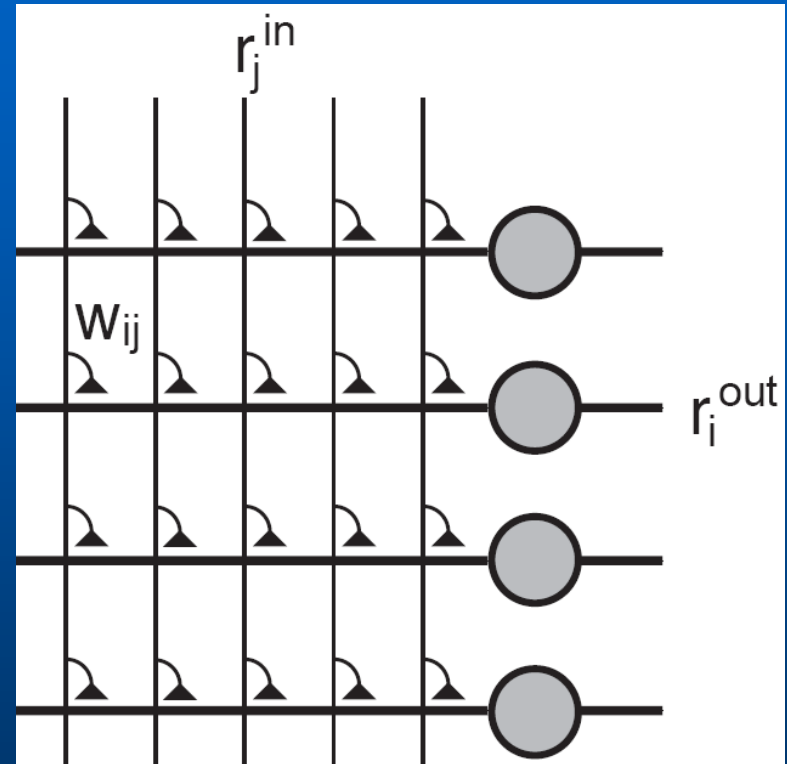


Fig. 4.2 A network of associative nodes

4.1.2 Associations (3)

- (A) $h = \sum_i w_i r_i^{in} = 3$ (4.1), threshold = 1.5

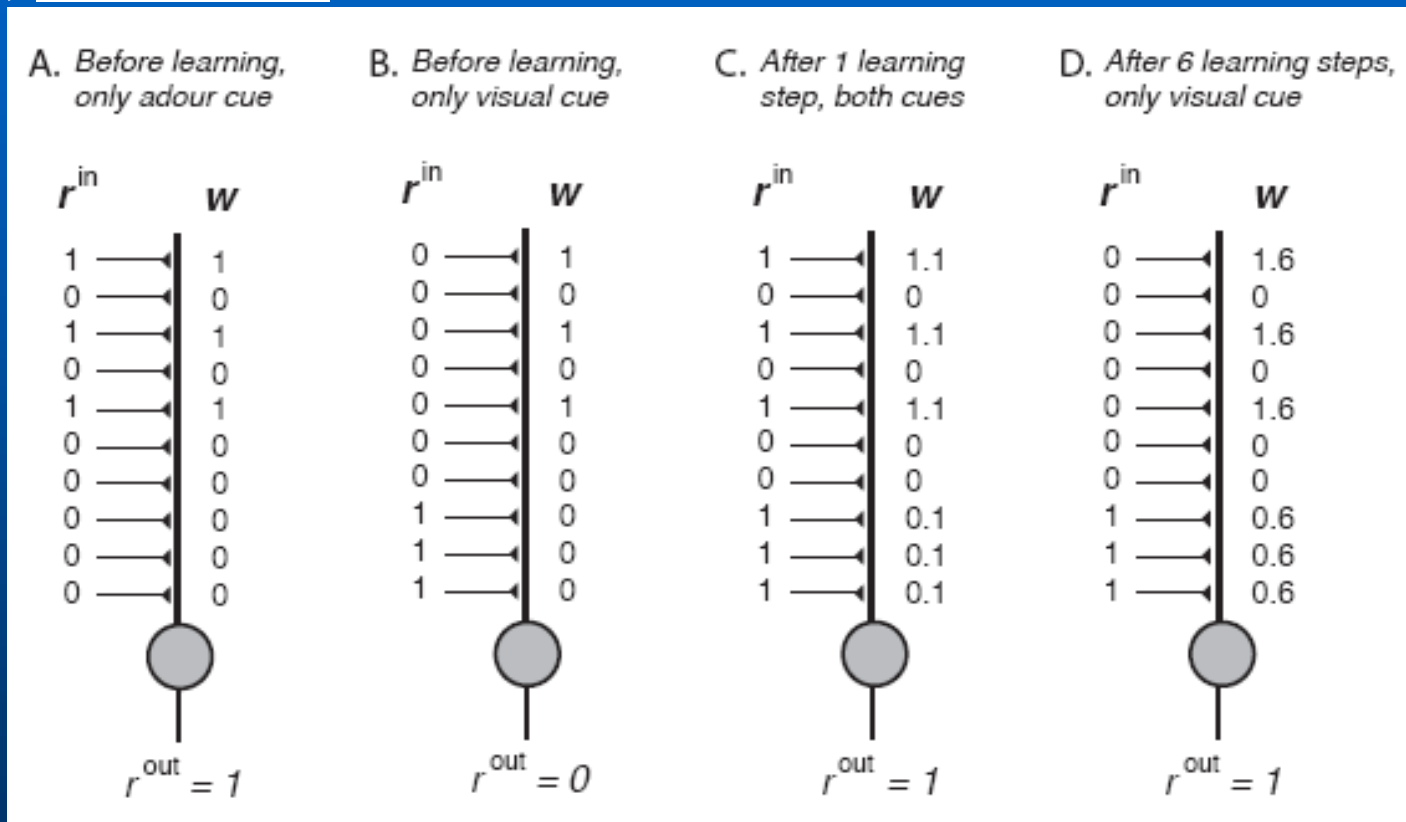


Fig. 4.3 Examples of an associative node that is trained on two feature vectors with a Hebbian-type learning algorithm that increases the synaptic strength by $\delta w = 0.1$ each time a presynaptic spike occurs in the same temporal window as a postsynaptic spike

4.1.3 Hebbian learning in the conditioning framework (1)

- The mechanisms of an associator
 - ◆ The first stimulus, the odour of the hamburger, was already effective in eliciting a response of neuron before learning
 - *Unconditioned stimulus (USC)*
 - Based on the random initial weight distribution
 - ◆ For the second input, the visual image of the hamburger, the response of the neuron changes during learning
 - *Conditioned stimulus (CS)*
- The input vector to the associator is a mixture of UCS and CS as illustrated in Fig. 4.4A

4.1.3 Hebbian learning in the conditioning framework (2)

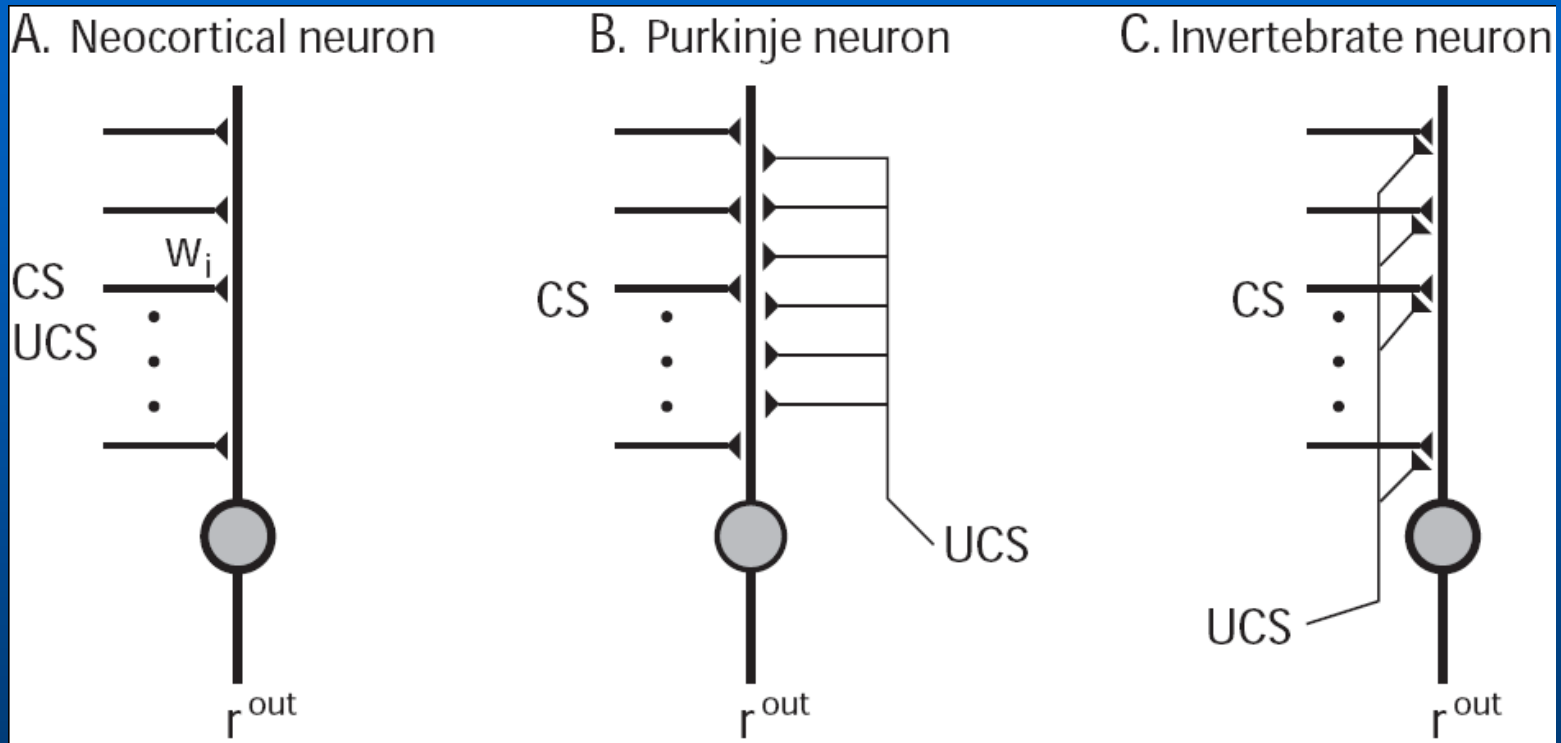


Fig. 4.4 Different models of associative nodes resembling the principal architecture found in biological nervous systems

4.1.4 Features of associators and Hebbian learning

- Pattern completion and generalization
 - ◆ *Recall from partial input*
 - ◆ The output node responds to all patterns with a certain similarity to the trained pattern
- Prototypes and extraction of central tendencies
 - ◆ The ability to extract central tendencies
 - ◆ *Noise reduction*
- Graceful degradation
 - ◆ The loss of some components of system should not make the system fail completely.
 - ◆ *Fault tolerance*

4.2 The physiology and biophysics of synaptic plasticity

- Synaptic machinery can change
 - ◆ The number of release sites
 - ◆ The possibility of neurotransmitter release
 - ◆ The number of transmitter receptors
 - ◆ The conductance and kinetics of ion channels

4.2.1 Typical plasticity experiments (1)

- The experiment by Bliss and Lomo (1973) in hippocampus cultures
 - ◆ LTP
 - High-frequency stimulus applied
 - Increased amplitude of EFP (Fig. 4.5A)
 - ◆ LTD
 - Low-frequency stimulus applied
 - Decreased amplitude of EFP (Fig. 4.5B)
- The experiment by Fine and Enoki in hippocampal slices of rats
 - High-frequency stimulus applied
 - Increased amplitude of EPSP (Fig. 4.6A)

4.2.1 Typical plasticity experiments (2)

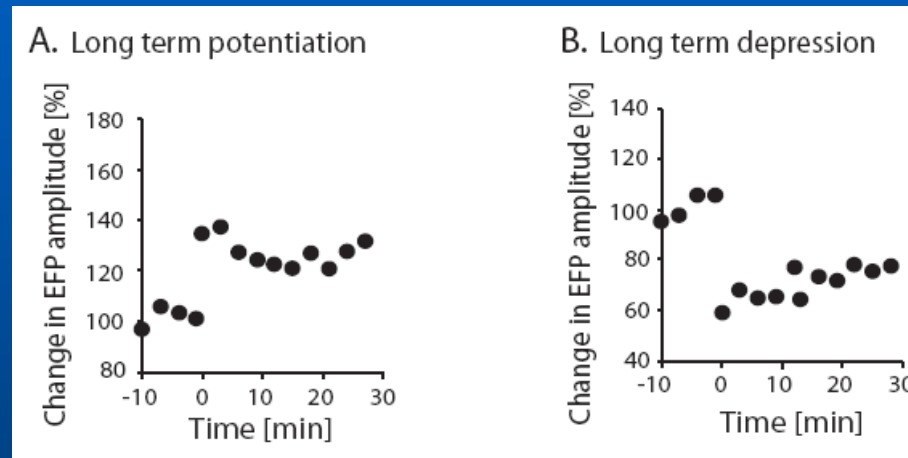


Fig. 4.5

4.2.1 Short-term plasticity

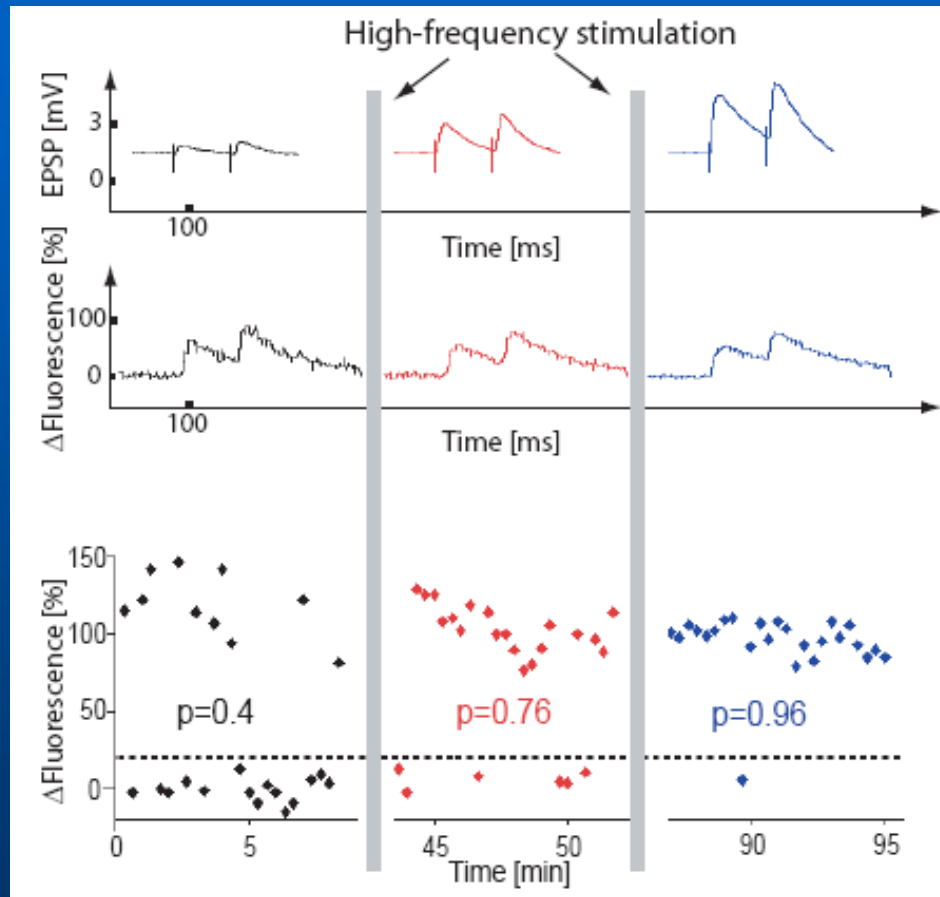
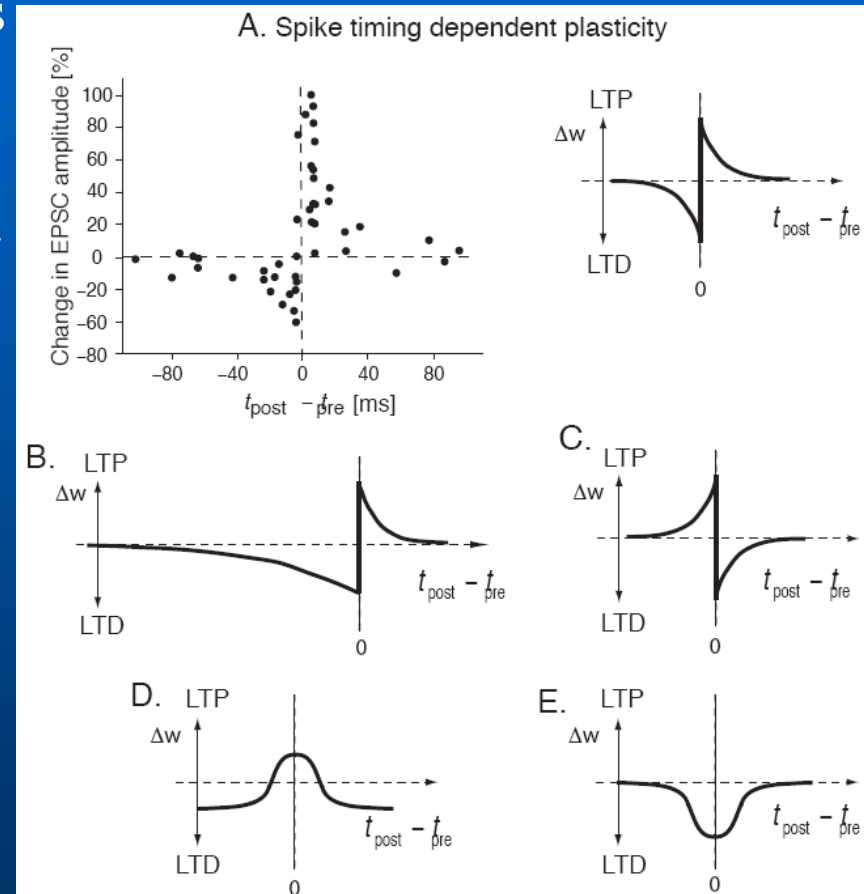


Fig. 4.6

4.2.2 Spike timing dependent plasticity

- Relative changes of EPSC amplitudes (and therefore weights) for different values of the time differences between pre- and postsynaptic spikes.
 - ◆ Asymmetrical Hebbian plasticity (Fig. 4.7B-C)
 - ◆ Symmetrical Hebbian plasticity (Fig. 4.7D-E)

Fig. 4.7 Several examples of the schematic dependence of synaptic efficiencies on the temporal relations between pre- and postsynaptic spikes



4.2.3 The calcium hypothesis and modeling chemical pathways

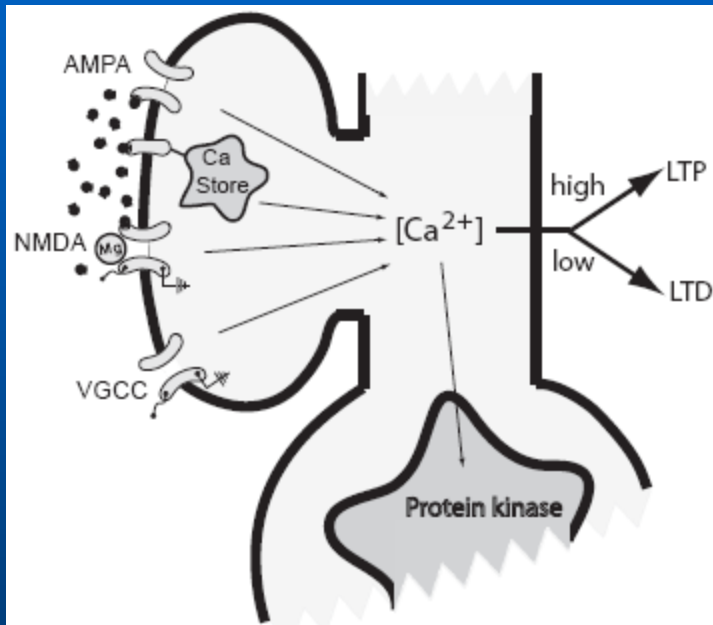


Fig. 4.8

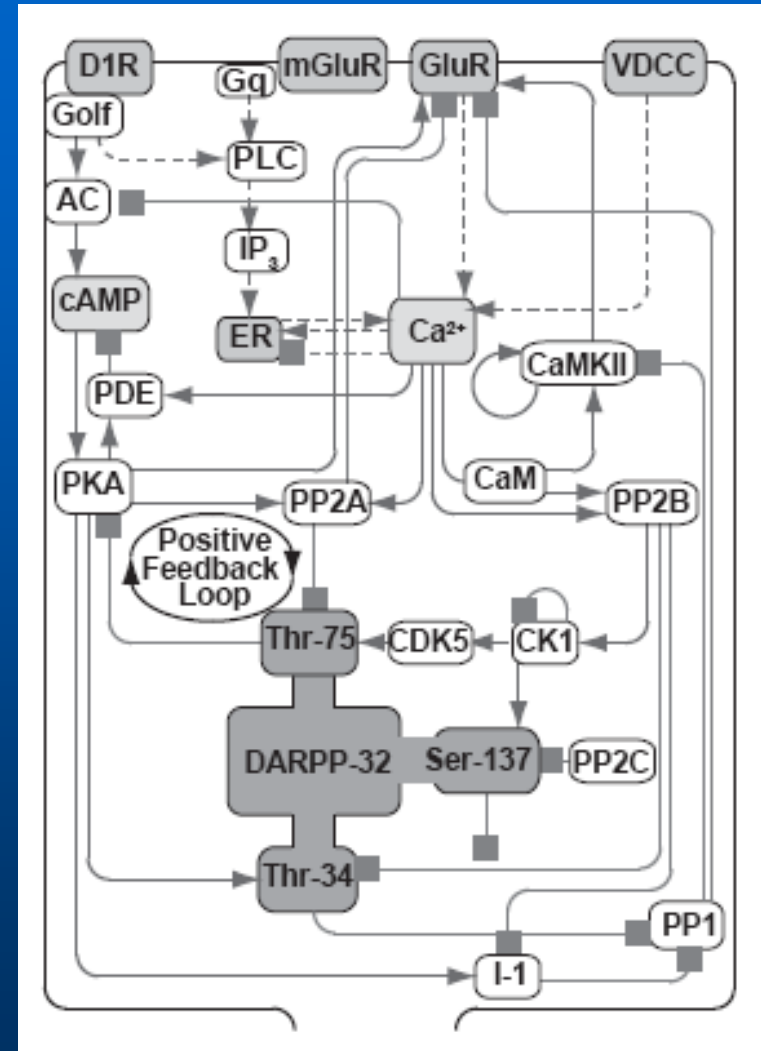


Fig. 4.8

4.3 Mathematical formulation of Hebbian plasticity

- Synaptic plasticity by a change of weight values
- The weight values are not static but can change over time
- The variation of weight values after time steps Δt in a discrete fashion as

$$w_{ij}(t + \Delta t) = w_{ij}(t) + \delta w_{ij}(t_i^f, t_j^f, \Delta t; w_{ij}) \quad (4.2)$$

- The dependence of the weight changes on various factors
 - ◆ Activity-dependent synaptic plasticity
 - Depend on the firing times of the pre- and postsynaptic neuron
 - ◆ The strength of synapse can vary within some interval

4.3.1 Spike timing dependent plasticity rules

- General form

$$\Delta w_{ij} = \varepsilon^{\pm}(w) K^{\pm}(t^{post} - t^{pre})$$

- ◆ Kernel function

$$K^{\pm}(t^{post} - t^{pre}) = e^{\mp \frac{t^{post} - t^{pre}}{\tau^{\pm}}} \Theta(\pm[t^{post} - t^{pre}])$$

- ◆ Additive rule

$$\varepsilon^{\pm} = \begin{cases} a^{\pm} & \text{for } w_{ij}^{\min} \leq w_{ij} \leq w_{ij}^{\max} \\ 0 & \text{otherwise} \end{cases}$$

- ◆ Multiplicative rule

$$\begin{aligned} \varepsilon^{+} &= a^{+}(w^{\max} - w_{ij}) \\ \varepsilon^{-} &= a^{-}(w_{ij} - w^{\min}). \end{aligned}$$

4.3.2 Hebbian learning in population rate models (1)

- The average behavior of neurons or cell assemblies

General: $\Delta W_{ij} = \epsilon(t, W)[f_{\text{post}}(r_i)f_{\text{pre}}(r_j) - f(r_i, r_j, W)]$

Mnemonic equation (Caianiello): $\Delta W_{ij} = \epsilon(W)[r_i r_j - f(W)]$

Basic Hebb: $\Delta W_{ij} = \epsilon r_i r_j$

Covariance rule: $\Delta W_{ij} = \epsilon(r_i - \langle r_i \rangle)(r_j - \langle r_j \rangle)$

BCM theory: $\Delta W_{ij} = \epsilon(f^{\text{BCM}}(r_i; \theta^M)(r_j) - f(W))$

ABS rule: $\Delta W_{ij} = \epsilon(f_{\text{ABS}}(r_i; \theta^-, \theta^+) \text{sign}(r_j - \theta^{\text{pre}}))$

4.3.2 Hebbian learning in population rate models (2)

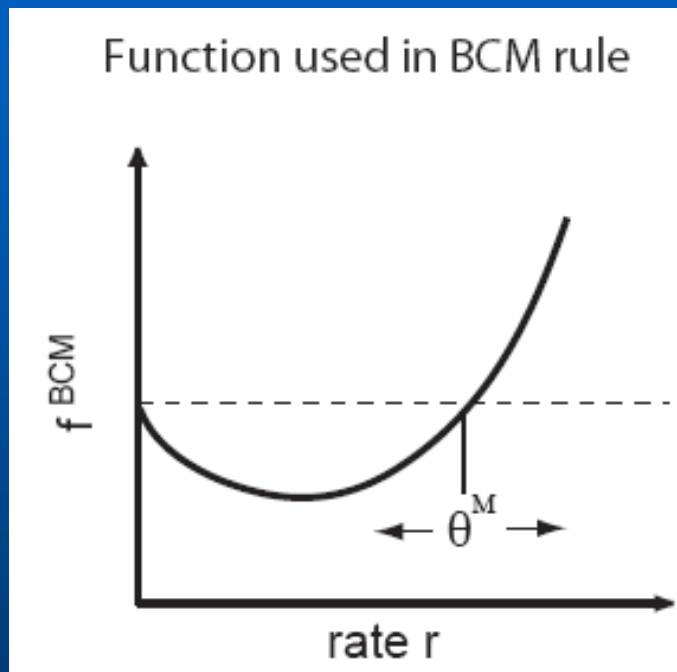


Fig. 4.10

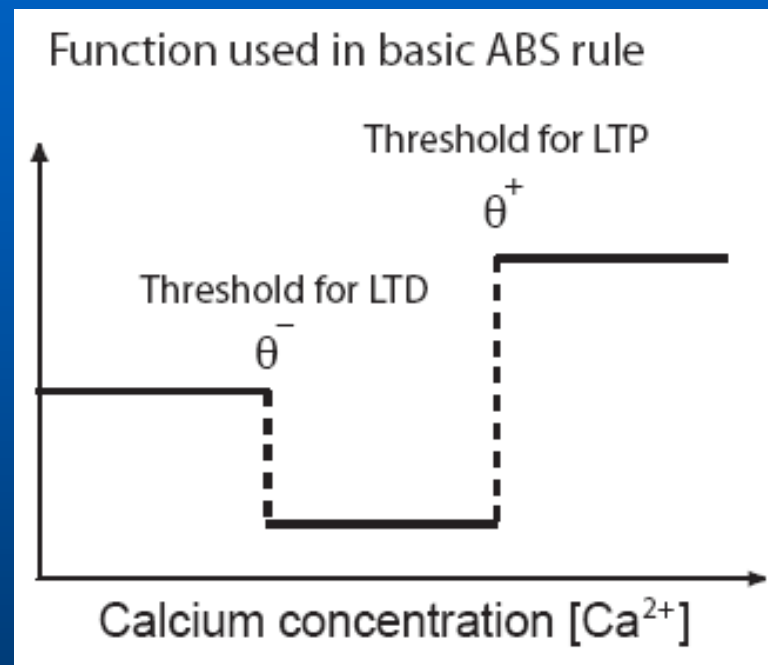


Fig. 4.11

4.3.3 Negative weights and crossing synapses

- In single neurons
 - ◆ Synaptic learning rules should not change the sign of weight values.
- In population nodes
 - ◆ Domain crossing of weight values is allowed.

4.4 Synaptic scaling and weight distribution

- Repeated application of additive association rules results in runaway (unstable) synaptic values.
- Real neural systems need some balance and competition between synapses to allow stable learning.

4.4.1 Examples of STDP with spiking neurons (1)

- Asymmetric Hebbian rules for spiking neurons

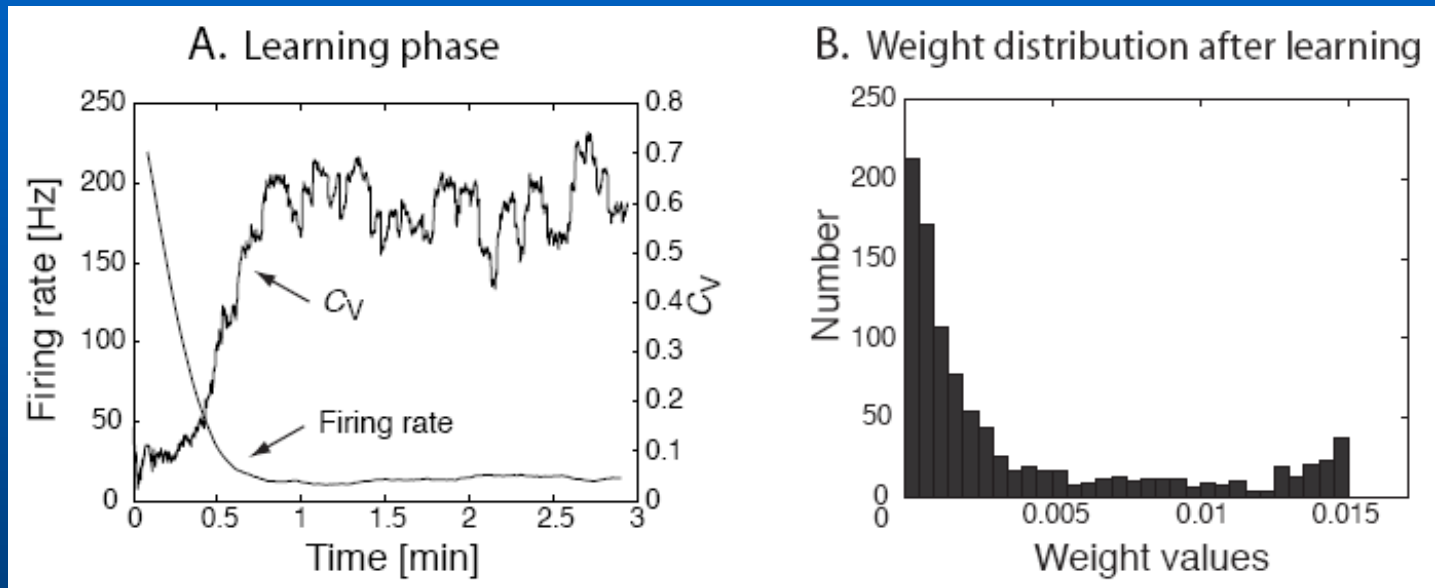


Fig. 4.12 (A) Firing rate (decreasing curve) and C_v , the coefficient of variation (increasing and fluctuating curve), of an IF-neuron that is driven by 1000 excitatory Poisson spike trains while the synaptic efficiencies are changed according to an additive Hebbian rule with asymmetric Gaussian plasticity windows. (B) Distribution of weight values after 5 minutes of simulated training time (which is similar to the distribution after 3 minutes). The weights were limited to be in the range of 0-0.015. The distribution has two maxima, one at each boundary of the allowed interval.

4.4.1 Examples of STDP with spiking neurons (2)

- The firing time of the IF-neuron is mainly determined by the average firing input current
- Measure this statement using *cross-correlation function*

$$C(n) = \langle s^{pre}(t)s^{post}(t+n\Delta t) \rangle - \langle s^{pre} \rangle \langle s^{post} \rangle$$

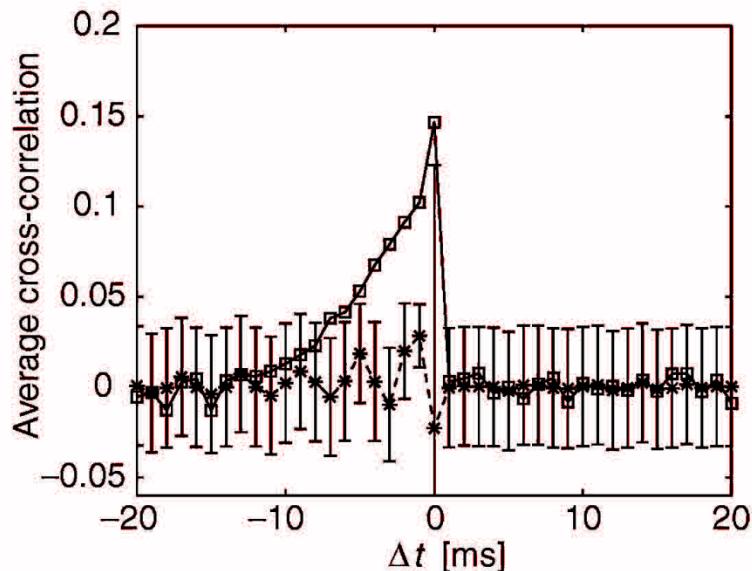


Fig. 4.13 Average cross-correlation function between pre-synaptic Poisson spike trains and the postsynaptic spike train (averaged over all presynaptic spike trains) in simulation of an IF-neuron with 1000 input channels. The spike trains that lead to the results shown by stars were generated with each weight value fixed to value 0.015. The cross-correlations are consistent with zero when considered within the variance indicated by the error bars. The squares represent the simulation results from simulations of the IF-neuron driven by the same presynaptic spike trains as before, but with the weight matrix after Hebbian learning shown in Fig. 7.9. Some presynaptic spike trains caused postsynaptic spiking with a positive peak in the average cross-correlation functions when the presynaptic spikes precede the postsynaptic spike. No error bars are shown for this curve for clarity.

4.4.2 Weight distributions in rate models

- After learning Np with Hebbian covariance rule (eq. 4.11), $w_{ij}^0 = 0$

$$w_{ij} = \frac{1}{\sqrt{Np}} \sum_{\mu} (r_i^{\mu} - \langle r_i \rangle)(r_j^{\mu} - \langle r_j \rangle)$$

- Rate models of recurrent networks trained with the Hebbian training rule on random patterns have Gaussian distribution weight component

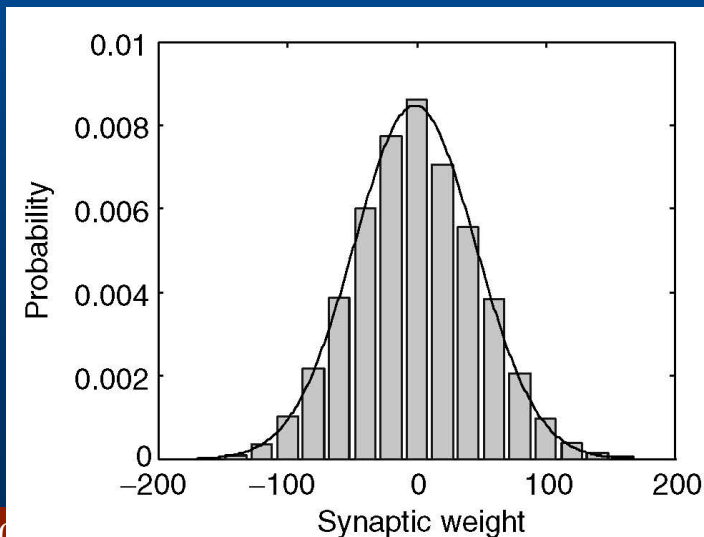


Fig. 4.14 Normalized histograms of weight values from simulations of a simplified neuron (sigma node) simulating average firing rates after training with the basic Hebbian learning rules 4.11 on exponentially distributed random patterns. A fit of a Gaussian distribution to the data is shown as a solid line.

4.4.3 Competitive synaptic scaling and weight decay (1)

- The dependence of overall synaptic efficiencies on the average postsynaptic firing rate
 - ◆ Crucial to keep the neurons in the regime of high variability
 - Keep neurons sensitive for information processing in the nervous systems
- Many experiments have demonstrated
 - ◆ Synaptic efficiencies are scaled by the average postsynaptic activity
- The threshold where LTP is induced can depend on the time-averaged recent activity of the neuron
- Weight normalization
- Weight decay

4.4.3 Competitive synaptic scaling and weight decay (2)

Explicit normalization: $W_{ij} \leftarrow \frac{W_{ij}}{\sum_j W_{ij}}$

Basic decay: $\Delta W_{ij} = r_i r_j - c W_{ij}$

Willshaw rule: $\Delta W_{ij} = (r_i - W_{ij}) r_j$

Oja rule: $\Delta W_{ij} = r_i r_j - (r_i)^2 W_{ij}$

4.4.4 Oja's rule and principal component analysis (PCA)

- Oja's rule (in the previous section) also implements efficiently an algorithm called PCA
- PCA is to reduce the dimension of high-dimensional data.

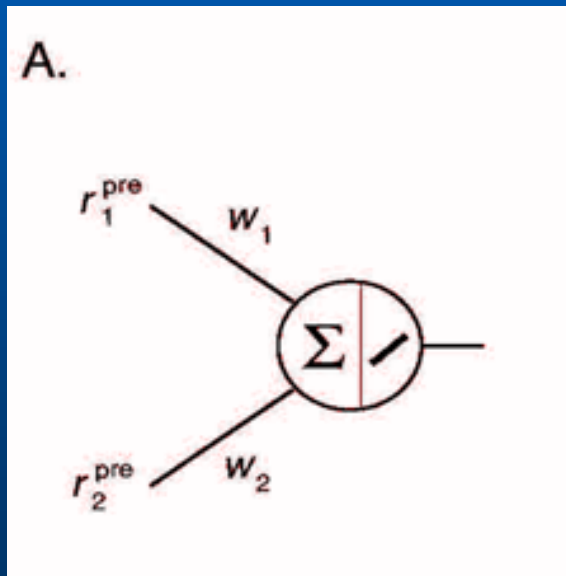


Fig. 4.15

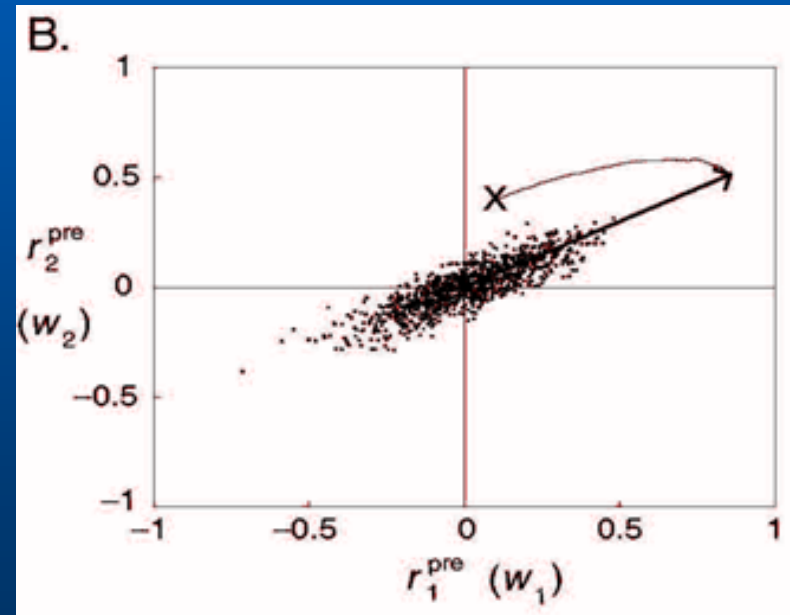


Fig. 4.16