

Plasticity

- Hebbian learning and memory
- Hopfield model and some generalizations
- Experimental evidence

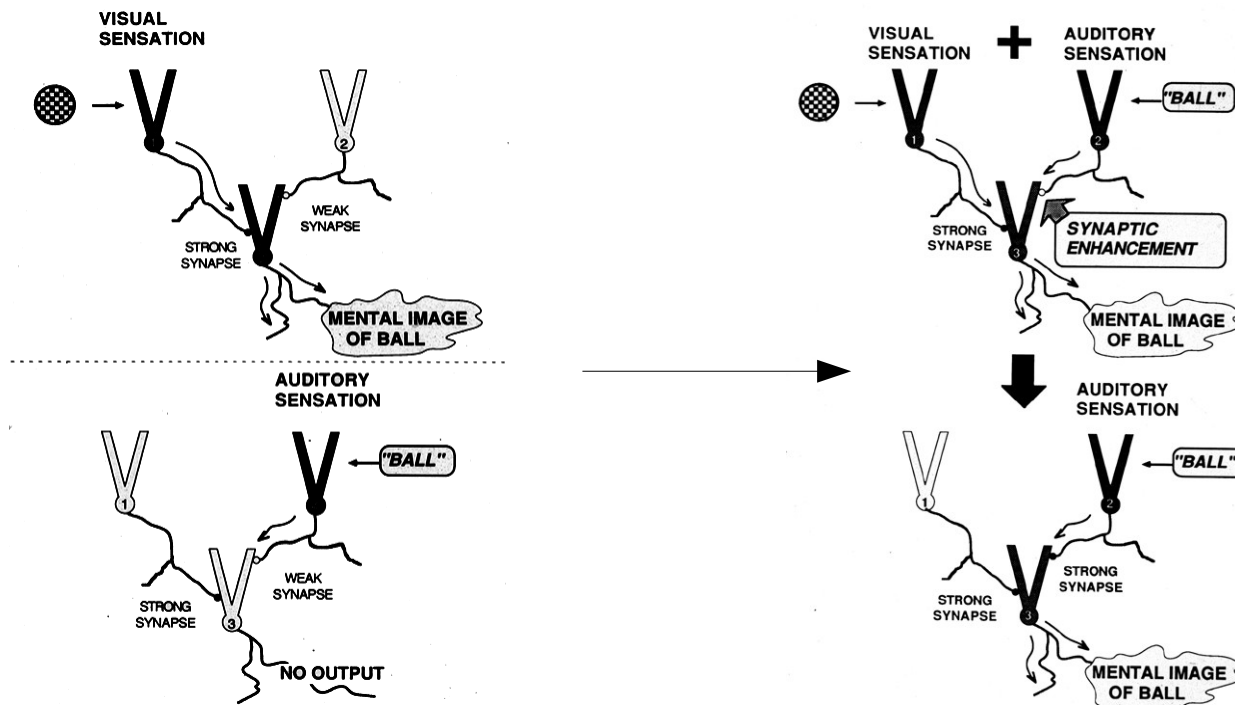
Hebbian Learning

- It is a process in which neurons that are simultaneously active reinforce their connections
- “Neurons that fire together wire together”



Hebbian Learning

- What would be the possible results of this mechanism?
- Create associations



Hebbian Learning

- What would be the possible results of this mechanism?
- Create self-sustaining patterns of activity

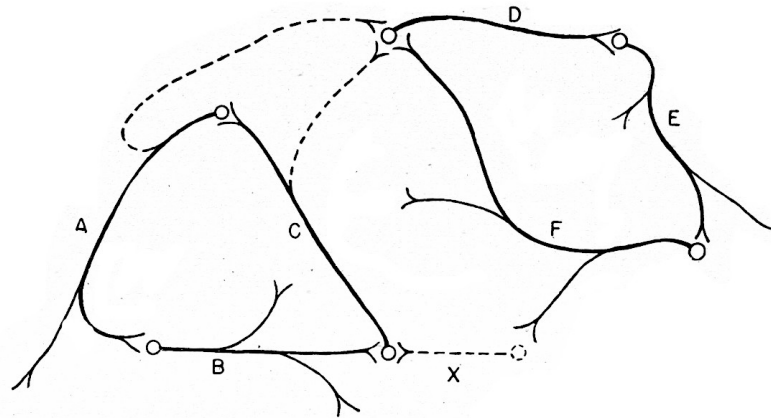
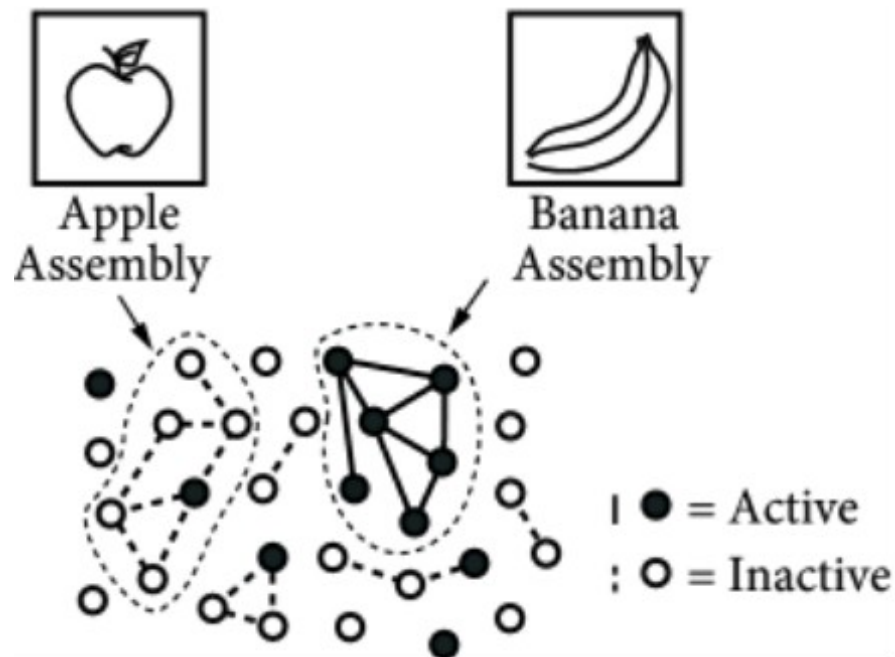


Figure 43. To illustrate the way in which learning might modify the functioning of cortical circuits and establish a cell-assembly. It is assumed that *A-B-C* and *D-E-F*, in association cortex, are excited by the same sensory event (axons from the sensory cortex are not shown, but it is assumed that they excite these cells separately). If *A* then delivers impulses to *B* at the moment when *B* is being fired by axons from sensory cortex, the synapse *A-B* will be “strengthened,” and similarly with the other synapses. As a result of this strengthening the excitation of one cell may become able to set up reverberation in the circuit. Broken lines show possible connections between the two circuits, which would permit them to function as one system.

Hebbian Learning

- What would be the possible results of this mechanism?
 - Create self-sustaining patterns of activity



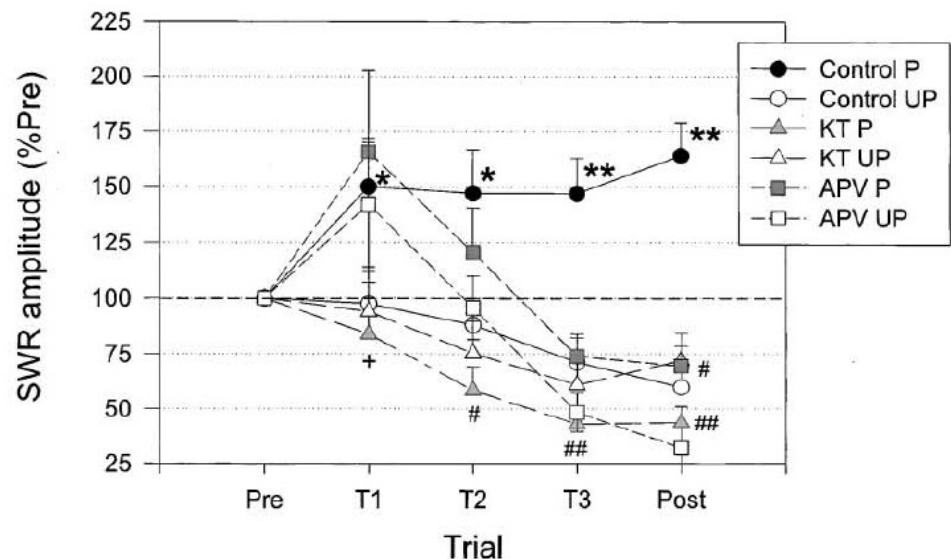
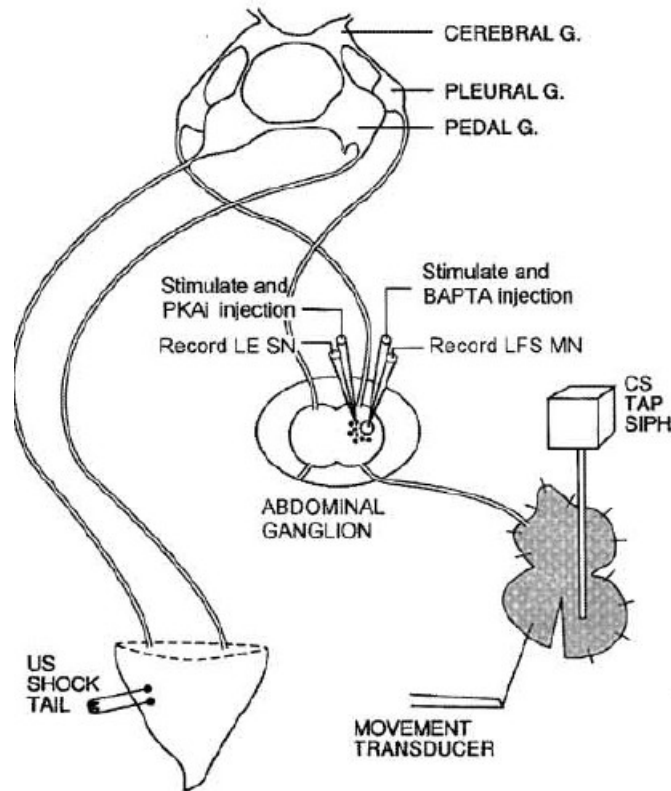
Hebbian Learning

- The first case gives a mechanism for classical conditioning
 - This was shown in 1974 by Kandel in a set of experiments in *Aplysia* (Antonov et al., Neuron, 2003)
 - The animal can associate a conditioned stimulus (tactile) to a unconditioned stimulus (electric) to withdraw its siphon
 - By perturbing molecular signaling it was shown that both pre- and post-synaptic mechanisms are relevant and that they are not independent but interact via retrograde signaling



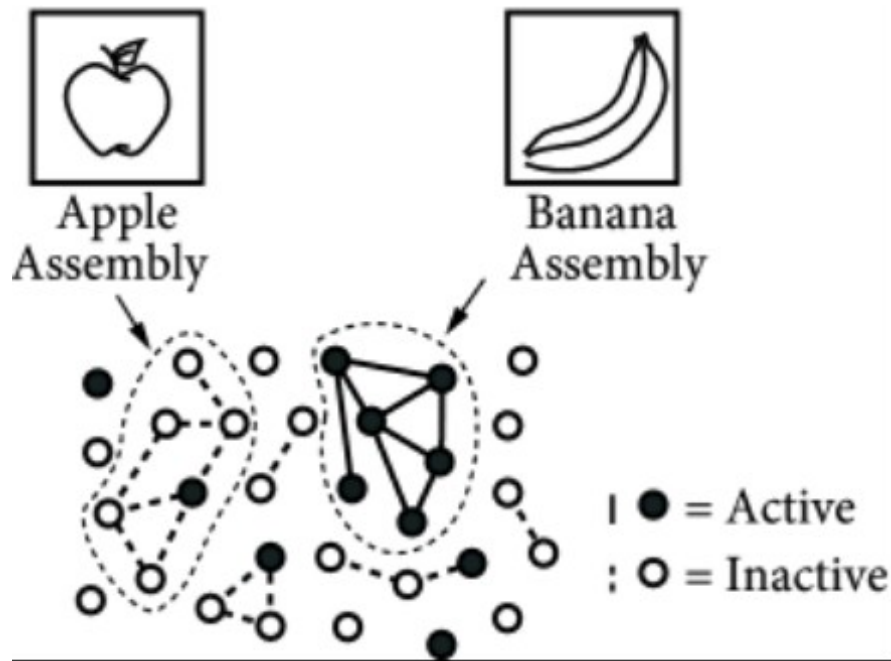
Hebbian Learning

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Hebbian Learning

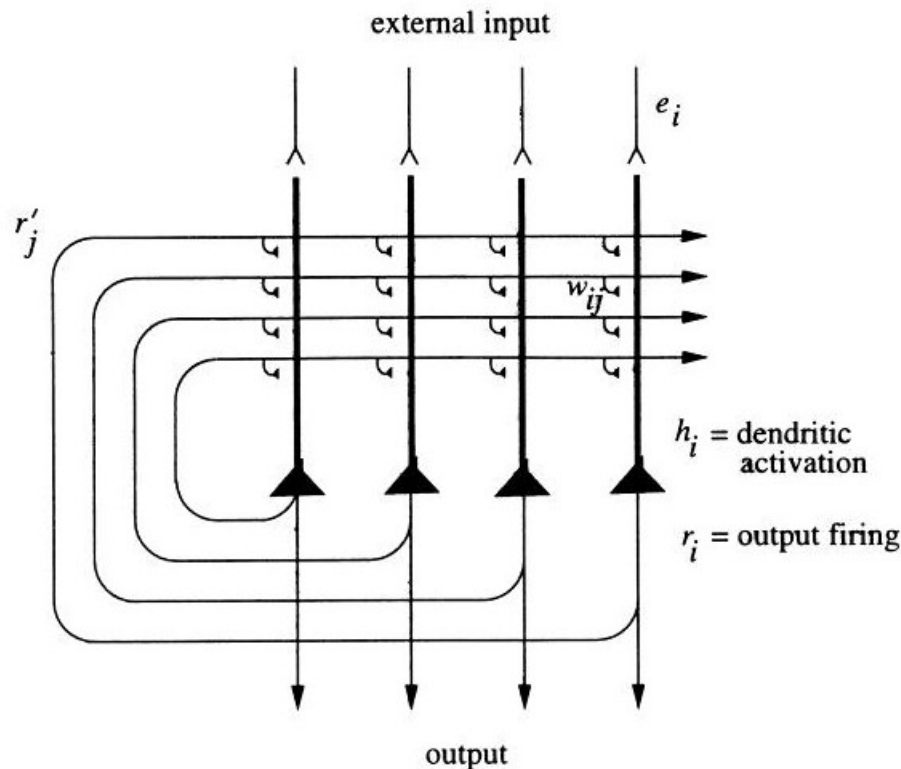
- Self-sustaining patterns of activity



- This can be the basis of memory
- The memory has a retrieval mechanism based on content (instead of address)

Hebbian Learning

- This is sometimes called *auto-association*



- The states of the neurons changes until it converges to a *fixed point*

Hebbian Learning

Autoassociators

- Complete a partial cue
- Can continue a sequence
- Generalize
- Gracefully degrade/fault tolerant
- Extract prototypes / reduce fluctuations

Are also fast, but their feedback may sustain short term memory

p_c is again proportional to N and grows with decreasing average activity level

Hebbian Learning

- How can we study all these properties?
- Let us simplify to keep the most simple ingredients
- Binary neurons
- Purely Hebbian connectivity matrix
- Simple threshold dynamics: neurons are active if their input is larger than a certain threshold
(Little, 1974; Hopfield, 1982)

Hebbian Learning

- Updating

$$s_i = 1 \text{ if } \sum_j w_{ij} s_j - \Theta_i > 0$$

$$s_i = -1 \text{ if } \sum_j w_{ij} s_j - \Theta_i \leq 0$$

The updating can be sequential or in parallel

- Hebbian learning determines the synaptic efficacies

$$w_{ij} = (1/N) \sum_{\mu} \xi_i^{\mu} \xi_j^{\mu} \quad (w_{ii}=0)$$

where $\xi_i^{\mu} = \pm 1$ is the state of the neuron i in pattern μ ($i=1, \dots, N$)

Hebbian Learning

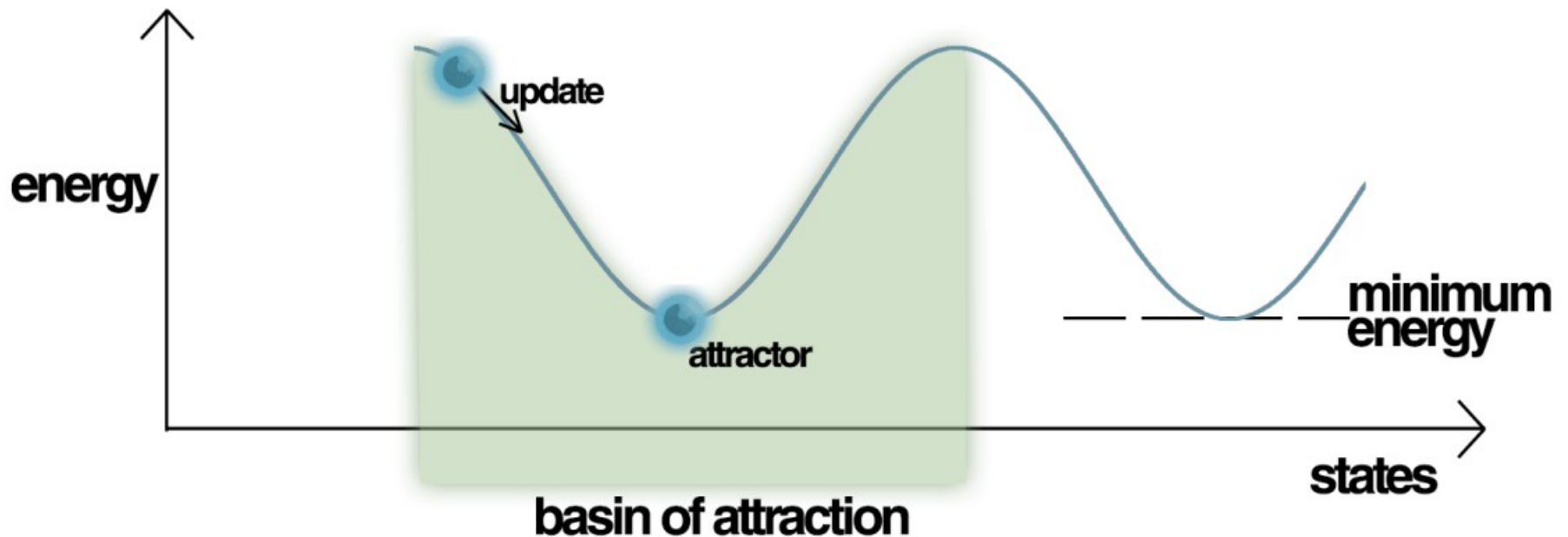
- Why this dynamics should converge to a fixed point?
- There is a *Lyapunov* (or energy) function

$$E = \frac{1}{2} \sum_{ij} w_{ij} s_i s_j - \sum_i \Theta_i s_i$$

- This function always decreases.
- After one step of the updating it must be $E' \leq E$
- The system must converge to a local minimum of E

Hebbian Learning

- The system must converge to a local minimum of E



- Every initial condition in the *basin of attraction* will converge to the same attractor

Hebbian Learning

- The system will work as a *content addressable memory*
- But how can be sure the minima of E are in the correct places?
- Let us consider the simplest case: we have only one memory to store:

$$w_{ij} = (1/N) \xi_i^1 \xi_j^1$$

- What happens if we use this pattern as initial condition of the dynamics:

$$s_i = 1 \text{ if } \sum_j w_{ij} s_j - \Theta_i > 0$$

$$s_i = -1 \text{ if } \sum_j w_{ij} s_j - \Theta_i \leq 0$$

Hebbian Learning

$$s_i = 1 \text{ if } (1/N) \sum_j \xi_i^1 \xi_j^1 \xi_j^1 - \Theta_i > 0$$

$$s_i = -1 \text{ if } (1/N) \sum_j \xi_i^1 \xi_j^1 \xi_j^1 - \Theta_i \leq 0$$

- But as the ξ are +/-1 we have

$$s_i = 1 \text{ if } \xi_i^1 - \Theta_i > 0$$

$$s_i = -1 \text{ if } \xi_i^1 - \Theta_i \leq 0$$

- If we take $\Theta_i = 0$ it must be

$$s_i = \xi_i^1$$

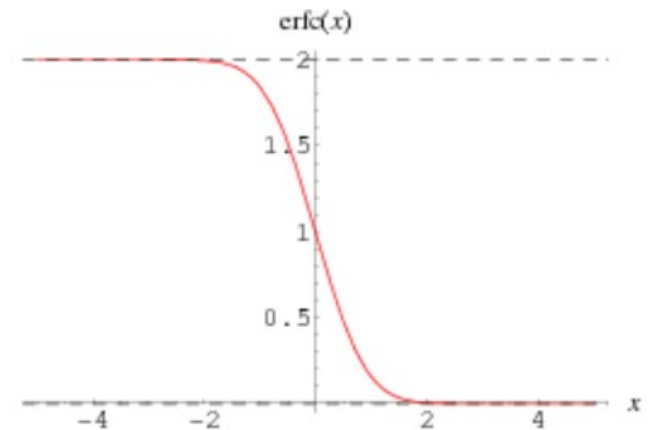
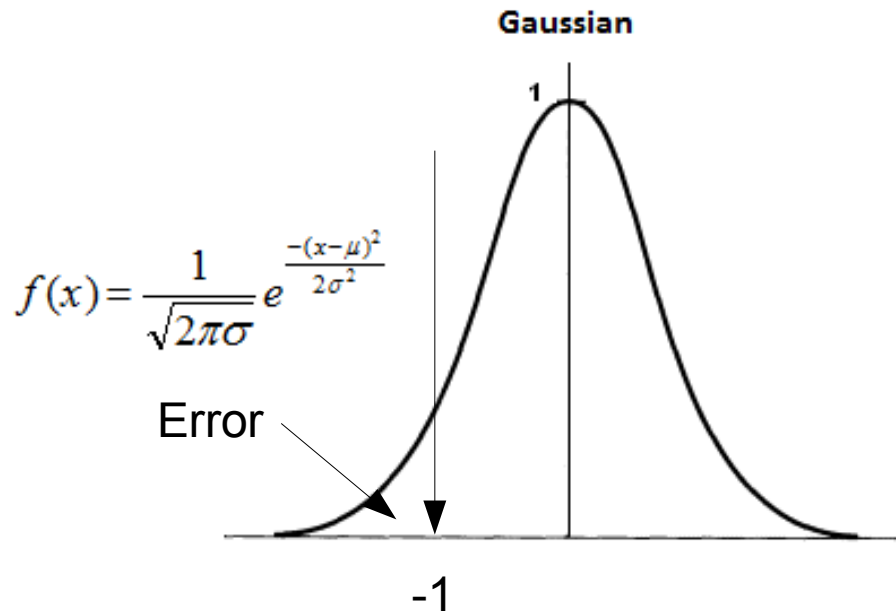
Hebbian Learning

- What happens if we try to store p memories?
$$s_i = 1 \quad \text{if} \quad \xi_i^1 + (1/N) \sum_{j,\mu > 1} \xi_i^\mu \xi_j^\mu \xi_j^1 > 0$$
$$s_i = -1 \quad \text{if} \quad \xi_i^1 - (1/N) \sum_{j,\mu > 1} \xi_i^\mu \xi_j^\mu \xi_j^1 \leq 0$$
- In principle the quantity $(1/N) \sum_{j,\mu > 1} \xi_i^\mu \xi_j^\mu \xi_j^1$ could be up to order p and it has a sign that seems unrelated to ξ_i^1
- Let us take the case where ξ_i^μ are independent random variables ± 1 with equal probability
- Now $(1/N) \sum_{j,\mu > 1} \xi_i^\mu \xi_j^\mu \xi_j^1$ is a Gaussian variable with 0 mean and variance $(p-1)/N$

Hebbian Learning

- The probability of one error is

$$P(\text{error}) = \text{erfc}(\sqrt{N/(2(p-1))})/2$$



$$\text{erfc}(x) \rightarrow \exp(-x^2)/(x\pi^{1/2})$$

Hebbian Learning

- It can be proved that the probability of error for ONE memory goes to 0 in the limit of large N if

$$p < N / (2 \ln(N))$$

- If we want that the probability of error goes to 0 for ALL the p memories it must be

$$p < N / (4 \ln(N))$$

Hebbian Learning

- Serious drawback of the model: spurious states
 - For instance $\xi_i^M = \text{sign}(\xi_i^1 + \xi_i^2 + \xi_i^3)$ is also a fixed point of the dynamics
- An the same for any odd number of symmetric combinations
- In real life the dynamics has also a random component (vesicle release is a Poisson process, opening and closing of the ionic channels, etc)

Hebbian Learning

- Stochastic dynamics:

$s_i = 1$ with probability $1/(1+\exp(-2h_i/T))$

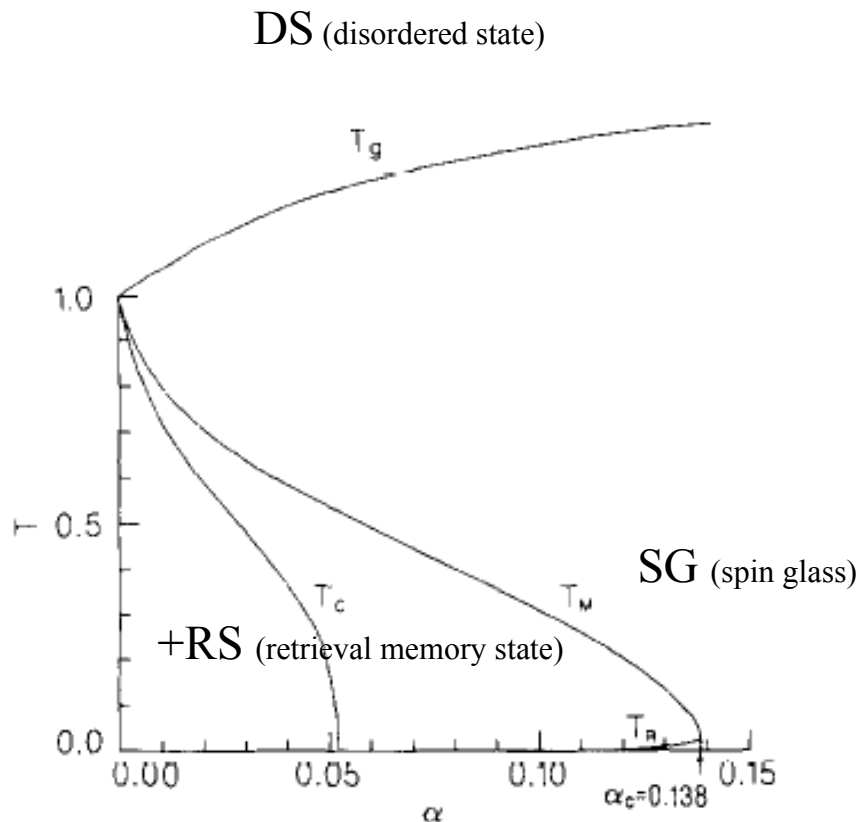
$s_i = -1$ with probability
 $\exp(-2h_i/T)/(1+\exp(-2h_i/T))$

where $h_i = \sum_j w_{ij} s_j$

- This problem can be solved using technique of statistical mechanics of disordered systems:

Hebbian Learning

- Phase diagram in the plane ($\alpha=p/N, T$) (Amit et al., 1987)



Hebbian Learning

- We will check numerically the capacity limit $\alpha_c = p_c/N$ in the tutorial this afternoon

Hebbian Learning

- Generalizations of the Hopfield model
 - Low level of activity
 - Dilution in the connectivity matrix
 - Partial asymmetry in the connections
 - Pattern with correlations
 - Continuous valued units
 - Storing temporal sequences...

Hebbian Learning

- Low level of activity
 - If $\xi = \pm 1$ with equal probability, then the neurons are spiking half of the time
 - In fact the level of activity is much lower
 - $P(\xi=1)=a$; $P(\xi=-1)=1-a$ with $a \ll 1$
- Now the Hebbian learn must be modified to incorporate this level of activity:

$$w_{ij} = (1/N) \sum_{\mu} (\xi_i^{\mu} - a)(\xi_j^{\mu} - a)$$

0

$$w_{ij} = (1/N) \sum_{\mu} \xi_i^{\mu} (\xi_j^{\mu} - a)$$

Hebbian Learning

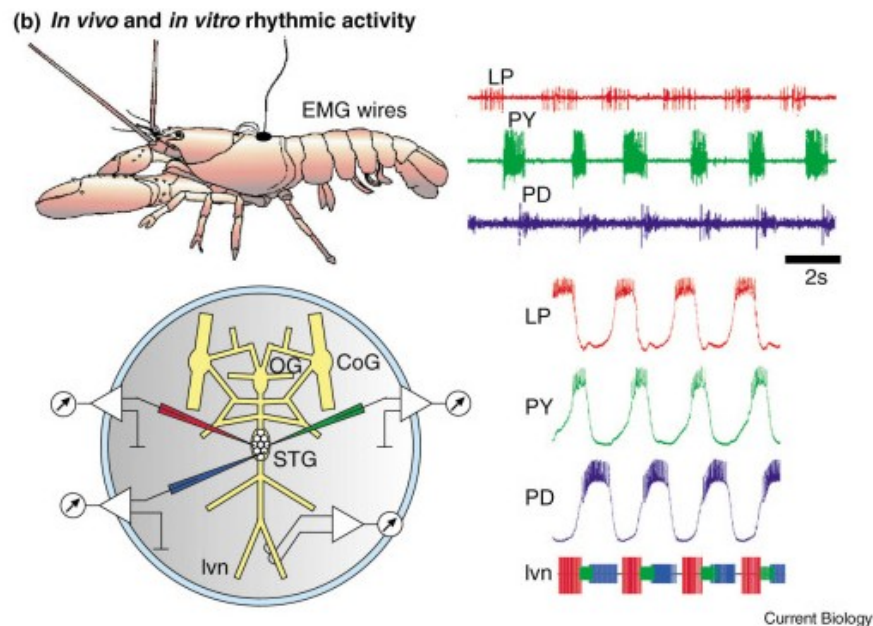
- Low level of activity
 - Both give similar retrieval properties
 - The capacity of the network is

$$p_c \sim -(a \ln(a))^{-1}$$

- The number of stored patterns diverges in the limit $a \rightarrow 0$
- But the amount of stored information remains finite

Hebbian Learning

- Storing temporal sequences
 - Central Pattern Generators (CPG)
 - The output of the network should be a periodic sequence of states, not a fixed point
 - Essential for locomotion, respiration, digestion...



Hebbian Learning

- Storing temporal sequences
 - How could I store a *temporal sequence* in a given network?
 - Patterns ξ_i^μ should appear in order
 - First approach: a non-symmetric matrix of synaptic weights
$$w_{ij}^s = (1/N) \sum_{\mu} \xi_i^{\mu} \xi_j^{\mu}$$
$$w_{ij}^a = (1/N) \sum_{\mu} \xi_i^{\mu+1} \xi_j^{\mu}$$
 - The second term will induce transitions from state μ to state $\mu+1$
 - But they are almost instantaneous.

Hebbian Learning

- Storing temporal sequences
 - The system cannot work as an associative memory
 - We need a *delay*.
 - The state of neuron i at time $t+1$ is chosen according to the sign of
 - $$h_i(t) = \sum_j w_{ij}^s s_j(t) + \lambda \sum_j w_{ij}^a s_j(t-\tau)$$
 - If λ and τ are chosen properly we find that the system stays in a given state the time enough to correct errors

Hebbian Learning

- Storing temporal sequences
 - For instance:

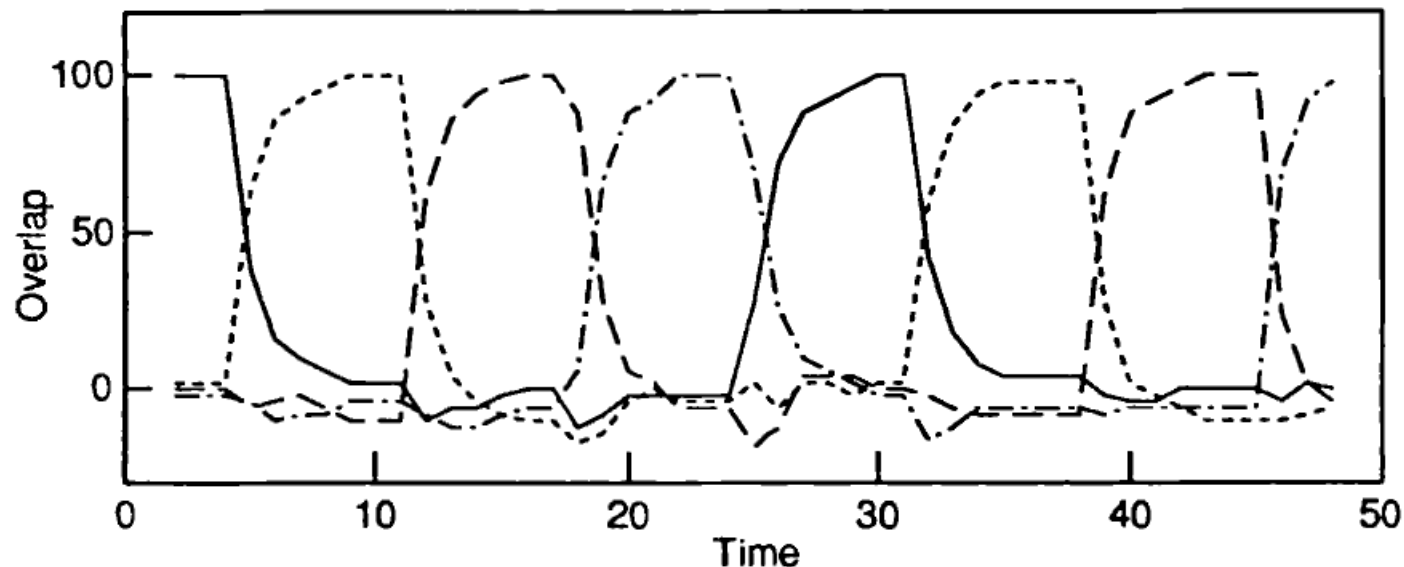


FIGURE 3.10 Example of sequence generation. The curves show the overlap of the state S_i at time t with each of the embedded patterns $\xi_i^1, \xi_i^2, \xi_i^3, \xi_i^4$. The overlaps were calculated using $\sum_i S_i \xi_i^\mu$. The parameters used were $N = 100, p = 4, \lambda = 2, \tau = 8$ using the step function kernel (3.59).

Hebbian Learning

- Storing temporal sequences
 - This is an active theme of research. See for instance *Spike-Based Bayesian-Hebbian Learning of Temporal Sequences*, Tully et al. *PLoS Comp. Biol.* (2016)
 - Here they study how to store temporal sequences in a spike-based network.

Hebbian Learning

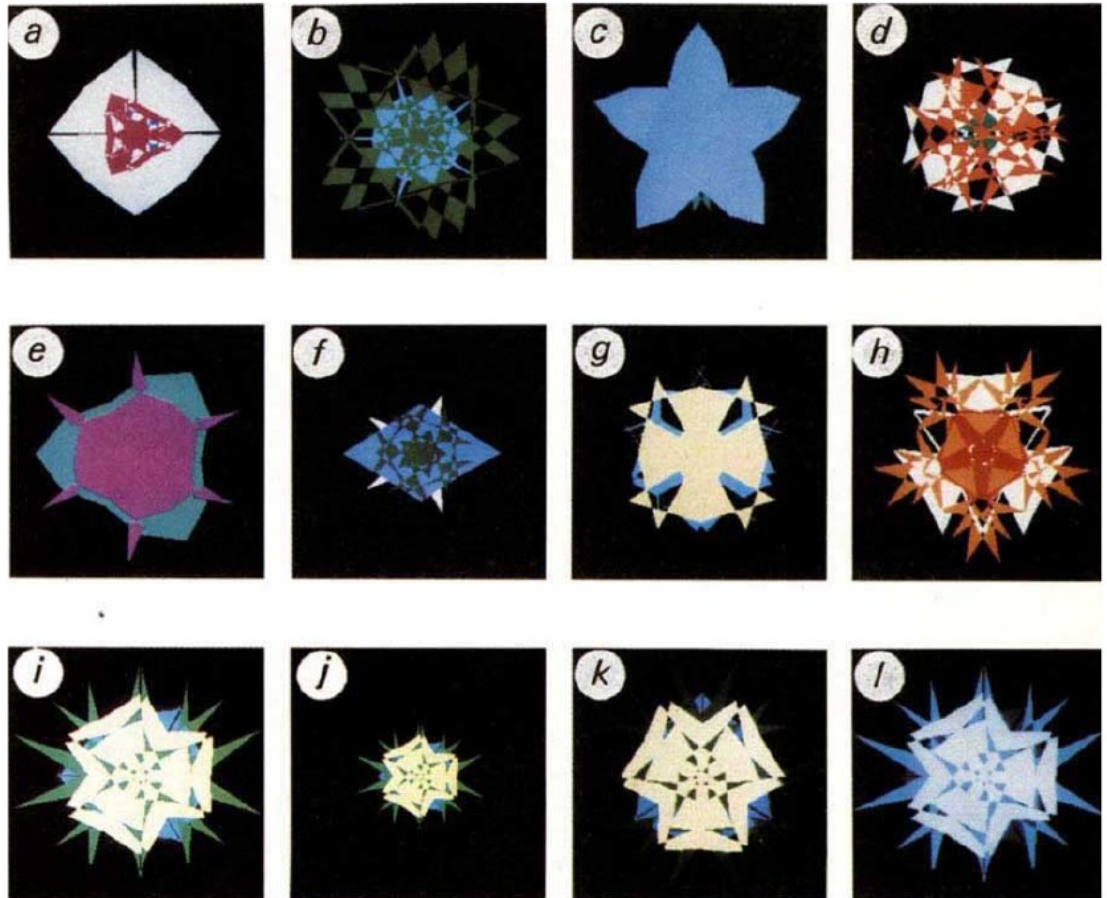
- What is the experimental evidence of the attractor theory for storing memories?
- What should we expect?
 - Some neurons show high firing rate (or at least higher than some baseline value) persistently even after the stimulus has been withdrawn
 - This persistent activity should be selective, i.e., some neurons should display it only for some stimuli but not for others

Hebbian Learning

- Miyashita & Chang: delayed match to sample task
 - One stimulus is briefly presented
 - After a delay period a second stimulus is shown (that can match the previous one or not)
 - The animal has to indicate whether the second stimulus is the same as the first one, receiving a reward if he gives the correct answer
 - During the experiments neuronal activity in the temporal cortex is being recorded

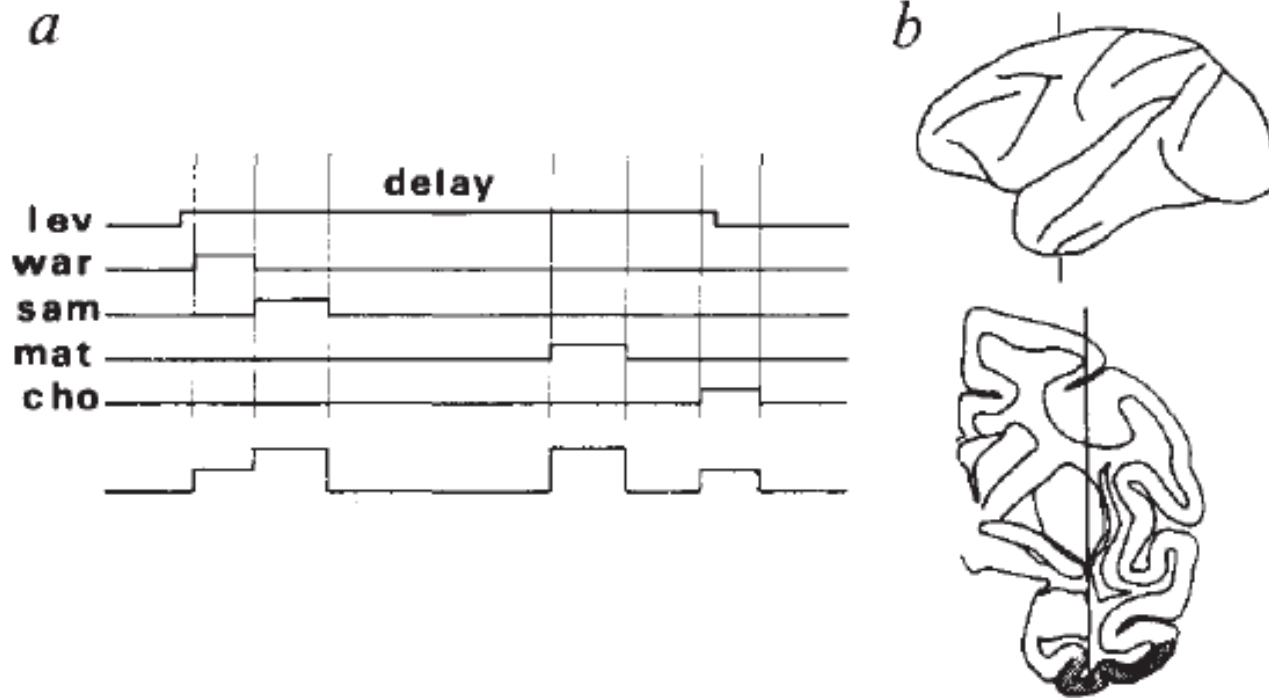
Hebbian Learning

- Miyashita & Chang: delayed match to sample task
 - Stimulus set



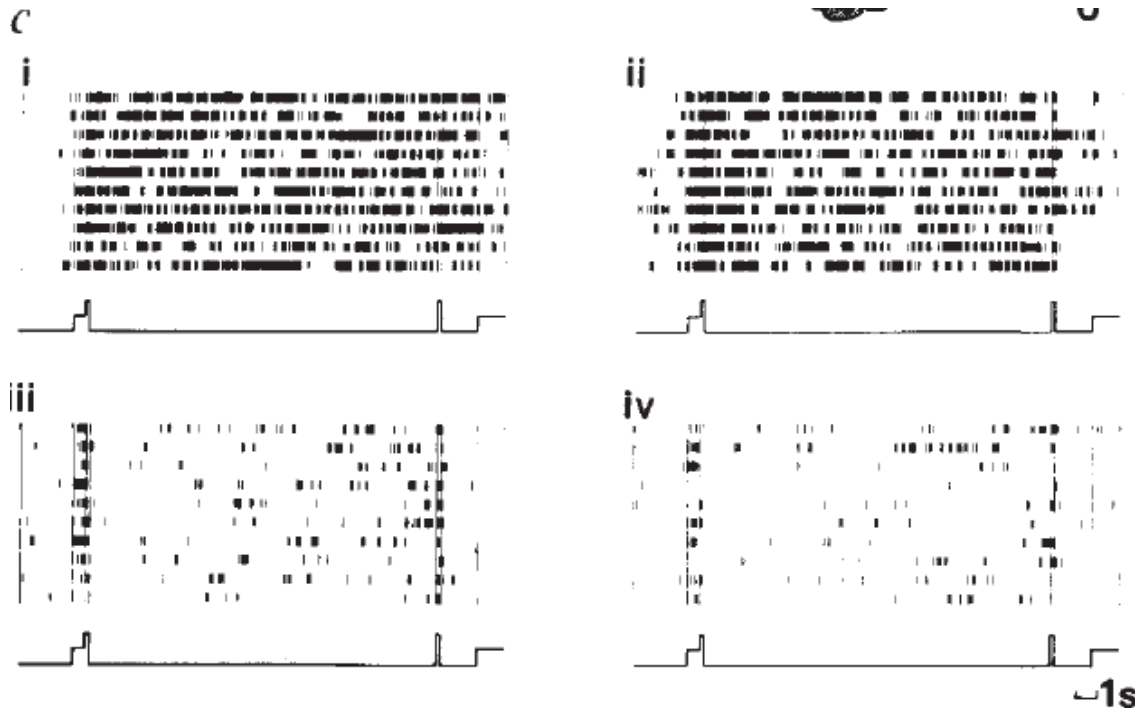
Hebbian Learning

- Miyashita & Chang: delayed match to sample task
 - Task



Hebbian Learning

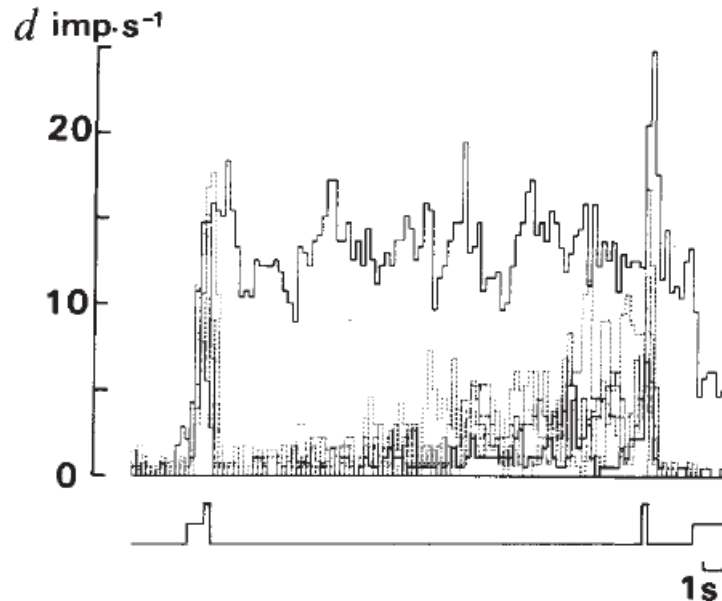
- Miyashita & Chang: delayed match to sample task
- Recordings



- Response of the same neuron to 4 different stimuli

Hebbian Learning

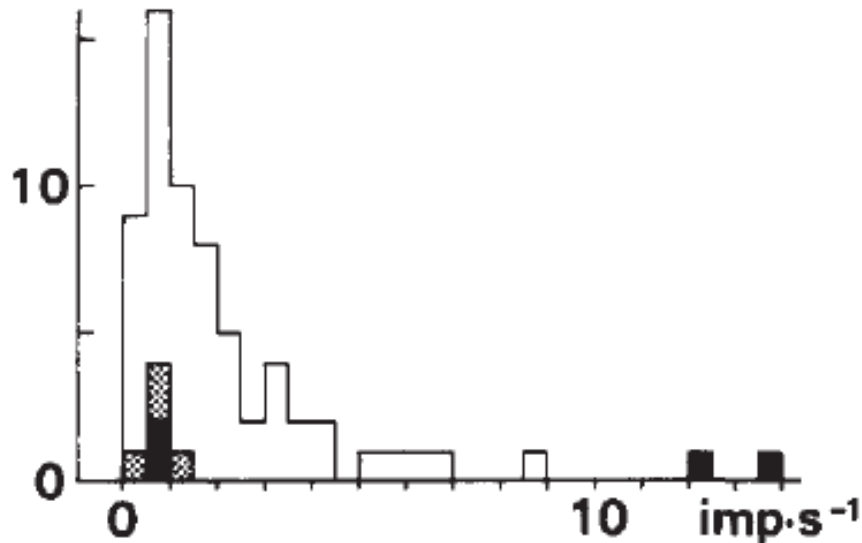
- Miyashita & Chang: delayed match to sample task
 - Recordings



- Averaged responses of the same neuron to 6 different stimuli (one effective and 6 ineffective)

Hebbian Learning

- Miyashita & Chang: delayed match to sample task
 - Recordings



- The code is *sparse*: the number of neurons with high rate during the delay period is very small

Hebbian Learning

- Miyashita (Nature, 1998) later showed that the few patterns for which a neuron was conjointly selective were frequently related to each other through stimulus-stimulus association imposed during training.
- The results indicate that the selectivity acquired by these cells represents a neuronal correlate of the associative long-term memory of pictures.

Learning and Plasticity

- Next lecture:
 - Short-term plasticity
 - Working memory