# Introduction to neural dynamics

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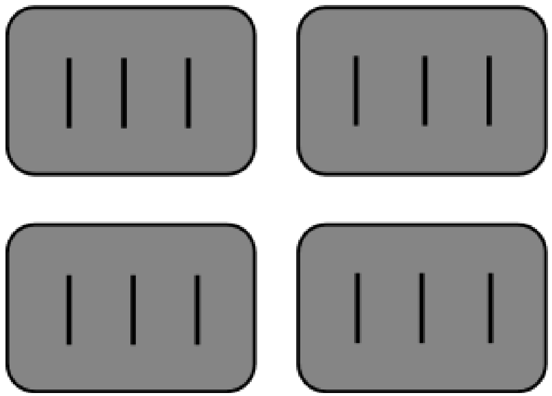
# Summary

- Decision Making
- Perceptual Decision Making in Monkeys
- Competition through Common Inhibition
- Associative Memory
- Memory Recall
- Neuronal Assemblies
- The Hebbian Paradigm
- The Hopfield Model

# Decision Making

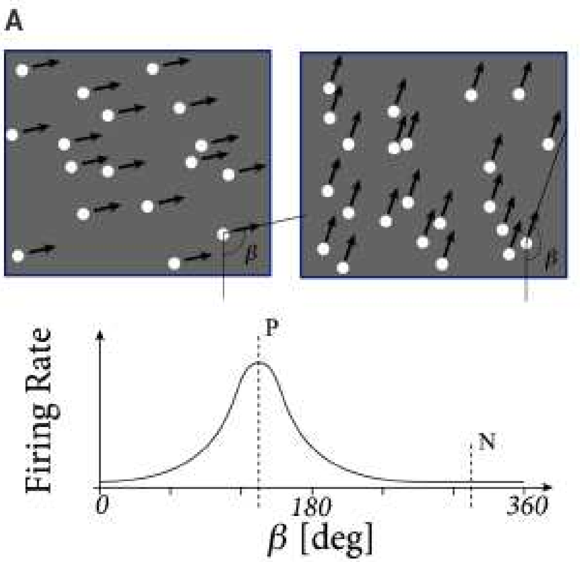


A subject should decide based on a short flash of three vertical black bars on a gray background if :

- Is the middle bar shifted to the left or to the right compared to a symmetric arrangement of the three bars where it is exactly in the center?
- The subject who holds a button in each hand, indicates his decision (left or right) by pressing the corresponding button.

If the shift is very small, or if the bars are presented with low contrast on a noisy screen, the question is difficult to answer. The subject reports his perception as a decision

# Perception of Motion




- Neurons in the middle temporal visual area (MT) are activated by stimuli in motion
- Different neurons in MT respond to different directions of motion, but just as in other parts of visual cortex, area MT has a columnar structure so that neighboring neurons have a similar preferred direction of motion
- At the beginning of a typical recording session with an extracellular electrode in MT, the preferred direction of motion of a single neuron or cluster of neighboring neurons is determined by varying the movement angle of the random dot stimulus.
- Once the receptive properties of the local MT neurons have been determined, only two different classes of stimuli are used, i.e., dots moving coherently in the preferred direction of the recorded neuron, and dots moving coherently in the opposite direction

# Saccade

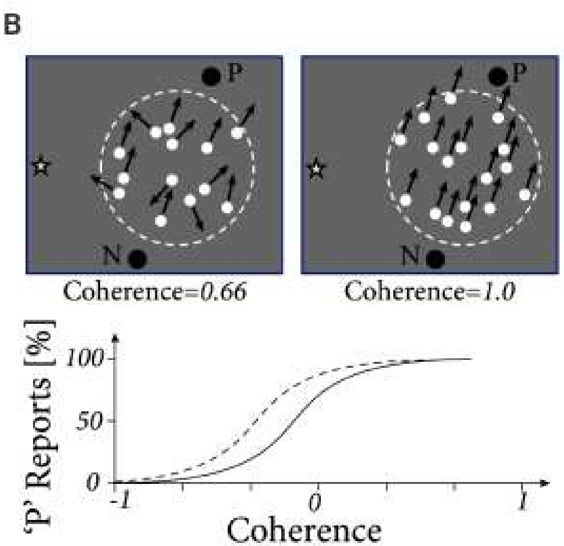
Wikipedia

- A saccade is a quick, simultaneous movement of both eyes between two or more phases of fixation in the same direction.
- When scanning immediate surroundings or reading, human eyes make saccadic movements and stop several times, moving very quickly between each stop. The speed of movement during each saccade cannot be controlled; the eyes move as fast as they are able.
- One reason for the saccadic movement of the human eye is that the central part of the retina, which provides the high-resolution portion of vision is very small in humans, only about 1–2 degrees of vision, but it plays a critical role in resolving objects.
- It is more efficient to move the eye so that small parts of a scene can be sensed with greater resolution, than by turning the head

FILM

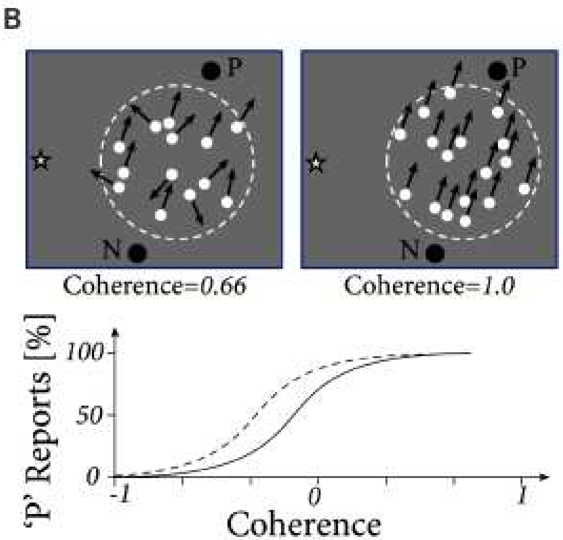
# Perceptual Decision Making in Monkeys

- The stimulus consists of a random pattern of moving dots, where most, but not necessarily all, of the dots move coherently in the same direction
- Two different directions of motion are used, e.g., upward or downward, in the preferred (opposite) direction of the recorded neurons
- The monkey has been trained to indicate the perceived motion direction by saccadic eye movements to one of two targets




- In the first phase of each trial, the monkey fixates on the star while a moving random dot stimulus is presented inside the receptive field (dashed circle) of a neuron.
- After visual stimulation is switched off, the monkey indicates by eye movements to one of the two targets (filled black circles, marked P and N) whether the perceived motion is in the direction 'P' or 'N'.

# Perceptual Decision Making in Monkeys




- The behavioral performance can be assessed with the psychometric function which represents the percentage of saccades to the target P as a function of coherence
- Coherence is the fraction of coherently moving dots
  - Coherence = 1 : all points move in the P direction
  - Coherence = 0.66 : 1/3 of the points move in a random direction
  - Coherence = -1 : all points in the 'N' direction
- An electrode in MT cannot only be used to record neural activity, but also to stimulate a cluster of neurons in the neighborhood of the electrode.
- Since neighboring neurons have similar preferred directions of motion, current injection into the electrode can bias the perception of the monkey in favor of the neurons' preferred direction, even if the random dot pattern has no or only a small amount of coherence

This indicates that the perceptual decision of the monkey relies on the motion information represented in the activity of MT neurons

# Perceptual Decision Making in Monkeys

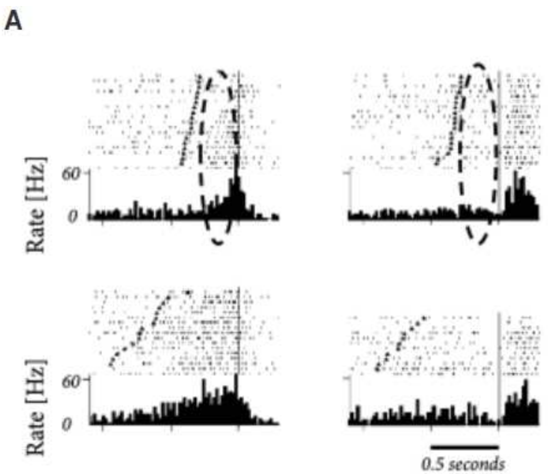
The monkey's perceptual decision is influenced by the stimulation of MT neurons, this result does not imply that the decision itself is made in MT. It is likely to be made at a later stage, in an area that uses the information of MT neurons

The experiment by Roitman & Shadlen

- The measurements are now done in the Lateral Intra-parietal Area (LIP) during experiments of perceptual decision making with moving random dot stimuli
- Area LIP is located in the visual processing stream between primary visual cortex and the Frontal Eye Field region involved in the control of saccadic eye movements
- Neurons in area LIP respond during the preparation of saccadic eye movements
- Different neurons in LIP have different receptive field field corresponding to a target region of eye movements.
- A LIP neuron responds just before a saccadic eye movement into its receptive field occurs.

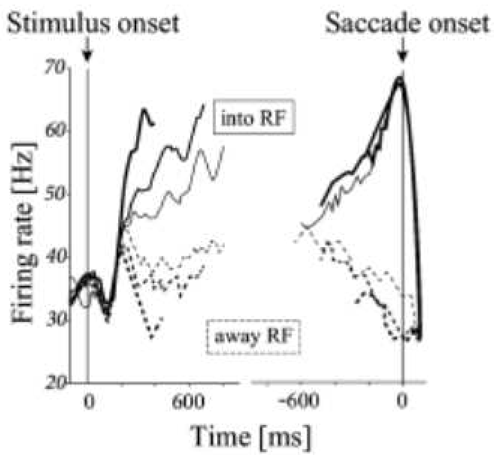
# The experiment by Roitman & Shadlen

- Monkeys are trained to indicate the direction of a moving dot pattern by saccadic eye movements to one of two visual targets
- The first target is located in the receptive field (RF) of a LIP neuron. Therefore, the recorded neuron is expected to respond whenever the monkey prepares a movement to the first target. The second target is located in the opposite direction.
- A random dot stimulus moving in direction of the first target implies that the monkey should make an eye movement toward it; the response to a stimulus moving in the opposite direction is a saccade to the second target




- The LIP neuron response is enhanced (suppressed) just before the saccade, if the saccadic movement is into (away from) its RF ( left right )
- Responses were faster for stimuli with larger coherence (top 51.2%) than smaller coherence (bottom 6.4%),
- Filled triangles indicate onset of motion stimulus.

# The experiment by Roitman & Shadlen



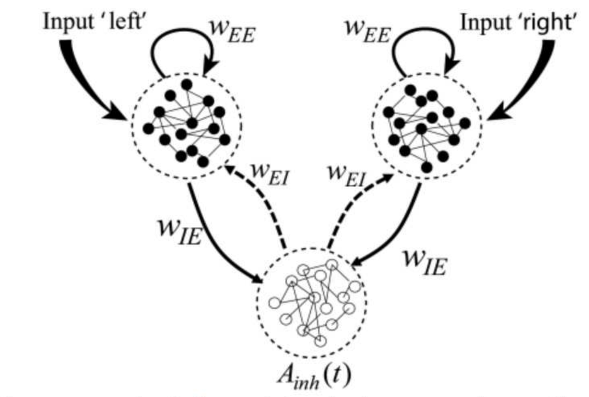

- Firing rate response of LIP neurons (averaged over 54 neurons) aligned to stimulus onset (left) or saccade onset (right).
- The stronger the coherence (solid lines: coherence 51.2%, 12.8% and 3.2%) of a random dot motion stimulus initiating a saccade 'into' the RF the faster the rise of the response of LIP neurons (left)
- Whatever the coherence, the LIP neurons always reach the same firing rate, at the moment when a saccade into the RF starts (right).
- The neurons activity are suppressed, if the monkey chooses the opposite saccadic target 'away RF' (dashed lines)

Conclusions

The decision to perform a saccade is taken when the firing rate of LIP neurons reaches a threshold value
For stimuli with higher coherence, the firing increases more rapidly, the threshold is reached earlier, and reaction times are shorter than for stimuli with lower coherence.

# Competition through common inhibition

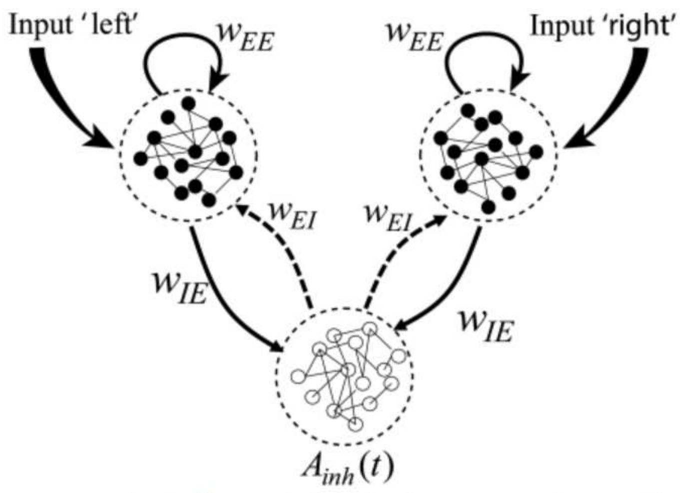
The essential features of the experiments of Roitman & Shadlen can be described by a simple model of decision making where neuronal populations compete with each other through shared inhibition




- A network of spiking neurons made of 2 excitatory populations interacting via a common pool of inhibitory neurons
- The neurons are randomly connected with synaptic coupling $w_{EE}$ within the excitatory populations and with coupling $w_{IE}$ ($w_{EI}$) to (from) the inhibitory population

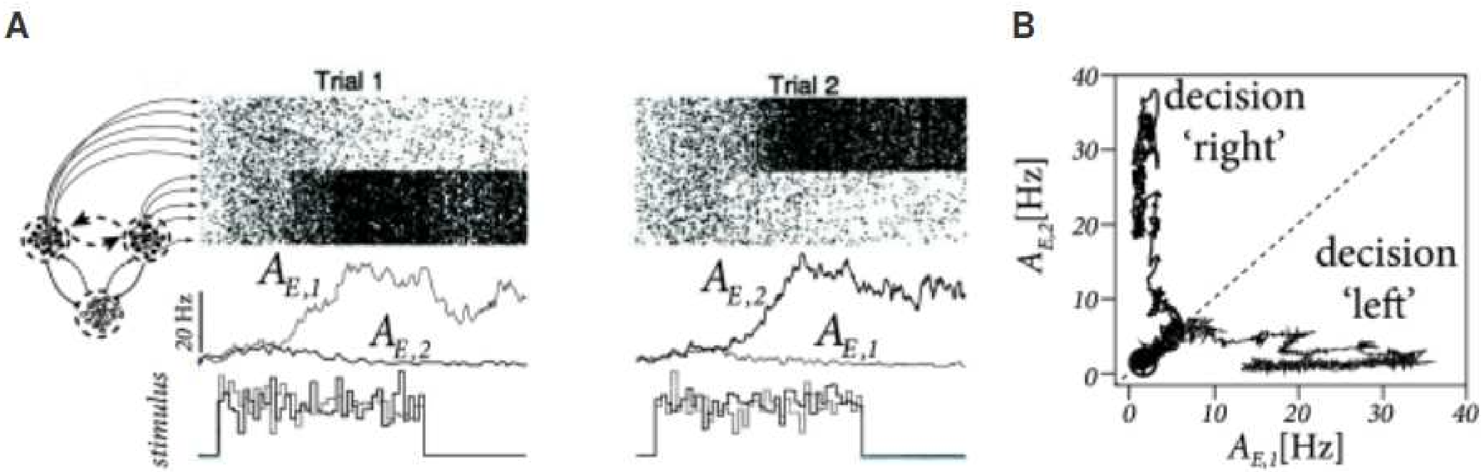
- The parameters are chosen such that in absence of stimulation all neurons exhibit spontaneous activity at low firing rates: asynchronous irregular firing
- Stimulation corresponds to a positive mean input into one or both excitatory populaions
- Input into population 1 (2) indicates coherent motion of the random dot pattern to the left (right)
- Since the stimulus in the experiments has a random component, the input into each population is described as a mean plus some noise

# Competition through common inhibition



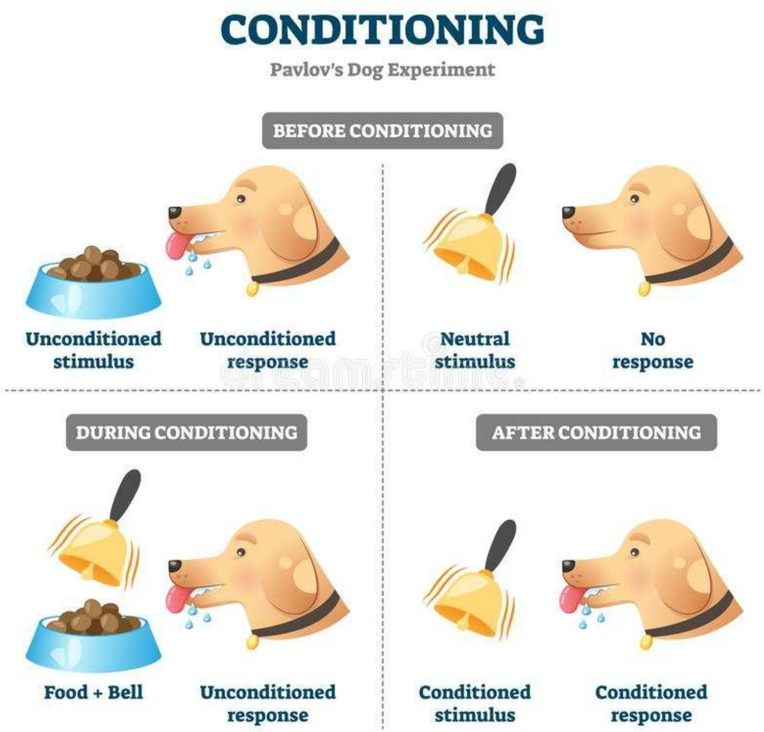

- If the pattern has a high degree of coherence and moves to the left, the mean input to population 1 is high. This induces a high activity $A_{E,1}$ which in turn excites the inhibitory population which transmits inhibition to both excitatory pools.
- Only the stimulated pool can overcome the inhibition so that the activity of the other excitatory population is suppressed
- At most one of the two populations can be active at the same time: the two populations are said to compete with each other.
- The competition is induced by the shared inhibition. If the external stimulus favors one of the two populations, the population receiving the stronger stimulus wins the competition.

# Competition through common inhibition




- To highlight the dynamics of competition, let us now focus on a strong, but unbiased stimulus : after stimulus onset, both excitatory populations receive an input of the same mean, but with a different noise realization
- Immediately after the onset of stimulation, both excitatory populations increase their firing rates.
- Soon afterward, however, one of the activities grows further at the expense of the other one, which is suppressed
- The population which develops a high activity is called the winner of the competition

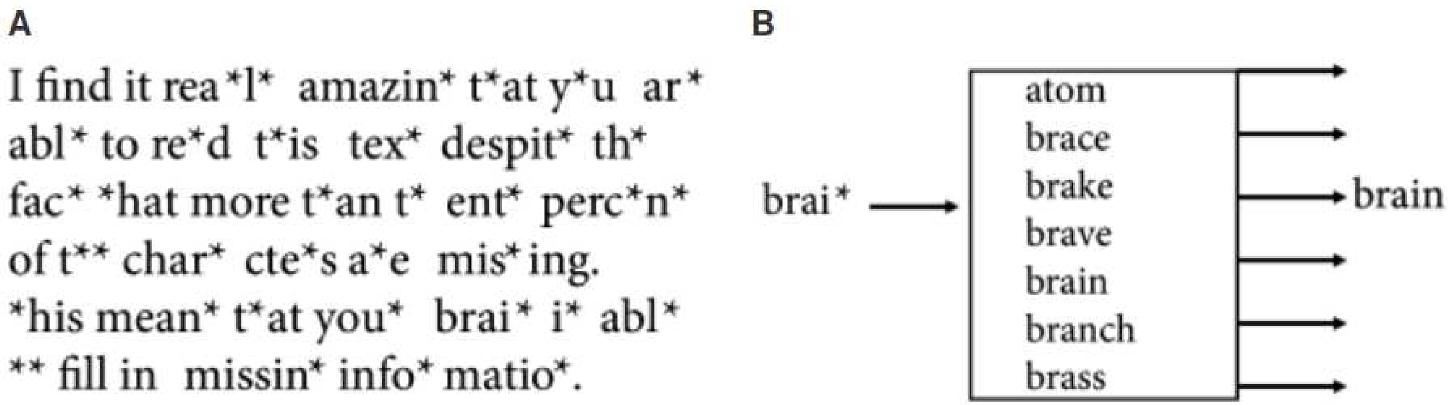
# Associative memory and attractor dynamics




- Memory works with associations. If you hear the voice of an old friend on the phone, you may spontaneously recall stories that you had not thought of for years.
- If you are hungry and see a picture of a banana, you might vividly recall the taste and smell of a banana . . . and thereby realize that you are indeed hungry.

A model of neural networks that describe the recall of previously stored items from memory is the Hopfield Model

# Associations and memory




- Memory recall works on association in the sense of completing partial information
- Nearly all words are incomplete, but your brain is able to cope with this situation,
- As you are able to follow a phone conversation over a noisy line, recognize a noisy image of a handwritten character or associate the picture of an orange with its taste so as retrieve your concept of an orange as a tasty fruit.
- Memory Recall : An incomplete word is compared to a list of all possible words. The most likely entry (i.e. the one which is most similar to the input) in the list is given as the output of memory recall.

# Memory Recall

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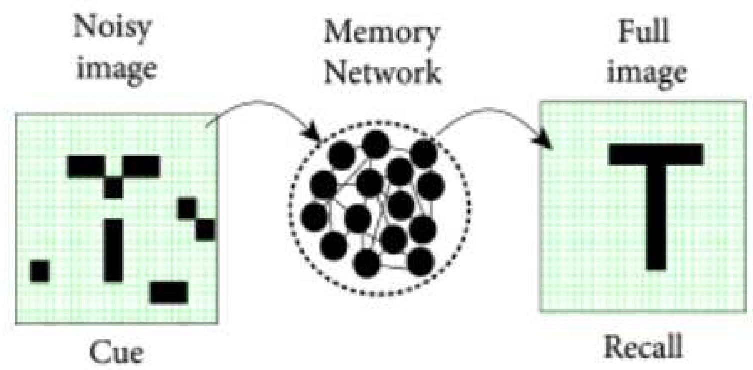
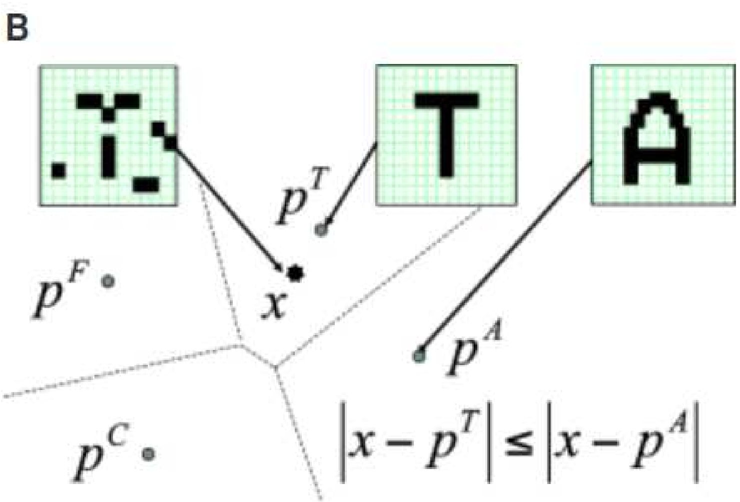



Noisy images of objects are recognized if the brain finds, among the memorized items, one which is highly similar

- Let us imagine that in your memory there are many memory items $p^{\mu}$ , where $\mu = A.B.C, \ldots T, \ldots$ are the possible noise-free letters stored in your memory.
- The memory items $p^{\mu}$ can be seen as points in some space $A$
- A noisy image (cue) $x$ corresponds to another point in the same space $A$
- How can I determine to which of the stored items $p^{\mu}$is more similar $x$ ?

# Memory Recall




- One should determine the distance of $x$ from all the memory items : $|x - p^\mu|$
- And determine the one at smallest distance

$$|x - p^T| \leq |x - p^\mu| \quad \forall \mu$$

- The interactions of neurons in the Hopfield Model embedded in a large network will find the item that corresponds best to the noisy cue without implementing any algorithm

# Neuronal Assemblies

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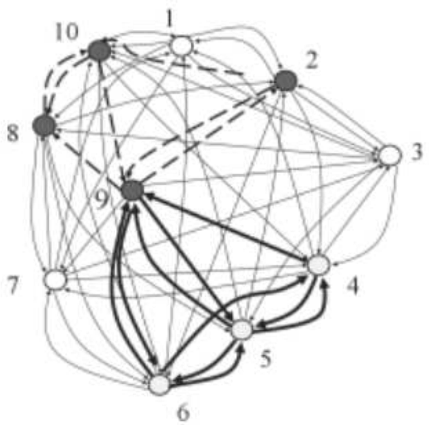
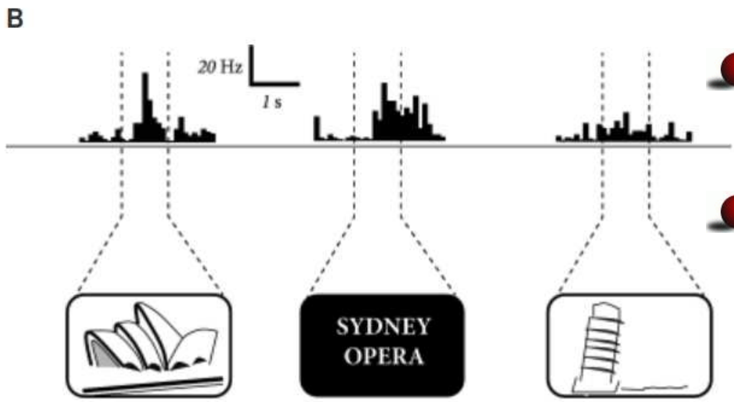



- Neuronal assemblies are sub-networks of strongly connected neurons that represent an abstract concept
- For example, your mental concept of a ‘banana’ containing the mental image of its form, color, taste and texture could be represented by one assembly of strongly connected neurons, while another one might represent your concept of Sydney with its famous opera house.
- Neurons belonging to an assembly do not have to be neighbors but can be widely distributed across one, or even several, brain areas

# The Quiroga et al. experiment (2005)




- Response of a single neuron in human hippocampus
- The same neuron responds strongly to an image of the Sydney opera house and the words Sydney opera, but much more weakly to images of other landmarks such as the Pisa tower

Three aspects are worth emphasizing.

- It is unlikely that the neuron responding to the Sydney opera house is the only one to do so. Therefore, we should not think of a single neuron as representing a concept or memory item, but rather a group of neurons
- The same neuron participates in several assemblies. In the experiments with a large collection of pictures of famous individuals and landmarks were used, each neuron showed strong responses to about 3 % of the stimuli
- Some, but not all, of the neurons showed prolonged responses that persisted after the end of stimulus presentation. This could potentially indicate that a memory item is retrieved and kept in the brain even after the stimulus has disappeared

R. Q. Quiroga et al. (2005) Nature 435, pp. 1102

# The Quiroga et al. experiment (2005)

**Figure 1: A single unit in the left posterior hippocampus activated exclusively by different views of the actress Jennifer Aniston.**


R. Q. Quiroga et al. (2005) Nature 435, pp. 1102

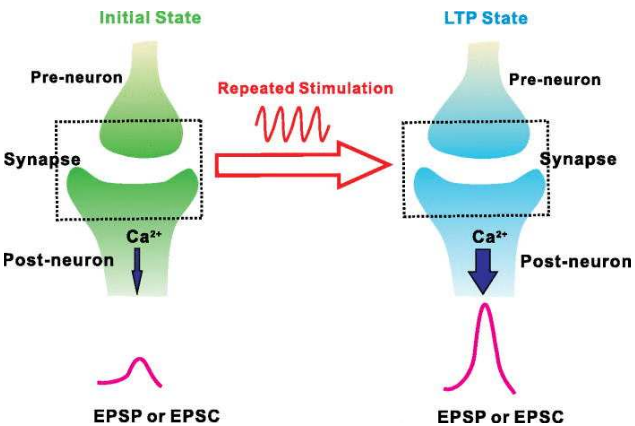
# The Hebbian Paradigm

In his 1949 book The Organization of Behavior, Donald Hebb predicted a form of synaptic plasticity with the following property:

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

Hebbian plasticity

In 1979 the phenomenon of long-term potentiation (LTP) was discovered, where the synapses conecting two neurons get potentiated whenever the two neuron fire together repetively.




- The EPSC/ EPSP amplitude get larger : the synaptic weights $W_{ij}$ get stronger

# The Hopfield Model

This is a neural network model, where Hebbian plasticity is used to store memory items

- A fully connected network of $N$ binary neurons $s_i$
  - active $s_i = +1$
  - inactive $s_i = -1$
- Neuron $j$ send a action potential to neuron $i$ with a synaptic weight $W_{ij}$ $(W_{ii} = 0)$
- The input postsynaptic potential stimulating neuron $i$ is $h_i(t) = \sum_{j=1}^{N} W_{ij} s_j(t)$
- The simultaneous update rule for the dynamics of the $N$ neurons is given by

$$s_i(t + \Delta t) = sgn\,(h_i(t)) = sgn\left(\sum_{j=1}^{N} W_{ij} s_j(t)\right) \qquad i = 1, \ldots, N$$

- A memory item to store in the network is represented by the value that the neurons should take in the network a pattern :

$$\xi^{\mu} = (+1, -1, +1, +1, -1, \ldots, -1)$$

# The Hopfield Model - Learning Phase

The network is firstly trained to recognize $P$ different patterns $\xi^\mu \quad \mu = 1, \ldots, P$ for a learning phase where initially the synaptice weights are set all to zero $W_{ij} = 0$

- The neuron values $\{s_i\}$ are set equal to those of the patterns $\{\xi_i^\mu\}$ in sequence
- Synaptic weights are updated with the Hebbian rule for each new presented pattern $\xi^\mu$

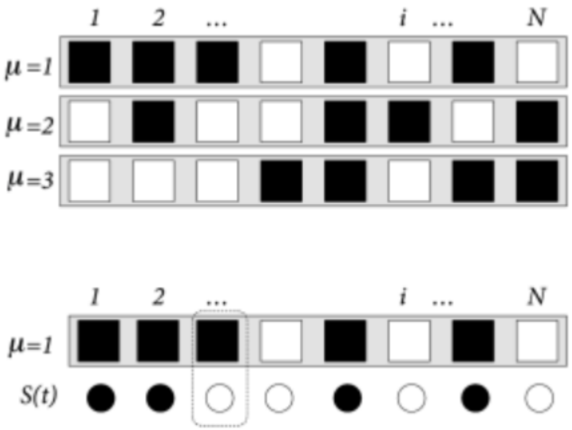
$$W_{ij} \to W_{ij} + \eta s_i s_j = W_{ij} + \eta \xi_i^\mu \xi_j^\mu \quad \eta > 0$$

  - The synapses is potentiated by $+\eta$ is the neurons are both active or inactive
  - The synapses is depressed by $-\eta$ if one neuron is active and the other inactive
- At the end of the learning phase we will obtain

$$W_{ij} = \frac{1}{N} \sum_{\mu=1}^{P} \xi_i^\mu \xi_j^\mu \qquad \eta = \frac{1}{N}$$

The Hopfield model works as an associative memory , if the network is initialized with a corrupted version of the pattern, the network converge to the complete pattern

# The Hopfield Model - Single Pattern




Let us suppose to store a single pattern in the network $(\xi_1, \xi_2, \ldots, \xi_N)$

- the synaptic weights are $W_{ij} = \frac{1}{N}\xi_i \xi_j$
- The evolution is

$$s_i(t + \Delta t) = sgn(\xi_i \frac{1}{N} \sum_{j=1}^{N} \xi_j s_j) = sgn(\xi_i m)$$

Where $m = \frac{1}{N} \sum_j \xi_j s_j$ is the overlap between the state $s$ and the pattern $\xi$ :

- In the figure $m = \frac{N-2}{N} = \frac{6}{8} = 0.75$
- If $s = \xi$ then $m = +1$ – If $s = -\xi$ then $m = -1$ - These are fixed points
- Since $s_i = \xi_i = sgn(+\xi_i)$ and $s_i = -\xi_i = sgn(-\xi_i)$

If I consider the case $\{s_i = \xi_i\}$ and I change sign to the first neuron $s_1 = -\xi_1$ the overlap will be $m = \frac{N-2}{N} > 0$ therefore $s_1(t + \Delta t) = sgn(\xi_1 m) = sgn(\xi_1)$

In one step the pattern is recoverered, therefore it is attractor for the dynamics: a stable fixed point

# The Hopfield Model - Many Patterns

If I store $P$ patterns $\xi^\mu \quad \mu = 1, \ldots, P$ in the network the synaptic coupling matrix will be

$$W_{ij} = \frac{1}{N} \sum_{\mu=1}^{P} \xi_i^\mu \xi_j^\mu$$

we can introduce $P$ overlap functions with the actual state $\{s_i(t)\}$ of the network as

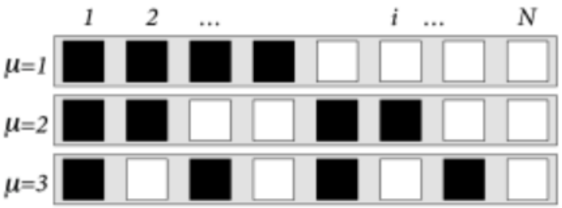
$$m^\mu(t) = \frac{1}{N} \sum_{i=1}^{N} s_i(t) \xi_i^\mu$$

The evolution dynamics is given by

$$s_i(t + \Delta t) = sgn(\sum_{\mu=1}^{P} \xi_i^\mu m^\mu(t))$$

the overlaps $m^\mu(t)$ completely determine the dynamics of the network

# Memory Retrivial




Let us suppose that the initial state $\{s_i(t=0)\}$ is orthogonal to all the stored patterns apart the pattern $\mu = 3$ i.e.

- $m^{\mu}(0) = 0 \quad \forall \mu \neq 3$ orthogonal
- $\mu^3(0) = 0.4$ significant overlap

The evolution of the neuronal dynamics is given in this case by

$$s_i(t+\Delta t) = sgn\left(\sum_{\mu=1}^{P} \xi_i^{\mu} m^{\mu}(t)\right) = sgn\left(\xi_i^3 0.4\right) = \xi_i^3 \quad \forall i$$

Hence, each neuron takes, after a single time step, the desired state corresponding to the pattern.
In other words, the pattern with the strongest similarity to the input is retrieved, as it should be.

# Memory Capacity

Which is the maximal number of patterns that can be stored in a network of $N$ neurons ?

- Memory retrieval implies pattern completion, starting from a partial cue
- A minimal condition for pattern completion is that at least the dynamics should not move away from the pattern, if the initial cue is identical to the complete pattern
- A network with initial state $s_i(t_0) = \xi_i^\nu$ for $i \leq i \leq N$ should remian in the pattern $\xi^\nu$
- Therefore pattern $\xi^\nu$ must be a fixed point under the dynamics.

We insert $s_j(t_0) = \xi_j^\nu$ in the dynamics and we get

$$s_i(t_0 + \Delta t) = sgn\left(\frac{1}{N}\sum_{j=1}^{N}\sum_{\mu=1}^{P}\xi_i^\mu\xi_j^\mu\xi_j^\nu\right) = \xi_i^\nu\, sgn\left(1 + \frac{1}{N}\sum_{j=1}^{N}\sum_{\mu\neq\nu}\xi_i^\mu\xi_i^\nu\xi_j^\mu\xi_j^\nu\right)$$

# Memory Capacity

$$s_i(t_0 + \Delta t) = \xi_i^\nu \, sgn\,(1 + a_i^\nu)$$

where $a_i^\nu = \frac{1}{N}\sum_{j=1}^{N}\sum_{\mu\neq\nu}\xi_i^\mu\xi_i^\nu\xi_j^\mu\xi_j^\nu$,

- If $1 + a_i^\nu > 0$ i.e. $a_i^\nu < -1$ The fixed point is stable
- Even if the network is initialized in perfect agreement with one of the patterns, it can happen that one or a few neurons flip their sign.
- The probability to move away from the pattern is equal to the probability of finding a value $a_i^\nu > 0$ for one of the neurons $i$

The capacity is the maximal number of patterns $P^{max}$ that can be stored in a network of $N$ neurons

$$C = \frac{P^{max}}{N} \simeq 0.138$$

D. J. Amit, H. Gutfreund and H. Sompolinsky (1985) Phys. Rev. Lett. 55, pp. 1530{1533.

# Bibliography


- Neuronal Dynamics (online book): From single neurons to networks and models of cognition, Wulfram Gerstner, Werner M. Kistler, Richard Naud and Liam Paninski
- Roitman, Jamie D., and Michael N. Shadlen. Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task Journal of neuroscience 22.21 (2002): 9475-9489.
- RQ Quiroga, L Reddy, G Kreiman, C Koch, I Fried Invariant visual representation by single neurons in the human brain Nature 435 (7045), 1102-1107
- Hopfield, J. J. (1982) Neural networks and physical systems with emergent collective computational properties Proc. Nat. Acad. Sci. (USA) 79, 2554-2558.