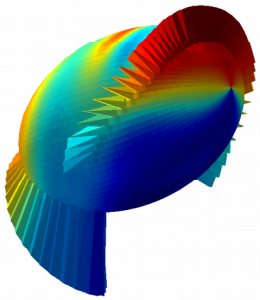
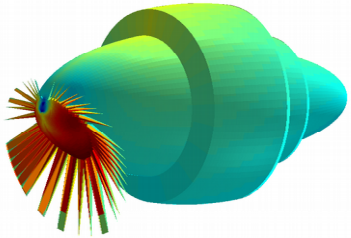
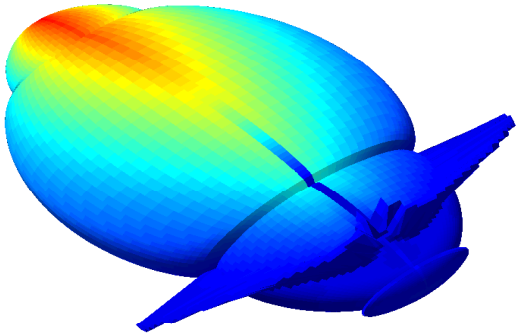
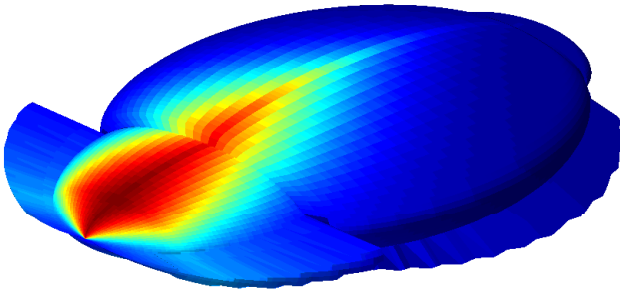


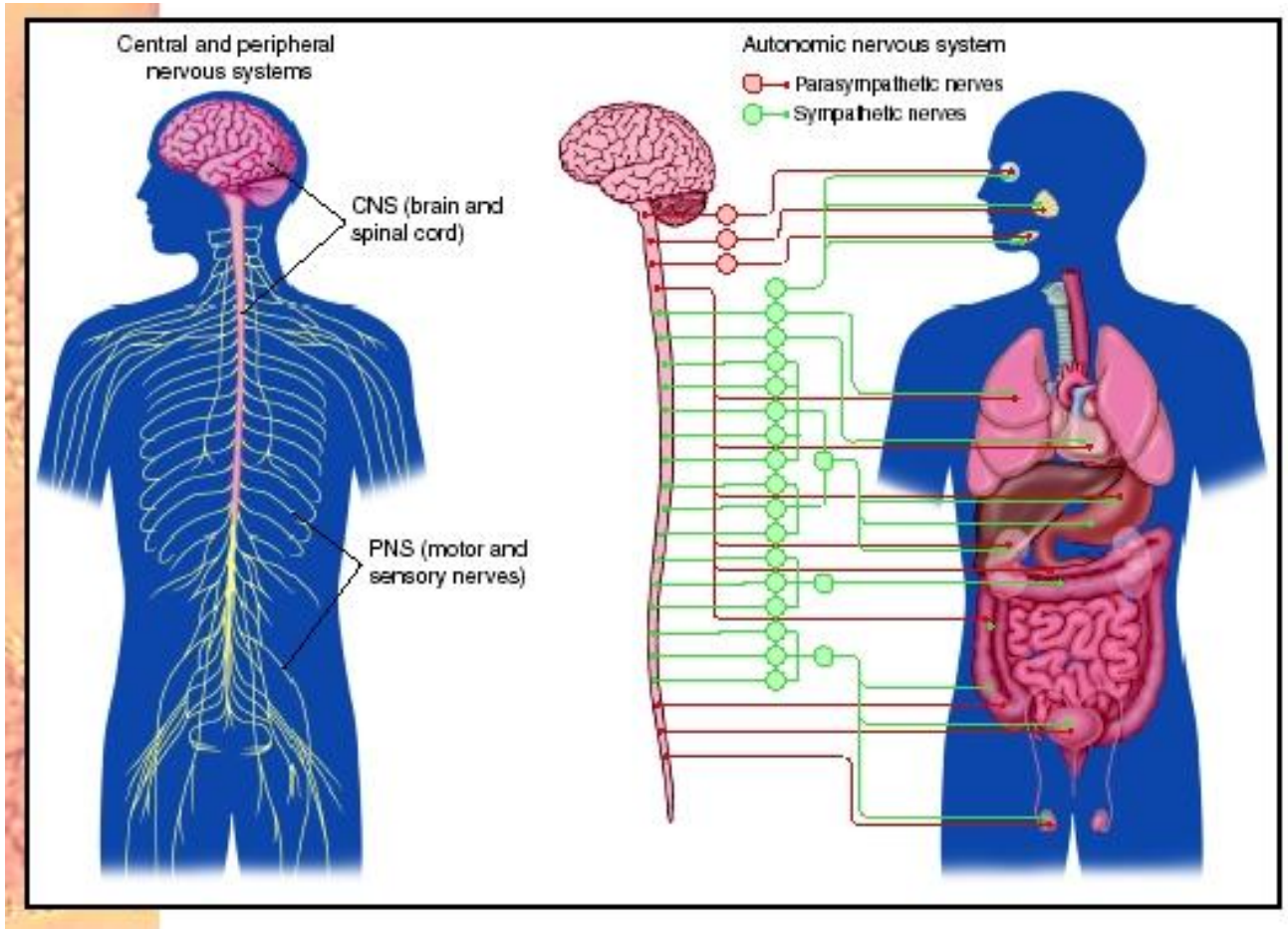


# Lecture 2
# Neural Computation



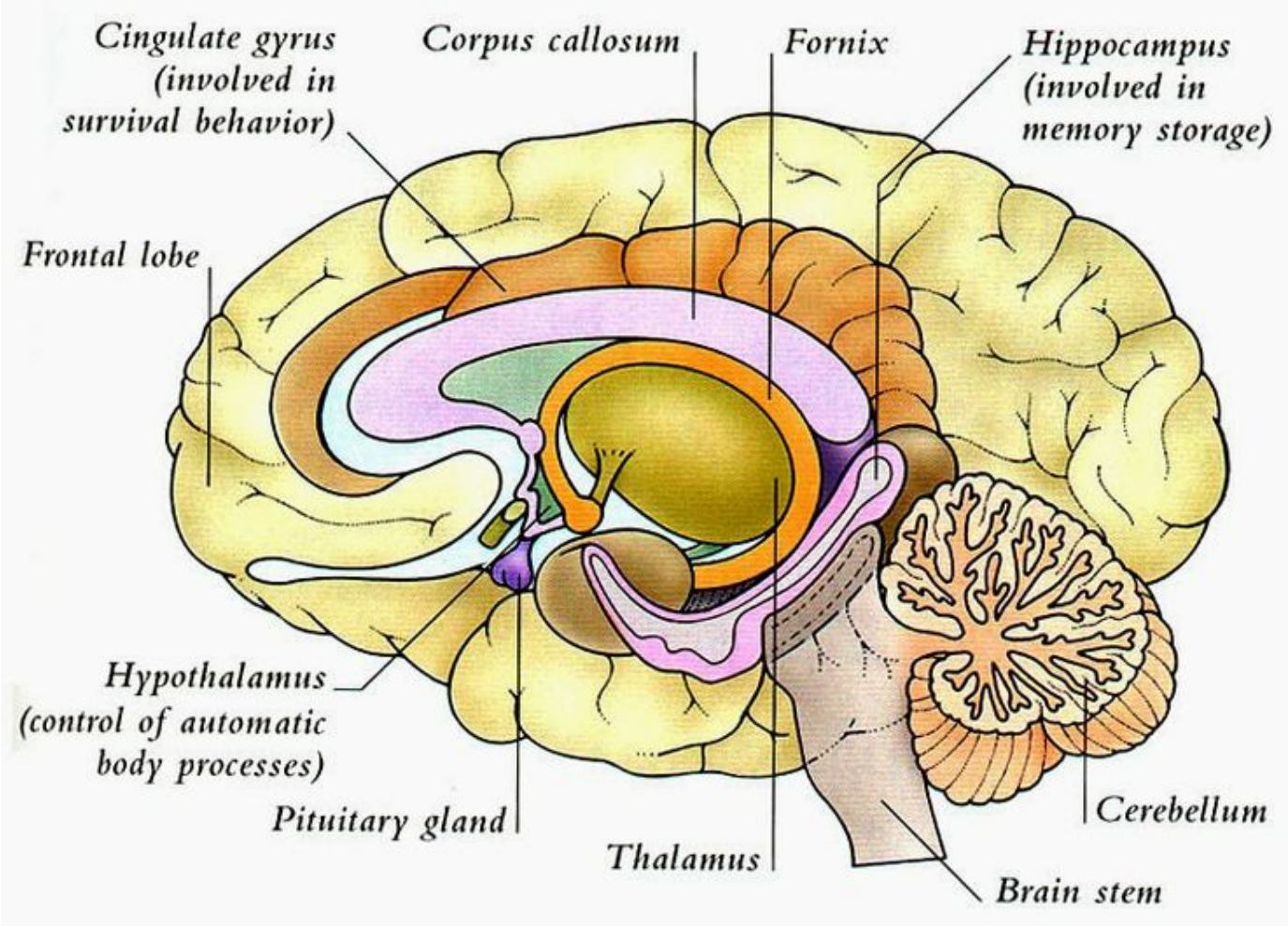


# The Nervous System




http://www.biologyreference.com/images/biol_03_img0336.jpg

# The Brain

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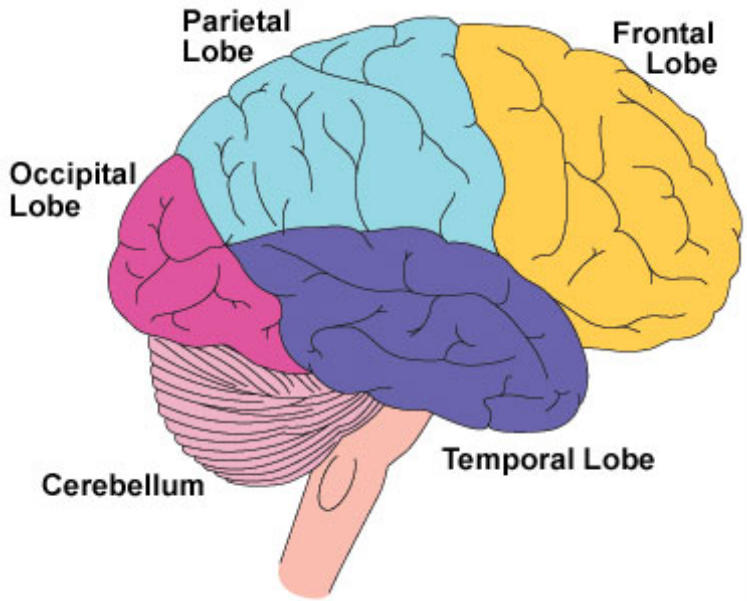
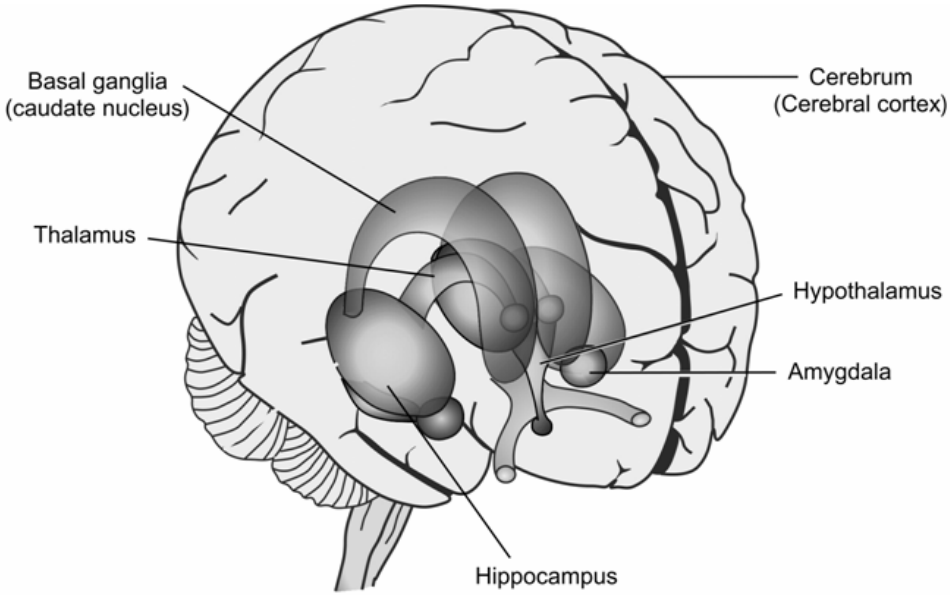



http://www.jodihouse.org/pictures/brain.jpg

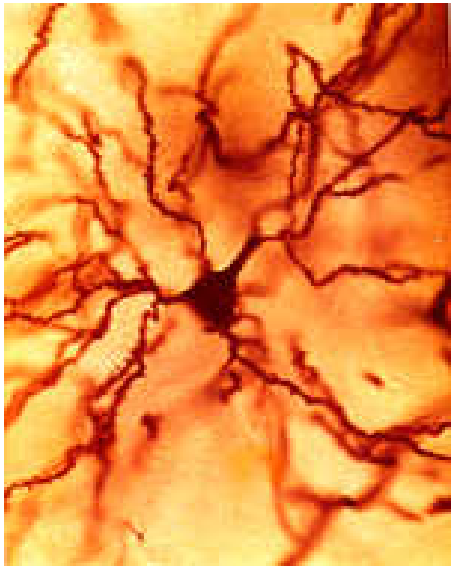
http://www.oecd.org/dataoecd/50/26/15355602.gif




# Brain Architecture

Inner structure of the human brain, including the limbic system.

# Neurons



Cortical Pyramidal Cells

Cerebellar Purkinje Cell

http://faculty.washington.edu/chudler/cellpyr.html

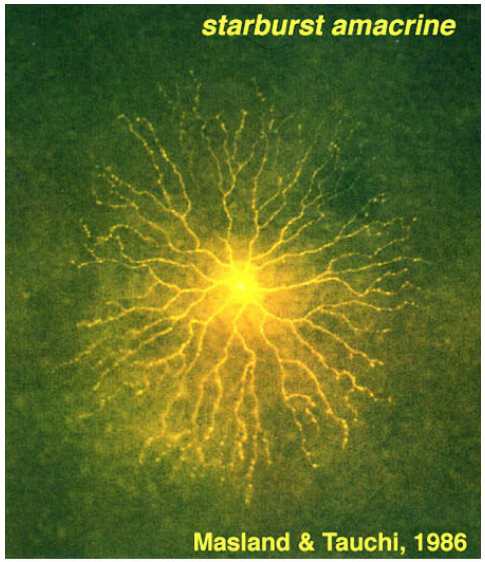


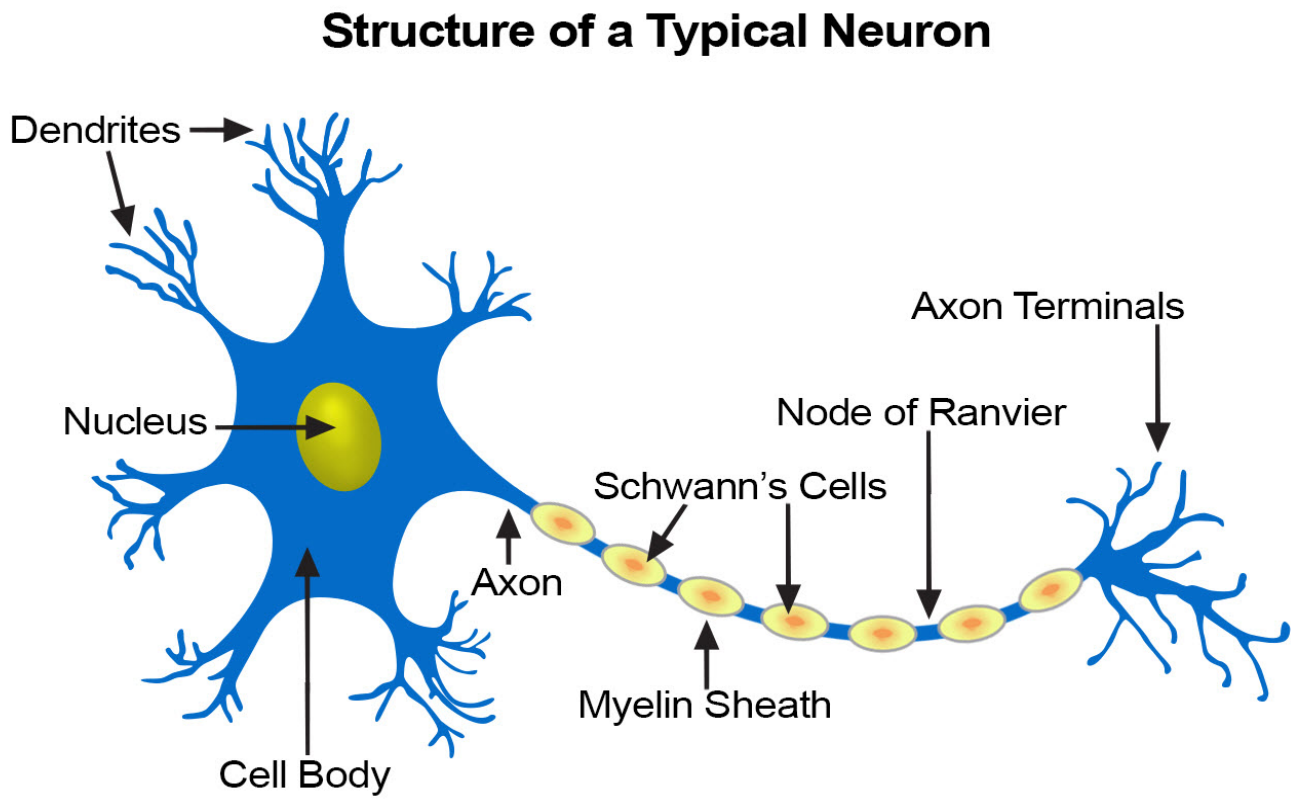

Fig. 36. Lucifer yellow labeling of a starburst amacrine cell in the rabbit retina.

Retinal Amacrine Cell

http://webvision.med.utah.edu/book/part-iv-neurotransmitters-in-the-retina-2/part-iv-neurotransmitters-in-the-retina/

Cool images at:
http://www.neuralimages.org

# Neuron Structure



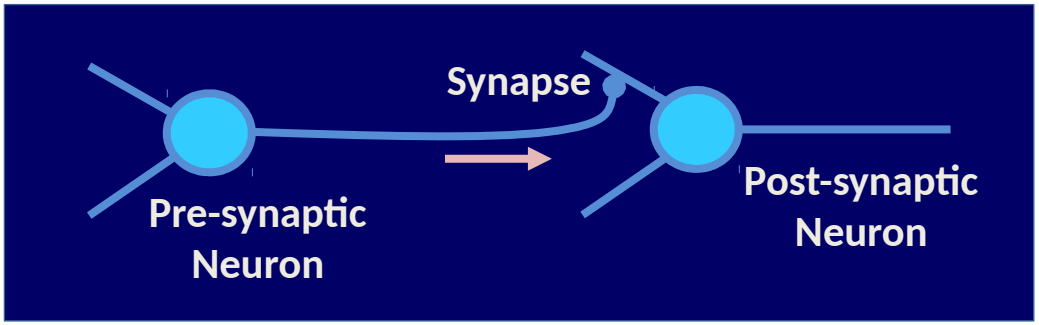

Source: https://training.seer.cancer.gov/anatomy/nervous/tissue.html

See the following link for an excellent intro to the brain:

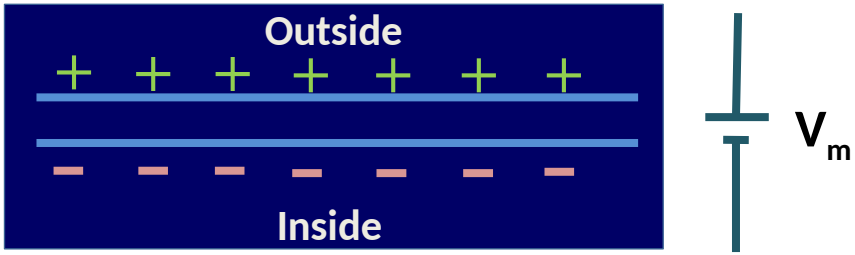
http://www.bristol.ac.uk/synaptic/basics/

# Basic Neuron Functionality

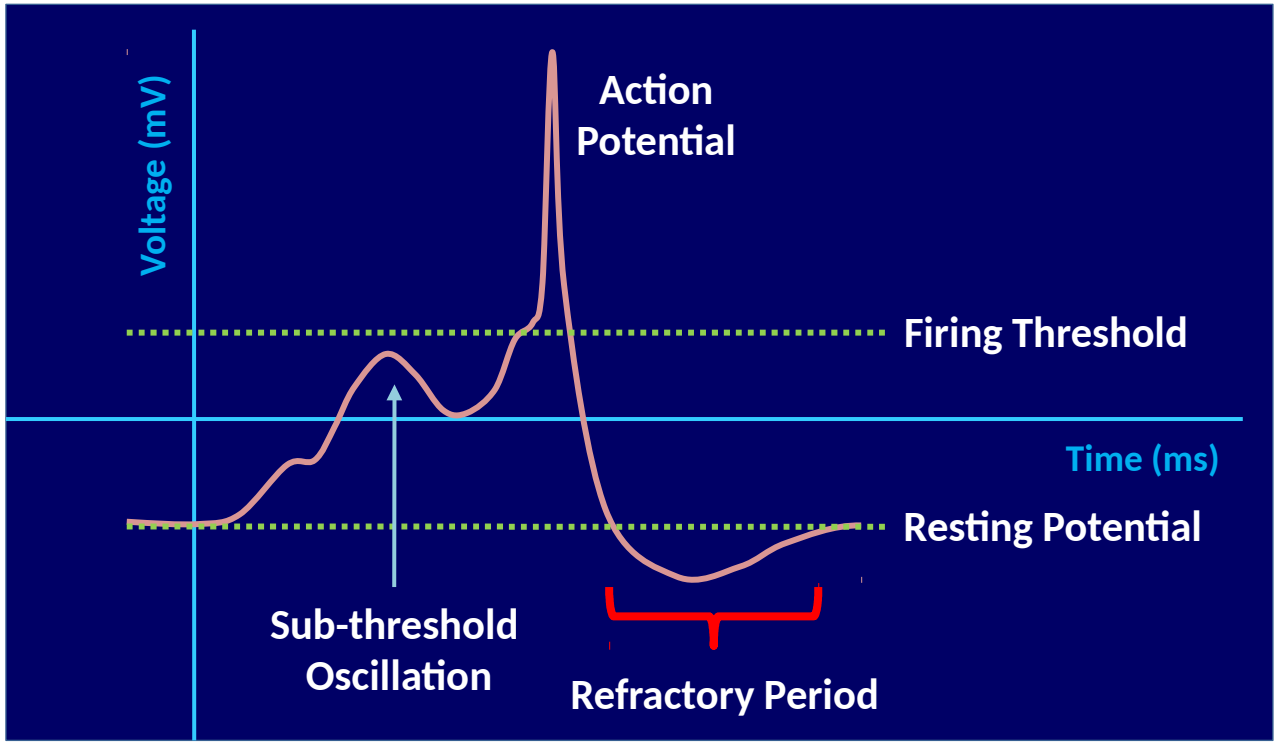
Neurons connect with each other at ***directed*** junctions called ***synpases***.
The neuron providing the input is called the ***pre-synaptic neuron***.
The neuron receiving the input is called the ***post-synaptic neuron***.



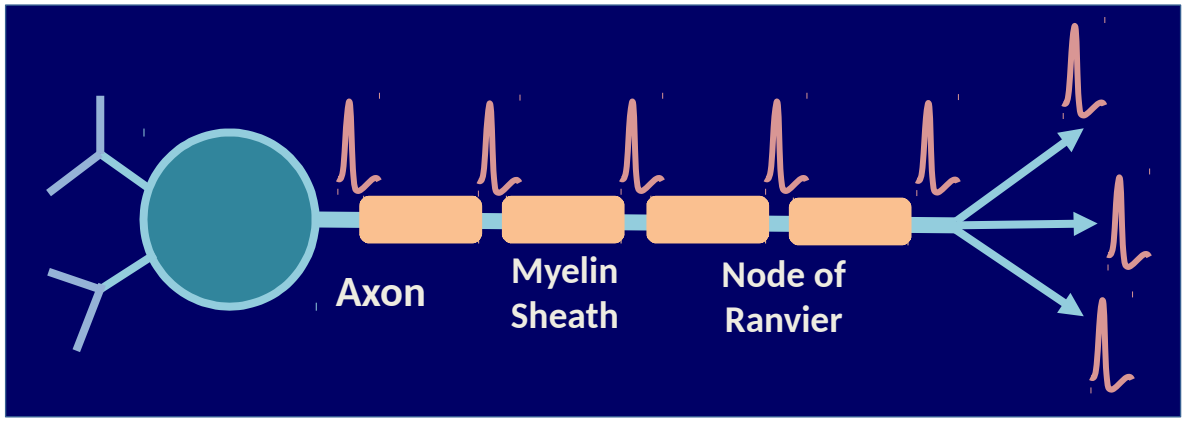

Every neuron has a voltage across its membrane – the ***membrane potential*** (usually around -65mV to -90mV, called the ***resting potential***)



If the membrane potential at the ***soma*** (body) of a neuron rises above a ***firing threshold*** (about +10 mV), the neuron fires a voltage spike called an ***action potential*** on its axon. The action potential rises to about +30mV and is about 1ms wide. After firing, a neuron temporarily enters a ***refractory period***, in which is cannot fire again.



The action potential travels down the axon of the neuron using a regenerative process called ***saltatory conduction***.

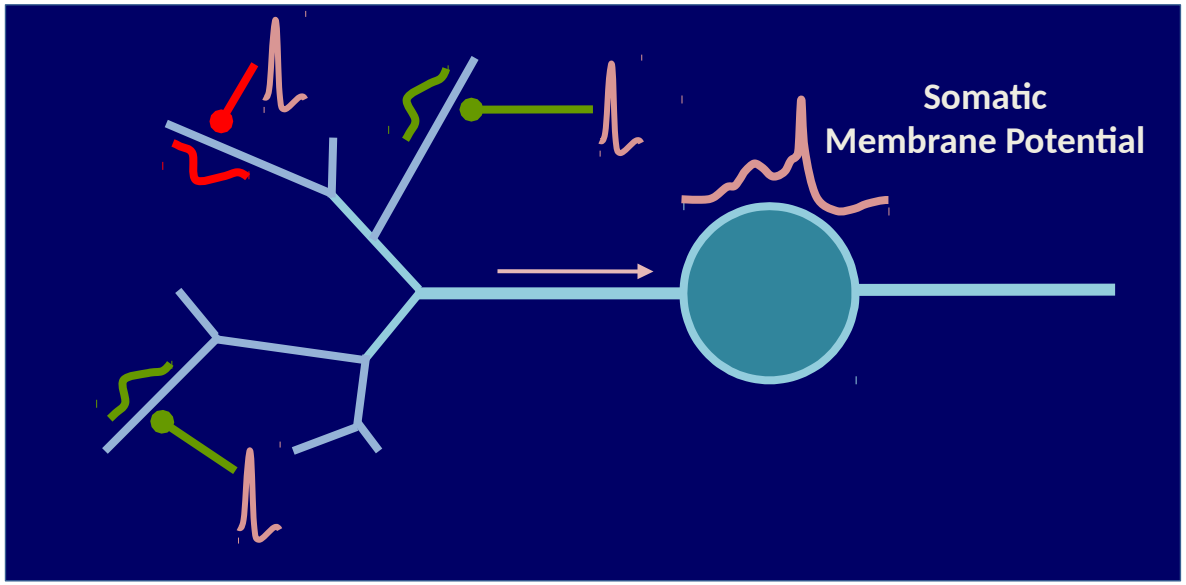



Saltatory conduction allows action potential to travel over long distances without getting weaker through two mechanisms:

- The ***myelin sheath*** acts as an insulator, preventing charge from leaking out, and allowing conduction over very long distances (e.g., from brain to spinal cord.)
- The action potential is ***regenerated*** at each ***node of Ranvier***.

When an action potential arrives at a synapse on another neuron, it changes the neuron's membrane potential transiently via a chemical called a ***neurotransmitter***.

These changes are called ***post-synaptic potentials***. They can be positive (***excitatory post-synaptic potential - EPSP***) or negative (***inhibitory post-synaptic potential – IPSP***).



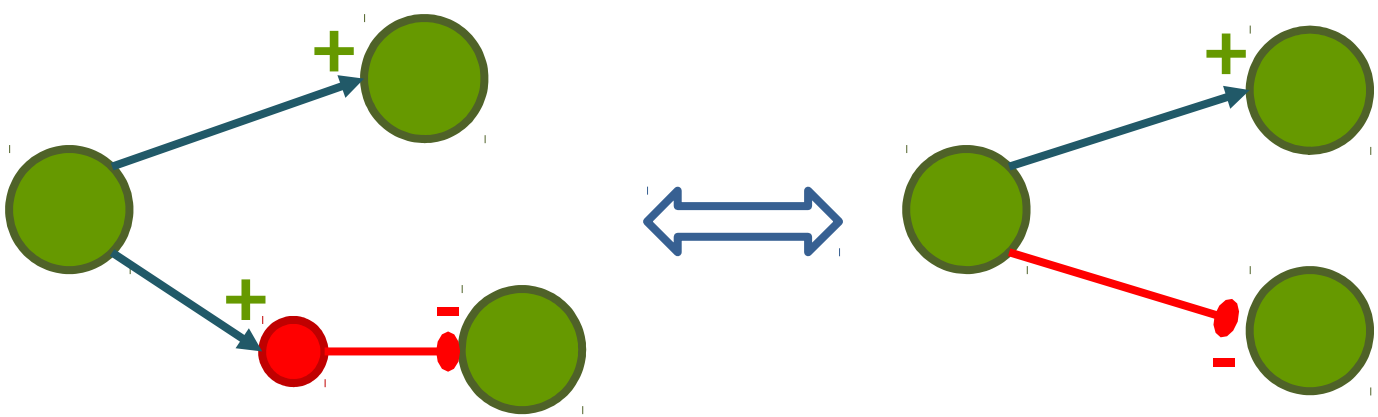

All the PSPs arriving at a neuron anywhere on its dendrites or soma are ***continuously integrated*** and ***conducted passively*** throughout the neuron, resulting in change of the membrane potential at the soma. If that reaches threshold, the neuron ***fires*** an action potential.

# Inhibitory and Excitatory Neurons

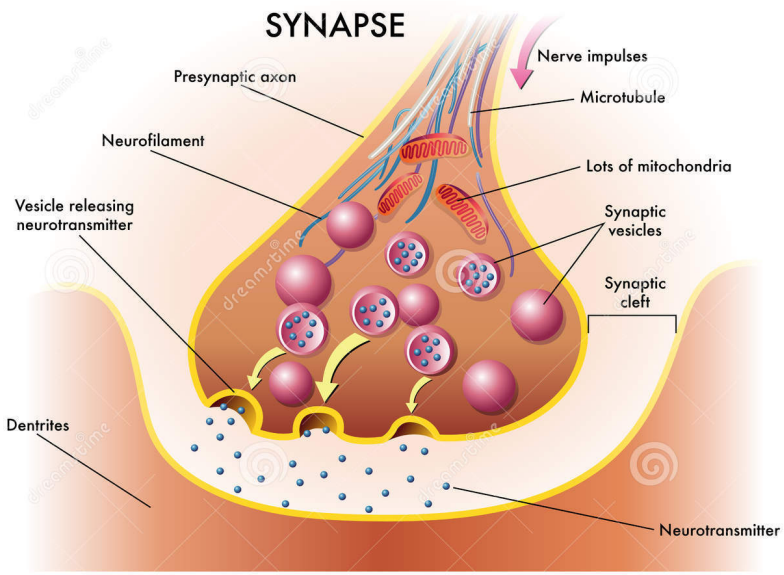
In the nervous system, a pre-synaptic neuron either excites all its targets (***excitatory neuron***), or inhibits all its targets (***inhibitory neuron***), depending on which neurotransmitter it secretes.

Thus, the only way from an excitatory neuron to inhibit another neuron is indirectly through an inhibitory neuron.

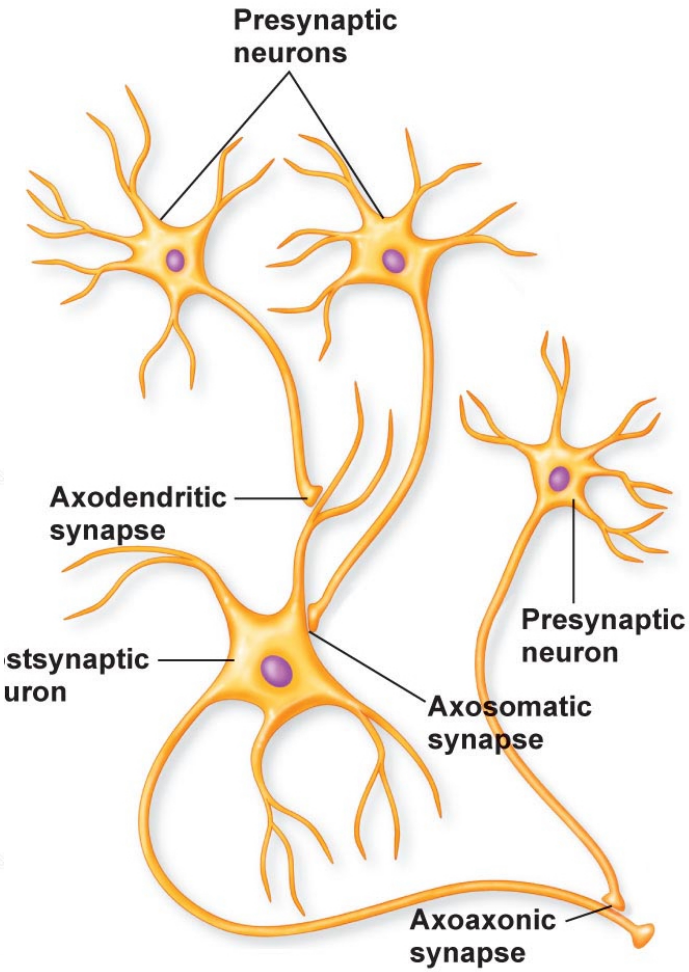
But ***artificial neural networks*** typically allow the same neuron to make excitatory (positive) and inhibitory (negative) synapses, with a ***synaptic weight*** determining the strength of the connection.



# Synapses




http://understandingcontext.com/2014/01/synapses-and-neurotransmitter/



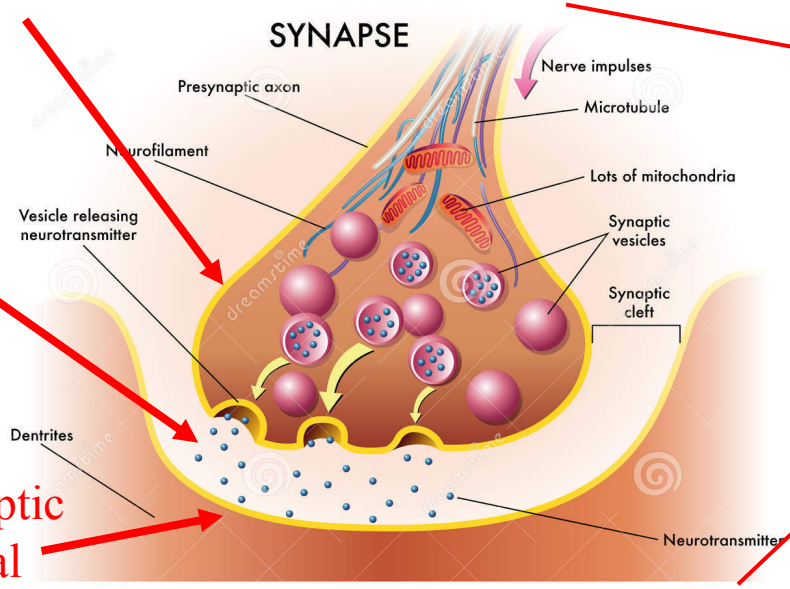

http://pittmedneuro.com/synaptic.html

# Synapses

Pre-synaptic Terminal

Synaptic Cleft

Post-synaptic Terminal

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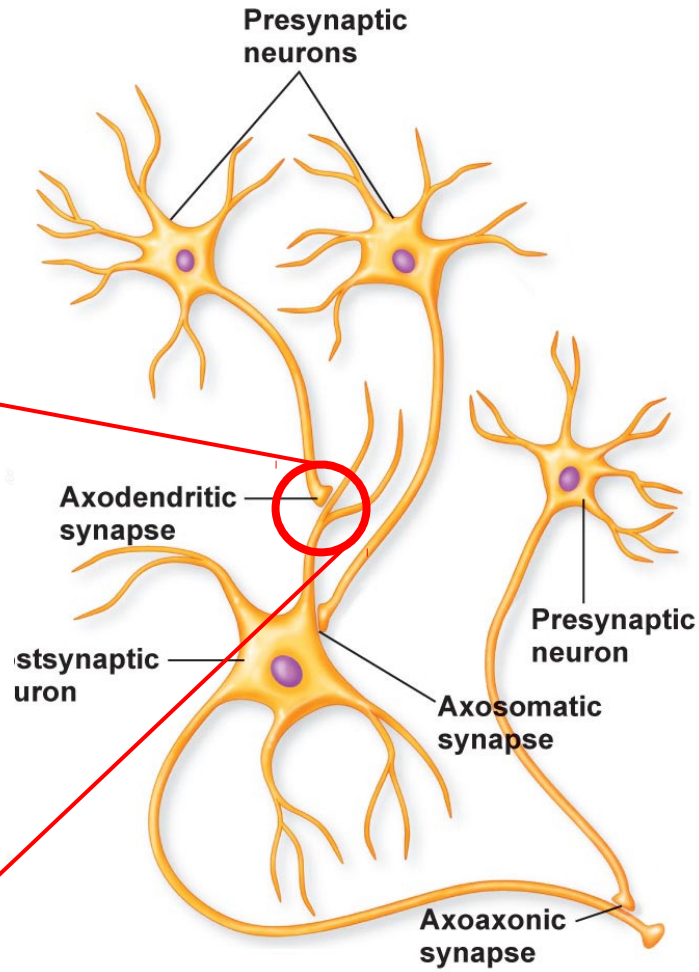


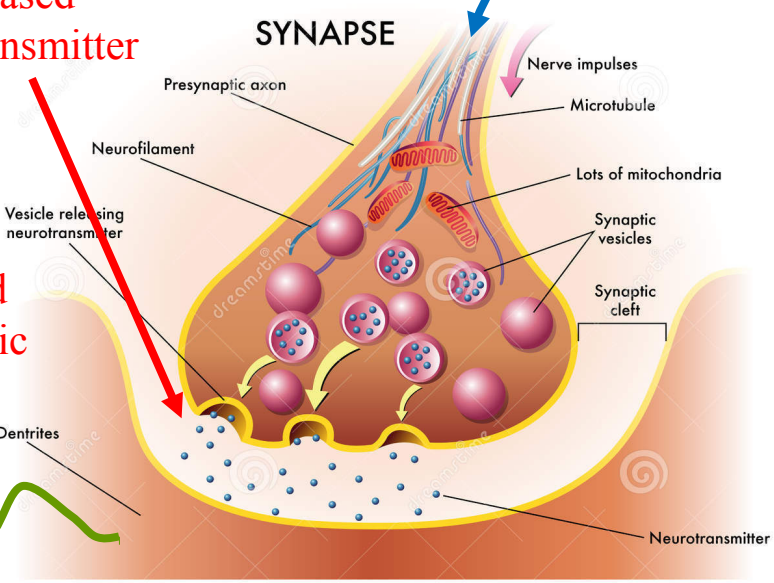

http://pittmedneuro.com/synaptic.html

# Synapses

Incoming action potential from pre-synaptic neuron

Released neurotransmitter

Generated post-synaptic Potential (PSP)

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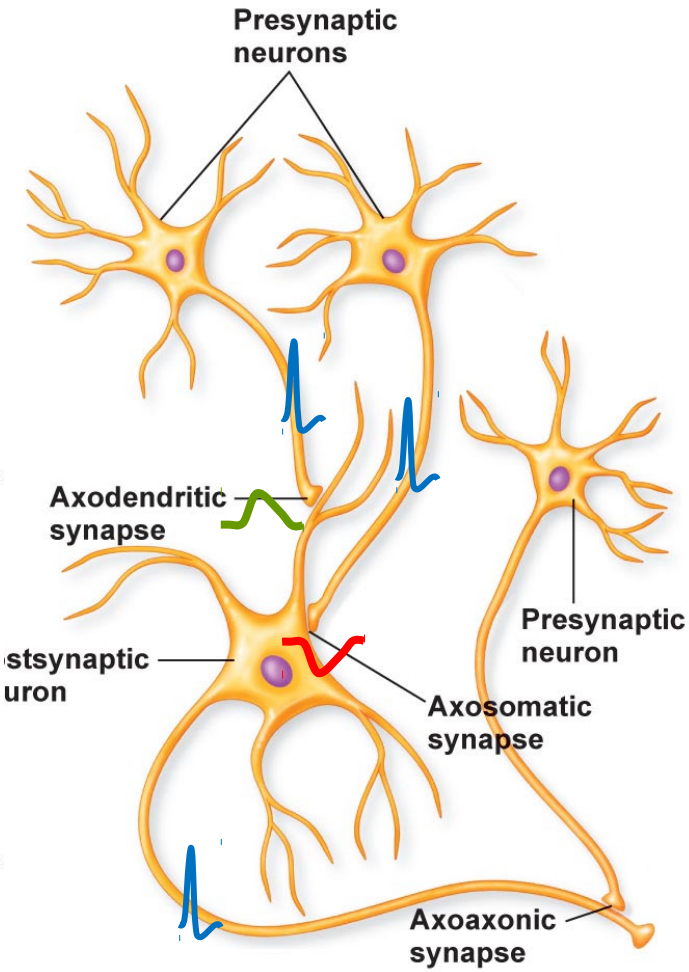
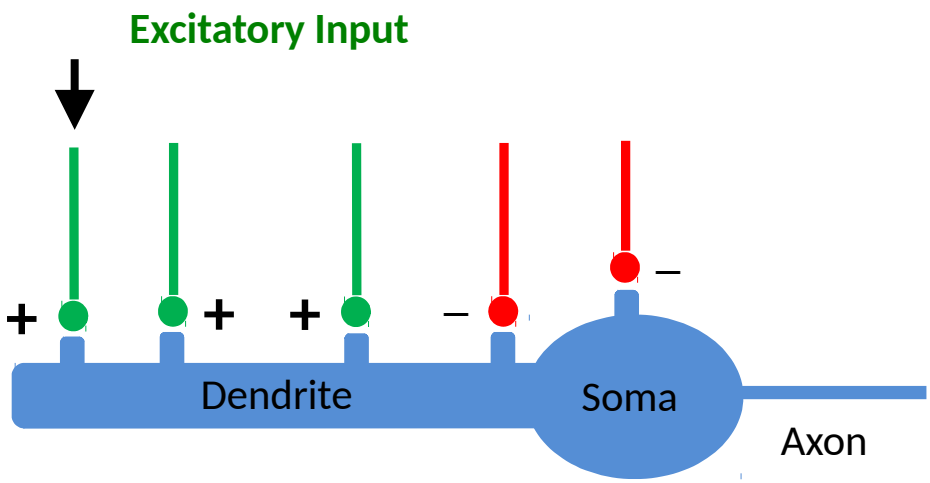
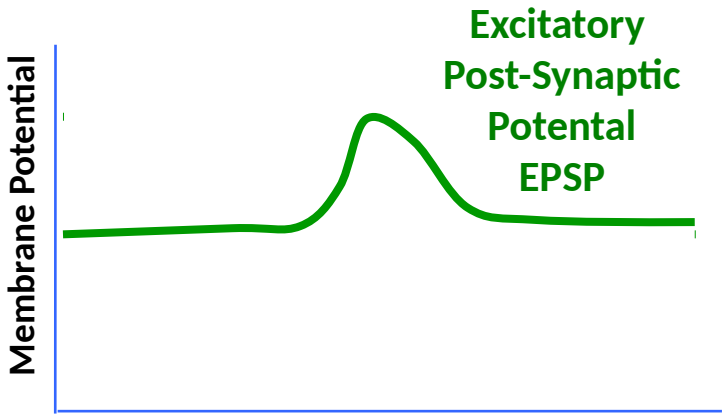
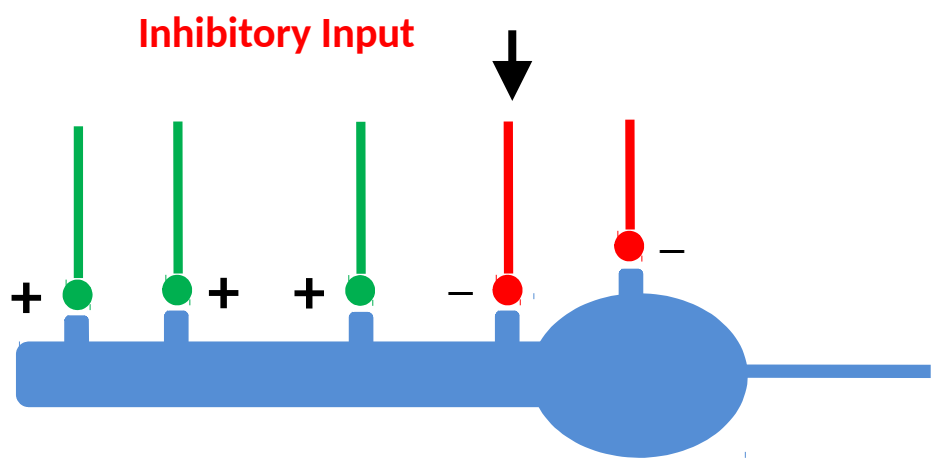


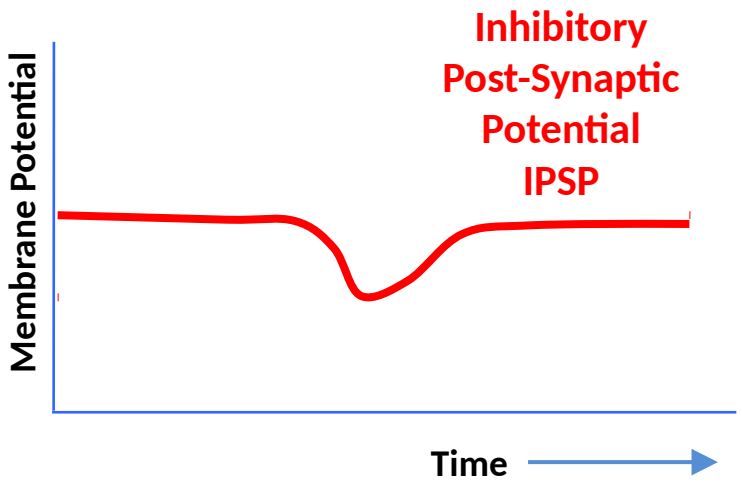

http://pittmedneuro.com/synaptic.html

# Excitatory and Inhibitory Synapses

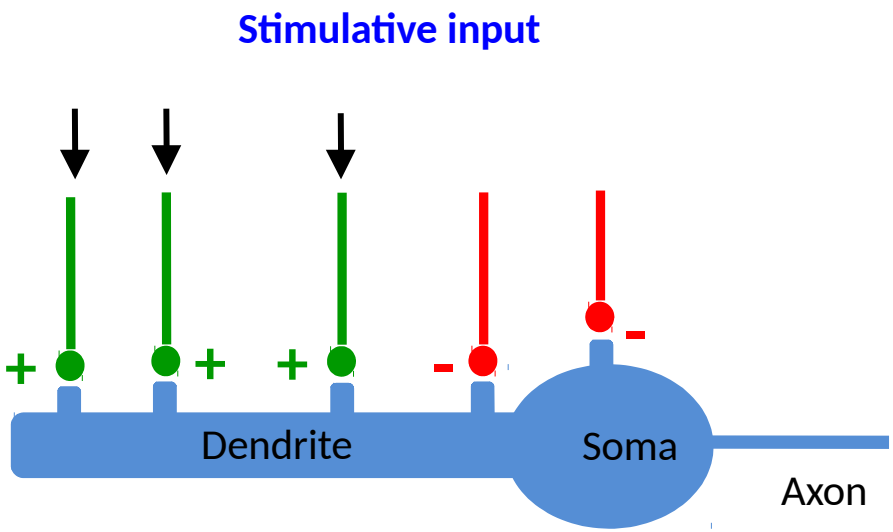


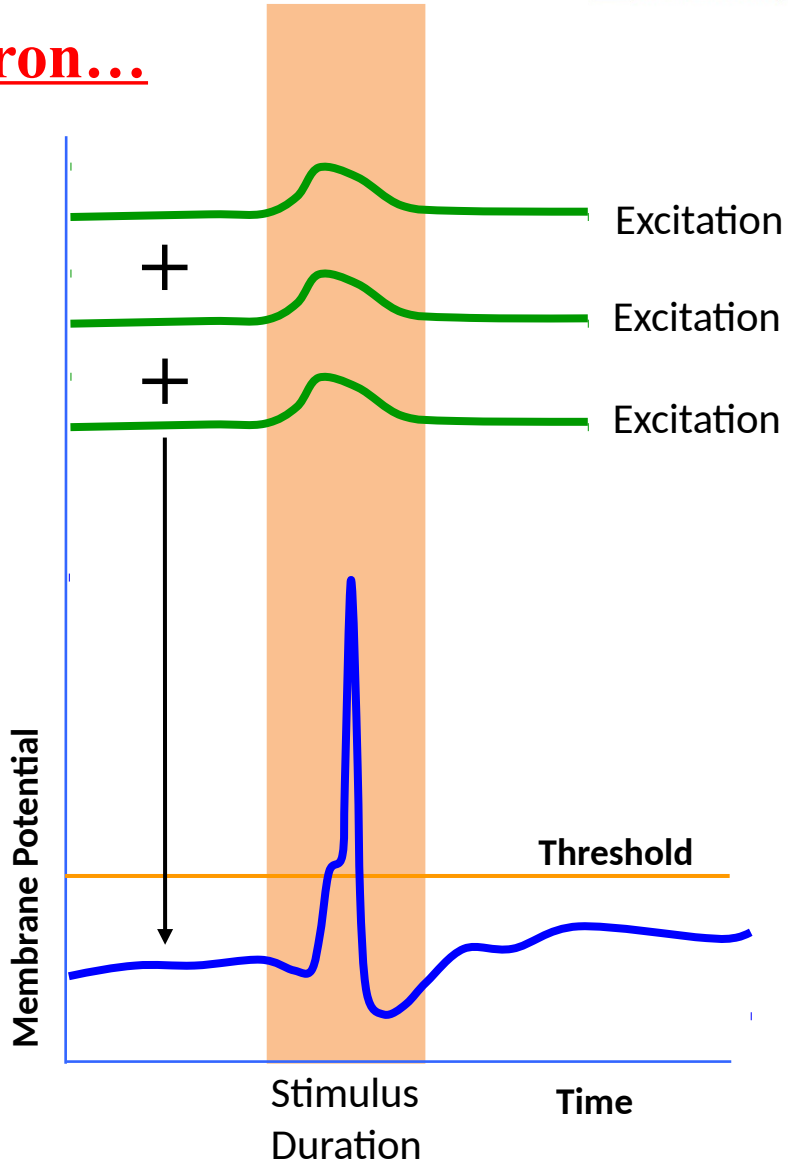



# Some input patterns activate the neuron…

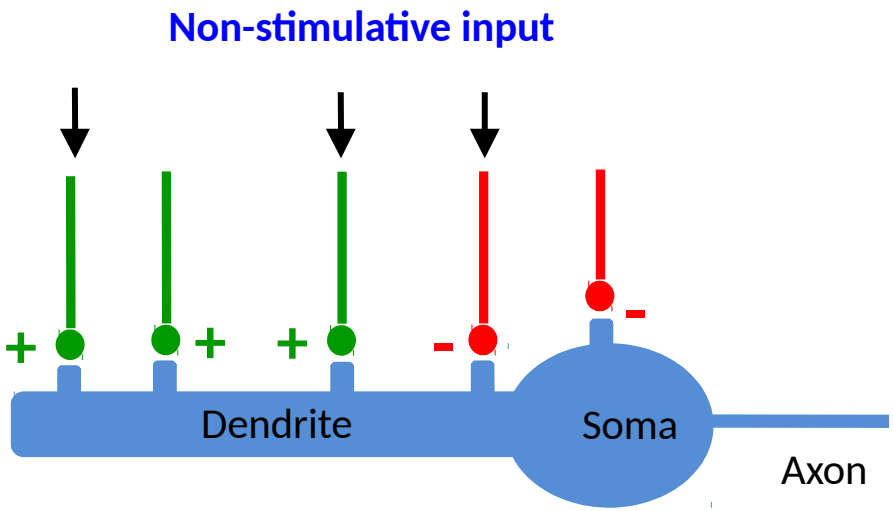


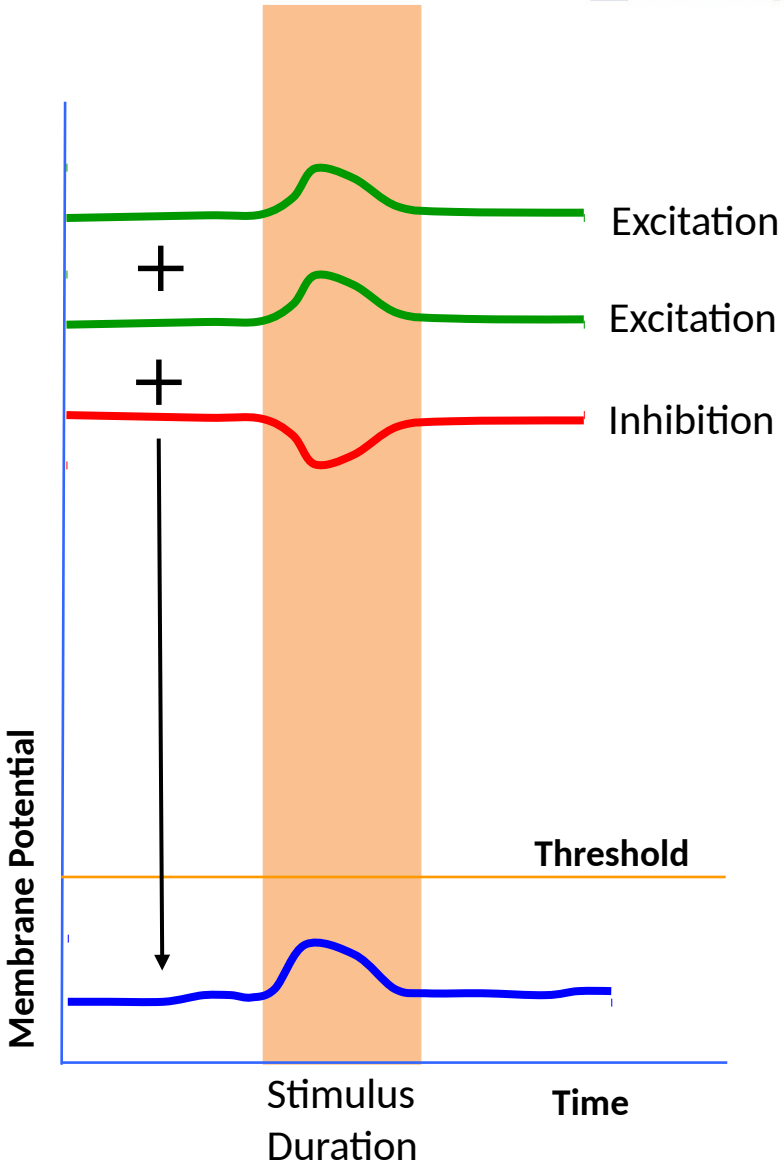

Total activation is higher than threshold → Action potential

# Information at the Cellular Level

## …. some do not.




Total activation is lower than threshold
→ No action potential



# Single Neuron Models

## Multi-Compartment Biophysical Models

- Neurotransmitter release
- Receptor dynamics
- Ion channel dynamics
- Second messengers
- Detailed cell morphology
- Dynamics of the membrane potential
- Shunting inhibition
- Action potential.

## Neurodynamical Models (Izhikevich)

## Integrate-and-Fire Models

- Single compartment
- Spiking model of action potential
- Synapses as integrators
- Threshold rule for response
- Phenomenological model of dynamics
- Discrete-event simulation.

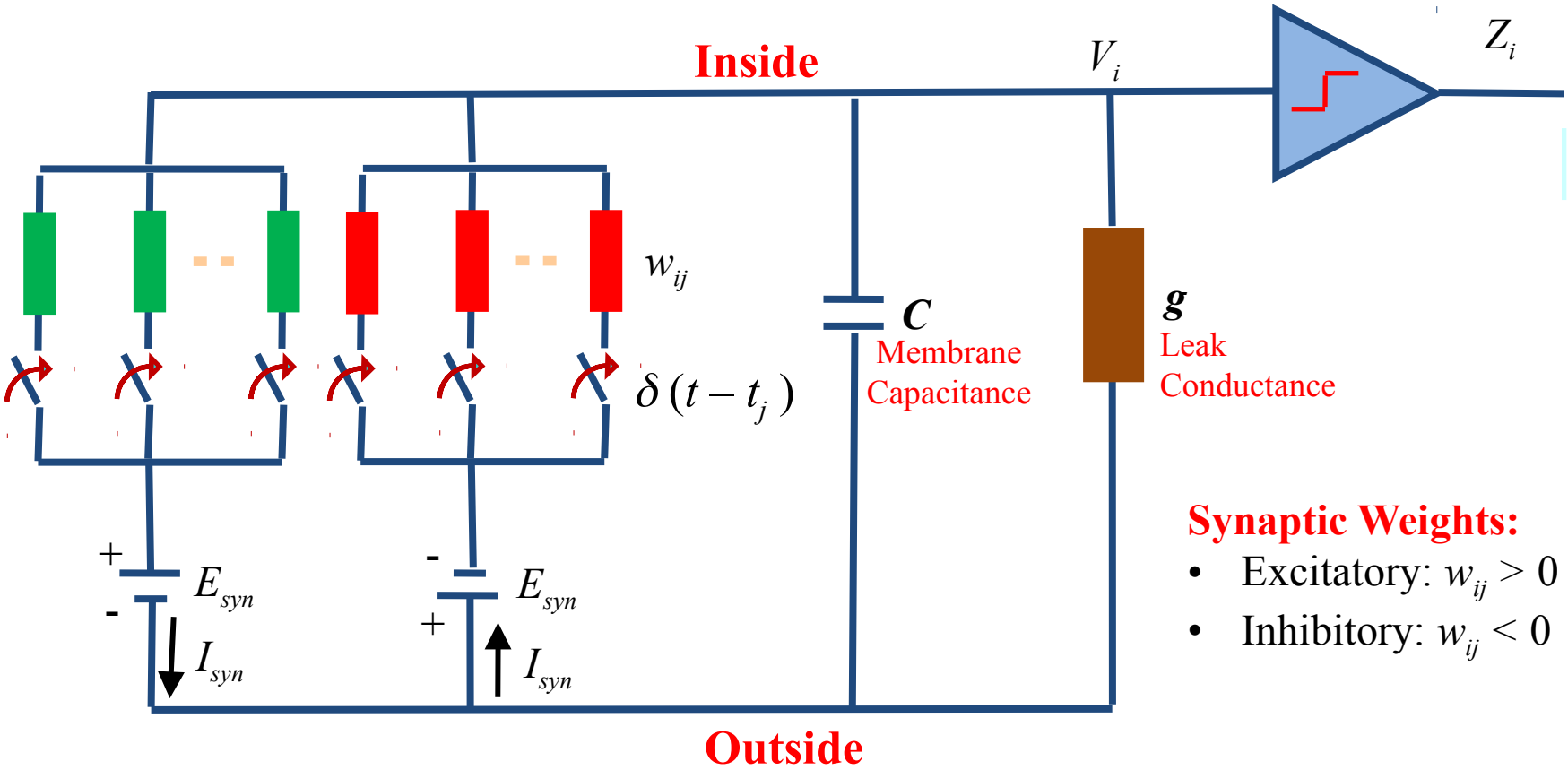
## Rate Models

- Summation of synaptic inputs
- No internal dynamics
- Simple response function.

## Threshold Models

- Summation of synaptic inputs
- No internal dynamics
- All-or-none response function

# Integrate-and-Fire Model




**Synaptic Weights:**

- Excitatory: $w_{ij} > 0$
- Inhibitory: $w_{ij} < 0$

$$C\frac{dV_i}{dt} = -g\,V_i + \sum_j w_{ij} \sum_k \delta(t - t_{jk})\,(E_{syn} - V_i)$$

$$Z_i(t) = \begin{cases} 1 & if\ V_i(t) > \theta \\ 0 & else \end{cases}$$

$V_i$ is reset after each spike

# Izhikevich Model

A very popular model for spiking neurons that actually models the shape of the action potential, unlike the integrate-and-fire model.

By changing the *a*, *b*, *c* and *d* parameters, many realistic neuron types can be modeled.

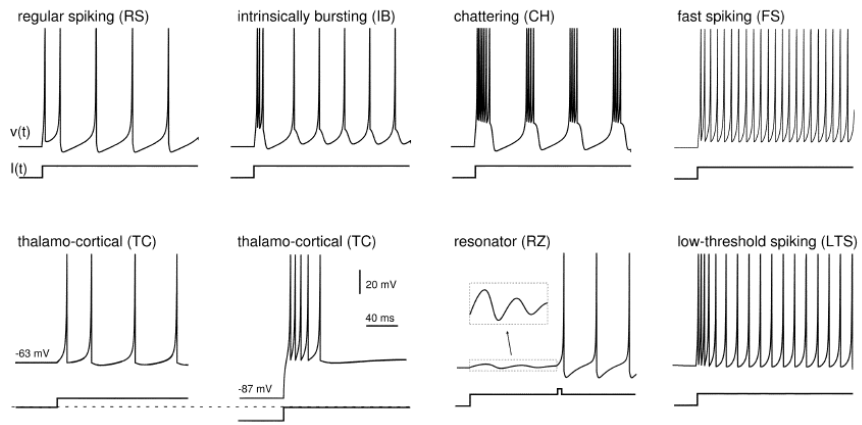
$$\frac{dV_i}{dt} = 5V_i + 0.04V_i^2 + 140 - U_i + I(t)$$

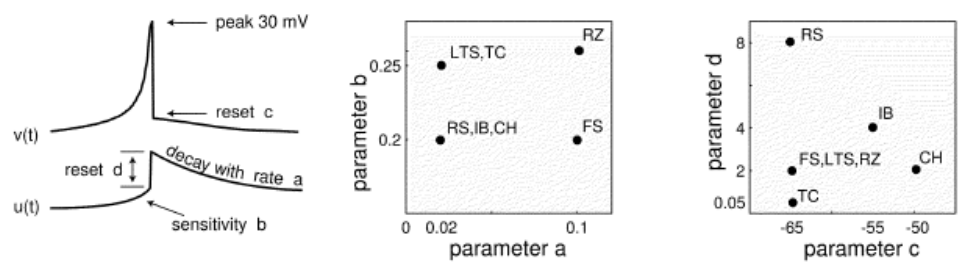
$$\frac{dU_i}{dt} = a(bV_i - U_i)$$

If $V_i > 30$: $\quad Z_i = 1, \quad V_i = c, \quad U_i = U_i + d$

Else: $\quad Z_i = 0$

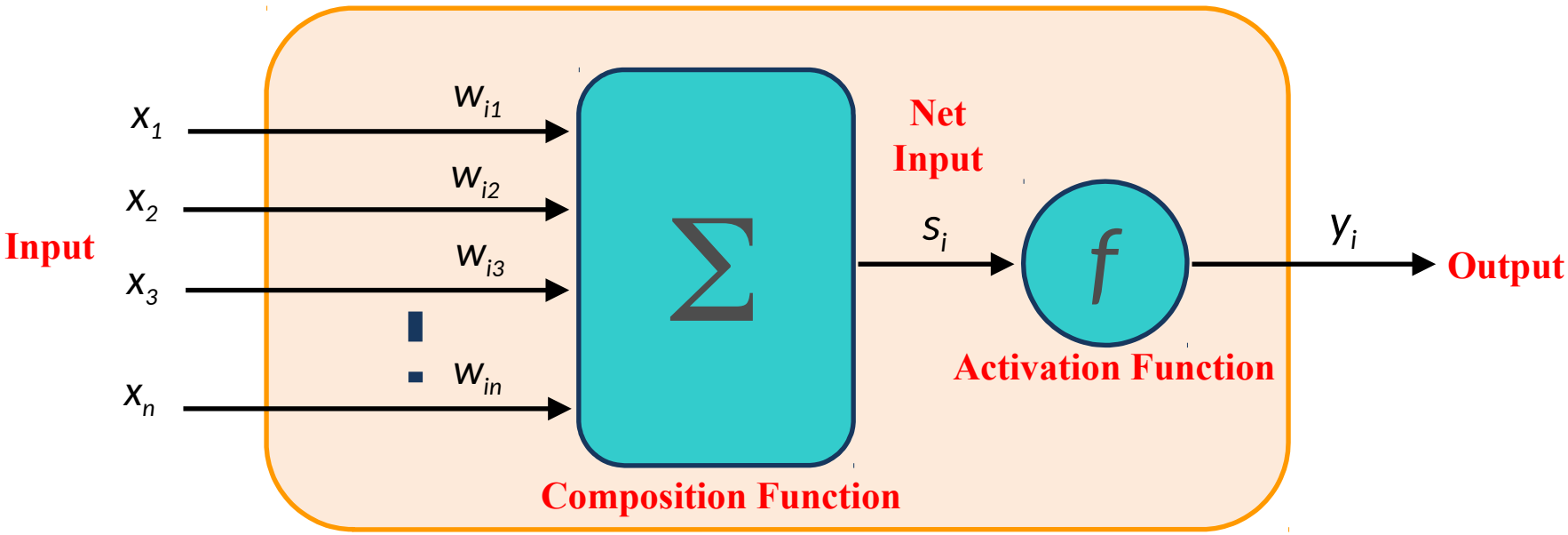
$$I(t) = \sum_j w_{ij} Z_j(t^-)$$



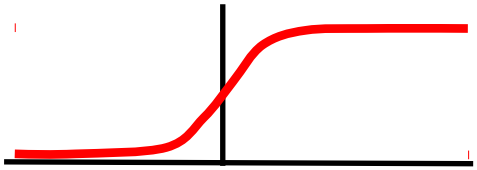

E.M. Izhikevich (2003) Simple models of spiking neurons. *IEEE Trans. On Neural Networks* 14: 1569-1572.

# Simple Neuron Model



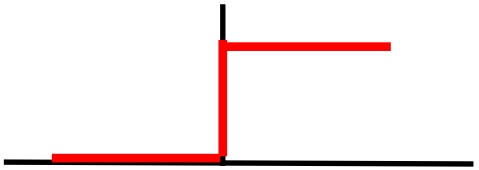

$$s_i = \sum_j w_{ij} x_j$$

$$y_i = f(s_i)$$



$$f(s) = \frac{1}{1+e^{-s}}$$

Rate Coding

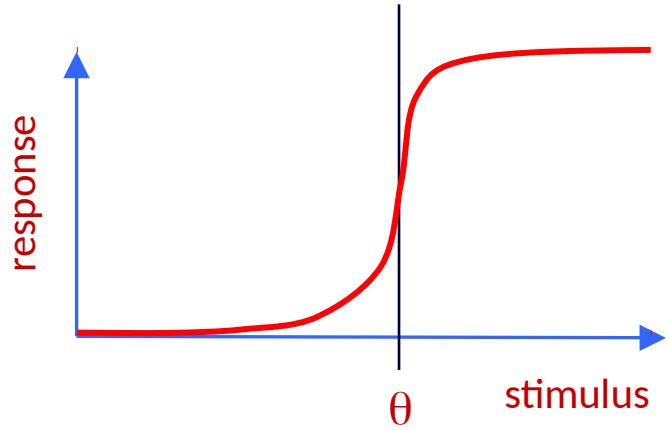


$$f(s) = \begin{cases} 1 & if\ s > 0 \\ 0 & else \end{cases}$$

All-or-None Coding

# What do neurons do?

## Discrimination:

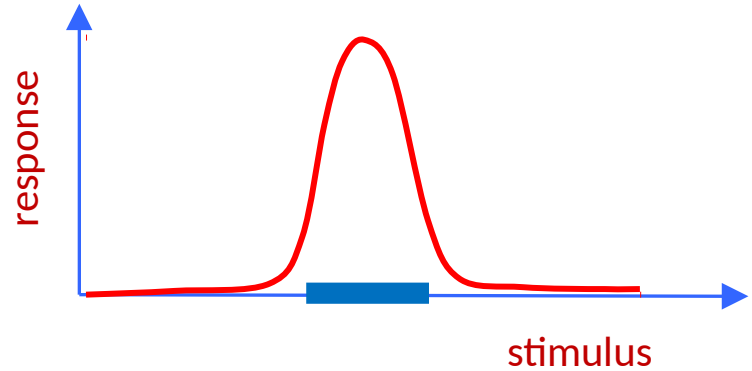



- stimulus > θ → large response
- stimulus < θ → small response

The neuron discriminates between two classes of inputs.

Discrimination is **classification**

## Tuning:




- α < stimulus < β → large response
- stimulus < α → small response
- stimulus > β → small response

The neuron is tuned to a specific range of inputs.

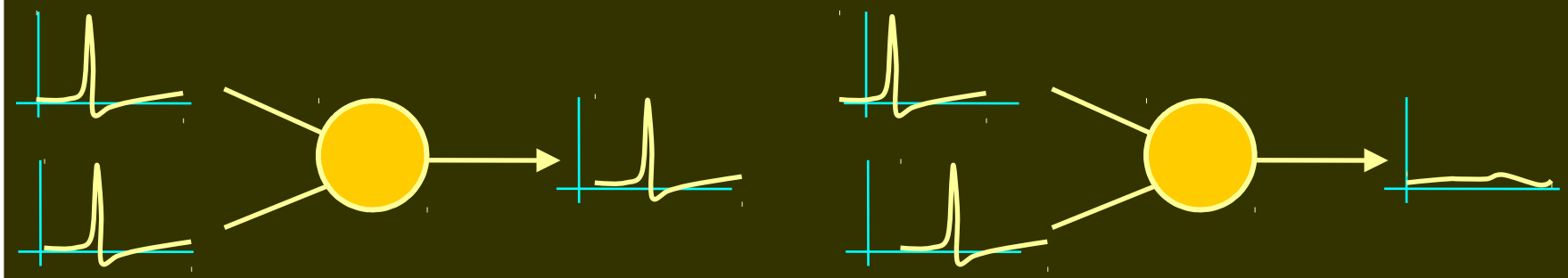
Tuning is a rough **measurement**

# Spatial and Temporal Discrimination

## Spatial Discrimination:

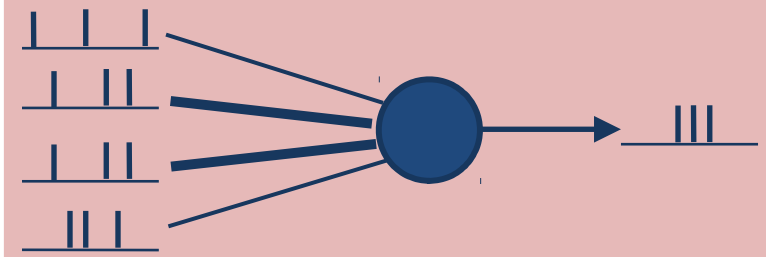
Some input patterns are coded with activity, other with inactivity

## Temporal Discrimination:



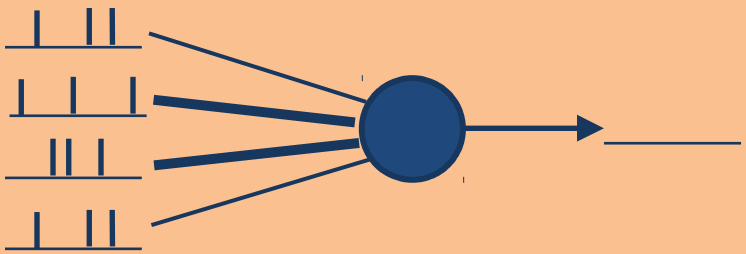
Some input spike sequences are coded with a spike, other with none

# Spatiotemporal Discrimination



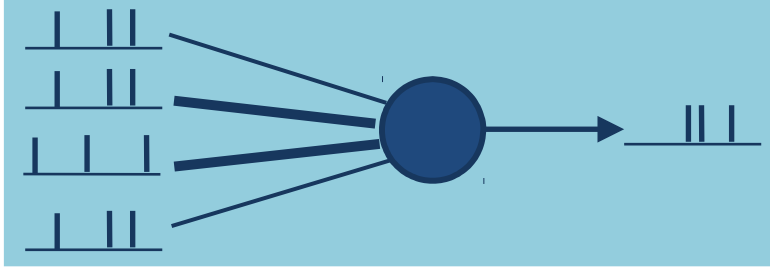
Strong inputs coincident
Weak not coincident

→ Strong Response



Weak inputs coincident
Strong inputs not coincident

→ No Response

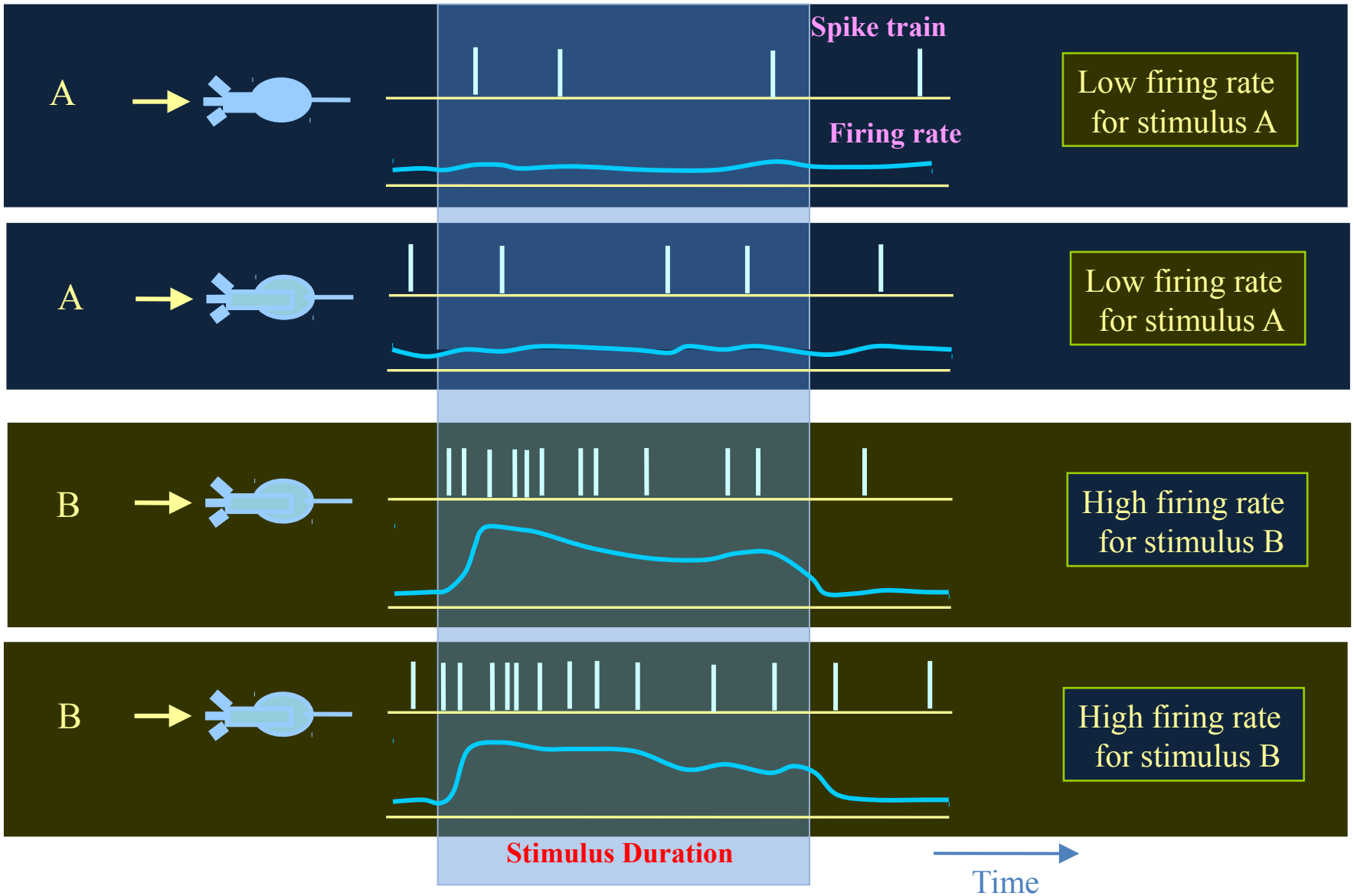


Weak inputs coincident
Some strong inputs coincident

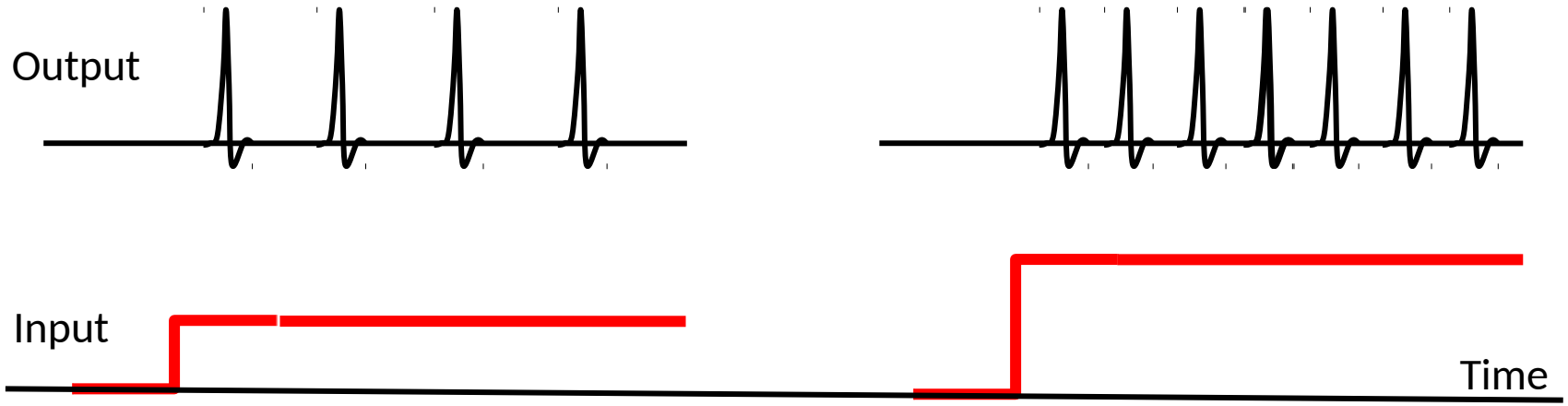
→ Strong Response

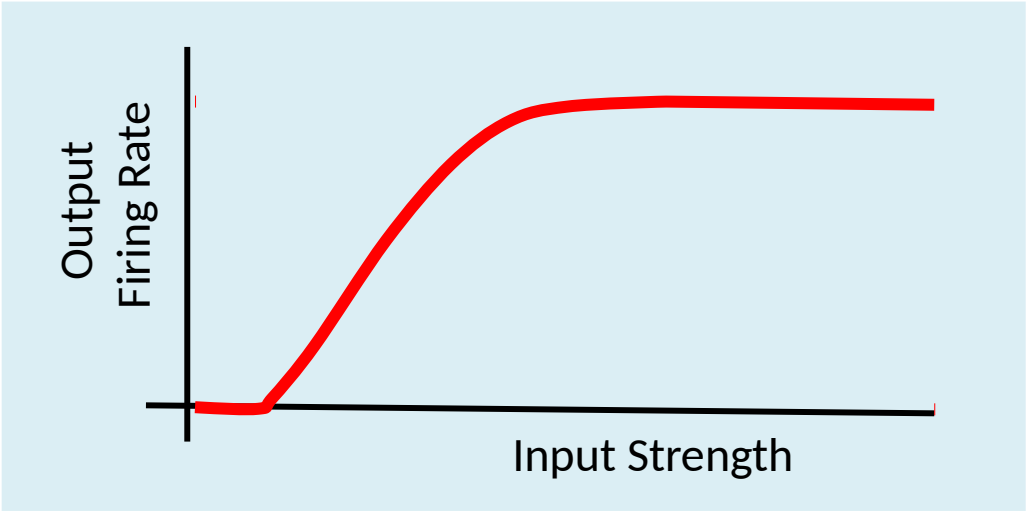
The same number of spikes in different spatiotemporal arrangements lead to different responses.

# Rate Coding

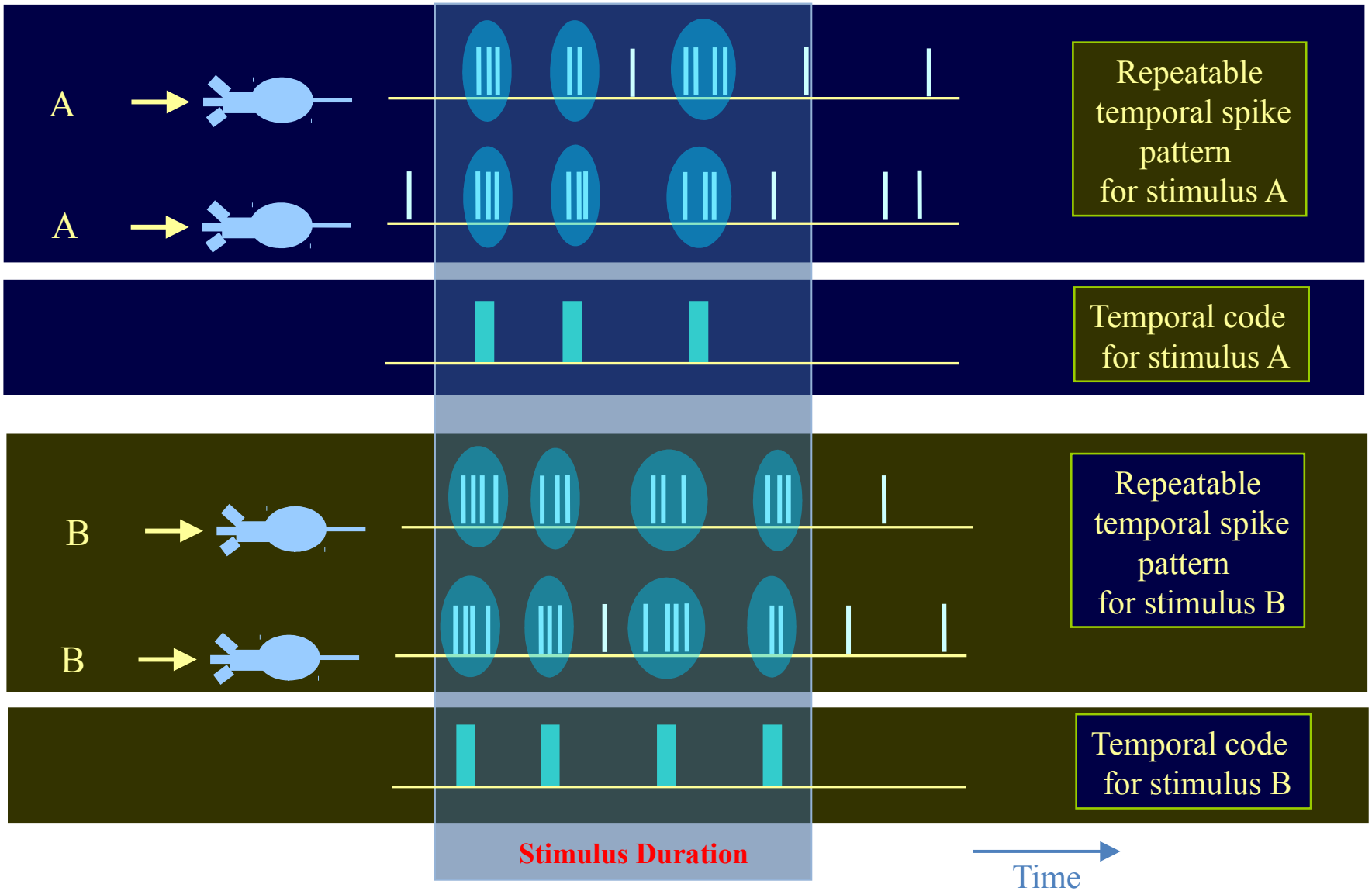

Spike train
Firing rate
A
Low firing rate for stimulus A
A
Low firing rate for stimulus A
B
High firing rate for stimulus B
B
High firing rate for stimulus B
Stimulus Duration
Time

# Rate Coding

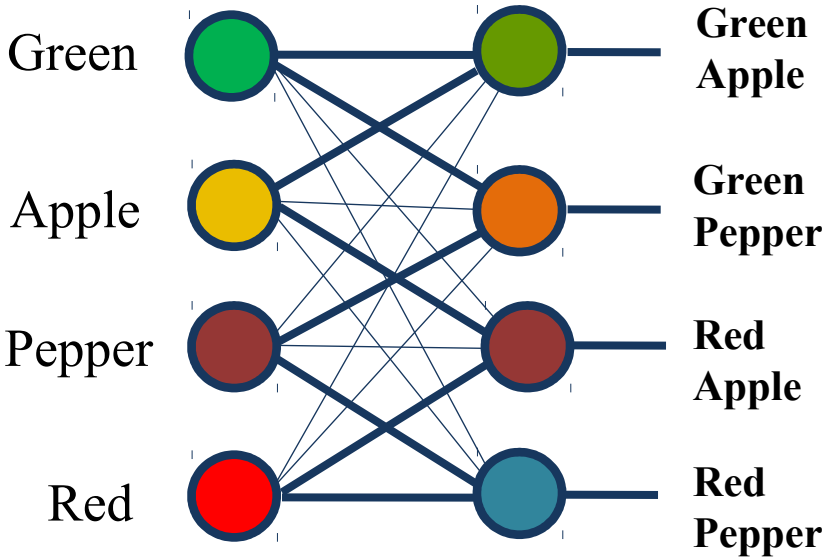


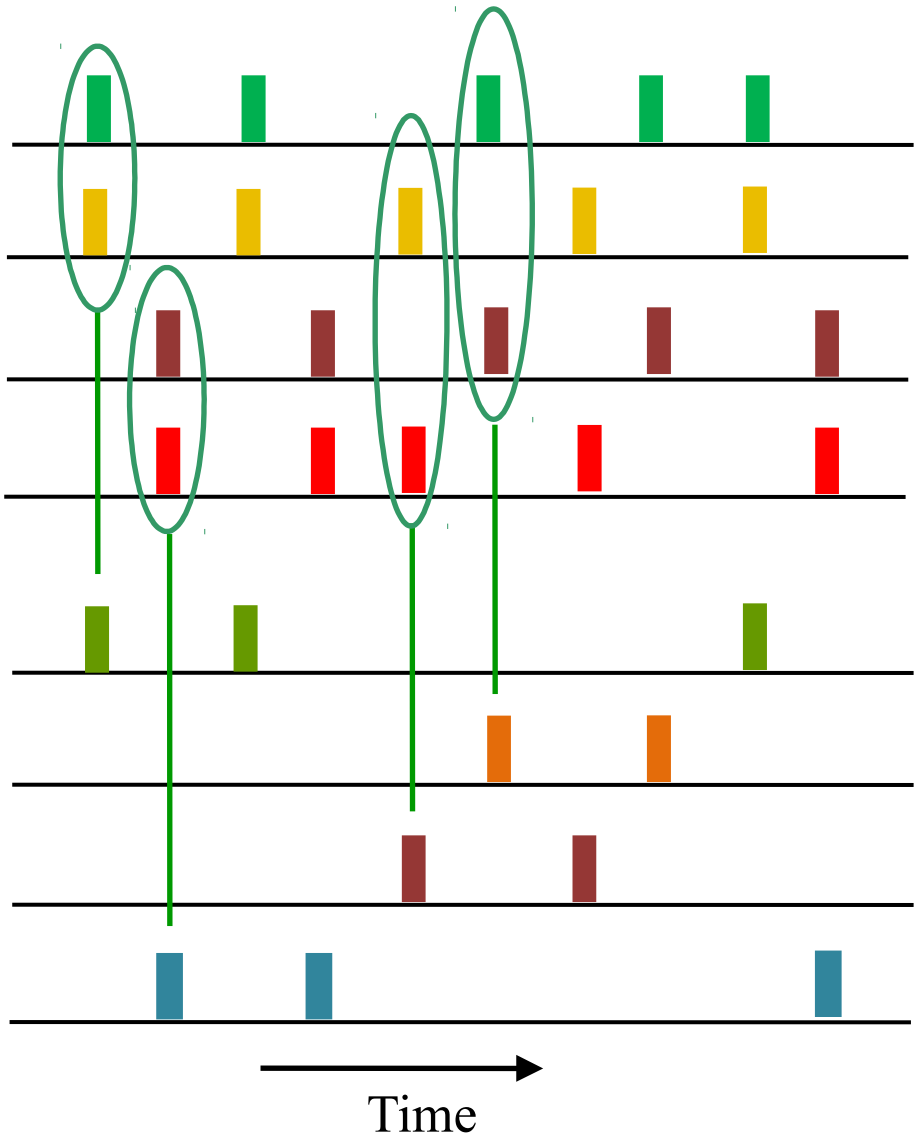



# Temporal Coding



# Synchrony-Based Coding



# Network Architectures

# Canonical Networks

**Central Pattern Generators:**
Networks that produce a repeating patterrn of activity to drive periodic processes e.g., gait, breathing, etc.

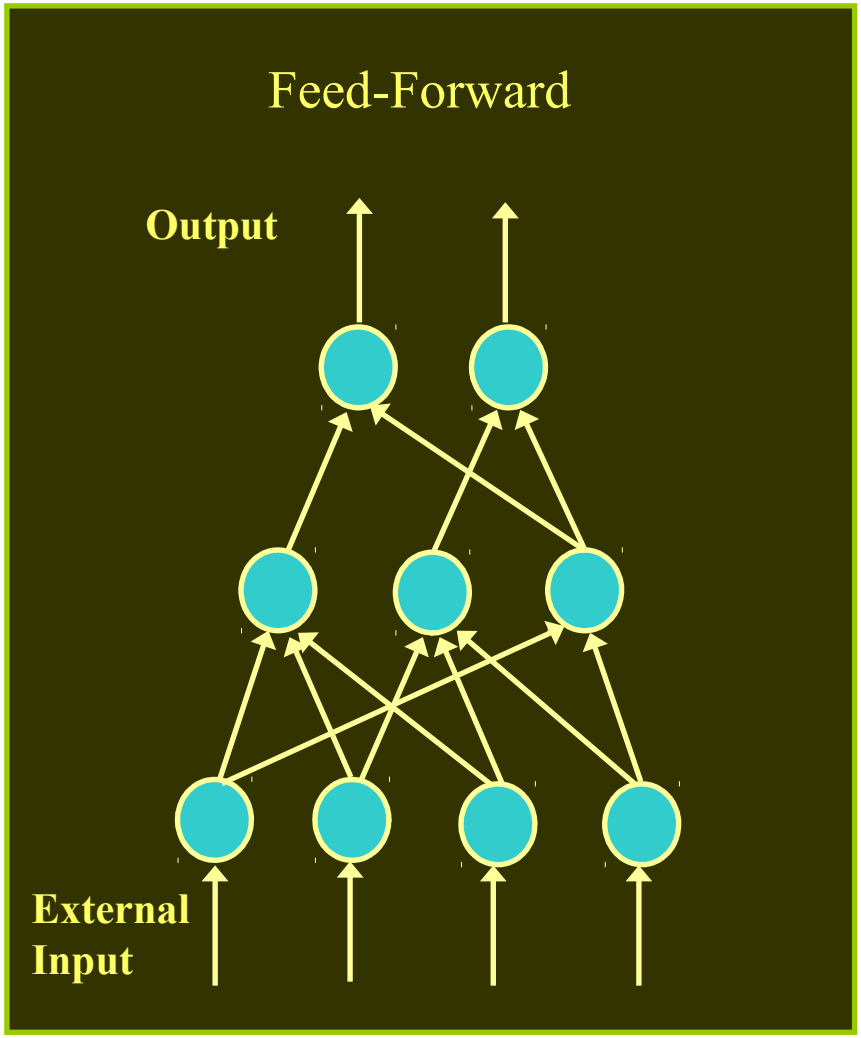
**Retinotopic Networks:**
Networks comprising multiple layers of neurons where the projections between successive layers maintain spatial relationships.
Example: Early visual system, somatosensory maps.

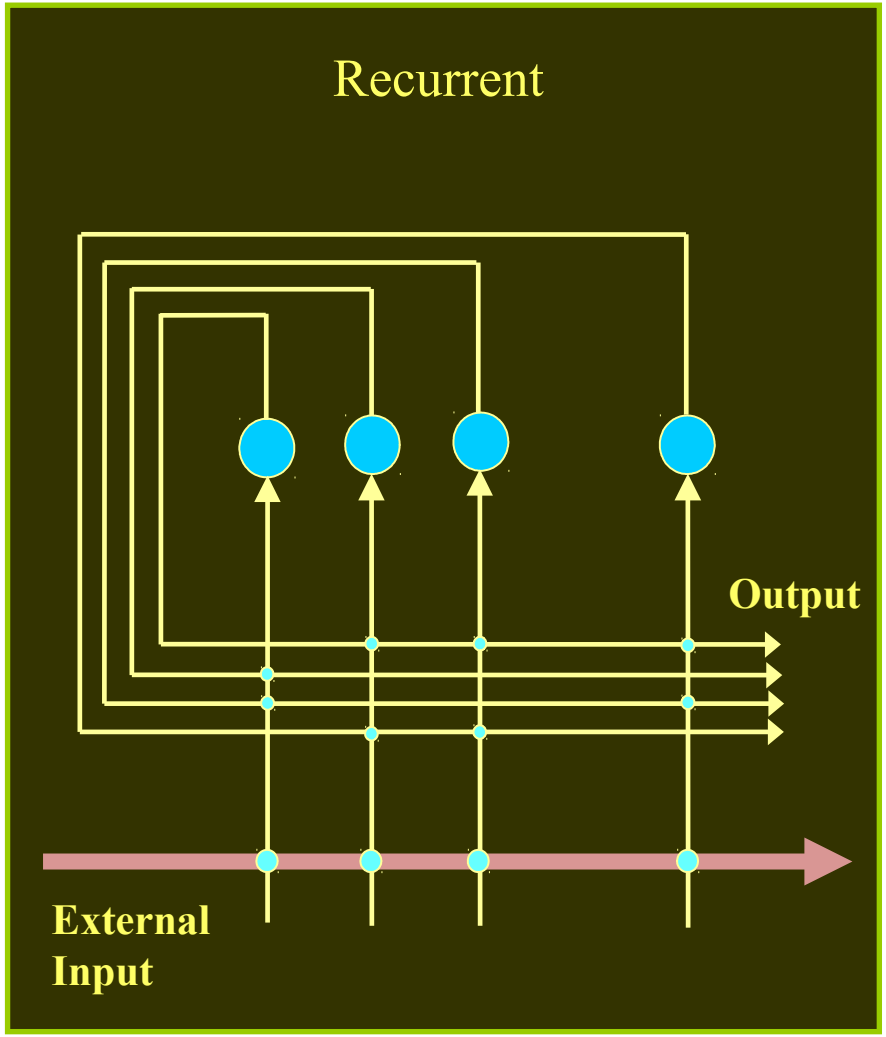
**Feed-Forward Networks:**
Networks where lower layers of neurons feed only to higher layers.

**Lateral Inhibition/Excitation Networks:**
Networks where each neuron inhibits/excites neurons close to it while exciting/inhibiting those further away.
Example: Winner-take-all networks, bump attractor networks

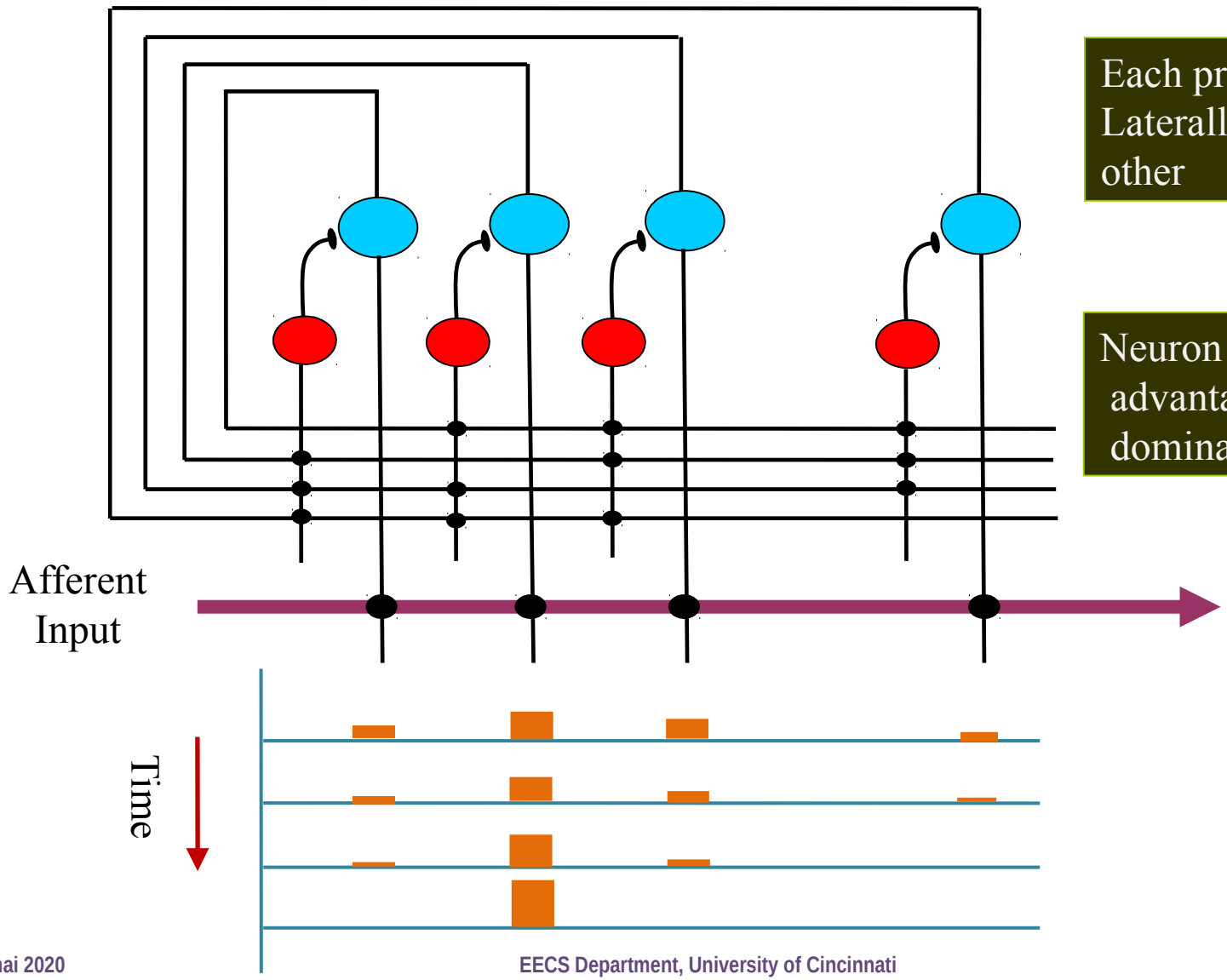
**Recurrent Networks:**
Networks where neurons receive connections from other neurons of the same or higher layers, leading to equilibria, sequences, chaotic attractors, etc.
Examples: Autoassociative memories, sequence generators.

# Two Basic Types of Neural Networks



# Winner-Take-All (WTA) Networks



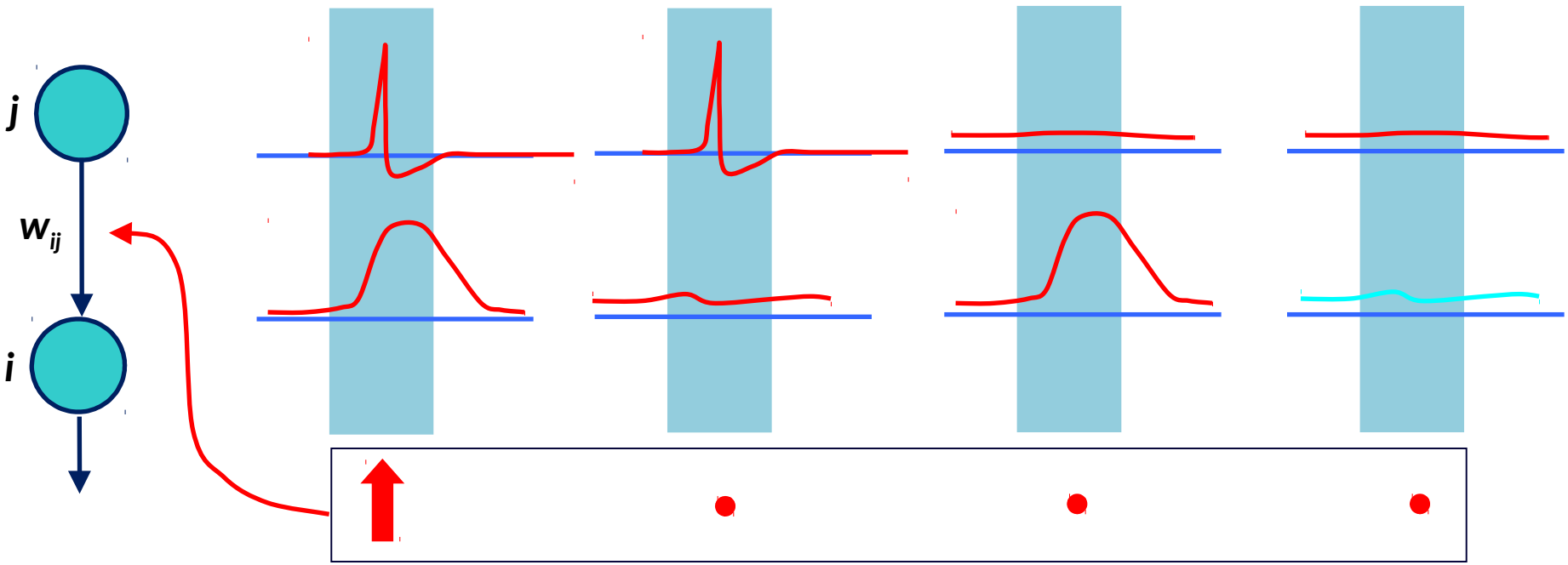

Each primary neuron Laterally inhibits every other

Neuron with initial advantage eventually dominates.

# Synaptic Plasticity

# The Hebb Rule for Learning

"Neurons that fire together wire together"




| | Low Output | High Output |
|---|---|---|
| Low Input | ● | ● |
| High Input | ● | ↑ |

$$\Delta w_{ij}(t) = \eta\, y_j(t)\, y_i(t)$$

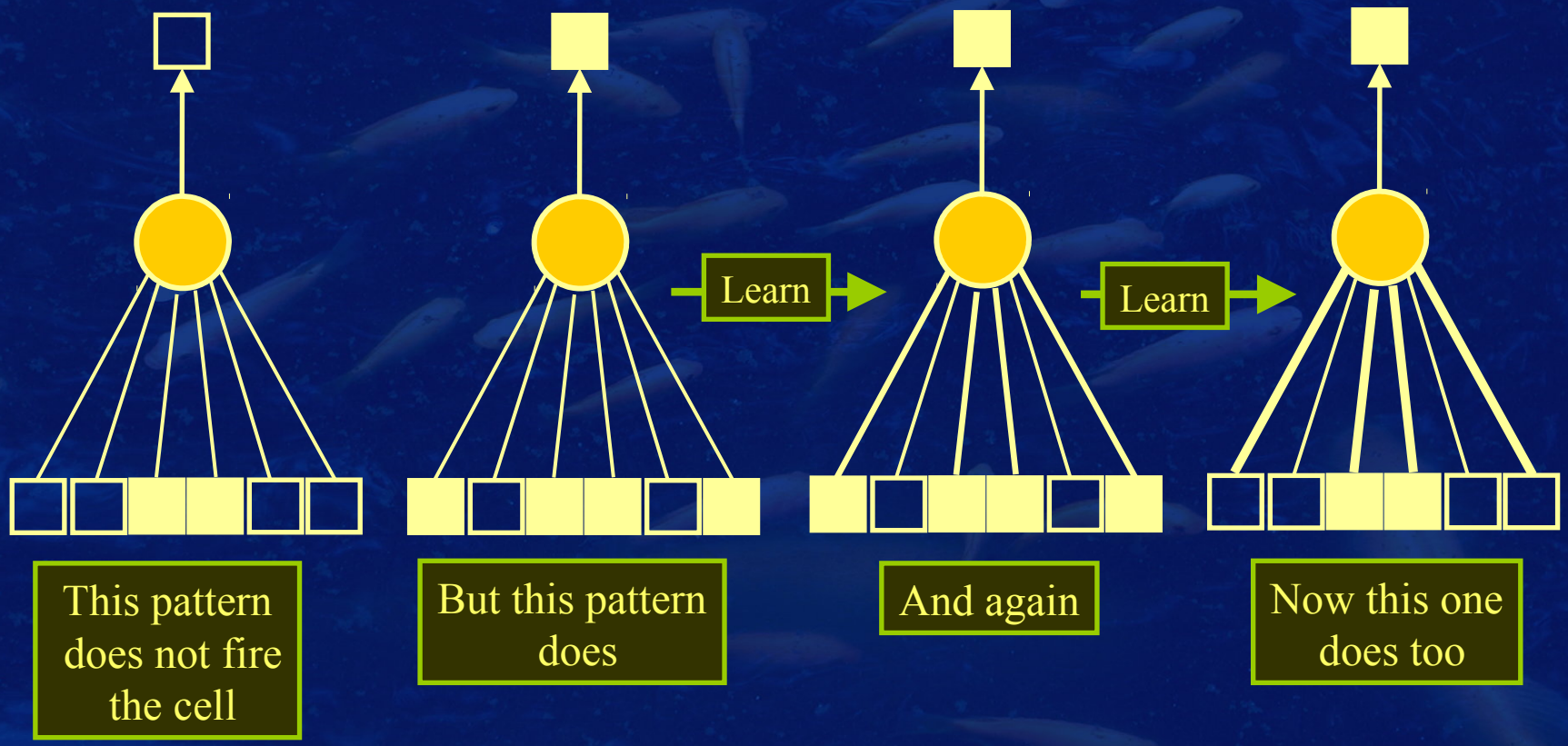
For binary $y_j$ and $y_i$ this leads to:

$$\bar{w}_{ij} \propto \langle y_i y_j \rangle$$

but is dynamically unstable

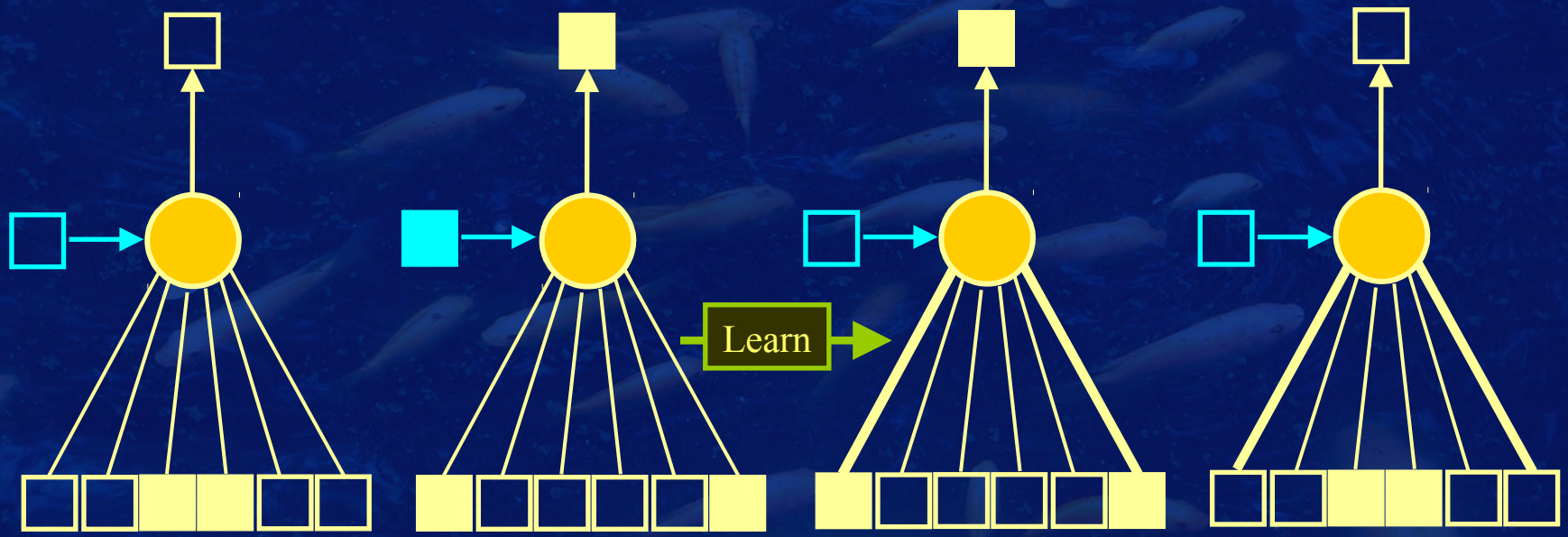
# Hebb Rule in Action

## Recognizing Partial Patterns



# Hebb Rule in Action

## Learning by Reinforcement



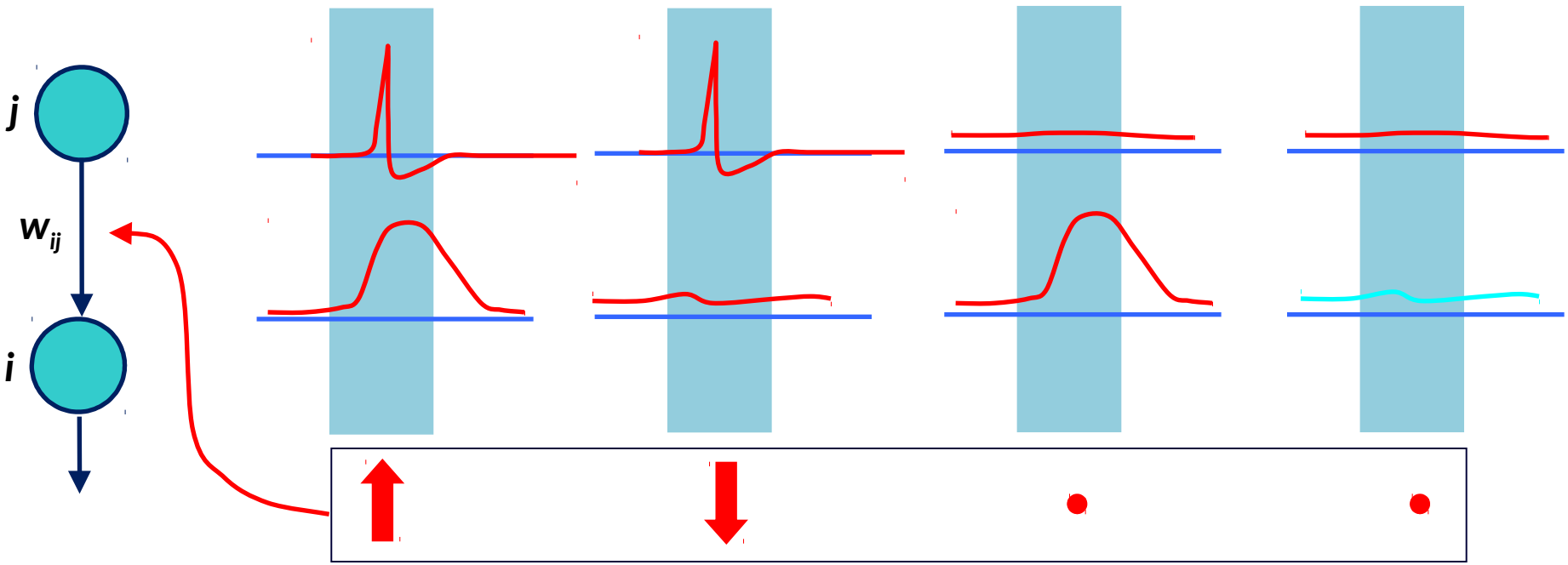

This pattern is shown without reinforcement

This pattern is shown with reinforcement

Now this pattern fires the cell without reinforcement

But this one still does not

# Pre-Synaptically-Gated Hebb Rule



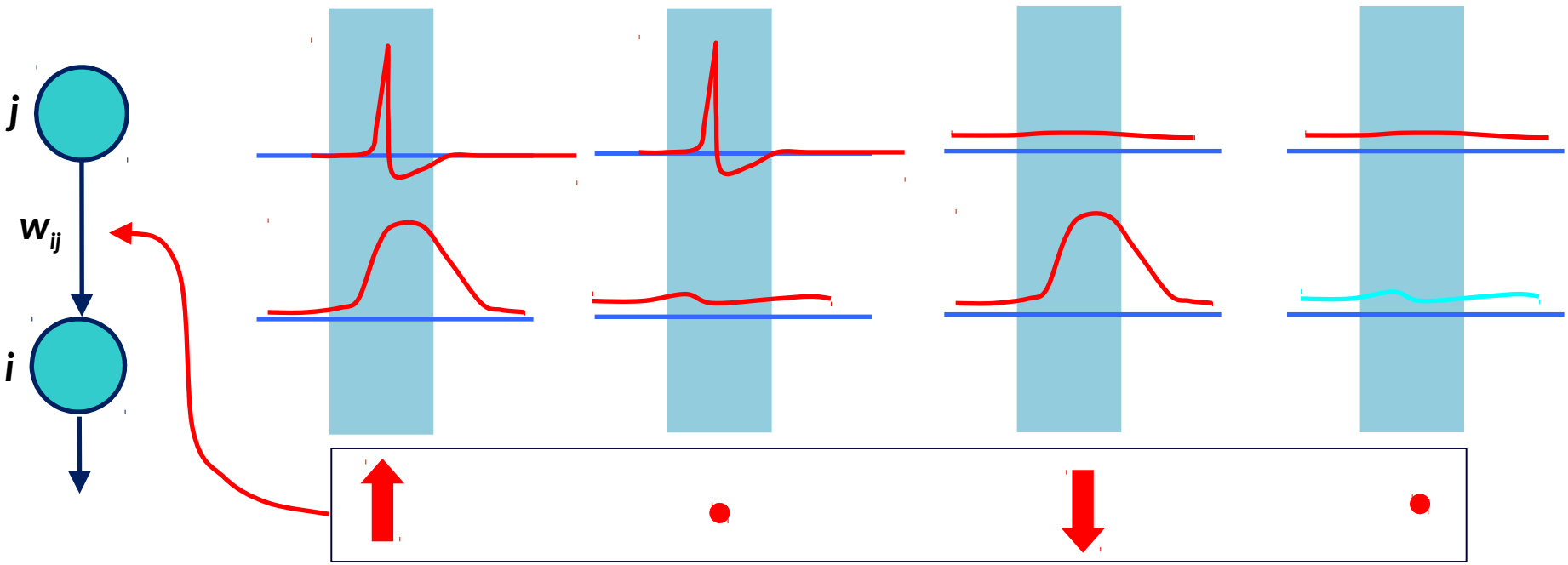

| | Low Output | High Output |
|---|---|---|
| Low Input | • | • |
| High Input | ↓ | ↑ |

$$\Delta w_{ij}(t) = \eta\, y_j(t)\,[y_i(t) - w_{ij}(t)]$$

For binary $y_j$ and $y_i$ this leads to:

$$\bar{w}_{ij} \approx p(y_i(t) = 1 \mid y_j(t) = 1)$$

# Post-Synaptically-Gated Hebb Rule




| | Low Output | High Output |
|---|---|---|
| Low Input | • | ↓ |
| High Input | • | ↑ |

$$\Delta w_{ij}(t) = \eta\, y_i(t)\,[y_j(t) - w_{ij}(t)]$$

For binary $y_j$ and $y_i$ this leads to:

$$\bar{w}_{ij} \approx p(y_j(t) = 1 \mid y_i(t) = 1)$$

Consider the pre-synaptically-gated rule:

$$\Delta w_{ij}(t) = \eta\, y_j(t)\,[\, y_i(t) - w_{ij}(t)\,]$$

First, note that if $\eta$ is small, the rule is self-stabilizing, i.e., $w_{ij}$ remains within the same limits as $y_i$

Now, taking expectations, we get

$$\langle \Delta w_{ij}(t) \rangle = \eta\, \langle y_j(t)\, y_i(t) \rangle - \eta \langle y_j(t)\, w_{ij}(t) \rangle$$

At convergence, we get (approximately)

$$0 = \langle y_j(t)\, y_i(t) \rangle - \langle y_j(t) \rangle\, \bar{w}_{ij}$$

where $\bar{w}_{ij}$ is the equilibrium weight

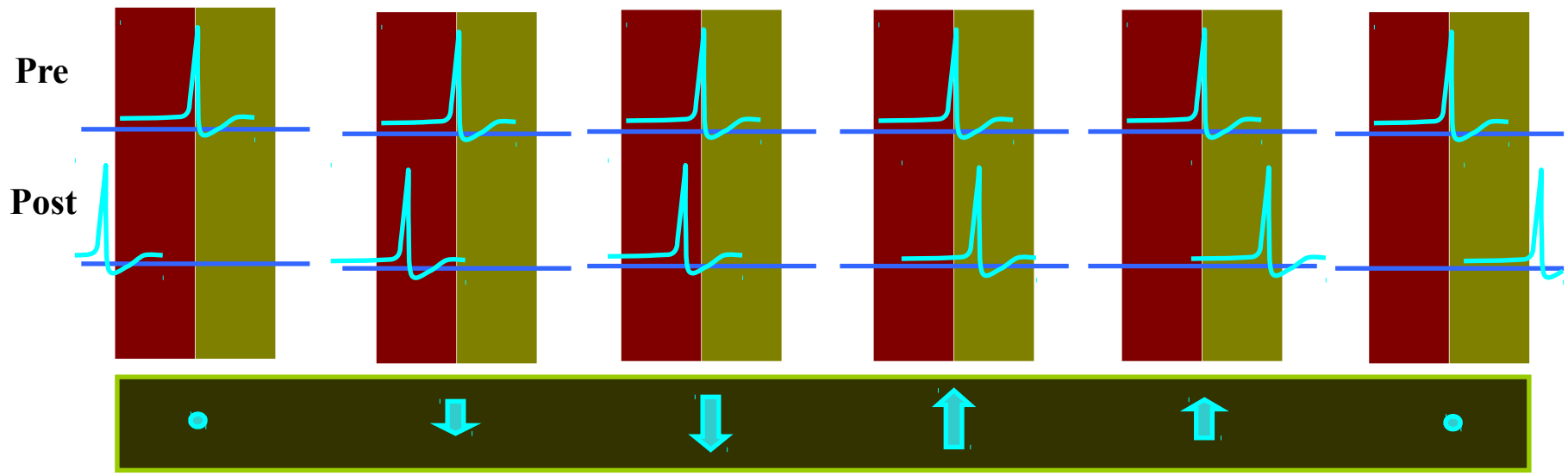
Giving

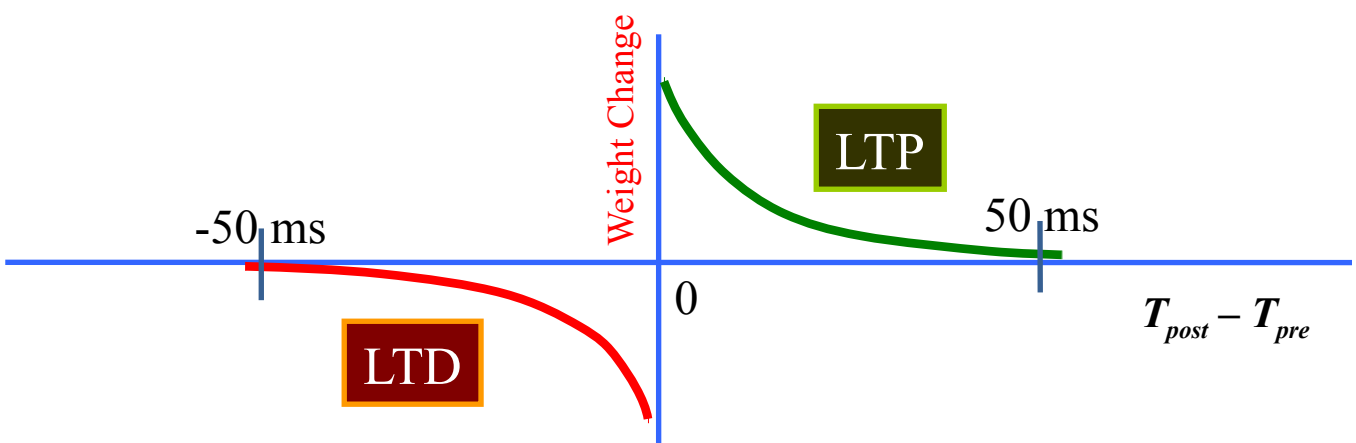
$$\bar{w}_{ij} = \frac{\langle y_j(t)\, y_i(t) \rangle}{\langle y_j(t) \rangle} = \frac{p(y_i(t) = 1, y_j(t) = 1)}{p(y_j(t) = 1)} = p(y_i(t) = 1 \mid y_j(t) = 1)$$

Similarly, $\Delta w_{ij}(t) = \eta\, y_i(t)\,[\, y_j(t) - w_{ij}(t)\,]$ gives $\bar{w}_{ij} = p(y_j(t) = 1 \mid y_i(t) = 1)$

# Spike Time-Dependent Plasticity (STDP)

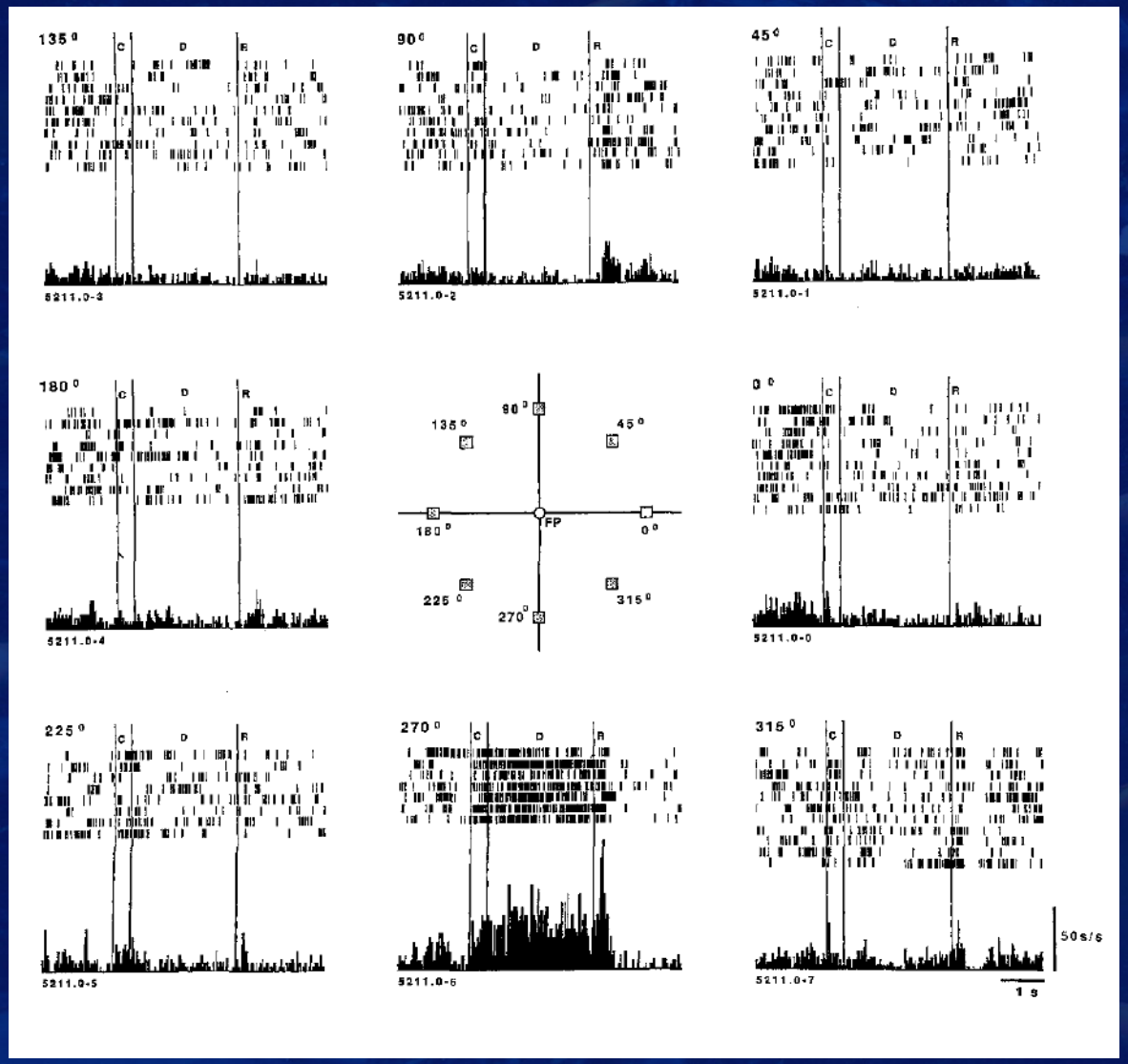
Markram, H., Lübke, J., Frotscher, M., and Sakmann, B. (1997).
Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. *Science*, 275:213-215.



# Examples of Neural Information Processing

# Direction- and Stimulus-Specific Working Memory Neuron




The neuron increases its activity only when this stimulus is presented at the 270 degree position

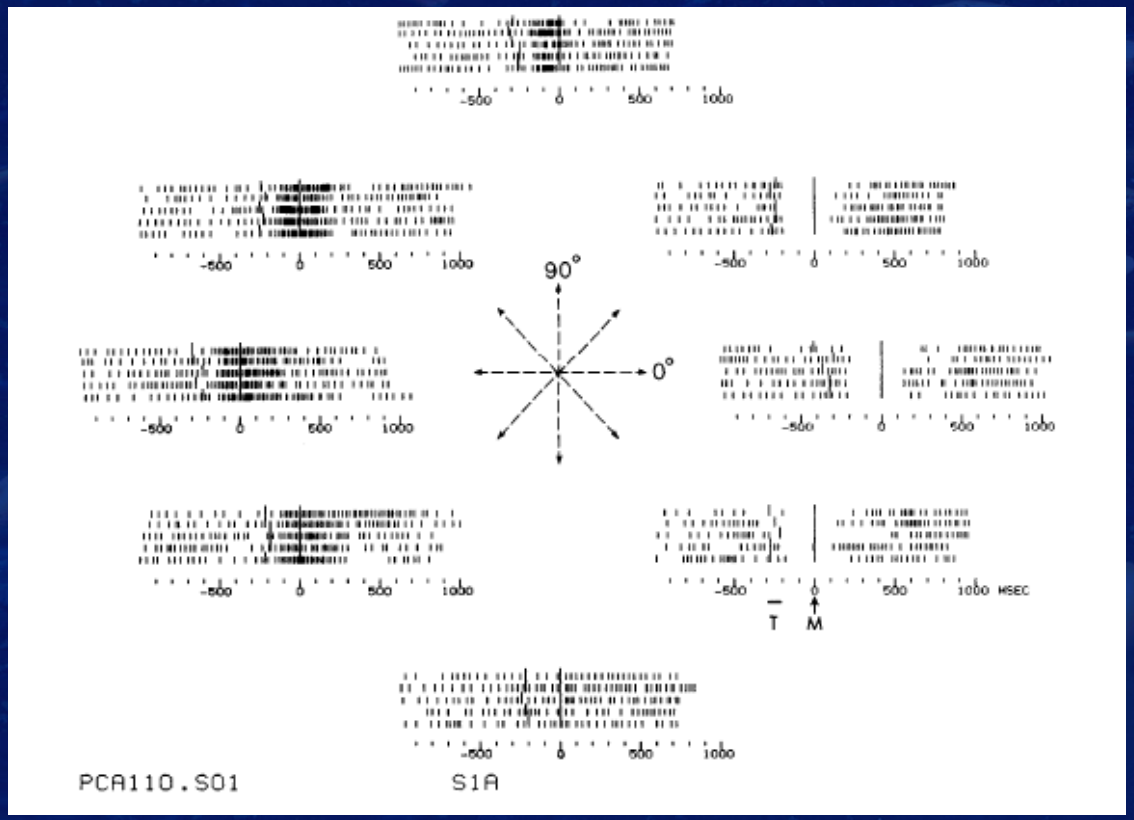
and

maintains its activity after the stimulus is switched off until the response has been produced.

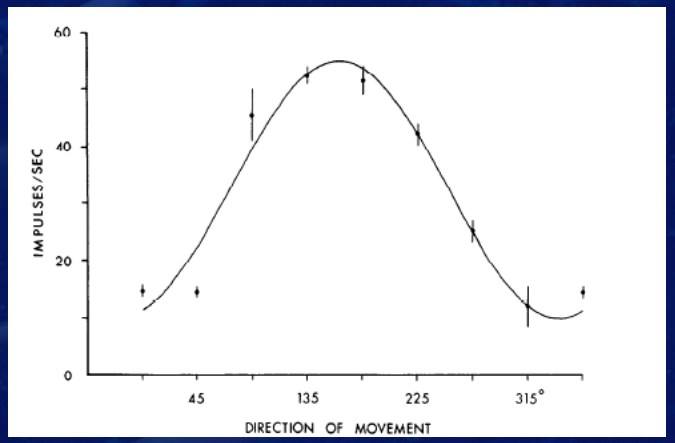
Funahashi, S., Bruce, C. J., and Goldman-Rakic, P. S. (1989). Mnemonic coding of visual space in the primate dorsolateral prefrontal cortex. J. Neurophysiol. *61,331-349.*

# Population Codes for Direction

A.P. Georgopoulos J. P. Kalaska, R. Caminiti & J.T. Massey (1982)
On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex, J. Neurosci 2: 1527-1537



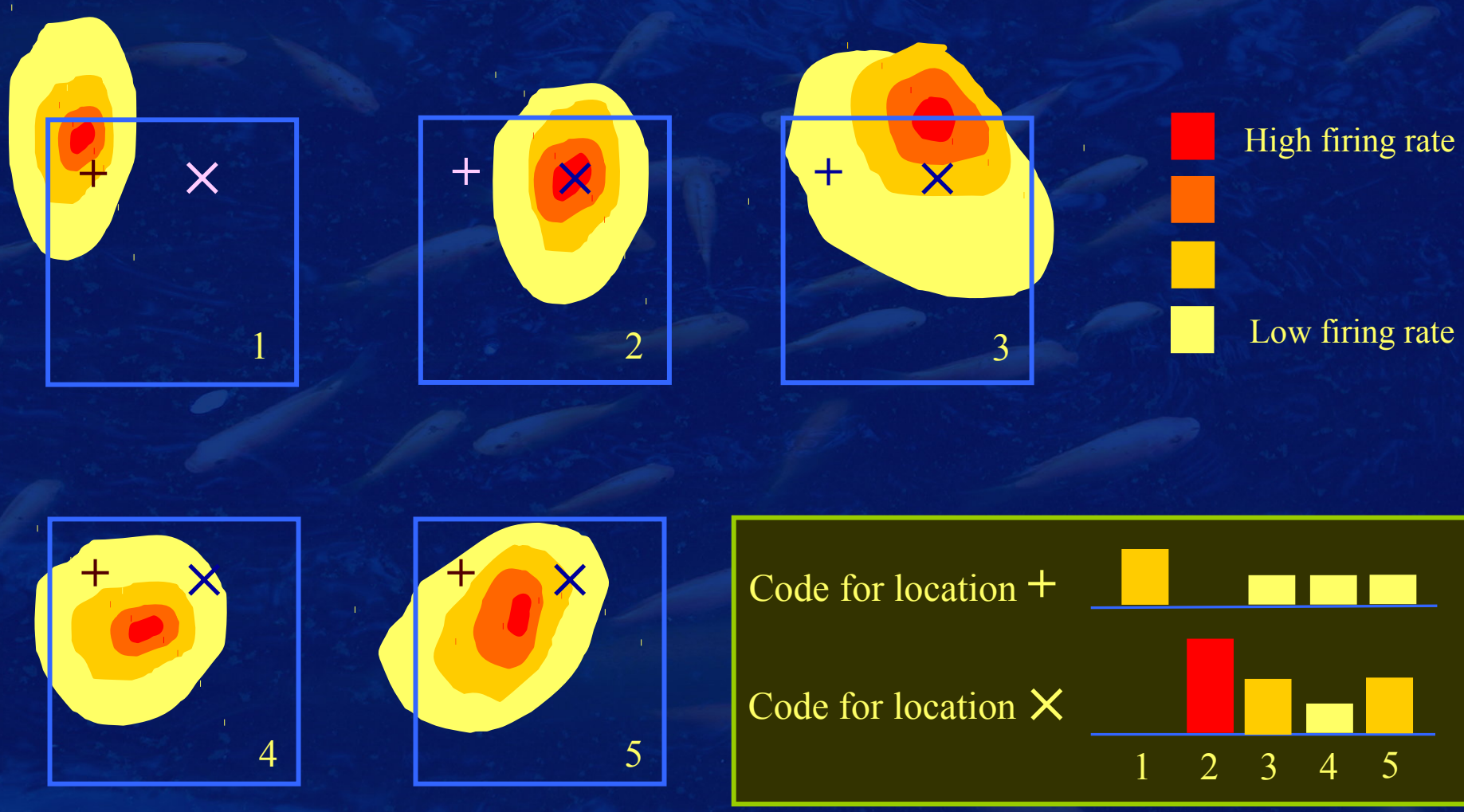

Firing of the cell is tuned to direction of movement

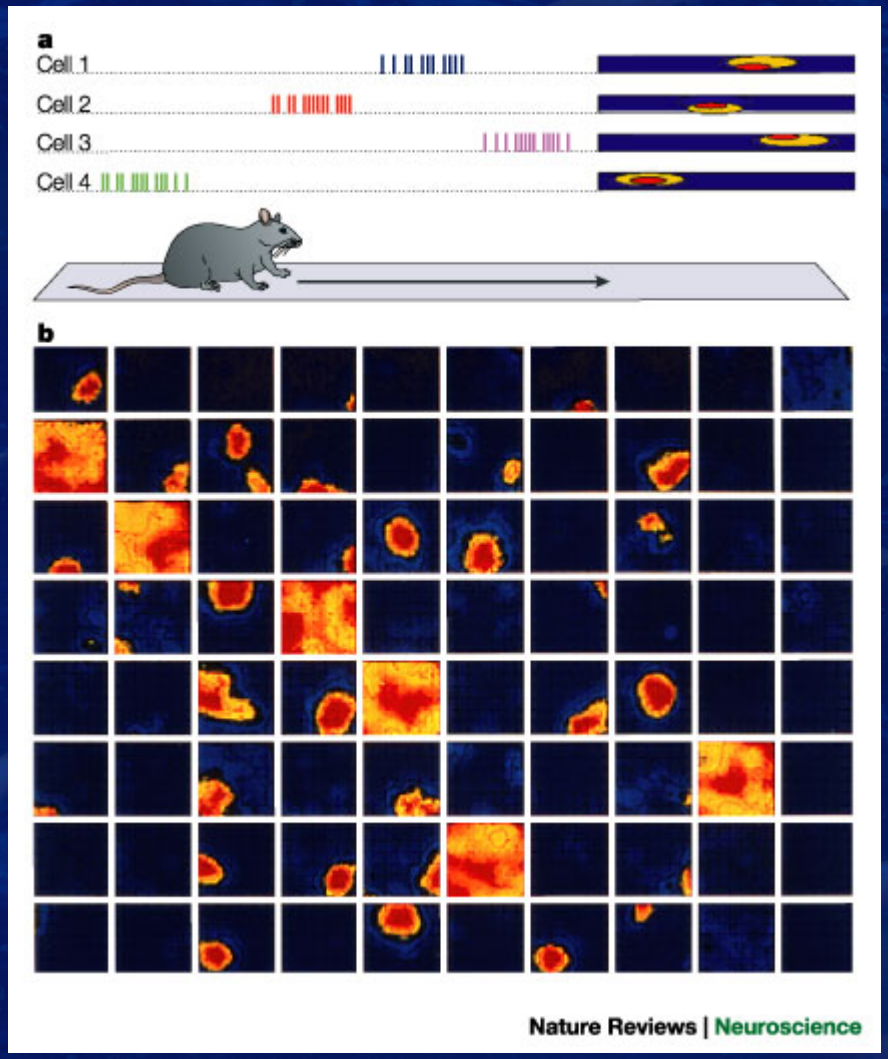



Tuning curve described by a cosine-like function

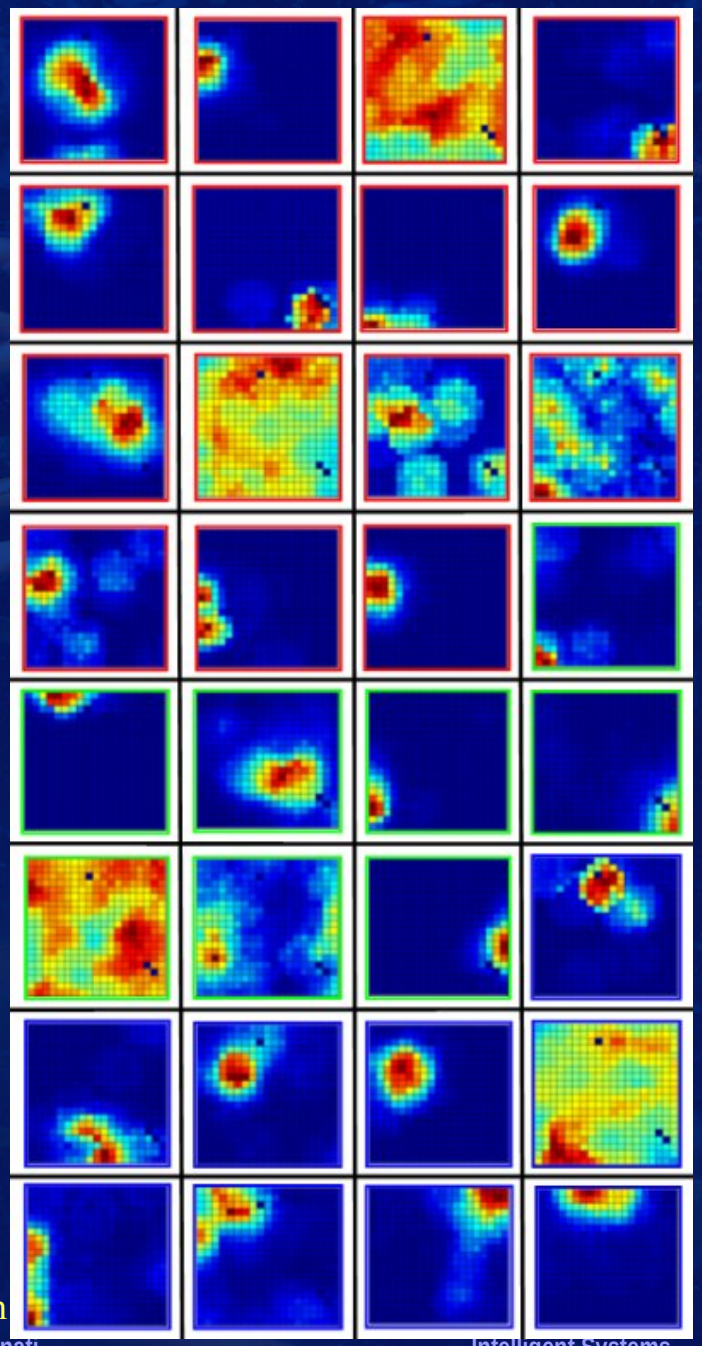
# Ensemble Coding: Distributed Codes

## Hippocampal Place Cells



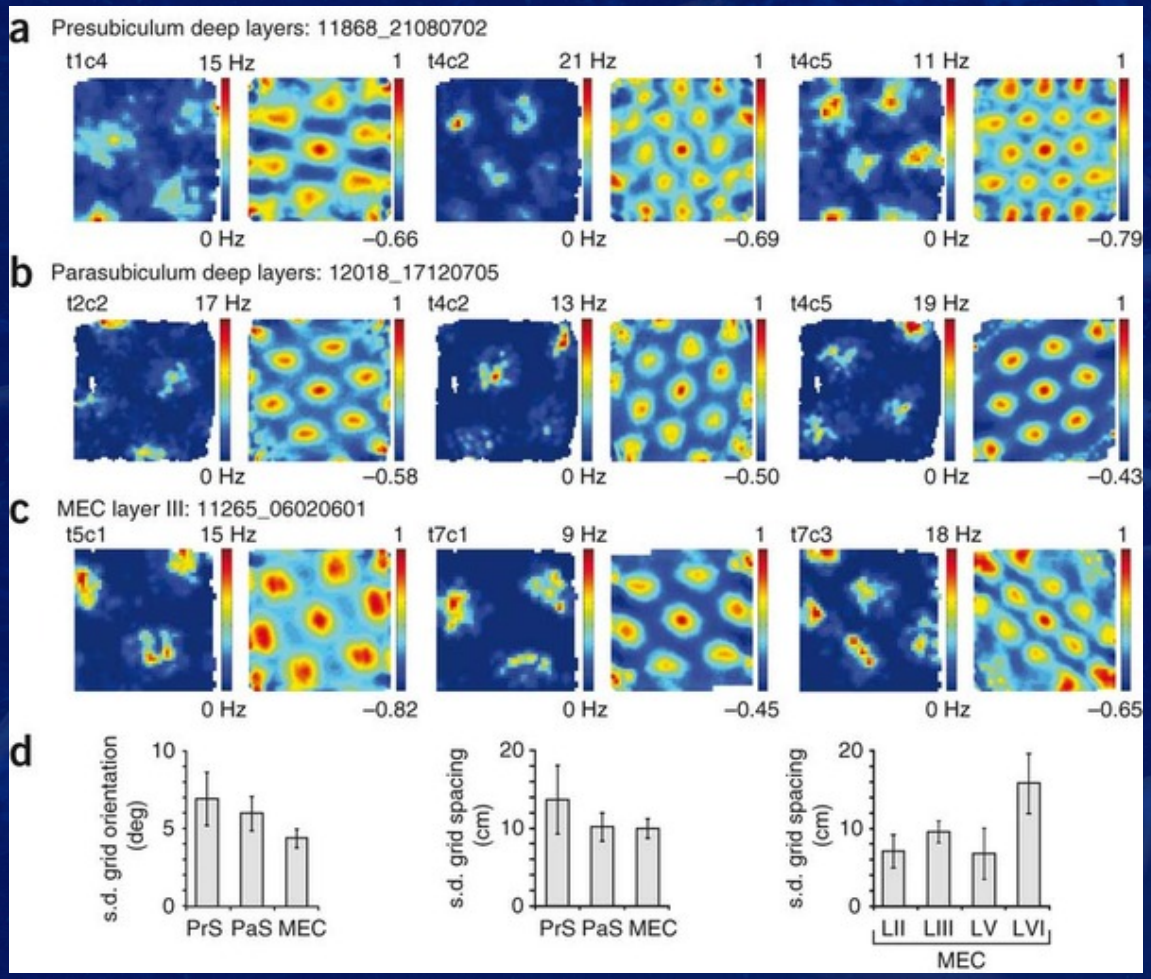



NMDA receptors, place cells and hippocampal spatial memory
Kazu Nakazawa, Thomas J. McHugh, Matthew A. Wilson & Susumu Tonegawa. Nature Reviews Neuroscience 5, 361-372 (May 2004)
doi:10.1038/nrn1385



http://hargreaves.swong.webfactional.com/place.htm

# Grid Cells




Grid cells have firing fields with a grid pattern.

Nearby cells have fields with similar spatial frequency and orientation, but a spatial offset.

Fields in different regions can have different spatial frequency and orientation.

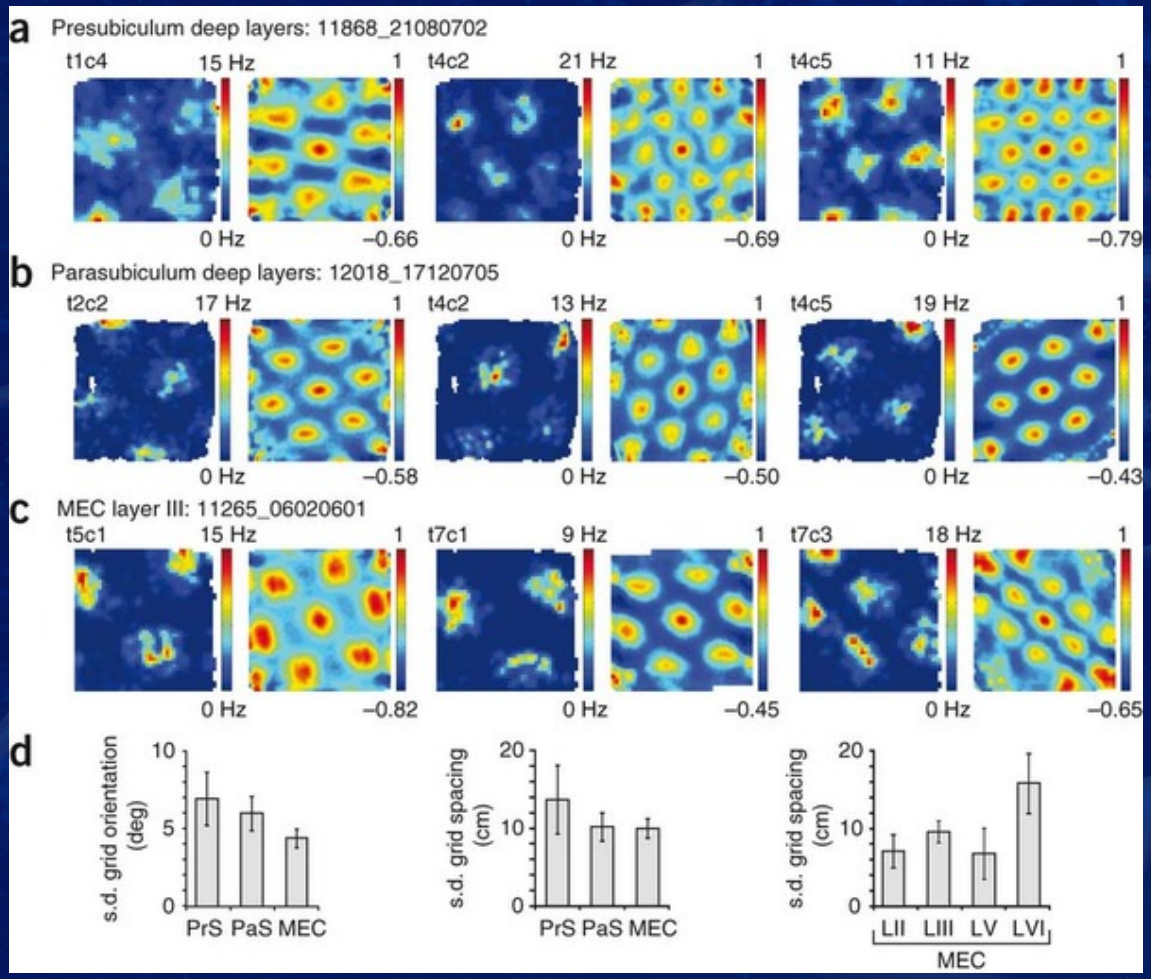
Grid cells are found in several brain regions, including the entorhinal cortex, the presubiculum, and the parasubiculum.

Grid cells are thought to work with hippocampal place cells to encode spatial representations.

The 2014 ***Nobel Prize*** in Physiology & Medicine was awarded to May-Britt Mozer, Edvard Mozer and John O'Keefe for their work on grid cells and place cells.

Boccara, C.N. et al (2010) Grid cells in pre- and para-subiculum. Nature Neurosciece 13: 987-994.

# Grid Cells

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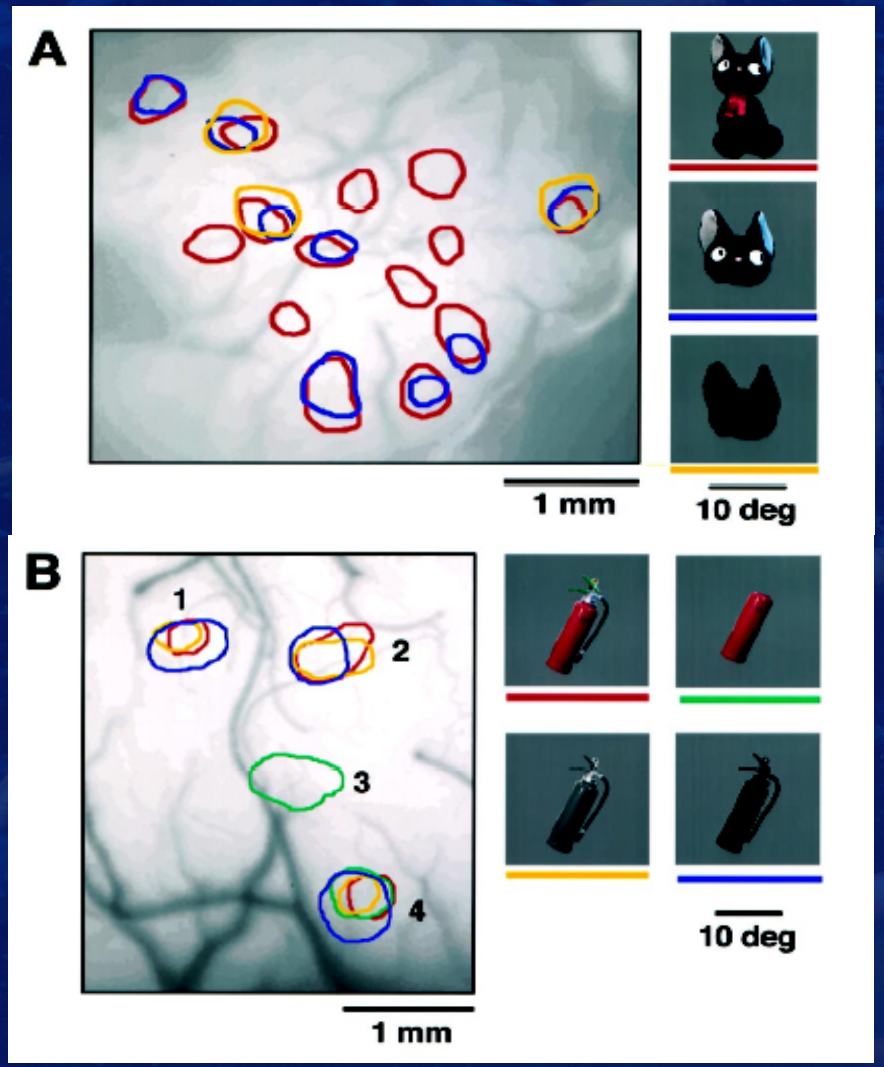
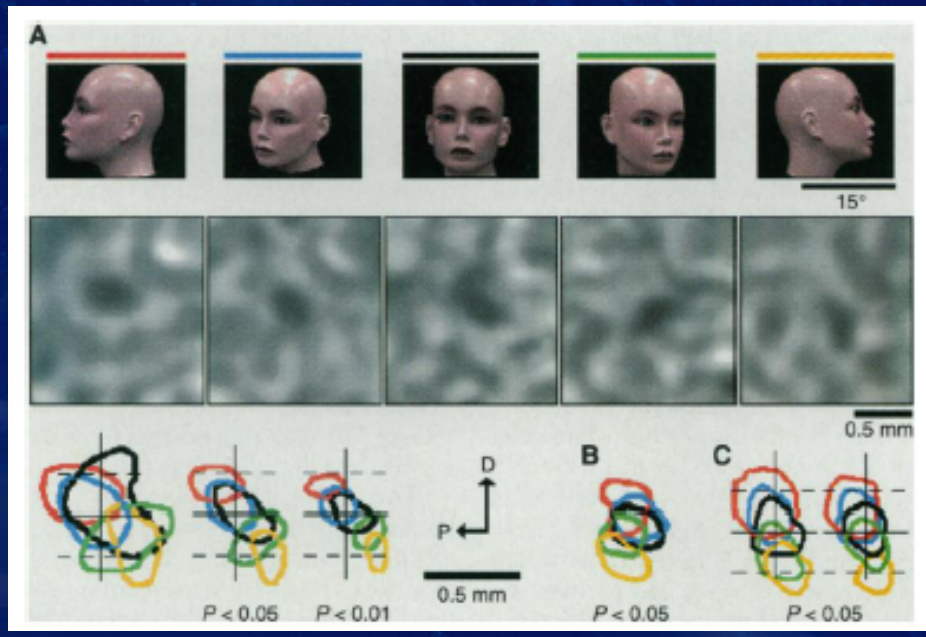
# Distributed Coding: Feature-Specific Activity in the Macaque Inferotemporal Cortex




Tsunoda K, Yamane Y, Nishizaki M, & Tanifuji M (2001) Complex objects are represented in macaque inferotemporal cortex by the combination of feature columns. *Nat Neurosci* **4**:832–838.

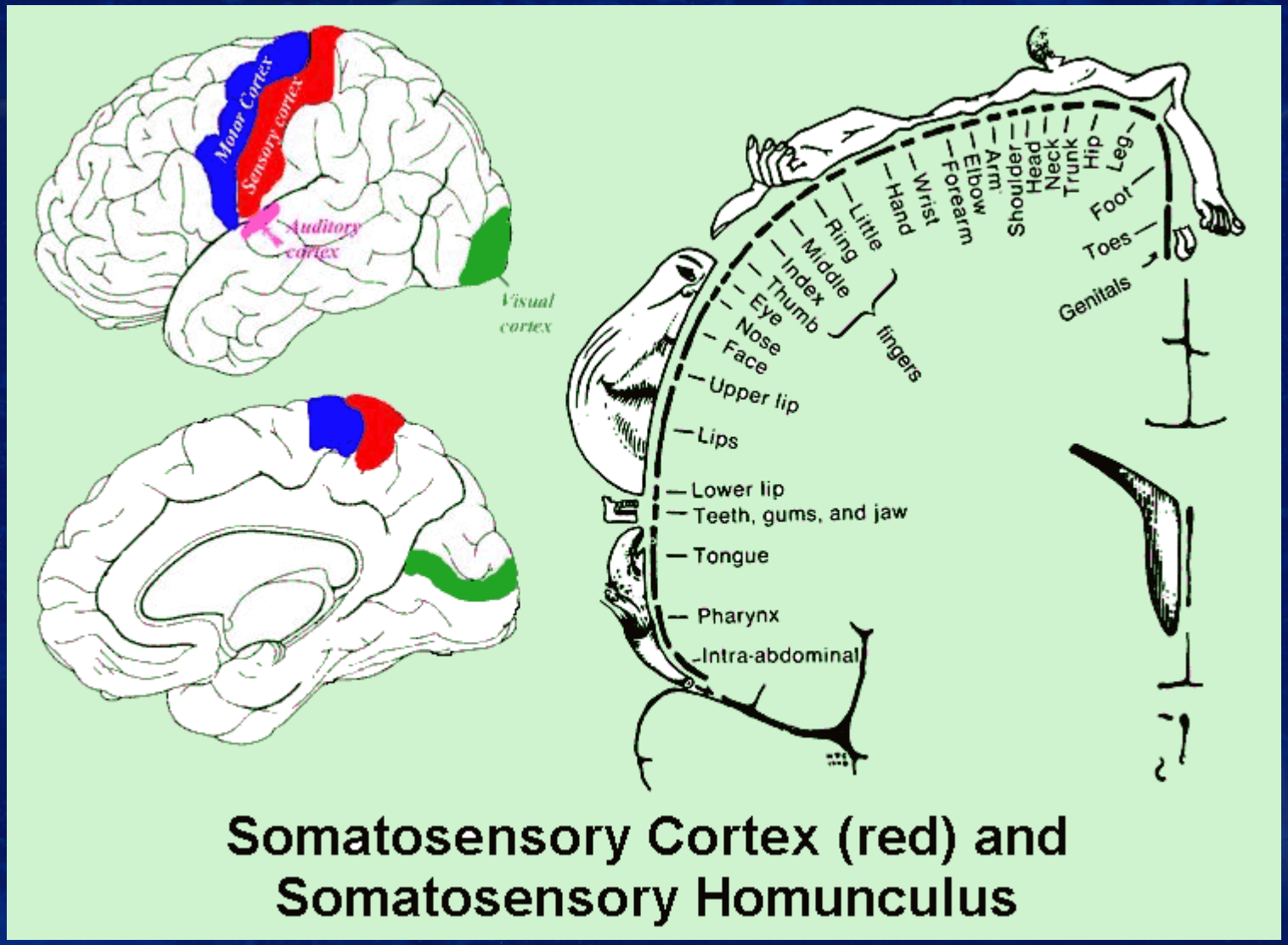
Specific features activate neurons in several spots

Activity region moves as stimulus is rotated




Wang, G., Tanaka, K. & Tanifuji M (2001) Optical imaging of functional organization in the monkey inferotemporal cortex. *Science* **272**:1665-1668.

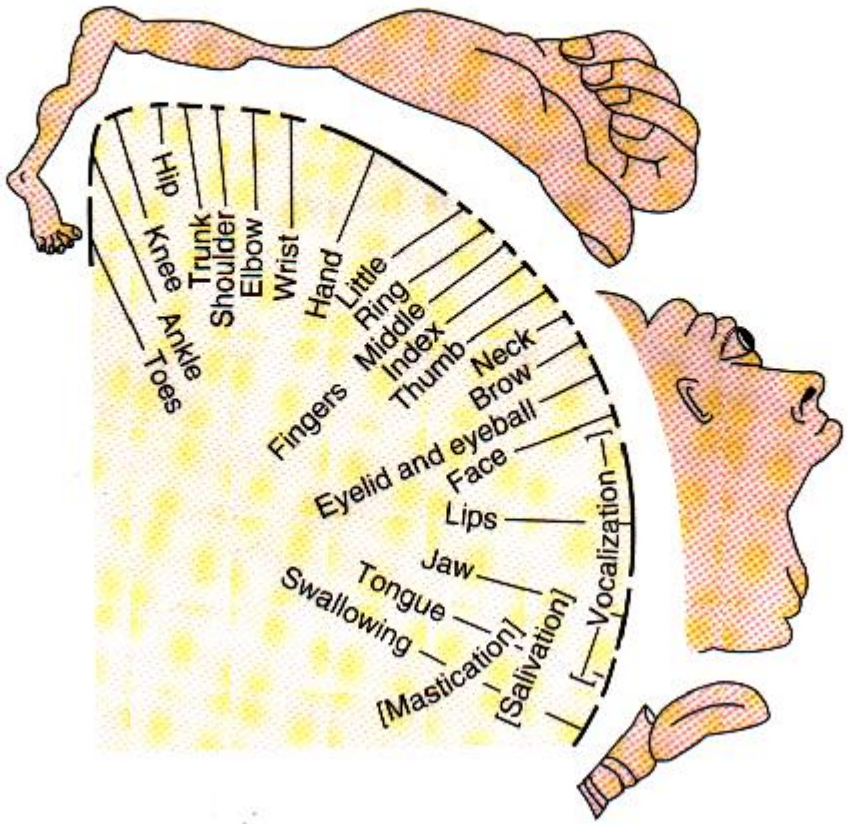
# The Somatosensory Homunculus




Somatosensory Cortex (red) and Somatosensory Homunculus

http://ww2.coastal.edu/kingw/psyc450/skin/fig_12-2-5.png

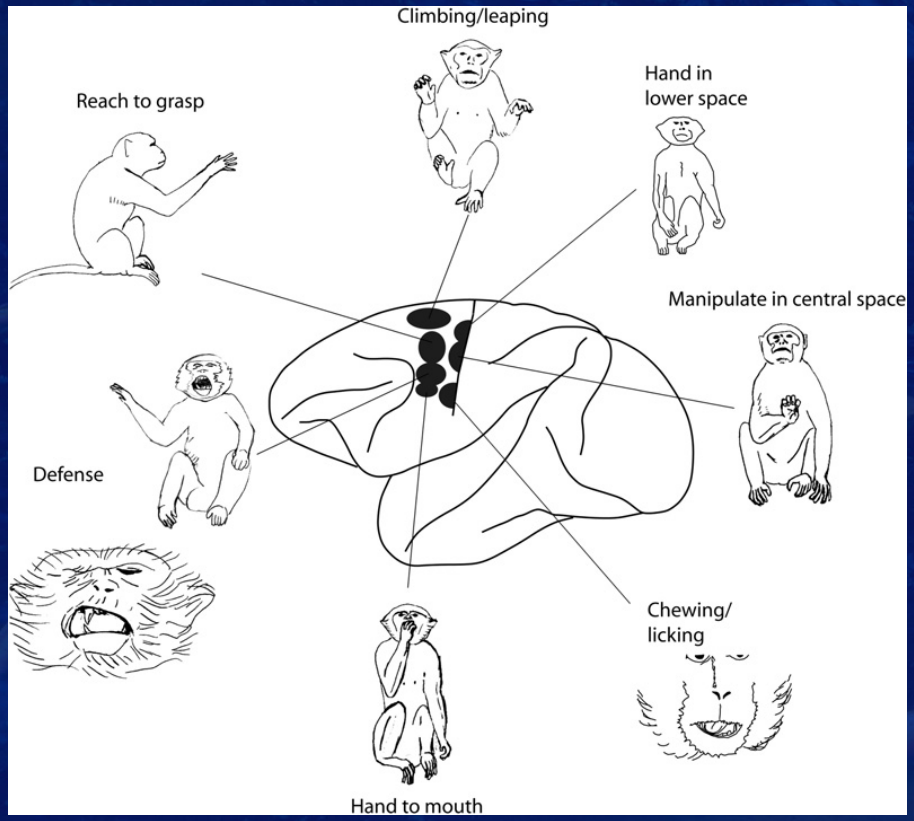
# The Motor Homunculus



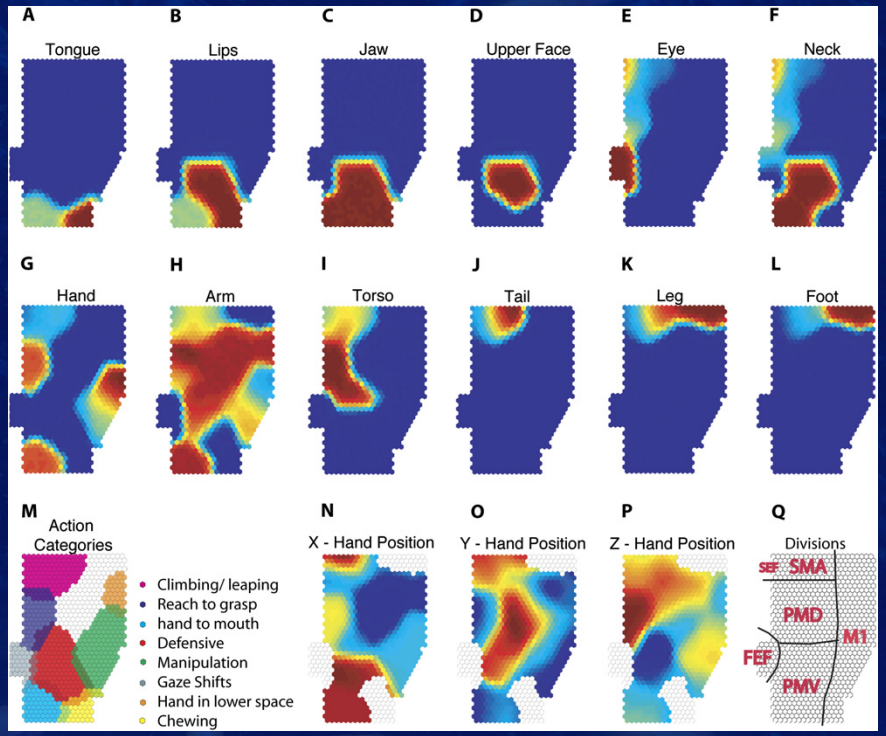

http://www.vis.caltech.edu/~zoltan/szeged8/img8.htm

# Stereotypical Actions

M.S.A. Graziano & T.N. Aflalo (2007) Mapping Behavioral Repertoire onto the Cortex, *Neuron* 56: 239-251.



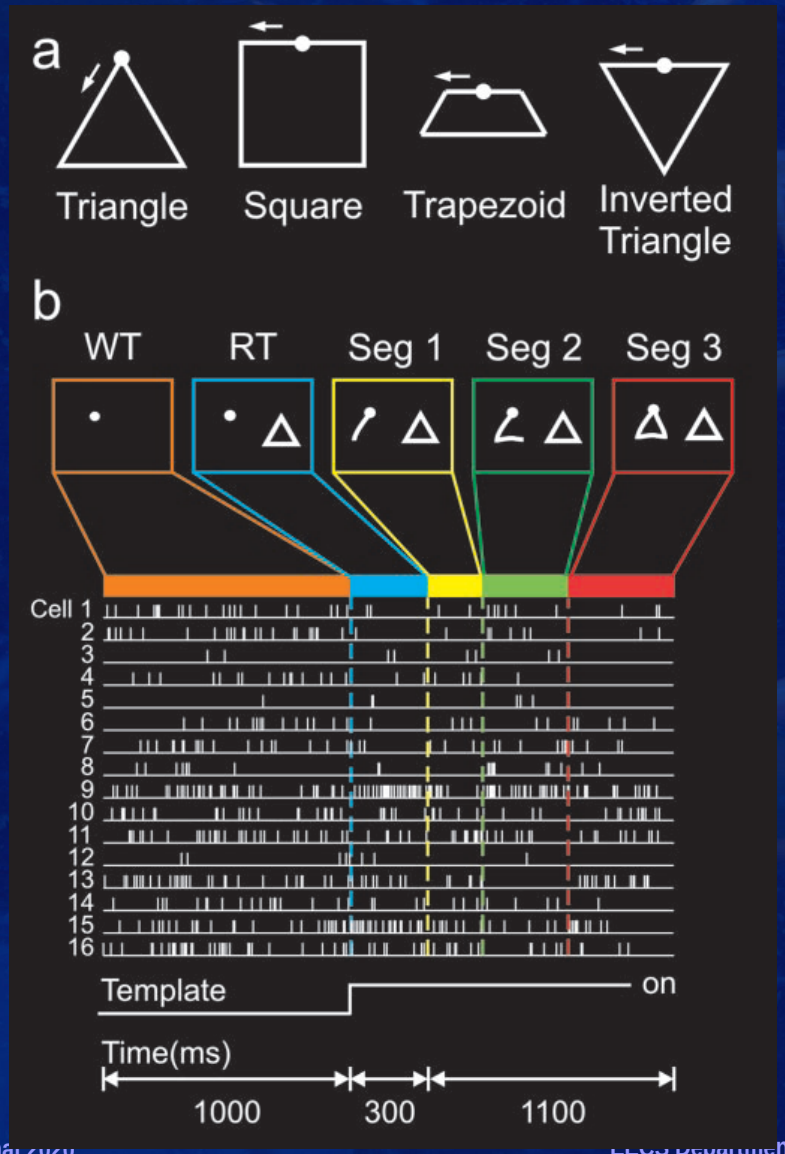

Actions resulting from sustained stimulation of various areas of the motor cortex.

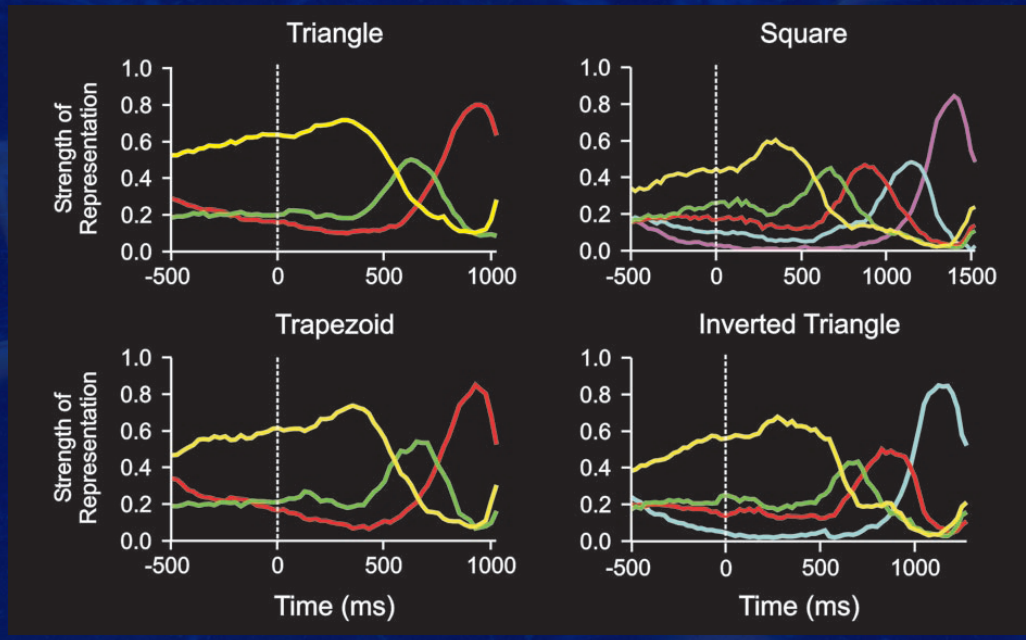


Cortical maps and simulated movements generated by a computational model

# Sequential Movement

B.B. Averbeck, M.V. Chafee, D.A. Crowe, A.P. Georgopoulos (2002)
Parallel processing of serial movements in prefrontal cortex, PNAS 99: 13172-13177.



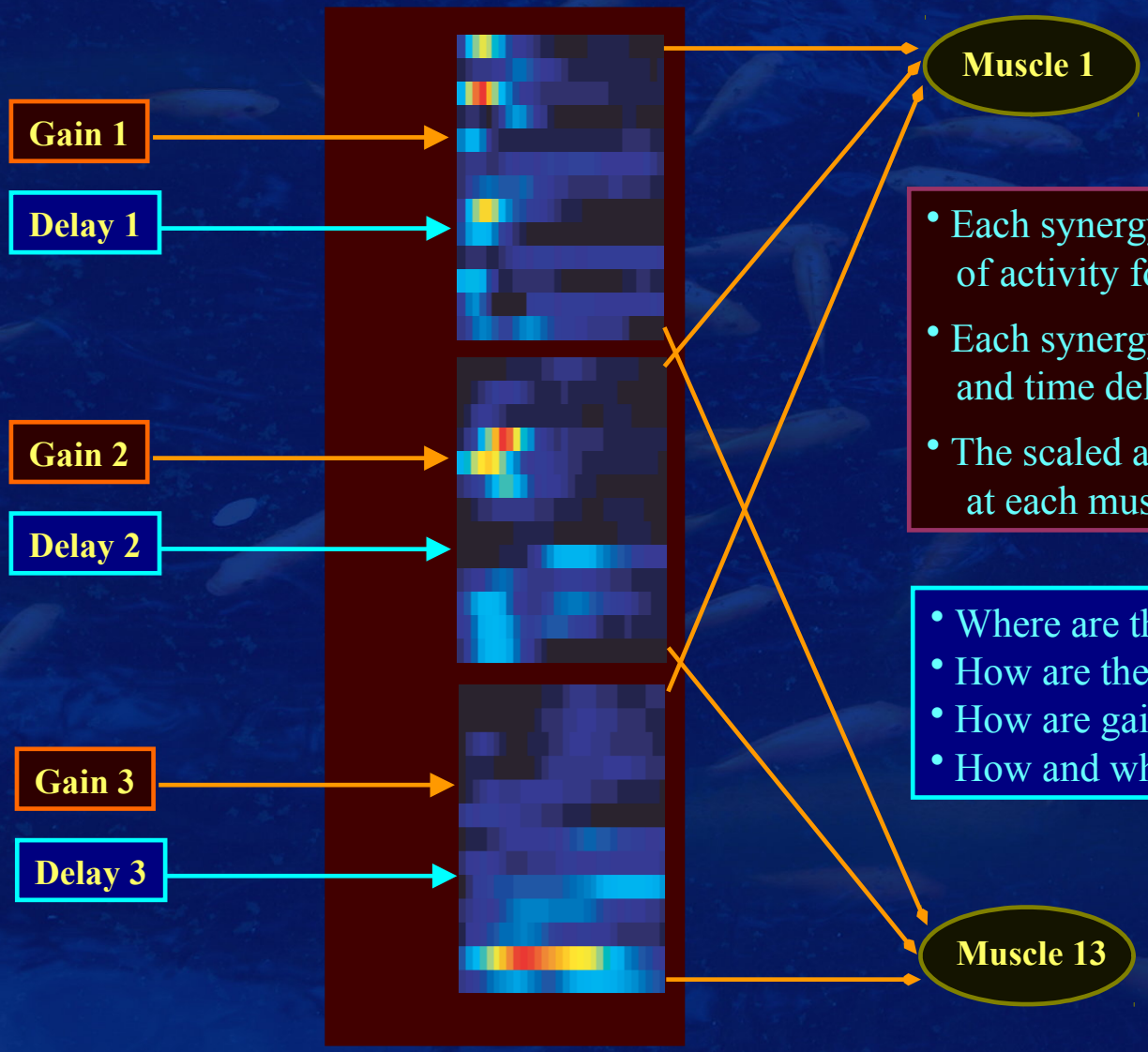




The code for the entire sequence turns on at the beginning, with amplitude indicating order of execution.

Neurons code for movement in specific directions, and for stages of execution

# The Motor Synergies Model

(d'Avella, A., Saltiel, P. and Bizzi, E. (2003) Nature Neurosci 6: 300-308)

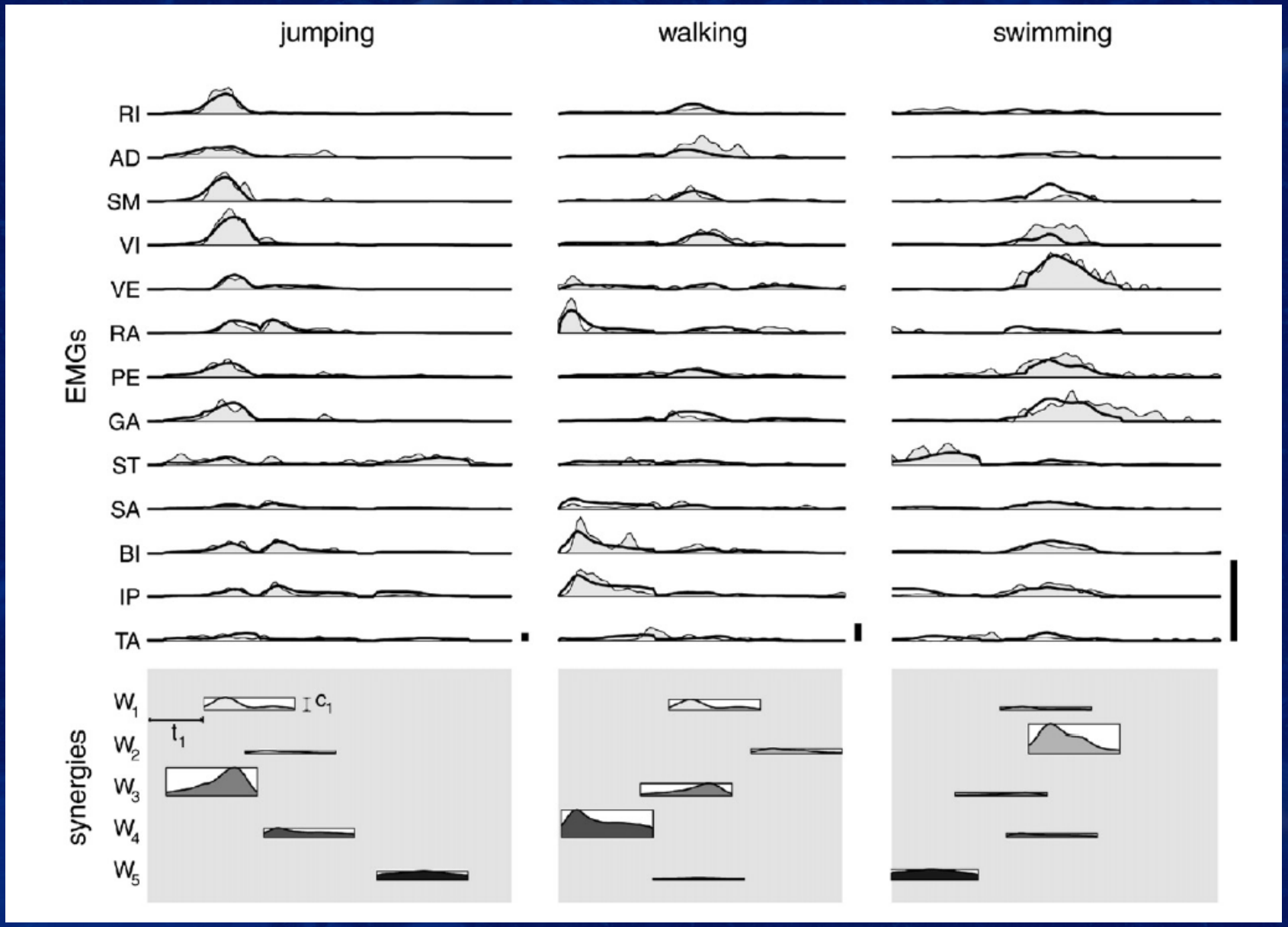



- Each synergy specifies a particular pattern of activity for each muscle.
- Each synergy is evoked with a specific gain and time delay for each action.
- The scaled and delayed synergies are summed at each muscle to produce the action.

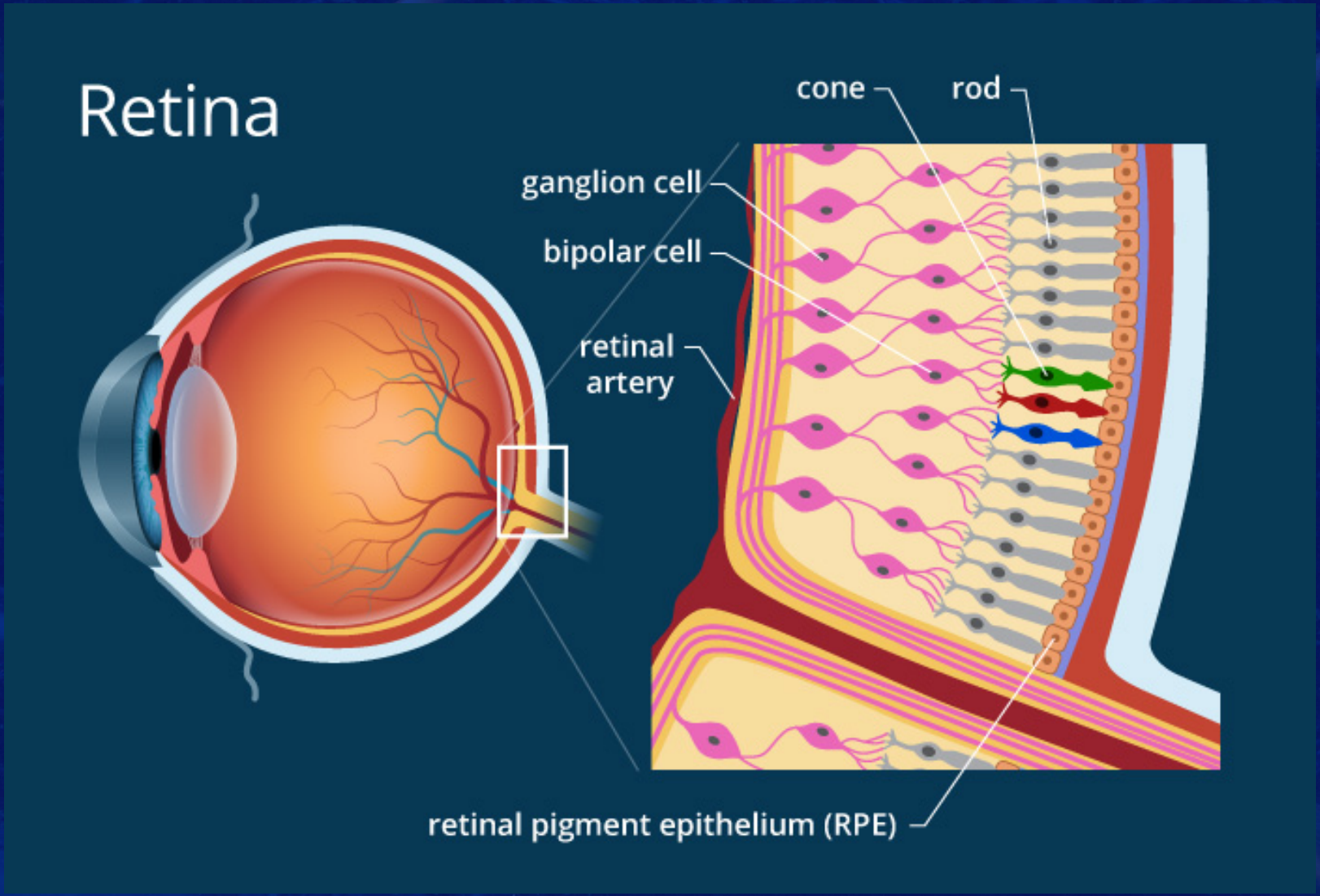
- Where are the synergies stored?
- How are they configured (genetic or learned)?
- How are gains and delays specified?
- How and where are new actions learned?

# The Motor Synergies Model

(Bizzi, E. et al (2008), Brain Research Reviews 57: 125-133)

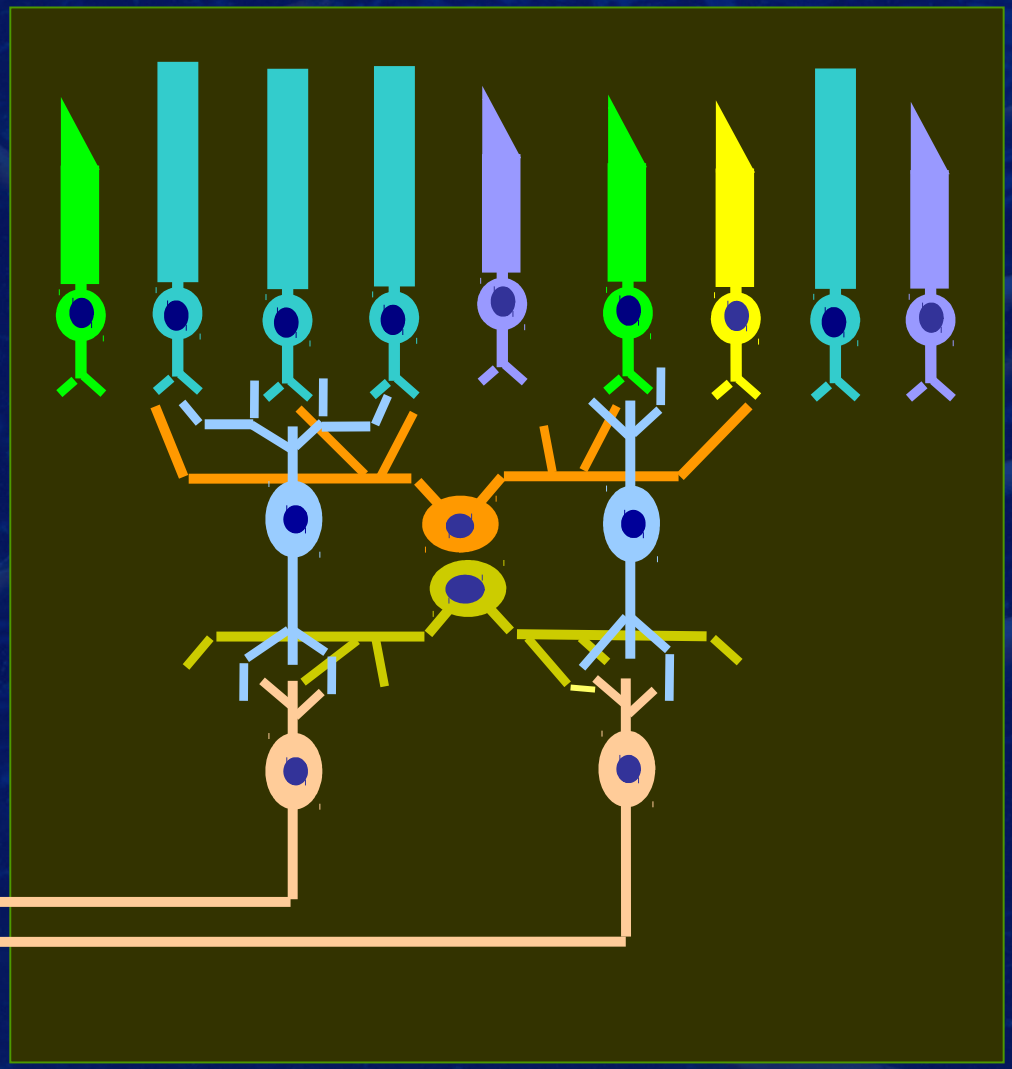


# The Retina




https://www.allaboutvision.com/resources/retina.htm

# The Retina



Photoreceptors
(rods and cones)

Bipolar Cells

Ganglion Cells

Optic Nerve
(to LGN)

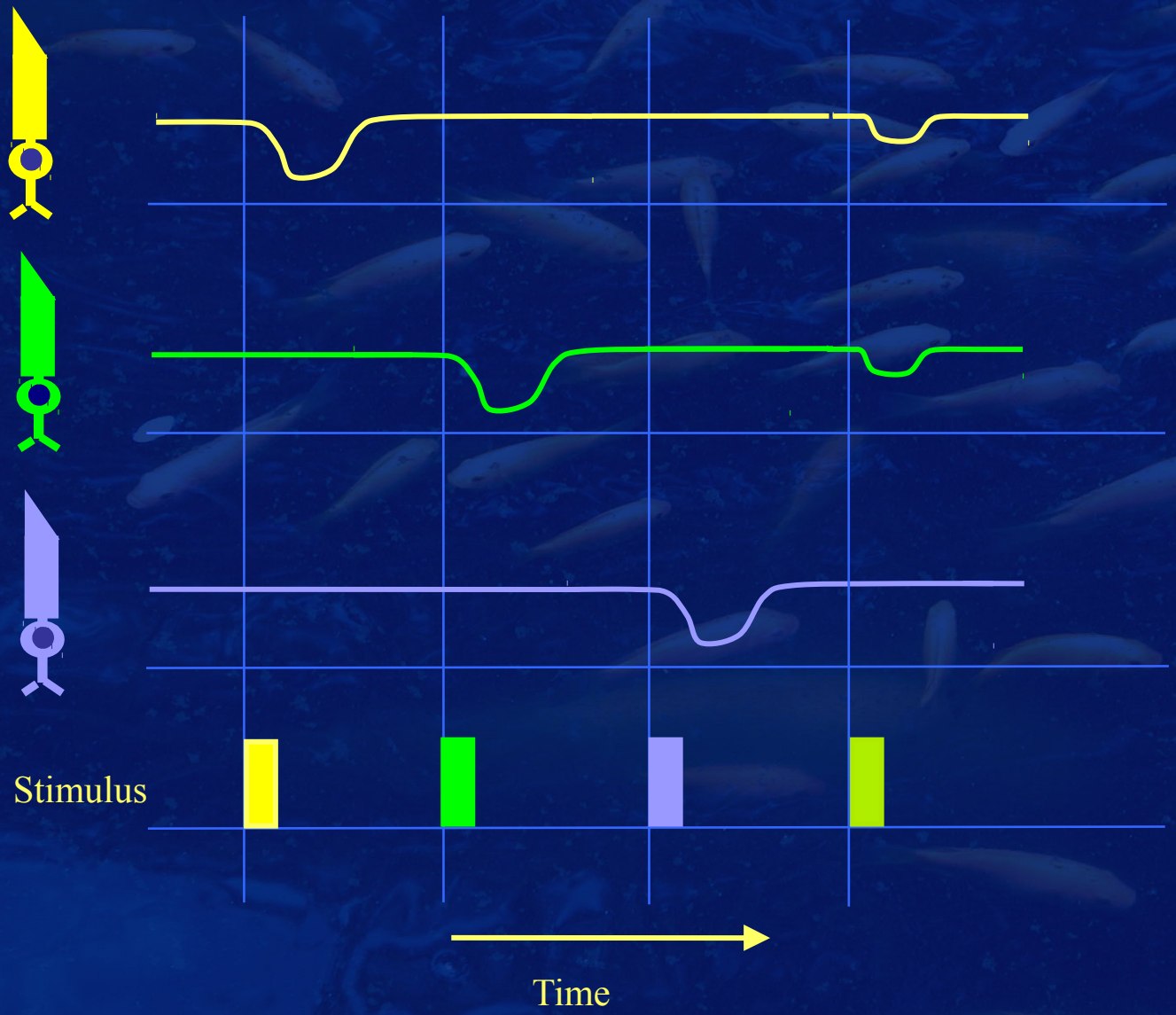
Horizontal Cells

Amacrine Cells

Light

# Cellular Information Processing

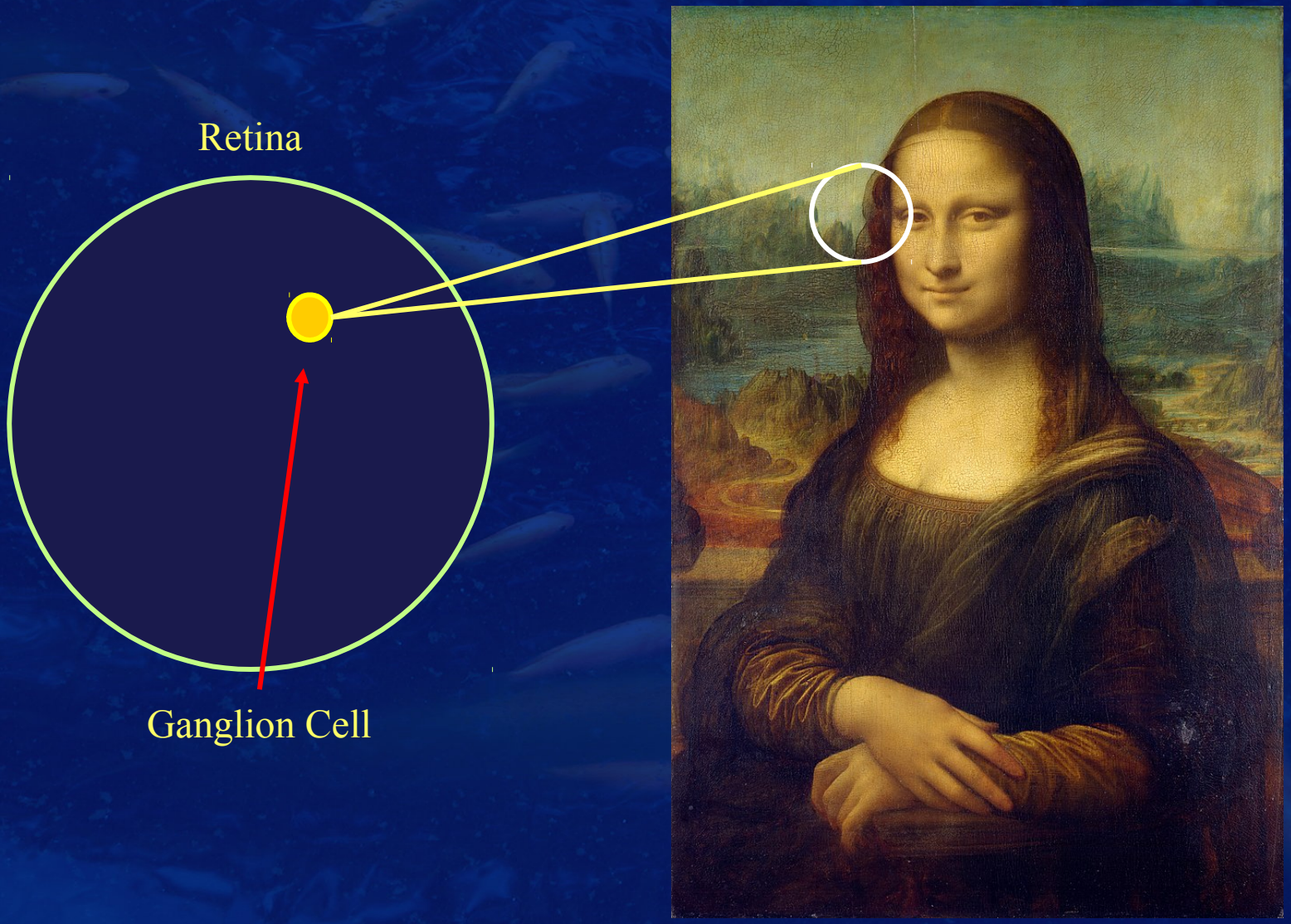
## Signal Detection in Retinal Receptors



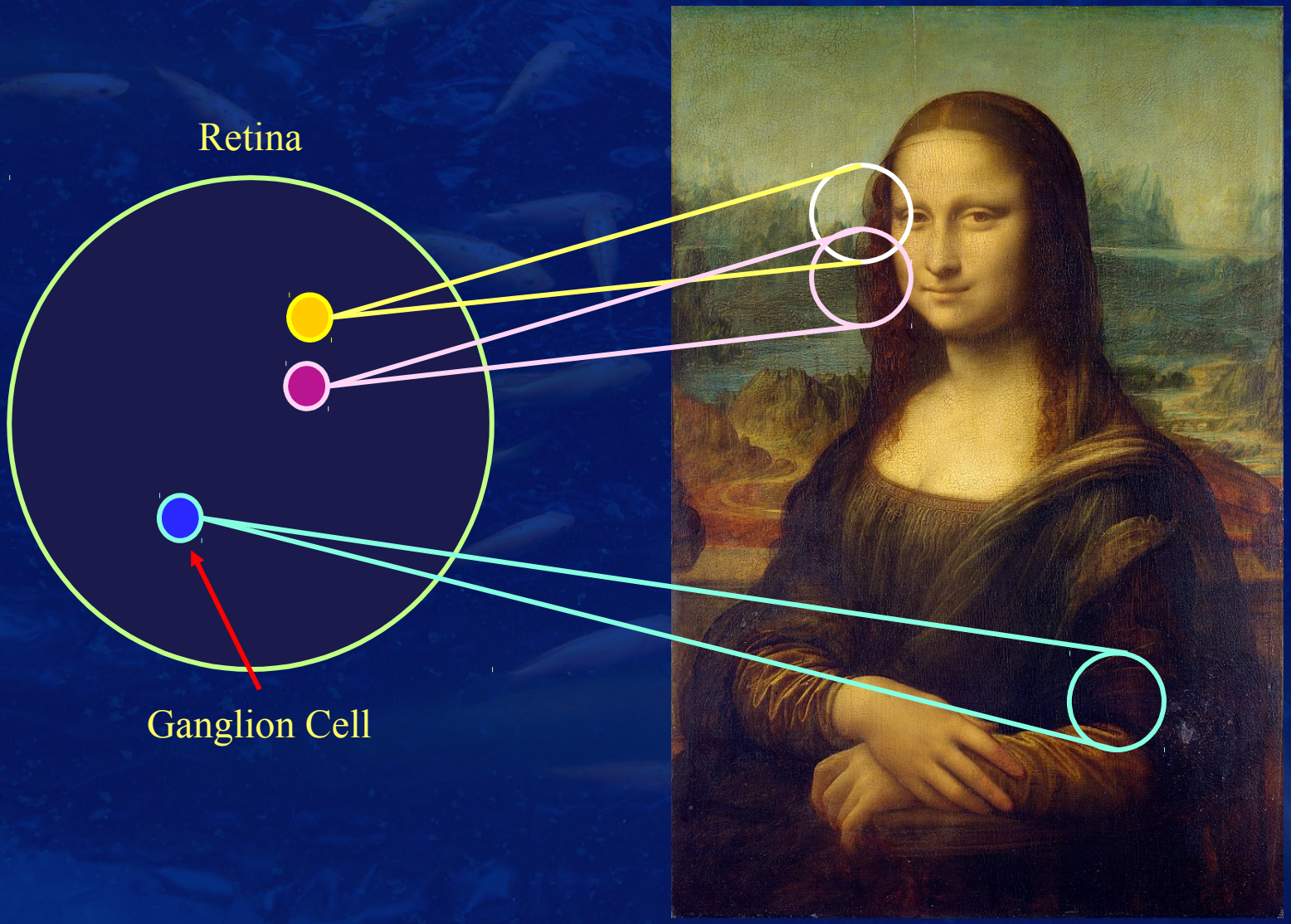

Yellow
Not green
Not blue

= **Information**

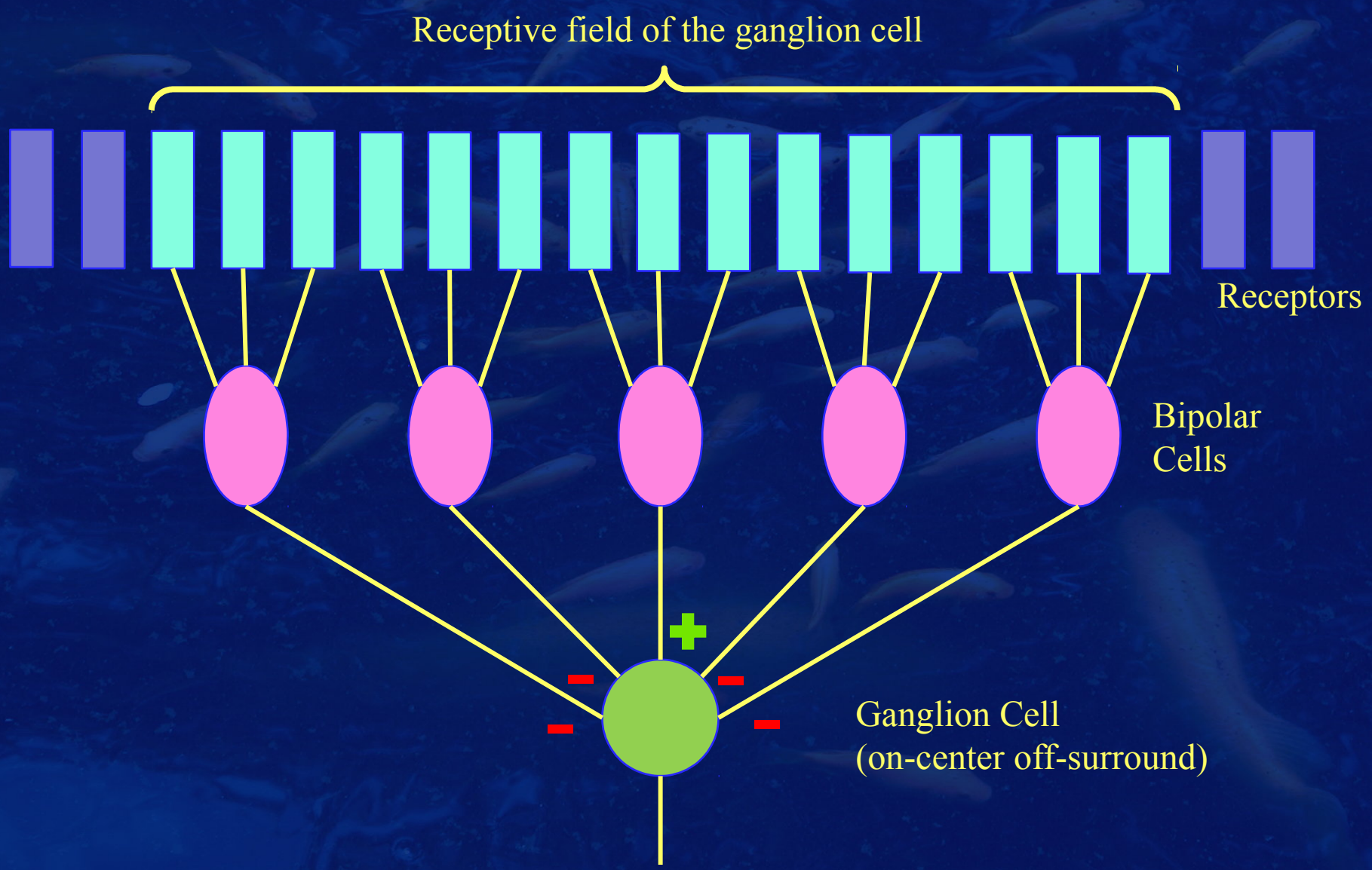
# Receptive Fields



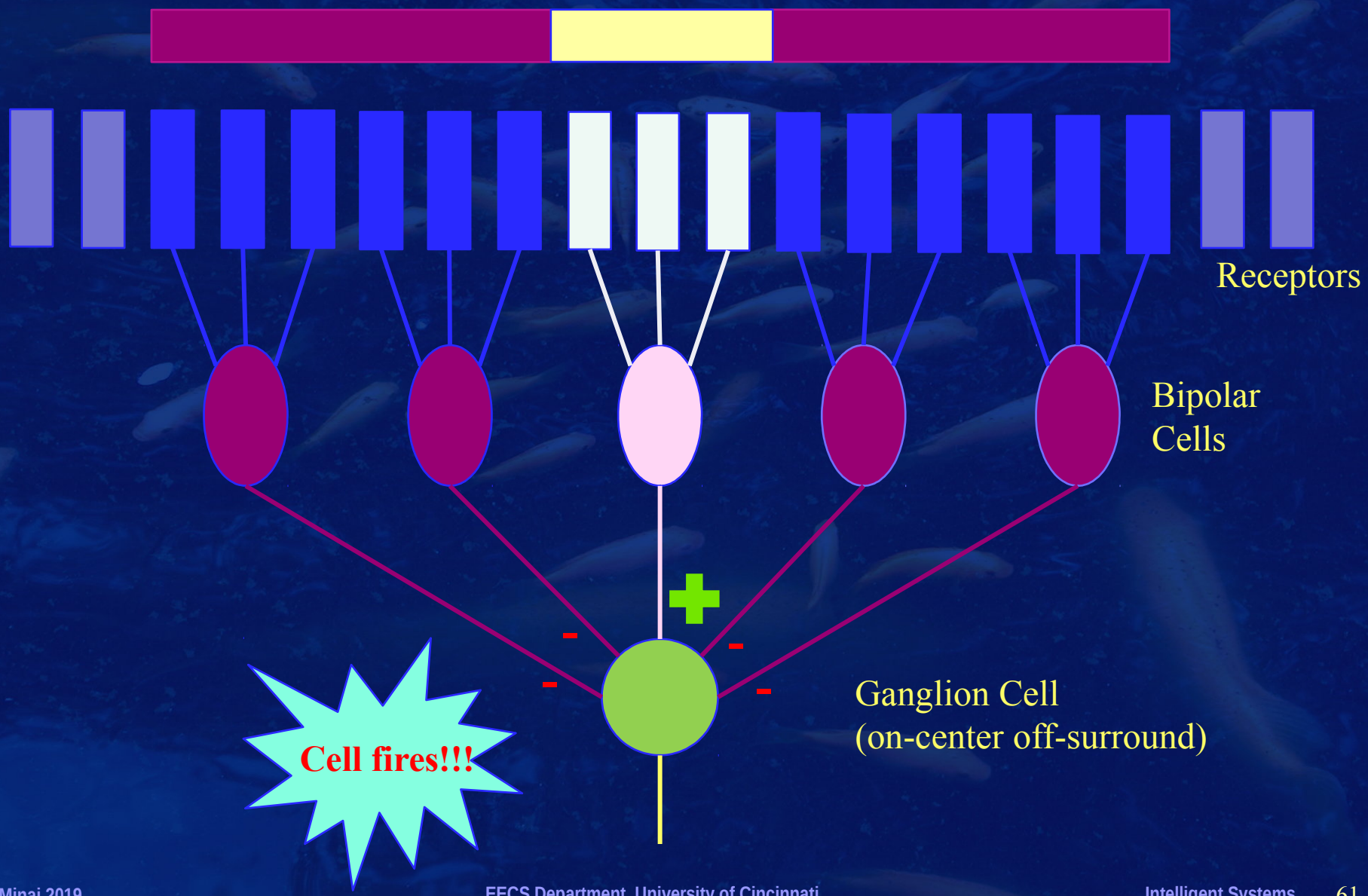
# Retinotopic Mapping



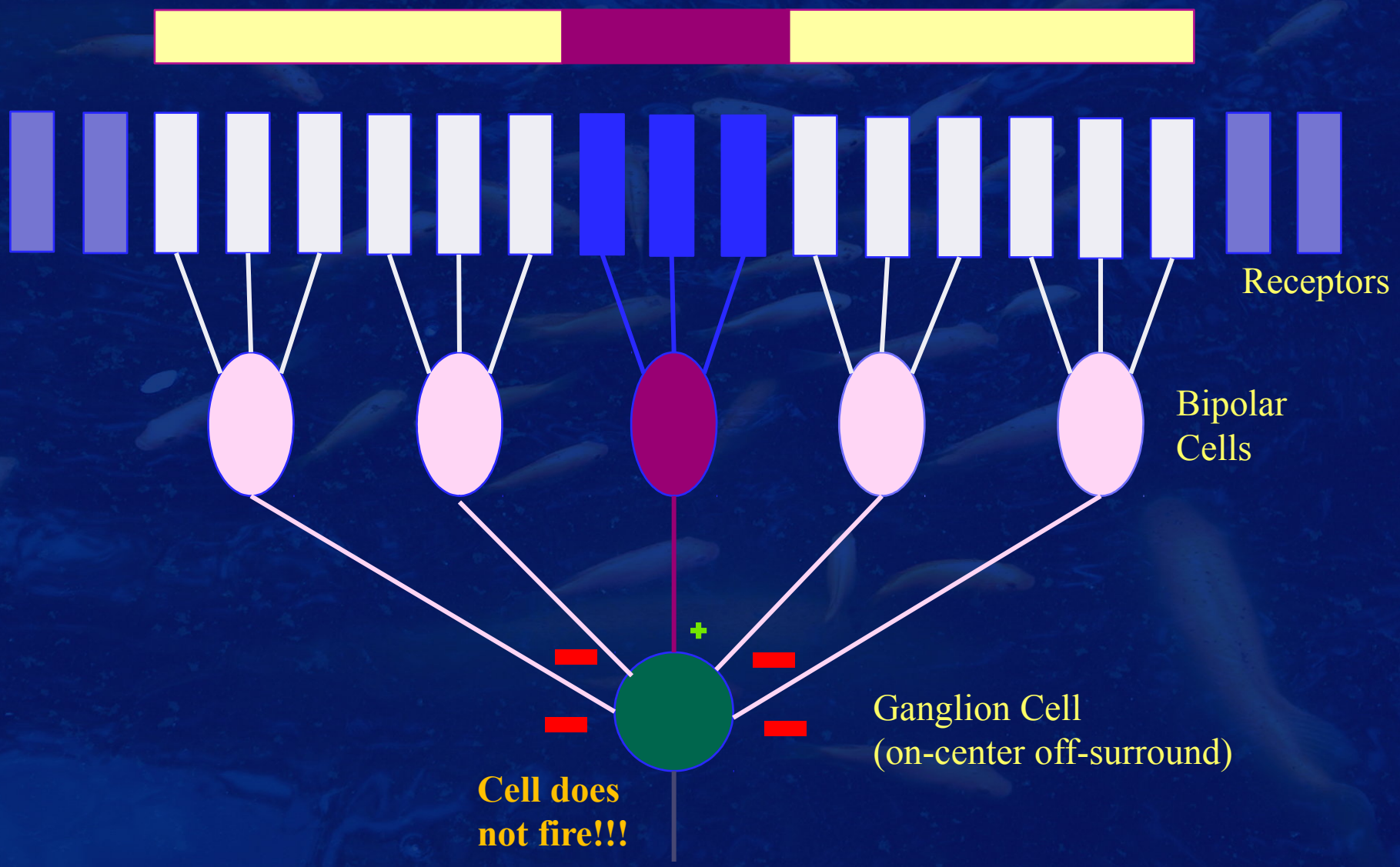
# Center-Surround Receptive Fields



Input with bright center and dark surround

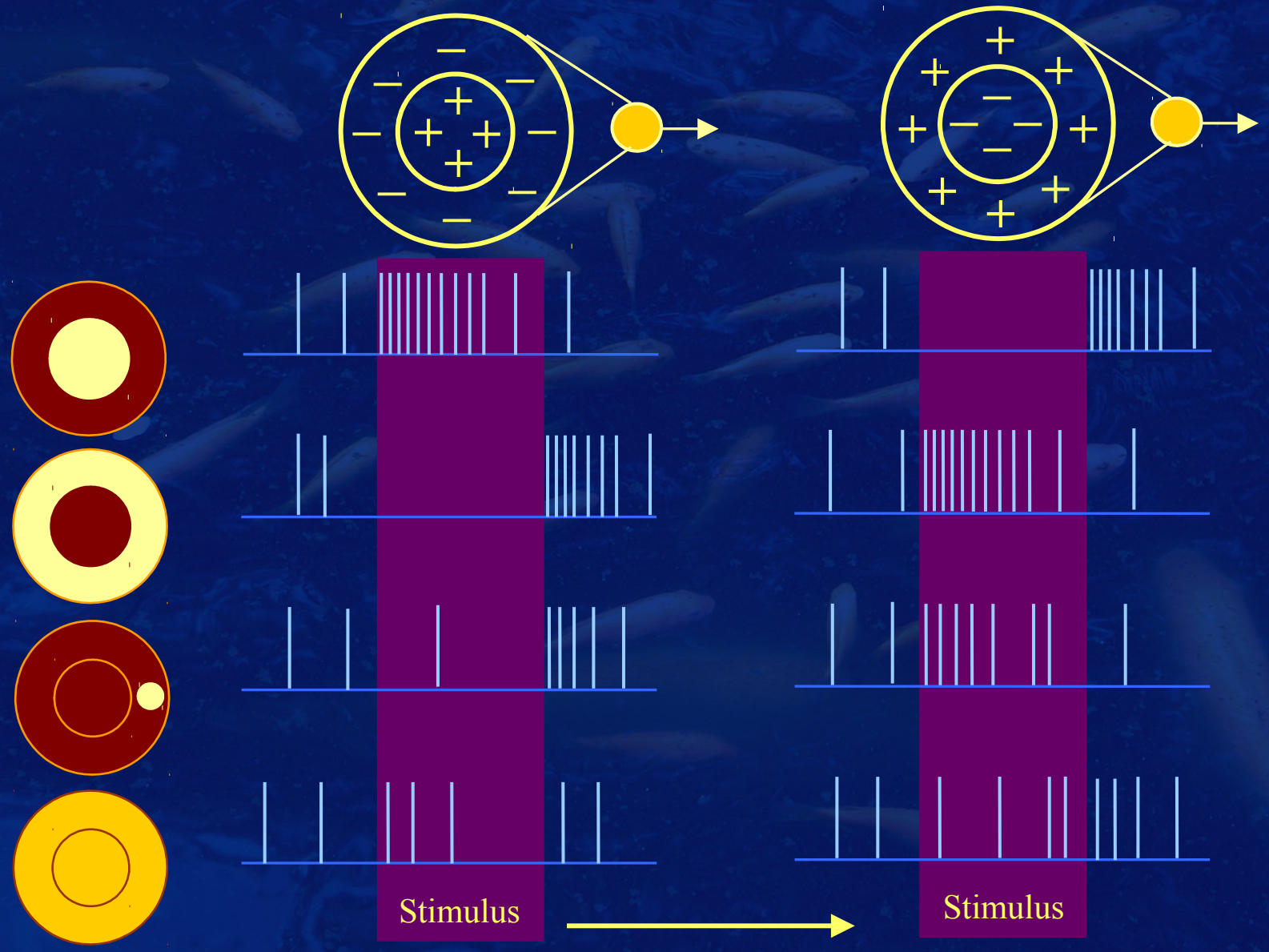


Input with bright center and dark surround



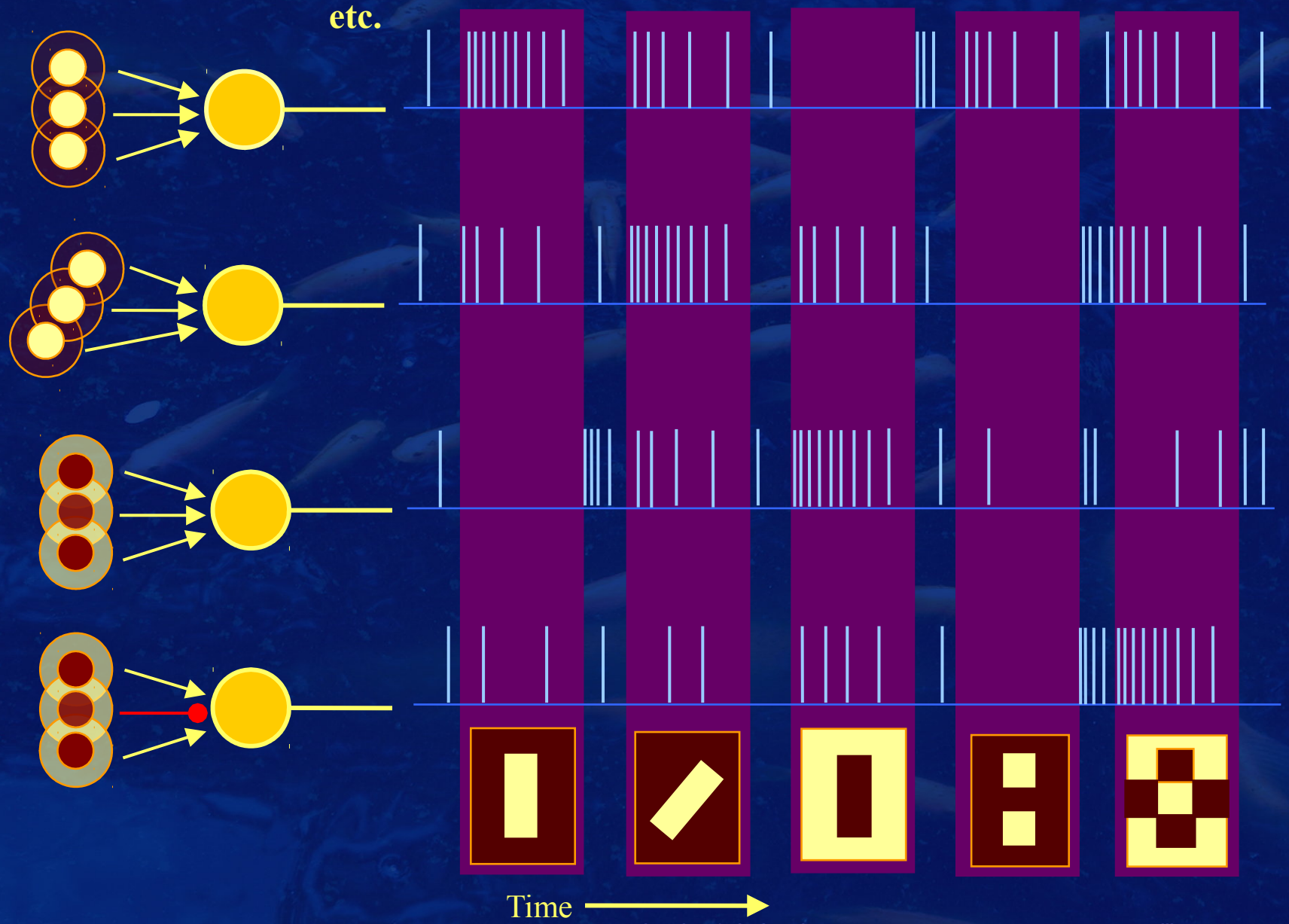
# Small Network Information Processing

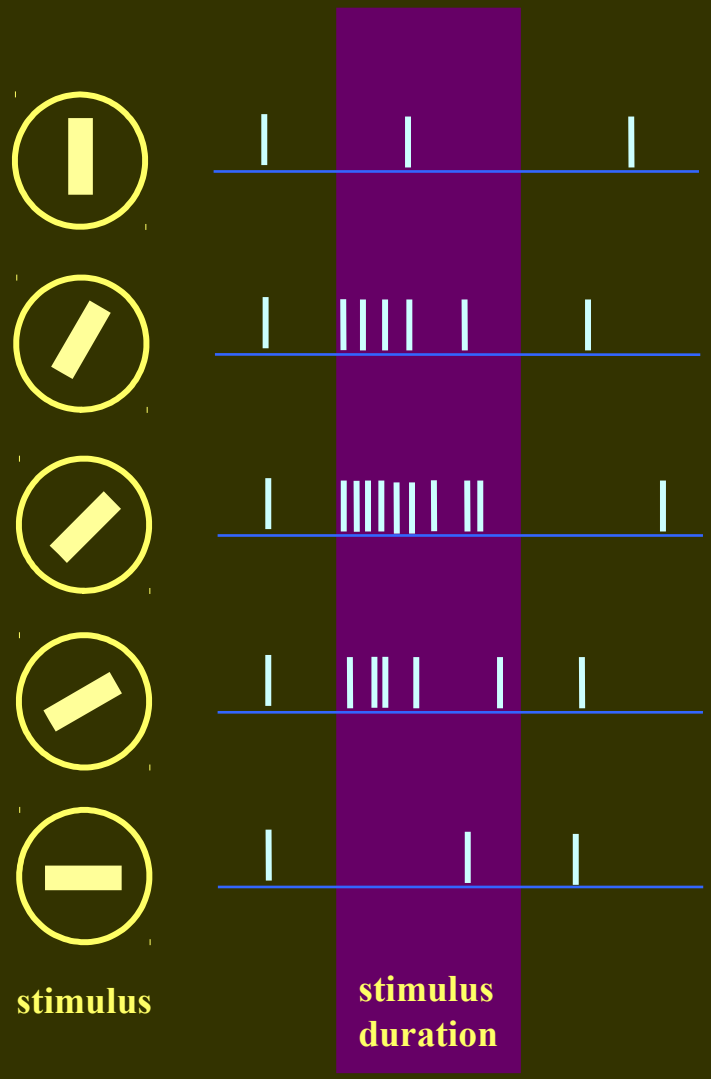
## Center-Surround Ganglion Cell Responses



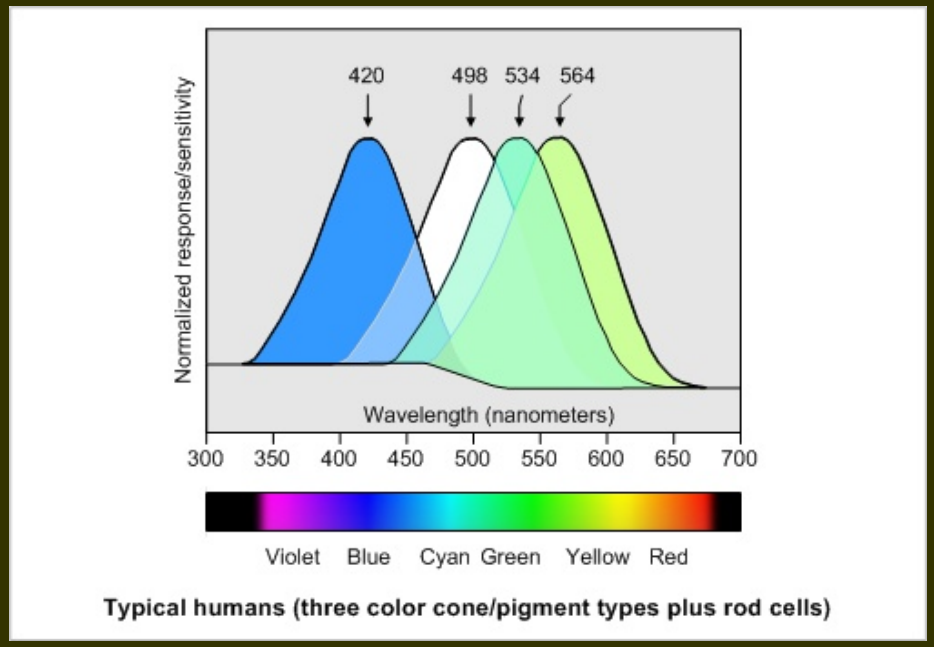
# Feature Detection by Visual Cortex Cells

**Edge-Detectors, Orientation Detectors, etc.**






**Orientation selective cells in the visual system**

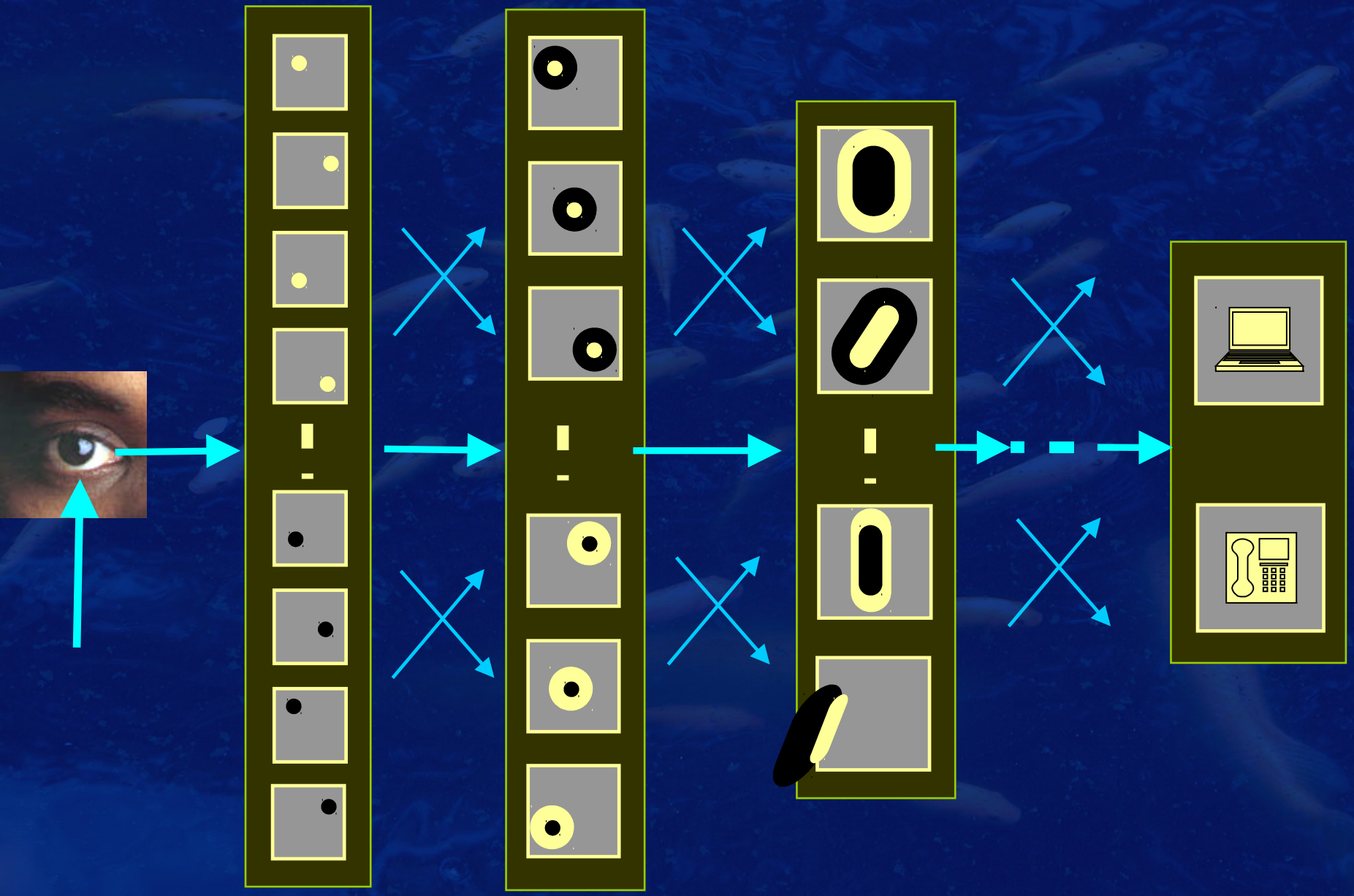



Source: http://www.diycalculator.com/sp-cvision.shtml

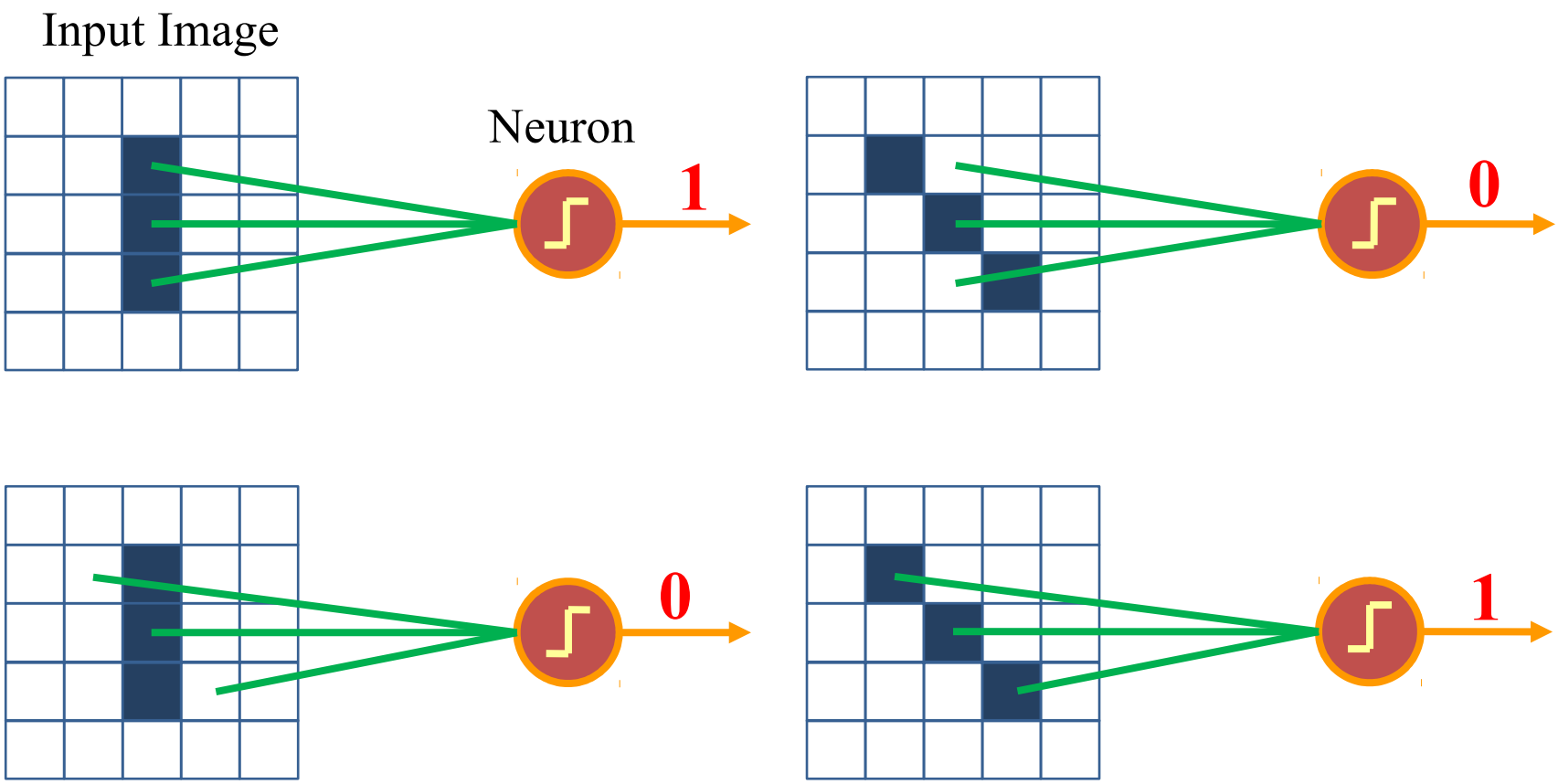
**Human visual receptors**

# Examples of Tuning

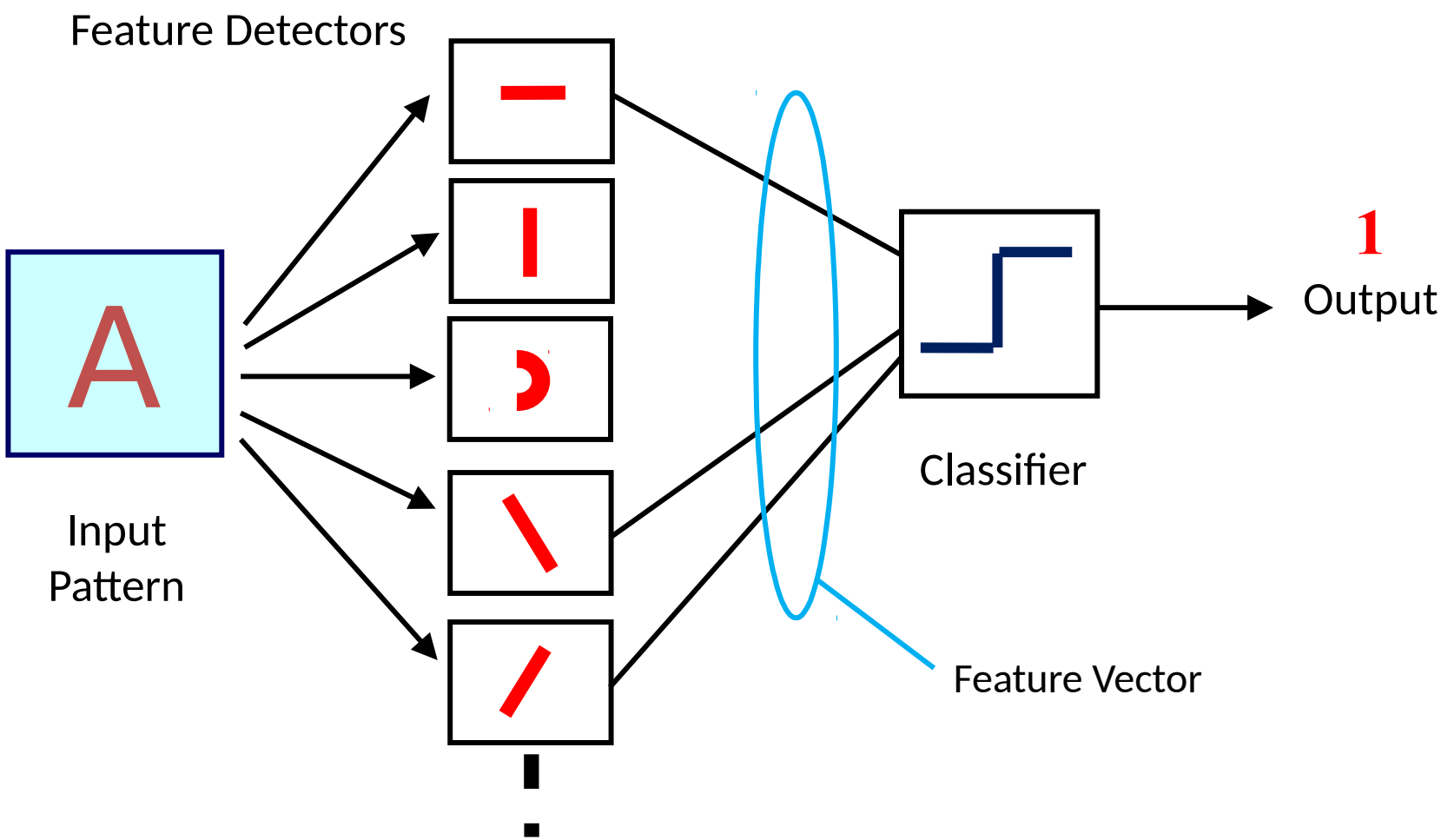
# Example: From Sensation to Recognition



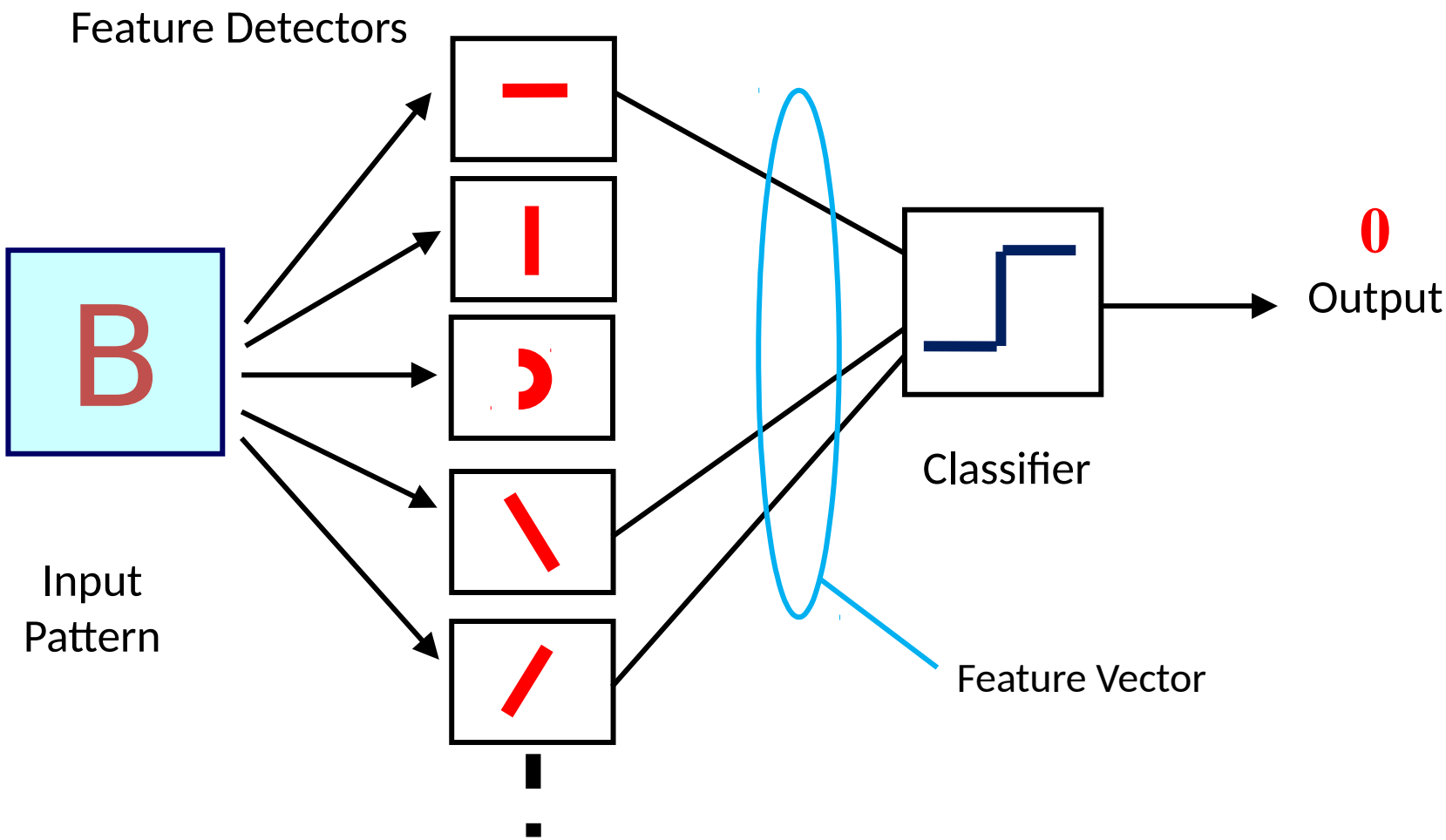
# Feature Detectors



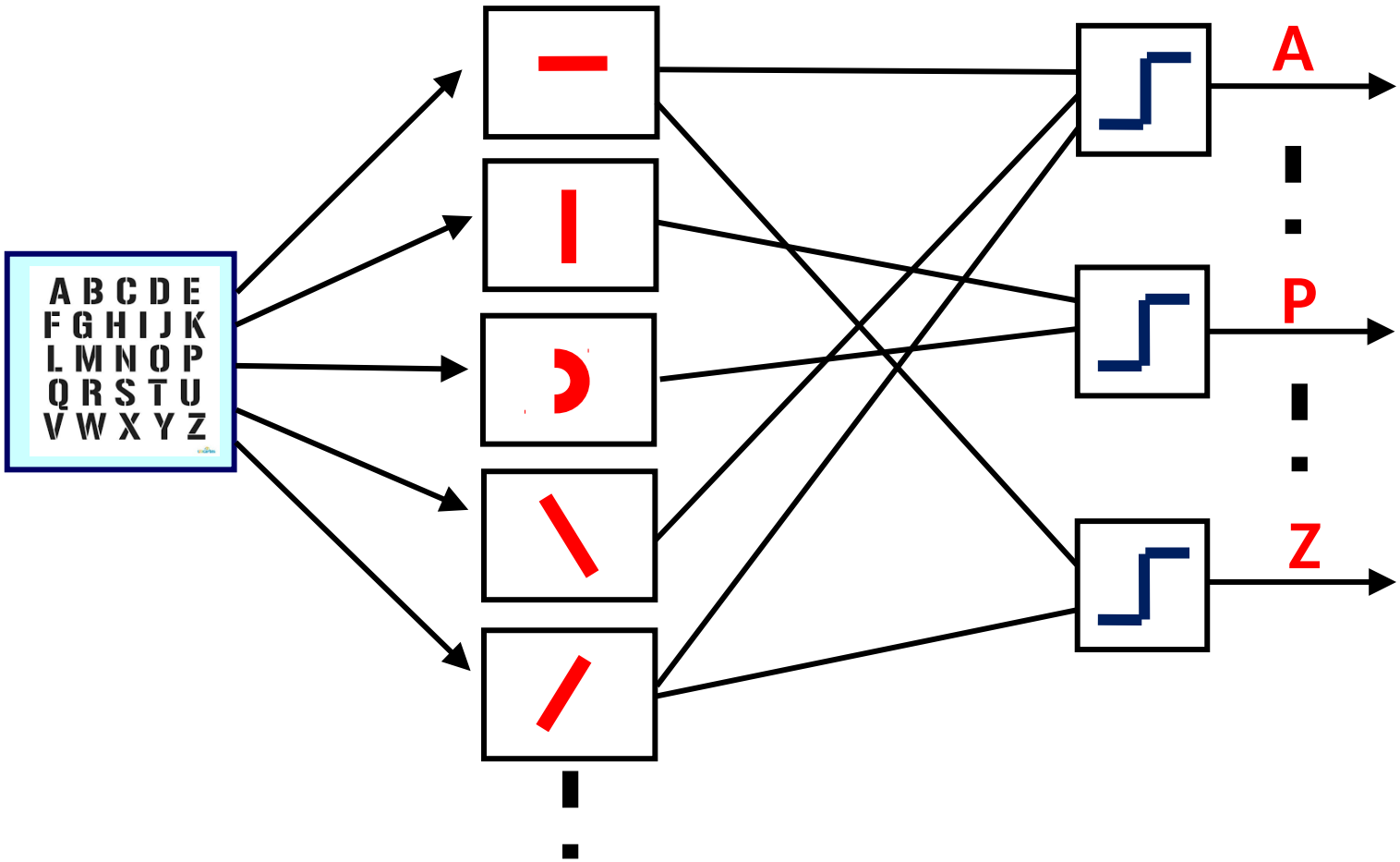
# An A-detector



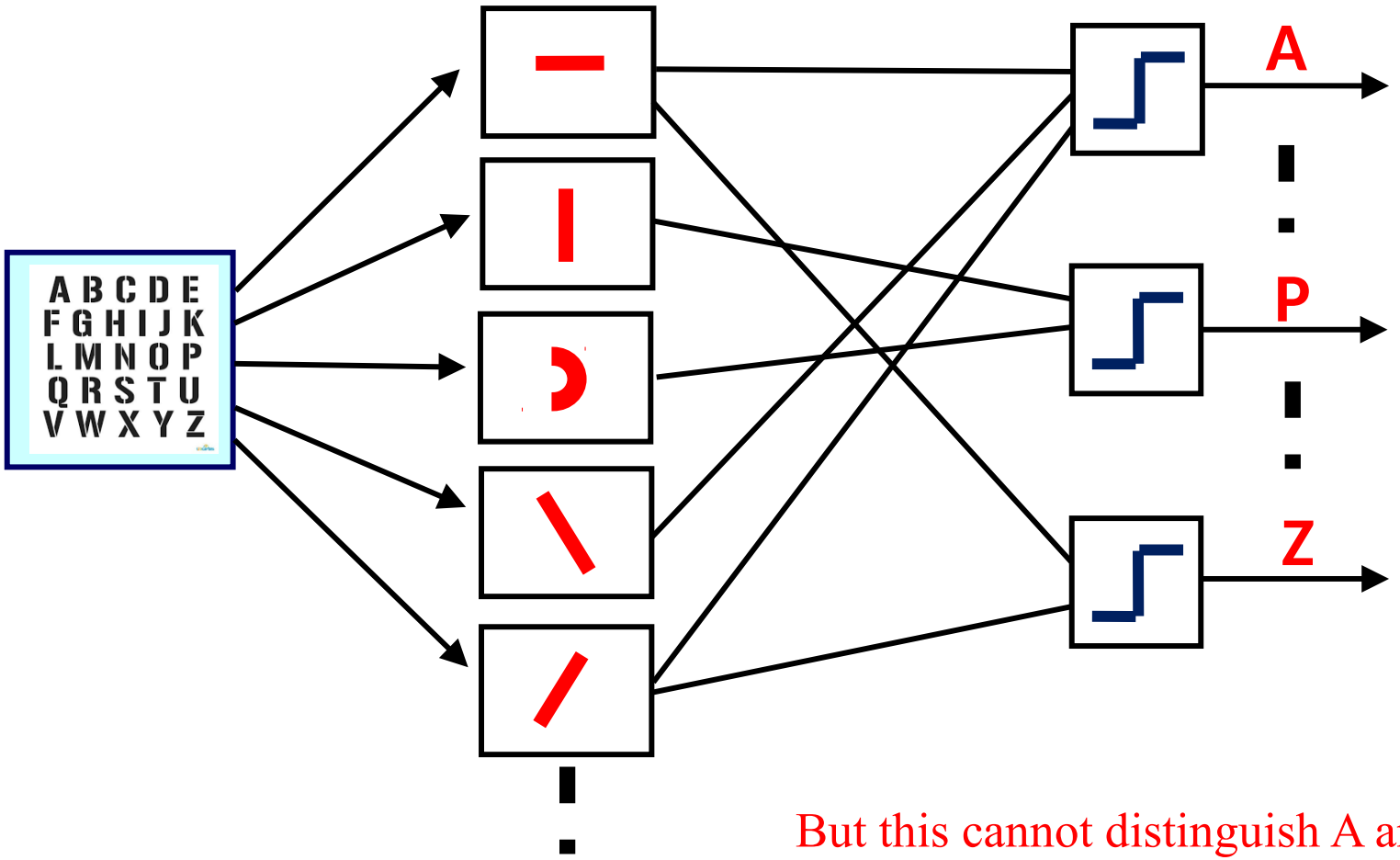
# An A-detector



# A Letter Recognizer

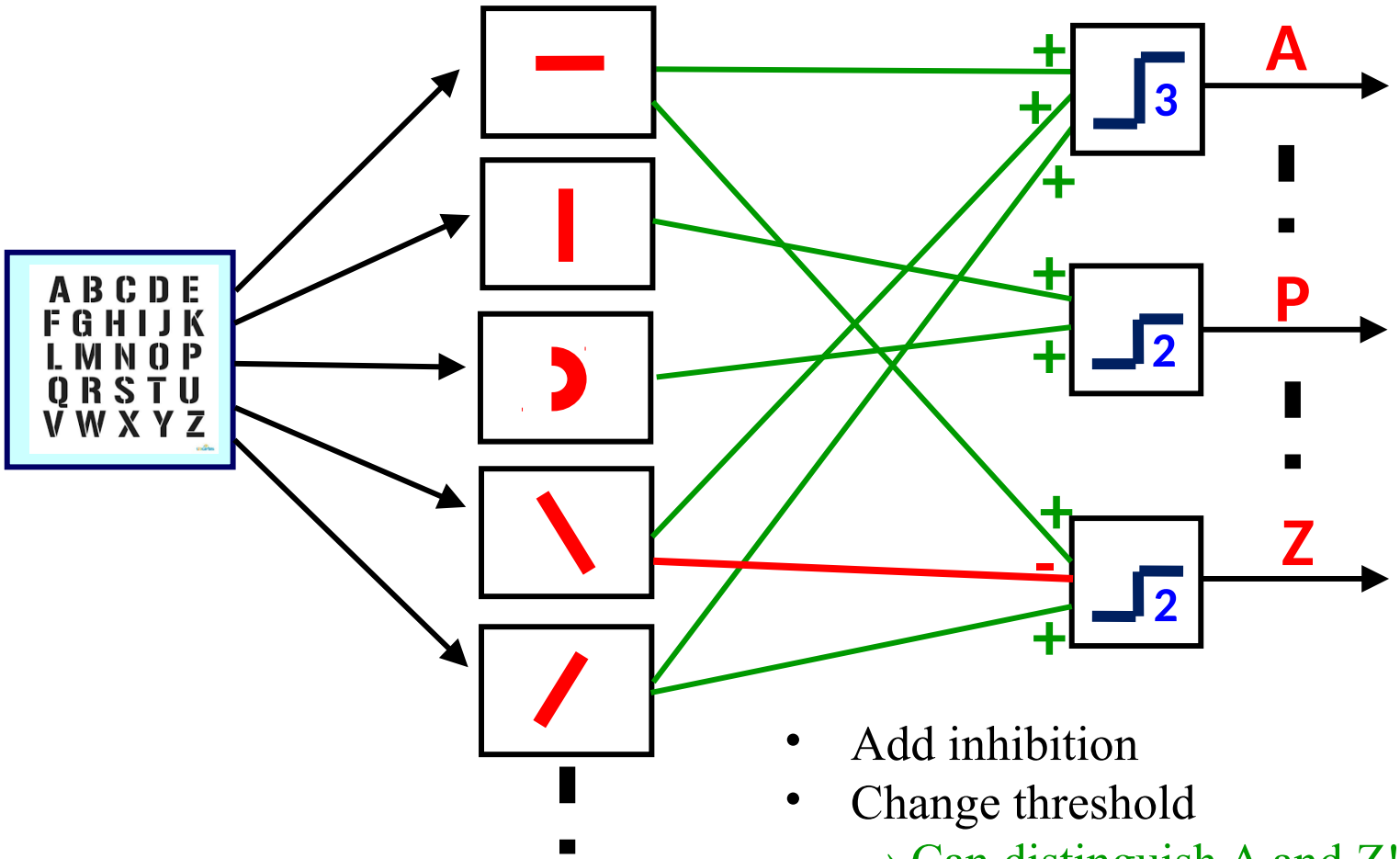


# A Letter Recognizer




But this cannot distinguish A and Z!

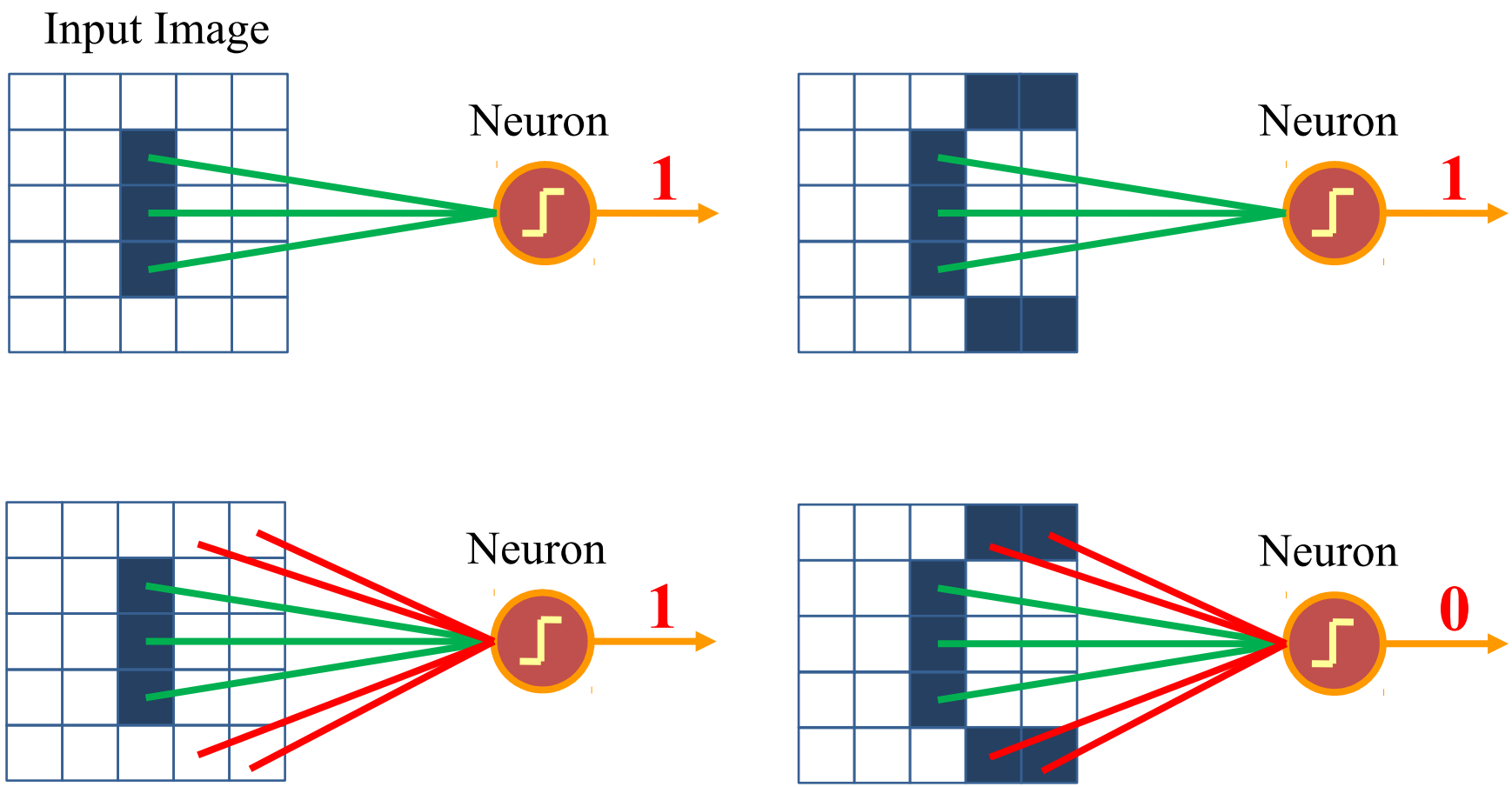
# A Letter Recognizer




- Add inhibition
- Change threshold

→ Can distinguish A and Z!

# Sharper Feature Detectors



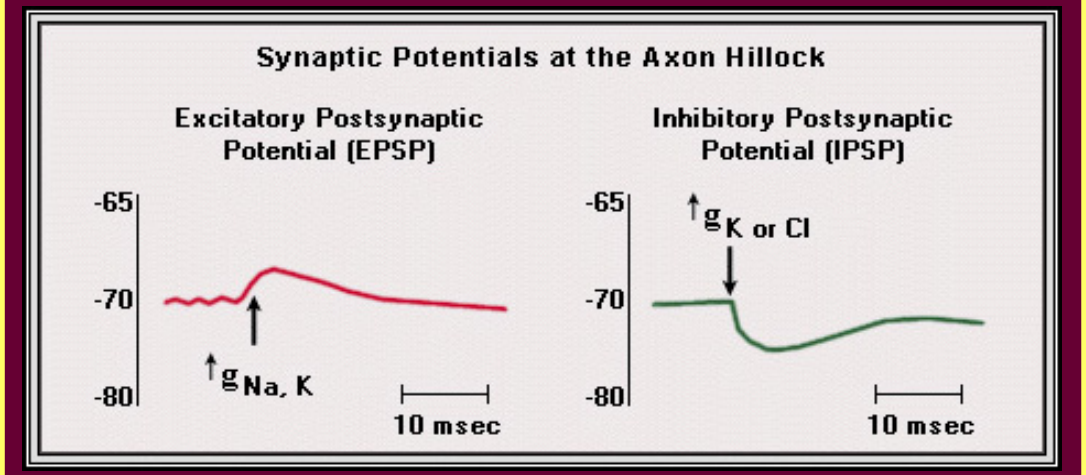

Rule: Excitation from some pixels, inhibition from the rest.

# Appendices

# Details of Neural Activation

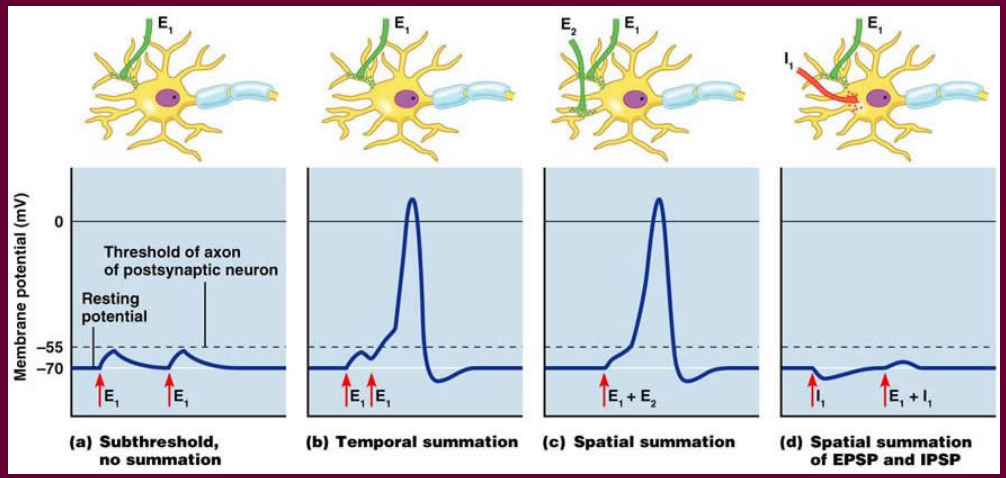
# Neural Activity

## Postsynaptic Potentials



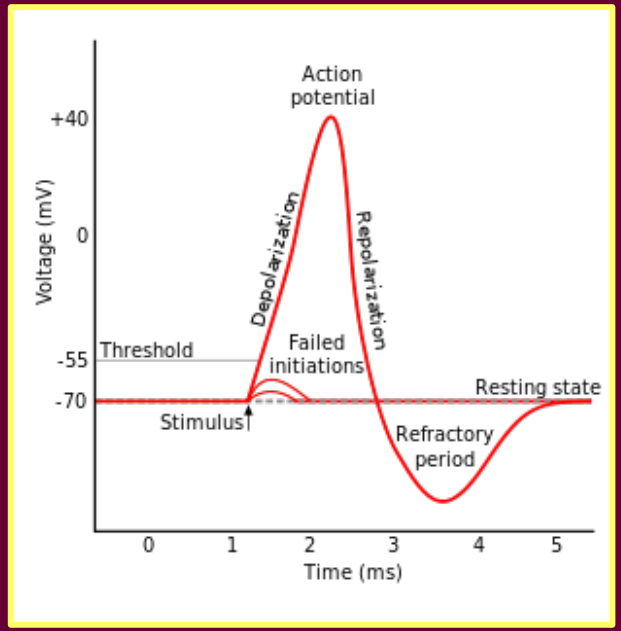

http://humanphysiology.tuars.com/program/section8/8ch1/s8ch1_37.htm

## Spatial and Temporal Summation




http://classes.midlandstech.edu/carterp/Courses/bio210/chap11/lecture1.html

## Action Potential



# Neural Signaling

Neurons form large and complex networks with specific connectivity to perform functions such as sensory processing, memory, motor control, etc.

→ Neural networks

**Membrane potential :**

There is usually an electrical voltage across the neuron's membrane caused by the asymmetric distribution of ions inside and outside the cell. This is called the membrane potential, $V_m$, of the neuron.

Outside

++++++++++++++++++++++++++++++++++++++++++++++

- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

Inside

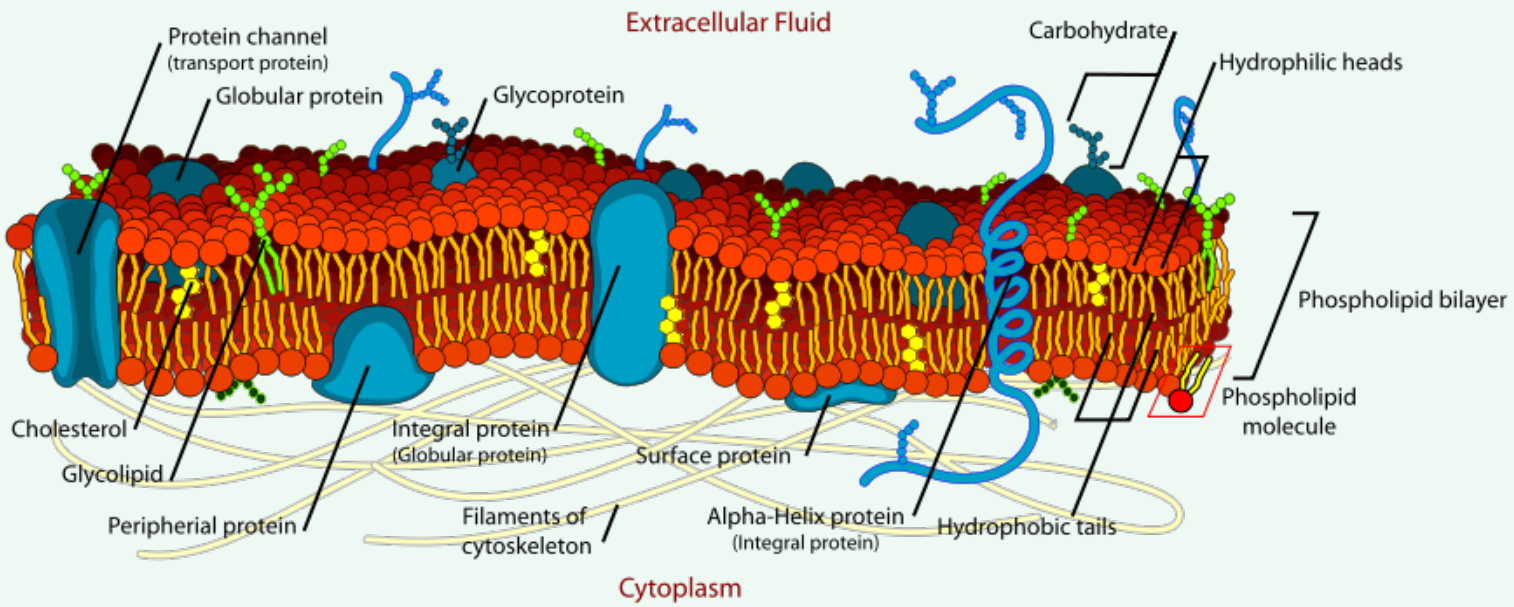
- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -

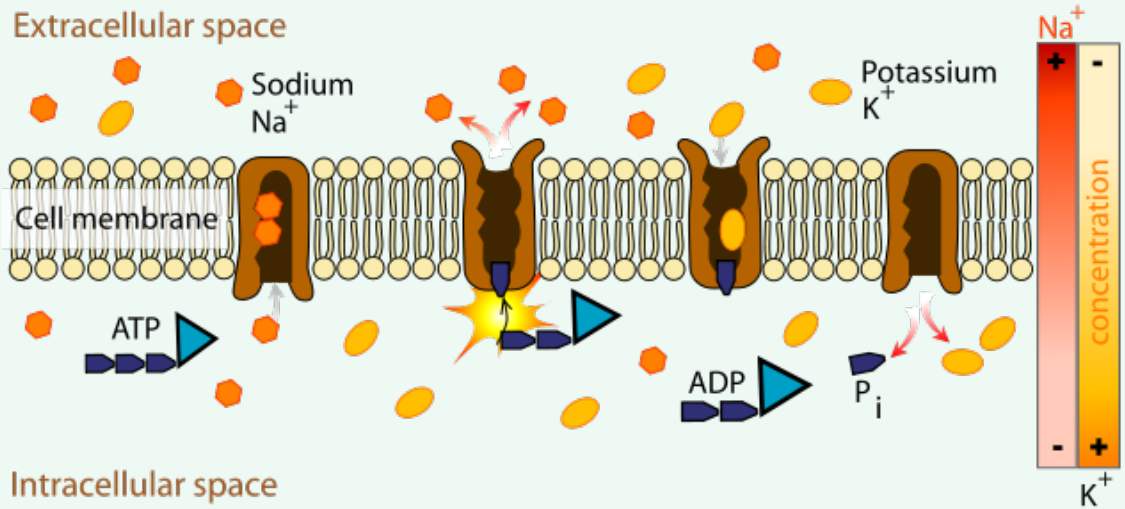
++++++++++++++++++++++++++++++++++++++++++++++

Outside

Neurons signal by changing their membrane potential.

# The Cell Membrane



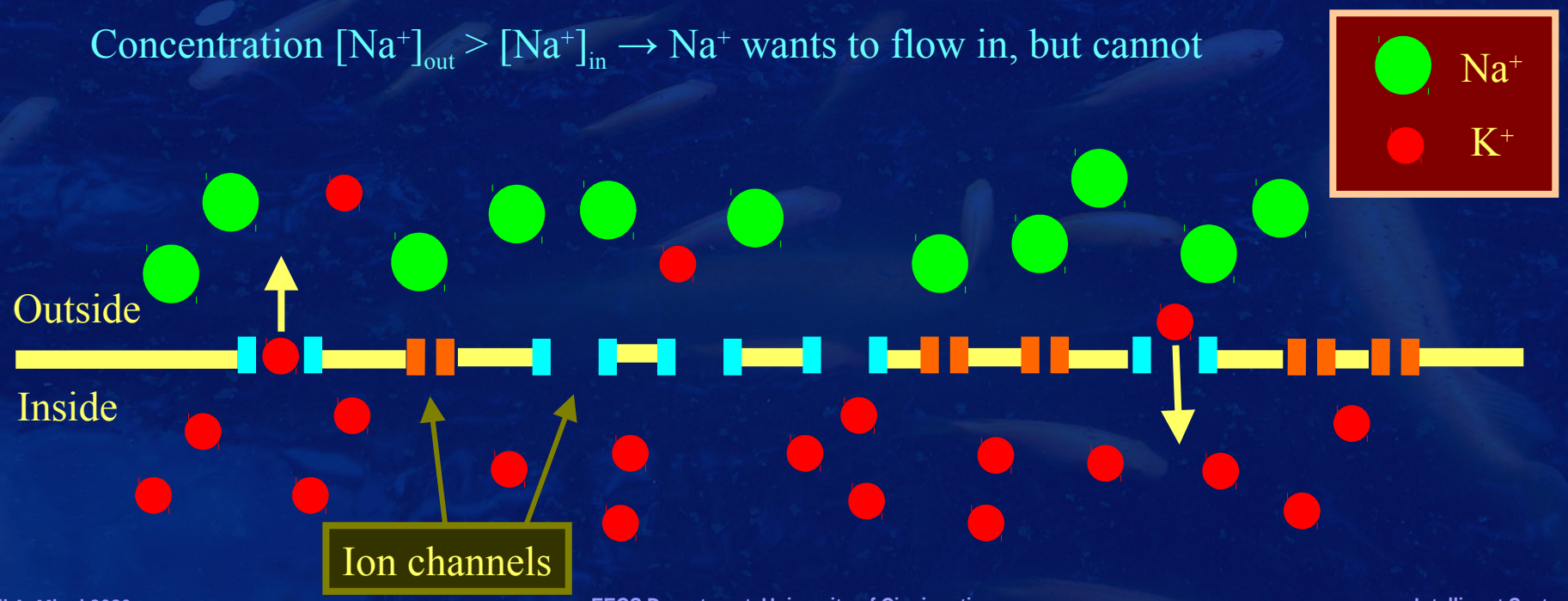

https://en.wikipedia.org/wiki/Membrane_potential#/media/File:Cell_membrane_detailed_diagram_en.svg

# The Membrane Potential

Assume no potential drop across the membrane.
$K^+$ concentration higher inside, $Na^+$ concentration higher outside.
$K^+$ ions can diffuse across the membrane, $Na^+$ cannot.

Concentration $[K^+]_{in} > [K^+]_{out} \rightarrow K^+$ flows out
$\rightarrow$ Negative charge builds inside the membrane
$\rightarrow$ Wants to pull $K^+$ back into the cell
$\rightarrow$ $[K^+]$ reaches asymmetric equilibrium where the two flows balance.

Concentration $[Na^+]_{out} > [Na^+]_{in} \rightarrow Na^+$ wants to flow in, but cannot



# The Resting Potential

Goldman-Hodgkin-Katz Equation

Membrane potential, $V_m$, is given by:

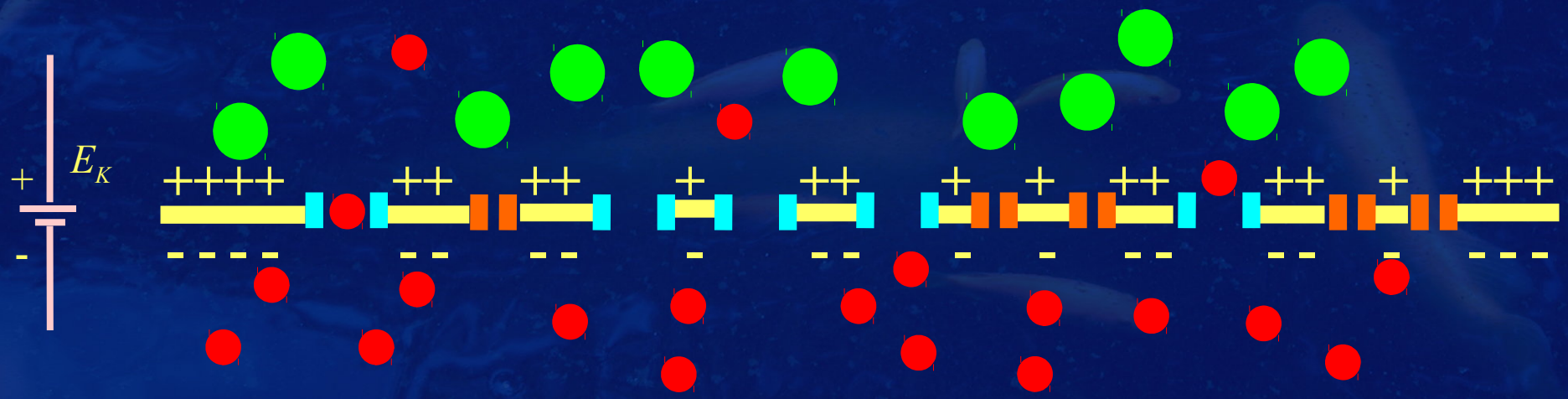
$$V_m = -61.5\log_{10}\frac{p_K[K^+]_{out} + p_{Na}[Na^+]_{out}}{p_K[K^+]_{in} + p_{Na}[Na^+]_{in}}\ mV$$

$p_L$ = permeability to ion L

Since $p_{Na} \approx 0$,

$$V_m = -61.5\log_{10}\frac{p_K[K^+]_{out}}{p_K[K^+]_{in}} \equiv E_K \approx -90mV$$

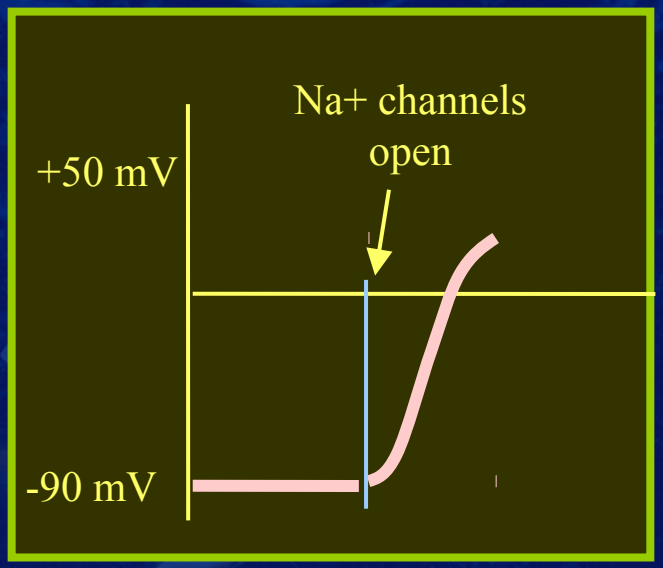
Equilibrium potential for $K^+$ $\approx$ Resting potential



# Membrane Depolarization

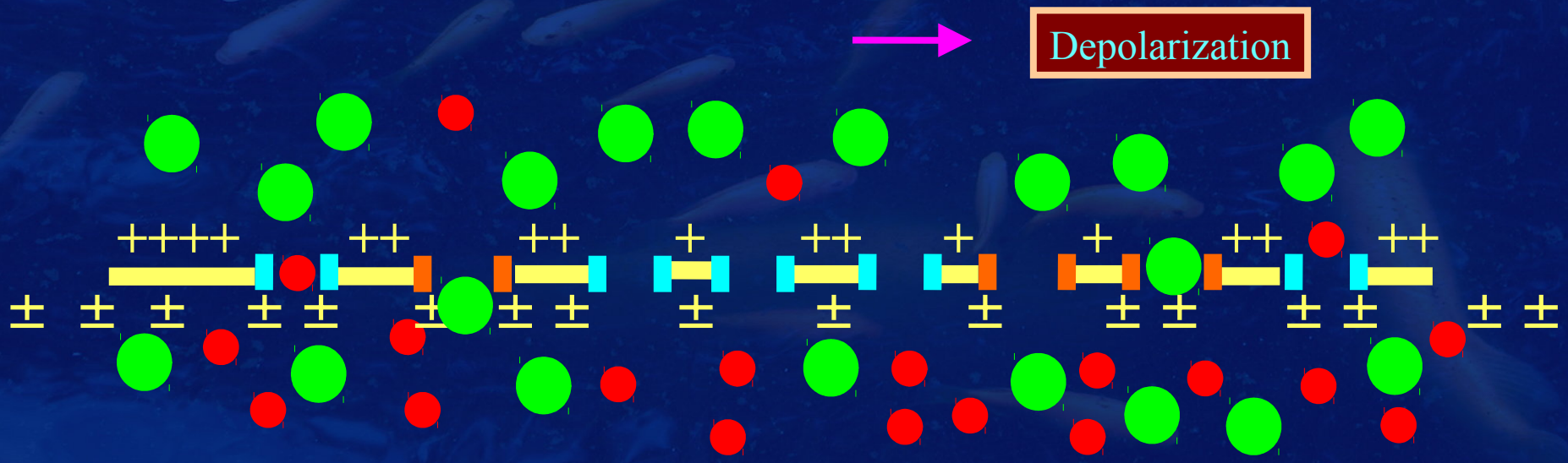
The equilibrium potential of $Na^+$ is

$$V_m = -61.5\log_{10}\frac{p_{Na}[Na^+]_{out}}{p_{Na}[Na^+]_{in}} \equiv E_{Na} \approx +50mV$$

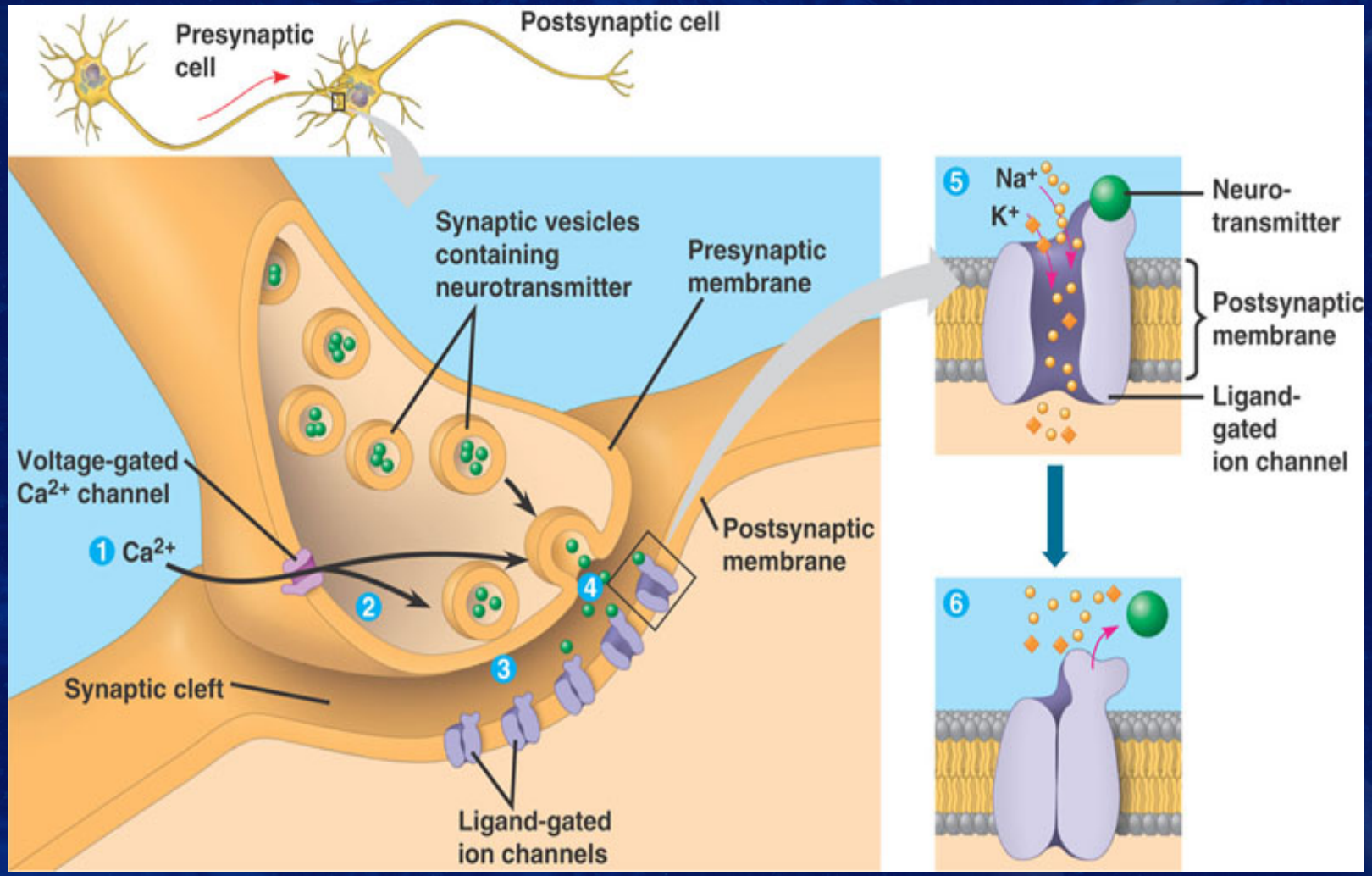



⇒ If the $Na^+$ channels (sodium channels) are opened

→ influx of $Na^+$ ions → $V_m$ rises towards 0 and becomes positive



# Synapses: Junctions between Neurons




kvhs.nbed.nb.ca/gallant/biology/synapse.html

# Ion Channels

Ion channels can be:

- Ligand-gated → opened and closed by the binding of a chemical messenger.
- Voltage-gated → opened and closed by the membrane potential at the channel.

Some channels are both ligand- and voltage-gated (e.g., the NMDA receptor)

## Channel Functions

Ligand-gated channels are found throughout the neuron and are responsible for:

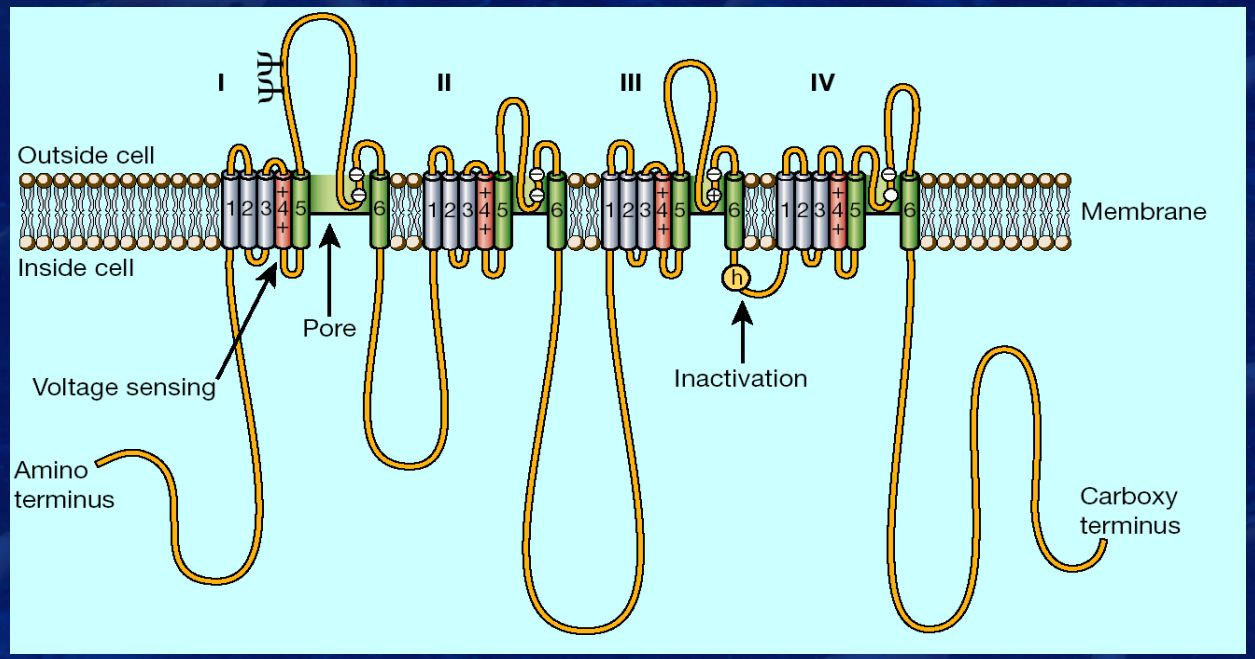
- Maintaining the membrane potential.
- Generating the post-synaptic potentials in response to incoming action potentials

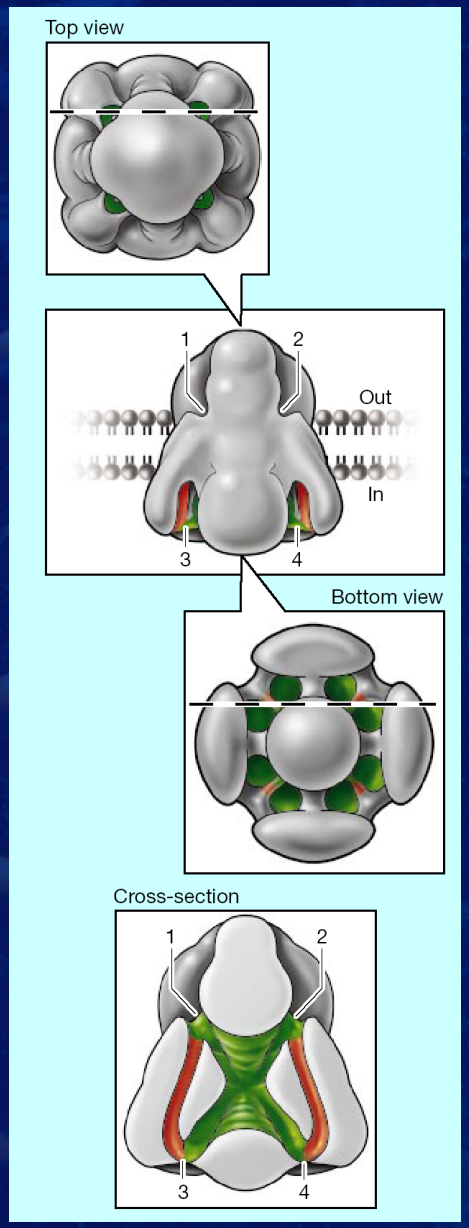
Post-synaptic potentials propagate diffusively along dendrites, and integrate.

Voltage-gated channels are found in the soma and axon, and are responsible for:

- Generating the action potential.
- Propagating the action potential by regeneration.

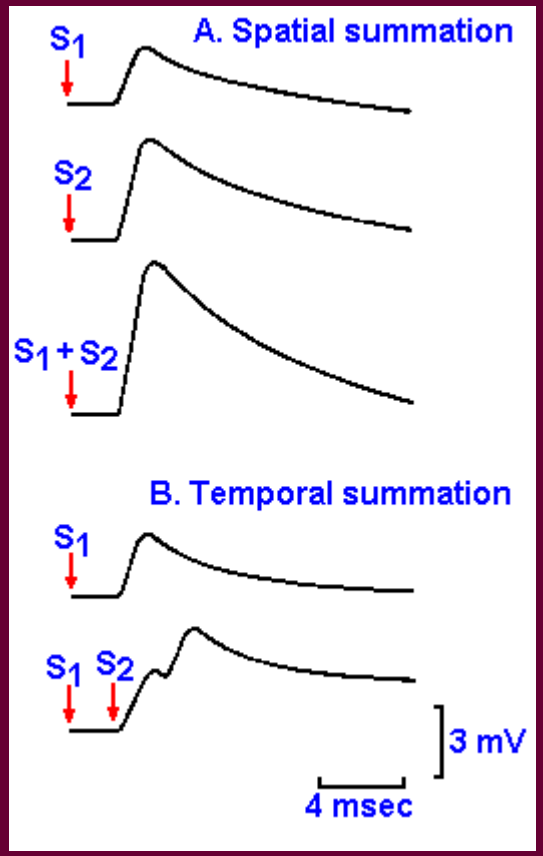
# Voltage-Gated Sodium Channel



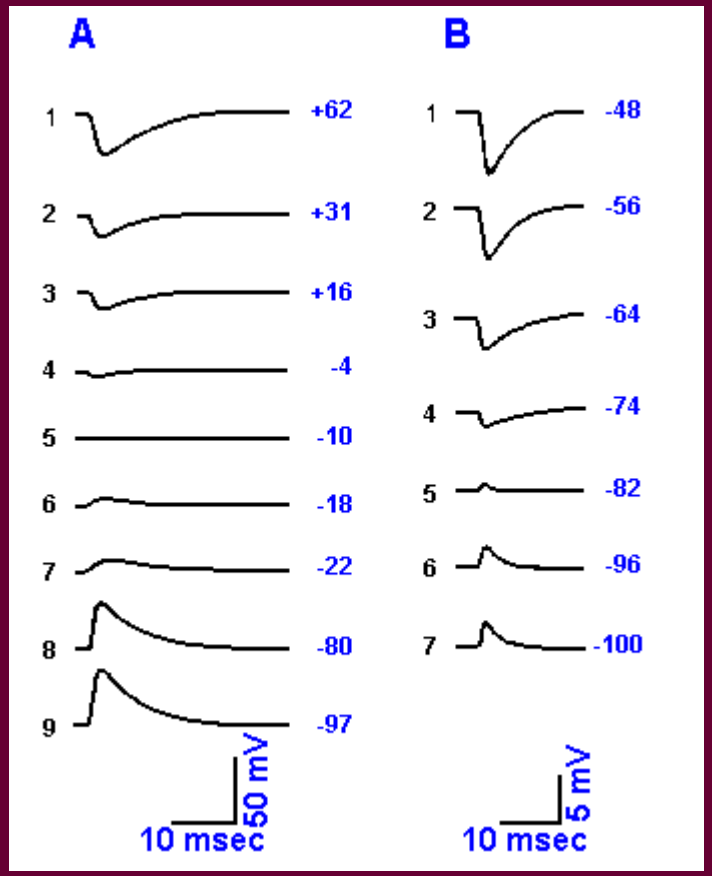




Images from:
W.A. Catterall (2001) A 3D view of sodium channels, *Nature* 409: 988-991

# EPSP and IPSP




Spatial and temporal summation of EPSPs

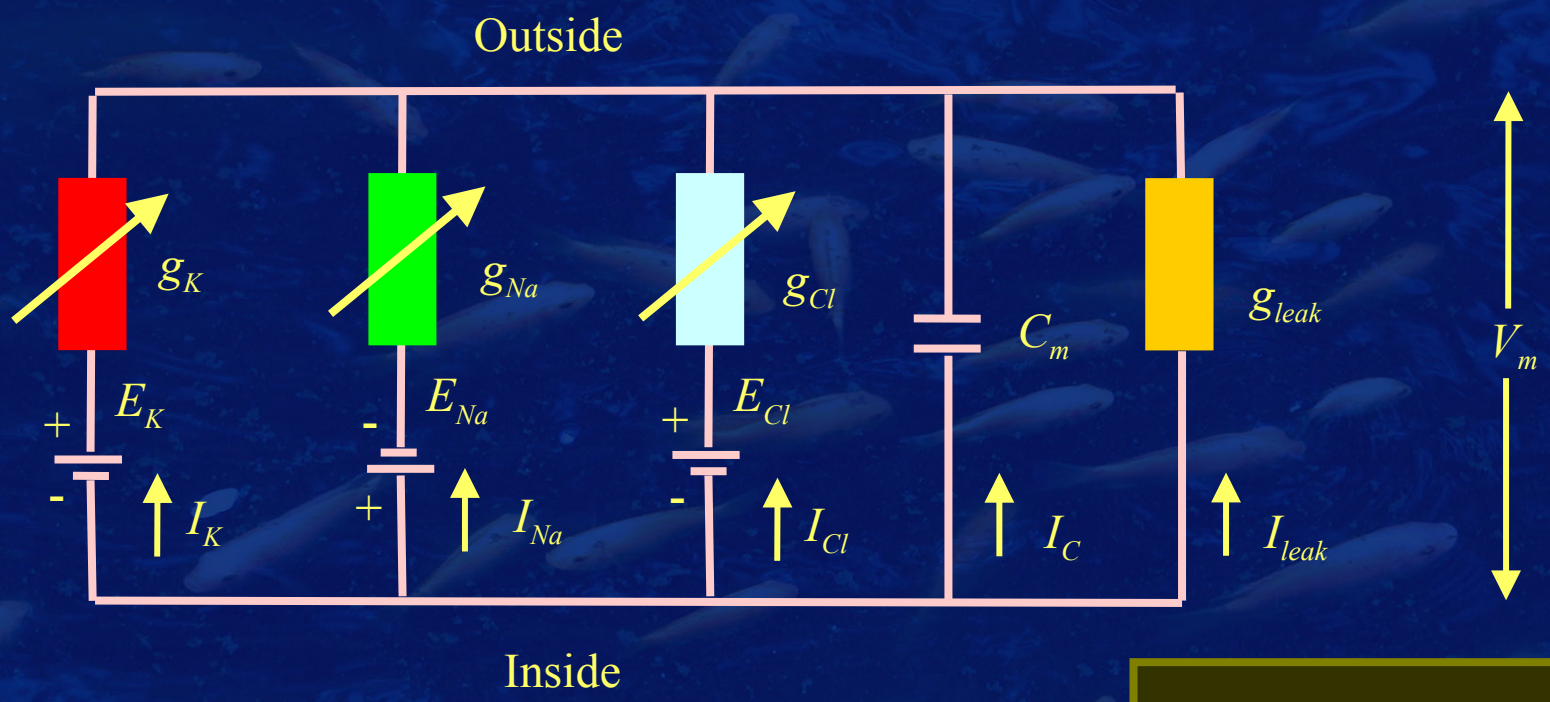



Dependence of EPSP and IPSP on membrane potential: Polarity reverses at the equilibrium potentials of $Na^+$ and $K^+$

http://michaeldmann.net/mann13.html

# Detailed Neuron Models

# A Simple Electrical Model of the Membrane




$$C\frac{dV_m}{dt} = -I_{Na} - I_K - I_{Cl} - I_{leak}$$

$$I_C = C\, dV_m / dt$$
$$I_{Na} = g_{Na}(V_m - V_{Na})$$
$$I_K = g_K(V_m - V_K)$$
$$I_{Cl} = g_{Cl}(V_m - V_{Cl})$$
$$I_{leak} = g_{leak} V_m$$

Membrane potential changes in response to changes in the ionic conductances based on channel activity

# Action Potential: The Hodgkin-Huxley Model

$$C\frac{dV_m}{dt} = -\boxed{g_{Na} m^3 h}(V_m - V_{Na}) - \boxed{g_K n^4}(V_m - V_K) - \boxed{g_r}(V_m - V_r) + I_{ext}$$

Na conductance
Voltage-dependent
Time-varying

K conductance
Voltage-dependent
Time-varying

Misc conductance
Fixed

*m*, *h* and *n* are called gating variables

They parameterize how the sodium and potassium conductances change with time and membrane potential.

# The Hodgkin-Huxley Model: Dynamics of Gating Variables

$$\frac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n$$

K conductance dynamics

$$\frac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m$$

$$\frac{dh}{dt} = \alpha_h(V_m)(1-h) - \beta_h(V_m)h$$

Na conductance dynamics

**Voltage Dependence:**

$$\alpha_n(v) = \frac{0.01\,(10-v)}{exp\,(1-0.1v)-1}$$

$$\beta_n(v) = 0.125\ exp\,(-v/80)$$

$$\alpha_m(v) = \frac{0.1\,(25-v)}{exp\,(2.5-0.1v)-1}$$

$$\beta_m(v) = 4\ exp\,(-v/18)$$

$$\alpha_h(v) = 0.07\ exp\,(-v/20)$$

$$\beta_h(v) = \frac{1}{exp\,(3-0.1v)-1}$$

http://icwww.epfl.ch/~gerstner//SPNM/node14.html

See also: http://www.klab.caltech.edu/~stemmler/sec1.html

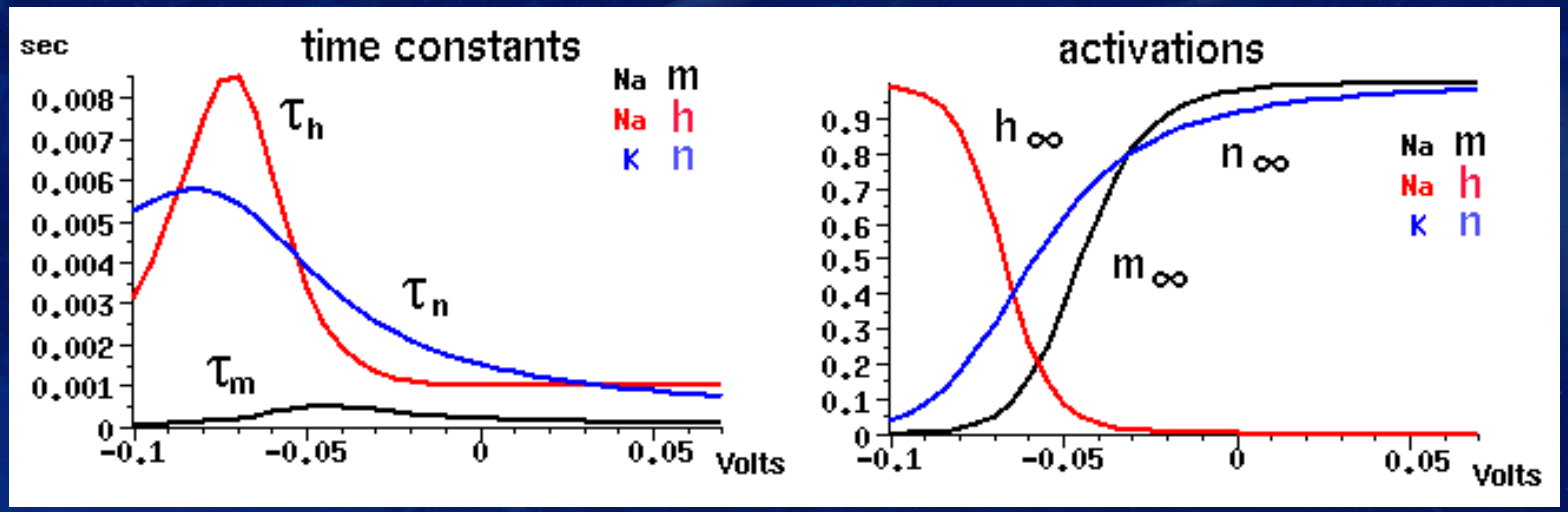
http://ece-www.colorado.edu/~ecen4831/HHsumWWW/HHsum.html

The equations for *m*, *h* and *n* can be rewritten in terms of steady states and time constants dependent upon $V_m$

$$\frac{dn}{dt} = \frac{n_\infty - n}{\tau_n} \qquad \frac{dm}{dt} = \frac{m_\infty - m}{\tau_m} \qquad \frac{dh}{dt} = \frac{h_\infty - h}{\tau_h}$$

Steady-State Gating Value: $q_\infty(v) = \dfrac{\alpha_q(v)}{\alpha_q(v) + \beta_q(v)}$ $\qquad q = n, m, h$

Gating Time Constant: $\tau_q(v) = \dfrac{1}{\alpha_q(v) + \beta_q(v)}$




http://ece-www.colorado.edu/~ecen4831/HHsumWWW/HHsum.html

# The Hodgkin-Huxley Model: Conductance Dynamics

**Sodium conductance** = $g_{Na}\, m^3 h$

The complementary forms for $\alpha_m$ , $\beta_m$ vs. $\alpha_h$ , $\beta_h$ (previous slide) ensure that:

- $m$ increases with increasing $V_m$ $\Rightarrow$ Sodium conductance increases with $V_m$
- $h$ decreases with increasing $V_m$ $\Rightarrow$ Sodium conductance decreases with $V_m$

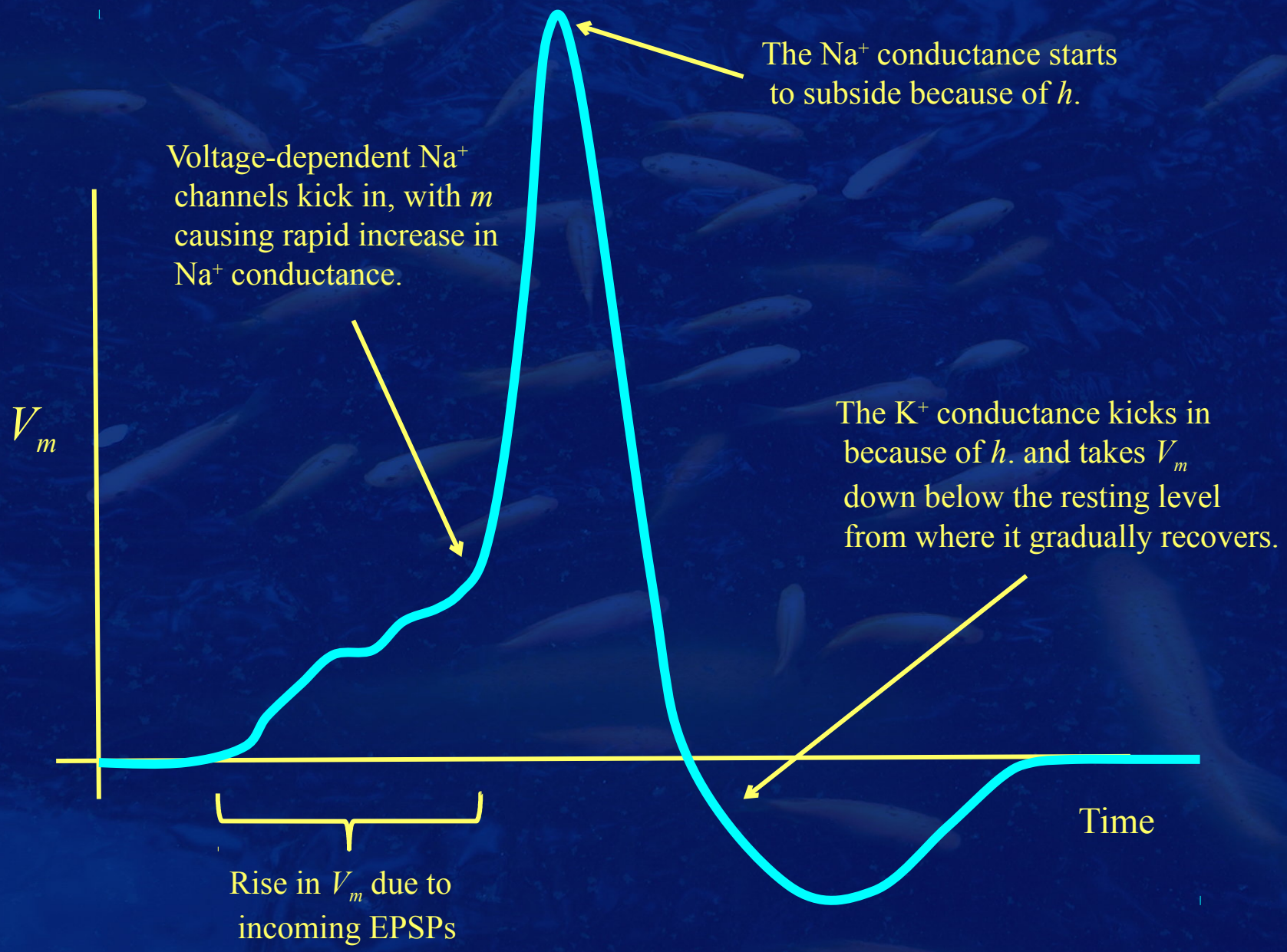
But the *timing* of the two effects is different because

- $\alpha_m$ , $\beta_m$ vs. $\alpha_h$ , $\beta_h$ are themselves functions of $V_m$ with different parameters
- The growth curves for both are nonlinear with saturation effects.
- $m$ enters the conductance as $m^3$ but $h$ only as $h^1$.

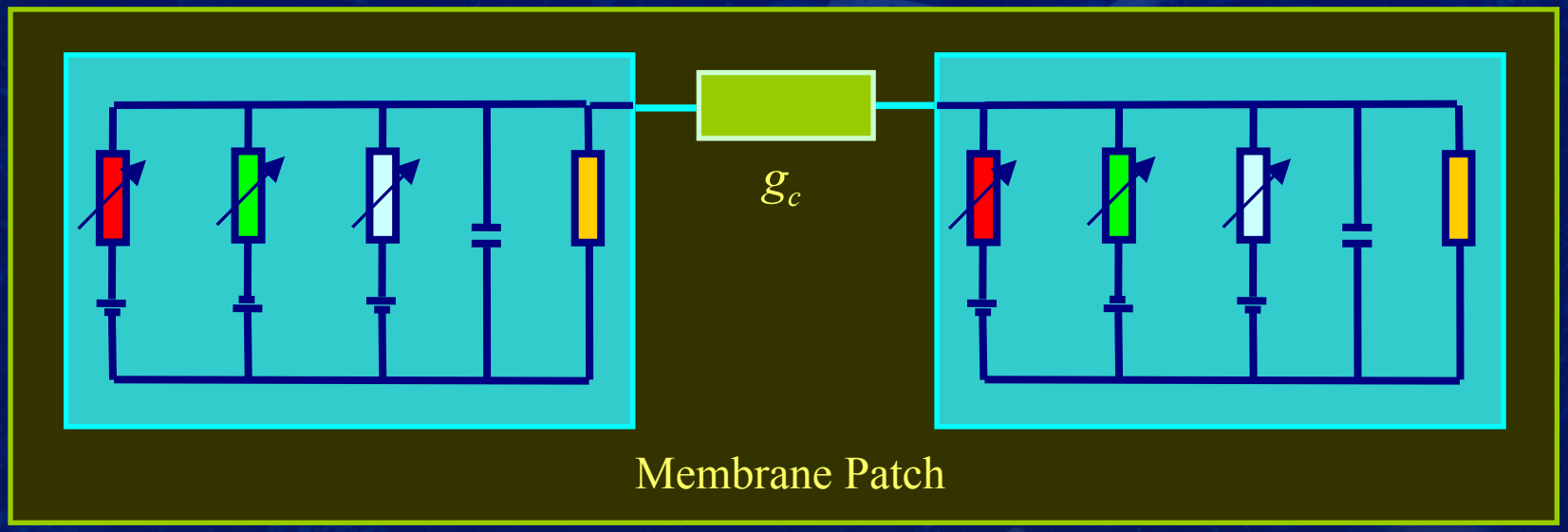
Thus, the net effect is an initial rapid rise in Sodium conductance (due to $m^3$ and low $\tau_m$) and then a decrease (because of $h$ and larger $\tau_h$), mimicking the actual behavior of Sodium channels.

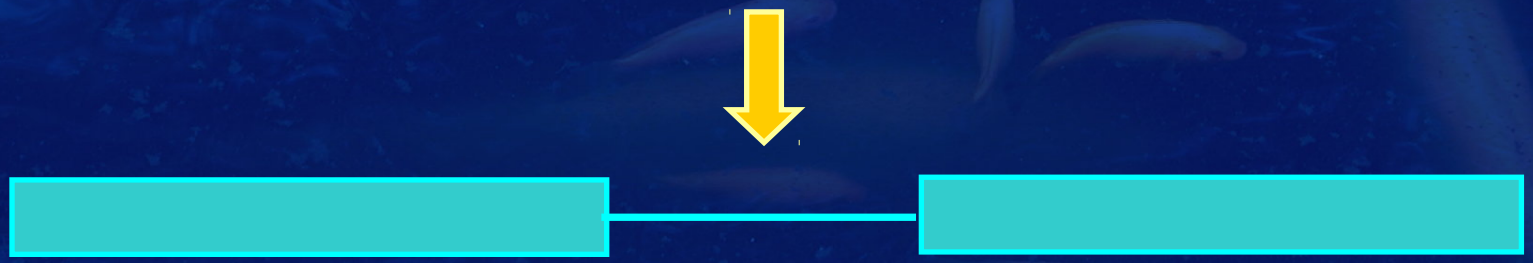
**Pottasium conductance** = $g_K\, n^4$ is simpler, and just activates slowly, leading to hyperpolarization and the refractory period, but the decreasing $V_m$ eventually brings $n$ back down to 0 because its steady-state value at low voltage is near 0.

# Generation of the Action Potential

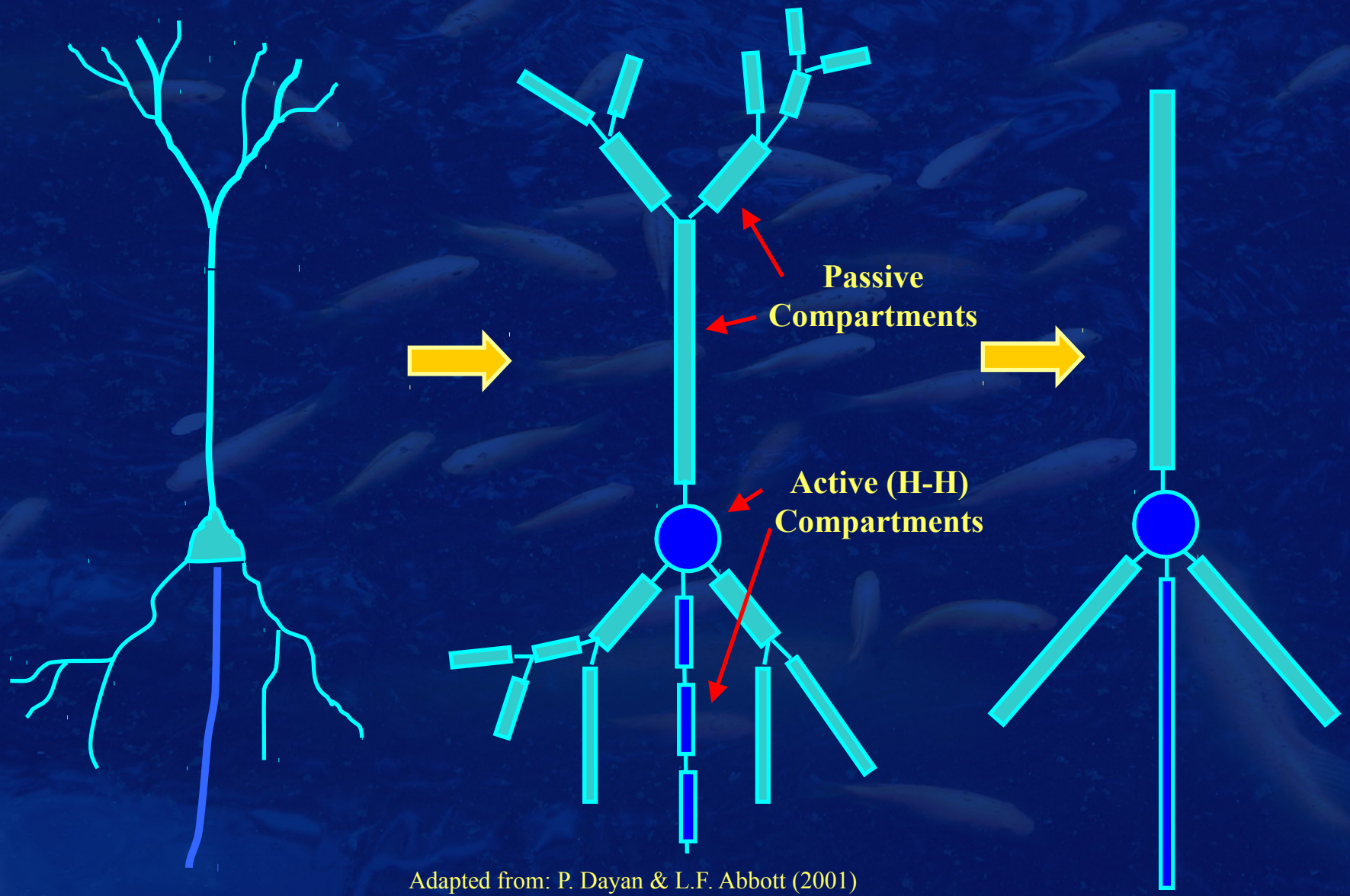


# Compartmental Models



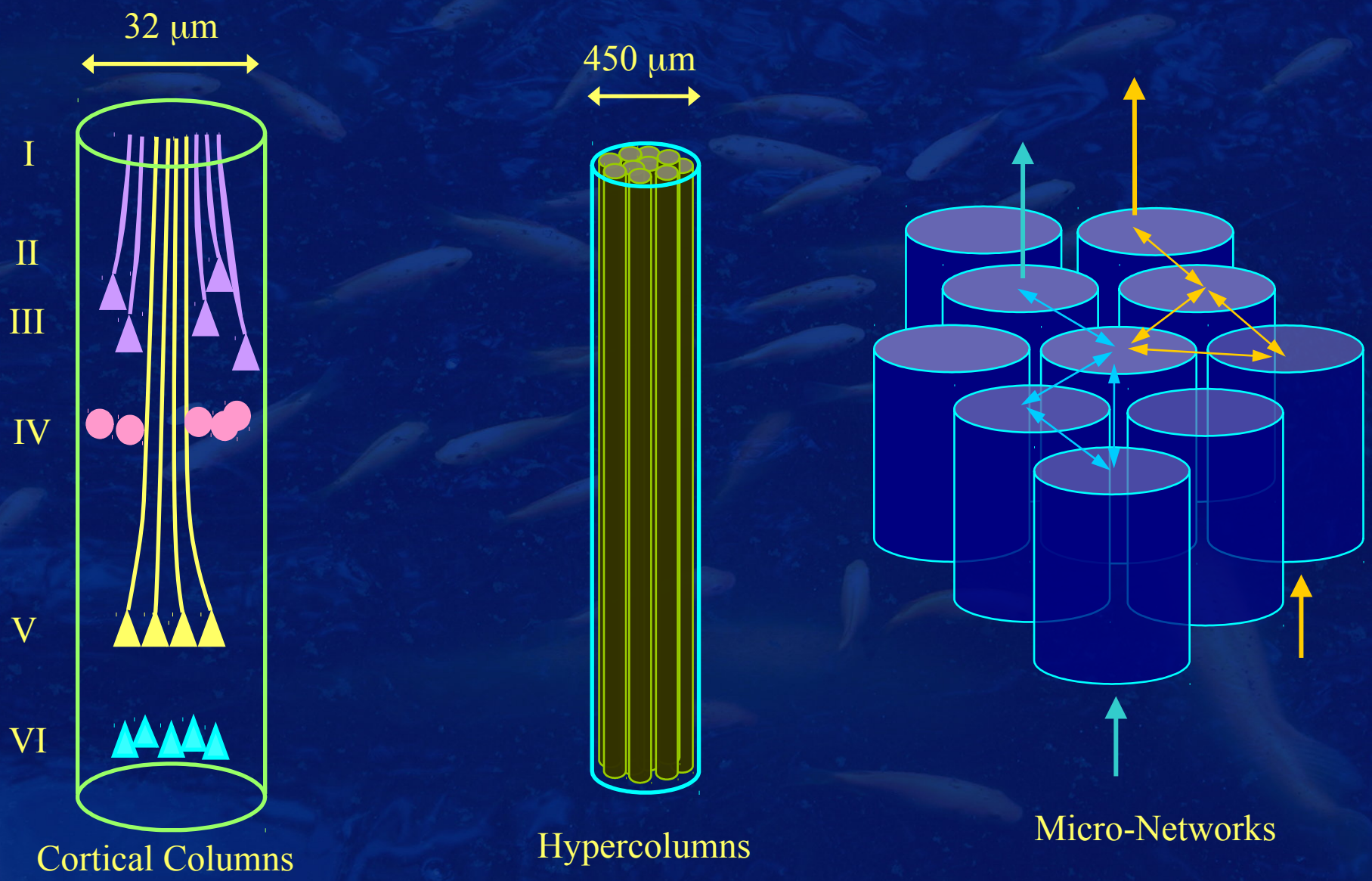
# Compartmental Model of Neurons




Adapted from: P. Dayan & L.F. Abbott (2001)
Theoretical Neuroscience, MIT Press.

# Large-Scale Brain Networks

# Multi-Scale Modularity in the Cortex

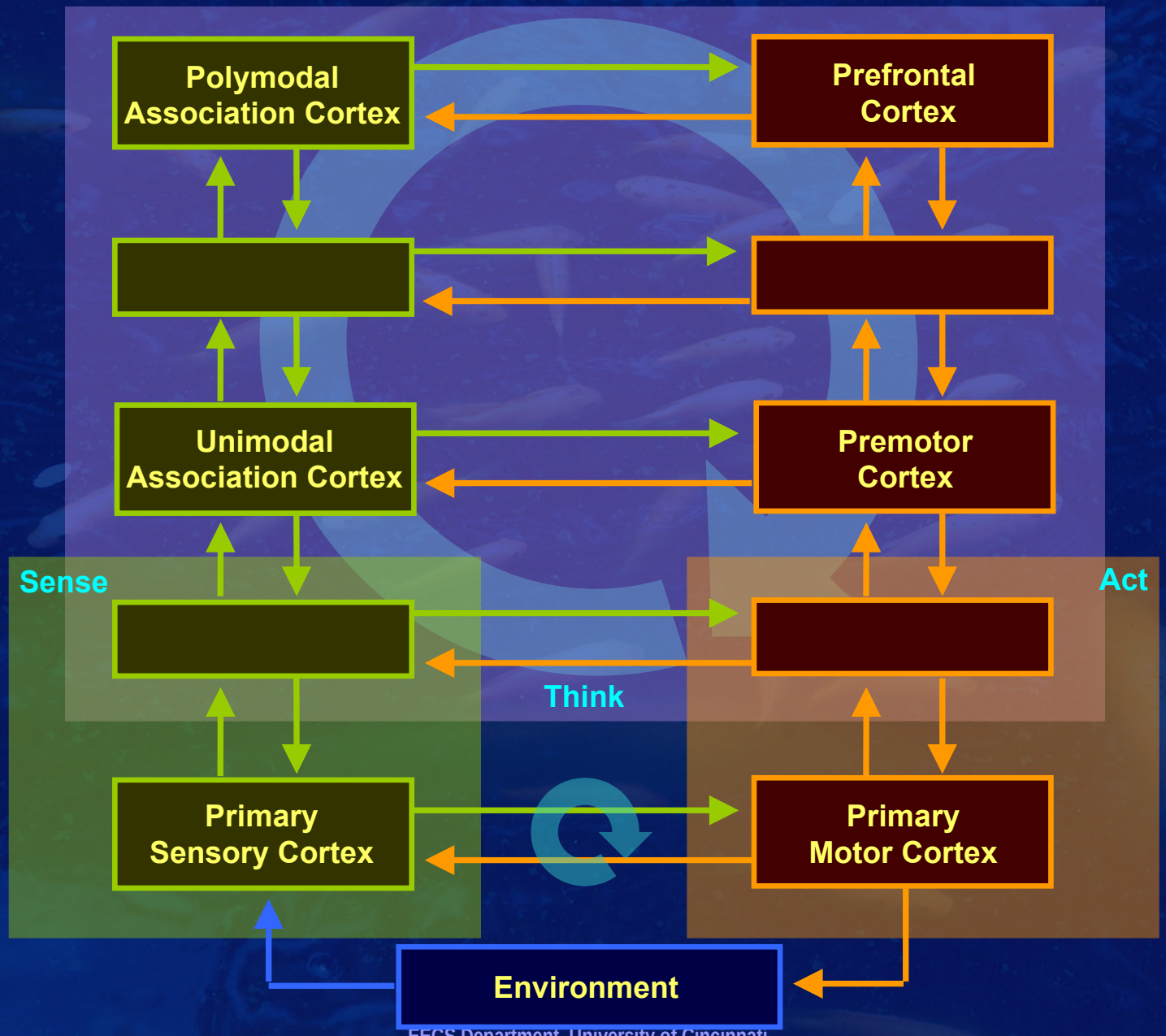


# Phenomenological Time-Scales

| Time Scale | Phenomena |
|---|---|
| Fixed | Natural laws. |
| 100,000 – 1,000,000 years<br>(~ 1,000 – 100,000 gen) | General climate, habitat, ecosystem, geography, etc.<br>General behavior of most other macro-organisms. |
| 1,000 – 10,000 years<br>(10 – 5,000 gen) | Details of climate, habitat, ecosystem, geography, etc.<br>Migration and competition. |
| 100 – 1,000 years<br>(1 – 50 gen) | Variation in species populations.<br>Specific ecological factors (e.g., rainfall patterns) |
| 1 – 100 years<br>(1 lifetime) | Specific ecological factors (e.g., availability of food).<br>Patterns of experience, Social relationships. |
| 1 day – 1 year | Growth and development.<br>Natural phenomena (day/night, seasons, etc.) |
| 1 sec – 1 day | Behavior of self and other individuals.<br>Specific experiences (episodes). |
| 100 msec – 1 sec | Perception, cognition and action |

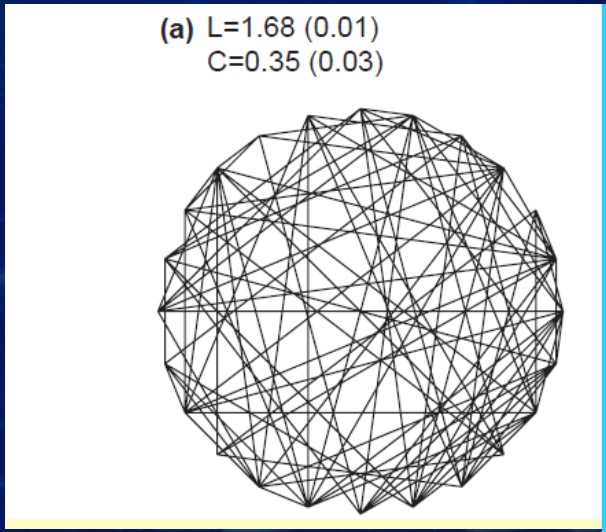
# The Perception-Action Cycle

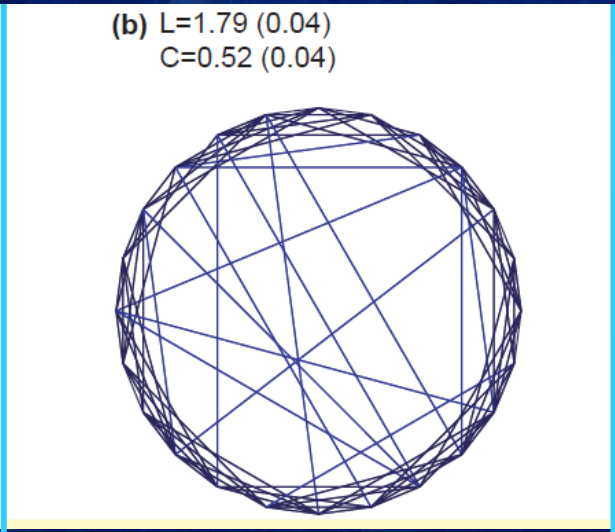
Redrawn from:
Fuster, 1995

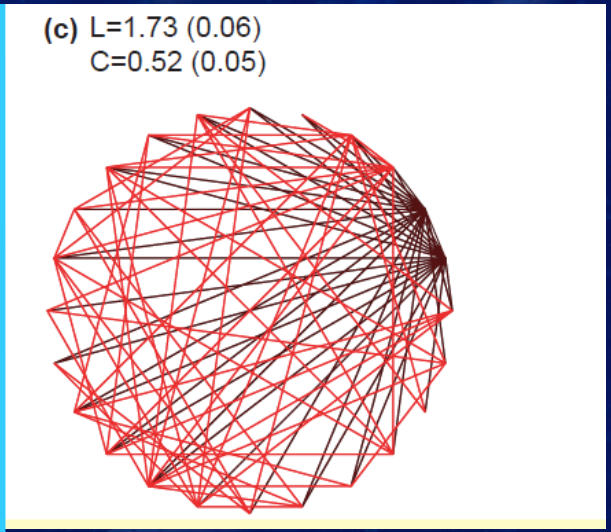


# Network Structures

Sporns, O. et al. (2004) Organization, development and function of complex brain networks, Trends in Cognitive Sciences 8: 418-425



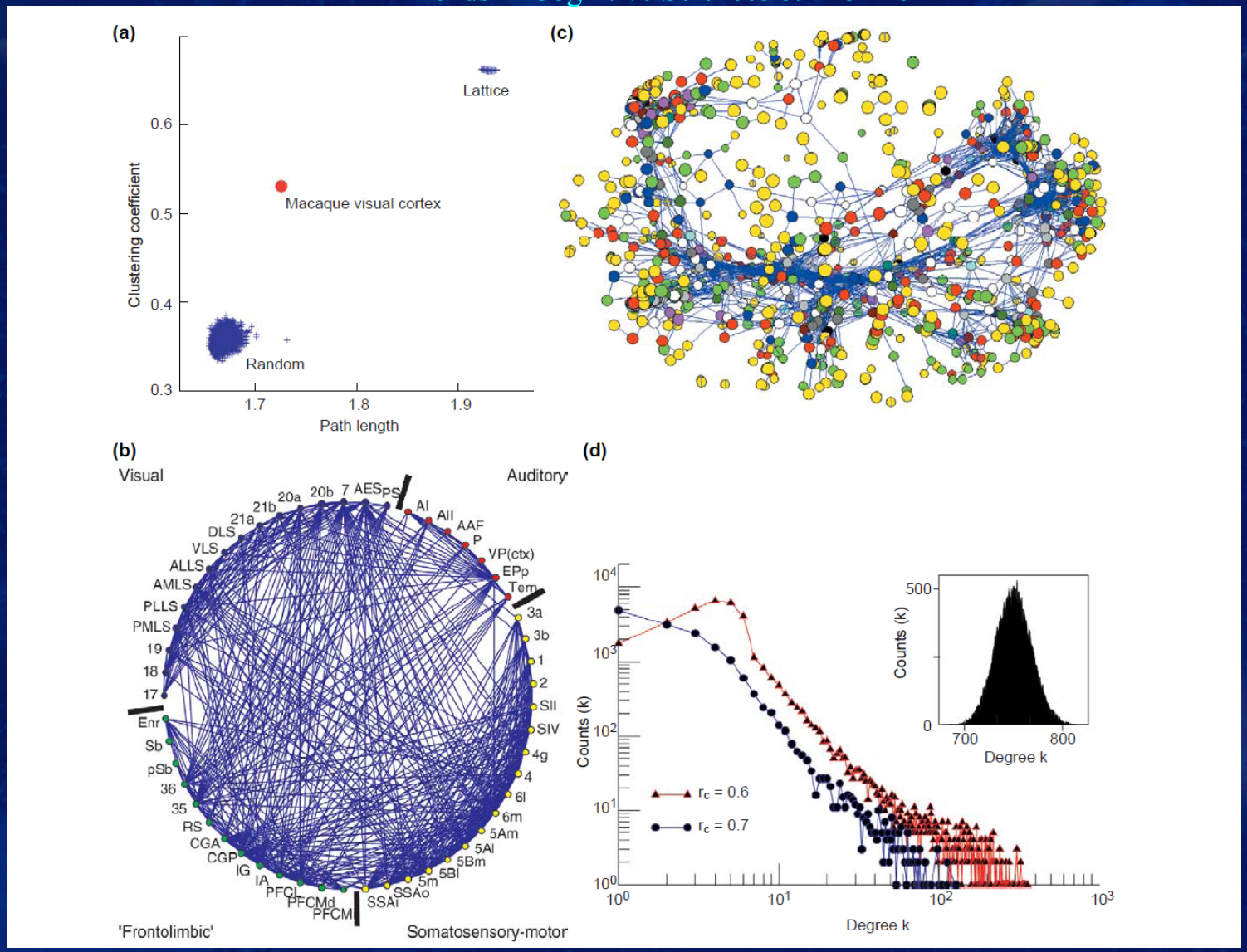




| **Random** | **Small World** | **Fat-Tailed** |
|---|---|---|
| Nodes connect randomly to any other node | Nodes connect mainly to nearby nodes, with some shortcuts | Most nodes have few links but a few have many |
| • Short paths<br>• Low clustering | • Short paths<br>• High clustering | • Short paths<br>• Low clustering |
| Connectivity is:<br>• Poisson | Connectivity could be:<br>• Poisson<br>• Power law | Connectivity could be:<br>• Power law<br>• Bimodal |

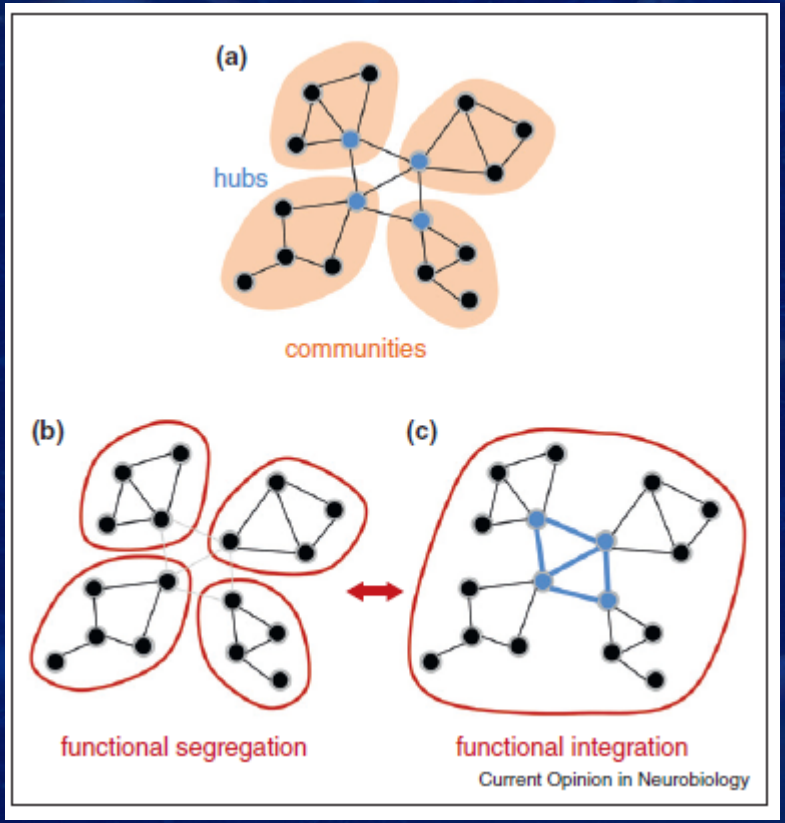
# Structure of Brain Networks

Sporns, O. et al. (2004) Organization, development and function of complex brain networks, Trends in Cognitive Sciences 8: 418-425



# Integration and Segregation in Neural Communities

O. Sporns (2013) Network attributes for segregation and integration in the human brain. Current Opinion in Neurobiology 23: 162-171




The blue "core" comprises a "rich club" of high-degree, strongly connected nodes.

Functional communities are linked by the core

→ Separate processing when core inactive
→ Integrated processing when core active.

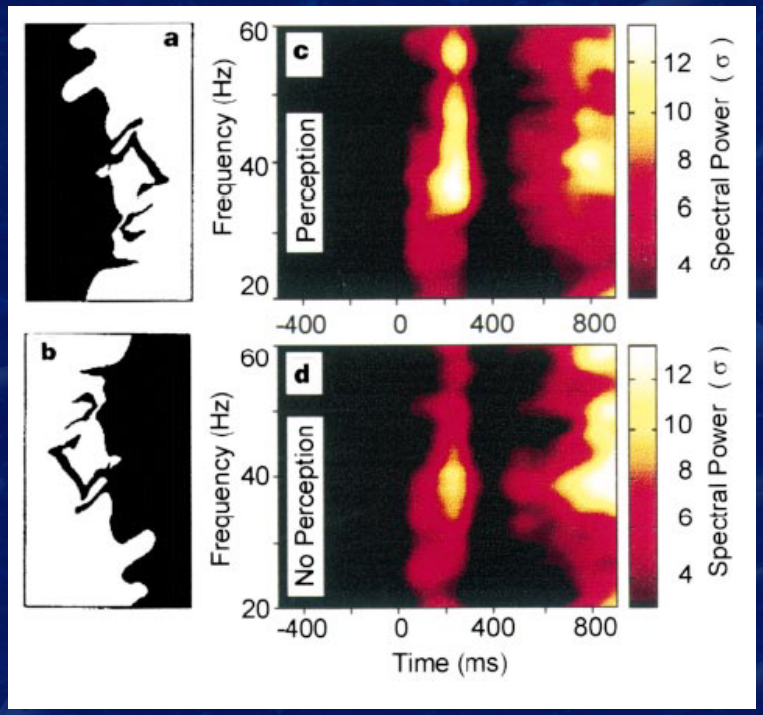
A very large number of experiments have shown that:

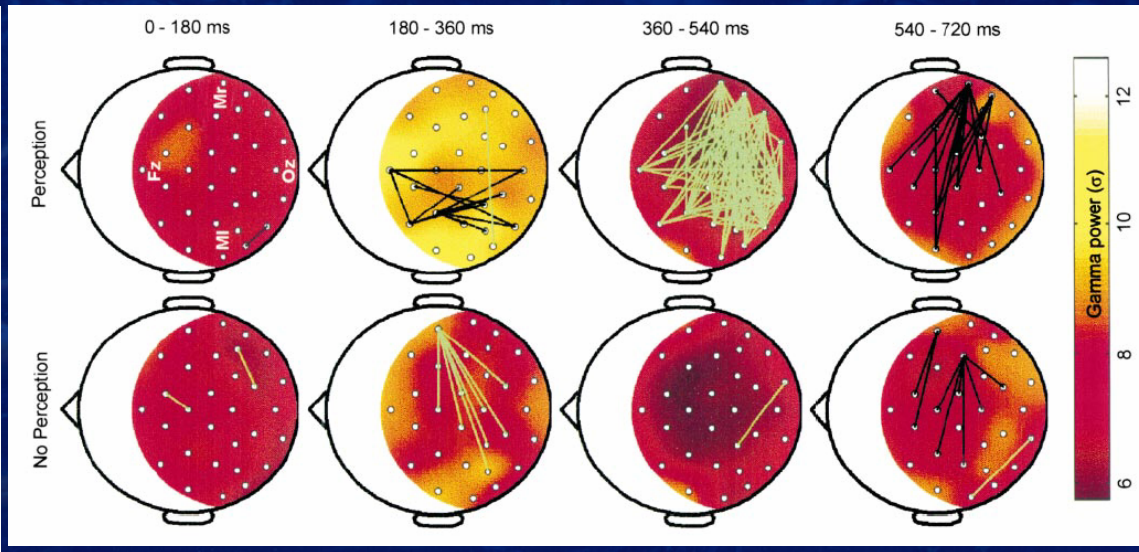
- Brain sub-systems can perform unconscious functions on their own.
- Conscious functions require the emergence of brain-wide integration of activity.

**So is there a rich club?**

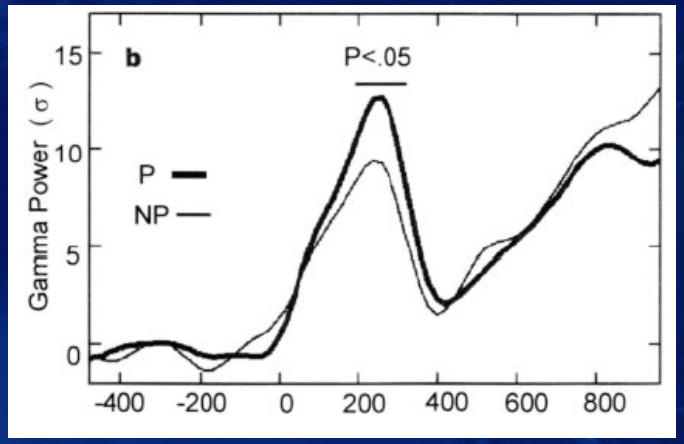
# Synchronization Across Modules

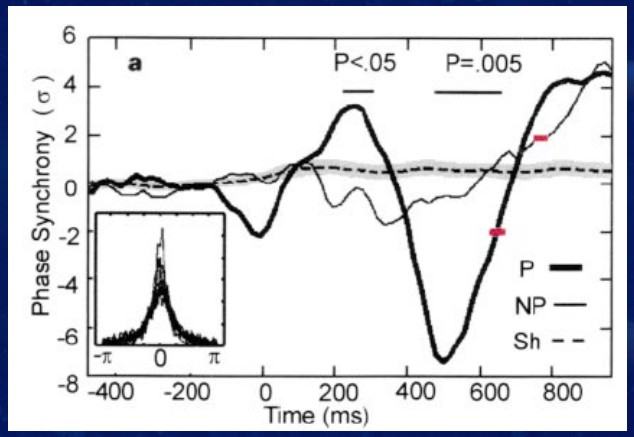
## The Signature of Emergent Coordination




Gamma power is similar in perception and no perception



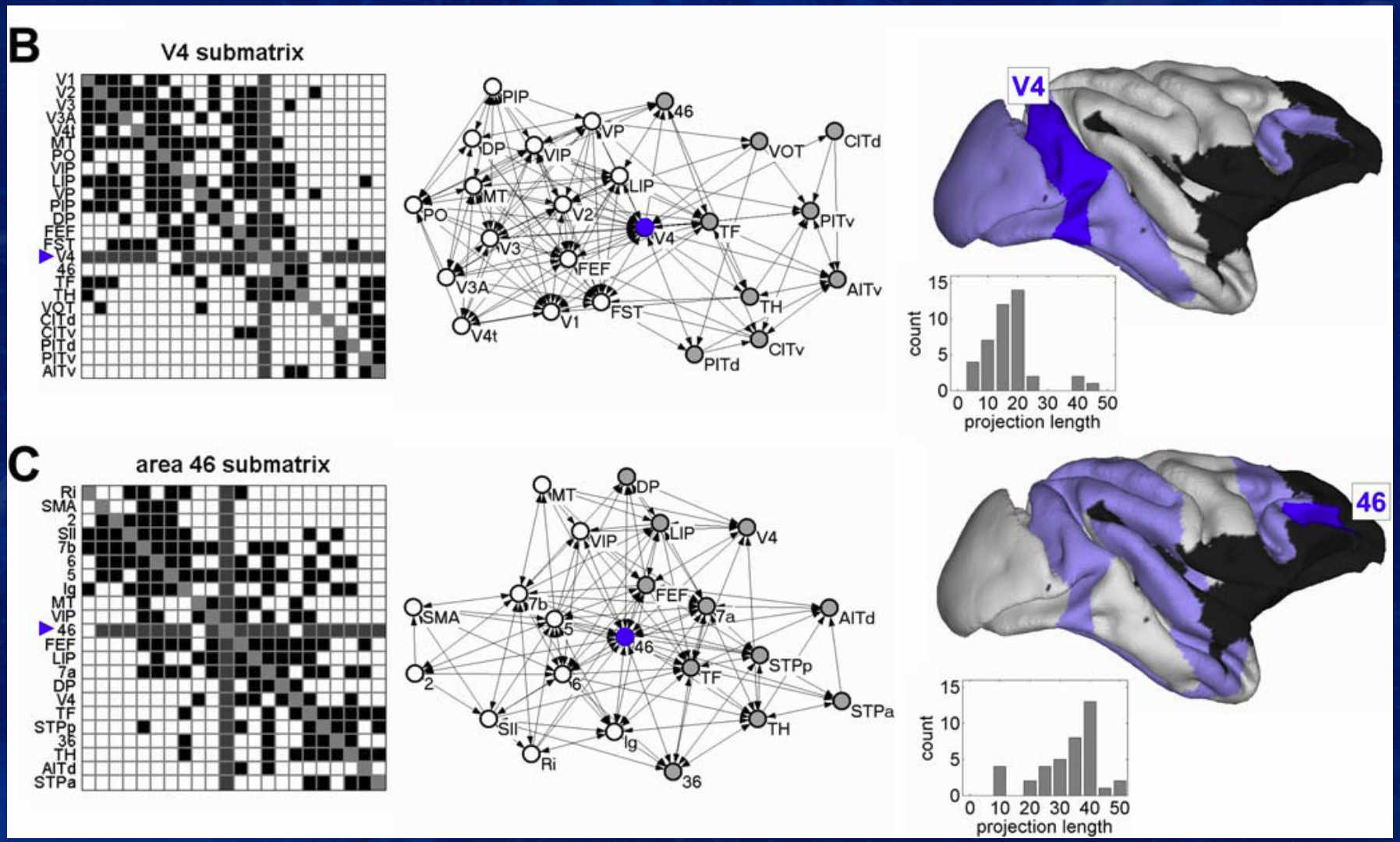




But cross-regional coherence is much higher for the perception case.

Rodriguez, E., et al (1999) Perception's shadow: long-distance Synchronization of human brain activity, Nature 397: 430-433.

# Structural Hubs in the Brain

O. Sporns, C.J. Honey, R. Kötter, R. (2007) Identification and Classification of Hubs in Brain Networks. PLoS ONE e1049.




Structural outward connectivity of two important sub-regions in the cortex.

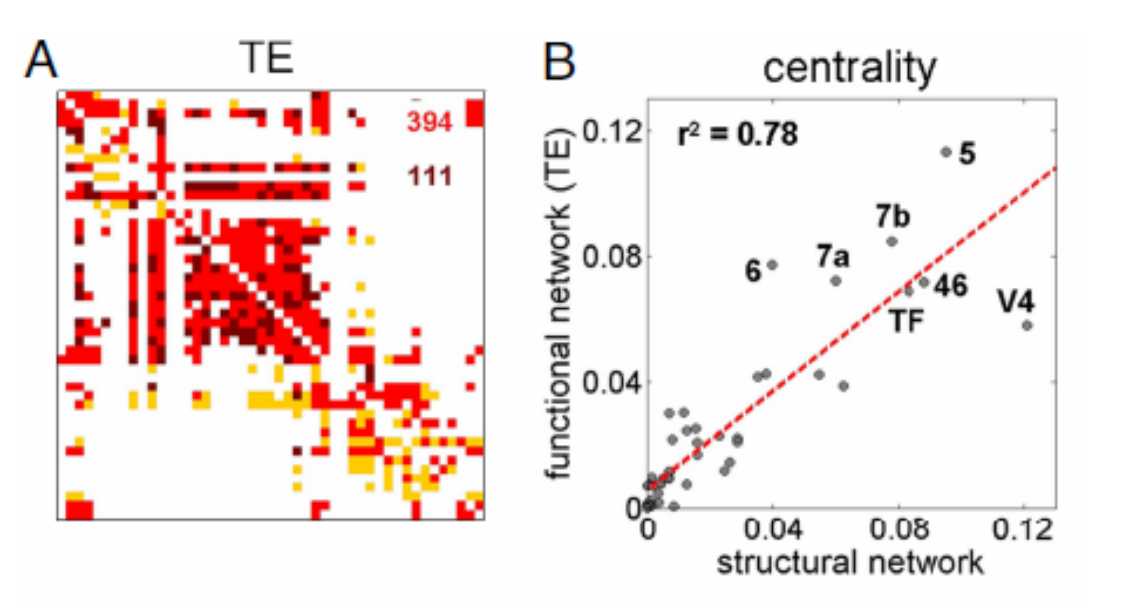
# Extracting Functional Connectivity

O. Sporns, C.J. Honey, R. Kötter, M. Breakspear, and O. Sporns,(2007) Network structure of cerebral cortex shapes functional connectivity on multiple time scales. PNAS 104: 10240–10245

Functional connectivity between nodes in brain images is determined using ***transfer entropy*** (TE):

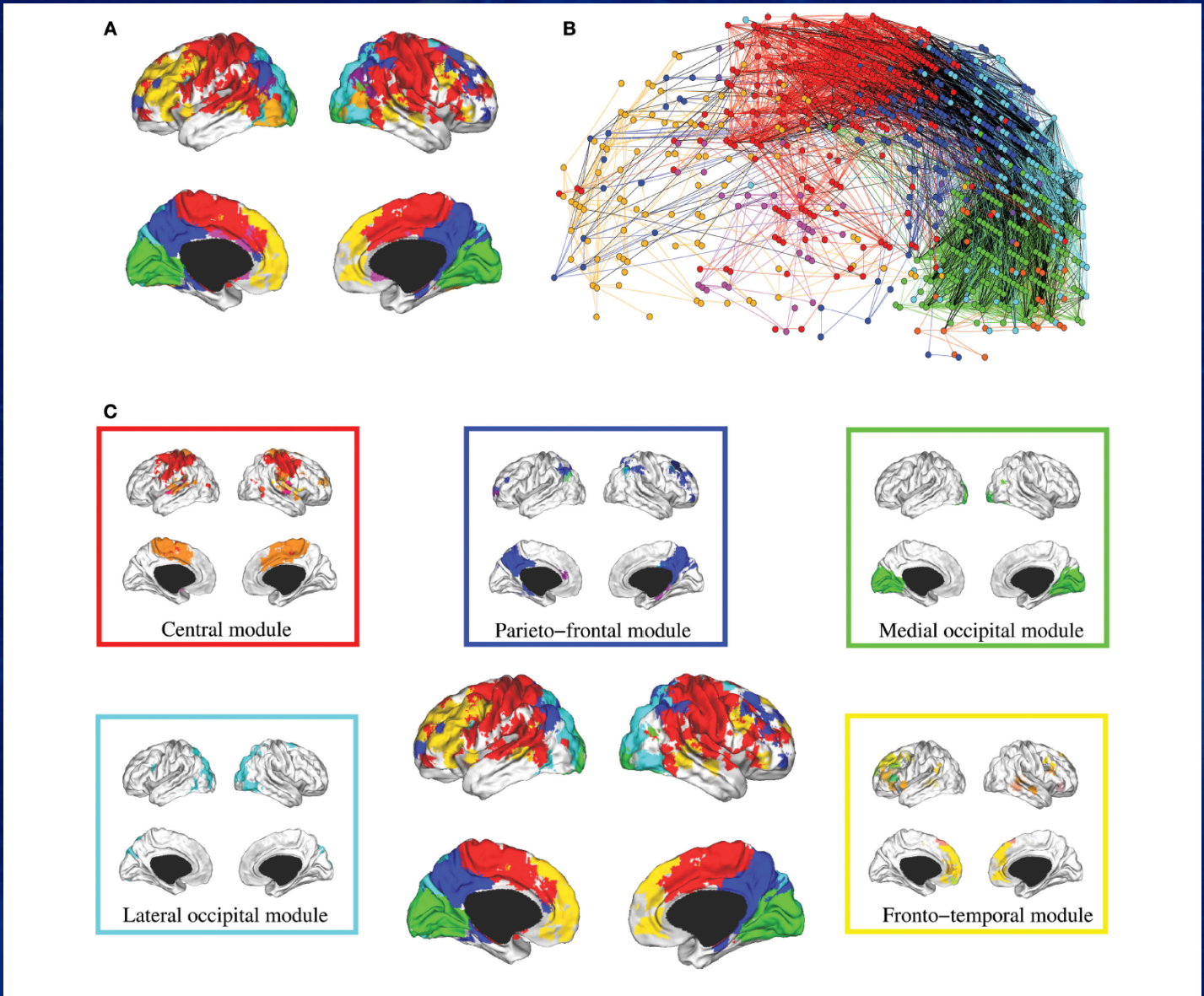
$$T_{Y \to X} = \sum p(x_{t+1}, x_t, y_t) \log \frac{p(x_{t+1} \mid x_t, y_t)}{p(x_{t+1} \mid x_t)}$$

If TE $\neq$ 0, it indicates that $y_t$ has causal influence on $x_{t+1}$

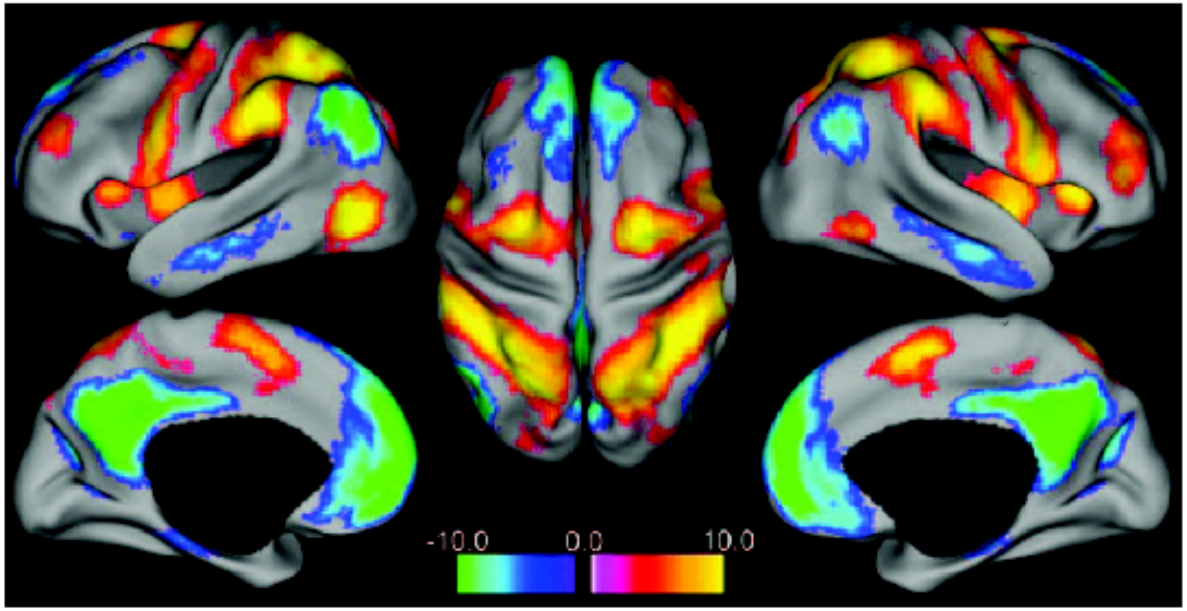



Centralities in a TE-based functional network are highly correlated with centralities in the corresponding structural network.

# Functional Networks of the Brain




Meunier, D. et al. (2009) Hierarchical modularity in human brain functional networks, Frontiers in Neuroinformatics doi: 10.3389/neuro.11.037.2009

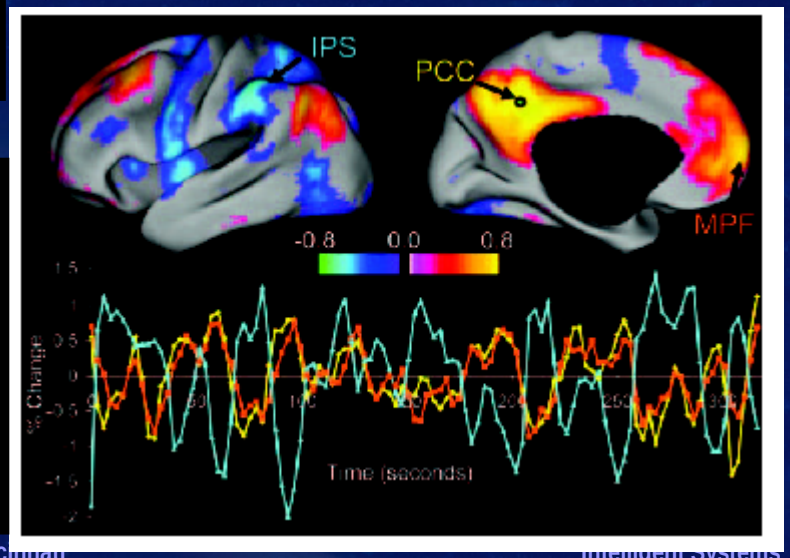



Fox, M.D., Snyder, A.Z., Vincent, J.L., Corbetta, M., Van Essen, D.C., and Raichle, M.E. (2005) The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences USA* **102**: 9673-9678.

Blue/Green = Regions positively correlated with task-negative nodes in the brain and negatively correlated with task-positive nodes.

Red/Yellow = Regions positively correlated with task-positive nodes in the brain and negatively correlated with task-negative nodes.

# Two Intrinsic Functional Networks




Activity time series for three regions showing phase opposition between task-positive and task-negative areas.

- PCC = Posterior cingulate/precuneus (task-negative)
- MPF = Medial prefrontal cortex (task-negative).
- IPS = Intraperietal sulcus (task-positive)

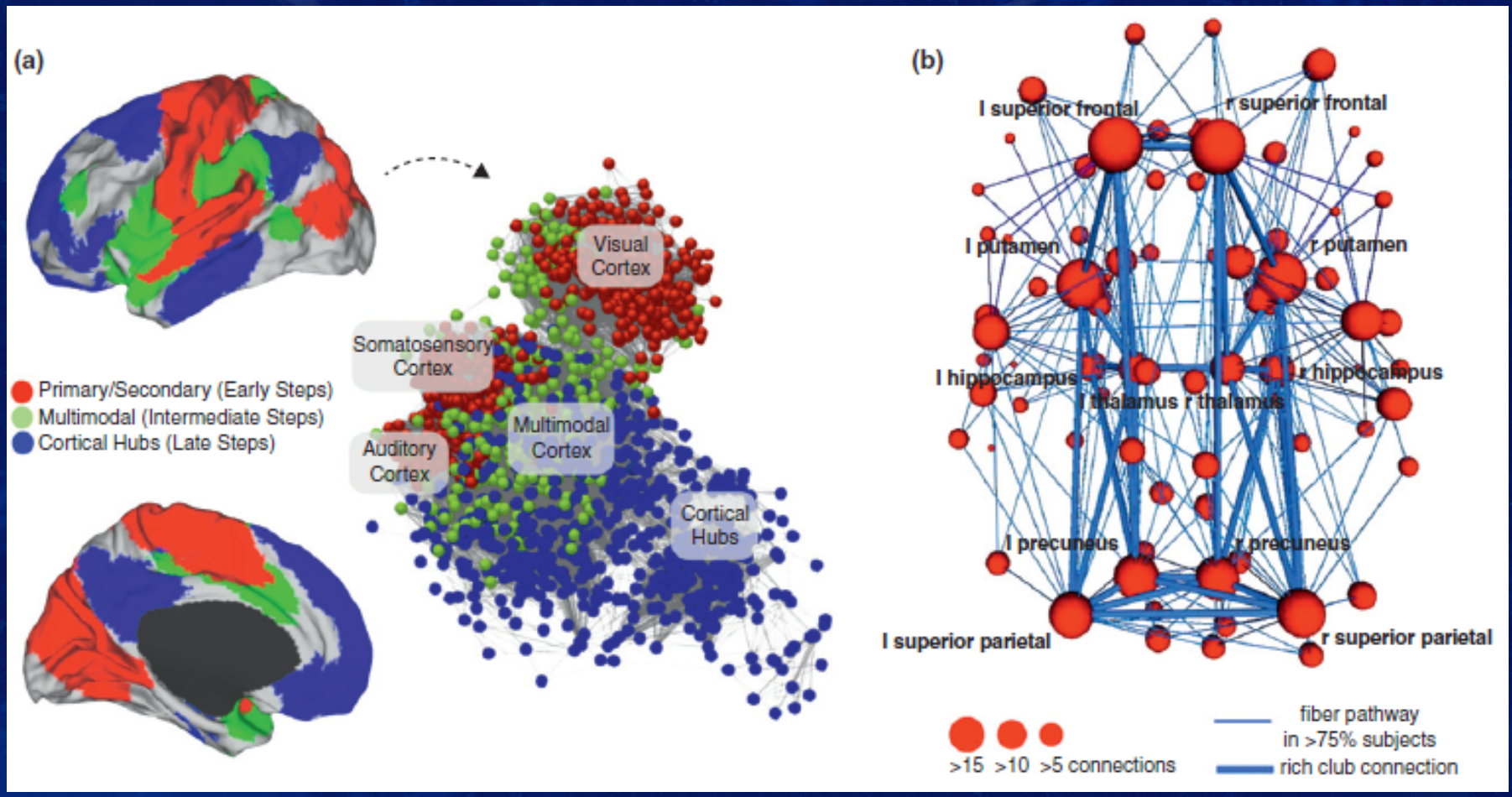
Top map shows correlation with PCC activity.

# Structural and Functional Connectivity

O. Sporns (2013) Network attributes for segregation and integration in the human brain. Current Opinion in Neurobiology 23: 162-171

Functional Communities

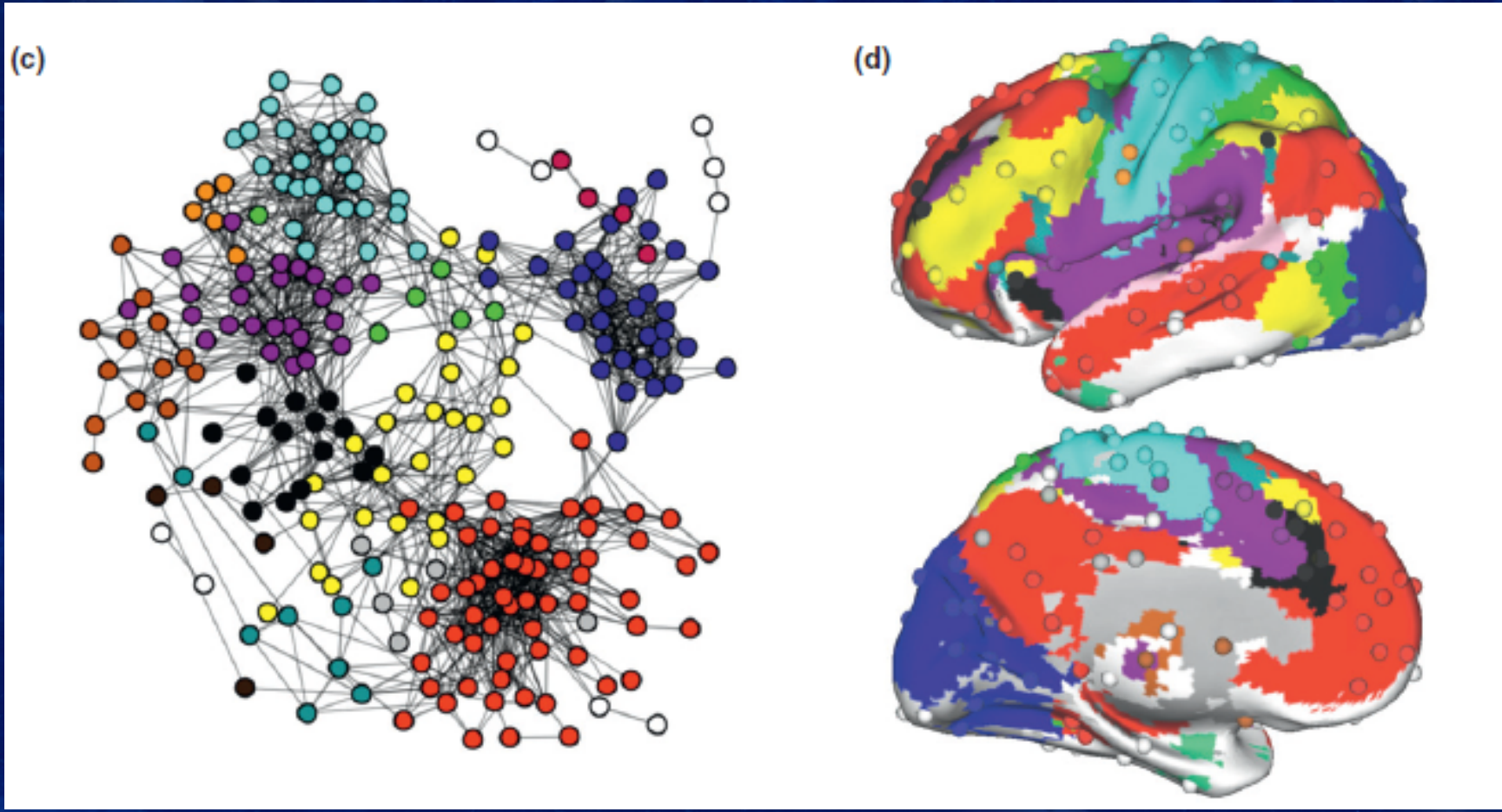
Structural Connectivity




Highly connected hubs form the "rich club" and represent a core/backbone network

# Functional Communities in the Human Cortex

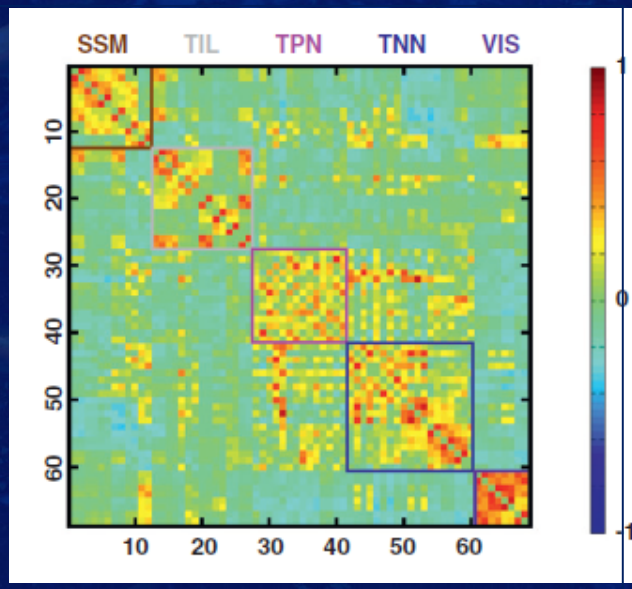
O. Sporns (2013) Network attributes for segregation and integration in the human brain. Current Opinion in Neurobiology 23: 162-171

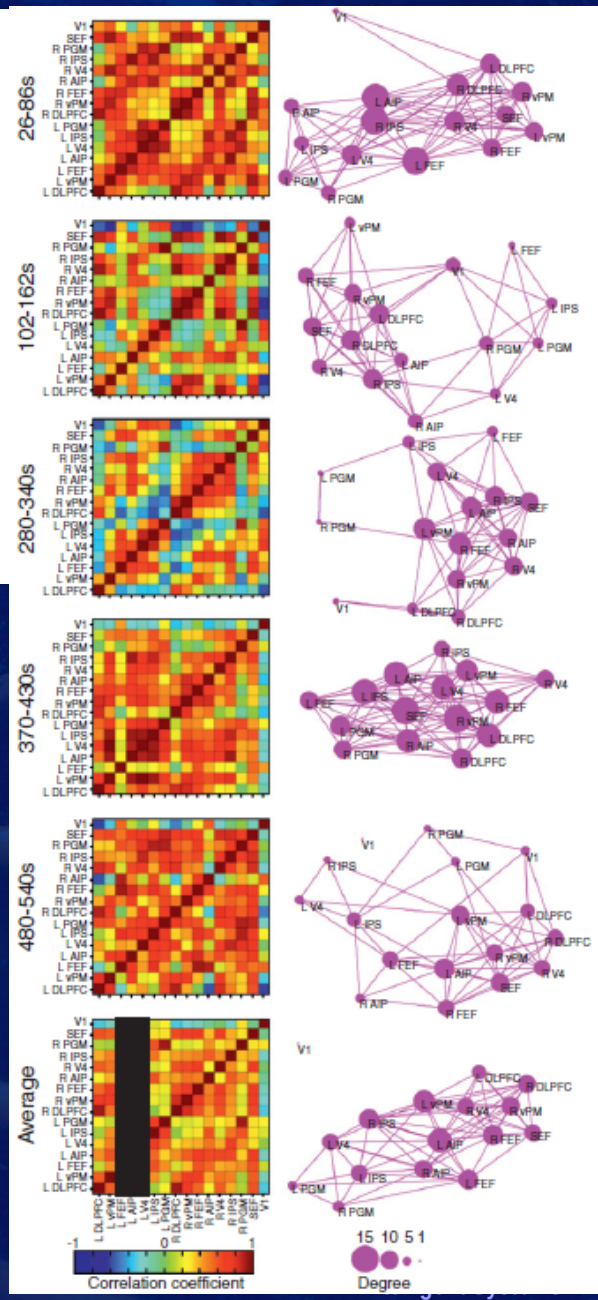


# Dynamics of Functional Brain Communities

Inter-regional average connectivity pattern for one subject, showing five functional communities:

- Somatosensory-motor (SSM)
- Temporal/insular/limbic (TIL)
- Task-positive (TPN)
- Task-negative (TNN)
- Visual (VIS)




Inter-regional connectivity for the same subject in different 60s windows during task performance – and the average connectivity (last panel).

Note the dramatic changes in functional connectivity over time.

O. Sporns (2013) Current Opinion in Neurobiology 23: 162-171

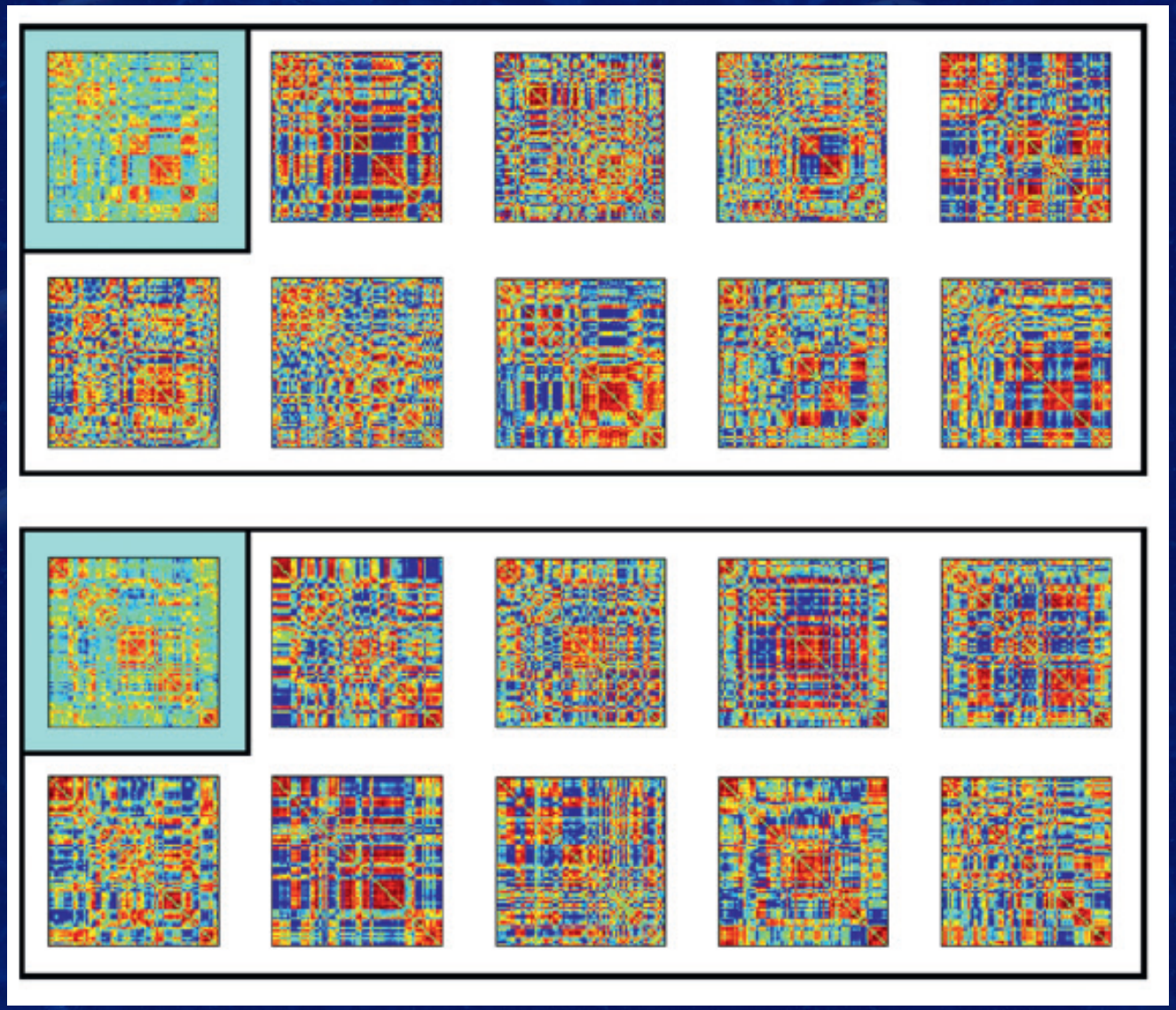
# Dynamics of Functional Brain Communities

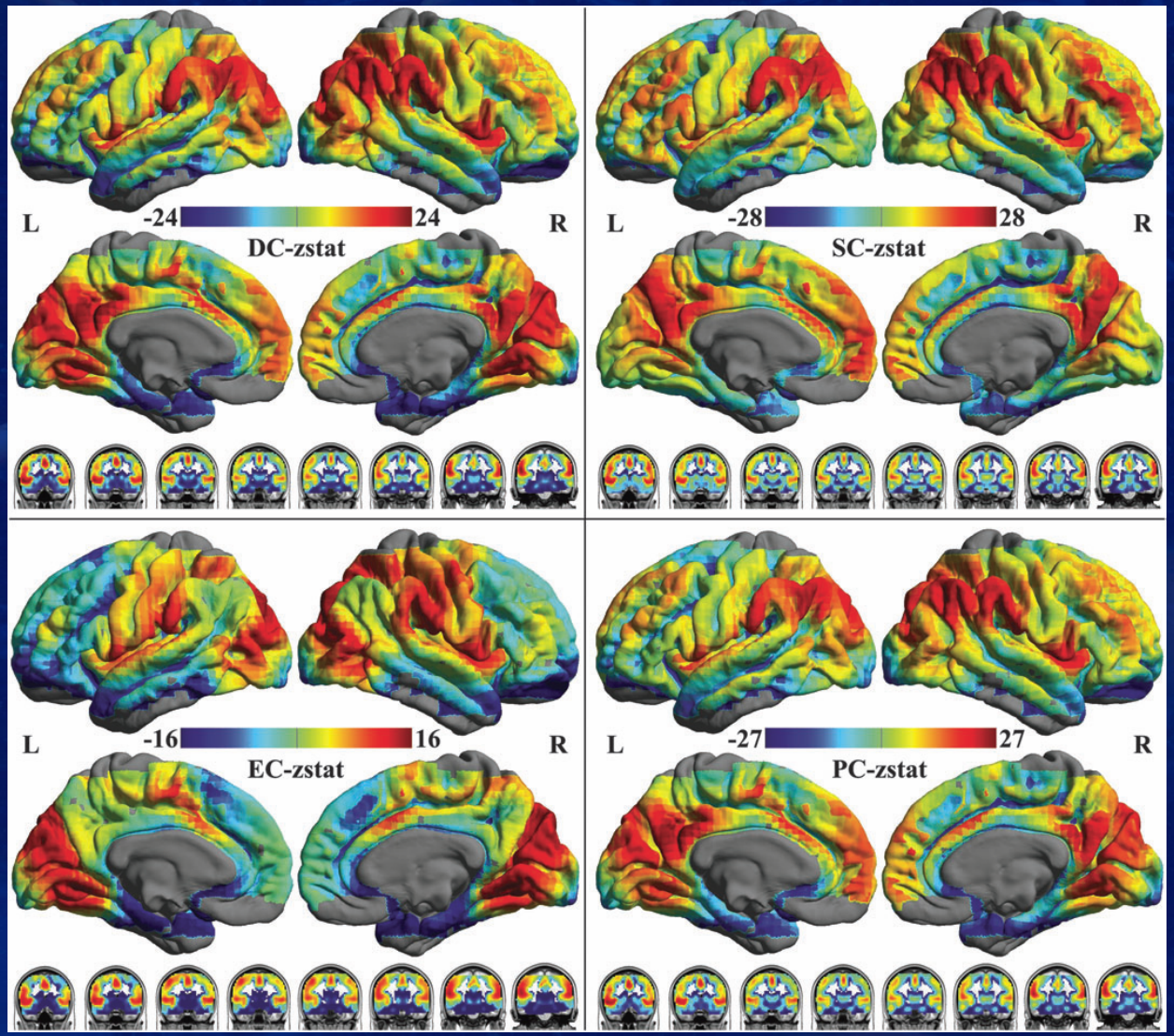
O. Sporns (2013) Current Opinion in Neurobiology 23: 162-171

Connectivity patterns for two different subjects over time.

The top left picture shows the time-averaged connectivity matrix.

The rest show connections in small successive time windows.



# Regions with High Functional Centrality

X.-N. Zuo, R. Ehmke, M. Mennes, D. Imperati, F.X. Castellanos, O. Sporms and M.P. Milham (2011)
Network centrality in the human functional connectome. Cerebral Cortex doi:10.1093/cercor/bhr269