Introduction to computational neuroscience : from single neurons to network dynamics

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What's the brain good for ?

Tree
no neurons

C.elegans
302 neurons

Fly
1 000 000 neurons

Rat
1 000 000 000 n.

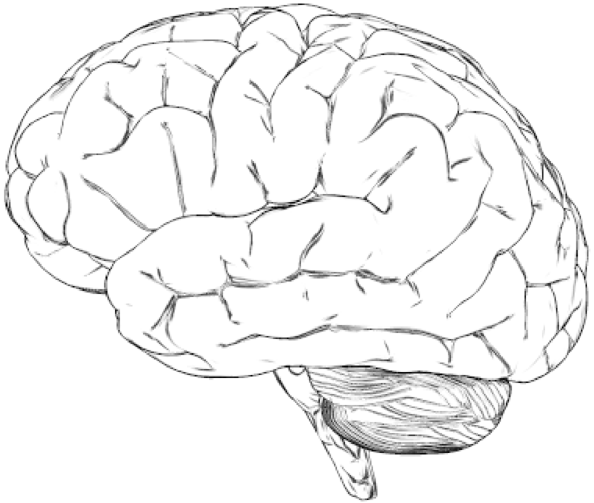
Human
80 000 000 000 000 n.

The brain generates motion (=behavior)

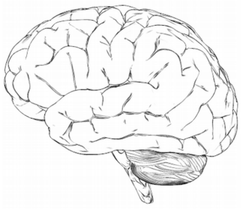
more complex brains generate a greater variety of behaviors

more complex brains can learn more behaviors

Cognitive processing

stimulus →  → response

What's the brain good at ?

			
chess	1	:	0
scrabble	1	:	0
Jeopardy!	1	:	0
video games	1	:	0
Go	1	:	0
Object recognition	1	:	1

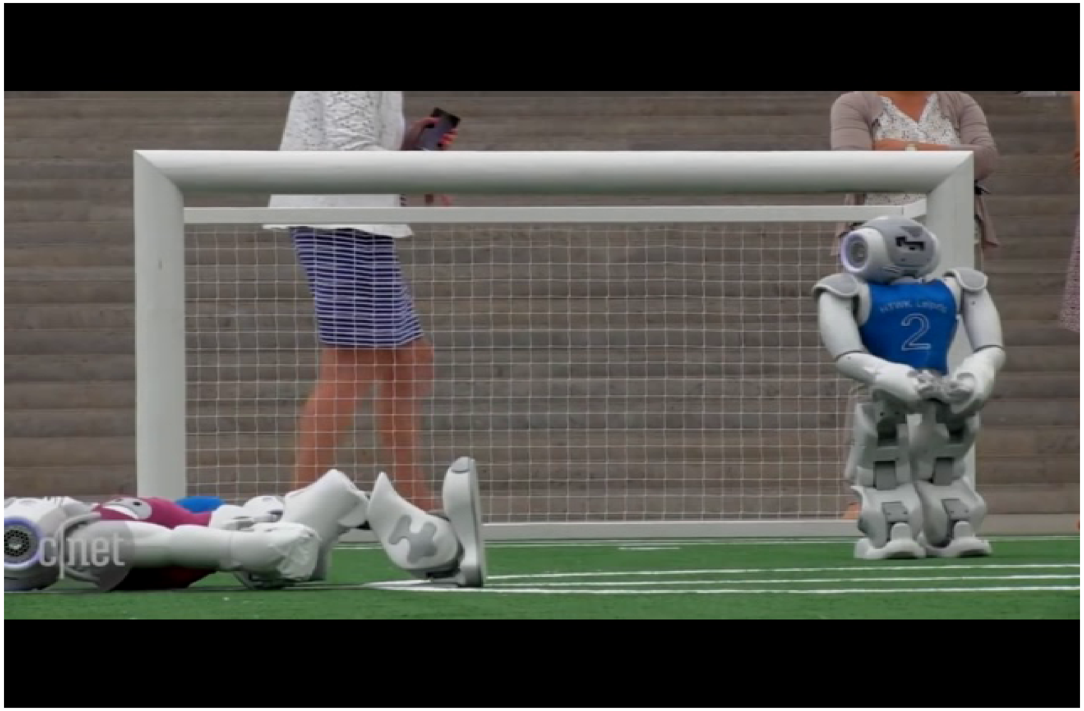
Computers outperform humans in algorithmic tasks and tasks involving database mining.

What's the brain good at ?

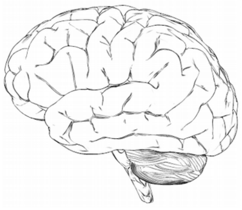
Lionel Messi – Barcelona : Getafe CF 2007

What's the brain good at ?

RoboCup 2016



What's the brain good at ?

			
soccer			
	0	:	1
numerous tasks	0	:	1

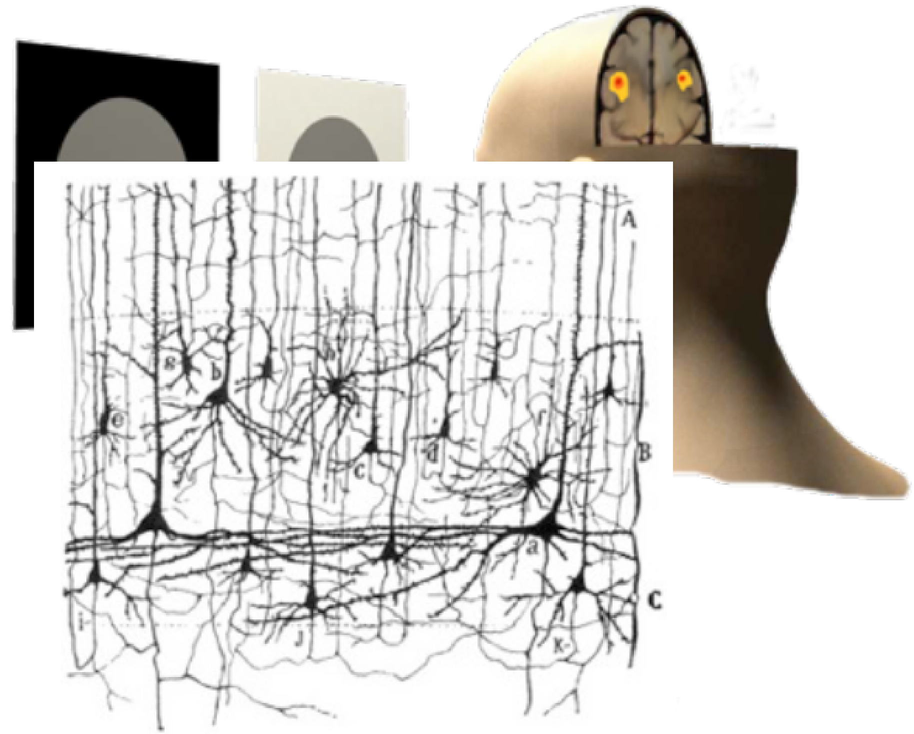
Brains are better in tasks involving interactions with the real world.

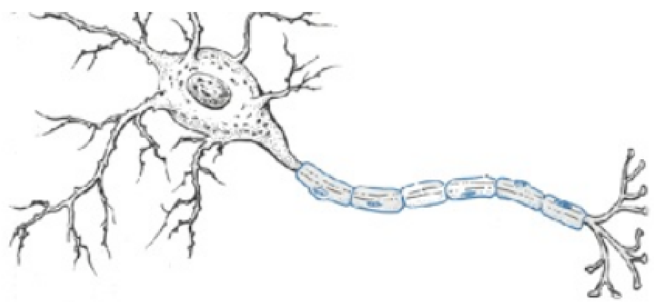
Why model the brain ?

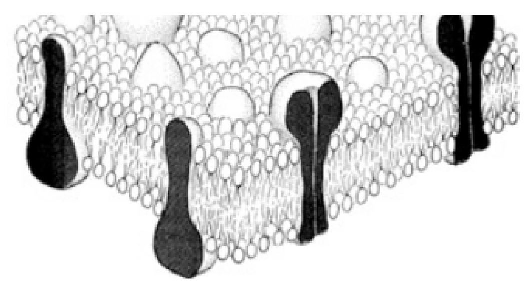
- → to understand it
- → to repair/improve it
- → to get inspired

The many spatial scales of the brain

CNS	1 m
Systems	10 cm
Maps	1 cm
Networks	1 mm
Neurons	100 µm
Synapses	1 µm
Molecules	1 nm







How does the brain work ?

A physics/engineering approach

just rebuild the whole thing

→ reverse engineering the brain

The quest for mechanisms :
Constructing the systems from parts

CNS	1 m
Systems	10 cm
Maps	1 cm
Networks	1 mm
Neurons	100 µm
Synapses	1 µm
Molecules	1 nm

The quest for mechanisms :
Constructing the systems from parts

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Lecture outline :

Introduction to Computational Neurosciences

1. Introduction :

- A couple of brain questions

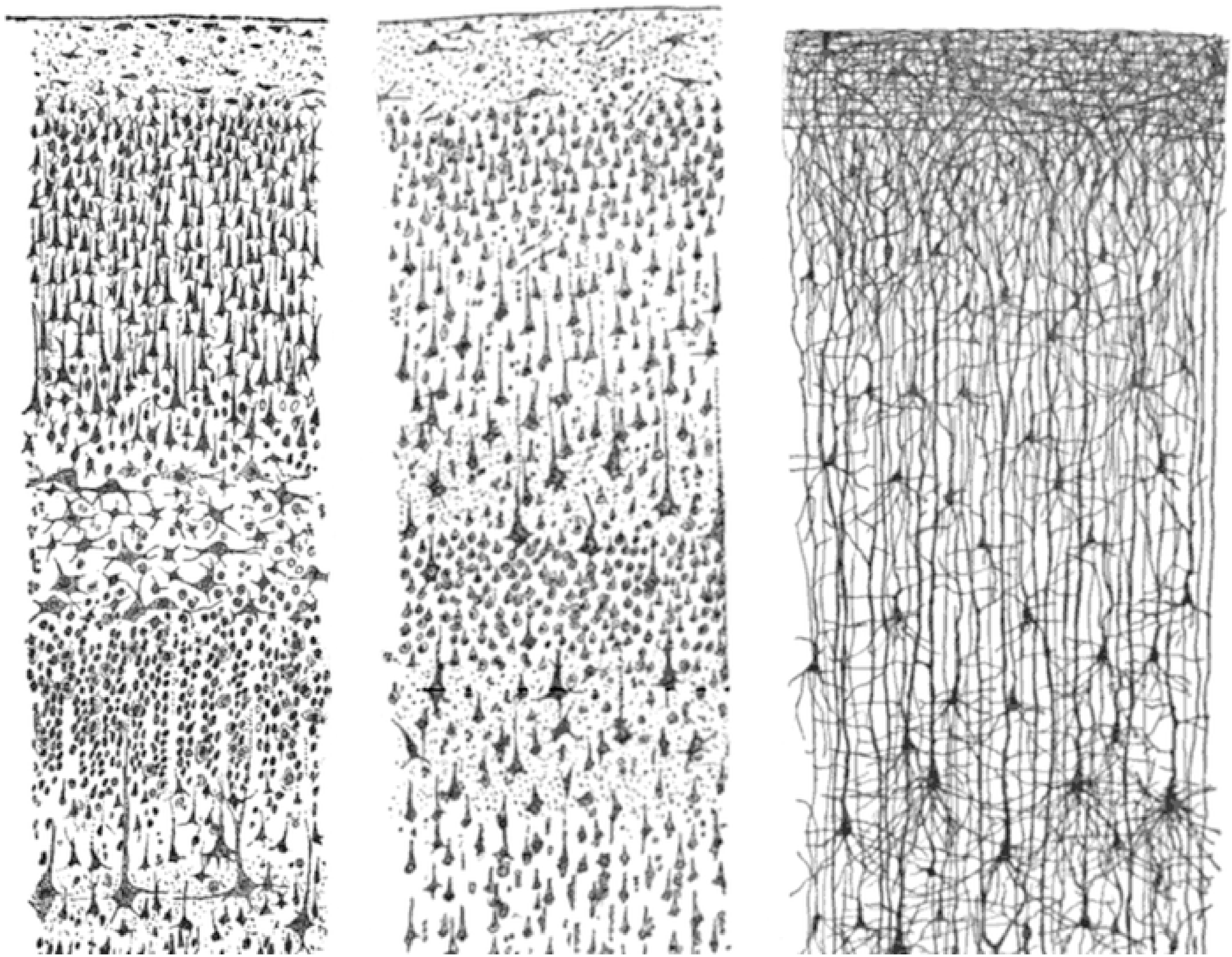
2. The Neuron :

- Hodgkin-Huxley model
- Integrate-and-Fire model
- Rate model
- Cable theory

3. Neural networks :

- Rate models
- Spiking neuron models
- Examples

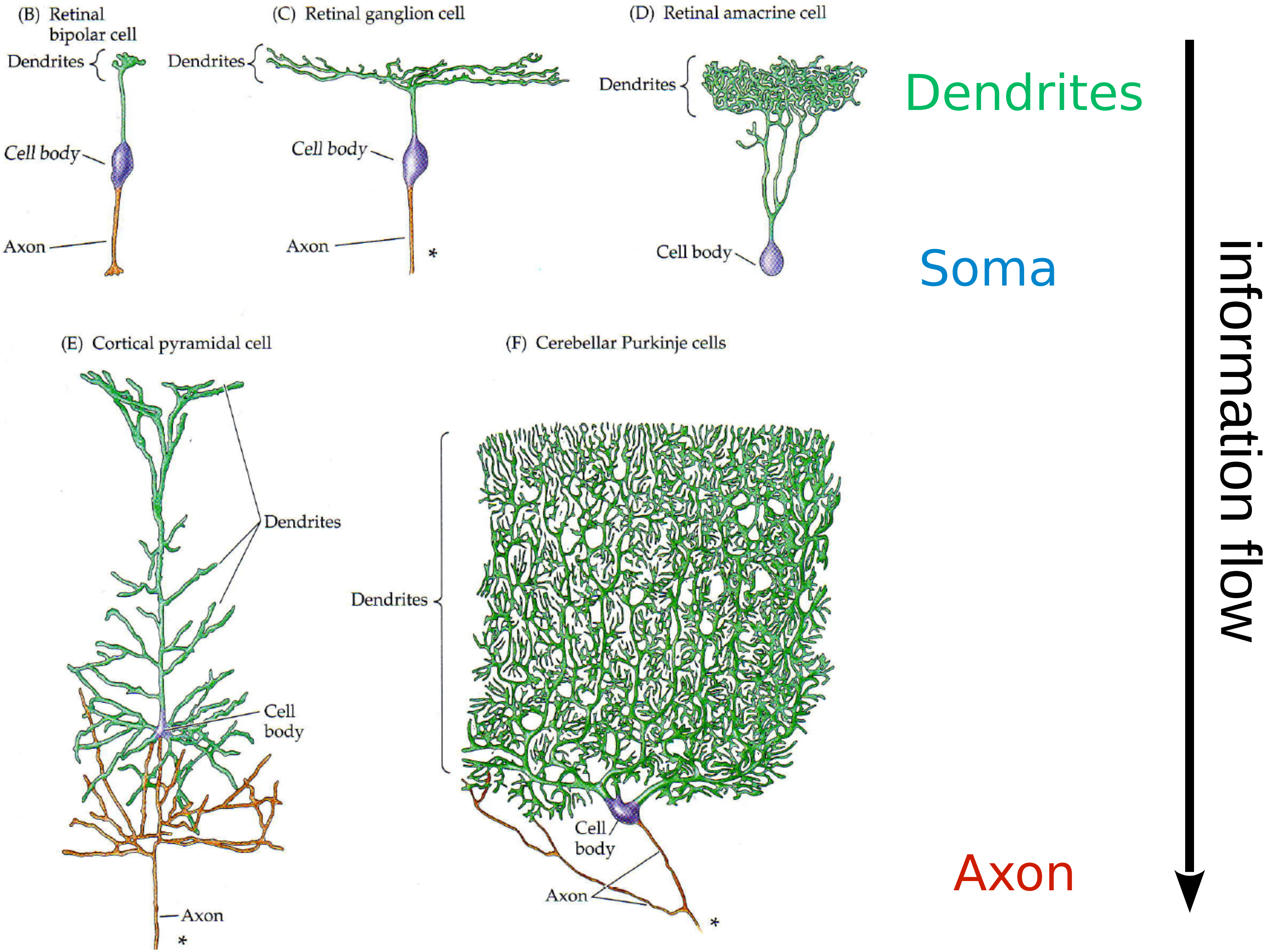
What does the hardware look like ?



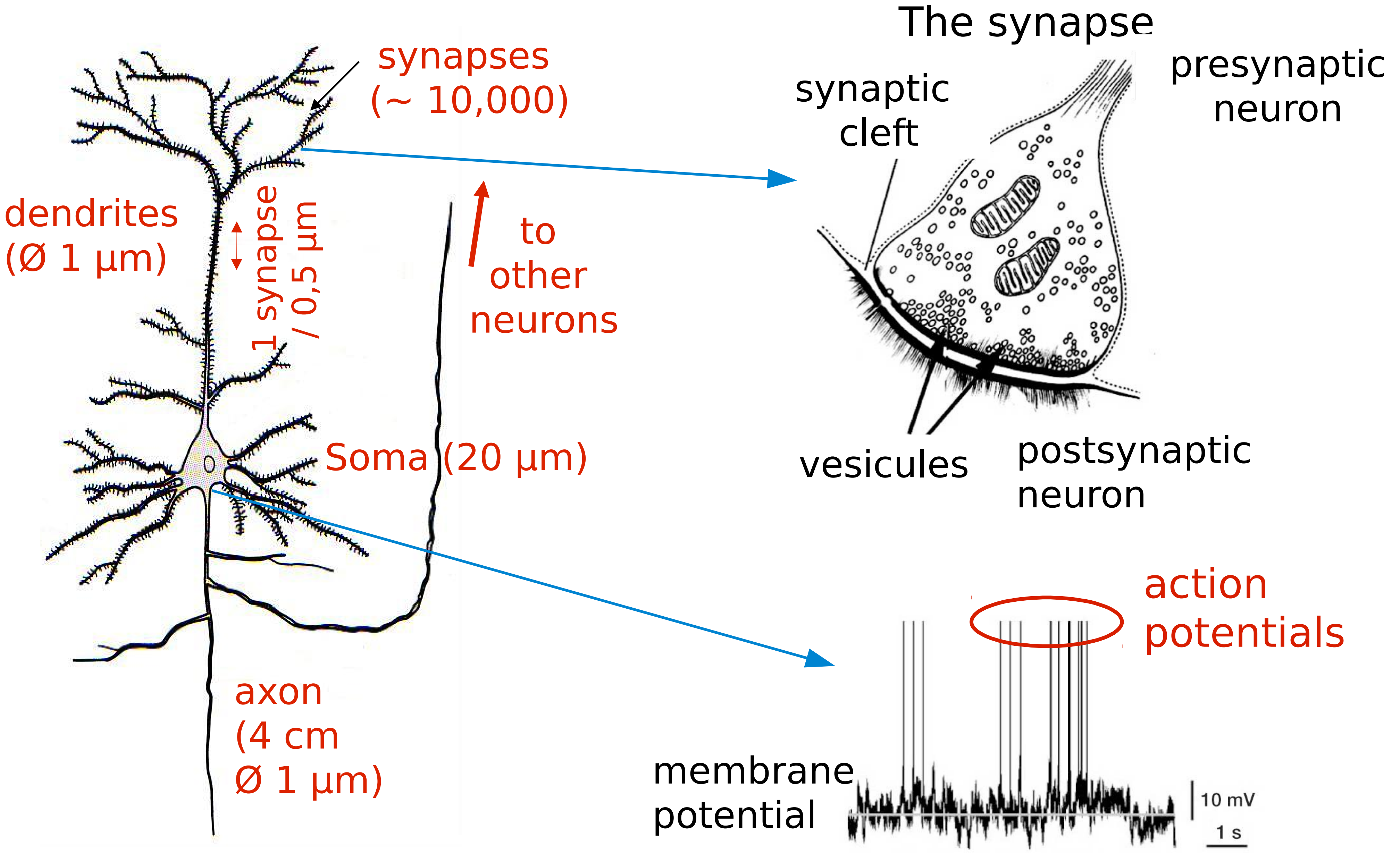
Ramon y Cajal (Nobel Prize 1906) → neuron doctrine

Joseph von Gerlach (1871), Camillo Golgi → ~~Reticular theory~~

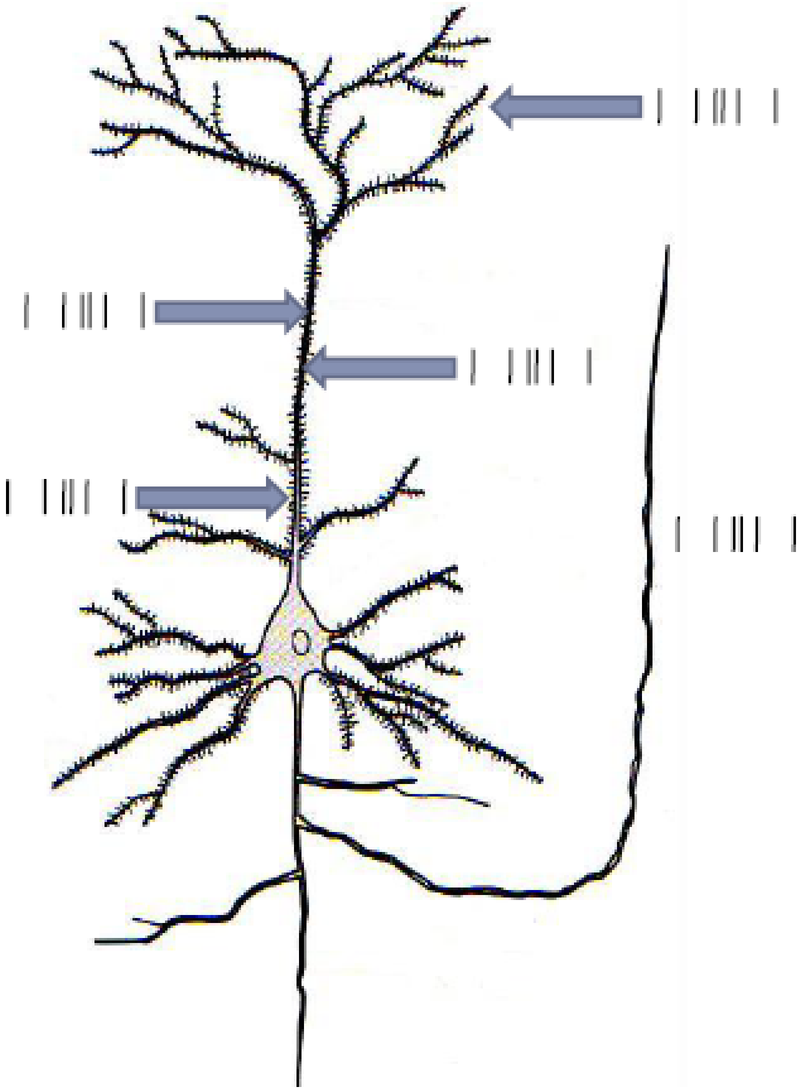
Neurons = basic units of computation

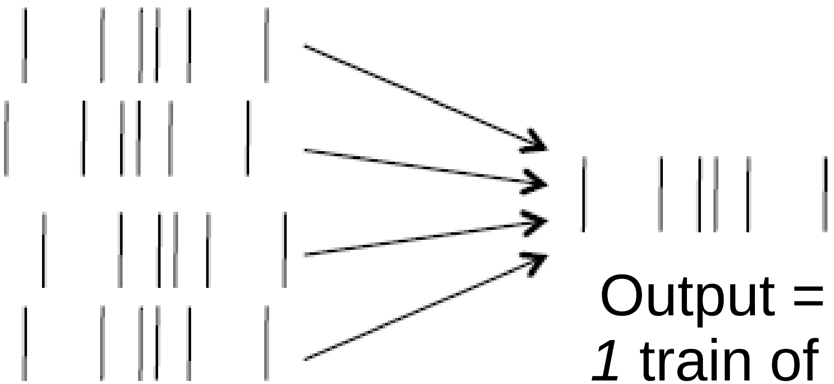


The typical cortical neuron



Neural integration





Output =
1 train of
action potentials

Input =
N trains of
action potentials

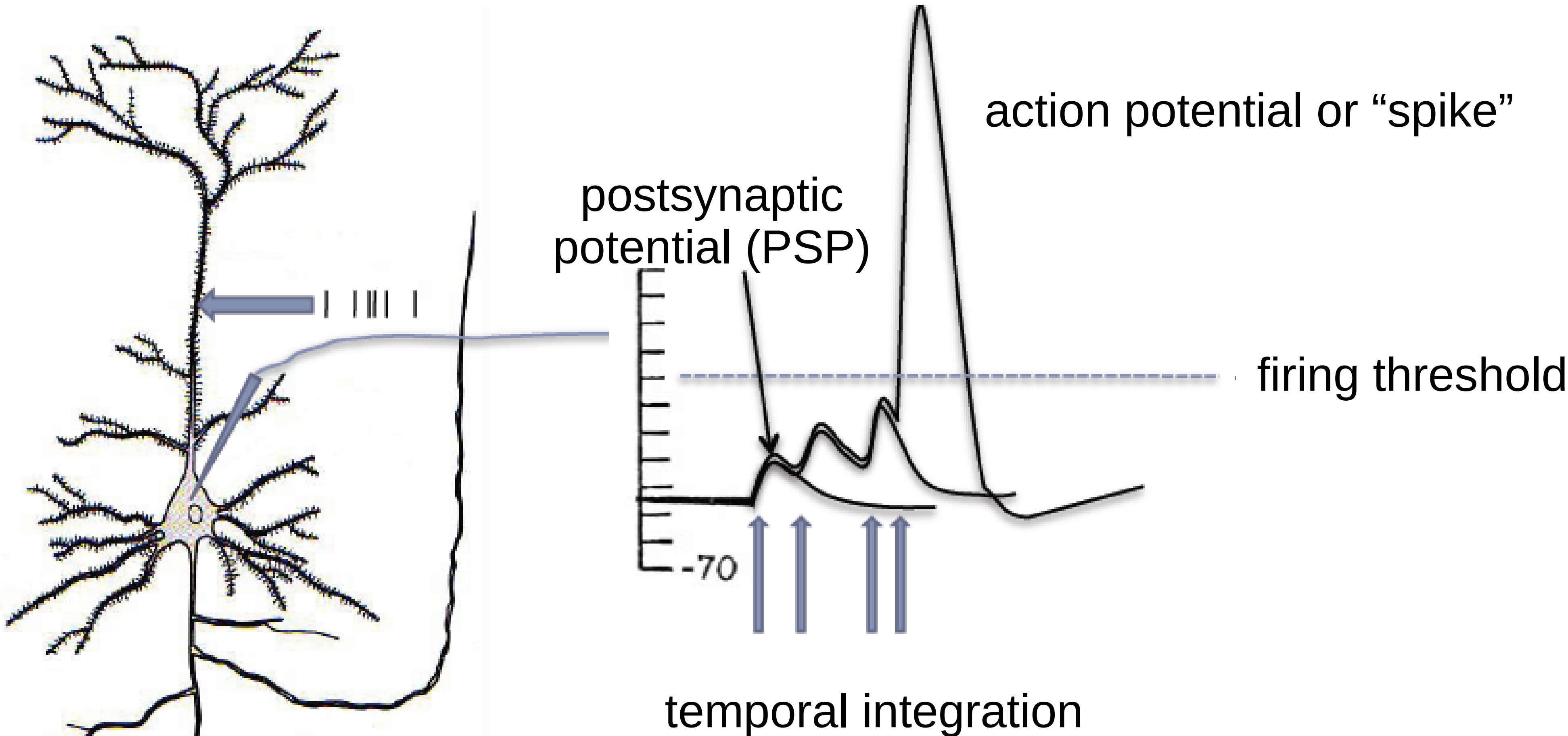
Synaptic current :

$$I_s = G_{max}\,\Delta V\,\alpha(t) = w_{ij}\,\alpha(t)$$

Total synaptic current in neuron *i* at time *t* :

$$I^{i}_{syn}(t) = \sum_j w_{ij} \sum_k \alpha(t - t_j^{(k)})$$

Neural integration



$$I^{i}_{syn}(t) = \sum_{j} w_{ij} \sum_{k} \alpha(t - t_{j}^{(k)})$$

Statistics of spike trains

- Spike train (action potentials) :
  → A sequence of spike times t^k
  → A signal

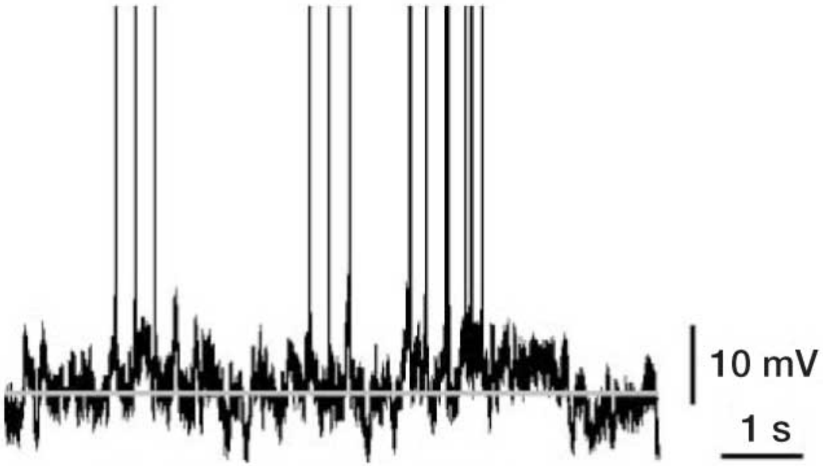
$$S(t) = \sum_k \delta(t - t^k)$$

- Inter-spike interval (ISI) :

$$\mathrm{ISI} = t^{n+1} - t^n$$

- Firing rate :
  → number of spikes / time
  → mean of S :

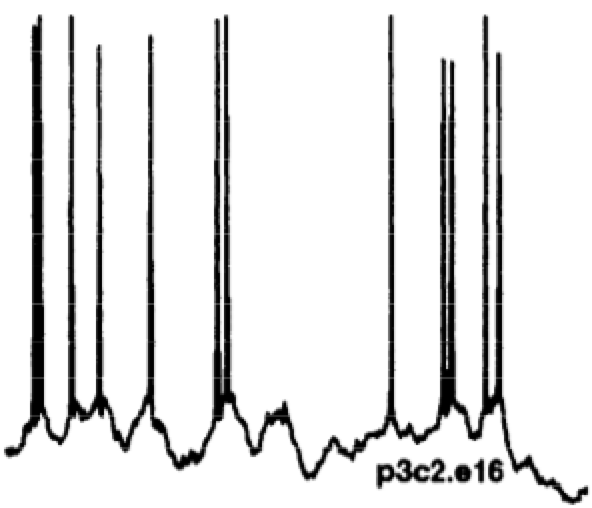
$$r = \langle S(t) \rangle = \lim_{T \to +\infty} \frac{1}{T} \int_0^T S(t)\, dt$$



Statistics of spike trains

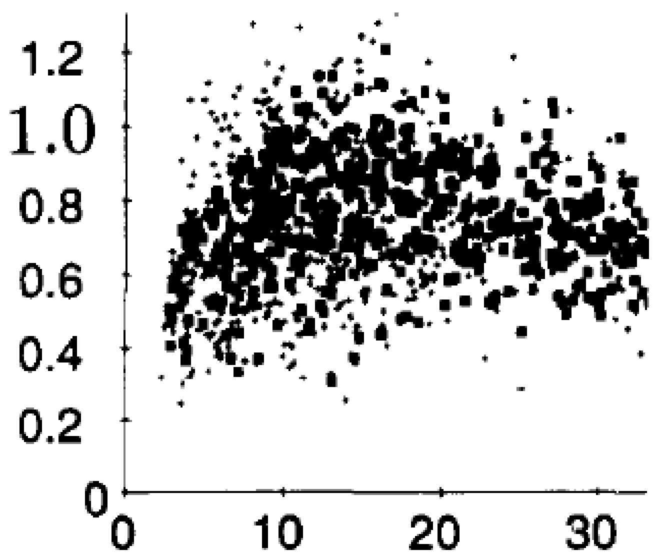
- Spike trains are irregular and vary from one trial to another :
  →probabilistic description
- The statistics of cortical spike trains resemble a "Poisson process" :

visual stimulation
in vivo



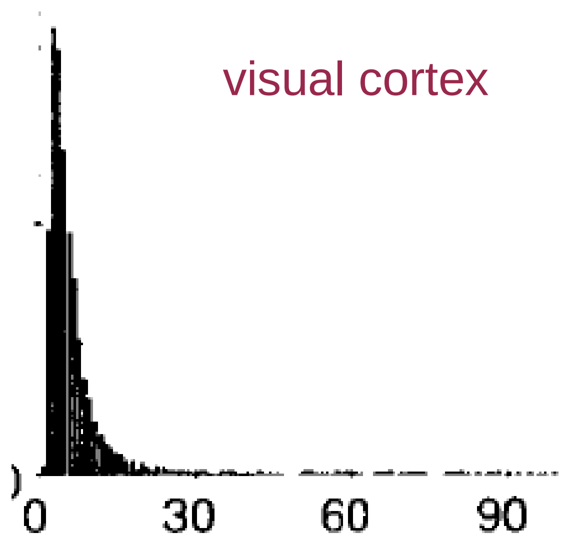
[Holt *et al.*, 1996]

Coefficient of Variation
CV



firing rate

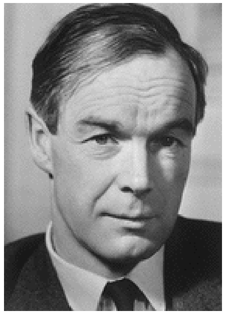
ISI distribution

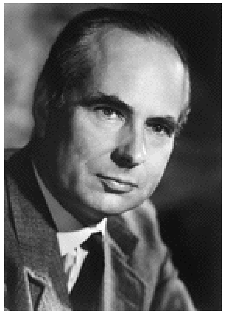


ISI (ms)

Single neuron models

- **Hodgkin Huxley model** : description of ion channel dynamics (Hodgkin & Huxley, 1952)





Hodgkin Huxley

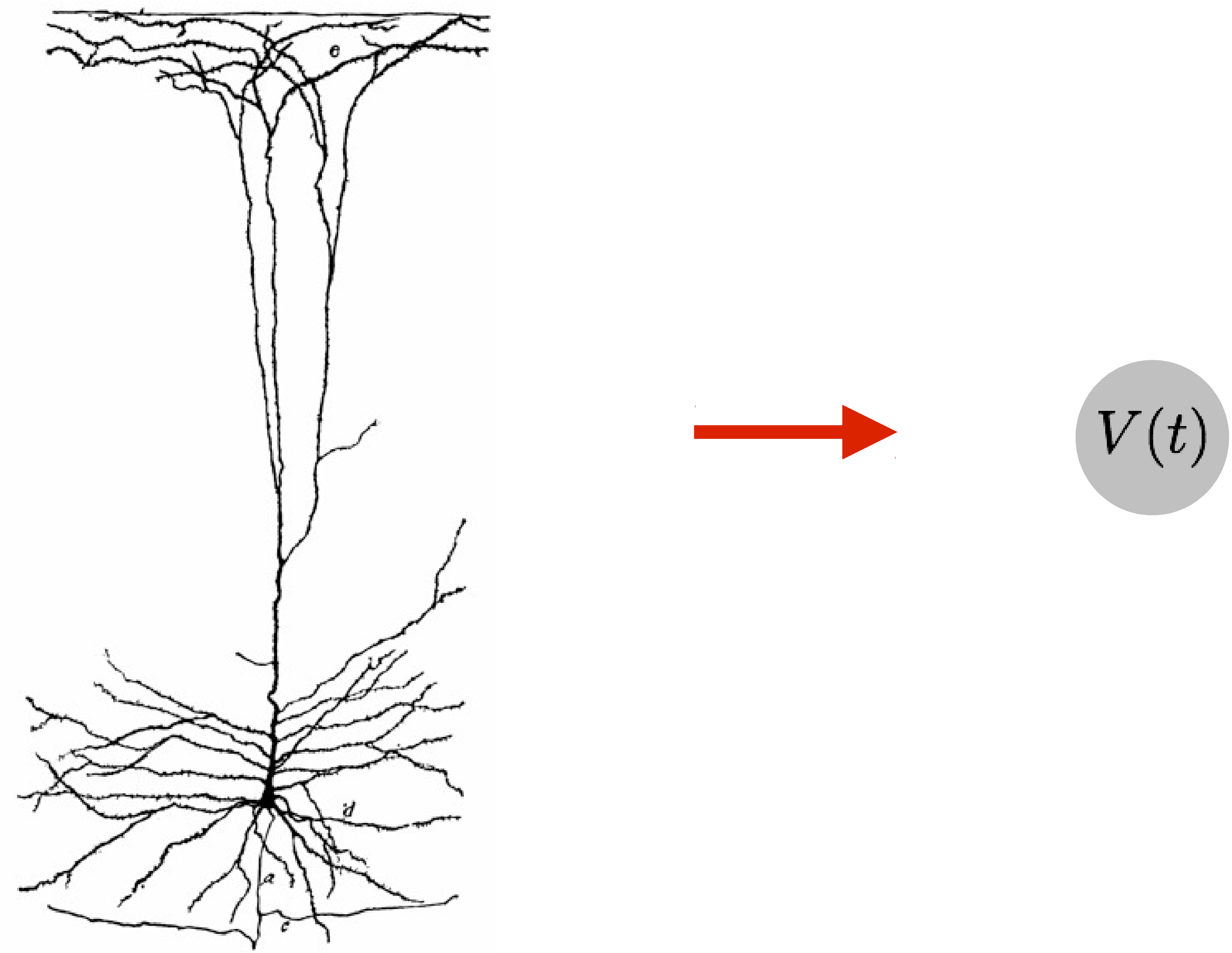
- **integrate-and-fire model** : description of input integration membrane potential dynamics (LaPicque, 1907)

- **rate model** : description of the mean firing rate dynamics

- **cable theory** : description of input propagation along the dendrites (Rall, 1962)

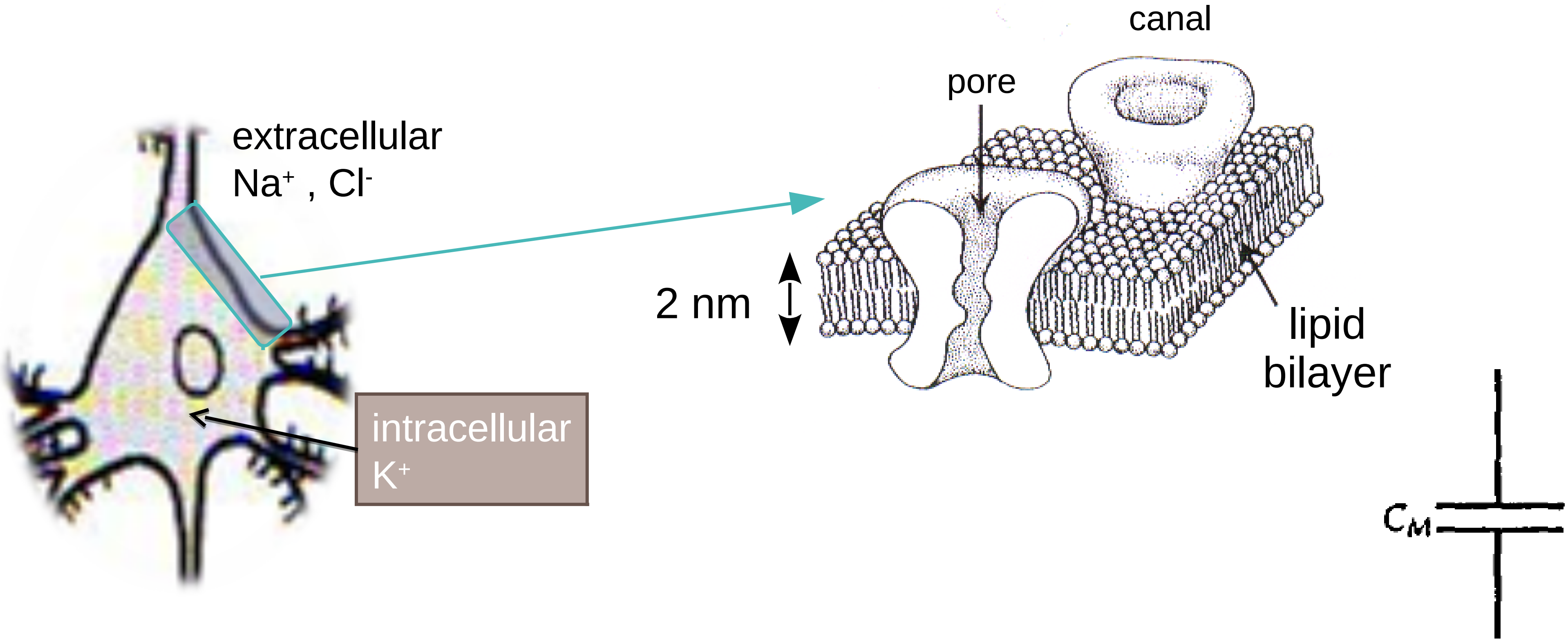
Wilfrid Rall

simplified single neuron : single compartment model



The membrane

- Lipid bilayer (= capacitance) with pores (channels = proteines)



specific capacitance 1 μF/cm²

total specific capacitance = specific capacitance * surface

Physics reminder

Ohm's law :

The current flowing through a resistor is directly proportional to the voltage drop across the resistor.

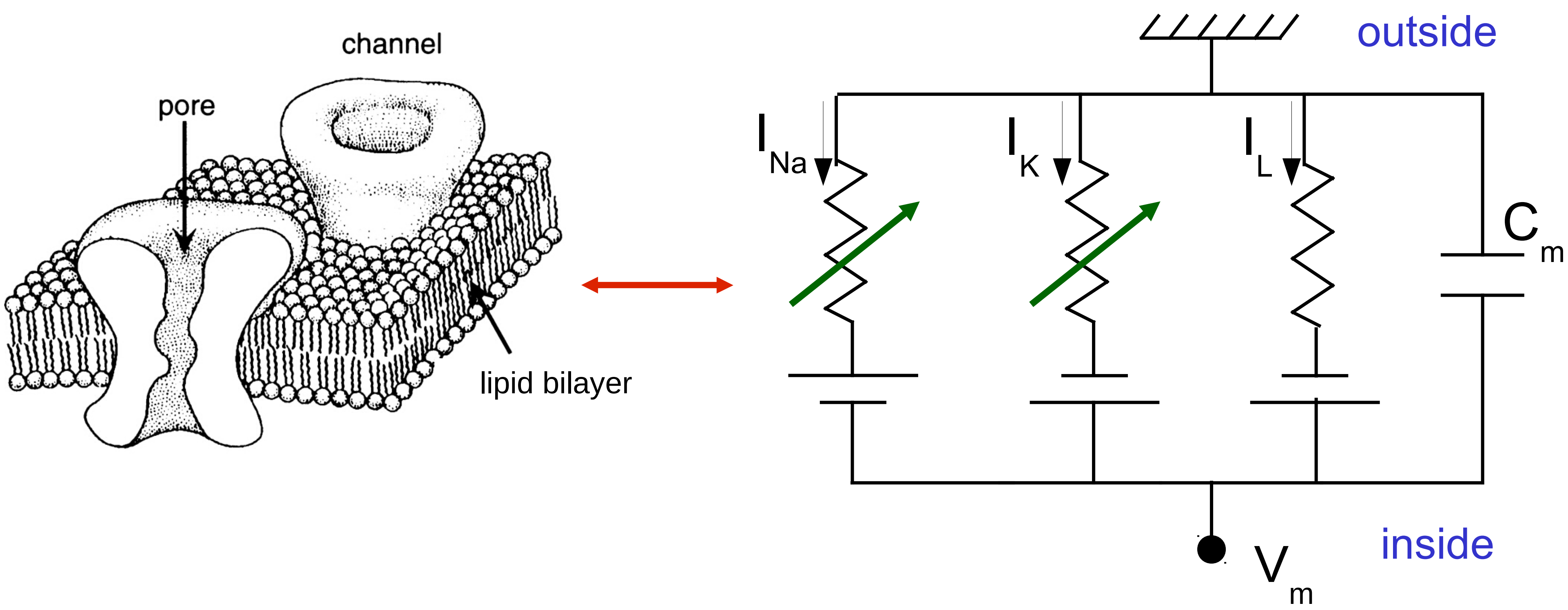
$$I = \frac{V}{R} \qquad R = \frac{1}{g}$$

Kirchoff's law :

The sum of currents flowing into a point is equal to the sum of currents flowing out of that point..

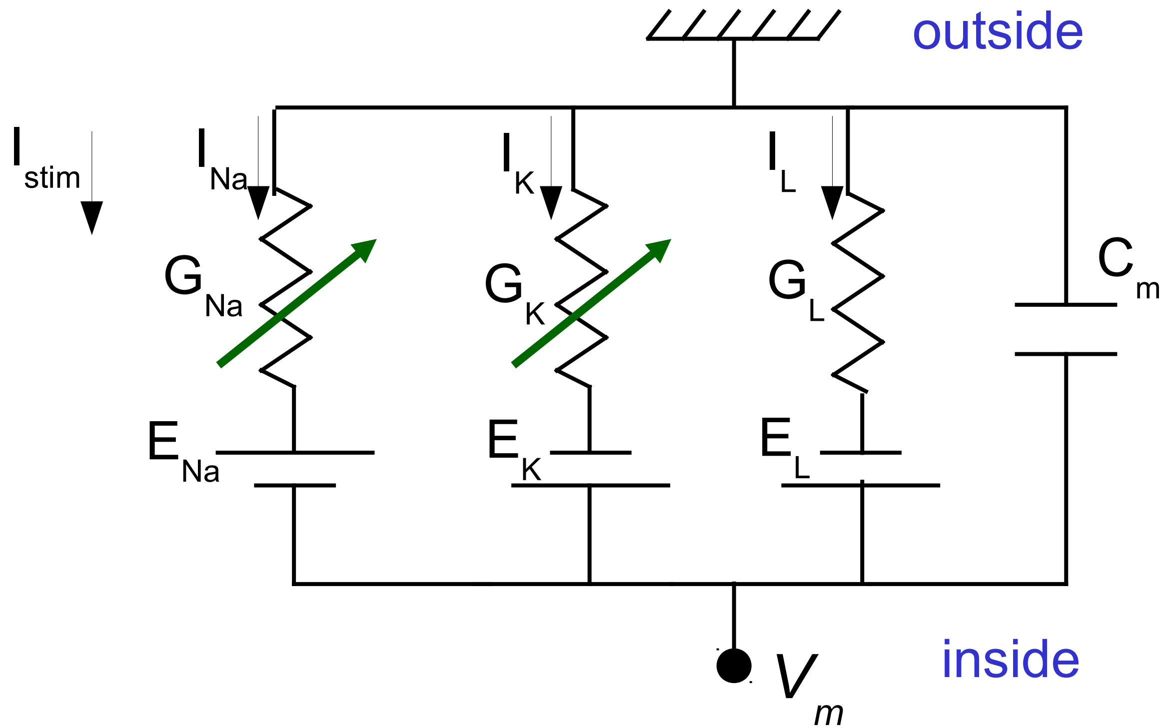
$$I_1 + I_2 + I_3 + \cdots = 0$$

Membrane properties : equivalent circuit



- The membrane potential V_m varies due to the opening/closing of different types of ion channels.
- **“Active membrane”** : Ion channel conductance varies with the membrane potential.

Hodgkin-Huxley model : membrane potential equation



Kirchhoff's law :

$$I_{stim} = I_{Na} + I_k + I_L + I_C$$

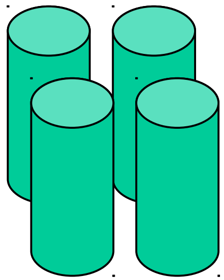
Ohm's law :

$$R = \frac{\Delta V}{I} \rightarrow I = \frac{\Delta V}{R} = g\left(V_m - V_{rev}\right)$$

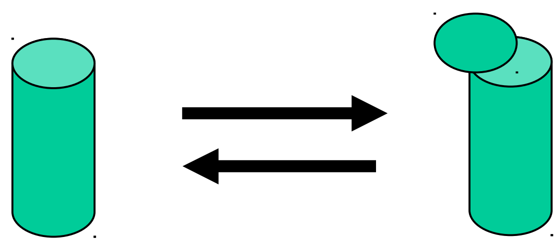
$$\rightarrow I_{stim} = g_{Na}(t)\left(V_m - V_{Na}\right) + g_K(t)\left(V_m - V_K\right) + g_L\left(V_m - V_L\right) + C\frac{dV_m}{dt}$$

Hodgkin-Huxley model : potassium channel

- 4 similar sub-units



- Each subunit can be « open » or « closed » :



- The channel is « open » if and only if all the sub-units are « open »

Hodgkin-Huxley model : potassium channel

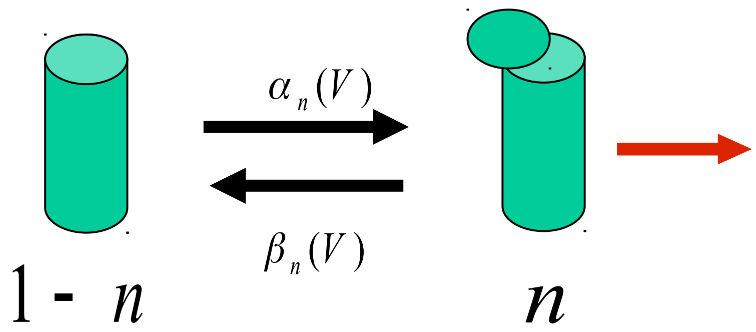
- probability that one sub-unit is « open » : $n(t)$
- probability that all sub-units are « open » : $n(t)^4$
- maximal K+ conductance, when all channels are open : $\bar{g}_K$
- K^+ conductance : $g_k = \bar{g}_K n(t)^4$

$$C\frac{dV}{dt} = g_{Na}(t)(V_{Na} - V) + g_K(t)(V_K - V) + g_L(V_L - V) + I_{stim}$$

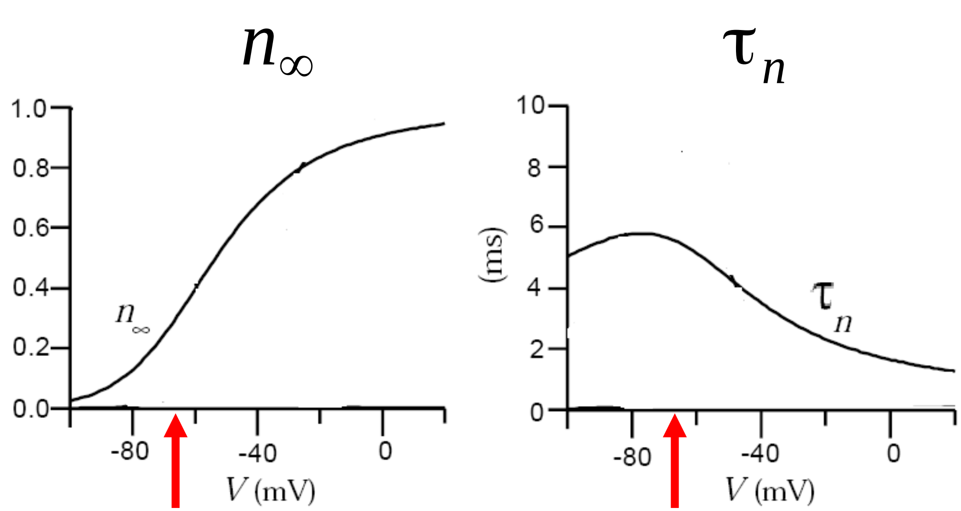
↓

$$C\frac{dV}{dt} = g_{Na}(t)(V_{Na} - V) + \bar{g}_K n(t)^4 (V_K - V) + g_L(V_L - V) + I_{stim}$$

Hodgkin-Huxley model : potassium channel

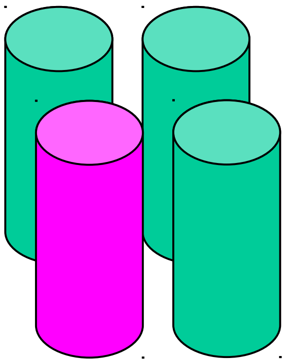


- dynamics equation: $$\tau_n \frac{dn}{dt} = -n + n_\infty$$
- time constant: $$\tau_n = \frac{1}{\alpha_n + \beta_n}$$
- asymptotic value: $$n_\infty = \frac{\alpha_n}{\alpha_n + \beta_n}$$

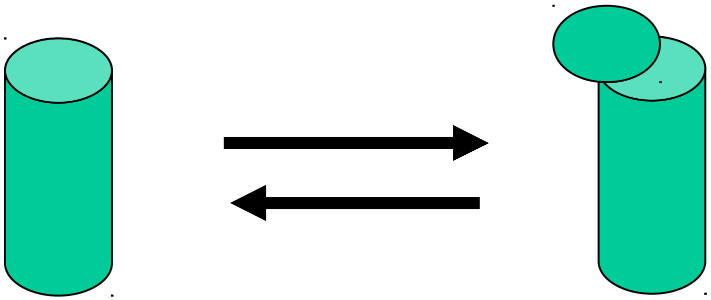


- The potassium channel is closed at resting potential.

Hodgkin-Huxley model : sodium channel



- The sodium channel has 3 similar « fast » esub-units and 1 « slow » subunit
- Each sub-unit can be « open » or « closed »



➔ The channel is « open » if and only if all the sub-units are « open »

modèle Hodgkin-Huxley : canal de sodium

- Probability that the « fast « sub-unit is « open » : m
- Probability that the « slow » sub-unit is « open » : h
- Probability that the channel is « open » : $m^3 h$
- Maximal Na+ condutance, when all channels are open : $\bar{g}_{Na}$
- Na+ conductance : $g_{Na} = \bar{g}_{Na} m^3 h$

$$C\frac{dV}{dt} = g_{Na}(V_{Na} - V) + g_K(V_K - V) + g_L(V_L - V) + I_{ext}$$

$$C\frac{dV}{dt} = \bar{g}_{Na} m^3 h (V_{Na} - V) + \bar{g}_K n^4 (V_K - V) + g_L (V_L - V) + I_{stim}$$

modèle Hodgkin-Huxley : canal de sodium

dynamics of the of the fast sub-unit

$$\tau_m \frac{dm}{dt} = -m + m_\infty$$

$$\tau_m = \frac{1}{\alpha_m + \beta_m}$$

$$m_\infty = \frac{\alpha_m}{\alpha_m + \beta_m}$$

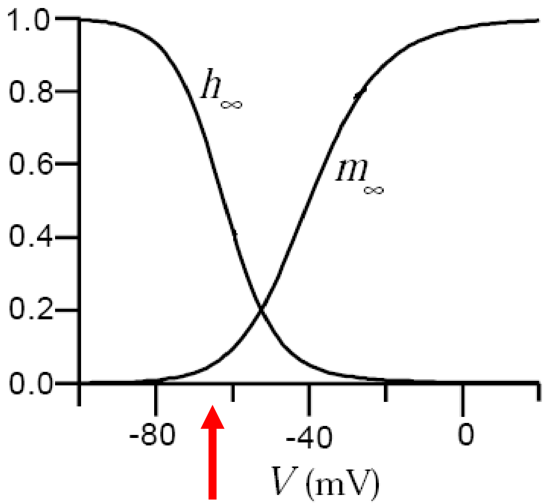
dynamics of the slow sub-unit :

$$\tau_h \frac{dh}{dt} = -h + h_\infty$$

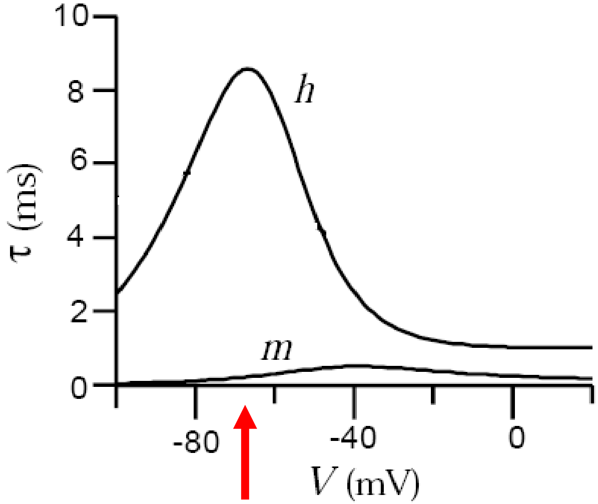
$$\tau_h = \frac{1}{\alpha_h + \beta_h}$$

$$h_\infty = \frac{\alpha_h}{\alpha_h + \beta_h}$$

asymptotic values



time constants



- The fast sub-unit is closed at resting potential.
- The slow sub-unit is open at resting potential.
- The sodium channel is closed at resting potential.

Complete equations of the Hodgkin-Huxley model

$$C\frac{dV}{dt}=\bar{g}_{Na}m^3h(V_{Na}-V)+\bar{g}_K n^4(V_K-V)+g_L(V_L-V)+I_{stim}$$

$$\tau_n\frac{dn}{dt}=-n+n_\infty \quad ,\tau_n=\frac{1}{\alpha_n+\beta_n},n_\infty=\frac{\alpha_n}{\alpha_n+\beta_n}$$

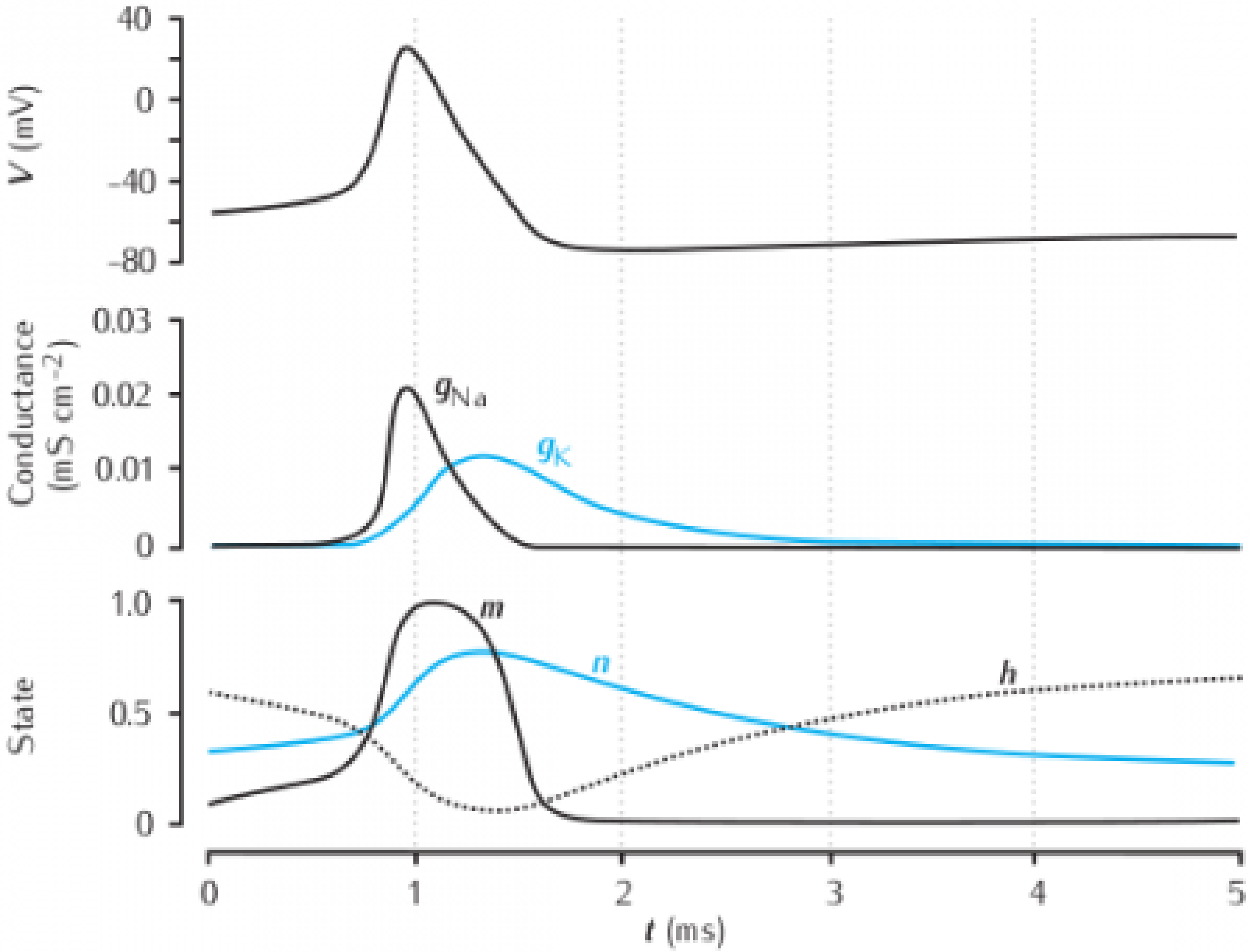
$$\tau_m\frac{dm}{dt}=-m+m_\infty \quad ,\tau_m=\frac{1}{\alpha_m+\beta_m},m_\infty=\frac{\alpha_m}{\alpha_m+\beta_m}$$

$$\tau_h\frac{dh}{dt}=-h+h_\infty \quad ,\tau_h=\frac{1}{\alpha_h+\beta_h},h_\infty=\frac{\alpha_h}{\alpha_h+\beta_h}$$

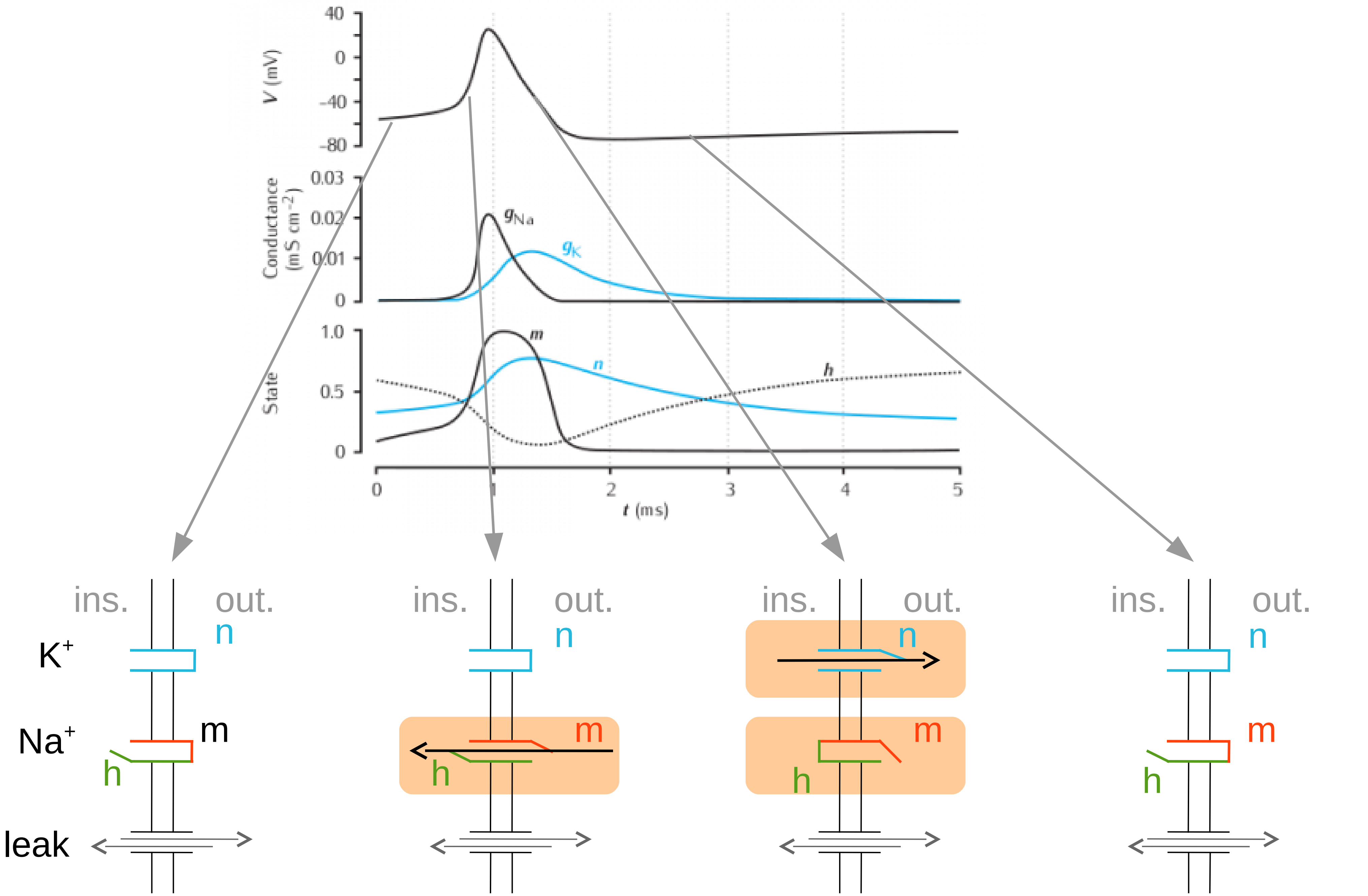
$$\alpha_n(V)=\frac{(0.1-0.01V)}{e^{1-0.1V}-1} \qquad \alpha_m(V)=\frac{(2.5-0.1V)}{e^{2.5-0.1V}-1} \qquad \alpha_h(V)=0.07e^{-\frac{V}{20}}$$

$$\beta_n(V)=0.125e^{-\frac{V}{80}} \qquad \beta_m(V)=4e^{-\frac{V}{18}} \qquad \beta_h(V)=\frac{1}{e^{3-0.1V}+1}$$

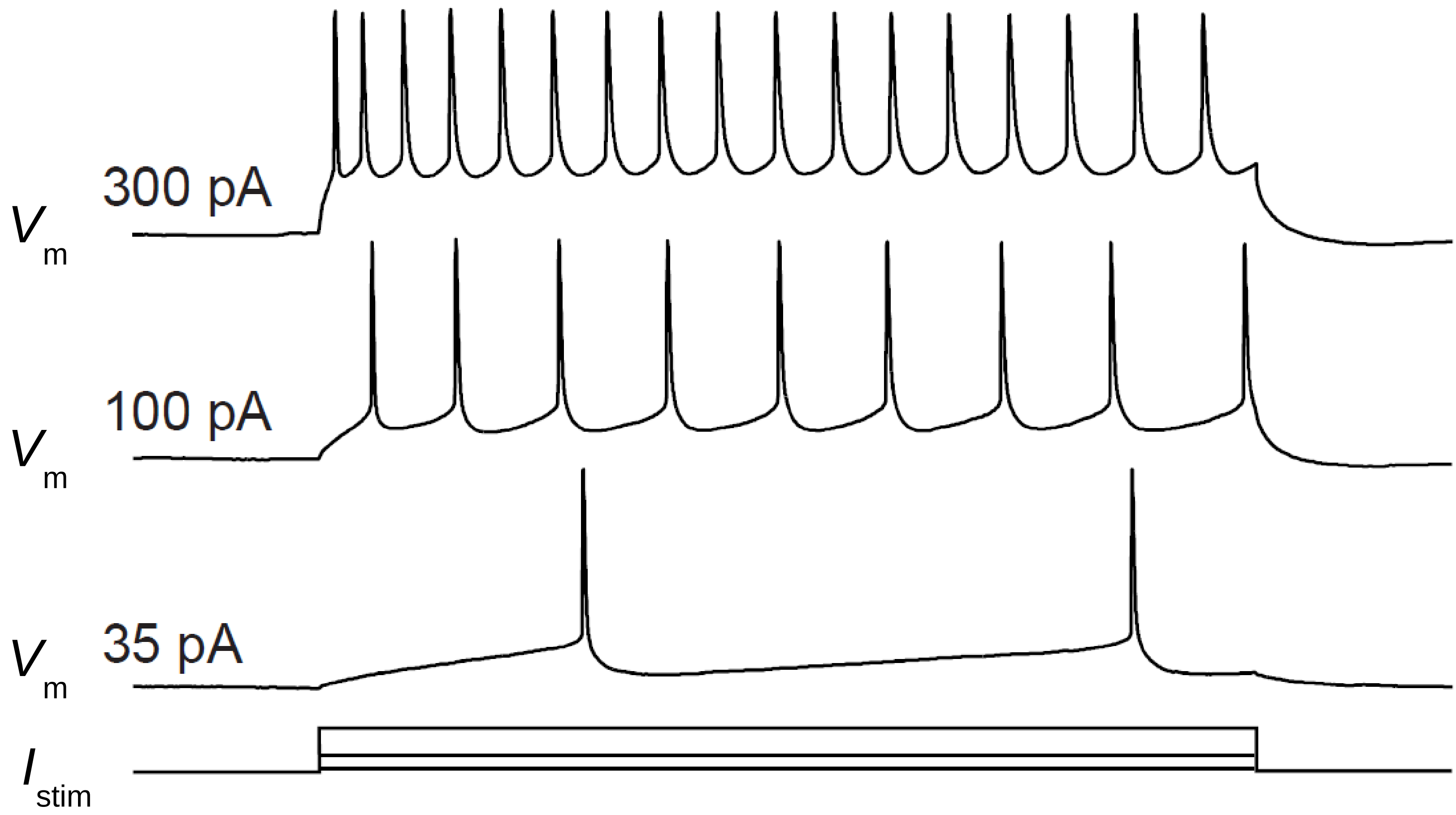
Hodgkin-Huxley model : the action potential



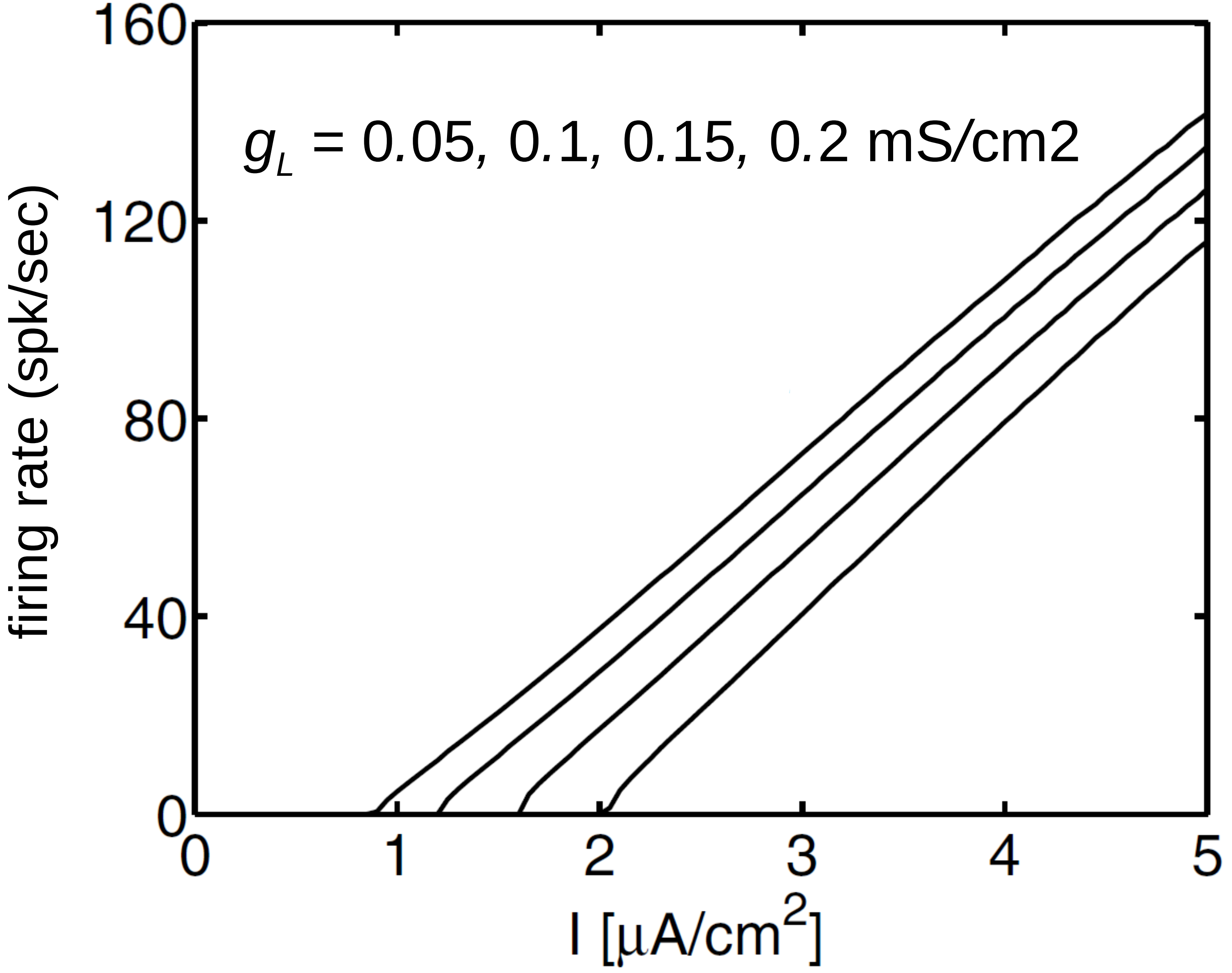
Hodgkin-Huxley model : the action potential



Hodgkin-Huxley model : current injection



Hodgkin-Huxley model : F-I curve



Integrate-and-Fire model : derivation

simplification : no active currents → $g(t) = const.$

→ The shape of the action potential is not described !

$$C\frac{dV}{dt} = g_{Na}(V_{Na} - V) + g_K(V_K - V) + g_L(V_L - V) + I_{stim}$$

$$C\frac{dV}{dt} = \underbrace{g_{Na}V_{Na} + g_K V_K + g_L V_L}_{} - \underbrace{(g_{Na} + g_K + g_L)}_{G_{tot}} V + I_{stim}$$

$$C\frac{dV}{dt} = G_{tot}(V_0 - V) + I_{stim}$$

$$\tau = \frac{C}{G_{tot}}$$

$$\boxed{\tau\frac{dV}{dt} = (V_0 - V) + \frac{I_{stim}}{G_{tot}}}$$

Integrate-and-Fire model : membrane potential equation

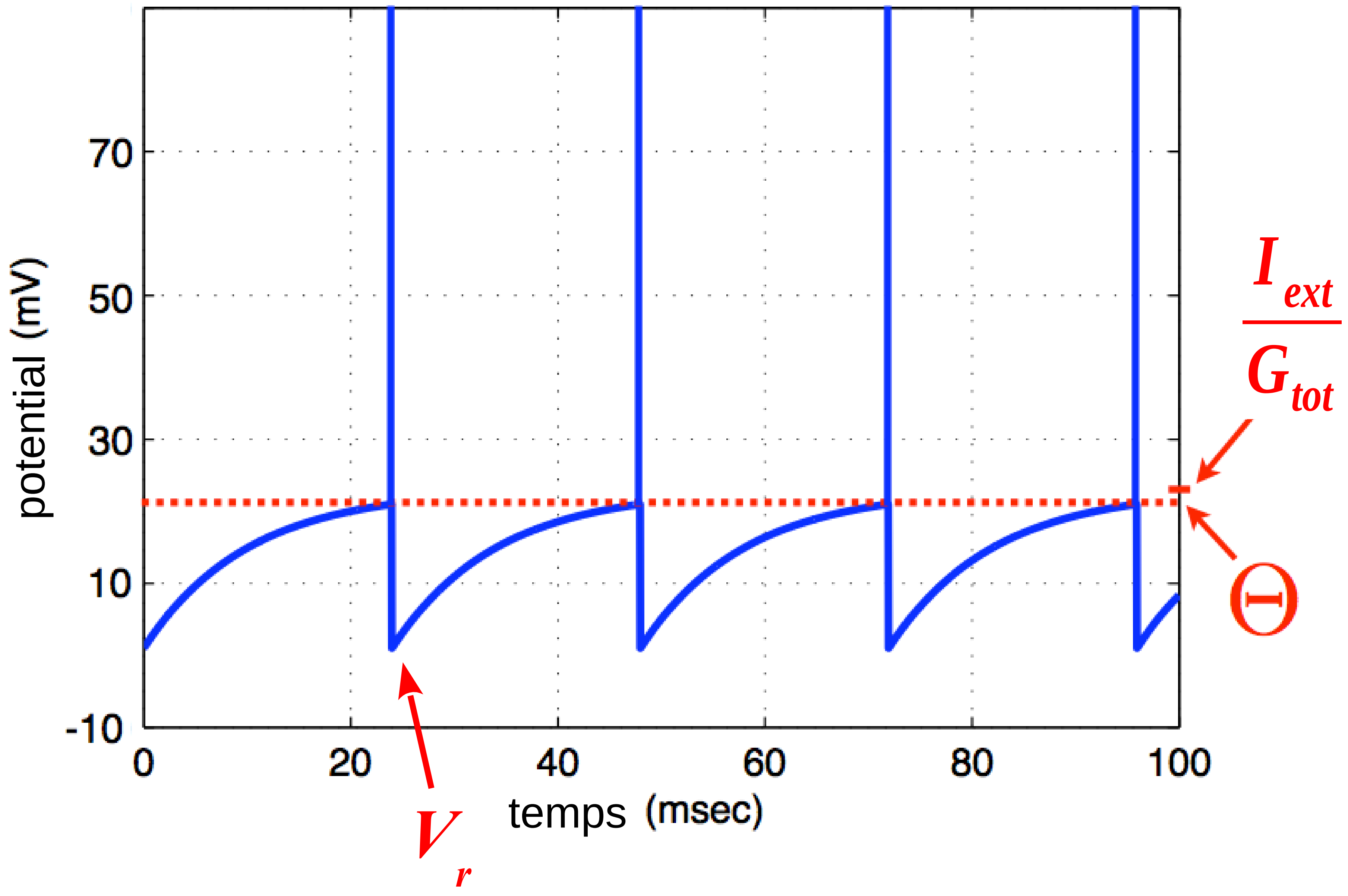
$$\tau \frac{dV}{dt} = (V_0 - V) + \frac{I_{ext}}{G_{tot}}$$

- V_0 resting membrane potential
- τ membrane time constant
- I_{ext} external current (synaptic)
- G_{tot} total conductance

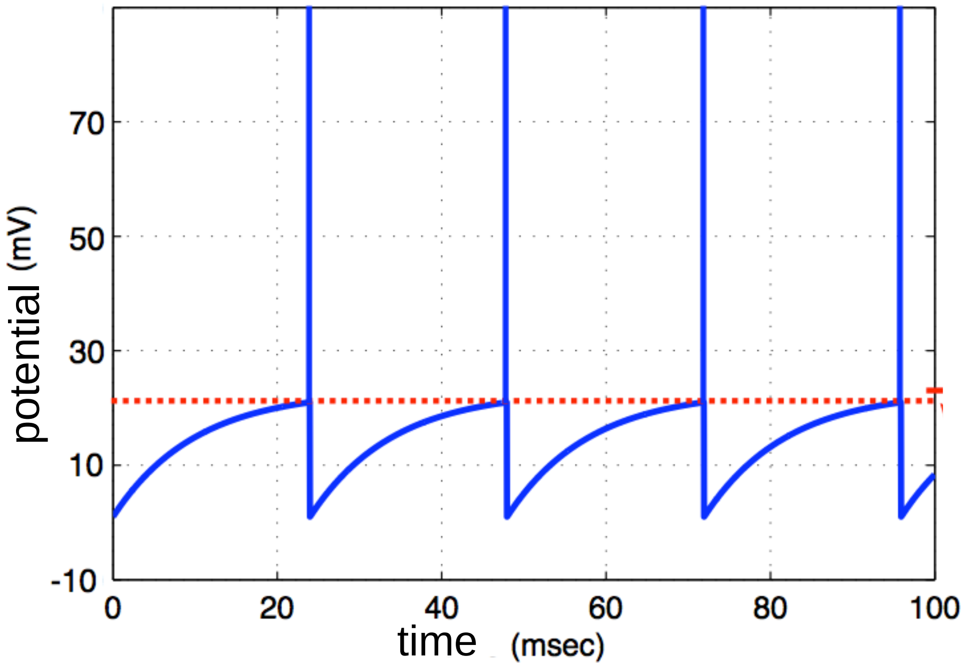
generation of the action potential :

- Θ firing threshold
- V_r reset potential
- if $V > \Theta$:
  → the neuron fires an action potential
  → after the action potential, the membrane potential is reset to V_r

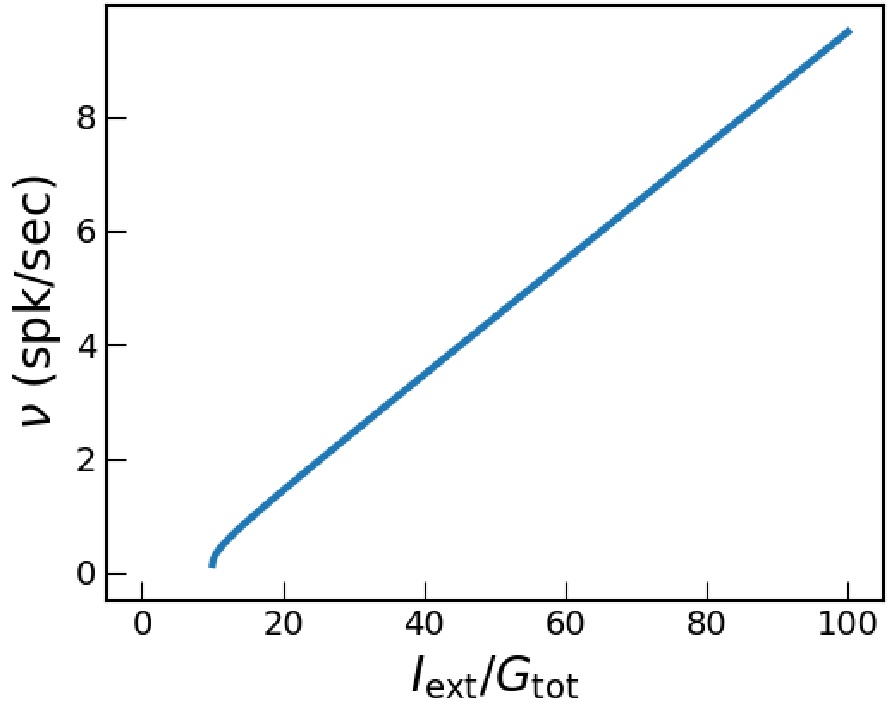
Integrate-and-Fire model : dynamics



Integrate-and-Fire model : dynamics

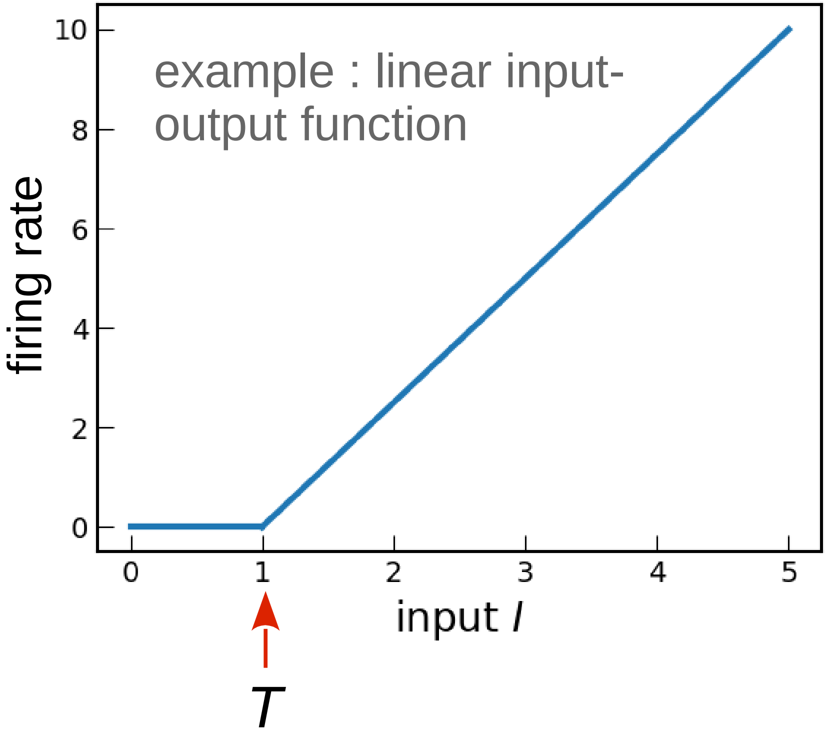


F-I curve



Rate model

Phenomenological description of the input-output function :



$$\tau \frac{dm}{dt} = - m + F(I_{syn} + I_{ext} - T)$$

m: output of the neuron – firing rate

τ : membrane time constant

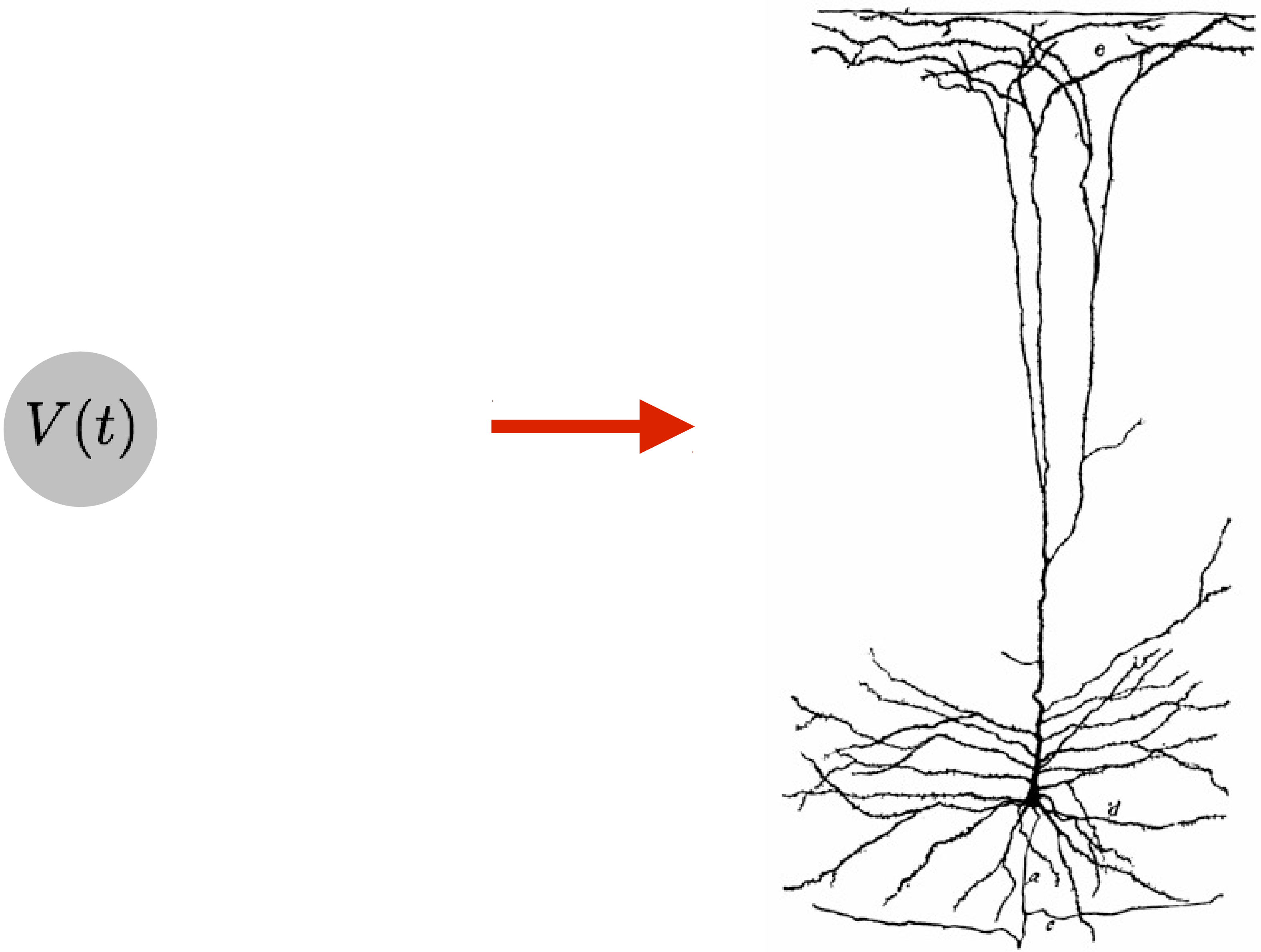
F : input-output transfer function

$\boldsymbol{I_{syn}}$: synaptic input

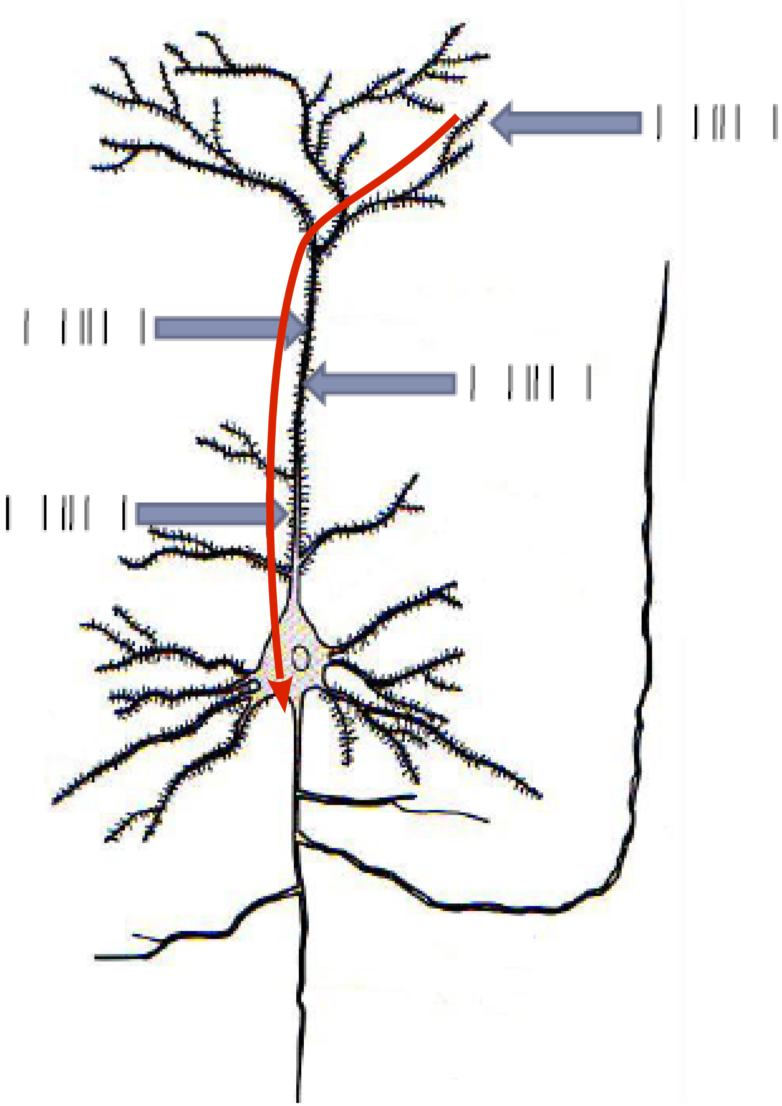
$\boldsymbol{I_{ext}}$: external current

T : firing threshold

How do potentials propagate along the dendritic tree ?

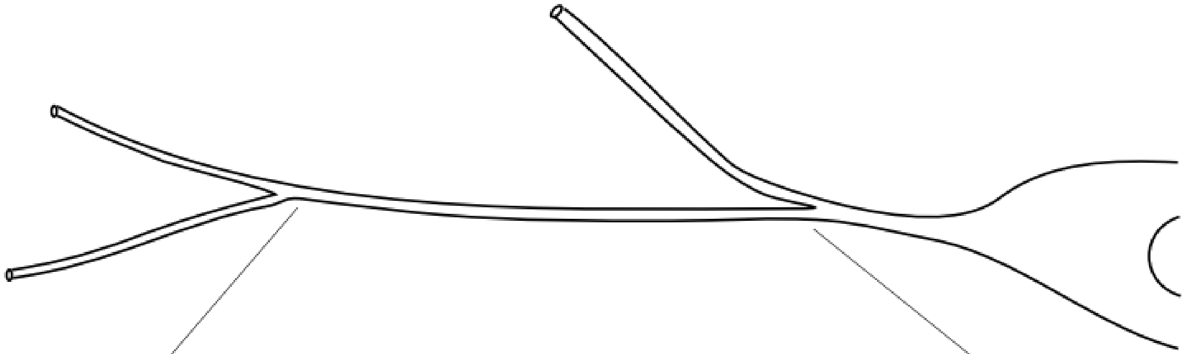


Cable theory

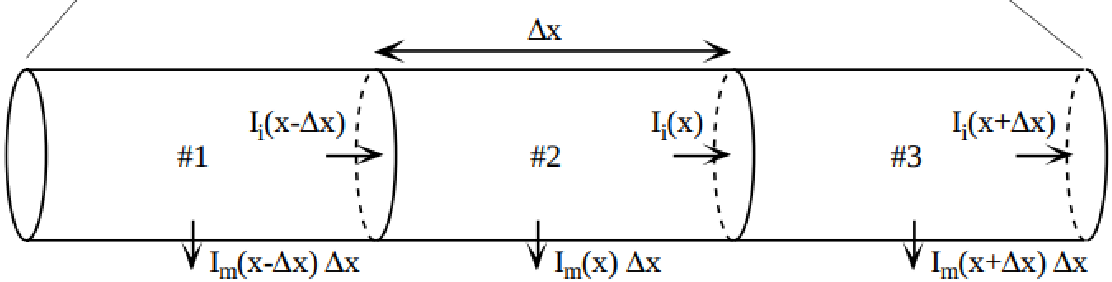


- how do synaptic inputs propagate to the soma or the axon initial segment
- how do input interact between each other
- how does the input location along the dendritic tree impact its functional importance for the neuron

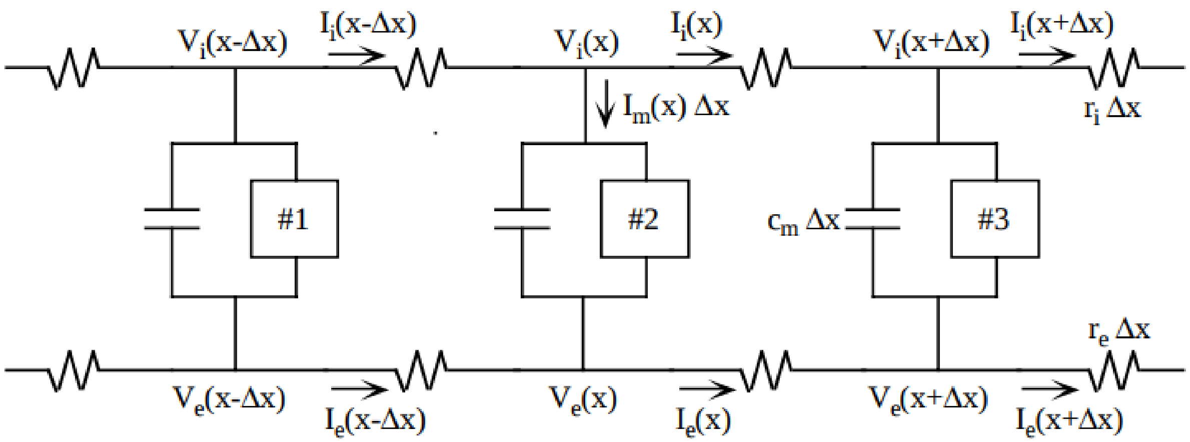
Abstraction of the dendritic membrane of a neuron



Soma and dendritic branch



Portion of the secondary dendrite divided in three sub-cylinders



Discrete electric model of the three sub-cylinders

Non-linear cable equation

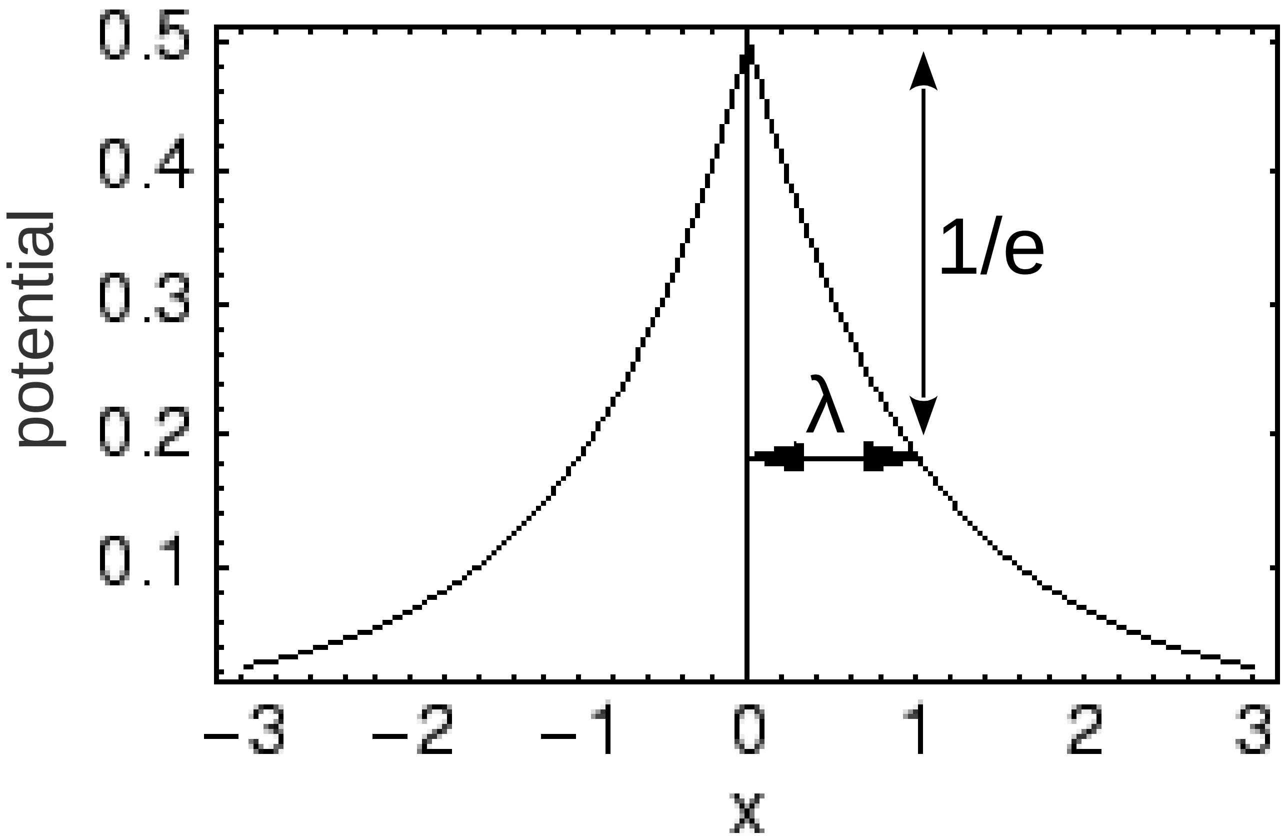
models the membrane potential distribution along a membrane cylinder

$$\frac{1}{r_i + r_e} \frac{\partial V}{\partial x^2} = c_m \frac{\partial V}{\partial t} + I_{ion}$$

current which propagates between neighboring points along the cylinder

typical membrane potential equation of the point neuron model

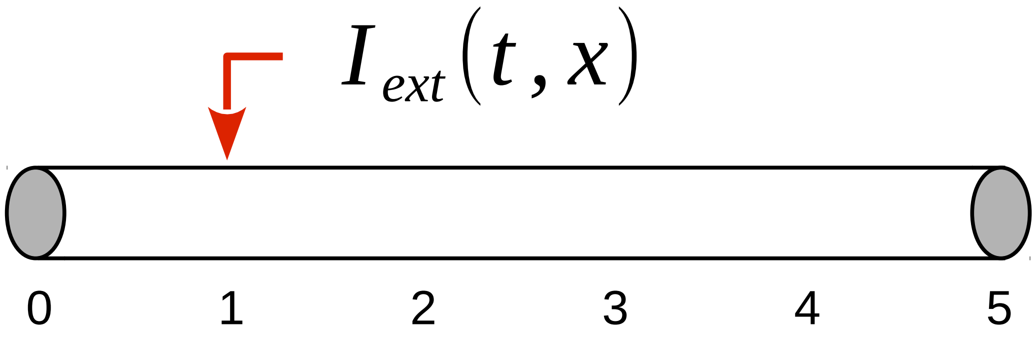
Stationary solution of the cable equation



λ length constant

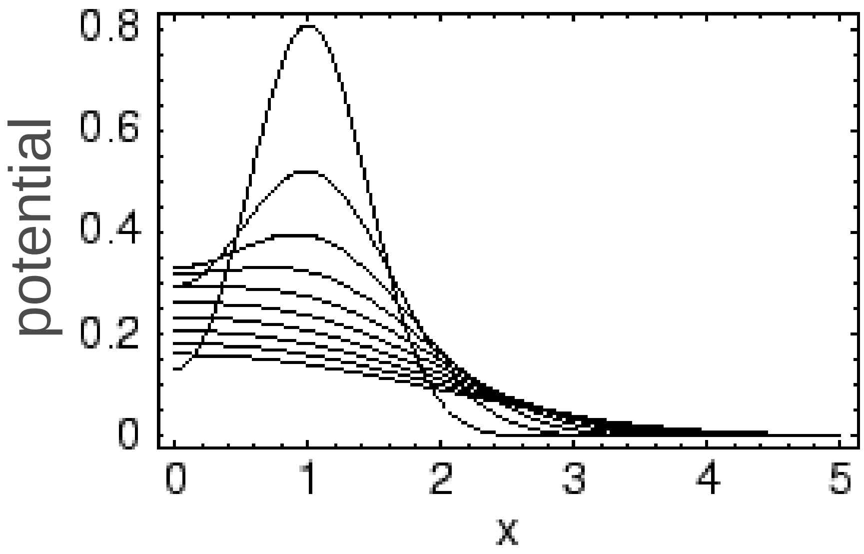
$$I_{ext}(t,x) = \delta(x)$$

Spatial and temporal distribution of the potential along the membrane



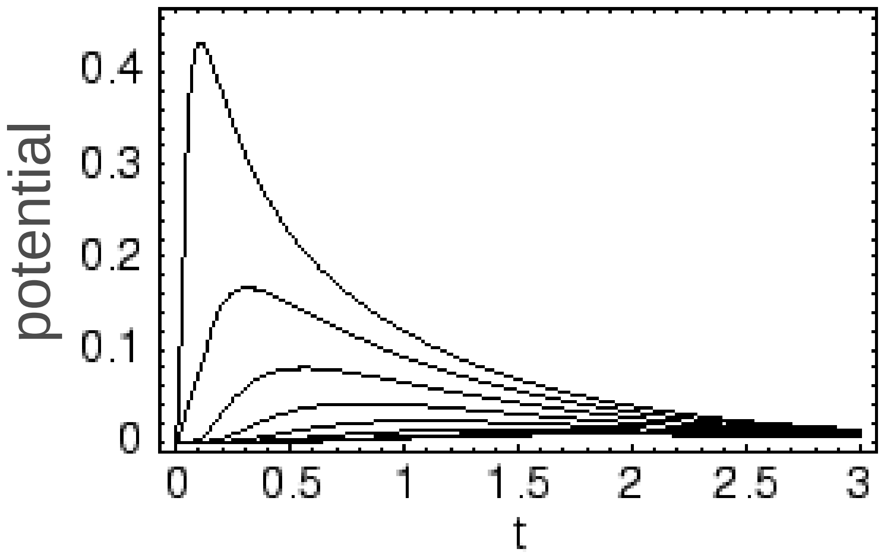
sealed cable

different time points



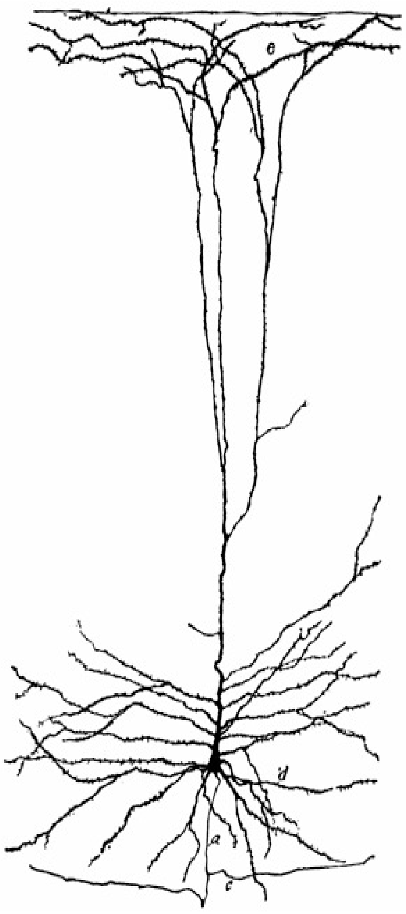
t = 0.1, 0.2, ... , 1.0

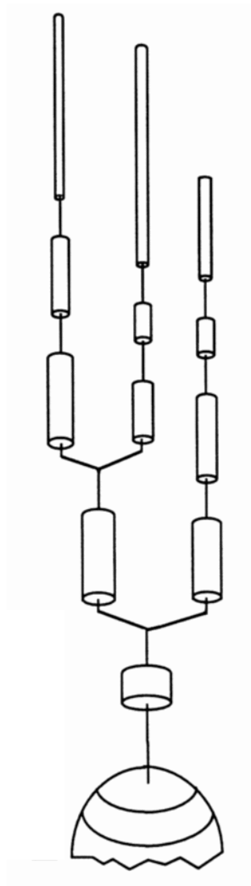
different locations

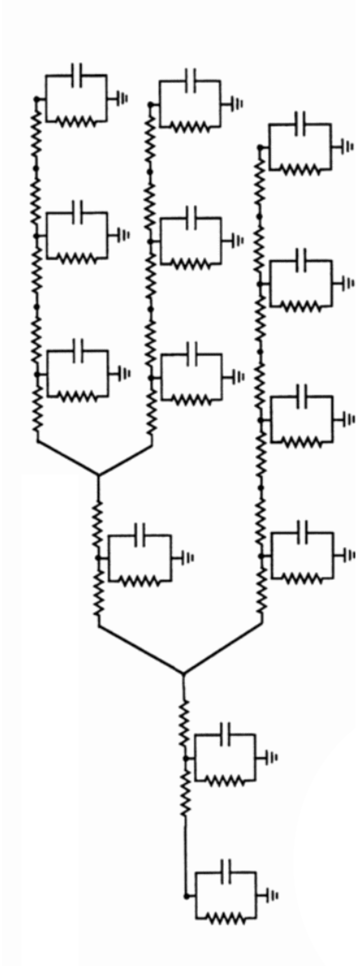


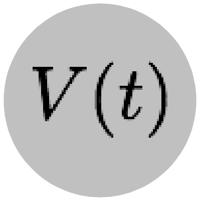
x = 1.5, 2.0, 2.5, ... , 5.0

Single neuron models


real
neuron

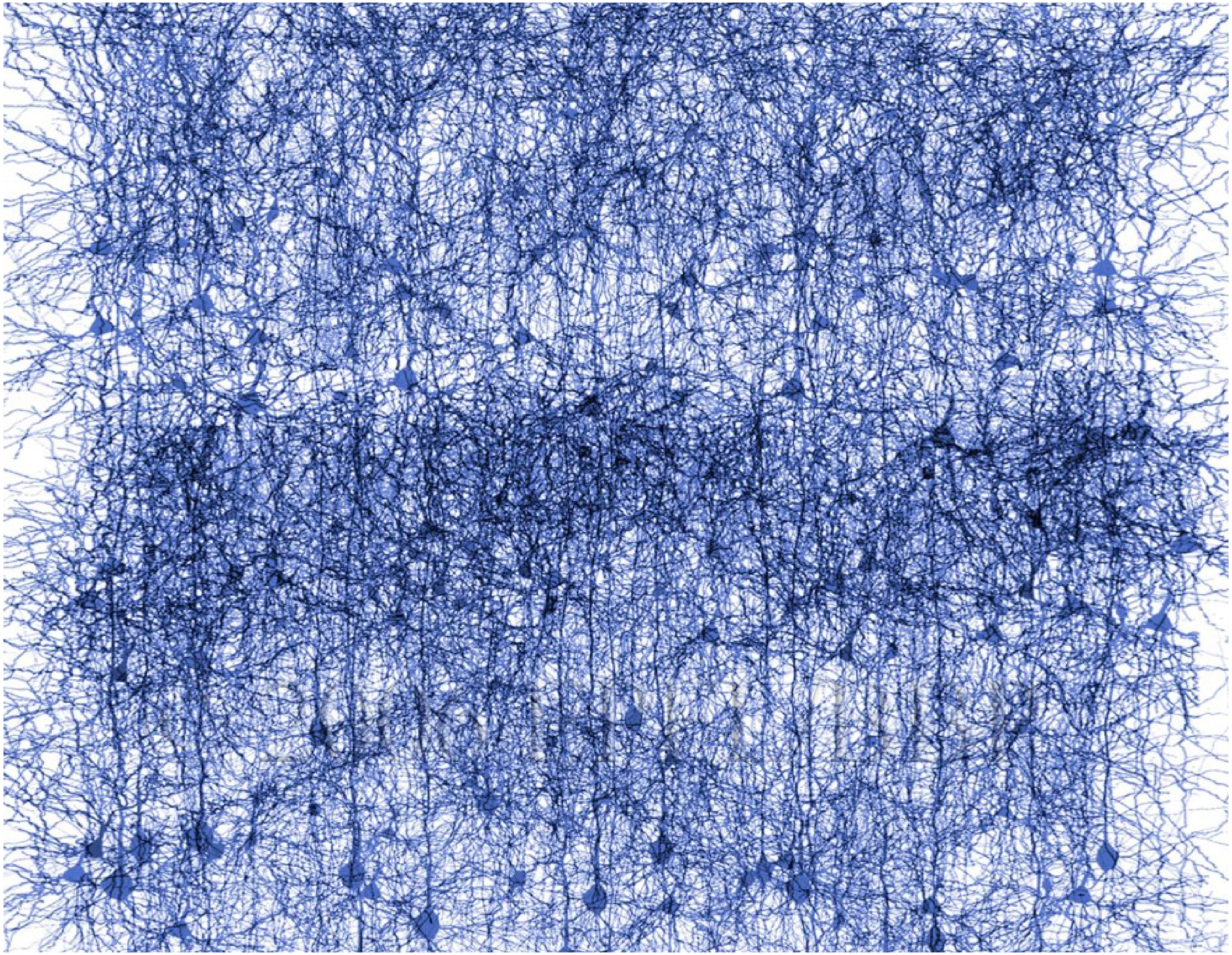

cable
theory


compartmental
model



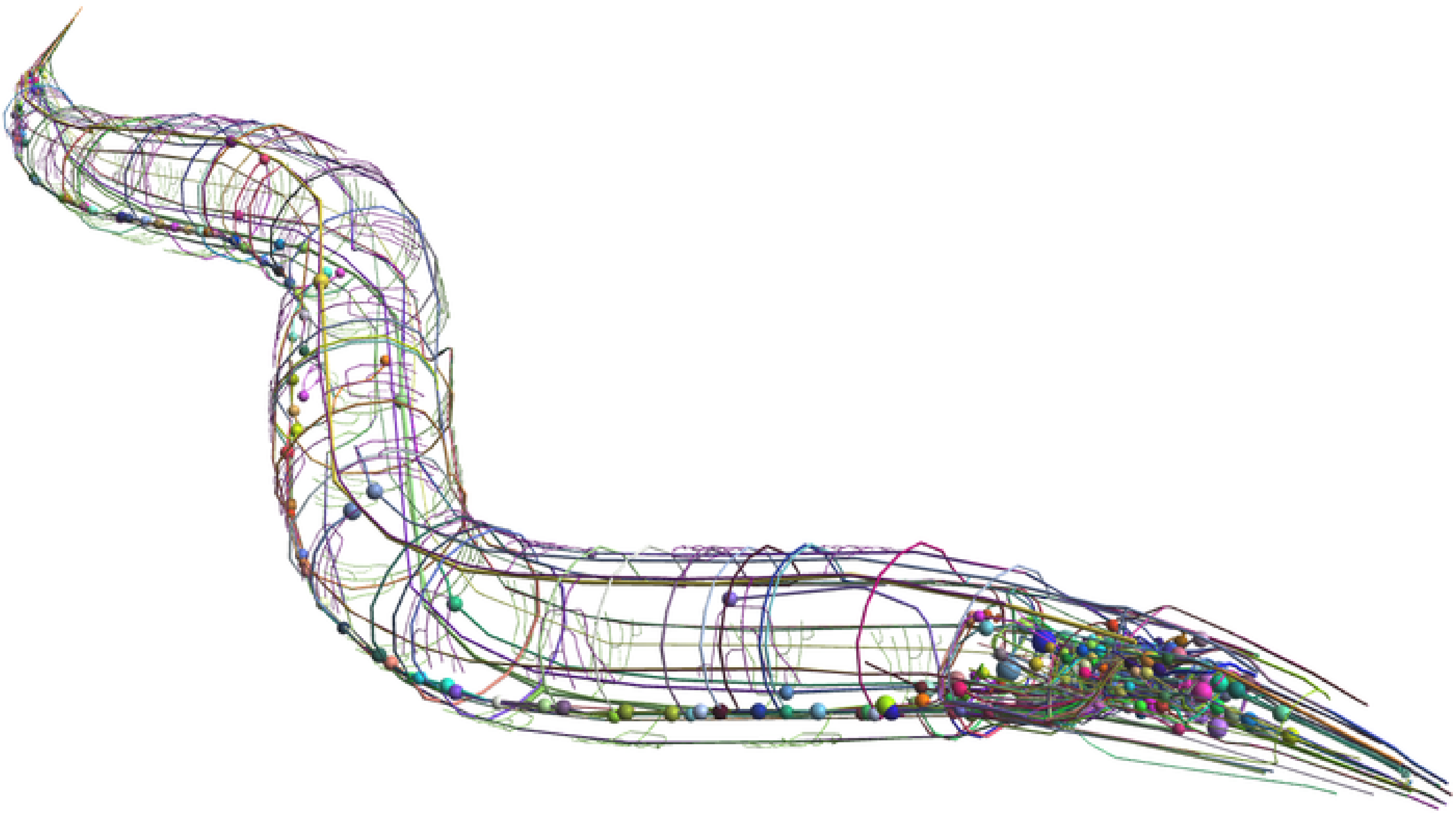
point
neuron

Neurons form networks



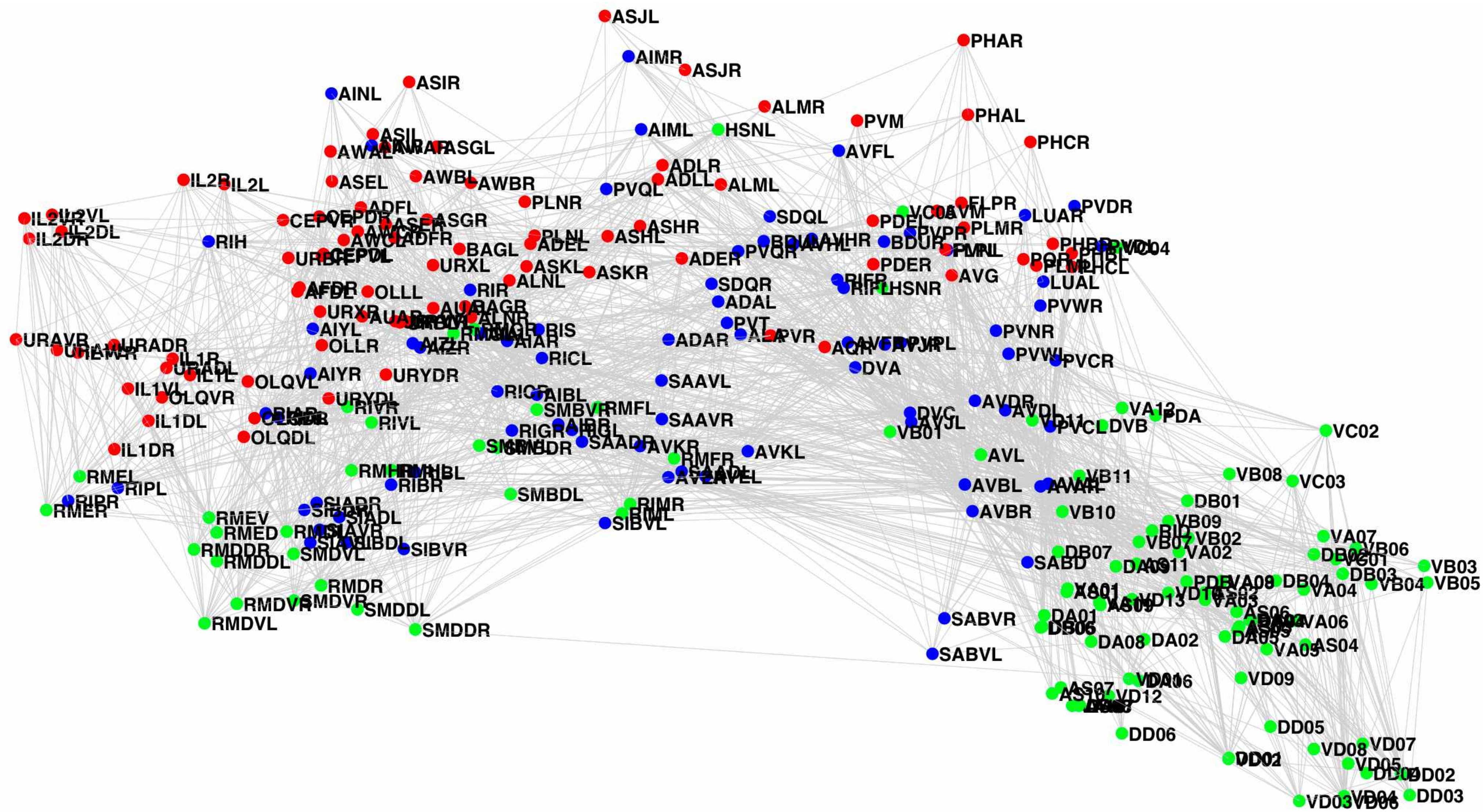
The brain : a network of 10^{11} neurons connected by 10^{15} synapses

C elegans : brain network



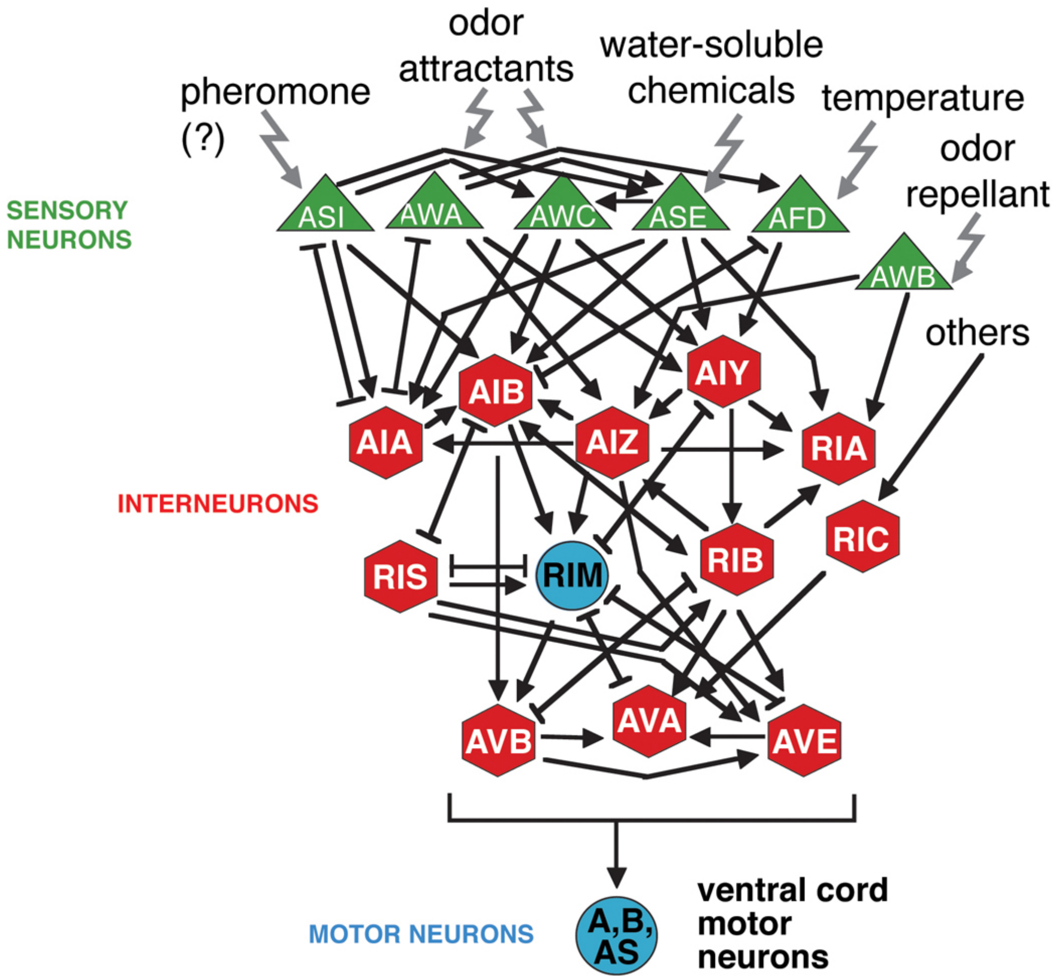
C elegans brain : 302 neurons

C elegans : brain network



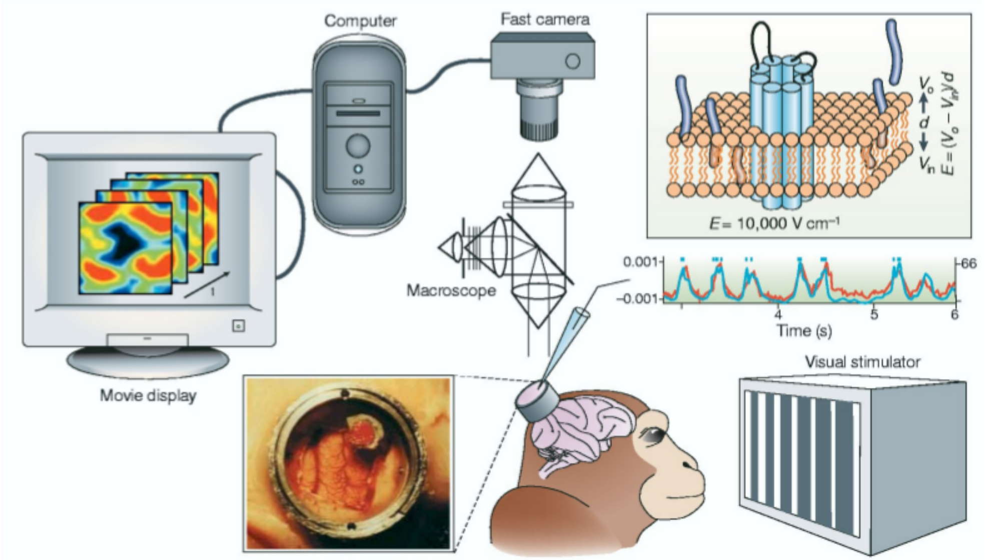
C elegans brain : 302 neurons – each of them a highly specialized analog computer

Brain network : from sensory to motor

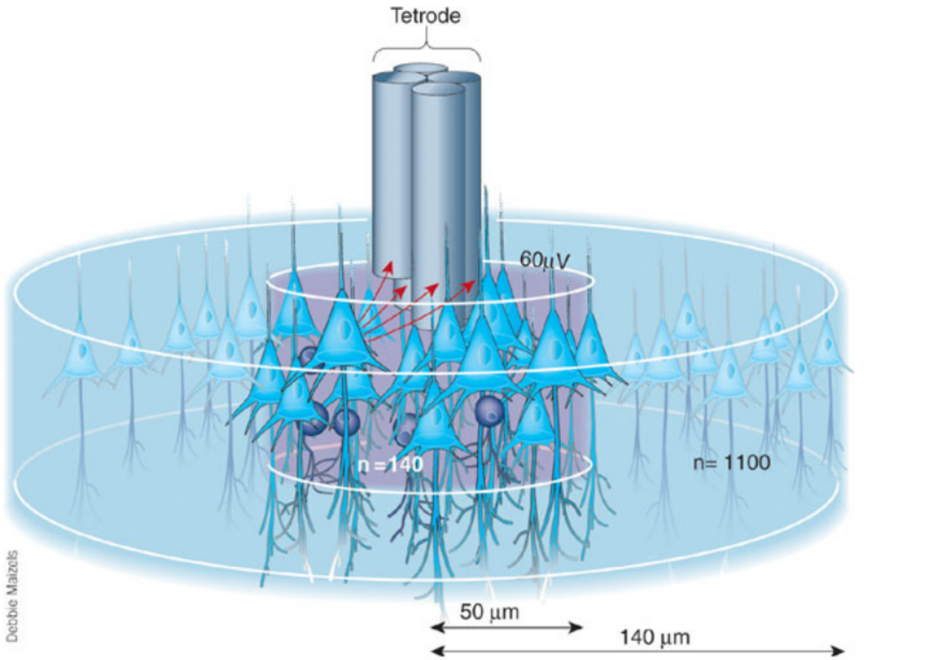


Descriptions of neural network dynamics

- **Rate models** (neural mass models) : describe the activity of a whole population of neurons by a single ‘average firing rate’ variable : *m(x, t)*



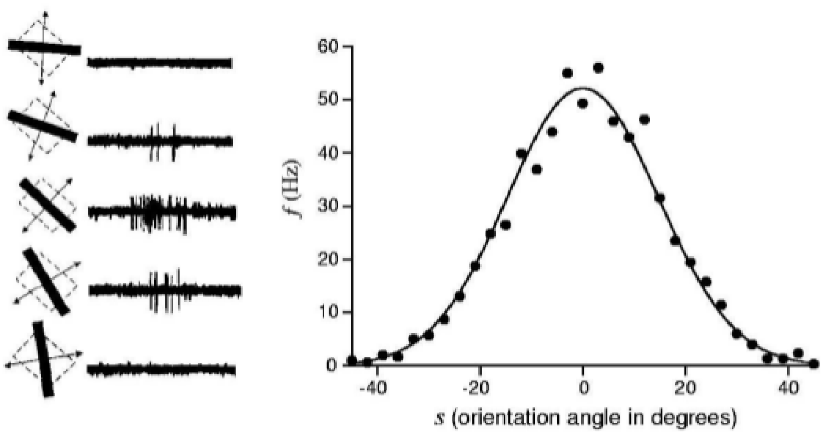
- **Networks of spiking neurons :** describe the activity of a population of *N* neurons coupled through network connectivity matrix by *O(N)* coupled differential equations.

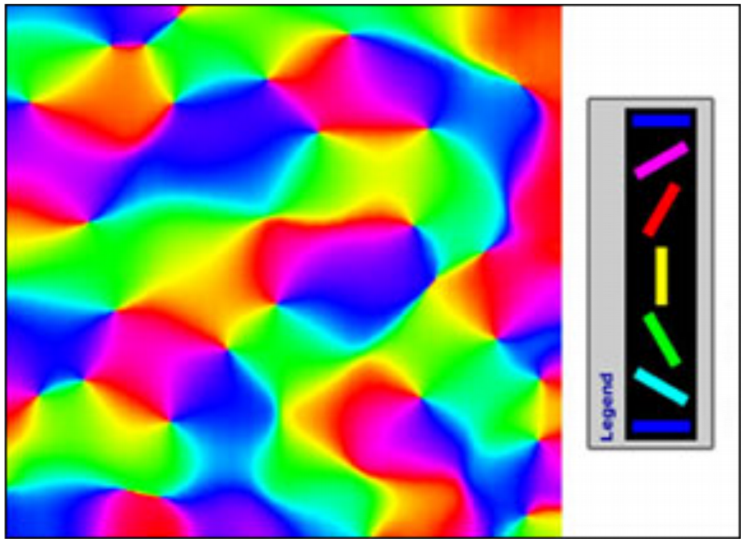


Rate models : spatial selectivity

In many brain regions, neighboring neurons share similar selectivity to external inputs

→ There is a topographical organization of selectivity.





Example : In many areas of the brain, neurons show selectivity to spatial variables:.

- **Primary visual cortex** : orientation
- **MT** : direction of movement
- **Posterior parietal cortex, prefrontal cortex:** spatial location (present and past)
- **FEF**: location of a saccade
- **Motor cortex** : direction of arm

 ...

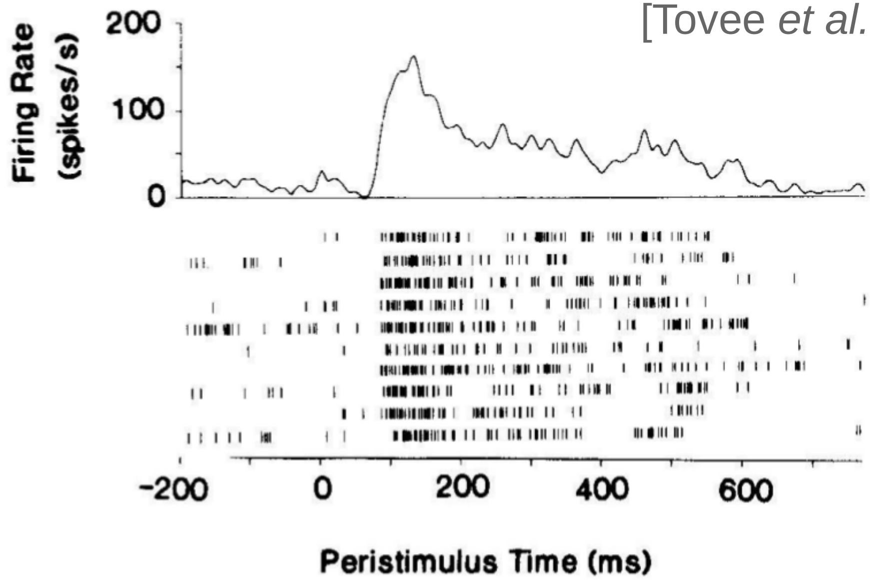
→ **What are the mechanisms of spatial selectivity?**

Networks of spiking neurons : irregularity

Spontaneous vs. selective/evoked activity :

- Spontaneous activity : 1-20 spk/s
- In presence of external stimuli: in many parts of cortex, instantaneous firing rate (PSTH) depends on (carries information about) external stimuli.

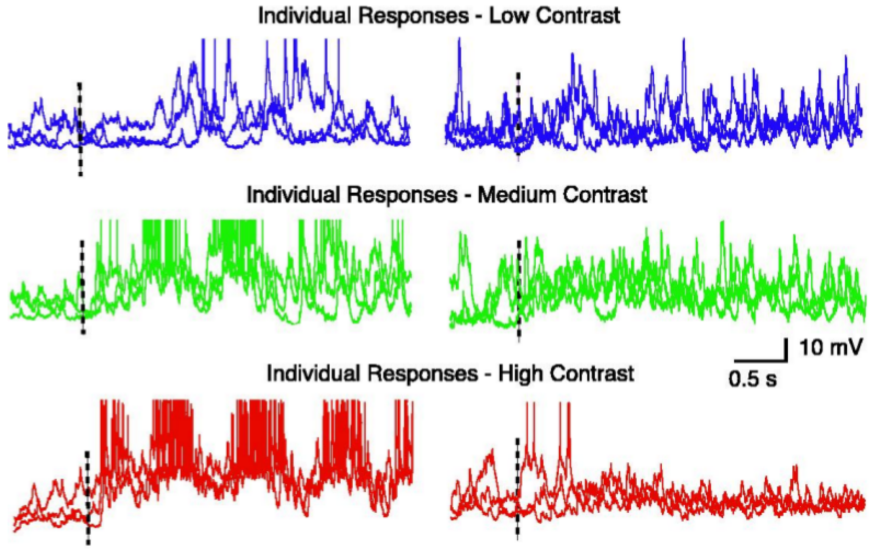
[Tovee *et al.* 1993]



Statistics of neural activity :

- very irregular firing (close to Poisson process – CV close to 1)
- Large membrane potential fluctuations (~ 5mV)

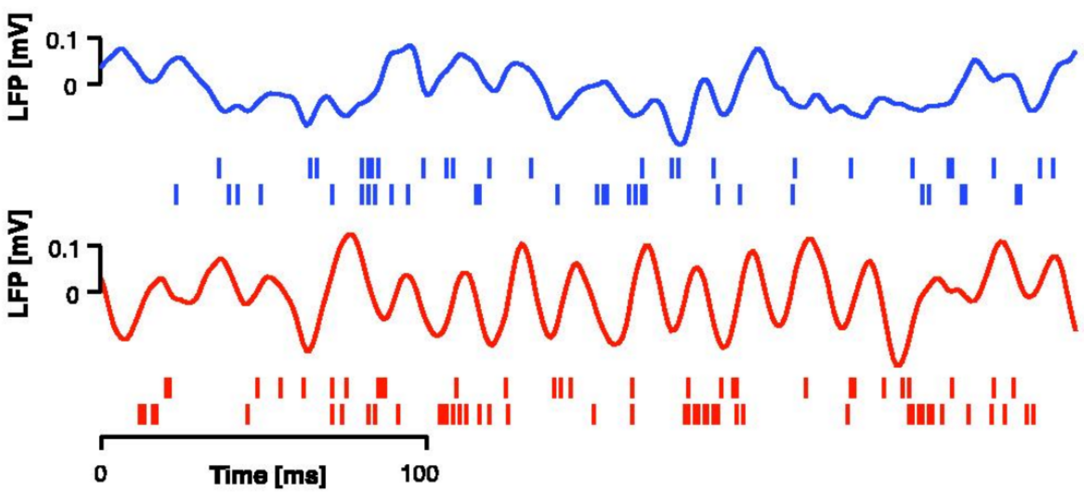
➡ **What are the mechanisms of irregular activity?**



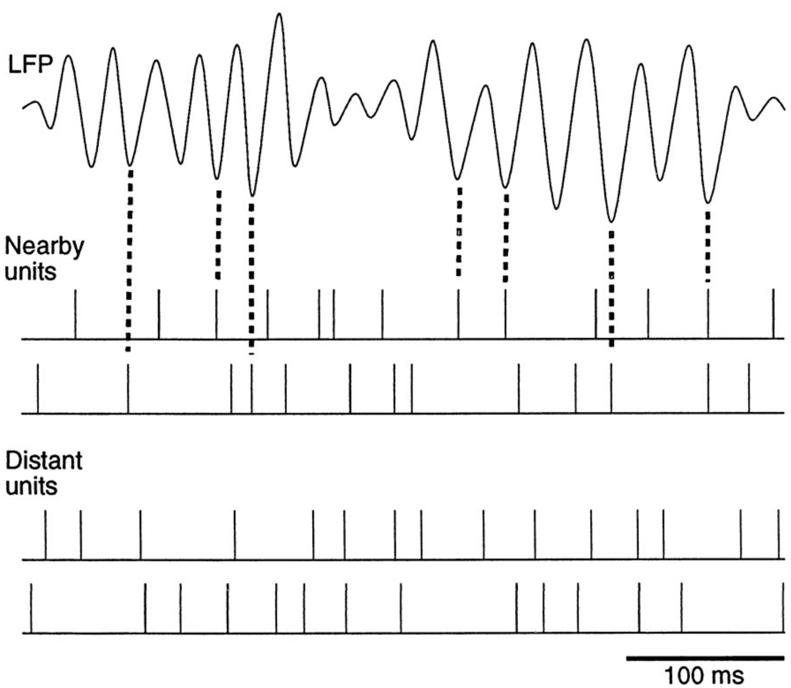
[Anderson *et al.* 2000]

Networks of spiking neurons : oscillations

- LFP recordings : reflect local network activity
- Various oscillatory patterns in wake and sleep



[Fries *et al.* 2001]



[Destexhe *et al.* 1999]

➡ **What are the mechanisms of synchronized oscillations?**

Network models : parts list

- How many neuron types ?

  How many neurons of each type ?

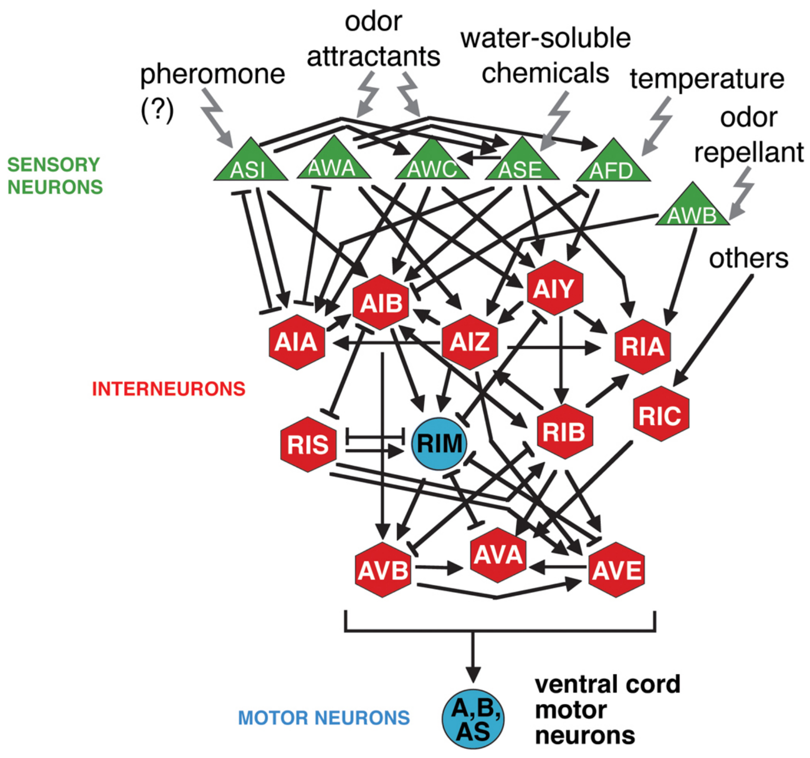
- How are the neurons connected

  (What is the connectivity matrix) ?

- What are the external inputs ?

- What is(are) the neuron model(s) ?

- What is(are) the synapse model(s)?



Types and numbers of neurons

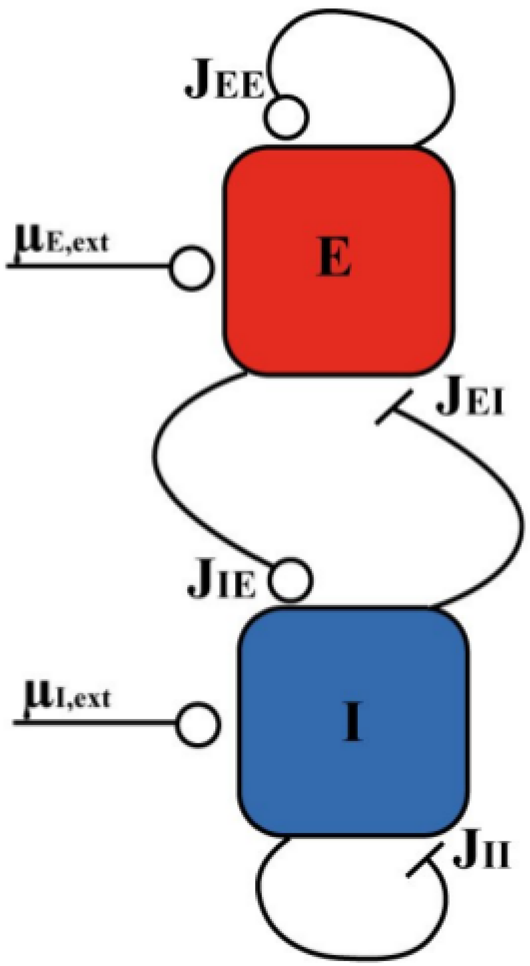
- How many types of neurons? How many neurons in each type?

  - Depends on the system modeled

  - Classic example :
    Two population cortical network (E-I)

  - Numerical simulations : $N \sim 10^3$-10^4 (single workstations), much more (clusters, dedicated supercomputers)

  - Analytical calcuations : $N \to \infty$



Connectivity matrix

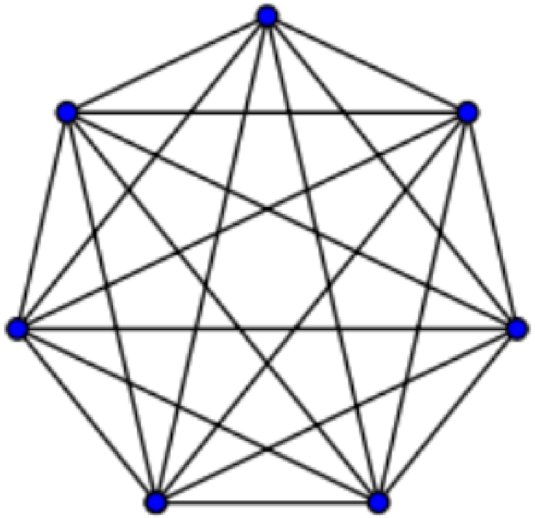
- How are neurons connected (what is the connectivity matrix)?

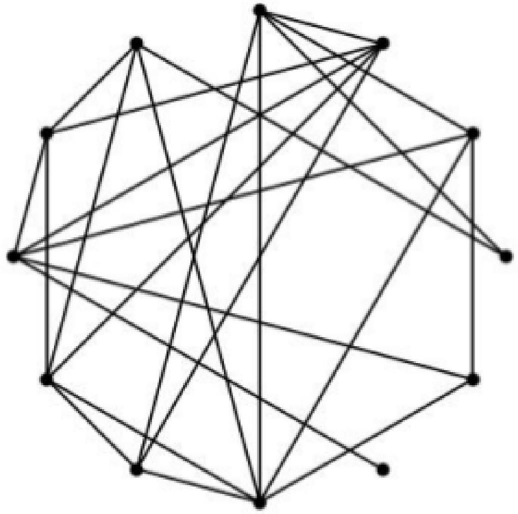
  - Fully connected (all-to-all)

  - Randomly connected (par ex. Erdos-Renyi)

  - Spatial structure

  - With a structure imposed by learning





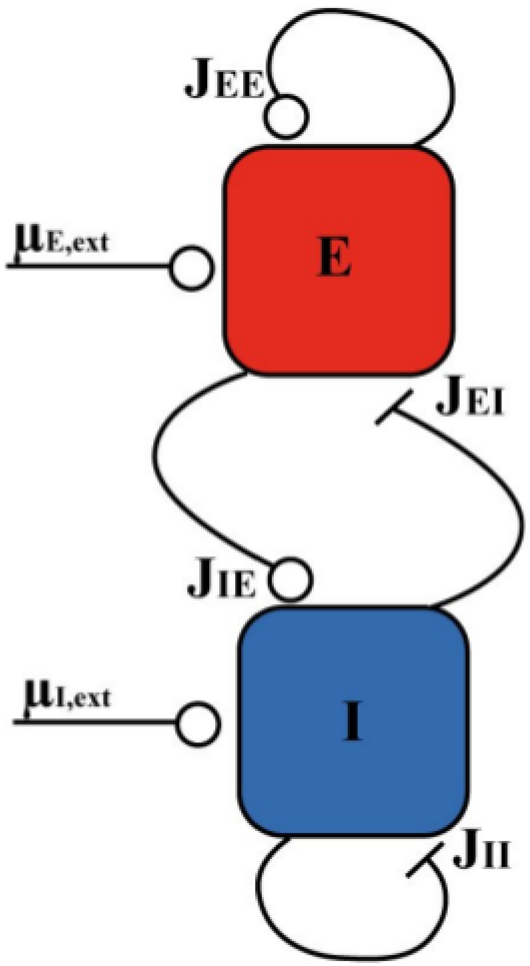
External inputs

- What are the external inputs ?

  - Constant

  - Stochastic (e.g. independent Poisson processes; independent white noise)

  - Temporally/spatially structured

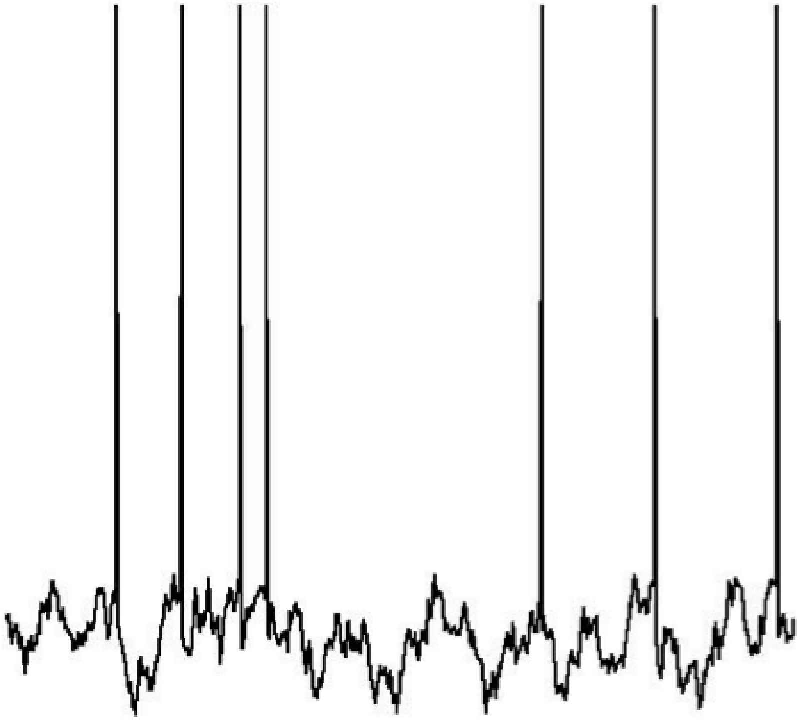


Neuron models

- What is(are) the neuronal model(s) ?

  - Binary

  - Spiking (LIF, NLIF, HH-type, etc. ...)



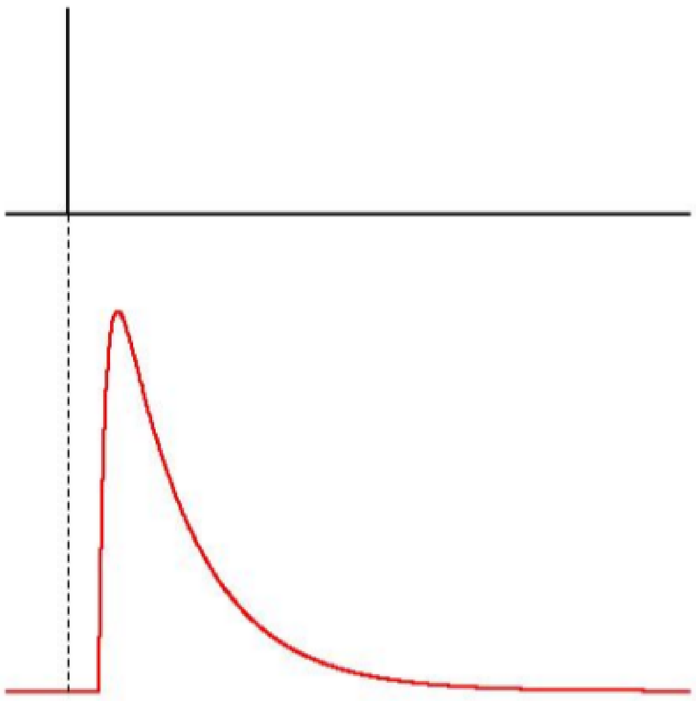
Synapse models

- What is(are) the synapse model(s)?

  - Fixed number (synaptic weight, binary networks)

  - Temporal kernel (spiking networks)

  - Non-plastic vs. plastic



Questions

- **Dynamics:** What are the intrinsic dynamics of networks (**spontaneous activity**, in the absence of structured inputs)?
- **Coding:** What is the effect of external inputs on network dynamics? How do networks encode external inputs?
- **Learning and memory:** How are external inputs learned/memorized?

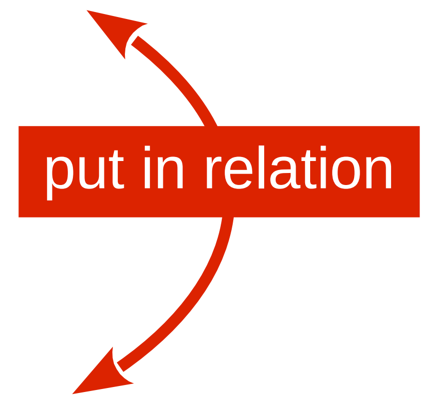
  - How do external inputs modify network connectivity through synaptic plasticity? How is learning implemented?

  - What is the impact of structuring in the connectivity on network dynamics?
- **Computation:** How do networks perform computations?

How to investigate a neural network model's behavior ?

1st Step: *a simplified network for mathematical analysis*

- Simple neuron model (rate model with linear transfer function, or Integrate-and-Fire model)
- All-to-all connectivity or simple connectivity scheme (Gaussian)
- No noise, no heterogeneity



Étape 2 : *numerical simulations of a more “realistic” model*

- “Realistic” neuron model (non-linear input-output function, H&H, conductance-based currents ...)
- “Realistic” connectivity scheme (with some randomness)
- Synaptic noise
- Heterogeneity in the single neuron parameters (threshold, gain, conductances, ...)

Rate model

- In a ‘rate model’ (also called: ‘firing rate model’, ‘neural mass model’, neural field model’, ‘Wilson-Cowan model’), one describes the activity (instantaneous firing rate) of a population of neurons at a given location by a single analog variable:

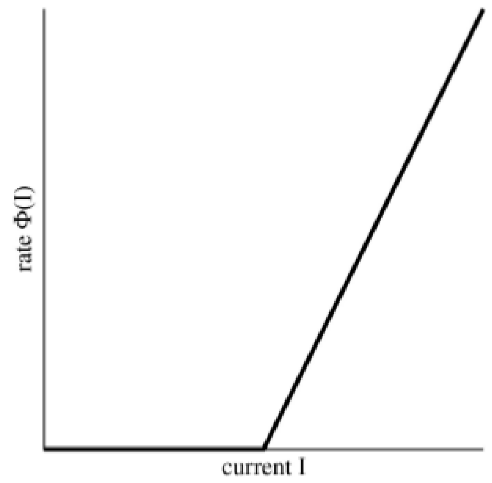
$$\tau \dot{r}(x,t) = -r(x,t) + \Phi\left(I(x,t) + \int dy\, J(|x-y|)\, r(y,t)\right)$$

- τ : time constant of firing rate dynamics
- *r (x, t)*: firing rate of neurons at location *x* at time *t*
- Φ (.) : transfer function (f-I curve)
- *I (x, t)* : external input
- *J (x, y)*: strength of synaptic connections between neurons at locations *x* and *y*

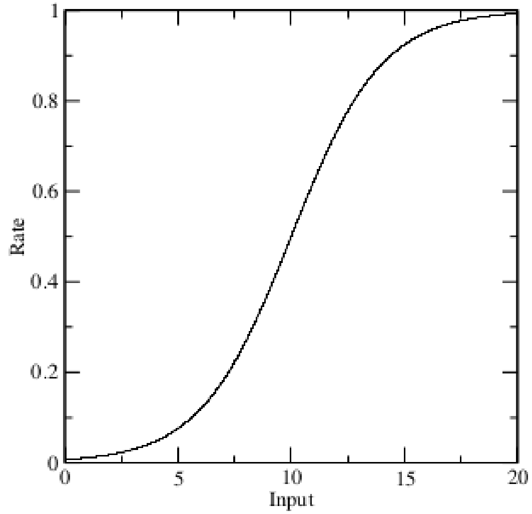
[Amari 1972, Wilson and Cowan 1972]

The transfer function Φ (.)

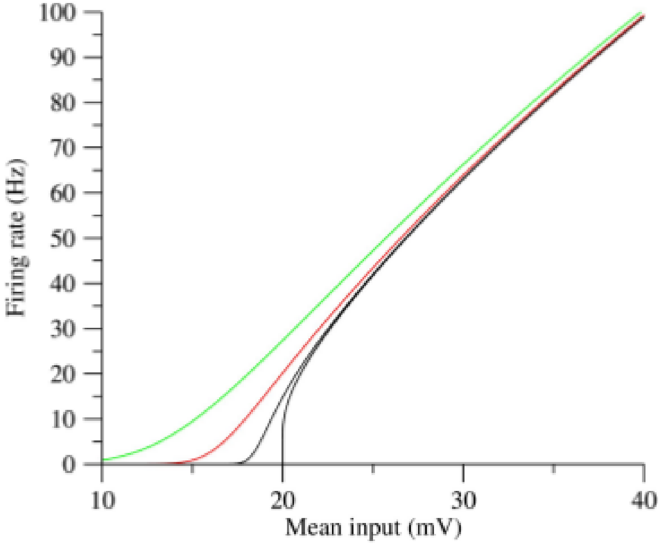
Threshold linear $\Phi(x)=[x-T]_+$



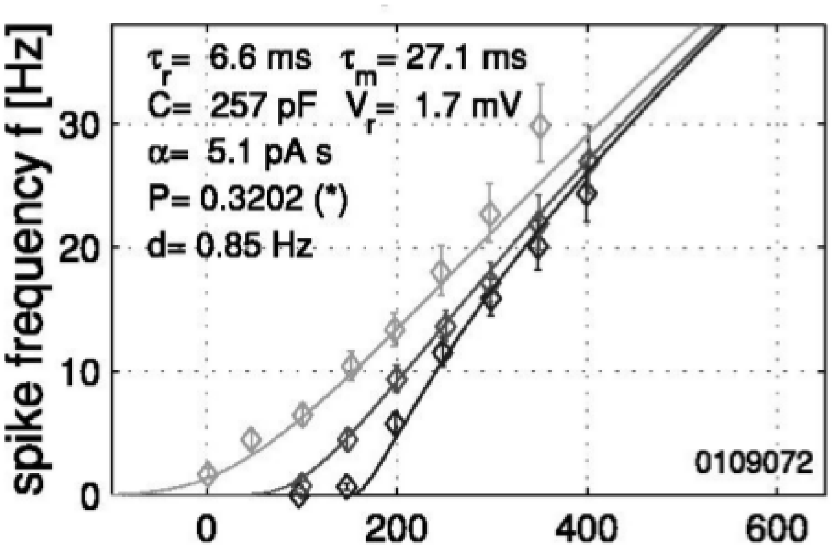
Sigmoidal $\Phi(x)=1/(1+\exp(-\beta(x-T)))$



f-I curve of a specific spiking neuron model



f-I curve of a real neuron [Rauch et al 2003]



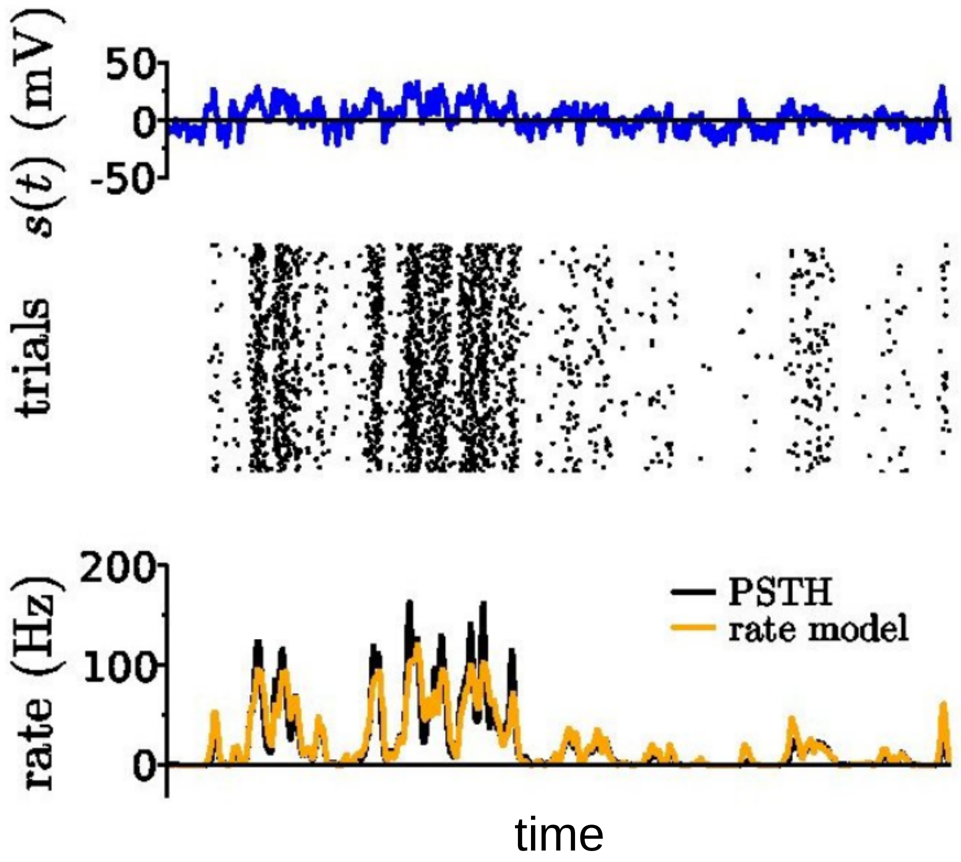
From populations of individual neurons to a rate model

The population activity of homogeneous populations of

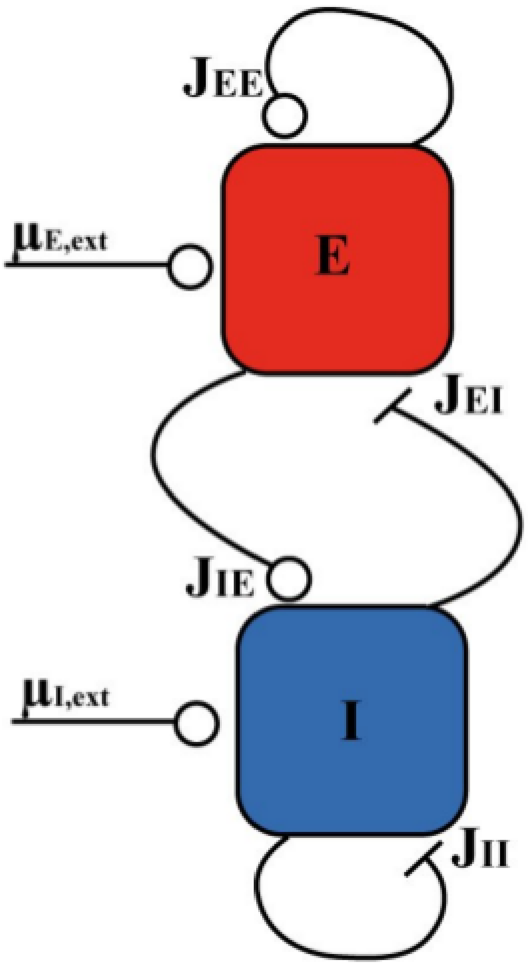
- Stochastic binary neurons
- Stochastic spiking neurons (EIF)

can sometimes be shown to be well approximated by firing rate equations

$$\tau \frac{dr}{dt} = -r(t) + \Phi\left(I(t) + \boldsymbol{J}\, r(t)\right)$$



Rate models of local networks of neurons



- *n* sub-populations described by their average firing rate r_i, $i = 1, \ldots, n$

$$\tau_i \dot{r}_i = -r_i + \Phi_i\left(I + \sum_j J_{ij} r_j\right)$$

- **Example** : E-I network (Wilson and Cowan 1972)

$$\tau_E \dot{r}_E = -r_E + \Phi_E\left(I_{EX} + J_{EE} r_E - J_{EI} r_I\right)$$

$$\tau_I \dot{r}_I = -r_I + \Phi_I\left(I_{IX} + J_{IE} r_E - J_{II} r_I\right)$$

Analysis of rate models

$$\tau \dot{r} = -r + \Phi\left(I + \boldsymbol{J} r\right)$$

- Solve the equations for fixed point(s) :

$$r_0 = \Phi\left(I + \boldsymbol{J} r\right)$$

- Check linear stability of fixed points :
  - A small perturbation *δr* around the fixed point obeys the linearized dynamics

$$\dot{\delta} r = \frac{\left(-1 + \Phi' \boldsymbol{J}\right)}{\tau} \delta r$$

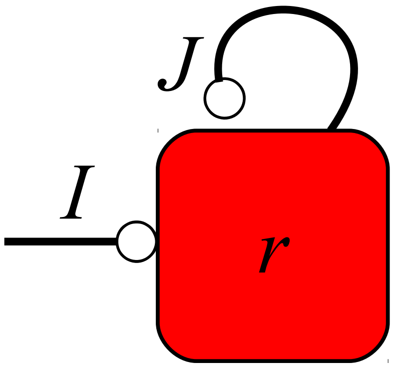
  - Compute eigenvalues λ of the Jacobian matrix (-1 + Φ**J**)

  - Fixed point stable if all eigenvalues have negative real parts;
  - "Rate" instability (saddle node bifurcation) when λ = 0
  - Oscillatory instability (Hopf bifurcation) when λ = ± *iw* and *w≠0*

- Weakly non-linear analysis close to bifurcation ⇒ normal form ⇒ nature of bifurcation (super or subcritical)

Simplest case :
1 population, linear Φ

$$\tau \dot{r} = -r + \left(I + J r \right)$$



- Unstable if *J* > *1* (' rate instability')
- Perfect integrator if *J* = *1* :

$$r(t) = \frac{1}{\tau} \int^{t} I(t')dt'$$

- Stable if *J* < *1* :

$$\frac{\tau}{(1-J)} \frac{dr}{dt} = -r + \frac{I}{(1-J)}$$

- Excitatory network (0 < *J* < 1): amplification of inputs, slow response
- Inhibitor network (J < 0): attenuation of inputs, fast response

Network dynamics of spiking networks

Binary networks

Spiking networks

- Neurons receive inputs (both from the outside and from the network itself)...

$$I_i = I_{iX} + \sum_j J_{ij} S_j(t)$$

$$I_i = I_{iX} + \sum_{j,k} J_{ij} S_{ij}(t - t_j^k)$$

- Neurons decide whether to be active or not, as a function of those inputs

$$S_i(t+dt) = \Theta(I_i(t) - T)$$

Membrane potential : $V_i(t)$

$$\tau_i \frac{dV_i}{dt} = -V_i + I_i(t)$$

Spike emitted whenever $V_i(t) = V_T$

After the spike, voltage is reset to V_R

Visualizing network activity

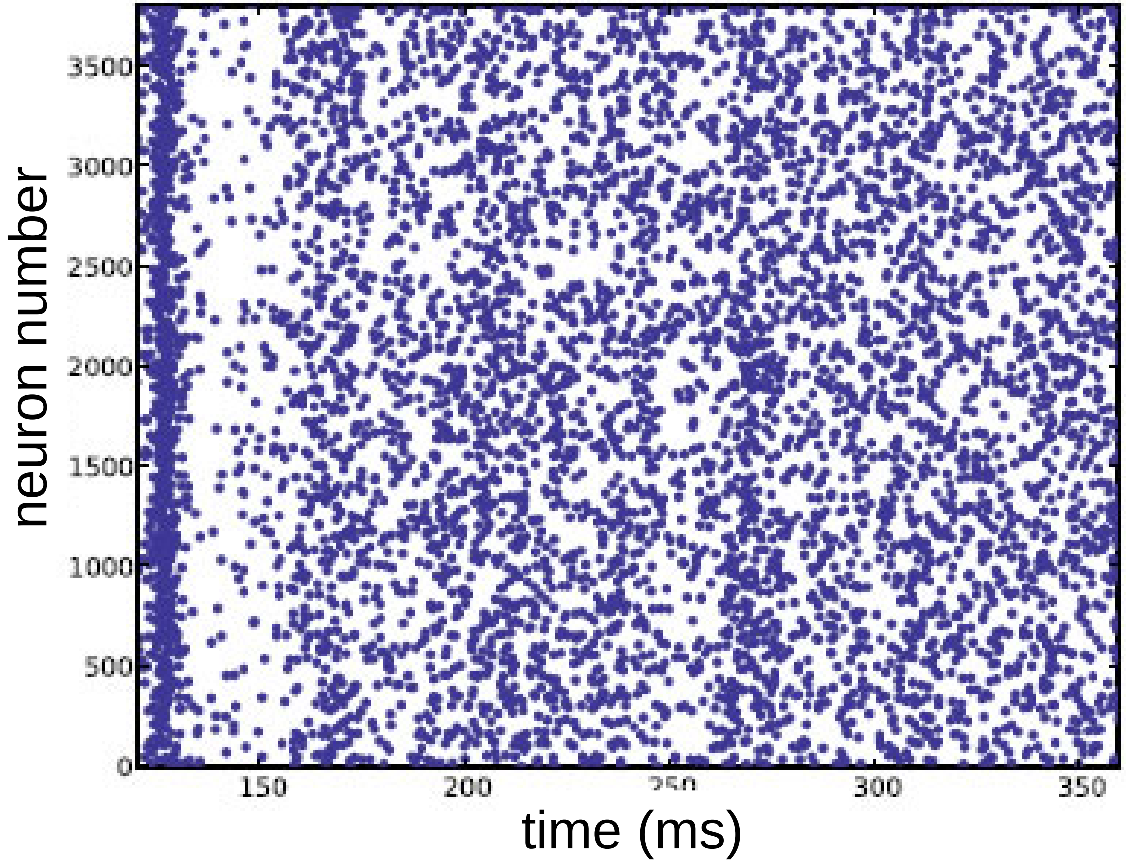
Binary network

Spiking network

- **Raster plot :** spiking activity of whole network vs time

$$S_i(t) = 1,0$$

$$S_i(t) = \sum_k \delta(t - t_i^k)$$



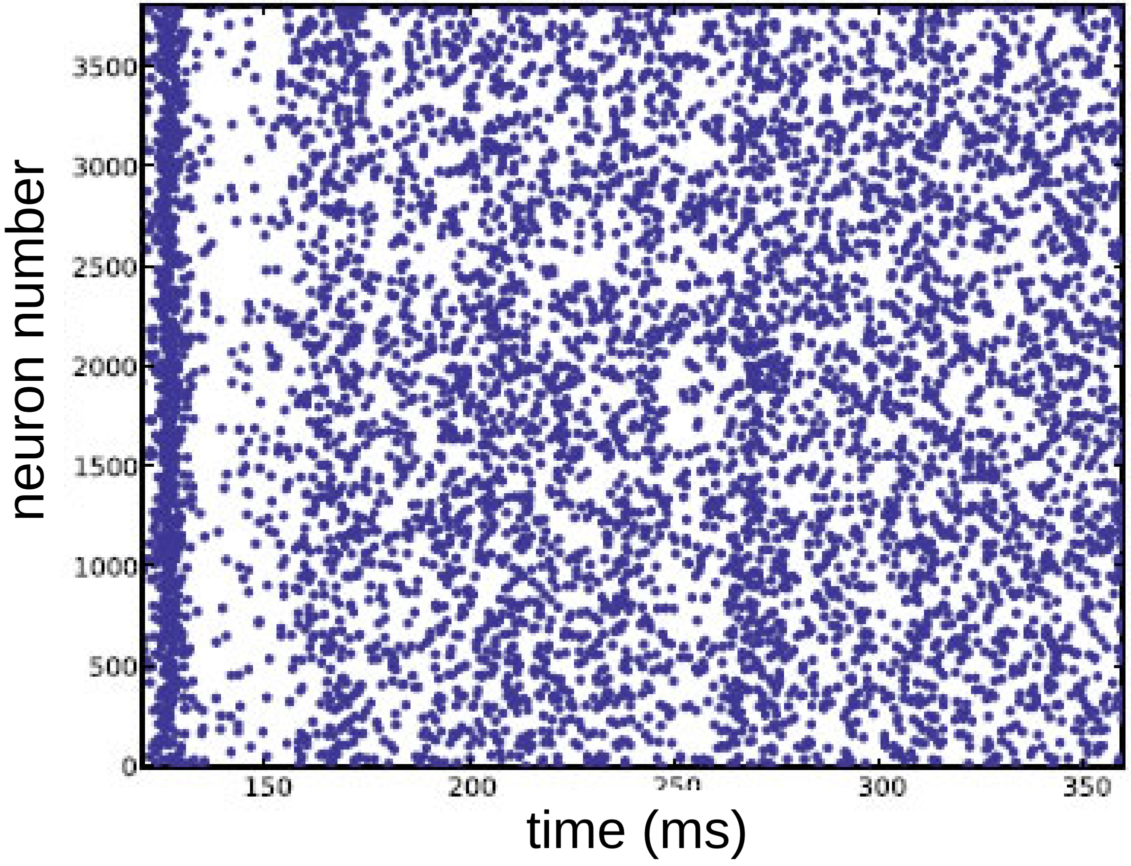
Firing rate

Binary network *Spiking network*

- Averaging over time: average firing rates of single neurons

$$\nu_i = \frac{1}{T} \sum_i S_i(t)\, dt$$

$$\nu_i = \frac{1}{T} \int_0^T S_i(t)\, dt$$



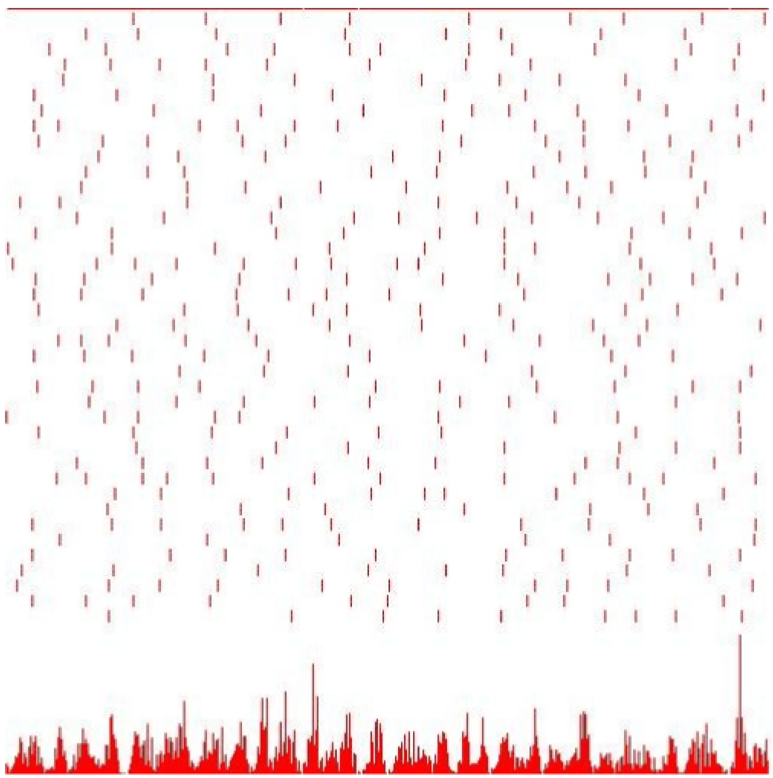
Population activity

Binary networks *Spiking networks*

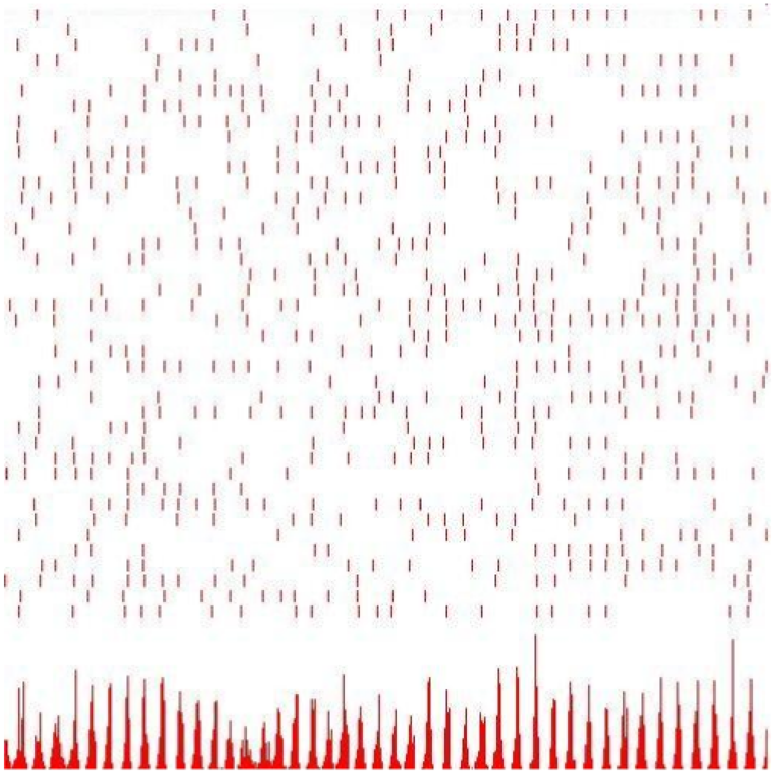
- Averaging over neurons: instantaneous average rate (vs time)

$$\nu(t) = \frac{1}{N\,dt} \sum_i S_i(t)$$

neuron number

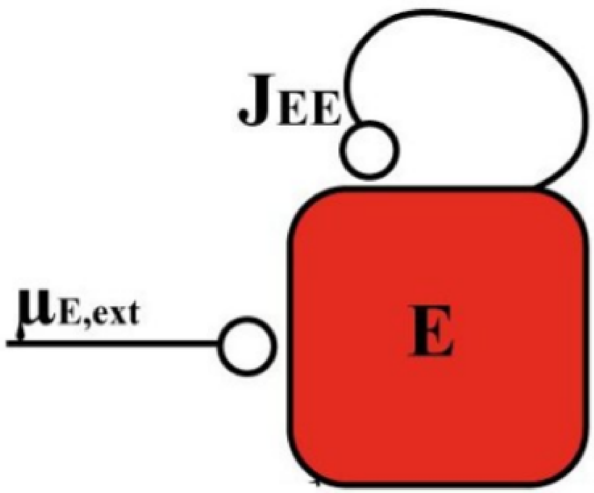


time (ms)



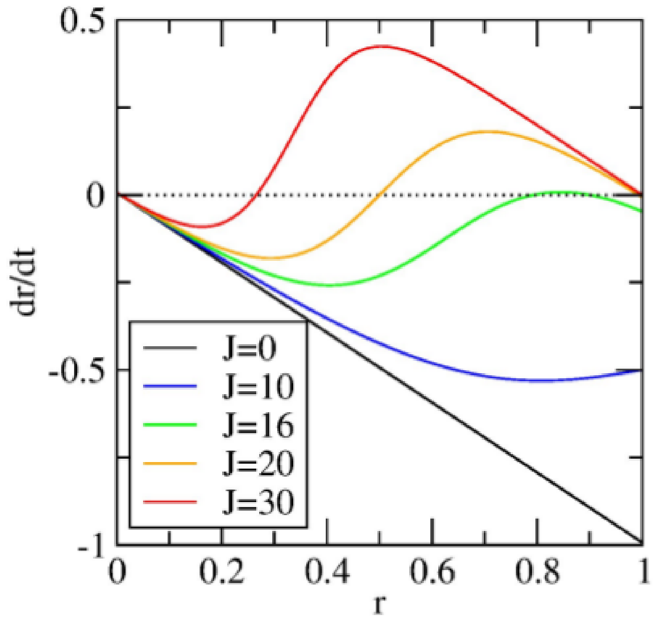
time (ms)

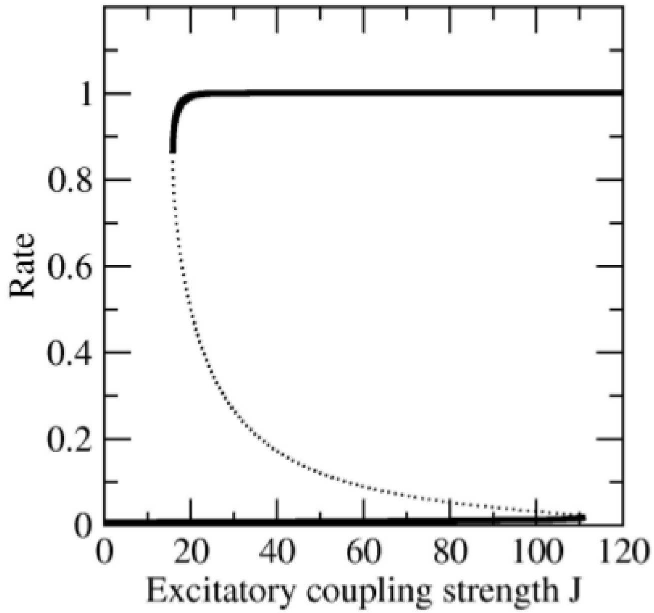
Example 1 :
E network rate model with bistability



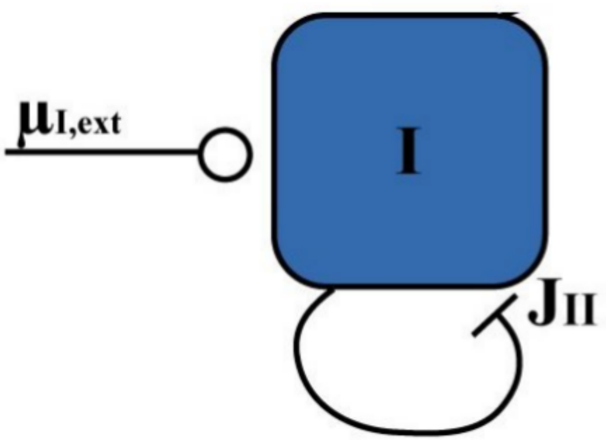
$$\tau \frac{dr}{dt} = -r + \Phi\left(I + Jr\right)$$

Sigmoidal transfer function Φ



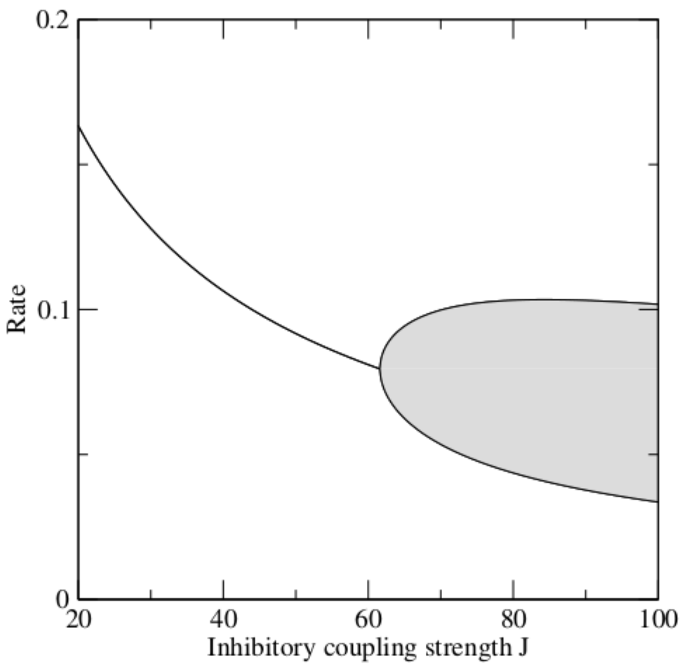


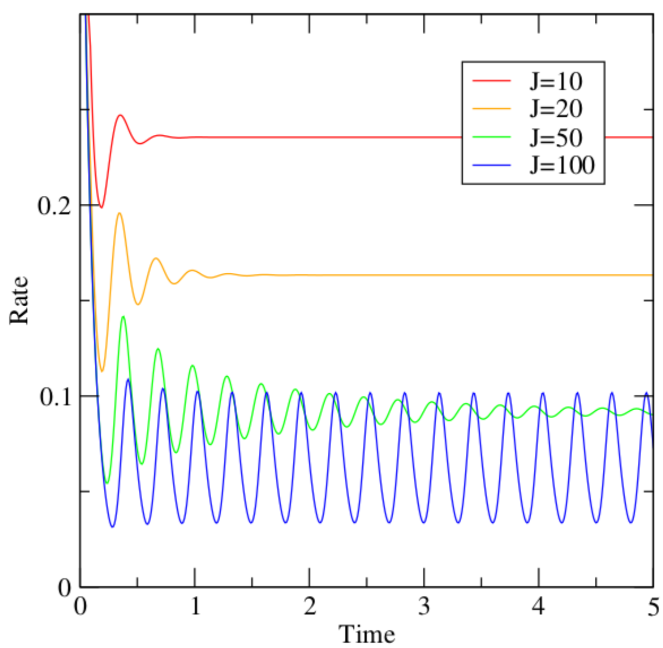
Example 2 : I network rate model with delays - oscillations



$$\tau \frac{dr_I}{dt} = -r_I + \Phi[I_{IX} - J_{II} r_I(t-D)]$$

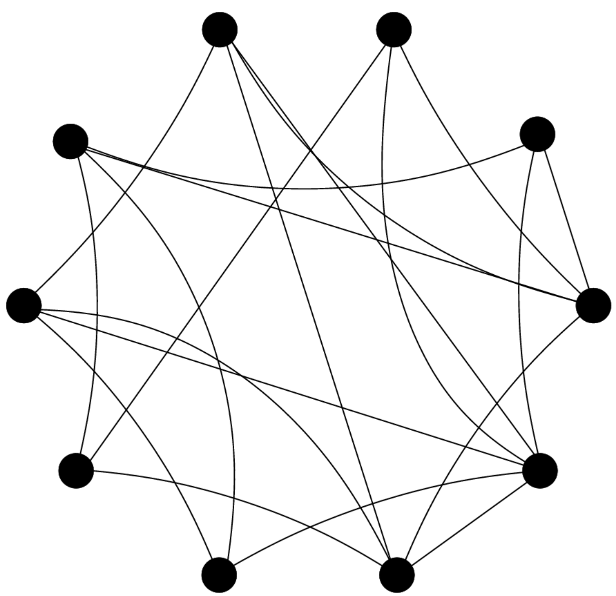
- oscillations at a frequency f_c appear when $\tilde{J}_{II} > J_c$
- For $D \ll \tau, J_c \sim \pi\tau/(2D), f_c \sim 1/(4D)$
- Frequency controlled by synaptic delays
  ⇒ fast oscillations in cortex/hippocampus?





Example 2 : I network rate spiking neuron model with delays - oscillations

- sparsely connected network of inhibitory integrate-and-fire neurons, delay $D = 2$ ms
- Individual neurons fire irregularly at low rates but the network exhibits an synchronized, oscillatory population activity



$p = 0.2$

N=5000