

# Introduction to computational neuroscience : from single neurons to network dynamics

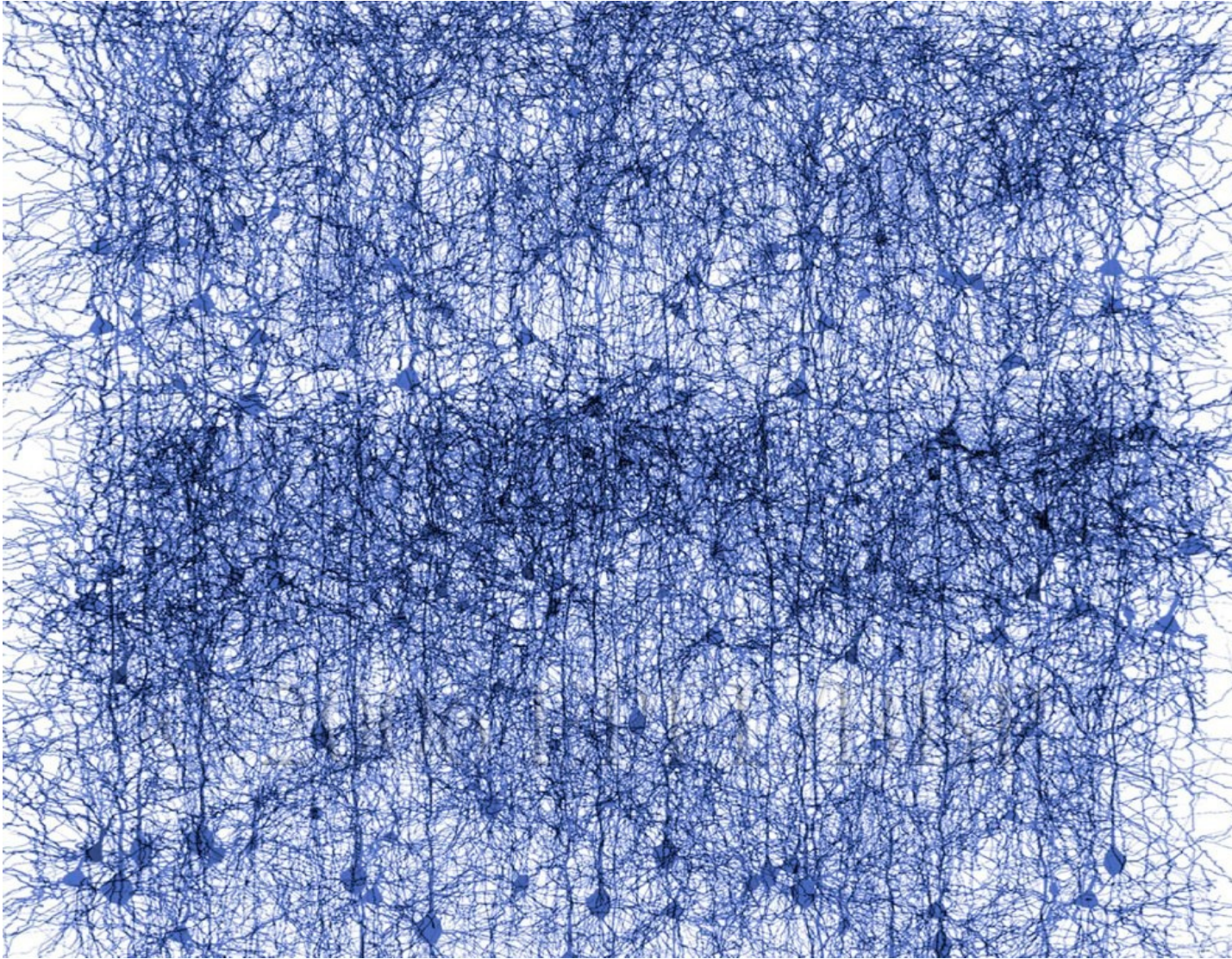


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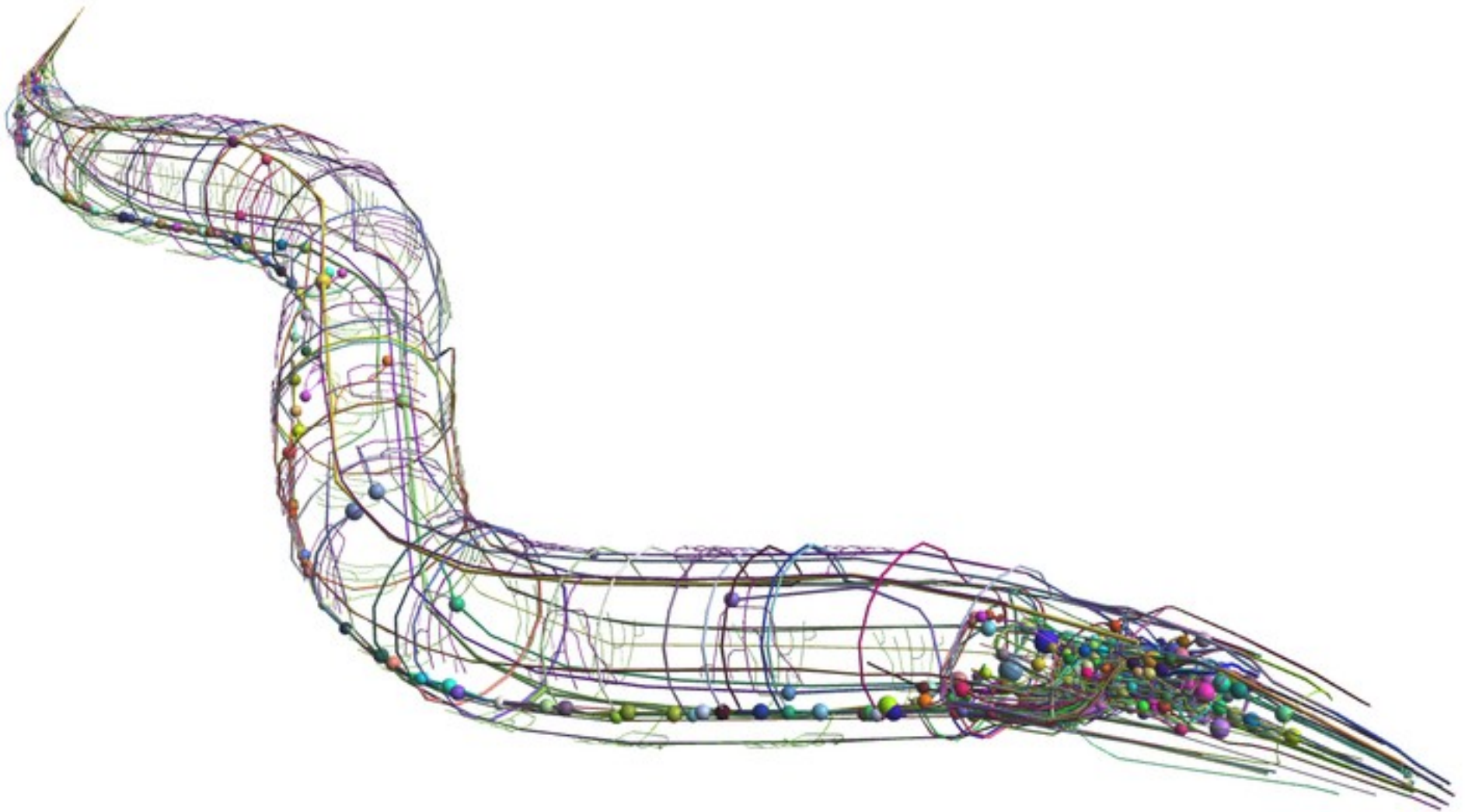
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# Neurons form networks



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

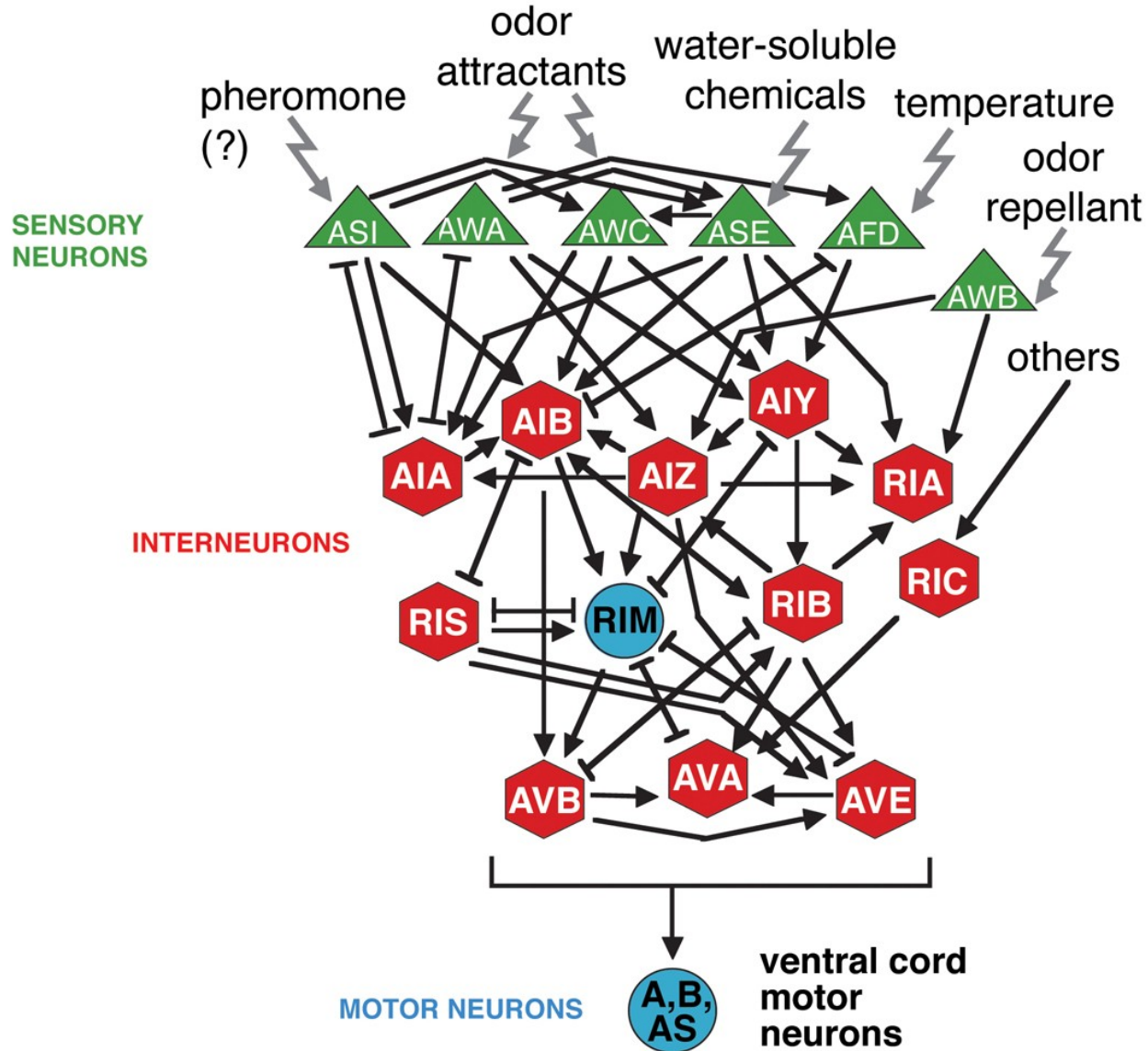
# C elegans : brain network



**C elegans brain** : 302 neurons, ~7,000 connections



# Brain network : from sensory to motor

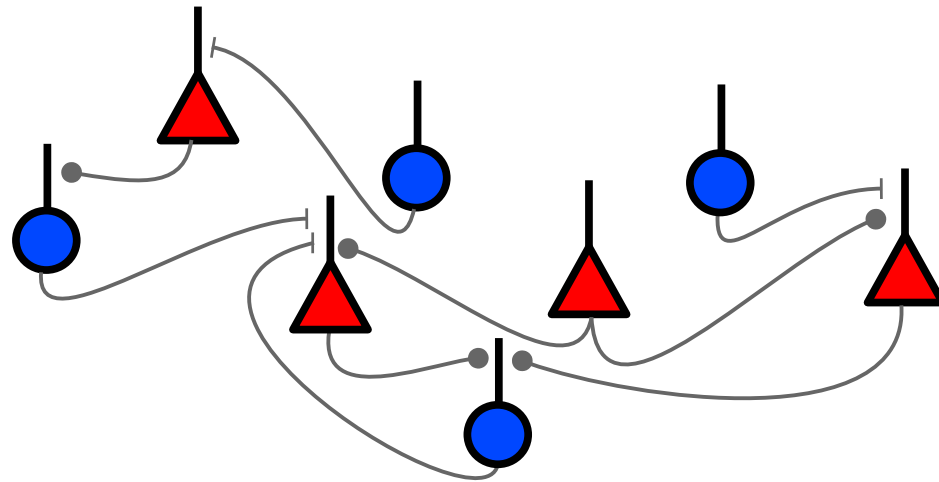


# Two classes of neural network models

- **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.

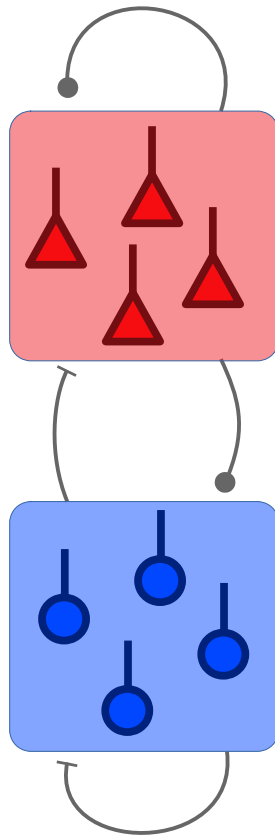
# Network models : rate vs. spiking neural network

neural network



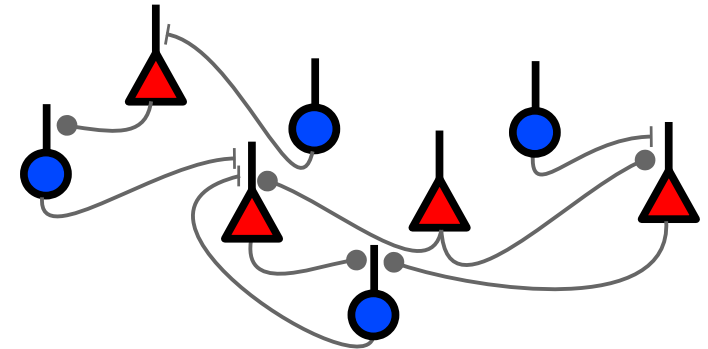
# Network models : rate vs. spiking neural network

**Rate model**



groups of similar neurons are  
grouped together

**Spiking neuron model**

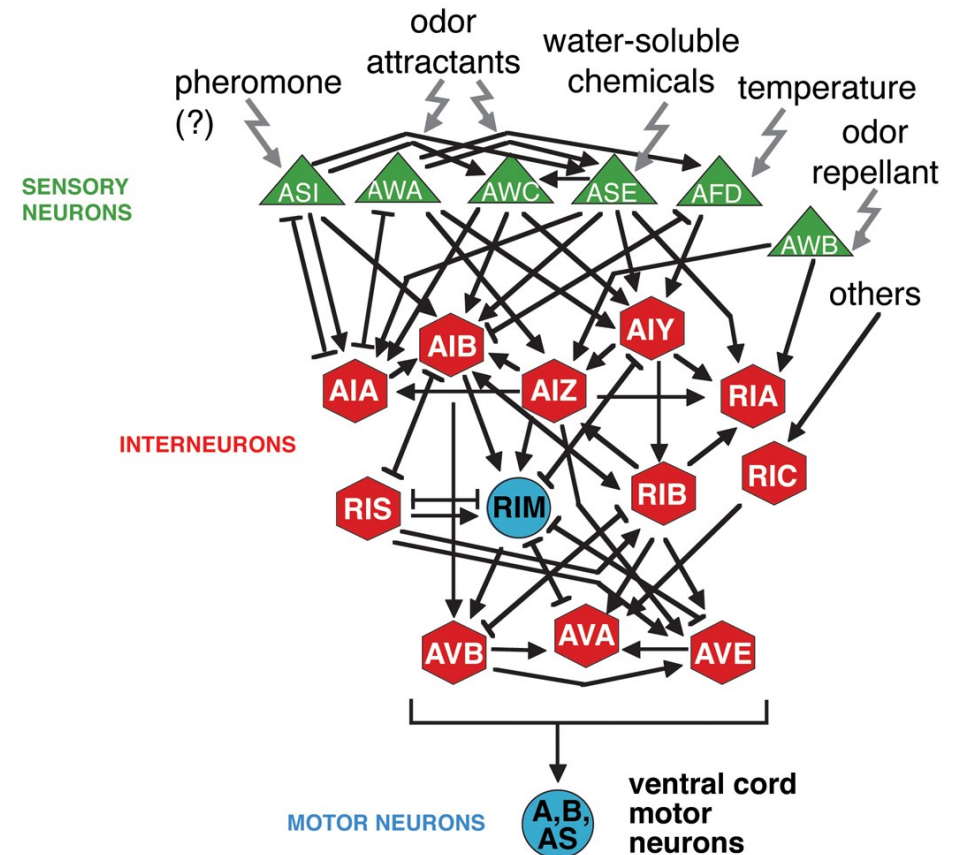


each individual neuron is described



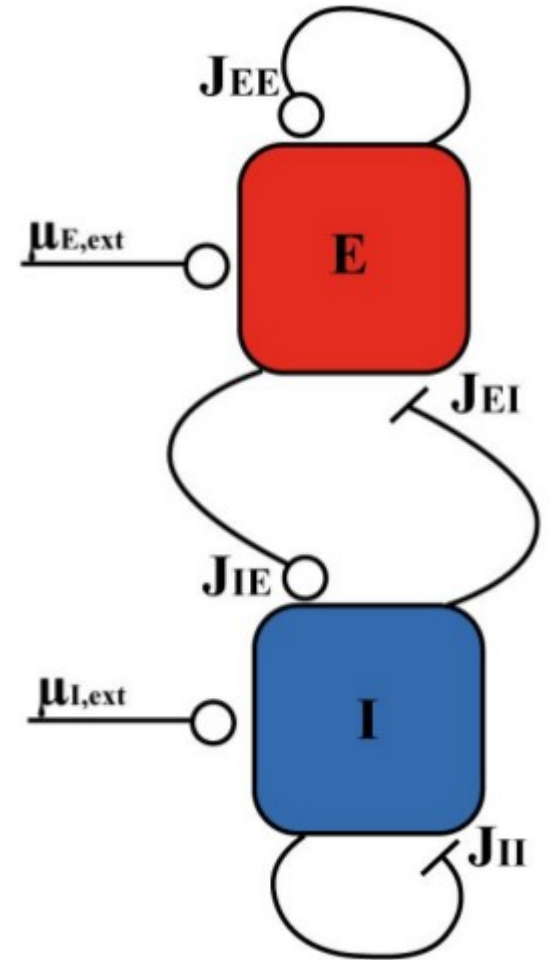
# Network models : parts list

- 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)?



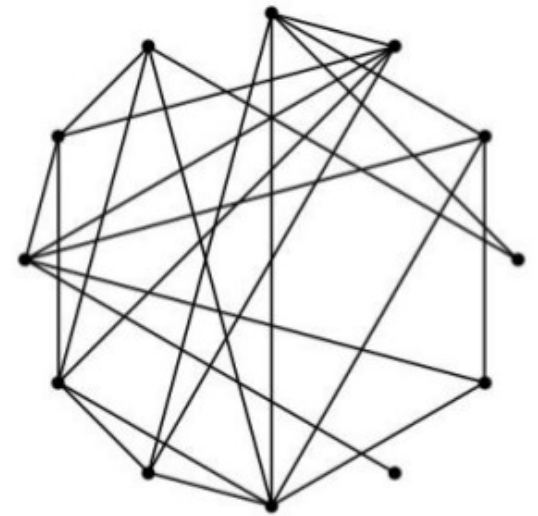
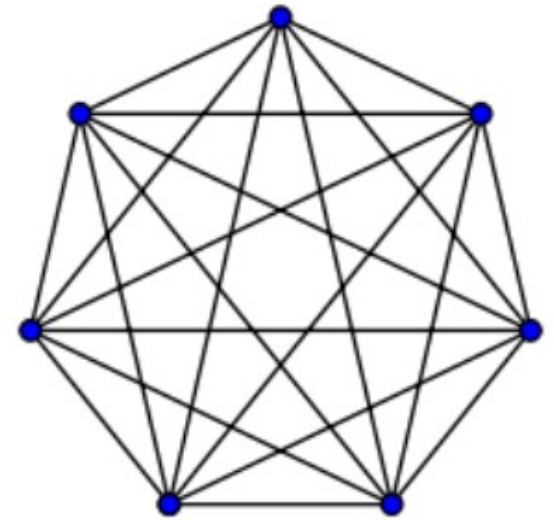
# Types and numbers of neurons

- 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 of spiking neurons:  
 $N \sim 10^3-10^4$  (single workstations), much more (clusters, dedicated supercomputers)
  - Analytical calculations :  $N \rightarrow \infty$



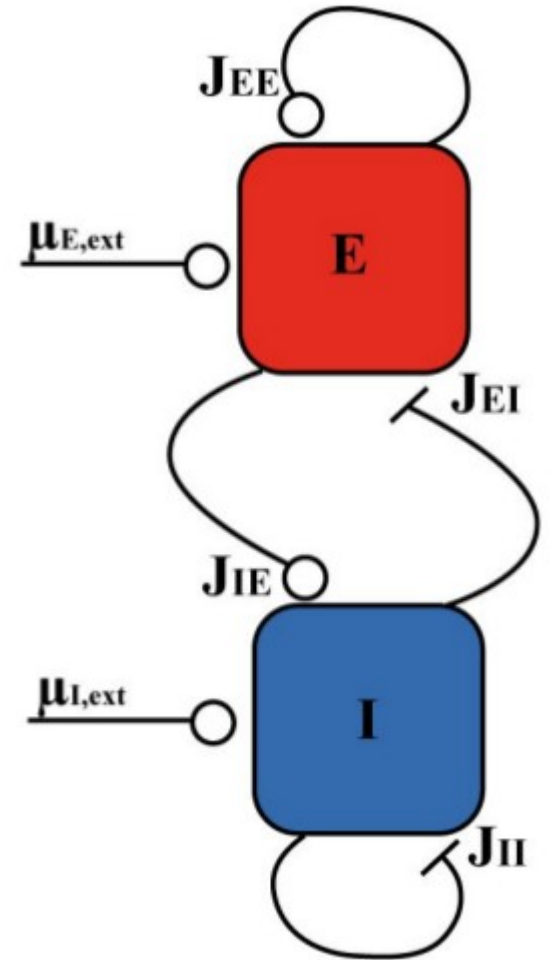
# Connectivity matrix

- 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



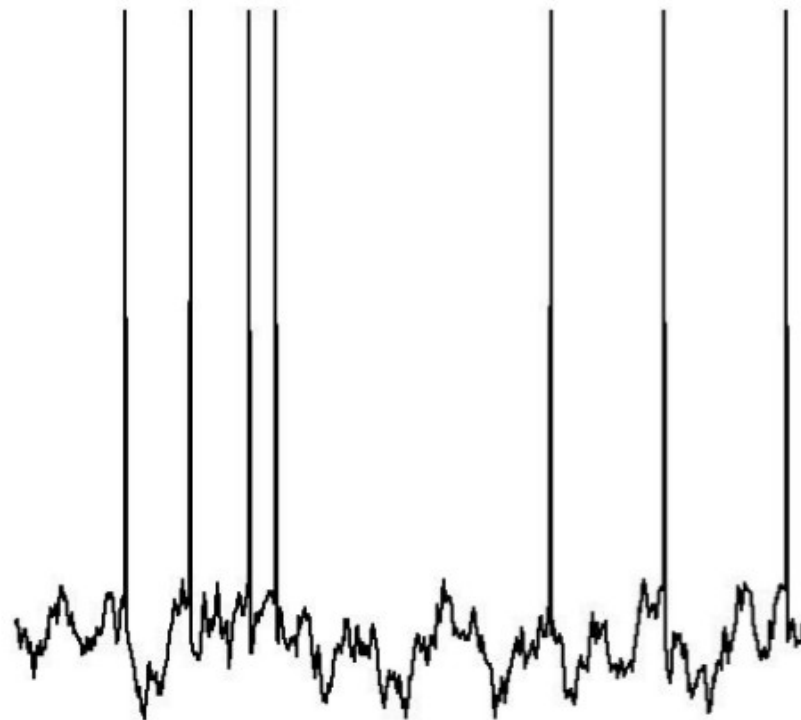
# External inputs

- What are the external inputs ?
  - Constant
  - Stochastic (e.g. independent Poisson processes; independent white noise)
  - Temporally/spatially structured

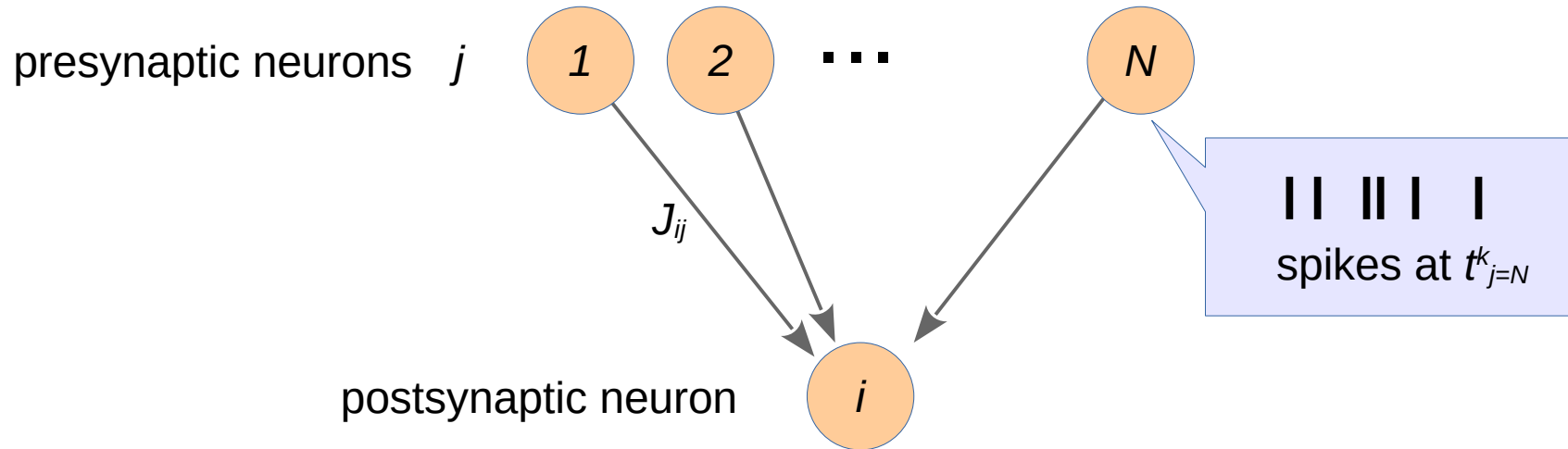


# Neuron models

- What is(are) the neuronal model(s) ?
  - Binary
  - Spiking (LIF, NLIF, HH-type, etc. ...)
  - rate units (groups of neurons)



# Neuron models of spiking networks



## Binary networks

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

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

## Spiking networks

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

# Neuron models of spiking networks

## Binary networks

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

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

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

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

Neuron active :  $S = 1$

or inactive :  $S = 0$

## Spiking networks

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

Membrane potential :  $V_i(t)$

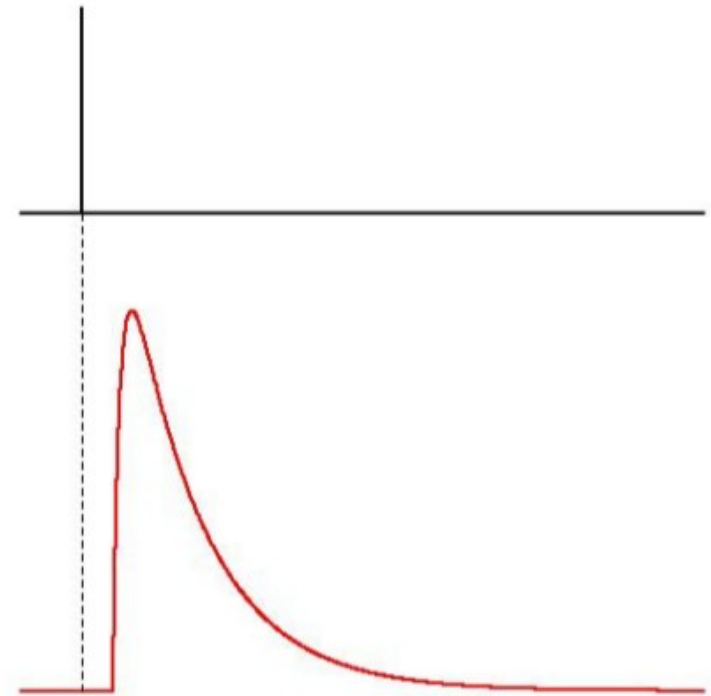
$$\tau_i \frac{dV_i}{dt} = -V_i + I_i(t)$$

Spike emitted whenever  $V_i(t) = V_T$

After the spike, voltage is reset to  $V_R$

# Synapse models

- What is(are) the synapse model(s)?
  - Fixed number (synaptic weight, binary networks)
  - Temporal kernel (spiking networks)
  - Non-plastic vs. plastic





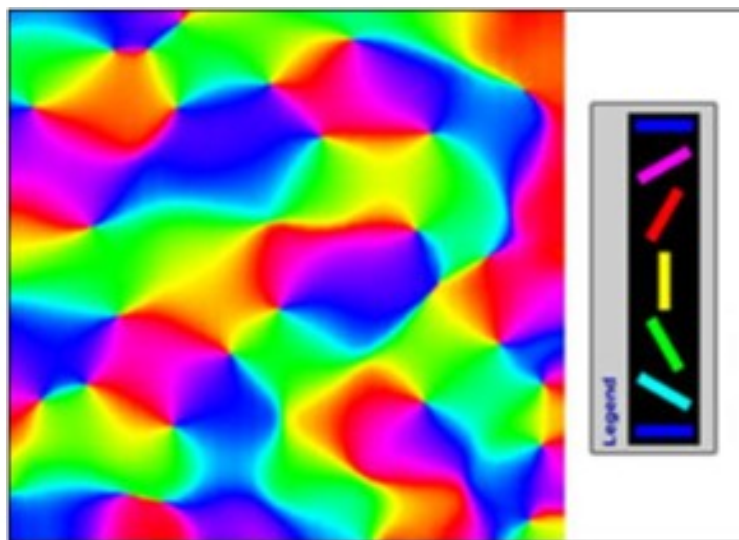
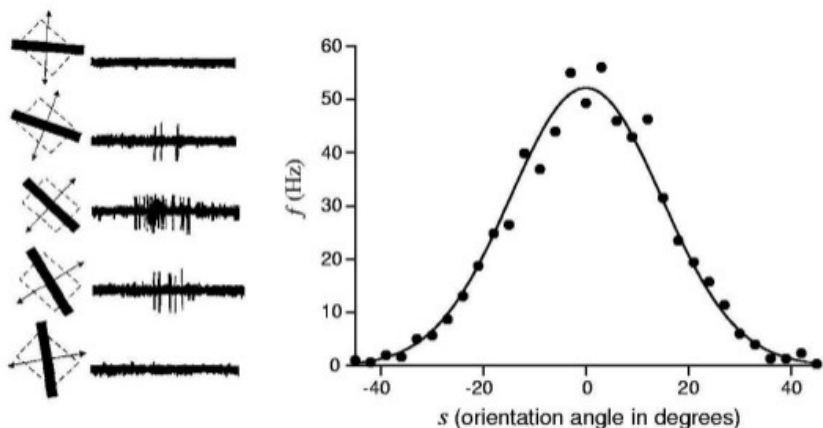
# Questions

- **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?

# 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

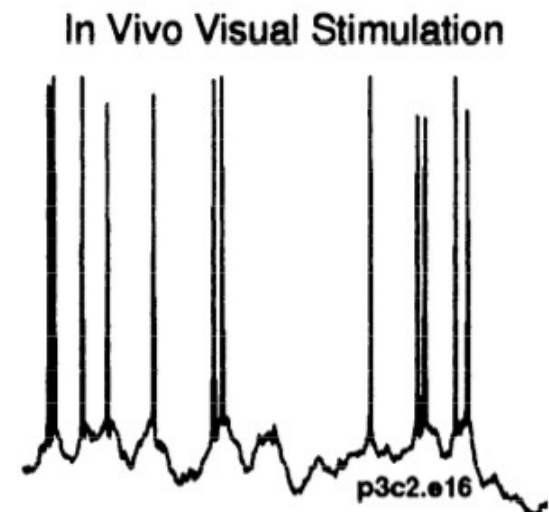
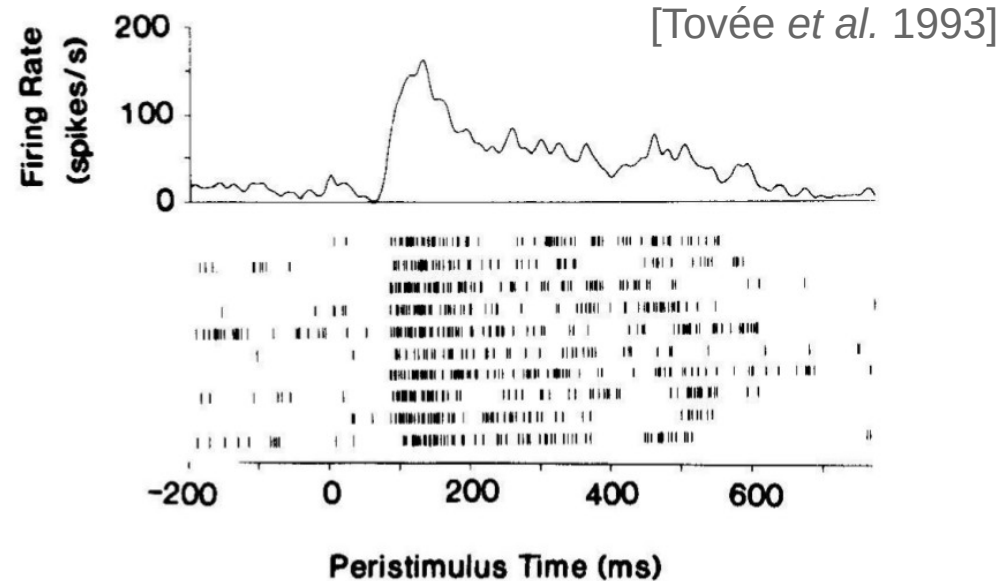
## Spontaneous vs. selective/evoked activity :

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

## Statistics of neural activity :

- very irregular firing (close to Poisson process – CV close to 1)
- Large membrane potential fluctuations ( $\sim 5\text{mV}$ )

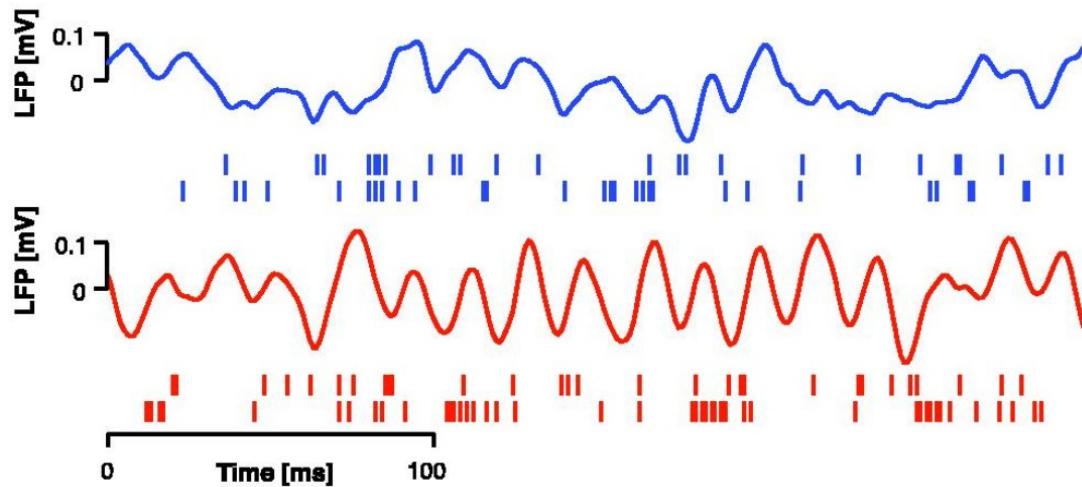
**→ What are the mechanisms of irregular activity and large potential fluctuations ?**



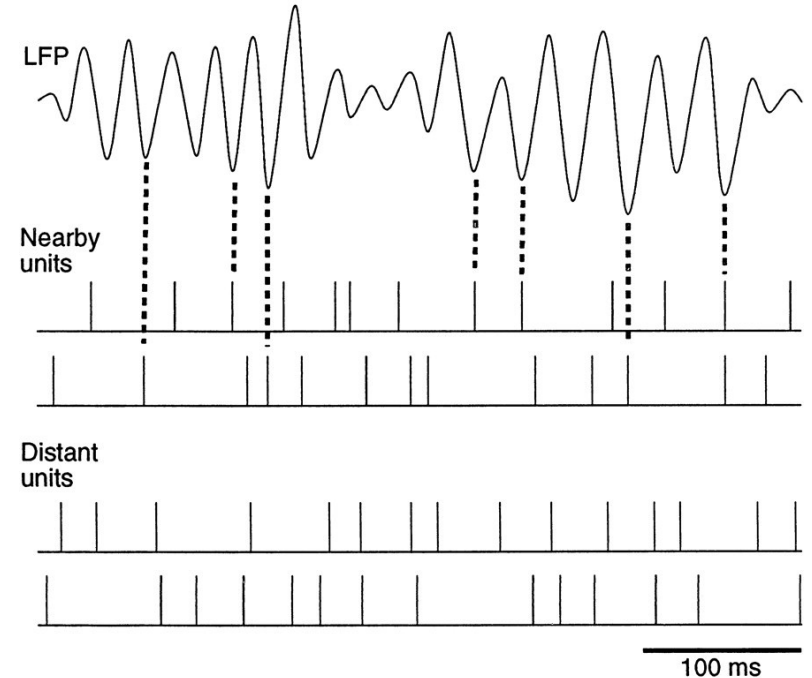
[Holt *et al.*, 1996]

# 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?**

# How to investigate a neural network model's behavior ?

## **1<sup>st</sup> 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, ... )



put in relation

# Rate model

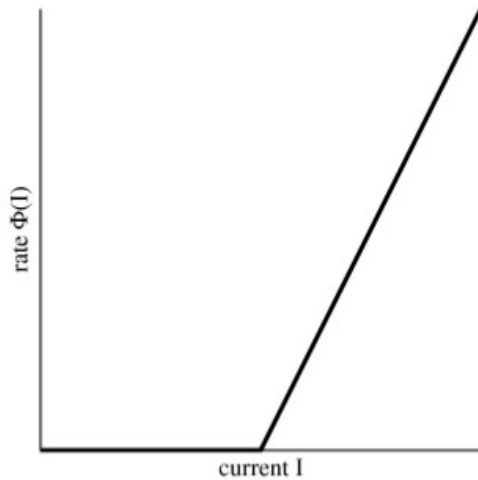
- In a 'rate model' (also called: 'firing rate model', 'neural mass model', 'neural field model', 'Wilson-Cowan model'), one describes the activity (instantaneous firing rate) of a population of neurons at a given location by a single analog variable:

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

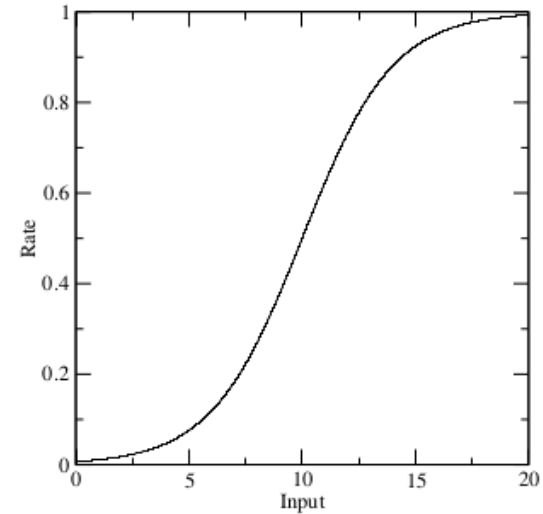
- $\tau$  : time constant of firing rate dynamics
- $r(x, t)$ : firing rate of neurons at location  $x$  at time  $t$
- $\Phi(\cdot)$  : transfer function (f-I curve)
- $I(x, t)$  : external input
- $J(x, y)$ : strength of synaptic connections between neurons at locations  $x$  and  $y$

# The transfer function $\Phi(\cdot)$

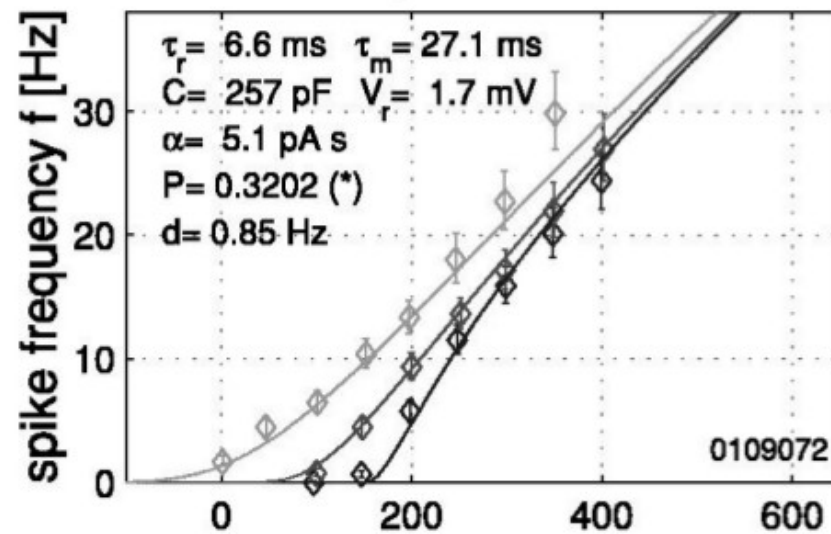
Threshold linear  $\Phi(x) = [x - T]_+$



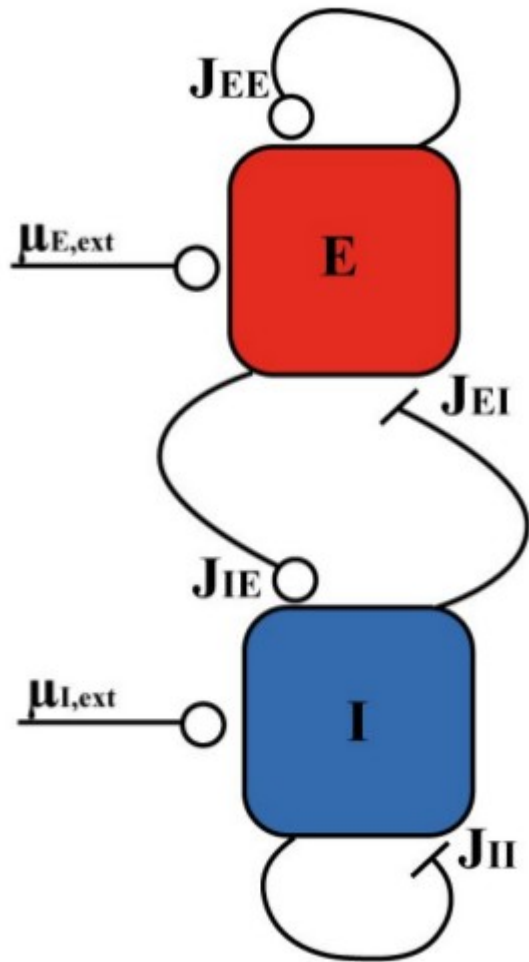
Sigmoidal  $\Phi(x) = 1 / (1 + \exp(-\beta(x - T)))$



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



# Example : Rate models of local and discrete networks of neurons



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

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

- **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 model dynamics

$$\tau \dot{r} = -r + \Phi(I + \mathbf{J} r)$$

- Solve the equations for fixed point(s), i.e., where  $\dot{r} = 0$  :

$$r_0 = \Phi(I + \mathbf{J} r)$$

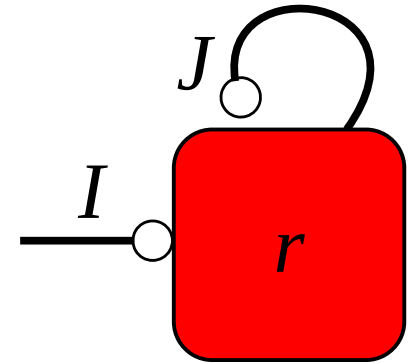
- Check linear stability of fixed points :
  - A small perturbation  $\delta r$  around the fixed point obeys the linearized dynamics

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

- Compute eigenvalues  $\lambda$  of the Jacobian matrix  $(-1 + \Phi \mathbf{J})$
- Fixed point stable if all eigenvalues have negative real parts;
- “Rate” instability (saddle node bifurcation) when  $\lambda = 0$
- Oscillatory instability (Hopf bifurcation) when  $\lambda = \pm i\omega$  and  $\omega \neq 0$

# Simplest case : 1 population, linear $\Phi$

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



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

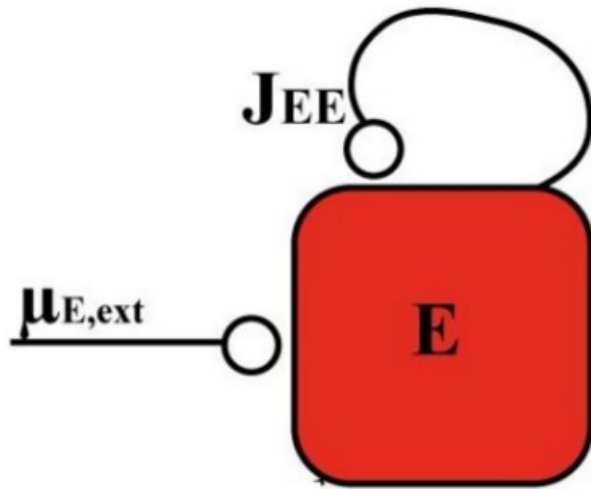
$$r(t) = \frac{1}{\tau} \int^t I(t') dt'$$

- Stable if  $J < 1$  :

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

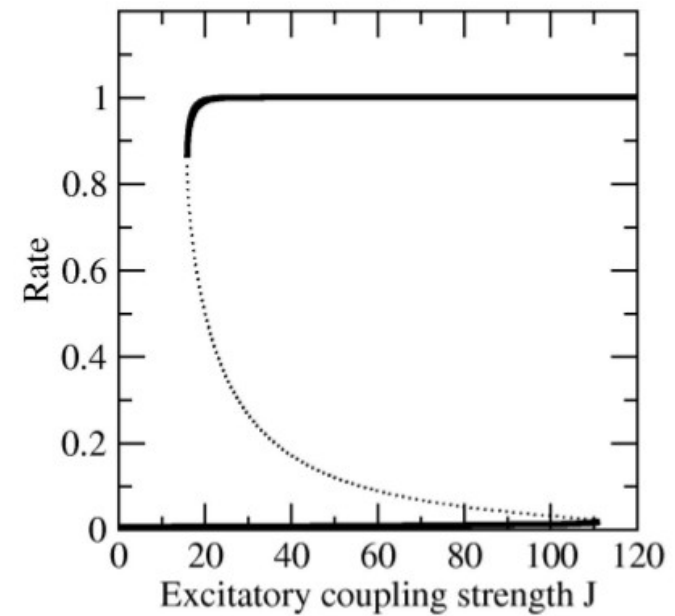
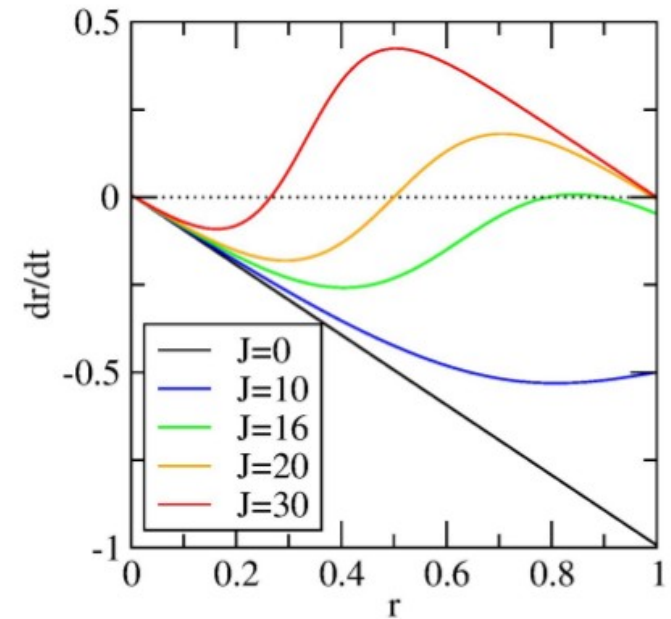
- Excitatory network ( $0 < J < 1$ ): amplification of inputs, slow response
- Inhibitor network ( $J < 0$ ): attenuation of inputs, fast response

# Example 2 : E network rate model with bistability

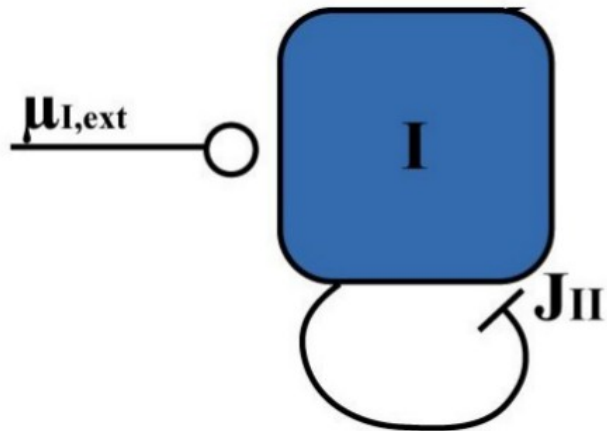


$$\tau \frac{dr}{dt} = -r + \Phi(I + Jr)$$

Sigmoidal transfer function  $\Phi$

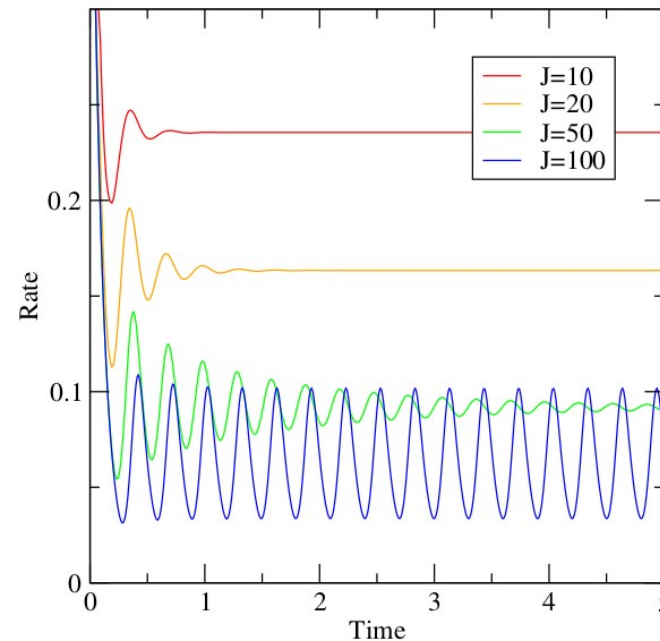
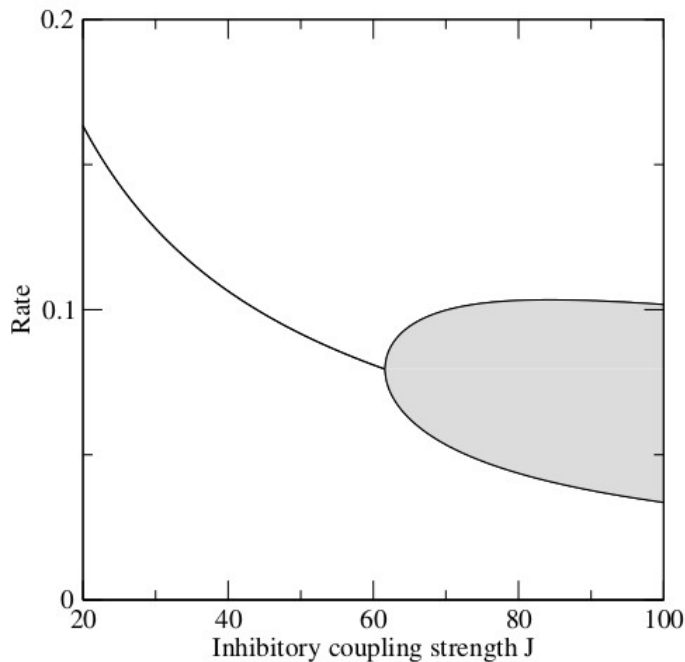


# Example 3 : I network rate model with delays - oscillations



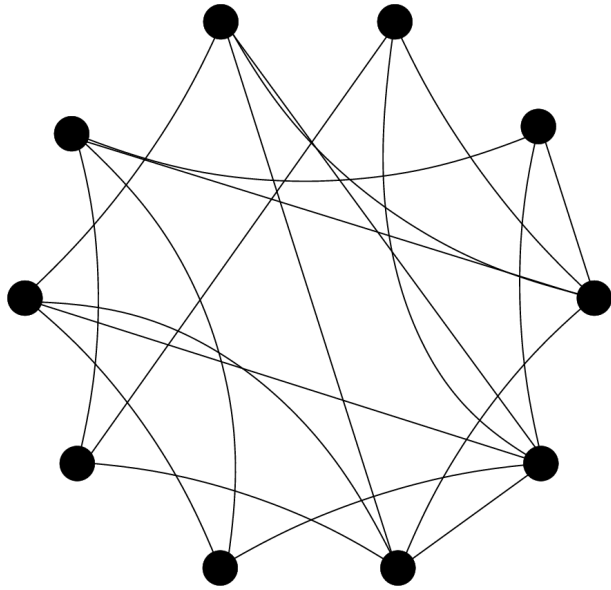
$$\tau \frac{dr_I}{dt} = -r_I + \Phi [I_{IX} - J_{II} r_I(t - D)]$$

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



# Example 3 : 1 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



$p = 0.2$

