Introduction to computational neuroscience : from single neurons to network dynamics

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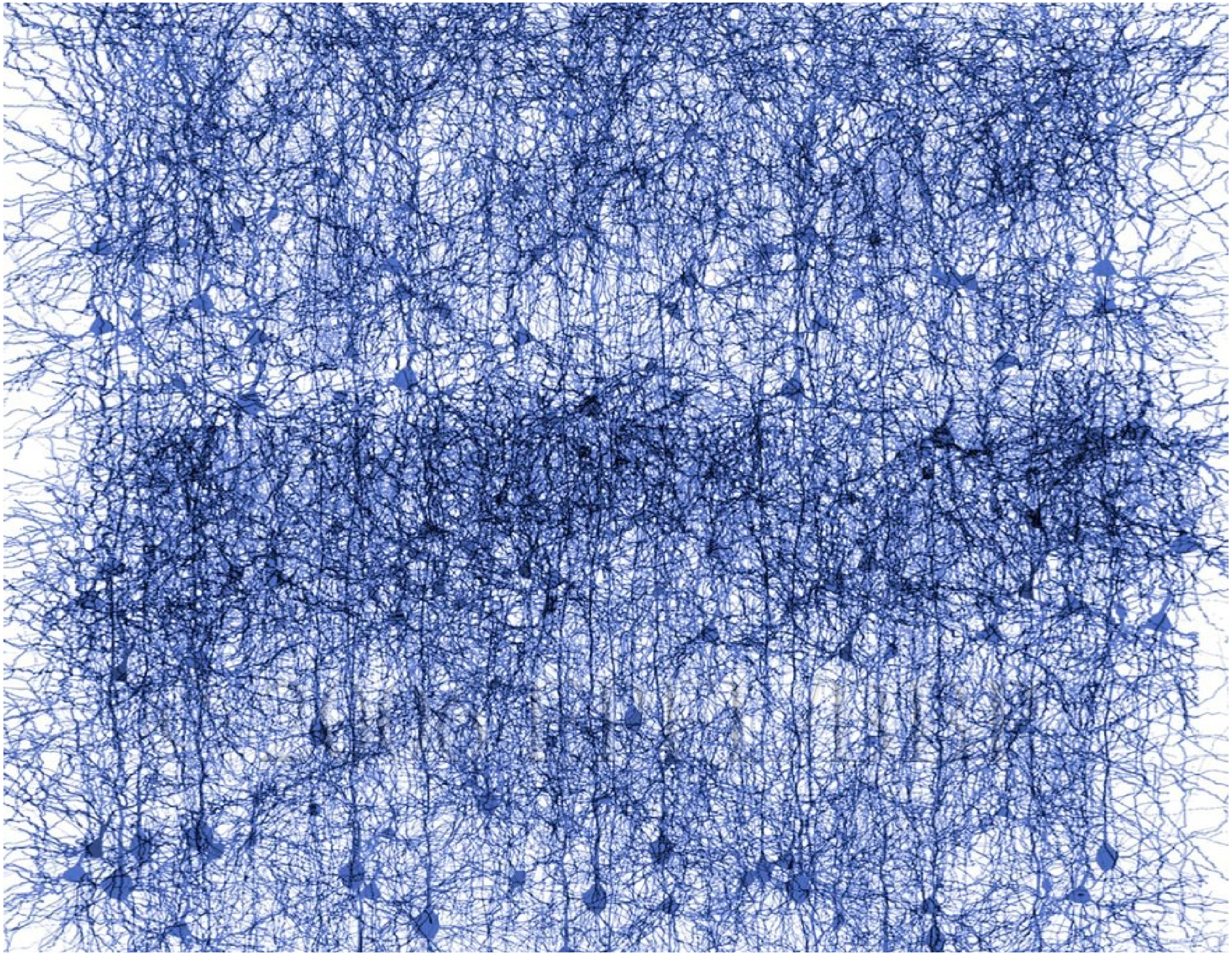
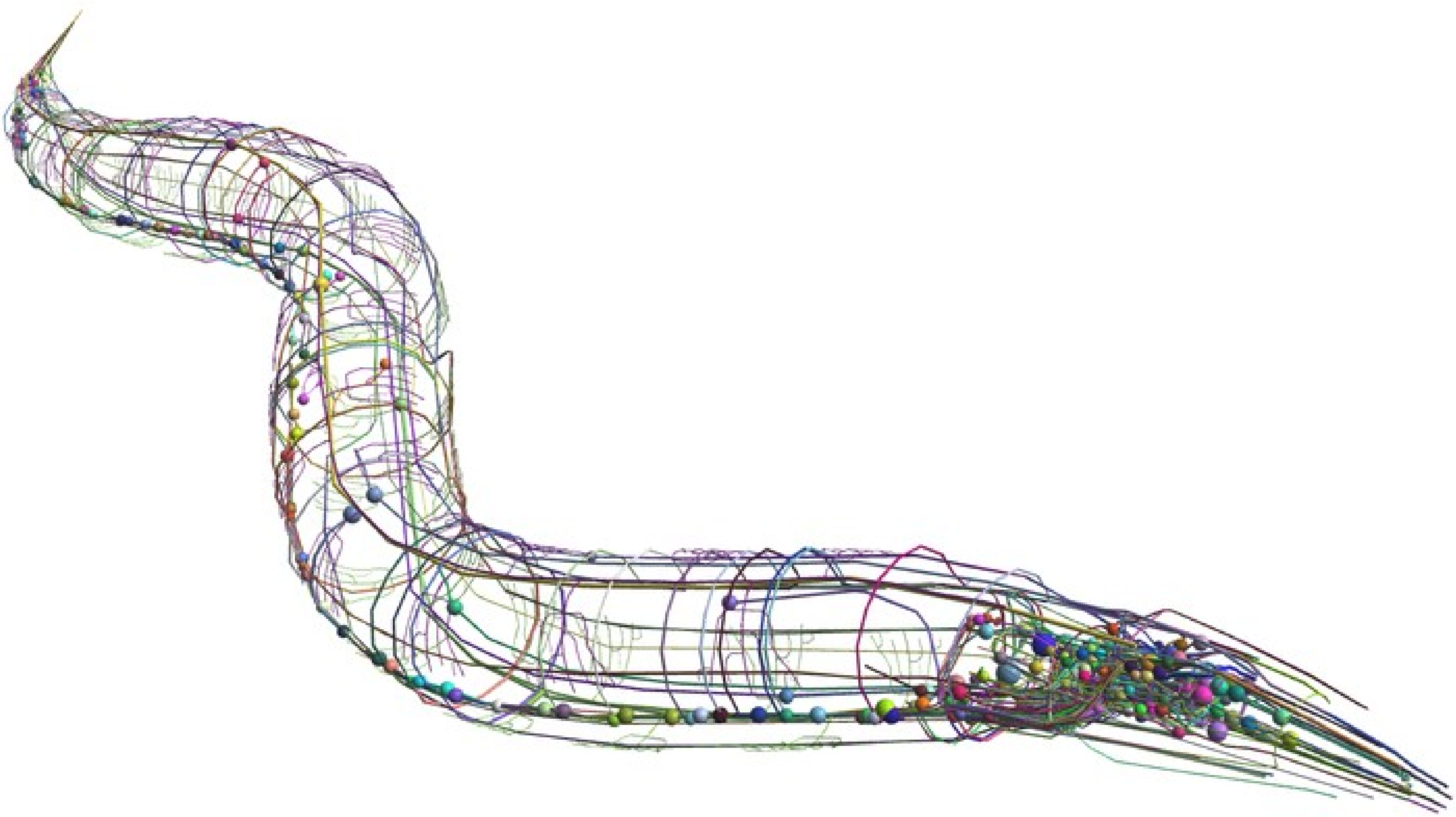
Neurons form networks



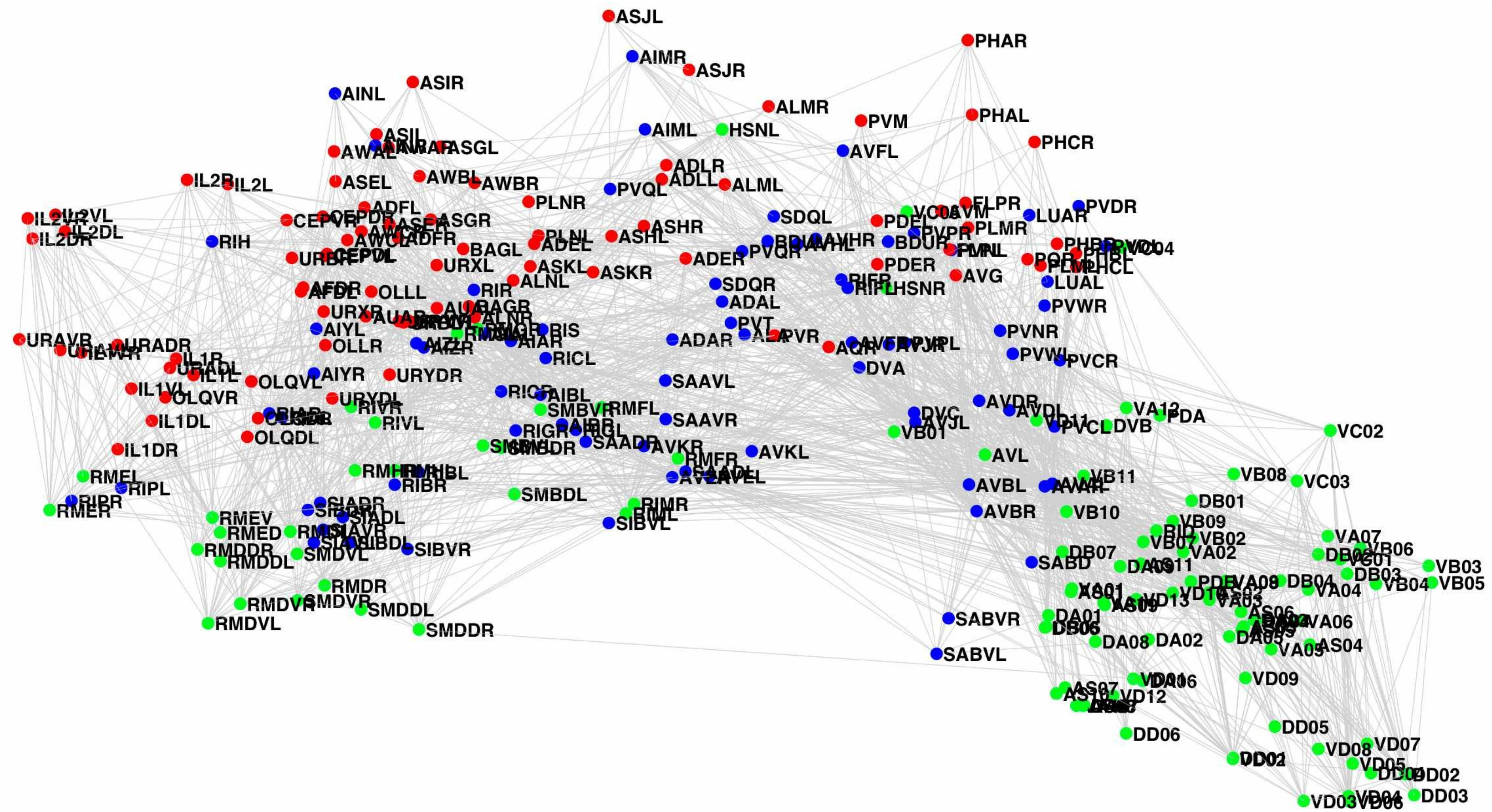
The brain : a network of 10^{11} neurons connected by 10^{15} synapses

C elegans : brain network



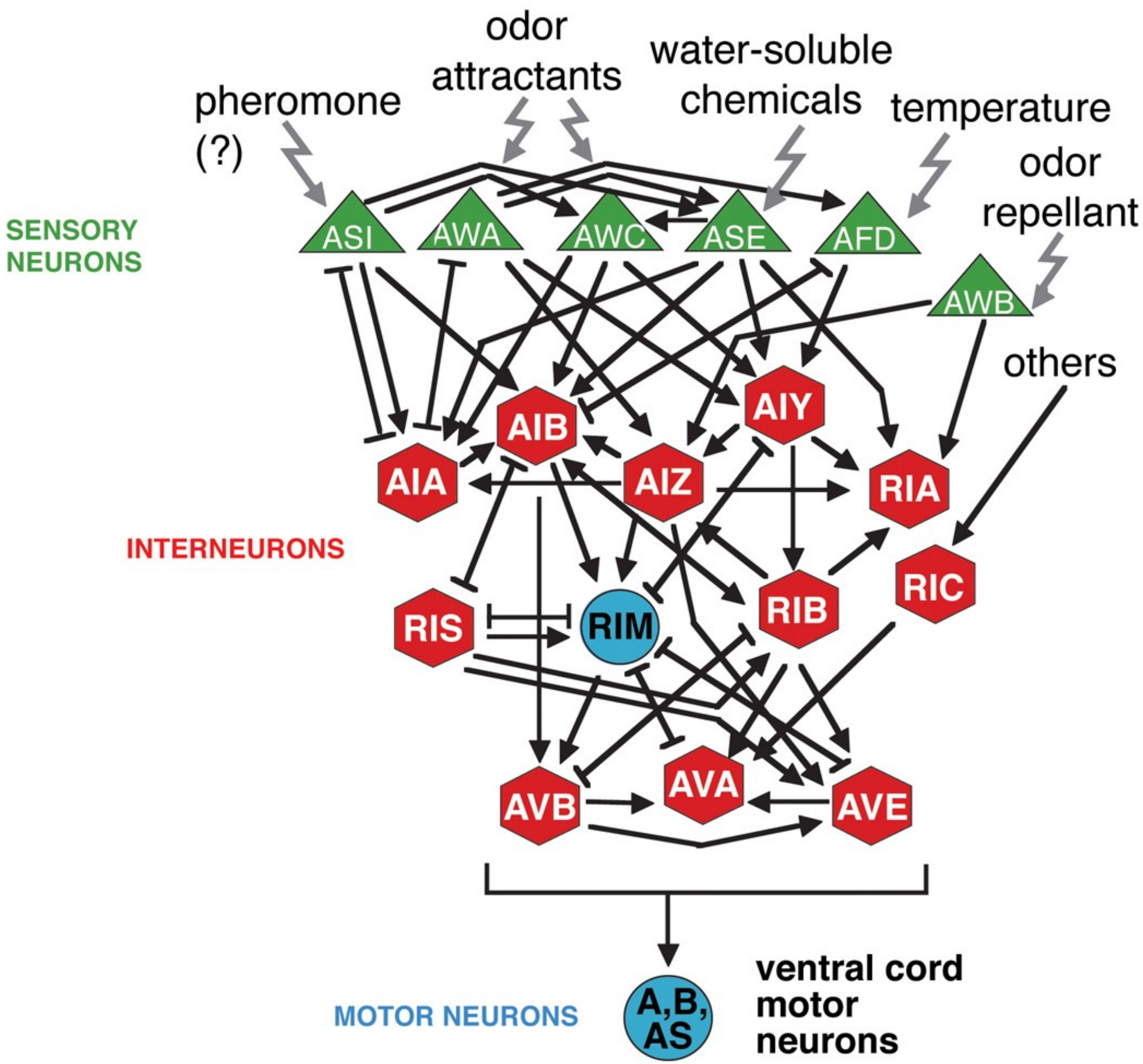
C elegans brain : 302 neurons, ~7,000 connections

C elegans : brain network



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

Brain network : from sensory to motor



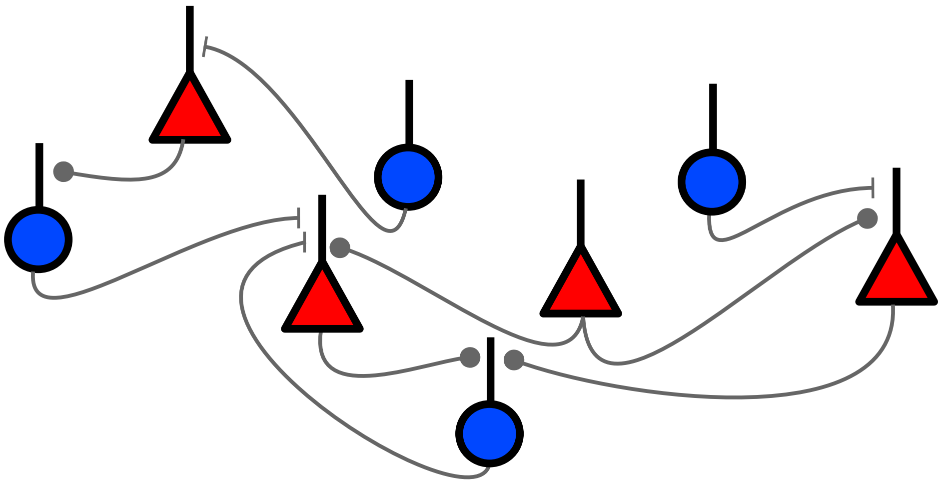
Two classes of neural network models

- **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.

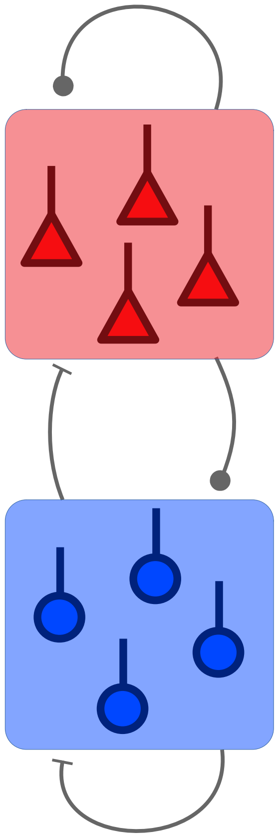
Network models :
rate vs. spiking neural network

neural network



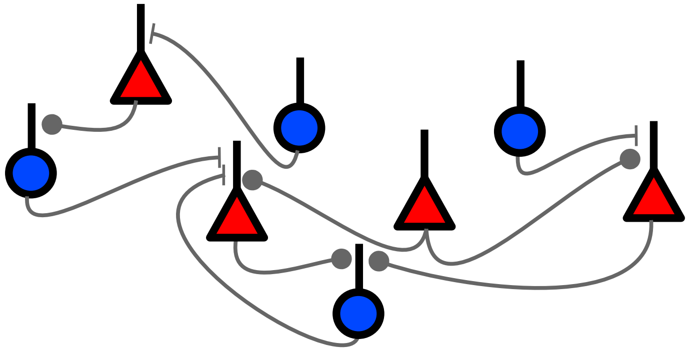
Network models :
rate vs. spiking neural network

Rate model



ensembles 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 ?

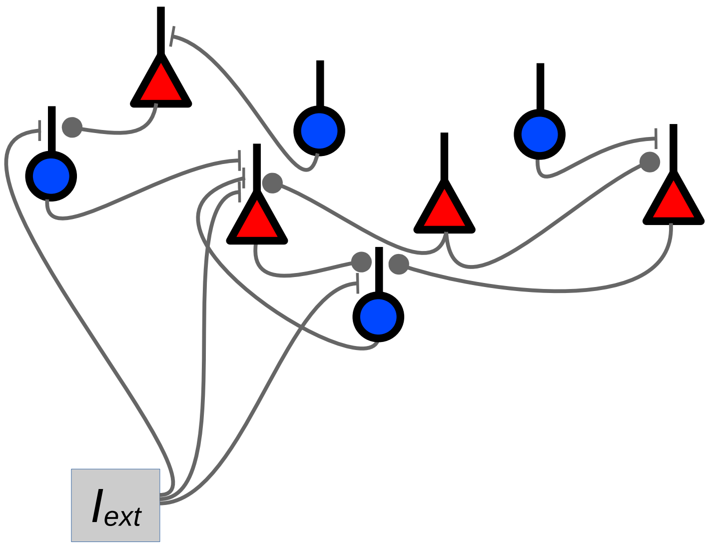
- How are the neurons connected

  (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

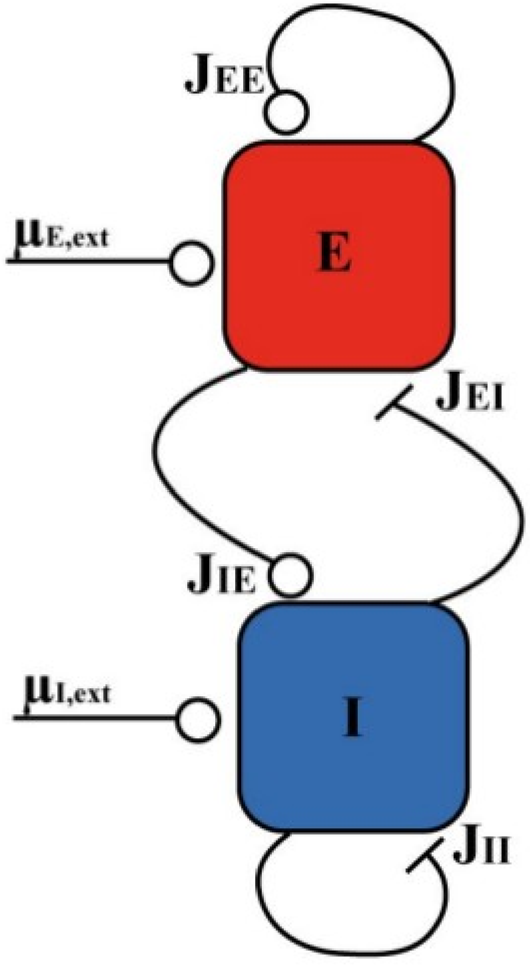
- How many types of neurons? How many neurons in each type?

  - 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 : $N \to \infty$



Connectivity matrix

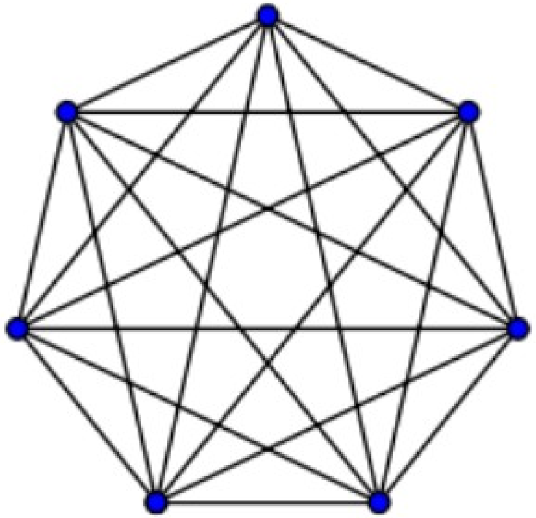
- How are neurons connected (what is the connectivity matrix)?

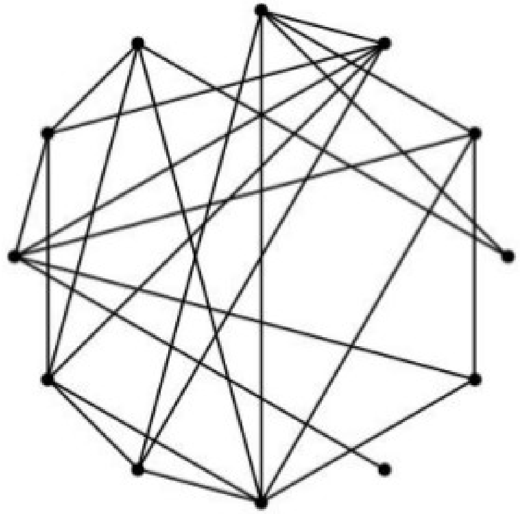
  - Fully connected (all-to-all)

  - Randomly connected (par ex. Erdos-Renyi)

  - Spatial structure

  - With a structure imposed by learning





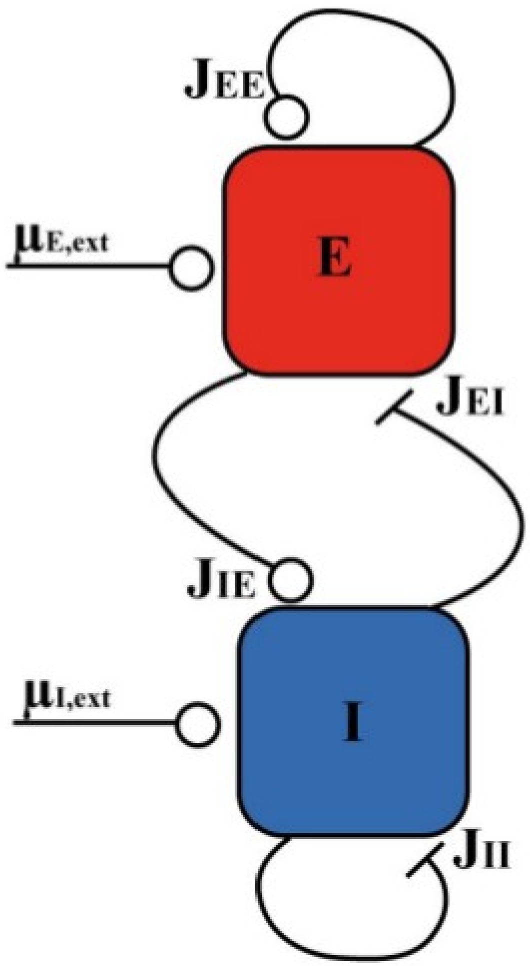
External inputs

- What are the external inputs ?

  - Constant

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

  - Temporally/spatially structured



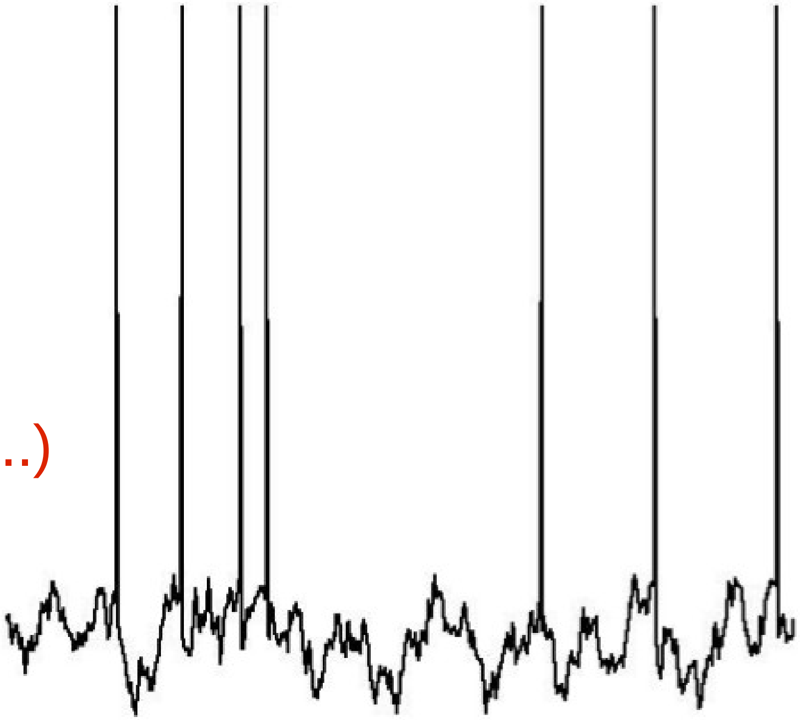
Neuron models

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

  - Binary

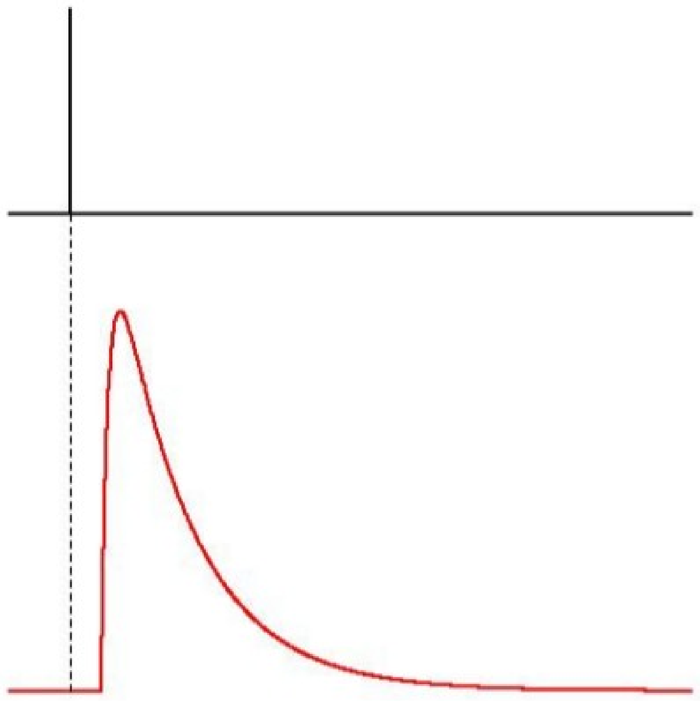
  - Spiking (Integrate-and-Fire, HH-type, etc. ...)

  - rate units (groups of neurons)



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?

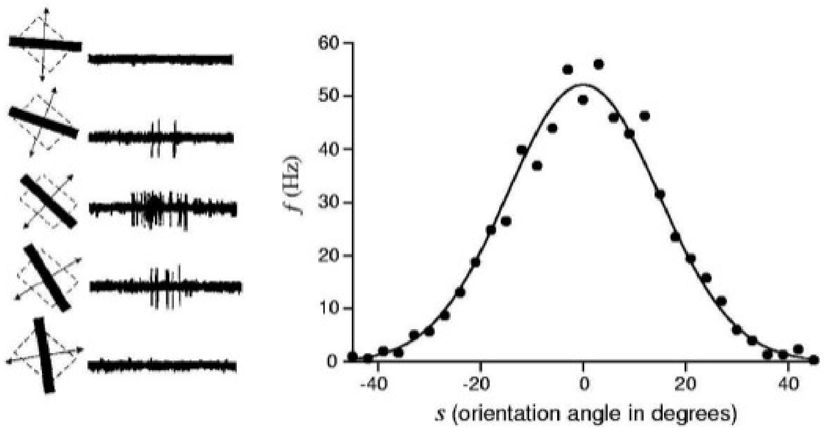
  - How do external inputs modify network connectivity through synaptic plasticity? How is learning implemented?

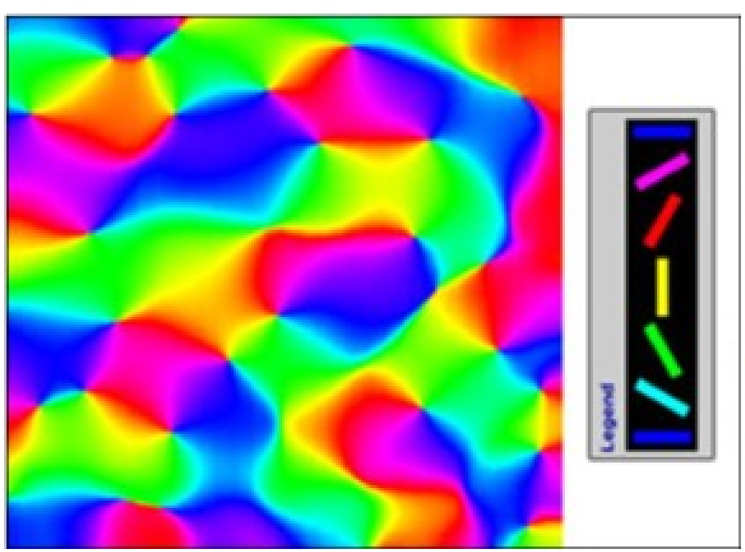
  - What is the impact of structuring in the connectivity on network dynamics?
- **Computation:** How do networks perform computations?

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

  ...

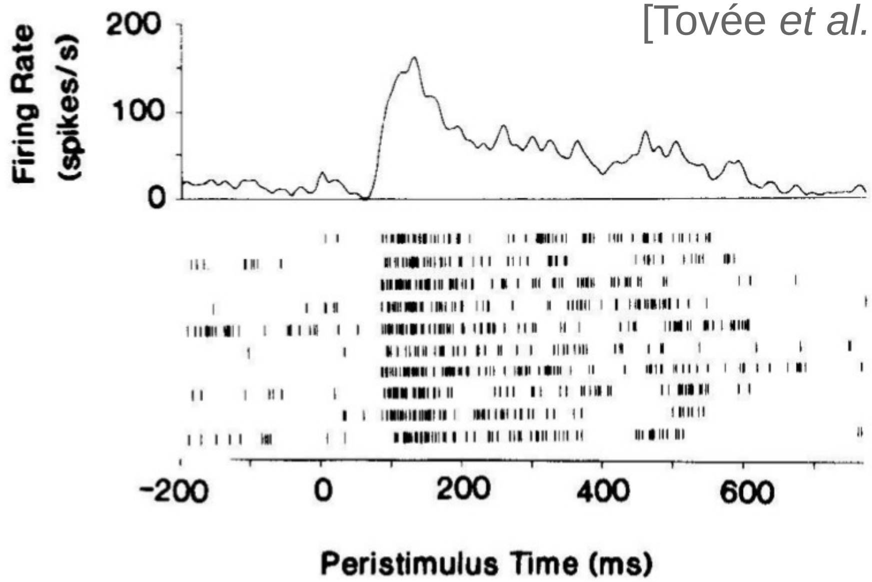
➡ **What are the mechanisms of spatial selectivity?**

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

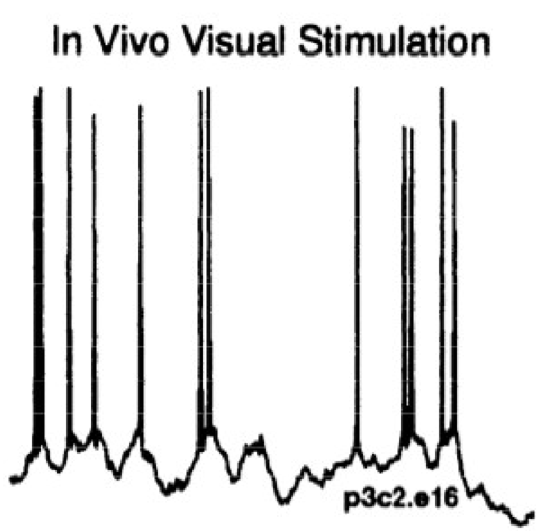
[Tovée *et al.* 1993]



Statistics of neural activity :

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

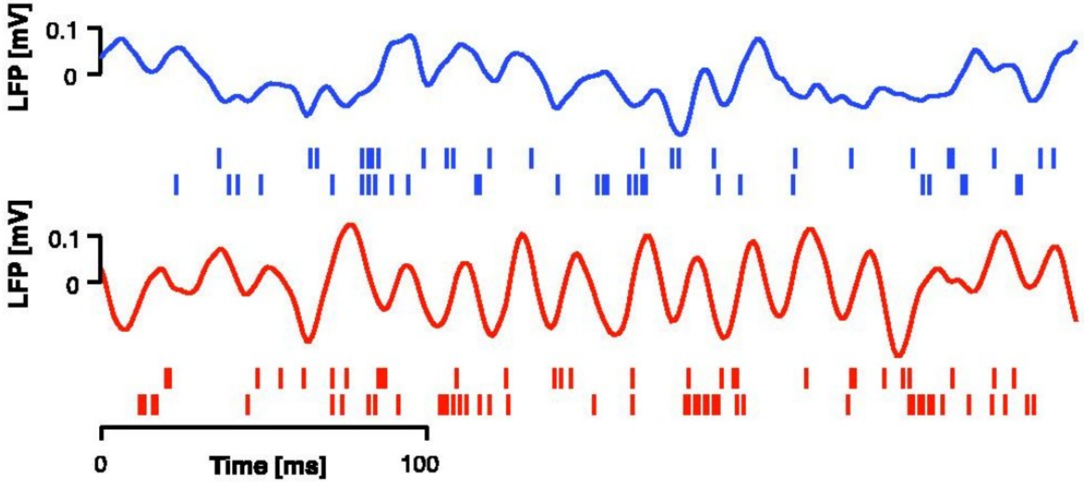
➡ **What are the mechanisms of irregular activity and large potential fluctuations ?**



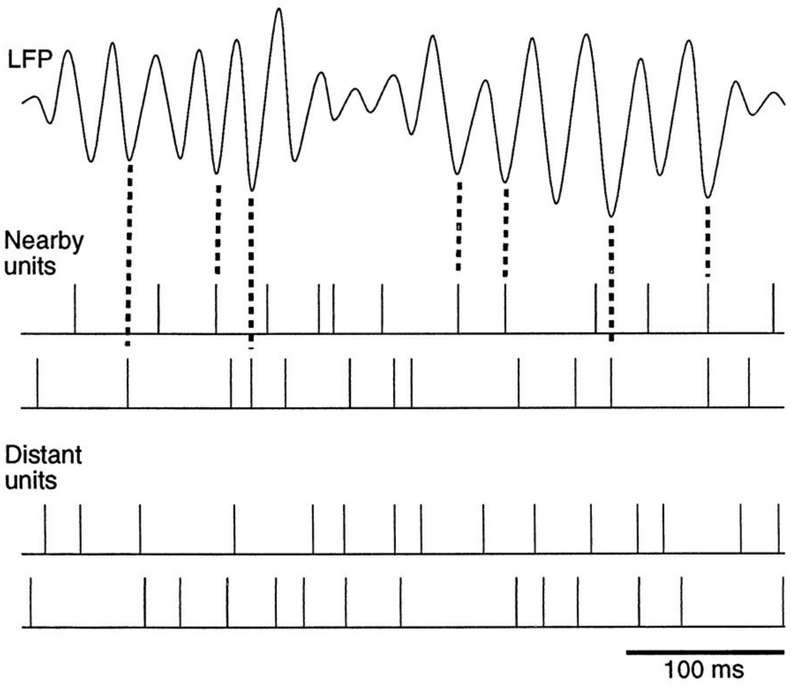
[Holt *et al.*, 1996]

Networks of spiking neurons : oscillations

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



[Fries *et al.* 2001]



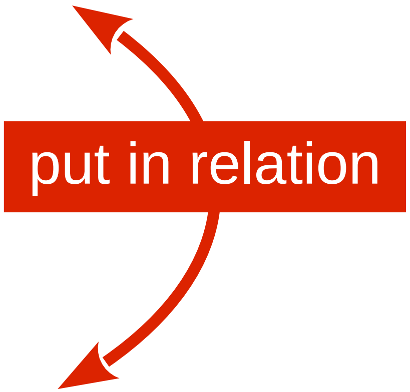
[Destexhe *et al.* 1999]

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

How to investigate a neural network model's behavior ?

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:

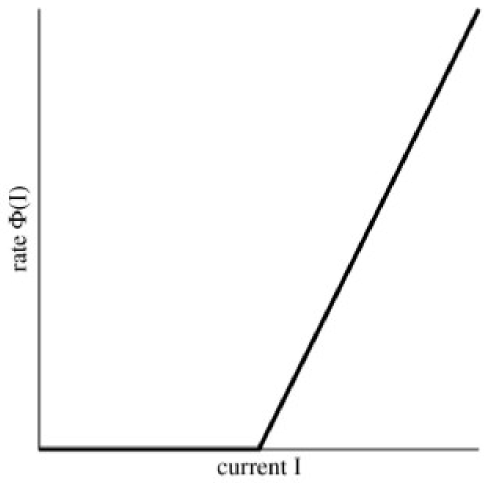
$$\tau \dot{r}(x,t) = -r(x,t) + \Phi\left(I(x,t) + \int dy\, J(|x-y|)\, r(y,t) \right)$$

- 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*

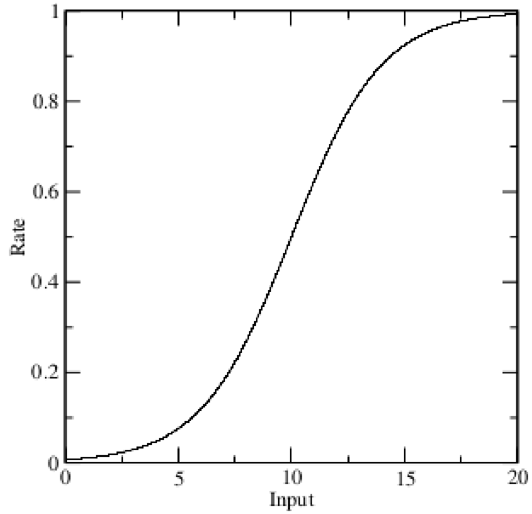
[Amari 1972, Wilson and Cowan 1972]

The transfer function Φ (.)

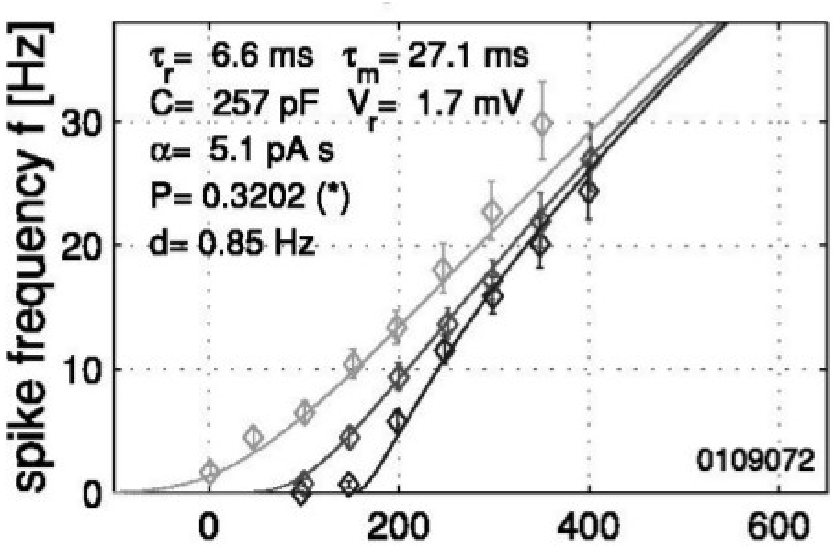
Threshold linear $\Phi(x)=[x-T]_+$



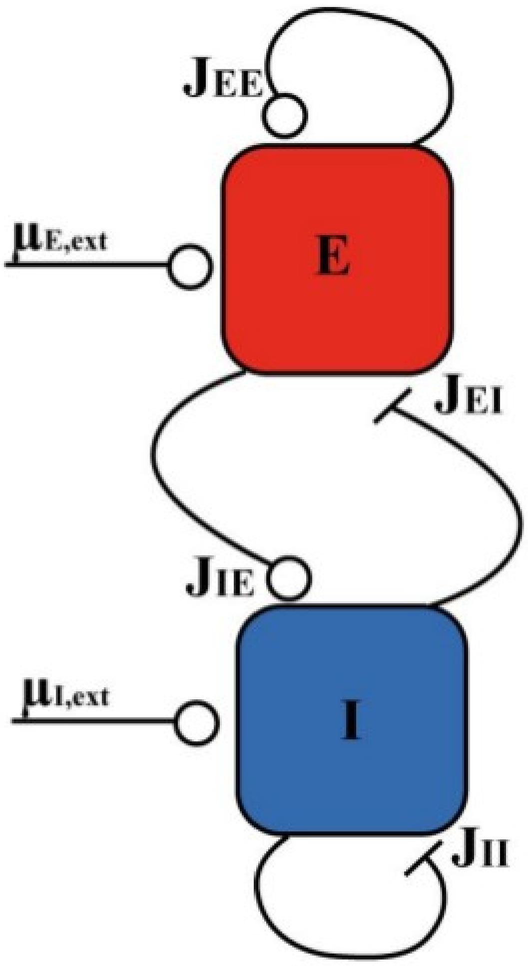
Sigmoidal $\Phi(x)=1/(1+\exp(-\beta(x-T)))$



f-I curve of a 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, $i = 1, \ldots, n$

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

- **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 model dynamics

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

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

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

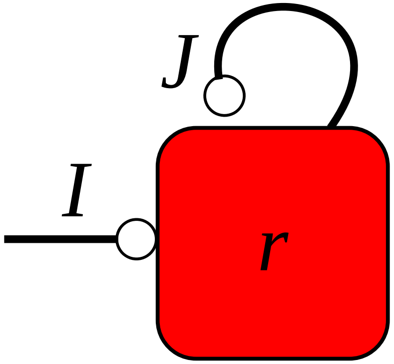
- Check linear stability of fixed points :
  - A small perturbation *δr* around the fixed point obeys the linearized dynamics

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

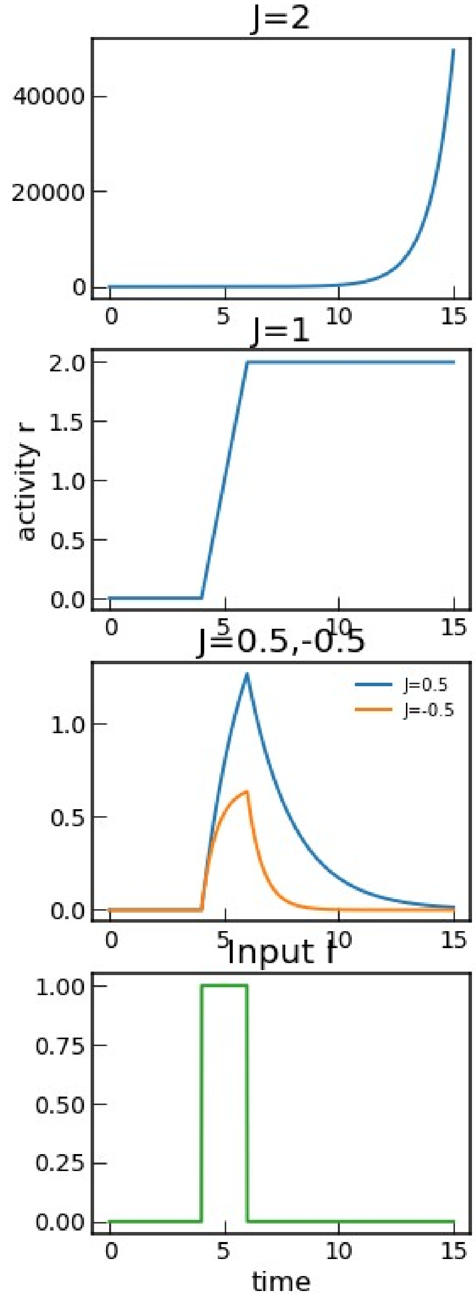
  - Compute eigenvalues λ of the Jacobian matrix (-1 + Φ**J**)

  - 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*

Example 1 - Simplest case : 1 population, linear Φ



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



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

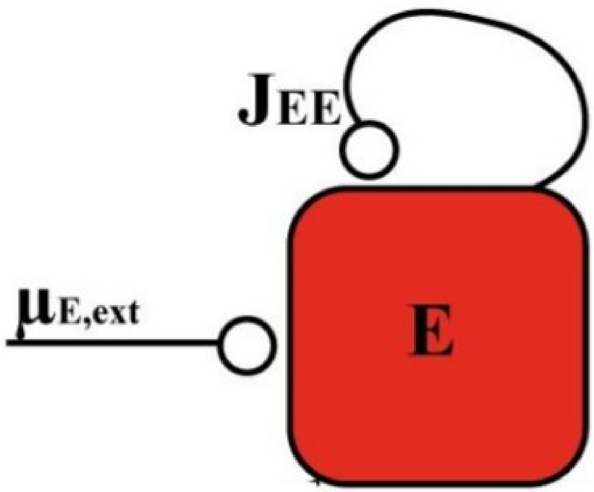
$$r(t) = \frac{1}{\tau} \int^{t} I(t')dt'$$

- Stable if *J < 1* :

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

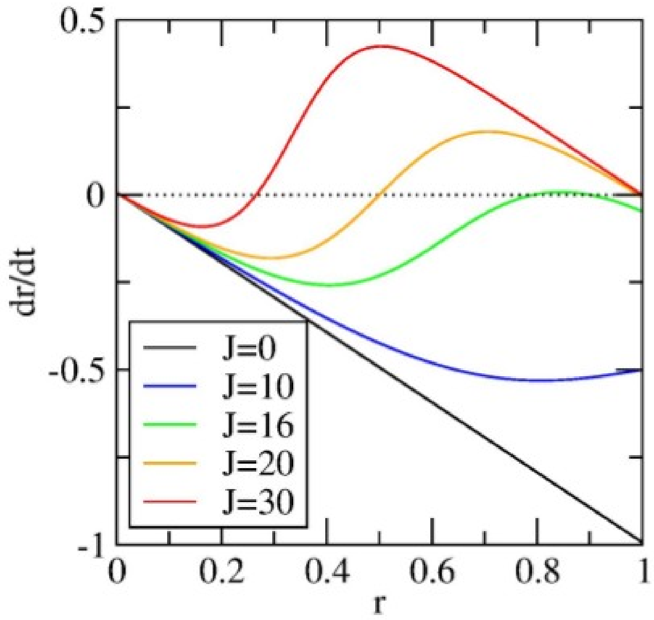
- Excitatory network (0 < *J* < 1): amplification of inputs, slow response
- Inhibitor network (J < 0): attenuation of inputs, fast response

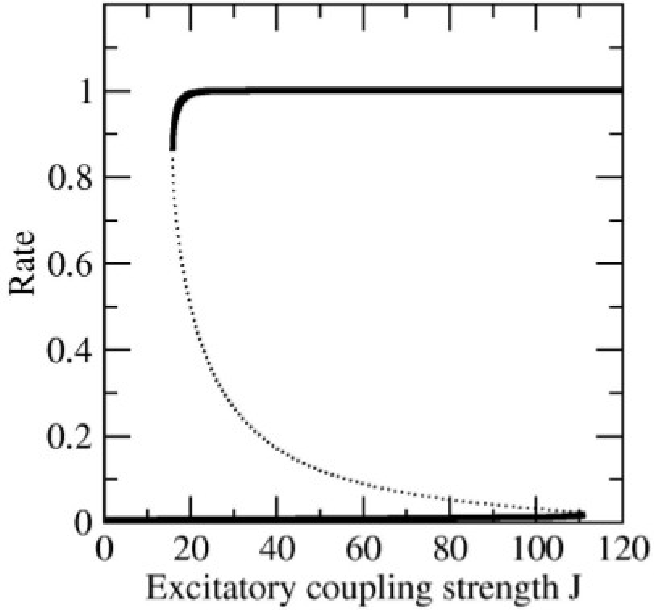
Example 2 :
E network rate model with bistability



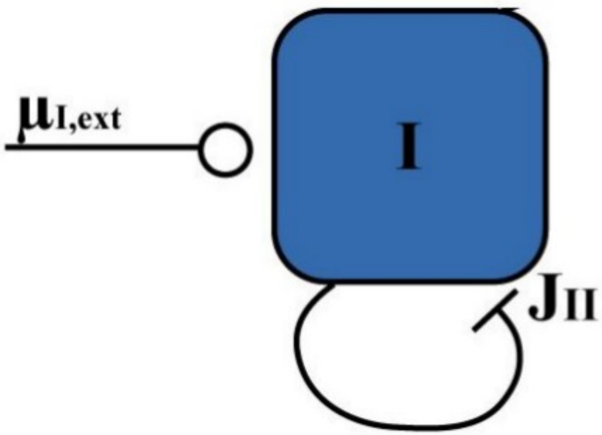
$$\tau \frac{dr}{dt} = -r + \Phi\left(I + Jr\right)$$

Sigmoidal transfer function Φ



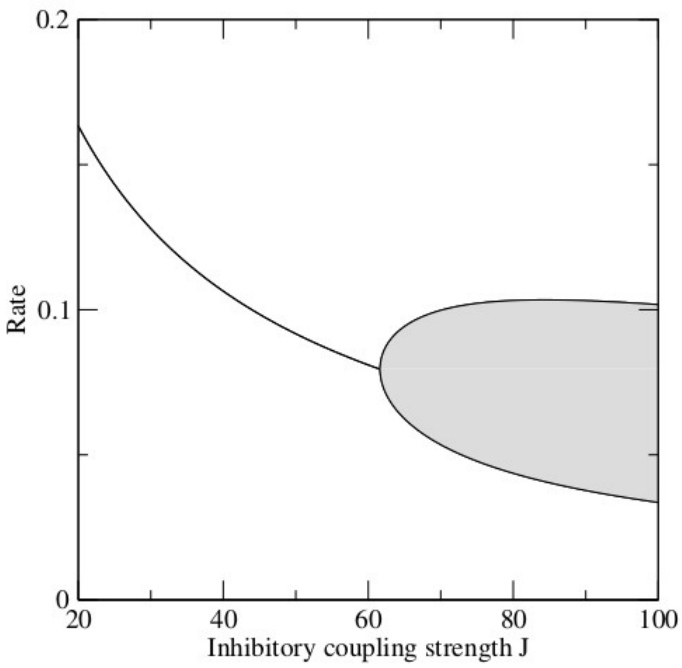


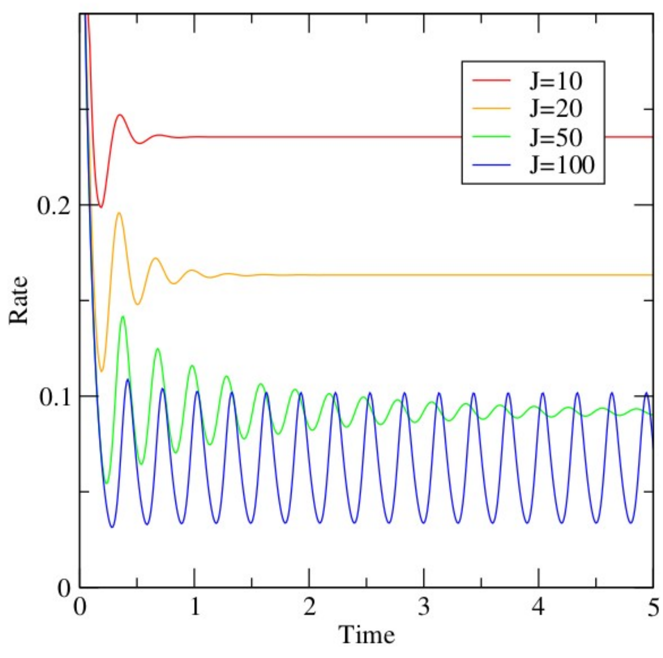
Example 3 : I network rate model with delays - oscillations



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

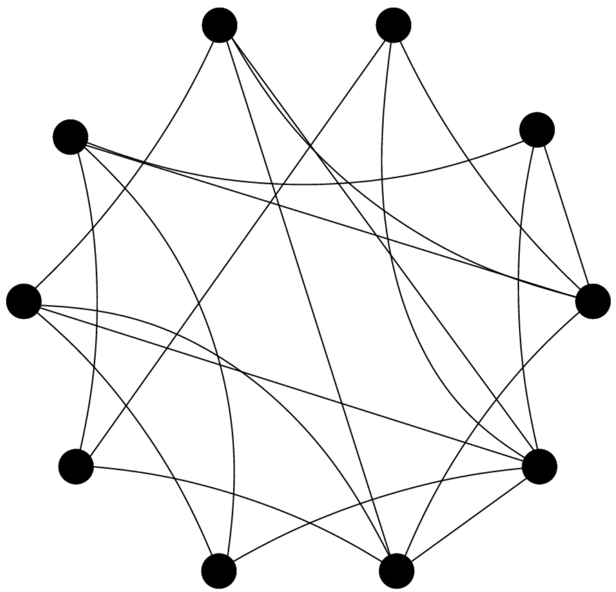
- oscillations at a frequency f_c appear when $\tilde{J}_{II} > J_c$
- For $D \ll \tau, J_c \sim \pi\tau/(2D), f_c \sim 1/(4D)$
- Frequency controlled by synaptic delays
  ⇒ fast oscillations in cortex/hippocampus?





Example 3 : 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