

Introduction to computational neuroscience : from single neurons to network dynamics

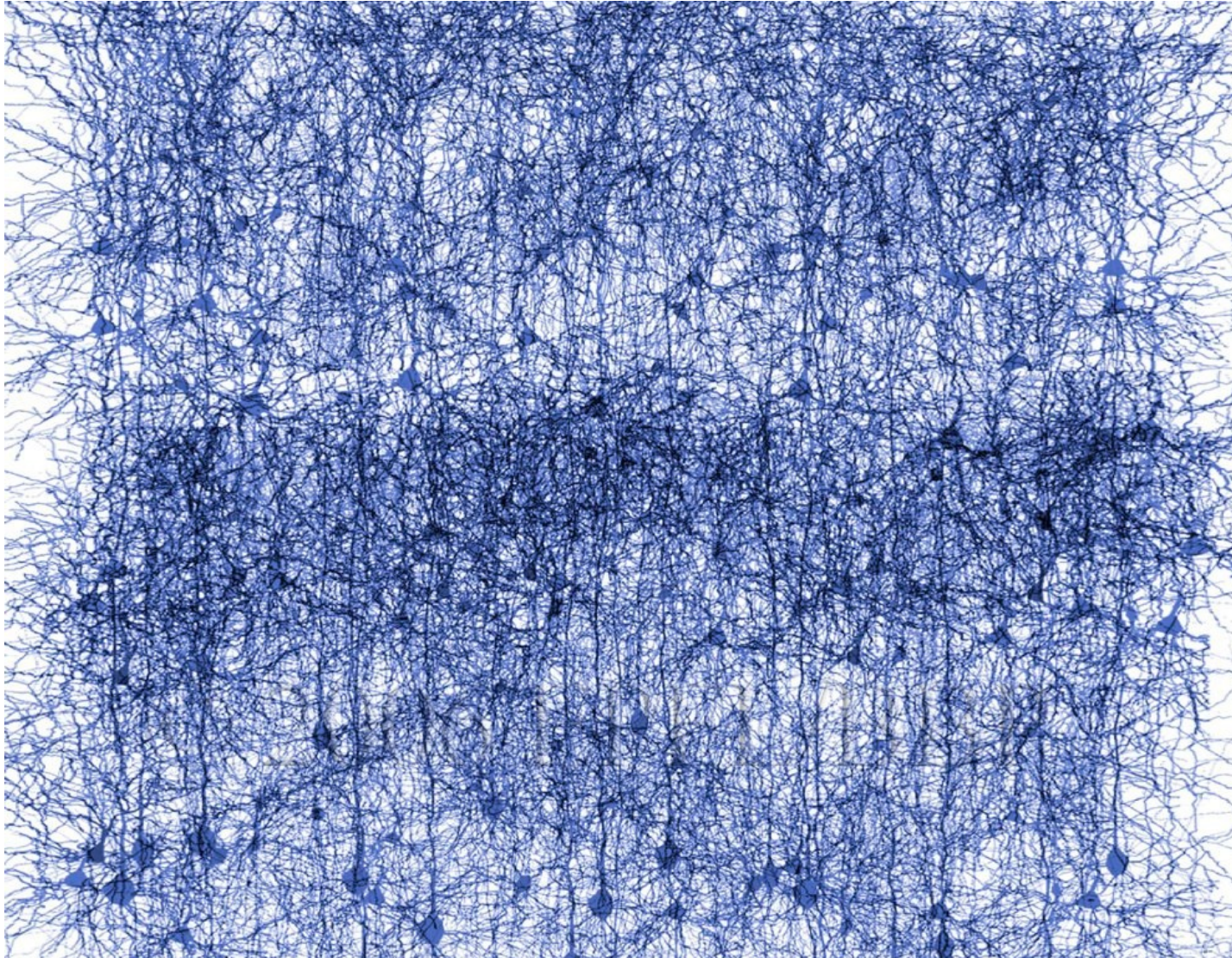


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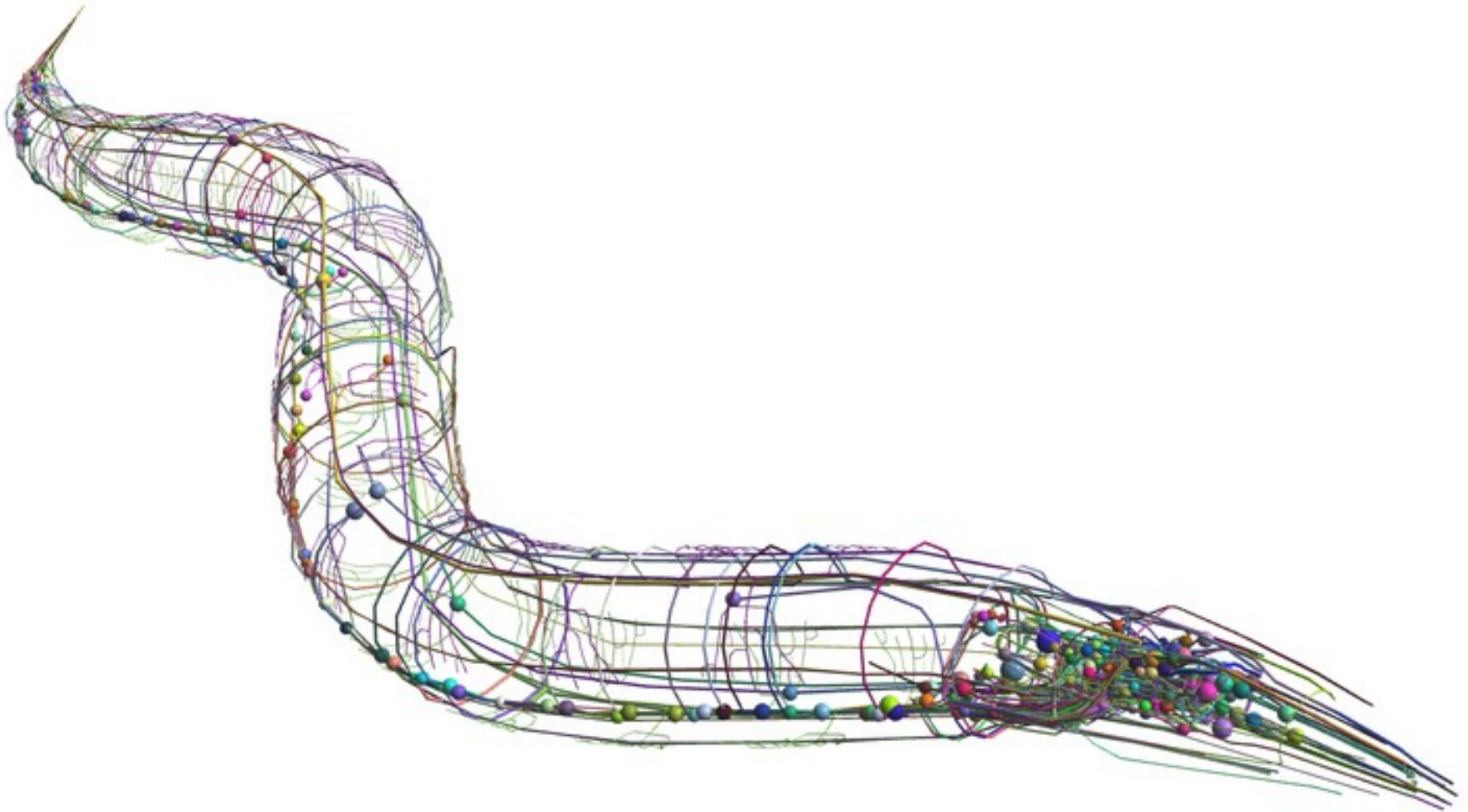
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Neurons form networks



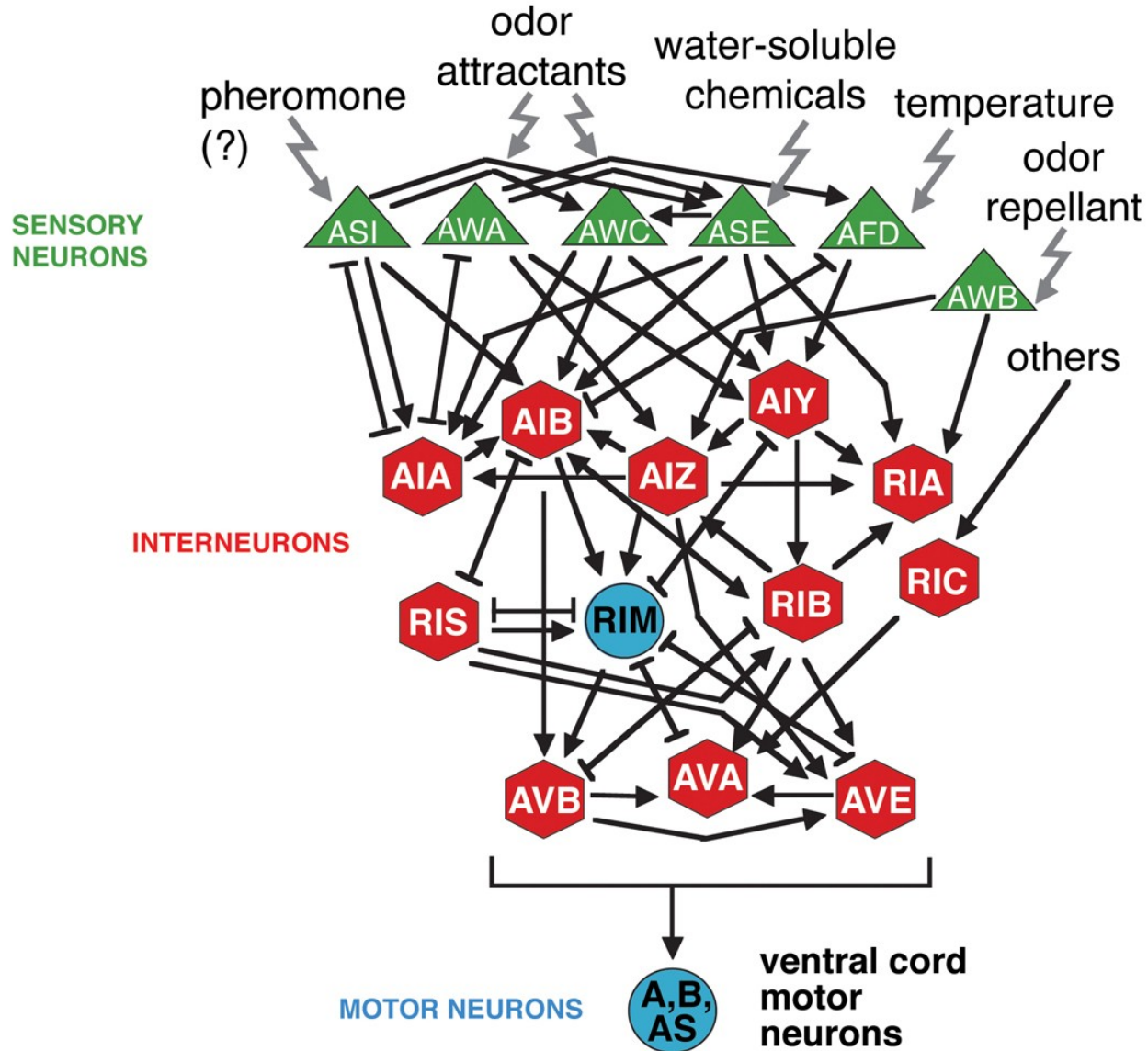
The brain : a network of 10^{11} neurons connected by 10^{15} synapses

C elegans : brain network



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

Brain network : from sensory to motor

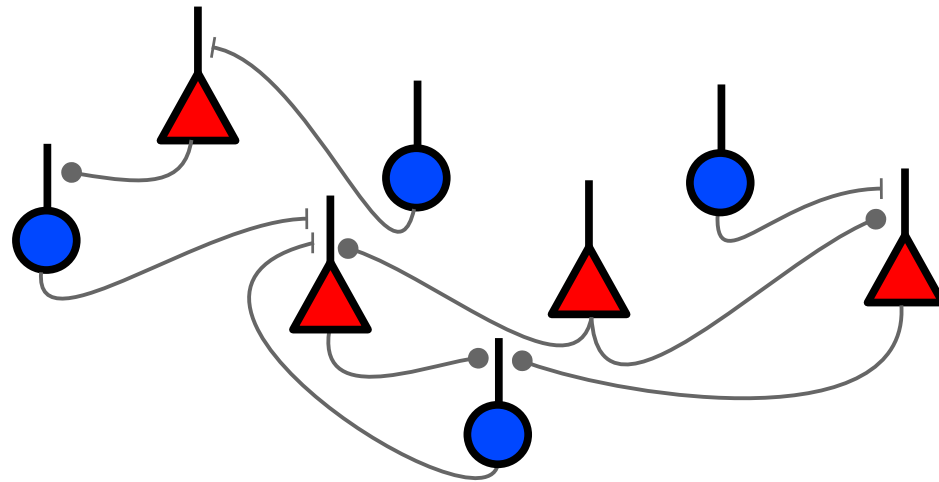


Two classes of neural network models

- **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.

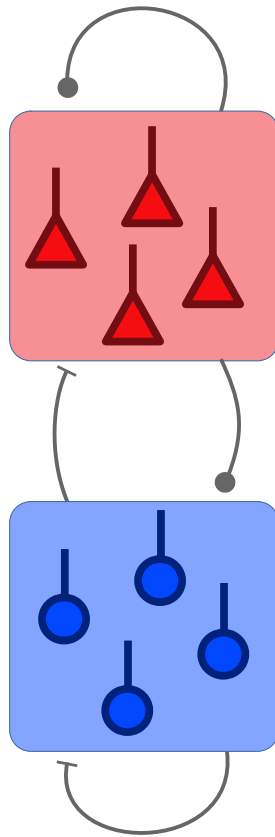
Network models : rate vs. spiking neural network

neural network



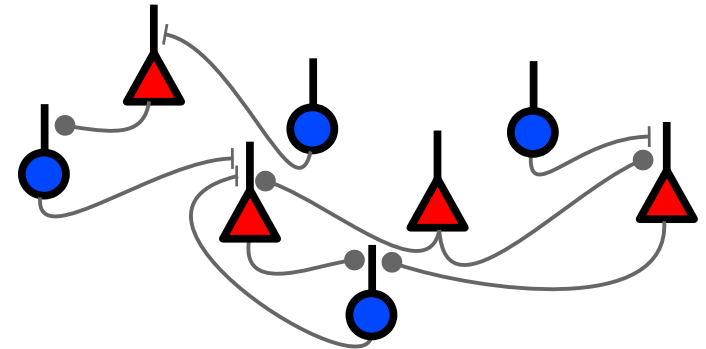
Network models : rate vs. spiking neural network

Rate model



ensembles of similar neurons are
grouped together

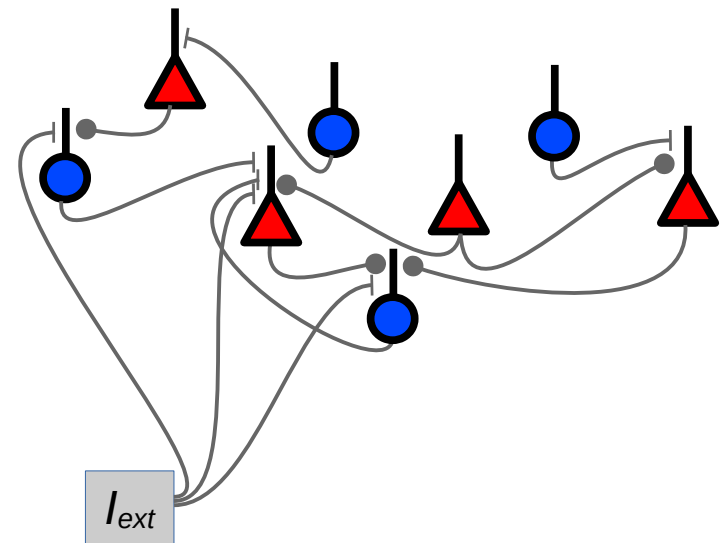
Spiking neuron model



each individual neuron is described

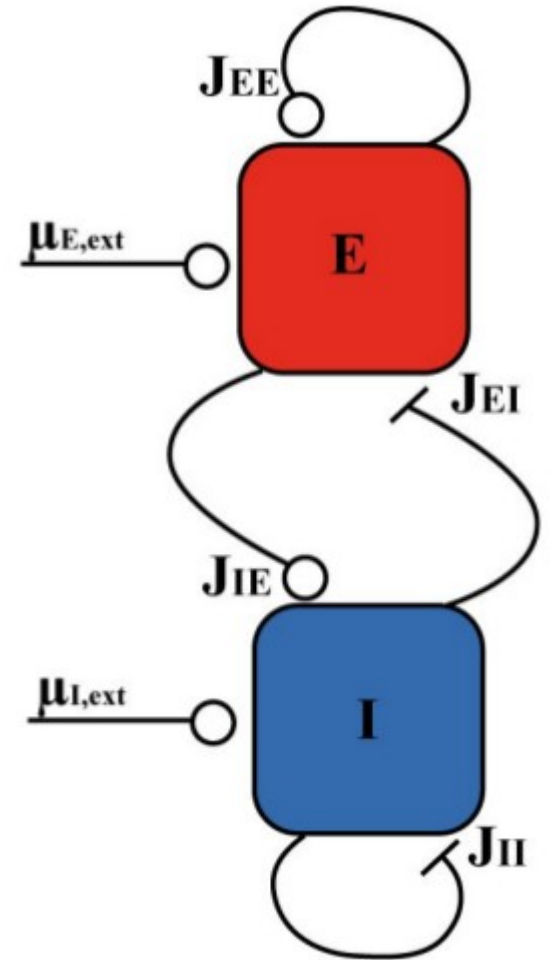
Network models : parts list

- 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) ?



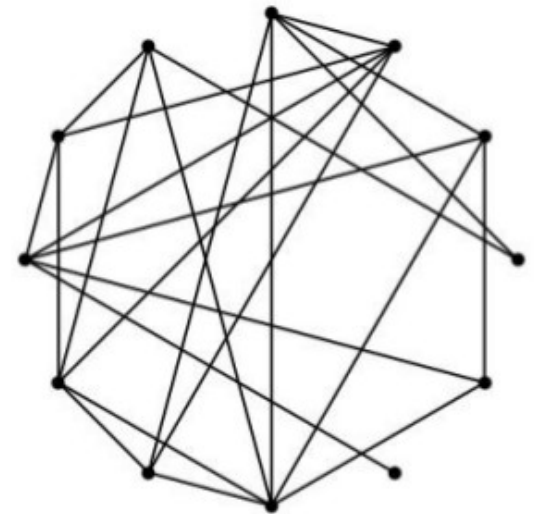
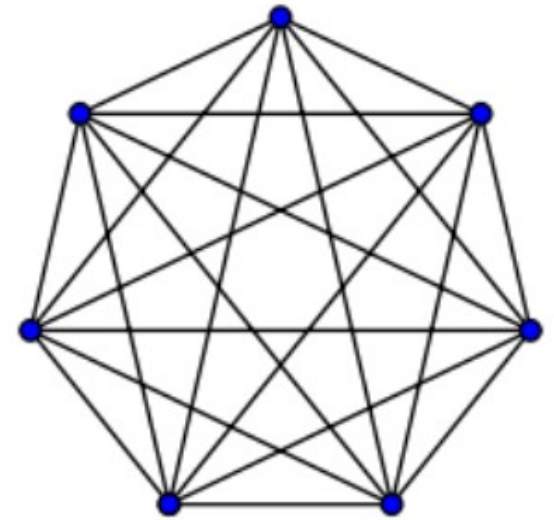
Types and numbers of neurons

- 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 : $N \rightarrow \infty$



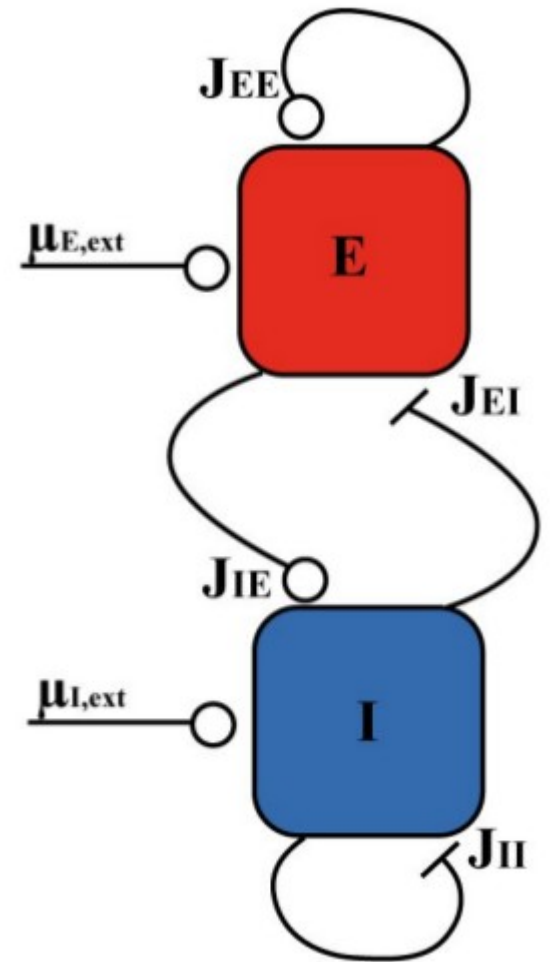
Connectivity matrix

- 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



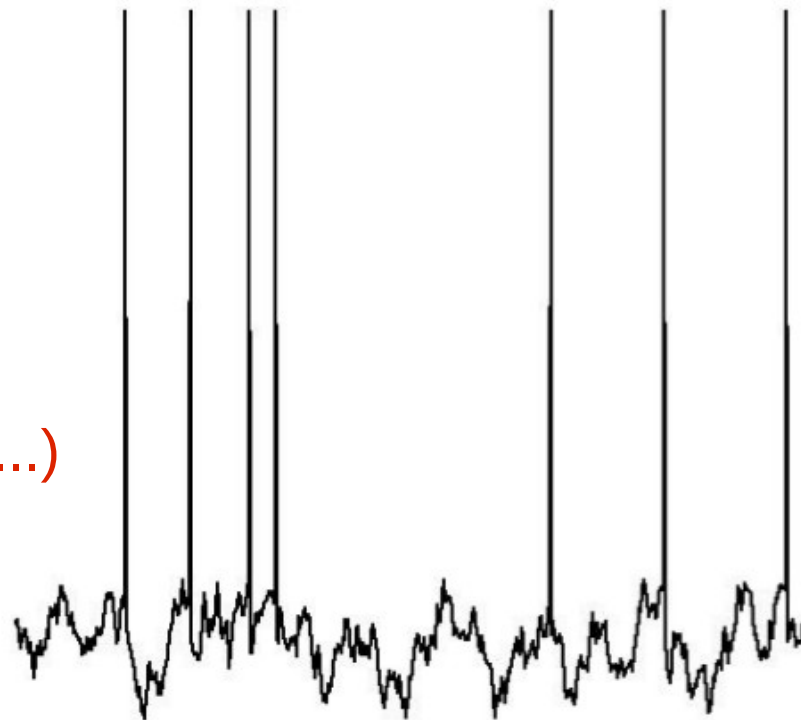
External inputs

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



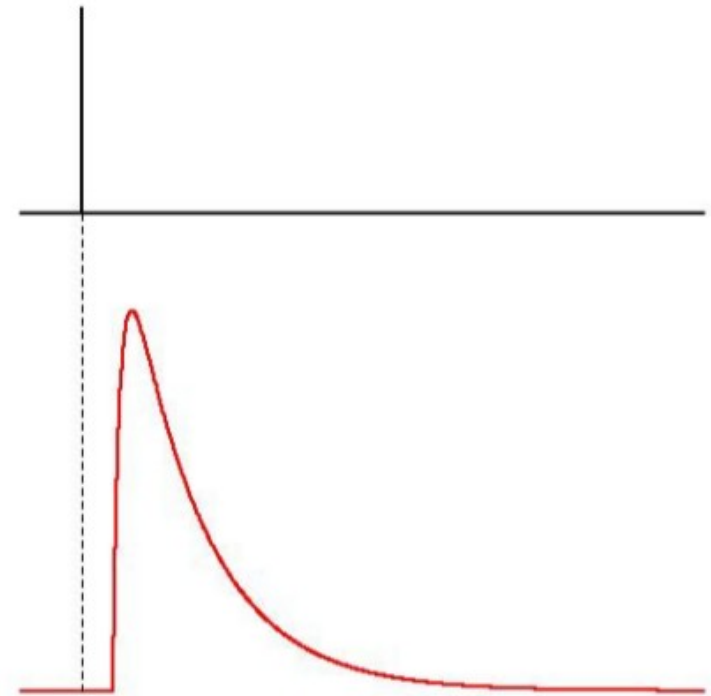
Neuron models

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



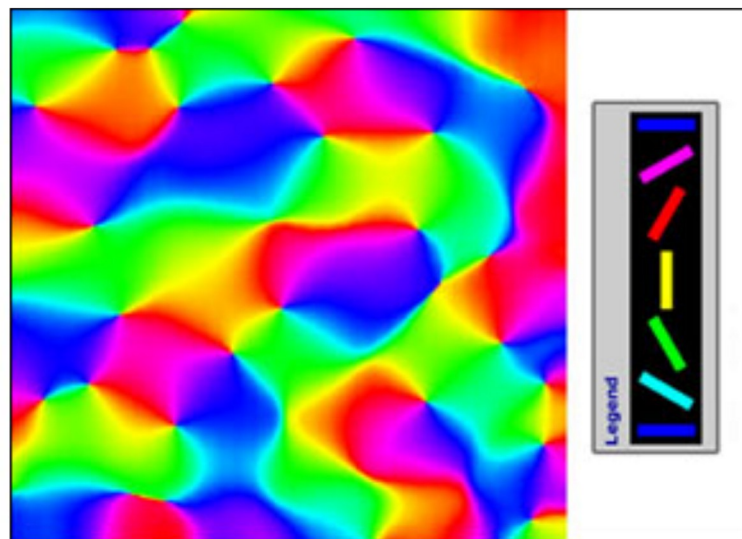
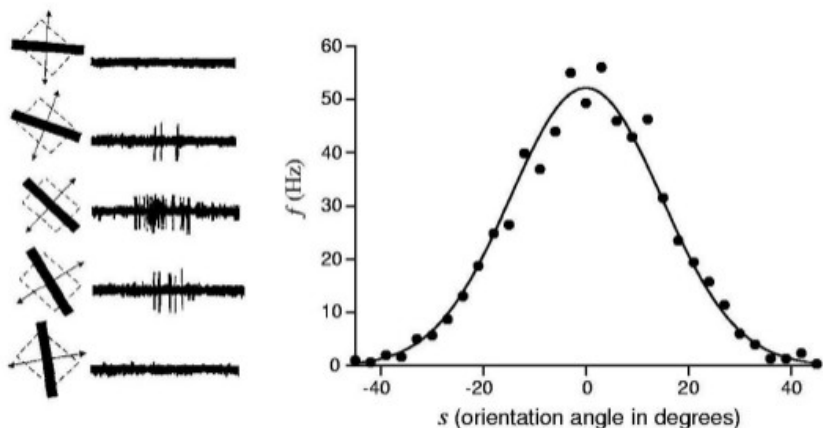
Questions

- **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

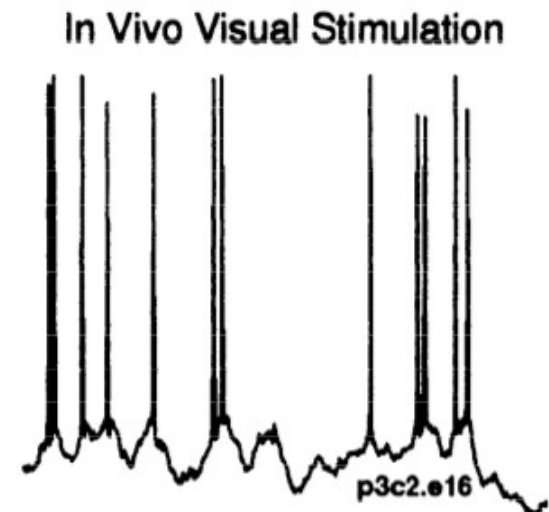
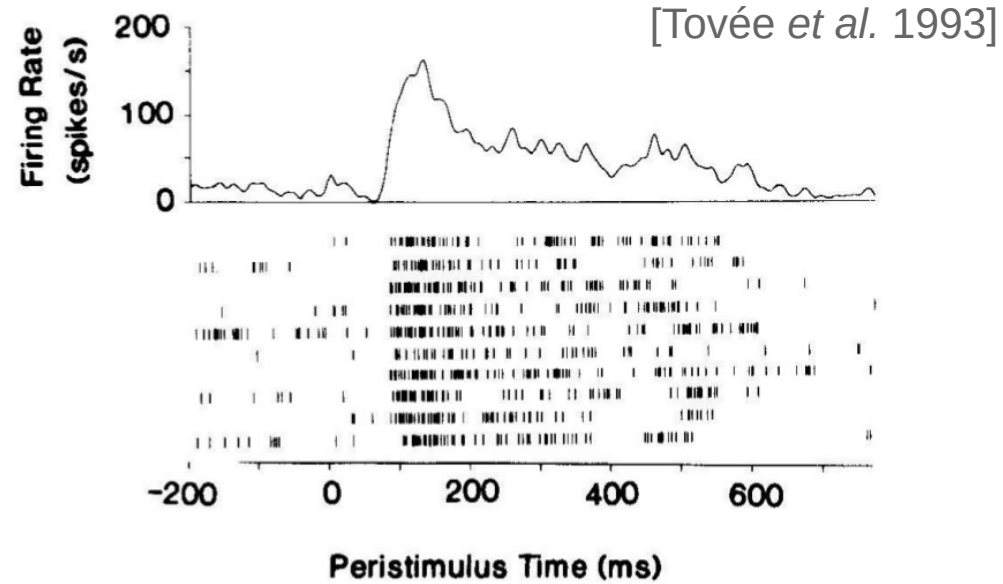
Spontaneous vs. selective/evoked activity :

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

Statistics of neural activity :

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

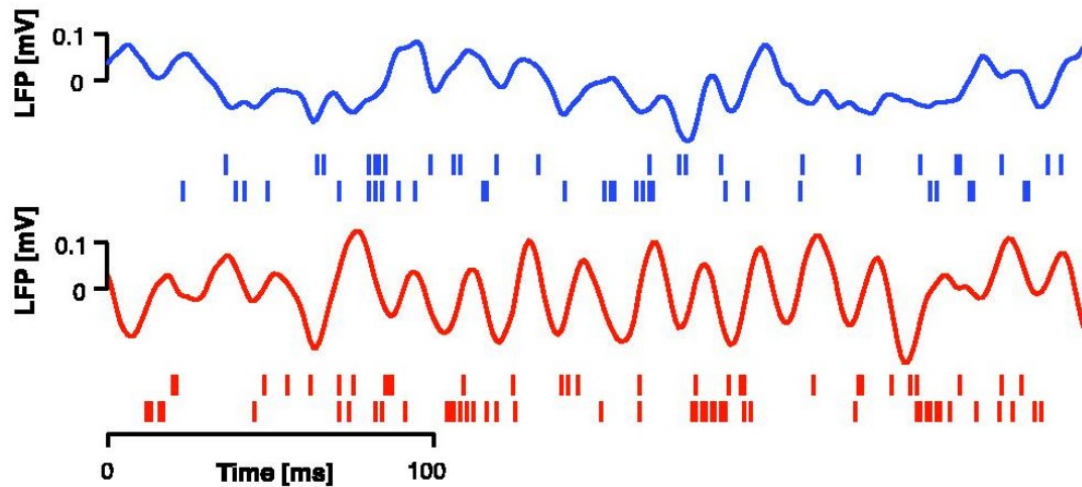
→ What are the mechanisms of irregular activity and large potential fluctuations ?



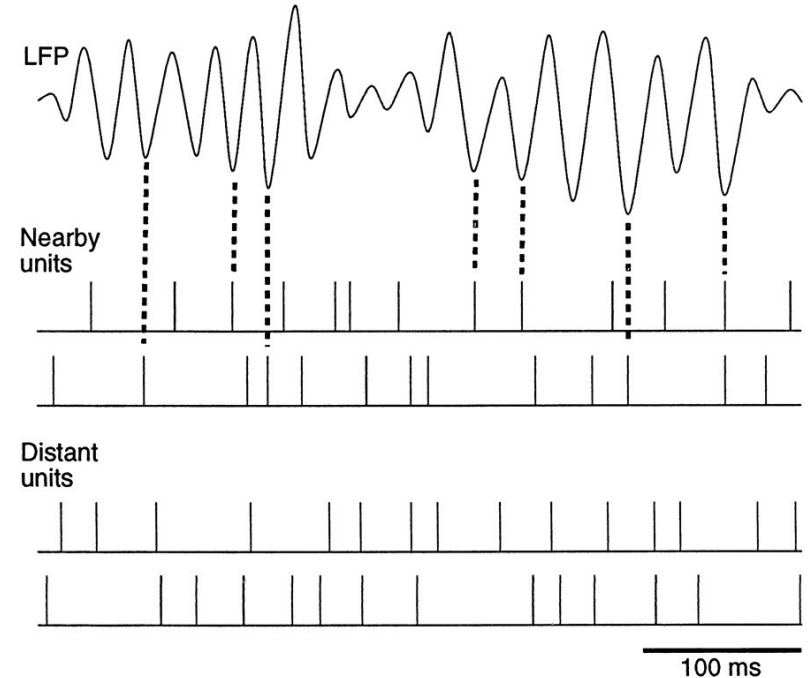
[Holt *et al.*, 1996]

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 ?

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

2nd Step : *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

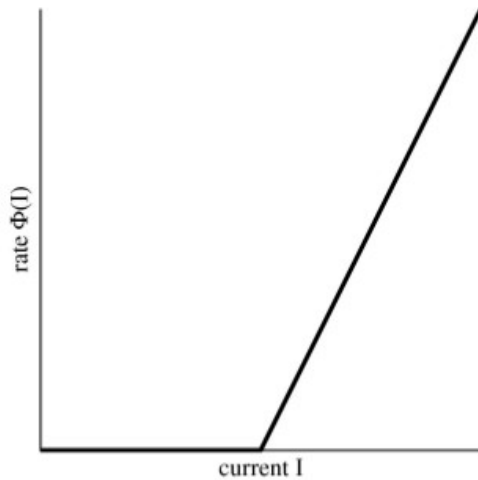
- In a 'rate model' (also called: 'firing rate model', 'neural mass model', 'neural field model', 'Wilson-Cowan model'), one describes the activity (instantaneous firing rate) of a population of neurons at a given location by a single analog variable:

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

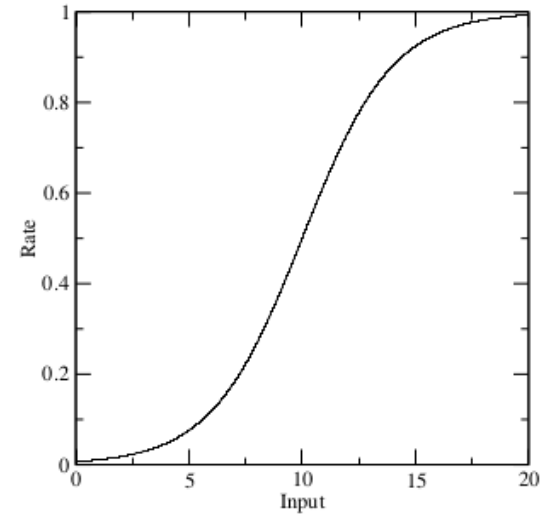
- τ : time constant of firing rate dynamics
- $r(x, t)$: firing rate of neurons at location x at time t
- $\Phi(\cdot)$: transfer function (f-I curve)
- $I(x, t)$: external input
- $J(x, y)$: strength of synaptic connections between neurons at locations x and y

The transfer function $\Phi(\cdot)$

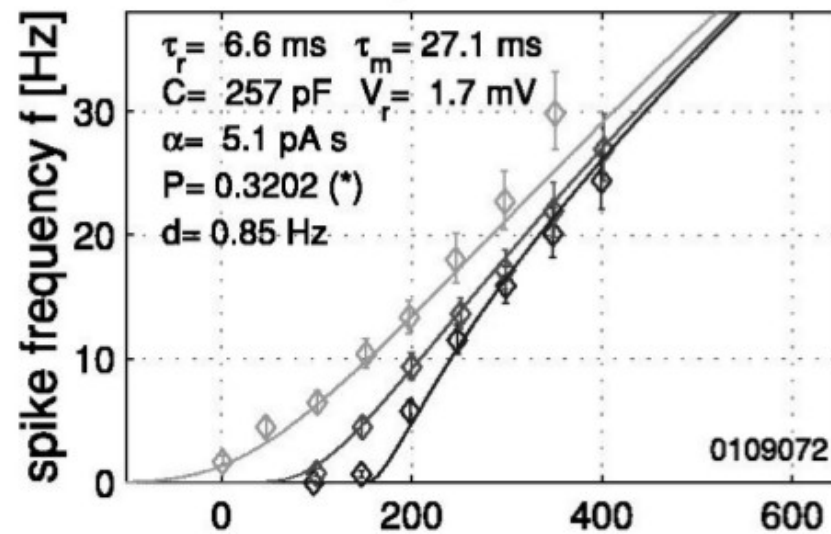
Threshold linear $\Phi(x) = [x - T]_+$



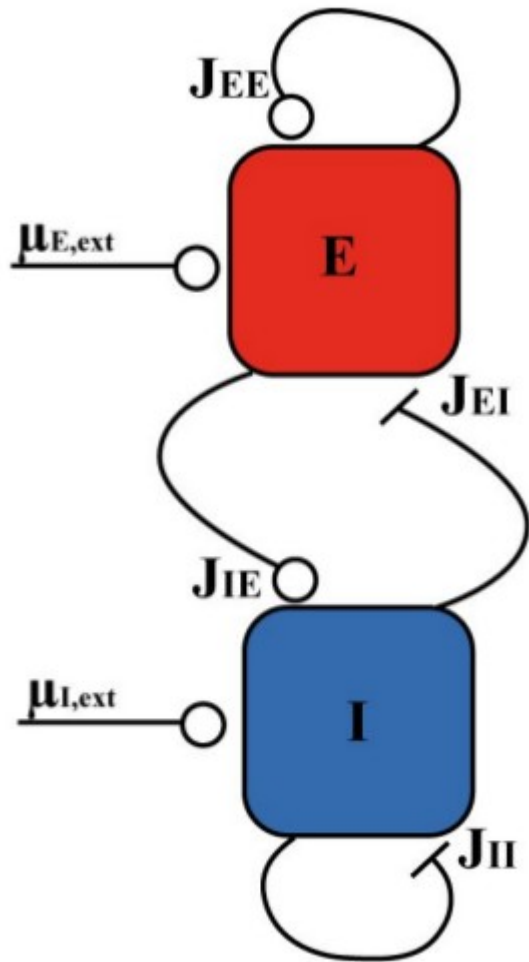
Sigmoidal $\Phi(x) = 1 / (1 + \exp(-\beta(x - T)))$



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 $\dot{r} = 0$:

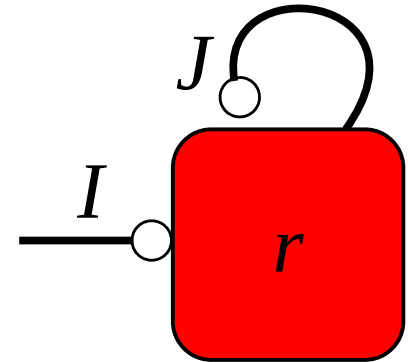
$$r_0 = \Phi(I + \mathbf{J} r)$$

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

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

- Compute eigenvalues λ 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 $\omega \neq 0$

Example 1 - Simplest case : 1 population, linear Φ



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

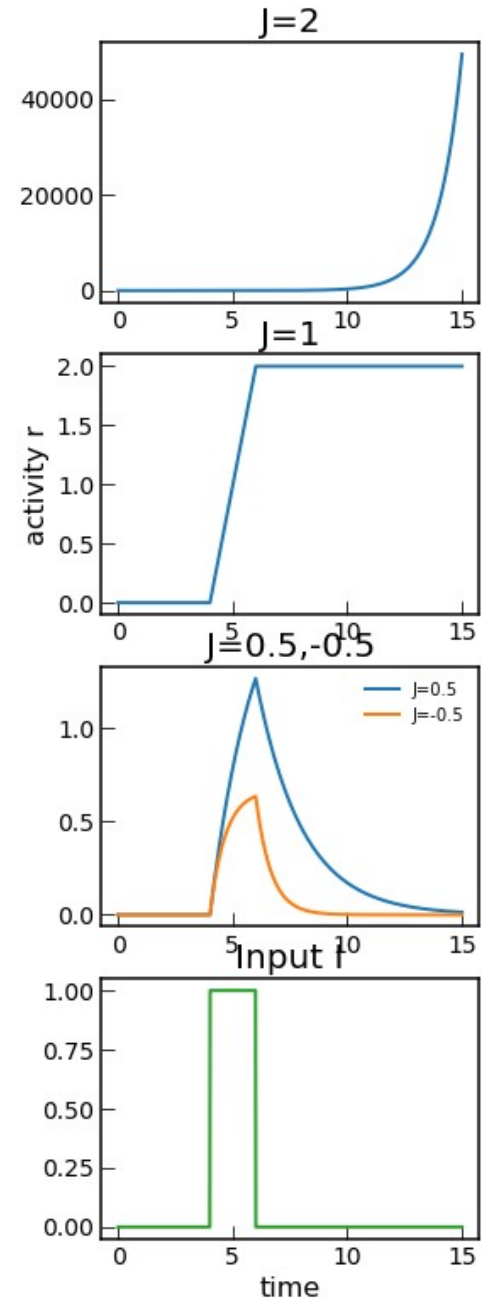
- Unstable if $J > 1$ ('rate instability')
- Perfect integrator if $J = 1$:

$$r(t) = \frac{1}{\tau} \int_0^t I(t') dt'$$

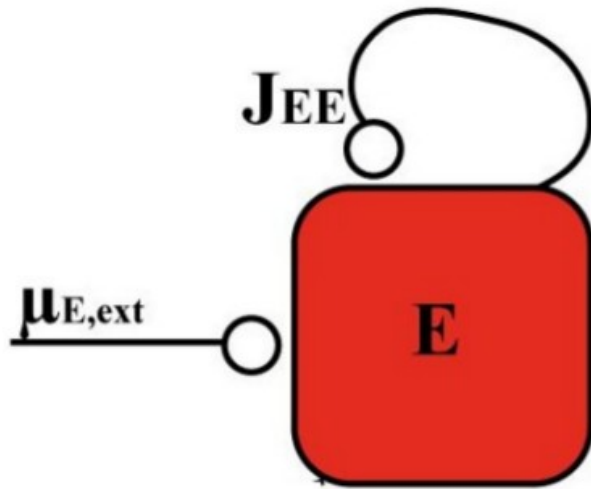
- Stable if $J < 1$:

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

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

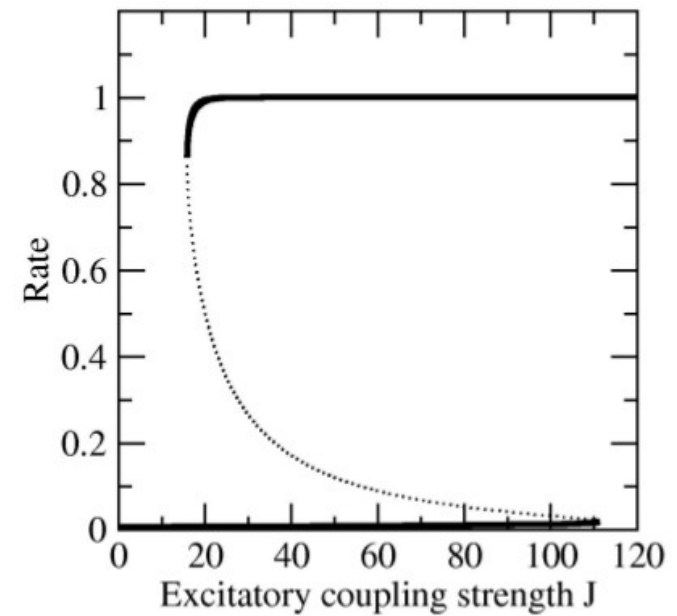
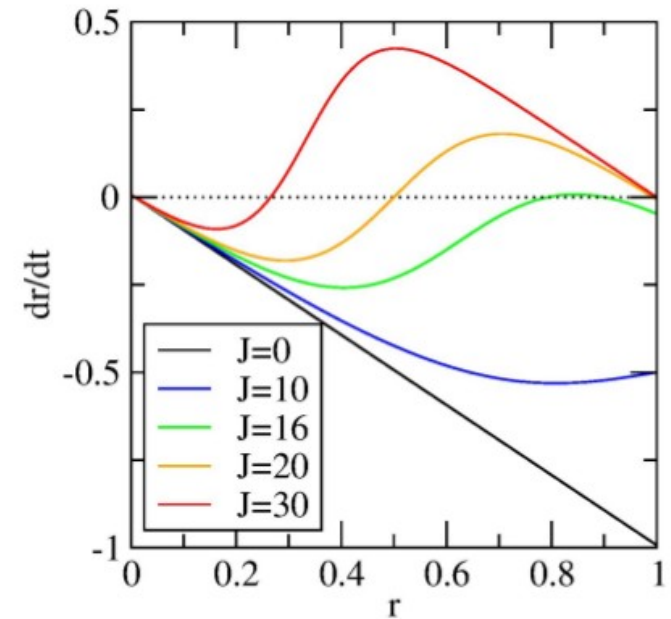


Example 2 : E network rate model with bistability

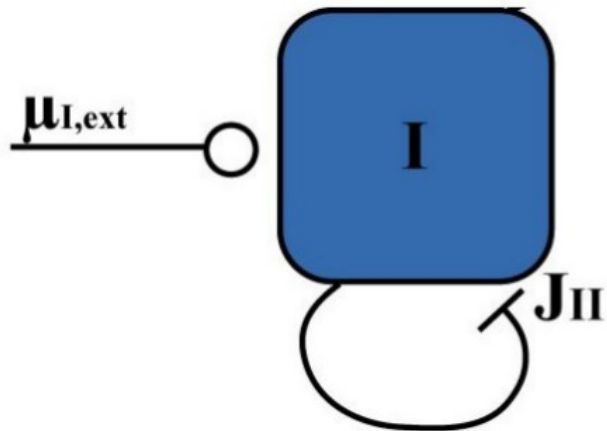


$$\tau \frac{dr}{dt} = -r + \Phi(I + Jr)$$

Sigmoidal transfer function Φ

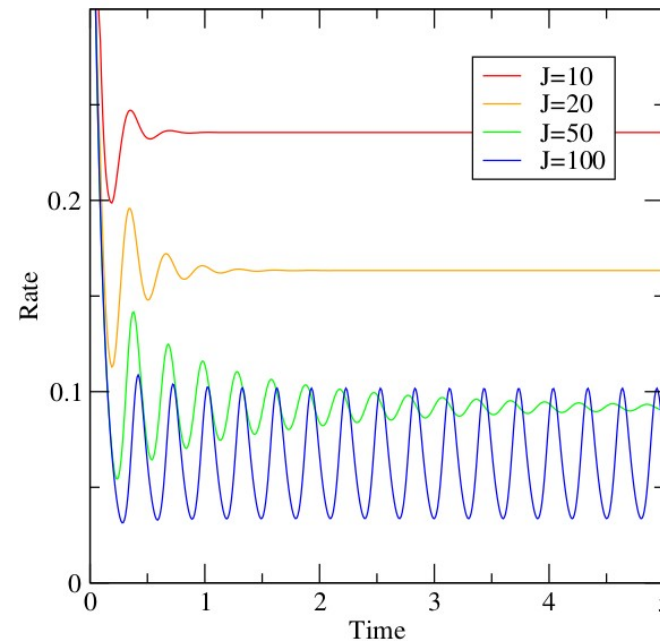
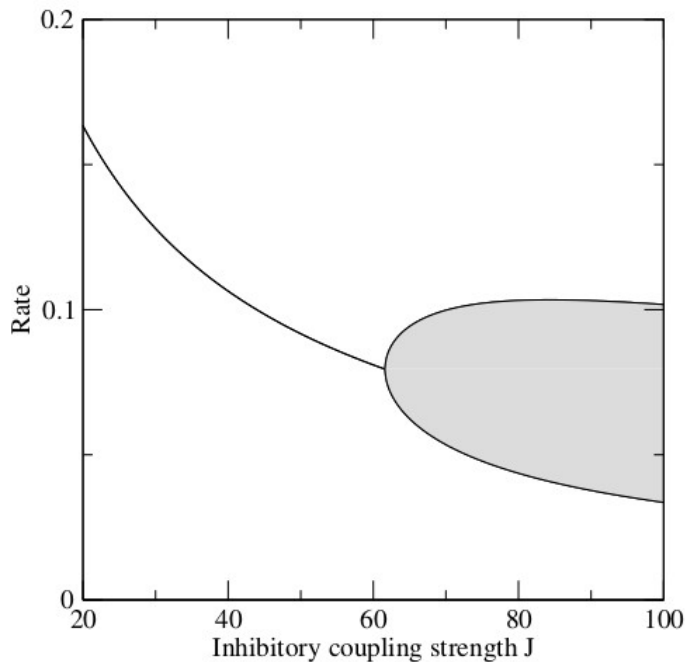


Example 3 : I network rate model with delays - oscillations



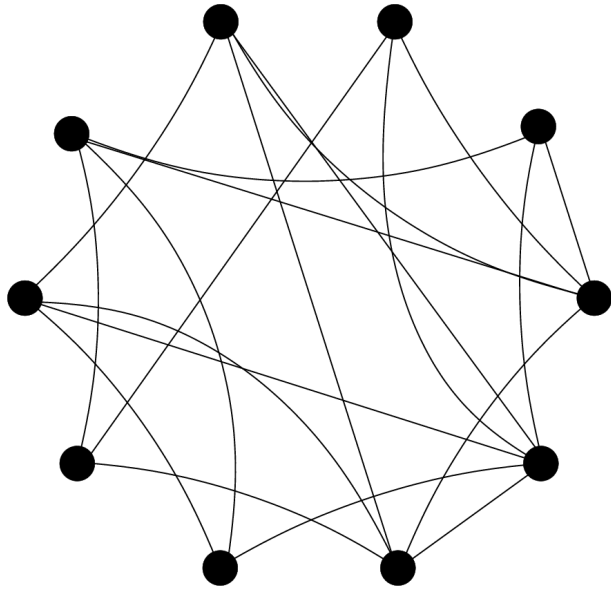
$$\tau \frac{dr_I}{dt} = -r_I + \Phi [I_{IX} - J_{II} r_I(t - D)]$$

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



$p = 0.2$

