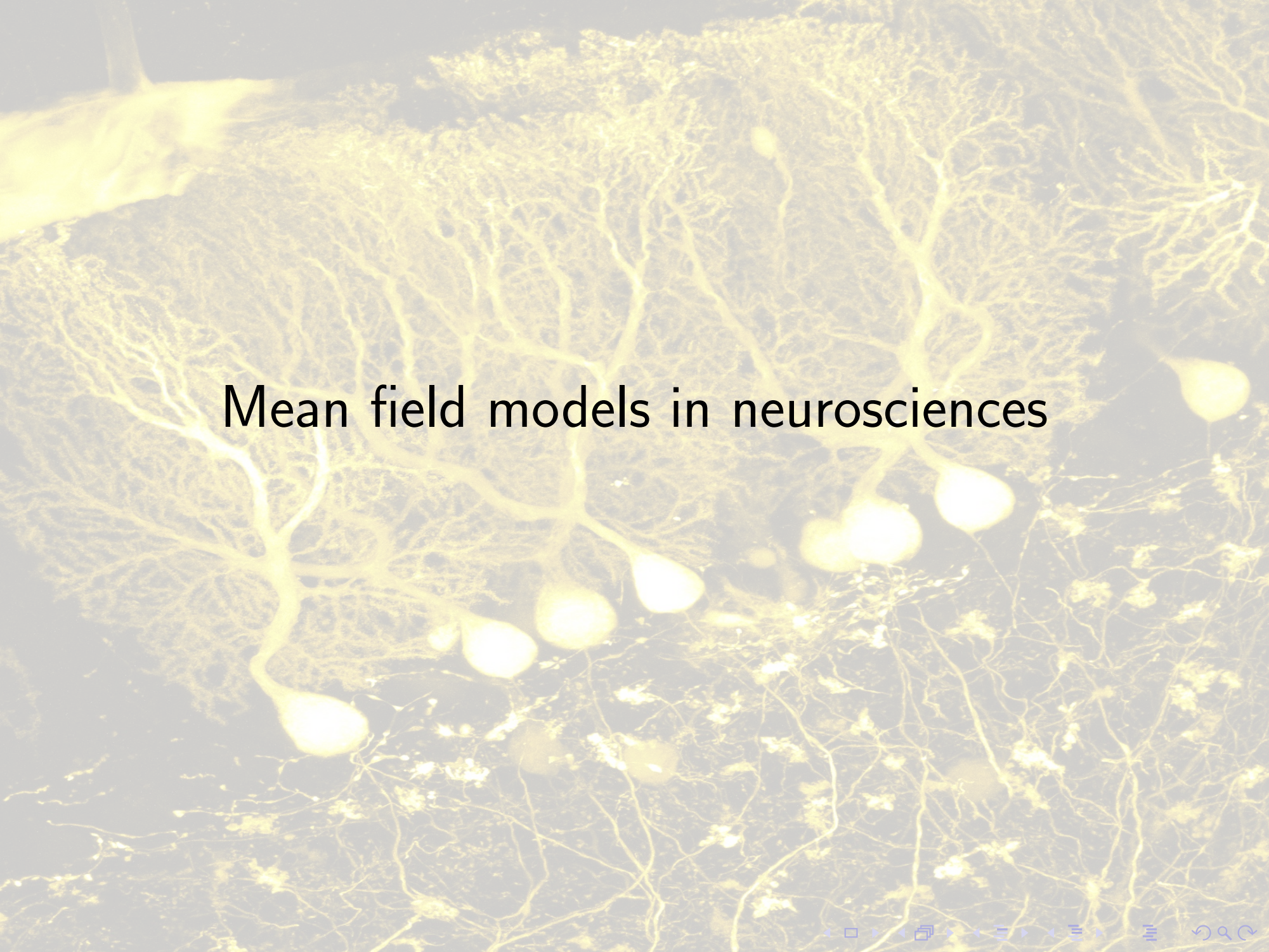

Mean field models in neurosciences

Introduction

In the study of higher function (e.g. sensory information processing, learning and pattern recognition) the focus on single neurons is not the best approach.

- The number of neurons involved is too vast.
- Higher functions are global processes, involving entire microcircuits. Local processes, e.g. the behaviour of a single neuron, are not too important.
- Random local interactions between neurons (short range interactions) give rise to precise long-range interactions at circuit level.

We can introduce a model which emphasizes the properties of a population of cells instead of focusing on individual neurons. We replace the interactions between the single neurons with a mean field, an average interaction.

Mean field - An idea from physics

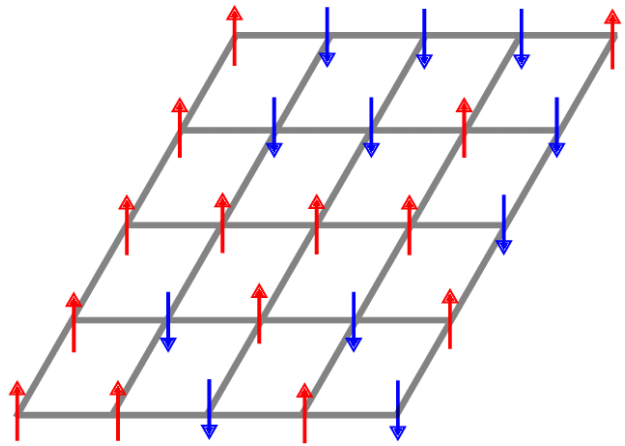
The idea to replace all interactions of the elements in a system with an average or effective interaction, first appeared in physics to describe phase transitions [Weiss (1907), Lenz (1920), Ising (1925)].

The prototypical model for the mean field is the Ising model, a mathematical model of ferromagnetism in statistical mechanics.

Mean field - An idea from physics

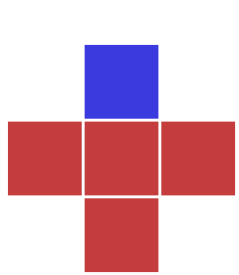
The model consists of discrete variables that represent magnetic dipole moments of atomic (spins) that can be in one of two states:

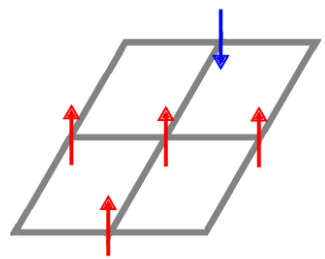
- $+1, \uparrow$: Updward magnetization.
- $-1, \downarrow$: Downward magnetization.



Picture from 'Thermalisation and Relaxation of Quantum Systems', S. S. Wald, HAL science ouverte.

The spins are arranged in a lattice and each spin can interact with its nearest neighbors.





The Ising model

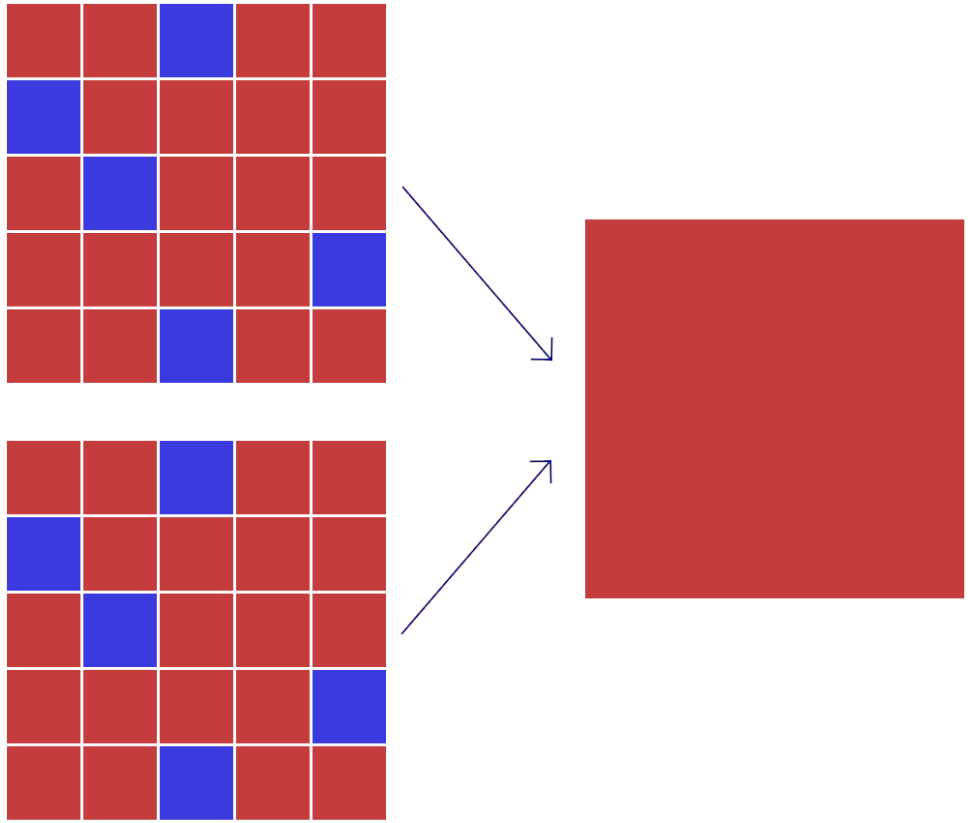
The energy of the system is given by

$$H = -J \underbrace{\sum_{i,j}^{N} S_i S_j}_{\substack{\text{Each molecule} \\ \text{interacts with its} \\ \text{neighbrohoods}}}$$

Neighboring spins that agree ($\uparrow\uparrow$ or $\downarrow\downarrow$) have a lower energy than those that disagree; the system tends to the lowest energy but heat disturbs this tendency, thus creating the possibility of different structural phases. The interactions between the microscopic magnetization of the atoms in the ferromagnet give rise to a macroscopic magnetic field that we can measure.

The Ising model

Different microscopic configurations correspond the the same macroscopic magnetic field.



To study the macroscopic behavior we do not need to know the fine details of the system.

The Ising model

The probability to find the system in a certain microscopic configuration is proportional to the Boltzmann factor

$$p \propto e^{-\beta H(S_1, S_2, \cdots, S_N)}$$

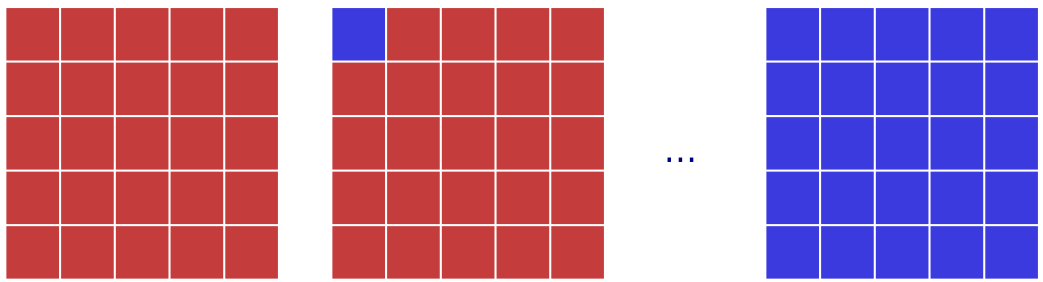
The parameter $\beta \propto 1/T$, with T the temperature of the system, controls the degree of order of the system.

The Ising model

We normalize this probability using the partition function, computed summing the Boltzmann factors of every possible microscopic configuration.

$$Z = \sum_{\substack{\text{All the configurations} \\ \text{of the spins}}} e^{-\beta H} = \sum_{S_1=\pm 1} \sum_{S_2=\pm 1} \cdots \sum_{S_N=\pm 1} e^{-\beta H}$$

$$Z = e^{-\beta H(\uparrow\uparrow\ldots\uparrow)} + e^{-\beta H(\downarrow\uparrow\ldots\uparrow)} + \cdots + e^{-\beta H(\downarrow\downarrow\ldots\downarrow)}$$



The Ising model

The partition functions allows us to connect the microscopic and the microscopic worlds.

$$p(S_1, S_2, \cdots, S_N) = \frac{1}{Z} e^{-\beta H(S_1, S_2, \cdots, S_N)}$$

For example

$$p(\downarrow\downarrow \ldots \downarrow) = \frac{e^{-\beta H(\downarrow\downarrow \ldots \downarrow)}}{Z} = \frac{-e^{\beta H(\downarrow\downarrow \ldots \downarrow)}}{e^{-\beta H(\uparrow\uparrow \ldots \uparrow)} + \ldots + e^{-\beta H(\downarrow\downarrow \ldots \downarrow)}}$$

The Ising model

Now we can compute the macroscopic (average) values corresponding to microscopic observables.

For example the total average magnetization of the material is

$$M = \langle \sum_{i=1}^{N} S_i \rangle = p(\uparrow\uparrow \ldots \uparrow) \sum_{i=1}^{N} S_i + \ldots + p(\downarrow\downarrow \ldots \downarrow) \sum_{i=1}^{N} S_i$$

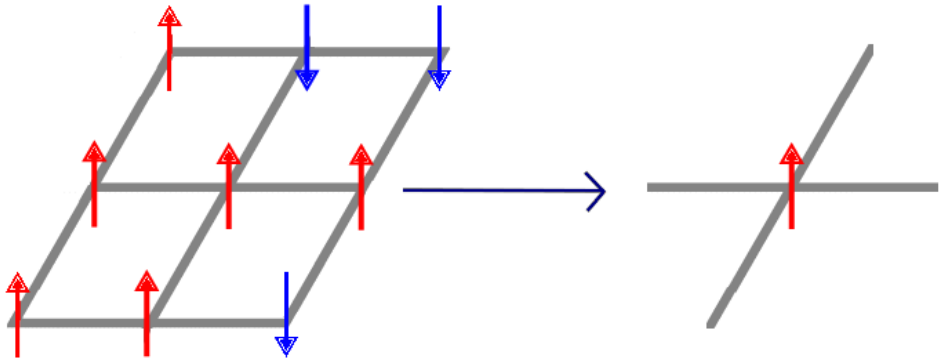
or

$$M = \langle \sum_{i=1}^{N} S_i \rangle = \frac{1}{Z} \sum_{\mathcal{C}} \sum_{i} S_i e^{\beta H(\mathcal{C})} = \sum_{\mathcal{C}} \left(p(\mathcal{C}) \sum_{i} S_i \right)$$

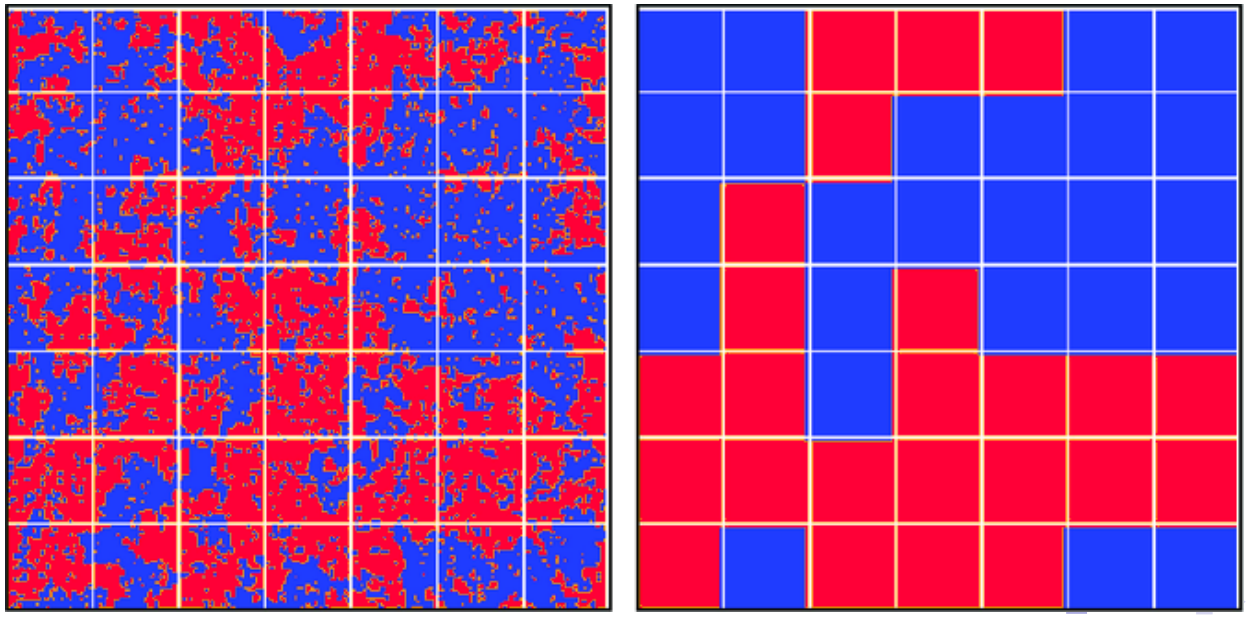
Problem: There are too many configurations
$\rightarrow$ This sum is difficult to compute.

Coarse graining

Instead of observing the single spin, we group several molecules considering a square grid and we assign to each square the average magnetization of the group of spins.

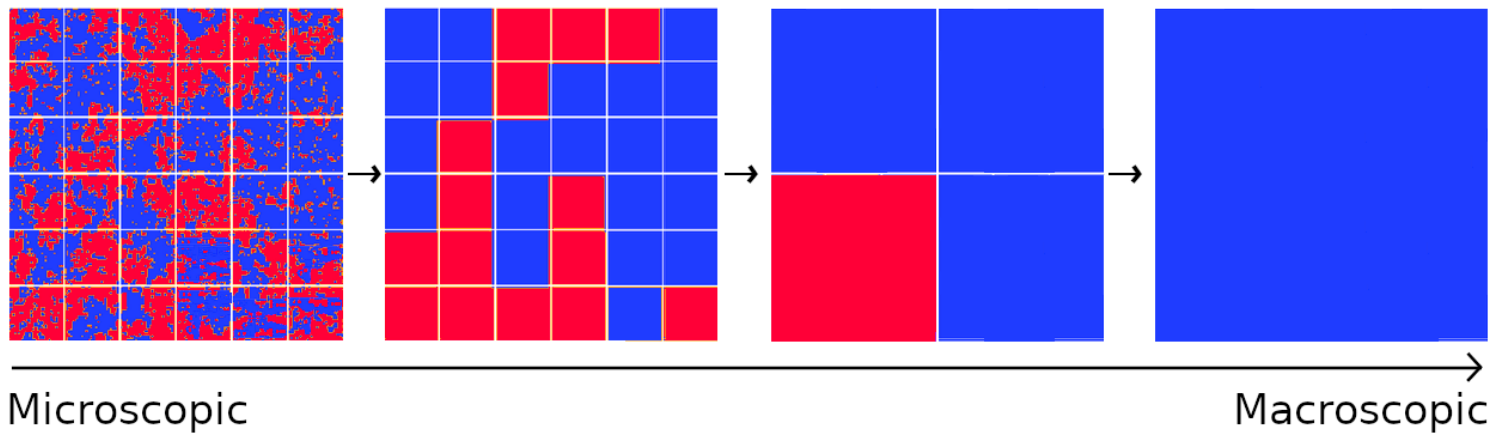


We place the averaged spins on a new coarser lattice.



Coarse graining

If we are interested in a macroscopic description, we can consider greater and greater grids as we move away from the microscopic scale.



At the macroscopic scale we take the mean value of the magnetic field of the whole material.

Mean field for the Ising model

The average magnetic field is the mean of the N spins in the material.

$$M = \frac{S_1 + S_2 + \cdots + S_N}{N}$$

This is a good approximation if the number of spins which are close to M is high. We neglect the fluctuations $M - S_i$.

Using this assumption

$$J \sum_{ij}^{N} \underbrace{S_i S_j}_{\substack{\text{Each molecule interacts} \\ \text{with its neighbrohoods}}} \approx J \sum_{i}^{N} \underbrace{S_i M}_{\substack{\text{Each molecule interacts} \\ \text{with the mean field}}}$$

Mean field for the Ising model

Now we can define the mean field energy

$$H_{MF} = -J \sum_{i=1}^{N} S_i M$$

which contains only interactions of single spins with the mean magnetic field. The corresponding partition function

$$Z = \sum_{\text{All the configurations}} e^{-\beta H_{MF}}$$

can be evaluated and the result is

$$Z = 2^N \left[Cosh\left(\beta JM\right) \right]^N$$

Mean field for the Ising model

Now we can compute the total mean magnetization from Z.

$$M = \langle \sum_{i=1}^{N} S_i \rangle = p(\uparrow\uparrow \ldots \uparrow) \sum_{i=1}^{N} S_i + \ldots + p(\downarrow\downarrow \ldots \downarrow) \sum_{i=1}^{N} S_i$$

Result:

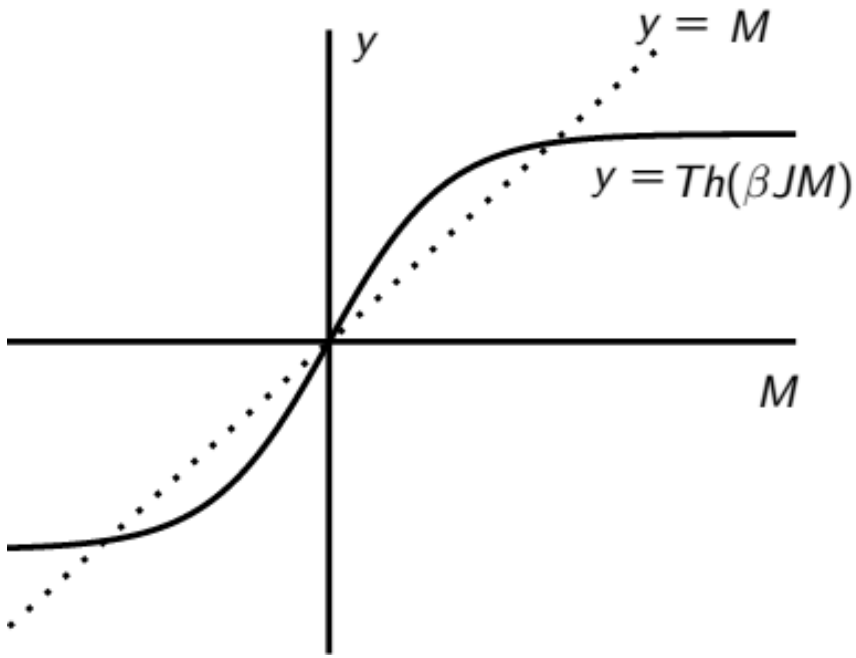
$$M = Th(\beta J M)$$

M appears at both the left and the right and side of the (nonlinear) equation.

This is an example of self consistent equation depending on an external parameter (β).

A solution M is called a fixed point.

Mean field for the Ising model



If β is high enough ($\beta > \beta_C$) we find three solutions, three different behavior of the material.

- $M = 0$: No magnetization.
- $M = +\mathfrak{M}$: Upward magnetization.
- $M = -\mathfrak{M}$: Downward magnetization.

If β is low enough ($\beta < \beta_C$) we find only one solution, $M = 0$.

Mean field in neurosciences

Now let us apply the previous ideas to neuroscience.

Let us consider a small volume of the granular layer in the cerebellar cortex.

In this region we find more than half of the neurons in the entire brain
$\Rightarrow$ Studying the activity of all the neurons is impossible!

We need to find a simplified model.

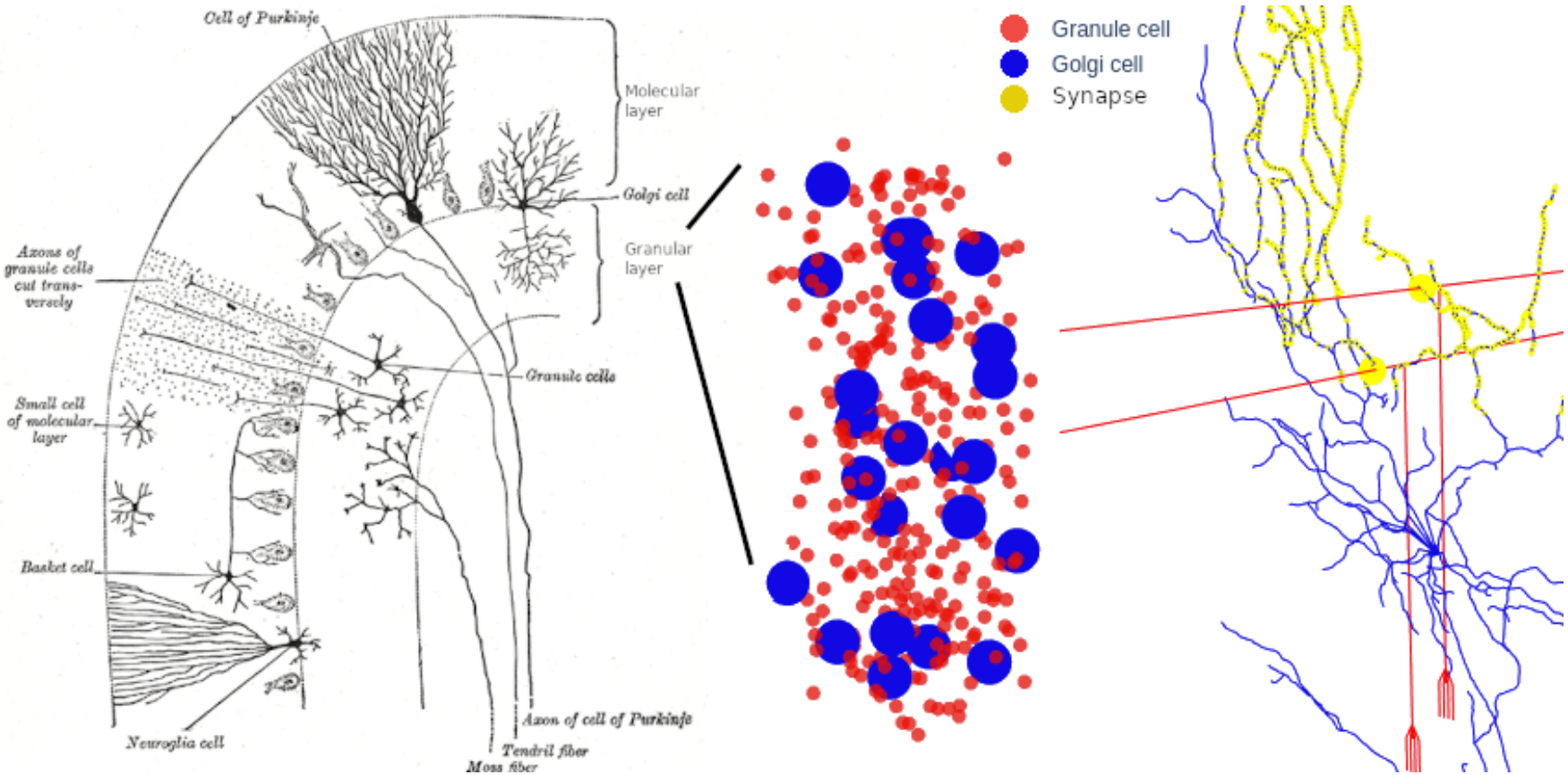
Mean field in neurosciences

Many nervous processes of any complexity are dependent upon the interaction of excitatory and inhibitory subpopulations. This hypothesis is supported by many works: Hardtline & Ratliff (1958), Hubey & Wiesel (1963), Freeman (1967),...

We need a two-variable description of the whole population.

Mean field in neurosciences

Example: granule cells (excitatory) and Golgi cells (inhibitory) in the cerebellar cortex.



Wilson-Cowan model - Hypotheses

A simple mean field model for populations of neurons is the Wilson-Cowan model (1972).

This model describes the dynamics of a spatially localized population containing both excitatory and inhibitory neurons.

Wilson-Cowan model - Hypotheses

Assumption on the population

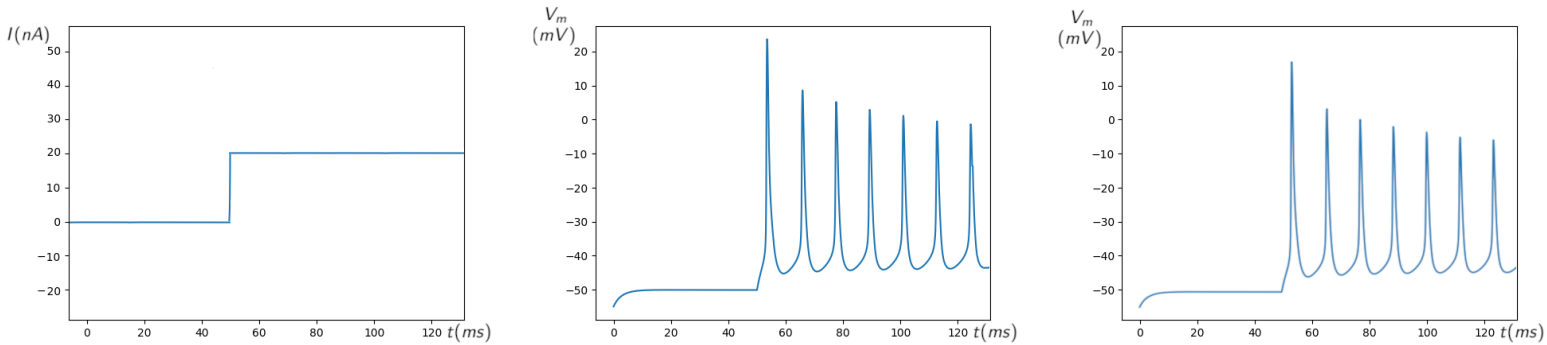
- The cells of these populations are in close spatial proximity.
- The interconnections are random, but dense enough so that there is at least one (direct or indirect) path connecting any two cells within the population.

Under these assumptions we can neglect spatial interactions, therefore we can just deal with the temporal dynamics of the aggregate of neurons. The relevant variable is the proportion of active cells per unit time: not the single spike of a neuron, but the spike frequency.

Wilson-Cowan model - Hypotheses

In relatively small volumes of cortical tissues there are many cells with nearly identical responses to identical stimuli. These hypotheses are well supported by experimental evidences:

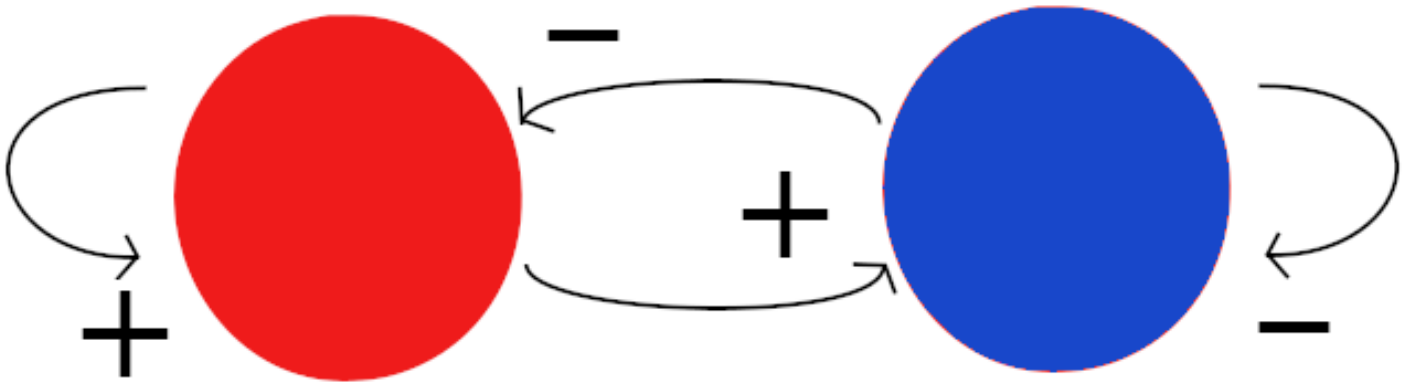
- Physiological evidences for local redundancy: Mountcastle (1957), Hubel & Wiesel (1965), ...
- Anatomical evidences for local redundancy: Szentá gothai (1967), Colonnier (1965), ...



Membrane potential of two granule cells (central and right panel) in response to a current injection into the soma (right panel).

Mean field in neurosciences

This assumption allows us to perform a coarse graining in space, grouping all the neurons of the same kind in a microcircuit in a single entity.



Instead of single neurons we consider the inhibitory end the excitatory subpopulations as our object of study.

Wilson Cowan model - Dynamical variables

Dynamical variables

$E(t) =$ Proportion of excitatory cells firing per unit time at the instant t.

$I(t) =$ Proportion of inhibitory cells firing per unit time at the instant t.

$E(t) = 0, I(t) = 0$ is the resting state, a state of low-level background activity.

Wilson Cowan model - Mean field equations

Neurons not in a refractory state respond to stimuli with a spike after a small timestep τ. The value of $E(t+\tau)$ and $I(t+\tau)$ are equal to the proportion of neuron which are sensitive and which also receive at least threshold excitation of time t. Suppose that the refractory period has a duration of r milliseconds. Then the proportion of excitatory cells which are refractory is

$$\frac{1}{N_E}\int_{t-r}^{t} E(s)ds$$

where N_E is a normalization constant. Therefore the proportion of excitatory cells which are sensitive is

$$1-\frac{1}{N_E}\int_{t-r}^{t} E(s)ds$$

In the following, for the sake of simplicity, we assume that E is already normalized and we set $N_E = 1$. A similar expression holds true for the inhibitory population.

Wilson Cowan model - Mean field equations

Denote with $\mathcal{S}_E$ and $\mathcal{S}_I$ the functions giving the expected proportions of the subpopulations receiving at least threshold excitation per unit time as a function of the average levels of excitation within the subpopulations. $\mathcal{S}_E$ and $\mathcal{S}_I$ are called response functions because they give the expected proportion of cells in a subpopulation which would respond to a given level of excitation if none of them were initially in the absolute refractory state. Since the neurons in a population are slightly different from each other, we assume that there is a probability distribution D of individual thresholds. The subpopulation response function $\mathcal{S}(x)$ to a stimulus x, is then given by

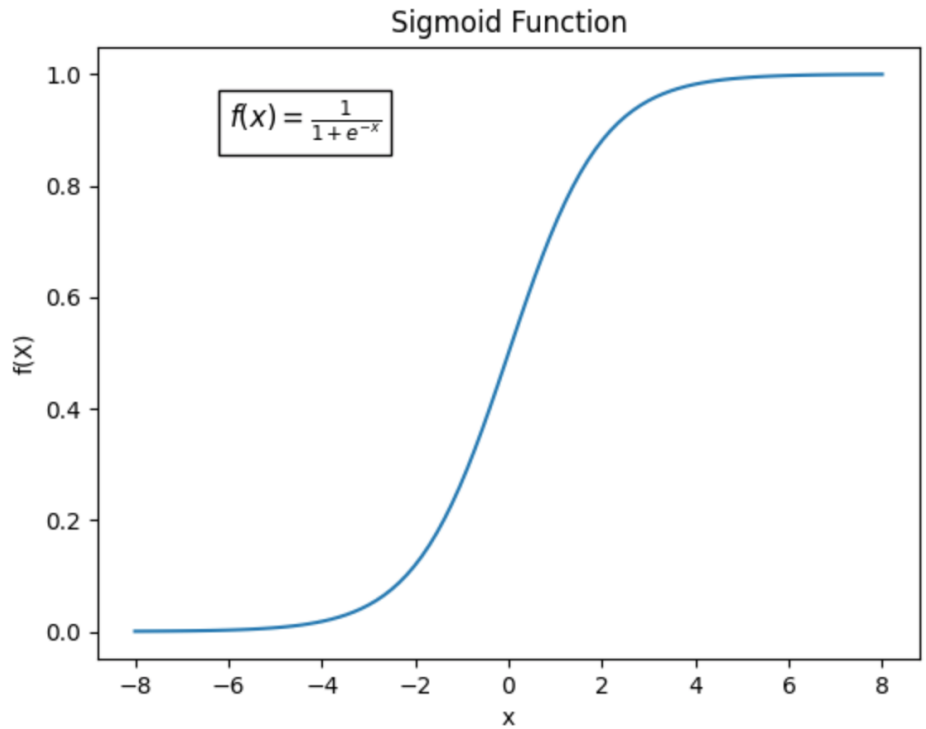
$$\mathcal{S}(x) = \int_0^x D(\theta) d\theta$$

Wilson Cowan model - Mean field equations

By definition of probability distribution, the integral

$$\mathcal{S}(x) = \int_0^x D(\theta) d\theta$$

is a monotonic function of the input x, with lower asymptote of 0 and upper asymptote of 1. The prototypical response function is the logistic function, also known as sigmoid.



Wilson Cowan model - Mean field equations

Phenomenological meaning of the sigmoidal shape

- Low excitation fails to excite any elements of the population.
- Strong excitation can excite all the members of the population.
- Experimental studies shows that both single cells response (Kernell, 1965) and populations responses (Rall, 1955) follow sigmoidal curves.

Wilson Cowan model - Mean field equations

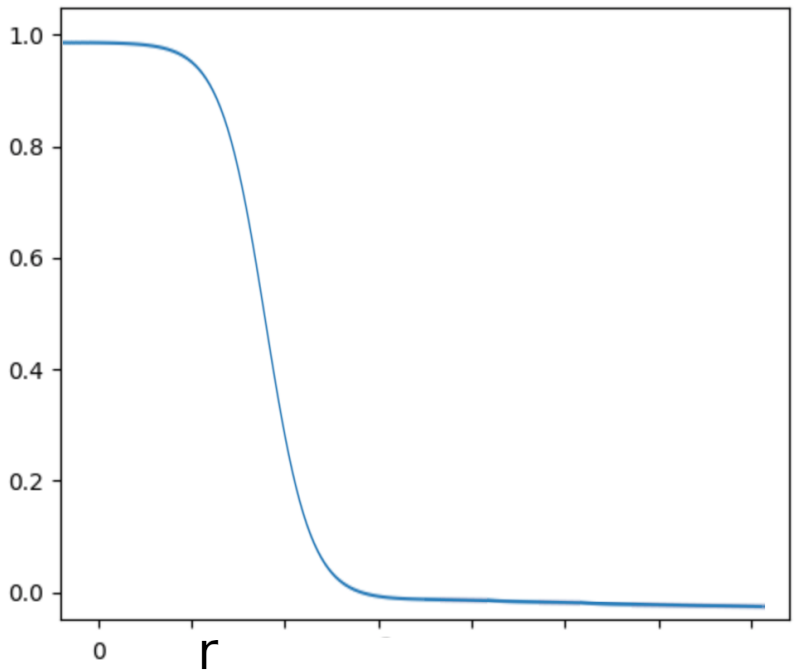
Suppose that the effect of the stimulation decays with a time course $\alpha(t)$. Since individual neurons sum their inputs, the average level of excitation generated in an excitatory cell at time t is

$$\int_{-\infty}^{t} \alpha(t-s)\left[c_1 E(s) - c_2 I(s) + P(s)\right] ds$$

where $P(s)$ is an external stimulus at time s and c_1, c_2 are positive numbers representing the average number of excitatory and inhibitory synapses per cell.

Wilson Cowan model - Mean field equations

The stimulation decays α is 1 for $t < r$ and goes rapidly to zero for $t > r$.



In the previous integral α and E, I, P are considered at different times: $t - s$ and s respectively. The retarded action of α is a complication for the model.

Wilson Cowan model - Mean field equations

A similar expression holds true also for the inhibitory population.
The differences in the coefficients reflect the different morphologies of the two cell types, while the differences in the external stimuli depend on the specific afferents to the subpopulations.

Wilson Cowan model - Mean field equations

If the probability that a cell is sensitive is independent of the probability that a cell is currently excited above its threshold, then acitivity of the excitatory population in a small time period δt is given by

$$\underbrace{\left[1 - \int_{t-r}^{t} E(s)ds\right]}_{Neurons\ \ not\ \ refractory} \underbrace{\mathcal{S}(x)}_{Excitation} \ \ \delta t$$

Wilson Cowan model - Mean field equations

Therefore we arrive to

$$E(t+\tau) = \left[1 - \int_{t-r}^{t} E(s)ds\right] \mathcal{S}_E \left\{\int_{-\infty}^{t} \alpha(t-s)[c_1 E(s) - c_2 I(s) + P_E(s)]ds\right\}$$

In the same way we obtain

$$I(t+\tau) = \left[1 - \int_{t-r}^{t} I(s)ds\right] \mathcal{S}_I \left\{\int_{-\infty}^{t} \alpha(t-s)[c_3 E(s) - c_4 I(s) + P_I(s)]ds\right\}$$

These are the equations governing the dynamics of the localized subpopulations of neurons.

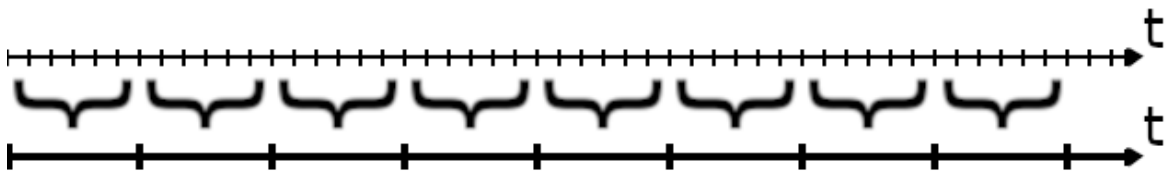
Wilson Cowan model - Mean field equations

These two equation are complex to study because they involve nonlinear terms ($\mathcal{S}_E$ and $\mathcal{S}_I$) and temporal integrals whose terms are evaluated at different times. We need to simply the model.

- The nonlinearities due to the response functions are a fundamental characteristic of biological control systems.
- The presence of temporal integrals is an aspect of lesser significance biologically, therefore we can simplify them.

Wilson Cowan model - Mean field equations

To remove the temporal integrals, we follow the strategy suggested by the Ising model, this time applied to time. We make use of a time coarse graining, averaging the activity over a properly chosen time interval.



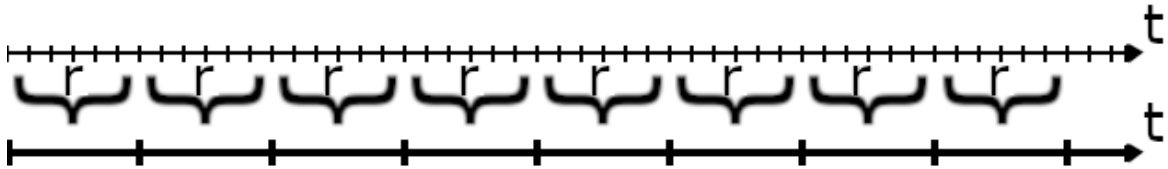
A coarse grained variable $\overline{f}(t)$ is given by

$$\overline{f}(t) = \frac{1}{s} \int_{t-s}^{s} f(\tau) d\tau$$

Caveat: we lose any information on fast processes, on any temporal variations on time scales shorter than s.

Wilson Cowan model - Mean field equations

The stimulation decays α appearing in the integrals goes to zero for $t > r$, therefore we can take average on the refractory period ($s = r$).



Using the coarse grained variable $\overline{E}$ we can make the following substitutions:

$$E(t) \to \overline{E}(t)$$

$$\int_{t-r}^{t} E(s)ds \to r\overline{E}(t)$$

$$\int_{-\infty}^{t} \alpha(t-s)E(s)ds \to C\overline{E}(t)$$

with C a constant depending on the shape of α. We can apply the same argument to the integrals containing $I(t)$.

Wilson Cowan model - Mean field equations

The dynamical equations for become

$$\overline{E}(t+\tau) = \left[1 - r\overline{E}(t)\right] \mathcal{S}_E \left\{ kc_1 \overline{E}(t) - kc_2 \overline{I}(t) k\overline{P_E}(t) \right\}$$

$$\overline{I}(t+\tau) = \left[1 - r\overline{I}(t)\right] \mathcal{S}_I \left\{ kc_3 \overline{E}(t) - kc_4 \overline{I}(t) + k\overline{P_I}(t) \right\}$$

For small timesteps τ, we can replace $E(t+\tau)$ and $I(t+\tau)$ with the first order Taylor expansion of the coarse grained variables at $\tau = 0$.

$$\overline{E}(t+\tau_E) \approx \overline{E}(t) + \tau_E \frac{d\overline{E}}{dt}(t)$$

$$\overline{I}(t+\tau_I) \approx \overline{I}(t) + \tau_I \frac{d\overline{I}}{dt}(t)$$

Wilson Cowan model - Mean field equations

We arrive to the equations

$$\tau_E \frac{d\overline{E}}{dt}(t) = -\overline{E}(t)\left[1 - r\overline{E}(t)\right]\mathcal{S}_E\left\{kc_1\overline{E}(t) - kc_2\overline{I}(t)k\overline{P_E}(t)\right\}$$

$$\tau_I \frac{d\overline{I}}{dt}(t) = -\overline{I}(t)\left[1 - r\overline{E}(t)\right]\mathcal{S}_I\left\{kc_3\overline{E}(t) - kc_4\overline{I}(t) + k\overline{P_I}(t)\right\}$$

Since the refractory period r is small, we can approximate terms $1 - r\overline{E}$ and $1 - r\overline{I}$ with 1, arriving to the system of differential equations

$$\begin{cases} \tau_E \frac{d\overline{E}}{dt}(t) &= -\overline{E}(t) + \mathcal{S}_E\left\{c_1\overline{E}(t) - c_2\overline{I}(t) + \overline{P_E}(t)\right\} \\ \tau_I \frac{d\overline{I}}{dt}(t) &= -\overline{I}(t) + \mathcal{S}_I\left\{c_3\overline{E}(t) - c_4\overline{I}(t) + \overline{P_I}(t)\right\} \end{cases}$$

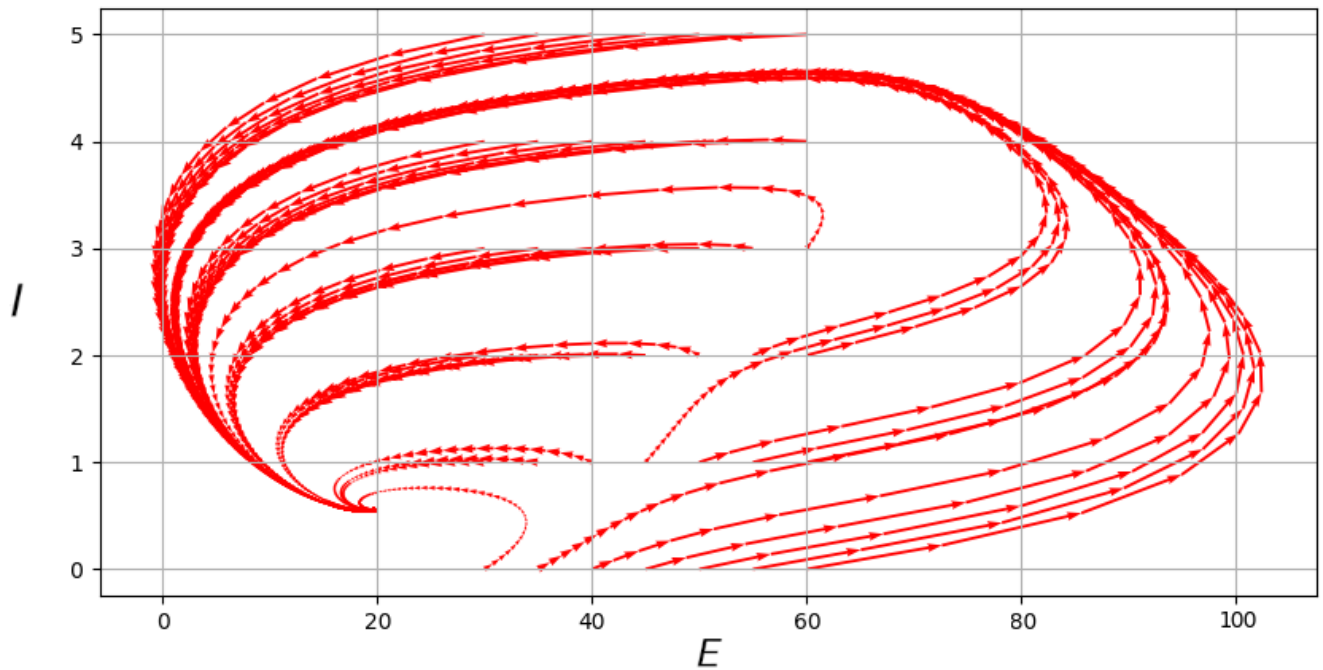
where we also adsorbed the constant k in c_1, c_2, c_3, c_4.

Wilson Cowan model - Mean field equations

The most important mathematical advantage gained from the removal of the time integrals is that we can apply the phase plane analysis to extract the qualitative features of the solutions of the dynamical equations for E and I and their dependence on the parameter of the model, for example the external currents P_E and P_I. A common tools to visualize the the behavior of dynamical systems is the phase portrait.

A phase portrait is a geometric representation of the trajectories of a dynamical system in the plane of the dynamical variables – For us the plane $(E - I)$.

To each initial condition – a starting point (E^*, I^*) – is associated a solution $(E(t), I(t))$ which may be represented by a curve or a point.



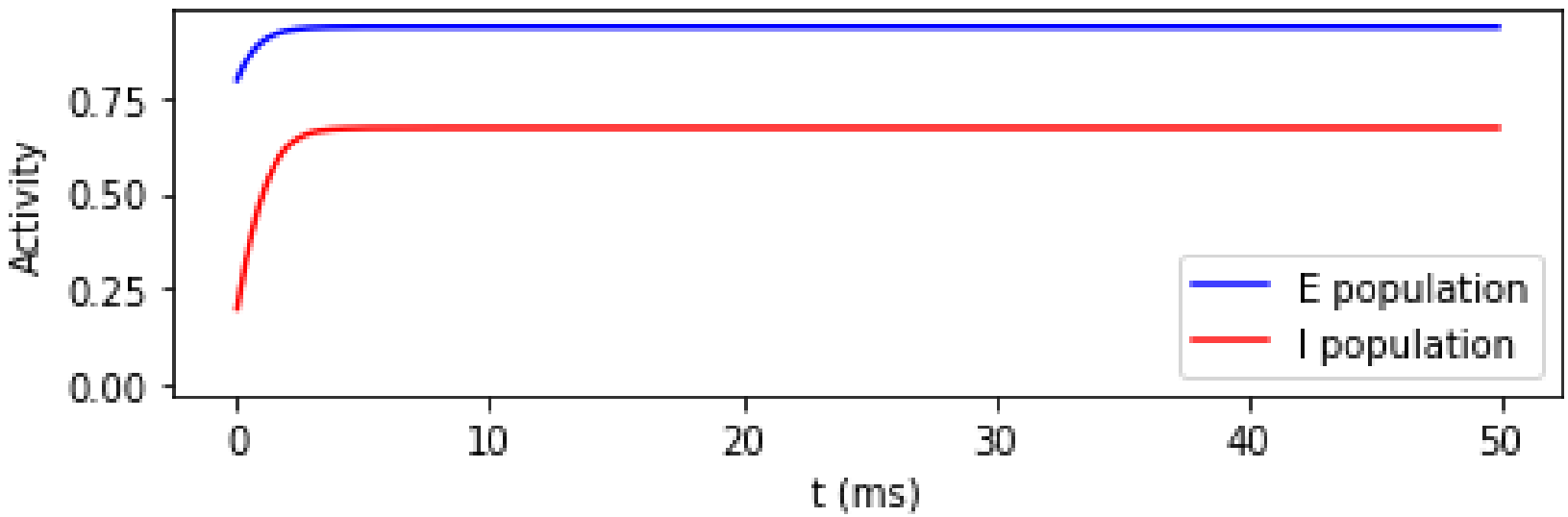
A rest state may attract or push away the curve representing the solutions.

How do we draw a phase portrait?

1) We select a set of initial data, for example on a grid in the space of the dynamical variables.
2) For each initial datum we solve the equations of the model.
3) For each initial datum, we plot the dynamical variables at different times, for example with a fixed time step Δt.

Steady states

The first interesting feature of the model are steady states, namely states in which the firing rates E and I become constant in time, eventually after a transient.



We can study the steady states of the model finding the critical points (or fixed points) of the dynamical system.

A critical point is a point at witch $dE/dt = 0$ and $dI/dt = 0$ for every time $t > t_0$.

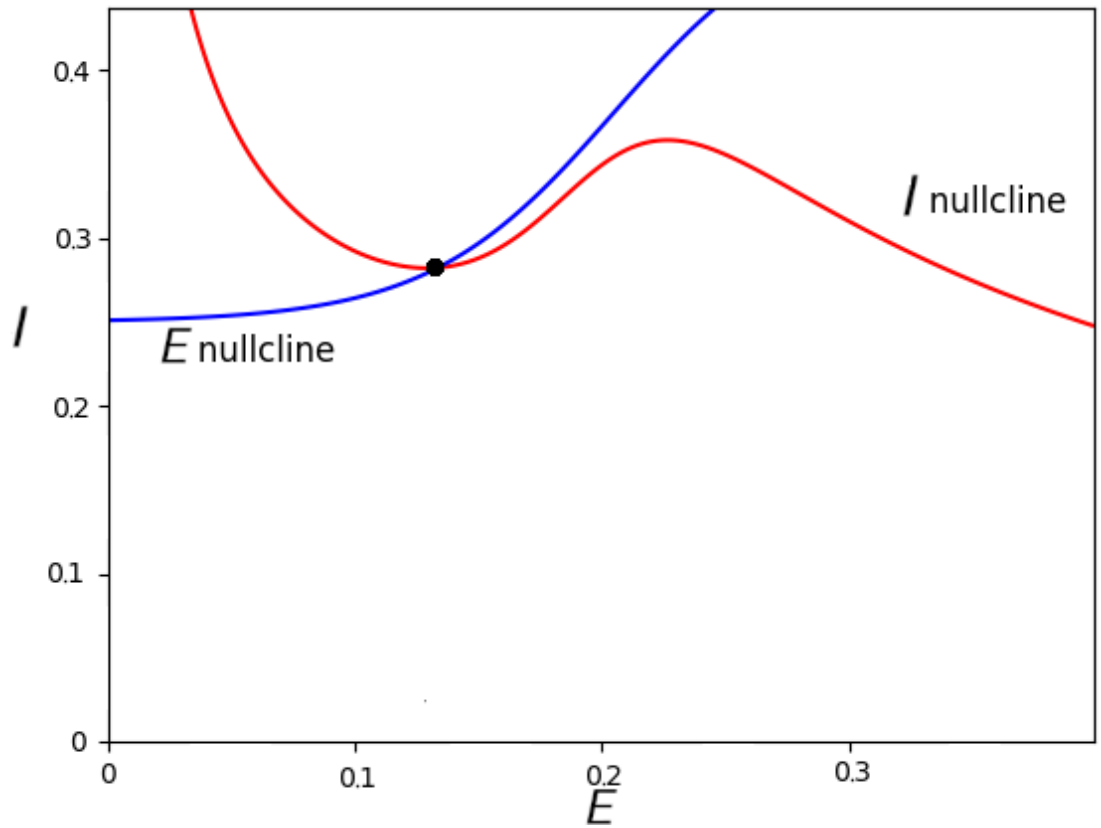
In a two variables model of the form

$$\begin{cases} \dfrac{dE}{dt} = F(E, I) \\ \\ \dfrac{dI}{dt} = G(E, I) \end{cases}$$

The critical points are the solutions of the nonlinear system,

$$\begin{cases} F(E, I) = 0 \\ G(E, I) = 0 \end{cases} \tag{1}$$

The curves $F(E, I) = 0$ and $G(E, I) = 0$ are called nullclines. Since at a critical point both the equations must be satisfied, we can find the critical points graphically at the intersection of the nullclines.



A model can admit different kinds of rest states.

$$\begin{cases} \dfrac{dE}{dt} = F(E, I) \\ \\ \dfrac{dI}{dt} = G(E, I) \end{cases}$$

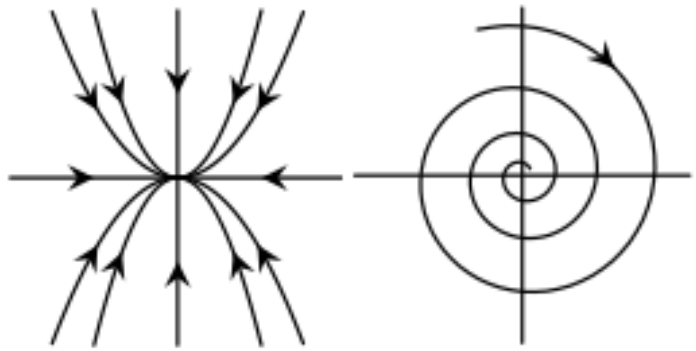
To study the stability of a critical point (E^*, I^*) it is sufficient to know the Jacobian matrix evaluated at the critical point

$$J := \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} \dfrac{\partial F}{\partial E}(E^*, I^*) & \dfrac{\partial F}{\partial I}(E^*, W^*) \\ \\ \dfrac{\partial G}{\partial E}(E^*, I^*) & \dfrac{\partial G}{\partial I}(E^*, I^*) \end{pmatrix}$$

We can study the nature of the critical point (V^*, w^*) examining the eigenvalues of J, which are the roots of the equations

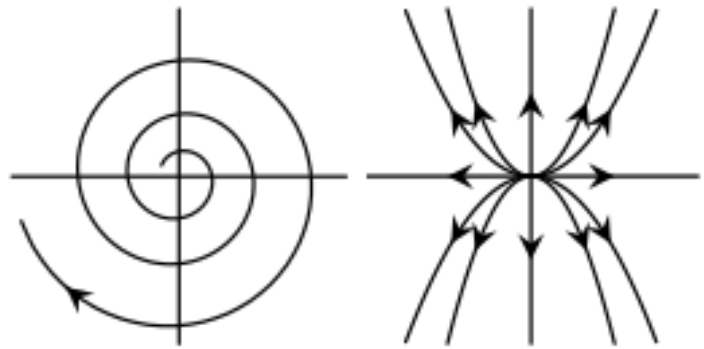
$$\lambda^2 - (a + d)\lambda + (ad - bc) = 0$$

If the real part of the roots of this equation is negative, the rest point is stable (an attractor or sink).



In a model describing a neuron only spiral sinks may correspond to a single action potential.

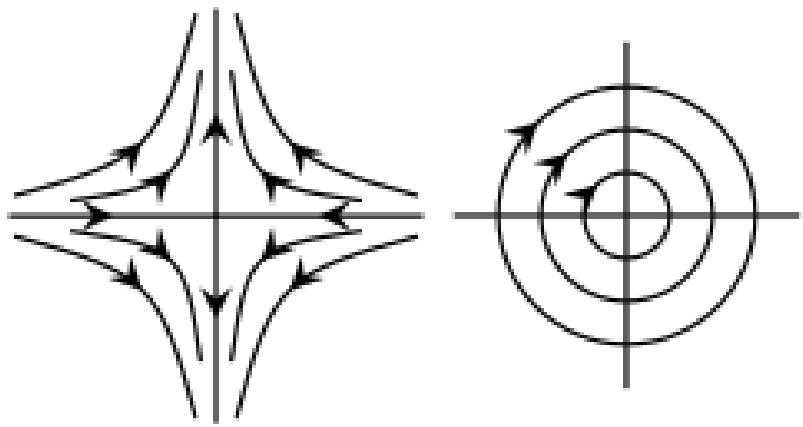
If the real part of both the eigenvalues is positive, the rest point is a repulsor (or source).



These critical points correspond to unstable equilibrium, related to oscillatory behaviors.

If both the eigenvalues are real, but with opposite signs , the critical point is a saddle, corresponding to an unstable equilibrium in some directions and to a stable equilibrium along other ones.

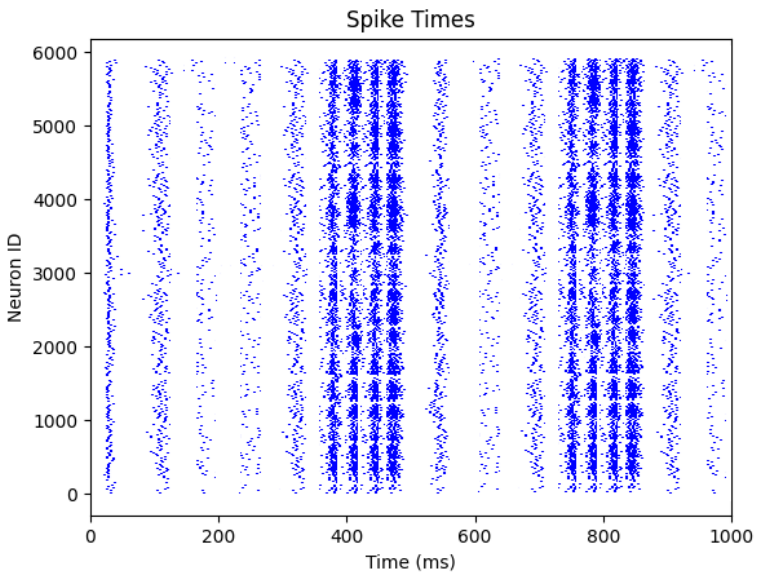
If both the eigenvalues are imaginary numbers, the critical point is a center, corresponding to a periodic motion (with the form of a sine or a cosine).

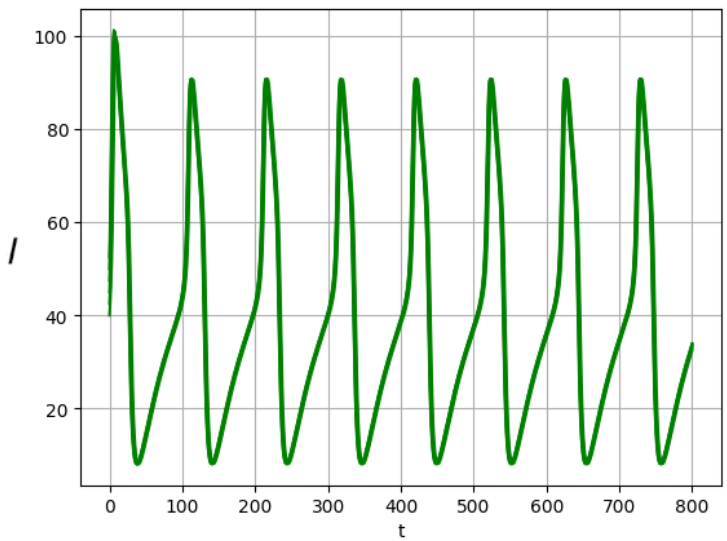


saddle center

Oscillations

Some populations of neurons (for example the excitatory unipolar brush cells and the inhibitory Golgi cells in the cerebellar cortex) may show an oscillatory behavior, with the spiking rates of the two populations cyclically varying between a maximum and a minimum.

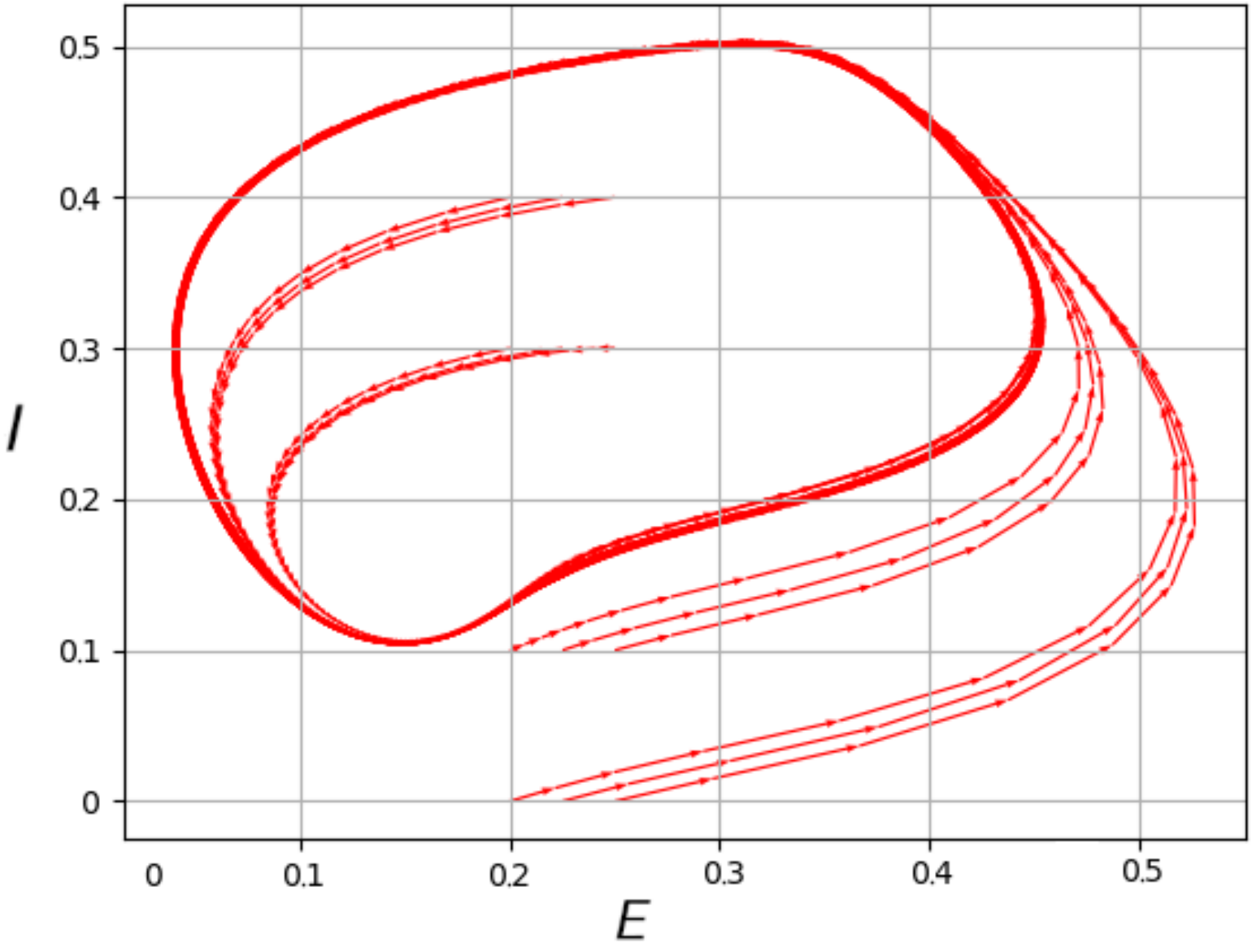




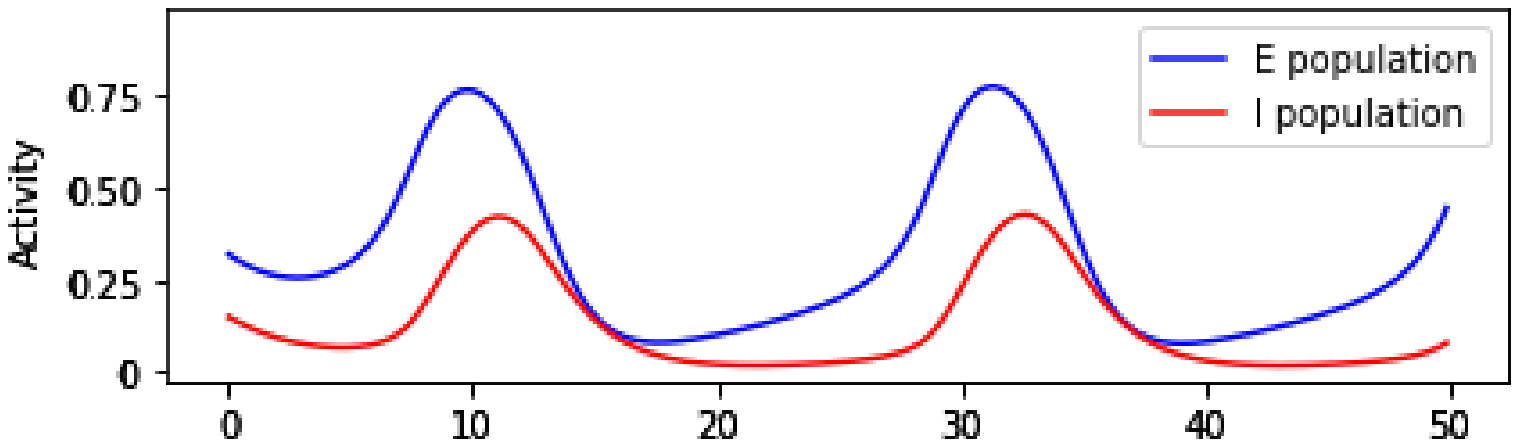
In addition to equilibrium points, we can also find *equilibrium curves*, called limit cycles.

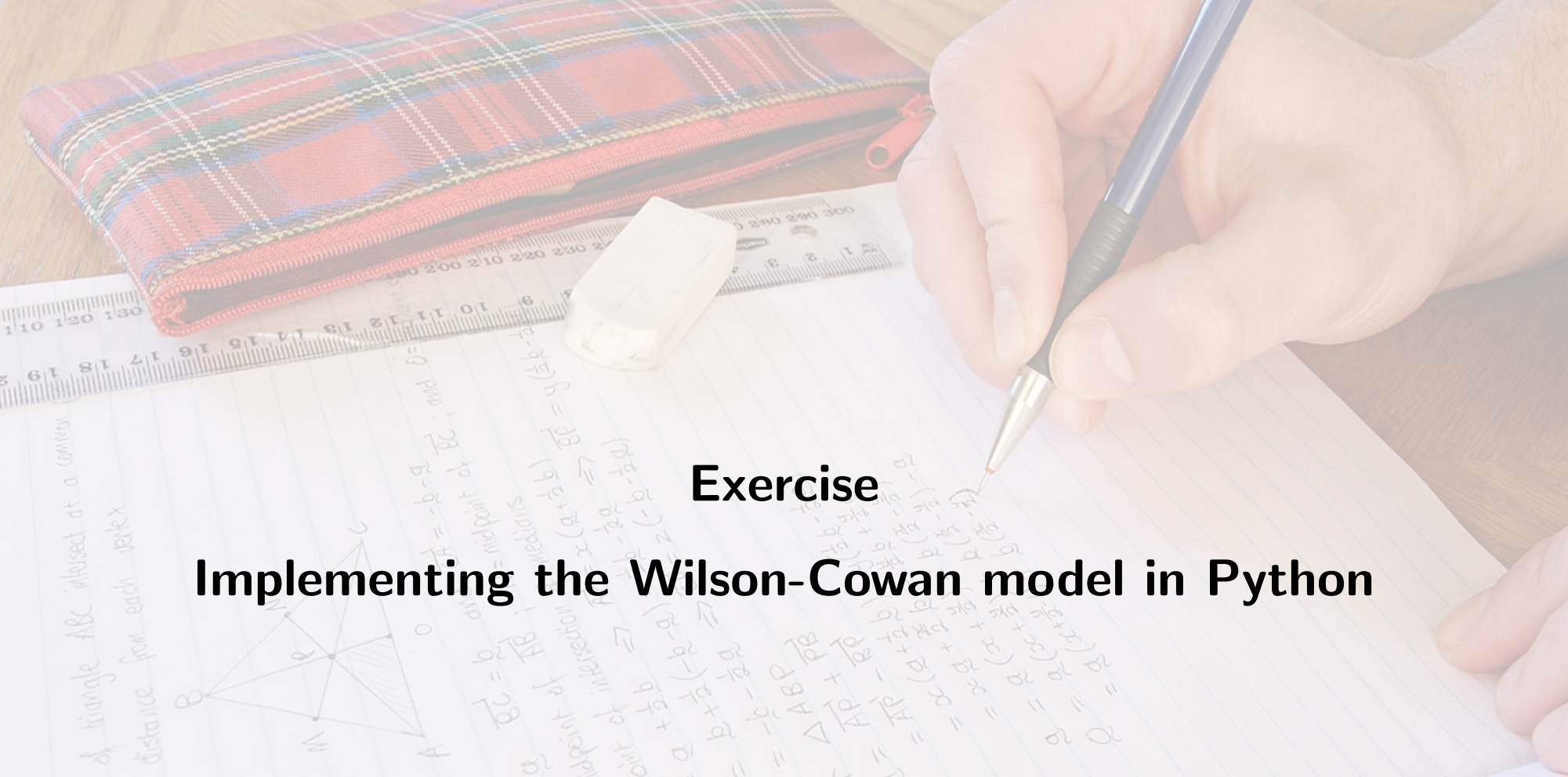
If the initial point of a trajectory is on a limit cycle, the trajectory remains on the limit cycle forever in absence of external stimuli.

As for equilibrium points the trajectory of a point near a limit cycle can follows two paths: It may be attracted by a limit cycle or it may be pushed away from it.


0.5
0.4
0.3
0.2
0.1
0
I
0
0.1
0.2
0.3
0.4
0.5
E

A limit cycle describes a periodic solution in the $E - t$ and $I - t$ planes, a cyclical change of the activity of the two subpopulations.





Exercise

Implementing the Wilson-Cowan model in Python

Nonlinear term

The dynamic of the Wilson-Cowan model is governed by the following system of equations

$$\begin{cases} \frac{dE}{dt}(t) &= \frac{1}{\tau_E}\left[-E(t) + \mathcal{S}_E\left\{c_1 E(t) - c_2 I(t) + P_E(t)\right\}\right] \\ \\ \frac{dI}{dt}(t) &= \frac{1}{\tau_I}\left[-I(t) + \mathcal{S}_I\left\{c_3 E(t) - c_4 I(t) + P_I(t)\right\}\right] \end{cases}$$

where the nonlinear functions $\mathcal{S}_E$ and $\mathcal{S}_I$ are given by

$$\mathcal{S}_E(x) = \frac{1}{1 + exp(1.2 * (x - 2.8))} - \frac{1}{z + exp(3.36)}$$

$$\mathcal{S}_I(x) = \frac{1}{1 + exp(1 * (x - 4))} - \frac{1}{z + exp(4)}$$

and the time constants are $\tau_E = 1\ ms$, $\tau_I = 2\ ms$. Set $c_1 = 9$, $c_2 = 4$, $c_3 = 13$ and $c_4 = 11$.

Nonlinear term

We can see the system also in a vectorial form

$$\frac{d}{dt}\begin{pmatrix} E(t) \\ I(t) \end{pmatrix} = \begin{pmatrix} \tau_E^{-1}\left[-E(t) + \mathcal{S}_E\left\{c_1 E(t) - c_2 I(t) + P_E(t)\right\}\right] \\ \tau_I^{-1}\left[-I(t) + \mathcal{S}_I\left\{c_3 E(t) - c_4 I(t) + P_I(t)\right\}\right] \end{pmatrix}$$

where the nonlinear functions $\mathcal{S}_E$ and $\mathcal{S}_I$ are given by

$$\mathcal{S}_E(x) = \frac{1}{1 + exp(1.2 * (x - 2.8))} - \frac{1}{z + exp(3.36)}$$

$$\mathcal{S}_I(x) = \frac{1}{1 + exp(1 * (x - 4))} - \frac{1}{z + exp(4)}$$

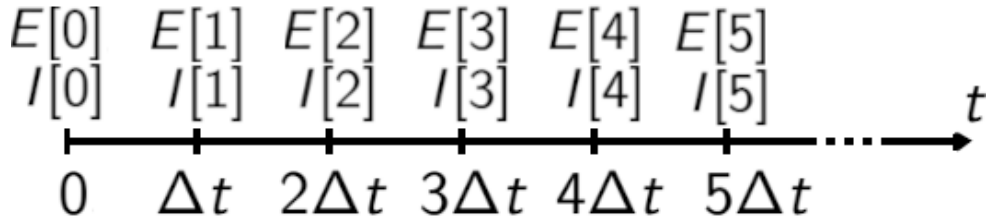
and the time constants are $\tau_E = 1\ ms$, $\tau_I = 2\ ms$. Set $c_1 = 9$, $c_2 = 4$, $c_3 = 13$ and $c_4 = 11$.

Tasks:

- Write a function implementing the sigmoidal nonlinear term.
- Write a function to compute the rhs of the equation above.

Numerical integration of the equations of motion

We can integrate the equations of the Wilson-Cowan model numerically using the Euler method. The dynamics of E and I subpopulations can be simulated on a time-grid of stepsize Δt. Denote with $E[k]$ and $I[k]$ the values of E and I at the time $k\Delta t$, $k \in \mathbb{N}$.



At each time step we update the firing rates E and I as follows:

$$\begin{cases} E[k+1] = E[k] + \Delta E[k] \\ I[k+1] = I[k] + \Delta I[k] \end{cases}$$

where the increments $\Delta E[k]$, $\Delta I[k]$ are given by

$$\begin{cases} \Delta E[k] = \dfrac{\Delta t}{\tau_E}\left(-E[k] + \mathcal{S}_E(c_1 E[k] - c_2 I[k] + P_E[k])\right) \\ \Delta I[k] = \dfrac{\Delta t}{\tau_I}\left(-I[k] + \mathcal{S}_I(c_3 E[k] - c_4 I[k] + P_I[k])\right) \end{cases}$$

Numerical integration of the equations of motion

At each time step we update the firing rates E and I as follows:

$$\begin{cases} E[k+1] = E[k] + \Delta E[k] \\ I[k+1] = I[k] + \Delta I[k] \end{cases}$$

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Tasks:

- Write a function to perform the numerical integration of the dynamical equations.
- Plot the evolution of the firing rates E and I starting from the initial conditions $E(0) = 0.2$ and $I(0) = 0.2$.

Phase portrait

Task:

- Draw a phase portrait of the Wilson-Cowan model studying what happens near the initial conditions $E(0) = 0.2$ and $I(0) = 0.2$.