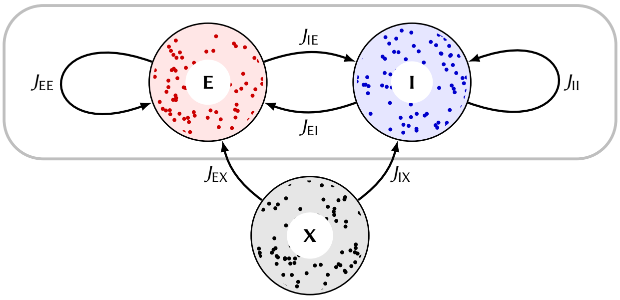
Long tutorial – balanced networks

In this question, you will investigate the asynchronous and irregular dynamical regime of cortical circuits in a simple model network (cf lecture). **The network will be built up and analysed incrementally**. We start by giving the full specifications of the network in its final form; later sections will dissect each of the main components, and guide you towards their implementation in python (or any other programming language of your choice).

You are expected to work in groups, and to prepare a 30-min presentation (one per group) to report on your findings. Each group should make a common set of slides, and speaking time should be divided near-equally between group members.

1 Full network specifications

Architecture In its final form, the network will be composed of three populations of N neurons each: one excitatory ('E') population, one inhibitory ('I') population, and a third, "external" population ('X') which will provide baseline input to the network:



Index notation In the following, i and j will be used to denote neuron indices within populations – thus, $i, j \in \{1, 2, \dots, N\}$. We will use greek letters α and β to denote population identities – thus $\alpha, \beta \in \{\mathrm{E}, \mathrm{I}, \mathrm{X}\}$.

Connectivity Every single neuron in the E- and I-populations receives input from K randomly chosen E-neurons, K randomly chosen I-neurons, and K randomly chosen X-neurons. We will use the notation $C_i^{\alpha\beta}$ to denote the set that contains the indices of those K neurons in population β that have been randomly chosen to connect onto the i^{th} neuron of population α (the proliferation of subscripts and superscripts is admitedly intimidating, but helpful later at implementation stage!). The weights associated with these connections (see also "dynamics" below) are given by $J_{\alpha\beta}/\sqrt{K}$; thus, all connections of the same "type" have the same weight. Note also that $J_{\alpha I} < 0$ (inhibitory connections), while $J_{\alpha E} > 0$ and $J_{\alpha X} > 0$ (excitatory connections) – whatever the identity α of the postsynaptic population.

Dynamics The neurons in the X-population are artificial "Poisson neurons", i.e. they fire action potentials independently of each other, according to Poisson processes with rate r_{X}. The neurons in

notation	value	description
V_{th}	1	spiking threshold
δ_t	0.1 ms	integration time step
τ	20 ms	membrane time constant
N	1000	number of neurons in each population
K	100	number of presynaptic partners (per neuron) from each population
r_{X}	10 Hz	firing rate of the Poisson neurons in population X

Table 1: Table of parameters.

the E- and I-populations are modelled as simple "leaky integrate-and-fire" (LIF) neurons, as follows. The membrane potential V_i^α of the i^{th} neuron in population α obeys first-order dynamics given by

$$\frac{dV_i^\alpha}{dt} = -\frac{V_i^\alpha(t)}{\tau} + \sum_{\beta \in \{\text{E,I,X}\}} \frac{J_{\alpha\beta}}{\sqrt{K}} \sum_{j \in C_i^{\alpha\beta}} S_j^\beta(t) \tag{1}$$

where τ is the membrane time constant, and $S_j^\beta(t)$ is the spike train of the j^{th} neuron in population β. Here, a spike train is modelled as a sum of Dirac delta functions placed at the times at which the neuron fires its action potentials (cf. lecture). Note, therefore, that the outer sum (over β) says that "neurons in population α receive input from other neurons belonging to all 3 populations" (which includes α itself), and the inner sum (over j) is gathering input from the K specific presynaptic partners found in each population.

Finally, when $V_i^\alpha(t)$ grows above a threshold value V_{th}, the neuron emits an action potential (which will therefore appear as a Dirac delta function in $S_i^\alpha(t)$), and V_i^α is instantaneously reset to 0.

Time discretization Although the model is specified in continuous time, your computer implementation will have to be in discrete time. Therefore, any continuous process $f(t)$ (e.g. a spike train $S(t)$, or a voltage $V(t)$) will need to be discretised, i.e. specified only at integer multiples of a time bin δ_t (value given in the table). We will adopt the intuitive notation $\tilde{f}(k) = f(k\delta_t)$ for integer k.

Unless indicated otherwise, you will use the set of default parameters given in Table 1.

2 Generating Poisson spike trains

1. Sample the activity of the X-population for 2 seconds, i.e. generate a set of N independent, 2 second-long Poisson spike trains $\{\tilde{S}_i(k)\}_{i=1,\dots,N}$ with rate r_{X}. Plot the result in a "raster plot", i.e. a plot in which a dot appears at coordinates $(k\delta_t, i)$ if neuron i fires at time $k\delta_t$ (that is, if $\tilde{S}_i(k) \neq 0$). One way to check that your code is correct is by counting the number of spikes fired by each neuron, and then averaging this number across neurons. What should this average number be, in theory?

   Hint For a Poisson process with constant rate r_{X} (expected number of events per second), the probability of an event (a spike) falling between t and $t + \delta_t$ (for δ_t very small) is approximately

$r_X\delta_t$, independent of t. Thus, a discretised Poisson process can be generated by sampling the value $\tilde{S}(k)$ in each bin independently from a Bernoulli distribution:

$$\tilde{S}(k) \leftarrow \frac{1}{\delta_t} \begin{cases} 1 & \text{with probability } r_X\delta_t \\ 0 & \text{with probability } (1 - r_X\delta_t) \end{cases} \tag{2}$$

3 Single LIF neuron with one input spike train

1. Simulate the membrane potential dynamics and spiking activity of a single LIF neuron, which receives input from a single Poisson neuron with rate r_X. Set the value of the (only) synaptic weight to $w = 0.9$. Plot the time-varying membrane potential $V_i(t)$, as well as the input and output spike trains $S_j(t)$ and $S_i(t)$ using dots as in the previous question.

   Hint Here, Equation (1) reduces to $dV_i/dt = -V_i(t)/\tau + wS_j(t)$ where $S_j(t)$ is the single input Poisson spike train. The discrete-time version can be obtained through forward Euler integration, i.e.

$$\tilde{V}(0) \leftarrow 0 \qquad \text{and} \qquad \tilde{V}(k) \leftarrow \tilde{V}(k-1) + \delta_t \left[-\frac{\tilde{V}(k-1)}{\tau} + w\tilde{S}_j(k-1) \right] \tag{3}$$

   followed by

$$\tilde{S}_i(k) \leftarrow \frac{1}{\delta_t} \begin{cases} 1 & \text{if } \tilde{V}(k) > V_{\text{th}} \\ 0 & \text{otherwise} \end{cases} \qquad \text{and finally} \qquad \text{if } \tilde{V}(k) > V_{\text{th}} \text{ then } \tilde{V}(k) \leftarrow 0 \tag{4}$$

4 Single LIF neuron with many input spike trains

Consider now a single LIF neuron receiving inputs from K independent Poisson neurons, each firing at a constant rate r_X. The K corresponding synaptic weights are all set to some constant w. Thus, the dynamics are described by

$$\frac{dV_i(t)}{dt} = -\frac{V_i(t)}{\tau} + \underbrace{\frac{w}{K}\sum_{j=1}^{K} S_j(t)}_{h(t)} \tag{5}$$

1. First, disable the spike-and-reset mechanism (i.e. simulate Equation (5) only; do not reset $V_i(t)$ to zero when it crosses the threshold). How does $V_i(t)$ behave for $w = 1$? Plot a 2 second-long sample.

(difficult) After about 100 ms, the fluctuations of $V_i(t)$ become stationary, and approximately normally distributed with a mean μ and a variance σ^2. By first calculating the mean and covariance function of $h(t)$, derive the theoretical values of μ and σ^2, as functions of w, K, r_X and τ. Write down your derivations.

Hint You might want to rewrite Equation (5) in discrete time and work from there.

2. Plot μ and σ^2 as a function of K (keeping the other parameters fixed at their default values given in the table, and $w = 1$). On top of these smooth curves, plot μ and σ^2 obtained from simulations for $K = 0, 10, 100, 1000$ (you will want to simulate the dynamics for over 10 seconds, discard the initial 100 ms transient, and compute the average and variance of $V_i(t)$). Do your simulations agree with your theoretical predictions?

3. Calculate (analytically) the value that w must take such that, whatever the value of K, the mean potential μ be equal to V_{th}. Confirm your prediction in simulations, by setting $K = 100$ and w to your predicted value.

4. Now, enable the spike-and-reset mechanism, and proceed by trial and error to find the value of w that makes the output firing rate approximately equal to 10 Hz (all other parameters being set to their default values given in the table). For this value of w, compute the Fano factor of the output spike train, using a counting window of 100 ms. Is this close to the amount of spike count variability usually measured in the cortex?

   Hint The Fano factor can be estimated by counting spikes in a sliding window of length 100 ms. By sliding the window in time, you will obtain many different counts: the Fano factor is defined as the variance of those counts, divided by their mean.

5 Single LIF neuron with many E and I Poisson inputs

Consider again a single LIF neuron, now receiving excitatory input from K independent Poisson neurons, and inhibitory input from another K independent Poisson neurons. Each of these Poisson neurons fire at a constant rate r_X. Take the corresponding K excitatory (resp. inhibitory) synaptic weights to be $w/\sqrt{K}$ (resp. $-w/\sqrt{K}$).

1. What are the theoretical values of the mean μ and variance σ^2 of the membrane potential? Give expressions for both, as a function of w, r_x, and τ.

2. Through trial and error, find the value of w such that the neuron fires an agerage of 10 spikes per second. For this value of w, compute the Fano factor numerically. Is this now closer to the values usually found in the cortex?

6 Full network

Now, assemble the full network as specified in Section 1. In particular, this will involve generating random connectivity, i.e. generating for each neuron in population α, 3 sets $C_i^{\alpha\beta}$ of K randomly chosen indices of presynaptic partners from population β, as previously explained in Section 1. Use the following synaptic weight parameters: $J_{\text{EE}} = J_{\text{IE}} = 1$, $J_{\text{EI}} = -2.5$, $J_{\text{II}} = -2$, $J_{\text{EX}} = 2$ and $J_{\text{IX}} = 1$.

1. Using the theoretical arguments developed in the lecture, what values would you predict for the mean firing rate r_{E} in population E, and mean firing rate r_{I} in population I?

2. Simulate the network for 2 seconds. How many spikes per second do neurons in the E and I population fire, on average? Is that roughly in line with your theoretical predictions?
3. According to the theory, how would r_E and r_I vary with increasing r_X? Check this prediction in your simulations by repeating question 6.2 for different values of r_X (e.g. 5, 10, 15, and 20 Hz).