Lecture 2.2 Exercises: Firing rate models

2.1 Linear 2D dynamical system

A linear 2D dynamical system can be written in general as

$$\dot{x} = ax + by \qquad (1)$$
$$\dot{y} = cx + dy \qquad (2)$$

1. What is the fixed point of this dynamical system?

2. Compute the eigenvalues of the stability matrix, as a function of its determinant *D* and its trace *T*.

3. Write down the conditions on *D* and *T* to observe the 5 different possible types of stability (2 real positive eigenvalues; 1 real positive and one real negative eigenvalue; 2 real negative eigenvalues; 2 complex conjugate eigenvalues with positive real part; 2 complex conjugate eigenvalues with negative real part).

4. Plot the different regions with their boundaries in the *T* − *D* plane. Indicate the region where the fixed point is stable, and draw the 2 different bifurcation lines which bound this stability region.

2.2 Excitatory-inhibitory network

Consider the recurrent excitatory-inhibitory network defined by the rate equations

$$\tau_E \partial_t r_E = -r_E + \varphi(\mathrm{J_{EE} r_E - J_{EI} r_I + I_E}) \qquad (1)$$
$$\tau_I \partial_t r_I = -r_I + \varphi(\mathrm{J_{IE} r_E - J_{II} r_I + I_I}) \qquad (2)$$

where r_E and r_I are the rates of excitatory and inhibitory neurons respectively, and J_{EE}, J_{EI}, J_{IE}, J_{II}>0 are the weights of the recurrent couplings. Assume, for the sake of simplicity that $\tau_E = \tau_I = 1$. The external inputs I_E and I_I are constant in time and may be either positive (corresponding to excitatory input) or negative (corresponding to inhibitory input). Finally, the transfer function is given by

$$\varphi(x) = \begin{cases} 0 & \text{if } x < 0 \\ x & \text{if } 0 \leq x \leq 1 \\ 1 & \text{if } x > 1 \end{cases} \quad (3)$$

1. The fixed point of the dynamics is given by the intersection of the nullclines $\partial_t r_E = 0$ and $\partial_t r_I = 0$. This system of equation gives rise to qualitatively different kinds of fixed points, depending of the parameters: it may have $r_E = 0$ or 1, $r_I = 0$ or 1, or $0 < r_E, r_I < 1$. Focus on the case of nullclines such that the fixed point has $0 < r_E, r_I < 1$. The system displays two qualitatively different behaviors for $J_{EE} < 1$ and $J_{EE} > 1$. Draw two plots of the nullclines in the (r_E, r_I)-plane (r_E on the x axis, r_I on the y axis), one plot for each of these two conditions (in the case $J_{EE} > 1$, restrict yourself to the case in which the r_I nullcline has a larger slope than the r_E nullcline). Indicate the directions of the flows of r_E and r_I with small arrows in each of the four regions separated by the nullclines.

2. In the vicinity of such a fixed point (with $0 < r_E, r_I < 1$), the rate equations become linear:

$$\partial_t r_E = -r_E + J_{EE} r_E - J_{EI} r_I + I_E \quad (4)$$
$$\partial_t r_I = -r_I + J_{IE} r_E - J_{II} r_I + I_I \quad (5)$$

   Calculate the location of the fixed point (r_E^*, r_I^*) of the dynamics as a function of J_{EE}, J_{EI}, J_{IE}, and J_{II}.

3. The stability of the fixed point is dictated by the value of the eigenvalues of the matrix

$$\begin{pmatrix} J_{EE} - 1 & -J_{EI} \\ J_{IE} & -J_{II} - 1 \end{pmatrix} \quad (6)$$

   derived from the linear rate equations above. Calculate the two eigenvalues in terms of J_{EE}, J_{EI}, J_{IE}, and J_{II}.

4. The fixed point is stable if the real part of each eigenvalue is negative. Translate this condition into a condition on the couplings J_{EE}, J_{EI}, J_{IE}, and J_{II}. You should consider two cases separately: in the first case the eigenvalues are real and in the second case the eigenvalues are complex.

5. We first consider parameters for which the fixed point is stable, and investigate how the system reacts to changes in external inputs. How does the fixed point change in response to an increase in inputs to the inhibitory population by an amount $\Delta I_I > 0$, in each of the two cases ($J_{EE} < 1$ and $J_{EE} > 1$)? (Note: your plots in question 1 can help you

check the correctness of your results, if you think of how the nullclines move following a change in I_I.), you should find a counter-intuitive answer. Explain, in words, why is the behavior in the case $J_{EE} > 1$ counter-intuitive?. If the rate of the inhibitory population, r_I, is kept fixed, is the dynamics of the excitatory population stable?

6. If the fixed point is unstable and the eigenvalues are complex, r_E and r_I undergo an oscillation with growing magnitude. Since Eqs. (1,2) saturate for small and large values of r_E and r_I, the dynamics converge to a limit cycle. Choose a set of parameters such that the dynamics converge to a limit cycle, and simulate the equations of the model with such parameters. Plot nullclines and the limit cycle obtained from the simulation on the (r_E, r_I)-plane.

2.3 Robust integrator network

Take a network of excitatory neurons whose activity $r(t)$ evolves according to

$$\tau \frac{dr(t)}{dt} = -r(t) + I(t) + Jr(t) \qquad (9)$$

where τ is the time constant of the rate dynamics, J is the strength of the excitatory feedback, and $I(t)$ is the external input. Here we focus on the special case of an integrator network, $J \sim 1$. One of the motivations for studying this special case is the part of the oculomotor system which is responsible for holding still the position of the eyes in between saccades. This system has been studied in detail in particular in the goldfish, where those neurons are located in so called area 1. The activity of those neurons has been shown to be proportional to eye position. They seem to integrate transient inputs they receive during saccades (fast eye movements between fixations, during that time $I(t)$ is proportional to the amplitude of the saccade), and to be able to maintain their firing rate stable in absence of those inputs in between saccades (during that time $I(t) = 0$) - a phenomenon called persistent activity. In this paper, we focus on the robustness properties of the model.

1. Solve the equations for arbitrary time-varying inputs in the case $J = 1.2$.

2. It is unrealistic to assume that the value of a biological parameter can be fine-tuned exactly to some fixed value, here $J = 1$. What happens when there is a small deviation around 1, $J = 1 + \varrho$?

3. It can be shown that the eye is not perfectly stable over very long times, but there is a drift on time scales of about 10s. Assuming a firing rate time constant τ of about 10ms, what does it tell us about the degree of fine tuning in the system, as measured by Q?

4. A possible way of achieving robustness is to introduce dynamics of the synaptic weights of the type

$$\frac{dJ}{dt} = -\gamma r \frac{dr}{dt} \tag{10}$$

   In the following we take $J(t = 0) = J_0$, $r(t = 0) = r_0$, and $I(t) = 0$. What are the fixed points of the coupled equations for r and J?

5. Linearize the equations about the fixed points and discuss the stability of the solutions.

6. In the (r, J) plane, sketch the solutions close to the fixed points.

7. What is the trajectory of the system in the (r, J) plane, starting from arbitrary initial conditions? (Hint: integrate Eq. (10) with respect to time.) For what range of initial conditions does the system act as an integrator?

Comment [JB1]: Is this right?