Tutorial: planar models

The FitzHugh-Nagumo model

The FitzHugh-Nagumo model (FNM) is written as follows

$$\dot{V} = V(V-a)(1-V) - w + I$$
$$\dot{w} = \epsilon(V - \gamma w)$$

where $a < 1$, $0 < \epsilon < 1$, $\gamma \geq 0$.

Steady state stability

Assume $I = 0$, and prove the following statements

- S1: The FNM admits an equilibrium at $(V_*, w_*) = (0, 0)$.
- S2: If $a > 0$, then $(0, 0)$ is linearly stable.
- S3: If $a < -1/\gamma$, or $a > -1/\gamma$ and $a < -\epsilon\gamma$, then $(0, 0)$ is linearly unstable.

Excitable regime

Let us test S2 using numerical methods. Write code that simulates the FNM, with $a = 0.1$, $\epsilon = 0.01$, $\gamma = 2$, $I = 0$, and show that it displays excitable behaviour in this regime. In particular:

- Plot the nullclines of the model
- Time step the model with two initial conditions of the form $(0.2, w_0)$ where w_0 is taken slightly above and below the V-nullcline, respectively.
- Plot $V(t)$ in both cases.
- Plot both orbits in the phase plane, and superimpose them to the nullclines.
- The examples above give an indication of an **excitable behaviour**. Vary initial conditions to familiarise yourself with this behaviour.

Relaxation oscillations

Let us now test S3. Set $a = -0.1$ and keep all other parameters as above.

- Check that this parameter choice respects the hypotheses of S3.
- Verify that the system supports a periodic orbit. Plot the orbit in the phase plane, as well as the solution profile $V(t)$, as a function of t. Note the sharp "jumps" of the voltage, followed by slower segments. This orbit is called a **relaxation oscillation**.
- By changing initial conditions, provide numerical evidence that the steady state at (0,0) is unstable, and that the relaxation oscillation is attracting.

Slowly-increasing currents

Set $a = 0.1$, $\epsilon = 0.02$, $\gamma = 1$, and take $I(t)$ to be a slowly increasing function, for instance

$$I(t) = \rho t,$$

where $\rho > 0$ is **small**. This mimics a quasi-static increase in the injected current.

- Setup a simulation in which I increases from 0 to 0.8, and plot $V(t)$.
- Estimate the values of I at which oscillations are born and destroyed (a rough estimate would suffice!).
- Describe how the period of oscillations varies as I increases. Support your description with numerical evidence. This question is deliberately vague: you are requested to read your data, choose your argument, make a conjecture. It's a more open-ended question. The statement can be as simple as "This is what I see... and this is how I decided to show it...". You are not requested to explain "why" you observe this trend, but just "what" you see, and "how" you see it.

More analysis on the FNM

Let us return to the FNM model, for some further analytical work. The objective of this exercise is to make general statements about the number of steady states of the FNM, and about their stability. Also, you will be able to predict the onset and termination of oscillations in the "Slowly-increasing currents" section.

- Find an expression for the nullclines of the model. Draw a qualitative sketch, and plot representative arrows for each subregion in phase space.
- Prove that steady states (V_*, w_*) satisfy

$$w_* = V_*/\gamma, \qquad h(V_*) - I = 0, \qquad h(V) = V/\gamma - V(V-a)(1-V)$$

- Using h or otherwise, prove the following statements:

  S4: if $\gamma < 3/(1 - a + a^2)$, then for each value of I there exists a unique equilibrium to the FNM.
  S5: if $\gamma \geq 3/(1 - a + a^2)$, then for each value of I there exist 1 or 3 equilibria.

  Hint: consider the cubic polynomial $p(V) = h(V) - I$. Note that this polynomial is different from the one in the first equation of the FNM (which is also a cubic)!. Study the sign of $p'(V)$. For S4 you find that $p'(V) > 0$ for all V, and you conclude that $p(V)$ is strictly monotone increasing.
- Assume $\gamma < 3/(1 - a + a^2)$, so that there is only one stationary state for each value of I. Prove that, if $3\epsilon\gamma < a^2 - a + 1$, then there exist two values of the currents I, say I_{*1} and $I_{*,2}$, such that:
  1. The FNM has equilibria at $E_1 = (V_{*1}, V_{*1}/\gamma)$, and $E_2 = (V_{*1}, V_{*1}/\gamma)$, with $I_{*1} = h(V_{*1})$ and $I_{*2} = h(V_{*2})$, respectively.
  2. The Jacobians $J(E_1)$ and $J(E_2)$ of the FNM at E_1 and E_2, respectively, have trace zero, and positive determinant.
  3. The eigenvalues of $J(E_1)$ and $J(E_2)$, are purely imaginary, and of the form $\lambda = \pm i\omega$.
- Use the previous results to predict the onset/death of oscillations in the Slowly-increasing current experiment. In that experiment, we selected parameters so that $\gamma < 3/(1 - a + a^2)$ and $3\epsilon\gamma < a^2 - a + 1$ so that the analysis above applies (check it!). Also, in that experiment $I(t)$ changes very slowly from 0 to 0.8. You should be able to check that I_{*1} and I_{*2} in the previous exercise correspond to value of the currents where the oscillations are born, or die out. This phenomenon is visible because the current traverses slowly 2 Hopf bifurcations, at I_{*1} and I_{*2}, respectively (we will discuss this more clearly in the following lectures). The ω in the previous exercise are related to the period of the solution near onset/termination. Judging from your calculations of ω, how can you make the period at the onset/death increase/decrease?

Explore the Morris-Lecar model using the software pplane

In this exercise, you get to familiarize yourselves with phase plane analysis using a tool called **pplane**, originally developed by D. Polking. The software is relatively old, and sort of maintained by the community because it is intuitive and enables most of the analysis we would like to achieve. If there is a downside, then it is the relatively low numerical accuracy. This could be made more strict at the expense of slowing it down considerably.

First, take the file "pplane9.m" from the ELO, and place this file into some folder and change Matlab's working directory to that folder. Next, on the command line, type "pplane9". A setup window appears with some menu items and several fields. Here, you can specify a planar system at the top, some expressions and parameters in the middle, and at the bottom you have several options to change the layout of the output. By default, some standard system is already specified. Without making any changes now, press the lower right button "Proceed". A "pplane9 Display"-window appears with arrows corresponding to the vector field. You can now click on a point in the phase plane. The result will show the orbit with this point as initial condition, both in forward an.d backward time. Following the arrows, you can trace the direction of time. Click on a few more points to get a pretty figure. We could analyze this system, but instead we now turn to the Morris-Lecar model.

In the "Setup" window, insert the following fields, with v and w in the left boxes, and the ODEs on the right:

```
v'=(-4.4*minf*(v-120)-8*w*(v-(-84))-2*(v-(-60))+Iapp)/20
w'=phi*(winf-w)/tauw
```

Next, we need to specify the following expressions and parameters:

```
minf=(1+tanh((v+1.2)/18))/2
tauw=1/cosh((v-2)/(2*30))
winf=(1+tanh((v-2)/30))/2
Iapp=80
phi=.04
```

Note that the parameters v3=2 and v4=30 have been substituted already. The general formula is given by:

```
tauw=1/cosh((v-v3)/(2*v4))
winf=(1+tanh((v-v3)/v4))/2
```

Finally, set tick the box "Nullclines" instead of arrows, and set the display Window to: [–80,50] x [0,1]

After all fields are filled, it is time to press "Proceed". The Display-window is updated. The first result is that the nullclines from the lecture are reproduced. The magenta V-nullcline indeed has the shape of a cubic, while the shap of the yellow W-nullcline is sigmoidal. We can now do a few numerical experiments.

- For Iapp=80, the system is excitable. First in the Display-window, select the option "Solutions|Find an equilibrium point." and select the intersection point of the nullclines. A pop-up window appears showing the coordinates and the linearization of the equilibrium. Verify this point is stable. Now click to the right of the point, i.e. starting near V=–30 till V=–20. Initially, the orbits will spiral to the equilibrium immediately, but at some point they will first make a large excursion. This is the sign of excitability. Some more remarks;
  1. If you find the simulation takes too long, you can press the "Stop"-button on the right.
  2. Time-varying inputs are not possible in this tool.
- For Iapp=90, the system is bistable. Update the parameter to this new value in the Display-window and press "Proceed" to get the new phase plane. First, verify that the steady state is still stable. Next, click near (V,W)=(–50,0). What do you observe? To check that we do two things. First, in the Display-window select "Solutions|Find a nearly closed orbit|Forward" and click on the orbit you just computed. You will get a message "a closed orbit of period 102". Second, select "Graph|Both" and click on the orbit to inspect the time series of V and W. The blue line shows periodic spiking, and if you select only W, then the red line shows this periodicity too. We conclude we have two attractors for this parameter value. Some unstable object must be in between separating the basins of attraction. To get a feeling for that, click on a point near the right maximum of the V-nullcline. What invariant object does the orbit approach in backward time?
- For Iapp=218 and higher, the system exhibits depolarization block. There is a stable steady state at the right branch. Unless you first apply an inhibitory perturbation, the system will not exhibit an action potential anymore.
- Experiment with a few other values for Iapp. You can also repeat your earlier analysis for the Fitzhugh-Nagumo model.