

Objectives

- Understand one of the processes via which neurons change the stability of their quiescent and spiking states.
- 2 Understand what a Hopf bifurcation is.
- Show the existence and calculate the direction of a Hopf bifurcation in a 2D neuron model.

• Consider the differential system given by Eq.(1) with a parameter $\mu \in \mathbb{R}$ such that

$$\frac{dx}{dt} = \begin{pmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{pmatrix} = \begin{pmatrix} f_1(x_1, x_2, \mu) \\ f_2(x_1, x_2, \mu) \end{pmatrix} = f(x, \mu), \tag{1}$$

- The parameter μ can modify the behavior of the solutions of the system. Thus, it should be useful to represent the evolution of the fixed point x_e according to the variation of the parameter μ_0 .
- For a differential system $dx/dt = f(x, \mu_0)$, μ_0 is called a *bifurcation* parameter if a topological change of a solution occurs when the parameter μ_0 changes.
- It is called a bifurcation parameter because it can completely change the behavior of the solutions.
- There are many types of bifurcations but in this course, only the Andronov-Hopf bifurcation (or Hopf bifurcation for short) is discussed in detail, as it is crucial for the spiking phenomenon we are interested in.

- For a fixed point x_e of a differential system $dx/dt = f(x, \mu)$, the pair (x_e, μ_0) is called a *Andronov-Hopf bifurcation point* when

 - 2 Det $D_x f(x_e, \mu_0) = \omega(\mu) > 0$,
- The first Lyapunov coefficient $L_1 \neq 0$ defined as:

$$\begin{split} L_1 &= \frac{1}{16(\omega(\mu_0))} \left[\frac{\partial^2 f_1}{\partial x_1 \partial x_2} \left(\frac{\partial^2 f_1}{\partial x_1^2} + \frac{\partial^2 f_1}{\partial x_2^2} \right) + \frac{\partial^2 f_2}{\partial x_1 \partial x_2} \left(\frac{\partial^2 f_2}{\partial x_1^2} + \frac{\partial^2 f_1}{\partial x_2^2} \right) - \frac{\partial^2 f_1}{\partial x_1^2} \frac{\partial^2 f_2}{\partial x_1^2} + \frac{\partial^2 f_1}{\partial x_2^2} \frac{\partial^2 f_2}{\partial x_2^2} \right] \\ &+ \frac{1}{16} \left[\frac{\partial^3 f_1}{\partial x_1^3} + \frac{\partial^3 f_1}{\partial x_1 \partial x_2^2} + \frac{\partial^3 f_2}{\partial x_1^2 \partial x_2} + \frac{\partial^3 f_2}{\partial x_2^2} \right], \end{split}$$

determines the criticality (direction) of the Andronov-Hopf bifurcation. The Andronov-Hopf bifurcation is super-critical if $L_1<0$ and sub-critical if $L_1>0$. When conditions 1,2, and 3 above hold, a unique isolated periodic solution (limit cycle — self-sustained spiking activity) bifurcates when the value of the parameter μ passes $\mu_0.$

In the theory of bifurcations, a Hopf bifurcation is a critical point where a system's stability switches and a periodic solution arises.

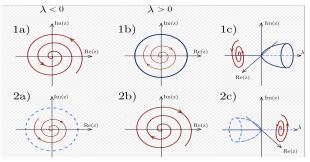


Figure: Dynamics of the Hopf bifurcation is governed by eigenvalue value $z=\lambda+i\omega$. Possible trajectories are in red, stable structures are in dark blue, and unstable structures are in dashed light blue. Super-critical Hopf bifurcation $(L_1<0)$: 1a) stable fixed point 1b) unstable fixed point, stable limit cycle 1c) phase space dynamics. Subcritical Hopf bifurcation $(L_1>0)$: 2a) stable fixed point, unstable limit cycle 2b) unstable fixed point 2c) phase space dynamics.

- It is helpful to draw the bifurcation diagram (one of the variables versus the bifurcation parameter) to understand how the system is modified when the parameter μ changes.
- To illustrate this, we consider equation

$$\begin{cases}
dv = (v - \frac{v^3}{3} - w + I)dt, \\
dw = \varepsilon(d + v)dt,
\end{cases}$$
(3)

with $0 < \varepsilon \ll 1$. The nullclines of the system are:

$$\begin{cases} v_{null}: w = v - \frac{v^3}{3} + I, \\ w_{null}: v = -d, \end{cases}$$
 (4)

and therefore, the fixed point is

$$(v_e, w_e) = (-d, -d + \frac{d^3}{3} + I).$$
 (5)

- Here, *d* is a bifurcation parameter that can drastically change the neuron's behavior.
- To see this, we study the behavior of the linearized system in the neighborhood of the fixed point by looking at the Jacobian matrix at (v_e, w_e) :

$$J(v_e, w_e) = \left(\begin{array}{cc} 1 - v_e^2 & -1 \\ \varepsilon & 0 \end{array} \right),$$

where $\det J = \varepsilon$ and $\operatorname{tr} J = 1 - v_e^2$. The eigenvalues of the Jacobian at (v_e, w_e) are

$$\lambda_{1,2} = \frac{1}{2} \left[(1 - d^2) \pm \sqrt{(1 - d^2)^2 - 4\varepsilon} \right].$$
 (6)

Following the table given in Lecture 8, depending on the value of the parameter d, we identify the following three cases:

- If |d| > 1, then (v_e, w_e) is stable node. At this point, it is important to point out that a neuron is said to be in an *excitable state* when starting with some initial condition in the basin of attraction of a *unique stable fixed point* will result in at *most one* large non-monotonic excursion (spike) into the phase space after which the phase trajectory returns and stays at this fixed point.
- ② If |d| < 1, then (v_e, w_e) is an unstable node and there exists a stable periodic cycle around it. The neuron is said to be in oscillatory state.
- ③ If d=1, the fixed point at $(v_e,w_e)=(-1,-2+I)$ is a Andronov-Hopf bifurcation point, for all $I \geq 0$. Furthermore, the value and, most importantly, the sign of the first Lyapunov coefficient is given by $L_1=-8.0$. This implies that the fixed point at $(v_e,w_e)=(-1,-2+I)$ undergoes a super-critical Hopf bifurcation; i.e., the stable fixed becomes unstable by creating a stable limit cycle (spiking) surrounding it.

 The bifurcation diagram for Eq.(3) above is shown in the Figure below, where we can see the range of values of the bifurcation parameter d for which we have either a no spiking (no limit cycle) or spiking (limit cycle).

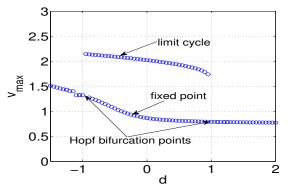


Figure: Bifurcation diagram computed with the maximum values (v_{max}) of the membrane potential variable. The blue circles represent a stable fixed point for |d| > 1. When |d| = 1 a Hopf bifurcation occurs. When |d| < 1 the system has an unstable fixed point and a stable limit cycle, $\varepsilon = 0.05$. I = 0.001.

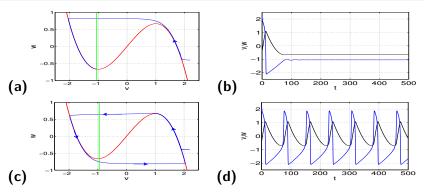


Figure: In (a) and (c) the red curve represents the cubic v-nullcline, the green vertical line is the w-nullcline which intersects the red curve at the fixed point at $(v_e, w_e) = (-d, -d + \frac{d^3}{3} + I)$. The blue curve with arrow shows the behavior of a trajectory with initial conditions at $(v_i, w_i) = (2.25, -0.35)$ for d = 1.05 in (a), and d = 0.95 in (c). (b) and (d) show the time series of v (in blue) and v (in black) of the phase portraits (a) and (c) respectively. In (b) the model is in the excitable state with no possibility of a limit cycle solution, while in (d), there is a limit cycle (Spiking). $\varepsilon = 0.05$, I = 0.001.

Remark: The stimulus current I in Eq. (3) is not a bifurcation parameter. Fixing d and varying $I \geq 0$ only moves the red curve representing the v-nullcline upward if I is increased or downward if I is decreased. Since the w-nullcline is vertical, changing I does not change the position of the v-coordinate of the fixed point at $(v_e, w_e) = (-d, -d + \frac{d^3}{3} + I)$ and therefore, the fixed point remains stable if |d| > 1 or unstable if |d| < 1. This can also be easily seen by looking at Eq.(6) above, which determines the stability of the unique fixed point (v_e, w_e) , which is independent of I.