1 Two Dimensional Neuron

In this problem we will study the dynamics of a neuron described by a membrane potential variable $V$ and a recovery variable $W$. The dynamics of the neuron are in general:

$$\frac{d}{dt} \begin{pmatrix} V \\ W \end{pmatrix} = \begin{pmatrix} \dot{V} \\ \dot{W} \end{pmatrix} = \begin{pmatrix} F_1(V, W) \\ F_2(V, W) \end{pmatrix}. \quad (1)$$

Assume that for all values of $V$ and $W$: $\frac{\partial F_1(V, W)}{\partial W} < 0$, $\frac{\partial F_2(V, W)}{\partial W} < 0$, $\frac{\partial F_2(V, W)}{\partial V} > 0$.

- **An equilibrium (fixed) point** $(V_0, W_0)$ is the point where $\dot{V} = F_1(V_0, W_0) = 0$ and $\dot{W} = F_2(V_0, W_0) = 0$.
- **Nullclines** are the lines where either $\dot{V}$ or $\dot{W}$ are 0. If the nullclines intersect, that is an equilibrium point. We will call the $F_1 = 0$ line the “$V$ nullcline” (because $\dot{V} = 0$ on that line) and the $F_2 = 0$ line the “$W$ nullcline”.

1.1 **Stability Analysis.** Suppose that at the equilibrium point $\frac{\partial F_1}{\partial V} < 0$. Show that the equilibrium is stable.

A specific model

We will work with **FitzHugh-Nagumo model** of the form:

$$F_1(V, W) = f(V) - W + I, \quad \text{where} \quad f(V) = \left(1 - \frac{V}{\sqrt{3}}\right) \cdot V \cdot \left(1 + \frac{V}{\sqrt{3}}\right) = V - \frac{V^3}{3}, \quad (2)$$

$$F_2(V, W) = \phi(V - bW). \quad (3)$$

Note that $\frac{1}{\phi}$ sets the time scale for the slow variable $W$, and therefore $0 < \phi \ll 1$.

1.2 **Plot the nullclines of the model** (solve for $W(V)$ such that $F_1 = 0$) or $F_2 = 0$, see Fig. [1] for the sketch) with the parameters $I = 3$, $b = 1/2$. Note that the $V$ nullclines have three “branches” and the $W$ nullcline is monotonic.

1.3 **Stability Analysis.** Find parameters such that the equilibrium is in the middle branch of the $V$ nullcline. Compute $\frac{\partial F_2}{\partial W}$ at the equilibrium and show that it is positive. Given your answer to 1.1, what does that say about the equilibrium point? Are you able to determine the stability as straightforward as 1.1?

1.4 Now find two sets of parameters and plot the nullclines for each of them:

---

1Problem courtesy of Bard Ermentrout. A good resource that can help with some background is chapter 3 of Bard’s book: Mathematical Foundations of Neuroscience. The eBook is available for free through [http://roger.ucsd.edu/](http://roger.ucsd.edu/)
(a) One such that the equilibrium is in the middle branch of the V nullcline and the slope of the V nullcline is smaller than the slope of the W nullcline at the equilibrium point.

(b) Another such that the equilibrium is in the middle branch of the V nullcline and the slope of the V nullcline is greater than the slope of the W nullcline at the equilibrium point.

Use linear stability analysis to show that in the first case the equilibrium is a node and that in the second case it is a saddle. Can you use the nullcline plots to explain this graphically? The range of each parameter: $b > 0, 0 < \phi \ll 1$ and $I \in \text{Real}$.

1.5 Run the dynamics. Plot examples of spike trains and discuss the different regimes you identified in 1.4.

2 Two Oscillators with Exponential-decay Coupling

Consider the two weakly coupled phase oscillations,

$$\frac{d\psi_i}{dt} = \omega + \epsilon \vec{Z}(\psi_i) \cdot \vec{P}(\psi_i, \psi_j), \quad i, j = \{1, 2\}$$

the two perturb each other with a small phase shift, $\psi_i = \delta \psi_i + \omega t$,

$$\frac{d\delta \psi_i}{dt} = \epsilon \vec{Z}(\delta \psi_i + \omega t) \cdot \vec{P}(\delta \psi_i + \omega t, \delta \psi_j + \omega t).$$

Since $\frac{d\delta \psi_i}{dt} \ll \omega$, we can average the perturbation over a full cycle,

$$\frac{d\delta \psi_1}{dt} = \Gamma(\delta \psi_1, \delta \psi_2)$$
$$\frac{d\delta \psi_2}{dt} = \Gamma(\delta \psi_2, \delta \psi_1)$$

where $\Gamma(\delta \psi_1, \delta \psi_j)$ represents the averaged perturbation of oscillator $j$ on oscillator $i$ over a full cycle,

$$\Gamma(\delta \psi_1, \delta \psi_j) = \frac{\epsilon}{2\pi} \int_{-\pi}^{\pi} d\theta \vec{Z}(\delta \psi_i + \theta) \cdot \vec{P}(\delta \psi_i + \theta, \delta \psi_j + \theta),$$

$\Gamma$
note that we have replaced $\omega t = \theta \in \{-\pi, \pi\}$. Similar to what we did in the lecture, assume that the perturbation $\vec{P} (\cdots)$ solely depends on the phase of the other oscillator, i.e., $\vec{P}(\delta \psi_i + \theta, \delta \psi_j + \theta) \rightarrow \vec{P}(\delta \psi_j + \theta)$,

$$\Gamma (\delta \psi_i, \delta \psi_j) = \frac{e}{2\pi} \int_{-\pi}^{\pi} d\theta \vec{Z}(\delta \psi_i + \theta) \cdot \vec{P}(\delta \psi_j + \theta),$$
change of variable $\theta \rightarrow \theta - \delta \psi_j$

$$\Rightarrow \Gamma (\delta \psi_j - \delta \psi_i) = \frac{e}{2\pi} \int_{-\pi}^{\pi} d\theta \vec{Z}(\theta - (\delta \psi_j - \delta \psi_i)) \cdot \vec{P}(\theta), \text{ let } \Delta_{ji} = \delta \psi_j - \delta \psi_i$$

$$\Rightarrow \Gamma (\Delta_{ji}) = \frac{e}{2\pi} \int_{-\pi}^{\pi} d\theta \vec{Z}(\theta - (\Delta_{ji})) \cdot \vec{P}(\theta), \quad (7)$$

where the sensitivity of phase to the perturbation is

$$Z(\phi) = \sin (\phi), \quad (8)$$

and the perturbation $\vec{P}(\cdots)$ is given by an exponential function

$$\vec{P}(\phi) = \begin{cases} 0, & \phi < 0 \\ g_{\text{syn}} e^{-\phi/\omega \tau}, & \phi \geq 0. \end{cases} \quad (9)$$

Eq. (4) and (5) become

$$\frac{d\delta \psi_1}{dt} = \Gamma (\delta \psi_2 - \delta \psi_1) = \Gamma (\Delta_{21}),$$

$$\frac{d\delta \psi_2}{dt} = \Gamma (\delta \psi_1 - \delta \psi_2) = \Gamma (\Delta_{12}).$$

Subtracting these two equations, we get the equation of motion for the phase difference between the two oscillators,

$$\Rightarrow \frac{d (\delta \psi_1 - \delta \psi_2)}{dt} = \Gamma (\delta \psi_2 - \delta \psi_1) - \Gamma (\delta \psi_1 - \delta \psi_2),$$

$$\Rightarrow \frac{d (\Delta_{12})}{dt} = \Gamma (\Delta_{21}) - \Gamma (\Delta_{12}),$$

$$= 2\Gamma_{\text{odd}} (\Delta_{21}) = 2\Gamma_{\text{odd}} (-\Delta_{12}), \quad (10)$$

$$= -2\Gamma_{\text{odd}} (\Delta_{12}), \quad (11)$$

where $\Gamma_{\text{odd}} (\cdots)$ is the odd part of the function $\Gamma (\cdots)$.

\textbf{2.1} Calculate the averaged perturbation $\Gamma (\Delta)$ and then find the odd function $\Gamma_{\text{odd}} (\Delta)$ \textit{(Hint: see the foot note)}.

\textbf{2.2} Analysis the stability for the case where two oscillators have

(a) excitatory connections $g_{\text{syn}} = g_{\text{excitatory}} > 0$; (b) inhibitory connections $g_{\text{syn}} = g_{\text{inhibitory}} < 0$.

For each case, do the two oscillators tend to be in-phasic or anti-phasic?

\footnote{The integral (Eq. 7) can be done by extending the range of integration over all time, i.e., $\int_{-\infty}^{\infty}$. Since $\vec{P}(\phi) = 0$ when $\phi < 0$, the integral in Eq. 7 becomes $\int_{0}^{\infty}$. For more detail, please cf. Sec. 5.3.1 of Week 4 lecture notes.}