Lecture 11: Slow-fast analysis, singular Hopf bifurcation, phase plane analysis, and excitability in a slow-fast neuron model (Continuation of Lecture 10)

The slow-fast analysis of FitzHugh-Nagumo neuron model

- Now we consider the FHN model given by:

$$\begin{cases} \varepsilon \frac{dx_\tau}{d\tau} & = & F(x_\tau, y_\tau) = x_\tau(a - x_\tau)(1 - x_\tau) - y_\tau, \\ \frac{dy_\tau}{d\tau} & = & G(x_\tau, y_\tau, c) = bx_\tau - cy_\tau, \end{cases} \tag{1}$$

or

$$\begin{cases} \frac{dx_t}{dt} & = & F(x_t, y_t) = x_t(a - x_t)(1 - x_t) - y_t, \\ \frac{dy_t}{dt} & = & \varepsilon G(x_t, y_t) = \varepsilon(bx_t - cy_t), \end{cases} \tag{2}$$

where $b > 0$ and $c > 0$ is a co-dimension one Hopf bifurcation, $0 < a < 1$, and $0 < \varepsilon := \frac{\tau}{t} \ll 1$.

- We shall focus on the slow-fast analysis of Eqs.(1) and (2), which allows us to analytically and geometrically understand the mechanism behind the dynamical behaviors of the FHN neuron model during excitability and spiking.
- For the slow-fast analysis of Eqs. (1) and (2), we take the singular limit $\varepsilon = 0$.

The slow-fast analysis of FitzHugh-Nagumo neuron model

- The singular limit in Eq.(2) yields:

$$\begin{cases} \frac{dx}{dt} & = & x(a-x)(1-x)-y, \\ \frac{dy}{dt} & = & 0, \end{cases} \tag{3}$$

Eq.(3) is called the fast subsystem of the FHN model, and it is an ODE parametrized by y (which is now a constant). The flow of the fast subsystem is called the fast flow.

- The singular limit in Eq.(1) yields:

$$\begin{cases} 0 & = & x(a-x)(1-x)-y, \\ \frac{dy}{d\tau} & = & bx-cy, \end{cases} \tag{4}$$

Eq.(4) is a differential-algebraic equation called the slow subsystem of the FHN model, and the flow of the slow subsystem is called the slow flow.

The slow-fast analysis of FitzHugh-Nagumo neuron model

- The algebraic constraint of Eq.(4) defines the critical manifold $\mathcal{M}_0$ of the FHN neuron (which is exactly the x-nullcline).

$$\mathcal{M}_0 := \{(x, y) \in \mathbb{R}^2 | F(x, y) = x(x-a)(1-x) - y = 0\} \quad (5)$$

- Note that points on $\mathcal{M}_0$ are fixed points of the fast subsystem in Eq.(3).
- The FHN neuron model is normally hyperbolic (i.e., $\partial_x F \neq 0$) away from the local maximum and a minimum of the critical manifold $\mathcal{M}_0$. At the special points defined by

$$(x_s, y_s) := \{(x, y) \in \mathbb{R}^2 | \partial_x F = \frac{dy}{dx} = -3x^2 + 2(a+1)x - a = 0\} \quad (6)$$

$\mathcal{M}_0$ looses normal hyperbolicity (since $\partial_x F = 0$) at its fold points (x_s, y_s), also known as singular points.

- Note: In general, the solution to an ordinary differential equation (ODE) may or may not be unique at a particular point. Whether or not a solution is unique depends on the properties of the ODE and the conditions imposed on the problem. The existence and uniqueness theorem for ODEs states that a first-order ODE will have a unique solution that satisfies specific initial or boundary conditions under certain conditions. This theorem guarantees the uniqueness of the solution in a certain interval or domain. However, it's important to note that the solution might not be unique in some cases. Non-uniqueness can occur when the ODE is singular or ill-posed, meaning that it lacks sufficient conditions to guarantee the existence of a unique solution.

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- At the fold point (x_s, y_s), the existence and uniqueness theorem of first-order ODEs does not hold, and the solutions (trajectories) of the slow subsystem in Eq.(4) are forced to leave $\mathcal{M}_0$ precisely at the singular points (x_s, y_s).

- So, since the critical manifold $\mathcal{M}_0$ of the FHN neuron model looses its hyperbolicity at the (x_s, y_s), the slow flow in Eq.(4) must detach from $\mathcal{M}_0$ and should become fast, that is $\frac{dy}{d\tau} = 0$, and horizontally jump from one attracting branch of $\mathcal{M}_0$ to another.
- To see this more clearly, it is more convenient to use an alternative procedure to derive the slow flow on $\mathcal{M}_0$ in terms of the fast variable x. We implicitly differentiate $F(x, y) = y - h(x) = 0$ with respect with τ

$$\frac{dy}{d\tau} = G(x, y) = h'(x)\frac{dx}{d\tau} \Rightarrow \frac{dx}{d\tau} = \frac{G(x, y)}{h'(x)}.$$

Using the constraint $y = h(x)$ (i.e., the critical manifold $\mathcal{M}_0$), we have the expression of the slow flow of the fast variable x on $\mathcal{M}_0$ as

$$\frac{dx}{d\tau} = \frac{G(x, h(x))}{h'(x)}, \tag{7}$$

which becomes singular at the fold point x_s with $h'(x_s) = 0$.

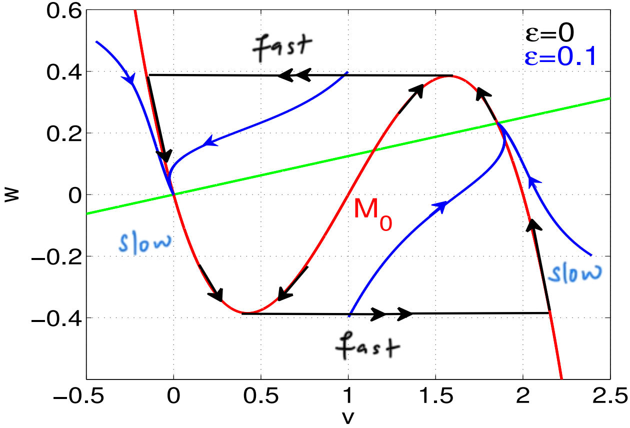


Figure: In the singular limit (i.e., when $\varepsilon = 0$), black single and double arrows indicate slow and fast flow, respectively. Blue trajectories represent some solutions of the FHN when $\varepsilon \neq 0$.

- A fold point (x_s, y_s) is said to be a folded singularity at the bifurcation parameter value $c = c_0$, if it satisfies the assumptions of a nondegenerate fold point, i.e.,

$$\begin{cases} F(x_s, y_s, c_0) = 0, \\ \partial_x F(x_s, y_s, c_0) = 0 \\ \partial_y F(x_s, y_s, c_0) \neq 0 \\ \partial_{xx} F(x_s, y_s, c_0) \neq 0 \\ G(x_s, y_s, c_0) = 0. \end{cases} \tag{8}$$

- A folded singularity of the FHN model is called generic if

$$\begin{cases} \partial_x G(x_s, y_s, c_0) \neq 0 \\ \partial_c G(x_s, y_s, c_0) \neq 0 \end{cases} \tag{9}$$

- Exercise 3B: Are the fold points defined in Eq. (6) above (which you must explicitly calculate) generic fold points or not?

- An arbitrary point $p \in \mathcal{M}_0$ at which a slow and a fast segment are concatenated is called
  - a jump point if the fast flow is directed away from $\mathcal{M}_0$,
  - a drop point if the fast flow is directed toward $\mathcal{M}_0$.

  At a generic fold point (x_s, y_s), the slow subsystem in Eq.(4) is singular, and solutions reach (x_s, y_s) in finite forward or backward time. This makes the generic fold point (x_s, y_s) a *jump point*, an ingredient necessary for the existence of deterministic relaxation oscillations.

- For the full FHN model (i.e., $\varepsilon > 0$), the fixed point are defined by

$$(x_e, y_e) := \{(x, y) \in \mathbb{R}^2 | F(x, y) = G(x, y) = 0\} \tag{10}$$

From Eq. (1), we obtain the fixed point equations given as

$$\begin{cases} \frac{b}{c}x = -x^3 + (a+1)x^2 - ax \\ y = \frac{b}{c}x \end{cases} \tag{11}$$

- Eq.(11) has solutions for x

$$\begin{cases} x_0 = 0 \\ x_1 = \frac{a+1}{2} - \sqrt{\frac{(a-1)^2}{4} - \frac{b}{c}} \\ x_2 = \frac{a+1}{2} + \sqrt{\frac{(a-1)^2}{4} - \frac{b}{c}} \end{cases} \tag{12}$$

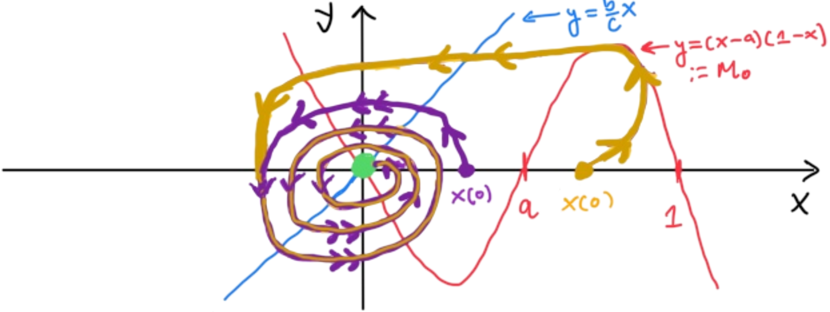
- Note that x_1 and x_2 exist (i.e., $x_1, x_2 \in \mathbb{R}$) only if $\frac{(a-1)^2}{4} > \frac{b}{c}$.
- See that if $(a-1)^2 < \frac{4b}{c} \implies x_0$ is the unique fixed point.
- Also, because $b > 0$, $c > 0$ and $0 < a < 1$, the set of fixed points in Eq.(12) becomes ordered, i.e., $x_0 < a < x_{1,2} < 1$.

The slow-fast analysis of FitzHugh-Nagumo neuron model

- A bifurcation is said to occur if some or all of the fixed points in Eq. (12) coincide.
- For example, $x_1 = x_2$ if and only if $\frac{(a-1)^2}{4} = \frac{b}{c}$
- For this course, we shall consider x_0 to be the only fixed point. The stability of x_0 is given by the eigenvalues of the Jacobian matrix of Eq.(2) (*From your previous exercises, this should now be a pretty easy check!*). We consider our unique fixed point $(x_0, y_0) = (0, 0)$ to be stable.
- With a unique and stable fixed point, the neuron is said to be in the excitable regime. The excitable regime of a neuron can thus be defined as a state where, starting from an initial condition within the basin of attraction of a *unique stable fixed point*, the neuron experiences at *most one* significant non-monotonic excursion (spike) in the phase space. After this spike, the phase trajectory returns to the fixed point and remains there until further perturbation.

Excitability of FitzHugh-Nagumo neuron model

- Phase portrait of the excitable regime of the FHN neuron.



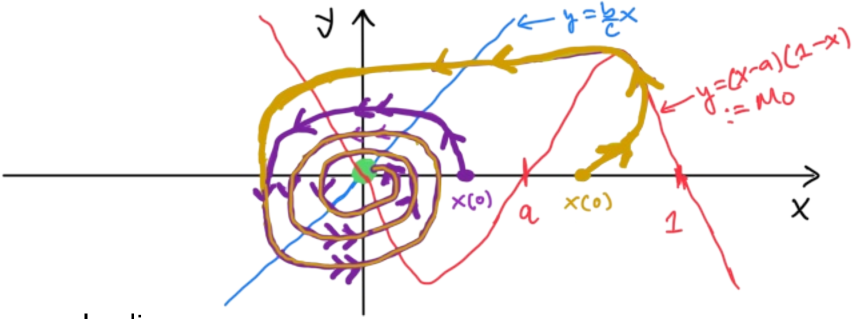
- The evolution of a trajectory in the excitable regime is constrained by the isoclines of the FHN neuron given by:

$$\frac{dy}{dx} = \frac{\varepsilon(bx - cy)}{x(x-a)(1-x) - y} \tag{13}$$

- Exercise 3C: Using the slow-fast FHN neuron model written in the fast timescale t, show how the isocline in Eq.(13) is obtained?

Excitability of FitzHugh-Nagumo neuron model

- Phase portrait of the excitable regime of the FHN neuron.



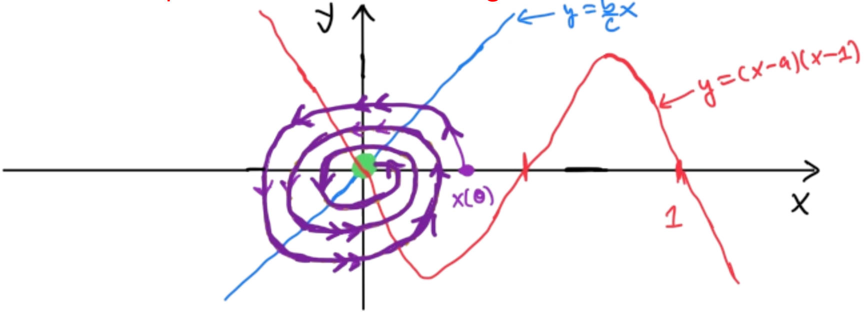
- Isoclines:

$$\frac{dy}{dx} = \frac{\varepsilon(bx - cy)}{x(x-a)(1-x) - y} \tag{14}$$

- If $y = \frac{b}{c}x \implies \frac{dy}{dx} = 0$ in Eq.(14)
- If $y = x(x-a)(1-x) \implies \frac{dy}{dx} = \infty$ in Eq.(14)
- If $0 < x < a$, then $\frac{dy}{dx} < 0$
- If $a < x < 1$, then $\frac{dy}{dx} > 0$

Excitability of FitzHugh-Nagumo neuron model

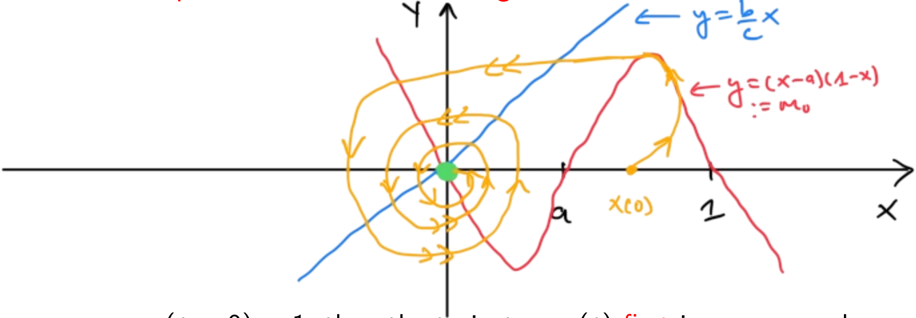
- Phase portrait of the excitable regime of the FHN neuron.



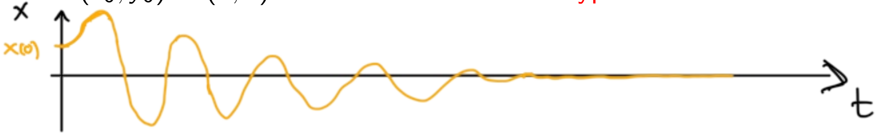
- $0 < x(t=0) < a$, then the trajectory moves directly to the unique and stable fixed point located at $(x_0, y_0) = (0, 0)$ and the voltage $x(t)$ of the neuron immediately starts to decrease to zero — the resting state of the neuron.

Excitability of FitzHugh-Nagumo neuron model

- Phase portrait of the excitable regime of the FHN neuron.

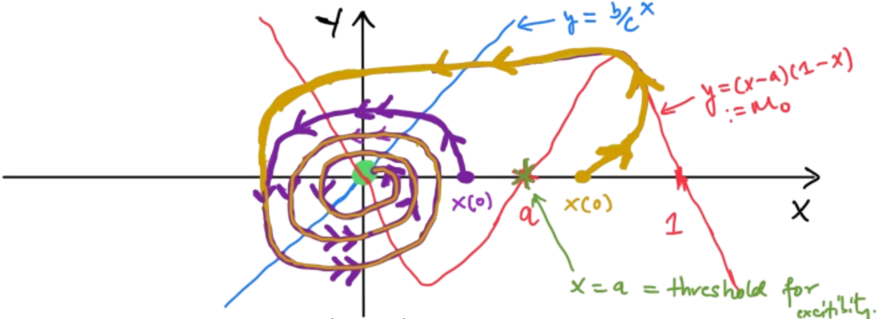


- $a < x(t = 0) < 1$, then the trajectory $x(t)$ first increases, and the FHN "fires" or "spikes". The trajectory undergoes a long excursion in phase space before returning to the fixed point at $(x_0, y_0) = (0, 0)$. This make the FHN a Type II neuron model.



Excitability of FitzHugh-Nagumo neuron model

- Phase portrait of the excitable regime of the FHN neuron.



- Thus, we see that $x(t = 0) = a$ acts a threshold between different behaviors called excitability.
- $x(t) \geq a$ can also be used as a threshold that determines whether at a time t there is a spike or not.

- In summary, 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 trajectory returns and stays at this fixed point. Self-sustained spiking is not possible in the excitable regime unless a parameter is changed such that a Hopf bifurcation occurs.

Singular Hopf bifurcation in the slow-fast FHN neuron

- Self-sustained spiking can be achieved in the FHN neuron model only via a Hopf bifurcation, making, as we shall see later, the FHN neuron model a Type II neuron model, in contrast to Type I neuron model.
- The slow-fast FHN neuron model (and, in general, any 2D slow-fast dynamical system) is said to undergo a singular Hopf bifurcation (SHB) if the linearized center manifold of the system has a pair of singular eigenvalues $\lambda(\varepsilon, c)$ at the Hopf bifurcation point $c = c_H$. That is, if we have $\lambda(\varepsilon, c) = \mu(\varepsilon, c) + i\beta(\varepsilon, c)$ such that $\mu(\varepsilon, c = c_H) = 0$ and $\frac{d}{dc}\mu(\varepsilon, c = c_H) \neq 0$, then the FHN undergoes a SHB if:
  1. $\lim_{\varepsilon \to 0} |\beta(\varepsilon, c)| = \infty$ on the slow time-scale τ, and
  2. $\lim_{\varepsilon \to 0} \beta(\varepsilon, c) = 0$ on the fast time-scale t.
- Exercise 3D: For $\varepsilon = 0.001$, show that the slow-fast FHN neuron given in Eqs. (1) and (2) can undergo a SHB at $c = c_H$. Simulate this FHN neuron on each timescale (i.e., on τ and t) and show the corresponding time series with at least 5 spikes, where a spike is counted only when $x \geq 1$.