Neural Networks and Biological Modeling

Professor Wulfram Gerstner
Laboratory of Computational Neuroscience

Answers to question set 3

Reminder: linear stability of a fixed point

We assume you have studied simple dynamical system before. Here, we give you a quick reminder. If you need more background information, we recommend you the following resources:

- Chapter 4.3 in "Neuronal Dymamics": http://neuronaldynamics.epfl.ch/online/Ch4.S3.html
- Chapter 5 in "Steven Strogatz, Nonlinear Dynamics and Chaos" (available in the library)
- Or just search the internet for what you need... http://wcherry.math.unt.edu/math2700/diffeq.pdf

Here's the compact summary: consider the dynamical system

$$\dot{x} = F(x)$$

where $x \in \mathbb{R}^n$ and $F : \mathbb{R}^n \to \mathbb{R}^n$. The fixed points of such a system are the points that satisfy $\dot{\mathbf{x}} = 0$, i.e., they are the solutions of $F(x) = 0$. In order to determine the stability of a fixed point x^*, we linearize the system about x^*:

$$\frac{d(x - x^*)}{dt} = \underbrace{F(x^*)}_{=0} + F'(x^*)(x - x^*) + \dots$$

where

$$F' = \begin{pmatrix} \frac{\partial F_1}{\partial x_1} & \cdots & \frac{\partial F_1}{\partial x_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial F_n}{\partial x_1} & \cdots & \frac{\partial F_n}{\partial x_n} \end{pmatrix}$$

is the jacobian matrix of F. If this matix has n distinct eigenvalues λ_k (real or complex), the system can be diagonalized, and the solutions can be expressed as combinations of exponentials of the form $e^{\lambda_k t}$. Therefore, $x - x^* \to 0$ if all the eigenvalues have a negative real part. If one or more eigenvalues have positive real part, $|x - x^*| \to \infty$. Therefore,

- The fixed point x^* is *stable* if all the eigenvalues of $F'(x^*)$ have negative real part.
- The fixed point x^* is *unstable* if one or more eigenvalues of $F'(x^*)$ have positive real part.
- If some eigenvalues have a vanishing real part (which occurs for pairs of eigenvalues since they are complex conjugates), the linear stability analysis is not sufficient to determine the stability of the fixed point.

Exercise 1: Separation of time scales

A. One-dimensional system

1.1 We set $\tau \frac{dx}{dt} = -x + c = 0$ and find the fixed point at $x = c$.

1.2 The general solution of this equation is $x(t) = x_0 e^{-t/\tau} + c(1 - e^{-t/\tau})$. (If you are not sure of how to find this solution, review the ODE primer given in the week one solutions and do the derivation with $a = -\frac{1}{\tau}$ and $q(t) = \frac{c}{\tau}$.)

We see from the general solution solution that any initial value x_0 decays to 0 while the second term approaches c with time constant τ. This shows that for any initial condition, the solution converges to the fixed point which is therefore stable (here, the eigenvalue is $\lambda = -1/\tau < 0$).

1.3 We need to solve the equations

$$\begin{array}{rll} (i) & \tau\dot{x} = -x & \text{for } t \in (-\infty, 0) \\ (ii) & \tau\dot{x} = -x + c_0 & \text{for } t \in (0, 1) \\ (iii) & \tau\dot{x} = -x & \text{for } t \in (1, +\infty) \end{array}$$

with the requirement that $x(t)$ be continuous. We obtain

$$x(t) = \begin{cases} 0 & \text{for } t \in (-\infty, 0) \\ c_0(1 - e^{-t/\tau}) & \text{for } t \in (0, 1) \\ c_1 e^{-(t-1)/\tau} & \text{for } t \in (1, +\infty) \end{cases}$$

where $c_1 = x(1) = c_0(1 - e^{-1/\tau})$.

1.4 We plot x(t) for $\tau = 0.01$ and $\tau = 0.5$ and observe the different timescales: compared to the blue curve, the red one almost instantanously reaches its target value.

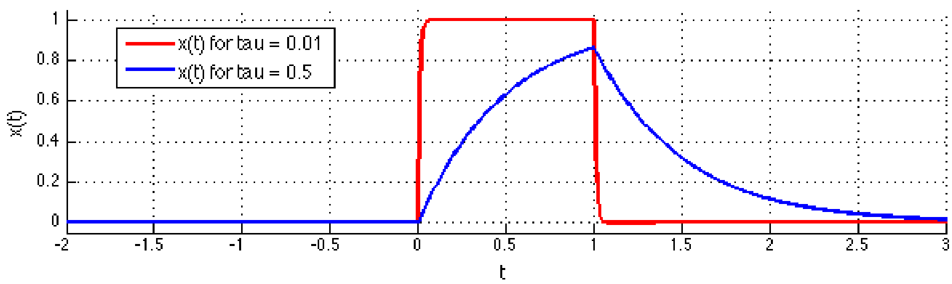


Figure 1: Evolution of x(t) for two different timescales.

B. Separation of time scales

1.5 The time constant of $u(t)$ is 1 whereas the m-variable evolves much faster with $\epsilon = 0.01$. In the limit $\frac{\epsilon}{1} \to 0$, m immediately converges to it's fixed point $c(u)$. We can therefore replace m with $c(u)$ in the first equation and are left with a single equation:

$\frac{du}{dt} = f(u) - c(u)$

1.6 The u-equation then becomes

$$\frac{du}{dt} = F(u) = -au + b - \tanh(u) \; .$$

The fixed points are given by $F(u) = 0 \Leftrightarrow f(u) = c(u)$. As you can see in figure 2, the two curves have exactly one intersection for all values of b. That fixed point is stable if $F'(u^*) = -a - tanh'(u^*) < 0$, which is always true since $a > 0$ and $tanh'(u) = 1 - tanh^2(u) > 0$.

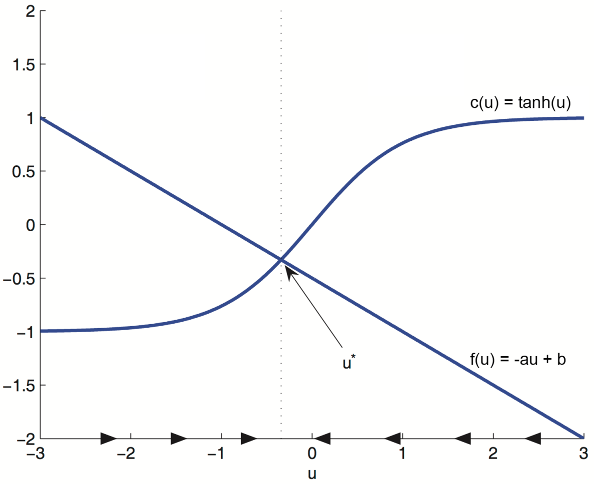


Figure 2: The fixed point u^* is given by the intersection of the two curves $f(u) = -ax + b$ and $c(u) = \tanh(u)$. On the left of the fixed point, we have $f(u) > c(u)$ and thus $F > 0$, whereas on the right of the fixed point $F < 0$. Therefore, $u(t)$ always moves towards the fixed point (in the direction of the arrows on the u-axis).

Exercise 2: Phase space stability analysis

2.1 Linear system

We study the following system

$$\begin{cases} \dfrac{du}{dt} &= \alpha u - w \\ \dfrac{dw}{dt} &= \beta u - w \end{cases} \tag{1}$$

If you had difficulties to analyze this system, we recommend to sketch the phase plane for a couple of different values for α and β. This will help you to become familiar with the notion of nullclines and eigenvectors. You will not get the point from looking at figure 3 - take a pen and paper.

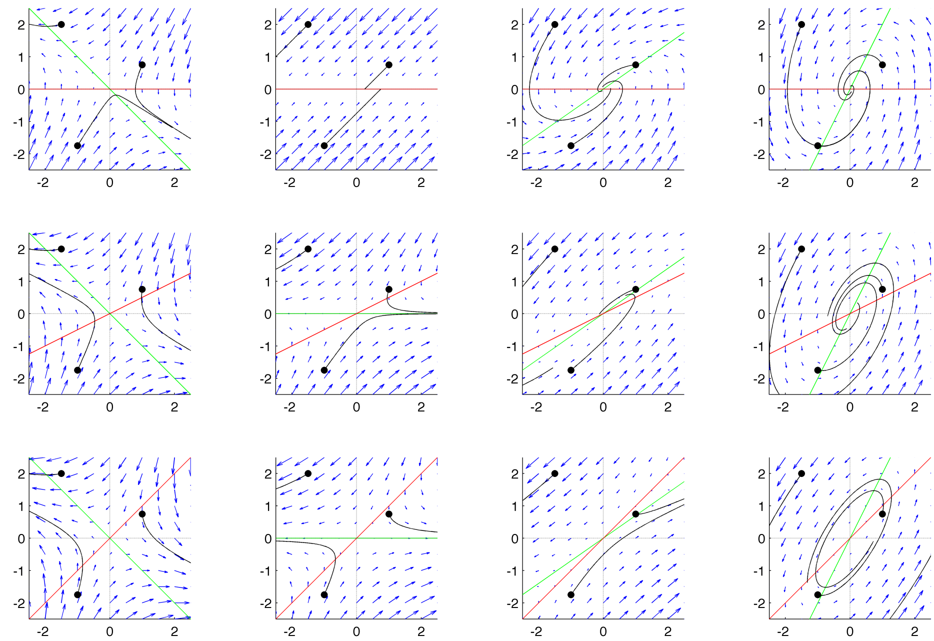


Figure 3: We plot the direction field for different combinations of $\alpha \in \{0, 0.5, 1\}$ and $\beta \in \{-1, 0, 0.7, 2\}$. The u-nullcline is plotted in green, the w-nullcline in red. The black lines are the trajectories we get when we initialize the system at the small black circle and let it evolve from t=0 to t=5.7. We observe that for some combinations, the system evolves in spirals. This is the case when it has complex eigenvalues. For real eigenvalues, we can estimate the eigendirection of the system from the graph.

The system can be rewritten as $\frac{d}{dt}x = Ax$ where $x = \begin{pmatrix} u \\ w \end{pmatrix}$ and $A = \begin{pmatrix} \alpha & -1 \\ \beta & -1 \end{pmatrix}$. The eigenvalues of A are the roots of the characteristic polynomial $P(\lambda) = \lambda^2 - \lambda \mathrm{Tr}A + \mathrm{Det}A$. They are given by

$$\lambda_\pm = -\frac{1}{2}\left[(1-\alpha) \pm \sqrt{(1-\alpha)^2 - 4(\beta-\alpha)}\right] . \tag{2}$$

Let us first study the case of real eigenvalues, that is, when $\beta \leq \frac{(1+\alpha)^2}{4}$ and $\alpha \neq 1$ holds. Since $\beta > \alpha$, we have $\sqrt{(1-\alpha)^2 - 4(\beta-\alpha)} < |1-\alpha|$. We can conclude that $\mathrm{sign}(\lambda_\pm) = \mathrm{sign}(\alpha - 1)$. In this situation,

$\alpha < 1 \Longrightarrow \lambda_\pm < 0$: The point $(0,0)$ is a stable fixed point.

$\alpha > 1 \Longrightarrow \lambda_\pm > 0$: The point $(0,0)$ is an unstable fixed point.

In the case $(1-\alpha)^2 - 4(\beta-\alpha) < 0$, the eigenvalues are complex conjugates. In that case,

$\alpha > 1 \Longrightarrow \mathrm{Re}(\lambda_\pm) > 0$: The point $(0,0)$ is an unstable fixed point.

$\alpha < 1 \Longrightarrow \mathrm{Re}(\lambda_\pm) < 0$: The point $(0,0)$ is a stable fixed point.

$\alpha = 1 \Longrightarrow \mathrm{Re}(\lambda_\pm) = 0$: In the case of a linear system the solution is a periodic orbit around the fixed point.

Remark : When $\beta < \alpha$, we have $\mathrm{sign}(\lambda_+\lambda_-) = -1$ (because $\sqrt{(1-\alpha)^2 - 4(\beta-\alpha)} >| 1-\alpha |$), and thus the fixed point is always unstable.

2.2 Piecewise linear Fitzhugh-Nagumo model

We study here the simplified Fitzhugh-Nagumo model:

$$\left[\begin{aligned} \frac{du}{dt} &= f(u) - w + I \\ \frac{dw}{dt} &= bu - w \end{aligned}\right. \tag{3}$$

(i) The fixed points are given by

$$\begin{aligned} w &= f(u) + I \\ u &= \frac{w}{b} . \end{aligned}$$

By sketching the nullclines, we see that there is only one fixed point. As I increases, this fixed point moves to the right along $f(u)$ (see figure 5).

(ii) The linearized system is

$$\frac{d}{dt}\begin{pmatrix} u-u^* \\ w-w^* \end{pmatrix} = \begin{pmatrix} p & -1 \\ b & -1 \end{pmatrix}\begin{pmatrix} u-u^* \\ w-w^* \end{pmatrix} \tag{4}$$

where $p = df/du\,|_{u^*}$ is the slope of $f(u)$ at the location of the fixed point (u^*, w^*). The eigenvalues are

$$\lambda_\pm = \frac{1}{2}\left[p - 1 \pm \sqrt{(p-1)^2 - 4(b-p)}\right] . \tag{5}$$

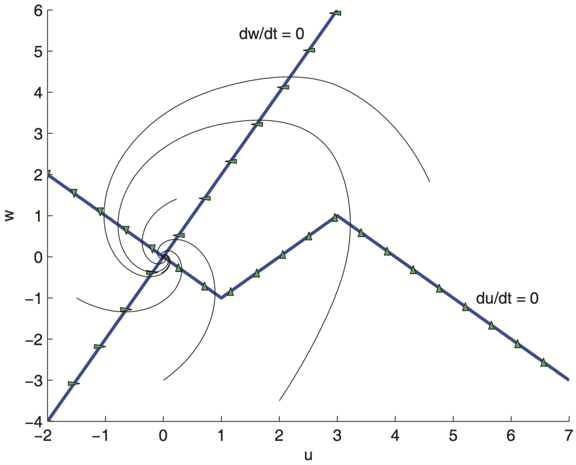
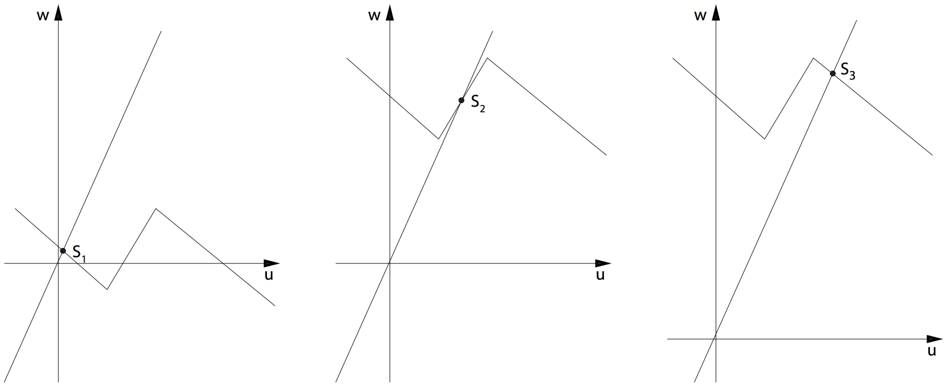


Figure 4: Nullclines of the Fitzhugh-Nagumo model for $a = 1$ and $b = 2$. A few trajectories are also shown.

With $a < 1$ and $b > 1/a$, we can apply the results of exercise 2.1, with $\alpha = p$ and $\beta = b$. We thus obtain the following classification:

$\mathbf{1^{st}}$ and $\mathbf{3^{rd}}$ segments of $\mathbf{f(u)}$, $\mathbf{p = -1}$. The fixed points (denoted S_1 and S_3 on Fig. 5) are stable.

$\mathbf{2^{nd}}$ segment of $\mathbf{f(u)}$, $\mathbf{p = \frac{1}{a}}$. Since $a < 1$, we have $1 < p < b$ and thus this fixed point (denoted S_2) is unstable.



(a) $I \leq b + 1$ (b) $b + 1 \leq I \leq b(1 + 2a) - 1$ (c) $I \geq b(1 + 2a) - 1$

Figure 5: Nullclines for the simplified Fitzhugh-Nagumo model. The input current shifts the u-nullcline and thereby affects the location (and stability) of the fixed point.