Dynamical Systems in Neuroscience: Elementary Bifurcations

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1 Introduction

In a dynamical system representing the stimulation of neurons, bifurcations arise due to the fact that when stimulated by a constant amplitude current to drive the cell of the neuron to fire, the membrane goes from having a resting potential voltage to an oscillatory voltage as a result of the bifurcation of the input into the dynamical systems.

There are a multitude of bifurcations that exist in representing the behavior of neurons, however the use cases of each depends on the specific experiment that is being conducted. For single neuron dynamics, the saddle node on a an invariant circle (SNIC) and the Hopf Bifurcation are the most common bifurcations to arise out of the most common models for neuronal behavior, namely Hodgkin-Huxley and Morris-Lecar equations.

In a small neuronal network, the bifurcations that arise have some edge cases in when they may oscillate as a network. As such, expressing the bifurcations in terms of the single neuron bifurcations is not going to be sufficient and instead we will look at how they function as a group.

2 Definitions

Dynamical System: A system in which a function describes the time dependence of a point in geometrical space. Usually represented as a differential equation of the following form,

$$\frac{dx}{dt} = F(x, \mu) \tag{1}$$

where x is an n-dimensional vector of unknowns and μ is an m-dimensional vector of parameters, and F is simply a function that depends on both.

Bifurcation Theory: A family of differential equations that depending on a parameter α such that

$$Y'(t) = F(\alpha, Y(t)) \tag{2}$$

where $Y(t) \in \mathbb{R}^n$. Bifurcation theory examines the changes in the qualitative behavior as α varies in the dynamical system. For the sake of this paper we will be referencing the most elementary types of bifurcations that is, equilibrium bifurcations.

Equilibrium Bifurcation: Qualitative changes that relate to changes in the properties of of an equilibrium in a system.

3 Hodgkin-Huxley Model

Also known as the conductance based model, the Hodgkin-Huxley model is a 2 dimensional model that simulates the response of action potentials in neurons. The model represents the cell as a circuit with lipid bilayer of the cell has some capacitance C_m, each ion channel within the cell has some conductance g_n where n denotes a specific ion channel, g_L the conductance of the Leak channels, and finally E_n and E_L denote the emf generated by the difference in electrochemical ions, in this case, sodium and potassium ions.

The leak current can be expressed by the following balance

$$I_L = I_{cap} + I_{ion}$$

where

$$I_{cap} = C_m \frac{dV_m}{dt}$$

and

$$I_{ion} = g_n(V_m - V_{ion})$$

Therefore the total current through the membrane with sodium and potassium channels mentioned prior is,

$$I_{total} = I_{cap} + I_{K^+} + I_{Na^+} + I_L$$

which is

$$I_{total} = C_m \frac{dV_m}{dt} + g_K(V_M - E_K) + g_{Na}(V_m - E_{Na}) + g_L(V_M - E_L) \tag{3}$$

Furthermore, in the Hodgkin-Huxley model, there exist gating variables which determine the probability of a channel opening. From empirical analysis we have that the probability that the potassium channel opens is n^4 and for sodium we have that it is m^3. There is also the probability that the sodium inactivation gate is open, that is something that is a result of the inhibitory process due to bursting or a refractory period so to speak and this has the variable h usually denoting it. Therefore our Hodgkin-Huxley model now takes the form,

$$I_{total} = C_m \frac{dV_m}{dt} + \overline{g}_K n^4(V_M - E_K) + \overline{g}_{Na} m^3 h(V_m - E_{Na}) + \overline{g}_L(V_M - E_L) \tag{4}$$

It is also important to know that each of these gating variables have their own first-order differential equation that they satisfy.

$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n \tag{5}$$

$$\frac{dm}{dt} = \alpha_m(V)(1-m) - \beta_m(V)m \tag{6}$$

$$\frac{dh}{dt} = \alpha_h(V)(1-h) - \beta_h(V)h \tag{7}$$

Now if we let $p = n, m$ or h then we have that,

$$p_\infty(V) = \frac{\alpha_p(V)}{\alpha_p(V) + \beta_p(V)} \tag{8}$$

and

$$\tau_p(V) = \frac{1}{\alpha_p(V) + \beta_p(V)} \tag{9}$$

4 Morris-Lecar Model

Similar to the Hodgkin-Huxley model, this model instead of being based off a sodium channel, it is instead based off a calcium channel. The model follows quite similarly to the Hodgkin-Huxley and takes the form of the following,

$$C_M \frac{dV}{dt} = I - g_L(V - E_L) - g_K n(V - E_K) - g_{Ca} m_\infty(V)(V - E_{Ca} \tag{10}$$

$$\frac{dn}{dt} = \phi(n_\infty(V) - n)/\tau_n(V) \tag{11}$$

where

$$m_\infty(V) = \frac{1}{2}[1 + \tanh((V - V_1)/2)] \tag{12}$$

$$\tau_n(V) = 1/\cosh((V - V_3)/(2V_4)) \tag{13}$$

$$n_\infty(V) = \frac{1}{2}[1 + \tanh((V - V_3)/V_4)] \tag{14}$$

and V_1, V_2, V_3 and V_4 are chosen parameters such that they satisfy the voltage-clamp data or satisfy the steady state and time constant and ϕ is a reference frequency.

5 Stability

Before progressing on, it is important that we discuss when our linear and non-linear differential equations are stable due to the fact that we will be discussing equilibrium bifurcations.

5.1 Linear ODE

For linear ODE's of the first order we can find their points of stability by solving and examining the eigenvalues of the autonomous function,

$$Ax = \lambda x \tag{15}$$

We say that this solution is asymptotically as $t \to \infty$ if and only if for all eigenvalues of A, $\text{Re}(\lambda) < 0$. It is asymptotically stable for $t \to -\infty$ if and only if for all eigenvalues of A, $\text{Re}(\lambda) > 0$.

5.2 Non-linear ODE

Taking the linearization of a system of two differential equations at a fixed point, we can find stability by taking the Jacobian of that matrix.

Similar to our linear reference we have that if both of the eigenvalues of the two dimensional Jacobian matrix have negative real values.

In the case of our models it would be similar to the following,

$$\frac{dV}{dt} = f(V, n) \tag{16}$$

$$\frac{dn}{dt} = g(V, n) \tag{17}$$

Let M denote the linearized Jacobian matrix about a fixed point, then we have that,

$$M = \begin{vmatrix} \frac{\partial f}{\partial V}(V_R, n_R) & \frac{\partial f}{\partial n}(V_R, n_R) \\ \frac{\partial g}{\partial V}(V_R, n_R) & \frac{\partial g}{\partial n}(V_R, n_R) \end{vmatrix} \tag{18}$$

6 Andronov-Hopf Bifurcation

As a parameter is varied in the Morris-Lecar model, it naturally will follow that points of stability will become unstable. What Andronov-Hopf bifurcation looks at in particular is the transition of stability from a complex eigenvalue to another part in the imaginary axis.

The Hopf bifurcation theorem states that there exists values of the parameter I near I_1 and I_2 such that there exist periodic solutions that lie near fixed points $(V_R(I), n_R(I))$. That is to say there is a critical point such that the dynamical system's stability switches and periodic solutions arise.

In most cases the Hopf bifurcation is a two dimensional prototype, in this case let us consider a function $F : \mathbb{R} \times \mathbb{R}^2 \to \mathbb{R}^2$. If

1. $F(x, 0) = 0$ for some x in a neighborhood of x_0
2. $DF(x, 0)$ has two non-real eigenvalues $|\lambda(x)|$ and $\overline{\lambda}(x)$ for x in a neighborhood of x_0 and that the modulus of eigenvalue about x_0 is 1
3. $\frac{d}{dx}|\lambda(x)| > 0$ at $x = x_0$
4. $\lambda^k(_0) \neq 1$ for $k = 1, 2, 3, 4$

Then there exists a smooth x-dependent change of coordinates bringing F into the form $F(x, \mu) = f(x, \mu) + O(||x||^5)$. This is due to the fact that the map we are looking at is a C^4 map so we don't want our eigenvalue to satisfy the first four roots of unity as well as getting an order of degree 5 on the mapping function.

Now we want to represent this in terms of polar coordinates as it is easier to handle, that is we now have,

$$f = \begin{vmatrix} |\lambda(x)|r - \alpha(x)r^3 \\ \theta + \gamma(x) + \beta(x)r^2 \end{vmatrix} \tag{19}$$

where $\alpha(x)$, $\beta(x)$, and $\gamma(x)$ are smooth arbitrary functions.

We consider the bifurcation subcritical if the term $\alpha(x_0) < 0$ and the case of $\alpha(x_0) = 0$ is undetermined.

We consider the bifurcation supercritical if the function is determinable at $\alpha(x_0) = 0$ is asymptotically stable about that point and furthermore that the term itself $\alpha(x_0) > 0$.

Do note that there are more specific Hopf bifurcations such as the Hopf-Hopf Bifurcation, normal form Hopf Bifurcation, but in this context we are simply just talking about the generic Hopf bifurcation.

7 Saddle Node on an Invariant Circle Bifurcation

To begin with we will go over what a Saddle Node Bifurcation is and then progress onto the case of it being on the invariant circle.

7.1 Saddle Node Bifurcation Normal Form

A saddle node bifurcation is a bifurcation that has the properties that as one varies the parameter α the appearance of fixed points being equilibrium will collide and eventually disappear. The saddle node bifurcation differential equation often takes the form of,

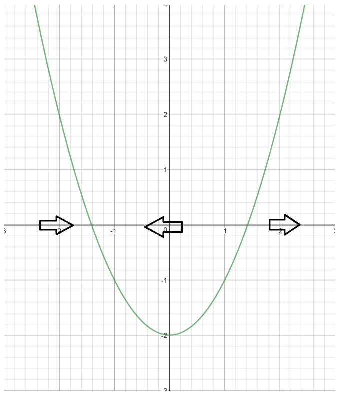
$$Y'(t) = \alpha + Y(t)^2 \tag{20}$$

where α is a our varying parameter. Solving for stability we see that the equilibria points only exist at the solution to the quadratic equation,

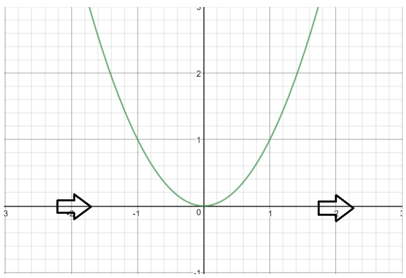
$$Y(t) = \pm\sqrt{-\alpha} \tag{21}$$

Now notice that we have three scenarios,

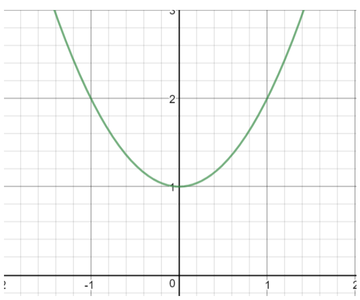
1. If $\alpha < 0$ we have that there exists two equilibrium points, one at $-\sqrt{\alpha}$ and one at $\sqrt{-\alpha}$. Notice furthermore, the stable equilibrium point is at the negative value and unstable at the positive. This can be represented by the following diagram of the quadratic equation,



2. If $\alpha = 0$ we see that we only have one point of equilibria and that is at the origin, however this equilibria is upon a saddle point, therefore unsurprisingly we call it a saddle node bifurcation,



3. Finally if $\alpha > 0$ we see that r can only be imaginary meaning that there is no equilibria on the real domain, therefore we have no equilibria and a graph that looks as following,



Therefore the term saddle-node bifurcation comes about because you either have a stable point or a saddle node point for bifurcations. Furthermore, the visualization that as α changes over time we see that the we go from a stable equilibria to the colliding of them before the disappearance of the equilibria altogether.

7.2 Saddle Node Bifurcation Two Dimensions

In two dimensions we have the following form that the differential equations tend to take,

$$\frac{dx}{dt} = \alpha - x^2 \tag{22}$$

$$\frac{dy}{dt} = -y \tag{23}$$

For this section there will be no diagrams depicting the stability and instability of the equilibria as I am incapable of producing such diagrams.

However similar to the normal form we have 3 cases that are a result of the changing parameter α.

1. The first in this case is when $\alpha < 0$ we notice that this time because of how the differential equation is set up in respect to $\frac{dx}{dt}$ we have that there are no equilibrium points.

2. The second is when $\alpha = 0$, we once again have that there exists a saddle point.

3. Finally when we have $\alpha > 0$ this time we have that these are where the two points of equilibrium, but this time however one of the points is a saddle point and the other is a node, one that will either attract (stable) or repel (unstable).

Once again with the varying α we see in this case in reverse that we have that there exist a two equilibrium that collide before disappearing.

7.3 Saddle Node on an Invariant Circle

The SNIC is a standard saddle node bifurcation except that it occurs on an invariant circle. Furthermore, the path that the varying parameter takes is that of a heteroclinic trajectory, or a orbital path in phase space that joins the two equilibrium points together. Note that if the equlibrium point start and end desintation is the same, then we call this a homoclinic trajectory. We call the circle an invariant because any solution that starts on the circle remains on the circle.

So for the SNIC, we have that we have a heteroclinic trajectory connecting the node and the saddle that were mentioned in section 7.2. As we know about saddle node bifurcations, the node and the saddle point will eventually coalesce, as this happens, the direct trajectory shrinks, our heteroclinic trajectory that is larger slowly becomes a homoclinic trajectory on the invariant circle because the equilibrium has become one. Finally once the point disappears, we get that the circle becomes a limit-cycle, which is simply when a trajectory becomes closed and infinite.

8 Relation to Neuroscience

The bifurcations are important because when a neuron is in it's resting state, it is excitable and we can treat that mathematically that it is near a bifurcation. Therefore when we inject a ramp current, that is as we increase the amount of DC current going into the neuron, we are causing the parameters to change or varying α at this point.

The reason the two aforementioned bifurcations were chosen for this is because as the current changes we have two bifurcations that result in part due to the eigenvalues of the Jacobian of our dynamical system,

1. We get a negative eigenvalue that increases and becomes zero which happens at the saddle-node bifurcation, and as we know from above this causes the equilibrium to disappear entirely.

2. The next is that we have two complex-conjugate eigenvalues with negative real parts. These real parts become purely imaginary as we vary current, and in this case this is exactly the Andronov-Hopf Bifurcation previously mentioned, so we see that the equilibrium becomes unstable but unlike the saddle node bifurcation it does not disappear.

As such these two bifurcations are quintessential to modeling the behavior of how neurons act with regard to current ramp injections. The current ramp injections are a means of essentially activating the action potential and getting the neuron to fire.

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