# Bifurcation Analysis, Phase Model of Izhikevich Model

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# 1 Introduction

A neuron is a cell in the human brain that can propagate electric signals along its axon and transmit information to other neurons, enabling a range of functionalities such as cognition and muscle control. The firing of electric signals, also referred to as spiking, occurs when the membrane potential of the neuron reaches a certain threshold. Naturally, people are interested in modeling the membrane potential of the neuron and developing models that can mimic important properties of neurons.

The Izhikevich model [4], developed by Eugene M. Izhikevich, is a planar fast-slow system that can model various firing patterns of a neuron. A very important feature of this model is the existence of subthreshold oscillation, which distinguishes a neuron from an integrator to a resonator. Mathematically, the transition from integrator to resonator occurs via a co-dimension 2 Bogdanov-Takens bifurcation, with the integrator corresponding to a saddle-node on invariant circle bifurcation and the resonator corresponding to an Andronov-Hopf bifurcation. In this report, we develop the bifurcation conditions for the aforementioned bifurcations to occur. Furthermore, we use the Phase Response Curve (PRC) and the Frequency-Current Curve (F-I curve) to show the transition of the neuron from integrator to resonator. After completing the analysis of the single-neuron case, we proceed to investigate the effect of bifurcation on the synchronization of two neurons. However, during the investigation, we found that parameter $d$ has a significant effect on the synchronization of the neuron. Therefore, we use the infinitesimal Phase Response Curve (iPRC) to investigate the effect of parameter $d$ on the uncoupled neuron. The iPRC could be then used to investigate the effect of parameter $d$ on the weakly coupled neuron by computing the phase model.

# 2 Bifurcation Analysis of Izhikevich Model

## 2.1 The Model Itself

Similar to integrate and fire model, the Izhikevich model has a resetting condition, but, this model also have a current variable u that modulates the faster voltage variable v. The dimensional Izhikevich model is as follows:

$$\begin{aligned} C\dot{v} &= k(v-v_r)(v-v_t) - u + I_{\text{app}} & \qquad \text{if } v \geq v_{\text{peak}},\ \text{then} \\ \dot{u} &= a(b(v-v_r)-u) & \qquad v \to c, u \to u+d \end{aligned} \tag{1}$$

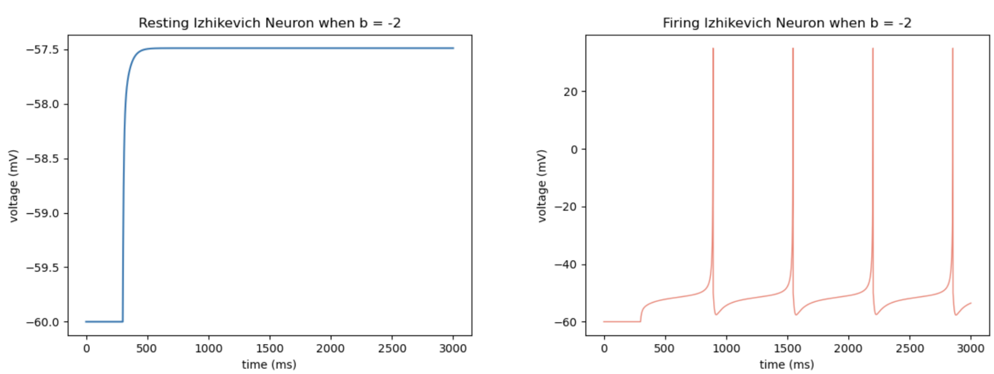
In a biological neuron, the membrane of the neuron has various gates that open and closes depending on the concentration of various chemicals that are generated from stimulation. The voltage dependent slow variable u aims to reproduce the same effect on the neuron, and hence we could have a vector of u, a and b[4].

The Izhikevich model aims to produce the subthreshold behaviours that are observed in the biological neuron model such as Hodgkin-Huxley model[4]. Through tuning the parameter b, the neuron can transition from an integrator to resonator[4]. Therefore, we can only look at the behaviour of the model for $v < v_{\text{peak}}$ when analyzing for the bifurcation condition. The rest of parameter can be chosen to model spiking patterns of biological neuron such as Regular Spiking, Intrinsically Bursting and etc. We are particularly interested in regular spiking neurons, so we choose the parameter in [4],

| C | a | k | $v_r$ | $v_t$ | $v_{\text{peak}}$ | c | d |
|---|---|---|---|---|---|---|---|
| 100 | 0.03 | 0.7 | -60 | -40 | 35 | -50 | 100 |

## 2.2 The Role of $I_{\text{app}}$

Generally, the neuron has two states, the resting states in which neuron does not fire, and the spiking state state in which neuron fire in different patterns. The transition of a neuron from rest to fire happens via 4 types of bifurca-



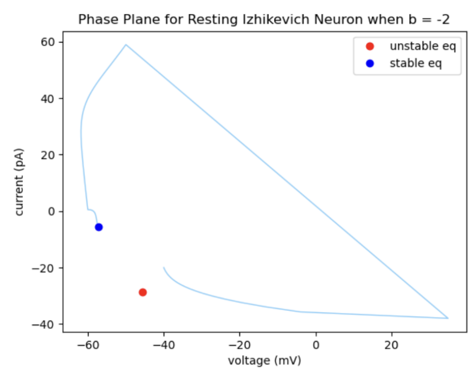

Resting

Regular Spiking

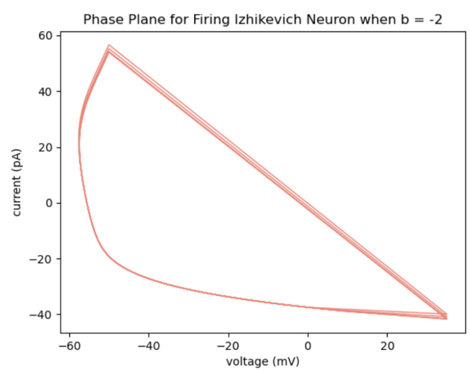
Figure 1: Two States of Neuron

tions, Saddle Node Bifurcation, Saddle-Node on Invariant Circle Bifurcation, Subcritical Andronov-Hopf Bifurcation, and Supercritical Andronov-Hopf Bifurcation. In the case of Izhikevich neuron, when the $I_{\text{app}}$ is sufficiently large, the neuron will spike via either Saddle-Node on Invariant Circle Bifurcation or Subcritical Andronov-Hopf Bifurcation[4] depending on the value of b. To maintain Regular Spiking, we need to maintain the sufficiently large current. Therefore, $I_{\text{app}}$ is our bifurcation parameter. Depending on the value of b, the neuron will either be an integrator or a resonator.

In the view of dynamical system, when a neuron is resting, the solutions near the stable equilibrium points are attracted to it, and the solutions near the unstable equilibrium are repelled from it. In Figure 2, when $I_{\text{app}}$ is low, the neuron is at rest, so a large perturbation might cause the neuron to fire, but eventually settles down to a steady state solution. Once the neuron is in Regular Spiking, we then have stable limit cycles that attract nearby solutions.




Resting




Regular Spiking

Figure 2: Dynamical System View of Two States of the Neuron

## 2.3 Jacobians, Equilibrium Points, and Nullclines

The v-nullcline and u-nullcline can be found by setting $\dot{v} = 0, \dot{u} = 0$.

$$
\begin{aligned}
u &= I_{\text{app}} + k(v - v_r)(v - v_t) \\
u &= b(v - v_r)
\end{aligned}
$$

Unlike the usual biological neuron model, we have a parabola nullcline rather than a cubic nullcline. The equilibrium points can be found by setting the nullcline equal to each other.

$$
\begin{aligned}
v_{\text{eq},1} &= \frac{kv_t + kv_r + b + \sqrt{(v_r - v_t)^2 k^2 + (-2v_r b + 2bv_t - 4I_{\text{app}})k + b^2}}{2k} \\
u_{\text{eq},1} &= b(v_{\text{eq},1} - v_r) \\
v_{\text{eq},2} &= \frac{kv_t + kv_r + b - \sqrt{(v_r - v_t)^2 k^2 + (-2v_r b + 2bv_t - 4I_{\text{app}})k + b^2}}{2k} \\
u_{\text{eq},2} &= b(v_{\text{eq},2} - v_r)
\end{aligned}
$$

Plotting the nullcline and equilibrium points give us an idea of how the saddle node on invariant circle bifurcation happens

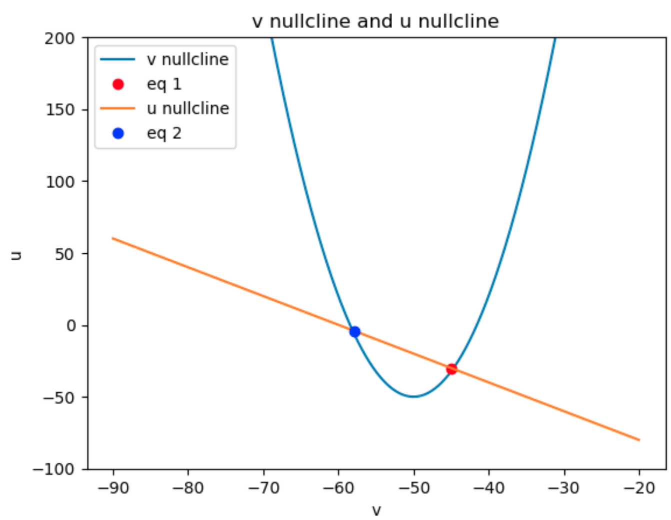



Figure 3: Nullclines

As we increase the current applied, the quadratic nullcline will be shifted upwards, and two equilibrium points eventually collides and we have a saddle node. To derive the condition for the Andronov-Hopf bifurcation to happen, we compute the Jacobians of the system,

$$
J = \begin{bmatrix} \frac{k(2v - v_t - v_r)}{C} & \frac{-1}{C} \\ ab & -a \end{bmatrix} \tag{2}
$$

The eigenvalue of the Jacobian are

$$
\lambda_2 = -\frac{\eta - Ca + \sqrt{\eta^2 + 2Ca\eta + Ca(Ca - 4b)}}{2C}
$$

where $\eta = 2k(v - \frac{v_r}{2} - \frac{v_t}{2})$. For a Andronov-Hopf Bifurcation to occur, we need to have two eigenvalues with purely imaginary part, so we should set $\eta = 0$,

$$v_{\text{hopf}} = \frac{Ca + k(v_t + v_r)}{2k} \tag{3}$$

to zero the term in front of the radicand. Then, the eigenvalue becomes

$$\lambda_{\text{hopf}} = \pm\frac{\sqrt{Ca(Ca-b)}}{C}$$

Therefore, we see that if $\boldsymbol{Ca < b}$, we will have **Andronov-Hopf Bifurcation**. The current at which $v_{\text{hopf}}$ occurs can be found by equating the equilibrium points with $v_{\text{hopf}}$, which is

$$I_{\textbf{hopf}} = \frac{-((v_r - v_t)k + Ca - 2b)((v_t - v_r)k + Ca)}{4k} \tag{4}$$

Furthermore, when $\boldsymbol{Ca = b}$, the two eigenvalues will be zero, which means we have **Bogdanov-Takens Condition**. For Saddle-Node on invariant circle bifurcation, we can set the two equilibrium points equal to each other, and obtain

$$I_{\text{sn}} = \frac{((v_t - v_r)k + b)^2}{4k} \tag{5}$$

When $I_{\text{app}} = I_{\text{sn}}$, the equilibrium points for v is

$$v_{\text{sn}} = \frac{b + k(v_t + v_r)}{2k} \tag{6}$$

Substitute $v_{\text{sn}}$ into the eigenvalues, we have $\lambda_1 = -\frac{Ca-b-|Ca-b|}{2C}$, $\lambda_2 = -\frac{Ca-b+|Ca-b|}{2C}$. In both cases of $Ca > b, Ca < b$, we will have a saddle node bifurcation at $v_{\text{sn}}$ when $I_{\text{app}} = I_{\text{sn}}$. Then, if $Ca < b$, and we are at $I_{\text{hopf}}$, we will have Andronov-Hopf Bifurcation. The $I_{\text{sn}}$ and $I_{\text{hopf}}$ can be plotted against b to give a graphical visualization of the two bifurcation parameters,

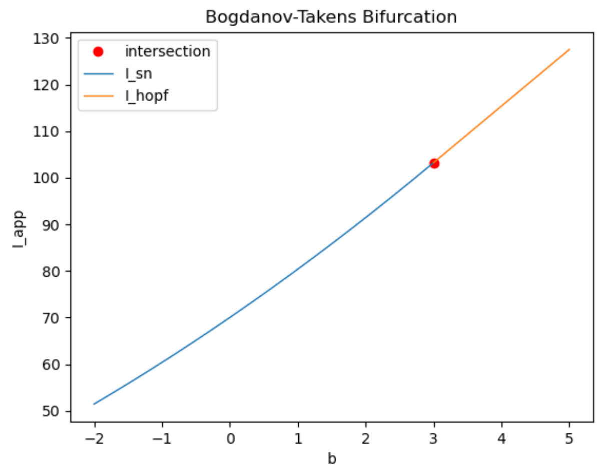
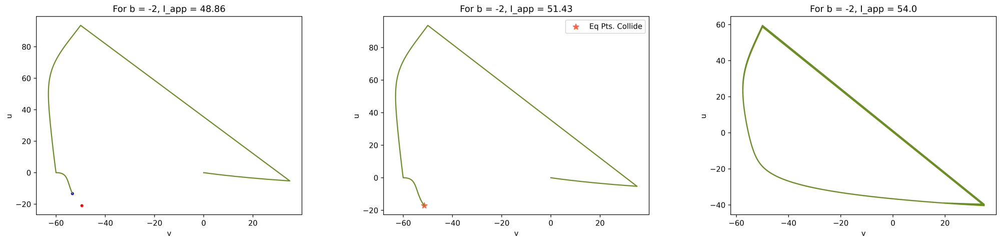



Figure 4: Bifurcation Plot

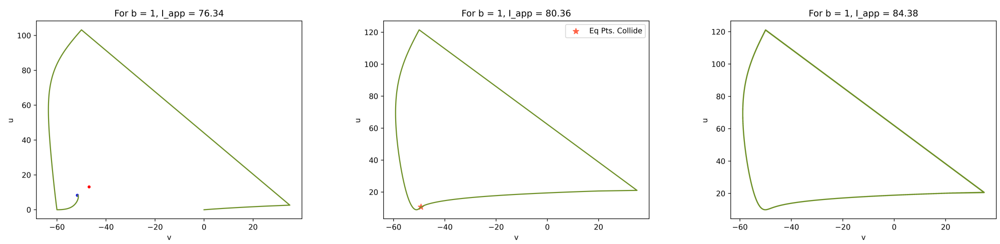
### 2.4 Phase Plane Simulation

For b = -2, 1, 3, 5, we plot the phase plane in python for different values of $I_{\text{app}}$ in the form of a step function. From 5, we can see in figure (a), the blue dot is a stable equilibrium point that attract solutions, and the red dot is an unstable equilibrium point which no solution want to be near of it. Then in figure (b), we did see the voltage reset and two equilibrium collide, but the trajectory is not closed. As we increase the current, we have stable limit cycle with no equilibrium points as the equilibrium points becomes imaginary. When b = 1, we do have a saddle node on invariant circle bifurcation in (b) of Figure 6 because the saddle node is on the limit cycle, and also, one side of the saddle node attracts the solution, and the other side repels the solution. At the Bogdanov-Takens point with b = 3, in figure (a)7, we have an unstable limit cycle that is attracted to a stable equilibrium point, and a saddle. Then, we have a saddle node and the non saddle disappears via Subcritical Andronov-Hopf bifurcation, and in figure(c), we have stable limit cycles. For b = 5, we predict a Subcritical Andronov-Hopf bifurcation, in figure (a) from 8, we have a stable equilibrium point and an unstable equilibrium point, and the stable equilibrium point attracts the unstable limit cycle. Then, the two equilibrium collide, and the solution approaches the stable limit cycle.



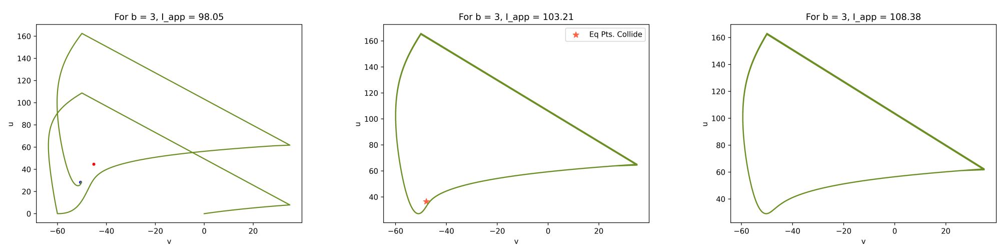

(a) $I_{\text{app}} = 0.95I_{\text{sn}}$ (b) $I_{\text{app}} = I_{\text{sn}}$ (c) $I_{\text{app}} = 1.05I_{\text{sn}}$

Figure 5: Phase Plane for b = -2



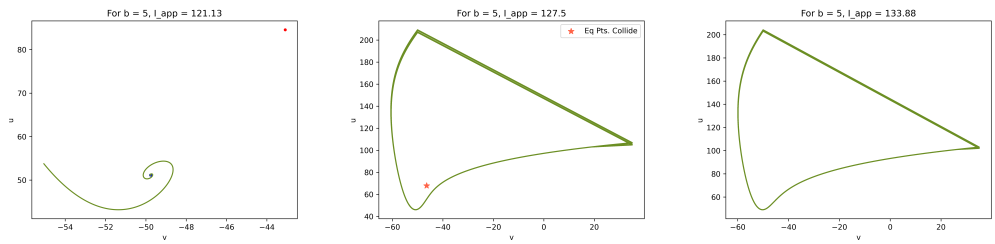

(a) $I_{\text{app}} = 0.95I_{\text{sn}}$ (b) $I_{\text{app}} = I_{\text{sn}}$ (c) $I_{\text{app}} = 1.05I_{\text{sn}}$

Figure 6: Phase Plane for b = 1




(a) $I_{\text{app}} = 0.95I_{\text{hopf}}$ (b) $I_{\text{app}} = I_{\text{hopf}}$ (c) $I_{\text{app}} = 1.05I_{\text{hopf}}$

Figure 7: Phase Plane for b = 3

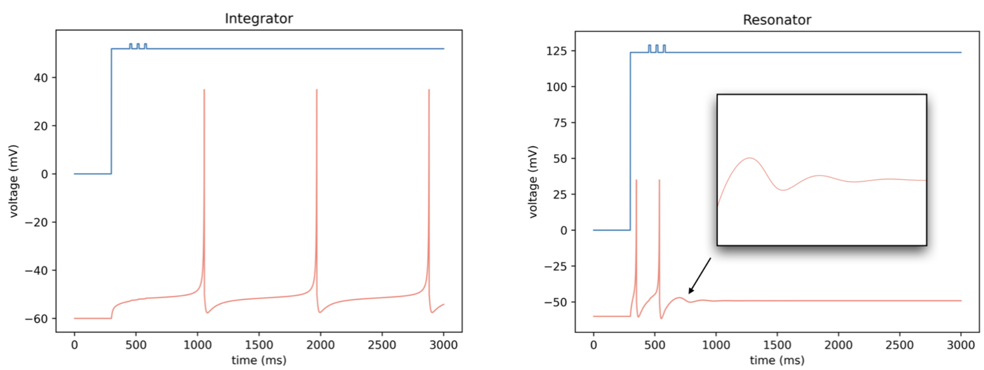



(a) $I_{\text{app}} = 0.95 I_{\text{hopf}}$ (b) $I_{\text{app}} = I_{\text{hopf}}$ (c) $I_{\text{app}} = 1.05 I_{\text{hopf}}$

Figure 8: Phase Plane for b = 5

## 2.5 Integrator vs. Resonator

The subthreshold oscillation refers to fluctuations in the membrane potential below the threshold for firing action potential. The existence of subthreshold oscillation distinguishes a resonator neuron from an integrator neuron. After



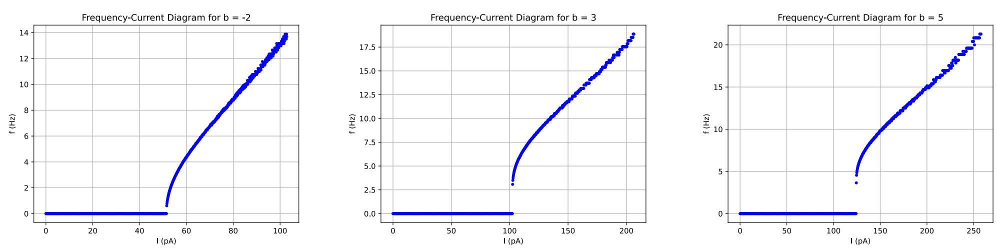

Integrator for b = -2 Resonator for b = 5

Figure 9: Integrator and Resonator

we increase the value of b beyond Ca = 3, the solution becomes oscillatory because the eigenvalues of the equilibrium points becomes imaginary, and we just have sinusoidal terms in our solution. Moreover, as the value of b increase, the frequency of oscillation becomes stronger9.

## 2.6 Frequency Current Curve

The F-I curve is a diagram that relates the neuron's firing frequency with the magnitude of current applied $I_{\text{app}}$. In general, there are two types of F-I curves, a continuous F-I curve that suggests the neuron can fire at arbitrarily low frequency, and a F-I curve that has a jump discontinuity at some $I_{\mathbf{app}}$. The type of F-I curves is determined by the bifurcation of the neuron. In particular, Saddle-Node on Invariant Circle bifurcation produce continuous F-I curve, while Subcritical Andronov-Hopf bifurcation produce discontinuous F-I curve[4]. Therefore, we should expect to observe continuous F-I curve for $b < 3$, and discontinuous F-I curve. To measure the F-I curve, we follow the method introduced in [1], we inject a step current into the Izhikevich neuron, and if there are more than spikes, the frequency is $\frac{1000}{t_4 - t_3}$, where $t_3$ and $t_3$ is the time of the third and fourth spike respectively. Otherwise, we set the frequency to be zero. In 10, we have a jump at BT point, and for b = 5, our F-I curve is discontinuous.




(a) F-I curve for b = -2 (b) F-I curve for b = 3 (c) F-I curve for b = 5

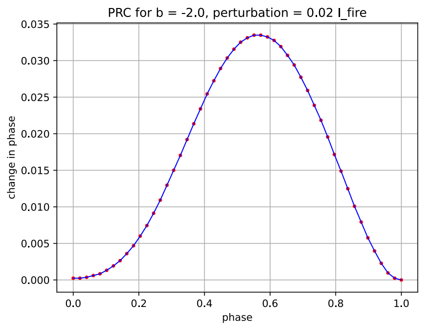
Figure 10: F-I curves for various b

## 2.7 Phase Response Curve

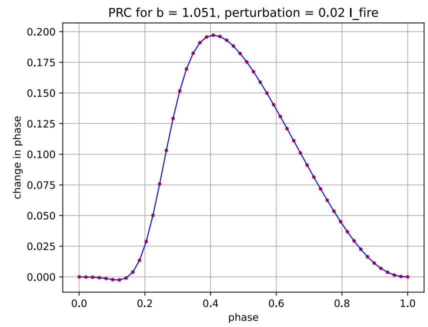
The Regular Spiking neuron can be viewed as a stable oscillator, and therefore a small perturbation along its limit cycle will not cause chaotic behavior. In addition, in the human brain, the neuron is often connected with other neurons and will receive stimulation from other neurons and surrounding environment. In the view of dynamical systems, the stimulation on the neuron means perturbation on a limit cycle of the oscillator, and observing the change in the period of the new limit cycle is the idea of the PRC. To implement the PRC, we choose a step current and find the vary the current until we have at least 6 spikes. Then, we take the interval between the fifth and fourth spike to be the reference limit cycle with period $T_{\text{ref}}$. Along the reference limit cycle, we apply a small perturbation along the reference limit cycle for a very small period of time. The x scale would then be the starting time we applied the perturbation, denote it by $\phi = \frac{t}{T}$. Then, we observe the new period $T_{\text{new}}$ between the fifth and fourth spike by using

$$\Delta\phi = \frac{T_{\text{ref}} - T_{\text{new}}}{T_{\text{ref}}} \tag{7}$$

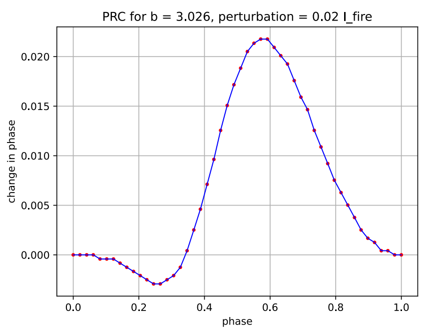
from [3]. The simulation result is shown in 11. As you can see, there are two types of PRCs, one where we only have positive phase change, called Type I PRC near Saddle-Node on Invariant Circle bifurcation. The Type II PRC is one with both positive and negative phase change and it is near Andronov-Hopf bifurcation [3]. From the bifurcation analysis, we have shown for b = 3, we have a Bodganov-Takens bifurcation, and for $b < 3$, we have Saddle-Node on Invariant Circle bifurcation, and for $b > 3$, we have Subcritical Andronov-Hopf bifurcation. However, the BT bifurcation is complicated, and the change may not happen exactly at the BT. Nevertheless, we observed the qualitative change in shape, and this confirms our previous bifurcation analysis.



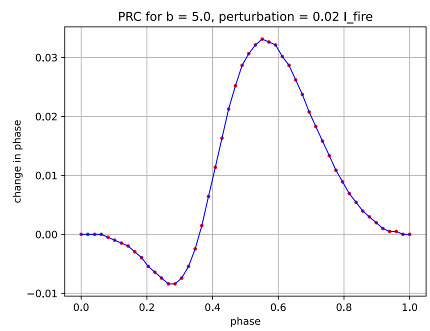

(a) PRC for b = -2




(b) PRC for b = 1




(c) PRC for b = 3




(d) PRC for b = 5

Figure 11: PRC plots

# 3 Neuron Synchronization

The analysis for uncoupled neuron is complete, and now we proceed to simulate synchronization of a weakly coupled two neuron system by connecting a synaptic current between them, which results in the following dynamical system [6],

$$
\begin{aligned}
\frac{dv_i}{dt} &= k(v_i - v_r)(v_i - v_t) - u + I_{\text{app}} - g_{\text{syn}} s_j (v_i - v_{\text{syn}}) \\
\frac{du_i}{dt} &= a(b(v_i - v_r) - u_i) \\
\frac{ds_i}{dt} &= \alpha(1 - s_i) H_\infty(v_i - v_{\text{peak}}) - \beta s_i \\
&\text{if } v \geq v_{\text{peak}} \\
(v, u) &\rightarrow (c, u + d)
\end{aligned}
\tag{8}
$$

where i = 1, 2, $j \neq i$. The s state is the voltage gated channel, $g_{\text{syn}}$ is the channel conductance, $v_{\text{syn}}$ is set based on whether we want inhibitory or excitory input, and $H_\infty(v_i - v_{\text{peak}})$ is a step function. The equation (8) tells us whenever $v_i \geq v_{\text{peak}}$, we turn on the synaptic input, and afterward, the synaptic input decays exponentially at the rate of $\beta$.

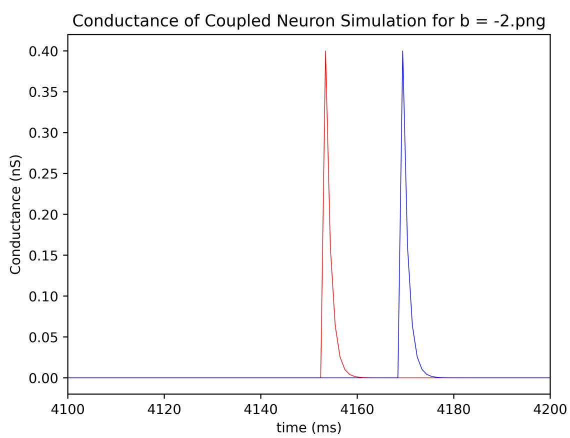



Figure 12: Example of Conductance

We predict for $b \geq 3$, the neurons are more likely to synchronize because is the PRC of the resonator have both positive phase change and negative phase change, and hence the synaptic current can cause the spike of two neurons to move forward and backward, since the limit cycle is stable, both will eventually converge to the same limit cycle. We also need to observe the anti-phase behaviour that's seen in biological neuron. However, for d =

100, we did not observe anti-phase behaviour, and spikes are close to each other for all values of b13. For d = 50, we are able to observe anti-phase

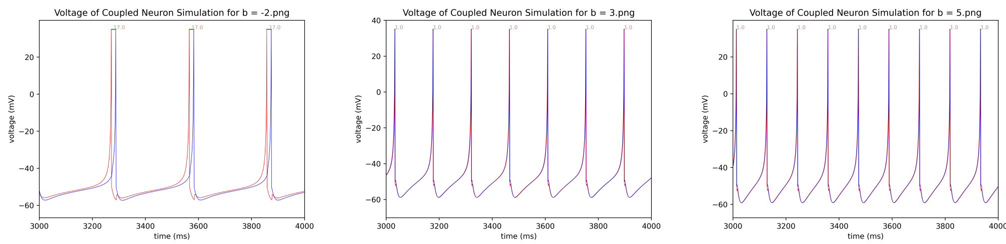



Figure 13: Coupled Neuron Plot with d = 100

behaviour, and when b increases, the neurons synchronize 14 To understand

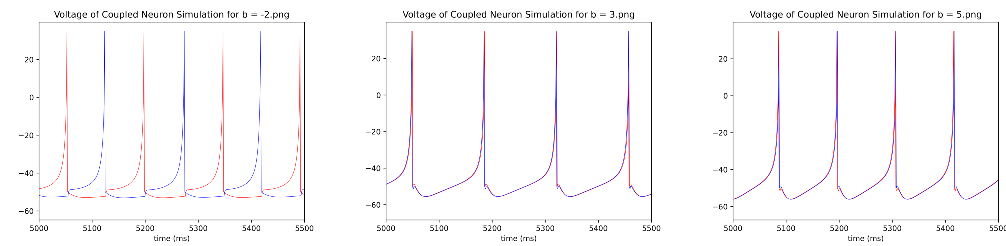



Figure 14: Coupled Neuron Plot with d = 50

the effect of parameter d, we proceed to use the phase model.

# 4 Phase Model

To analyze the effect of parameter d, we need a more robust method that can deal with discontinuity. We can avoid dealing with the discontinuity by using iPRC to compute the phase model, which considers the adjoint of the linearized system. Then, we use phase reduction to compute the interaction of two neurons by measuring the phase difference[2][6].

## 4.1 infinitesimal Phase Response Curve

Consider our dynamical system 1, from figure 2, we can observe that it has a stable limit cycle with period T, and we call it $\bar{x}$. In our case, $\bar{x} = (\bar{v}, \bar{u})^T$

for $t \in [0, T)$. Then, we can define the phase function $\Theta(x(\bar{\phi}))$ using the isochron of the stable limit cycle because very point in the isochron will converge to $\Theta(x(\bar{\phi}))$ as time reach infinity[2]. Hence, if we start at a state that is arbitrarily close to one state, its difference will be the change in phase, which is

$$\Delta\phi(x) = \Theta(x+y) - \Theta(x) = \nabla_x \Theta(x) y + O(y^2) \approx Z(t)y \tag{9}$$

where $Z(t) = \nabla_x \Theta(x)$[6]. Moreover, if we linearize 1 around the limit cycle, then y should satisfy the following linear differential equation,

$$\frac{dy}{dt} = \begin{bmatrix} \frac{k(2v(t) - v_t - v_r)}{C} & \frac{-1}{C} \\ ab & -a \end{bmatrix} y = A(t)y \tag{10}$$

Since the phase is asymptotic in the neighborhood of attraction of x, then we can say the derivative of phase with respect to time is zero, which means $\frac{d\Delta\phi(x)}{dt} = 0$, but $\Delta\phi(x) = Z(t)y$. Therefore, we have [6]

$$\begin{aligned} 0 &= \frac{d}{dt} Z(t)y(t) \\ 0 &= \left[\frac{dZ}{dt} + A(t)^T Z(t)\right] y \\ 0 &= \frac{dZ}{dt} + A(t)^T Z(t) \text{ since y is arbitrary} \end{aligned}$$

$$\begin{bmatrix} \frac{dZ^v}{dt} \\ \frac{dZ^u}{dt} \end{bmatrix} = \begin{bmatrix} \frac{-k(2\bar{v} - v_t - v_r)}{C} Z^v - abZ^u \\ \frac{Z^v}{C} + aZ^u \end{bmatrix} \tag{11}$$

If we assume $y = (a, 0)$, then we are only perturbing the voltage, and $Z^v$ is our iPRC. Furthermore, $\phi = \Theta(x(\phi))$ by definition, differentiating both sides with respect to $\phi$ gives $Z(\phi) \cdot \frac{dx(\phi)}{d\phi} = 1$. Moreover, since 1 is discontinuous at the end of the limit cycle, to ensure the iPRC is continuous, we impose the boundary condition [5],

$$Z^u(0) = Z^u(T^-) \tag{12}$$

To implement the above boundary value problem in python, we need to obtain $\bar{v}$, which is from the reset condition $v = c$ to the voltage peak

$v = v_{\text{peak}}$. An example is given in 15. Then, we use the boundary value problem solver from scipy.

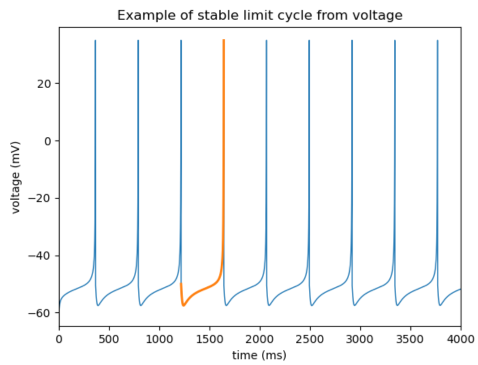
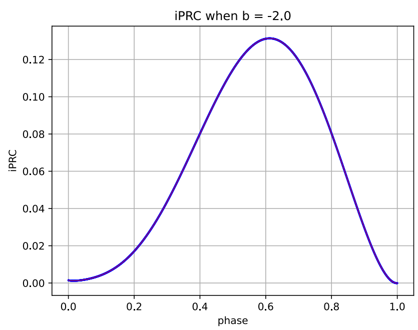


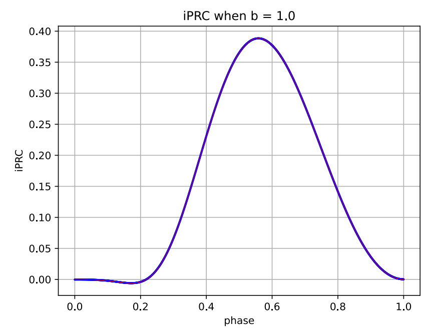

Figure 15: Nullclines

The simulation result is shown in 16, the plotting style is still the same as 11. However, we can't see the red points in the iPRC because we have a fine mesh, so it looks like we have a line. Although the amplitude of iPRC is significantly larger than then PRC, the shape of the PRC and iPRC agree with each other since we have Type I PRC for $b < 1$, and Type II PRC for $b > 1$. However, negative phase change is first observed in iPRC when b = 0.8 as opposed to b = 1 in the PRC. Furthermore, we can use iPRC to compute the case when we have a smaller value of d, which we could not compute using the PRC. The result of the simulation is shown in 17. We initially have a downward curve, but as b increases, the curve resembles more like 16. Since in the neuron synchronization section, the chosen value was d = 50, we should look at the effect of d = 50 on our iPRC, which is the 18.

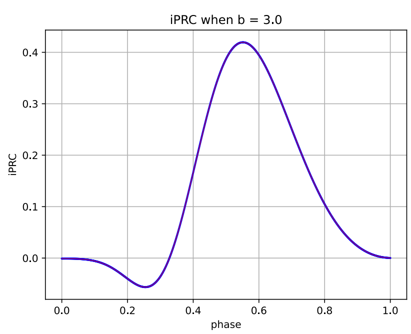
We can observe for b = -2, the iPRC plot is slightly higher on the left hand side than plot (a) in 16. As values of b goes higher, the iPRC plots becomes more alike the iPRC plots for d = 100.



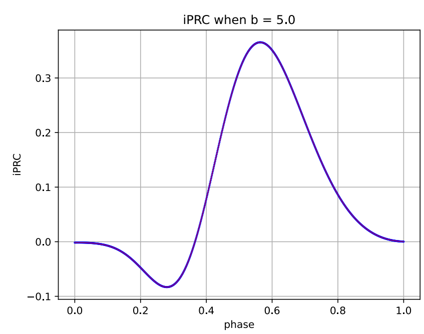

(a) iPRC for b = -2




(b) iPRC for b = 1

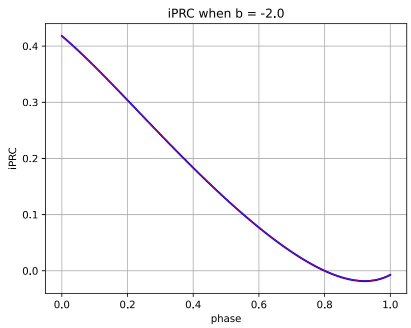



(c) iPRC for b = 3

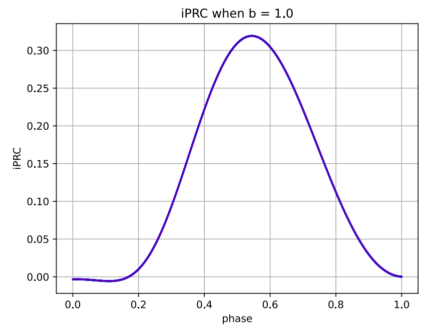



(d) iPRC for b = 5

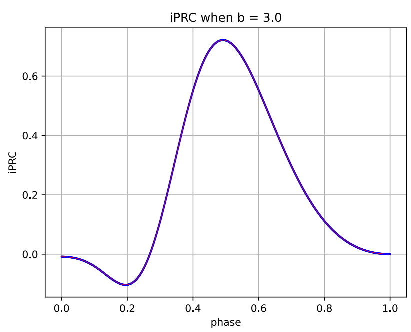
Figure 16: iPRC plots for d = 100



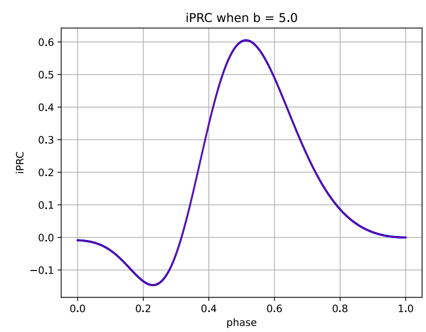

(a) iPRC for b = -2




(b) iPRC for b = 1

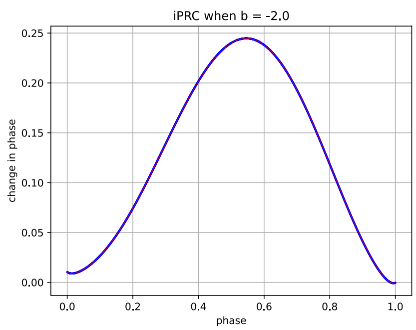



(c) iPRC for b = 3

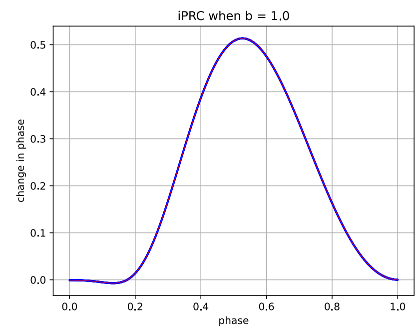



(d) iPRC for b = 5

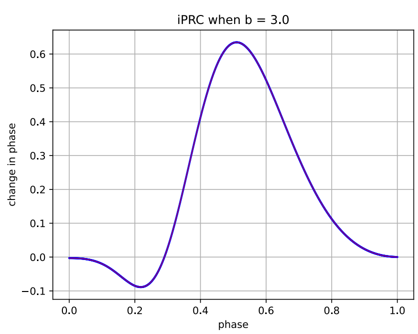
Figure 17: iPRC plots for d = 20



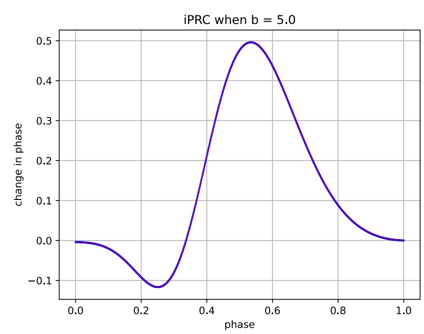

(a) iPRC for b = -2




(b) iPRC for b = 1




(c) iPRC for b = 3




(d) iPRC for b = 5

Figure 18: iPRC plots for d = 50

# 5 Appendix

## References


[1] Christoph Börgers. *An Introduction to Modeling Neuronal Dynamics*. Springer, 2017.

[2] Sue Ann Campbell. *Coupled Nonlinear Oscillators*. 2019. URL: https://www.math.uwaterloo.ca/~sacampbe/grpmeeting/phasemodels.pdf (visited on 08/13/2024).

[3] Carmen C. Canavier. *Phase response curve*. 2006. URL: http://www.scholarpedia.org/article/Phase_response_curve (visited on 08/13/2024).

[4] Eugene M. Izhikevich. *Dynamical Systems in Neuroscience. The Geometry of Excitability and Bursting*. The MIT Press, 2007.

[5] Ladenbauer J Augustin M Shiau L Obermayer K. "Impact of Adaptation Currents on Synchronization of Coupled Exponential Integrate-and-Fire Neurons". In: *PLoS Comput Biol* 8.4 (2012).

[6] G. Bard Ermentrout · David H. Terman. *Mathematical Foundations of Neuroscience*. Springer, 2010.


### 5.1 Links to Code

1. The code for the iPRC is here.
2. The code for the PRC is here.
3. The code for the Neuron Synchronization is here.