Cornell University Mathematics Department Senior Thesis

Chaos in the Hodgkin-Huxley Equations: The Takens-Bodganov Cusp Bifurcation

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"Turning and turning in the widening gyre

The falcon cannot hear the falconer;

Things fall apart; the centre cannot hold;

Mere anarchy is loosed upon the world. . ."

William Butler Yeats-*"The Second Coming"*

Abstract

The Hodgkin-Huxley equation is a fundamental biological model of the action potential in giant squid axons. The original bifurcation diagrams of the Hodgkin-Huxley equation are examined with the facilitation of new techniques in both computational and theoretical dynamical systems, thus providing the originally proposed bifurcation diagrams even stronger numerical support. The codimension three bifurcation, called the Takens-Bogdanov Cusp bifurcation, is analyzed in the context of identification and existence. This analysis provides grounds for examining the Takens-Bogdanov Cusp bifurcation in the Hodgkin-Huxley equation. Within a highly accurate numerical approximation (order of 10^{-8}), values for the equilibrium point and the parameters at the Takens-Bogdanov Cusp are found. Also, a local topological form is found and proven for the bifurcation. Lastly, for completeness of the analysis, the computational methods used are proven. The new results presented here are the examination of the bifurcation diagrams and the approximation of the values corresponding to the Takens-Bogdanov Cusp point.

Acknowledgments

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Contents

Abstract ii

Acknowledgments iii

Contents iv

List of Figures v

1 Introduction 1
- 1.1 Introduction to Hodgkin and Huxley Model 1
- 1.2 The Hodgkin-Huxley Equations 3
- 1.3 Topological Equivalence, Normal Forms, and Types of Bifurcation 5

2 Bifurcation of the HH Equations Revisited 9

3 The Takens-Bogdanov Cusp Bifurcation 17
- 3.1 Motivation: Local Bifurcation 17
- 3.2 Definitions of Certain Bifurcation 22
- 3.3 Takens-Bogdanov Cusp Bifurcation 25
- 3.4 Computational Evidence 34
  - 3.4.1 Existence by verification 35
  - 3.4.2 Local Topological Equivalence 38

4 Computational Methods 41

5 Conclusion 47

Bibliography 48

List of Figures

2.1 Deformed Bifurcation diagram of HH equations 1a. 11
2.2 Deformed Bifurcation diagram of HH equations 1b. 13
2.3 Deformed Bifurcation diagram of HH equations 2a. 14
2.4 Deformed Bifurcation diagram of HH equations 2b. 16

3.1 Deformed bifurcation diagrams in the locality of the Cusp and Takens-Bogdanov points with various $\bar{g}_K$ values. 18

Chapter 1

Introduction

1.1 Introduction to Hodgkin and Huxley Model

The Nobel prize winning work done by Hodgkin and Huxley in 1950's has created much advancement in the fields of physiology and biophysics. Originally proposed as a model for the various electrical behaviors of giant squid axons observed experimentally, the model has forged new ground for the fields of biology, physiology, and biophysics [1]. More recently, the equation has been shown to have chaotic behavior as a dynamical systems. The mathematical importance of the Hodgkin and Huxley model can be seen in both the pure and applied sense, providing physical examples for certain chaotic behaviors while also providing a dynamical system with a various array of codimension one, two, and three bifurcations.

Physiologically, the nervous system is built up of nerve cells, called neurons, which convey information from one cell to another by electrical signals. The pulses of electrical charge that travel through the neuron's membrane are called action potentials. The action potential is one type of electrical response given by the nerves when they become electrically excited. These electrical responses are controlled by chemical processes in which ions flow through the neuron's membrane depending on their concentration gradients. The main ionic currents are the: sodium (Na) and potassium (K) currents and the passive current (L). Modeled as an electrical circuit system, the space-clamped Hodgkin-Huxley equations describe the behavior of the potential difference across the neuron when the neuron is exposed to an external electrical stimulus. The model relates the membrane potential to physical variables which govern the transmission of electrical currents in the particular channel, conductances, ionic reversal potentials, temperature, voltage dependence of channel gating, and external current. The equations themselves and the parameter values are based on experimental data. The Hodgkin-Huxley equations provide a quantitative depiction of the qualitative physiological behavior that was already well documented. Therefore, it is clear the initial applications to physiology, biology, and biophysics were incredibly valuable. Yet over a half century later, the mathematical analysis of the nonlinear differential equation is still not entirely understood [1].

Since the formulation of the HH equations, many have modified the equations both for accuracy and simplicity [1]. One common method of modification has been the reduction of the variables. The four dimensions of the model are the voltage difference and three gating variables that were included as fitting parameters to the experimental observations. One notable reduction is the FitzHugh-Nagumo model, which reduces the equations to two dimensions:

the voltage and a recovery variable. Another reduction is found when one of the gating parameter is assumed to reach equilibrium instantaneously and may be taken as a constant, thereby reducing the system to a three dimensional model. This reduction to a three dimensional model is also implicitly a part of the Fitzhugh-Nagumo reduction. Although the reductions may aid in a quantitative approximation to experimental measurements, the vast mathematical analysis is greatly deprived by these dimensional simplifications. Many of the dynamic behaviors that arise in the HH equations vanish as the variables are reduced [1].

1.2 The Hodgkin-Huxley Equations

Although the Hodgkin-Huxley equations are a four dimension partial differential equation which depends on both space and time, the quantitative description that results in a laboratory is set up by a space-clamp experiment. This removes the dependence on position and creates a four dimension nonlinear differential equation dependent only on time. The coordinates of the state space are the voltage, V, across the neuron and the three gating parameters, m, n, and h. The experimental parameters are the external current *(I)*, the temperature (T), the conductance *(g)* for the sodium, potassium, and leakage channels, the equilibrium potentials $(\bar{V})$, and additional parameters in the gating variables. The space-clamped Hodgkin-Huxley Equations are:

$$\dot{V} = -G(V, m, n, h) + I$$

$$\dot{m} = \Phi(T)[(1 - m)\alpha_m(V) - m\beta_m(V)]$$

$$\dot{n} = \Phi(T)[(1 - n)\alpha_n(V) - n\beta_n(V)]$$

$$\dot{h} = \Phi(T)[(1-h)\alpha_h(V) - h\beta_h(V)].$$

The function $\Phi(T) = 3^{(T-6.3)/100}$ takes into account the effect of temperature on the electrical behavior of the neuron. The function G is defined as:

$$G(V,m,n,h) = \bar{g}_{Na}m^3h(V-\bar{V}_{Na}) + \bar{g}_K n^4(V-\bar{V}_K) + \bar{g}_L(V-\bar{V}_L)$$

.

The equations for the variations of the permeability of the sodium, potassium, and leakage are define as:

$$\alpha_m(V) = \Psi(\tfrac{V+25}{10}) \qquad \beta_m(V) = 4exp(V/18)$$

$$\alpha_n(V) = 0.1\Psi(\tfrac{V+10}{10}) \qquad \beta_n(V) = 0.125exp(V/80)$$

$$\alpha_h(V) = \Psi(\tfrac{V+10}{10}) \qquad \beta_n(V) = (1+exp(\tfrac{V+30}{10}))^{-1}$$

where

$$\Psi(x) = x/(exp(x)-1).$$

Note: We define $\Psi(0) = 1$.

The values that are used throughout this paper were taken from the original experimental data. The parameters $\bar{g}_K, \bar{V}_K$, and I are varied while we set $\bar{g}_{Na} = 120mS/cm^2, \bar{g}_L = 0.3mS/cm^2, \bar{V}_{Na} = -115mV, \bar{V}_L = 10.599mV$, and $T = 6.3C$. The differential equation and the values set above will be periodically referred to as HH [6]. Note: Modern conventions reverse the sign of currents and shift the zero of the membrane potential.

1.3 Topological Equivalence, Normal Forms, and Types of Bifurcation

A system of differential equations defines a vector field whose solution comprise a dynamical system. To understand all behaviors of the dynamical system for a certain parameter value, all possible orbits (also called *trajectories*) defined by the vector field are examined. We call the collection of all possible orbits for a specific parameter the *phase portrait.* In order to compare the qualitative structures of the phase portraits for given dynamical systems, we must define an equivalence class that can relate their respective behaviors. If there exists a time preserving homeomorphism (a continuous invertible map whose inverse is continuous) which takes orbits of one dynamical system onto the other dynamical system, then the dynamical systems are said to be *topologically equivalent.* As the parameters are varied, points of topological non-equivalency may occur. These events are called *bifurcations* of the vector field [7]. The study of bifurcations describes the qualitative differences in the dynamical system that occur at each type of bifurcation. *Bifurcation diagrams* graph the division within the parameter space between regions of topologically non-equivalent phase portraits. At a point of bifurcation, if there is a dynamical systems which is topologically equivalent to all dynamical systems with the same bifurcation, then that system is called the *topological normal form.* The normal form aids as a tool for comparing different systems and provides simplifications in the analysis of the behaviors which occur in various bifurcations [5].

In order to give the reader a better sense of both the behavior and the numerics of key bifurcations that will arise throughout this paper, the following list is provided:

Codimension One Bifurcation:

Saddle node or Limit point (SN): The linearization at the equilibrium point has one (usually simple) zero eigenvalue [5]. Two equilibrium points combine and vanish [6].

Hopf(H): The linearization of the equilibrium point has a simple pair of pure imaginary eigenvalues. All other eigenvalues have non-zero real parts [5]. The amplitude of a periodic orbit decreases to a point and vanishes as the parameter approaches the equilibrium point. Also, the period limits to a finite positive value [6].

Homoclinic (HB)/Twisted Homoclinic (THB): As the parameter approaches the bifurcation value, the point of periodic orbits is unbounded and an equilibrium point approaches the periodic orbit [7]. The homoclinic orbits are trajectories which include the equilibrium point [6]. There is a line bundle along the homoclinic orbit whose evolution is described by the induced flow on the tangent vectors. The homoclinic case is homeomorphic to a cylinder, while the twisted homoclinic bifurcation is homeomorphic to the Mobius band.

Limit point of Cycles or Saddle Node of Cycles (LPC): A stable periodic orbit and a saddle periodic orbit combine to become an unstable periodic orbit and then vanish [7]. The limit point of cycles can be thought of as a turning point for the periodic orbits [2].

Period Doubling (PD): The linearization at the equilibrium point has an eigenvalue of negative one [5]. An orbit with period T changes stability and combines with another orbit which has period 2T and vanishes [6].

Codimension Two Bifurcation:

Cusp (C): The cusp is found on saddle node curves and occurs when a non-degeneracy condition on the second derivatives of the vector field fails. Near the cusp point is a region with three nearby equilibrium points [6].

Takens-Bogdanov (TB): The linearization at the equilibrium point has a zero eigenvalue with algebraic multiplicity two. The bifurcation diagram of its normal form reveals the occurrence of three codimension one bifurcations stemming from this point, namely, the Homoclinic, Hopf, and Saddle Node bifurcations [7].

Neutral Saddle (NS)/Twisted Neutral Saddle (TNS): Occurs when the sum of two eigenvalues in the linearization is zero [7]. This is equivalent to a point of changing stability. The twisted neutral saddles are neutral saddles that occur on twisted homoclinic orbits. Limit point of cycles end at a Neutral Saddle. For the Twisted Neutral Saddle bifurcation, we expect the occurrence of Homoclinic, Twisted Homoclinic, and Period doubling bifurcation to develop [6].

Saddle Node Loop (SNL): A homoclinic orbit that arises from a saddle node. Connected to the Saddle Node Loop are Homoclinic and Saddle Node bifurcation curves [6].

Generalized Hopf or Degenerate Hopf (GH): The generalized Hopf bifurcation occurs when the first Lyapunov coefficient vanishes while the linearization at the equilibrium point has a simple pair of pure imaginary eigenvalues [7]. The behavior is characterized by degeneracy in the manner in which periodic orbits combine with a Hopf bifurcation point [6].

Codimension Three Bifurcation:

Takens-Bogdanov Cusp (TBC): The TBC bifurcation occurs when a Takens-Bogdanov bifurcation point on a saddle node curve combines with a Cusp [6]. The invariant center manifold is of degree two, the linearization is nilpotent, and the second derivative in the 'direction' of the zero eigenvalues is zero.

Chapter 2

Bifurcation of the HH Equations Revisited

The work done by Guckenheimer and Labouriau detailed the bifurcation diagrams of the HH equations for codimension two bifurcations and presented numerical evidence for the existence of a Takens-Bogdanov Cusp bifurcations. The method used for the original bifurcation diagrams resulted from explicit calculations of saddle node and Hopf curves of equilibrium and studying a vast number of individual phase portraits and searching for boundaries of topological non-equivalence within the parameter space [6]. In this section, the bifurcation diagrams are revisited under new computational techniques that support their work numerically.

Using MatCont, a continuation program for bifurcation of dynamical systems, and the theory of unfolding of codimension two bifurcation, more numerical evidence is found that supports the original findings of Guckenheimer and Labouriau [2]. We start the analysis by setting $\bar{g}_K = 36mS/cm^2$ and varying $\bar{V}_K$ and I. Figure 2.1 on the next page depicts the (partial) bifurcation diagram for the HH equations and $\bar{g}_K = 36mS/cm^2$. Many of the curves are extremely close, so for the visibility of the reader the diagrams have been deformed (scaled and stretched). Note that this does not affect the partitioning of the parameter space into topological equivalence classes. First, by searching for equilibrium points of the HH equations whose linearization has a simple eigenvalue of zero, the curves of saddle nodes are easily found. The computation is done by evaluating the determinant of the derivative of the differential equation at the equilibrium. When this determinant is zero, there exists a zero eigenvalue of the linearization at the equilibrium. Along the saddle node curve,when a nondegeneracy condition on the second derivatives of the vector field fails, the cusp point is detected [7]. A Takens-Bogdanov bifurcation occurs on the top branch of the saddle node curve. The TB point is detected on a saddle node by the appearance of a second zero eigenvalue. From the TB point, a Hopf curve emanates and crosses over the lower branch of the saddle node curve. The detection of the Hopf bifurcation is done by examining the sums of any two eigenvalues. When the sum is zero and the eigenvalues are purely imaginary the bifurcation is found. Along the Hopf curve which originated from the TB point, a generalized Hopf bifurcation is located. This happens when the first Lyapunov coefficient becomes zero. The GH bifurcation divides the Hopf curve into two parts, one containing a stable equilibrium and another containing an unstable equilibrium [7]. From the generalized Hopf point, a limit point of cycles emerges and continues past the lower branch of the saddle node curve. Returning to the beginning of the upper saddle node branch and varying the parameters vertically, a period doubling bifurcation occurs below the top branch of the saddle node. HH equations' level of difficulty prevented the computational analysis to progress much past this.

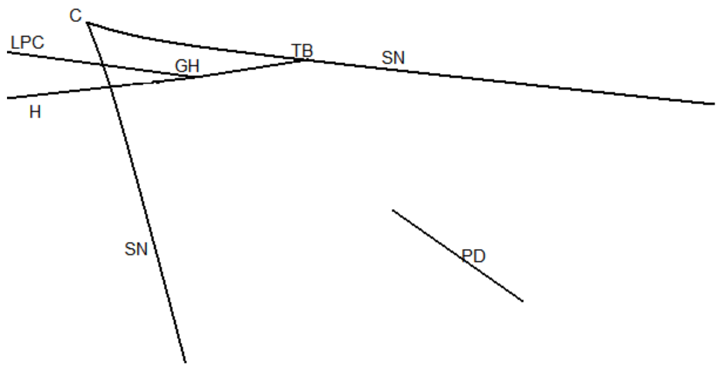


Figure 2.1: Deformed Bifurcation diagram of HH equations 1a.

However, where direct numerical methods failed mathematical intuition dominated. The bifurcation diagram has shown numerically the existence of Hopf and saddle node curves adjacent to the TB bifurcation. But, the unfolding of the normal form for the Takens-Bogdanov bifurcation reveals the existence of two saddle node curves, a Hopf curve, and a Homoclinic bifurcation curve stemming from the TB point [5]. Therefore, there should exist a Homoclinic curve originating from TB point. Although the Homoclinic bifurcation could not be found directly, indirectly there is strong evidence for its position within the parameter space. Examining the period of orbits along the Hopf bifurcation curve between the generalized Hopf point and the Hopf curve's intersection with the lower branch of the saddle node curve, there are two points of very long periods. The periods found in some intervals of the curve are on the order of 10^5, and when the parameters were slowly varied the periods became undefined near where the Homoclinic curve is predicted to intersect the Hopf curve. Between the two points where the period became undefined, the parameters were varied away from the Hopf curve in both directions. This revealed more regions of undefined periods. Returning to the Takens-Bogdanov point and searching below the saddle node curve shows the same pattern. Repeating the path following method for the period doubling points found earlier shows the existence of a Homoclinic curve between the period doubling points and the upper saddle node curve and a Homoclinic curve below the period doubling points. By interpolation (qualitatively), the Homoclinic bifurcation curve is determined. This period chasing technique yields strong numerical evidence to the occurrence and shape of the Homoclinic curve. Combining this information with the numerical methods of Matcont reveal an identical bifurcation diagram to that done by Guckenheimer. Figure 2.1 is the complete bifurcation diagram for $\bar{g}_K = 36mS/cm^2$.

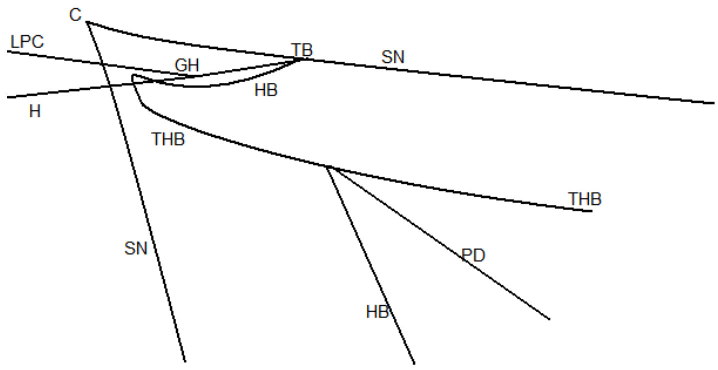


Figure 2.2: Deformed Bifurcation diagram of HH equations 1b.

The analysis of the HH equations are continued by setting $\bar{g}_K = 12mS/cm^2$ and varying $\bar{V}_K$ and I. The analysis is similar to that which was done for $\bar{g}_K = 36mS/cm^2$ and the bifurcation diagram is displayed below(see Figure 2.4 on page 16). First, the saddle node curves and the cusp bifurcation were found. In this case, the Takens-Bogdanov bifurcation has passed the cusp point and now occurs on the lower branch of the saddle node curve. From the Takens-Bogdanov bifurcation a Hopf curve emerges. On the upper saddle node curve, a limit point of cycles was detected; however, for only a small interval. A collection of neutral saddle points were found between the two saddle node branches near the limit point of cycles. Also, a period doubling bifurcation was found by starting near the beginning of the upper saddle node branch and varying the parameters vertically. Repeating the path following method from the period doubling points reveals the existence of some Homoclinic points. Returning to the Takens-Bogdanov bifurcation and studying the periods of periodic orbits reveals the emergence of a Homoclinic bifurcation. Even with some qualitative interpolation, the bifurcation diagram is far from complete. Figure 2.3 is the partial bifurcation diagram for $\bar{g}_K = 12mS/cm^2$.

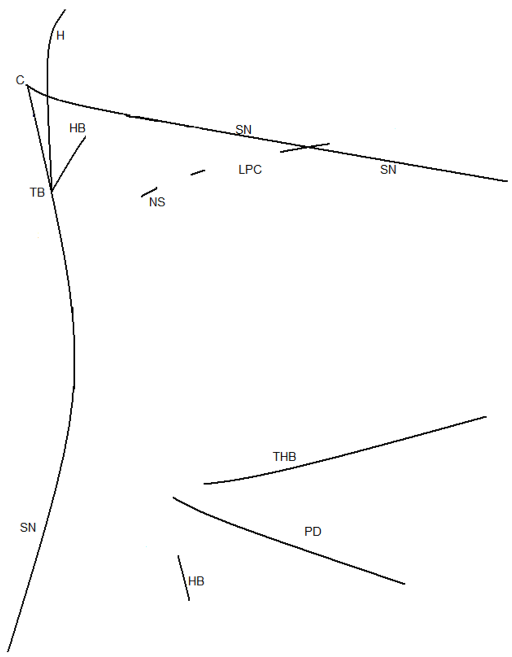


Figure 2.3: Deformed Bifurcation diagram of HH equations 2a.

Although the bifurcation diagram for $\bar{g}_K = 12mS/cm^2$ is not complete, there is enough support to justify filling in the missing bifurcation curves. From Guckenheimer's work, the homoclinic curve originating from the TB point approaches the upper saddle node curve and becomes a saddle node loop. The neutral saddle loop does not intersect the homoclinic bifurcation which terminates at the Takens-Bogdanov point, rather, it encounters a homoclinic orbit touching the two saddle node branches at saddle node loops. From the unfolding of twisted neutral saddle loops, it can be shown that the period doubling curve intersects the homoclinic and twisted homoclinic curves at a twisted neutral saddle loop, which then becomes a saddle node loop at the lower branch of the saddle node curve. And finally, a limit point of cycles is known to end at the neutral saddle [6]. Therefore, theory justifies the assumptions needed to complete the bifurcation diagram. Figure 2.4 on the next page is the complete bifurcation diagram for $\bar{g}_K = 12mS/cm^2$.

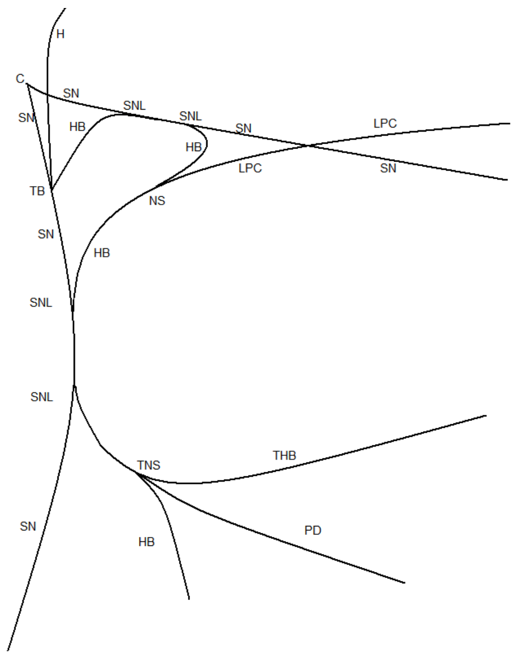


Figure 2.4: Deformed Bifurcation diagram of HH equations 2b.

Note that the Takens-Bogdanov bifurcation has switch from one saddle node branch to another as $\bar{g}_K$ decreased from $36mS/cm^2$ to $12mS/cm^2$. In order for the Takens-Bogdanov point to move smoothly from the upper saddle node branch to the lower one, the TB point must combine with the cusp bifurcation. This codimension three bifurcation is dealt with in great detail in the next chapter.

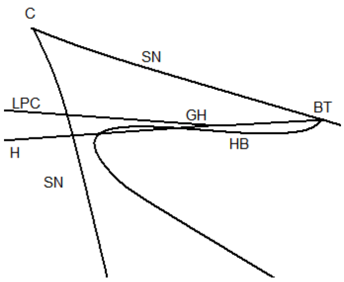
Chapter 3

The Takens-Bogdanov Cusp Bifurcation

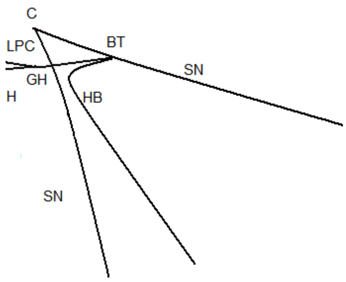
Motivated by its appearance in the Hodgkin-Huxley equations, this chapter shifts the attention to analyzing the Takens-Bogdanov Cusp Bifurcation and showing its existence in the model.

3.1 Motivation: Local Bifurcation

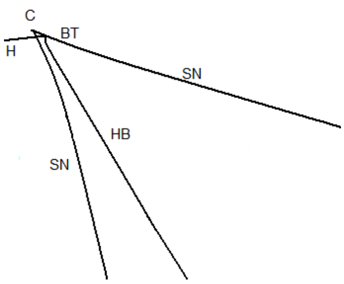
The flip in the relative positions of the Cusp and Takens-Bogdanov points in the bifurcation diagrams with $\bar{g}_K = 36$ and $\bar{g}_K = 12$ brings into question the possible existence of parameter values in which the two bifurcations coincide. By varying $\bar{g}_K$, we examine the bifurcation diagrams near the two points to find numerical bounds on the possible values. Figure 3.1 below depicts the local bifurcation diagram (scaled for visibility) for various $\bar{g}_K$ values.



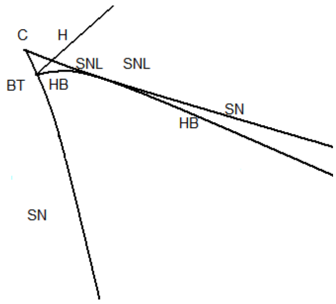
(a) $\bar{g}_K = 36$



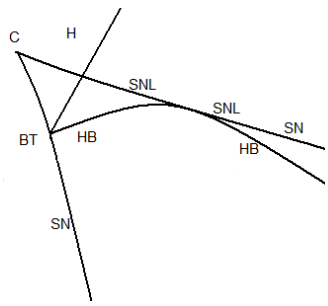
(b) $\bar{g}_K = 30$



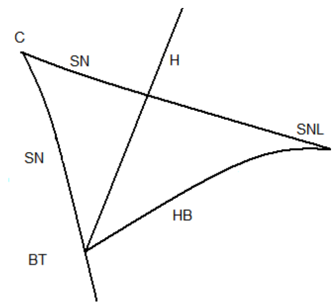
(c) $\bar{g}_K = 28$



(d) $\bar{g}_K = 26$



(e) $\bar{g}_K = 18$



(f) $\bar{g}_K = 12$

Figure 3.1: Deformed bifurcation diagrams in the locality of the Cusp and Takens-Bogdanov points with various $\bar{g}_K$ values.

As $\bar{g}_K$ is varied, the following values are computed: the eigenvalues for both bifurcations, the coordinates and parameters for both bifurcations, and the quadratic coefficient in the Takens-Bogdanov normal form. Starting with $\bar{g}_K =$ 36 the Takens-Bogdanov bifurcation is found at the equilibrium (V,m,n,h)= (-4.047081, 0.084264, 0.381090, 0.451565) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-5.385798, 0.219929, 36). The eigenvalues are 0 (multipliticity 2), -4.66429, and -0.2346. The normal form coefficient of the quadratic term is -.001855435. The cusp occurs at (V,m,n,h)= (0.220284, 0.051574, 0.314307, 0.603803) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-4.481471, -0.316520, 36). In the variable space, the points are relatively seperated with respect to V. The eigenvalues for the cusp point are 0, -4.69997, -0.426224, and -0.1004533. Observe that the nonzero eigenvalues are all negative. The first three eigenvalues of the cusp are close to the eigenvalues associated with the Takens-Bogdanov point. The local bifurcation diagram is depicted in Figure 3.1(a). The value of $\bar{g}_K$ is reduced to 30 and the bifurcation locally is displayed in Figure 3.1(b). The Takens-Bogdanov point is found at the equilibrium (V,m,n,h)= (-3.293224, 0.077427, 0.369121, 0.478431) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-4.320207, -0.618804 , 30). The nonzero eigenvalues are -4.59195 and -0.216656. The normal form coefficient of the quadratic term decreases to -.0006135526. The cusp occurs at (V,m,n,h)= (-1.633052, 0.064051, 0.342972, 0.538113) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-4.190451, -0.684437, 30). In the parameter space, the two bifurcation points are slowly approaching one another. The nonzero eigenvalues for the cusp point are -4.58025, -0.28513, and -0.076059, all still negative. Now, decreasing further, $\bar{g}_K = 28$, the Takens-Bogdanov's equilibrium is located at (V,m,n,h)= (-3.056617, 0.075383, 0.365374, 0.486915) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-3.962541, -0.842698, 28). Notice that the value of the gating variables change very little as $\bar{g}_K$ varies. The nonzero eigenvalues are -4.57633 and -0.211155. The normal form coefficient of the quadratic term decreases again to -.0002038274. The cusp occurs at (V,m,n,h)= (-2.469612, 0.070513, 0.356105, 0.508020) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-3.946649, -0.850363, 28). In the parameter space, the Takens-Bogdanov point has moved along one branch of the saddle node curve and is now very close to the cusp point(See Figure 3.1(c)). The nonzero eigenvalues for the cusp point are -4.56673, -0.239175, and -0.0364764, all still negative. The third nonzero eigenvalue of the cusp linearization seems to be decreasing more rapidly than the others.

Setting $\bar{g}_K = 26$ causes the Takens-Bogdanov point to switch relative position with respect to the cusp point. For previous values of $\bar{g}_K$, the Takens-Bogdanov point remained on the top branch of the saddle node curve; however, it now resides on the lower part (See Figure 3.1(d)). The points new located is (V,m,n,h)= (-2.826639, 0.073441, 0.361738, 0.495176) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-3.598883, -1.043601, 26). The nonzero eigenvalues are -4.56428 and -0.205902. The normal form coefficient of the quadratic term switches signs and is equal to .0002035363. If the normal form coefficient is continous with respect to $\bar{g}_K$ (which is varied continously) on the interval $[26, 28]$ and the normal form coeffiecient is positive on one endpoint and negative on the other, by Bolzano's Theorem, there exists a point where the normal form coefficient vanishes. The cusp is located at (V,m,n,h)= (-3.450110, 0.078809, 0.371608, 0.472817) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-3.581186, -1.051771, 26). The nonzero eigenvalues for the cusp point are -4.58169, -0.192865, and 0.0510321. This time, the third eigenvalue is positive, which reveals that for $\bar{g}_K$ between 26 and 28, there is a value in which the linearization of the cusp point becomes nilpotent. The other two nonzero eigenvalues have approached the values of the Bogdanov-Takens point. The parameters and coordinates are still relatively close. It is worth mentioning that the coefficient to the cusp bifucation switches signs and is now positive and will remain so for all lesser values of $\bar{g}_K$. Now, setting $\bar{g}_K = 18$ causes the Takens-Bogdanov point to move away from the cusp point (See figure 3.1(e)). Its location is (V,m,n,h)= (-1.966642, 0.066562, 0.348197, 0.526123) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-1.983194, -1.660766, 18). The nonzero eigenvalues are -4.54527 and -0.187354. The normal form coefficient of the quadratic term stays positive and increases to .001802218. The cusp is located at (V,m,n,h)= (-8.123521, 0.130699, 0.445989, 0.316162) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (0.247835, -2.525355 , 26). The nonzero eigenvalues for the cusp point are -5.004, -0.17693, and 0.802583. The two bifurcation points are now moving away from each other both in variable and parameter space.

Lastly, for $\bar{g}_K = 12$ the Takens-Bogdanov point drastically moves away from the cusp point, relative to the values of 26 and 28 (See figure 3.1(f)). The Takens-Bogdanov point's location is (V,m,n,h) = (-1.377520, 0.062184, 0.338981, 0.547278) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (-0.267227, -1.974591, 12). The nonzero eigenvalues are -4.5546 and -0.175895. The normal form coefficient of the quadratic term stays positive and increases to .002956026. The cusp is now extremely distant from the Takens-Bogdanov point, located at (V,m,n,h)= (-11.019640, 0.174616, 0.491289, 0.236392) with parameter values of $(\bar{V}_K, I, \bar{g}_K)$= (8.945909, -4.738952, 26). The nonzero eigenvalues for the cusp point continue to move away from zero and are -5.37245, -0.192093, and 1.40223. As we decrease the value of $\bar{g}_K$, we see that this separation continues along the lower branch of the saddle node curve.

3.2 Definitions of Certain Bifurcation

In the HH equations, the Takens-Bogdanov bifurcation was shown to occur on both sides of a cusp bifurcation along a saddle node curve. Therefore, before studying the Takens-Bogdanov Cusp bifurcation, the basic material and its relevance to our analysis is built up. Consider a dynamical system(3.1):

$$\dot{x} = f(x, \alpha)$$

where $x \epsilon \mathbb{R}^n$ and $\alpha \epsilon \mathbb{R}^m$.

As mentioned in the introduction, a saddle node bifurcation occurs when the eigenvalue of the linearized differential equation is zero. The definition below formalizes that statement [7].

Definition 3.1: For all $m > 0$, the dynamical system (3.1) with equilibrium x_0 has a *saddle node bifurcation* when $\alpha = \alpha_0$ if $\partial_x f(x_0, \alpha_0)$ has a simple zero eigenvalue and no other eigenvalues with zero real parts.

The dynamical system may be reduced to a more convenient form for further analysis. We shall omit the parameter α temporarily. The existence of a locally smooth invariant manifold near a non-hyperbolic equilibrium is guaranteed by the Center Manifold Theorem [5]. By separating the eigenbasis of $\partial_x f(x_0)$ into k eigenvectors corresponding to eigenvalues with zero real parts and r eigenvectors corresponding to eigenvalues with nonzero real parts (r+k=n), Shoshitaishvili's theorem reduces the differential equation to a decoupled system [8]:

$$\dot{w} = Aw + \Psi(w, \Phi(w))$$

$$\dot{z} = Bz$$

where the new coordinates are w ϵ $\mathbb{R}^k$ and z ϵ $\mathbb{R}^r$, A is a k-by-k matrix with all eigenvalues having zero real parts, B is a r-by-r matrix with all eigenvalues having nonzero real parts, and $\Phi : \mathbb{R}^k \to \mathbb{R}^r$ is a smooth function for the Center Manifold. The differential equation (3.1 without the parameter) is locally topologically equivalent to the reduction above. Since the differential equation is locally equivalent and the z component of the second differential equation only has simple exponential solutions, attention now can be focused on the equation for w. The first equation in the reduction of the differential equation is the restriction to the center manifold [7].

Returning back to the saddle node bifurcation, we may simplify the differential equation by restricting it to its center manifold and apply Shoshitaishvili's theorem. It is easy to show that this yields:

$$\dot{w} = aw^2 + O(w^3)$$

where w ϵ $\mathbb{R}$ and a is nonzero. Along the saddle node curve, the differential equation is locally equivalent for various nonzero a's for each equilibrium. When a vanishes (which corresponds to the $\partial_{xx} f$ vanishing) the cusp bifurcation occurs. We take $f : \mathbb{R} \to \mathbb{R}$, restricting it to the center manifold.

Definition 3.2: For all $m > 0$, the dynamical system with equilibrium x_0 has a *cusp bifurcation* when $\alpha = \alpha_0$ if $\partial_x f(x_0, \alpha_0)$ has a simple zero eigenvalue and no other eigenvalues with zero real parts and $\partial_{xx} f(x_0, \alpha_0)$ vanishes.

Continuing along the saddle node curve, when a second eigenvalue of $\partial_x f$ becomes zero the Takens-Bogdanov bifurcation occurs. Now our restriction onto the center manifold goes from one dimensional to two dimension.

Definition 3.3: For all $m > 1$, the dynamical system with equilibrium x_0 has a *Takens-Bogdanov bifurcation* when $\alpha = \alpha_0$ if $\partial_x f(x_0, \alpha_0)$ has a zero eigenvalue with an algebraic multiplicity of two and no other eigenvalues with zero real parts.

Locally, the dynamical system (3.1) near a Takens-Bogdanov point is topologically equivalent to either of the following differential equations [5]:

$$\dot{x} = y + ax^2$$

$$\dot{y} = bx^2$$

or

$$\dot{x} = y$$

$$\dot{y} = ax^2 + bxy$$

for nonzero a and b. It is not difficult to show that both determine the vector field locally.

3.3 Takens-Bogdanov Cusp Bifurcation

The collision of the Takens-Bogdanov bifurcation and the cusp bifurcation creates the occurrence of a codimension three bifurcation. From the perspective of the Takens-Bogdanov bifurcation, the codimension three bifurcation retains the zero eigenvalue with an algebraic multiplicity of two; however, one genericity condition is violated: one of its normal form coefficients vanishes [4]. Looking at it from the cusp's point of view, the simple zero eigenvalue becomes a zero eigenvalue with an algebraic multiplicity of two, but the vanishing second derivative is preserved. The center manifold is now two dimensional. The following definition is provided:

Definition 3.4: For all $m > 2$, the dynamical system with equilibrium x_0 has a *Takens-Bogdanov Cusp bifurcation* when $\alpha = \alpha_0$ if (i) $\partial_x f(x_0, \alpha_0)$ has a zero eigenvalue with an algebraic multiplicity of two and no other eigenvalues with zero real parts and (ii) the expression $< p, B[q, q] >$ evalutes to zero, where p and q are the left and right eigenvectors, respectively, corresponding to the zero eigenvalue and B is the bilinear form, defined component wise as:

$$B_i[x, y] = \sum_{j,k} [\partial_{z_j z_k} f_i(0)] x_j y_j$$

where j,k run from 1 to n..

Condition (i) corresponds to the linearization of the Takens-Bogdanov bifurcation and Condition (ii) corresponds to the cusp condition on the second derivatives. When the cusp and the Takens-Bogdanov bifurcations coincide, the center manifold of the resulting system is of dimension two. Although the cusp's center manifold is dimension one, the Takens-Bogdanov's center manifold is dimension two. The determining factor for the behavior of the center manifold lies with the eigenvalues of the linearized vector field. It is clear that real parts of the eigenvalues of the Takens-Bogdanov bifurcation do not change when becoming a Takens-Bogdanov Cusp, thus it is expected that a topological normal form of the Takens-Bogdanov Cusp bifurcation should be very similar to that of a Takens-Bogdanov. The theorem below provides the 3-jet normal form of the codimension three bifurcation.

Theorem 3.1: For m=2, assuming f ϵ C^r and the dynamical system (3.1) has a Takens-Bogdanov Cusp bifurcation at the equilibrium $x = x_0$ with $\alpha = \alpha_0$, then the system is topologically equivalent to:

$$\dot{x} = y + O(|(x, y)|^3)$$

$$\dot{y} = bxy \pm x^3 + O(|(x,y)|^3)$$

$$\dot{\gamma} = \gamma$$

$$\dot{\zeta} = -\zeta$$

where b is nonzero, x,y ϵ $\mathbb{R}$, γ ϵ $\mathbb{R}^{d_+}$, and ζ ϵ $\mathbb{R}^{d_-}$ ($d_\pm$ are the number of positive/negative eigenvalues).

Proof:

Without loss of generality, α is omitted.

By restricting $\dot{x} = f(x)$ to its center manifold and applying Shoshitaishvili's theorem, the differential equation is reduced to the decoupled differential equation:

$$\dot{u} = Au + g(u)$$

$$\dot{\vartheta} = B\vartheta$$

where the new coordinate is u ϵ $\mathbb{R}^2$, A is a 2-by-2 nilpotent matrix, B is a matrix with all eigenvalues having nonzero real parts, and g ϵ C^r is the restriction onto the center manifold. By simple scaling, it is clear that the second equation for ϑ is topologically equivalent to:

$$\dot{\gamma} = \gamma$$

$$\dot{\zeta} = -\zeta$$

where γ ϵ $\mathbb{R}^{d_+}$, and ζ ϵ $\mathbb{R}^{d_-}$. The first equation can be linearly transformed to a new basis such that the nilpotent matrix A becomes:

$$A = \begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}$$

Denote the linear part of the first equation at the equilibrium by $L = Ax$ [6]. The induced map called the adjoint endomorphism, ad L, on the linear space H_2 of vector fields (homogeneous polynomials of degree 2) is defined as the Lie bracket operation:

$$adL(Y) = [Y, L] = DLY - DYL$$

which for this case, component wise, is:

$$adL \begin{pmatrix} Y^1 \\ Y^2 \end{pmatrix} = \begin{pmatrix} Y^2 - \partial_x Y^1 y \\ -\partial_x Y^2 y \end{pmatrix}$$

The standard basis elements of H_2 are

$$\begin{pmatrix} x^2 \\ 0 \end{pmatrix}, \begin{pmatrix} xy \\ 0 \end{pmatrix}, \begin{pmatrix} y^2 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ x^2 \end{pmatrix}, \begin{pmatrix} 0 \\ xy \end{pmatrix}, \begin{pmatrix} 0 \\ y^2 \end{pmatrix}$$

and applying the map to the standard basis results in:

$$adL \begin{pmatrix} x^2 \\ 0 \end{pmatrix} = \begin{pmatrix} -2xy \\ 0 \end{pmatrix} \qquad adL \begin{pmatrix} xy \\ 0 \end{pmatrix} = \begin{pmatrix} -y^2 \\ 0 \end{pmatrix}$$

$$adL \begin{pmatrix} y^2 \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \qquad adL \begin{pmatrix} 0 \\ x^2 \end{pmatrix} = \begin{pmatrix} x^2 \\ -2xy \end{pmatrix}$$

$$adL\begin{pmatrix} 0 \\ xy \end{pmatrix} = \begin{pmatrix} xy \\ -y^2 \end{pmatrix} \qquad adL\begin{pmatrix} 0 \\ y^2 \end{pmatrix} = \begin{pmatrix} y^2 \\ 0 \end{pmatrix}$$

Therefore, we see that the range of the operator, R[ad L], is spanned by four basis vectors in H_2. Thus, the chosen two dimensional subspace, G_2, below completes the space.

$$R[adL] = span(\begin{pmatrix} x^2 \\ 0 \end{pmatrix}, \begin{pmatrix} xy \\ 0 \end{pmatrix}, \begin{pmatrix} y^2 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ y^2 \end{pmatrix})$$

$$G_2 = span(\begin{pmatrix} 0 \\ x^2 \end{pmatrix}, \begin{pmatrix} 0 \\ xy \end{pmatrix})$$

therefore $H_2 = adL + G_2$.

Now repeating the process for H_3 (homogeneous polynomials of degree 3) where the standard basis elements are:

$$\begin{pmatrix} x^3 \\ 0 \end{pmatrix}, \begin{pmatrix} x^2y \\ 0 \end{pmatrix}, \begin{pmatrix} xy^2 \\ 0 \end{pmatrix}, \begin{pmatrix} y^3 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ x^3 \end{pmatrix}, \begin{pmatrix} 0 \\ x^2y \end{pmatrix}, \begin{pmatrix} 0 \\ xy^2 \end{pmatrix}, \begin{pmatrix} 0 \\ y^3 \end{pmatrix},$$

and applying the map to the standard basis results in:

$$adL\begin{pmatrix} x^3 \\ 0 \end{pmatrix} = \begin{pmatrix} -3x^2y \\ 0 \end{pmatrix} \qquad adL\begin{pmatrix} x^2y \\ 0 \end{pmatrix} = \begin{pmatrix} -2xy^2 \\ 0 \end{pmatrix}$$

$$adL\begin{pmatrix} xy^2 \\ 0 \end{pmatrix} = \begin{pmatrix} -y^3 \\ 0 \end{pmatrix} \qquad adL\begin{pmatrix} y^3 \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$$adL\begin{pmatrix} 0 \\ x^3 \end{pmatrix} = \begin{pmatrix} x^3 \\ -3x^2y \end{pmatrix} \qquad adL\begin{pmatrix} 0 \\ x^2y \end{pmatrix} = \begin{pmatrix} x^2y \\ -2xy^2 \end{pmatrix}$$

$$adL\begin{pmatrix} 0 \\ xy^2 \end{pmatrix} = \begin{pmatrix} xy^2 \\ -y^3 \end{pmatrix} \qquad adL\begin{pmatrix} 0 \\ y^3 \end{pmatrix} = \begin{pmatrix} y^3 \\ 0 \end{pmatrix}$$

Therefore, we see that the range of the operator, R[ad L], is spanned by six basis vectors in H_3. Thus, the chosen two dimensional subspace, G_3, below completes the space.

$$R[adL] = span(\begin{pmatrix} x^3 \\ 0 \end{pmatrix}, \begin{pmatrix} x^2y \\ 0 \end{pmatrix}, \begin{pmatrix} xy^2 \\ 0 \end{pmatrix}, \begin{pmatrix} y^3 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ xy^2 \end{pmatrix}), \begin{pmatrix} 0 \\ y^3 \end{pmatrix}))$$

$$G_3 = span(\begin{pmatrix} 0 \\ x^3 \end{pmatrix}, \begin{pmatrix} 0 \\ x^2y \end{pmatrix})$$

therefore $H_3 = adL + G_3$.

Now, applying the Normal Form Theorem [5], for our chosen spaces for G_2 and G_3 there is an analytic change of coordinates in a neighborhood of the equilibrium that maps the differential equation onto:

$$\dot{x} = y + O(|(x,y)|^3)$$

$$\dot{y} = ax^2 + bxy + cx^2y + dx^3 + O(|(x,y)|^3)$$

Next, we scale the equations (ignoring the remainder terms) by setting

$$x = \epsilon^2 u$$

$$y = \epsilon^3 u$$

and rescale time from t to ϵt, for $\epsilon \geq 0$. The differential equations now become:

$$\dot{u} = v$$

$$\dot{v} = au^2 + b\epsilon uv + c\epsilon^3 u^2 v + d\epsilon^2 u^3$$

For ϵ small, we see that the $u^2 v$ term has the least effect. This suggests that the $x^2 y$ term does not greatly affect the dynamics and therefore may be neglected.

It can (and will be) shown that the coefficient a can be defined as [7]:

$$a = \frac{1}{2} < p, B[q, q] >$$

where $<, >$ is the standard complex inner product, p is the eigenvector of the transpose matrix with eigenvalue zero, B is the bilinear form as described in definition (3.4 ii), and q is the eigenvector corresponding to the zero eigenvalue. By definition of the Takens-Bogdanov Cusp, we see that a must vanish, yielding:

$$\dot{y} = bxy + dx^3 + O(|(x, y)|^3)$$

Lastly, the transformation $\tilde{x} = \sqrt{d}x$ and $\tilde{y} = \sqrt{d}y$ removes the coefficient on the x^3 term yielding:

$$\dot{y} = bxy \pm x^3 + O(|(x,y)|^3)$$

for a new, nonzero b.

Combining both reductions of the two equations in the decoupled differential equations results in:

$$\dot{x} = y + O(|(x,y)|^3)$$

$$\dot{y} = bxy \pm x^3 + O(|(x,y)|^3)$$

$$\dot{\gamma} = \gamma$$

$$\dot{\zeta} = -\zeta$$

where b is nonzero, x,y ϵ $\mathbb{R}$, $\gamma \, \epsilon \, \mathbb{R}^{d_+}$, and $\zeta \, \epsilon \, \mathbb{R}^{d_-}$. **QED**

The normal form of the Takens-Bogdanov Cusp bifurcation is exactly what was expected. A natural next question would be: Up to what order can this form be used for determinacy? The next theorem answers this question.

Theorem 3.2: The Takens-Bogdanov Cusp Bifurcation is determined locally by the 3-jet:

$$\dot{x} = y$$

$$\dot{y} = bxy \pm x^3$$

$$\dot{\gamma} = \gamma$$

$$\dot{\zeta} = -\zeta$$

where b is nonzero, x,y ϵ $\mathbb{R}$, $\gamma \, \epsilon \, \mathbb{R}^{d_+}$, and $\zeta \, \epsilon \, \mathbb{R}^{d_-}$.

"Proof:"

In [5], it is proven, using the method of "blowing up", that the 2-jet:

$$\dot{x} = y + ax^2$$

$$\dot{y} = bx^2$$

determines the vector field locally for nonzero b. The proof is independent of a, thus the 2-jet of the Takens-Bogdanov Cusp bifurcation:

$$\dot{x} = y$$

$$\dot{y} = bx^2$$

is sufficient for determinacy. Therefore, the 3-jet also is sufficient for determinacy.

In the proof of theorem 3.1, the choice of complement basis gives two normal forms for Takens-Bogdanov Cusp:

$$\dot{x} = y + O(|(x, y)|^3)$$

$$\dot{y} = bxy \pm x^3 + O(|(x, y)|^3)$$

and

$$\dot{x} = y + O(|(x, y)|^3)$$

$$\dot{y} = bx^2 \pm x^3 + O(|(x, y)|^3)$$

which are both locally topologically equivalent to the original differential equation (3.1). Topological equivalence is an equivalence relation for the group of vector fields, therefore by definition the relation is transitive. So if the second form is equivalent to (3.1) locally and (3.1) is locally equivalent to the first form, then the two forms must be equivalent to each other. From [5], the second form has been shown to determine the local topological structure of the differential equation, therefore, by equivalence so must the first. **QED**

Although the 3-jet is sufficient for determining the local vector field, it fails to provide a universal unfolding of the codimension three bifurcation. However, the local structure is all that is needed for proving existence.

3.4 Computational Evidence

The analysis above provides a basis for proving the existence of the Takens-Bogdanov Cusp bifurcation in the Hodgkin-Huxley equations, with parameters $\bar{g}_K$, $\bar{V}_K$, and I. In this section a given set of values for the parameters are studied in order to reveal such existence.

Claim: For the HH equations with parameters $\bar{g}_K$, $\bar{V}_K$, and I, there exists a Takens-Bogdanov Cusp bifurcation at (or extremely near) the equilibrium:

$$\begin{pmatrix} V \\ m \\ n \\ h \end{pmatrix} = \begin{pmatrix} -2.9409168 \\ 0.74400691 \\ 0.36354434 \\ 0.49106969 \end{pmatrix}$$

with parameters equal to:

$$\begin{pmatrix} \bar{g}_K \\ \bar{V}_K \\ I \end{pmatrix} = \begin{pmatrix} 27.000082480 \\ -3.7818334 \\ -0.94578507 \end{pmatrix}$$

3.4.1 Existence by verification

The existence of the bifurcation relies on showing that the claim above satisfies the definition for the Takens-Bogdanov Cusp bifurcation. This can be done by verify the claim directly. By tedious manual computation, the jacobian is found to be:

$$\partial HH = \begin{pmatrix} \partial_V HH & \partial_m HH & \partial_n HH & \partial_h HH \end{pmatrix}$$

where

$$\partial_V HH = \begin{pmatrix} -(\bar{g}_{Na} m^3 h + \bar{g}_K n^4 + \bar{g}_L) \\ \Phi(T)[(m-1)(\frac{e^{\frac{V+25}{10}}(x+15)+10}{100(e^{\frac{V+25}{10}}-1)^2}) - \frac{2}{9} m e^{\frac{V}{18}}] \\ \Phi(T)[(n-1)(\frac{e^{\frac{V+10}{10}}-10}{1000(e^{\frac{V+10}{10}}-1)^2}) - \frac{1}{640} n e^{\frac{V}{80}}] \\ \Phi(T)[\frac{7}{2000}(1-h)e^{V/20} + \frac{h e^{\frac{V+30}{10}}}{10(1+e^{\frac{V+30}{10}})}] \end{pmatrix}$$

$$\partial_m HH = \begin{pmatrix} 3\bar{g}_{Na} m^2 h(V - \bar{V}_{Na}) \\ -(\frac{\frac{V+25}{10}}{e^{\frac{V+25}{10}} - 1} + 4e^{\frac{V}{18}}) \\ 0 \\ 0 \end{pmatrix}$$

$$\partial_n HH = \begin{pmatrix} 4\bar{g}_K n^3 (V - \bar{V}_K) \\ 0 \\ -(\frac{\frac{V+10}{100}}{e^{\frac{V+10}{10}} - 1} + \frac{1}{8}e^{\frac{V}{80}}) \\ 0 \end{pmatrix}$$

$$\partial_h HH = \begin{pmatrix} \bar{g}_{Na} m^3 (V - \bar{V}_{Na}) \\ 0 \\ 0 \\ -(\frac{1}{7}e^{\frac{V}{20}} + (1 + e^{\frac{V+30}{10}})^{-1}) \end{pmatrix}$$

Evaluating the Jacobian at the equilibrium and at the claimed parameters and then solving for its eigenvalues returns 0 with multiplicity 2, -4.56989, and -.2085. Therefore, condition (i) in definition (3.3) is verified.

Due to the level of computational complexity, the second condition can be verified by a computer. First, the right and left eigenvectors v and u, respectively, corresponding to the eigenvalue zero is computed. Then the second order bilinear form is found. The bilinear form for the quadratic term, B[x,y], is defined component wise as [7]:

$$B_i[x, y] = \sum_{j,k} [\partial_{z_j z_k} f_i(0)] x_j y_j$$

where j,k run from 1 to n. And by computing $< u, B[v, v] >$ we find that this expression evaluates to zero. Thus the second condition in definition (3.3) is found to be true. Therefore, by definition (3.3), at the values stated there exists a Takens-Bogdanov Cusp bifurcation.

Theorem 3.3: For the HH equations with parameters $\bar{g}_K$, $\bar{V}_K$, and I, there exists a Takens-Bogdanov Cusp bifurcation with the following values (up to order 10^{-8}):

$$\begin{pmatrix} V \\ m \\ n \\ h \end{pmatrix} = \begin{pmatrix} -2.9409168 \\ 0.74400691 \\ 0.36354434 \\ 0.49106969 \end{pmatrix}$$

$$\begin{pmatrix} \bar{g}_K \\ \bar{V}_K \\ I \end{pmatrix} = \begin{pmatrix} 27.000082480 \\ -3.7818334 \\ -0.94578507 \end{pmatrix}$$

[Note: The values stated and the verification is done up to order 10^{-8}. Thus, those values are true up to the numerical approximation.]

3.4.2 Local Topological Equivalence

Since it has been shown that the values stated above are indeed the values for the Takens-Bogdanov Cusp bifurcation, a reasonable next step is to calculate its normal form. Theorem (3.2) stated that near the bifurcation, the differential equation is locally equivalent to

$$\dot{x} = y$$

$$\dot{y} = bxy \pm x^3$$

$$\dot{\gamma} = \gamma$$

$$\dot{\zeta} = -\zeta$$

where b is nonzero, x,y ϵ $\mathbb{R}$, $\gamma \ \epsilon \ \mathbb{R}^{d_+}$, and $\zeta \ \epsilon \ \mathbb{R}^{d_-}$.

The eigenvalues were shown to be: 0 with multiplicity 2, -4.56989, and -.2085. Therefore, $\zeta \ \epsilon \ \mathbb{R}^2$ and there is no need for γ. The coefficient, b, can be calculated several ways. One way is by finding four eigenvectors, $v_{0,1}$ and $u_{0,1}$ in $\mathbb{R}^n$ such that the following hold:

$$Av_0 = 0 \ Av_1 = v_0 \ A^T u_0 = u_1 \ A^T u_1 = 0$$

$$< u_0, v_0 >=< u_1, v_1 >= 1$$

$$< u_0, v_1 >=< u_1, v_0 >= 0$$

where A is the linearized matrix and A^T is its transpose [7]. Then we can write b as:

$$b =< u_0, B[v_0, v_0] > + < u_1, B[v_0, v_1] >$$

This formulation will be derived later. The calculated value for b is 0.007194659. This yields the following corollary:

Corollary 3.1: The HH equations near the Takens-Bogdanov Cusp Bifurcation is locally topologically equivalent to:

$$\dot{x} = y$$

$$\dot{y} = 0.007194659xy - x^3$$

$$\dot{\zeta} = -\zeta$$

where x,y ϵ $\mathbb{R}$ and ζ ϵ $\mathbb{R}^2$.

Note that the sign on the x^3 term is negative. It is not difficult to check that if it were positive, then there would exist heteroclinic orbits around the bifurcation, which is not true for the HH equations.

It is worth mentioning that a weaker analysis with similar conclusions has been done for a three dimensional reduction of the HH equations. As seen, the gating parameter m does not vary much. Thus assuming that m has reached its equilibrium value instantaneously, the HH equations are reduced to:

$$\dot{V} = -G(V, m, n) + I$$
$$\dot{n} = \Phi(T)[(1 - n)\alpha_n(V) - n\beta_n(V)]$$
$$\dot{h} = \Phi(T)[(1 - h)\alpha_h(V) - h\beta_h(V)]$$

where G is now define as

$$G(V,m,n,h) = \bar{g}_{Na}(\frac{\alpha_m(V)}{\alpha_m(V)+\beta_m(V)})^3 h(V-\bar{V}_{Na}) + \bar{g}_K n^4(V-\bar{V}_K) + \bar{g}_L(V-\bar{V}_L)$$

This system displays the same behavior as the four dimensional HH equations.

Chapter 4

Computational Methods

The dynamical system near a Takens-Bogdanov Cusp bifurcation has been proven to be locally equivalent to the 3-jet:

$$\dot{x} = y$$

$$\dot{y} = bxy \pm x^3$$

$$\dot{\gamma} = \gamma$$

$$\dot{\zeta} = -\zeta$$

Although the differential equation below provides the universal unfolding of the codimension three bifurcation [7]:

$$\dot{x} = y$$

$$\dot{y} = a_1 + a_2x + a_3y + a_4x^3 + a_5xy + a_6x^2y$$

$$\dot{\gamma} = \gamma$$

$$\dot{\zeta} = -\zeta$$

for the purposes of determinacy, the proven normal form is sufficient.

To complete the analysis, this chapter outlines Kuznetsov's proof for the normal form computations used in the previous chapters [7].

Outline of Computational Derivation:

Consider the dynamical system,with equilibrium $x = 0$ when $\alpha = 0$:

$$\dot{x} = f(x, \alpha)$$

where $x \epsilon \mathbb{R}^n$ and $\alpha \epsilon \mathbb{R}^m$.

Define $f(x)$ as $f(x) = f(x, 0)$ and Taylor expand the function with respect to the equilibrium:

$$f(x) = Ax + \frac{1}{2}B[x, x] + O(x^3)$$

where

$$A = \partial_x f(0, 0)$$

and

$$B_i[x, y] = \sum_{j,k} [\partial_{z_j z_k} f_i(0)] x_j y_j$$

for j,k running from 1 to n.

Also, in order to restrict the new differential equation to the center manifold we change coordinates to:

$$x = \Phi(w)$$

where $\Phi : \mathbb{R}^2 \rightarrow \mathbb{R}^n$ is a smooth function defined on the center manifold.

By applying Shoshitaishvili's theorem we reduce the differential equation to its invariant manifold [8]:

$$w = \Psi(w)$$

where $\Psi : \mathbb{R}^2 \rightarrow \mathbb{R}^2$ is a smooth function defined on the center manifold. Returning to the differential equation, the restriction on the center manifold yields:

$$\dot{x} = \dot{\Phi}(w) = \Phi_w(w)\dot{w} = \Phi_w(w)\Psi(w) \Rightarrow$$

$$\Phi_w(w)\Psi(w) = f(\Phi(w))$$

which is called the homological equation. Since we have assumed that both $\Phi(w)$ and $\Psi(w)$ are smooth we may Taylor expand them for all nonzero multiindex i

$$\Phi(w) = \sum \frac{1}{i!}\phi_i w^i$$

$$\Psi(w) = \sum \frac{1}{i!}\psi_i w^i$$

By definition of the Takens-Bogdanov Cusp bifurcation, there exists four eigenvectors, $v_{0,1}$ and $u_{0,1}$ in $\mathbb{R}^n$ such that the following hold:

$$Av_0 = 0 \; Av_1 = v_0 \; A^T u_0 = u_1 \; A^T u_1 = 0$$

$$< u_0, v_0 >=< u_1, v_1 >= 1$$

$$< u_0, v_1 >=< u_1, v_0 >= 0$$

where A is the linearized matrix and A^T is its transpose.

Decomposing a vector in the center subspace of A leads to:

$$r =< u_0, r > v_0+ < u_1, r > v_1 = yv_0 + zv_1$$

Therefore, the homological equation is

$$\Phi_y \dot{y} + \Phi_z \dot{z} = f(\Phi(y, z))$$

with

$$\Phi(x, y) = yv_0 + zv_1 + \frac{1}{2}\phi_{2,0}y^2 + \phi_{1,1}yz + \frac{1}{2}\phi_{0,2}z^2$$

$$f(\Phi) = A\Phi + \frac{1}{2}B[\Phi, \Phi]$$

ignoring all order 3 terms since our concern is with order 2 or less terms. The normal form (2-jet) as we defined it earlier is:

$$y = z$$

$$z = ay^2 + byz$$

where a and b must be determined. Using the homological expression, a can be found by:

$$\frac{1}{2}A\phi_{2,0} = av_1 - \frac{1}{2}B[v_0, v_0]$$

By Fredholm's Alternative [3], there exist a solution to the linear system if and only if $< u_1, \frac{1}{2}A\phi_{2,0} >= 0$, and since $< u_1, v_1 >= 1$:

$$a = \frac{1}{2} < u_1, B[v_0, v_0] >$$

For b we have:

$$A\phi_{1,1} = bv_1 + \phi_{2,0} - B[v_0, v_1]$$

again applying Fredholm's Alternative yields:

$$b = - < u_1, \phi_{2,0} > + < u_1, B[v_0, v_1] >$$

which can be simplified by using the homological expression for a

$$b =< u_0, B[v_0, v_0] > + < u_1, B[v_0, v_1] >$$

Then we can write b as:

$$b =< u_0, B[v_0, v_0] > + < u_1, B[v_0, v_1] >$$

This provides a nice computational method for determining the coefficients in the Takens-Bogdanov normal form. **QED**

Applying this to computations for the Takens-Bogdanov Cusp bifurcation simplifies the numerics significantly. Recall that the 3-jet locally topologically equivalent form is:

$$\dot{x} = y$$

$$\dot{y} = bxy \pm x^3$$

where a in the Takens-Bogdanov normal form vanishes. We can determine

b by using:

$$b =< u_0, B[v_0, v_0] > + < u_1, B[v_0, v_1] >$$

thereby determining the Takens-Bogdanov Cusp normal form.

Chapter 5

Conclusion

The complete chaotic behavior of the Hodgkin-Huxley equation still remains unsolved. The bifurcation diagrams presented in this paper revealed many codimension one and two bifurcations and one codimension three. The use of new computational programs (Matcont), numerical methods, and dynamical systems theory supported the original bifurcation diagrams given by [6]. Proving the 3-jet determinacy for the Takens-Bogdanov Cusp bifurcation provided a framework for proving the existence of this bifurcation in the Hodgkin-Huxley equation. Within the accurate numerical approximation (order of 10^{-8}), the values for the equilibrium point and the parameters at the TBC bifurcation were found to be (V,m,n,h)=(-2.9409168, 0.74400691, 0.36354434, 0.49106969) and ($\bar{g}_K$,$\bar{V}_K$, I)=(27.000082480, -3.7818334, -0.94578507), respectively. Also, the local topological form was found and proven to be:

$$\dot{x} = y \qquad \dot{y} = 0.007194659xy - x^3 \qquad \dot{\zeta} = -\zeta$$

where x,y ϵ $\mathbb{R}$ and ζ ϵ $\mathbb{R}^2$.

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