Normal form analysis of a mean-field inhibitory neuron model

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A Thesis in

The Department of Mathematics

and Statistics

Presented in partial fulfilment of the requirements for the degree of Master of Science (Mathematics) at Concordia University

Montreal, Quebec, Canada

April 2012

CONCORDIA UNIVERSITY

School of Graduate Studies

This is to certify that the thesis prepared

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Entitled: Normal form analysis of a mean-field inhibitory neuron model

and submitted in partial fulfilment of the requirements for the degree of

Master of Science (Mathematics)

complies with the regulations of the University and meets the accepted standards with respect to originality and quality.

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Abstract

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In neuroscience one of the open problems is the creation of the alpha rhythm detected by the electroencephalogram (EEG). One hypothesis is that the alpha rhythm is created by the inhibitory neurons only. The mesoscopic approach to understand the brain is the most appropriate to mathematically modelize the EEG records of the human scalp. In this thesis we use a local, mean-field potential model restricted to the inhibitory neuron population only to reproduce the alpha rhythm. We perform extensive bifurcation analysis of the system using AUTO. We use Kuznetsov's method that combines the center manifold reduction and normal form theory to analytically compute the normal form coefficients of the model. The bifurcation diagram is largely organised around a codimension 3 degenerate Bogdanov-Takens point. Alpha rhythm oscillations are detected as periodic solutions.

Acknowledgements

Completing a Master of Science program demands intellectual, financial and major psychological support throughout the entire procedure. During these four years, from the time that I decided to continue my graduate studies until today, many people provided me with priceless support in various aspects, thus helping me to become a better educated person.

I am immensely grateful to my principal supervisor Dr Lennaert van Veen from the UOIT for introducing me to the magical field of Bifurcation Theory, for his helpful guidance and endless patience. I had the opportunity to work with him during the first years of his career as a university professor and I am confident that he will become a successful, inspiring professor hopefully with better students. I would like to thank also Dr Eusebius Doedel from Concordia University for his useful feedback on this thesis. Special thanks to my friend, office and class mate Alexandra Lemus Rodriguez for sharing technical skills, knowledge and panic during the initiation to bifurcation theory, parameter continuation and dynamical systems.

Undertaking and completing this project would never be possible without the ample resources provided by of Concordia University. I would like to thank the graduate department of mathematics and statistics, all the professors involved in the graduate committee and the support stuff, for the encouragement, the help and the financial support. For the latter I am particularly grateful to the Hellenic Scholarship foundation and the Hellenic Community of Greater Montreal.

Finally, position not removing anything from importance, I would like to thank my family for the psychological support that offered me generously all these four years. I also owe a particular thanks to my friends: the Greeks, the step parents, the cook, the accountant, the lawyer, the doctor, the real doctor, the nurse and her parents, the dentist that left, my French and German roommates for tolerating and denying the veracity of my insecurities all these years. A special thanks to the first pet that I loved for teaching me that life has a meaning only when an entire existence depends on you.

To my sister

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Introduction

The work presented in this thesis has two main components: brain modelling and normal form analysis. We dedicate Chapter 1 to the presentation of the model and the brain's basic functions and Chapters 2 and 3 to dynamical systems and normal form theory. In Chapter 4 we explain the application of the theory to our model and make the connection with the brain functions, in particular with the alpha rhythm. Finally in the conclusion we summarize the method, the theory and the results.

More specifically in Chapter 1 we describe the basic morphology of the brain and the interaction between its parts, the various approaches used to mathematically model the brain, in particular the mesoscopic approach and its immediate relation with the EEG. We present the initial model and its restriction to the inhibitory neuron population only. This restriction yields a three-variable, autonomous, nonlinear set of ordinary differential equations that we will analyse by means of dynamical systems theory.

In Chapter 2 we define dynamical systems and we present stability and bifurcation theory as well as simplification methods like center manifold reduction and normal form theory. Specific examples are given for each method.

In Chapter 3 we describe a method to apply center manifold reduction and compute the coefficients of the normal forms of a dynamical system at the same time. This method was introduced by Kuznetsov [13] and can be applied analytically as well as numerically to our model.

In Chapter 4 we describe the application of the method presented in Chapter 3 to our model. We do the bifurcation analysis of the system and we present the relation with our initial goal, that is to describe the creation of the alpha rhythm. We show that the behaviour of our model is largely organized by a degenerate Bogdanov-Takens bifurcation. We present an explicit example of a bifurcation diagram in which stable periodic motion generates an alpha peak in the power spectrum.

Chapter 1

Neuroscientific motivation

1.1 Introduction

Understanding the way the brain functions is an issue that persists since the times of ancient cultures' philosophers. The earliest reference to the brain comes from a papyrus of the 17th century BC, where the symptoms, diagnosis and prognosis of two patients wounded on the head are described. In the second half of the first millennium BC Greek philosophers developed theories on the functions of the brain. For example Aristotle believed that the seat of intelligence is the heart and the brain was a cooling mechanism of the blood [17]. During the Roman empire the anatomist Galen made a description of the nervous system and its parts. During the renaissance, Vesalius and Descartes contributed to the development of neuroscience [17]. Studies of the brain became more sophisticated after the development of a staining procedure used to reveal the structures of individual neurons. Santiago Ramón y Cajal used this technique to formulate the neuron doctrine, that is the hypothesis that the functional unit of the brain is the neuron [16]. Since then, various experiments, observations and calculations with the help of technological advances permitted the scientists to have an acurate description of the neuron and its networks.

1.2 Brain modeling

As systems seen from outside, brains take inputs in the form of stimuli and give outputs in the form of logically coherent responses. Neurobiologists usually begin not with the whole brain but with the smallest functional unit of the brain. For many purposes this is the neuron [7]. The brain is composed of a great number of neurons, cells which consist of a collection of structures embedded in a watery substance called *cytoplasm* and bounded by a thin layer off a fatty material called the *membrane*. Each neuron has a nucleus embedded in the cytoplasm and the expanded region of the cytoplasm including the nucleus is the *cell* body or *soma*. From the soma extend one or more filaments of two types: the axon and the dendrite. These two types are distinguished by morphological characteristics and there is only one axon for each neuron, but a neuron may have several dendrites. The point of connection between the soma and the axon is called the axon hillock. The dendritic membrane forms contacts with the axon tips of other neurons, which are the *synapses* [10].

1.2.1 Microscopic aspect

In the microscopic approach the principal unit that scientists analyze is that of the neuron and its networks. In general the functional and structural properties of neurons and their local networks are known, so mathematical models have been developed to describe the activity of a single neuron, its axon and dendrites [7]. In the late 19th century, Bois-Reymond, Müller and von Helmholtz demonstrated that neurons were electrically excitable and that their activity affected the state of nearby neurons. The dendrites receive input from as many as 10^5 axons tips of other neurons, combine them and deliver what results to the initial segment of the axon as follows: Electrical charges produced at the synapses propagate to the soma and create a postsynaptic potential. If this potential exceeds a threshold value, typically a depolarisation of

10-15 mV, the neuron generates a brief electrical pulse that is called a spike or action potential at its axon hillock. The spikes traverse the axon and reach the synapses that transfer the information to another neuron [6]. It can be shown that at a resting nerve fibre a small electric potential between its inner and outer side is present. This potential is called the resting potential. The inner part of the nerve fibre is negatively charged as compared to the outer liquid. The difference potential is about 70 mV [10].

There are two major classes of neurons determined by the effect they produce on other neurons. Synaptic inputs that depolarize the neuron and increase its pulse rate are called excitatory as are the input neurons and the synapses, and synaptic inputs that decrease its pulse rate and hyperpolarize the neuron are called inhibitory. Most neurons receive inputs from both inhibitory and excitatory neurons but their output is either excitatory or inhibitory but not both [6]. Neurons are able to produce trains of individual spikes, by which information is exchanged between the neurons. Scientists believe that correlations between spike trains play an important role in brain activity [10]. Two kinds of approach are currently being undertaken to develop models that explain the brain behaviour. One approach rests in data from single neurons, which are believed to coordinate their firing patterns, so as to constitute sparsely connected neural nets and nerve cell assemblies. The other approach is directed toward understanding the formation of neural ensembles with state variables representing pulse and wave densities that are continuous in time and space [7]. This approach is called the mesoscopic approach or mean field theory and is the focus of this thesis.

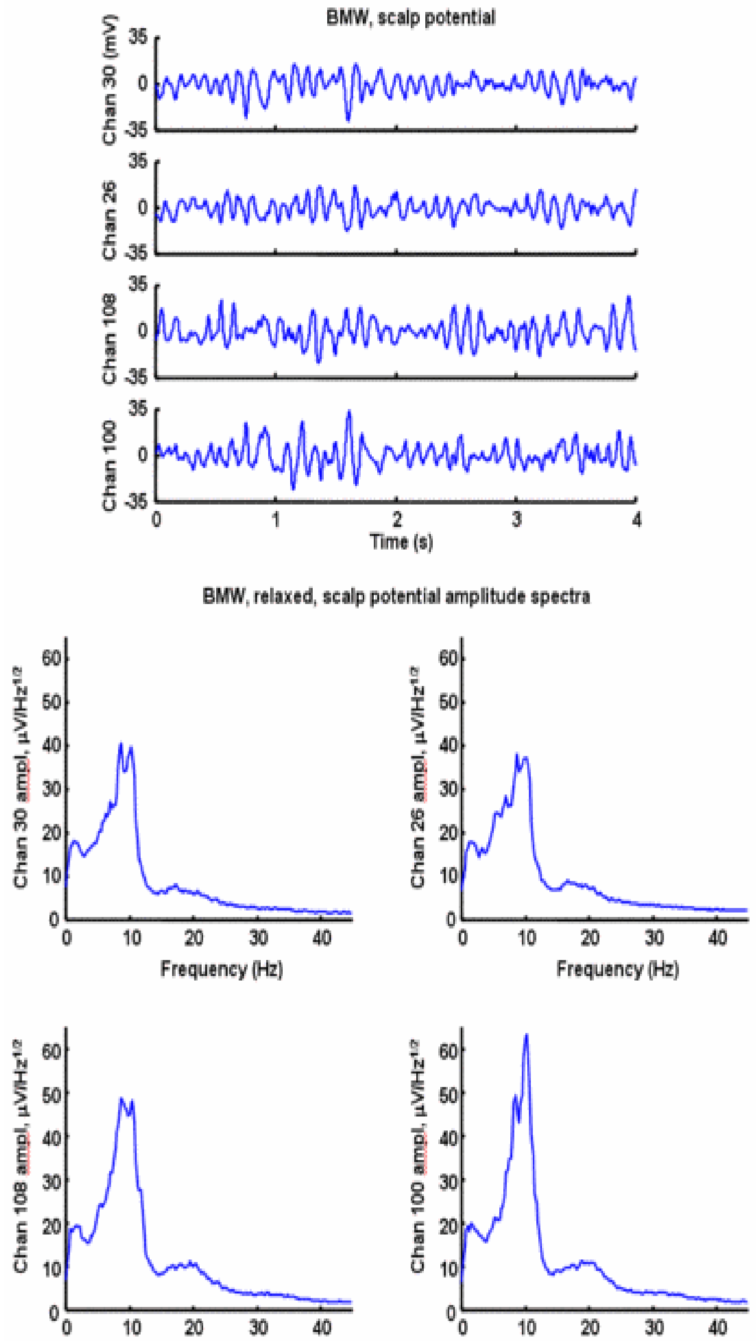
1.2.2 Mesoscopic approach and mean field models of the electroencephalogram

The pioneers in understanding how information is conveyed over long distances by action potentials were Hodgkin and Huxley [21]. In 1952 they presented a mathematical model for transmission of electrical charges between the axons of a squid, action potentials, and how they were initiated and propagated. Then Katz's work revealed how synapses transfer information from one neuron to another and to effector cells. Finally in 1972 Wilson and Cowan proposed a model that describes the dynamics between populations of excitatory and inhibitory neurons. Extensions of this model are widely used in neuronal modeling and one of this extension proposed by Liley, Cadush and Dafilis in 1999 is going to be the initial point in this thesis [3].

The mesoscopic approach in modeling the brain functions is closely related to the electroencephalogram, henceforth EEG. The EEG measures the potential difference between electrodes placed on the scalp. This difference of electrical activity reflects the summed activity of thousands or millions of neurons. The detected electrical activity by the scalp's EEG varies between 1-40 Hz. This activity has been divided into bands of frequency that have a characteristic spatial distribution over the scalp and are associated with different states of brain functions. A famous oscillation observed is the alpha rhythm whose frequency range is 8-13 Hz and emerges with the closing of the eyes and relaxation [20]. In figure 1.1 we can see how the EEG detects this kind of rhythm. Scientists now use some of these particular oscillations, alpha, beta and gamma rhythms, to make diagnostics on the brain's state. On the other hand open questions persist about how the alpha rhythm is created. One of the hypotheses, that we are going to explore in this thesis, is that the alpha rhythm is created by the inhibitory neuron population only.

In the mesoscopic approach cortical tissue is treated as a spatial continuum. This

Figure 1.1: (Top) Alpha rhythm recorded from a healthy relaxed subject with closed eyes using an electrode on the neck as reference. Four seconds of data are shown from four scalp locations. The amplitude is given in microvolts. This EEG was recorded at the Brain Sciences Institute in Melbourne. (Bottom) The corresponding amplitude spectra based on the full five minute record reveals dominant activity in the alpha (8-13 Hz) band. Reproduced from Nunez and Srinivasan (2006) [20].



approach is more suitable for the description of EEG as it relies on some form of spatial averaging by implicitly defining a spatial scale while the EEG is a spatial or population average that depends on the geometry of recording. The mean field models can be used to explain how local masses of neurons of the brain cortex can organize their activity when they are destabilized by microscopic sensory inputs. One of the key findings in support of this approach to neurodynamics is the value of the EEG as a means of estimating the magnitude of the mesoscopic state variable of neural populations. The definition of mesoscopic state variables requires consideration of the fact that the local mean fields that govern these states are created by synaptic interactions, in which each neuron transmits (in round numbers) to 10000 and receives from 10000 others. Because the dendritic current manifested in the EEG is formed by summation in the volume conductor of the local areas of cortex, it is the best available assay of the local mean field intensities of cortical populations. Moreover, the surface EEG is by far the better measure of the output of a cortical population, whereas the activity of its individual neurons is the better measure of the cortical response to its input [10].

1.3 The model and the simplification

As stated previously we start with the model presented in Liley, Cadush and Dafilis [3] as an extension of the Wilson and Cowan model. We simplify the model by setting the spatial derivatives to zero and neglecting the long-range cortical-cortical connections, as presented in van Veen and Liley [23]. The simplified model can be regarded as a model of the local mean-field potential, without direct coupling to the rest of the cortex. The mesoscopic EEG model presented in van Veen and Liley locally describes the cortical activity by the mean soma membrane potentials of the excitatory and the inhibitory neuron population, h_e and h_i respectively, along with the mean synaptic activities I_{ee},I_{ei},I_{ie} and I_{ii}, each modeling the interaction between two populations as indicated by the subscripts. The first two dynamical equations are

$$\begin{aligned}
\tau_e \dot{h}_e &= h_{er} - h_e + \frac{h_{eeq} - h_e}{|h_{eeq} - h_{er}|} I_{ee} + \frac{h_{ieq} - h_e}{|h_{ieq} - h_{er}|} I_{ie} \\
\tau_i \dot{h}_i &= h_{ir} - h_i + \frac{h_{eeq} - h_i}{|h_{eeq} - h_{ir}|} I_{ei} + \frac{h_{ieq} - h_i}{|h_{ieq} - h_{ir}|} I_{ii}
\end{aligned} \tag{1.1}$$

where h_{er} and h_{ir} are the resting potentials, h_{eeq} and h_{ieq} are the equilibrium potentials and τ_e and τ_i are the relaxation time scales. These equations describe the response of the mean soma membrane of excitatory and inhibitory neuronal populations as indicated by the subscripts to synaptic current. Now, the synaptic activity is modeled by the eight following equations considering the local feedforward and feedback excitatory (I_{ee}, I_{ei}) and inhibitory (I_{ie}, I_{ii}) synaptic activity.

$$\begin{aligned}
\ddot{I}_{ee} &+ 2a\dot{I}_{ee} + a^2 I_{ee} = Aae[N_{ee} S_e(h_e) + p_{ee}] \\
\ddot{I}_{ie} &+ 2b\dot{I}_{ie} + b^2 I_{ie} = Bbe N_{ie} S_i(h_i) \\
\ddot{I}_{ei} &+ 2a\dot{I}_{ei} + a^2 I_{ei} = Aae[N_{ei} S_e(h_e) + p_{ei}] \\
\ddot{I}_{ii} &+ 2b\dot{I}_{ii} + b^2 I_{ii} = Bbe N_{ii} S_i(h_i)
\end{aligned} \tag{1.2}$$

where A and B are the postsynaptic potential peak amplitudes, a and b the synaptic rate constants and e Euler's number. Now, excitatory (inhibitory) neurons receive a total of $N_{ee}(N_{ei})$ synapses from nearby excitatory neurons and $N_{ie}(N_{ii})$ synapses from nearby inhibitory neurons. The functions S_q convert the mean membrane potential of the neuron populations to an equivalent mean firing rate, and are given by

$$S_q(h_q) = m_q \left(1 + \exp(-\sqrt{2}(h_q - \theta_q)/s_q)\right)^{-1}$$

where $q = e, i$. In this system of equations the principal parameters are p_{ee} and p_{ei}, the excitatory input from distant excitatory cortical and subcortical neurons to excitatory or inhibitory neurons, according to the subscript. Choosing physiologically admissible parameters, these equations can reproduce the main features of spontaneous human EEG. In the study presented by van Veen and Liley [23], when p_{ei} is much larger than p_{ee} the only possible limit state is an equilibrium solution of the systems (1.1) and (1.2), which means that the mean soma potentials attain a certain equilibrium value. Then, when we increase the value of p_{ee}, a periodic solution appears at a certain frequency, which is the first detection of alpha rhythm. Further increase of p_{ee} leads to irregular behaviour of the mean soma membrane potentials in the alpha band.

Our study was motivated by the hypothesis that the alpha rhythm and the corresponding frequencies might be caused by the inhibitory neuron populations of the brain only. So from the system (1.1) and (1.2) we delete the equations and the terms which involve excitatory neurons to obtain

$$\begin{aligned} \tau_i \dot{h}_i &= h_{ir} - h_i + \frac{h_{ieq} - h_i}{|h_{ieq} - h_{ir}|} I_{ii} \\ \ddot{I}_{ii} + 2b\dot{I}_{ii} + b^2 I_{ii} &= BbeN_{ii} S_i(h_i). \end{aligned}$$

We first shift the membrane potential by h_{ir} and scale time and potential by τ_i and $|h_{ieq} - h_{ir}|$, respectively. This leads to

$$\begin{aligned} \dot{\tilde{h}}_i &= -\tilde{h}_i + (sign(h_{ieq} - h_{ir}) - \tilde{h}_i)\tilde{I}_{ii} \\ \ddot{\tilde{I}}_{ii} + 2\tilde{b}\dot{\tilde{I}}_{ii} + \tilde{b}^2 \tilde{I}_{ii} &= \frac{\tilde{t}_i^2}{|h_{ieq} - h_{ir}|} BbeN_{ii} S_i(|h_{ieq} - h_{ir}|\tilde{h}_i + h_{ir}) = \\ &= \tilde{B}\tilde{b}eN_{ii} \frac{\tilde{m}_i}{1 + \exp(-\sqrt{2}(\tilde{h}_i - \tilde{\theta}_i)/\tilde{s}_i)} \end{aligned}$$

where

$$\begin{aligned}
\tilde{h}_i &= \frac{h_i - h_r}{|h_{ieq} - h_{ir}|}, \qquad \tilde{I}_{ii} = \frac{I_{ii}}{|h_{ieq} - h_{ir}|}, \qquad \tilde{t} = \frac{t}{\tau_i} \\
\tilde{B} &= \frac{B}{|h_{ieq} - h_{ir}|}, \qquad \tilde{m}_i = \tau_i m_i, \qquad \tilde{\theta}_i = \frac{\theta_i - h_{ir}}{|h_{ieq} - h_{ir}|} \\
\tilde{s}_i &= \frac{s_i}{|h_{ieq} - h_{ir}|}, \qquad \tilde{b} = \tau_i b
\end{aligned}$$

Finally we introduce

$$x_1 = \tilde{h}_i, \qquad x_2 = (d/d\tilde{t} + \tilde{b})\tilde{I}_{ii}, \qquad x_3 = \tilde{I}_{ii}$$

which gives the first order system

$$\begin{aligned}
\dot{x}_1 &= -x_1 + (\sigma - x_1)x_3 + p_1 \\
\dot{x}_2 &= -\tilde{b}x_2 + \frac{\tilde{M}}{1 + \exp(-\sqrt{2}(x_1 - \tilde{\theta}_1)/\tilde{s}_1)} + p_2 \\
\dot{x}_3 &= \tilde{b}x_3 + x_2
\end{aligned} \tag{1.3}$$

where $\tilde{M} = \tilde{B}\tilde{b}eN_{ii}\tilde{m}_i$ and $\sigma = \pm 1$. The parameter p_2 is the inhibitory input to inhibitory neurons p_{ii} and we introduce the parameter p_1 to help us throughout our study of the reduced model. Without loss of generality, we can assume σ to be positive, because of the symmetry

$$(x_1, x_2, x_3, \sigma, p_1, p_2, b, \theta, s) \rightarrow (-x_1, x_2, x_3, -\sigma, -p_1, p_2, b, -\theta, -s).$$

Chapter 2

Dynamical systems

2.1 Introduction

A dynamical system is one whose state changes with time, usually described by a differential or a difference equation. These equations characterize the evolution of a system with respect to time, the parameters and the initial conditions. Examples of dynamical systems are the mathematical models for the swinging of a clock pendulum and atmospheric convection. Depending on the type of the differential equation, ordinary, partial, linear or nonlinear, we can solve analytically or use computational techniques to approximate the solutions. Solving a differential equation permits us to know the state of the system at any time in the future or in the past given a starting point in the state space. In general, however, interesting phenomena are modelled by differential equations that are impossible to solve. In these cases numerical methods provide solutions and their dependence on a particular initial point. Bifurcation analysis permits us to know the evolution of such solutions in a range of parameter values.

So, one of the considerations of dynamical systems theory is to find solutions of the system that do not change with respect to time called steady states or fixed points. Other important solutions are periodic solutions, that is solutions that repeat themselves after a certain amount of time. Then we are interested in finding the dependence of these solutions on small perturbations and on variation of the parameters. This part of the theory is called stability theory and deals with the asymptotic behaviour of nearby orbits of solutions. In particular, we seek the set of points, called the attractor, towards which the solutions of a dynamical system tend in positive time. Furthermore, bifurcation theory studies the change in the number, the type and the properties of solutions of dynamical systems with respect to changes made in the parameters.

2.2 Stability theory

We start by introducing basic concepts of stability theory using a fairly simple linear dynamical system:

$$\dot{x} = Ax, \qquad x \in \mathbb{R}^n \tag{2.1}$$

where A is an $n \times n$ matrix with constant coefficients. By a solution of (2.1) we mean a flow $\phi(t, x_0)$, depending on time t and the initial condition x_0. The origin is *stable* if any solution starting close to $\mathbf{0}$ at a given time stays close to it for all later times. It is *asymptotically stable* if nearby solutions converge to it when $t \to \infty$. By the theory of Ordinary Differential Equations, henceforth ODE, we know that solutions of (2.1) are given by $\phi(t, x_0) = e^{tA}x_0$ and that the topological properties of the flow depend on the eigenvalues of the matrix A. In particular, if all the eigenvalues have negative real part $\phi(t, x_0) \to \mathbf{0}$ and if at least one eigenvalue has positive real part $|\phi(t, x_0)| \to \infty$.

To proceed with more general theory, we consider a nonlinear vector field:

$$\dot{x} = f(x), \qquad x \in \mathbb{R}^n, \qquad x(0) = x_0 \tag{2.2}$$

Definition 2.1. A *fixed point* of (2.2) is a point $\bar{x} \in \mathbb{R}^n$ such that $f(\bar{x}) = 0$.

Recall also by the theory of ODE that for smooth functions $f(x)$, the solution to this problem is defined locally in some neighbourhood of the fixed point. So a local flow $\phi(t, x_0)$ is defined in analogy to the one defined in the linear case. To discuss stability of $\bar{x}$, we need to study nearby solutions, so it seems reasonable to study the associated linear system near $\bar{x}$:

$$\dot{\xi} = \mathbf{D}f(\bar{x})\xi, \qquad \xi \in \mathbb{R}^n \tag{2.3}$$

where $\mathbf{D}f = [\dfrac{\partial f_i}{\partial x_j}]$ is the Jacobian matrix of the first partial derivatives of the vector valued function f and $x = \bar{x} + \xi$, $|\xi| \ll 1$. Two very important results of dynamical systems theory, the Hartman-Grobman theorem and the stable manifold theorem of a fixed point, give us the relation between the solutions of the nonlinear and the associated linearised problem in a neighbourhood of a fixed point.

Theorem 2.1. (Hartman-Grobman) [8] *If $\mathbf{D}f(\bar{x})$ has no zero or purely imaginary eigenvalues then there is a homeomorphism h defined on some neighbourhood U of $\bar{x}$ in $\mathbb{R}^n$ locally taking orbits of the nonlinear flow $\phi(t, x_0)$ of (2.2), to those of the linear flow $e^{t\mathbf{D}f(\bar{x})}$ of (2.3). The homeomorphism preserves the sense of orbits and can also be chosen to preserve parametrization by time.*

In other words, the number of eigenvalues with positive and negative real parts determine the topological equivalence of the flow near $\bar{x}$. If there are eigenvalues with zero real parts, then the flow near $\bar{x}$ cannot be determined by linearization. When all the eigenvalues of the matrix $\mathbf{D}f$ have nonzero real parts, the corresponding fixed point is called an *hyperbolic fixed point.* If all of the eigenvalues of $\mathbf{D}f(\bar{x})$ have negative real parts, the point is asymptotically stable and is called a sink. When all of the eigenvalues of the matrix have positive real parts $\bar{x}$ is said to be a source and it is asymptotically unstable. Finally when some, but not all, of the eigenvalues have positive real parts, while the rest of them have negative real parts, the associated fixed point is called a saddle point. For further details on the classification of equilibrium points see [19]. Closed orbits which lead to the same saddle point in positive and negative time are called *homoclinic orbits*. Orbits that lead to different saddle points in positive and negative time are called *heteroclinic* orbits as defined in [11].

When at least one of the eigenvalues has a zero real part, the fixed point is called *nonhyperbolic*. The study of the cases with nonhyperbolic fixed points is called bifurcation theory and is going to be presented later on.

With this being said, we can represent $\mathbb{R}^n$ as the direct sum of the three subspaces E^s, E^u and E^c defined by $E^s = span\{\mathbf{p}_1, \mathbf{p}_2, ..., \mathbf{p}_s\}$, $E^u = span\{\mathbf{p}_{s+1}, \mathbf{p}_{s+2}, ..., \mathbf{p}_{s+u}\}$ and $E^c = span\{\mathbf{p}_{s+u+1}, \mathbf{p}_{s+u+2}, ..., \mathbf{p}_{s+u+c}\}$, where $\mathbf{p}_1, \mathbf{p}_2, ..., \mathbf{p}_s$ are the corresponding (generalised) eigenvectors corresponding to the eigenvalues of $\mathbf{D}f$ having negative real part, $\mathbf{p}_{s+1}, \mathbf{p}_{s+2}, ..., \mathbf{p}_{s+u}$ are the (generalised) eigenvectors corresponding to the eigenvalues of $\mathbf{D}f$ having positive real part and $\mathbf{p}_{s+u+1}, \mathbf{p}_{s+u+2}, ..., \mathbf{p}_{s+u+c}$ are the (generalised) eigenvectors corresponding to the eigenvalues of $\mathbf{D}f$ having zero real part.

These subspaces are called the *stable*, *unstable* and *center subspaces* respectively. The names reflect the fact that in linear systems the orbits starting in E^s decay to zero as $t \to \infty$, orbits starting in E^u become unbounded as $t \to \infty$ and orbits starting in E^c neither grow nor decay exponentially as $t \to \infty$. The stable manifold theorem explains the relation between the before mentioned subspaces of the linearised system and the ones of the initial nonlinear one.

Theorem 2.2. (Stable Manifold Theorem) [8] *Suppose that $\dot{x} = f(x)$ has a hyperbolic fixed point $\bar{x}$. Then there exist local stable and unstable manifolds $W^s_{loc}(\bar{x})$, $W^u_{loc}(\bar{x})$*

of the same dimension s and u as those of the eigenspaces E^s and E^u of (2.3), and tangent to E^s, E^u at $\bar{x}$. $W^s_{loc}(\bar{x})$, $W^u_{loc}(\bar{x})$ are as smooth as f.

The manifolds are invariant and the solutions starting on these manifolds tend to the fixed point when $t \to \infty$ and $t \to -\infty$ respectively.

Before we continue, we define another important class of solutions of (2.2):

Definition 2.2. A solution of (2.2) is said to be *periodic of period T* if there exists $T > 0$ such that $x(t) = x(t + T)$ for all $t \in \mathbb{R}$. By the period of an orbit we mean the smallest possible $T > 0$ such that the definition holds.

2.3 Bifurcation theory

The word "bifurcation" is used to indicate a qualitative change in the features of a system, such as the number and type of solutions, under the variation of one or more parameters on which the considered system depends. Locations in the phase and parameter space where these changes occur, are called bifurcation points. A bifurcation that requires at least m control parameters to occur is called a codimension-m bifurcation. We will start by discussing briefly codimension-one bifurcations.

We will consider a one-dimensional vector field which depends on a single parameter

$$\dot{x} = f(x, \mu), \qquad x \in \mathbb{R}, \qquad \mu \in \mathbb{R} \tag{2.4}$$

and suppose that it has a fixed point at $(x, \mu) = (0, 0)$. Following the theory of the previous section, we have to linearise f near $(0, 0)$ to determine the stability of the fixed point. The linear vector is given by

$$\dot{\xi} = D_x f(0, 0)\xi, \qquad \xi \in \mathbb{R}.$$

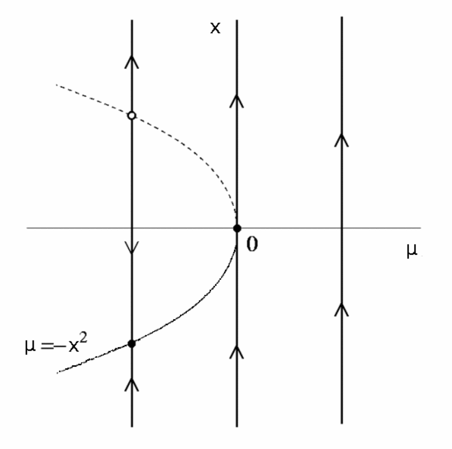
If the fixed point is hyperbolic, we know that its stability is determined by the values of the real parts of the eigenvalues of $\mathbf{D}f(\bar{x})$ and since they are all with values far from zero, changing slightly μ will not change the nature of stability of the fixed point. That is why we are concerned about cases where the fixed point is nonhyperbolic, that is when Df_x has eigenvalues with real part equal to zero. So in general, we consider that $f(0,0) = 0$ and $\frac{\partial f}{\partial x}(0,0) = 0$, that is one zero eigenvalue and one with nonzero real part. Further characterization of this type of bifurcation results from the geometry of the curve of fixed points in the μ-x plane in the neighbourhood of the fixed point. Further discussion on how these conditions are derived, one can find in the books by Guckenheimer and Holmes [8] and Wiggins [24]. We say that (2.4) undergoes a *saddle-node* bifurcation if $\frac{\partial f}{\partial x}(0,0) = 0$ and $\frac{\partial^2 f}{\partial x^2}(0,0) \neq 0$. Geometrically that means that as we vary μ a stable and an unstable solution of the system coincide on the bifurcation point and disappear. Remark that for certain values of the parameter there are no equilibrium points.

In figure 2.1 we see how we represent this in what we call a bifurcation diagram. In this (μ, x) plane, the continuous line represents the curve of stable solutions whereas the dotted line, the curve of unstable solutions. As we change μ the two solutions come closer till they coincide and disappear.

Other types of bifurcation occur involving systems that have a zero eigenvalue at the bifurcation point. In one case we have two equilibrium points for all parameter values, that exchange stability at the bifurcation point called a transcritical bifurcation. The other case involves the exchange of stability of a solution and the creation of a pair of solutions appearing only on one side of the bifurcation. We do not get into details on these bifurcations because they occur in symmetrical dynamical systems.

Now, let us consider a little more complicated case, to define the next most simple way that a fixed point can be nonhyperbolic. Consider

Figure 2.1: Saddle-node bifurcation in the $\dot{x} = \mu + x^2$ system. Figure reproduced from Scholarpedia [15].



$$\dot{y} = g(y, \mu), \qquad y \in \mathbb{R}^2, \mu \in \mathbb{R}, \tag{2.5}$$

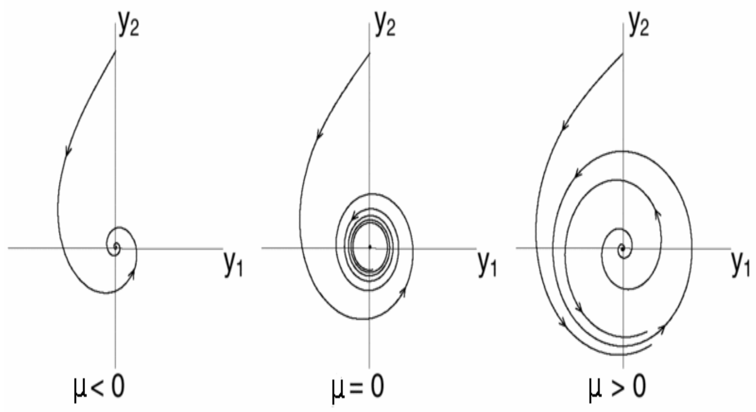
and suppose that it has a fixed point at $(y, \mu) = (0, 0)$. We linearise g near $(0, 0)$ to determine the stability and how it changes when we change μ. So, we consider

$$\dot{\xi} = D_y g(0, 0)\xi, \qquad \xi \in \mathbb{R}^n.$$

A Hopf bifurcation, also called Andronov-Hopf bifurcation, is said to occur at $(0, 0)$ if $D_y g$ has a pair of purely imaginary eigenvalues $\pm i\omega$ and there is a transversal or nonzero speed crossing of the imaginary axis, hence called a *transversality condition.* The transversality condition can be formulated by $\frac{d\lambda}{d\mu} \neq 0$ at $\mu = 0$ where $\lambda \pm i\omega$ is the pair of imaginary eigenvalues for $\mu \simeq 0$. When the above two conditions are satisfied, a periodic solution of period $\frac{2\pi}{\omega}$ is born at $(0, 0)$.

Definition 2.3. An Andronov-Hopf bifurcation can be supercritical or subcritical depending on the stability of the periodic solution that is born. When the periodic solution that is created is stable then the bifurcation is called supercritical and subcritical when the periodic solution is unstable.

Figure 2.2: Supercritical Andronov-Hopf bifurcation in the plane. Figure reproduced from Scholarpedia [14].



In the bifurcation diagram (2.2), the solutions now are represented in the plane since we are working in a two-dimensional system. We consider the variation of the parameter μ from the negative to the positive values. The bifurcation is supercritical since the solution that is created is stable.

2.4 Simplification of dynamical systems

2.4.1 Center manifold reduction

The center manifold theorem provides a means for systematically reducing the dimension of the state spaces which need to be considered when analysing bifurcations of a given type. A center manifold is an invariant manifold tangent to the center eigenspace. The local dynamical behaviour "transverse" to the center manifold is relatively simple, since it is controlled by the exponentially contracting or expanding flows in the local stable or unstable manifolds. We cannot define the center manifold in terms of the asymptotic behaviour of solutions in it, since solutions in the center manifold can be expanding or contracting. In order to define them we have to analyze higher order terms of the system. The center manifold reduction is used to reduce the order of the dynamical system first, and then the method of the normal forms is used to simplify the (nonlinear) structure of the reduced system.

A center manifold need not be unique and is generally less smooth than the vector field.

Theorem 2.3. (Center Manifold Theorem) [8] *Let f be a C^r vector field on $\mathbb{R}^r$ vanishing at the origin ($f(0) = 0$) and let $A = Df(0)$. Divide the spectrum of A into three parts, σ_s, σ_c and σ_u with*

$$Re(\lambda) \begin{cases} < 0 & \text{if } \lambda \in \sigma_s, \\ = 0 & \text{if } \lambda \in \sigma_c, \\ > 0 & \text{if } \lambda \in \sigma_u. \end{cases}$$

Let the (generalized) eigenspaces of σ_s, σ_c and σ_u be E^s,E^c, and E^u, respectively. Then there exist C^r stable and unstable invariant manifolds W^u and W^s tangent to E^u and E^s at 0 and a C^{r-1} center manifold W^c tangent to E^c at 0. The manifolds W^u, W^s and W^c are all invariant under the flow of f. The stable and unstable manifolds are unique, but W^c need not be.

Now consider the system

$$x' = Ax + f(x, y), \qquad y' = By + g(x, y), \qquad (x, y) \in \mathbb{R}^n \times \mathbb{R}^m \tag{2.6}$$

where all the eigenvalues of the matrix A have zero real parts and all the eigenvalues of the matrix B have non zero real parts. The functions f and g are sufficiently smooth, they contain elements of $O(|x|^r|y|^k)$, $O(|x|^s)$ and $O(|y|^p)$ where $r, k \geq 1$ and $s, p \geq 2$ and they satisfy the following conditions:

$$f(0, 0) = 0, \qquad Df(0, 0) = \mathbf{0}, \qquad g(0, 0) = 0, \qquad Dg(0, 0) = \mathbf{0}$$

where Df is the Jacobian matrix of f and Dg the Jacobian matrix of g. The general theory states that there exists a center manifold $y = h(x)$ for (2.6) and that the equation on the center manifold

$$u' = Au + f(u, h(u)), \qquad u \in \mathbb{R}^n$$

near $u = 0$ determines the dynamics of (2.6) near $(x, y) = (0, 0)$ [1]. If we replace $y = h(x)$ into the second equation of the system (2.6) and using the chain rule, we obtain

$$Dh(x)[Ax + f(x, h(x))] - Bh(x) - g(x, h(x)) = 0.$$

This is a partial differential equation that probably is more difficult to solve than our initial problem but the theory states that close to $(0, 0)$ we can approximate the center manifold as a Taylor series up to its degree of smoothness and up to any desired degree of accuracy depending on the bifurcation that we are studying and the smoothness of the vectorfield.

2.4.2 Normal forms

Assume that the center manifold theorem has been applied and we consider a flow restricted on the center manifold. The next step is to simplify the flow, eliminating the nonlinear parts, in order to proceed with the bifurcation analysis. The resulting simplified vector fields are called *normal forms*. The idea is to introduce successive coordinate changes in order to simplify a general vector field.

So, consider again the nonlinear vector field (2.2) where f is $\mathbf{C}^r$, with r to be specified as we go along. Suppose (2.2) has a fixed point at $\bar{x} = 0$. We first divide the system to its linear and nonlinear part and write (2.2) as follows

$$\dot{x} = Df(0)x + \bar{f}(x), \tag{2.7}$$

where $\bar{f}(x) \equiv f(x) - Df(0)x$. Then under the transformation $x = Ty$, where T is the matrix that transforms the matrix $Df(0)$ into Jordan canonical form, (2.7) becomes

$$\dot{y} = T^{-1}Df(0)Ty + T^{-1}\bar{f}(Ty). \tag{2.8}$$

Denoting the Jordan canonical form of $Df(0)$ by J, we have $J \equiv T^{-1}Df(0)T$, and we define $F(y) \equiv T^{-1}\bar{f}(Ty)$ so that (2.8) is alternately written as

$$\dot{y} = Jy + F(y), \qquad y \in \mathbb{R}^n. \tag{2.9}$$

Now, we proceed with the task of simplifying the nonlinear part, $F(y)$. We Taylor expand $F(y)$, so that (2.9) becomes

$$\dot{y} = Jy + F_2(y) + F_3(y) + \cdots + F_{r-1}(y) + O(|y|^r), \tag{2.10}$$

where F_i represent the i^{th} terms in the Taylor expansion of $F(y)$. We next introduce the coordinate transformation $y = z + h_2(z)$, where $h_2(z)$ is second order in z and (2.10) becomes

$$\begin{aligned} \dot{y} = (\mathbb{I} + Dh_2(z))\dot{z} = Jz + Jh_2(z) + & \\ + F_2(z + h_2(z)) + F_3(z + h_2(z)) + \cdots + F_{r-1}(z + h_2(z)) + O(|z|^r), & \end{aligned} \tag{2.11}$$

where $\mathbb{I}$ is the $n \times n$ identity matrix. Note that each term $F_k(z + h_2(z)), 2 \leq k \leq r - 1$ can be written as $F_k(z) + O(|z|^{k+1}) + \cdots + O(|z|^{2k})$, so that (2.11) becomes

$$\begin{aligned} (\mathbb{I} + Dh_2(z))\dot{z} = & \\ = Jz + Jh_2(z) + F_2(z) + \tilde{F}_3(z) + \cdots + \tilde{F}_{r-1}(z) + O(|z|^r), & \end{aligned} \tag{2.12}$$

where the terms $\tilde{F}_k(z)$ represent the $O(|z|^k)$ terms, modified by the transformation.

Now, for z sufficiently small, $(\mathbb{I} + Dh_2(z))^{-1}$ exists and can be represented in a series expansion as follows

$$(\mathbb{I} + Dh_2(z))^{-1} = \mathbb{I} - Dh_2(z) + O(|z|^2) \quad (2.13)$$

Substituting (2.13) in (2.12) gives

$$\dot{z} = Jz + Jh_2(z) - Dh_2(z)Jz + F_2(z) + \tilde{F}_3(z) + \cdots + \tilde{F}_{r-1}(z) + O(|z|^r) \quad (2.14)$$

Recall that the goal of this exercise was to simplify the nonlinear part of the vector field (2.9). So, we can choose $h_2(z)$ in order to eliminate $F_2(z)$, which would mean choose $h_2(z)$ such that

$$Dh_2(z)Jz - Jh_2(z) = F_2(z). \quad (2.15)$$

First, it should be clear that $h_2(z)$ and $F_2(z)$ can be viewed as elements of H_2, where H_k is the linear vector space formed by the set of all vector-valued monomials of degree k. Consequently the map $h_2(z) \longmapsto Dh_2(z)Jz - Jh_2(z)$ is a linear map of H_2 into H_2. So, solving (2.15) is like solving $Ax = b$ from linear algebra. Thus, (2.14) can be simplified to

$$\dot{z} = Jz + F_2^r(z) + \tilde{F}_3(z) + \cdots + \tilde{F}_{r-1}(z) + O(|z|^r)$$

where F_2^r are the $O(|z|^2)$ terms that are in the space complementary to $L_J(h_2(z))$, where $L_J(h_2(z)) \equiv -(Dh_2(z)Jz - Jh_2(z))$. So, if $L_J(H_2) = H_2$, then all second-order terms can be eliminated. We repeat the same method to eliminate the $O(|z|^3)$

terms and the procedure can be iterated up until the desired order. We generalize the procedure to obtain the following *normal form theorem*.

Theorem 2.4. (Normal Form Theorem) [24] *By a sequence of analytic coordinate changes (2.9) can be transformed into*

$$\dot{z} = Jz + F_2^r(z) + \cdots + F_{r-1}^r(z) + O(|z|^r), \tag{2.16}$$

where $F_k^r(z) \in G_k$*,* $2 \leq k \leq r-1$ *and* G_k *is a space complementary to* $L_J(H_k)$*. Equation (2.16) is said to be in normal form.*

Some normal forms resulting from the reduction on the center manifold cannot exhibit all possible bifurcations of the equilibria of the initial system. In order to explore all possible behaviours close to the original system, we add a finite number of small parameters to the normal form. If the original parameters satisfy all transversality conditions and the new ones do as well, then there exists an one-to-one map between the two. This procedure is called unfolding, an idea that is used in general to examine characteristics of a system that initially are neglected [18]. The number of the unfolding parameters is always equal to the codimension of the bifurcation.

Now suppose that the vector field (2.2) depends on a parameter μ and that the equilibrium undergoes a saddle-node bifurcation at $\mu = 0$, then the restriction of (2.2) in a neighbourhood of $\mu = 0$ to the one-dimensional center manifold is locally topologically equivalent to the normal form

$$\dot{w} = \beta_1 + aw^2$$

with $a \neq 0$. Observe that the normal form predicts the collision of two equilibria when the parameter β_1 passes zero and that the sign of the coefficient a determines on which side of the w-axis the equilibria exist.

If the equilibrium undergoes a Hopf bifurcation at $\mu = 0$, the normal form of the restriction of (2.5) to the two-dimensional center manifold has the form

$$\begin{aligned}\dot{w}_1 &= \beta w_1 - w_2 \pm (w_1 + w_2)^2 w_1 \\ \dot{w}_2 &= w_1 + \beta w_2 \pm (w_1 + w_2)^2 w_2\end{aligned}$$

The system undergoes a Hopf bifurcation at $\beta = 0$. Depending on the sign in front of the cubic terms of the normal form we have two kinds of Hopf bifurcations. The system has always an equilibrium point at the origin which is stable for $\beta < 0$ and unstable for $\beta > 0$. Now, when the sign in front of the cubic terms is positive there is an unstable periodic solution which disappears when β crosses zero from negative to positive values and the equilibrium solution at the origin is unstable at the critical parameter value. This bifurcation is called subcritical Hopf bifurcation. When the sign is negative, a stable periodic solution appears when β crosses zero from negative to positive values and the equilibrium solution is stable at the critical parameter value. This bifurcation is called supercritical.

Note that for systems that depend on a parameter vector μ, the procedure is the same for an extended system. For the center manifold reduction we have a function $y = h(x, \mu)$ and for the normal form calculations we seek coefficients that depend on the vector of parameters μ. However this can lead to computations involving thousands of coefficients of the multivariate Taylor expansions.

Example 2.1. Consider

$$\begin{aligned}\dot{x} &= x^2 + y \\ \dot{y} &= x - y + \alpha\end{aligned}$$

At $\bar{\alpha} = \frac{1}{4}$ we have a fixed point at $(\bar{x}, \bar{y}) = (-\frac{1}{2}, -\frac{1}{4})$. First we translate this fixed point to the origin by puting $x = -\frac{1}{2} + \tilde{x}$, $y = -\frac{1}{4} + \tilde{y}$ and $\alpha = \frac{1}{4} + \tilde{a}$ to obtain:

$$
\begin{aligned}
\dot{\tilde{x}} &= (\frac{1}{2} + \tilde{x})^2 - \frac{1}{4} + \tilde{y} = \tilde{x}^2 + \tilde{y} - \tilde{x} \\
\dot{\tilde{y}} &= -\frac{1}{2} + \tilde{x} + \frac{1}{4} - \tilde{y} + \frac{1}{4} + \tilde{\alpha} = \tilde{x} - \tilde{y} + \tilde{\alpha}
\end{aligned}
$$

We can drop the tildes, to work with the following system of equations

$$
\begin{aligned}
\dot{x} &= x^2 + y - x \\
\dot{y} &= x - y + \alpha
\end{aligned} \tag{2.17}
$$

which has a fixed point at $(0, 0)$ with $\alpha = 0$. The conditions for a general system to undergo a saddle-node bifurcation are that there is a unique curve of solutions that passes through $(0, 0)$ at $\alpha = 0$ and that the curve of solutions lies locally on one side of $\alpha = 0$ on the α-(x, y) space. It is trivial to see that the curve of solutions is uniquely defined by $(x, y)^T = (\pm\sqrt{-\alpha}, \pm\sqrt{-\alpha} - \alpha)^T$ only for negative values of α.

Now, we linearise this system about the critical fixed point and we calculate the eigenvalues and the eigenvectors of the Jacobian matrix. We obtain $\lambda_1 = 0$ and $\lambda_2 = -2$ with corresponding eigenvectors $(1, 1)$ and $(-1, 1)$. We introduce the following transformation $x = Tz$ where T is the matrix whose columns are the eigenvectors, we can write the system as follows:

$$
\dot{z} = \begin{pmatrix} ! & \dot{z}_1 \\ & \dot{z}_2 \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ 0 & -2 \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} + \begin{pmatrix} \frac{1}{2}(z_1 - z_2)^2 \\ -\frac{1}{2}(z_1 + z_2)^2 \end{pmatrix}
$$

By the center manifold theorem, there exists a center manifold for (2.17) which can locally be represented as $z_2 = h(z_1)$ about the fixed point. We are going to compute this manifold in Example 3.1.

2.5 Codimension-2 bifurcations

In the previous sections we studied equilibrium points and the changes on their topological properties as we vary one parameter of the system. As previously mentioned the codimension of a bifurcation is the number of parameters that have to be varied for the bifurcation to occur, so the bifurcations that we have seen up until now are all codimension-one bifurcations. We can learn many things by studying codimension-two bifurcations. In many cases interesting dynamics depend on more that one parameter. So, if we allow two parameters to vary, we take in account codimension-two bifurcation points which are points in the two-parameter plane where several curves of codimension-one bifurcations intersect transversally or tangentially. A codimension-two bifurcation can be detected along a curve of codimension-one bifurcation point as the change in the eigenvalues structure of the Jacobian matrix of the system or as the vanishing of a coefficient of the corresponding normal form of the system reduced on the center manifold. In general consider

$$\dot{x} = f(x, \mu) \qquad x \in \mathbb{R}^n, \mu \in \mathbb{R}^m, \tag{2.18}$$

where f is smooth.

2.5.1 The double zero eigenvalue

The first case that we will study is detected when the number of eigenvalues of the Jacobian matrix that are zero becomes two. This case, the double zero eigenvalue, was studied simultaneously and independently by Bogdanov and Takens [11] and is the case for which the theory is the most complete. The Bogdanov-Takens, henceforth, BT bifurcation occurs in systems whose Jacobian matrix can be transformed to

$$\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}.$$

Assume that at $\mu = 0$ the system (2.18) has a critical point $(x_1, x_2) = (0, 0)$ and that the Jacobian matrix evaluated at the critical values has a zero eigenvalue of multiplicity two, $\lambda_{1,2} = 0$. As discussed in [8], the normal form of this problem can be written as follows

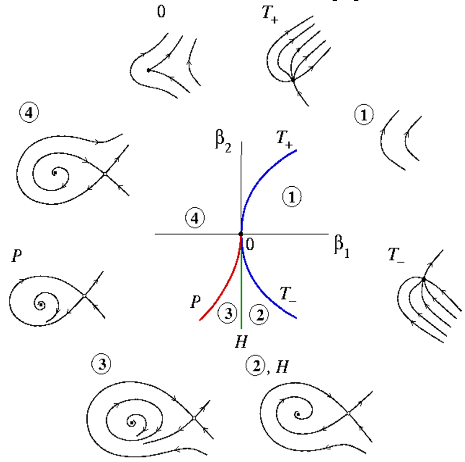
$$\begin{aligned} \dot{x_1} &= x_2 \\ \dot{x_2} &= a_2 x_1^2 + b_2 x_1 x_2 \end{aligned} \qquad (2.19)$$

Assuming that $a_2 b_2 \neq 0$ we proceed to the unfolding of this degenerate vector field to obtain

$$\begin{aligned} \dot{y_1} &= y_2 \\ \dot{y_2} &= \beta_1 + \beta_2 y_1 + y_1^2 \pm y_1 y_2. \end{aligned} \qquad (2.20)$$

For parameters near the critical point, we have two equilibrium points, a saddle and a non-saddle one which collide in a saddle-node bifurcation. Then the non-saddle point undergoes a Hopf bifurcation and a period orbit is created. The orbit homoclinic to the saddle point exists in some parameter range and then vanishes via a saddle homoclinic bifurcation as illustrated in the diagram 2.3.

Figure 2.3: Bogdanov-Takens bifurcation in planar system: $\dot{y_1} = y_2$, $\dot{y_2} = \beta_1 + \beta_2 y_1 + y_1^2 - y_1 y_2$. Figure reproduced from Scholarpedia [9].



2.5.2 Fold-Hopf bifurcation

The second case is detected again by a change of the eigenspace of the Jacobian matrix. This time we have one zero eigenvalue and a pair of purely imaginary eigenvalues. So, in this case, the fold-Hopf, henceforth FH, bifurcation occurs when the linear part of the Jacobian matrix can be transformed to

$$\begin{pmatrix} 0 & -\omega & 0 \\ \omega & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

Later on we will prove that this case is not possible in the model that we analyse in this thesis.

2.6 Codimension-3 bifurcation

Codimension-3 bifurcations occur when three degeneracy conditions hold simultaneously. These conditions can be three zero eigenvalues of the Jacobian matrix or two eigenvalues equal to zero and one of the coefficients of the normal form also. This is called the degenerate BT case.

2.6.1 Degenerate Bogdanov-Takens

In this thesis we are going to explore the case where the a_2 coefficient of the normal form (2.19) is equal to zero. If $a_2 = 0$, a generic three-parameter unfolding of (2.19) is locally topologically equivalent to

$$\begin{aligned} \dot{\xi_0} &= \xi_1, \\ \dot{\xi_1} &= \beta_1 + \beta_2\xi_0 + \beta_3\xi_1 + a_3\xi_0^3 + b_2\xi_0\xi_1 + b_3'\xi_0^2\xi_1. \end{aligned} \tag{2.21}$$

This bifurcation is called a degenerate BT bifurcation with a double equilibrium or cusp point. Actually in this case the BT point coincides with the cusp point, that is the point where two saddle-node curves meet tangentially. For an example of the bifurcation analysis of this case one can see also Baer, Kooi, Kuznetsov and Thieme [22]. Furthermore, assuming that $b_2 \geq 0$, we can distinguish three cases topologically different according to the sign of a_3, b_3' and of the expression $b_2^2 + 8a_3$. This last condition determines the stability of the equilibrium and gives respectively the saddle, focus and elliptic case as explained in [4].

Chapter 3

Practical computation of normal forms on center manifolds

3.1 Introduction

As we discussed previously Taylor expansions are used to explicitly compute equations of a system restricted to the center manifold up to a desired degree. These equations can then be normalized to eliminate as many nonlinear parts as possible. Recall also that this algorithm requires a linear transformation that puts the linear part of the system into Jordan form. Many authors have published computations of normal forms of two-dimensional systems up to fifth order. In addition there exist algorithms that allow these coefficients to be computed up to an arbitrary order using symbolic manipulation software.

The method that will be present below was initially developed by Coulet and Spiegel in [2] and then applied to all codimension-two bifurcations of equilibria of ODE's in a paper by Kuznetsov [12]. The method was used again in a paper by Kuznetsov that gave explicit computational formulas for normal forms on center manifolds at degenerate BT bifurcations up to fourth order in n-dimensional systems [13].

In this algorithm there is no preliminary linear transformation performed and the approximation of the center manifold and the normalization are combined using only critical (generalised) eigenvectors of the Jacobian matrix and its transpose.

3.2 The method

Consider (2.18) and suppose it has an equilibrium at the origin where $\mu = 0$. Write

$$\dot{x} = F(x) = f(x, 0), x \in \mathbb{R}^n \tag{3.1}$$

with

$$F(x) = Ax + \frac{1}{2}B(x,x) + \frac{1}{6}C(x,x,x) + \frac{1}{24}D(x,x,x,x) + \frac{1}{120}E(x,x,x,x,x) + O(\|x\|^6),$$

where $A = f_x(0,0)$ has n_c eigenvalues with zero real part and

$$\begin{aligned}
B_i(x,y) &= \sum_{j,k=1}^{n} \left.\frac{\partial^2 F_i(\xi)}{\partial \xi_j \partial \xi_k}\right|_{\xi=0} x_j y_k \\
C_i(x,y,z) &= \sum_{j,k,l=1}^{n} \left.\frac{\partial^3 F_i(\xi)}{\partial \xi_j \partial \xi_k \partial \xi_l}\right|_{\xi=0} x_j y_k z_l \\
D_i(x,y,z,v) &= \sum_{j,k,l,m=1}^{n} \left.\frac{\partial^4 F_i(\xi)}{\partial \xi_j \partial \xi_k \partial \xi_l \partial \xi_m}\right|_{\xi=0} x_j y_k z_l v_m \\
E_i(x,y,z,v,w) &= \sum_{j,k,l,m,s=1}^{n} \left.\frac{\partial^5 F_i(\xi)}{\partial \xi_j \partial \xi_k \partial \xi_l \partial \xi_m \partial \xi_s}\right|_{\xi=0} x_j y_k z_l v_m w_s
\end{aligned}$$

for $i = 1, 2, \ldots, n$. Note that the multilinear terms now called B_i, C_i, D_i and E_i were denoted F_i in the section describing the computation of normal forms. Now restrict the system to its n_c dimensional center manifold parametrized by $w \in \mathbb{R}^{n_c}$

$$x = H(w), \qquad H : \mathbb{R}^{n_c} \to \mathbb{R}^n. \tag{3.2}$$

The restricted equation can be written as

$$\dot{w} = G(w), \qquad G : \mathbb{R}^{n_c} \to \mathbb{R}^{n_c}. \tag{3.3}$$

Substitution of (3.2) and (3.3) into (3.1) gives the following homological equation

$$H_w(w)G(w) = F(H(w)). \tag{3.4}$$

Now expand the functions G and H in (3.4) into Taylor series

$$G(w) = \sum_{|\nu|\geq 1} \frac{1}{\nu!} g_\nu w^\nu, \qquad H(w) = \sum_{|\nu|\geq 1} \frac{1}{\nu!} h_\nu w^\nu,$$

where ν is a multivariable component and assume that the equation (3.3) is put into normal form up to a certain order. Equating the coefficients of equal order terms of the left and right hand side of (3.4), we find g_ν and h_ν, the coefficients of the normal form and those of the Taylor expansion for $H(w)$ respectively. Collecting the coefficients of the w^n-terms in (3.4) gives a linear system for the coefficient h_ν,

$$Ah_\nu = R_\nu. \tag{3.5}$$

Here the matrix A is the Jacobian matrix of F, while R_ν depends on the coefficients of G and H of order less or equal to $|\nu|$, as well on the corresponding terms of the Taylor expansion for F. For example, for the saddle-node case, define q and p such that

$$Aq = 0, \qquad \bar{A}^T p = 0, \qquad \langle p, q \rangle = 1 \tag{3.6}$$

the null-vectors of A and the adjoint matrix $\bar{A}^T$ respectively. Assume that R_ν involves only known quantities. System (3.5) has a solution, if and only if Fredholm's solvability condition $\langle p, R_\nu \rangle = 0$ holds.

In particular, when R_ν depends on the unknown coefficient g_ν of the normal form, A is singular and the above solvability condition gives the expression for g_ν. On the other hand, the unique solution h_ν to (3.5) satisfying $\langle p, h_\nu \rangle = 0$ can be obtained by solving the following non-singular $(n+1)$-dimensional system.

$$\begin{pmatrix} A & q \\ \bar{p}^T & 0 \end{pmatrix} \begin{pmatrix} h_\nu \\ s \end{pmatrix} = \begin{pmatrix} R_\nu \\ 0 \end{pmatrix}. \tag{3.7}$$

Actually we write $h_\nu = A^+ R_\nu$.

Then we have $H(w) = wq + \frac{1}{2}h_2 w^2 + O(|w|^3)$, $\dot{w} = aw^2 + O(|w|^3)$, $w \in \mathbb{R}$ and

$$F(H(w)) = A(wq+\frac{1}{2}h_2w^2)+\frac{1}{2}B(wq+\frac{1}{2}h_2w^2, wq+\frac{1}{2}h_2w^2) = \frac{1}{2}Ah_2w^2+\frac{1}{2}w^2B(q,q).$$

So the homological equation is

$$aqw^2 = \frac{1}{2}(Ah_2 + B(q,q))w^2$$

So, $Ah_2 = -B(q,q) + 2aq$ and by the solvability condition

$$\langle p, -B(q,q) + 2aq \rangle = -\langle p, B(q,q) \rangle + 2a\langle p, q \rangle = 0$$

and we can find

$$a = \frac{1}{2}\langle p, B(q,q) \rangle.$$

Example 3.1. Recall example 2.1

In this case we have $p = (1,0)^T$, $q = (1,0)^T$ the null vectors,

$$A = \begin{pmatrix} 0 & 0 \\ 0 & -2 \end{pmatrix}, \qquad \dot{z} = Az + \frac{1}{2}\begin{pmatrix} (z_1 - z_2)^2 \\ -(z_1 + z_2)^2 \end{pmatrix}$$

$z = H(w) = qw + h_2 w^2 + O(|w|^3)$ and $\dot{w} = aw^2 + O(|w|^3)$.

So the homological equation becomes

$$\begin{aligned} H_w \dot{w} &= F(H(w)) \\ (q + h_2 w)aw^2 &= A(qw + \frac{1}{2}h_2 w^2) + \frac{1}{2}B(H(w), H(w)) \end{aligned}$$

So, considering the w^2-coefficients, we get the following equation $aq = \frac{1}{2}Ah_2 + \frac{1}{2}B(q,q)$ and with the solvability condition we obtain $2a\langle p, q\rangle - \langle p, B(q,q)\rangle = 0$ and $a = \frac{1}{2}\langle p, B(q,q)\rangle = \frac{1}{2}\langle (1,0), (-1,0)\rangle = -\frac{1}{2}$.

3.3 Bogdanov-Takens

To apply the method for the BT case, we need to keep in mind that we now have two parameters and a double zero eigenvalue, so there exist two linearly independent (generalised) eigenvectors, $q_{0,1} \in \mathbb{R}^n$, such that $Aq_0 = 0$, $Aq_1 = q_0$ and two similar vectors $p_{1,0} \in \mathbb{R}^n$ of the transposed matrix A^T such that $A^T p_1 = 0$ and $A^T p_0 = p_1$. We can select these vectors to satisfy $\langle q_0, p_0\rangle = \langle q_1, p_1\rangle = 1$ and $\langle q_1, p_0\rangle = \langle q_0, p_1\rangle = 0$. Now the homological equation has the form

$$H_{w_0}\dot{w}_0 + H_{w_1}\dot{w}_1 = F(H(w_0, w_1)), \tag{3.8}$$

where $H(w_0, w_1) = w_0 q_0 + w_1 q_1 + \frac{1}{2}h_{20}w_0^2 + h_{11}w_0 w_1 + \frac{1}{2}h_{02}w_1^2 + O(\|(w_0, w_1)\|)^3$, with $h_{jk} \in \mathbb{R}^n$, and the corresponding normal form

$$\begin{aligned}\dot{w}_0 &= w_1 \\ \dot{w}_1 &= aw_0^2 + bw_0w_1\end{aligned}$$

Substituting these expressions into (3.8) and collecting the w_0^2-terms, gives the linear system for h_{20}

$$Ah_{20} = 2aq_1 - B(q_0, q_0) \tag{3.9}$$

The solvability condition for this system is

$$\langle p_1, 2aq_1 - B(q_0, q_0)\rangle = 2a\langle p_1, q_1\rangle - \langle p_1, B(q_0, q_0)\rangle = 0$$

which gives

$$a = \frac{1}{2}\langle p_1, B(q_0, q_0)\rangle$$

Now taking the scalar product of both sides of (3.9) with p_0 we obtain

$$\langle p_1, h_{20}\rangle = -\langle p_0, B(q_0, q_0). \tag{3.10}$$

On the other hand, the w_0w_1-terms in (3.8) give the linear system $Ah_{11} = h_{20} + bq_1 - B(q_0, q_1)$. Its solvability condition gives

$$\langle p_1, h_{20} + bq_1 - B(q_0, q_1)\rangle = \langle p_1, h_{20}\rangle + b\langle p_1, q_1\rangle - \langle p_1, B(q_0, q_1)\rangle = 0$$

Taking into consideration (3.9), we get

$$b = \langle p_0, B(q_0, q_0)\rangle + \langle p_1, B(q_0, q_1)\rangle$$

3.3.1 Degenerate Bogdanov-Takens

The same technique was used by Kuznetsov to derive similar expressions for all the normal form coefficients of degenerate BT bifurcation [13]. He applied the same technique in the case where the coefficient $a = 0$. Recall that if $a = 0$, a generic three parameter unfolding of the normal form is topologically equivalent to

$$\begin{aligned} \dot{\xi}_0 &= \xi_1, \\ \dot{\xi}_1 &= \beta_1 + \beta_2\xi_0 + \beta_3\xi_1 + a_3\xi_0^3 + b_2\xi_0\xi_1 + b_3'\xi_0^2\xi_1. \end{aligned}$$

Assuming also that b_2 is positive, Kuznetsov gives the three possible cases depending on the sign of the normal form coefficient of the cubic term. More precisely if a_3 is positive we have a saddle case, if it is negative, the expression $b_2^2 + 8a_3$ is negative and b_3' is different from zero, we have a focus case. Finally a_3 is negative and $b_2^2 + 8a_3$ positive we have an elliptic case. Later on we are going to use these expressions to compute the normal form coefficients of the system we are studying in this thesis and perform a similar analysis.

Chapter 4

Bifurcation analysis of the mean field model

4.1 Introduction

In this chapter we will apply the simplification techniques and the computation methods that we introduced in the previous chapter to do the bifurcation analysis of the model derived in the first chapter. Our goal is to describe the alpha rhythm using the model presented in van Veen and Liley [23] restricted to the inhibitory neuron population only.

So, dropping the tildes and the subscripts, and substituting the expression $\frac{1}{1+\exp(-\sqrt{2}(x_1-\theta)/s)}$ by S we have the following three-dimensional system of ODEs depending on six parameters. If we want to solve for the equilibrium of these equations, we have in total nine unknowns and three equations.

$$\begin{aligned} \dot{x_1} &= -x_1 + (1-x_1)x_3 + p_1 \\ \dot{x_2} &= -bx_2 + MS + p_2 \\ \dot{x_3} &= -bx_3 + x_2 \end{aligned} \tag{4.1}$$

We are going to describe any possible interactions of saddle-node and Hopf bifurcations of the solutions of this system. To do so, we first find expressions for the fixed points, that means the points where the three components of the vector field become zero. We then impose further restrictions according to the eigenspace of the bifurcation that we want to study. Like this, if we want to explore a codimension-3 bifurcation, our unknowns have to satisfy in total six algebraic conditions, so we can define six unknowns with respect to the other three. In this model, by a series of simplifications we will write five unknowns as a function of x_1 and we establish an equation which explains the relation between the six of them.

4.2 Linearisation about the fixed points

We first calculate the Jacobian matrix of this system:

$$J = \begin{pmatrix} -1 - x_3 & 0 & 1 - x_1 \\ MS' & -b & 0 \\ 0 & 1 & -b \end{pmatrix}.$$

Then we calculate the characteristic polynomial of the Jacobian matrix and extract the constant and the coefficients of the zeroth, first, second and third order terms

$$\begin{aligned} c_0 = Det(J) &= -b^2 - x_3 b^2 + MS' - MS'x_1 \\ c_1 = -\lambda_1\lambda_2 - \lambda_1\lambda_3 - \lambda_2\lambda_3 &= -2b - 4bx_3 - b^2 \\ c_2 = Tr(J) &= -1 - x_3 - 2b \\ c_3 &= -1 \end{aligned} \tag{4.2}$$

4.3 Codimension-two bifurcations

4.3.1 Fold-Hopf bifurcation

It is easy to prove that in this system we cannot have a case of FH bifurcation. Recall that this bifurcation occurs at a point where the Jacobian matrix evaluated at the bifurcation point has an eigenvalue equal to zero and a pair of purely imaginary eigenvalues. So, the c_0 and c_2 coefficients of the characteristic polynomial have to be zero and since c_3 is negative, c_1 has to be negative too for the FH bifurcation to occur. So, if we isolate b from the equation $c_2 = 0$ and we replace it in c_1 we obtain

$$\tilde{c}_1 = \frac{3}{4}(1 + x_3)^2$$

which is a perfect square and is positive for any value of x_3.

4.3.2 Bogdanov-Takens bifurcation

By a series of simplifications that we will describe right after, we find simple expressions for the coordinates of the fixed point as well as the parameters p_1 and p_2 with respect to M, S, S' and b at the point where the BT bifurcation occurs. We find also an equation that explains the relation between all parameters and the functions S and S'. More precisely we find

$$\begin{aligned}
\hat{\hat{x}}_2 &= -\frac{1}{2}b(2 + b) \\
\hat{\hat{x}}_3 &= -1 - \frac{1}{2}b \\
\hat{p_1} &= \frac{1}{4}\frac{4MS' - b^4}{MS'} \\
\hat{p_2} &= -b^2 - MS - \frac{1}{2}b^3
\end{aligned}$$

and

$$\hat{f}(x_1, M, \theta, s, b) = \frac{1}{4}\frac{b(-b^3 - 2MS' + 2MS'x_1)}{MS'} = 0.$$

In order to find these expressions, we start by considering the fixed point, that is the point where the vector field is zero. We start by expressing the fixed points $\bar{x}_2$ and $\bar{x}_3$ with respect to the other parameters equating the corresponding equations in (4.1) with zero.

$$\begin{aligned}\bar{x}_2 &= \frac{MS + p_2}{b} \\ \bar{x}_3 &= \frac{MS + p_2}{b^2}\end{aligned} \tag{4.3}$$

We continue the simplification by replacing the expression for $\bar{x}_3$ in the first equation of (4.1) and the equations of (4.2). Like this we obtain equations depending only on x_1 and the rest of the parameters as follows

$$f(x_1, M, \theta, s, b, p_2, p_1) = -x_1 + \frac{(1 - x_1)(MS + p_2)}{b^2} + p_1 = 0 \tag{4.4}$$

and

$$\begin{aligned}c_0 &= -b^2 - MS - p_2 + MS' - MS'x_1 \\ c_1 &= -b\left(2 + \frac{2(MS + p_2)}{b^2} + b\right)\end{aligned} \tag{4.5}$$

Recall from the theory presented that the condition to have a BT bifurcation is a double zero eigenvalue of the Jacobian matrix. So, the c_0 and the c_1 coefficients of the characteristic polynomial should be zero. We use these two equations to express p_1 and p_2 with respect to the rest of the parameters for the BT bifurcation to occur. We isolate p_2 from the equation $c_1 = 0$ and we replace it in the expression for c_0 to obtain

$$\hat{p}_2 = -b^2 - MS - \frac{1}{2}b^3 \tag{4.6}$$

and

$$\tilde{c}_0 = \frac{b^3}{2} + MS' - 2MS'x_1. \tag{4.7}$$

Now we isolate x_1 from the equation $\tilde{c}_0 = 0$ and we replace the expression in (4.4) to obtain

$$\tilde{f}(M, \theta, s, b, p_1, p_2) = b^3 + 2MS' + MSb + p_2 b - 2p_1 MS' = 0 \tag{4.8}$$

Recall that this equation is the first equation of the vector field (4.1) where we have replaced the expression for the third coordinate of the fixed point $\bar{x}_3$. Thus we can isolate p_1 from the equation $\tilde{f} = 0$ and in the resulting expression we replace the equation (4.6) to obtain

$$\hat{p}_1 = \frac{1}{4}\frac{4MS' - b^4}{MS'}. \tag{4.9}$$

We replace the expression found for $\hat{p}_2$ in the expressions for the fixed points $\bar{x}_3$ and $\bar{x}_2$ to obtain

$$\begin{aligned} \hat{\bar{x}}_2 &= -\frac{1}{2}b(2+b) \\ \hat{\bar{x}}_3 &= -1 - \frac{1}{2}b \end{aligned} \tag{4.10}$$

We replace the expressions for the two parameters (4.9) and (4.6) in (4.4) to obtain the following equation

$$\hat{f}(x_1, M, \theta, s, b) = \frac{1}{4}\frac{b(-b^3 - 2MS' + 2MS'x_1)}{MS'} = 0. \tag{4.11}$$

Now we have expressions for the two parameters p_1 and p_2 and for the second and third coordinates of the fixed points that depend only on the unknowns b, M, x_1

and the function S' which depends on θ, s and x_1. The equation (4.11) gives us the relation between all these unknowns.

Finally, we can isolate S' from the equation $\hat{f} = 0$ and we replace the expression in the matrix J as well as the expression for $\hat{\hat{x}}_3$ to obtain

$$A = \begin{pmatrix} \frac{1}{2}b & 0 & 1 - x_1 \\ \frac{1}{2}\frac{b^3}{-1+x_1} & -b & 0 \\ 0 & 1 & -b \end{pmatrix}.$$

4.4 Codimension-three bifurcations

4.4.1 Degenerate Bogdanov-Takens bifurcation

In order to analyse better the behavior of our system, we need to go to higher codimension. BT gives us a two parameter organising portrait, the degenerate BT will organise three parameter unfoldings and thus gives us more information. First, we need to determine the conditions where the BT point coincides with the cusp point. According to [4], this happens when the second order coefficient of the normal form is equal to zero and then we can distinguish three subcases depending on the sign of the third order coefficient of the normal form. We follow [13] where computations of the normal form coefficients are presented for degenerate BT bifurcations. In order to proceed with the analysis we consider the following normal form

$$\begin{aligned} \dot{w}_0 &= w_1 \\ \dot{w}_1 &= a_2 w_0^2 + b_2 w_0 w_1 + a_3 w_0^3 + b_3 w_0^2 w_1 + a_4 w_0^4 + b_4 w_0^3 w_1 + O(\|(w_0, w_1)\|^5) \end{aligned} \tag{4.12}$$

4.4.2 Computation of the normal form coefficients

In this section we use the matrix A as it resulted by the simplfications done in section 4.3.2, that is the Jacobian matrix of the system at the point where the BT bifurcation occurs, and Kuznetsov's method described in chapter 3 to find expressions for the normal form coefficients. We find the following expressions for the coefficients

$$
\begin{aligned}
a_2 &= -\frac{2}{3}\left(b + \frac{MS''(-1+x_1)^2}{b^2}\right) \\
b_2 &= \frac{4}{9}\frac{-b^3 + 2MS'' - 4MS''x_1 + 2MS''x_1^2}{b^3} \\
a_3 &= \frac{4}{81}\frac{1}{b^6}(8M^2S''^2x_1^4 - 9MS'''b^3x_1^3 - 32M^2S''^2x_1^3 - 14b^3MS''x_1^2 + 27MS'''b^3x_1^2 + \\
&+ 48M^2S''^2x_1^2 - 27MS'''b^3x_1 + 28b^3MS''x_1 - 32M^2S''^2x_1 + 5b^6 - 14b^3MS'' + \\
&+ 8M^2S''^2 + 9MS'''b^3)
\end{aligned}
$$

These relatively simple expressions along with the expressions for the coordinates of the fixed point and the parameters permit us to find explicit values for the position of the degenerate BT point and also conclude that only the saddle case of the degenerate BT bifurcation is possible in this system.

According to the method described in chapter 3, the only elements we need to calculate the normal form coefficients of the BT case is two linearly independent (generalised) eigenvectors $q_{01} \in \mathbb{R}^3$ such that $Aq_0 = 0$, $Aq_1 = q_0$ and two similar vectors p_{01} of the transposed matrix A^T such that $A^Tp_0 = 0$ and $A^Tp_1 = p_0$.

Doing the necessary calculations we find that A has a double zero and $-\frac{3}{2}b$ as eigenvalues, as we expected. The eigenvectors are respectively

$$
v_1 = r_1\left(-2\frac{1+x_1}{b}, b, 1\right)^T \qquad \text{and} \qquad v_3 = \left(\frac{1}{2}\frac{-1+x_1}{b}, -\frac{1}{2}b, 1\right)^T.
$$

The corresponding eigenvectors of the transposed matrix are

$$w_1 = r_2\left(-\frac{b}{-1+x_1}, \frac{1}{b}, 1\right)^T \qquad \text{and} \qquad w_3 = \left(\frac{1}{2}\frac{b}{-1-x_1}, -\frac{2}{b}, 1\right)^T.$$

Now we solve $Av_1 = v_2$ and $A^T w_1 = w_2$ and we obtain the respective generalised eigenvectors with t_1 and t_2 as free parameters

$$\begin{aligned} v_2 &= \left(2\frac{2r_1x_1 - bt + bt_1x_1 - 2r_1}{b^2}, bt_1 + r_1, t_1\right)^T \qquad \text{and} \\ w_2 &= \left(t_2, -\frac{-t_2 + t_2x_1 + 2r_2}{b^2}, -\frac{-t_2 + t_2x_1 + r_2}{b}\right)^T. \end{aligned}$$

Recall that the vectors have to verify the following conditions $\langle q_0, p_0\rangle = \langle q_1, p_1\rangle = 1$ and $\langle q_1, p_0\rangle = \langle q_0, p_1\rangle = 0$. We define the coefficients r_1, r_2 and the free parameters t_1, t_2 in order for the vectors to verify these conditions. Thus, we obtain

$$r_1 = 1, \qquad r_2 = -\frac{b}{3}, \qquad t_1 = -\frac{2}{3b}, \qquad \text{and} \qquad t_2 = 0$$

and the following vectors:

$$\begin{aligned} q_0 &= \left(\frac{2(-1+x_1)}{b}, b, 1\right)^T, \qquad q_1 = \frac{1}{3}\left(8\frac{x_1-1}{b^2}, 1, -\frac{2}{b}\right)^T, \qquad \text{and} \\ p_0 &= \frac{1}{3}\left(0, \frac{2}{b}, 1\right)^T, \qquad p_1 = \frac{1}{3}\left(\frac{b^2}{-1+x_1}, -1, -b\right)^T. \end{aligned}$$

Then we calculate the B_i and the C_j terms as described in section 3.2. In our case only the terms $B_1(x_1, x_3) = \frac{\partial^2 F_1}{\partial x_1 \partial x_3} = -1 = B_1(x_3, x_1)$, $B_2(x_1, x_1) = \frac{\partial^2 F_2}{\partial x_1^2} = MS''$ and $C_2(x_1, x_1, x_1) = \frac{\partial^3 F_2}{\partial x_1^3} = MS'''$ survive, the rest being equal to zero. Now, following the theory presented in chapter 3 and [13] we calculate:

$$a_2 = \frac{1}{2}\langle p_1, B(q_0, q_0)\rangle = -\frac{2}{3}\left(b + \frac{MS''(-1+x_1)^2}{b^2}\right) \tag{4.13}$$

and

$$\begin{aligned} b_2 &= \langle p_0, B(q_0,q_0)\rangle + \langle p_1, B(q_0,q_1)\rangle \\ &= \frac{4}{9}\frac{-b^3+2MS''-4MS''x_1+2MS''x_1^2}{b^3} \end{aligned} \tag{4.14}$$

Now, in order to compute the third order coefficient a_3 we need the vector h_{20}. Recall that $Ah_{20} = 2a_2q_1 - B(q_0, q_0)$, and we can compute the right hand side of this expression and solve with respect to h_{20} and a free parameter, say r_3. According to [13] h_{20} has to satisfy $2\langle p_0, h_{20}\rangle - 2\langle p_0, B(q_0, q_1)\rangle - \langle p_1, B(q_1, q_1)\rangle = 0$ and with this we determine the expression for the free parameter and we calculate $a_3 = \frac{1}{6}\langle p_1, C(q_0, q_0, q_0)\rangle + \frac{1}{2}\langle p_1, B(h_{20}, q_0)\rangle - \frac{a_2}{2}\langle p_1, B(q_1, q_1)\rangle$ which gives

$$\begin{aligned} a_3 = \frac{4}{81}\frac{1}{b^6}(&8M^2S''^2x_1^4 - 9MS'''b^3x_1^3 - 32M^2S''^2x_1^3 - 14b^3MS''x_1^2 + 27MS'''b^3x_1^2 + \\ &+ 48M^2S''^2x_1^2 - 27MS'''b^3x_1 + 28b^3MS''x_1 - 32M^2S''^2x_1 + 5b^6 - 14b^3MS'' + \\ &+ 8M^2S''^2 + 9MS'''b^3) \end{aligned} \tag{4.15}$$

Now, let's go back to our system and the unknowns. To locate the degenerate BT point, the last two conditions to impose are the vanishing of the first component of the vector field and of the second order coefficient of the normal form. We use the equations (4.11) and (4.13) to determine implicitly $\hat{\bar{x}}_1$ and $\hat{M}$ the expressions of the fixed point and the parameter M in order to have the degenerate BT bifurcation.

$$\begin{aligned} \hat{\bar{x}}_1 &= -\frac{2S' - S''}{S''} \\ \hat{M} &= -\frac{1}{4}\frac{S''b^3}{S'^2} \end{aligned} \tag{4.16}$$

Replacing these two expressions in the expression (4.15) for the third order coefficient of the normal form, we find the following expression

$$a_3 = -\frac{4}{9}\frac{-3S''^2 + 2S'''S'}{S''^2} \tag{4.17}$$

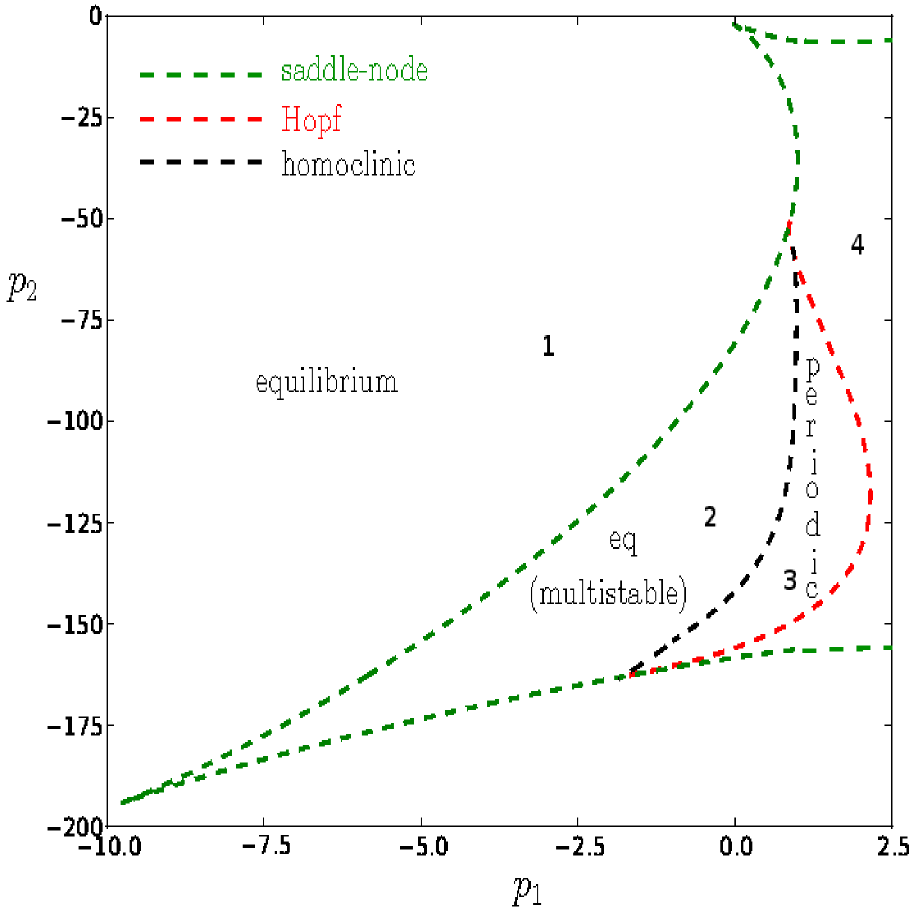
If we replace the expression for S', S'' and S''' we obtain $\hat{a}_3 = \frac{4}{9}\frac{(1+E)^2}{(E-1)^2}$ which is a positive definite expression, where $E = \exp(-\sqrt{2}(x_1 - \theta)/s)$. Thus we arrive to the conclusion that only the saddle case of the degenerate BT bifurcation occurs in this model.

4.4.3 Alpha rhythm

Recall now that our goal was to describe the alpha rhythm. In order to illustrate the organisation of our model around the degenerate BT point, we give an example using the following set of parameters: $(b, \theta, s, M) = (2.5, 1.5, 0.5, 150)$. We introduce these values in AUTO and we do parameter continuation to explore the organisation of the system as we expected it by the bifurcation analysis. In graph 4.1 we give an example of the unfolding near the degenerate BT point, in order to be able to see clearly the organisation. We can see a series of various bifurcations: In green the saddle-node curve and in red the Hopf bifurcation curve uniting the two BT points. The black line defines the set of parameters where the homoclinic orbit exists. Note that the degenerate BT point is the point where the two BT points coincide with the cusp point. We can compare this figure with the figure where the saddle-node case is illustrated in [4] and we can see that all the elements are present as predicted by the normal form analysis.

In addition, as we can see in figure 4.1 when $p_2 \leq -b^2$, all orbits seem to be bounded and there exists at least one stable equilibrium. Note that one stable equilibrium goes to infinity when $p_2 = -b^2$. Furthermore, for $p_2 > -b^2$ in one case all orbits diverge, situation that occurs in regions labeled 1 and 2. In the other case,

Figure 4.1: Bifurcation diagram at $p_1 = 0.8751$ and $p_2 = -50.6385$



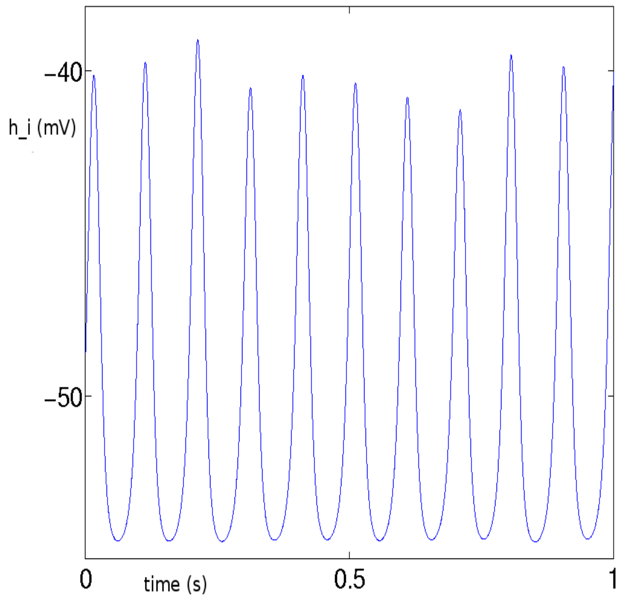
some orbits converge to an equilibrium, situation that occurs in region 4, or to a periodic orbit, which is the case in the region 3 while others diverge.

In our case, we observe a stable periodic solution in the region labeld 3 in the graph 4.1. Then we illustrated it in the graph 4.2 of the time series of h_i with some additive noise in p_2. We can see a periodical variation of the inhibitory neurons potential between around -55 and -40 mV.

What is more important is that in this example we actually detect oscillations that vary in the range of the alpha rhythm. If we fix τ_i at 40 ms, which is a physiologically reasonable value, then the period of the solution lies in the interval $(80, 120)$ ms which is $(12.5, 8.3)$ Hz.

Furthermore, in the graph 4.3 we can see how the signal of the inhibitory neurons

Figure 4.2: Time series of h_i with noise in p_2 at $p_1 = 1.03$ and $p_2 = -75$



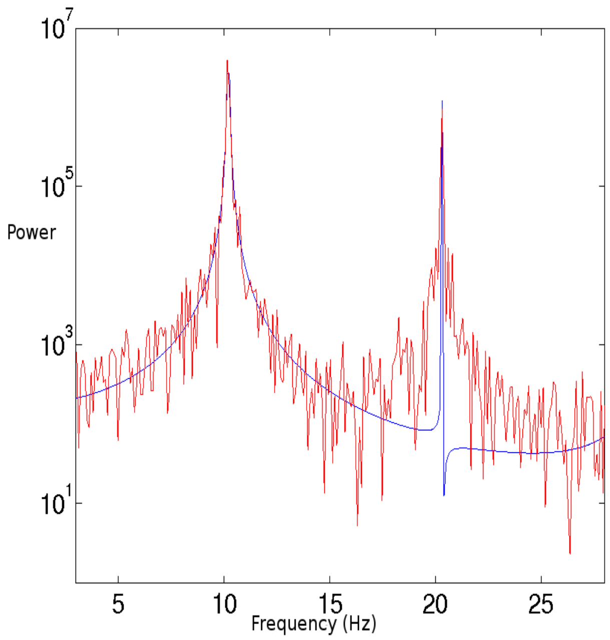
potential, h_i, is distributed in function of the frequency. We can clearly see a peak around 10 Hz and then around 25 Hz. We then superimposed to this graph the power spectrum with noise on p_2.

In our case all the parameters that we used to analyse the model, if we scale them to their real dimension, we see that they vary into physiologically logical ranges as described in [5]. In the following table we present the parameters, the values that we used in this thesis scaled to their real dimension and the physiologically logical ranges as described in [5].

parameters	value used	MIN	MAX	Units
h_{ir}	-65	-80	-60	mV
τ_i	40	5	150	ms
h_{ieq}	-75	-90	h_{ir}-5	mV
B	0.2	0.1	2	mV
b	62.5	10	500	s^{-1}
N_{ii}	111	100	1000	-
m_i	0.1	0.05	0.5	ms^{-1}
θ_i	-50	-55	-40	mV
s_i	5	2	7	mV

Table 4.1: The parameters, the values used and their physiologically logical range

Figure 4.3: Power spectrum of the time series with noise on p_2 at $p_1 = 1.03$ and $p_2 = -75$



Conclusion

In this thesis we explored an open question in neuroscience which is the generation of the alpha rhythm in the brain. This rhythm is an energy peak at around 10 Hz in the power spectrum of the signal detected between electrodes placed in the scalp. In other words, it is a common signal that we see in the EEG. For our analysis we used a mean field model which is better suited to describe the EEG in contrast with single-neuron models. In fact this model describes how local masses of neurons interact when they are destabilized by sensory inputs.

More precisely we used a simplification of a model proposed by Liley, Cadush and Dafilis [3] and then we simplified it more neglecting the long-range cortical-cortical connections and putting the spatial derivatives to zero as proposed in van Veen and Liley [23]. We base our analysis on the hypothesis that the alpha rhythm is generated by interaction between the inhibitory neurons only. Thus we consider only the equations that describe these connections and we obtain a three dimension system of nonlinear ordinary differential equations.

We then use center manifold reduction and normal form theory to simplify the equations. Actually we present Kuznetsov's method to calculate the normal form coefficients which combines the center manifold reduction and the calculation of the normal form coefficients. Applying it to our equations we surprisingly obtain very simple algebraic expressions for each one of them and the parameters of the system. We compute them and we use them to find the position of the degenerate BT point.

With further analysis we prove that in this system only the saddle-node case is possible according to the analysis presented in [4].

We then introduce the values that we found in AUTO and doing parameter continuation we explore the organisation of the system around the degenerate BT point. We find a stable periodic solution whose nondimensional period lies in the interval $(2, 3)$. If we put τ_i at 40 ms which a physiologically normal value, we get a period in the interval $(80, 120)$ ms which is in $(8.3, 15)$ Hz, where we usually detect the alpha rhythm. Furthermore, we see that the values that we used if converted in the corresponding dimensional values, they are physiologically admissible values as described in [5].

We conclude by presenting a numerical example where the alpha rhythm is detected as a stable periodic orbit. We also give an example of the organisation of our system close to the degenerate BT point.

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