# Synchronization and Phase Locking in Networks of Heterogeneous Model Neurons

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#### Abstract

This dissertation examines the effect of two types of system complexity, nonlinearity and heterogeneity, on oscillatory dynamics in networked systems. In particular, we focus on finding conditions for complete synchronization, where the dynamics of multiple systems are identical, phase locking, where the dynamics of multiple systems share critical features, and mixed mode oscillations (MMOs), where the dynamics of a single system demonstrate periodic oscillations with peaks of markedly different sizes. A fascinating application of these conditions is to networks of model neurons and the crucial role of synchronization in brain function.

We establish conditions for synchronization in networks of heterogeneous systems with nonlinear dynamics and diffusive coupling. We leverage a passivity-based Lyapunov approach to find a condition for complete synchronization in networks of identical nonlinear systems in terms of the network structure and the dynamics of individual systems. An application to networked model neurons with biologically relevant parameter values demonstrates improvement over alternative methods. Cluster synchronization is an extension of complete synchronization where the network can be partitioned into distinct subgroups of systems that are synchronized. We find conditions for cluster synchronization in networks of non-identical systems with nonlinear dynamics and diffusive coupling using a passivity-based Lyapunov approach and a contraction based approach.

We examine a system of two model neurons where the first neuron receives a constant external input and the second neuron receives input from the first through diffusive coupling. Large networks that are cluster synchronized can be represented by simpler systems; in particular, the dynamics of a network synchronized in two clusters can be represented by a system of two coupled model neurons. We use techniques from dynamical systems theory to characterize parameter regimes where each model neuron is resting, firing, or sustaining MMOs. The system of two model neurons and its extensions represent a foundation for investigating how network structure and external stimuli interact to influence the dynamics in networks of neurons.

Characterization of the conditions for when synchronization may arise in networks of heterogeneous nonlinear systems is a crucial step toward understanding complex networked systems.

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In memory of

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(November 2, 1918 - August 30, 2018)

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# Part I

# Conditions for Synchronization and Phase Locking in Networks

## Chapter 1

## Introduction

Synchronization and phase locking are compelling phenomena where systems are affected by one another or a common environment and develop related patterns of behavior. Synchronization plays a pivotal role in natural and man-made systems; for example, synchronized motion in animal groups is used to avoid predators [116], synchronized firing of lasers is leveraged to make precise measurements [105], and synchronized cells in the heart, called the sinoatrial node, generate the heartbeat [85]. In spring, the synchronous flashing of fireflies in the Great Smoky Mountains National Park attract thousands of parking lottery winners. This massive display of synchronization is an extremely popular attraction - the lottery was enacted because the previous first-come, first-served system would sell out in seconds. The emergence of synchronization in a universe characterized by disorder is a striking dynamic that captivates the imagination and is an active area of research in diverse fields of science and engineering.

In this dissertation, we find novel conditions for *complete synchronization*, where the states of individual systems are identical, and *phase locking*, where the phases of oscillating models are separated by a constant offset, in complex networked systems. We focus on two types of complexity: heterogeneity and nonlinearity. A network of stable oscillatory systems with identical dynamics that are all connected to one another through a linear coupling function will synchronize for any positive coupling strength. However, once heterogeneity is incorporated into the system dynamics or the coupling, this is no longer the case. In addition to heterogeneity, nonlinearity in the form of nonlinear dynamics introduces further complexity in the methods needed to prove conditions for synchronization or phase locking.

#### 1.1 Networked systems

A graph  $\mathcal{G} = (\mathcal{N}, \mathcal{E})$  is a mathematical object comprised of nodes  $\mathcal{N}$  that are connected by edges  $\mathcal{E}$  and can facilitate analysis of complex networked systems by providing a representation that is compact and straightforward to interpret. The nodes in a network can be agents in a multi-agent system, compartments in a compartmental model, or any other collection of systems that relates to one another in a pairwise fashion. The edges in a network represent pairwise connections between nodes. The structure is written in an adjacency matrix  $A = [a_{ij}]$ , where  $a_{ij} \geq 0$  is the weight of the edge from node i to node j. When there is no edge from node i to node j,  $a_{ij} = 0$ . Networks can be undirected, where  $a_{ij} = a_{ji}$  for all i and j in the set of nodes, or directed, where this condition does not need to be satisfied.

The term *connected graph* denotes a graph where a path, which is a series of edges that are connected sequentially, can be found between any two nodes. Common network structures include the complete graph, where each node is connected to every other node, the star graph, where a central node connects to all other nodes and there are no other connections, the cycle graph, where the nodes are connected in a cycle, and the tree graph, a connected graph with no cycles.

Throughout this dissertation, we repeatedly consider general networks of nonlinear systems connected by linear diffusive coupling. For a network of n systems, where

system i has state  $\mathbf{x}^i \in \mathbb{R}^N$ , the dynamics are written

$$\dot{\mathbf{x}}^i = \mathbf{f}^i(\mathbf{x}^i) + Bu^i, \text{ for } i = 1, \dots, n.$$
(1.1)

For the Lyapunov based approaches we take B to be a vector of zeros with a one in the first entry, indicating that coupling only influences the first variable. The coupling  $u^i$  is linear diffusive coupling, which is written

$$u^{i} = \sum_{j \in \mathcal{N}^{i}} \gamma a_{ij} (x_{1}^{j} - x_{1}^{i}), \qquad (1.2)$$

where  $x_1^i$  is the variable corresponding to the first variable of system  $i, \gamma > 0$  is the coupling strength, and  $\mathcal{N}^i$  is a collection of indices that represent the neighbors of node i.

The Laplacian matrix of  $\mathcal{G}$  is [4]

$$\mathcal{L}_{ij} = \begin{cases} \sum_{k \in \mathcal{N}^i} a^{ik} & i = j, \\ -a^{ij} & i \neq j, j \in \mathcal{N}^i, \\ 0 & \text{otherwise.} \end{cases}$$
(1.3)

In a connected graph, the smallest eigenvalue of the Laplacian,  $\lambda^{(1)}$ , is zero. For a connected and undirected graph, the rest of the eigenvalues are real and positive. The second smallest eigenvalue,  $\lambda^{(2)}$ , is called *algebraic connectivity* and corresponds to how connected the graph is, where a higher value of  $\lambda^{(2)}$  indicates higher connectivity.

# 1.2 Conditions for synchronization in networked systems

Synchronization is a ubiquitous phenomenon in natural and engineered systems, and has been observed and studied in a variety of fields [100]. In the brain, synchronization helps produce desired behavior [38,81], while excess synchronization can cause debilitating disorders such as Parkinson's disease [22] and epilepsy [75]. Complete synchronization is a type of synchronization where the state of a system in the network converge to the states of all other systems, such that  $\mathbf{x}^i = \mathbf{x}^j$ , for  $(i, j) = 1, \ldots, n$ after a transient period. Finding necessary and sufficient conditions for the existence of synchronization is a crucial step toward understanding and controlling complex oscillatory behavior.

In the literature, necessary and sufficient conditions for synchronization have been studied for a variety of networked systems. For networks of identical systems with nonlinear dynamics and arbitrary network structure, sufficient conditions are typically found using Lyapunov approaches that leverage passivity properties of the individual nonlinear systems [101, 124] or by employing a contraction-based approach [7, 118]. Our approach in Chapter 2 is to build on the semi-passivity method described in [101, 124] to provide a tighter bound on the required coupling strength for synchronization in biologically relevant model parameter regimes.

# 1.3 Conditions for cluster synchronization in networked systems

When a network is comprised of heterogeneous systems, complete synchronization is no longer possible. Instead, the network may become partitioned into subgroups of systems, where the systems in a subgroup synchronize with one another. In this dissertation, we define a synchronized cluster as a group of completely synchronized nodes [11, 121].

Finding necessary and sufficient conditions for cluster synchronization in networked systems is an active area of investigation. For nodes in a cluster to synchronize completely, it is necessary that the internal dynamics of each node are identical and that the sum of the edge weights from each other cluster is also identical for every node [11,51,125]. Sufficient conditions guarantee stability of the potential cluster partition. Such sufficient conditions have been found for networks where the dynamics are in terms of a single variable [19,92] and in terms of the network structure within clusters for networks of systems with more general nonlinear dynamics [45,79,134]. The contributions described in Chapter 2 on cluster synchronization use a contraction based approach to find a sufficient conditions. The improvement is partly due to the fact that the condition incorporates both the network structure within clusters and the network structure between clusters.

#### **1.4** Model neurons<sup>\*</sup>

The numerical simulations presented throughout this dissertation implement lowdimensional, nonlinear, conductance-based models of membrane potential dynamics that replicate features of neurons observed in experiment. Conductance-based models are biophysical models that represent the membrane potential of a neuron in terms of an electrical circuit with the following components: (1) batteries, which represent ion concentration gradients across the membrane, (2) resistors, which represent ion channels in the membrane, and (3) capacitors, which represent charge stored across the membrane [41].

<sup>\*</sup>The second and third paragraphs of this section are modified from [28] and parts are verbatim.

Mathematical efforts to model neuronal dynamics have a rich history, dating back to the pioneering work of Hodgkin and Huxley [59] on the action potential in the squid giant axon. The *Hodgkin-Huxley model* (HH) consists of four ordinary differential equations that model the membrane potential and three gating variables [63]. While the Hodgkin-Huxley model is directly based on experiment, the high dimension and large number of parameters result in issues with analytical tractability as the number of model neurons is scaled in a network setting.

A two-dimensional model that captures salient qualities of the four-dimensional Hodgkin-Huxley model was developed independently by FitzHugh [46, 47] and by Nagumo [90]. In this model, commonly known as the *FitzHugh-Nagumo model* (FN), one variable represents the membrane potential and the other represents a gating variable. A constant external input to the FN model neuron can produce quiescent, or resting, behavior (a low-voltage stable equilibrium point), firing (a stable limit cycle), or saturated behavior (a high-voltage stable equilibrium point). The FN model neuron captures realistic neuronal behavior such as spike accommodation, bistability, and excitability [63].

In this dissertation, we focus on the FN model and leverage the balance between analytical tractability and biologically realistic dynamics. We implement the FN model in Chapter 2 to illustrate applications of the theory for complete and cluster synchronization, and analyze the dynamics of two FN models and directed trees of FN models in Chapters 3 and 4.

## 1.5 Complex oscillatory patterns in networks of model neurons

The FN model is a fast-slow system characterized by dynamics that operate at two different timescales. The membrane potential dynamics are fast and the gating variable is slow; the difference in speeds is determined by a constant timescale separation parameter. In the single FN model neuron, the bifurcation parameter corresponding to external input determines whether the FN model is in a quiescent, firing, or saturated regime. When the external input is near the boundaries between these regimes, the dynamics follow *canard trajectories*. Canards are solutions that pass from a slow stable manifold, near a bifurcation point, and on to a slow unstable manifold, where they stay for a long time compared to the system timescale [15, 126, 139]. Canards only exist for a very small range of the bifurcation parameter in the single FN model, but are seen for a wider range of parameter values when multiple FN models are coupled together.

In Chapters 3 and 4, we study a system of two model neurons, the *directed two*-FN system, where the first neuron receives a constant external input and the second neuron receives an input from the first neuron. For certain combinations of external input and strength of coupling from the first neuron to the second, canard trajectories are observed numerically. The directed two-FN system has two fast and two slow variables, so the existence of canard trajectories, combined with a suitable return mechanism, can drive *mixed mode oscillations* (MMOs) [34,71]. MMOs are periodic solutions that alternate between small amplitude oscillations (SAOs) and much larger oscillations [84]. As noted in [28], the "existence of canard-driven MMOs has been described for systems in four dimensions [14, 126], systems with two slow variables and two fast variables [128], and generalized systems in arbitrary finite dimensions [138]." In a two-FN system, a necessary condition for MMOs was found in terms of a parameter corresponding to input to one of the two FN models [69]. In Chapters 3 and 4, we leverage these results to determine necessary conditions for existence of canards and canard-driven MMOs in the directed two-FN system in terms of two parameters: (1) the external input and (2) the coupling strength from the first FN model to the second.

#### 1.6 Outline

In Chapter 2, we present approaches to finding conditions for synchronization in networks of nonlinear systems and summarize results from Part II: Chapter 7 [29] and Chapter 8 [4]. The two main developments we highlight use a nonsmooth Lyapunov approach inspired by [37] and a contraction based approach [3] to find sufficient conditions for complete synchronization in networks of identical systems and cluster synchronization in networks of non-identical systems. The conditions are in terms of coupling strength and network connectedness. Applications of the theory to networks of FN model neurons demonstrate improvement over a sufficient condition calculated using a previously proposed method, the quadratic Lyapunov approach [124]. We provide numerical examples to illustrate applications and shortcomings of both approaches and to motivate the material in Chapter 3.

In Chapter 3, we characterize the parameter regimes where different dynamics are possible for networks of FN models and summarize results from the paper in Part II: Chapter 9 [28]. We begin by detailing the bifurcation structure of three systems of FN model neurons. The first is a single FN model neuron, the second is the directed two-FN system, and the third is a general directed tree of FN model neurons. The analysis builds off of the work presented in Chapter 2 by considering simple networks that can represent reductions of cluster synchronized networks. We go on to describe parameter regimes where canards and canard-driven MMOs are possible by relating the bifurcation structure of the directed two-FN system to a singularly perturbed system. We find necessary conditions for canard-driven MMOs in terms of two model parameters and provide a complementary sufficient condition for phase locking that we extend to directed trees of FN models.

In Chapter 4, we examine how synchronization and phase locking emerge in networks of model neurons with both excitatory and inhibitory coupling. We extend the analysis of the directed two-FN system presented in Chapter 3 to incorporate inhibitory coupling. Canards, MMOs, and phase locking are all exhibited in the inhibitory regime. We characterize regions of parameter space where MMOs may occur and where phase locking is guaranteed and generalize these conditions to directed trees of FN neurons with excitatory and inhibitory coupling.

Chapter 5 concludes Part I of this dissertation by summarizing the main contributions from each chapter and outlining future directions of inquiry.

### Chapter 2

# Conditions for Synchronization in Networks of Nonlinear Systems<sup>\*</sup>

This chapter summarizes the derivation of conditions that guarantee synchronization in networks of nonlinear systems which appear in the published papers [29] and [4]. Using the network model defined in Section 1.1, we consider synchronization in a network of identical nonlinear systems configured in an arbitrary network with linear coupling. A nonsmooth Lyapunov analysis is used to find a sufficient condition for synchronization of the nonlinear systems in the network. The condition is in terms of two quantities: 1) the overall coupling strength in the network and 2) the connectedness of the network structure. For high enough coupling strength and connectedness, a given network is guaranteed to exhibit synchronous dynamics.

To compare the sufficient condition to commonly used methods in the literature, we study a model of neuronal membrane potential dynamics, the Fitzhugh-Nagumo (FN) model. For a network of FN models, we compare the sufficient condition for synchronization derived through nonsmooth Lyapunov analysis to the sufficient con-

<sup>\*</sup>This chapter summarizes results from Davison, Dey, and Leonard [29] and Aminzare, Dey, Davison, and Leonard [4]. Further details and the full papers can be found in Chapters 7 and 8, respectively.

dition for synchronization derived through quadratic Lyapunov analysis in Section 2.2. Under biologically relevant model parameter regimes, the sufficient condition derived through nonsmooth Lyapunov analysis is tighter.

As a step toward more general networks, we incorporate two types of heterogeneity into our study of FN model neurons: 1) the network structure is arbitrary and 2) the models have non-identical external inputs. When the inputs to different models are non-identical, a phenomenon called cluster synchronization emerges. After a suitable transient, it is possible to reduce a cluster synchronized network to a network where each node represents a cluster [24, 112, 115]. By looking at the network structure of each cluster independently and applying the conditions derived through nonsmooth Lyapunov analysis, we find conditions that guarantee synchronization within clusters in Section 2.2.

Section 2.3 summarizes the development and application of a sufficient condition for cluster synchronization in networks of heterogeneous nonlinear systems using a contraction based approach. The condition was derived using contraction theory in [4]. We consider applications to networks of model neurons with FitzHugh-Nagumo and Hindmarsh-Rose dynamics. In the FN setting, we prove the sufficient condition found using the contraction approach represents a substantial improvement over the sufficient conditions derived using Lyapunov methods in Section 2.2. In part, this is because the contraction-based proof does not rely on a bound on the dynamics, which results in more conservative conditions. The sufficient conditions for cluster synchronization are in terms of the network structure, for a network where the intrinsic nonlinear dynamics of each node may differ. Finally, we provide numerical examples that illustrate the utility of the contraction based approach. In particular, we consider the same setting as the final example from Section 2.2 and show that the sufficient condition from contraction theory predicts the synchronized clusters more accurately than the sufficient condition from Lyapunov theory. We also illustrate the limitations of the sufficient condition derived using contraction theory and give an example of implementation when the clusters are comprised of different types of neuronal models.

#### 2.1 Definitions, background, and main results

In this section, we provide definitions from [29] and [4] that formalize the notions of complete synchronization and cluster synchronization. We describe two methods, contraction and Lyapunov stability, that are commonly used to find sufficient conditions for synchronization in terms of the graph structure and system dynamics. The main result from [29], a condition on the network connectivity and coupling strength for general nonlinear systems comprised of polynomial ordinary differential equations, is included. We also restate the main result from [4]. The main theorem in [4] implements contraction to find a sufficient condition for synchronization in terms of the network structure and the dynamics of systems in the network. We begin with definitions of the complete synchronization manifold and complete synchronization. Throughout this dissertation, we consider complete synchronization unless otherwise specified.

We consider a network of n general nonlinear models with dynamics  $\mathbf{x}^i \in \mathbb{R}^N$ . This can be described by (1.1), or more generally by

$$\dot{\mathbf{x}}^{i}(t) = \mathbf{f}^{i}\left(\mathbf{x}^{i}(t), t\right) + \sum_{j \in \mathcal{N}^{i}} \gamma^{ij} D\left(\mathbf{x}^{j}(t) - \mathbf{x}^{i}(t)\right) \qquad i = 1, \dots, n .$$
(2.1)

Here  $D \in \mathbb{R}^{n \times n} = \text{diag}(d_1, \ldots, d_n)$  is the *diffusion matrix*, a nonzero diagonal matrix with  $d_i \geq 0$ . Additionally,  $\gamma^{ij} = a_{ij}$ , the network graph edge weights. In (1.1),  $D = \text{diag}(\gamma, 0, \ldots, 0)$  and the  $\mathbf{f}^i$  are time independent. We consider the description in (1.1) for the Lyapunov based approach and the more general description in (2.1) for the contraction based approach. **Definition 2.1.1** (Complete synchronization manifold [29]). The complete synchronization manifold  $\mathscr{S}$  is an algebraic manifold in the state space of the full system wherein the states of individual systems are identical:

$$\mathscr{S} = \{\mathbf{x}^1, \dots, \mathbf{x}^n \in \mathbb{R}^N | x^i = x^j, \forall i, j = 1, \dots, n\}.$$

**Definition 2.1.2** (Complete synchronization [29]). The dynamics given in Equation (1.1) synchronize completely if, for any solution  $\mathbf{x}$  of Equation (1.1), there exists a solution  $\bar{\mathbf{x}} \in \mathscr{S}$  such that

$$\mathbf{x}(t) - \bar{\mathbf{x}}(t) \to 0 \quad as \ t \to \infty.$$

An extension of complete synchronization to networks of systems with heterogeneous parameters is cluster synchronization, which we define here and use throughout the chapter.

**Definition 2.1.3** (Cluster synchronization [4], modified for consistency). For any  $1 \le K \le n$  and any  $1 \le c_1, \ldots, c_K \le n$  such that  $c_1 + \cdots + c_K = n$ , let

$$\mathscr{S}_{K} := \left\{ \mathbf{x} \in \mathbb{R}^{nN} \mid \mathbf{x}^{1} = \cdots = \mathbf{x}^{c_{1}}, \ldots, \mathbf{x}^{n-c_{K}+1} = \cdots = \mathbf{x}^{n}, \mathbf{x}^{i} \in \mathbb{R}^{N} \right\}.$$

The dynamics given in Equation (2.1) synchronize in clusters if there exists  $1 \le K \le$ n such that all solutions of Equation (2.1) converge to  $\mathscr{S}_K$  in an appropriate norm.  $\mathscr{S}_K$  is called the K-cluster synchronization manifold.

In this chapter, we consider complete synchronization, which requires systems to have identical dynamics after initial transients, and complete synchronization in clusters, which requires the systems in a cluster be completely synchronized [100]. While this restriction fails to incorporate cases where systems are approximately synchronized [99,122], it is a good starting point due to the wide variety of theoretical tools that can be applied to the problem. One essential tool is the concept of Lyapunov stability. An equilibrium point  $\mathbf{x}_* \in \mathbb{R}^N$  of the nonlinear system  $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ , where  $\mathbf{f} \in \mathbb{R}^N$ , is stable if there exists a continuously differentiable function  $V(\mathbf{x}) : \mathcal{D} \to \mathbb{R}$ such that  $V(\mathbf{x}_*) = 0$ ,  $V(\mathbf{x}) > 0$  ( $V(\mathbf{x})$  is positive definite) in  $\mathcal{D} - {\mathbf{x}_*}$ , and  $\dot{V}(x) \leq 0$ ( $\dot{V}(x)$  is negative semidefinite) in  $\mathcal{D} - {\mathbf{x}_*}$ , where  $\mathcal{D}$  is a region in  $\mathbb{R}^N$  containing  $\mathbf{x}_*$  [66]. Extensions of Lyapunov stability are used to prove stability of equilibrium points and trajectories for various applications. Quadratic Lyapunov functions have been used to prove stability of synchronized solutions in general semi-passive systems [124] and networks of Hindmarsh-Rose model neurons [93]. To prove stability in [29], we use a nonsmooth Lyapunov function,

$$V(\mathbf{x}) = \sum_{k=1}^{N} \max_{i,j=1,\dots,n} (x_k^i - x_k^j).$$
(2.2)

The derivative  $\dot{V}(x)$  is replaced by an upper Dini derivative, which is defined in the following.

**Definition 2.1.4** (Upper Dini derivative [66]). The upper Dini derivative, also called the upper right hand derivative, of a real valued function  $V : \mathbb{R} \to \mathbb{R}$  is defined as

$$D^{+}V(t) = \limsup_{h \to 0^{+}} \frac{V(t+h) - V(t)}{h}.$$
(2.3)

It provides an upper bound for right hand derivatives of V.

We use the concept of strict semi-passivity to bound the system dynamics.

**Definition 2.1.5** (Strictly Semi-passive, [29]). A dynamical system  $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}) + B\mathbf{u}$ ,  $\mathbf{y} = C\mathbf{x}, \mathbf{x} \in \mathbb{R}^N, \mathbf{u}, \mathbf{y} \in \mathbb{R}^m$  is strictly semi-passive in a region  $\mathcal{D} \subset \mathbb{R}^N$  if there exists a nonnegative function  $V : \mathcal{D} \to \mathbb{R}_+$  such that  $\mathcal{D}$  is open, connected and invariant under the dynamics,  $V(\mathbf{x}) > 0$  for  $\mathbf{x} \in \mathcal{D} \setminus \{0\}$ , V(0) = 0, and  $\dot{V} \leq \mathbf{y}^T \mathbf{u} - H(\mathbf{x})$ , where  $H(\mathbf{x}) > 0$  when  $\|\mathbf{x}\| \geq r$  with the radius r being dependent on the system parameters.

Using the nonsmooth Lyapunov function and bounds on the dynamics that arise from strict semi-passivity, we prove stability of the complete synchronization manifold for sufficiently large  $\gamma \lambda^{(2)}(\mathcal{L})$ . This combination of terms represents the strength of coupling and connectedness of the graph.

**Theorem 2.1.6** ([29], modified for consistency). Consider the system described in (1.1) with a linear diffusive coupling on the first variable (1.2). Assume that (1.1) is strictly semi-passive and  $\mathbf{f}^i$  is equal for i = 1, ..., n. Then, whenever the coupling strength  $\gamma$  and the second smallest eigenvalue of the graph Laplacian  $\lambda^{(2)}(\mathcal{L})$  (representing network connectivity) satisfy

$$\gamma \lambda^{(2)}(\mathcal{L}) > \sum_{k=1}^{N} F_{1k} + h_1,$$
  
and 
$$\sum_{k=1}^{N} F_{jk} + h_j < 0 \quad \forall j = 2, \dots, N$$

the complete synchronization manifold S is globally asymptotically stable, where  $F_{ij}$ 's and  $h_i$ 's are functions of system parameters.

Assuming the intrinsic dynamics of all systems are equal, for an arbitrary system k, the (i, j)th element of  $F \in \mathbb{R}^{N \times N}$  is the linear term of  $x_j^k$  in the function  $f_i^k$ , and the function  $h_i$  is a function that bounds the nonlinear dynamics of  $f_i^k$ . For a detailed proof of Theorem 2.1.6, please see Chapter 7.

Another commonly used method to find conditions for synchronization is contraction [3]. Intuitively, for a system to be contractive, any two solutions of the system must grow closer together, as defined by a suitable norm, as time progresses. The formal definition for contraction follows. **Definition 2.1.7** (Contraction [4]). Consider the nonlinear dynamical system

$$\dot{\mathbf{x}}(t) = \mathbf{G}(\mathbf{x}(t), t) \tag{2.4}$$

on  $V \times [0, \infty]$ , where V is a convex subset of  $\mathbb{R}^N$ . Let the vector field **G** satisfy  $\mathbf{G}(\mathbf{x}, t)$ Lipschitz on  $\mathbf{x}$  and continuous on  $(\mathbf{x}, t)$  such that the existence and uniqueness of solutions of (2.4) is guaranteed. Equation (2.4) is contractive if there exist c < 0 and a norm  $\|\cdot\|$  on  $\mathbb{R}^N$  such that, for any two solutions  $\mathbf{x}$  and  $\mathbf{y}$ , the following inequality holds for any  $t \ge 0$ 

$$\|\mathbf{x}(t) - \mathbf{y}(t)\| \le e^{ct} \|\mathbf{x}(0) - \mathbf{y}(0)\|.$$
(2.5)

Contraction has been used to find conditions for synchronization in [5, 8, 78, 111, 112, 135]. For a thorough description of relating contraction theory and synchronization, please refer to [3]. The conditions derived using contraction approaches are in terms of the Jacobian,  $J_{\mathbf{G}}(\mathbf{x})$ , of the system dynamics  $\mathbf{G}(\mathbf{x})$  [5] and may also incorporate diffusion matrix D or the graph structure  $\mathcal{G}$  [8]. A common format for graph structure to be incorporated into synchronization conditions is in terms of the second smallest eigenvalue of the Laplacian of each cluster subgraph,  $\lambda_{\mathscr{C}_r}^{(2)}$  [29]. The main result from [4] contains more information about the graph structure by also including the second smallest eigenvalue of the Laplacian of the subgraph of interconnections between clusters,  $\bar{\lambda}^{(2)}$ . It relies on the following assumption of the arrangement of the clusters and cluster-input-equivalence.

**Assumption 2.1.8** ([4] modified for consistency). In the network described by Equation (2.1), we assume that

1. There exist  $K \leq n$  and  $c_1, \ldots, c_K \geq 2$ , such that  $c_1 + \cdots + c_K = n$ , and

$$\mathbf{f}^{i_1} = \cdots = \mathbf{f}^{i_{c_1}} =: \mathbf{f}_{\mathscr{C}_1}, \ldots, \mathbf{f}^{i_{n-c_K+1}} = \cdots = \mathbf{f}^{i_n} =: \mathbf{f}_{\mathscr{C}_K},$$
where  $\{i_1, \ldots, i_n\}$  is a permutation of  $\{1, \ldots, n\}$ . Without loss of generality, we can assume:

$$\mathbf{f}^1 = \cdots = \mathbf{f}^{c_1} =: \mathbf{f}_{\mathscr{C}_1}, \ldots, \ \mathbf{f}^{n-c_K+1} = \cdots = \mathbf{f}^N =: \mathbf{f}_{\mathscr{C}_K}.$$

Let  $\mathscr{C}_1, \ldots, \mathscr{C}_K$  denote K clusters of nodes. The nodes in cluster  $\mathscr{C}_1$  are defined by  $\mathbf{x}^1, \ldots, \mathbf{x}^{c_1}$  and they all have dynamics  $\mathbf{f}_{\mathscr{C}_1}$ , the nodes in cluster  $\mathscr{C}_2$  are defined by  $\mathbf{x}^{c_1+1}, \ldots, \mathbf{x}^{c_1+c_2}$  and they all have dynamics  $\mathbf{f}_{\mathscr{C}_2}$ , etc. For ease of notation in our calculations, we let

$$\mathbf{x}_{\mathscr{C}_{1}}^{1} = \mathbf{x}^{1}, \dots, \mathbf{x}_{\mathscr{C}_{1}}^{c_{1}} = \mathbf{x}^{c_{1}},$$

$$\mathbf{x}_{\mathscr{C}_{2}}^{1} = \mathbf{x}^{c_{1}+1}, \dots, \mathbf{x}_{\mathscr{C}_{2}}^{c_{2}} = \mathbf{x}^{c_{1}+c_{2}},$$

$$\vdots$$

$$\mathbf{x}_{\mathscr{C}_{K}}^{1} = \mathbf{x}^{n-c_{K}+1}, \dots, \mathbf{x}_{\mathscr{C}_{K}}^{c_{K}} = \mathbf{x}^{n}.$$
(2.6)

2. The cluster-input-equivalence condition defined in [11] holds. This implies that the following edge weight sums are equal: for any two nodes  $\mathbf{x}_{\mathscr{C}_r}^i, \mathbf{x}_{\mathscr{C}_r}^j, (i, j) \in \mathscr{C}_r$ ,

$$\eta_{\mathscr{C}_{r}\mathscr{C}_{s}} := \sum_{k \in \mathcal{N}_{\mathscr{C}_{s}}^{i}} \gamma^{ik} = \sum_{k \in \mathcal{N}_{\mathscr{C}_{s}}^{j}} \gamma^{jk}, \qquad (2.7)$$

where  $\mathcal{N}_{\mathcal{C}_s}^i$  denotes the indices of the neighbors of node *i* which are in cluster  $\mathcal{C}_s$ .

**Theorem 2.1.9** (Theorem 1, [4] modified for consistency). Consider Equation (2.1) with Assumption 2.1.8, and let

$$\mu := \max_{r=1,\dots,K} \sup_{(x,t)\in V\times[0,\infty)} \mu_{2,P} \left[ J_{\mathbf{f}_{\mathscr{C}_r}}(\mathbf{x},t) - \left(\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}\right) D \right],$$
(2.8)

where  $P \in \mathbb{R}^{N \times N}$  is a positive definite matrix chosen such that  $P^2D + DP^2$  is positive semidefinite. Then, for any solution  $\mathbf{x}$  of Equation (2.1) that remains in  $V^N$ , there exists  $\bar{\mathbf{x}}(t)$  such that

$$\|\mathbf{x}(t) - \bar{\mathbf{x}}(t)\|_{2,\mathcal{P}} \le e^{\mu t} \|\mathbf{x}(0) - \bar{\mathbf{x}}(0)\|_{2,\mathcal{P}},\tag{2.9}$$

where  $\mathcal{P} = I_n \otimes P^2$  and  $\|\cdot\|_{2,\mathcal{P}}$  is a  $\mathcal{P}$ -weighted  $L^2$  norm on  $\mathbb{R}^{nN}$ , defined by

$$\|\mathbf{x}\|_{2,\mathcal{P}} := \left\| \left( \left\| P^2 \mathbf{x}^1 \right\|_2, \dots, \left\| P^2 \mathbf{x}^n \right\|_2 \right)^\top \right\|_2,$$

for any  $\mathbf{x} = \left(\mathbf{x}^{1^{\top}}, \dots, \mathbf{x}^{n^{\top}}\right)^{\top} \in \mathbb{R}^{nN}$ . In particular, if  $\mu < 0$ , then for any pair of nodes  $i, j \in \mathscr{C}_r, \mathbf{x}^i_{\mathscr{C}_r}$  and  $\mathbf{x}^j_{\mathscr{C}_r}$  satisfy

$$\mathbf{x}_{\mathscr{C}_r}^i(t) - \mathbf{x}_{\mathscr{C}_r}^j(t) \to 0 \quad as \ t \to \infty.$$

For a detailed proof of this theorem and a table of induced matrix measures  $\mu$  in Table 8.1, please refer to Chapter 8.

# 2.2 Synchronization in networks of model neurons: Lyapunov approach

Here, we apply the general theory outlined in Theorem 2.1.6 to a network of FitzHugh-Nagumo (FN) model neurons [47,90]. We highlight the new result that the sufficient condition for synchronization derived using the nonsmooth Lyapunov approach is an improvement over the sufficient conditions derived using a quadratic Lyapunov function [124].

We consider two settings: (1) a network of n FN model neurons with identical model parameters and (2) a network of n FN model neurons with differing external inputs. In the first case, we find sufficient conditions for synchronization. In the second case, we find sufficient conditions for cluster synchronization. In both settings, the dynamics of each FN model are modeled by

$$\dot{y}^{i} = y^{i} - \frac{y^{i^{3}}}{3} - z^{i} + I^{i} + u^{i},$$

$$\dot{z}^{i} = \epsilon(y^{i} + a - bz^{i}), \text{ for } i = 1, \dots, n.$$
(2.10)

The two variables model the membrane voltage (y) and a recovery variable (z). They are separated by the timescale parameter  $\epsilon \ll 1$ , where  $\epsilon$  is a positive constant. The variables a and b are also positive constants that are common to all FN models in the network. The input to neuron i is written as two terms: a constant external input  $I^i$ and an input from all neighbors in the network  $u^i$ .

#### 2.2.1 Identical model parameters

In [29], we find a sufficient condition for synchronization in a network of FN models (2.10) with identical  $I^i$  by applying Theorem 2.1.6. The FN model (2.10) was shown to be strictly semi-passive [101] and we consider networks where  $u^i$  consists of linear diffusive coupling (1.2), so both assumptions in Theorem 2.1.6 are satisfied. The resulting sufficient condition is in terms of the coupling strength  $\gamma$  and the second smallest eigenvalue of the graph Laplacian  $\lambda^{(2)}(\mathcal{L})$ . The sufficient condition is given by

$$\gamma \lambda^{(2)}(\mathcal{L}) \ge 1 + \epsilon + \frac{\beta_1^2}{3}, \qquad (2.11)$$

where  $\beta_1$  is the bound on the dynamics of y given by strict semi-passivity. We compare the sufficient condition for synchronization found using the nonsmooth Lyapunov approach (2.11) to a sufficient condition for synchronization found using a quadratic Lyapunov approach. The quadratic Lyapunov function is used to find conditions for synchronization in networks of general strictly semi-passive systems [124] and Hindmarsh-Rose model neurons [93]. For FN model neurons, the sufficient condition is given by

$$\gamma \lambda^{(2)}(\mathcal{L}) > \frac{(\epsilon - 1)^2}{4b\epsilon} + 1 + \frac{\beta_1^2}{3}.$$
 (2.12)

We show that, when the FN models are arranged in a complete graph and the parameters satisfy  $\epsilon$  small and  $b \in [0, 1]$  - which corresponds to biologically plausible model behavior - the condition from the nonsmooth Lyapunov approach is an improvement on the condition from the quadratic Lyapunov approach and a contraction based approach [113]. We denote  $\lambda_m^*$  as the value of  $\lambda^{(2)}(\mathcal{L})$  where, for a given  $\gamma$ , (2.11) is satisfied. Similarly, we denote  $\lambda_s^*$  as the value of  $\lambda^{(2)}(\mathcal{L})$  where, for a given  $\gamma$ , (2.12) is satisfied. A comparison between these values for a range of model parameters is depicted in Figure 2.1, which illustrates the improvement.



Figure 2.1: Ratio of synchronization conditions for the nonsmooth and quadratic Lyapunov approaches. For the biologically relevant parameter ranges plotted, the bound derived from the nonsmooth approach is always tighter. Repeated from Figure 7.1.

Details of the calculations are contained in Chapter 7.

#### 2.2.2 Non-identical model parameters

Networks of systems with non-identical model parameters may experience cluster synchronization, where the network can be partitioned such that systems within a subgroup only synchronize with one another. The interplay between network structure and arrangement of model parameters determine how and whether cluster synchronization arises [12, 121]. In particular, input-equivalent systems have equivalent sums of the external input and input from neighbors in the graph over all time. We use input-equivalence [113] to extend Theorem 2.1.6 to cluster synchronized networks where the constant external input  $I^i$  is non-identical. See Corollary 7.5.2 and the corresponding proof for more details.

**Example 2.2.1** (Limitations of Lyapunov-based approach). To motivate the improvement in synchronization conditions from using a contraction based approach detailed next, we present two distinct limitations of the Lyapunov approach when finding sufficient conditions for cluster synchronization. In this example and throughout the remainder of this dissertation, we use the terminology "cluster" to denote a cluster synchronized group of nodes. The first limitation is the bound from semi-passivity,  $\beta_1$ , which is often much larger than the dynamics and so results in a loose bound for synchronization. The second limitation is that this method only considers the graph structure within clusters, and so misses situations where the synchronization in one cluster is mediated by the synchronization in another cluster.

The example system we consider is a graph composed of two clusters with structure depicted in Figure 2.2. The first is a complete graph on three nodes, which are colored orange in the figure. The second, colored blue, consists of six nodes that are connected to one of the nodes in the first cluster but are not connected to one another. The coupling within the first cluster (orange-orange), denoted  $\gamma_1$ , is set to 1. The coupling from the first cluster to the second (orange-blue), denoted  $\gamma_{12}$ , is set to 0.25. There is no coupling within the second cluster (blue-blue), so  $\gamma_2 = 0$ . The model parameters are a = 0.7, b = 0.8,  $\epsilon_1 = 0.3$ ,  $I_1 = 0$ ,  $\epsilon_2 = 0.08$ , and  $I_2 = 0.5$ , where  $I_1$  is the constant external input to each system in the first cluster and  $I_2$  is the constant external input to each system in the second cluster.



Figure 2.2: Graph structure (left) and y dynamics (right) for a graph with two clusters of FitzHugh-Nagumo model neurons.

We compute the synchronization bounds for each cluster and compare these to the corresponding graph measures in Table 2.1. In both clusters, the coupling is lower than the sufficient condition. The dynamics are depicted in Figure 2.2. In the orange cluster, the coupling is about a factor of two less than the sufficient condition, but the cluster synchronizes. This illustrates the limitation of the Lyapunov approach where the bounds are not tight. In the blue cluster, the coupling is infinitely smaller than the sufficient condition, but the cluster synchronizes. This illustrates the limitation of this approach where cluster synchronization mediated by other clusters is not taken into consideration. Both of these limitations are addressed and improved on in the following section where we present the contraction based approach.

Table 2.1: Sufficient conditions for cluster synchronization and graph measures for the graph in Figure 2.2.

Cluster $c$	$\lambda^{(2)}(\mathcal{L}_c)$	$\gamma_c \lambda_m^*$	Sufficient condition	Actual $\gamma_c$
Inner (orange)	3	5.3	$\gamma_1 > 1.77$	$\gamma_1 = 1$
Outer (blue)	0	5.08	Not satisfied for finite $\gamma$	$\gamma_2 = 0$

## 2.3 Synchronization in networks of model neurons: Contraction approach

In this section, we highlight an application of Theorem 2.1.9 to networks of cluster synchronized FN models and Hindmarsh-Rose (HR) models. Through numerical examples in Section 2.3.2, we illustrate several improvements on the sufficient conditions derived using the Lyapunov approach in Section 2.2.2.

### 2.3.1 Cluster synchronization in networks of heterogeneous FN and HR model neurons

We begin by considering a network of n FitzHugh-Nagumo models (2.10) with a linear gap diffusive coupling (1.2) on the first variable with coupling strength  $\gamma > 0$ . Furthermore, assume the network can be partitioned into  $K \ge 1$  clusters according to Assumption 2.1.8 and let model parameters  $a_{\mathscr{C}_r}, b_{\mathscr{C}_r}, \epsilon_{\mathscr{C}_r}$ , and  $I_{\mathscr{C}_r}$  be heterogeneous across clusters but the same within a given cluster  $\mathscr{C}_r$ , where  $r = 1, \ldots, K$ .

**Corollary 2.3.1.** ([4]) Consider Equation (2.10), with Assumption 2.1.8. For all  $r = 1, \ldots, K$ , let

$$\gamma > \frac{1 + \alpha_r}{\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}}$$

where  $\alpha_r = \frac{\left(\epsilon_{\mathscr{C}_r}p - 1/p\right)^2}{4b_{\mathscr{C}_r}\epsilon_{\mathscr{C}_r}}$  and p > 0 is a constant. Then for any pair of FN model neurons  $\{(y^i, z^i)^\top, (y^j, z^j)^\top\}$  such that  $(i, j) \in \mathscr{C}_r$ ,

$$y^{i}(t) - y^{j}(t) \rightarrow 0, \quad z^{i}(t) - z^{j}(t) \rightarrow 0, \quad as \ t \rightarrow \infty.$$

In particular, if  $p = \max_r \frac{1}{\sqrt{\epsilon_{\mathscr{C}_r}}}$ , then  $\alpha_r$  is minimized.

There are two FN model parameters that appear in the expression for the bound on  $\gamma$ . The first is  $\epsilon \ll 1$ , which is the timescale separation between y and z and controls the frequency of spiking. The second is b, which determines the ratio of the time for a spike to the refractory period. For a detailed proof and discussion, please refer to Chapter [4].

When K = 1, the network is represented by a single cluster and the sufficient condition from Corollary 2.3.1 becomes  $\gamma \lambda_{\mathscr{C}_1}^{(2)} > 1$ . The sufficient condition for synchronization found using the nonsmooth Lyapunov approach (2.11) is  $\gamma \lambda_{\mathscr{C}_1}^{(2)} \ge 1 + \epsilon + \frac{\beta_1^2}{3}$ . The constants  $\epsilon$  and  $\beta_1^2$  are both nonnegative, so the sufficient condition from 2.3.1 represents an improvement over previous results.

The second application of Theorem 2.1.9 we provide is a network of N modified Hindmarsh-Rose models with a linear gap diffusive coupling (1.2) on the first variable with coupling strength  $\gamma > 0$ . The two-dimensional Hindmarsh-Rose dynamics we consider are

$$\dot{y}^{i} = -y^{i^{3}} + c^{i}y^{i^{2}} + z^{i} + I^{i} + u^{i},$$
  

$$\dot{z}^{i} = \delta^{i}(1 - 5y^{i^{2}} - z^{i}), \text{ for } i = 1, \dots, n,$$
(2.13)

where y is the membrane potential, z is a recovery variable, c > 0 is a constant,  $0 < \delta^i \ll 1$  determines the time scale separation,  $I^i$  is a constant external input to HR model i and  $u^i$  is the collection of inputs from all neighbors of i in  $\mathcal{G}$ . Again, assume the network can be partitioned into  $K \ge 1$  clusters according to Assumption 2.1.8 and let model parameters,  $c_{\mathscr{C}_r}$ ,  $\delta_{\mathscr{C}_r}$ , and  $I_{\mathscr{C}_r}$  be heterogeneous across clusters but the same within a given cluster  $\mathscr{C}_r$ , where  $r = 1, \ldots, K$ .

**Corollary 2.3.2.** ([4]) Consider Equation (2.13), under Assumption 2.1.8. For all  $r = 1, \ldots, K$ , let

$$\gamma > \frac{1}{\lambda_{\mathscr{C}_{i}}^{(2)} + \bar{\lambda}^{(2)}} \max\left\{\frac{-(2c_{\mathscr{C}_{i}} - 5)^{2}}{4(25\delta_{\mathscr{C}_{i}}p^{2} - 3)} + \frac{1}{4\delta_{\mathscr{C}_{i}}p}, \frac{c_{\mathscr{C}_{i}}^{2}}{3} - \delta_{\mathscr{C}_{i}}\right\},\tag{2.14}$$

where p is a constant that satisfies  $0 . Then for any pair of HR models <math>\{(y^i, z^i)^\top, (y^j, z^j)^\top\}$  such that  $(i, j) \in \mathscr{C}_r$ ,

$$y^i(t) - y^j(t) \to 0, \quad z^i(t) - z^j(t) \to 0, \quad as \ t \to \infty.$$

In particular, if  $p = \max_r \frac{3}{5\delta_{\mathscr{C}_r}(5+|2c_{\mathscr{C}_r}-5|)}$ , then the first argument of the max operator in Equation (2.14) is minimized and has the value  $\frac{(5+|2c_{\mathscr{C}_r}-5|)^2}{12}$ .

For a detailed proof, please refer to Chapter 8.

#### 2.3.2 Numerical examples

This section contains numerical examples that illustrate the applications of Theorem 2.1.9 from Section 2.3.1. Three distinct examples are presented. The first revisits Example 2.2.1 and compares the bounds from the nonsmooth Lyapunov approach with the bounds from Corollary 2.3.1. The bounds from contraction theory are shown to be tighter and more useful in describing the behavior for both clusters. The second example is a case where multiple models are connected in the graph and illustrates how the contraction-based approach can be generalized. The third example depicts a scenario where the cluster synchronized steady state includes complex oscillatory dynamics that can be studied by reducing the cluster synchronized graph to a simpler graph. Chapter 3 provides an in-depth analysis of the scenario presented in the third example.

**Example 2.3.3** (Comparison of contraction and Lyapunov bounds). We again consider the example system from Figure 2.2. The first cluster (orange) is a complete graph on three nodes and the second cluster (blue) consists of six nodes that are connected to one of the nodes in the first cluster but are not connected to one another. The coupling within the first cluster (orange-orange), denoted  $\gamma_1$ , is set to 1. The coupling from the first cluster to the second (orange-blue), denoted  $\gamma_{12}$ , is set to 0.25.

There is no coupling within the second cluster (blue-blue), so  $\gamma_2 = 0$ . The model parameters are a = 0.875, b = 0.8,  $\epsilon_1 = 0.3$ ,  $I_1 = 0$ ,  $\epsilon_2 = 0.08$ , and  $I_2 = 0.5$ .

We compute the synchronization bounds using both the Lyapunov approach and the contraction approach for each cluster in Table 2.2. Neither cluster satisfies the sufficient condition for synchronization derived using the nonsmooth Lyapunov approach. However, both clusters do indeed synchronize. The inner cluster satisfies the sufficient condition for synchronization derived using the contraction approach. This is an example of how the improvement described in Section 2.3.1 is also present in a cluster synchronized network. The outer cluster does not satisfy the sufficient condition for synchronization derived using the contraction approach. This is a limitation for the contraction based approach - the bounds are still not necessary and sufficient and, while tighter than previous bounds, still do not capture all of the conditions where synchronization occurs. However, the connection between clusters is taken into account, which provides for a more accurate understanding of the system.

Table 2.2: Comparison of synchronization conditions derived through contraction and Lyapunov approaches for the graph in Figure 2.2. When the Lyapunov function approach is used, neither cluster satisfies the sufficient condition. When the contraction approach is considered, the inner cluster is guaranteed to synchronize and the outer cluster does not satisfy the sufficient condition.

Cluster $c$	$\gamma_c \lambda^{(2)}(\mathcal{L}_c)$	$\gamma_c \lambda_m^*$	Ns Lyapunov	$\gamma(\lambda^{(2)}(\mathcal{L}_c)+ar{\lambda}_2)$	Contraction
Inner (orange)	3	5.3	3 < 5.3 X	3.25	3.25 > 1 🗸
Outer (blue)	0	5.08	0 < 5.08 X	0.25	0.25 < 1 X

**Example 2.3.4** (Cluster synchronization in a network with both FN and HR models, adapted from [4]). In this example, we consider a network of 12 model neurons grouped into three clusters as depicted in Figure 2.3. The clustering, determined based on the

graph structure and nodal dynamics, satisfies Assumption 2.1.8. Parameters for the models in each cluster are described in the following.

- 1. Cluster  $\mathscr{C}_1$  (purple circles): four FN models;  $a_{\mathscr{C}_1} = 0.875$ ,  $b_{\mathscr{C}_1} = 0.8$ ,  $I_{\mathscr{C}_1} = 1$ , and  $\epsilon_{\mathscr{C}_1} = 0.08$ ;
- 2. Cluster  $\mathscr{C}_2$  (green squares): six HR models;  $c_{\mathscr{C}_2} = 2$ ,  $I_{\mathscr{C}_2} = 0.5$ , and  $\delta_{\mathscr{C}_2} = 0.01$ ;
- 3. Cluster  $\mathscr{C}_3$  (blue triangles): two HR models;  $c_{\mathscr{C}_3} = 3$ ,  $I_{\mathscr{C}_3} = 0.2$ , and  $\delta_{\mathscr{C}_3} = 0.08$ .

The intra-cluster coupling is 0.01 times the coupling in cluster 1, the coupling in cluster 2 is 0.5 times the coupling in cluster 1, and the coupling in cluster 3 is 2 times the coupling in cluster 1. The second smallest eigenvalues of the Laplacian of the three intra-cluster subgraphs and the inter-cluster subgraph are  $\lambda_{\mathscr{C}_1}^{(2)} = 2$ ,  $\lambda_{\mathscr{C}_2}^{(2)} = 1$ ,  $\lambda_{\mathscr{C}_3}^{(2)} = 4$ , and  $\bar{\lambda}^{(2)} = 0.01$ , respectively. By Corollaries 2.3.1 and 2.3.2, the clusters will synchronize if

$$\gamma > \max\left\{\frac{1}{\lambda_{\mathscr{C}_{1}}^{(2)} + \bar{\lambda}^{(2)}}, \frac{\frac{1}{8}\left(\frac{25}{p} - \frac{1}{p^{2} - 12}\right)}{\lambda_{\mathscr{C}_{2}}^{(2)} + \bar{\lambda}^{(2)}}, \frac{1.32}{\lambda_{\mathscr{C}_{2}}^{(2)} + \bar{\lambda}^{(2)}}, \frac{\left(\frac{25}{p} - \frac{1}{p^{2} - 12}\right)}{\lambda_{\mathscr{C}_{3}}^{(2)} + \bar{\lambda}^{(2)}}, \frac{2.92}{\lambda_{\mathscr{C}_{3}}^{(2)} + \bar{\lambda}^{(2)}}\right\}.$$

$$(2.15)$$

Taking p = 2.4 is close to the minimum for the second and fourth terms. The fourth term has the largest numerator, so a sufficient condition for cluster synchronization over all clusters is  $\gamma > 2.59$ . The right panel of Figure 2.3 shows three synchronized clusters in the network when  $\gamma = 2.6$ .

**Example 2.3.5** (Reduction example and motivation for two-FN analysis). In this example, we illustrate how cluster synchronization can be leveraged to reduce the number of nodes in a graph and consider the complex oscillations that emerge for coupling below the synchronization bound. We consider a complete graph on six nodes with identical FN model neuron dynamics. The parameters are a = 0.875, b = 0.8,



Figure 2.3: Graph structure (left) and y dynamics (right) for a graph on 12 nodes with three clusters. The purple cluster consists of FN models, while the green and blue clusters are formed of HR models with different dynamics. Adapted from Figure 8.1.

and  $\epsilon = 0.08$ , there is an input I = 0 to the dark blue node and I = 1 otherwise, and the coupling is  $\gamma = 0.016$  for edges connecting the dark blue node to all other nodes and is  $14\gamma = 0.224$  otherwise. This gives  $\lambda^{(2)}(\mathcal{L}_c) = 70$  and  $\bar{\lambda}_2 = 1$ , so  $\gamma(\lambda^{(2)}(\mathcal{L}_c) + \bar{\lambda}_2) = 1.136$  and, by Theorem 2.1.9, the complete graph on five nodes will synchronize.

This gives us a useful tool to study the complex oscillations seen in Figure 2.4. We can reduce the graph to a simple graph on two nodes, shown in the lower panel. The larger cluster is guaranteed to synchronize, so the steady state dynamics can be accurately modeled by a single FN model. In Chapter 3, we analyze the dynamics of the two-FN system in detail as the coupling and external input are varied.



Figure 2.4: Graph structure (top left) and y dynamics (top right) for a graph on six nodes with two clusters. The graph is a complete graph and the nodal dynamics are FN models with parameters a = 0.875, b = 0.8, and  $\epsilon = 0.08$ . The coupling is  $\gamma = 0.016$  for edges connecting the dark blue node to all other nodes and is  $14\gamma$ otherwise. The external input I = 1 to all FN models except the dark blue one, which receives an external input of I = 0. The system separates into two clusters: the first fires normally and the second exhibits oscillations at half the frequency of the first. Because it is synchronized after the transients, the system can be reduced to a graph on two nodes in the steady state (bottom).

## Chapter 3

# Conditions for Mixed-Mode Oscillations and Phase Locking in Coupled FN Model Neurons<sup>\*</sup>

In this chapter, we investigate networks of FN models coupled through linear gap diffusive coupling. We characterize the different dynamic behavior for values of external input and coupling strength and further investigate the complex oscillations observed numerically in Example 2.3.5. In Section 3.1, we provide definitions and background from multiple timescale systems theory.

In Sections 3.2, 3.3, and 3.4, we describe the bifurcation structure of three fundamental networks of FN models: (1) a single FN model with constant external input, (2) a unidirectionally coupled pair of FN models where the first receives a constant external input and the second receives only an input from the first (the *directed two-FN system*), and (3) directed trees of FN models. We characterize regions of bifurcation parameter space where the models are resting, firing with alternating small amplitude oscillations (SAOs), and phase locked. The boundaries between regions are charac-

<sup>\*</sup>The material presented in this chapter is based on Davison, Aminzare, Dey, and Leonard [28]. Please see Chapter 9 for detailed calculations.

terized by *Hopf bifurcations*, where varying a parameter results in a stability change for an equilibrium point as an isolated limit cycle appears or disappears from that equilibrium point. If the limit cycle is stable, the Hopf bifurcation is *supercritical*. If the limit cycle is unstable, the Hopf bifurcation is *subcritical*.

In Chapter 2, we noted that there are certain requirements on the FN model parameters for biologically realistic results. We formalize these requirements in the following assumption to ensure that the FN model has a unique equilibrium point for all constant external inputs I.

Assumption 3.0.1. ([28]) Parameters  $a, b, and \epsilon$  are such that the FN model (2.10) has a unique equilibrium point for all values of  $I \ge 0$ . This results in conditions 0 < a < 1 and 0 < b < 1.

For the remainder of this chapter and much of Chpater 4, we maintain this assumption.

#### **3.1** Definitions and background

In this section, we provide definitions of canards and mixed mode oscillations (MMOs), which are observed numerically in coupled systems of FN models. Examples of (a) small amplitude oscillations (SAOs) (b) MMOs, and (c) phase locking are shown in Figure 3.1.

In Chapter 2, we described  $\epsilon$  as the timescale separation parameter. It controls the difference in speed between the slow and fast dynamics. A general fast-slow system with m fast variables and n slow variables is typically studied by considering one of two subsystems, where  $\mathbf{y} \in \mathbb{R}^m$  are the fast variables and  $\mathbf{z} \in \mathbb{R}^n$  are the slow



Figure 3.1: Example of (a) SAOs, (b) MMOs, and (c) phase locking observed in simulation of the directed two-FN system. In all plots  $y_A$  is in blue and  $y_B$  is in magenta. (a) For I = 1 and  $\gamma = 0.05$ ,  $y_B$  follows small oscillations with the same frequency as the firing of model neuron A. (b) For I = 1 and  $\gamma = 0.08$ ,  $y_B$  exhibits MMOs. (c) For I = 1.4 and  $\gamma = 1.03$ ,  $y_A$  and  $y_B$  exhibit phase locking, i.e., they fire at a constant phase offset, even though the amplitude of the spikes and the waveforms are different. Modified from Figure 9.4.

variables. A general fast-slow system can be written

$$\epsilon \frac{d\mathbf{y}}{d\tau} = \boldsymbol{f}(\mathbf{y}, \mathbf{z}, \epsilon),$$

$$\frac{d\mathbf{z}}{d\tau} = \boldsymbol{g}(\mathbf{y}, \mathbf{z}, \epsilon).$$
(3.1)

The singular limit,  $\epsilon = 0$ , gives the *slow subsystem*, which is often referred to as the *reduced system* [72]. In networks of FN models, the functions **f** and **g** do not depend on  $\epsilon$ . Changing timescales by  $t = \frac{\tau}{\epsilon}$  gives

$$\frac{d\mathbf{y}}{dt} = \boldsymbol{f}(\mathbf{y}, \mathbf{z}, \epsilon), 
\frac{d\mathbf{z}}{dt} = \epsilon \boldsymbol{g}(\mathbf{y}, \mathbf{z}, \epsilon).$$
(3.2)

The singular limit,  $\epsilon = 0$ , gives the *fast subsystem*, which is often referred to as the *layer system* [72]. The set of equilibrium points of the layer system, where  $\mathbf{f}(\mathbf{y}, \mathbf{z}, 0) = 0$ , is called the *critical manifold* when the set is a submanifold of  $\mathbb{R}^m \times \mathbb{R}^n$  [72]. When the Jacobian at a point  $\mathbf{y}_*$  on the critical manifold,  $D_{\mathbf{y}}\mathbf{f}(\mathbf{y}_*)$ , has at least one eigenvalue with zero real part,  $\mathbf{y}_*$  is a *fold point* [139]. A *canard* is a solution of the singularly perturbed system that passes from an attracting slow manifold through a

fold point to a repelling slow manifold and stays within  $\mathscr{O}(\epsilon)$  of the repelling slow manifold for  $\mathscr{O}(1)$  in the slow timescale [126]. *Mixed mode oscillations* (MMOs) are periodic solutions of (3.2) comprised of SAOs and large amplitude oscillations (LAOs) with substantially different amplitudes [72].

To find conditions for canard-driven MMOs, we study a rescaling of the reduced system called the desingularized system. The derivation of the desingularized system proceeds as described in the following, quoted from [28].

To derive the desingularized system we first differentiate  $f(\mathbf{y}, \mathbf{z}) = 0$  with respect to  $\tau$  to get

$$(D_{\mathbf{y}}\boldsymbol{f}) \cdot \frac{d\mathbf{y}}{d\tau} + (D_{\mathbf{z}}\boldsymbol{f}) \cdot \frac{d\mathbf{z}}{d\tau} = \mathbf{0}.$$
(3.3)

Multiplying both sides of (3.3) by  $\operatorname{adj}(D_{\mathbf{y}}\boldsymbol{f})$ , the adjugate (or the transpose of the cofactor matrix) of  $D_{\mathbf{y}}\boldsymbol{f}$ , gives

$$-\det (D_{\mathbf{y}}\boldsymbol{f})\frac{d\mathbf{y}}{d\tau} = \operatorname{adj}(D_{\mathbf{y}}\boldsymbol{f})(D_{\mathbf{z}}\boldsymbol{f}) \cdot \boldsymbol{g}(\mathbf{y}, \mathbf{z}).$$
(3.4)

This system is singular when det  $(D_{\mathbf{y}} \mathbf{f}) = 0$ , namely at fold points. This means that standard existence and uniqueness results do not hold at the fold points. However, rescaling time in (3.4) by  $d\tau = -\det(D_{\mathbf{y}}\mathbf{f})d\tau_2$ yields the desingularized system

$$\frac{d\mathbf{y}}{d\tau_2} = \operatorname{adj}(D_{\mathbf{y}}\boldsymbol{f})(D_{\mathbf{z}}\boldsymbol{f}) \cdot \boldsymbol{g}(\mathbf{y}, \mathbf{z}).$$
(3.5)

Note that to obtain the corresponding flows of the reduced system from the desingularized system, due to the time scaling  $d\tau = -\det(D_{\mathbf{y}}\mathbf{f})d\tau_2$ , the direction of the flows of the desingularized system must be reversed on branches where  $\det(D_{\mathbf{y}}\mathbf{f}) > 0$ . There are two types of equilibrium points of the desingularized system: ordinary singularities and folded singularities. Ordinary singularities are also equilibrium points of the reduced system and are within  $\mathcal{O}(\epsilon)$  of the equilibrium points of the full system. When **f** and **g** do not depend on  $\epsilon$ , the ordinary singularities are the equilibrium points of the full system. Folded singularities are the fold points, or points where the Jacobian on the critical manifold has at least one eigenvalue with zero real part, of the reduced system.

In systems with two or more slow variables, the existence of MMOs with canard SAOs over a range of parameter space requires there exist (1) a stable folded node and (2) a global return mechanism to return the dynamics to near the stable folded node. A cubic-shaped critical manifold is the global return mechanism in the FN model. In a system with two fast and two slow variables, the eigendirections create a funnel. Trajectories of the full system pass from the attracting branch of the critical manifold close to the folded singularity to the repelling branch of the critical manifold. The corresponding trajectory eventually jumps away from the repelling branch [26, 137]. The global return mechanism is essential because it returns trajectories to the funnel [34, 71].

A Folded Saddle Node of Type II (FSN II) bifurcation in the desingularized system (3.5) corresponds to a Hopf bifurcation in the full system. In a FSN II bifurcation, there is a transcritical bifurcation where a folded saddle and stable ordinary singularity change stability and become a stable folded node and saddle ordinary singularity. An example FSN II bifurcation in the directed two-FN system is depicted in Figure 9.9, with corresponding phase planes shown in Figure 9.7.

#### 3.2 Single FN model

We begin by describing the bifurcation structure and dynamics of a single FN model with a constant external input I (2.10). In Figure 3.2, the bifurcation diagram of the FN model is depicted with bifurcation parameter I. The points where the unique equilibrium point changes stability are Hopf bifurcations. The stability of the limit cycle that emerges from a Hopf bifurcation point is determined by the cubic coefficient, also referred to as the first Lyapunov coefficient,  $\alpha$  (refer to Definition 9.2.3). According to Proposition 9.2.4, a Hopf bifurcation is supercritical if  $\alpha < 0$ , subcritical if  $\alpha > 0$ , and degenerate if  $\alpha = 0$ . For a single FN model, the cubic coefficient is

$$\alpha = \frac{1}{8} \left( \frac{2b - b^2 \epsilon - 1}{1 - b^2 \epsilon} \right)$$

Please refer to Chapter 9 for details. The Hopf bifurcations observed experimentally in neurons at the boundary between resting and firing are subcritical [10, 104]. We fix parameter values a = 0.875, b = 0.8, and  $\epsilon = 0.08$  that satisfy Assumption 3.0.1 that there be a unique equilibrium point and ensure subcritical Hopf bifurcations.

As I is increased from zero, there are six values of I that mark boundaries for dynamic regimes:  $I_{0sn}$ ,  $I_{0c}$ ,  $I_0$ ,  $I_1$ ,  $I_{1c}$ , and  $I_{1sn}$ . Behavior according to parameter ranges is described in the caption of Figure 3.2. Figure 3.2 was created using the numerical continuation software package MATCONT [36]. Note that the  $I_{sn}$ , which denote saddle node bifurcations of limit cycles, are almost indistinguishable in parameter space from the  $I_c$ , or canard explosion points [16,53,88]. A canard explosion is a sudden growth in size of limit cycles as the bifurcation parameter is varied. For the FN model, the canard explosion and saddle node bifurcation of limit cycles occur  $\mathscr{O}(\epsilon)$  away from the Hopf bifurcation point. Refer to Chapter 9 for details and a calculation of  $I_{0c}$  and  $I_{1c}$ .



Figure 3.2: Bifurcation diagram for a single FN model drawn with a numerical continuation software tool [36] for a = 0.875, b = 0.8, and  $\epsilon = 0.08$ . Green corresponds to stable equilibrium points or limit cycles and red corresponds to unstable equilibrium points or limit cycles. For most values  $I < I_0$ , the FN model is in the quiescent regime. For  $I_{0sn} \approx I_{0c} < I < I_0$ , the FN model is in the firing regime since it concurrently exhibits a stable equilibrium point, small unstable oscillations, and larger stable oscillations. The FN model is always in the firing regime when  $I_0 < I < I_1$ . For  $I_1 < I < I_{1c} \approx I_{1sn}$ , the FN model is also in the firing regime since it concurrently exhibits a stable equilibrium point, small unstable oscillations, and larger stable oscillations. For all other  $I > I_1$ , the FN model is in the saturated regime. Repeated from Figure 9.1

#### 3.3 Two FN models

The directed two-FN system consists of two FN models, A and B, arranged as in Figure 3.3. Parameter values a, b and  $\epsilon$  are identical for both FN models, A receives a constant external input I, and B receives no external input and receives a linear gap junction (1.2) input from A with strength  $\gamma$ . We characterize the regions of I- $\gamma$ parameter space where different dynamic behavior occurs.

The equations describing the directed two-FN system can be written as a pair of equations that describe a FN model with constant external input I and no coupling and a pair of equations that describe a FN model with no external input and a linear



Figure 3.3: A directed network of two FN model neurons, A and B. A receives an external input I and there is a unidirectional coupling from A to B with strength  $\gamma$ . Repeated from Figure 9.2.

coupling to the other FN model with strength  $\gamma$ . These equations are

$$\frac{dy_A}{dt} = y_A - \frac{y_A^3}{3} - a - z_A + I, \qquad (3.6a)$$

$$\frac{dz_A}{dt} = \epsilon (y_A - bz_A), \tag{3.6b}$$

$$\frac{dy_B}{dt} = y_B - \frac{y_B^3}{3} - a - z_B + \gamma(y_A - y_B), \qquad (3.6c)$$

$$\frac{dz_B}{dt} = \epsilon (y_B - bz_B). \tag{3.6d}$$

The desingularized system (3.5) gives us information about the types of folded singularities present for different parameter values and so can be used to calculate the regimes where canard-driven MMOs may be present. For the directed two-FN system, the desingularized system is given by

$$\frac{dy_A}{d\tau_2} = -(1 - y_B^2 - \gamma) \left( y_A - b \left( y_A - \frac{y_A^3}{3} - a + I \right) \right),$$

$$\frac{dy_B}{d\tau_2} = \gamma \left( y_A - \frac{y_A^3}{3} - a + I \right) - (1 - y_A^2) \left( y_B - b \left( y_B - \frac{y_B^3}{3} - a + \gamma (y_A - y_B) \right) \right).$$
(3.7)

Refer to Chapter 9 for details of the calculation. The desingularized system (3.7) has a single ordinary singularity and two, four, or six folded singularities for different values of I and  $\gamma$ . Refer to Chapter 9, Figure 9.5 for the signs of the real parts of the eigenvalues of the Jacobian evaluated at the ordinary singularity and Figure 9.6 for

the signs of the real parts of the eigenvalues of the Jacobian evaluated at each of the folded singularities.



Figure 3.4: Regions of behavior of the directed two-FN system (3.6) in the  $I-\gamma$  parameter space. Boundaries between regions are identified in the key. In regions (3), (5), (6), and (7), shaded gray, there is a stable limit cycle such that either A or B is firing. In region (3), with cross hatching, only B is firing. In regions (5) and (7), in darker gray, there is phase locking. In region (6), in light gray, A is firing and B may exhibit canard solutions. In region (8), in light gray, B may exhibits MMOs for some parameter values but the necessary conditions for canard-driven MMOs are not satisfied. HH denotes a Hopf-Hopf bifurcation and GH denotes a generalized Hopf bifurcation (also known as a degenerate Hopf or Bautin bifurcation). Adapted from Figure 9.3.

In what follows, we briefly describe the possible and numerically observed dynamics of FN models A and B for the eight distinct regions of I- $\gamma$  parameter space in Figure 3.4. Due to the time rescaling, the stability of the ordinary singularity of the desingularized system will be opposite of the stability of the equilibrium point of the full system, although they are the same point. Chapter 9 contains details about how these results were obtained. The Hopf bifurcations  $I_{0A}$ ,  $I_{1A}$ ,  $I_{0B}$  and  $I_{1B}$  are detailed in Propositions 9.5.1 and 9.5.4. In Chapter 9, a numerical error in calculating the imaginary parts of the eigenvalues of the folded singularities resulted in an inaccurate grouping of regions (6) and (8) as one region. They are distinct because there are no stable folded nodes in region (8), while a stable folded node exists in region (6). We have modified Figure 3.4 to include a separation between these regions.

- The equilibrium point of the directed two-FN system (3.6) is stable, so FN model A and FN model B are quiescent. Phase locking and MMOs are not possible. Refer to Section 9.5.1 for details.
- (2) The equilibrium point of the directed two-FN system (3.6) is stable. FN model A is saturated, resting at a higher voltage, and FN model B is quiescent, so phase locking and MMOs are not possible. Refer to Section 9.5.2 for details.
- (3) The equilibrium point of the directed two-FN system (3.6) is a saddle. FN model A is saturated and FN model B is firing. After a transient, this is analogous to a single firing FN model (B) with a constant external input (A, saturated), which has one fast and one slow variable so MMOs are not possible. Refer to Section 9.5.2, particularly Proposition 9.5.4, for details.
- (4) The equilibrium point of the directed two-FN system (3.6) is stable. FN models A and B are both saturated, so phase locking and MMOs are not possible. Refer to Section 9.5.2 for details.
- (5) The equilibrium point of the directed two-FN system 3.6 is a saddle. FN model A is firing and FN model B is phase locked with A. Canard-driven MMOs are not possible because there are no stable folded nodes in the desingularized system (3.7) for the parameter ranges in this region of *I*-γ space. Refer to Section 9.5.3 for details.
- (6) The equilibrium point of the directed two-FN system (3.6) is a saddle. FN model A is firing. Canard-driven MMOs are possible because there is a stable folded node in the desingularized system 3.7. Phase locking is also possible. Refer to Section 9.5.4 for details. The curve  $I_{**}$  is calculated numerically as the point

where the eigenvalues of the stable folded singularity transition from complex (left of  $I_{**}$ ) to real (right of  $I_{**}$ ).

- (7) The equilibrium point of the directed two-FN system (3.6) is unstable. FN models A and B are both firing and are phase locked. Canard-driven MMOs are not possible because there are no stable folded nodes in the desingularized system (3.7) for the parameter ranges in this region of *I*-γ space. Refer to Section 9.5.4 for details.
- (8) The equilibrium point of the directed two-FN system (3.6) is a saddle. FN model A is firing and FN model B exhibits various behavior according to the values of I and γ chosen. Canard-driven MMOs are not possible because there are no stable folded nodes in the desingularized system (3.7) for the parameter ranges in this region of I-γ space. However, MMOs are observed in numerical simulation, for example in Figure 3.1(b). Determining the generating mechanism for MMOs in this region is a compelling direction for further investigation because the low coupling regime is biologically relevant.

#### 3.4 Directed trees of FN models

The results from the directed two-FN system can be extended to directed trees of FN models with the same intrinsic model parameters and differing external inputs. The Jacobian of a directed tree has a lower block triangular structure. As a result, the eigenvalues of the blocks on the diagonal will determine local stability of the equilibrium point. From this, the parameter values where Hopf bifurcations occur can be determined. As in the directed two-FN system, when two or more FN models are firing, they are phase locked due to the identical  $\epsilon$ . Thus, the parameters for the Hopf bifurcations are also sufficient conditions for phase locking. Refer to Chapter 9 for details, including Figure 9.10 for an example simulation.

## Chapter 4

# Phase Locking in Excitatory -Inhibitory Networks

The work presented in Chapters 2 - 3 relies on the assumption that connections between model neurons follow a linear gap junction coupling  $\gamma_{ij}(x_j - x_i)$ , where *i* is the model neuron under consideration, *j* is summed over all its neighbors, and  $\gamma_{ij} > 0$  is the strength of coupling between model neurons *i* and *j*. In this chapter, we consider inhibitory coupling in addition to the excitatory coupling – this broadens our understanding of synchronization and phase locking in model neuronal systems.

In this chapter, we consider networks of FN model neurons with linear gap junction coupling, but remove the restriction that  $\gamma_{ij} > 0$ , which allows for inhibitory coupling. Our goal is to analyze the dynamics of a network of two unidirectionally coupled FN model neurons for different parameter values of the external input to the first FN model, I, and the coupling from the first FN model to the second,  $\gamma$ . In Section 4.1, as in Chapter 3, we study the stability properties of equilibrium points of the desingularized system. We classify the regions of parameter space where canards and MMOs may exist for  $\gamma < 0$  and provide a numerical example. We carefully study the bifurcation structure of the desingularized system as  $\gamma$  crosses 0 and interpret the changes that are exhibited in Section 4.2. A degenerate Hopf bifurcation characterizes the transition for certain folded singularities under conditions on the external input *I*. Finally, in Section 4.3, we use a numerical example to explore a directed tree of FN model neurons with both excitatory and inhibitory linear gap junction coupling.

## 4.1 Two-FN system with inhibitory electrical coupling

We consider the two-FN system (3.6) with  $\gamma \in \mathbb{R}$  and all other parameter ranges as in Assumption 3.0.1 when  $\gamma > 0$ . For  $\gamma < 0$  there are regions of the *I*- $\gamma$  parameter space where canards and MMOs exist. We describe conditions for which MMOs may be present when  $\gamma < 0$ .

The desingularization of the reduced two-FN system is given by (3.7):

$$\frac{dy_A}{d\tau_2} = -(1 - y_B^2 - \gamma) \left( y_A - b \left( y_A - \frac{y_A^3}{3} - a + I \right) \right),$$

$$\frac{dy_B}{d\tau_2} = \gamma \left( y_A - b \left( y_A - \frac{y_A^3}{3} - a + I \right) \right)$$

$$- (1 - y_A^2) \left( y_B - b \left( y_B - \frac{y_B^3}{3} - a + \gamma (y_A - y_B) \right) \right).$$
(4.1)

In Section 9.4.2, we solve for the equilibrium values and stability properties of the ordinary and folded singularities in the desingularized system (4.1) as a function of I and  $\gamma$ . The folded singularities are found using the same process for  $\gamma < 0$ . Assumption 3.0.1 guarantees a unique ordinary singularity for  $\gamma > 0$ , but there are regions of the I- $\gamma$  parameter space for  $\gamma < 0$  where there are three ordinary singularities. The conditions for the ordinary singularities are identical to those that give the equilibrium points of the original system (3.6):

$$0 = y_{A*} - b\left(y_{A*} - \frac{y_{A*}^3}{3} - a + I\right), \qquad (4.2a)$$

$$0 = y_{B*} - b \left( y_{B*} - \frac{y_{B*}^3}{3} - a + \gamma (y_{A*} - y_{B*}) \right).$$
(4.2b)

The process of determining the number of ordinary singularities is analogous to the process for determining the number of folded singularities in Section 9.4.2. The conditions on a, b, and I follow Assumption 3.0.1, so there is one solution to Equation (4.2a). Equation 4.2b can be written as a cubic equation

$$\beta_3 y_{B*}^3 + \beta_2 y_{B*}^2 + \beta_1 y_{B*} + \beta_0 = 0, \qquad (4.3)$$

where  $\beta_0 = ba - b\gamma y_{A*}$ ,  $\beta_1 = 1 - b + b\gamma$ ,  $\beta_2 = 0$ , and  $\beta_3 = \frac{b}{3}$ .

As in Section 9.4.2, the solutions of (4.3) for  $y_{B*}$  as a function of  $\gamma$  and I are given by

$$y_{A*,k} = -\frac{1}{3\beta_3} \left( \beta_2 + C_k + \frac{\beta_2^2 - 3\beta_1\beta_3}{C_k} \right),$$

where, for k = 1, 2, 3,

$$C_{k} = \left(\frac{\sqrt{-3}-1}{2}\right)^{k-1} \left(\frac{\sigma - \sqrt{-27\beta_{3}^{2}\Delta}}{2}\right)^{1/3},$$
$$\Delta = 18\beta_{3}\beta_{2}\beta_{1}\beta_{0} - 4\beta_{0}\beta_{2}^{3} + \beta_{2}^{2}\beta_{1}^{2} - 4\beta_{3}\beta_{1}^{3} - 27\beta_{3}^{2}\beta_{0}^{2},$$
$$\sigma = 2\beta_{2}^{2} - 9\beta_{3}\beta_{2}\beta_{1} + 27\beta_{3}^{2}\beta_{0}.$$

If  $\Delta > 0$ , there are three real solutions (three ordinary singularities), and, if  $\Delta < 0$ , there is one real solution (one ordinary singularity). When  $\gamma > 0$ ,  $\Delta < 0 \forall I$ . When  $\gamma < 0$ , there are regions of *I*- $\gamma$  parameter space where  $\Delta > 0$  and there are three ordinary singularities.

The signs of the real parts of the eigenvalues of the three ordinary singularities in the desingularized system (4.1) are plotted as a function of I and  $\gamma$  in Figure 4.1. In regions where there are three ordinary singularities, we do not describe the dynamics of A and B here. In regions where there is only one ordinary singularity, the dynamics are described in the following. When A and B are both quiescent or saturated, there is only one ordinary singularity and it is an unstable equilibrium in the desingularized system (4.1) with positive real parts of both eigenvalues, which corresponds to a stable equilibrium in the full system (2.10). The regions where Aand B are both quiescent or saturated are  $I < I_{0A}$  and  $I > I_{1A}$ , which correspond to the quiescent and saturated regions for A. In regions where there is only one ordinary singularity A is firing, and B may or may not be firing,  $I_{0A} < I < I_{IA}$ , the ordinary singularity is a saddle in the desingularized system (4.1) and the full system (2.10).



Figure 4.1: Regions in the I- $\gamma$  parameter space distinguishing local stability of the three ordinary singularities in the desingularized system (4.1). Each plot corresponds to one of the three ordinary singularities. In white regions, the ordinary singularity does not exist. In dark gray regions, the ordinary singularity is unstable. In light gray regions, the ordinary singularity is a saddle. In light blue regions, the ordinary singularity is stable. The Hopf bifurcations and distinguishing features of the original two-FN system (3.6), the boundaries in Figure 9.3, are plotted for comparison as five curves.

The equilibrium values and stability properties of all six folded singularities detailed in Section 9.4.2 can be extended to  $\gamma < 0$ . Figure 4.2 depicts regions in I- $\gamma$ parameter space according to the local stability of the folded singularities. The white regions in Figure 4.2 correspond to values of I and  $\gamma$  where the given folded singularity does not exist in the desingularized system (4.1) (i.e.  $\Delta < 0$ ). In dark gray regions, the folded singularity is unstable. In light gray regions, the folded singularity is a saddle. In light blue regions, the folded singularity is stable.

The two folded singularities in the bottom row of Figure 4.2 exhibit no changes in stability as  $\gamma$  changes from positive to negative. Two of the folded singularities  $y_{B*} = \sqrt{1-\gamma}$  persist as folded saddles as  $\gamma$  crosses zero, except for  $I < I_{0A}$  for the first (top row, right) and  $I > I_{1A}$  for the second (middle row, right). Two of the folded singularities  $y_{B*} = \sqrt{1-\gamma}$  exhibit the reverse – the first (top row, left) changes stability for  $I > I_{0A}$  and the second (middle row, left) changes stability for  $I < I_{1A}$ . These changes in stability as  $\gamma$  crosses zero are a feature we explore further in Section 4.2.

When the folded singularity is stable, it is either a stable folded node or a stable folded focus. Figure 4.3 depicts the regions of  $I-\gamma$  parameter space where the eigenvalues of each folded singularity are real.

Thus, the regions where robust families of canards could exist for  $\gamma < 0$  are the light blue regions that overlap between Figure 4.2 and Figure 4.3. This can be further refined by the condition that there be an ordinary singularity that is a saddle to ensure the return mechanism to the stable folded node that allows for MMOs to exist. Figure 4.4 depicts examples of small amplitude oscillations (SAOs) and MMOs for values of I and  $\gamma$  in regimes where stable folded singularities exist and there is a single ordinary singularity that is a saddle. The shape of the SAOs differ from the shape of the SAOs when  $\gamma > 0$ , as seen by comparing Figure 4.4 with Figure 3.1.

We check whether the eigenvalues of the singularities have an imaginary component for all six folded singularities and find that all stable folded singularities in the  $\gamma < 0$  regime are foci. The lack of stable folded nodes should indicate a lack of robust families of canard solutions in the full system, but both canard-like SAOs and MMO



Figure 4.2: Regions in the  $I-\gamma$  parameter space distinguishing local stability of the three folded singularities corresponding to  $y_{B*} = -\sqrt{1-\gamma}$  (top, middle, and bottom plots on the left) and the three folded singularities corresponding to  $y_{B*} = \sqrt{1-\gamma}$  (top, middle, and bottom plots on the right). This is modified from Figure 9.6 to include negative values for  $\gamma$ . In white regions, the folded singularity does not exist. In dark gray regions, the folded singularity is unstable. In light gray regions, the folded singularity is stable.

are present for  $\gamma < 0$  as seen in Figure 4.4. We also ran simulations for a range of values of I and  $\gamma < 0$  for which there are no stable folded nodes and observed both canard-like SAOs and MMOs. These results warrant further investigation.

#### **4.2** Bifurcations at $\gamma = 0$

In this section, we look at the transition between positive and negative  $\gamma$  in the desingularized two-FN system (4.1). We highlight degenerate Hopf bifurcations that occur at  $\gamma = 0$  and are the mechanism for the transitions in stability for the folded



Figure 4.3: Regions in the I- $\gamma$  parameter space distinguishing existence of imaginary parts of the eigenvalues for the three folded singularities corresponding to  $y_{B*} = -\sqrt{1-\gamma}$  (top, middle, and bottom plots on the left) and the three folded singularities corresponding to  $y_{B*} = \sqrt{1-\gamma}$  (top, middle, and bottom plots on the right). In white regions, the folded singularity does not exist. In dark gray regions, the folded singularity has imaginary or complex eigenvalues. In light blue regions, the folded singularity has real eigenvalues.



Figure 4.4: Examples of canard-like SAOs (left) and MMOs (right) in the two-FN system with negative coupling  $\gamma < 0$ . Parameters used in the simulation are I = 1,  $\gamma = -0.04$  (left) and I = 0.7,  $\gamma = -0.09$  (right). In both plots, the light purple trace is the voltage of FN model A, while the dark trace is the voltage of FN model B. The small oscillations in both panels are canards.

singularities at  $\gamma = 0$  depicted in Figure 4.2. Conditions for the existence and stability of degenerate Hopf bifurcations are provided for each folded singularity in terms of *I*.

At  $\gamma = 0$ , there is one ordinary singularity. It does not change stability, as seen in Figure 4.2. Two of the six folded singularities have large values for  $y_{A*}$  and do not experience stability changes across I- $\gamma$  parameter space. The other four are (-1, -1), (-1, 1), (1, -1), and (1, 1), i.e.,  $y_{A*}^2 - 1 = 0$  and  $y_{B*}^2 - 1 = 0$  for these four folded singularities. Here, we detail the bifurcations at  $\gamma = 0$  for the desingularized two-FN system. We begin with definitions of Hopf bifurcations and the coefficients used to determine type of Hopf bifurcations. The normal form for a Hopf bifurcation is described in [28], which we quote in the following.

The dynamics at a Hopf bifurcation at the origin of a two-dimensional system can be written as

$$\left(\begin{array}{c} \frac{dx_1}{dt}\\ \frac{dx_2}{dt} \end{array}\right) = \left(\begin{array}{c} 0 & -\omega\\ \omega & 0 \end{array}\right) \left(\begin{array}{c} x_1\\ x_2 \end{array}\right) + \left(\begin{array}{c} F(x_1, x_2)\\ G(x_1, x_2) \end{array}\right), \quad (4.4)$$

such that F and G satisfy F(0,0) = G(0,0) = 0 and  $D_{\mathbf{x}}F(0,0) = D_{\mathbf{x}}G(0,0) = \mathbf{0}$  where  $D_{\mathbf{x}}F$  is the Jacobian of F with respect to  $\mathbf{x}$  and  $\mathbf{x} = (x_1, x_2)^{\top}$ .

**Definition 4.2.1** (First Lyapunov coefficient [28, 53, 57]). Consider the system (4.4). The coefficient of the cubic term of the Taylor expansion of the RHS of (4.4) is expressed as

$$\alpha = \frac{1}{16} (F_{x_1 x_1 x_1} + F_{x_1 x_2 x_2} + G_{x_1 x_1 x_2} + G_{x_2 x_2 x_2}) \Big|_{(0,0)} + \frac{1}{16\omega} (F_{x_1 x_2} (F_{x_1 x_1} + F_{x_2 x_2}) - G_{x_1 x_2} (G_{x_1 x_1} + G_{x_2 x_2}) - F_{x_1 x_1} G_{x_1 x_1} + F_{x_2 x_2} G_{x_2 x_2}) \Big|_{(0,0)},$$

$$(4.5)$$

where  $F_{x_1x_2}$  denotes  $\frac{\partial^2 F}{\partial x_1 \partial x_2}$ , and so on.

**Proposition 4.2.2** (Theorem 3.4.2 (modified) [53], [28]). The system  $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mu)$ , admits a Hopf bifurcation for the parameter value  $\mu = \mu_0$  at an equilibrium point  $\mathbf{x} = \mathbf{0}$  if

- 1.  $D_{\mathbf{x}}\mathbf{f}(\mathbf{0},\mu_0)$  has a pair of pure imaginary eigenvalues and no other eigenvalues with zero real parts.
- 2.  $\frac{\partial}{\partial \mu} \Re(\lambda(\mu)) \Big|_{\mu=\mu_0} \neq 0$ , where  $\Re(\lambda)$  denotes the real part of the eigenvalue  $\lambda$ .
- The cubic coefficient of the Taylor expansion of f, denoted by α and defined in Definition 4.2.1, is nonzero.

Furthermore, if  $\alpha < 0$ , the Hopf bifurcation is supercritical, while, if  $\alpha > 0$ , the Hopf bifurcation is subcritical.

For details of the proof, refer to Chapter 9.

**Definition 4.2.3** (Second Lyapunov coefficient when  $\alpha = 0$  [73]). Consider the system (4.4), where the first and second conditions of Proposition 4.2.2 are satisfied and the first Lyapunov coefficient  $\alpha$  is zero. The second Lyapunov coefficient  $\beta$  is expressed as

$$\beta = \frac{1}{12\omega} \operatorname{Re}(g_{32}) + \frac{1}{12\omega^2} \operatorname{Im} \left[ g_{20}\bar{g}_{31} - g_{11} \left( 4g_{31} + 3\bar{g}_{22} \right) - \frac{1}{3}g_{02} \left( g_{40} + \bar{g}_{13} \right) - g_{30}g_{12} \right] \\ + \frac{1}{12\omega^3} \left\{ \operatorname{Re} \left[ g_{20} \left( \bar{g}_{11} (3g_{12} - \bar{g}_{30}) + g_{02} \left( \bar{g}_{12} - \frac{1}{3}g_{30} \right) + \frac{1}{3}\bar{g}_{02}g_{03} \right) \right. \\ \left. + g_{11} \left( \bar{g}_{02} \left( \frac{5}{3}\bar{g}_{30} + 3g_{12} \right) + \frac{1}{3}g_{02}\bar{g}_{03} - 4g_{11}g_{30} \right) \right] \operatorname{3Im} \left( g_{20}g_{11} \right) \operatorname{Im}(g_{21}) \right\} \\ \left. + \frac{1}{12\omega^4} \left\{ \operatorname{Im} \left[ g_{11}\bar{g}_{02} \left( \bar{g}_{20}^2 - 3\bar{g}_{20}g_{11} - 4g_{11}^2 \right) \right] + \operatorname{Im} \left( g_{20}g_{11} \right) \left[ \operatorname{3Re}(g_{20}g_{11}) - 2|g_{02}|^2 \right] \right\}$$

where  $g_{ij} = \langle p, B^{i+j}(\underbrace{s, \dots, s}_{i}, \underbrace{\overline{s}, \dots, \overline{s}}_{j}) \rangle$ , with

$$B^{i+j}(\underbrace{u,\ldots,u}_{i},\underbrace{w,\ldots,w}_{j}) = \left(u^{\top},\ldots,u^{\top}\right)^{\top} \frac{\partial^{i+j}\mathcal{F}(\mathbf{x},0)}{\partial \mathbf{x}^{i+j}}\Big|_{\mathbf{x}=\mathbf{0}} \begin{pmatrix} w \\ \vdots \\ w \end{pmatrix}$$
(4.6)

Here,  $\mathcal{F} = (F, G)^{\top}$ , s is an eigenvector of A that corresponds to an eigenvalue  $i\omega$ , and p is an eigenvector of  $A^{\top}$  that corresponds to eigenvalue  $-i\omega$ .

**Definition 4.2.4** (Degenerate Hopf bifurcation). Consider the conditions for a Hopf bifurcation given in Proposition 4.2.2 and let the first condition be satisfied. If either of the second or third conditions are not satisfied, the bifurcation is a degenerate Hopf bifurcation. If the first and second conditions are satisfied but the third is not, we call the resulting bifurcation a degenerate Hopf bifurcation Type I. If the first and third conditions are satisfied but the second is not, we call the resulting bifurcation a degenerate Hopf bifurcation Type II. Furthermore, if  $\beta < 0$ , the degenerate Hopf bifurcation is supercritical, while, if  $\beta > 0$ , the degenerate Hopf bifurcation is subcritical. Further classification of the bifurcation structure near degenerate Hopf bifurcations as a function of the bifurcation parameter can be found in [50].

Degenerate Hopf bifurcations have been studied in the Hodgkin-Huxley model neuron [74] and the FitzHugh-Nagumo model neuron when parameters a, b, I, and  $\epsilon$  are treated as bifurcation parameters [106]. In the following Proposition, we give conditions for degenerate Hopf bifurcations in terms of I for each of the four folded singularities at  $y_{A*}^2 = 1$  and  $y_{B*}^2 = 1$ .

**Proposition 4.2.5.** Consider the desingularized two-FN system (4.1) and Assumption 3.0.1. Then, for any fixed I > 0, two degenerate Hopf bifurcations occur at  $\gamma = 0$  as follows

- 1. For  $I < I_{0A}$ , the degenerate Hopf bifurcations occur at the folded singularities (-1,1) and (1,-1),
- 2. For  $I \in (I_{0A}, I_{1A})$ , the degenerate Hopf bifurcations occur at the folded singularities (-1, -1) and (1, -1),
- 3. For  $I > I_{1A}$ , the degenerate Hopf bifurcations occur at the folded singularities (-1,-1) and (1,1),

where  $I_{0A} = -\frac{1}{b} + \frac{2}{3} + a$ , and  $I_{1A} = \frac{1}{b} - \frac{1}{3} + a$ .

*Proof.* When  $\gamma = 0$ , the first condition of Proposition 4.2.2 is satisfied. We check the second and third conditions.

We begin by transforming the system (4.1) to the origin. Letting  $y_{0A} = y_A - y_{A*}$ and  $y_{0B} = y_B - y_{B*}$ , we obtain the equations

$$\frac{dy_{0A}}{d\tau_2} = -\left(1 - (y_{0B} + y_{B*})^2 - \gamma\right) \left(y_{0A} + y_{A*} - b\left(y_{0A} + y_{A*} - \frac{(y_{0A} + y_{A*})^3}{3} - a + I\right)\right),$$

$$\frac{dy_{0B}}{d\tau_2} = \gamma \left(y_{0A} + y_{A*} - b\left(y_{0A} + y_{A*} - \frac{(y_{0A} + y_{A*})^3}{3} - a + I\right)\right) - (1 - (y_{0A} + y_{A*})^2) \quad (4.7)$$

$$\cdot \left(y_{0B} + y_{B*} - b\left(y_{0B} + y_{B*} - \frac{(y_{0B} + y_{B*})^3}{3} - a + \gamma(y_{0A} + y_{A*} - (y_{0B} + y_{B*}))\right)\right).$$

At the bifurcation point,  $\gamma = 0$ , the value of the equilibrium points of the desingularized system can be solved from the relations  $y_{B*}^2 - 1 = 0$  and  $y_{A*}^2 - 1 = 0$ .

First, we check the transversality condition (Proposition 4.2.2, (2)) by showing that the eigenvalues of the Jacobian evaluated at  $(y_{0A}, y_{0B}) = (0, 0)$  cross the imaginary axis with non-zero speed as  $\gamma$  is changed. We do this by taking the partial derivative of the trace of  $D_{\mathbf{y}}\rho(0,0)$ , where  $\rho$  is the right hand side of (4.1), with respect to  $\gamma$  and evaluating at  $\gamma = 0$ . If that is nonzero, then the real parts of the eigenvalues are nonzero and the transversality condition is satisfied. The Jacobian of (4.1) is

$$D_{\mathbf{y}}\rho(0,0) = \begin{pmatrix} -(1-y_{B*}^2-\gamma)(1-b+by_{A*}^2) & 2y_{B*}(y_{A*}-bz_{A*}) \\ \gamma + 2y_{A*}(y_{B*}-bz_{B*}) & -(1-y_{A*}^2)(1-b(1-y_{B*}^2-\gamma)) \end{pmatrix},$$

with trace

$$\operatorname{Tr}(D_{\mathbf{y}}\rho(0,0)) = -\left(1 - y_{B*}^2 - \gamma\right)\left(1 - b + by_{A*}^2\right) - \left(1 - y_{A*}^2\right)\left(1 - b(1 - y_{B*}^2 - \gamma)\right).$$

The derivative of the trace of  $D_{\mathbf{y}}\rho(0,0)$  is given by

$$\begin{split} \frac{\partial}{\partial\gamma}\operatorname{Tr}(D_{\mathbf{y}}\rho(0,0)) &= \left(2y_{B*}\frac{\partial y_{B*}}{\partial\gamma} + 1\right)\left(1 - b + by_{A*}^2\right) + \left(2y_{A*}\frac{\partial y_{A*}}{\partial\gamma}\right)\left(1 - 2b(1 - y_{B*}^2 - \gamma)\right) \\ &+ \left(1 - y_{A*}^2\right)\left(2by_{B*}\frac{\partial y_{B*}}{\partial\gamma} + b\right). \end{split}$$

Evaluating at  $\gamma = 0$  and applying the relations  $y_{B*}^2 - 1 = 0$  and  $y_{A*}^2 - 1 = 0$  we obtain

$$\frac{\partial}{\partial \gamma} \operatorname{Tr}(D_{\mathbf{y}}\rho(0,0)) \Big|_{\substack{\gamma=0\\y_{A*}^2=1\\y_{B*}^2=1}} = \left(2y_{B*}\frac{\partial y_{B*}}{\partial \gamma} + 1\right) + 2y_{A*}\frac{\partial y_{A*}}{\partial \gamma}.$$

The values of the partial derivatives of the equilibrium points with respect to  $\gamma$  are

$$\frac{\partial y_{A*}}{\partial \gamma}\Big|_{\substack{y_{A*}^{2}=1\\y_{B*}^{2}=1}} = -\frac{y_{A*} - b\left(y_{A*} - \frac{y_{A*}^{3}}{3} - a + I\right)}{2y_{A*}\left(y_{B*} - b\left(y_{B*} - \frac{y_{B*}^{3}}{3} - a\right)\right)},$$
$$\frac{\partial y_{B*}}{\partial \gamma}\Big|_{\substack{y_{A*}^{2}=1\\y_{B*}^{2}=1}} = \mp \frac{1}{2}.$$
Substituting these to the expression we obtain for the partial derivative of the trace with respect to  $\gamma$ 

$$\frac{\partial}{\partial\gamma} \operatorname{Tr}(D_{\mathbf{y}}\rho(0,0))\Big|_{\substack{\gamma=0\\y_{A*}^2=1\\y_{B*}^2=1}} = -\frac{y_{A*} - b\left(y_{A*} - \frac{y_{A*}^3}{3} - a + I\right)}{\left(y_{B*} - b\left(y_{B*} - \frac{y_{B*}^3}{3} - a\right)\right)}$$

We check the conditions where this is equal to zero, which gives values of the system parameters where the transversality condition is not satisfied:

$$0 = y_{A*} - b\left(y_{A*} - \frac{y_{A*}^3}{3} - a + I\right).$$
(4.8)

For all other values of I, the second condition of Proposition 4.2.2 is satisfied.

Next, we transform the system into the form given by (4.4) by finding a change of coordinates that results in a matrix with the imaginary parts of the eigenvalues in the off-diagonal entries. The Jacobian of (4.1) evaluated at the equilibrium (0,0),  $\gamma = 0$ , and  $y_{A*}^2 = y_{B*}^2 = 1$  is

$$D_{\mathbf{y}}\rho(0,0)\Big|_{\substack{\gamma=0\\y_{A_*}^2=1\\y_{B_*}^2=1}} = \begin{pmatrix} 0 & 2y_{B_*}r\\ 2y_{A_*}q & 0 \end{pmatrix},$$
(4.9)

where  $r = y_{A*} - b\left(y_{A*} - \frac{y_{A*}^3}{3} - a + I\right)$  and  $q = y_{B*} - b\left(y_{B*} - \frac{y_{B*}^3}{3} - a\right)$ . The conditions  $a \in (0, 1)$  and  $b \in (0, 1)$  that arise from Assumption 3.0.1 give q > 0,  $\forall y_{B*}$ . The sign of r in terms of I for the four folded singularities of interest is shown in Table 4.1. The eigenvalues of the matrix (4.9) are given by  $\lambda = \pm 2\sqrt{y_{A*}y_{B*}qr}$ . When  $y_{A*}y_{B*}qr < 0$ , the eigenvalues are purely imaginary and  $\omega = 2\sqrt{-y_{A*}y_{B*}qr}$ . Conditions for when the eigenvalues are purely imaginary as a function of I are given in Table 4.1. When the eigenvalues are purely imaginary,  $\omega^2 = -4y_{A*}y_{B*}qr$ . The

Table 4.1: Type of folded singularity for  $\gamma = 0$  in the desingularized two-FN system as a function of I. The upper table depicts the computational steps to finding the values of the eigenvalues and the resulting type of equilibrium as a function of I. The top row denotes the folded singularity, the second row shows the value of  $y_{A*}$  multiplied by  $y_{B*}$  at that folded singularity, the third row shows the sign of q multiplied by r as a function of I, and the fourth row shows the type of folded singularity. The lower table depicts the type of folded singularity for the three regimes of I. In each entry of the right column, the lower left corresponds to the type of folded singularity for (1, -1), the upper right corresponds to the type of folded singularity for (1, 1), and the upper left corresponds to the type of folded singularity for (-1, 1).

$(y_{A*}, y_{B*})$	(-1, -1)		(+1, -1)		(-1, +1)		(1,1)	
$y_{A*}y_{B*}$	+1		-1		-1		+1	
$\operatorname{Sign}(qr)$	$I > I_{0A}$ <0	$I < I_{0A}$ $> 0$	$I > I_{1A}$ < 0	$I < I_{1A}$ $> 0$	$I > I_{0A}$ <0	$I < I_{0A}$ > 0	$I > I_{1A}$ < 0	$I < I_{1A}$ > 0
Type	Center	Saddle	Saddle	Center	Saddle	Center	Center	Saddle

I < Int	Center	Saddle
$I \leq I_{0A}$	Saddle	Center
	Saddle	Saddle
$I_{0A} < I < I_{1A}$	Center	Center
I > L	Saddle	Center
	Center	Saddle

corresponding eigenvectors are  $v_{1,2} = (\pm ic, 1)^{\top}$ , where  $c = \frac{2y_{B*}r}{\omega}$ . We let

$$T = \begin{pmatrix} 0 & c \\ 1 & 0 \end{pmatrix}, \text{ which gives } T^{-1} = \begin{pmatrix} 0 & 1 \\ \frac{1}{c} & 0 \end{pmatrix}.$$

Then, we have the desired relation

$$T^{-1}D_{\mathbf{y}}\rho(0,0)\Big|_{\substack{\gamma=0\\y_{A*}^2=1\\y_{B*}^2=1}}T = \begin{pmatrix} 0 & -\omega\\ \omega & 0 \end{pmatrix},$$

and the transformation  $\eta = T^{-1}(y_{0A}, y_{0B})^{\top}$  gives us the relation

$$\frac{d\eta}{dt} = T^{-1} D_{\mathbf{y}} \rho(0,0) \Big|_{\substack{\gamma=0\\y_{A_*}^2=1\\y_{B_*}^2=1}} T\eta + T^{-1} \mathbf{h}(T\eta).$$

The function  $\mathbf{h}(\mathbf{x})$  can be found by considering the nonlinear terms in (4.7) at  $\gamma = 0$ . Solving for the nonlinear terms, we obtain

$$\begin{pmatrix} h_1(y_{0A}, y_{0B}) \\ h_2(y_{0A}, y_{0B}) \end{pmatrix} = \begin{pmatrix} \begin{pmatrix} y_{0B}^2 \left( y_{0A} + y_{A*} - b \left( y_{0A} + y_{A*} - \frac{(y_{0A} + y_{A*})^3}{3} - a + I \right) \right) \\ + 2y_{0B}y_{B*} \left( y_{0A} - b \left( y_{0A} - \frac{y_{0A}^3}{3} - y_{0A}^2 y_{A*} - y_{0A} y_{A*}^2 \right) \right) \\ \begin{pmatrix} y_{0A}^2 \left( y_{0B} + y_{B*} - b \left( y_{0B} + y_{B*} - \frac{(y_{0B} + y_{B*})^3}{3} - a \right) \right) \\ + 2y_{0A}y_{A*} \left( y_{0B} - b \left( y_{0B} - \frac{y_{0B}^3}{3} - y_{0B}^2 y_{B*} - y_{0B} y_{B*}^2 \right) \right) \end{pmatrix} \end{pmatrix} \end{pmatrix}$$

The nonlinear terms,  $T^{-1}\mathbf{h}(T\eta)$  are

$$\begin{pmatrix} F(\eta_1, \eta_2) \\ G(\eta_1, \eta_2) \end{pmatrix} = \begin{pmatrix} h_2 \begin{pmatrix} c\eta_2 \\ \eta_1 \end{pmatrix} \\ \frac{1}{c} h_1 \begin{pmatrix} c\eta_2 \\ \eta_1 \end{pmatrix} \end{pmatrix}$$

•

This gives us

$$\begin{pmatrix} F(\eta_1, \eta_2) \\ G(\eta_1, \eta_2) \end{pmatrix} = \begin{pmatrix} \left( c^2 \eta_2^2 \left( \eta_1 + y_{B*} - b \left( \eta_1 + y_{B*} - \frac{(\eta_1 + y_{B*})^3}{3} - a \right) \right) \\ + 2c \eta_2 y_{A*} \left( \eta_1 - b \left( \eta_1 - \frac{\eta_1^3}{3} - \eta_1^2 y_{B*} - \eta_1 y_{B*}^2 \right) \right) \\ \left( \frac{1}{c} \eta_1^2 \left( c \eta_2 + y_{A*} - b \left( c \eta_2 + y_{A*} - \frac{(c \eta_2 + y_{A*})^3}{3} - a + I \right) \right) \\ + \frac{1}{c} 2\eta_1 y_{B*} \left( c \eta_2 - b \left( c \eta_2 - \frac{c^3 \eta_2^3}{3} - c^2 \eta_2^2 y_{A*} - c \eta_2 y_{A*}^2 \right) \right) \end{pmatrix} \end{pmatrix} \right)$$

The nonlinear functions satisfy F(0,0) = G(0,0) = 0. Taking derivatives, the nonlinear functions also satisfy  $D_{\eta}F(0,0) = D_{\eta}G(0,0) = 0$ . To compute the stability of the limit cycles resulting from the Hopf bifurcation, we check the sign of the cubic coefficient,  $\alpha$ , given in Definition 4.2.1. To find  $\alpha$ , we begin by computing the partial derivatives of F and G, which are given in Appendix A.1. The value of  $\alpha$  as a function of I is computed from these derivatives in Appendix A.2. When  $\gamma = 0$  and the first two conditions of Proposition 4.2.2 are satisfied,  $\alpha = 0$  for all values of I at all four folded singularities. Thus, the third condition of Proposition 4.2.2 is not satisfied and the bifrucation is a degenerate Hopf bifurcation Type I.

To obtain information about the stability of the limit cycles originating from the Hopf bifurcation, we calculate the second Lyapunov coefficient in Appendix A.3 using the method described in Definition 4.2.3. Table 4.2 compiles the information from this calculation. Figure 4.5 shows the sign of the second Lyapunov coefficient as calculated in Appendix A.3.

Table 4.2: Type of degenerate Hopf bifurcation for  $\gamma = 0$  in the desingularized two-FN system as a function of I. Each of the four fixed points that satisfy  $y_{A*}^2 = 1$  and  $y_{B*}^2 = 1$  is shown.  $I_{*-}$  and  $I_{*+}$  are the points where  $\beta = 0$  found in Appendix A.3.

$(y_{A*}, y_{B*})$	(-1, -1)	(+1, -1)	(-1, +1)	(+1, +1)
$I < I_{0A}$	none	subcritical	supercritical	none
$I_{0A} < I < I_{*-}$	supercritical	subcritical	none	none
$I_{*-} < I < I_{*+}$	subcritical	subcritical	none	none
$I_{*+} < I < I_{1A}$	subcritical	supercritical	none	none
$I_{1A} < I$	subcritical	none	none	supercritical

**Remark 4.2.6.** The values of I where the transversality conditions are not satisfied according to (4.8) are equivalent to  $I_{0A}$  and  $I_{1A}$  evaluated at  $y_{A*} = 1$ . These



Figure 4.5: Sign of the second Lyapunov coefficient  $\beta$  as a function of I for four folded singularities at  $\gamma = 0$ . In this figure, a = 0.875 and b = 0.8. The  $(y_{A*}, y_{B*})$  value of the folded singularity is given in parentheses. Red indicates that  $\beta > 0$ , so the degenerate Hopf bifurcation is subcritical, and green indicates that  $\beta > 0$ , so the degenerate Hopf bifurcation is supercritical.

correspond to the Hopf bifurcations as a function of I in the full system (3.6) and degenerate Hopf bifurcations of Type II in the desingularized system.

**Remark 4.2.7.** When  $\gamma = 0$  and the conditions for the degenerate Hopf bifurcations are met, the stability of the small limit cycles emerging from the degenerate Hopf bifurcation for a small range of  $\gamma$  around  $\gamma = 0$  can be determined by the second Lyapunov coefficient  $\beta$ . Further work is required to determine whether one or more saddle node of limit cycles bifurcations and subsequent changes in stability are present. A thorough classification of degenerate Hopf bifurcations can be found in [50].

When  $\gamma < 0$ , there are two distinct differences from  $\gamma > 0$  that we detailed in Section 4.1. First, for parameter values that satisfy Assumption 3.0.1 for  $\gamma > 0$ , there are regions of *I*- $\gamma$  parameter space for  $\gamma < 0$  that have three equilibrium points for system (3.6). It would be useful to find conditions on *a*, *b*, and  $\epsilon$  such that there is a single equilibrium point for all values of *I* and  $\gamma$  considered. Second, while canards and MMOs are exhibited in simulation, there are no stable folded nodes when  $\gamma < 0$ , which are a necessary condition for the robust families of canards that form the small oscillations in MMOs. This may be indicative of a different generating mechanism for MMOs and needs further study.

The transition between excitatory ( $\gamma > 0$ ) and inhibitory ( $\gamma < 0$ ) coupling is characterized by degenerate Hopf bifurcations in the desingularized system and no change to the single equilibrium point of the full system. A generalized Hopf bifurcation in the full system is a known generating mechanism for MMOs [25,52]. Further investigation is needed to determine whether the degenerate Hopf bifurcations in the desingularized system generate the MMOs present in the inhibitory directed two-FN system.

#### 4.3 Numerical example

In this section, we provide a numerical example of a directed tree of FN models with both excitatory and inhibitory coupling. As described in Section 9.6, a directed tree is composed of distinct directed chains that can be analyzed independently.

In Figure 4.6, we illustrate with the directed chain that starts with the light orange FN model and is directed to the right to the cyan FN model. The structure and inputs to the chain are the same as that illustrated in Section 9.6 but the coupling weights are different. The first FN model (light orange) receives an input I = 1.2, which ensures that it is firing. The coupling strength from the first FN model to the second FN model (dark orange) with input I = 0.4 is  $-\gamma$ , where  $\gamma = 0.4$ . This combination of coupling strength of inputs ensures that the second FN model is firing. The coupling strength to the third FN model (dark cyan) with zero input is  $-0.2\gamma$ . In this case, MMOs induced by canards are exhibited. The input to the fourth FN model (cyan) is an MMO. The strong positive coupling from the third FN model to the fourth FN model,  $\gamma = 0.4$ , ensures the frequency of spiking in the fourth FN model is the same as the frequency of the third FN model.

The graph structure and inputs in this simulation is the same as the example presented in Section 9.6, but the different coupling strengths illustrate similarities and differences in firing patterns in the presence of inhibitory coupling. The main similarity we highlight here is the presence of canards and MMOs for low strength excitatory and inhibitory coupling. A crucial difference between the excitatory and inhibitory regimes is the offset in spike timing. The following assumes the FN models in a chain are firing. When the coupling is excitatory ( $\gamma > 0$ ), the spikes of consecutive FN models in the chain occur close to one another in time. As the magnitude of  $\gamma$  is increased, the timing of spikes grows increasingly similar. This is depicted in Figure 9.10. When the coupling is inhibitory, ( $\gamma < 0$ ), the spikes of consecutive FN models in the chain are phase locked but are out of phase. As the magnitude of  $\gamma$  is increased, the spike of the n + 1th FN model aligns with the point where the nth FN model repolarizes. This is depicted in the first two FN models in Figure 4.3. When there are multiple FN models with MMOs and the large oscillations of one occur during the SAOs of another, the resulting behavior is called "leap-frogging." Leap-frogging oscillations have been observed in FN models with inhibitory coupling [42].



Figure 4.6: Numerical simulation of a directed tree graph of FN model neurons with heterogeneous external inputs. The directed tree is the same as the network from Figure 9.10, but incorporates both excitatory ( $\gamma > 0$ ) and inhibitory ( $\gamma < 0$ ) coupling strengths. Panel (a) depicts a directed tree graph of FN model neurons with heterogeneous external inputs  $I_i$  and edge weights as shown, where  $\gamma = 0.4$ . A representative chain is selected and indicated by vertices with colors matching simulation results, which are shown in panel (b).

## Chapter 5

# Final Remarks<sup>\*</sup>

In this dissertation, we derived novel bounds for synchronization in arbitrary networks of heterogeneous nonlinear systems in terms of the network structure and examined the dynamics of coupled model neurons. We implemented nonsmooth Lyapunov functions to compute sufficient conditions for cluster synchronization in networks of heterogeneous nonlinear systems coupled through linear gap junctions. These bounds represent an improvement over the synchronization bounds previously reported in the literature and incorporate two key types of heterogeneity: (1) differences in model parameters and (2) arbitrary network structure. Reductions of cluster synchronized networks motivated the detailed analysis of a network of two FitzHugh-Nagumo model neurons with heterogeneous parameters and unidirectional coupling. We found necessary conditions for canards and MMOs for excitatory coupling and used the resulting bounds to draw conclusions about phase locking in directed trees of FN models. We showed that canard-driven MMOs do not exist for the inhibitory directed two-FN system. However, we observed MMOs in numerical simulation and will investigate the generating mechanism in future work.

<sup>\*</sup>Some material from the Conclusion sections of [28, 29] appears in this chapter; the first two paragraphs of Section 5.2 are verbatim.

The bounds for synchronization and detailed bifurcation analysis of the two-FN system presented here are an excellent starting point for further investigation into the onset of firing and synchronization in systems of model neurons. In this section, we detail potential directions of future investigation into further improvement and extension of the synchronization conditions presented in Chapter 2. We go on to discuss extensions of the conditions on canards and MMOs presented in Chapter 3 to diverse network structures and heterogeneous nodal dynamics. Finally, the results presented in Chapter 4 form an exciting first step toward further inquiry into the dynamics of networks with both excitatory and inhibitory coupling.

# 5.1 Improvement and generalization of synchronization conditions

In Chapter 2, we improved upon existing sufficient conditions for synchronization by implementing a nonsmooth Lyapunov function which had been previously used to find tight bounds for synchronization in a complete graph of identical systems [19]. Sufficient conditions for synchronization in systems with nonlinear coupling, time delays, and heterogeneous intrinsic nodal dynamics have been found using quadratic Lyapunov and contraction analyses in [21, 65, 80]. We expect that such bounds may also be improved by implementing nonsmooth Lyapunov functions or a contraction based approach that takes clusters into consideration [4]. A key limitation of the work presented in Chapter 2 and [4] is the requirement that synchronization be complete. Systems with both heterogeneous nodal dynamics and asymmetric coupling will not synchronize according to this definition. More realistic network configurations could be studied if the complete synchronization requirement were extended. Two possible extensions are phase synchronization, where clusters have critical features such as peaks that occur at the same time [13, 19, 92, 130], and approximate synchronization, where nodes within a cluster may have dynamics that slightly differ [43, 44, 99, 122]. Finding bounds that address a wider range of coupling types and intrinsic dynamics is a critical step toward understanding the dynamics of heterogeneous networks of model neurons.

# 5.2 Canards and MMOs in systems with arbitrary network topology and heterogeneous nodal dynamics

The following two paragraphs are an excerpt from the conclusion of [28].

Further investigation of the two-FN system is necessary to determine the threshold between MMOs and canard solutions without MMOs, which have been observed in simulation. Firing onset has historically been difficult to analyze in the FN model because MMOs are a direct result of spike threshold accommodation and the threshold curve in the FN model is not analytically defined [41, 86, 131]. The threshold has been studied numerically, as well as the chaotic behavior at the boundaries between types of MMOs, e.g., in [60]. Canards have been shown to play a role in threshold phenomena in FitzHugh-Nagumo model neurons, Hodgkin-Huxley model neurons, and a compartmental model of a cerebellar Purkinje cell [68,86,88,139]. An analytical description of the threshold phenomena involved in the onset of firing in the two-FN system would add significantly to the literature on canards and MMOs.

Another promising future direction of study includes consideration of more diverse graph structures, e.g. loops within the graph, and a more detailed analysis of the MMOs in these systems. General results have been found for finite dimensional fast-slow systems, which could be applied in this context [138]. More complex graph structures could be built from a set of motifs that are well understood: the unidirectional two-FN model presented in Chapter 3, a bidirectional two-FN system with heterogeneous coupling strengths, and larger chains and loops that extend from these cases. With these building blocks in place, it would be possible to prove conditions for MMO and phase locking in a diverse class of networks.



Figure 5.1: Isospike diagram for the spike ratio of FN model B to FN model A as a function of  $\gamma$  and the timescale parameter,  $\epsilon$ , in the two-FN system. The dark blue on the lower right indicates that B never spikes, while the dark red on the upper left indicates that B spikes exactly once for every input spike from A. There are discrete steps between each type of MMO with chaotic dynamics at the boundaries.

Heterogeneous intrinsic model parameters and different types of coupling have not yet been incorporated into the analysis of MMOs and phase locking in Chapter 3. Changing  $\epsilon$  changes the frequency of oscillation and the timescale of the FN model, so a network of FN models with differing values of  $\epsilon$  would be a compelling system for exploring canard phenomena in three or more distinct timescales. Figure 5.1 shows how the regimes where MMOs are found vary as a function of both  $\gamma$  and  $\epsilon$ . Heterogeneous  $\epsilon$  parameters result in differing dynamics even given similar inputs and coupling. Exploring the effects of variation in  $\epsilon$  and other model parameters forms a compelling next direction of research. Canards and MMOs have been analytically studied in a variety of neural systems. In Chapters 3 and 4 we presented conditions for canards and MMOs in coupled FN models. The role of canards has also been examined in models of cerebellar Purkinje cells [68], neural field models [9], model dopaminergic neurons [70], among others. Experimental observations of canards and MMOs have been made in cells of the entorhinal cortex layer II and III [2, 40] and in mouse spinal motorneurons [62]. Developments in the theory of multiple timescale systems have advanced understanding of the conditions for existence of canards and mixed mode oscillations in neuronal models. However, further experimentation is needed to clarify how the analytical results presented here and in related work correspond to systems of biological neurons.

# Part II

# Papers

## Chapter 6

# Overview

Part II of this dissertation is comprised of three published papers. Some differences in formatting may be present between the published versions and the versions presented here. The following sections outline the structure of this part and designate the author contributions.

#### 6.1 Outline

Chapter 7 presents a general framework for the use of nonsmooth Lyapunov functions to find a sufficient condition for synchronization in networks of nonlinear systems with polynomial dynamics. The condition is applied to networks of identical and non-identical FN models and is an improvement over previous methods.

Chapter 8 details the use of a contraction based approach to find a sufficient condition for cluster synchronization in networks of heterogeneous nonlinear systems. A novel aspect of this approach is use of connections within and between clusters in the condition. Improvement over the condition for networks of FN models in Chapter 7 is demonstrated.

Chapter 9 consists of a detailed investigation into the dynamics of networks of FN models. Bifurcation theory and multiple timescale systems theory are leveraged to

characterize the parameter values for which different dynamic behavior may occur, including phase locking and mixed mode oscillations.

#### 6.2 Author Contributions

For the papers [29] and [28], I am the lead author and the lead contributor to the framing of the questions, the literature survey, the development and performance of the analysis, the discussion, the creation of the numerical illustrations, and the writing. Early versions of some of the material in [29] have been presented at Princeton Bioengineering Day 2015, APS March Meeting 2016, and the 54th Annual Allerton Conference on Communication, Control and Computing (where the conference paper appeared). Early versions of some of the material in [28] have been presented at SIAM DS17, APS March Meeting 2018, and Janelia conference on Distributed, Collective Computation in Biological and Artificial Systems in 2018. My dissertation advisor, Naomi Ehrich Leonard, advised me on all aspects of this work.

I am grateful to my co-authors, Biswadip Day and Naomi Ehrich Leonard on the paper [29], and my co-authors Zahra Aminzare, Biswadip Day, and Naomi Ehrich Leonard on the papers [28] and [4]. In all cases, I discussed ideas and approach with my co-authors. They also provided valuable guidance, helped check mathematical results, and contributed to the editing and revision of the papers. Some specific contributions are described here.

• In Chapter 7, Naomi Ehrich Leonard and Vaibhav Srivastava suggested looking at synchronization in FitzHugh-Nagumo models. Biswadip Dey suggested also including a result for a network of general nonlinear systems and helped with formulation and notation. Naomi Leonard, Biswadip Dey, and I planned the structure of the paper.

- In Chapter 8, Zahra Aminzare proposed applying a contraction based approach to study cluster synchronization based on our conversations about the paper [29], wrote and proved the main theorem, and described the theory for using contraction to prove synchronization. Naomi Ehrich Leonard checked the theory and provided valuable guidance on clear and succinct writing. Biswadip Dey wrote code and performed the numerical simulations. I contributed to the introduction, conclusions, the application to two types of model neuron, checking the theory, and editing.
- In Chapter 9, Naomi Ehrich Leonard first suggested I consider the directed two-FN system and, along with Biswadip Dey, provided feedback and direction in the early stages of the project. Zahra Aminzare advised me on writing the propositions and definitions, particularly in Section 9.4, and shared code that I used to effectively visualize phase planes. Zahra Aminzare, Biswadip Dey, and I structured the paper, with advice and guidance from Naomi.

## Chapter 7

# Synchronization Bound for Networks of Nonlinear Oscillators<sup>\*</sup>

#### Elizabeth N. Davison, Biswadip Dey and Naomi Ehrich Leonard

Investigation of synchronization phenomena in networks of coupled nonlinear oscillators plays a pivotal role in understanding the behavior of biological and mechanical systems with oscillatory properties. We derive a general sufficient condition for synchronization of a network of nonlinear oscillators using a nonsmooth Lyapunov function, and we obtain conditions under which synchronization is guaranteed for a network of Fitzhugh-Nagumo (FN) oscillators in biologically relevant model parameter regimes. We incorporate two types of heterogeneity into our study of FN oscillators: 1) the network structure is arbitrary and 2) the oscillators have non-identical external inputs. Understanding the effects of heterogeneities on synchronization of oscillators with inputs provides a promising step toward control of key aspects of networked oscillatory systems.

<sup>\*</sup>This chapter appears in the paper Davison, Dey, and Leonard (2016) [29].

#### 7.1 Introduction

Synchronization phenomena in networks of nonlinear oscillators have critical implications in biology, communications, computer science, power networks, and diverse other disciplines. In biological neuronal networks, synchronization can be beneficial, allowing for production of complex behavior, or detrimental, causing disorders such as Parkinson's disease [75] and epilepsy [22]. Understanding the principles underlying synchronization and related behavior in complex interconnected oscillatory systems is a necessary first step toward effective control for enhancement of desired dynamics and suppression of undesired dynamics.

Among multiple existing methods for finding necessary and sufficient conditions to determine stability of synchronization in nonlinear systems, the master stability function (MSF) approach establishes a necessary condition for synchronization in systems of oscillators with linear coupling [95]. Complementary sufficient conditions can be found by leveraging passivity properties of the oscillators [101] or by employing approaches based on contraction theory [7,118]. However, the majority of synchronization conditions expressed in terms of a lower bound on network coupling strength are too loose to accurately describe the emergence of synchronization. Our approach is to build on the semi-passivity method described in [101, 124] to provide a tighter bound on the required coupling strength for synchronization in biologically relevant model parameter regimes.

In this paper, we present a new sufficient condition for synchronization in a network of nonlinear oscillators whose dynamics can be represented by ordinary differential equations composed of polynomial functions of the state. This class of models generalizes well-known oscillator models including the Van der Pol oscillator, the FitzHugh-Nagumo (FN) neuronal model [47,90], and the Hindmarsh-Rose neuronal model [58]. We consider dynamics that are strictly semi-passive and use a nonsmooth Lyapunov function [37] to find a sufficient condition for full synchronization in terms of a lower bound on coupling strength in an arbitrary network of oscillators with identical parameters. We apply this result to compute the bound for a network FN oscillators with identical external inputs to fully synchronize, and we show it is a tighter bound than bounds derived from related methods for relevant parameter regimes.

We then introduce the concepts of input-equivalence [113] and cluster synchronization [12, 121] to extend the nonsmooth Lyapunov analysis to networks of FN oscillators with non-identical external inputs. We calculate the sufficient condition for synchronization in clusters in a representative system to illustrate the utility of the nonsmooth Lyapunov method.

An understanding of how and when synchronization occurs promises to be an invaluable tool for informing experimental studies of oscillator ensembles and a basis for examining mechanisms for the emergence of abnormal synchronization.

#### 7.2 Network Model

In this paper, we consider a network of n nonlinear oscillators with identical internal dynamics, and assume they interact over a connected, undirected graph  $\mathcal{G}$ . We let  $\mathbf{x}^i \in \mathbb{R}^N$  denote the state of the *i*-th node, and we define the underlying dynamics as

$$\dot{\mathbf{x}}^i = \mathbf{f}(\mathbf{x}^i) + Bu^i \tag{7.1}$$

for i = 1, ..., n. Each component of  $\mathbf{f} : \mathbb{R}^N \to \mathbb{R}^N$  is a polynomial function of the state of the oscillator.  $B \in \mathbb{R}^{N \times 1}$  captures how the social input  $u^i$  (due to influence from neighbors) affects the individual states of the *i*-th node. We assume B to be a vector of zeros with a one in its first row, thereby implying that the social input

has a direct impact on only the first variable<sup>†</sup> of the state  $\mathbf{x}^i$ . The dynamics of an oscillator may also depend on an external input  $I^i$ . We examine the influence of identical and non-identical external inputs in Sections 7.4 and 7.5, respectively, in the case of Fitzhugh-Nagumo oscillators.

We assume the social input  $u^i$  provides a linear diffusive coupling between neighbors in the graph  $\mathcal{G}$ . Let  $A = [a_{ij}]$  with  $a_{ij} \in [0, 1]$  represent the weighted adjacency matrix of  $\mathcal{G}$ . We represent the linear diffusive coupling term  $u^i$  as

$$u^{i} = \sum_{j=1}^{n} \gamma a_{ij} (x_{1}^{j} - x_{1}^{i}), \qquad (7.2)$$

where the parameter  $\gamma > 0$  is the coupling strength. Next, we define  $\mathbf{x}_1 = [x_1^1, x_1^2, \dots, x_1^n]^T$  and  $\mathbf{u} = [u^1, u^2, \dots, u^n]^T$  to represent the vectors of first variables of the system states and social inputs, respectively. The diffusive coupling between individual oscillators becomes

$$\mathbf{u} = -\gamma (D - A)\mathbf{x}_1 = -\gamma L \mathbf{x}_1,\tag{7.3}$$

where  $D = \text{diag}\{d_1, d_2, \dots, d_n\}, d_i = \sum_{j=1}^n a_{ij}$ , and L = D - A denotes the Laplacian of the underlying graph.

We restrict our analysis to systems where the dynamics are strictly semi-passive, which allows us to bound the dynamics of each variable for each oscillator.

**Definition 7.2.1** (Strictly Semi-passive). A dynamical system  $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}) + B\mathbf{u}$ ,  $\mathbf{y} = C\mathbf{x}$ ,  $\mathbf{x} \in \mathbb{R}^N$ ,  $\mathbf{u}, \mathbf{y} \in \mathbb{R}^m$  is strictly semi-passive in a region  $\mathcal{D} \subset \mathbb{R}^N$  if there exists a nonnegative function  $V : \mathcal{D} \to \mathbb{R}_+$  such that  $\mathcal{D}$  is open, connected and invariant under the dynamics,  $V(\mathbf{x}) > 0$  for  $\mathbf{x} \in \mathcal{D} \setminus \{0\}$ , V(0) = 0, and  $\dot{V} \leq \mathbf{y}^T \mathbf{u} - H(\mathbf{x})$ , where  $H(\mathbf{x}) > 0$  when  $\|\mathbf{x}\| \geq r$  with the radius r being dependent on the system parameters.

<sup>&</sup>lt;sup>†</sup>In a neuronal oscillator context, the first variable  $x_1^i$  is typically interpreted as the underlying membrane potential.

A strictly semi-passive system behaves like a passive system whenever the system state is sufficiently away from the origin. As the trajectories of a semi-passive system eventually return to the ball of radius r around the origin, the trajectories of the system are ultimately bounded. Furthermore, when a group of n such semi-passive systems are interconnected by a linear diffusive coupling, the closed-loop system has ultimately bounded solutions [101,102]. We let  $\{\beta_1, \beta_2, \ldots, \beta_N\}$  represent the bounds on the state variables for individual oscillators.

#### 7.3 Nonsmooth Lyapunov Analysis

In this section, we derive a sufficient condition for synchronization in the class of systems described in Section 7.2. To do so, we first define the manifold of synchronized states, and then perform a stability analysis using a nonsmooth Lyapunov approach. By exploiting the properties of Dini derivatives of the associated nonsmooth Lyapunov function, our analysis yields the sufficient condition in terms of coupling strength and network connectivity.

**Definition 7.3.1** (Complete synchronization manifold). The complete synchronization manifold S is an algebraic manifold in the state space of the full system wherein the states of individual systems are identical:

$$\mathcal{S} = \{\mathbf{x}^1, \dots, \mathbf{x}^n \in \mathbb{R}^N | x^i = x^j, \forall i, j = 1, \dots, n\}.$$

**Definition 7.3.2** (Upper Dini derivative [66]). The upper Dini derivative, also called the upper right hand derivative, of a real valued function  $v : \mathbb{R} \to \mathbb{R}$  is defined as

$$D^{+}v(t) = \limsup_{h \to 0^{+}} \frac{v(t+h) - v(t)}{h}.$$
(7.4)

It provides an upper bound for right hand derivatives of v.

**Theorem 7.3.3.** Consider the system described in (7.1) with a linear diffusive coupling on the first variable (7.2). Assume that (7.1) is strictly semi-passive. Then, whenever the coupling strength  $\gamma$  and the second smallest eigenvalue of the graph Laplacian  $\lambda_2(L)$  (representing network connectivity) satisfy

$$\gamma \lambda_2(L) > \sum_{k=1}^N F_{1k} + h_1,$$
  
and 
$$\sum_{k=1}^N F_{jk} + h_j < 0 \quad \forall j = 2, \dots, N,$$

the complete synchronization manifold S is globally asymptotically stable, where  $F_{ij}$ 's and  $h_i$ 's are functions of system parameters.

*Proof.* Earlier studies [37] have shown the effectiveness of nonsmooth Lyapunov functions in deriving the critical coupling strength for a complete graph of Kuramoto oscillators. Due to our interest in deriving a sufficient condition for synchronization in terms of a tight lower bound on the coupling strength we follow a similar philosophy, and introduce the following Lyapunov function:

$$V_0(\mathbf{x}) = \sum_{k=1}^{N} \max_{i,j=1,\dots,n} (x_k^i - x_k^j).$$
(7.5)

The Dini derivative of this nonsmooth Lyapunov function can be expressed as

$$D^{+}V_{0}(\mathbf{x}) = \sum_{k=1}^{N} \dot{x}_{k}^{m_{k}} - \dot{x}_{k}^{l_{k}}, \qquad (7.6)$$

where  $m_k$  and  $l_k$  are defined as

$$m_k = \underset{i=1,\dots,n}{\arg \max} (x_k^i),$$
$$l_k = \underset{i=1,\dots,n}{\arg \min} (x_k^i).$$

As the dynamics of individual systems are identical, we can rewrite the Dini derivative as

$$D^+V_0(\mathbf{x}) = \left(u^{m_1} - u^{l_1}\right) + \sum_{k=1}^N \left(f_k(\mathbf{x}^{m_k}) - f_k(\mathbf{x}^{l_k})\right),$$

where  $f_k : \mathbb{R}^N \to \mathbb{R}$  represents the k-th component of the vector-valued function **f**. Let  $L^i \in \mathbb{R}^{1 \times n}$  denote the *i*-th row of the graph Laplacian L. Then, we have

$$u^{m_1} - u^{l_1} = \gamma (-L^{m_1} + L^{l_1}) \mathbf{x}_1 = (\mathbf{e}_{l_1} - \mathbf{e}_{m_1})^\top \gamma L \mathbf{x}_1$$

where  $\{\mathbf{e}_1, \mathbf{e}_2, \dots, \mathbf{e}_n\}$  constitutes the natural basis for  $\mathbb{R}^n$ . We can further simplify this expression in terms of the second smallest eigenvalue of the graph Laplacian by bounding the product  $L\mathbf{x}_1$  as

$$(\mathbf{e}_l - \mathbf{e}_m)^\top \gamma L \mathbf{x}_1 \le \gamma \lambda_2(L) (\mathbf{e}_l - \mathbf{e}_m)^\top \mathbf{x}_1 = \gamma \lambda_2(L) (x_1^{l_1} - x_1^{m_1}).$$

This gives an expression for the derivative in terms of the internal dynamics and second smallest eigenvalue of the graph Laplacian:

$$D^{+}V_{0}(\mathbf{x}) = \sum_{k=1}^{N} \left( f_{k}(\mathbf{x}^{m_{k}}) - f_{k}(\mathbf{x}^{l_{k}}) \right) + \gamma \lambda_{2}(L)(x_{1}^{l_{1}} - x_{1}^{m_{1}}).$$

Now we perform a change of coordinates, where  $w_k = x_k^{m_k} - x_k^{l_k} > 0$  for all k. Then by separating each function into a linear term and a higher order term as

$$f_k(\mathbf{x}^{m_k}) = \mathbf{a}_k \cdot \mathbf{x}^{m_k} + g_k(\mathbf{x}^{m_k}),$$

we have

$$\left(f_k(\mathbf{x}^{m_k}) - f_k(\mathbf{x}^{l_k})\right) = \mathbf{a}_k \cdot \mathbf{w} + g_k(\mathbf{x}^{m_k}) - g_k(\mathbf{x}^{l_k}).$$

This allows us to capture the effect of nonlinearities by putting a bound on  $g_k(\mathbf{x}^{m_k}) - g_k(\mathbf{x}^{l_k})$ , and bound the Dini derivative as

$$D^+V_0(\mathbf{w}) \leq \mathbf{1} \cdot F\mathbf{w} + \mathbf{1} \cdot \tilde{h}(\beta_1, \beta_2, \dots, \beta_N)\mathbf{w} - \gamma \lambda_2(L)w_1.$$

Here, **1** is the vector of all ones,  $F \in \mathbb{R}^{N \times N}$  has rows equal to the  $\mathbf{a}_k$ . The nonlinear behavior is captured by an  $N \times N$  matrix  $\tilde{h} \triangleq \text{diag}\{h_1, h_2, \dots, h_N\}$ , where the functions  $h_1, \dots, h_N$  depend on the bounds  $\beta_1, \dots, \beta_N$  introduced in Section 7.2.

By construction, each element of **w** is positive, so we have  $D^+V_0(\mathbf{w}) \leq 0$  whenever

$$\gamma \lambda_2(L) > \frac{1}{w_1} \left( \mathbf{1} \cdot F \mathbf{w} + \mathbf{1} \cdot \tilde{h}(\beta_1, \beta_2, \dots, \beta_N) \mathbf{w} \right)$$

We can write this as N separate conditions:

$$\gamma \lambda_2(L) > \sum_{k=1}^N F_{1k} + h_1$$
 (7.7)

$$\sum_{k=1}^{N} F_{jk} + h_j < 0 \quad \forall j = 2, \dots, N.$$
(7.8)

Thus,  $D^+V_0(\mathbf{w}) \leq 0$ , and increasing  $\lambda_2$  will not change this property. So we have found a sufficient condition for local Lyapunov stability of the equilibrium state  $\mathbf{w} = 0$ , which is equivalent to the manifold  $\mathcal{S}$ . Further, there exists a real number  $\phi > 0$  such that  $D^+V_0(\mathbf{w}) \leq -\phi \|\mathbf{w}\|_1$ .

To show that  $\mathcal{S}$  is attractive, we consider the following integral [55]:

$$V_0(\mathbf{w}(t)) - V_0(\mathbf{w}(0)) \le -\int_0^t \phi \|\mathbf{w}(t)\|_1 dt$$
  

$$\Rightarrow V_0(\mathbf{w}(0)) \ge V_0(\mathbf{w}(t)) + \int_0^t \phi \|\mathbf{w}(t)\|_1 dt.$$

As  $V_0(\mathbf{w}(t)) \ge 0$  for all  $t \ne 0$  by construction, taking the limit  $t \rightarrow \infty$  we have

$$V_0(\mathbf{w}(0)) \ge \phi \int_0^\infty \|\mathbf{w}(t)\|_1 dt.$$
 (7.9)

So the integral in (7.9) is less than or equal to  $V_0(\mathbf{w}(0))/\phi$ , which takes a finite value, and the integrand is uniformly continuous. By Barbalat's Lemma,  $\mathbf{w} \to 0$  as  $t \to \infty$ . Since  $x_k^i$  are bounded for all i and k, this means that  $\mathcal{S}$  is attractive if there are trajectories that originate outside the set. Thus, the complete synchronization manifold  $\mathcal{S}$  is globally asymptotically stable.

# 7.4 FitzHugh-Nagumo Network With Identical External Inputs

The general argument presented in Section 7.3 can be specialized to a particular oscillator model in order to better understand the bound and to compare it with the bounds from other methods. Here, we specialize the bound in Theorem 7.3.3 to find a sufficient condition for synchronization of a network of FitzHugh-Nagumo (FN) oscillators [47,90].

The FN model is a two-dimensional reduction of the four-dimensional Hodgkin-Huxley model of the membrane potential dynamics of neurons [59]. It is a comparatively simple model, but captures the distinct quiescent, firing, and saturated states of the system, which depend on the input into the model. We choose to analyze the FN model due to this combination of simplicity and range of possible dynamics. We consider a network of n FN neuronal oscillators. Each FN oscillator  $i = 1, \ldots, n$  has two states (N = 2) with dynamics modeled as

$$\dot{x}_{1}^{i} = x_{1}^{i} - \frac{x_{1}^{i}}{3}^{3} - x_{2}^{i} + I^{i} + u^{i}$$

$$\dot{x}_{2}^{i} = \epsilon(x_{1}^{i} + a - bx_{2}^{i}).$$
(7.10)

The model parameters  $\epsilon \ll 1$ , a and b are all positive and the same for every oscillator i. The variable  $x_1^i$  represents the membrane potential and operates at a faster timescale than  $x_2^i$ , which is the recovery variable. We consider constant external inputs  $I^i$  that can be independently assigned to each oscillator in the network.

#### 7.4.1 FN Network as a Strictly Semi-passive System

In [101] it was shown that a single FN neuronal oscillator model with dynamics (7.10) is strictly semi-passive, and thus a network of FN oscillators is ultimately bounded. Following [124], a network of FN oscillators with linear diffusive coupling (7.2) was shown also to be strictly semi-passive. This can be done using a non-negative function

$$V_P = \sum_{i=1}^n \left( \frac{1}{2} x_1^{i^2} + \frac{1}{2\epsilon} x_2^{i^2} \right),$$

which has derivative satisfying

$$\dot{V_P} \le \underbrace{\sum_{i=1}^n x_1^i u^i}_{\mathbf{x}_1^T \mathbf{u}} - \underbrace{\sum_{i=1}^n \left( \frac{x_1^i}{3} \left( x_1^{i^3} - 3x_1^i - 3I^i \right) + bx_2^i \left( x_2^i - \frac{a}{b} \right) \right)}_{H(\mathbf{x}_1, \mathbf{x}_2)}.$$

It follows that if a single FN neuronal oscillator model is strictly semi-passive, then any network of FN oscillators connected by the linear diffusive coupling is also a strictly semi-passive system with ultimately bounded dynamics [124].

### 7.4.2 Synchronization Bound: Nonsmooth Lyapunov Function

In this section we apply the constructive proof of Theorem 7.3.3 to compute the corresponding sufficient condition for global asymptotic stability of the complete synchronization manifold S for a network of FN oscillators with dynamics (7.10), identical constant external inputs  $I^i$ , and linear diffusive coupling (7.2). From Section 7.4.1, the system is strictly semi-passive. Following (7.5), the nonsmooth Lyapunov function is

$$V(\mathbf{x}_1, \mathbf{x}_2) = \max_{i,j=1,\dots,n} (x_1^i - x_1^j) + \max_{i,j=1,\dots,n} (x_2^i - x_2^j).$$

The Dini derivative of this Lyapunov function is  $D^+V(\mathbf{x}_1, \mathbf{x}_2) = \dot{x}_1^m - \dot{x}_1^l + \dot{x}_2^m - \dot{x}_2^l$ . When the external inputs are identical, we can follow the general procedure of the proof and bound  $D^+V(\mathbf{x}_1, \mathbf{x}_2)$  as follows:

$$D^{+}V(\mathbf{x}_{1},\mathbf{x}_{2}) \leq \left(1+\epsilon+\frac{\beta_{1}^{2}}{3}\right)(x_{1}^{m}-x_{1}^{l})+\gamma\lambda_{2}(L)(x_{1}^{l}-x_{1}^{m})-(1+b\epsilon)(x_{2}^{m}-x_{2}^{l}).$$

Here,  $\beta_1$  is the ultimate bound for the  $x_1$  variable. Since each oscillator model has the same parameters, this bound is the same for each oscillator, independent of its position in the graph. Since the parameters b and  $\epsilon$  are always positive,  $x_2^m > x_2^l$ . Thus,  $-(1 + b\epsilon)(x_2^m - x_2^l) < 0$  and the condition (7.8) for synchronization is always satisfied.

To satisfy condition (7.7) we must have

$$\gamma \lambda_2(L) \ge 1 + \epsilon + \frac{\beta_1^2}{3} = \gamma \lambda_m^*. \tag{7.11}$$

This provides a sufficient condition for full synchronization of a network of FN oscillators with linear diffusive coupling and identical constant external inputs as a lower bound on the product of the coupling strength  $\gamma$  and the second smallest eigenvalue of the graph Laplacian  $\lambda_2(L)$ .

#### 7.4.3 Synchronization Bound: Quadratic Lyapunov Function

In this section we use a quadratic Lyapunov function to compute a bound on  $\gamma \lambda_2(L)$ that is sufficient for synchronization of a network of FN oscillators with linear diffusive coupling and identical inputs. This approach is an application of the procedure outlined in [124]. Earlier studies have evaluated similar bounds with quadratic Lyapunov functions for networks of Hindmarsh-Rose neurons [93].

**Theorem 7.4.1.** Consider a network of FN oscillators with dynamics (7.10), identical constant external inputs, and linear diffusive coupling (7.2). Suppose the coupling strength  $\gamma$  and second smallest eigenvalue of the graph Laplacian  $\lambda_2(L)$  satisfy

$$\gamma \lambda_2(L) > \frac{(\epsilon - 1)^2}{4b\epsilon} + 1 + \frac{\beta_1^2}{3} = \gamma \lambda_s^*.$$
 (7.12)

Then the complete synchronization manifold S is globally asymptotically stable.

*Proof.* Let  $V_Q(\mathbf{w}_1, \mathbf{w}_2) = \frac{1}{2}(\|\mathbf{w}_1\|_2^2 + \|\mathbf{w}_2\|_2^2)$  be a positive-definite Lyapunov function, where  $\mathbf{w}_1$  and  $\mathbf{w}_2$  are transformed coordinates that represent the differences between states in  $\mathbf{x}_1$  and between states in  $\mathbf{x}_2$ , respectively.

The derivative of  $V_Q(\mathbf{w}_1, \mathbf{w}_2)$  can be computed as

$$\dot{V}_Q(\mathbf{w}_1, \mathbf{w}_2) = \frac{1}{2} \frac{d}{dt} \|\mathbf{w}_1\|_2^2 - b\epsilon \|\mathbf{w}_2\|_2^2 + \epsilon \mathbf{w}_1 \cdot \mathbf{w}_2.$$
(7.13)

Using,  $u^i = -\gamma L \mathbf{x}_1$ ,  $\mathbf{w}_1 \cdot L \mathbf{w}_1 \ge \lambda_2(L) \|\mathbf{w}_1\|_2^2$ , and  $|x_1^i| \le \beta_1$ , we can write

$$\dot{V}_Q \le \left(1 - \gamma \lambda_2 + \frac{\beta_1^2}{3}\right) \|\mathbf{w}_1\|_2^2 + (1 - \epsilon)\mathbf{w}_1 \cdot \mathbf{w}_2 - b\epsilon \|\mathbf{w}_2\|_2^2$$

When 
$$\gamma \lambda_2(L) = \gamma \lambda_s^* = \frac{(\epsilon - 1)^2}{4b\epsilon} + 1 + \frac{\beta_1^2}{3}$$
, we have

$$\dot{V}_Q \leq -\left(\sqrt{b\epsilon} \|\mathbf{w}_2\|_2 - \frac{|\epsilon - 1|}{2\sqrt{b\epsilon}} \|\mathbf{w}_1\|_2\right)^2.$$

Thus,  $\dot{V}_Q \leq 0$ , and increasing  $\gamma$  will not change this property. So we have found a sufficient condition for Lyapunov stability of the equilibrium state  $\mathbf{w}_1 = \mathbf{w}_2 = 0$  (and thus the complete synchronization manifold  $\mathcal{S}$ ). Further, there is some  $\kappa$  such that  $\dot{V}_Q \leq -\kappa (\|\mathbf{w}_1\|_2^2 + \|\mathbf{w}_2\|_2^2)$ .

To show that S is attractive, we can evaluate the integral of  $\dot{V}_Q$  as we did for the integral of the Dini derivative in the proof of Theorem 7.3.3. This completes the proof.

#### 7.4.4 Synchronization Bound: Master Stability Function

The Master Stability Function (MSF) approach is commonly used to calculate necessary conditions on coupling for synchronization in oscillator networks [95]. Given a particular coupling scheme, the MSF approach carries out a local stability analysis of the linearized dynamics, and derives a necessary condition for synchronization in terms of a lower bound on the coupling strength. Following the steps presented in [95], it can be shown that for an undirected network of FN oscillators connected with linear diffusive coupling, this necessary condition can be expressed as

$$\gamma \lambda_2(L) \ge 1 - b\epsilon - \beta_1^2. \tag{7.14}$$

#### 7.4.5 Comparison of Bounds

We first compare the different bounds on  $\gamma \lambda_2(L)$  computed above for global asymptotic stability of S in the case of a complete network graph of FN oscillators, i.e., there is a connection between every pair of oscillators. In this case the graph Laplacian is

$$L = (n-1)\mathbb{I}_n - \mathbf{1}_n \mathbf{1}_n^T,$$

and  $\lambda_2(L) = n$ .

Our new bound using the nonsmooth Lyapunov function can be compute from (7.11) as

$$\gamma n > 1 + \epsilon + \frac{\beta_1^2}{3},$$

whereas the bound computed using the quadratic Lyapunov function is given by

$$\gamma n > \frac{(\epsilon - 1)^2}{4b\epsilon} + 1 + \frac{\beta_1^2}{3}.$$

An earlier work [113], used a contraction analysis, and the corresponding sufficient condition was given as

$$\gamma n > \frac{1}{\epsilon}.$$

On the other hand, the master stability function based approach yields the following necessary condition:

$$\gamma n \ge 1 - b\epsilon - \beta_1^2.$$

Whenever  $\epsilon/(1-\epsilon) < 1/(2\sqrt{b})$ , our new bound from the nonsmooth analysis is tighter than the bound from the quadratic Lyapunov function. Additionally, when  $\epsilon < 3/(3 + 3\epsilon + \beta_1^2)$ , our new bound is tighter than the contraction theory based bound as well. For biologically plausible firing behavior of an FN oscillator, numerical simulations typically use  $b \in [0, 1]$  and small values of  $\epsilon \ (\approx \frac{1}{12})$ , which in turn tends to result in  $\beta_1 \approx 2$ . In this parameter regime, our nonsmooth analysis yields a tighter bound compared to the bounds obtained from earlier approaches based on the quadratic Lyapunov function and contraction theory. We next compare the bounds for a general network graph. In Figure 7.1 we compare the bound from the nonsmooth Lyapunov approach with the bound from the quadratic Lyapunov function approach by ploting the ratio of  $\lambda_m^*$  to  $\lambda_s^*$ . The ratio is plotted for  $\epsilon \in [0, 0.3]$  and  $b \in [0, 1]$ , which are parameter values commonly used to provide biologically relevant behavior with the FN model. For these conditions,  $\lambda_m^* < \lambda_s^*$ , and the ratio gets smaller with decreasing  $\epsilon$ . This implies that in these parameter regimes, the bound from our new nonsmooth approach is tighter than the bound from the quadratic Lyapunov function approach.



Figure 7.1: **Bound comparison:** Ratio of synchronization conditions for the nonsmooth and quadratic Lyapunov approaches. For the biologically relevant parameter ranges plotted, the bound derived from the nonsmooth approach is always tighter.

Comparing the bound from the nonsmooth Lyapunov stability analysis, which is sufficient for synchronization, with the bound from the MSF approach, which is necessary for synchronization, provides insight into where the bounds perform well and how we can improve them in further work [111]. The necessary condition is  $\gamma\lambda_2 \geq 1 - b\epsilon - \beta_1^2$ , and the sufficient condition is  $\gamma\lambda_2 \geq 1 + \epsilon + \frac{\beta_1^2}{3}$ . The difference between these bounds is  $\epsilon(1 + b) + \frac{4}{3}\beta_1^2$ . For models with a small  $\epsilon$  parameter, as are typical, the accuracy of these bounds is limited by the bound on the dynamics,  $\beta_1^2$ . This suggests that to get closer to a condition that is both necessary and sufficient for synchronization, we should use a method that does not rely on the bound on the dynamics.

# 7.5 FitzHugh-Nagumo Network with Non-Identical External Inputs

When the external inputs  $I^i$  to individual FN oscillators in a network are not the same, the network separates into synchronized clusters, i.e. groups of oscillators with identical behavior, depending both on the distribution of external inputs and on the network structure [12, 121]. Oscillators must be input-equivalent in order for synchronization to occur [113]. Here, we use the notion of input-equivalence to extend our analysis to networks of nonlinear oscillators with non-identical constant external inputs  $I^i$ .

**Definition 7.5.1** (Input-equivalence). Two FN oscillators i and j are inputequivalent if

$$I^i + u^i(t) = I^j + u^j(t) \quad \forall t.$$

#### 7.5.1 Nonsmooth Lyapunov Analysis

We now extend our result from Section 7.4 to a network of FN oscillators with nonidentical inputs. We provide a sufficient condition under which each of a set of oscillators that are input-equivalent will synchronize as a cluster.

**Corollary 7.5.2.** Consider a network of FN oscillators with dynamics (7.10), nonidentical constant external inputs, and linear diffusive coupling (7.2). Suppose that the oscillators can be partitioned into C distinct sets  $C_k$ , k = 1, ..., C such that all pairs in each set are input-equivalent [113]. Let  $L_k$  be the Laplacian of the subgraph for the oscillators in  $C_k$ . Define the cluster synchronization manifold as

$$\mathcal{S}_{\mathcal{C}} = \{\mathbf{x}^1, \dots, \mathbf{x}^n \in \mathbb{R}^2 : x^i = x^j, \forall i, j \in \mathcal{C}_k, \forall k\}.$$

 $\mathcal{S}_{\mathcal{C}}$  is globally asymptotically stable if for all k

$$\gamma \lambda_2(L_k) > 1 + \epsilon + \frac{\beta_{1,k}^2}{3}.$$

*Proof.* By input-equivalence, we treat each set of FN oscillators separately. Since the internal dynamics of each oscillator are identical, we can use the result from Theorem 7.3.3 for FN oscillators as in (7.11) for each set  $C_k$ .

**Example 7.5.3** (Cluster Synchronized Graph). We illustrate our result by considering a network of FN oscillators interacting over undirected graph (refer Figure 7.2) which can be partitioned into three (C = 3) input-equivalent sets: (1) a cycle graph  $C_m$ , (2) a complete graph  $K_m$ , and (3) a single central node connected to every element in both  $K_m$  and  $C_m$ . We simulate such a system with m = 50, and external



Figure 7.2: Graph used in the example illustrated in the case m = 4.

input 0 to elements in  $C_m$ , external input 0.1 to the central node, and external input 0.4 to elements in  $K_m$ . When b = 0.8,  $\epsilon = 0.08$ , and  $\gamma = 0.1$  for all connections, we observe the dynamics represented in Figure 7.3. All oscillators in the complete graph synchronize, while those in the cycle graph do not. We calculate the second smallest eigenvalues of the graph Laplacians for each subgraph, and find that  $\lambda_2(L_K) = 50$ , while  $\lambda_2(L_C) = 0.0158$ . Since the oscillator parameters are homogeneous,  $\beta_{1,k} \approx 2$ for both  $C_m$  and  $K_m$ . Thus, the sufficient condition for synchronization is  $\lambda_m^* = 2.41$ for each subgraph, so  $\lambda_2(L_K)$  is above the synchronization bound, while  $\lambda_2(L_C)$  is far below. In this example, we have used the synchronization condition as a guideline to design a system that exhibits different types of dynamic behavior.



Figure 7.3: **Dynamics of cluster synchronization:** The  $x_1$  and  $x_2$  dynamics for 101 FN oscillators arranged according to the graph structure depicted in Figure 2 with m = 50. Cluster synchronization is apparent in one cluster, but the other inputequivalent cluster does not synchronize. These results are consistent with the bounds from Corollary 7.5.2.

#### Conclusion

We have used a nonsmooth Lyapunov function to determine new sufficient conditions for synchronization in networks of nonlinear oscillators. This function was previously used to find tight bounds for synchronization in a complete graph of Kuramoto oscillators. We provide a general framework and a specialization to the FN model that illustrates its effectiveness. The bounds reported for the FN model improve on previously reported bounds as well as the bound we calculate in this work using an alternative method [113,124]. Finding sufficient conditions for synchronization in systems with nonlinear coupling, time delays, and heterogeneous node dynamics has been explored using the quadratic Lyapunov and contraction analyses in [21,65,80]. We expect that these bounds may also be improved with nonsmooth Lyapunov functions. This research was supported in part by the Office of Naval Research under ONR grant N00014-14-1-0635 and by the National Science Foundation under Grant No. DGE-1656466.
# Chapter 8

# Cluster Synchronization of Diffusively-Coupled Nonlinear Systems: A Contraction Based Approach<sup>\*</sup>

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Finding the conditions that foster synchronization in networked nonlinear systems is critical to understanding a wide range of biological and mechanical systems. However, the conditions proved in the literature for synchronization in nonlinear systems with linear coupling, such as has been used to model neuronal networks, are in general not strict enough to accurately determine the system behavior. We leverage contraction theory to derive new sufficient conditions for cluster synchronization in terms of the network structure, for a network where the intrinsic nonlinear dynam-

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ics of each node may differ. Our result requires that network connections satisfy a cluster-input-equivalence condition, and we explore the influence of this requirement on network dynamics. For application to networks of nodes with FitzHugh-Nagumo dynamics, we show that our new sufficient condition is tighter than those found in previous analyses that used smooth or nonsmooth Lyapunov functions. Improving the analytical conditions for when cluster synchronization will occur based on network configuration is a significant step toward facilitating understanding and control of complex networked systems.

## 8.1 Introduction

Synchronization has been observed and studied in diverse fields. Its presence has been characterized in symmetric networks of identical mechanical systems or identical biological systems, as well as those with differing types of individual components and nonuniform coupling [100]. The role of synchronization has been studied in a multitude of both natural and engineered settings including collective motion [116], power-grid networks [89], robotics [91], sensor networks [117], circadian rhythms [141], bioluminescence in fireflies [119], pacemaker cells in the heart [85], neuronal ensembles [23], and numerous others. In the human brain, synchronization at the neuronal or regional level can be beneficial, allowing for production of a vast range of behaviors [38,81], or detrimental, causing disorders such as Parkinson's disease [22] and epilepsy [75]. Applications for control of neural dynamics may involve regulating patterns of synchronized phenomena among nodes or subsystems that have different intrinsic dynamics and are connected in an arbitrary network [1,140]. Most generally, nodes can be agents in a multi-agent system, compartments in a compartmental system, or other units that interact with one another in a pairwise framework. Characterizing the emergence and persistence of synchronization in a system with multiple heterogeneous nodes is the first step towards effective control of desired behavior.

Heterogeneous nodes and nonuniform coupling structure in a network often lead to complex patterns of synchronization. Under certain conditions, it is possible to partition the network into clusters of nodes that are synchronized within clusters but not across clusters. In a cluster synchronized network, nodes in the same cluster will have similar behavior after a transient. The cluster synchronized network can thus be reduced to a network where each node corresponds to a cluster, commonly referred to as the *quotient network* [24, 113, 115]. The simplified dynamics represent a powerful tool for facilitating analysis of the dynamics of cluster synchronized systems.

Cluster synchronization has been defined in various ways in the literature. According to one common definition for phase oscillators, clusters are subgroups of oscillators that share common phases [19,92]. Recent works (e.g. [13,130]) have also assumed similar definition for cluster synchronization. Another definition is based on approximate cluster synchronization, wherein nodes within a given cluster can have slightly different behaviors [43, 44, 99, 122]. In the present work, we define cluster synchronnization as convergence to an invariant manifold, called the cluster synchronization manifold, on which the states of all nodes in a cluster evolve identically [11, 121].

A necessary condition for cluster synchronization is the existence of an invariant manifold. In this work, we assume "cluster-input-equivalence", which ensures existence of such a manifold. Cluster-input-equivalence was proposed in [51, 125], under the name "balanced equivalence", and in [11, Eq. 13]. Subsequently this condition was used to show existence of an invariant manifold for cluster synchronization [110, 115, 123].

Another important problem is the establishment of sufficient conditions that guarantee stability of a cluster synchronization manifold. The problem has been well studied for networks where the dynamics can be described by reduced phase oscillators, e.g., [19,92]. The problem has also been studied for networks of more general nonlinear dynamics. For example, in [79,134] conditions that rely on intra-cluster network structure have been explored. Specialized network graphs have been considered in [96]. In [142] time-delay and negative coupling have been explored as mechanisms to realize cluster synchronization in a network with homogeneous dynamics.

In the present paper, we propose a new sufficient condition for cluster synchronization that applies to general network structure and heterogeneous nonlinear dynamics. The method leverages contraction theory, which has been used to analyze the stability of invariant dynamics, including cluster synchronization [99]. Here, we use contraction theory to find a sufficient condition for cluster synchronization that incorporates a novel measure of connectivity between clusters not found in previous work on the subject.

Contraction theory is a powerful tool for understanding synchronization phenomena in networked systems. The proper tool for characterizing contractivity for nonlinear systems is provided by the logarithmic norms, or matrix measures [32], of the Jacobian of the vector field, evaluated at all possible states. This idea is a classical one, and can be traced back at least to work of D.C. Lewis in the 1940s [76].

Dahlquist's 1958 thesis under Hörmander used matrix measures to show contractivity of differential equations, and more generally of differential inequalities, the latter applied to the analysis of convergence of numerical schemes for solving differential equations [27]. Several authors have independently rediscovered the basic ideas. For example, in the 1960s, Demidovič [30, 31] established basic convergence results with respect to Euclidean norms, as did Hartman [56] and Yoshizawa [143, 144]. In control theory, the field attracted much attention after the work of Lohmiller and Slotine [77]. We refer the reader especially to the careful historical analysis given in [64]. Other useful historical references are [94] and the survey [120]. An introductory tutorial to basic results in contraction theory for nonlinear control systems is given in [6]. Results on synchronization using contraction-based techniques are described, for example, in [5,8,78,111,113,135].

The main contributions of the present paper are as follows. We extend contraction theory to a setting where the nodal dynamics may have heterogeneous intrinsic dynamics and the network satisfies the cluster-input-equivalence condition. Using this extension of contraction theory, we prove new sufficient conditions for cluster synchronization in a network of heterogeneous nodal dynamics. We improve upon our earlier analysis of synchronization in networks of homogeneous FitzHugh-Nagumo (FN) oscillators [29], and show that the proposed result yields a tighter bound on the algebraic connectivity of the associated undirected graph. The bound is a significant advance over previous results because it incorporates terms that reflect inter- and intra- cluster network structure.

The paper proceeds as follows. In Section 8.2, we review relevant concepts and results from the contraction theory literature. In Section 8.3, we present our main result, an extension of the existing theory to a cluster synchronized setting. In Section 8.4, we consider networks of neuronal oscillators, modeled by FitzHugh-Nagumo and Hindmarsh-Rose dynamics, and demonstrate how the proposed approach provides sufficient conditions for cluster synchronization. We conclude in Section 8.5.

## 8.2 A review of contraction theory

In what follows, we review notations, definitions, and main results in contraction theory that will be applied in later sections.

**Definition 8.2.1** (Logarithmic norm [120]). For any matrix  $A \in \mathbb{R}^{n \times n}$  and any given norm  $\|\cdot\|$  on  $\mathbb{R}^n$ , the logarithmic norm (also called the matrix measure) of A induced by the norm  $\|\cdot\|$  is defined by

$$\mu[A] = \lim_{h \to 0^+} \sup_{x \neq 0 \in \mathbb{R}^n} \frac{1}{h} \left( \frac{\|(I+hA)x\|}{\|x\|} - 1 \right), \tag{8.1}$$

where I is the identity matrix of size n.

Notation 1. For any  $1 \le p \le \infty$  and any  $n \times n$  positive definite matrix Q, let  $\|\cdot\|_p$ denote the  $L^p$  norm on  $\mathbb{R}^n$ , and  $\|\cdot\|_{p,Q}$  denote the Q-weighted  $L^p$  norm on  $\mathbb{R}^n$  defined by  $\|x\|_{p,Q} := \|Qx\|_p$ . By  $\mu_p[A]$ , we mean the logarithmic norm of A induced by  $\|\cdot\|_p$ and by  $\mu_{p,Q}[A]$ , we mean the logarithmic norm of A induced by  $\|\cdot\|_{p,Q}$ . Note that  $\mu_{p,Q}[A] = \mu_p[QAQ^{-1}].$ 

Notation 2. For any matrix A, denote A positive semidefinite as  $A \ge 0$ .

**Remark 8.2.2.** In Table 8.1, the algebraic expression of logarithmic norms induced by the  $L^p$  norm for p = 1, 2, and  $\infty$  are shown. For proofs, see for instance [32].

vector norm, $\ \cdot\ $	induced matrix measure, $\mu[A]$
$  x  _1 = \sum_{i=1}^n  x_i $	$\mu_1[A] = \max_j \left( a_{jj} + \sum_{i \neq j}  a_{ij}  \right)$
$\ x\ _{2} = \left(\sum_{i=1}^{n}  x_{i} ^{2}\right)^{\frac{1}{2}}$	$\mu_2[A] = \max_{\lambda \in \operatorname{spec} \frac{1}{2}(A+A^T)} \lambda$
$\ x\ _{\infty} = \max_{1 \le i \le n}  x_i $	$\mu_{\infty}[A] = \max_{i} \left( a_{ii} + \sum_{i \neq j}  a_{ij}  \right)$

Table 8.1: Standard matrix measures for a real  $n \times n$  matrix,  $A = [a_{ij}]$ .

**Definition 8.2.3** (Contraction). Consider the following nonlinear dynamical system on  $V \times [0, \infty]$ , where V is a convex subset of  $\mathbb{R}^n$ . Consider appropriate conditions on vector field G (e.g. G(x,t) Lipschitz on x and continuous on (x,t)) that guarantee existence and uniqueness of solutions of

$$\dot{x}(t) = G(x(t), t).$$
 (8.2)

Equation (8.2) is contractive if there exist c < 0 and a norm  $\|\cdot\|$  on  $\mathbb{R}^n$  such that, for any two solutions x and y of Equation (8.2), the following inequality holds for any  $t \ge 0$ :

$$||x(t) - y(t)|| \le e^{ct} ||x(0) - y(0)||.$$
(8.3)

**Proposition 8.2.4** (Theorem 1, [6]). Consider Equation (8.2) and assume that G is a continuously differentiable function on its first variable. Let  $c := \sup_{(x,t)} \mu[J_G(x,t)]$ , where  $\mu$  is the logarithmic norm induced by an arbitrary norm on  $\mathbb{R}^n$ , and  $J_G$  is the Jacobian of G. Then for any two solutions x and y of Equation (8.2), and  $t \ge 0$ ,

$$||x(t) - y(t)|| \le e^{ct} ||x(0) - y(0)||.$$

In particular, when c < 0, Equation (8.2) satisfies Equation (8.3) and is contractive.

Throughout the paper, we denote the Jacobian of the vector field f(x,t) evaluated at (x,t) as  $J_f(x,t)$ , i.e.,  $J_f(x,t) = \frac{\partial f}{\partial x}(x,t)$ .

We consider a network of N nodes, with states  $\{X^1, \ldots, X^N\}$  and intrinsic dynamics  $F^i$ :

$$\dot{X}^{i}(t) = F^{i}\left(X^{i}(t), t\right) \; .$$

Here,  $X^i$  and  $F^i$  have dimension  $n \ge 1$ . For a fixed convex subset  $V \subset \mathbb{R}^n$ ,  $F^i \colon V \times [0, \infty) \to \mathbb{R}^n$ , defined by  $F^i = F^i(z, t)$ , is Lipschitz on z and continuous on (z, t). We also assume that the nodes are diffusively connected through an undirected weighted graph  $\mathcal{G} = (\mathcal{V}, \mathcal{E})$  and describe the dynamics of the network as follows:

$$\dot{X}^{i}(t) = F^{i}\left(X^{i}(t), t\right) + \sum_{j \in \mathcal{N}^{i}} \gamma^{ij} D\left(X^{j}(t) - X^{i}(t)\right) \qquad i = 1, \dots, N .$$
(8.4)

The indices in  $\mathcal{N}^i$  represent the neighbors of node *i*. Without loss of generality<sup>†</sup>, we can assume that the *diffusion matrix* D is a nonzero diagonal matrix of size n,  $D = \text{diag}(d_1, \ldots, d_n)$ , where  $d_i \geq 0$ . The positive constants  $\gamma^{ij}$  represent the edge weights of  $\mathcal{G}$ . The products of the elements in D and the edge weights  $\gamma^{ij}$  represent the coupling strengths between the nodes. This allows representation of all possible diffusive coupling structures by manipulation of the diagonal elements of D and the edge weights.

Let  $\mathcal{L} = (\mathcal{L}_{ij})$  be the Laplacian matrix of  $\mathcal{G}$ :

$$\mathcal{L}_{ij} = \begin{cases} \sum_{k \in \mathcal{N}^i} \gamma^{ik} & i = j, \\ -\gamma^{ij} & i \neq j, j \in \mathcal{N}^i, \\ 0 & \text{otherwise.} \end{cases}$$
(8.5)

We denote the eigenvalues of  $\mathcal{L}$  as  $0 = \lambda^{(1)} \leq \lambda^{(2)} \leq \cdots \leq \lambda^{(N)}$ . The second smallest eigenvalue,  $\lambda^{(2)}$ , is called the *algebraic connectivity* of the graph. This number helps to quantify "how connected" the graph is. The number of the zero eigenvalues is equal to the number of connected components of  $\mathcal{G}$ .

Using the notation of the Laplacian matrix, Equation (8.4) can be written in closed form:

$$\dot{X}(t) = \mathcal{F}(X(t), t) - (\mathcal{L} \otimes D)X(t), \qquad (8.6)$$

where  $X = (X^{1^T}, \dots, X^{N^T})^T$ ,  $\mathcal{F} = (F^{1^T}, \dots, F^{N^T})^T$ , and  $\otimes$  represents the Kronecker product.

Definition 8.2.5 (Complete synchronization). Let

$$\mathscr{S}_1 := \left\{ X \in \mathbb{R}^{nN} \mid X^1 = \dots = X^N, \ X^i \in \mathbb{R}^n \right\}.$$

<sup>&</sup>lt;sup>†</sup>If D is not diagonal, an appropriate change of coordinate can render it diagonal.

The dynamics given in Equation (8.4) synchronize completely if any solution of Equation (8.4) converges to  $\mathscr{S}_1$  in an appropriate norm. In other words, let X be a solution of Equation (8.4). Then there exists a solution  $\bar{X} \in \mathscr{S}_1$  such that, in an appropriate norm,

$$X(t) - \bar{X}(t) \to 0 \quad as \ t \to \infty.$$

 $\mathscr{S}_1$  is called the synchronization manifold.

We will use synchronization and complete synchronization alternatively.

**Definition 8.2.6** (Cluster synchronization). For any  $1 \le K \le N$  and any  $1 \le c_1, \ldots, c_K \le N$  such that  $c_1 + \cdots + c_K = N$ , let

$$\mathscr{S}_K := \left\{ X \in \mathbb{R}^{nN} \mid X^1 = \dots = X^{c_1}, \ \dots, \ X^{N-c_K+1} = \dots = X^N, \ X^i \in \mathbb{R}^n \right\}.$$

The dynamics given in Equation (8.4) synchronize in clusters if there exists  $1 \le K \le$ N such that all solutions of Equation (8.4) converge to  $\mathscr{S}_K$  in an appropriate norm.  $\mathscr{S}_K$  is called the K-cluster synchronization manifold.

The 1-cluster synchronization manifold is the same as the synchronization manifold (Definition 8.2.5).

In the following two propositions, we consider Equation (8.4) with homogeneous  $F^i = F$ , and state two sufficient conditions that guarantee that Equation (8.4) synchronizes.

**Proposition 8.2.7** (Proposition 1, [7]). Consider Equation (8.4) with homogeneous  $F^i = F$ . Assume that there exists a norm on  $\mathbb{R}^n$  such that

$$\sup_{(x,t)} \mu[J_F(x,t)] < 0.$$
(8.7)

Then Equation (8.4) synchronizes.

In [113], Proposition 8.2.7 has been generalized<sup>‡</sup> to  $F^i$  with heterogeneous elements. The work shows that, under some conditions on the weights of the interconnected graph, if each node has contractive dynamics, then Equation (8.4) synchronizes in clusters. In Section 8.4, we provide an example (with FitzHugh-Nagumo and Hindmarsh-Rose oscillators) that synchronizes in clusters and supports our theory derived in the next section but does not satisfy the condition provided in [113].

Note that the sufficient condition provided in Proposition 8.2.7 depends only on the dynamics of each isolated node, namely  $J_F$ . The next proposition from [8] provides a sufficient condition for complete synchronization less restrictive than Equation (8.7), which depends on  $J_F$ , the diffusion matrix D, and the graph  $\mathcal{G}$ . It is based on the weighted  $L^2$  norms. For some special graphs, the result has been generalized to weighted  $L^p$  norms [7].

**Proposition 8.2.8** (Theorem 4 (modified), [8]). Consider Equation (8.4) with homogeneous  $F^i = F$ . Assume that there exists a positive definite matrix P such that  $P^2D + DP^2$  is also positive definite, and let

$$c := \sup_{(x,t)\in V\times[0,\infty)} \mu_{2,P} \left[ J_F(x,t) - \lambda^{(2)} D \right].$$

Then for any solution X of Equation (8.4) that remains in  $V^N$ , there exists a solution  $\overline{X}$  such that

$$||X(t) - \bar{X}(t)||_{2, I_N \otimes P^2} \le e^{ct} ||X(0) - \bar{X}(0)||_{2, I_N \otimes P^2}$$

Moreover, if c < 0, then Equation (8.4) synchronizes, i.e., for any pair  $i, j \in \{1, \ldots, N\}$ ,

$$X^{i}(t) - X^{j}(t) \to 0 \quad as \ t \to \infty.$$

<sup>&</sup>lt;sup>‡</sup>The statement of Theorem 3 in [113] is correct; however, the proof needs revision to be complete.

In the following section, we present the main result of this work – we generalize Proposition 8.2.8 to heterogeneous  $F^i$  and provide sufficient conditions for cluster synchronization.

### 8.3 Main result: Cluster synchronization

In this section, we provide sufficient conditions on heterogeneous intrinsic dynamics  $F^i$ , the graph  $\mathcal{G}$ , and the diffusion matrix D, that guarantee cluster synchronization of the network described in Equation (8.4).

**Assumption 8.3.1.** In the network described by Equation (8.4), we assume that

1. There exist  $K \leq N$  and  $c_1, \ldots, c_K \geq 2$ , such that  $c_1 + \cdots + c_K = N$ , and

$$F^{i_1} = \dots = F^{i_{c_1}} =: F_{\mathscr{C}_1}, \ \dots, \ F^{i_{N-c_K+1}} = \dots = F^{i_N} =: F_{\mathscr{C}_K},$$

where  $\{i_1, \ldots, i_N\}$  is a permutation of  $\{1, \ldots, N\}$ . Without loss of generality, we can assume:

$$F^1 = \dots = F^{c_1} =: F_{\mathscr{C}_1}, \ \dots, \ F^{N-c_K+1} = \dots = F^N =: F_{\mathscr{C}_K}.$$

Let  $\mathscr{C}_1, \ldots, \mathscr{C}_K$  denote K clusters of nodes. The nodes in cluster  $\mathscr{C}_1$  are defined by  $X^1, \ldots, X^{c_1}$  and they all have dynamics  $F_{\mathscr{C}_1}$ , the nodes in cluster  $\mathscr{C}_2$  are defined by  $X^{c_1+1}, \ldots, X^{c_1+c_2}$  and they all have dynamics  $F_{\mathscr{C}_2}$ , etc. For ease of notation in our calculations, we let

$$X_{\mathscr{C}_{1}}^{1} = X^{1}, \dots, X_{\mathscr{C}_{1}}^{c_{1}} = X^{c_{1}},$$
$$X_{\mathscr{C}_{2}}^{1} = X^{c_{1}+1}, \dots, X_{\mathscr{C}_{2}}^{c_{2}} = X^{c_{1}+c_{2}},$$
$$\vdots$$
(8.8)

$$X^1_{\mathscr{C}_K} = X^{N-c_K+1}, \dots, X^{c_K}_{\mathscr{C}_K} = X^N.$$

The cluster-input-equivalence condition defined in [11] holds. This implies that
the following edge weight sums are equal: for any two nodes X<sup>i</sup><sub>𝔅r</sub>, X<sup>j</sup><sub>𝔅r</sub>, (i, j) ∈
𝔅<sub>r</sub>,

$$\eta_{\mathscr{C}_{r}\mathscr{C}_{s}} := \sum_{k \in \mathscr{N}^{i}_{\mathscr{C}_{s}}} \gamma^{ik} = \sum_{k \in \mathscr{N}^{j}_{\mathscr{C}_{s}}} \gamma^{jk}, \tag{8.9}$$

where  $\mathcal{N}_{\mathcal{C}_s}^i$  denotes the indices of the neighbors of node *i* which are in cluster  $\mathcal{C}_s$ .

Assumption 8.3.1 ensures that the K-cluster synchronization manifold is invariant, which is a necessary condition for cluster synchronization.

Next we provide sufficient conditions to show that  $\mathscr{S}_K$  is (globally) stable, i.e., any solution of Equation (8.4) converges to  $\mathscr{S}_K$ .

Recall that the network graph is  $\mathcal{G} = (\mathcal{V}, \mathcal{E})$ . Denote the subgraph for the nodes in  $\mathscr{C}_r$  by  $\mathcal{G}_{\mathscr{C}_r} = (\mathcal{V}_{\mathscr{C}_r}, \mathcal{E}_{\mathscr{C}_r})$ . The set  $\mathcal{V}_{\mathscr{C}_r}$  consists of all the nodes in  $\mathscr{C}_r$  and the set  $\mathcal{E}_{\mathscr{C}_r}$ consists of all edges that have both end points in  $\mathcal{V}_{\mathscr{C}_r}$ . Then

$$\mathcal{G} = \left(\bigcup_{r=1}^{K} \mathcal{G}_{\mathscr{C}_r}\right) \bigcup \bar{\mathcal{G}},$$

where  $\bar{\mathcal{G}} = (\mathcal{V}, \mathcal{E} \setminus \cup_r \mathcal{E}_{\mathscr{C}_r})$  is the graph describing connections among the clusters  $\mathscr{C}_r$ .

Let  $\mathcal{L}_{\mathscr{C}_r}$  denote the Laplacian matrix of  $\mathcal{G}_{\mathscr{C}_r}$  with eigenvalues  $0 = \lambda_{\mathscr{C}_r}^{(1)} \leq \lambda_{\mathscr{C}_r}^{(2)} \leq \dots \leq \lambda_{\mathscr{C}_r}^{(c_r)}$  and  $\bar{\mathcal{L}}$  denote the Laplacian matrix of  $\bar{\mathcal{G}}$  with eigenvalues  $0 = \bar{\lambda}^{(1)} \leq \bar{\lambda}^{(2)} \leq \dots \leq \bar{\lambda}^{(N)}$ . In the special case of K = 1, we set  $\bar{\lambda}^{(2)} = 0$ . Then  $\mathcal{L}$ , the Laplacian matrix of  $\mathcal{G}$ , can be written as follows:

$$\mathcal{L} = \mathcal{L}_{\mathscr{C}} + \bar{\mathcal{L}},\tag{8.10}$$

where  $\mathcal{L}_{\mathscr{C}}$  is a block diagonal matrix with the form:

$$\mathcal{L}_{\mathscr{C}} = \begin{pmatrix} \mathcal{L}_{\mathscr{C}_{1}} & & \\ & \ddots & \\ & & \mathcal{L}_{\mathscr{C}_{K}} \end{pmatrix}.$$

$$(8.11)$$

With these definitions, Equation (8.6) can be written as

$$\dot{X}(t) = \mathcal{F}(X(t), t) - (\mathcal{L}_{\mathscr{C}} \otimes D)X(t) - (\bar{\mathcal{L}} \otimes D)X(t).$$
(8.12)

**Theorem 8.3.2.** Consider Equation (8.4), or equivalently Equation (8.12), with Assumption 8.3.1, and let

$$\mu := \max_{r=1,\dots,K} \sup_{(x,t)\in V\times[0,\infty)} \mu_{2,P} \left[ J_{F_{\mathscr{C}_r}}(x,t) - \left(\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}\right) D \right],$$
(8.13)

where  $P \in \mathbb{R}^{n \times n}$  is a positive definite matrix chosen such that  $P^2D + DP^2$  is positive semidefinite. Then, for any solution X of Equation (8.4) that remains in  $V^N$ , there exists  $\bar{X}(t)$  such that

$$||X(t) - \bar{X}(t)||_{2,\mathcal{P}} \le e^{\mu t} ||X(0) - \bar{X}(0)||_{2,\mathcal{P}},$$
(8.14)

where  $\mathcal{P} = I_N \otimes P^2$  and  $\|\cdot\|_{2,\mathcal{P}}$  is a  $\mathcal{P}$ -weighted  $L^2$  norm on  $\mathbb{R}^{nN}$ , defined by

$$||x||_{2,\mathcal{P}} := \left\| \left( \left\| P^2 x^1 \right\|_2, \dots, \left\| P^2 x^N \right\|_2 \right)^T \right\|_2,$$

for any  $x = (x^{1^T}, \dots, x^{N^T})^T \in \mathbb{R}^{nN}$ . In particular, if  $\mu < 0$ , then for any pair of nodes  $i, j \in \mathscr{C}_r, X^i_{\mathscr{C}_r}$  and  $X^j_{\mathscr{C}_r}$  satisfy

$$X^i_{\mathscr{C}_r}(t) - X^j_{\mathscr{C}_r}(t) \to 0 \quad as \ t \to \infty.$$

**Remark 8.3.3.** Theorem 8.3.2 provides a sufficient condition for cluster synchronization that depends on the dynamics of each isolated cluster  $J_{F_{\mathscr{C}_r}}$ , the diffusion matrix D, the structure  $\lambda_{\mathscr{C}_r}^{(2)}$  of each subgraph  $\mathcal{G}_{\mathscr{C}_r}$  describing connections among the nodes in cluster  $\mathscr{C}_r$ , and the structure  $\bar{\lambda}^{(2)}$  of the subgraph  $\bar{\mathcal{G}}$  describing connections among the clusters. Proposition 8.2.8 is a special case of Theorem 8.3.2 when K = 1 and  $\bar{\lambda}^{(2)} = 0$ . One can still apply Proposition 8.2.8 to K > 1 clusters to show cluster synchronization. However, Theorem 8.3.2 provides a less restrictive sufficient condition for cluster synchronization because it makes use of coupling structure both within and between clusters.

**Remark 8.3.4.** For systems that satisfy  $\mu < 0$ , the rate of convergence to the K-cluster synchronization manifold can be approximated by  $\mu$ . In addition to the dependence on the dynamics in each cluster  $J_{F_{\mathscr{C}_r}}$  and the diffusion matrix D, the rate of convergence depends on the structure of the coupling within  $(\lambda_{\mathscr{C}_r}^{(2)})$  and between  $(\bar{\lambda}^{(2)})$  clusters.

In the proof of Theorem 8.3.2, we need the following key lemmas. We first state the Courant-Fischer minimax Theorem, from [61].

**Lemma 8.3.5.** Let L be a positive semidefinite matrix in  $\mathbb{R}^{l \times l}$ . Let  $\lambda^{(1)} \leq \cdots \leq \lambda^{(l)}$ be l eigenvalues with  $e^1, \cdots, e^l$  corresponding normalized orthogonal eigenvectors. For any  $v \in \mathbb{R}^l$ , if  $v^T e^j = 0$  for  $1 \leq j \leq k - 1$ ,  $1 \leq k \leq l$ , then

$$v^T L v > \lambda^{(k)} v^T v.$$

**Lemma 8.3.6.** [6, Lemma 3] Suppose that P is a positive definite matrix and A is an arbitrary matrix. If  $\mu_{2,P}[A] = \mu$ , then  $P^2A + A^T P^2 \leq 2\mu P^2$ .

Proof of Theorem 8.3.2

Let  $w := X - \bar{X}$ , where

$$X = \left(X_{\mathscr{C}_1}^{1}, \dots, X_{\mathscr{C}_1}^{c_1 T}, \dots, X_{\mathscr{C}_K}^{1}, \dots, X_{\mathscr{C}_K}^{c_K T}\right)^T,$$

is a solution of (8.4) and

$$\bar{X} = \left( \left( \mathbf{1}_{c_1} \otimes x_1 \right)^T, \dots, \left( \mathbf{1}_{c_K} \otimes x_K \right)^T \right)^T,$$

with  $x_r := \frac{1}{c_r} \sum_{i=1}^{c_r} X_{\mathscr{C}_r}^i$  and  $\mathbf{1}_{c_r} \in \mathbb{R}^{c_r}$  is a vector of ones. Let  $w = (w_1^T, \dots, w_K^T)^T$ , where  $w_r := \left( (X_{\mathscr{C}_r}^1 - x_r)^T, \dots, (X_{\mathscr{C}_r}^{c_r} - x_r)^T \right)^T \in \mathbb{R}^{c_r n}$ , and define

$$\Phi(w) := \frac{1}{2} w^T \mathcal{P} w = \frac{1}{2} \sum_{r=1}^K w_r^T \left( I_{c_r} \otimes P^2 \right) w_r .$$

Since  $\Phi(w) = \frac{1}{2} \|\mathcal{P}w\|_2^2$ , to prove (8.14), it suffices to show that

$$\frac{d}{dt}\Phi(w) \le 2\mu\Phi(w)$$

Let

$$\mathcal{F}(X,t) = \left(F_{\mathscr{C}_1}^T(X_{\mathscr{C}_1}^1,t),\ldots,F_{\mathscr{C}_1}^T(X_{\mathscr{C}_1}^{c_1},t),\ldots,F_{\mathscr{C}_K}^T(X_{\mathscr{C}_K}^1,t),\ldots,F_{\mathscr{C}_K}^T(X_{\mathscr{C}_K}^{c_K},t)\right)^T,$$

and

$$\bar{\mathcal{F}}(X,t) = \left( \left(\mathbf{1}_{c_1} \otimes y_1\right)^T, \dots, \left(\mathbf{1}_{c_K} \otimes y_K\right)^T \right)^T \quad \text{where} \quad y_r = \frac{1}{c_r} \sum_{i=1}^{c_r} F_{\mathscr{C}_r}(X^i_{\mathscr{C}_r}, t).$$

Standard calculations show that the derivative of  $\Phi$  is as follows:

$$\frac{d\Phi}{dt}(w) = w^{T} \mathcal{P}\left(\mathcal{F}(X,t) - \bar{\mathcal{F}}(X,t)\right) - w^{T} \mathcal{P}(\mathcal{L}_{\mathscr{C}} \otimes D)w - w^{T} \mathcal{P}(\bar{\mathcal{L}} \otimes D)w$$

$$= w^{T} \mathcal{P}\left(\mathcal{F}(X,t) - \mathcal{F}(\bar{X},t)\right) + w^{T} \mathcal{P}\left(\mathcal{F}(\bar{X},t) - \bar{\mathcal{F}}(X,t)\right) - w^{T} \mathcal{P}(\mathcal{L}_{\mathscr{C}} \otimes D)w - w^{T} \mathcal{P}(\bar{\mathcal{L}} \otimes D)w$$

$$= w^{T} \mathcal{P}\left(\mathcal{F}(X,t) - \mathcal{F}(\bar{X},t)\right) - w^{T} \mathcal{P}(\mathcal{L}_{\mathscr{C}} \otimes D)w - w^{T} \mathcal{P}(\bar{\mathcal{L}} \otimes D)w$$

$$(8.15)$$

In the second equation, we added and subtracted  $w^T \mathcal{PF}(\bar{X}, t)$ , where  $\mathcal{F}(\bar{X}, t)$  is written as

$$\mathcal{F}(\bar{X},t) = \left( \left( \mathbf{1}_{c_1} \otimes F_{\mathscr{C}_1}(x_1,t) \right)^T, \ldots, \left( \mathbf{1}_{c_K} \otimes F_{\mathscr{C}_K}(x_K,t) \right)^T \right)^T.$$

The last equality holds because  $w_r^T(\mathbf{1}_{c_r} \otimes I_n) = 0$  implies that

$$w^{T}\mathcal{P}\left(\mathcal{F}(\bar{X},t)-\bar{\mathcal{F}}(X,t)\right) = \sum_{r=1}^{K} w_{r}^{T}\left(I_{c_{r}}\otimes P^{2}\right)\left(\mathbf{1}_{c_{r}}\otimes\left(F_{\mathscr{C}_{r}}^{T}(x_{r},t)-y_{r}^{T}\right)\right)$$
$$= \sum_{r=1}^{K} w_{r}^{T}\left(\mathbf{1}_{c_{r}}\otimes P^{2}\left(F_{\mathscr{C}_{r}}^{T}(x_{r},t)-y_{r}^{T}\right)\right)$$
$$= \sum_{r=1}^{K} w_{r}^{T}\left(\mathbf{1}_{c_{r}}\otimes I_{n}\right)P^{2}\left(F_{\mathscr{C}_{r}}^{T}(x_{r},t)-y_{r}^{T}\right)$$
$$= 0.$$

Step 1. We show that

$$-w^{T} \mathcal{P}(\mathcal{L}_{\mathscr{C}} \otimes D) w \leq -\sum_{r=1}^{K} \lambda_{\mathscr{C}_{r}}^{(2)} w_{r}^{T} \left( I_{c_{r}} \otimes P^{2} D \right) w_{r} .$$

$$(8.16)$$

Since  $P^2D + DP^2$  is positive semidefinite, Cholesky decomposition yields an upper triangular matrix M such that  $P^2D + DP^2 = 2M^T M$ . For any r = 1, ..., K,

$$\begin{split} -w_r^T \left( I_{c_r} \otimes P^2 \right) \left( \mathcal{L}_{\mathscr{C}_r} \otimes D \right) w_r &= -w_r^T \left( \mathcal{L}_{\mathscr{C}_r} \otimes P^2 D \right) w_r \\ &= -\frac{1}{2} w_r^T \left( \mathcal{L}_{\mathscr{C}_r} \otimes \left( P^2 D + D P^2 \right) \right) w_r \\ &= -w_r^T \left( \mathcal{L}_{\mathscr{C}_r} \otimes \left( M^T M \right) \right) w_r \\ &= -w_r^T \left( I_{c_r} \otimes M^T \right) \left( \mathcal{L}_{\mathscr{C}_r} \otimes I_n \right) \left( I_{c_r} \otimes M \right) w_r \\ &\leq -\lambda_{\mathscr{C}_r}^{(2)} \left( \left( I_{c_r} \otimes M \right) w_r \right)^T \left( I_{c_r} \otimes M \right) w_r \\ &= -\lambda_{\mathscr{C}_r}^{(2)} w_r^T \left( I_{c_r} \otimes M^T M \right) w_r \\ &= -\lambda_{\mathscr{C}_r}^{(2)} w_r^T \left( I_{c_r} \otimes P^2 D \right) w_r \,. \end{split}$$

Note that the inequality holds by Lemma 8.3.5. To apply Lemma 8.3.5, we need to show that

$$((I_{c_r} \otimes M) w_r)^T (\mathbf{1}_{c_r} \otimes I_n) = 0.$$

By definition of  $w_r$ ,  $w_r^T \mathbf{1}_{nc_r} = 0$  and hence

$$\left(\left(I_{c_r}\otimes M\right)w_r\right)^T\left(\mathbf{1}_{c_r}\otimes I_n\right) = w_r^T\left(I_{c_r}\otimes M^T\right)\left(\mathbf{1}_{c_r}\otimes I_n\right) = w_r^T\left(\mathbf{1}_{c_r}\otimes M^T\right)$$
$$= \sum_{i=1}^{c_r} (X_{\mathscr{C}_r}^i - x_r)^T M^T = \left(\sum_{i=1}^{c_r} (X_{\mathscr{C}_r}^i - x_r)^T\right)M^T = 0.$$

Both  $\mathcal{P}$  and  $\mathcal{L}_{\mathscr{C}}$  are block diagonal with blocks of same sizes,  $c_1, \ldots, c_K$ , so we have:

$$-w^T \mathcal{P}(\mathcal{L}_{\mathscr{C}} \otimes D)w = -\sum_{r=1}^K w_r^T \left( I_{c_r} \otimes P^2 \right) \left( \mathcal{L}_{\mathscr{C}_r} \otimes D \right) w_r \le -\sum_{r=1}^K \lambda_{\mathscr{C}_r}^{(2)} w_r^T \left( I_{c_r} \otimes P^2 D \right) w_r .$$

Step 2. We show that

$$-w^{T}\mathcal{P}(\bar{\mathcal{L}}\otimes D)w \leq -\sum_{r=1}^{K}\bar{\lambda}^{(2)}w_{r}^{T}\left(I_{c_{r}}\otimes P^{2}D\right)w_{r}.$$
(8.17)

The proof is analogous to the previous step.

$$-w^{T}\mathcal{P}(\bar{\mathcal{L}}\otimes D)w = -w^{T}(I_{N}\otimes P^{2})(\bar{\mathcal{L}}\otimes D)w$$

$$= -w^{T}(\bar{\mathcal{L}}\otimes P^{2}D)w$$

$$= -\frac{1}{2}w^{T}(\bar{\mathcal{L}}\otimes (P^{2}D + DP^{2}))w$$

$$= -w^{T}(\bar{\mathcal{L}}\otimes M^{T}M)w$$

$$= -w^{T}(I_{N}\otimes M^{T})(\bar{\mathcal{L}}\otimes I_{n})(I_{N}\otimes M)w$$

$$\leq -\bar{\lambda}^{(2)}w^{T}(I_{N}\otimes M^{T})(I_{N}\otimes M)w$$

$$= -\bar{\lambda}^{(2)}w^{T}(I_{N}\otimes M^{T}M)w$$

$$= -\bar{\lambda}^{(2)}w^{T}(I_{N}\otimes P^{2}D)w$$

$$= -\sum_{r=1}^{K}\bar{\lambda}^{(2)}w_{r}^{T}(I_{c_{r}}\otimes P^{2}D)w_{r}.$$

Step 3. We show that

$$w^{T}\mathcal{P}(\mathcal{F}(X,t) - \mathcal{F}(\bar{X},t)) = \sum_{r=1}^{K} \sum_{i=1}^{c_{r}} \int_{0}^{1} (X^{i}_{\mathscr{C}_{r}} - x_{r})^{T} P^{2} J_{F_{\mathscr{C}_{r}}} \left( x_{r} + \tau (X^{i}_{\mathscr{C}_{r}} - x_{r}) \right) (X^{i}_{\mathscr{C}_{r}} - x_{r}) d\tau.$$
(8.18)

Note that  $w^T \mathcal{P}(\mathcal{F}(X,t) - \mathcal{F}(\bar{X},t)) = \sum_{r=1}^K w_r^T (I_{c_r} \otimes P^2) \tilde{\mathcal{F}}_r(X_{\mathscr{C}_r})$ , where

$$\tilde{\mathcal{F}}_r(X_{\mathscr{C}_r}) = \left(F_{\mathscr{C}_r}^T(X_{\mathscr{C}_r}^1, t) - F_{\mathscr{C}_r}^T(x_r, t), \dots, F_{\mathscr{C}_r}^T(X_{\mathscr{C}_r}^{c_r}, t) - F_{\mathscr{C}_r}^T(x_r, t)\right)^T.$$

By the Mean Value Theorem for integrals, for any  $r = 1, \ldots, K$ ,

$$w_{r}^{T} \left( I_{c_{r}} \otimes P^{2} \right) \tilde{\mathcal{F}}_{r}(X_{\mathscr{C}_{r}}) = \sum_{i=1}^{c_{r}} (X_{\mathscr{C}_{r}}^{i} - x_{r})^{T} P^{2} \left( F_{\mathscr{C}_{r}}(X_{\mathscr{C}_{r}}^{i}, t) - F_{\mathscr{C}_{r}}(x_{r}, t) \right)$$
$$= \sum_{i=1}^{c_{r}} \int_{0}^{1} (X_{\mathscr{C}_{r}}^{i} - x_{r})^{T} P^{2} J_{F_{\mathscr{C}_{r}}} \left( x_{r} + \tau (X_{\mathscr{C}_{r}}^{i} - x_{r}) \right) (X_{\mathscr{C}_{r}}^{i} - x_{r}) d\tau.$$

Adding over r, r = 1, ..., K, we obtain Equation (8.18).

Note that the sum of the left hand side of Equations (8.16)-(8.18), is equal to  $\frac{d\Phi}{dt}$ . Combining Steps 1-3, we have shown that

$$\frac{d\Phi}{dt} \le \sum_{r=1}^{K} \phi_r,$$

where for any  $r = 1, \ldots, K$ ,

$$\begin{split} \phi_r &\coloneqq w_r^T \left( I_{c_r} \otimes P^2 \right) \tilde{\mathcal{F}}_r(X_{\mathscr{C}_r}) - w_r^T \left( I_{c_r} \otimes P^2 \right) \left( I_{c_r} \otimes \lambda_{\mathscr{C}_r}^{(2)} D \right) w_r - w_r^T \left( I_{c_r} \otimes P^2 \right) \left( I_{c_r} \otimes \bar{\lambda}^{(2)} D \right) w_r \\ &= \sum_{i=1}^{c_r} \int_0^1 (X_{\mathscr{C}_r}^i - x_r)^T P^2 \left[ J_{F_{\mathscr{C}_r}} \left( x_r + \tau(X_{\mathscr{C}_r}^i - x_r) \right) - \lambda_{\mathscr{C}_r}^{(2)} D - \bar{\lambda}^{(2)} D \right] (X_{\mathscr{C}_r}^i - x_r) d\tau \\ &\leq \sum_{i=1}^{c_r} \frac{2\mu}{2} \int_0^1 (X_{\mathscr{C}_r}^i - x_r)^T P^2 (X_{\mathscr{C}_r}^i - x_r) d\tau \\ &= \frac{2\mu}{2} w_r^T \left( I_{c_r} \otimes P^2 \right) w_r \,. \end{split}$$

$$(8.19)$$

The inequality holds by applying Lemma 8.3.6 to Equation (8.13): we obtain, for any r = 1, ..., K, and any  $(x, t) \in V \times [0, \infty)$ ,

$$P^{2}\left[J_{F_{\mathscr{C}_{r}}}(x,t) - \left(\lambda_{\mathscr{C}_{r}}^{(2)} + \bar{\lambda}^{(2)}\right)D\right] + \left[J_{F_{\mathscr{C}_{r}}}^{T}(x,t) - \left(\lambda_{\mathscr{C}_{r}}^{(2)} + \bar{\lambda}^{(2)}\right)D\right]P^{2} \le 2\mu P^{2}.$$

Summing both sides of Equation (8.19) over r, for r = 1, ..., K, we obtain the desired result,  $\frac{d\Phi}{dt}(w) \leq 2\mu\Phi(w)$ .

### 8.4 Applications and numerical examples

In this section, we apply Theorem 8.3.2 to two types of nonlinear neuronal oscillator dynamics: FitzHugh-Nagumo dynamics and Hindmarsh-Rose dynamics. We then present numerical simulations for heterogeneous networks that include nodal dynamics of both types. In a second numerical example we show partial cluster synchronization, which results when  $\gamma$  takes an intermediate value below the bound.

## 8.4.1 Application to networks of heterogeneous FitzHugh-Nagumo neuronal oscillators

Here, we apply Theorem 8.3.2 to a network of N FitzHugh-Nagumo (FN) neuronal oscillators with graph  $\mathcal{G}$ . Let  $(y^i, z^i)^T \in \mathbb{R}^2$  be the state of oscillator i and  $I^i$  be the external input to oscillator i, for i = 1, ..., N.  $y^i$  and  $z^i$  represent the membrane potential and the recovery variable, respectively. The input current for oscillator i is  $I^i$ . The FN dynamics are

$$\dot{y}^{i} = f^{i}(y^{i}) - z^{i} + I^{i} + \gamma \sum_{j \in \mathcal{N}^{i}} \gamma^{ij}(y^{j} - y^{i}),$$

$$\dot{z}^{i} = \epsilon^{i}(y^{i} - b^{i}z^{i}),$$
(8.20)

where  $f^i$  is a cubic function,  $f^i(y) = y - \frac{y^3}{3} - a^i$ ,  $\gamma > 0$ ,  $a^i > 0$ ,  $0 < b^i < 1$ ,  $0 < \epsilon^i \ll 1$ are constant, and  $\mathcal{N}^i$  denotes the set of all the neighbors of node *i* in the network. In the FN model,  $\epsilon^i$  represents the time-scale separation between  $y^i$  and  $z^i$ , which affects oscillation frequency. The model parameter  $b^i$  controls the shape of the spike by changing the ratio of the duration of the spike to the refractory period. Using the notation of Theorem 8.3.2, n = 2,  $X^i = (y^i, z^i)^T$ ,  $F^i(X^i, t) =$  $(f^i(y^i) - z^i + I^i, \epsilon^i(y^i - b^i z^i))^T$ ,  $D = \text{diag}(\gamma, 0)$  is the diffusion matrix, and the  $\gamma^{ij}$ are the edge weights on the graph  $\mathcal{G}$ .

Assume that there exist  $K \geq 1$  clusters  $\mathscr{C}_1, \ldots, \mathscr{C}_K$  of FN oscillators such that  $a^i = a_{\mathscr{C}_r}, b^i = b_{\mathscr{C}_r}, \epsilon^i = \epsilon_{\mathscr{C}_r}$ , and  $I^i = I_{\mathscr{C}_r}$  for all FN oscillators  $i \in \mathscr{C}_r$  and all clusters  $r = 1, \ldots, K$ .

In what follows we show that, for K = 1 cluster, if  $\gamma \lambda^{(2)} > 1$ , then Equation (8.20) synchronizes, and, more generally, if K > 1, and for all  $r = 1, \ldots, K$ ,  $\epsilon_{\mathscr{C}_r} = \epsilon$ , and  $\gamma \left(\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}\right) > 1$ , then Equation (8.20) converges to its K-cluster synchronization manifold.

**Proposition 8.4.1.** Consider Equation (8.20), with Assumption 8.3.1. For all  $r = 1, \ldots, K$ , let

$$\gamma > \frac{1 + \alpha_r}{\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}},$$

where  $\alpha_r = \frac{\left(\epsilon_{\mathscr{C}_r} p - 1/p\right)^2}{4b_{\mathscr{C}_r}\epsilon_{\mathscr{C}_r}}$  and p > 0 constant. Then for any pair of FN oscillators  $\{(y^i, z^i)^T, (y^j, z^j)^T\}$  such that  $(i, j) \in \mathscr{C}_r$ ,

$$y^i(t) - y^j(t) \to 0, \quad z^i(t) - z^j(t) \to 0, \quad as \ t \to \infty.$$

In particular, if  $p = \max_r \frac{1}{\sqrt{\epsilon_{\mathscr{C}_r}}}$ , then  $\alpha_r$  is minimized.

*Proof.* To apply Theorem 8.3.2, we find a positive definite matrix P such that  $P^2D + DP^2$  is positive semidefinite and

$$\mu := \max_{r} \sup_{(y,z)^{T} \in \mathbb{R}^{2}} \mu_{2,P} \left[ J_{F_{\mathscr{C}_{r}}}(y,z) - \left( \lambda_{\mathscr{C}_{r}}^{(2)} + \bar{\lambda}^{(2)} \right) D \right] < 0.$$

Let P = diag(1, p) so that  $P^2D + DP^2 = \text{diag}(2\gamma, 0)$ , which is positive semidefinite. Then

$$\mu_{2,P} \left[ J_{F_{\mathscr{C}_{r}}}(y,z) - \left(\lambda_{\mathscr{C}_{r}}^{(2)} + \bar{\lambda}^{(2)}\right) D \right] = \mu_{2} \left[ P \left( J_{F_{\mathscr{C}_{r}}}(y,z) - \left(\lambda_{\mathscr{C}_{r}}^{(2)} + \bar{\lambda}^{(2)}\right) D \right) P^{-1} \right]$$
$$= \lambda_{\max} \left[ \left( \begin{array}{cc} 1 - y^{2} - \gamma \lambda_{\mathscr{C}_{r}}^{(2)} - \gamma \bar{\lambda}^{(2)} & \frac{\epsilon_{\mathscr{C}_{r}}p}{2} - \frac{1}{2p} \\ \frac{\epsilon_{\mathscr{C}_{r}}p}{2} - \frac{1}{2p} & -b_{\mathscr{C}_{r}}\epsilon_{\mathscr{C}_{r}} \end{array} \right) \right].$$
$$(8.21)$$

To see this recall that  $\mu_{2,P}[A] = \mu_2[PAP^{-1}]$ , and, by Remark 8.2.2,  $\mu_2[A] = \lambda_{\max}\left[\frac{A+A^T}{2}\right]$ , where  $\lambda_{\max}[B]$  denotes the largest eigenvalue of B. Note that the matrix shown in the second line, call it  $\mathcal{B}$ , is the symmetric part of  $P\left(J_{F_{\mathscr{C}_r}}(y,z) - \left(\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}\right)D\right)P^{-1}$ . Standard calculations show that if  $\gamma > \frac{1+\alpha_r}{\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}} \ge \frac{1}{\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}}$  then the trace and the

determinant of  $\mathcal{B}$  satisfy

$$\operatorname{Tr}[\mathcal{B}] = 1 - y^2 - \gamma \lambda_{\mathscr{C}_r}^{(2)} - \gamma \bar{\lambda}^{(2)} - b_{\mathscr{C}_r} \epsilon_{\mathscr{C}_r} < 0,$$
$$\operatorname{Det}[\mathcal{B}] = -b_{\mathscr{C}_r} \epsilon_{\mathscr{C}_r} \left( 1 - y^2 - \gamma \lambda_{\mathscr{C}_r}^{(2)} - \gamma \bar{\lambda}^{(2)} + \alpha_r \right) > 0$$

Therefore,  $\lambda_{\max}[\mathcal{B}] < 0$  and Theorem 8.3.2 yields the desired result.

In Proposition 8.4.1, the parameter  $\gamma$  can be interpreted as the diffusion matrix,

D, that represents the overall strength of graph coupling. For a system of Fitzhugh-Nagumo oscillators, the sufficient condition depends on a parameter,  $\epsilon$ , that controls the frequency of oscillations through the time scale separation between the voltage variable and gating variable. In general, as the value of  $\epsilon$  for a given cluster is increased, the value of  $\gamma$  needed to guarantee synchronization in that cluster is also increased. Furthermore, for values of  $\epsilon$  in a biologically relevant range (0.02, 0.2), increasing the minimum  $\epsilon$  over all clusters also increases the value of  $\gamma$  required for cluster synchronization. This indicates that systems with a lower frequency of oscillation synchronize more rapidly than those with higher oscillation frequencies. The other parameter that influences the sufficient condition for cluster synchronization is b that controls the ratio of the time over which the neuron is spiking to the refractory period. As this parameter is increased (for biologically realistic results, it is required to stay in the range (0,1), a smaller overall graph coupling is required to guarantee cluster synchronization for the entire network.

Remark 8.4.2. In Proposition 8.4.1:

1. If we assume that, for all r = 1, ..., K,  $\epsilon_{\mathscr{C}_r} = \epsilon$ , then  $\alpha_r = 0$  and we obtain a smaller lower bound for  $\gamma$ , namely

$$\gamma > \frac{1}{\lambda_{\mathscr{C}_i}^{(2)} + \bar{\lambda}^{(2)}}.$$

- 2. Non-diagonal P does not give a smaller lower bound for  $\gamma$ . If P is not diagonal, the condition for positive determinant is quadratic in terms of  $\gamma$ . This contradicts the positiveness of  $\gamma$  and so cannot be used to improve the bound for diagonal P.
- 3. Theorem 8.3.2 does not require constant system parameters, so it can be used to derive an analogous condition for a network of FN oscillators with time-varying parameters.

**Remark 8.4.3.** In the previous work [29], we showed that for K = 1, if  $\gamma \geq \frac{1+\epsilon+\beta^2/3}{\lambda_{\mathscr{C}_1}^{(2)}}$ , where  $\beta$  is the ultimate bound for the y variable, then Equation (8.20) synchronizes. By Proposition 8.4.1 we have found a smaller lower bound for  $\gamma$ ,  $\gamma > \frac{1}{\lambda_{\mathscr{C}_1}^{(2)}}$ , that guarantees synchronization.

## 8.4.2 Application to networks of heterogeneous Hindmarsh-Rose neuronal oscillators

Here, we apply Theorem 8.3.2 to a network of N two-dimensional modified Hindmarsh-Rose (HR) neuronal oscillators with graph  $\mathcal{G}$ . Let  $(y^i, z^i)^T \in \mathbb{R}^2$  be the state of oscillator i for  $i = 1, \ldots, N$ .  $y^i$  and  $z^i$  represent the membrane potential and the recovery variable, respectively. The input current for oscillator i is  $I^i$ . The two-dimensional HR dynamics are

$$\dot{y}^{i} = g^{i}(y^{i}) + z^{i} + I^{i} + \gamma \sum_{j \in \mathcal{N}^{i}} \gamma^{ij}(y^{j} - y^{i}),$$

$$\dot{z}^{i} = \delta^{i}(1 - 5y^{i^{2}} - z^{i}),$$
(8.22)

where  $g^i(y) = -y^{i^3} + c^i y^{i^2}$ ,  $\gamma, c^i > 0$ ,  $0 < \delta^i \ll 1$  is a parameter that determines the time-scale separation between the fast and slow dynamics, and  $\mathcal{N}^i$  denotes the set of all the neighbors of node *i* in the network. Using the notation of Theorem 8.3.2, n = 2,  $X^i = (y^i, z^i)^T$ ,  $F^i(X^i, t) = \left(g^i(y^i) + z^i + I^i, \delta^i(1 - 5y^{i^2} - z^i)\right)^T$ ,  $D = \text{diag}(\gamma, 0)$  is the diffusion matrix, and the  $\gamma^{ij}$  are the edge weights on the graph  $\mathcal{G}$ .

Assume there exist  $K \ge 1$  clusters  $\mathscr{C}_1, \ldots, \mathscr{C}_K$  of HR oscillators such that  $c^i = c_{\mathscr{C}_r}$ ,  $\delta^i = \delta_{\mathscr{C}_r}$ , and  $I^i = I_{\mathscr{C}_r}$  for all HR oscillators  $i \in \mathscr{C}_r$  and all clusters  $r = 1, \ldots, K$ .

**Proposition 8.4.4.** Consider Equation (8.22), under Assumption 8.3.1. For all r = 1, ..., K, let

$$\gamma > \frac{1}{\lambda_{\mathscr{C}_{i}}^{(2)} + \bar{\lambda}^{(2)}} \max\left\{\frac{-(2c_{\mathscr{C}_{i}} - 5)^{2}}{4(25\delta_{\mathscr{C}_{i}}p^{2} - 3)} + \frac{1}{4\delta_{\mathscr{C}_{i}}p}, \frac{c_{\mathscr{C}_{i}}^{2}}{3} - \delta_{\mathscr{C}_{i}}\right\},\tag{8.23}$$

where p is a constant that satisfies  $0 . Then for any pair of HR oscillators <math>\{(y^i, z^i)^T, (y^j, z^j)^T\}$  such that  $(i, j) \in \mathscr{C}_r$ ,

$$y^i(t) - y^j(t) \to 0$$
,  $z^i(t) - z^j(t) \to 0$ , as  $t \to \infty$ .

In particular, if  $p = \max_r \frac{3}{5\delta_{\mathscr{C}_r}(5+|2c_{\mathscr{C}_r}-5|)}$ , then the first argument of the max operator in Equation (8.23) is minimized and takes value  $\frac{(5+|2c_{\mathscr{C}_r}-5|)^2}{12}$ . *Proof.* To apply Theorem 8.3.2, we find a positive definite matrix P such that  $P^2D + DP^2$  is positive semidefinite and

$$\mu := \max_{r} \sup_{(y,z)^{T} \in \mathbb{R}^{2}} \mu_{2,P} \left[ J_{F_{\mathscr{C}_{r}}}(y,z) - \left( \lambda_{\mathscr{C}_{r}}^{(2)} + \bar{\lambda}^{(2)} \right) D \right] < 0.$$

Let P = diag(1, p) so that  $P^2D + DP^2 = \text{diag}(2\gamma, 0)$ , which is positive semidefinite. Then

$$\mu_{2,P} \left[ J_{F_{\mathscr{C}_{r}}}(y,z) - \left(\lambda_{\mathscr{C}_{r}}^{(2)} + \bar{\lambda}^{(2)}\right) D \right] = \mu_{2} \left[ P \left( J_{F_{\mathscr{C}_{r}}}(y,z) - \left(\lambda_{\mathscr{C}_{r}}^{(2)} + \bar{\lambda}^{(2)}\right) D \right) P^{-1} \right]$$
$$= \lambda_{\max} \left[ \begin{pmatrix} -3y^{2} + 2c_{\mathscr{C}_{r}}y - \gamma\lambda_{\mathscr{C}_{r}}^{(2)} - \gamma\bar{\lambda}^{(2)} & \frac{1}{2p} - 5\delta_{\mathscr{C}_{r}}py \\ \frac{1}{2p} - 5\delta_{\mathscr{C}_{r}}py & -\delta_{\mathscr{C}_{r}} \end{pmatrix} \right].$$
$$(8.24)$$

We denote this matrix as  $\mathcal{C}$ .

If 
$$\gamma(\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}) > \frac{c_{\mathscr{C}_r}^2}{3} - \delta_{\mathscr{C}_r}$$
, then we have  
 $\gamma\left(\lambda_{\mathscr{C}_r}^{(2)} + \bar{\lambda}^{(2)}\right) + \delta_{\mathscr{C}_r} > \frac{c_{\mathscr{C}_r}^2}{3} > \frac{c_{\mathscr{C}_r}^2}{3} - 3\left(y - \frac{c_{\mathscr{C}_r}}{3}\right)^2 = -3y^2 + 2c_{\mathscr{C}_r}y.$ 

Therefore, the trace of  $\mathcal{C}$  satisfies

$$\operatorname{Tr}[\mathcal{C}] = -3y^2 + 2c_{\mathscr{C}_r}y - \gamma\lambda_{\mathscr{C}_r}^{(2)} - \gamma\bar{\lambda}^{(2)} - \delta_{\mathscr{C}_r} < 0.$$

Further, if  $\gamma > \frac{-(2c_{\mathscr{C}_r}-5)^2}{4(25\delta_{\mathscr{C}_r}p^2-3)} + \frac{1}{4\delta_{\mathscr{C}_r}p}$ , then, under the condition that  $p^2 < \frac{3}{25\delta_{\mathscr{C}_r}}$ , the determinant of  $\mathcal{C}$  satisfies

$$\operatorname{Det}[\mathcal{C}] = -\delta_{\mathscr{C}_r} \left( -3y^2 + 2cy - \gamma \lambda_{\mathscr{C}_r}^{(2)} - \gamma \bar{\lambda}^{(2)} \right) - \left( \frac{1}{2p} - 5\delta_{\mathscr{C}_r} py \right)^2 > 0.$$

Therefore,  $\lambda_{\max}[\mathcal{C}] < 0$  and Theorem 8.3.2 yields the desired result.

#### 8.4.3 Numerical examples

**Example 8.4.5.** In this example, we consider the network of 17 neuronal oscillators shown in the left panel of Figure 8.1. This network can be grouped into three different clusters based on the individual nodal dynamics:

(i) Cluster  $\mathscr{C}_1$  (orange circles): six FN oscillators;  $a_{\mathscr{C}_1} = 0.5$ ,  $b_{\mathscr{C}_1} = 0.1$ ,  $I_{\mathscr{C}_1} = -2$ , and  $\epsilon_{\mathscr{C}_1} = 0.08$ ;

(ii) Cluster  $\mathscr{C}_2$  (green squares): seven HR oscillators;  $c_{\mathscr{C}_2} = 2$ ,  $I_{\mathscr{C}_2} = 2$ , and  $\delta_{\mathscr{C}_2} = 0.02$ ; (iii) Cluster  $\mathscr{C}_3$  (blue triangles): four HR oscillators;  $c_{\mathscr{C}_3} = 3$ ,  $I_{\mathscr{C}_3} = 4$ , and  $\delta_{\mathscr{C}_3} = 0.01$ . The second smallest eigenvalues of the Laplacian of the three intra-cluster subgraphs and the inter-cluster subgraph are  $\lambda_{\mathscr{C}_1}^{(2)} = 1.83$ ,  $\lambda_{\mathscr{C}_2}^{(2)} = \lambda_{\mathscr{C}_3}^{(2)} = 2$ , and  $\bar{\lambda}^{(2)} = 0.262$ , respectively. It follows directly from Propositions 8.4.1 and 8.4.4 that the clusters will synchronize if  $\gamma$  satisfies the following inequality:

$$\gamma > \max_{p \in (0,\sqrt{6})} \left\{ \frac{1 + 31.25(\frac{p}{12.5} - \frac{1}{p})^2}{\lambda_{\mathscr{C}_1}^{(2)} + \bar{\lambda}^{(2)}}, \frac{\frac{12.5}{p} - \frac{1}{2p^2 - 12}}{\lambda_{\mathscr{C}_2}^{(2)} + \bar{\lambda}^{(2)}}, \frac{1.3133}{\lambda_{\mathscr{C}_2}^{(2)} + \bar{\lambda}^{(2)}}, \frac{\frac{25}{p} - \frac{1}{p^2 - 12}}{\lambda_{\mathscr{C}_3}^{(2)} + \bar{\lambda}^{(2)}}, \frac{2.99}{\lambda_{\mathscr{C}_3}^{(2)} + \bar{\lambda}^{(2)}}\right\}.$$

$$(8.25)$$

For p = 2.4,  $\gamma > 4.6$  provides a sufficient condition for cluster synchronization. As shown in Figure 8.1, the network indeed stabilizes to three synchronized clusters when  $\gamma = 4.7$ .

**Example 8.4.6.** In this example we consider a large network of 200 FN oscillators illustrated in the left panel of Figure 8.2. The network is obtained through interconnection of two clusters:

(i) Cluster  $\mathscr{C}_1$  (magenta squares): A complete graph of 100 FN oscillators;  $a_{\mathscr{C}_1} = 0.9$ ,  $b_{\mathscr{C}_1} = 0.5$ ,  $I_{\mathscr{C}_1} = 2.0$ , and  $\epsilon_{\mathscr{C}_1} = 0.08$ ;

(ii) Cluster  $\mathscr{C}_2$  (green triangles): A star graph of 100 FN oscillators;  $a_{\mathscr{C}_2} = 0.7$ ,  $b_{\mathscr{C}_2} = 0.8$ ,  $I_{\mathscr{C}_2} = 0.3$ , and  $\epsilon_{\mathscr{C}_2} = 0.08$ .

Each node in the first cluster is connected to a unique node in the second cluster



Figure 8.1: Cluster synchronization in a network of 17 heterogeneous neuronal oscillators shown on the left: six FitzHugh-Nagumo oscillators (orange circles) with  $a_{\varphi_1} = 0.5$ ,  $b_{\varphi_1} = 0.1$ ,  $I_{\varphi_1} = -2$ ,  $\epsilon_{\varphi_1} = 0.08$ , seven Hindmarsh-Rose oscillators (green squares) with  $c_{\varphi_2} = 2$ ,  $I_{\varphi_2} = 2$ ,  $\delta_{\varphi_2} = 0.02$ , and four Hindmarsh-Rose oscillators (blue triangles) with  $c_{\varphi_3} = 3$ ,  $I_{\varphi_3} = 4$ ,  $\delta_{\varphi_3} = 0.01$ . The states converge to the 3-cluster synchronization manifold for  $\gamma = 4.7$ .

with coupling strength 0.25. Note that the cluster-input-equivalence condition holds in this case. For this network  $\lambda_{\mathscr{C}_1}^{(2)} = 100$ ,  $\lambda_{\mathscr{C}_2}^{(2)} = 1$  and  $\bar{\lambda}^{(2)} = 0$ . By choosing  $\gamma = 0.02$ such that  $\gamma > 1/(\lambda_{\mathscr{C}_1}^{(2)} + \bar{\lambda}^{(2)})$  but  $\gamma < 1/(\lambda_{\mathscr{C}_2}^{(2)} + \bar{\lambda}^{(2)})$  we do not obey the sufficient condition. However, numerical simulation (Figure 8.2) shows that the magenta cluster ( $\mathscr{C}_1$ ) synchronizes nevertheless as suggested by the fact that  $\gamma > 1/(\lambda_{\mathscr{C}_1}^{(2)} + \bar{\lambda}^{(2)})$  is satisfied. Our future work will explore more along this direction.

## 8.5 Conclusion

In this paper, we consider the patterns of synchronization that emerge in networks where individual nodes may have different intrinsic nonlinear dynamics. We leverage the cluster-input-equivalence condition, developed in [11,125] and extended with a useful graph-theoretical perspective in [115], to provide a starting framework for proving sufficient conditions for synchronization within clusters based on properties of the nodes and network structure. By adopting an approach based on contraction theory [3], our work proves a new sufficient condition for cluster synchronization, and provides its characterization in terms of the intra-cluster network structure and



Figure 8.2: Synchronization of only one (magenta) of two clusters in a large network of heterogeneous FN oscillators when the coupling strength takes an intermediate value. There are 100 oscillators in one cluster connected through a star graph (green triangles) and 100 oscillators in a second cluster connected through a complete graph (magenta squares). The network on the left illustrates the connections between clusters (in gray) in the case of 5 oscillators in each cluster.

the inter-cluster network structure. The inter-cluster network structure has not been explicitly used in previous works on finding sufficient conditions for cluster synchronization; our work improves on sufficient conditions by incorporating significantly more information about network structure.

Another key contribution of our work is an improvement on previous sufficient conditions for cluster synchronization [29] in networks with heterogeneous intrinsic dynamics. We have detailed an approach to finding sufficient conditions for synchronization independent of nonlinear model and network structure. However, the strict requirements imposed by studying complete synchronization within clusters that manifest in the cluster-input-equivalence condition limit the amount of heterogeneity in the nodal dynamics and asymmetry in the network that can be addressed. Future generalizations of our results should include relaxations of the complete synchronization requirement which would allow for more complex and realistic network configurations. A concrete first relaxation would be to combine the robustness result for contracting systems, as in [99], with the results from this work to study a system perturbed from a cluster-input-equivalence state by Brownian noise.

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# Chapter 9

# Mixed-Mode Oscillations and Phase Locking in Coupled FitzHugh-Nagumo Model Neurons<sup>\*</sup>

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We study the dynamics of a low-dimensional system of coupled model neurons as a step towards understanding the vastly complex network of neurons in the brain. We analyze the bifurcation structure of a system of two model neurons with unidirectional coupling as a function of two physiologically relevant parameters: the external current input only to the first neuron and the strength of the coupling from the first to the second neuron. Leveraging a timescale separation, we prove necessary con-

<sup>\*</sup>This chapter appears as Davison, Aminzare, Dey, and Leonard (2019) [28]. In Chapter 3, a mistake in the condition for MMOs is described and Figure 3.4 depicts an update to Figure 9.3 with the correct condition.

ditions for multiple timescale phenomena observed in the coupled system, including canard solutions and mixed mode oscillations. For a larger network of model neurons, we present a sufficient condition for phase locking when external inputs are heterogeneous. Finally, we generalize our results to directed trees of model neurons with heterogeneous inputs.

Efforts to gain insight into the complex dynamics of the brain benefit from a detailed understanding of neurons and their interactive dynamics. We study a system of two model neurons where the first neuron receives a constant external input and the second neuron receives an input from the first neuron. Systems of two coupled model neurons exhibit rich dynamical patterns that can represent large networks comprised of two distinct clusters. This makes them fascinating in their own right and useful as a starting point for studying more general networks. Using bifurcation theory, we find bounds on external input and coupling strength that predict firing, mixed mode oscillations, and phase locking. We extend these conditions to more general networks. Our results provide foundations for investigating the interplay between structure and external stimuli in networks of neurons.

## 9.1 Introduction

The study of model neurons has a rich history, dating back to the pioneering work of Hodgkin and Huxley [59] on the action potential in the squid giant axon. A twodimensional model that captures salient qualities of the four-dimensional Hodgkin-Huxley model was developed independently by FitzHugh [46,47] and by Nagumo[90]. In this model, commonly known as the FitzHugh-Nagumo (FN) model, one variable represents the membrane potential and the other represents a gating variable. A constant external input to the FN model neuron can produce quiescent behavior (a low-voltage stable equilibrium point), firing (a stable limit cycle), or saturated behavior (a high-voltage stable equilibrium point). The FN model neuron captures realistic neuronal behavior such as spike accommodation, bistability, and excitability [63].

A system of two coupled neurons can represent a larger network of neurons that cluster into two groups in which neurons within each group synchronize but neurons in different groups do not. A cluster synchronized network can be reduced to a quotient network [113,115] by leveraging balanced conditions on coupling and graph structure [123], as well as bounds on coupling strength [4, 29]. A system of two FN model neurons with gap junction diffusive coupling (two-FN system) has been studied numerically and analytically in the symmetric case [20,60], where both neurons receive the same external input and are coupled bidirectionally (undirected coupling). Gap junction diffusive coupling is modeled as a difference between the membrane potentials of the two model neurons multiplied by a parameter that represents the coupling strength. The two-FN system has also been studied numerically [60] in a context where the intrinsic properties of both models are the same but the neurons are coupled unidirectionally (directed coupling). Here, we add to the existing literature by analytically describing the bifurcation structure of the directed two-FN system in terms of two parameters, the external input to the first model neuron and the unidirectional coupling strength from the first model neuron to the second.

The FN model neuron is a classic example of a fast-slow system, and the coupled pair of FN model neurons exhibits rich dynamics characterized by the timescale separation. Under certain conditions on external input and coupling strength, the system exhibits *canard solutions*, which are solutions that pass from a stable to an unstable manifold in the slow system and stay near the unstable manifold for a long time relative to the slow system timescale [15, 72, 126]. Canard solutions result from the presence of two distinct types of folded singularities, stable folded nodes and folded saddles. In particular, stable folded nodes give rise to robust families of canard solutions [126, 137]. When combined with a suitable return mechanism, canard solutions can lead to mixed mode oscillations (MMOs), which are periodic oscillations that alternate between canard-driven oscillations and a relaxation oscillation [84]. The existence of canards and MMOs has been described for systems in four dimensions [14, 126], systems with two slow variables and two fast variables [128], and generalized systems in arbitrary finite dimensions [138]. The folded saddle node of type I (FSN I) and folded saddle node of type II (FSN II) have been identified as mechanisms for the onset of MMOs in fast-slow systems [26, 33, 34, 71, 84]. We leverage these results to determine the regions of parameter space where canards and MMOs may be present in the directed two-FN system, which has two slow variables and two fast variables and two fast variables.

Canard-induced MMOs have been studied analytically in numerous systems including chemical reactions [87,98], the Hodgkin-Huxley neuronal model [109], cortical grid cells [108], and a self-coupled FN model neuron [35]. In a two-FN system, the onset of firing, as coupling strength is increased, can be characterized by the appearance of canard solutions, and by MMOs, as the coupling is increased further. The existence of canard solutions in a two-FN system was first proven using nonstandard analysis in the case of model neurons with identical parameters [129]. Necessary conditions were found in terms of a model parameter that controls the slope of the linear nullcline of the system. Conditions for different stability types of folded singularities were found in terms of the same model parameter in a slightly modified, but still symmetric, model [48]. Here, we fix the corresponding parameter within the range where canard solutions may be present and find conditions for existence of canardinduced MMOs in terms of two parameters that break symmetry: external input and coupling strength. A condition for the onset of MMOs in a two-FN system was shown as an application of a method developed to study MMOs in systems with two fast variables and two slow variables [69]. There are no symmetry requirements and the main result is a necessary condition for MMO onset in terms of a parameter corresponding to the input to one of the neurons. In the spirit of this work, we prove explicit necessary conditions for existence of canard solutions and MMOs in the directed two-FN system in terms of both the external input and the coupling strength. First, we take the singular limit of the system, and obtain necessary conditions on the bifurcation parameters for existence of transcritical bifurcations. The transcritical bifurcations in the singularly perturbed system delineate regions in parameter space where MMOs exist in the original system.

We show, further, that the original system admits Hopf bifurcations within a distance of order  $\epsilon$  around the point in the parameter space where the singularly perturbed system admits transcritical bifurcations. This we use to derive novel bounds for phase-locking in representative networks of model neurons. Phase locking is a generalization of synchronization where the phases of oscillating models remain separated by a constant offset, while amplitudes and waveforms may vary [107]. A common phenomenon in nature, phase locking has been studied in cardiac rhythms [49,54,132], in the firing patterns of squid axons [82], in two coupled phase oscillators [67], in local field potential measurements of neurons in the human brain [114, 136], and in the brain as a mechanism for coordination between groups of neurons [133].

Finally, we consider the more general problem of n FN model neurons linked by unidirectional gap junction diffusive coupling in a directed tree, with heterogeneous coupling strengths and heterogeneous external inputs. As in the directed two-FN system, this can represent a class of large networks that contain cluster synchronized groups of model neurons and satisfy conditions on graph structure [123] and connectivity[4,29] so they can be reduced to a quotient network [113,115]. An analogous problem with homogeneous coupling strength has been analyzed in detail in the strong coupling limit where the dynamics are reduced using singular perturbation theory[83]. Here, we leverage an analysis of the singular perturbation of the directed two-FN system to provide necessary conditions for the existence of MMOs and sufficient conditions for phase locking in the original n-FN system.

Our contributions towards understanding the dynamics of networked nonlinear model neurons are as follows. First, we explain how the bifurcation structure of the directed two-FN system relates to the bifurcation structure of the reduced, singularly perturbed system that is used to study canard solutions. This is critical because the reduced system can be used to explain features of the original system and the original system can be used to understand the reduced system. Second, we provide necessary conditions for canards and MMOs in the directed two-FN system in terms of two model parameters; this is an extension of the conditions found in terms of one parameter in the literature. Third, we provide a sufficient condition for phase locking given heterogeneous external inputs in the directed two-FN system. We generalize these conditions to directed trees of FN model neurons.

The paper is organized as follows. In Section 9.2, we review the standard analysis of a single FN model neuron and give a biophysical rationale for bounds on model parameters used throughout the paper. In Section 9.3, we define the directed two-FN system and find conditions for Hopf bifurcations. In Section 9.4, we compute the singular perturbation of the directed two-FN system. We prove necessary conditions for the transcritical bifurcations in the singularly perturbed system and canards and MMOs in the original system in Section 9.5. In Section 9.6, we generalize the results to directed trees of FN model neurons. We provide a numerical example to illustrate our results.

## 9.2 Single FitzHugh-Nagumo model neuron

The FN model is a two-dimensional simplification of the four-dimensional Hodgkin-Huxley (HH) model that retains conceptually relevant properties of the activation and deactivation dynamics of the neuronal action potential. By letting y and z represent the membrane potential and a slow gating variable, respectively, its dynamics are given by

$$\frac{dy}{dt} = \psi(y) - z + I,$$

$$\frac{dz}{dt} = \epsilon(y - bz),$$
(9.1)

where  $\psi(y)$  is a cubic polynomial. For our purposes, we use  $\psi(y) = y - \frac{y^3}{3} - a$ . In this model, *I* corresponds to an external input,  $0 < \epsilon \ll 1$  is a positive timescale separation constant, and *a* and *b* are positive constants.

The FN model is far simpler to analyze than the full HH model due to the lower dimension. Despite the lower dimension, the FN model captures key characteristics of the HH model and a range of physiologically meaningful regimes and behaviors [63, 106]. The FN model is a suitable choice for network analysis because it is both dynamically rich and analytically tractable.

Hopf bifurcations are distinguishing features of the FN model dynamics. A *Hopf bifurcation* occurs when the variation in a parameter leads to the appearance or disappearance of an isolated limit cycle from an equilibrium point and a simultaneous change in stability of the equilibrium inside the limit cycle. In a *supercritical Hopf bifurcation*, the limit cycle is stable, while in a *subcritical Hopf bifurcation*, the limit cycle is stable.

A necessary condition [103] for the FN model to exhibit distinct quiescent, firing, and saturated regimes is the existence of a unique equilibrium point for all values of the bifurcation parameter I. In this paper we assume the following:
Assumption 9.2.1. Parameters a, b, and  $\epsilon$  are such that the FN model (9.1) has a unique equilibrium point for all values of  $I \ge 0$ . This results in conditions 0 < a < 1 and 0 < b < 1.

The condition on a corresponds to a simple voltage offset requirement and the condition on b corresponds to a requirement that the slope of the linear nullcline of (9.1) must be greater than that of the cubic nullcline of (9.1).

By Assumption 9.2.1, there is one equilibrium point for all values of I. There are six key features in the bifurcation structure of the FN model as the external input parameter, I, is varied:

- $I = I_{0sn}$  As I is increased from zero, stable and unstable limit cycles appear through a saddle node bifurcation of limit cycles at  $I = I_{0sn}$  for some  $I_{0sn} > 0$ , while the unique equilibrium point is stable. The large limit cycles are relaxation oscillations. The bifurcation at  $I_{0sn}$  defines the beginning of the firing regime and the small region of bistability.
- $I = I_{0c}$  As I is increased slightly, through the point  $I = I_{0c}[16, 53]$ , there is a region of bistability during which there occurs a *canard explosion*, which is an abrupt transition from small limit cycle oscillations to larger limit cycle oscillations. The unique equilibrium point is still stable. By Ref. [88], the saddle node of limit cycles and the canard explosion occur at essentially the same parameter value, i.e.,  $I_{0c} \approx I_{0sn}$ . We calculate an approximation to  $I_{0c}$  later in this section.
- $I = I_0$  As I is increased further, through a subcritical Hopf bifurcation at  $I = I_0$ , where  $I_0 > I_{0c}$ , the unstable limit cycles disappear, the stable equilibrium point becomes unstable, and the large stable limit cycles remain. The bifurcation at  $I_0$  defines the end of the small region of bistability.
- $I = I_1$  For  $I_0 < I < I_1$ , for some  $I_1 > 0$ , there are only an unstable equilibrium point and the large stable limit cycle oscillations. At  $I = I_1$ , through another

subcritical Hopf bifurcation, the equilibrium becomes stable and small unstable limit cycles appear. The bifurcation at  $I_1$  defines the beginning of a second small region of bistability.

- $I = I_{1c}$  For  $I_1 < I < I_{1c}$ , the equilibrium is stable and there is again a region of bistability characterized by a canard explosion with the unique equilibrium point stable[16,53]. We calculate an approximation to  $I_1$  later in this section.
- $I = I_{1sn}$  As I is increased slightly, through the point  $I = I_{1sn}$ , there is another saddle node bifurcation of limit cycles. The bifurcation at  $I_{1sn}$  defines the end of the firing regime and the second small region of bistability. By Ref. [88], the saddle node of limit cycles and the canard explosion occur at essentially the same parameter value, i.e.,  $I_{1sn} \approx I_{1c}$ .

Figure 9.1 depicts the bifurcation diagram of the FN model when I is varied.

The following proposition from Ref. [53] describes the stability of the unique equilibrium point of (9.1) given Assumption 9.2.1 and conditions on I for Hopf bifurcations.

**Proposition 9.2.2.** (Ref. [53]) Let Assumption 9.2.1 hold. Then, there exists  $I_0 < I_1$ such that the equilibrium point is stable for  $I < I_0$  and, as I increases, it will undergo a transition to an unstable equilibrium point through a Hopf bifurcation at  $I_0$ . As I is increased further it will undergo a transition from unstable to stable through a second Hopf bifurcation at  $I_1$ .

We review the approach to analyzing stability of the limit cycles arising from the Hopf bifurcations following the methods of Chapter 3 of Ref. [53] and the application to the FN model in Ref. [39]. We generalize the approach to networks of FN model neurons in later sections.



Figure 9.1: Bifurcation diagram for a single FN model drawn with a numerical continuation software tool [36] for a = 0.875, b = 0.8, and  $\epsilon = 0.08$ . Green corresponds to stable equilibrium points or limit cycles and red corresponds to unstable equilibrium points or limit cycles. For most values  $I < I_0$ , the FN model is in the quiescent regime. For  $I_{0sn} \approx I_{0c} < I < I_0$ , the FN model is in the firing regime since it concurrently exhibits a stable equilibrium point, small unstable oscillations, and larger stable oscillations. The FN model is always in the firing regime when  $I_0 < I < I_1$ . For  $I_1 < I < I_{1c} \approx I_{1sn}$ , the FN model is also in the firing regime since it concurrently exhibits a stable equilibrium point, small unstable oscillations, and larger stable oscillations. For all other  $I > I_1$ , the FN model is in the saturated regime.

The dynamics at a Hopf bifurcation at the origin of a two-dimensional system can be written as

$$\begin{pmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \end{pmatrix} = \begin{pmatrix} 0 & -\omega \\ \omega & 0 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} + \begin{pmatrix} F(x_1, x_2) \\ G(x_1, x_2) \end{pmatrix},$$
(9.2)

such that F and G satisfy F(0,0) = G(0,0) = 0 and  $D_{\mathbf{x}}F(0,0) = D_{\mathbf{x}}G(0,0) = \mathbf{0}$ where  $D_{\mathbf{x}}F$  is the Jacobian of F with respect to  $\mathbf{x}$  and  $\mathbf{x} = (x_1, x_2)^{\top}$ .

**Definition 9.2.3** (Cubic coefficient [53, 57]). Consider the system (9.2). The coefficient of the cubic term of the Taylor expansion of the RHS of (9.2) is expressed as

$$\alpha = \frac{1}{16} (F_{x_1 x_1 x_1} + F_{x_1 x_2 x_2} + G_{x_1 x_1 x_2} + G_{x_2 x_2 x_2}) \Big|_{(0,0)}$$

$$+ \frac{1}{16\omega} (F_{x_1x_2}(F_{x_1x_1} + F_{x_2x_2}) - G_{x_1x_2}(G_{x_1x_1} + G_{x_2x_2}) - F_{x_1x_1}G_{x_1x_1} + F_{x_2x_2}G_{x_2x_2}) \Big|_{(0,0)},$$

$$(9.3)$$

where  $F_{x_1x_2}$  denotes  $\frac{\partial^2 F}{\partial x_1 \partial x_2}$ , and so on.

**Proposition 9.2.4** (Theorem 3.4.2 (modified) [53]). The system  $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mu)$ , admits a Hopf bifurcation for the parameter value  $\mu = \mu_0$  at an equilibrium point  $\mathbf{x} = \mathbf{0}$  if

D<sub>x</sub>f(0, μ<sub>0</sub>) has a pair of pure imaginary eigenvalues and no other eigenvalues with zero real parts.
 ∂/∂μ ℜ(λ(μ)) | ≠ 0, where ℜ(λ) denotes the real part of the eigenvalue λ.
 The cubic coefficient of the Taylor expansion of f, denoted by α and defined in Definition 9.2.3, is nonzero.

Furthermore, if  $\alpha < 0$ , the Hopf bifurcation is supercritical, while, if  $\alpha > 0$ , the Hopf bifurcation is subcritical.

The cubic coefficient is also called the first Lyapunov coefficient. For the FN model, the cubic coefficient is given by

$$\alpha = \frac{1}{8} \left( \frac{2b - b^2 \epsilon - 1}{1 - b^2 \epsilon} \right).$$

In this paper we choose parameters that ensure Assumption 9.2.1 holds and the bifurcations are subcritical Hopf ( $\alpha > 0$ ); these yield biologically realistic dynamics [10, 104]. We fix a = 0.875, b = 0.8, and  $\epsilon = 0.08$ , and we consider  $I \ge 0$  as a bifurcation parameter.

The value of the bifurcation parameter I where canards exist near each Hopf bifurcation is close to the respective saddle node bifurcation of limit cycles and can be found following Ref. [17]. Let **f** represent the dynamics of (9.1) and let F and G be defined as in (9.2) for (9.1) where  $x_1 = y$  and  $x_2 = z$ . Following Equation (3.23) of Ref. [17] we compute

$$I_{ic} = I_i - 8 \frac{a_1}{F_{xx}\delta_i} \epsilon + \mathscr{O}(\epsilon^2), \qquad i = 0, 1,$$

where  $I_i$  is the value of I at the Hopf bifurcation,

$$a_1 = \frac{1}{16} (F_{yy}(F_z G_{yy} - F_{yy} G_z) + G_y(F_{yz} F_{yy} - F_z F_{yyy})),$$

and

$$\delta_i = \frac{\partial}{\partial I} \left[ \operatorname{Tr} \left( D_{\mathbf{x}} \mathbf{f}(\mathbf{p}, I) \right) \right] \Big|_{I = I_i}$$

For the FN model (9.1),  $I_{0c} = I_0 - 0.09\epsilon + \mathcal{O}(\epsilon^2)$  and  $I_{1c} = I_1 + 0.09\epsilon + \mathcal{O}(\epsilon^2)$ . So canards exists for  $I_{0c} < I < I_0$  and for  $I_1 < I < I_{1c}$ , as illustrated in Figure 9.1.

## 9.3 Directed two-FN model neuron system

The directed two-FN model neuron system is shown in Figure 9.2. The first model neuron is denoted A and it receives external input I. The second model neuron is denoted B and it receives no external input. The coupling is unidirectional from A to B, with coupling strength  $\gamma$ . A and B have the same intrinsic dynamics, i.e., the same values of a, b, and  $\epsilon$  as defined above. We let I and  $\gamma$  be bifurcation parameters.



Figure 9.2: A directed network of two FN model neurons, A and B. A receives an external input I and there is a unidirectional coupling from A to B with strength  $\gamma$ .

The two-FN system can be used to study cluster synchronized graphs containing two clusters. In this case, the dynamics can be reduced to a simplified quotient graph [112, 115]. When there are many more model neurons in one cluster than the other, the coupling from the large cluster to the small cluster is much stronger than the coupling from the small cluster to the large cluster. Thus, we can disregard the coupling from the small cluster to the large cluster and the simplified graph can be approximated by the directed two-FN system.

The equations for the directed two-FN system are

$$\frac{dy_A}{dt} = \zeta_A(y_A, z_A, y_B, z_B) = y_A - \frac{y_A^3}{3} - a - z_A + I, \qquad (9.4a)$$

$$\frac{dz_A}{dt} = \epsilon \,\xi_A(y_A, z_A, y_B, z_B) = \epsilon \,(y_A - bz_A),\tag{9.4b}$$

$$\frac{dy_B}{dt} = \zeta_B(y_A, z_A, y_B, z_B) = y_B - \frac{y_B^3}{3} - a - z_B + \gamma(y_A - y_B), \qquad (9.4c)$$

$$\frac{dz_B}{dt} = \epsilon \,\xi_B(y_A, z_A, y_B, z_B) = \epsilon \,(y_B - bz_B).$$
(9.4d)

Here,  $y_A(y_B)$  is the membrane potential of A(B) and  $z_A(z_B)$  represents a slow gating variable in A(B).

The bifurcation structure of directed and undirected two-FN systems have been studied extensively from a numerical perspective [60]. The bifurcation structure of the undirected system has been studied through analytical methods that leverage symmetry-based arguments or assume symmetric or near-symmetric FN models [20, 48, 129]. In contrast we examine the system with asymmetry in both the external input and the coupling.

We begin by classifying the behavior of the two model neurons A and B in the  $I-\gamma$  parameter space, as shown in Figure 9.3. Let  $I_{iA}$ ,  $I_{icA} \approx I_{isnA}$  for i = 0, 1 be the points associated to the FN model A for lower and upper Hopf bifurcations, canard explosions, and saddle node bifurcations, as defined in Section 9.2. Regions (1)-(7) are described as follows:

- (i) For  $I < I_{0cA}$ , both A and B will be quiescent at a stable equilibrium point. This corresponds to region (1) of Figure 9.3. See Section 9.5.1 for details.
- (ii) For  $I > I_{1cA}$ , A becomes saturated and, as  $\gamma$  varies, there are three distinct behaviors for B. See Section 9.5.2 for details. For  $I > I_{1cA}$ , there exist  $I_{0cB}(I)$ and  $I_{1B}(I)$  such that
  - (a) For γ < I<sub>0cB</sub>(I), B is quiescent. This corresponds to region (2) in Figure 9.3.
  - (b) For  $I_{0cB}(I) < \gamma < I_{1B}(I)$ , B is firing. This corresponds to region (3) in Figure 9.3.
  - (c) For  $\gamma > I_{1B}(I)$ , B is saturated. This corresponds to region (4) in Figure 9.3.
- (iii) For  $I_{0cA} < I < I_{1cA}$ , A is firing and there are three distinct behaviors for B:
  - (a) When γ > 1 bε, B is phase locked with A, where the phases of the oscillating models remain separated by a constant offset, while amplitudes and waveforms may vary. This corresponds to region (5) of Figure 9.3. See Section 9.5.3 for details.
  - (b) When γ < 1 bε and I is below a curve, denoted by I<sub>\*</sub>(γ), MMOs or small canard oscillations may be present. This corresponds to region (6) of Figure 9.3. See Section 9.4 for the derivation and Section 9.5.4 for details.
  - (c) When γ < 1 − bε and I is above I<sub>\*</sub>(γ), B is firing and is phase locked with A. This corresponds to region (7) of Figure 9.3. See Section 9.4 for the derivation and Section 9.5.4 for details.

In Section 9.4 we study the system (9.4) by applying geometric singular perturbation techniques. Leveraging fast-slow dynamics of (9.4), we reduce it to a twodimensional singular limit. We analyze the resulting second-order dynamics and draw conclusions about canards and MMOs for the original dynamics (9.4) in Section 9.5.



Figure 9.3: Regions of behavior of the directed two-FN system (9.4) in the  $I-\gamma$  parameter space. Boundaries between regions are identified in the key. In regions (3), (5), (6), and (7), shaded gray, there is a stable limit cycle such that either A or B is firing. In region (3), with cross hatching, only B is firing. In regions (5) and (7), in darker gray, there is phase locking. In region (6), in light gray, A is firing and B may exhibit canard solutions. All boundaries are computed analytically. HH denotes a Hopf-Hopf bifurcation and GH denotes a generalized Hopf bifurcation.

# 9.4 Fast-slow phenomena in the directed two-FN

## system

In this section, we assume A is firing and study the onset of firing in B as  $\gamma$  increases. This corresponds to region (6) of Figure 9.3. We begin by providing definitions of canards and MMOs, which are observed numerically at the transition from quiescent to firing in B as shown in Figure 9.4. For a general fast-slow system expressed as

$$\frac{d\mathbf{y}}{dt} = \boldsymbol{f}(\mathbf{y}, \mathbf{z}), 
\frac{d\mathbf{z}}{dt} = \epsilon \boldsymbol{g}(\mathbf{y}, \mathbf{z}),$$
(9.5)

 $\mathbf{y} \in \mathbb{R}^m$  are fast variables,  $\mathbf{z} \in \mathbb{R}^n$  are slow variables, and  $0 < \epsilon \ll 1$  is the timescale separation parameter. The singular limit corresponding to  $\epsilon = 0$  is called the *layer* system,  $\frac{d\mathbf{y}}{dt} = \mathbf{f}(\mathbf{y}, \mathbf{z})$ , where the slow variables  $\mathbf{z}$  are parameters in this limiting system.

**Definition 9.4.1** (Critical manifold). Given system (9.5) with  $\epsilon = 0$ ,

 $C = \{(\mathbf{y}, \mathbf{z}) \in \mathbb{R}^m \times \mathbb{R}^n : \mathbf{f}(\mathbf{y}, \mathbf{z}) = \mathbf{0}\} \text{ is called the critical manifold and corresponds}$ to the equilibrium points of the layer system.

**Definition 9.4.2** (Normal hyperbolicity). A subset  $C_h \subset C$  is called normally hyperbolic if all the points of  $C_h$  are hyperbolic equilibrium points of the layer system, i.e., if  $D_{\mathbf{y}} \mathbf{f}$  has no eigenvalues with zero real part.  $C_h$  is called attracting (respectively, repelling) if the eigenvalues have negative (respectively, positive) real part.  $C_h$  is a saddle if it in neither attracting nor repelling.

**Definition 9.4.3** (Fold points[139]). Denote the set of points in C that are not normally hyperbolic ( $D_{\mathbf{y}} \mathbf{f}$  has at least one eigenvalue with zero real part) as

$$L := \left\{ \left. (\mathbf{y}, \mathbf{z}) \in C \right| \begin{array}{c} \operatorname{rank}(D_{\mathbf{y}} f(\mathbf{y}, \mathbf{z})) = m - 1 \\ \mathbf{l} \cdot D_{\mathbf{y}}^2 f(\mathbf{y}, \mathbf{z})(\mathbf{r}, \mathbf{r}) \neq 0 \\ \mathbf{l} \cdot D_{\mathbf{z}} f(\mathbf{y}, \mathbf{z}) \neq \mathbf{0} \end{array} \right\},$$

where  $\mathbf{l}$  and  $\mathbf{r}$  are corresponding left and right eigendirections of  $D_{\mathbf{y}} \mathbf{f}$ . L denotes the fold points of the critical manifold C. L locally divides the critical manifold C into subsets with different stability properties.

**Definition 9.4.4** (Canard). A solution of (9.5) is called a canard if it stays within  $\mathcal{O}(\epsilon)$  of a repelling branch of the critical manifold for a time that is  $\mathcal{O}(1)$  on the slow timescale,  $\tau_1 = t\epsilon$ .

**Definition 9.4.5** (Mixed mode oscillation (MMO) [72]). Periodic solutions of (9.5) with peaks of substantially different amplitudes are called MMOs. Canard solutions often comprise the small oscillations present in MMOs.

**Definition 9.4.6** (Phase locking). Two oscillating signals are said to be phase locked if the phases of the signals remain separated by a constant offset. An example of a canard solution, MMOs, and phase locking found in the directed two-FN system are shown in Figure 9.4.



Figure 9.4: Example of (a) canard solutions, (b) MMOs, and (c) phase locking observed in simulation of the directed two-FN system. In all plots  $y_A$  is in blue and  $y_B$ is in magenta. (a) For I = 1 and  $\gamma = 0.05$ ,  $y_B$  follows a canard solution exhibited as small oscillations with the same frequency as the firing of model neuron A. (b) For I = 1 and  $\gamma = 0.08$ ,  $y_B$  exhibits MMOs where the small oscillations are a canard solution. (c) For I = 1.4 and  $\gamma = 1.03$ ,  $y_A$  and  $y_B$  exhibit phase locking, i.e., they fire at a constant phase offset, even though the amplitude of the spikes and the waveforms are different.

One of our goals is to show the existence of canards and MMOs in the two-FN system. In what follows we review how the equilibrium points and the fold points of a fast-slow system play important roles in the existence of canards and MMOs. To this end, we study the behavior of the slow system on the critical manifold, which is called the reduced system. By Fenichel Theory, the equilibrium points of the full system lie within an  $\mathcal{O}(\epsilon)$  neighborhood of the equilibrium points of the reduced system. However, the solutions of the reduced system blow up in finite time at the fold points. To remove these solutions, we study the desingularized system, which is obtained from the reduced system by an appropriate time rescaling. The equilibrium points of the equilibrium points of the full system are within an  $\mathcal{O}(\epsilon)$  neighborhood of the equilibrium points of the equilibrium points of the full system the reduced system by an appropriate time rescaling. The equilibrium points of the full system and the fold points.

In the slow timescale  $\tau_1 = t\epsilon$  system (9.5) becomes

$$\epsilon \frac{d\mathbf{y}}{d\tau_1} = \boldsymbol{f}(\mathbf{y}, \mathbf{z}),$$

$$\frac{d\mathbf{z}}{d\tau_1} = \boldsymbol{g}(\mathbf{y}, \mathbf{z}).$$
(9.6)

For this system, the singular limit corresponding to  $\epsilon = 0$  is called the *reduced system* which is the differential algebraic equation corresponding to the slow dynamics  $\frac{d\mathbf{z}}{d\tau_1} = \mathbf{g}(\mathbf{y}, \mathbf{z})$  defined on the critical manifold C. Note that the full and reduced systems have the same equilibrium points.

To derive the desingularized system we first differentiate  $f(\mathbf{y}, \mathbf{z}) = 0$  with respect to  $\tau_1$  to get

$$(D_{\mathbf{y}}\boldsymbol{f}) \cdot \frac{d\mathbf{y}}{d\tau_1} + (D_{\mathbf{z}}\boldsymbol{f}) \cdot \frac{d\mathbf{z}}{d\tau_1} = \mathbf{0}.$$
(9.7)

Multiplying both sides of (9.7) by  $\operatorname{adj}(D_{\mathbf{y}}\boldsymbol{f})$ , the adjugate (or the transpose of the cofactor matrix) of  $D_{\mathbf{y}}\boldsymbol{f}$ , gives

$$-\det (D_{\mathbf{y}}\boldsymbol{f})\frac{d\mathbf{y}}{d\tau_1} = \operatorname{adj}(D_{\mathbf{y}}\boldsymbol{f})(D_{\mathbf{z}}\boldsymbol{f}) \cdot \boldsymbol{g}(\mathbf{y}, \mathbf{z}).$$
(9.8)

This system is singular when det  $(D_y f) = 0$ , namely at fold points. This means that standard existence and uniqueness results do not hold at the fold points. However, rescaling time in (9.8) by  $d\tau_1 = -\det(D_y f) d\tau_2$  yields the desingularized system

$$\frac{d\mathbf{y}}{d\tau_2} = \operatorname{adj}(D_{\mathbf{y}}\boldsymbol{f})(D_{\mathbf{z}}\boldsymbol{f}) \cdot \boldsymbol{g}(\mathbf{y}, \mathbf{z}).$$
(9.9)

Note that to obtain the corresponding flows of the reduced system from the desingularized system, due to the time scaling  $d\tau_1 = -\det(D_y f)d\tau_2$ , the direction of the flows of the desingularized system must be reversed on branches where  $\det(D_y f) > 0$ .

The desingularized system (9.9) has two types of equilibrium points, which are called ordinary and folded singularities, respectively. **Definition 9.4.7** (Ordinary singularity). An equilibrium point of the desingularized system is an ordinary singularity if it corresponds to an equilibrium point of the reduced system and lies within an  $\mathcal{O}(\epsilon)$  neighborhood of an equilibrium point of the full system. Conditions for an ordinary singularity are

$$\boldsymbol{g}(\mathbf{y}, \mathbf{z}) = 0, \ \det(D_{\mathbf{y}}\boldsymbol{f}) \neq 0, \ adj(D_{\mathbf{y}}\boldsymbol{f})(D_{\mathbf{z}}\boldsymbol{f}) \cdot \boldsymbol{g}(\mathbf{y}, \mathbf{z}) \neq \mathbf{0}$$

**Definition 9.4.8** (Folded singularity). An equilibrium point of the desingularized system is a folded singularity if it corresponds to a fold point of the reduced system. Conditions for a folded singularity are

$$\det (D_{\mathbf{y}} \boldsymbol{f}) = 0, \ adj(D_{\mathbf{y}} \boldsymbol{f})(D_{\mathbf{z}} \boldsymbol{f}) \cdot \boldsymbol{g}(\mathbf{y}, \mathbf{z}) = \boldsymbol{0}$$

Suppose that the desingularized system (9.9) possesses a stable folded singularity  $\mathbf{y}^*$  that is a node. Let the eigenvalues of the linearization of (9.9) at  $\mathbf{y}^*$  be  $\lambda_s$  and  $\lambda_w$ , where  $\lambda_s < \lambda_w < 0$ . The trajectory tangent to the eigendirection corresponding to  $\lambda_s$ , called the *strong singular canard*, corresponds to a trajectory in the full system that passes through a point close to  $\mathbf{y}^*$  from the attracting branch to the repelling branch of the critical manifold. It creates a *funnel* such that all the trajectories in the full system that enter the funnel pass through the same point from the attracting branch to the repelling branch to the repelling branch of the critical manifold. It was shown [137] that these trajectories rotate about the eigendirection corresponding to  $\lambda_w$ , called the *weak singular canard*, and eventually leave the funnel and jump away from the point near  $\mathbf{y}^*$  [26]. If there exists a *return mechanism* to return these trajectories back to the funnel, then MMOs occur[34,71].

The remainder of this section details the calculations involved in the transformation of (9.4) into a two-dimensional desingularized system. In Section 9.5, we show conditions on I and  $\gamma$  such that the desingularized system possesses a stable folded node and thus a strong singular canard. We also explain the existence of a return mechanism and provide conditions for regions where MMOs are possible.

# 9.4.1 The critical manifold and fold points of the directed two-FN system

The critical manifold of system (9.4) with  $\epsilon = 0$  is

$$C = \left\{ y_A, y_B, z_A, z_B \middle| \begin{array}{l} z_A = y_A - \frac{y_A^3}{3} - a + I \\ z_B = y_B - \frac{y_B^3}{3} - a + \gamma(y_A - y_B) \end{array} \right\},$$
(9.10)

By Fenichel's Theorem, the slow dynamics of the two-FN system (9.4) will lie  $\mathscr{O}(\epsilon)$ away from  $C_h$ , the normally hyperbolic submanifold of C, on a normally hyperbolic slow invariant manifold  $C_{\epsilon}$  with the same stability properties as  $C_h$ . [72, 139]

We next identify fold points by checking the three conditions that determine the set L from Definition 9.4.3. The first eigenvalue of  $D_{\mathbf{y}}\boldsymbol{\zeta}$  is  $1 - y_A^2$ , with left and right eigenvectors  $\mathbf{l}_1 = (1, (\gamma - y_A^2 + y_B^2)/\gamma)$  and  $\mathbf{r}_1 = (0, 1)^{\top}$ . The second eigenvalue of  $D_{\mathbf{y}}\boldsymbol{\zeta}$  is  $1 - y_B^2 - \gamma$ , with left and right eigenvectors  $\mathbf{l}_2 = (0, 1)$  and  $\mathbf{r}_2 = (1, (-\gamma + y_A^2 - y_B^2)/\gamma)^{\top}$ .

The first condition is satisfied, i.e.,  $\operatorname{rank}(D_{\mathbf{y}}\boldsymbol{\zeta}) = 1$ , if either  $1 - y_A^2 = 0$  or  $1 - y_B^2 - \gamma = 0$ , but not both. The second condition is satisfied if

$$\mathbf{l} \cdot D_{\mathbf{y}}^{2} \boldsymbol{\zeta} (\mathbf{r}, \mathbf{r}) = \mathbf{l} \cdot \begin{pmatrix} -2y_{A} & 0 & 0 & 0 \\ 0 & 0 & 0 & -2y_{B} \end{pmatrix} \begin{pmatrix} \mathbf{r} \\ \mathbf{r} \end{pmatrix} \neq 0$$

For each eigenvalue, the condition becomes  $y_B \left( (1 - y_A^2) - (1 - y_B^2 - \gamma) \right) \neq 0$ , which is satisfied if the first condition is satisfied and  $y_B \neq 0$ . The third condition is always satisfied.

### 9.4.2 Desingularization of the directed two-FN system

According to (9.9), the desingularization of the reduced system of the two-FN system is

$$\frac{d\mathbf{y}}{d\tau_2} = \operatorname{adj}(D_{\mathbf{y}}\boldsymbol{\zeta})(D_{\mathbf{z}}\boldsymbol{\zeta}) \cdot (\mathbf{y} - b\mathbf{z}), \qquad (9.11)$$

or equivalently,

$$\frac{dy_A}{d\tau_2} = \rho_1(y_A, y_B) = -(1 - y_B^2 - \gamma)(y_A - bz_A), 
\frac{dy_B}{d\tau_2} = \rho_2(y_A, y_B) = \gamma(y_A - bz_A) - (1 - y_A^2)(y_B - bz_B),$$
(9.12)

where  $z_A$  and  $z_B$  are defined as

$$z_A = y_A - \frac{y_A^3}{3} - a + I,$$
  

$$z_B = y_B - \frac{y_B^3}{3} - a + \gamma(y_A - y_B).$$
(9.13)

In what follows we study the stability type of the ordinary singularity and the folded singularities of (9.12). These points correspond to the equilibrium point and the fold points of the two-FN system, respectively. However, due to the time reversal step, the stability in the desingularized system is not identical to the stability of the full system.

By Definition 9.4.7 the ordinary singularity in (9.12) satisfies

$$\mathbf{y} - b\mathbf{z} = 0$$
, det $(D_{\mathbf{y}}\boldsymbol{\zeta}) \neq 0$ , adj $(D_{\mathbf{y}}\boldsymbol{\zeta})(D_{\mathbf{z}}\boldsymbol{\zeta}) \cdot (\mathbf{y} - b\mathbf{z}) \neq \mathbf{0}$ .

Figure 9.5 depicts regions in I- $\gamma$  parameter space according to the local stability of the ordinary singularity. Changes in stability in (9.12) correspond to Hopf bifurcations in (9.4). However, the curves in I- $\gamma$  space that delineate the different signs of the real parts of the eigenvalues are slightly different from the Hopf bifurcation curves because predictions from singular perturbation analysis are accurate up to  $\mathcal{O}(\epsilon)$ . In regions where A and B are both quiescent or saturated (dark gray), the real parts of both eigenvalues are positive and the ordinary singularity is an unstable equilibrium. In regions where both A and B are firing (light blue), the real parts of both eigenvalues are negative and the ordinary singularity is a stable equilibrium. In regions where either A or B is firing (light gray), the ordinary singularity is a saddle.



Figure 9.5: Regions in the  $I-\gamma$  parameter space distinguishing local stability of the ordinary singularity in the desingularized system (9.12). Dark gray indicates an unstable node, light blue indicates a stable node, and light gray indicates a saddle. The Hopf bifurcations and distinguishing features of the original two-FN system (9.4), the boundaries in Figure 9.3, are plotted for comparison as five curves.

By Definition 9.4.8 the folded singularities of (9.12) satisfy

det 
$$(D_{\mathbf{y}}\boldsymbol{\zeta}) = 0$$
, and  $\operatorname{adj}(D_{\mathbf{y}}\boldsymbol{\zeta})(D_{\mathbf{z}}\boldsymbol{\zeta}) \cdot (\mathbf{y} - b\mathbf{z}) = \mathbf{0}$ ,

or equivalently

$$(1 - y_{B*}^2 - \gamma)(1 - y_{A*}^2) = 0, \qquad (9.14a)$$

$$(1 - y_{B*}^2 - \gamma)(y_{A*} - bz_{A*}) = 0, \qquad (9.14b)$$

$$(1 - y_{A*}^2)(y_{B*} - bz_{B*}) - \gamma(y_{A*} - bz_{A*}) = 0.$$
(9.14c)

(9.14a) is satisfied when  $y_{A*} = \pm 1$  or  $y_{B*} = \pm \sqrt{1 - \gamma}$ . If (9.14b) and (9.14c) are satisfied but (9.14a) is not satisfied, the corresponding singularity is an ordinary singularity.

First consider the case in which  $y_{A*} = \pm 1$ . By (9.14b)-(9.14c), either  $z_{A*} = \frac{1}{b}y_{A*}$ or  $\gamma = 0$  and  $y_{B*} = \pm 1$ . If  $z_{A*} = \frac{1}{b}y_{A*}$  then, by (9.13),  $I = \pm \frac{1}{b} \mp \frac{2}{3} + a$ . Thus, we do not consider the case  $y_{A*} = \pm 1$  further, since either  $\gamma = 0$  or I is independent of  $\gamma$ .

When  $y_{B*} = \pm \sqrt{1 - \gamma}$ , we use (9.13) to solve (9.14c) for  $y_{A*}$ , which is equivalent to solving the cubic equation

$$\beta_3 y_{A*}^3 + \beta_2 y_{A*}^2 + \beta_1 y_{A*} + \beta_0 = 0, \qquad (9.15)$$

,

where

$$\beta_{0} = b\gamma(I-a) + y_{B*} + b\left(-y_{B*} + \frac{y_{B*}^{3}}{3} + a + \gamma y_{B*}\right)$$
  

$$\beta_{1} = -\gamma,$$
  

$$\beta_{2} = -y_{B*} + b\left(y_{B*} - \frac{y_{B*}^{3}}{3} - a - \gamma y_{B*}\right),$$
  

$$\beta_{3} = \frac{2b\gamma}{3}.$$

The solutions of (9.15) for  $y_{A*}$  as a function of  $\gamma$  and I are given by

$$y_{A*,k} = -\frac{1}{3\beta_3} \left( \beta_2 + C_k + \frac{\beta_2^2 - 3\beta_1\beta_3}{C_k} \right),$$

where, for k = 1, 2, 3,

$$C_{k} = \left(\frac{\sqrt{-3}-1}{2}\right)^{k-1} \left(\frac{\sigma - \sqrt{-27\beta_{3}^{2}\Delta}}{2}\right)^{1/3},$$
  
$$\Delta = 18\beta_{3}\beta_{2}\beta_{1}\beta_{0} - 4\beta_{0}\beta_{2}^{3} + \beta_{2}^{2}\beta_{1}^{2} - 4\beta_{3}\beta_{1}^{3} - 27\beta_{3}^{2}\beta_{0}^{2},$$
  
$$\sigma = 2\beta_{2}^{2} - 9\beta_{3}\beta_{2}\beta_{1} + 27\beta_{3}^{2}\beta_{0}.$$

If  $\Delta > 0$ , there are three real solutions, i.e., three folded singularities, and, if  $\Delta < 0$ , there is one real solution, i.e., one folded singularity.

The Jacobian of (9.12) for the folded singularities with  $y_{B*} = \pm \sqrt{1-\gamma}$  has the form:

$$D_{\mathbf{y}}\boldsymbol{\rho}(y_{A*}, y_{B*}) = \begin{pmatrix} 0 & 2y_{B*}\xi_A \\ \gamma + 2y_{A*}\xi_B & -(1 - y_{A*}^2) \end{pmatrix},$$

where  $\boldsymbol{\rho} = (\rho_1, \rho_2)^{\top}$ ,  $\xi_A = y_{A*} - bz_{A*}$ , and  $\xi_B = y_{B*} - bz_{B*}$ . To classify each folded singularity, we use the trace and determinant of the Jacobian, which are

Tr 
$$(D_{\mathbf{y}}\boldsymbol{\rho}(y_{A*}, y_{B*})) = -(1 - y_{A*}^2),$$
  
det  $(D_{\mathbf{y}}\boldsymbol{\rho}(y_{A*}, y_{B*})) = -2y_{B*}\xi_A (\gamma + 2y_{A*}\xi_B).$ 

When det  $(D_{\mathbf{y}}\boldsymbol{\rho}(y_{A*}, y_{B*})) > 0$ , the real parts of the eigenvalues have the same sign, so the singularity is a folded node or focus. The stability can be determined by looking at the sign of the trace. When det  $(D_{\mathbf{y}}\boldsymbol{\rho}(y_{A*}, y_{B*})) < 0$ , the real parts of the eigenvalues have opposite signs, and the singularity is a folded saddle.

Figure 9.6 depicts regions in I- $\gamma$  parameter space according to the local stability of the folded singularities. The white regions in this figure correspond to values of Iand  $\gamma$  where the given folded singularity does not exist in the desingularized system (9.12) (i.e.  $\Delta < 0$ ).



Figure 9.6: Regions in the  $I-\gamma$  parameter space distinguishing local stability of the three folded singularities corresponding to  $y_{B*} = -\sqrt{1-\gamma}$  (top, middle, and bottom plots on the left) and the three folded singularities corresponding to  $y_{B*} = \sqrt{1-\gamma}$  (top, middle, and bottom plots on the right). In white regions, the folded singularity does not exist. In dark gray regions, the folded singularity is unstable. In light gray regions, the folded singularity is a saddle. In light blue regions, the folded singularity is stable.

## 9.5 Dynamics by region

In this section, we apply the analytical results for the desingularized system (9.12) to draw conclusions about the original system (9.4). In so doing we provide details of the computations used to produce Figure 9.3 and the characterization of each of the seven regions, as described in Section 9.3. We prove the stability of limit cycles of the Hopf bifurcations in model neuron B. We prove necessary conditions for MMOs and sufficient conditions for phase locking in terms of I and  $\gamma$ .

In the following proposition, we compute the value of the unique equilibrium point of (9.4), when Assumption 9.2.1 holds, and its stability as a function of I and  $\gamma$ .

**Proposition 9.5.1.** Consider the directed two-FN system (9.4) and let Assumption 9.2.1 hold. For any fixed I and  $\gamma$ , there exists a unique equilibrium point denoted by  $\mathbf{p}_* = (y_{A*}(I), z_{A*}(I), y_{B*}(I, \gamma), z_{B*}(I, \gamma))$ . Then,

1.  $\mathbf{p}_*$  is nonhyperbolic if I and  $\gamma$  satisfy

$$\sigma_1(I,\gamma) = 1 - b\epsilon - y_{A*}^2 = 0,$$
  
or  $\sigma_2(I,\gamma) = 1 - b\epsilon - \gamma - y_{B*}^2 = 0,$  (9.16)

where  $\sigma_1$  is the sum of the first two eigenvalues of the Jacobian of (9.4) evaluated at  $\mathbf{p}_*$  and  $\sigma_2$  is the sum of the second two eigenvalues of the Jacobian of (9.4) evaluated at  $\mathbf{p}_*$ .

2. p<sub>\*</sub> is hyperbolic if I and γ do not satisfy (9.16). If σ<sub>1</sub>(I, γ) < 0 and σ<sub>2</sub>(I, γ) <</li>
0, p<sub>\*</sub> is attracting. If σ<sub>1</sub>(I, γ) > 0 and σ<sub>2</sub>(I, γ) > 0, p<sub>\*</sub> is repelling. If σ<sub>1</sub>(I, γ)σ<sub>2</sub>(I, γ) < 0, p<sub>\*</sub> is a saddle.

*Proof.* Solving for the equilibrium point of (9.4), we first compute  $y_{A*}$  as a function of I as

$$y_{A*} = \left(\frac{3(I-a)}{2} + \sqrt{\frac{(3(I-a))^2}{4} + \tilde{b}^3}\right)^{1/3} + \left(\frac{3(I-a)}{2} - \sqrt{\frac{(3(I-a))^2}{4} + \tilde{b}^3}\right)^{1/3},$$
(9.17)

where  $\tilde{b} = \frac{1}{b} - 1$ . Similarly, by leveraging (9.17), we can write  $y_{B*}$  as a function of Iand  $\gamma$  as

$$y_{B*} = \left(\frac{3(\gamma y_{A*} - a)}{2} + \sqrt{\frac{9(\gamma y_{A*} - a)^2}{4} + \left(\tilde{b} + \gamma\right)^3}\right)^{1/3} + \left(\frac{3(\gamma y_{A*} - a)}{2} - \sqrt{\frac{9(\gamma y_{A*} - a)^2}{4} + \left(\tilde{b} + \gamma\right)^3}\right)^{1/3}$$
(9.18)

Then  $z_{A*} = \frac{1}{b}y_{A*}$  and  $z_{B*} = \frac{1}{b}y_{B*}$ .

We compute the linearization of (9.4) around  $\mathbf{p}_*$ . We let  $\boldsymbol{\nu}_A = (y_A, z_A)$ ,  $\boldsymbol{\nu}_B = (y_B, z_B)$ , and  $\boldsymbol{\xi} = (\zeta_A, \epsilon \xi_A, \zeta_B, \epsilon \xi_B)$ . The Jacobian of (9.4) evaluated at  $\mathbf{p}_*$  is

$$D_{(\boldsymbol{\nu}_{A},\boldsymbol{\nu}_{B})}\boldsymbol{\xi}(\mathbf{p}_{*}) = \begin{pmatrix} 1 - y_{A*}^{2} & -1 & 0 & 0\\ \epsilon & -b\epsilon & 0 & 0\\ \gamma & 0 & 1 - y_{B*}^{2} - \gamma & -1\\ 0 & 0 & \epsilon & -b\epsilon \end{pmatrix}$$

The linearization is block triangular, so the eigenvalues of the Jacobian are the union of the eigenvalues of the diagonal blocks. This means that local stability can be determined through linearization of each FN model separately. The eigenvalues for the first and second blocks are

$$\lambda_{1,2} = \frac{1}{2} \left( 1 - b\epsilon - y_{A*}^2 \right) \pm \frac{1}{2} \sqrt{(1 - b\epsilon - y_{A*}^2)^2 - 4\epsilon(1 - b + y_{A*}^2 b)},$$
  
$$\lambda_{3,4} = \frac{1}{2} \left( 1 - b\epsilon - \gamma - y_{B*}^2 \right) \pm \frac{1}{2} \sqrt{(1 - b\epsilon - \gamma - y_{B*}^2)^2 - 4\epsilon(1 - b + y_{B*}^2 b + b\gamma)}.$$

The sign of the real part of the eigenvalues will be determined by the sign of the first term. The first term of  $\lambda_{1,2}$  is zero when  $\sigma_1(I,\gamma) = \lambda_1 + \lambda_2 = 1 - b\epsilon - y_{A*}^2 = 0$ . The first term of  $\lambda_{3,4}$  is zero when  $\sigma_2(I,\gamma) = \lambda_3 + \lambda_4 = 1 - b\epsilon - \gamma - y_{B*}^2 = 0$ . Thus,  $\mathbf{p}_*$  is nonhyperbolic when  $\sigma_1 = 0$  or  $\sigma_2 = 0$ .

The stability of  $\mathbf{p}_*$  when  $\sigma_1 \sigma_2 \neq 0$  is derived from the signs of the real parts of the eigenvalues of  $D_{(\boldsymbol{\nu}_A, \boldsymbol{\nu}_B)} \boldsymbol{\xi}$ .

**Remark 9.5.2.** The one-dimensional manifolds of nonhyperbolic equilibrium points in I- $\gamma$  space,  $\{(I, \gamma) : \sigma_1(I, \gamma) = 0 \text{ or } \sigma_2(I, \gamma) = 0\}$ , correspond to the points where Aand B undergo Hopf bifurcations.

**Remark 9.5.3.** The corresponding flows of the full system and desingularized system have opposite sign when det  $(D_y f) > 0$  due to the time rescaling step,  $d\tau_1 =$   $-\det(D_{\mathbf{y}}\mathbf{f})d\tau_2$ . One consequence is that when the ordinary singularity in the desingularized system is an unstable node, the unique equilibrium in the full system is stable. Likewise, when the ordinary singularity in the desingularized system is a stable node, the unique equilibrium point in the full system is unstable.

#### 9.5.1 Quiescence: Region (1)

Given the two-FN system (9.4) and Assumption 9.2.1, if  $I < I_{0cA}$  then A converges to a single stable equilibrium point,  $(y_{A*}, z_{A*})$ , which is quiescent. The value  $y_{A*}$ , independent of  $\gamma$ , is too low to induce firing in B, i.e., B is quiescent.

To fully understand the behavior of B, we examine the desingularized system (9.12), which has seven singularities for the parameter values in region (1). These include one unstable ordinary singularity (corresponding to the unique stable equilibrium point), one unstable folded node, two stable folded singularities, and three saddle folded singularities.

Due to the presence of a stable folded node when  $\gamma$  is close to 1 and  $I < I_0$ , robust families of canards that compose small oscillations of B could arise for these parameter values in the original system (9.4) in region (1) as described in Section 9.4.

## 9.5.2 Hopf bifurcations in B: Regions (2), (3), and (4)

For the two-FN system (9.4), if  $I > I_{1cA}$  then A is saturated. We prove conditions for when B will be quiescent, firing, or saturated and provide illustrative examples of the desingularized system nullclines and phase plane for representative parameter values.

**Proposition 9.5.4.** Consider the two-FN system (9.4) and Assumption 9.2.1. Let  $I > I_{1cA}$  and  $\gamma < 1 - b\epsilon$ . There exist two curves of Hopf bifurcations defined by

$$I_{1B,0B}(\gamma) = \tilde{b}y_{A*\pm} + \frac{y_{A*\pm}^3}{3} + a$$

where

$$y_{A*\pm} = \pm \frac{1}{\gamma} \left( \frac{1}{3} (1 - \epsilon b - \gamma)^{3/2} + \left( \tilde{b} + \gamma \right) \sqrt{1 - \epsilon b - \gamma} + a \right).$$

The bifurcation structure of B in the small parameter range around the transition from quiescent to firing is analogous to the single FN model in Section 9.2. There is a saddle node bifurcation of limit cycles at  $I = I_{0sn}(\gamma)$ , canard explosion at  $I = I_{0cB}(\gamma)$ , and Hopf bifurcation at  $I = I_{0B}(\gamma)$ . B transitions from firing to saturated through a supercritical Hopf bifurcation at  $I = I_{1B}(\gamma)$ .

Moreover, there exists  $\gamma_*$  such that, for  $I < I_{0B}(\gamma_*)$ , the following holds. If  $\gamma < \gamma_*$ , the Hopf bifurcation at  $I_{0B}(\gamma)$  is subcritical and, if  $\gamma > \gamma_*$ , the Hopf bifurcation at  $I_{0B}(\gamma)$  is supercritical.

*Proof.* The Hopf bifurcations in *B* occur at nonhyperbolic equilibrium points, which are  $y_{B*\pm} = \pm \sqrt{1 - \gamma - b\epsilon}$  by Proposition 9.5.1.

Substituting  $y_{B*\pm} = \pm \sqrt{1 - \gamma - b\epsilon}$  and (9.4d) into the equilibrium solution for (9.4c) gives the critical values

$$y_{A*\pm} = \pm \frac{1}{\gamma} \left( \frac{1}{3} (1 - \epsilon b - \gamma)^{3/2} + \left( \tilde{b} + \gamma \right) \sqrt{1 - \epsilon b - \gamma} + a \right).$$

Substituting  $y_{A*\pm}$  and (9.4b) into (9.4a) gives the values

$$I_{1B,0B} = \tilde{b}y_{A*\pm} + \frac{y_{A*\pm}^3}{3} + a.$$

For a fixed  $\gamma$ , we check the conditions of Proposition 9.2.4 for the bifurcation parameter *I*. First, we transform  $(y_{B*}, z_{B*})$  to the origin (0, 0), by introducing  $y_0 = y_B - y_{B*}$  and  $z_0 = z_B - z_{B*}$ . With this change of variables, the dynamics of *B*  (9.4c)-(9.4d) can be expressed as

$$\frac{dy_0}{dt} = (1 - \gamma - y_{B*}^2)y_0 - \frac{y_0^3}{3} - y_0^2 y_{B*} - z_0, 
\frac{dz_0}{dt} = \epsilon(y_0 - bz_0),$$
(9.19)

and the Jacobian of (9.19) evaluated at the origin is

$$J_B(0,0) = \begin{pmatrix} 1 - y_{B*}^2 - \gamma & -1 \\ \epsilon & -b\epsilon \end{pmatrix}.$$

Now we apply Proposition 9.2.4.

Condition 1 of Proposition 9.2.4: This condition holds because  $Tr(J_B(0,0)) = 0$ at the bifurcation values  $I = I_{0B}$  and  $I = I_{1B}$ .

Condition 2 of Proposition 9.2.4: The second condition holds as well because

$$\left. \frac{\partial}{\partial I} \Re(\lambda_{3,4}(I)) \right|_{I=I_{0B,1B}} \neq 0,$$

where  $\lambda_{3,4}$  are given in the proof of Proposition 9.5.1.

Condition 3 of Proposition 9.2.4: The cubic coefficient  $\alpha$  of the Taylor expansion of (9.4c)–(9.4d) (Definition 9.2.3), which determines whether the Hopf bifurcation is subcritical or supercritical [53], is

$$\alpha = \frac{1}{8} \left( \frac{2b - 2b\gamma - b^2\epsilon - 1}{1 - b^2\epsilon} \right).$$

At  $\gamma = \gamma_*$ ,  $\alpha = 0$  and *B* undergoes a "generalized Hopf", or Bautin, bifurcation, depicted in Figure 9.3 as the point GH[50, 127]. For  $\gamma > \gamma_*$ ,  $\alpha < 0$  and the limit cycles resulting from the Hopf bifurcations are stable (supercritical). Otherwise, the limit cycles are unstable and the bifurcations are subcritical, as for *A*. **Remark 9.5.5.** For the two-FN system (9.4), given Assumption 9.2.1, if A is saturated, then B transitions from quiescent to firing to saturated as a function of I and  $\gamma$ .

In region (2), the desingularized system (9.12) has seven singularities, one ordinary singularity and six folded singularities. The ordinary singularity is unstable, and there are three unstable folded singularities and three folded saddles. This is a region where A is saturated and B is quiescent, so the full two-FN system has a unique stable equilibrium point.

In region (3), the desingularized system (9.12) has seven singularities for small  $\gamma$ , and five singularities for large  $\gamma$ .

The transition from seven to five singularities occurs through a saddle node bifurcation between a folded saddle point and an unstable folded singularity. The ordinary singularity is a saddle and the unique equilibrium point of the full system is also a saddle.

In region (4) the desingularized system (9.12) can have one, three, five, or seven singularities. Parameter choices for (9.12) in which  $\gamma > 1$ , which corresponds to  $\gamma > 1 - b\epsilon$  in the two-FN system, result in one singularity. Since  $\gamma > 1$  for (9.12) in region (4), the folded singularities corresponding to  $y_{B*} = \pm \sqrt{1 - \gamma}$  no longer exist. The ordinary singularity is unstable and the unique equilibrium point of the full system is stable.

#### 9.5.3 Phase-locking: Region (5)

Consider the two-FN system (9.4) with  $I_{0cA} < I < I_{1cA}$  such that A is firing. Region (5) corresponds to this range of I and  $\gamma > 1 - b\epsilon$ . For  $I_{0A} < I < I_{1A}$  and  $\gamma > 1 - b\epsilon$ , the linearization of (9.4) around the equilibrium point  $\mathbf{p}_*$  has two eigenvalues  $\lambda_{1,2}$ with positive real part, and two eigenvalues  $\lambda_{3,4}$  with negative real part. Thus, B will follow the limit cycle from A. **Remark 9.5.6.** For the two-FN system (9.4), given Assumption 9.2.1, if A is firing and  $\gamma > 1 - b\epsilon$ , B is firing and A and B are phased locked.

For the desingularized system (9.12),  $\gamma > 1$  and the singularities at  $y_{B*} = \pm \sqrt{1-\gamma}$  no longer exist. The ordinary singularity is a saddle and the unique equilibrium point of the full system is also a saddle. Note that there are still folded singularities corresponding to  $y_{A*} = \pm 1$ , but they are the points,  $I_{0A}$  and  $I_{1A}$ , where the stability changes in the ordinary singularity.

#### 9.5.4 Mixed mode oscillations: Regions (6) and (7)

Now consider the two-FN system (9.4) when  $I_{0cA} < I < I_{1cA}$  and  $\gamma < 1 - b\epsilon$ . In this case a range of dynamics is observed in simulation. For  $\gamma \ll 1$ , the influence of A is small, so B exhibits only small oscillations that stay close to  $(y_{B*}, z_{B*})$ . As  $\gamma$  is increased, the influence of oscillation A can be large enough to yield a mixed mode oscillation (MMO), see Figure 9.4(b). As  $\gamma$  is increased further and the influence of A becomes increasingly strong, B approaches firing at the same frequency as A.

To better understand these transitions, we study the bifurcation diagrams and phase planes of the desingularized system (9.12). We prove necessary conditions for the existence of MMOs as a function of I and  $\gamma$ .

In region (6) there are seven singularities for the desingularized system (9.12), seen in Figures 9.7(a) and 9.7(b). In this region, the ordinary singularity of the desingularized system (9.12) is a saddle (corresponding to a saddle in the full system), whereas the folded singularities include three saddles, one stable folded singularity, and two unstable singularities. Trajectories, nullclines, and singularities are shown in Figure 9.7(a) for parameters in region (6). Co-existence of the stable folded node and a global return mechanism due to the S-shaped critical manifold allows existence of canard-induced MMOs in this region of parameter space for the two-FN system [34]. Figure 9.7(b) zooms in on the area around the ordinary singularity and stable folded node for the same parameter values as Figure 9.7(a). Critical features for canard existence are present in this region. An unstable manifold of the ordinary singularity, which is a saddle, connects to the stable folded node, shown in red. The strong singular canard of the stable folded node is shown in green, and the stable manifold of the ordinary saddle singularity is shown in blue. All trajectories between the stable manifold of the ordinary singularity and the stable manifolds of the two folded saddles to the right of the stable folded node will be funneled to the stable folded node, and thus will pass from the attracting to repelling parts of the critical manifold in the full system. This results in the family of canard solutions seen in the full system.

In region (7) there are seven singularities. In this region, the ordinary singularity of the desingularized system (9.12) is stable (corresponding to an unstable equilibrium in the full system), whereas the folded singularities include four saddles and two unstable singularities. As a consequence, canard-induced MMOs do not exist in the two-FN system, and both A and B are firing and phase-locked.

We next compute the boundary between regions (6) and (7), shown by  $I_*$  in Figure 9.3. The boundary is defined by points at which there is a transcritical bifurcation between the ordinary singularity and a folded singularity, called FSN type II bifurcation, where the ordinary singularity transitions from a saddle to a stable node and the folded singularity transitions from a stable node to a saddle. This transcritical bifurcation is a known location for the onset of MMOs, [69] so computing  $I_*$  gives necessary conditions for the existence of MMOs. Figure 9.7(c) depicts the phase plane near the ordinary singularity at the transcritical bifurcation. The strong stable canard trajectory and connecting unstable manifold of the ordinary singularity are no longer present. Figure 9.7(d) depicts the phase plane near the ordinary singularity as



Figure 9.7: Nullclines and phase planes for the desingularized system (9.12) near the boundary between regions (6) and (7). For all panels, the folded singularities are shown as smaller circles and the ordinary singularity is a larger circle. Green represents a stable singularity, gray represents a saddle, and red represents an unstable singularity. Trajectories of the system are shown in black. The  $y_A$  (blue dashed) and  $y_B$  (pink dashed) nullclines are also shown. Panels (a) and (b) show the phase plane for I = 0.9 and  $\gamma = 0.4$  (in region (6)) for differing ranges of  $y_A$  and  $y_B$ . Panel (b) shows the stable (blue) and unstable (red) manifolds of the ordinary singularity, which is a saddle, along with the strong canard (green) associated with the stable folded node. Panel (c) shows the phase plane for I = 1.0633 and  $\gamma = 0.4$  on the boundary between regions (6) and (7). Panel (d) shows the phase plane for I = 1.3and  $\gamma = 0.4$  in region (7), where A is firing and B is phase locked with A in the two-FN system (9.4). The stable (light blue) and unstable (light red) manifolds of the folded saddle are shown.

I is increased beyond the transcritical bifurcation. In this region, there is no longer a stable folded node.

**Proposition 9.5.7** (Theorem 3.4.1 (modified) [53]). A system  $\dot{\mathbf{x}} = \boldsymbol{f}(\mathbf{x}, \mu)$ , admits a transcritical bifurcation at  $(\mathbf{x}_0, \mu_0)$  if

- 1.  $D_{\mathbf{x}} \mathbf{f}(\mathbf{x}_0, \mu_0)$  has a simple 0 eigenvalue with right eigenvector v and left eigenvector w.
- 2.  $\boldsymbol{w} D_{\mathbf{x}\mu}^2 \boldsymbol{f}(\mathbf{x}_0, \mu_0) \boldsymbol{v} \neq 0.$
- 3.  $\boldsymbol{w} D_{\mathbf{x}}^2 \boldsymbol{f}(\mathbf{x}_0, \mu_0) (\boldsymbol{v}^\top, \boldsymbol{v}^\top)^\top \neq 0.$

**Proposition 9.5.8.** Consider the desingularized system (9.12) with fixed  $\gamma < 1$  and let

$$I_*(\gamma) = \frac{1}{3b^3\gamma^3} \left(\sqrt{1-\gamma} + \frac{2b\sqrt[3]{1-\gamma}}{3} - ba\right)^3 + a.$$
(9.20)

Then system (9.12) admits a transcritical bifurcation at  $(\mathbf{p}, I_*(\gamma))$ , where  $\mathbf{p} = (y_{A*}, y_{B*})^{\top}$  is an ordinary singularity of (9.12), i.e.,  $\mathbf{p}$  solves (9.14b) and (9.14c).

*Proof.* To show the transcritical bifurcation, we apply Proposition 9.5.7 to (9.12). The Jacobian,  $D_{\mathbf{y}}\boldsymbol{\rho}$ , of (9.12) is

$$\left(\begin{array}{cc} -(1-y_B^2-\gamma)(1-b+by_A^2) & 2y_B(y_A-bz_A) \\ \gamma+2y_A(y_B-bz_B) & -(1-y_A^2)(1-b+by_B^2+b\gamma) \end{array}\right).$$

Condition 1 of Proposition 9.5.7: Evaluating the Jacobian of (9.12) at  $(y_A, y_B)^{\top} = \mathbf{p}$ and  $I = I_*$  gives

which has a zero eigenvalue with a left eigenvector  $\boldsymbol{w} = (1, 0)$  and a right eigenvector  $\boldsymbol{v} = \left(1, \frac{\gamma}{-(1-y_{A*}^2)}\right)^{\top}$ .

Condition 2 of Proposition 9.5.7: Taking the derivative of  $D_{\mathbf{y}}\rho$  with respect to Iand evaluating at  $(y_A, y_B)^{\top} = \mathbf{p}$  and  $I = I_*$  gives

$$D_{\mathbf{y}I}^{2}\boldsymbol{\rho}(\boldsymbol{p},I_{*}) = \begin{pmatrix} 0 & -2by_{B*} \\ 0 & 0 \end{pmatrix}.$$

Then, multiplying  $D^2_{\mathbf{y}\gamma}\boldsymbol{\rho}(\boldsymbol{p},I_*)$  from left by  $\boldsymbol{w}$  and from right by  $\boldsymbol{v}$ , we have

$$\boldsymbol{w}\left(D_{\boldsymbol{y}\gamma}^{2}\boldsymbol{\rho}(\boldsymbol{p},I_{*})\right)\boldsymbol{v}=rac{2b\gamma y_{B*}}{1-y_{A*}^{2}},$$

which is always nonzero.

Condition 3 of Proposition 9.5.7: Evaluating  $D_{\mathbf{y}}^2 \boldsymbol{\rho}$  at  $\boldsymbol{p} = (y_A, y_B)^{\top}$  and  $I = I_*$  gives

$$D_{\mathbf{y}}^{2}\boldsymbol{\rho}(\mathbf{p},I_{*}) = \begin{pmatrix} 0 & 2y_{B*}(1-s) & 0 & 2y_{A*} \\ 2y_{B*}(1-s) & 0 & 2y_{A*} & -2y_{B*}s \end{pmatrix}$$

where  $s = b(1 - y_{A*}^2)$ . Then, multiplying  $D_{\mathbf{y}}^2 \boldsymbol{\rho}$  from left by  $\boldsymbol{w}$  and from right by  $(\boldsymbol{v}^{\top}, \boldsymbol{v}^{\top})^{\top}$ , we have

$$\boldsymbol{w} \left( D_{\boldsymbol{y}}^{2} \boldsymbol{\rho}(\boldsymbol{p}, I_{*}) \right) \begin{pmatrix} \boldsymbol{v} \\ \boldsymbol{v} \end{pmatrix}$$
$$= \frac{-2\gamma}{1 - y_{A*}^{2}} \left( y_{B*}(1 - b(1 - y_{A*}^{2})) + y_{A*} \right), \qquad (9.21)$$

which is also nonzero as shown in Figure 9.8.



Figure 9.8: Regions in the I- $\gamma$  parameter space distinguishing the sign of (9.21). In the light blue regions, the sign is positive. In the light gray regions, the sign is negative. At the boundaries, the sign becomes zero. For all  $(I, \gamma)$  pairs on  $I_*$  (shown by the green dashed line), the sign of (9.21) is nonzero, except where  $I_*$  intersects  $I_{1A}$ . The bifurcation at the intersection is a codimension two bifurcation.

A necessary condition for canard-induced MMOs is the existence of a stable folded node with a return mechanism, since the family of canard solutions that form the small oscillations are only found in this context [18,69]. The stable folded node has a corresponding family of canard solutions because there are many trajectories that

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cross from the attracting to the repelling branch of the critical manifold through the stable folded node. Furthermore, the return mechanism is required for MMOs because, after each relaxation oscillation or canard trajectory, the dynamics must return near the singularity in order for the MMO to persist.

**Global return mechanism:** For all coupling strengths  $\gamma < 1-b\epsilon$ , the projection of the critical manifold in one fast and two slow dimensions is S-shaped, with two attracting branches connected by a repelling branch in the center and two fold lines. The relaxation oscillations in this setting provide a global return mechanism for the system [34, 69].

Stable folded node: In the directed two-FN system, MMOs are only possible for  $I < I_*(\gamma)$ , since that is where there is a stable folded node.

**Remark 9.5.9.** Consider the two-FN system (9.4). For  $I_{0cA} < I < I_*(\gamma)$ , this system exhibits MMOs and if  $I_*(\gamma) < I < I_{1cA}$ , it exhibits phase locking.

**Remark 9.5.10.** A special case of the transcritical (FSN II) bifurcations occurs when  $\gamma$  and I satisfy  $I_*(\gamma) = I_{1A}$ . In this case, there is a codimension two bifurcation where the real parts of the eigenvalues of the linearization of (9.12) about the ordinary singularity and the eigenvalues of the linearization of (9.12) about the folded singularity,  $y_{B*} = -\sqrt{1-\gamma}$ , are equal to zero. The codimension two bifurcation is illustrated by the orange star in the bifurcation diagram of (9.12) in Figure 9.9(a), for  $\gamma = 0.22$ . If we fix  $I_{0cA} < I < I_{1cA}$  and decrease the value of  $\gamma$  below the codimension two value, then MMOs are always possible.

To highlight the location of the transcritical bifurcation (FSN II) and compare to features in Figure 9.3, we show it as the blue star in the bifurcation diagram of (9.12) in Figure 9.9(b). Here, by treating I as the bifurcation parameter, and maintaining  $\gamma$  fixed at value 0.4, we can observe that the ordinary singularity transitions from unstable (thick dashed red) to saddle (thick gray) at  $I = I_{0A}$  (red star). Simultaneously, a stable folded singularity (thin green) becomes a folded saddle (thin gray)



Figure 9.9: This figure shows the bifurcation diagrams of the desingularized system (9.12) with bifurcation parameter I for two different values of  $\gamma$ . The insert shows the locations of the two diagrams (dashed lines correspond to the *I*-axis) in I- $\gamma$  parameter space matching Figure 9.5. (a) When  $\gamma = 0.22$ , the desingularized system admits a codimension two bifurcation (orange star) where the ordinary singularity remains a saddle, while one folded singularity switches from a stable folded singularity to an unstable folded singularity. (b) When  $\gamma = 0.4$ , a transcritical bifurcation (FSN II) occurs between the ordinary singularity and a folded singularity (blue star). For this choice of  $\gamma$ , the desingularized system admits another folded singularity (unstable folded singularity) at  $y_{A*} \approx 6$ , which is not shown in either figure.

and a folded saddle becomes an unstable folded singularity (thin dashed red). The concurrent existence of a stable folded node and a folded saddle allows for *composite canards*, which are trajectories that follow canard solutions of at least two different folded singularities and produce complex small-amplitude oscillations [97].

At  $I = I_*(\gamma)$  (blue star), derived in Proposition 9.5.8, the ordinary singularity and a folded singularity swap stability properties in a transcritical bifurcation, which can be classified as an FSN II bifurcation. Also, this FSN II bifurcation in the desingularized system (9.12) corresponds to the generalized Hopf bifurcation in the two-FN system (9.4). For  $I > I_*$ , (9.4) exhibits phase locking and MMOs are no longer possible.

At  $I = I_{1A}$  (magenta star), the ordinary singularity returns to a saddle and two folded saddles become two unstable folded singularities. For  $I > I_{1A}$ , phase locking in (9.4) is no longer possible. We also note that when I is just above  $I_{1A}$ , one folded saddle merges with an unstable folded singularity through a saddle node bifurcation.

## 9.6 Directed Tree of FN model neurons

In this section, we consider an extension of the previous results to a directed chain of coupled FN models. We leverage the connection between the desingularized system and the directed two-FN system to find sufficient conditions for phase locking.

Consider a system of k FN model neurons with dynamics

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mathbf{I}, \boldsymbol{\gamma}),$$

where  $\mathbf{x} \in \mathbb{R}^{2k}$ ,  $\mathbf{I} \in \mathbb{R}^{k-1}$ , and  $\boldsymbol{\gamma} \in \mathbb{R}^{k-1}$ . All FN models receive an external input except for the last in the chain. Then, by allowing heterogeneity in the external inputs and coupling strengths, the linearization around the equilibrium point can be expressed as

$$D_{\mathbf{x}}\mathbf{f} = \begin{pmatrix} J_1 & 0_{2\times 2} & 0_{2\times 2} & 0_{2\times 2} & \cdots & 0_{2\times 2} \\ \Gamma_1 & J_2 & 0_{2\times 2} & 0_{2\times 2} & \cdots & 0_{2\times 2} \\ 0_{2\times 2} & \Gamma_2 & J_3 & 0_{2\times 2} & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \ddots & 0_{2\times 2} \\ 0_{2\times 2} & 0_{2\times 2} & \ddots & \Gamma_{k-2} & J_{k-1} & 0_{2\times 2} \\ 0_{2\times 2} & 0_{2\times 2} & \cdots & 0_{2\times 2} & \Gamma_{k-1} & J_k \end{pmatrix},$$

where the first diagonal block is given by

$$J_1 = \left( \begin{array}{cc} 1 - y_1^2 & -1 \\ \\ \epsilon & -b\epsilon \end{array} \right),$$

and the subsequent diagonal blocks are given by

$$J_i = \begin{pmatrix} 1 - y_i^2 - \gamma_{i-1} & -1 \\ \epsilon & -b\epsilon \end{pmatrix}, \quad i \in \{2, \dots, k\}.$$

The blocks on the lower diagonal are

$$\Gamma_i = \gamma_i \begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}, \quad i \in \{1, \dots, k-1\}.$$

Due to the lower block triangular structure of the linearization, local stability of the equilibrium can be determined by studying the eigenvalues of the diagonal blocks. Similar to the analysis at the beginning of Section 9.5, we begin by solving for the equilibrium point. The equilibrium of the first model neuron is given by

$$y_{1*} = \left(\frac{3(I_1 - a)}{2} + \sqrt{\frac{(3(I_1 - a))^2}{4} + \tilde{b}^3}\right)^{1/3} + \left(\frac{3(I_1 - a)}{2} - \sqrt{\frac{(3(I_1 - a))^2}{4} + \tilde{b}^3}\right)^{1/3}.$$

The equilibrium of the i-th model neuron is given by

$$y_{i*} = \left(\frac{3\tilde{I}}{2} + \sqrt{\frac{(3\tilde{I})^2}{4} + (\tilde{b} + \gamma_{i-1})^3}\right)^{1/3} + \left(\frac{3\tilde{I}}{2} - \sqrt{\frac{(3\tilde{I})^2}{4} + (\tilde{b} + \gamma_{i-1})^3}\right)^{1/3},$$

where  $\tilde{I} = \gamma_{i-1}y_{i-1*} + I_i - a, i \in \{2, \dots, k\}$ . The eigenvalues of the individual diagonal blocks are

$$\lambda_{1,2} = \frac{1}{2} \left( 1 - y_{1*}^2 - b\epsilon \right) \pm \frac{1}{2} \sqrt{(y_{1*}^2 + b\epsilon - 1)^2 - 4\epsilon(1 - b + y_{1*}^2 b)},$$
  
$$\lambda_{2i-1,2i} = \frac{1}{2} \left( 1 - y_{i*}^2 - \gamma_{i-1} - b\epsilon \right) \pm \frac{1}{2} \sqrt{(y_{i*}^2 + \gamma_{i-1} + b\epsilon - 1)^2 - 4\epsilon(1 - b + y_{i*}^2 b + \gamma_{i-1})},$$

where i = 2, ..., k. The Hopf bifurcations in the *i*-th model neuron occur at

$$I_{H\pm} = \pm \frac{1}{3} (1 - \gamma_{i-1} - b\epsilon)^{3/2} \quad \pm \sqrt{1 - \gamma_{i-1} - b\epsilon} \left(\tilde{b} + \gamma_{i-1}\right) - \tilde{I}.$$
(9.22)

As a directed tree can be decomposed into a collection of directed chains, these results generalize to directed trees as well. In Figure 9.10, we illustrate with the directed chain that starts with the light orange FN model and is directed to the right to the cyan FN model. The first FN model (light orange) receives an input I = 1.2, which ensures that it is firing. The coupling strength to the second FN model (dark orange) with input I = 0.4 ensure that the second FN model is in region (6) where MMOs are possible. However, in this case no MMOs are exhibited. The coupling strength to the third FN model (dark cyan) with zero input ensure that it too is in region (6). In this case, MMOs induced by canards are exhibited. The active signal has frequency half that of the first and second FN models. As a result, the input to the fourth FN model (cyan) is an MMO; this case was not covered in our two-FN system analysis. The fourth FN model responds to incoming canards with almost no activity and incoming spikes with a small canard. The frequency of the small canards in the fourth FN model is the same as the frequency of the active signal of the third FN model.

## 9.7 Discussion

In this work, we study a system of two FN model neurons in a setting where the first FN model has a constant external input I, the second FN model has no input, and there is a unidirectional coupling with strength  $\gamma$  from the first FN model to the second. We study and rigorously characterize all of the different regions of dynamic behavior for the two-FN system in  $I-\gamma$  space. We prove new necessary conditions in terms of both I and  $\gamma$  for the existence of canards and MMOs. We leverage this result



Figure 9.10: Panel (a) depicts a directed tree graph of FN model neurons with heterogeneous external inputs  $I_i$ . All edge weights have coupling strength  $\gamma = 0.07$ . A representative chain is selected and indicated by vertices with colors matching simulation results, which are shown in panel (b). The frequency of the cyan FN models is half of the frequency of the orange FN models.

to find a similarly new sufficient condition for phase locking and extend to systems of FN models in directed tree networks. We illustrate for a directed chain of four FN models, where canards, MMOs, and frequency halving is observed as predicted.

Further investigation of the two-FN system is needed to determine the threshold between MMOs and canard solutions without MMOs, which have been observed in simulation. This threshold has been studied numerically, as well as the chaotic behavior at the boundaries between types of MMOs, e.g., in [60]. An analytical understanding of the threshold phenomena involved in the onset of firing in systems of FN models would add significantly to the literature on canards and MMOs.

Future directions include consideration of more diverse graph structures that include loops within the graph and a more detailed analysis of the MMOs in these systems. General results have been found for finite dimensional fast-slow systems, which could be applied in this context [138]. Incorporating heterogeneous model parameters is another area of future investigation. Changing  $\epsilon$  changes the frequency of oscillation and the timescale of the FN model, so a network of FN models with differing values of  $\epsilon$  would be a compelling system for exploring canard phenomena in three or more distinct timescales.

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# Appendix A

# First and Second Lyapunov Coefficients for the Desingularized Two-FN System at $\gamma = 0$

### **A.1** Derivatives of $F(\eta_1, \eta_2)$ and $G(\eta_1, \eta_2)$

To compute the Lyapunov coefficients of (9.12) at the Hopf bifurcation at  $\gamma = 0$ , we first compute the partial derivatives of  $F(\eta_1, \eta_2)$  and  $G(\eta_1, \eta_2)$  up to fifth order. The functions  $F(\eta_1, \eta_2)$  and  $G(\eta_1, \eta_2)$  are given by

$$\begin{pmatrix} F(\eta_1, \eta_2) \\ G(\eta_1, \eta_2) \end{pmatrix} = \begin{pmatrix} c^2 \eta_2^2 \left( \eta_1 + y_{B*} - b \left( \eta_1 + y_{B*} - \frac{(\eta_1 + y_{B*})^3}{3} - a \right) \right) \\ + 2c\eta_2 y_{A*} \left( \eta_1 - b \left( \eta_1 - \frac{\eta_1^3}{3} - \eta_1^2 y_{B*} - \eta_1 y_{B*}^2 \right) \right) \\ \begin{pmatrix} \frac{1}{c} \eta_1^2 \left( c\eta_2 + y_{A*} - b \left( c\eta_2 + y_{A*} - \frac{(c\eta_2 + y_{A*})^3}{3} - a + I \right) \right) \\ + \frac{1}{c} 2\eta_1 y_{B*} \left( c\eta_2 - b \left( c\eta_2 - \frac{c^3 \eta_2^3}{3} - c^2 \eta_2^2 y_{A*} - c\eta_2 y_{A*}^2 \right) \right) \end{pmatrix} \end{pmatrix} \right)$$

$$\begin{split} F_{\eta_{1}} \bigg|_{\mathbf{0}} &= (2c\eta_{2}y_{A*} + c^{2}\eta_{2}^{2})\left(1 - b + b\eta_{1}^{2} + 2b\eta_{1}y_{B*} + by_{B*}^{2}\right)\bigg|_{\mathbf{0}} = 0, \\ F_{\eta_{1}\eta_{1}\eta_{1}} \bigg|_{\mathbf{0}} &= (2c\eta_{2}y_{A*} + c^{2}\eta_{2}^{2})(2b\eta_{1} + 2by_{B*})\bigg|_{\mathbf{0}} = 0, \\ F_{\eta_{1}\eta_{1}\eta_{1}\eta_{1}} \bigg|_{\mathbf{0}} &= F_{\eta_{1}\eta_{1}\eta_{1}\eta_{1}\eta_{1}}\bigg|_{\mathbf{0}} = 0, \\ F_{\eta_{1}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} &= (2c\eta_{2}y_{A*} + c^{2}\eta_{2}^{2})(1 - b + b\eta_{1}^{2} + 2b\eta_{1}y_{B*} + by_{B*}^{2})\bigg|_{\mathbf{0}} = 2cy_{A*}, \\ F_{\eta_{1}\eta_{2}} \bigg|_{\mathbf{0}} &= (2cy_{A*} + 2c^{2}\eta_{2})\left(1 - b + b\eta_{1}^{2} + 2b\eta_{1}y_{B*} + by_{B*}^{2})\bigg|_{\mathbf{0}} = 2cy_{A*}, \\ F_{\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} &= 2c^{2}\left(1 - b + b\eta_{1}^{2} + 2b\eta_{1}y_{B*} + by_{B*}^{2}\right)\bigg|_{\mathbf{0}} = 2c^{2}, \\ F_{\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} &= F_{\eta_{1}\eta_{2}\eta_{2}\eta_{2}\eta_{2}}\bigg|_{\mathbf{0}} = 0, \\ F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} &= (2c^{2})\left(2b\eta_{1} + 2by_{B*}\right)\bigg|_{\mathbf{0}} = 4cby_{A*}y_{B*}, \\ F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} &= (2c^{2})\left(2b\eta_{1} + 2by_{B*}\right)\bigg|_{\mathbf{0}} = 4c^{2}by_{B*}, \\ F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} &= (2c^{2})\left(2b\right)\bigg|_{\mathbf{0}} = 4c^{2}b, \\ F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} &= (2c^{2})\left(2b\right)\bigg|_{\mathbf{0}} = 4c^{2}b, \\ F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} &= 0, \\ F_{\eta_{2}}\bigg|_{\mathbf{0}} &= 2c^{2}\eta_{2}\left(\eta_{1} + y_{B*} - b\left(\eta_{1} + y_{B*} - \frac{(y_{B*} + \eta_{1})^{3}}{3} - a\right)\right)\right)\bigg|_{\mathbf{0}} = 0, \\ F_{\eta_{2}\eta_{2}}\bigg|_{\mathbf{0}} &= 2c^{2}\left(\eta_{1} + y_{B*} - b\left(\eta_{1} - \frac{\eta_{1}^{3}}{3} - \eta_{1}^{2}y_{B*} - \eta_{1}y_{B*}^{2}\right)\bigg)\bigg|_{\mathbf{0}} = 0, \\ F_{\eta_{2}\eta_{2}\eta_{2}}\bigg|_{\mathbf{0}} &= 2c^{2}\left(\eta_{1} + y_{B*} - b\left(\eta_{1} + y_{B*} - \frac{(y_{B*} + \eta_{1})^{3}}{3} - a\right)\right)\bigg)\bigg|_{\mathbf{0}} = 2c^{2}q, \\ F_{\eta_{2}\eta_{2}\eta_{2}}\bigg|_{\mathbf{0}} &= 2c^{2}\left(\eta_{1} + y_{B*} - b\left(\eta_{1} + y_{B*} - \frac{(y_{B*} + \eta_{1})^{3}}{3} - a\right)\right)\bigg)\bigg|_{\mathbf{0}} = 2c^{2}q, \\ F_{\eta_{2}\eta_{2}\eta_{2}\eta_{2}}\bigg|_{\mathbf{0}} &= C^{2}\left(\eta_{1} + y_{B*} - b\left(\eta_{1} + y_{B*} - \frac{(y_{B*} + \eta_{1})^{3}}{3} - a\right)\right)\bigg)\bigg|_{\mathbf{0}} = 2c^{2}q, \\ F_{\eta_{2}\eta_{2}\eta_{2}\eta_{2}}\bigg|_{\mathbf{0}} &= C^{2}\left(\eta_{1} + y_{B*} - b\left(\eta_{1} + y_{B*} - \frac{(y_{B*} + \eta_{1})^{3}}{3} - a\right)\bigg)\bigg)\bigg|_{\mathbf{0}} = 2c^{2}q, \\ F_{\eta_{2}\eta_{2}\eta_{2}\eta_{2}}\bigg|_{\mathbf{0}} &= C$$

$$\begin{split} G_{\eta_1}\Big|_{\mathbf{0}} &= \frac{1}{c} 2\eta_1 \left( c\eta_2 + y_{A*} - b \left( c\eta_2 + y_{A*} - \frac{(c\eta_2 + y_{A*})^3}{3} - a + I \right) \right) \\ &+ \frac{1}{c} 2y_{B*} \left( c\eta_2 - b \left( c\eta_2 - \frac{c^3\eta_2^3}{3} - c^2\eta_2^2 y_{A*} - c\eta_2 y_{A*}^2 \right) \right) \Big|_{\mathbf{0}} = 0, \\ G_{\eta_1\eta_1}\Big|_{\mathbf{0}} &= \frac{2}{c} \left( c\eta_2 + y_{A*} - b \left( c\eta_2 + y_{A*} - \frac{(c\eta_2 + y_{A*})^3}{3} - a + I \right) \right) \right) = \frac{2r}{c}, \\ G_{\eta_1\eta_1}\Big|_{\mathbf{0}} &= G_{\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = 0, \\ G_{\eta_1\eta_2}\Big|_{\mathbf{0}} &= (2\eta_1 + 2y_{B*}) \left( 1 - b \left( 1 - c^2\eta_2^2 - 2c\eta_2 y_{A*} - y_{A*}^2 \right) \right) \Big|_{\mathbf{0}} = 2y_{B*}, \\ G_{\eta_1\eta_2\eta_2}\Big|_{\mathbf{0}} &= (2\eta_1 + 2y_{B*}) \left( 2c^2b\eta_2 + 2cby_{A*} \right) \Big|_{\mathbf{0}} = 4cby_{A*}y_{B*}, \\ G_{\eta_1\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} &= (2\eta_1 + 2y_{B*}) \left( 2c^2b) \Big|_{\mathbf{0}} = 4c^2by_{B*}, \\ G_{\eta_1\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} &= 0, \\ G_{\eta_1\eta_1\eta_2\eta_2}\Big|_{\mathbf{0}} &= 2 \left( 1 - b \left( 1 - c^2\eta_2^2 - 2c\eta_2 y_{A*} - y_{A*}^2 \right) \right) = 2, \\ G_{\eta_1\eta_1\eta_2\eta_2}\Big|_{\mathbf{0}} &= 2 \left( 2c^2b\eta_2 + 2cby_{A*} \right) \Big|_{\mathbf{0}} = 4cby_{A*}, \\ G_{\eta_1\eta_1\eta_2\eta_2}\Big|_{\mathbf{0}} &= 2 \left( 2c^2b\eta_2 + 2cby_{A*} \right) \Big|_{\mathbf{0}} = 0, \\ G_{\eta_1\eta_1\eta_2\eta_2}\Big|_{\mathbf{0}} &= 4c^2b, \\ G_{\eta_1\eta_1\eta_2\eta_2}\Big|_{\mathbf{0}} &= 4c^2b, \\ G_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} &= 6\eta_{\eta_1\eta_1\eta_1\eta_2\eta_2} = G_{\eta_1\eta_1\eta_1\eta_1\eta_2}\Big|_{\mathbf{0}} = 0, \\ G_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} &= b(\eta_1^2 + 2\eta_1y_{B*}) \left( 1 - b \left( 1 - c^2\eta_2^2 - 2c\eta_2y_{A*} - y_{A*}^2 \right) \right) \Big|_{\mathbf{0}} = 0, \\ G_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} &= b(\eta_1^2 + 2\eta_1y_{B*}) \left( 2c^2\eta_2 + 2cy_{A*} \right) \Big|_{\mathbf{0}} = 0, \\ G_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} &= b(\eta_1^2 + 2\eta_1y_{B*}) \left( 2c^2\eta_2 + 2cy_{A*} \right) \Big|_{\mathbf{0}} = 0, \\ G_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} &= b(\eta_1^2 + 2\eta_1y_{B*}) \Big|_{\mathbf{0}} = 0, \\ G_{\eta_2\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} &= C^2b(\eta_1^2 + 2\eta_1y_{B*}) \Big|_{\mathbf{0}} = 0. \end{aligned}$$

#### A.2 Computation of the first Lyapunov coefficient

In this section, we calculate the first Lyapunov coefficient, also known as the cubic coefficient. By Definition 9.2.3, the first Lyapunov coefficient is

$$\alpha = \frac{1}{16} (F_{x_1 x_1 x_1} + F_{x_1 x_2 x_2} + G_{x_1 x_1 x_2} + G_{x_2 x_2 x_2}) \Big|_{(0,0)} + \frac{1}{16\omega} (F_{x_1 x_2} (F_{x_1 x_1} + F_{x_2 x_2}) - G_{x_1 x_2} (G_{x_1 x_1} + G_{x_2 x_2}) - F_{x_1 x_1} G_{x_1 x_1} + F_{x_2 x_2} G_{x_2 x_2}) \Big|_{(0,0)}.$$
(A.1)

The sign of the cubic coefficient determines whether the Hopf bifurcation is subcritical or supercritical. We use the derivatives of  $F(\eta_1, \eta_2)$  and  $G(\eta_1, \eta_2)$  computed in Section A.1. Recall that  $r = y_{A*} - b\left(y_{A*} - \frac{y_{A*}^3}{3} - a + I\right)$ ,  $q = y_{B*} - b\left(y_{B*} - \frac{y_{B*}^3}{3} - a\right)$ , and  $\omega^2 = -4y_{A*}y_{B*}qr$ . For the desingularized system at  $\gamma = 0$  at the folded singularities  $y_{A*} = \pm 1$  and  $y_{B*} = \pm 1$ , the cubic coefficient is

$$\begin{aligned} \alpha &= \frac{1}{8}(c^2 + 1) + \frac{1}{4\omega} \left( c^3 y_{A*}q + \frac{y_{B*}r}{c} \right), \\ &= \frac{1}{8} \left( \frac{4y_{B*}^2 r^2}{\omega^2} + 1 \right) + \frac{1}{4\omega} \left( \frac{8y_{B*}^3 r^3}{\omega^3} y_{A*}q - \frac{\omega}{2} \right), \\ &= \frac{1}{8} \left( \frac{4y_{B*}^2 r^2}{-4y_{A*}y_{B*}qr} + 1 \right) + \frac{2y_{B*}^3 r^3 y_{A*}q}{16y_{A*}^2 y_{B*}^2 q^2 r^2} - \frac{1}{8}, \\ &= 0. \end{aligned}$$

# A.3 Computation of the second Lyapunov coefficient

In this section, we calculate the second Lyapunov coefficient when  $\alpha = 0$ . By Definition 4.2.3, the second Lyapunov coefficient for the system  $\mathbf{x} = A\mathbf{x} + F(\mathbf{x}, \gamma)$  is

$$\beta = \frac{1}{12\omega} \operatorname{Re}(g_{32}) + \frac{1}{12\omega^2} \operatorname{Im} \left[ g_{20}\bar{g}_{31} - g_{11} \left( 4g_{31} + 3\bar{g}_{22} \right) - \frac{1}{3}g_{02} \left( g_{40} + \bar{g}_{13} \right) - g_{30}g_{12} \right] \\ + \frac{1}{12\omega^3} \left\{ \operatorname{Re} \left[ g_{20} \left( \bar{g}_{11} (3g_{12} - \bar{g}_{30}) + g_{02} \left( \bar{g}_{12} - \frac{1}{3}g_{30} \right) + \frac{1}{3}\bar{g}_{02}g_{03} \right) \\ + g_{11} \left( \bar{g}_{02} \left( \frac{5}{3}\bar{g}_{30} + 3g_{12} \right) + \frac{1}{3}g_{02}\bar{g}_{03} - 4g_{11}g_{30} \right) \right] + 3\operatorname{Im} \left( g_{20}g_{11} \right) \operatorname{Im}(g_{21}) \right\} \\ + \frac{1}{12\omega^4} \left\{ \operatorname{Im} \left[ g_{11}\bar{g}_{02} \left( \bar{g}_{20}^2 - 3\bar{g}_{20}g_{11} - 4g_{11}^2 \right) \right] + \operatorname{Im} \left( g_{20}g_{11} \right) \left[ 3\operatorname{Re}(g_{20}g_{11}) - 2|g_{02}|^2 \right] \right\}.$$

Here, we perform the calculations to obtain the second Lyapunov coefficient for the desingularized two-FN system when  $\gamma = 0$ , which is written as

$$\begin{aligned} \frac{d\eta}{dt} &= T^{-1}D_{\mathbf{y}}\rho(0,0) \Big|_{\gamma=0} T\eta + T^{-1}\mathbf{h}(T\eta). \end{aligned}$$
Here,  $A &= T^{-1}D_{\mathbf{y}}\rho(0,0) \Big|_{\gamma=0} T = \begin{pmatrix} 0 & -\omega \\ \omega & 0 \end{pmatrix}, \ \omega &= 2\sqrt{-y_{A*}y_{B*}q_{T}}, \text{ and} \end{aligned}$ 

$$T^{-1}\mathbf{h}(T\eta) &= \begin{pmatrix} F(\eta_{1},\eta_{2}) \\ G(\eta_{1},\eta_{2}) \end{pmatrix} = \begin{pmatrix} \begin{pmatrix} c^{2}\eta_{2}^{2} \left(\eta_{1} + y_{B*} - b\left(\eta_{1} + y_{B*} - \frac{(\eta_{1} + y_{B*})^{3}}{3} - a\right)\right) \\ + 2c\eta_{2}y_{A*} \left(\eta_{1} - b\left(\eta_{1} - \frac{\eta_{1}^{3}}{3} - \eta_{1}^{2}y_{B*} - \eta_{1}y_{B*}^{2}\right)\right) \\ \begin{pmatrix} \frac{1}{c}\eta_{1}^{2} \left(c\eta_{2} + y_{A*} - b\left(c\eta_{2} + y_{A*} - \frac{(c\eta_{2} + y_{A*})^{3}}{3} - a + I\right)\right) \\ + \frac{1}{c}2\eta_{1}y_{B*} \left(c\eta_{2} - b\left(c\eta_{2} - \frac{c^{3}\eta_{2}^{3}}{3} - c^{2}\eta_{2}^{2}y_{A*} - c\eta_{2}y_{A*}^{2}\right)\right) \end{pmatrix} \end{aligned}$$

We choose vectors s and p such that s is an eigenvector of A that corresponds to the eigenvalue  $\lambda$  and p is an eigenvector of  $A^{\top}$  that corresponds to the eigenvalue  $\bar{\lambda}$ as follows

$$s = p = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 \\ -i \end{pmatrix}.$$

For ease of computation, we compute each order of terms separately.

#### Second order terms

We begin by calculating the second order terms  $g_{20}$ ,  $g_{11}$ , and  $g_{02}$  and disregarding the terms of F and G derivatives that were found to be zero in section A.1. First, we compute

$$g_{20} = \langle p, B^2(s,s) \rangle = \bar{p}^\top B^2(s,s) = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} B_1^2(s,s) \\ B_2^2(s,s) \end{pmatrix}.$$

The components of the multilinear function B are

$$B_{1}^{2}(s,s) = \sum_{j,k=1}^{2} \frac{\partial^{2}F(\eta,0)}{\partial\eta_{j}\partial\eta_{k}} \Big|_{\mathbf{0}} s_{j}s_{k} = \sum_{j=1}^{2} s_{j} \left( \frac{\partial F_{\eta_{1}}}{\partial\eta_{j}} \Big|_{\mathbf{0}} s_{1} + \frac{\partial F_{\eta_{2}}}{\partial\eta_{j}} \Big|_{\mathbf{0}} s_{2} \right),$$
  

$$= s_{1}^{2}F_{\eta_{1}\eta_{1}} \Big|_{\mathbf{0}} + 2s_{1}s_{2}F_{\eta_{1}\eta_{2}} \Big|_{\mathbf{0}} + s_{2}^{2}F_{\eta_{2}\eta_{2}} \Big|_{\mathbf{0}},$$
  

$$B_{2}^{2}(s,s) = \sum_{j,k=1}^{2} \frac{\partial^{2}G(\eta,0)}{\partial\eta_{j}\partial\eta_{k}} \Big|_{\mathbf{0}} s_{j}s_{k} = \sum_{j=1}^{2} s_{j} \left( \frac{\partial G_{\eta_{1}}}{\partial\eta_{j}} \Big|_{\mathbf{0}} s_{1} + \frac{\partial G_{\eta_{2}}}{\partial\eta_{j}} \Big|_{\mathbf{0}} s_{2} \right),$$
  

$$= s_{1}^{2}G_{\eta_{1}\eta_{1}} \Big|_{\mathbf{0}} + 2s_{1}s_{2}G_{\eta_{1}\eta_{2}} \Big|_{\mathbf{0}} + s_{2}^{2}G_{\eta_{2}\eta_{2}} \Big|_{\mathbf{0}}.$$
  
(A.2)

In Section A.1, we found that  $F_{\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$ , so we can disregard those terms. Plugging (A.2) into the expression for  $g_{20}$  gives

$$g_{20} = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} -iF_{\eta_1\eta_2} \Big|_{\mathbf{0}} - \frac{1}{2}F_{\eta_2\eta_2} \Big|_{\mathbf{0}} \\ \frac{1}{2}G_{\eta_1\eta_1} \Big|_{\mathbf{0}} - iG_{\eta_1\eta_2} \Big|_{\mathbf{0}} \end{pmatrix},$$
$$= \frac{1}{\sqrt{2}} \begin{pmatrix} -iF_{\eta_1\eta_2} \Big|_{\mathbf{0}} - \frac{1}{2}F_{\eta_2\eta_2} \Big|_{\mathbf{0}} + \frac{i}{2}G_{\eta_1\eta_1} \Big|_{\mathbf{0}} + G_{\eta_1\eta_2} \Big|_{\mathbf{0}} \end{pmatrix}.$$

For the  $g_{02}$  term,  $\bar{s}_1\bar{s}_2 = -s_1s_2$ , so we can use the calculations above to obtain

$$g_{02} = \langle p, B^{2}(\bar{s}, \bar{s}) \rangle = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} iF_{\eta_{1}\eta_{2}} \Big|_{\mathbf{0}} - \frac{1}{2}F_{\eta_{2}\eta_{2}} \Big|_{\mathbf{0}} \\ \frac{1}{2}G_{\eta_{1}\eta_{1}} \Big|_{\mathbf{0}} + iG_{\eta_{1}\eta_{2}} \Big|_{\mathbf{0}} \end{pmatrix},$$
$$= \frac{1}{\sqrt{2}} \left( iF_{\eta_{1}\eta_{2}} \Big|_{\mathbf{0}} - \frac{1}{2}F_{\eta_{2}\eta_{2}} \Big|_{\mathbf{0}} + \frac{i}{2}G_{\eta_{1}\eta_{1}} \Big|_{\mathbf{0}} - G_{\eta_{1}\eta_{2}} \Big|_{\mathbf{0}} \right).$$

Finally,  $s_1\bar{s}_2 = -\bar{s}_1s_2$ , so the cross terms cancel for  $g_{11}$ .

$$g_{11} = \langle p, B^2(s, \bar{s}) \rangle = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} -\frac{1}{2} F_{\eta_2 \eta_2} \Big|_{\mathbf{0}} \\ \frac{1}{2} G_{\eta_1 \eta_1} \Big|_{\mathbf{0}} \end{pmatrix},$$
$$= \frac{1}{\sqrt{2}} \begin{pmatrix} -\frac{1}{2} F_{\eta_2 \eta_2} \Big|_{\mathbf{0}} + \frac{i}{2} G_{\eta_1 \eta_1} \Big|_{\mathbf{0}} \end{pmatrix}.$$

#### Third order terms

The  $g_{ij}$  in the equation for  $\beta$  where i + j = 3 are  $g_{30}$ ,  $g_{03}$ ,  $g_{12}$ , and  $g_{21}$ . We compute the expressions for these three quantities in terms of the derivatives of F and G in this section. First,

$$g_{30} = \langle p, B^3(s, s, s) \rangle = \bar{p}^\top B^3(s, s, s) = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} B_1^3(s, s, s) \\ B_2^3(s, s, s) \end{pmatrix}$$

The  $B_i^3$  are computed in the following

$$B_{1}^{3}(s,s,s) = \sum_{j,k,l=1}^{2} \frac{\partial^{3} F(\eta,0)}{\partial \eta_{j} \partial \eta_{k} \partial \eta_{l}} \bigg|_{\mathbf{0}} s_{j} s_{k} s_{l},$$
  
$$B_{1}^{3}(s,s,s) = F_{\eta_{1}\eta_{1}\eta_{1}} \bigg|_{\mathbf{0}} s_{1}^{3} + 3F_{\eta_{1}\eta_{1}\eta_{2}} \bigg|_{\mathbf{0}} s_{1}^{2} s_{2} + 3F_{\eta_{1}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} s_{1} s_{2}^{2} + F_{\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} s_{2}^{3},$$

Note that  $B_2^3(x, y, z)$  is  $B_1^3(x, y, z)$  with the difference that  $G(\eta_1, \eta_2, \gamma)$  replaces  $F(\eta_1, \eta_2, \gamma)$ . Recall from Section A.1 that  $F_{\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = F_{\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$ . Furthermore,  $s_1^2s_2 = \frac{-i}{2\sqrt{2}}$  and  $s_1s_2^2 = \frac{-1}{2\sqrt{2}}$ . This results in

$$g_{30} = \frac{3}{4} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} -iF_{\eta_1\eta_1\eta_2} \middle|_{\mathbf{0}} - F_{\eta_1\eta_2\eta_2} \middle|_{\mathbf{0}} \\ -iG_{\eta_1\eta_1\eta_2} \middle|_{\mathbf{0}} - G_{\eta_1\eta_2\eta_2} \middle|_{\mathbf{0}} \end{pmatrix},$$
$$= \frac{3}{4} \begin{pmatrix} -iF_{\eta_1\eta_1\eta_2} \middle|_{\mathbf{0}} - F_{\eta_1\eta_2\eta_2} \middle|_{\mathbf{0}} + G_{\eta_1\eta_1\eta_2} \middle|_{\mathbf{0}} - iG_{\eta_1\eta_2\eta_2} \middle|_{\mathbf{0}} \end{pmatrix}$$

Similarly, we compute  $g_{03} = \langle p, B^3(\bar{s}, \bar{s}, \bar{s}) \rangle$ . Again, we can use the formula for  $B_i^3$  as computed above

$$B_1^3(s,s,s) = 3F_{\eta_1\eta_1\eta_2} \bigg|_{\mathbf{0}} \bar{s}_1^2 \bar{s}_2 + 3F_{\eta_1\eta_2\eta_2} \bigg|_{\mathbf{0}} \bar{s}_1 \bar{s}_2^2,$$

where the substitution  $F_{\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = F_{\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$  has already been made. Furthermore,  $\bar{s}_1^2 \bar{s}_2 = \frac{i}{2\sqrt{2}}$  and  $\bar{s}_1 \bar{s}_2^2 = \frac{-1}{2\sqrt{2}}$ . This results in

$$g_{03} = \frac{3}{4} \left( iF_{\eta_1\eta_1\eta_2} \Big|_{\mathbf{0}} - F_{\eta_1\eta_2\eta_2} \Big|_{\mathbf{0}} - G_{\eta_1\eta_1\eta_2} \Big|_{\mathbf{0}} - iG_{\eta_1\eta_2\eta_2} \Big|_{\mathbf{0}} \right).$$

The next third order term we compute is  $g_{12} = \langle p, B^3(s, \bar{s}, \bar{s}) \rangle$ . The  $B^3$  terms are

$$B_1^3(s,s,s) = F_{\eta_1\eta_1\eta_2} \bigg|_{\mathbf{0}} (2s_1\bar{s}_1\bar{s}_2 + s_2\bar{s}_1^2) + F_{\eta_1\eta_2\eta_2} \bigg|_{\mathbf{0}} (s_1\bar{s}_2^2 + 2s_2\bar{s}_1\bar{s}_2),$$

where the substitution  $F_{\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = F_{\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$  has already been made. Furthermore,  $2s_1\bar{s}_1\bar{s}_2 + s_2\bar{s}_1^2 = \frac{i}{2\sqrt{2}}$  and  $s_1\bar{s}_2^2 + 2s_2\bar{s}_1\bar{s}_2 = \frac{1}{2\sqrt{2}}$ . This results in

$$g_{12} = \frac{1}{4} \left( iF_{\eta_1\eta_1\eta_2} \bigg|_{\mathbf{0}} + F_{\eta_1\eta_2\eta_2} \bigg|_{\mathbf{0}} - G_{\eta_1\eta_1\eta_2} \bigg|_{\mathbf{0}} + iG_{\eta_1\eta_2\eta_2} \bigg|_{\mathbf{0}} \right).$$

The final third order term we compute is  $g_{21} = \langle p, B^3(s, s, \bar{s}) \rangle$ . The  $B^3$  terms are

$$B_1^3(s,s,s) = F_{\eta_1\eta_1\eta_2} \bigg|_{\mathbf{0}} (2\bar{s}_1 s_1 s_2 + \bar{s}_2 s_1^2) + F_{\eta_1\eta_2\eta_2} \bigg|_{\mathbf{0}} (\bar{s}_1 s_2^2 + 2\bar{s}_2 s_1 s_2),$$

where the substitution  $F_{\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = F_{\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$  has already been made. This value for  $g_{21}$  is

$$g_{21} = \frac{1}{4} \left( -iF_{\eta_1\eta_1\eta_2} \bigg|_{\mathbf{0}} + F_{\eta_1\eta_2\eta_2} \bigg|_{\mathbf{0}} + G_{\eta_1\eta_1\eta_2} \bigg|_{\mathbf{0}} + iG_{\eta_1\eta_2\eta_2} \bigg|_{\mathbf{0}} \right).$$

#### Fourth order terms

The  $g_{ij}$  in the equation for  $\beta$  where i + j = 4 are  $g_{40}$ ,  $g_{31}$ ,  $g_{22}$  and  $g_{13}$ . We begin by finding

$$g_{40} = \langle p, B^4(s, s, s, s) \rangle = \bar{p}^\top B^4(s, s, s, s) = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} B_1^4(s, s, s, s) \\ B_2^4(s, s, s, s) \end{pmatrix}.$$

 $B_1^4$  is computed in the following. Note that  $B_2^4$  is just  $B_1^4$  with G substituted for F.

$$\begin{split} B_{1}^{4}(s,s,s,s) &= \sum_{j,k,l,m=1}^{2} \frac{\partial^{4}F(\eta,0)}{\partial\eta_{j}\partial\eta_{k}\partial\eta_{l}\partial\eta_{m}} \bigg|_{\mathbf{0}} s_{j}s_{k}s_{l}s_{m}, \\ B_{1}^{4}(s,s,s,s) &= F_{\eta_{1}\eta_{1}\eta_{1}\eta_{1}} \bigg|_{\mathbf{0}} s_{1}^{4} + 4F_{\eta_{1}\eta_{1}\eta_{1}\eta_{2}} \bigg|_{\mathbf{0}} s_{1}^{3}s_{2} + 6F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} s_{1}^{2}s_{2}^{2} + 4F_{\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} s_{1}s_{2}^{3} \\ &+ F_{\eta_{2}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} s_{2}^{4}. \end{split}$$

We input the relations  $F_{\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = F_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0,$  $s_1^3 s_2 = -\frac{i}{4}, \ s_1^2 s_2^2 = -\frac{1}{4}, \ \text{and} \ s_1 s_2^3 = \frac{i}{4}.$  This results in the expression

$$g_{40} = \frac{1}{4\sqrt{2}} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} -4iF_{\eta_1\eta_1\eta_1\eta_2} \middle|_{\mathbf{0}} - 6F_{\eta_1\eta_1\eta_2\eta_2} \middle|_{\mathbf{0}} + 4iF_{\eta_1\eta_2\eta_2\eta_2} \middle|_{\mathbf{0}} \\ -4iG_{\eta_1\eta_1\eta_1\eta_2} \middle|_{\mathbf{0}} - 6G_{\eta_1\eta_1\eta_2\eta_2} \middle|_{\mathbf{0}} + 4iG_{\eta_1\eta_2\eta_2\eta_2} \middle|_{\mathbf{0}} \end{pmatrix}$$
$$= \frac{1}{4\sqrt{2}} \begin{pmatrix} -4iF_{\eta_1\eta_1\eta_1\eta_2} \middle|_{\mathbf{0}} - 6F_{\eta_1\eta_1\eta_2\eta_2} \middle|_{\mathbf{0}} - 6iG_{\eta_1\eta_1\eta_2\eta_2} \middle|_{\mathbf{0}} - 4G_{\eta_1\eta_2\eta_2\eta_2} \middle|_{\mathbf{0}} \end{pmatrix},$$

where we substitute  $F_{\eta_1\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1\eta_2}\Big|_{\mathbf{0}} = 0$  from Section A.1. Next, we compute  $g_{31} = \langle p, B^4(s, s, s, \bar{s}) \rangle$  by first finding  $B^4(s, s, s, \bar{s})$  as follows

$$B^{4}(s, s, s, \bar{s}) = F_{\eta_{1}\eta_{1}\eta_{1}\eta_{2}} \Big|_{\mathbf{0}} (s_{1}^{3}\bar{s}_{2} + 3s_{1}^{2}s_{2}\bar{s}_{1}) + F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}} \Big|_{\mathbf{0}} (3s_{1}^{2}s_{2}\bar{s}_{2} + 3s_{1}s_{2}^{2}\bar{s}_{1}) + F_{\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \Big|_{\mathbf{0}} (3s_{1}s_{2}^{2}\bar{s}_{2} + s_{2}^{3}\bar{s}_{1}),$$

where  $F_{\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = F_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$  has already been made. We find  $(s_1^3\bar{s}_2 + 3s_1^2s_2\bar{s}_1) = (3s_1s_2^2\bar{s}_2 + s_2^3\bar{s}_1) = -2i$  and  $(3s_1^2s_2\bar{s}_2 + 3s_1s_2^2\bar{s}_1) = 0$ , so the expression for  $g_{31}$  becomes

$$g_{31} = \frac{1}{4\sqrt{2}} \begin{pmatrix} 1 & i \end{pmatrix} \begin{pmatrix} -2iF_{\eta_1\eta_1\eta_1\eta_2} \\ -2iG_{\eta_1\eta_1\eta_1\eta_2} \\ 0 \\ -2iG_{\eta_1\eta_1\eta_1\eta_2} \\ 0 \\ 0 \end{pmatrix} = \frac{1}{4\sqrt{2}} \begin{pmatrix} -2iF_{\eta_1\eta_1\eta_1\eta_2} \\ 0 \\ -2iF_{\eta_1\eta_1\eta_1\eta_2} \\ 0 \\ 0 \end{pmatrix} + 2G_{\eta_1\eta_2\eta_2\eta_2} \\ 0 \\ 0 \end{pmatrix}.$$

To find  $g_{13}$ , we apply the relationships  $(\bar{s}_1^3 s_2 + 3\bar{s}_1^2 \bar{s}_2 s_1) = -(s_1^3 \bar{s}_2 + 3s_1^2 s_2 \bar{s}_1)$  and  $(3\bar{s}_1 \bar{s}_2^2 s_2 + \bar{s}_2^3 s_1) = -(3s_1 s_2^2 \bar{s}_2 + s_2^3 \bar{s}_1)$ . Thus,

$$g_{13} = -g_{31} = \frac{1}{4\sqrt{2}} \left( 2iF_{\eta_1\eta_1\eta_1\eta_2} \bigg|_{\mathbf{0}} - 2G_{\eta_1\eta_2\eta_2\eta_2} \bigg|_{\mathbf{0}} \right).$$

The final fourth order term we compute is  $g_{22}$ . After applying  $F_{\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = F_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$ , we obtain

$$B^{4}(s, s, \bar{s}, \bar{s}) = F_{\eta_{1}\eta_{1}\eta_{1}\eta_{2}} \bigg|_{\mathbf{0}} (2s_{1}^{2}\bar{s}_{1}\bar{s}_{2} + 2s_{1}s_{2}\bar{s}_{1}^{2}) + F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} (s_{1}^{2}\bar{s}_{2}^{2} + s_{2}^{2}\bar{s}_{1}^{2} + 4s_{1}s_{2}\bar{s}_{1}\bar{s}_{2}) + F_{\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} (2s_{1}s_{2}\bar{s}_{2}^{2} + 2s_{2}^{2}\bar{s}_{1}\bar{s}_{2}).$$

The coefficients are found to be  $(2s_1^2\bar{s}_1\bar{s}_2 + 2s_1s_2\bar{s}_1^2) = (2s_1s_2\bar{s}_2^2 + 2s_2^2\bar{s}_1\bar{s}_2) = 0$  and  $(s_1^2\bar{s}_2^2 + s_2^2\bar{s}_1^2 + 4s_1s_2\bar{s}_1\bar{s}_2) = 2$ . Inputting these to the expression for  $g_{22}$  gives

$$g_{22} = \frac{1}{4\sqrt{2}} \left( 2F_{\eta_1\eta_1\eta_2\eta_2} \Big|_{\mathbf{0}} + 2iG_{\eta_1\eta_1\eta_2\eta_2} \Big|_{\mathbf{0}} \right).$$

#### Fifth order terms

There is only one term  $g_{ij}$  with i + j = 5 to compute in the expression for  $\beta$ . It can be written as  $g_{32} = \langle p, B^5(s, s, s, \bar{s}, \bar{s}) \rangle$ . The multilinear function  $B^5(s, s, s, \bar{s}, \bar{s})$  is

$$\begin{split} B_{1}^{5}(s,s,s,\bar{s},\bar{s},\bar{s}) &= \sum_{j,k,l,m,n=1}^{2} \frac{\partial^{5}F(\eta,0)}{\partial\eta_{j}\partial\eta_{k}\partial\eta_{l}\partial\eta_{m}\partial\eta_{n}} \bigg|_{\mathbf{0}} s_{j}s_{k}s_{l}\bar{s}_{m}\bar{s}_{n}, \\ B_{1}^{5}(s,s,s,\bar{s},\bar{s},\bar{s}) &= F_{\eta_{1}\eta_{1}\eta_{1}\eta_{1}\eta_{2}} \bigg|_{\mathbf{0}} (2s_{1}^{3}\bar{s}_{1}\bar{s}_{2} + 3s_{1}^{2}s_{2}\bar{s}_{1}^{2}) \\ &+ F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} (s_{1}^{3}\bar{s}_{2}^{2} + 6s_{1}^{2}s_{2}\bar{s}_{1}\bar{s}_{2} + 3s_{1}s_{2}^{2}\bar{s}_{1}^{2}) \\ &+ F_{\eta_{1}\eta_{1}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} (3s_{1}^{2}s_{2}\bar{s}_{2}^{2} + 6s_{1}s_{2}^{2}\bar{s}_{1}\bar{s}_{2} + s_{2}^{3}\bar{s}_{1}^{2}) \\ &+ F_{\eta_{1}\eta_{2}\eta_{2}\eta_{2}\eta_{2}} \bigg|_{\mathbf{0}} (3s_{1}s_{2}^{2}\bar{s}_{2}^{2} + 2s_{2}^{3}\bar{s}_{1}\bar{s}_{2}), \end{split}$$

where we set  $F_{\eta_1\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = F_{\eta_2\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1\eta_1\eta_1}\Big|_{\mathbf{0}} = G_{\eta_2\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$  as found in Section A.1. Solving for the coefficients, we obtain

$$g_{32} = \frac{1}{8} \left( \begin{array}{c} 1 & i \end{array} \right) \left( \begin{array}{c} -iF_{\eta_1\eta_1\eta_1\eta_1\eta_2} \Big|_{\mathbf{0}} + 2F_{\eta_1\eta_1\eta_1\eta_2\eta_2} \Big|_{\mathbf{0}} - 2iF_{\eta_1\eta_1\eta_2\eta_2\eta_2} \Big|_{\mathbf{0}} + F_{\eta_1\eta_2\eta_2\eta_2\eta_2} \Big|_{\mathbf{0}} \right)$$
$$= \frac{1}{8} \left( 2F_{\eta_1\eta_1\eta_1\eta_2\eta_2} \Big|_{\mathbf{0}} + 2G_{\eta_1\eta_1\eta_1\eta_2\eta_2\eta_2} \Big|_{\mathbf{0}} \right),$$

where the relations  $F_{\eta_1\eta_1\eta_1\eta_1\eta_2}\Big|_{\mathbf{0}} = F_{\eta_1\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1\eta_1\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_2\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$ and  $F_{\eta_1\eta_1\eta_2\eta_2\eta_2}\Big|_{\mathbf{0}} = G_{\eta_1\eta_1\eta_1\eta_2\eta_2}\Big|_{\mathbf{0}} = 0$  have been substituted following the results from Section A.1.

#### Computing the $g_{ij}$

In this section, we find expressions for the  $g_{ij}$  calculated above in terms of the desingularized two-FN system parameters by incorporating the values of the derivatives from Section A.1. The expressions for of the  $g_{ij}$  where i + j = 2 are

$$g_{20} = \frac{1}{\sqrt{2}} \left( -i2cy_{A*} - c^2q + i\frac{r}{c} + 2y_{B*} \right),$$
  

$$g_{02} = \frac{1}{\sqrt{2}} \left( i2cy_{A*} - c^2q + i\frac{r}{c} - 2y_{B*} \right),$$
  

$$g_{11} = \frac{1}{\sqrt{2}} \left( -c^2q + i\frac{r}{c} \right).$$

The expressions for the  $g_{ij}$  where i + j = 3 are

$$g_{30} = \frac{3}{2} \left( -4icby_{A*}y_{B*} - c^2 + 1 \right),$$
  

$$g_{03} = \frac{3}{2} \left( -c^2 - 1 \right),$$
  

$$g_{21} = \frac{1}{2} \left( c^2 + 1 \right)$$
  

$$g_{12} = \frac{1}{2} \left( 4icby_{A*}y_{B*} + c^2 - 1 \right).$$

The expressions for the  $g_{ij}$  where i + j = 4 are

$$g_{40} = \frac{1}{\sqrt{2}} \left( -10icby_{A*} - 10c^2 by_{B*} \right),$$
  

$$g_{31} = \frac{1}{\sqrt{2}} \left( -2icby_{A*} + 2c^2 by_{B*} \right),$$
  

$$g_{13} = \frac{1}{\sqrt{2}} \left( 2icby_{A*} - 2c^2 by_{B*} \right),$$
  

$$g_{22} = \frac{1}{\sqrt{2}} \left( 2c^2 by_{B*} + 2icby_{A*} \right).$$

Lastly, for i+j=5, the expression for the  $g_{ij}$  of interest in calculating  $\beta$  is  $g_{32}=2c^2b$ .

#### Computing $\beta$

In this section, we substitute the expressions for the  $g_{ij}$  into the expression for  $\beta$  from Equation (4.6). The sign of  $\beta$  determines the stability of the limit cycles that arise from the degenerate Hopf bifurcation. We also incorporate the relations  $y_{A*}^2 = 1$ ,  $y_{B*}^2 = 1$ ,  $\omega = 2\sqrt{-y_{A*}y_{B*}qr}$ ,  $\omega^2 = -4y_{A*}y_{B*}qr$ , and  $c = \frac{2y_{B*}r}{\omega}$  and simplify using symbolic Matlab operations to obtain the following expression:

$$\beta = (q^2r^2 + 4q^2 - 16r^2 + 4q^2ry_{A*} - 6q^3r^2y_{B*} + 2qry_{A*}y_{B*} + 3q^2r^3y_{A*} - 7qr^2y_{B*} - 2q^2ry_{A*} - q^3ry_{A*}y_{B*} + 32bqr^2y_{B*} + 11qr^3y_{A*}y_{B*} + 7q^2r^2 - 7qr^2y_{B*} - 6qry_{A*}y_{B*} + 8bq^2r^2 + 32bqr^2y_{B*})(192\sqrt{-y_{A*}y_{B*}qr}q^3ry_{A*}y_{B*})^{-1}.$$

We can evaluate this expression for each of the four folded singularities of interest at  $\gamma = 0$  to determine what type of degenerate Hopf bifurcation occurs. Given our parameter choices to satisfy Assumption 9.2.1,  $I_{0A} > 0$  and  $I_{1A} > 0$ . We also use b = 0.8 here; b can however be kept general in the expression above and be used as an additional bifurcation parameter. The results for each point are summarized here. We denote the second Lyapunov coefficients  $\beta_{xx}$  where  $x \in \{-,+\}$  and signifies to which singularity the coefficient corresponds.

- $(y_{A*}, y_{B*}) = (-1, -1) \implies q = I_{0A}, r = I_{0A} I$ . The point undergoes a degenerate Hopf bifurcation when  $I > I_{0A}$ . Evaluating with b = 0.8, we find that there is a value of I, which we denote  $I_{*-}$ , such that  $\beta_{--} < 0 \forall I_{0A} < I < I_{*-}$  and  $\beta_{--} > 0 \forall I > I_{*-}$ . The degenerate Hopf bifurcation switches from supercritical to subcritical at  $I_{*-}$ , which is a Hopf bifurcation of higher degeneracy.
- $(y_{A*}, y_{B*}) = (+1, -1) \implies q = I_{0A}, r = I_{1A} I$ . The point undergoes a degenerate Hopf bifurcation when  $I < I_{1A}$ . Evaluating with b = 0.8, we find that there is a value of I, which we denote  $I_{*+}$ , such that  $\beta_{+-} > 0 \forall 0 < I < I_{**}$  and  $\beta_{+-} < 0 \forall I_{*+} > I > I_{1A}$ . The degenerate Hopf bifurcation switches from subcritical to supercritical at  $I_{*+}$ , which is a Hopf bifurcation of higher degeneracy.

- $(y_{A*}, y_{B*}) = (-1, +1) \implies q = I_{1A}, r = I_{0A} I$ . The point undergoes a degenerate Hopf bifurcation when  $I < I_{0A}$ . Evaluating with b = 0.8, we find that  $\beta_{-+} < 0 \forall I < I_{0A}$ . The degenerate Hopf bifurcation at (-1, +1), when it exists, is supercritical. The small limit cycles emerging from the Hopf bifurcation are stable and exist when  $\gamma < 0$ .
- $(y_{A*}, y_{B*}) = (+1, +1) \implies q = I_{1A}, r = I_{1A} I$ . The point undergoes a degenerate Hopf bifurcation when  $I > I_{1A}$ . Evaluating with b = 0.8, we find that  $\beta_{++} < 0 \forall I > I_{1A}$ . The degenerate Hopf bifurcation at (+1, +1), when it exists, is supercritical. The small limit cycles emerging from the Hopf bifurcation are stable and exist when  $\gamma > 0$ .

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