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Networks of Izhikevich Neurons
Synchronization and Network Inference

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> “¿Qué duda cabe que el mundo que conocemos es el resultado del reflejo de la parte de cosmos del horizonte sensible en nuestro cerebro? Este reflejo unido, contrastado, con las imágenes reflejadas en los cerebros de los demás hombres que han vivido y que viven, es nuestro conocimiento del mundo, es nuestro mundo. ”
>
> *Pio Baroja*

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Abstract

In this thesis, we delve into two interconnected realms: the stability of synchronized states in networks of Izhikevich neurons and the challenge of network inference within complex systems. The motivation stems from the ubiquity of complex networks in nature, where synchronization often occurs, presenting an intricacy when the underlying network structure is unknown.

The analytical foundation of our investigation lies in the application of the Master Stability Function (MSF) formalism to study the stability of synchronized states in networks of Izhikevich neurons. Despite the Izhikevich model's widespread use, this study represents the first application of the MSF to the Izhikevich model, which was made possible by using the Saltation Matrices approach.

Through this analytical framework, we explore total synchronized states and cluster synchronized states in networks with electrical and chemical couplings. Notably, the study reveals the nuanced behavior of synchronization, with the presence of a riddled basin of attraction near synchronization thresholds. The MSF, while a valuable tool, is shown to be susceptible to discrepancies, emphasizing the need for a cautious interpretation.

Transitioning to the second part of the thesis, we address the problem of network inference using the Unscented Kalman filter (UKF). The UKF is first tested on an isolated Izhikevich neuron, demonstrating remarkable accuracy in inferring parameters even under the influence of varying input currents. Extending the application to networks, the UKF successfully infers both electrical and electrical-chemical coupling structures.

In a novel approach, we employ the UKF for network inference based on event timing data. Associating a phase with timing events, we assimilate this information into the Kuramoto model, revealing in some cases, superior performance compared to mutual information and cross-correlation on synthetic data. However, computational costs make the approach impractical for large networks.

Keywords: Synchronization; Izhikevich Neuron; Master Stability Function; Kalman Filter; Complex Networks; Network Inference.
Knowledge Area: Physics; Non-linear Dynamics; Complex Networks; Time Series Analysis.

Resumo

Nesta tese, exploramos dois domínios interconectados: a estabilidade de estados sincronizados em redes de neurônios Izhikevich e o desafio da inferência de redes em sistemas complexos. A motivação advém da ubiquidade de redes complexas na natureza, onde a sincronização frequentemente ocorre, apresentando uma complexidade quando a estrutura subjacente da rede é desconhecida.

A base analítica de nossa investigação reside na aplicação do formalismo da *Função de Estabilidade Mestra* (MSF) para estudar a estabilidade de estados sincronizados em redes de neurônios Izhikevich. Apesar do uso generalizado do modelo Izhikevich, este estudo representa a primeira aplicação da MSF ao modelo Izhikevich, tornada possível pelo uso da abordagem de matrizes de saltos.

Através deste arcabouço analítico, exploramos estados totalmente sincronizados e estados sincronizados em aglomerados em redes com acoplamentos elétricos e químicos. Notavelmente, o estudo revela o comportamento sutil da sincronização, com a presença de uma bacia de atração *riddled* próxima aos limiares de sincronização. A MSF, embora uma ferramenta valiosa, mostra-se suscetível a discrepâncias, enfatizando a necessidade de uma interpretação cuidadosa.

Transitando para a segunda parte da tese, abordamos o problema da inferência de redes usando o filtro de Kalman *Unscented* (UKF). O UKF é primeiro testado em um neurônio Izhikevich isolado, demonstrando uma precisão notável na inferência de parâmetros mesmo sob a influência de correntes de entrada variáveis. Estendendo a aplicação para redes, o UKF infere com sucesso as estruturas de acoplamento elétrico e elétrico-químico.

Em uma abordagem inovadora, empregamos o UKF para inferência de redes com base em dados de temporização de eventos. Associando uma fase a eventos de temporização, assimilamos essa informação no modelo de Kuramoto, revelando em alguns casos, desempenho superior em comparação com informações mútuas e correlação cruzada em dados sintéticos. No entanto, os custos computacionais tornam a abordagem impraticável para grandes redes.

Palavras Chaves: Sincronização; Neurônios de Izhikevich; Função de Estabilidade Mestra; Filtro de Kalman; Redes Complexas; Inferência de redes.
Áreas do Conhecimento: Física; Dinâmica Não-Linear; Redes Complexas; Análise de Séries Temporais.

Contents

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Part I

Introduction

1 Introduction

1.1 Izhikevich Model

Neurons are the building blocks of the brain. These structures can display a rich variety of dynamics depending on their type and the inputs that it receives from other neurons [1]. Although many features of neurons remain unclear, models are capable of reproducing their observed dynamics. The seminal work of Hodgkin-Huxley (HH) introduced a neuron model based on the giant axon of the squid [2]. As it is biophysically accurate, this model has become a standard for ordinary differential equation (ODE)-based neuron models. Naturally, the collective dynamics of neurons are also of interest, and unfortunately, networks of complex models like the HH can be difficult to deal with both, analytically and computationally. With this in mind, E. M. Izhikevich proposed a neuron model that combines biological features of complex models, like the HH, with computational efficiency [3].

The equations of the model are the following:

$$\begin{bmatrix} x(t) \\ y(t) \end{bmatrix} = \begin{bmatrix} 0.04x^2 + 5x + 140 - y + I(t) \\ a(bx - y) \end{bmatrix} \tag{1.1}$$

with the after-spike reset given by

$$\text{if} \quad x \geq 30, \quad \text{then} \begin{cases} x \to c \\ y \to y + d \end{cases} \tag{1.2}$$

Where the variables x and y represent the membrane potential and a membrane recovery variable respectively. a is associated with the time scale of y while b describes the sensibility of x to subthreshold oscillations of y. The parameters c and d are related to the after-spike dynamics of the variables x and y. The parameter I takes into account synaptic currents or injected dc-currents [3]. The different types of neuronal activity that the Izhikevich model (IM) can emulate are shown in Fig. 1.1.

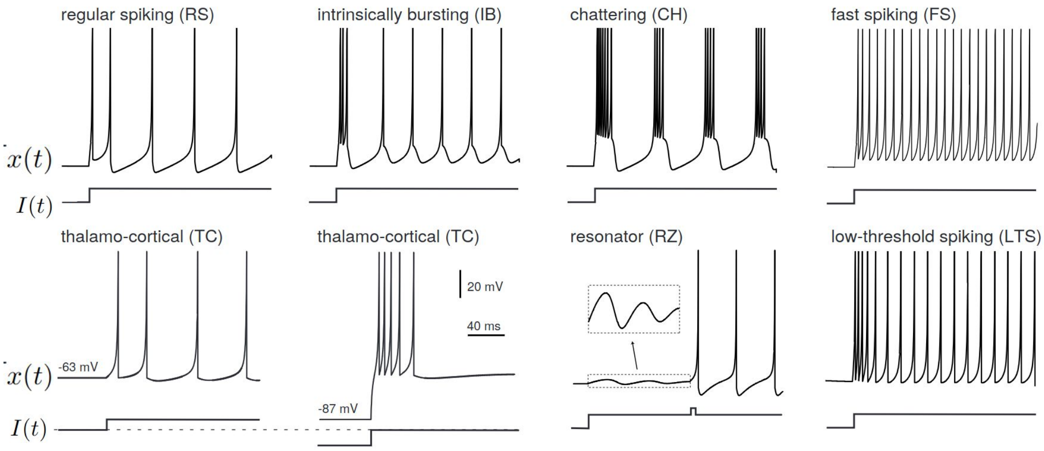

Figure 1.1: Some of the neuronal activity types that the IM (1.1) is capable of displaying for different values of (a, b, c, d) in response to a step of current $I(t)$. Adapted from [3].

Due to these characteristics, the IM has been implemented in the study of networks of spiking neurons, including large-scale models [4, 5]. Such models can be used to deepen our understanding of how the interplay between synaptic and neuronal processes produces collective behaviors. Of great interest is the emergence of rhythms and synchronization of neural activity, as it suggests that the high-dimensional dynamics of neuronal networks can collapse into low-dimensional oscillatory modes [6].

1.2 Synchronization

Synchronization occurs when a set of oscillators, interacting with each other (coupled) in some way, adjust their rhythms due to this interaction. As an example, we can mention the story of the Dutch researcher Christiaan Huygens, who observed and described the phenomenon of synchronization in the 17th century. What fascinated Huygens was the fact that the pendulum swings of two clocks fixed on the same wooden beam, reached a state of complete agreement, so much so that their sounds were heard simultaneously. This state was disrupted by interference, but after a short period, it was restored. As he pointed out, the explanation for this phenomenon is that the movement of one clock's pendulum transmitted vibrations through the beam to which it was attached and consequently to the case of the other clock, affecting the other pendulum's motion [7].

However, synchronization goes far beyond the clocks observed by Huygens, probably being the first non-linear effect studied scientifically [8]. It occurs daily in our bodies and nature. This is because biochemical and biophysical rhythms are omnipresent features in living beings, from rapid oscillations in cell membranes to the slow cycles of ovulation in mammals and circadian cycles [9].

Since Huygens' studies on synchronization, many other researchers have tackled this problem and nowadays synchronization is an established field of research in nonlinear sciences. From the analytical part, we highlight the work of Winfree, who saw synchronization as the result of a cooperative phenomenon. Drawing an analogy between synchronization and order from statistical physics, he described the transition to synchronization as a phase transition [10, 11]. Likewise, the work of Kuramoto, who is responsible for the first mathematically tractable model for synchronization [12, 13]. Finally, Pecora and Carroll's work summarizes the efforts to study the stability of synchronized states [14]. While the latter is commonly employed in studying synchronized states, in this thesis we present the first attempt to apply it to networks of Izhikevich neurons.

This holds significance as synchronization plays a crucial role in neuroscience, with studies suggesting its importance for communication between cortical areas and information processing [15–18]. However, synchronization is also associated with various brain pathologies such as Parkinson's disease, Alzheimer's, schizophrenia, and epilepsy [19, 20]. The case of epilepsy may be related to the presence of domains of synchronized activity coexisting with domains of asynchronous brain activity, known as chimeras [21, 22]. Since the observed patterns of synchronization in nature are far from being fully understood, their study is of great relevance.

But, to bridge the gap between synchronization in models and nature, unavoidably, we have to delve into the data from experiments and measurements, as time series analysis allows us to learn many characteristics of a system. We can identify, for example, whether the system in question is periodic, stochastic, or chaotic, and also the interaction and synchronization between elements [23–25]. And, more importantly, as we will study in this thesis, the analysis can also help us to have a better understanding of the underlying structure of these systems, i.e., the networks that encode the interactions between the elements of the system under study.

1.3 Network inference

Unraveling the structure of a network from observed data is a crucial open challenge in complexity science and, mathematically, an undetermined problem [26], implying that a singular solution does not exist [27]. The inherent significance of this problem is inevitable, given that many natural systems can be perceived as complex networks. Consequently, the interactions dictated by these networks impact the data obtained from such systems [28].

Among the many applications of network inference [29], like epidemiology [30], ecology [31], and social networks [32], one of the most famous is computational biology - which elucidates interactions between genes and cellular processes [33]. In this framework networks can help when describing processes, which are thought of as links of the networks, between proteins, enzymes, and genes, the nodes of the resulting networks.

Climate networks, in turn, encode relationships within environmental subsystems with complex dynamics like ecosystems and the atmosphere [34, 35]. The study of such networks can be helpful in understanding and mitigating the effects of climate change.

In the field of neuroscience, one can explore networks that span various scales, from expansive cortical areas to intricate individual neurons [36, 37]. While significant advancements have been achieved in exploring the connection between brain topology and dynamics, researchers have yet to attain a comprehensive understanding. [38, 39]. Thus, the study of such networks is important to better understand the functioning of the brain and its disorders.

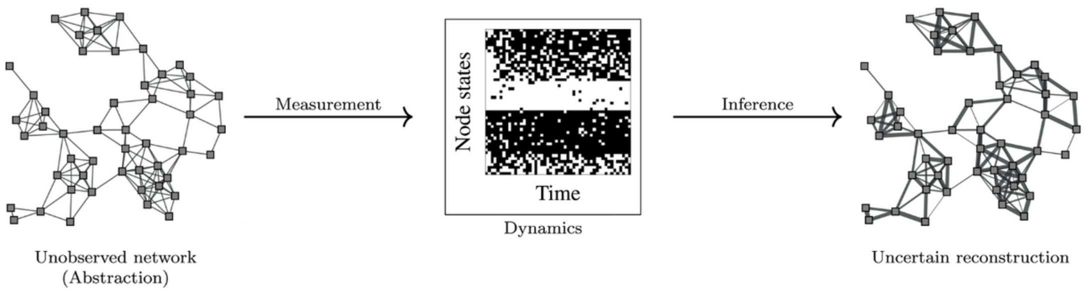

Figure 1.2: Framework for network inference using information (dynamics) obtained through measurements. Adapted from [29].

As represented in Fig. 1.2, the real network is not usually observed. This means we can say that the links are hidden variables, and we can only perform measurements on the units of the system (in the best-case scenario one can measure all the units) which will give us some feature (variable) of the system. With this in hand, we try to perform the network inference. One of the challenges of network inference is that, when using time series data, usually only one or a few variables can be observed (often not simultaneously), the observed variables can be recorded during a limited time interval, with limited temporal resolution, and with often unavoidable observational noise [27, 29].

On top of that, many times we rely solely on the data, without having a model for our system. Thus, deciding on a model that best encodes the network relationships of the variables observed becomes rather non-trivial. In such cases, researchers may end up using ad-hoc tuning of network model parameters [27, 28].

Naturally, it comes as no surprise that the list of methods proposed for network inference is as long as the number of applications for it. A popular approach is to perform some analysis between the time series of each node, like measuring the correlation between them, and the result one obtains is a matrix representing the measurement between all pairs of nodes. Then, a matrix representing the connections can be obtained by thresholding the covariance matrix. This approach can be used with other types of measures of similarity.

Moreover, we also find dedicated methods based on machine learning algorithms[40–42] bayesian inference[29, 43, 44] model-based [45–47] or model-independent approaches [48–54], among other types [55–59]. Here, we will build upon the work presented in [60], which utilized the Kalman filter [61] as a data assimilation tool to infer the connectivity of a network of Rössler oscillators [62]. In this continuation, our emphasis will shift to the study of networks of Izhikevich neurons.

1.4 Objectives

As we have seen, synchronization is present in many systems in nature that can be modeled as networks. On top of that, information about the underlying network is often missing, which can limit the analysis of such systems, and inferring the network from data is a challenging task.

With this in mind and drawing inspiration from neuroscience, the goal of this thesis is to explore these two themes using the IM as our framework. Part of the motivation stems from the fact that the examination of synchronization in networks of IM has yet to incorporate the application of the Master Stability Function. Additionally, our objective extends to inferring the network structure when the only available data is the timing of events, such as inter-spike intervals of neurons.

1.5 Outline

This thesis is divided into five parts, each comprising specific chapters. The first part serves as an introduction to the subjects and the motivation behind the thesis, paving the way for the subsequent discussions.

Transitioning from the introduction, Part II begins the core of the thesis, exploring synchronization in networks of Izhikevich neurons.

Chapter 2 is dedicated to introducing the Master Stability Function (MSF), the tool we use for analyzing both total synchronized and cluster-synchronized states in networks of Izhikevich neurons.

In the third Chapter, building upon the MSF revised in Chapter 2, we present the results of applying the MSF formalism to networks of Izhikevich neurons. We specifically focus on studying the stability of total and cluster synchronized states in small networks of electrically and chemically coupled neurons.

Transitioning from the study of synchronization in Part II, Part III is dedicated to the problem of network inference and the utilization of Kalman filters to address this challenge.

In Chapter 4, we shift our focus to network inference, introducing the concept of Bayesian filters and, specifically, the Kalman filter. Given our objective of studying nonlinear problems, we explore the Unscented Kalman filter —a version designed to handle nonlinearities— and discuss how these tools can be employed to infer the parameters of a given model.

In Chapter 5, we present the results of applying the Unscented Kalman filter (UKF) to infer the parameters of a given model, using the time series data of an Izhikevich neuron. Additionally, we extend our exploration to network inference, investigating small networks of Izhikevich neurons with both electrical and chemical couplings.

Closing Part III, Chapter 6 addresses the challenging problem of network inference when only event timing data, such as the spikes of a neuron, is available. In this chapter, we introduce a novel approach by combining the Kalman filter with the Kuramoto model to effectively fit the data. The results of this method are presented using interspike interval data from Izhikevich neurons and experimental data from an electronic circuit.

Part IV is dedicated to summarizing the conclusions and discussions arising from the results presented in the thesis. Finally, the thesis concludes with some perspectives, presenting future avenues of research.

Following the conclusions chapter, four appendices are included. Appendix A complements the theoretical framework used in Chapter 3, while Appendix B covers the mathematical details of Chapter 4. Additionally, Appendices C and D contain supplementary material related to the findings in Chapters 5 and 6. These appendices were placed at the end to ensure the fluidity of the main text and the core chapters of the thesis.

Part IV

Conclusion

7

Conclusion and final remarks

In this thesis, we investigated two topics, first the stability of synchronized states and second network inference. The connection between these two topics comes from the large amount of systems in nature that can be described as complex networks. In these systems, synchronization often occurs, and since the underlying network structure is unknown, understanding the phenomena becomes a rather trivial task. On the analytical side, we applied the master stability function formalism to study the stability of synchronized solutions in networks of Izhikevich neurons.

The first motivation to study the Izhikevich (IM) model comes from the ability of this model to display many neuronal patterns while being computationally efficient. In addition to it, the original paper by Izhikevich, where the model was introduced, accumulates more than five thousand citations. Similarly, the paper that introduced the Master Stability Function, by Pecora and Carroll, has received almost three thousand. Nevertheless, even twenty years after the publication of these works, our study marks the first application of the MSF to the IM. This stems from the challenges associated with calculating Lyapunov exponents in systems with discontinuities, like the IM. To overcome this, we applied the formalism of Saltation matrices to evaluate the Lyapunov exponents associated with the synchronized solutions.

With this framework (MSF + SM), we first analyzed the stability of total synchronized states, considering electrical and chemical couplings between neurons. To quantify the synchronization, we used the synchronization error (Err), i.e., the mean difference between the trajectories of the x variables of each neuron. By varying the coupling strength, we found that the synchronization error aligns well with MSF analysis when only one type of coupling is taken into account. While the network of electrically coupled neurons reached synchronization, the chemically one did not. However, introducing electrical coupling to a network solely connected chemically leads to synchronization. In this last case, we found that near the threshold for synchronization predicted by the MSF, a complex basin of attraction, also known as riddled. This leads to a coexistence of synchronized and non-synchronized solutions in this region, and as the coupling strength increased, this basin vanished, and all the solutions ended up synchronized.

Continuing with MSF analysis, we studied cluster synchronized states, where similar results were obtained. Nevertheless, when we considered the action of both types of coupling, on average, high-quality synchronization (Err ≈ 0) was not achieved in the range of coupling strength studied. We expected that synchronized solutions would be observed for coupling strengths $g \geq g_{th}$, instead, they only appear for higher coupling strengths. Similarly to the case of total synchronization, we found a riddled basin of attraction, characterized by a small uncertainty exponent.

These results underscore that the MSF is not a definitive diagnosis about the stability of synchronized solutions. Being dependent on a linear approximation, it is susceptible to such discrepancy. In resume, obtaining a negative MLE for the synchronized state is essential but does not assure its existence. On top of that its application to real-world systems is difficult since it is based on the assumption of identical oscillators, the absence of noise, and that usually we do not know the network of the system under study.

In the second part of this thesis, we tackled the last of the problems mentioned: network inference. To do so, we applied the Unscented Kalman filter (UKF) to the IM. As a warm-up to the network inference, we tested whether the UKF was capable of inferring the parameter of an isolated Izhikevich neuron. For the case where the x variable was measured at the same rate as the sampling time, the UKF proved to be very accurate for this task for all parameters, even in the case of a varying input current. Next, we considered networks of Izhikevich neurons with only electrical coupling and electrical + chemical couplings. In both situations, we quantified the precision of the UKF by measuring the distance between the real matrix and the estimated one. In both cases, the UKF was capable of inferring the networks.

Building upon these results, we decided to analyze UKF in inferring the connectivity structure of coupled oscillators based on event timing. To employ the UKF in this case, we associated a phase with timing events and then attempted to assimilate it into the Kuramoto model. Utilizing simulated neural spike times and experimental data from chaotic electronic circuits, we compared the efficacy of UKF with that of mutual information (MI) and cross-correlation (CC). Results on synthetic data reveal that averaging UKF predictions over multiple instances achieves perfect coupling topology reconstruction, outperforming MI and CC. However, this enhanced performance of UKF is accompanied by a considerable computational cost, rendering it impractical for large networks. In real-world experimental data, neither method fully recovered the network, with UKF and MI exhibiting comparable performance, while CC lagged significantly. Both UKF and MI benefit from averaging, with UKF excelling at weak coupling and MI at higher coupling.

Future work will be devoted to searching for a theoretical foundation to better understand the UKF performance in the case of strong coupling, for which not only the phase but also the amplitude dynamics may have to be considered. In addition, we plan to test the UKF's ability to infer directed pulsed interactions such as chemical couplings. It would also be interesting to analyze whether a more detailed, tailored phase model—instead of the generic Kuramoto model—or if a more advanced phase-extraction procedure (for example, using the Hilbert phase) could improve performance. It will also be interesting to consider whether other methods to analyze the set of inferred coupling coefficients (rather than k-means clustering) could lead to improved performance.

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