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How single node dynamics enhances synchronization in neural networks with electrical coupling

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ABSTRACT

The stability of the completely synchronous state in neural networks with electrical coupling is analytically investigated applying both the *Master Stability Function* approach (MSF), developed by Pecora and Carroll (1998), and the *Connection Graph Stability* method (CGS) proposed by Belykh et al. (2004). The local dynamics is described by Morris–Lecar model for spiking neurons and by Hindmarsh–Rose model in spike, burst, irregular spike and irregular burst regimes. The combined application of both CGS and MSF methods provides an efficient estimate of the synchronization thresholds, namely bounds for the coupling strength ranges in which the synchronous state is stable. In all the considered cases, we observe that high values of coupling strength tend to synchronize the system. Furthermore, we observe a correlation between the single node attractor and the local stability properties given by MSF. The analytical results are compared with numerical simulations on a sample network, with excellent agreement.

1. Introduction

During the last decades the importance of collective and self-organized behavior has been recognized in many different areas of science. In particular, investigation of the effect of synchronization in systems of coupled oscillators nowadays provides a unifying framework for emergent phenomena arising in various fields such as optics, chemistry, biology and ecology. Collective behaviors are also believed to play an important role in information processing in the brain, both at macroscopic and cellular levels. It is conjectured that synchronous brain activity is the most likely mechanism for many cognitive functions, such as attention and feature binding, as well as learning, development and memory formation. However, synchronization is not useful all the time because brain disorders, such as schizophrenia, epilepsy, Alzheimer's and Parkinson's diseases, have been linked to high levels of synchronization in the neuronal activities [1,2].

Recently, complex networks have become an established framework for the study of synchronization of dynamical units, based on the interplay between complexity

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in the overall topology and local dynamical properties of the coupled units [3]. The dynamics of a complex network can be modeled by N nodes, each of them described by a vector of state variables $\boldsymbol{x}_i(t) \in \mathbb{R}^m,\ i = 1, \ldots, N,$ interacting pairwise through a set of links, that encode the network topology. The evolution of the whole network can be expressed by a system of coupled $N \cdot m$ differential equations. Such systems can exhibit many types of synchronization [4]; in this paper we are interested in complete synchronization in neural networks. This is the simplest form of synchronization, and consists in a perfect convergence of trajectories of identical (maybe chaotic) systems in the course of time [4], if some kind of coupling between them is introduced. The dynamical network is said to achieve globally (locally) *asymptotic synchronization* if the synchronous state, namely the trajectory in which $\boldsymbol{x}_i(t) = \boldsymbol{x}^*(t)\ \forall i = 1, \ldots, N,$ is globally (locally) asymptotically stable.

Typically, in networks of continuous time oscillators, a central question is to find the bounds on the coupling strength so that the stability of synchronization is guaranteed [5]. To this end, we consider two mathematical methods to study the stability of synchronous state: the *Master Stability Function* (MSF) and the *Connection Graph Stability* (CGS). The first approach, developed by Pecora and Carroll [6], is based on the calculation of the maximum Lyapunov exponent of the transversal modes to the synchronous manifold and it provides conditions for the local stability of the synchronous state, through linearization techniques. The method is widely used in the study of neural synchronization and there are several extensions that allow to investigate group and cluster synchronization, delay-coupled networks [7] and also non-smooth dynamical networks [8]. The second one, developed by Belykh et al. [5,9], provides a threshold for the coupling strength above which the synchronous state is globally stable. Its calculation is based on the construction of a Lyapunov function for an auxiliary dynamical network of two nodes. The method provides only a sufficient condition for the global stability, being the threshold often an overestimation of the coupling strength required for the synchronization.

The main strength of MSF and CGS methods is that they both allow one to separate the contribution of the network structure from its dynamical properties. While the MSF approach is widely used in different fields [4], the application of CGS method, despite its stronger results, is restricted to more specific frameworks due to its restrictive hypotheses. We also point out that the CGS method cannot be applied if an increasing in the coupling strength desynchronizes the system (even considering only two coupled nodes), e.g. in x-coupled Rössler system [6]. Moreover, in literature the CGS results were rarely related to the MSF ones. In this paper we prove that the application of CGS leads to an efficient use of the MSF method.

Studies of neuronal synchronization based on different neuronal models can be separated into two categories: those using threshold models of integrate-and-fire type (I&F) and those with conductance-based realizations, such as Hodgkin–Huxley type models [10]. The first category is the most widely used in computational neuroscience, because the structure of the mathematical model enables an easy implementation; as regards the analytical treatment, a recent extension of the MSF formalism to non-smooth dynamical systems [8] can be used to study these threshold models, whereas the CGS method does not apply, due to the lack of regularity. On the other hand, large networks of conductance-based models are expensive to simulate, but they can be studied with both MSF and CGS analytical techniques. In particular, the Hodgkin–Huxley model [11] is biophysically meaningful but extremely expensive in terms of computational cost, and thus often reduced models are used, such as Morris–Lecar [12] and Hindmarsh–Rose [13], which we consider in this paper. Also communication between neurons is typically of two types: electrical connections via gap junctions and excitatory/inhibitory connections via chemical synapses [14,15]. Electrical connection is bidirectional, while the communication between two neurons through chemical synapses is unidirectional, from a presynaptic cell to the postsynaptic one. Chemical synapses are the principal way through which neurons communicate in the brain and are usually related to short and long term memory, according to their potentiation or depression under high activity periods [15,16]. Nevertheless, electrical coupling through gap-junctions has been observed to be responsible for neurons communication and for their overall activity [17]. As an example, in [17] the activity of GABAergic neurons in the Ventral Tegmental Area crucially changes when gap-junctions are cut off, suggesting them to be arranged over a network of electrically connected neurons. In this paper we consider the electrical coupling, which permits several analytical treatments hardly to perform in more complex coupling models and also reflects an observed type of communication between neurons.

Recent results focus on numerical investigation or on MSF approach and generally link the synchronization to the structural attributes of the underlying network, such as clustering coefficient, average network distance or connectivity distribution. These results are typically obtained for networks of Hindmarsh–Rose regular bursting neurons [1,2,18–20], while the synchronization properties of networks of neurons in the irregular bursting regime has not yet been investigated. Conversely, the only neuronal model studied via CGS method is the Hindmarsh–Rose, in the full range of its parameters [21]. Actually, the stability of the synchronous state in irregular burst regime turns out to be of particular interest because it reminds the firing activity of a network of neurons detected in “in vitro” cultures, where events in which neurons fire at high frequency in a short time interval (namely bursts) are followed by sporadic activity [22]. Furthermore, either the firing patterns in each burst or the time interval between two consecutive bursts are not regular [22]. A similar scenario can be found in the synchronized state of the irregular bursting regime, while, on the contrary, in the regular regime the bursts and the interspike intervals are identical.

Our aim is to study the synchronization behavior in such particular regimes using both CGS and MSF methods. Their combined application allows us to restrict the range of investigation needed in the MSF method, leading to a great saving in computational time. Moreover, in some particular cases, with these two methods it is possible to