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Dependence of inter-neuronal effective connectivity on synchrony dynamics in neuronal network motifs

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ABSTRACT

Effective connectivity, characterized as directional causal influences among neural units, is functionally significant to be reconstructed. Various dynamic regimes have been considered to underlie reshaping of the effective connections. In this work, the impact of zero-lag synchronization on the reconstruction of effective connectivity in neuronal network motifs is investigated. The synchronization analysis and effective connectivity estimation by using Granger causality (GC) method are performed. It is shown that the synchronization of the neurons at zero lag contributes to the reconstruction of reciprocal effective connections without synaptic connections. In addition, delay-induced zero-lag synchronous transition facilitates dynamic transformation of the causal interactions. With the increase of synaptic coupling strength, the causal interplay undergoes the transition to be statistically significant at a critical value. Furthermore, it can be found that multiple effective motifs are extracted from different synchronization states of the underlying structural motifs. GC measures of effective connectivity are proved to be reliable compared with the Information Flow for causal analysis. The obtained results may be helpful to future research about information processes.

1. Introduction

Revealing and understanding brain connectivity is one of the most significant problems in neuroscience [1]. The variety of inter-connective states is believed to underlie diverse cognitive functions of human brain [2]. Meanwhile, a number of neurological disorders, such as Parkinson's disease, are proved to be related to the disorders in cerebral connections [3]. Consequently, the information provided by the connective relationship is valuable for theoretical and applied neurobiological research. It is an important issue to extract connectivity, especially effective connectivity, from the neural recordings for neuronal systems. In particular, effective connectivity is defined as the directional causal influences of one neural element on another one [4] whether any two units are connected physically or not, which helps to understand the related dynamic behaviors of neuronal circuits [5].

In terms of the relations between effective connectivity and the other modes of brain connectivity, the mapping from effective connectivity to structural connectivity, formed by physical links anatomically, has been extensively explored [6]. It is suggested that the anatomical connectivity can be correctly inferred from the estimated interplay of each neuron pairs under some conditions, which is one of the potential applications of effective connectivity estimation. However, due to the dynamically changing strength of synaptic connections resulting from neuromodulation and time-dependent plasticity [7,8], as well as the possible transformations of causal effects induced by network activities [9], structural connectivity is not sufficient and timely enough to contain all changing situations of the connective states. Notably, it is inherently required of tracking the dynamical effective interactions instead of only specifying synaptic connection changes [10]. In addition, the notion of

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functional connectivity which is defined as statistical correlations among all units of a neurophysiological system has been applied in brain connectivity research [11]. Characterization about the observed correlations provides functional interactions between neurons without any reference to the underlying structural model [12]. The obtained functional network has been proved to exhibit properties like small-world effect, as well as dynamical behaviors reflected by the original physical organization of the structural connectivity [13–15]. However, effective connectivity is often associated to ongoing neuronal circuit dynamics [16] and thus dynamical causal relationship can be reconstructed from the activities of neuron units [17]. It is an intriguing problem that how distinct dynamical states of underlying structural networks could help to reflect the corresponding effective networks [18].

Experimental and theoretical studies have explored reconfiguration of effective connectivity under different scales of structural networks with its dynamic mechanisms [19,20]. It is convincingly reported that effective interactions of neuronal units are not always directly corresponding to their anatomical correlates, but are state-dependent, such as oscillatory patterns and phase relationships, which are relevant to efficient information exchange [21,22]. By extension, synchronization is regarded as one of the coordinating mechanisms which allows for effectively 'coupling' neuronal dynamics distributed among separated regions of brain [23]. It could reasonably conduce to forming different and significant interactions between neuronal groups [24,25]. Therefore, various synchronization regimes and also their related properties-with respect to delay, synaptic strength and phase pattern [26,27], could play vital roles in reshaping a rich repertoire of effective networks within certain structural modules [28,29]. Particularly, synchronization dynamics in the relative simple networks like neural motifs are prominent [30], especially in a more realistic way of delay-coupled [31–35]. Among them, zero-lag synchrony termed as a kind of isochronal synchronization arising between spatially remote cortical areas is being widely discussed [36]. It has been realized in delay-coupled triplets either by using physical circuits [37], or by means of neuronal model simulations [38]. The reciprocally connected resonance pair forming a so-called dynamical relaying is demonstrated to promote the generation of zero-lag synchrony in network motifs [39,40]. Due to functional integration significance [41], it is a question of interest to us to associate effective connectivity reconstruction with this synchrony regime [42]. Herein, how zero-lag synchrony influences the causal interactions in individual neuron circuits is systematically explored.

It has been reported that identifying effective connectivity and establishing precise brain rhythm can both range from microscopic level to macroscopic scale [43,44]. Remarkably, synchronic modulation of the microscopic neuronal signals, such as spikes, is exactly appropriate to explicate how brain organizes information processing at the degree of single cell [45]. So estimating effective interactions based on individual neuron firing is a good rule of thumb and our research is in the framework of network motifs composed of single neurons. Furthermore, Time Series Inference (TSI) concerning the temporal relations, dynamic correlations, mutual or transfer information as well as information flow, has been exploited to tackle the problem of causal interplay estimation in the brain [46-51] (see Section 4). The dynamical effective influences can be computed out from neural activities and it is also related with several dynamic behaviors [52]. As the type of TSI, Granger causality connectivity analysis (GCCA) is a widely used approach in neuroscience to measure directed causal connectivity [53]. Deriving from the field of economics [54], the Granger causality (GC) method has developed into a variety of forms that are applicable to different processes and requirements [55]. For example, the GC method has been utilized to characterize dynamically changing effective connections from the microelectrode recordings during necessary phases of a cognitive task [56]. Here GC with a proper pattern is chosen to provide us with an efficient and easy way to characterize effective connectivity as well as their changes in accordance with zero-lag synchronization dynamics.

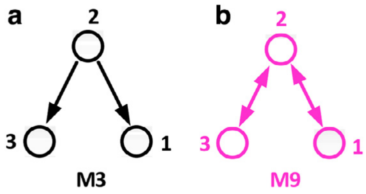

Fig. 1. Connecting patterns of the network motifs, denoted by M3, and M9. The notation we adopt for the motifs of three nodes follows the notation in [57].

In this work, the fundamental role of zero-lag synchronization in reconstructing effective connectivity is investigated. We primarily address this issue in two motifs [57]. By adjusting network parameters, effective connections change with the corresponding synchrony dynamics. Accordingly, the remainder of this paper is arranged as follows: in Section 2, the model of individual neuron and selected motifs are described. Then, we briefly introduce the basic principle of GC method and define an index to quantify zero-lag synchronization. In Section 3, the impacts of zero-lag synchronization on effective interactions among different motif networks are explored. In Section 4, the GC method is compared with other ways of causal measure and the features of effective connectivity deriving from zero-lag synchrony dynamics are briefly discussed. Finally, conclusions are given in Section 5.

2. Model and method

2.1. Model

Following the evolutionary dynamics of zero-lag synchronization, we conduct effective connectivity analysis under two configurations of the motifs [44]. These small network building blocks exist disproportionally in many biological systems with distinct numbers of vertices and patterns of interconnections, which account for structural complexity of brain network [58]. Adopted from the notation in [57], structural frameworks of the considered motifs are shown in Fig. 1, where the two selected motifs are denoted as M3 and M9. For M3, nodes 1 and 3 are commonly driven by node 2. Through adding two feedback connections, node 2 reciprocally connects to nodes 1 and 3 in M9.