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Stability and synchronization of random brain networks with a distribution of connection strengths

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Abstract

The impact of stability and synchronization of electrical activity on the structure of random brain networks with a distribution of connection strengths is investigated using a physiological model of brain activity. Connection strength is measured by the gain of the connection, which describes the effect of changes in the firing rate of neurons in one component on the neurons of another component. The stability of a network is calculated from the eigenvalue spectrum of the network's matrix of gains. Using random matrix theory, we predict and numerically verify the eigenvalue spectrum of randomly connected networks with gain values determined by a probability distribution. From the eigenvalue spectrum, the probability that a network is stable is calculated and shown to constrain the structural and physiological parameters of the network. In particular, stability constrains the variance of the gains. The complex vector of component amplitudes, or mode, corresponding to each dispersion root is an eigenvector of the network's gain matrix and is used to calculate the synchronization of each component's electrical activity. Synchronization is shown to decrease as the variance of the connection gain increases and inhibitory connections become more likely. Brain networks with large gain variance are shown to have multiple eigenvalues close to the stability boundary and to be partially synchronized. Such a network would have multiple partially synchronized modes strongly excited by a stimulus.

Keywords: Cortical networks; Stability analysis; Oscillatory networks; Network spectra; Synchronization; Random matrices

1. Introduction

Analysis of large-scale brain structure has shown that the brain is an interconnected network of neuronal populations with distinct anatomical characteristics. A number of experimentally determined connection networks for animal cortices have been published [18,19,23,47,59] showing that connections between brain components are not random but have a hierarchical structure with properties similar to those of small world networks [3].

The physical and evolutionary reasons for the brain to display this type of network structure have yet to be explained fully. A number of studies have shown that brain networks may have evolved so that the "cost" of wiring the connections between components, such as the volume of axons and dendrites, is minimized [7–9]. However, a recent study has shown that neural systems are not exclusively optimized for minimal global wiring but for a variety of factors including the minimization of processing steps [25]. An information theoretic approach has also been used [50–52] to study cortical network connectivity. By searching for networks that maximized a complexity measure connection matrices with similar properties to experimentally determined cortical networks were generated [52,55]. However, as noted in [52], this shifts the question from why

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the brain has this structure to why the brain maximizes this complexity measure.

The study of brain networks is part of the wider study of complex networks, which have been investigated extensively in years, see [3] for an extensive recent review. The main focus of this research has been on the structural properties of networks; however, a number of studies have recently looked at the dynamics of complex networks, including randomly connected networks [26,45,60]. Though the structure of brain networks, particularly cortical networks, has been widely analyzed, there has been little research on the dynamics of these networks using physiologically based models. Complementing the previous studies of brain network structure, we study brain networks using a physiologically based model of the brain's electrical activity. Our aim is to investigate the dynamics of networks of brain components with the goal of finding physical constraints on their possible structure.

Physiologically based modelling of the brain's electrical activity in recent years [6,41,43] suggests that an important constraint on brain structure is the linear stability of the electrical activity of the brain in response to an external input. If the brain is unstable, an input would lead to a continual increase in electrical activity, likely resulting a disorder. For example, there is evidence that instabilities in the corticothalamic system correspond to epileptic seizures [6,41,43,39]. It is possible that a linear instability leads to a stable nonlinear state (e.g., a limit cycle). However, this is not necessarily the case and requires study in the nonlinear regime to determine in general. Another important linear property is the synchronization of activity between brain structures. In epilepsy, synchronization increases between different cortical areas before and during seizure [53], and structures in the basal ganglia become more synchronized in Parkinson's disease [5,48]. Synchronization between different regions in the visual cortex is also argued to be involved in the binding problem [46].

Previously, we applied a physiological model to randomly connected excitatory brain networks and showed that stability constrains their physiology and structure [16]. That work only considered networks with a constant excitatory gain. Here, we extend that work by letting the gain vary within a network. The gain of a connection is determined by a probability distribution that allows the possibility of inhibitory connections. We also investigate the synchronization of the electrical activity of the components in a brain network. Even though large-scale brain networks are known to have a specific nonrandom connectivity, it is useful, as discussed in [13], to explore the stability and synchronization of randomly connected networks. First, we can obtain insight into why evolution selected a particular connectivity in the brain out of the space of all possible connectivities. Alternatively, we can interpret randomly connected networks with a distribution gain value to be networks with random or fluctuating interactions and we can investigate how the stability and synchronization of a network change as the input into each component fluctuates over time. Section 2 describes the representation of brain networks using directed networks and their corresponding connection matrices. The simple physiological model used to describe the dynamics of a brain network is presented in Section 3. A central role is played by the gain matrix of a brain network. In Section 4, we describe the important features of the gain matrix of a brain network and explain how the stability and synchronization are determined from its eigenvalues and eigenvectors. Using random matrix theory, we predict the eigenvalue distribution of brain networks with arbitrary connection distribution and arbitrary gain distribution in Section 5. These predictions are confirmed in Section 6 for randomly connected brain networks with similar parameters to experimentally determined brain networks and normally distributed gain. The stability and synchronization of these networks as the gain variance changes are presented in Section 7. Finally, results for the spectral distribution and synchronization of brain networks with fixed randomly generated connections and gains are presented in Section 8.

2. Brain networks

A brain network of n neuronal populations is represented here by a directed graph N and its corresponding connection matrix $\mathbf{C}(N) = [C_{ij}]$. Each vertex represents a specific neuronal population or brain component and an edge in the graph signifies a connection from one component to another along which an electrical signal is sent. The neurons constituting each component can belong to physically distinct regions of the brain, for example the visual and motor cortices, or can be intermixed with the neurons of another component such as the excitatory and inhibitory neurons in the cortex. If there is a connection from component j to component i, then $C_{ij} = 1$ and if there is no connection $C_{ij} = 0$. If $C_{ij} = C_{ji}$ for all i and j we say that the network is symmetric; otherwise it is asymmetric. When $C_{ij} = C_{ji}$, then components i and j are reciprocally, or symmetrically, connected. The fraction of connections for which a reciprocal connection exists will be denoted by the parameter q. In this work, we consider the stability of brain networks with randomly connected components and $0 \leqslant q \leqslant 1$. The probability of an edge existing between components is denoted by p. When $p = 0$, the network has no connections and when $p = 1$, the network is fully connected. In our analysis, we focus on networks that are strongly connected [4], ignoring networks that are made up of disconnected portions. This ensures that all the vertices in a network have at least one input and one output; i.e., there are no "sources" or "sinks" of electrical activity. If

$$p > (5 + \ln n)/n, \tag{1}$$

then a randomly connected network will almost surely be strongly connected [4]. In this work, we use values of p that satisfy Eq. (1) to ensure strong connectivity.