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The complex hierarchical topology of EEG functional connectivity

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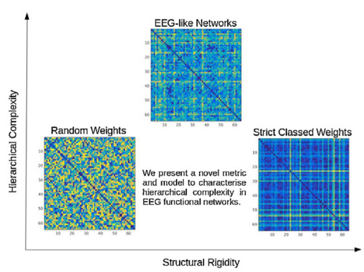
HIGHLIGHTS

- A novel framework for functional connectivity networks is presented.
- A metric to analyse the hierarchical complexity of networks is introduced.
- A functional connectivity null model for complete weighted networks is introduced.
- The null model attains highest complexity when mimicking EEG phase-lag networks.
- Key network concepts – integration, regularity, topological randomness – are refined.

GRAPHICAL ABSTRACT



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ABSTRACT

Background: Understanding the complex hierarchical topology of functional brain networks is a key aspect of functional connectivity research. Such topics are obscured by the widespread use of sparse binary network models which are fundamentally different to the complete weighted networks derived from functional connectivity.

New methods: We introduce two techniques to probe the hierarchical complexity of topologies. Firstly, a new metric to measure hierarchical complexity; secondly, a Weighted Complex Hierarchy (WCH) model. To thoroughly evaluate our techniques, we generalise sparse binary network archetypes to weighted forms and explore the main topological features of brain networks – integration, regularity and modularity – using curves over density.

Results: By controlling the parameters of our model, the highest complexity is found to arise between a random topology and a strict 'class-based' topology. Further, the model has equivalent complexity to EEG phase-lag networks at peak performance.

Comparison to existing methods: Hierarchical complexity attains greater magnitude and range of differences between different networks than the previous commonly used complexity metric and our WCH model offers a much broader range of network topology than the standard scale-free and small-world models at a full range of densities.

Conclusions: Our metric and model provide a rigorous characterisation of hierarchical complexity. Importantly, our framework shows a scale of complexity arising between 'all nodes are equal' topologies at one extreme and 'strict class-based' topologies at the other.

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1. Introduction

Graph theory is an important tool in functional connectivity research for understanding the interdependent activity occurring over multivariate brain signals (Bullmore and Sporns, 2009; Stam, 2014; Papo et al., 2014). In this setting, Complete Weighted Networks (CWNs) are produced from all common recording platforms including the Electroencephalogram (EEG), the Magnetoencephalogram (MEG) and functional Magnetic Resonance Imaging (fMRI), where every pair of nodes in the network share a connection whose weight is the output of some connectivity measure. Complex hierarchical structures are known to exist in real networks (Ravasz and Barabási, 2003), including brain networks (Bullmore and Sporns, 2009; Meunier et al., 2010), for this reason it is important to find methods to specifically evaluate hierarchical complexity of network topology. Here we introduce methods specific to this end.

Complexity is understood neither to mean regularity, where obvious patterns and repetition are evident, nor randomness, where no pattern or repetition can be established, but attributed to systems in which patterns are irregular and unpredictable such as in many real world phenomena (Costa et al., 2005). Particularly, the brain is noted to be such a complex system (Tononi et al., 1994) and this is partly attributed to its hierarchical structure (Meunier et al., 2010). Hierarchical complexity is thus concerned with understanding how the hierarchy of the system contributes to its complexity. Here we introduce a new metric aptly named hierarchical complexity, R, which is based on targeting the structural consistency at each hierarchical level of network topology. We compare our metric with network entropy (Solé and Valverde, 2004) and find that we can offer a greater magnitude and density range for establishing differences in complexity of different graph topologies.

Alongside this, we introduce the Weighted Complex Hierarchy (WCH) model which simulates hierarchical structures of weighted networks. This model works by modifying uniform random weights by addition of multiples of a constant, which is essentially a weighted preferential selection method with a highly unpredictable component provided by the original random weights. We show that it follows very similar topological characteristics of networks formed from EEG phase-lag connectivity. Intrinsic to our model is a strict control of weight ranges for hierarchical levels which offers unprecedented ease, flexibility and rigour for topological comparisons in applied settings and for simulations in technical exploration for brain network analysis. This also provides an unconvoluted alternative to methods which randomise connections (Watts and Strogatz, 1998; Sporns, 2006) or weights (Rubinov and Sporns, 2011) of the original network.

Any rigorous evaluation of brain networks should address their inherent complete weighted formulation (Fallani et al., 2014). However, the current field has largely lacked any concerted effort to build an analytical framework specifically targeted at CWNs, preferring instead to manipulate the functional connectivity CWNs into sparse binary form (e.g. (Sporns, 2006; Li et al., 2011; Tewarie et al., 2015) as well as wide-spread use of the Watts-Strogatz (Watts and Strogatz, 1998) and Albert–Barabasi (Barabasi and Albert, 1999) models) and using the pre-existing framework built around other research areas which have different aims and strategies in mind (Newman, 2010). In our methodological approach we propose novel generalisations of pre-existing sparse binary models to CWN form and thus allow a full density range comparison of our techniques. Due to the intrinsic properties of these graph types we find minimal and maximal topologies which can help to shed light on a wide variety of topological forms and their possible limitations (Solé and Valverde, 2004) in a dense weighted framework.

Further, as part of our study we seek after straightforward metrics to evaluate other main aspects of network topology for comparisons (Solé and Valverde, 2004; Sporns, 2010) and, in this search, found it necessary to revise key network concepts of integration–segregation (Stam, 2014; Watts and Strogatz, 1998; Rubinov and Sporns, 2010) and scale-freeness (Barabasi and Albert, 1999; Eguiluz et al., 2005). We provide here these revisions: (i) That the clustering coefficient, C, is enough to analyse the scale of integration and segregation, finding it unnecessary and convoluted to use the characteristic path length, L, as a measure of its opposite, as generally accepted (Bullmore and Sporns, 2009; Watts and Strogatz, 1998). (ii) We provide mathematical justification that the degree variance, V, and thus network irregularity (Snijders, 1981) is a strong indicator of the scale-free factor of a topology.

Our study of hierarchical complexity, using a comprehensive methodological approach, provides mathematical quantification of the hierarchical complexity of EEG functional connectivity networks and reveals new insights into key aspects of network topology in general. Our model provides improved comparative abilities for future clinical and technical research.

2. Network science: proposed methods and key revisions

We adopt the notation in Sandryhaila and Moura (2013) so that a graph, $G(\mathcal{V}, \mathbf{W})$, is a set of n nodes, $\mathcal{V}$, connected according to an $n \times n$ weighted adjacency matrix, $\mathbf{W}$. Entry W_{ij} of $\mathbf{W}$ corresponds to the weight of the connection from node i to node j and can be zero. An unweighted graph is one in which connections are distinguished only by their existence or non-existence, so that, without loss of generality, all existing connections have weight 1 and non-existent connections have weight 0. The graph is undirected if connections are symmetric, which gives symmetric $\mathbf{W}$. A simple graph is unweighted, undirected, with no connections from a node to itself and with no more than one connection between any pair of nodes. This corresponds to a graph with a symmetric binary adjacency matrix with zero diagonal. Such graphs are easy to study and measure (Newman, 2010). The degree, k_i, of node i is defined as the number of its adjacent connections, which is the number of non zero entries of the ith column of $\mathbf{W}$. Then, for a simple graph, $k_i = \sum_{j=1}^{n} W_{ij}$. For a graph with $2m$ edges, the connection density, P, of a graph is $P = 2m/n(n-1)$. A CWN is represented by a symmetric adjacency matrix with zero diagonal (no self-loops) and weights, $W_{ij} \in [0, 1]$, elsewhere. To analyse CWNs it is beneficial to convert it to simple form by binarising the adjacency matrix using a threshold, where a percentage of strongest connections are set to 1 and the remaining values set to 0. This stays true to the network activity (Fallani et al., 2014) whilst reducing computational complexity and weight issues found with weighted metrics (Stam, 2014). Hereafter, all mathematics will refer to simple graphs.

In this section we present the contributions of this study. We first present the hierarchical complexity metric and the WCH model, which are the key novel contributions of this paper. Thereafter we detail revisions and clarification of integration and segregation as a scale evaluated by C and scale-freeness as a factor evaluated by V. Finally, we outline the generalisation of key network archetypes to CWN form, full details of which can be found in the supplementary material.

2.1. Hierarchical complexity metric

The ideas of order and complexity are well known in the discussion of networks (indeed, real world networks are often called complex networks (Bullmore and Sporns, 2009; Papo et al., 2014; McAuley et al., 2007)). In mathematics, the graphs studied derive from some theoretical principles. These can involve set