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Comment

Multilayer network modeling creates opportunities for novel network statistics
Comment on "Network science of biological systems at different scales: A review" by Gosak et al.

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As described in the review by Gosak et al., the field of network science has had enormous success in providing new insights into the structure and function of biological systems [1]. In the complex networks framework, system elements are network nodes, and connections between nodes represent some form of interaction between system elements [2]. The flexibility to define network nodes and edges to represent different aspects of biological systems has been employed to model numerous diverse systems at multiple scales.

The use of network approaches at the cellular scale is not as common as at other scales, and Gosak et al. provide an excellent description of how network analysis can be useful in characterizing the cellular dynamics in islets of Langerhans [1] which will hopefully spur others to perform network analysis at this level. In addition to emphasizing the utility of network analysis across scales, the authors also point out that traditional network modeling is unable to capture certain dynamical features of cells and identify multilayer networks as the next emerging technique in modeling biological systems. As nicely described in the review, traditional network modeling approaches limit researchers to modeling static networks where only a single type of interaction is captured in the model. However, multilayer networks overcome these limitations by introducing a framework for modeling more complex interactions and relationships [3,4]. The multilayer network framework allows one to build multidimensional networks where a single layer describes a traditional network, and inter-layer links provide connections between single layers, thus linking scales, time, modalities, or a multitude of other network features.

Gosak et al. also discuss how multilayer networks can be used to introduce new modeling paradigms and link dimensions of data that could not previously be integrated in order to gain insight into system properties. In their review, they focus on the diverse range of biological systems that can be more thoroughly described by multilayer modeling approaches. The adoption of multilayer modeling to better characterize multiple types of interactions across scales and time in these systems is certainly exciting and worth encouraging. However, many challenges and opportunities remain that will need to be addressed as the use of the multilayer formalism is increasingly adopted by the complex networks community.

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Multilayer networks introduce a uniting framework to give coherent descriptions of systems across multiple scales, features, and/or time, but the mathematical analysis of the structure of multilayer networks requires the development and advancement of network statistics that are defined to work within this new framework. Indeed, many traditional network statistics such as those for detecting centrality [5,6], motifs [7], and community structure [8,9] have been extended to the multilayer setting. However, one must be careful in the interpretation of these metrics, as the construction of the network requires one to define both intra- and inter-layer links describing interactions between nodes. Intra-layer links can be interpreted in the same sense as connections in a traditional network, but the interpretation of inter-layer edges requires additional scrutiny and will be dependent on the specific construction of the network. Although some work such as that described by Gosak et al. has explored defining inter-layer edges experimentally by measuring time delay [10], calculating correlations between frequency bands [11], or using decay functions to model time-dependent relationships between network layers [12], in many applications, inter-layer connections are a parameter of the network construction that is set by the user. For example, when constructing either categorical or temporal networks and applying dynamic modularity maximization, inter-layer connections represent self-identity links that indicate the same node throughout layers [8]. However, the strength of these connections is a parameter of the modularity function, and different choices of strength can impact the resulting community detection. While some work has explored the effects of various parameter choices [13,14], more efforts are needed to address this important aspect of dynamic community detection.

Although much work remains in understanding the role and characterization of inter-layer links, the use and analysis of multilayer networks have already proven to be a useful tool in modeling complex biological systems. This is especially true in the emerging field of network neuroscience [15,16] where their use has led to insights into brain structure-function relationships, network evolution, multi-scale relationships, and disease [17]. Many new approaches to characterizing brain networks have utilized the extension of the popular method of modularity maximization to define community structure in the multilayer setting. When applied to temporal brain networks, this results in the detection of brain communities throughout time. By defining a coherent description of communities throughout time, researchers have also been able to define novel metrics such as flexibility [18], cohesion and disjointedness [19], and promiscuity [20] which describe how brain regions move between communities to work together over time or task.

The adoption of multilayer modeling techniques to understand biological systems is still in its early stages and Gosak et al. are correct in their observation that multilayer modeling represents the future of complex networks. However, as more researchers adopt this exciting new paradigm, we must also place a special importance on evaluating how to properly characterize and interpret multilayer network structure, as much of the mathematical formalism is still in its infancy. This should not be seen as a disadvantage of using multilayer modeling techniques, but instead as a motivation for researchers to ask difficult questions about how to interpret multilayer models and to develop novel network statistics, driven by the many diverse applications and uses of multilayer network modeling.

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