BMC Neuroscience



Poster presentation

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The complex world of the small brain Michelle Rudolph* and Alain Destexhe

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from Sixteenth Annual Computational Neuroscience Meeting: CNS*2007 Toronto, Canada. 7–12 July 2007

Published: 6 July 2007

BMC Neuroscience 2007, 8(Suppl 2):P21 doi:10.1186/1471-2202-8-S2-P21

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Since Stanley Milgram's "six degrees of separation", the interest in the topological structure of network graphs and implications for their functional role experienced a dramatic surge. 40 years later, small-world and scale-free properties, with the latter being generally viewed as a crucial prerequisite for complex dynamical behaviours, are identified as a unifying feature of many real-world networks. However, the study and characterisation of complexity at the level of neuronal populations such as cortical microcircuits, large-scale functional networks or, ultimately, the whole brain still remains a technically and mathematically difficult and, therefore, widely unsolved task. Moreover, recent research shows that small-world and scale-free connectivity are just two out of a vast plethora of applicable graph-theoretical measures to yield a more accurate characterisation of the networks structural or functional properties.

In this contribution we provide a detailed comparative characterisation of publicly available brain networks. The latter include structural areal connectivity graphs from the cat cortex, macaque and macaque visual cortex, as well as cellular networks of C. elegans and corresponding subnetworks formed by chemical synapses and gap junctions only. Graph theoretical tools applied include node degree and correlation, edge distance, clustering and cycle, entropy, hierarchical, centrality, spectral and complexity measures, as well as the study of subgraphs and fractal properties. Moreover, extensions of these measures incorporating weight and spatial information are proposed and applied to graphs where such data were available.

Our analysis shows that, first, in agreement with numerous previous studies, all investigated systems exhibit small-world properties (i.e. small average geodesic distance and high clustering coefficient) when relational graphs are considered. Second, for many other measures, marked differences (e.g. for efficiency and vulnerability) between the investigated networks were found, thus revealing a rich universe of structural qualities. We argue that the latter forces a re-evaluation of the question about structural prerequisites for functionally complex dynamical behaviours. Third, the incorporation of weight and spatial information qualitatively alters some conclusions drawn from the analysis of corresponding relational graphs, thus arguing for a careful re-evaluation of realworld networks in the context weighted and spatial graph theory.

In summary, our study suggests that a deeper understanding of the functional dynamics and role, and possible differences in the latter, of neural and brain networks necessitate their detailed structural characterisation beyond small-world and scale-free qualities. Moreover, a detailed graph-theoretical characterisation of structural and functional brain networks will allow to constraint developmental mechanisms which lead to the preference of specific network topologies over others. Finally, studying structural and functional patterns on the global scale with the full weight of graph theory could provide an alternative way to argue for complexity as an emergent quality of brain networks which goes beyond a pure description of the wealth of structural and functional properties observed in isolated neural systems.