NeuroImage 96 (2014) 174–182

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Rich club organization supports a diverse set of functional network configurations

Mario Senden [a,*], Gustavo Deco [b,c], Marcel A. de Reus [e], Rainer Goebel [a,d], Martijn P. van den Heuvel [e]

[a] Department of Cognitive Neuroscience, Faculty of Psychology and Neuroscience, Maastricht University, 6200 MD Maastricht, The Netherlands
[b] Center for Brain and Cognition, Computational Neuroscience Group, Department of Information and Communication Technologies, Universitat Pompeu Fabra, Roc Boronat 138, Barcelona 08018, Spain
[c] Institució Catalana de la Recerca i Estudis Avançats (ICREA), Universitat Pompeu Fabra, Passeig Lluís Companys 23, Barcelona 08010, Spain
[d] Department of Neuroimaging and Neuromodeling, Netherlands Institute for Neuroscience, an Institute of the Royal Netherlands Academy of Arts and Sciences (KNAW), 1105BA Amsterdam, The Netherlands
[e] Brain Center Rudolf Magnus, Department of Psychiatry, University Medical Center Utrecht, Brain Center Rudolf Magnus, 3508 GA Utrecht, The Netherlands

ARTICLE INFO

Article history:
Accepted 24 March 2014
Available online 31 March 2014

Keywords:
Rich club
Functional repertoire
Connectivity
Spin glass model
Connectome

ABSTRACT

Brain function relies on the flexible integration of a diverse set of segregated cortical modules, with the structural connectivity of the brain being a fundamentally important factor in shaping the brain's functional dynamics. Following up on macroscopic studies showing the existence of centrally connected nodes in the mammalian brain, combined with the notion that these putative brain hubs may form a dense interconnected 'rich club' collective, we hypothesized that brain connectivity might involve a rich club type of architecture to promote a repertoire of different and flexibly accessible brain functions. With the rich club suggested to play an important role in global brain communication, examining the effects of a rich club organization on the functional repertoire of physical systems in general, and the brain in particular, is of keen interest. Here we elucidate these effects using a spin glass model of neural networks for simulating stable configurations of cortical activity. Using simulations, we show that the presence of a rich club increases the set of attractors and hence the diversity of the functional repertoire over and above the effects produced by scale free type topology alone. Within the networks' overall functional repertoire rich nodes are shown to be important for enabling a high level of dynamic integrations of low-degree nodes to form functional networks. This suggests that the rich club serves as an important backbone for numerous co-activation patterns among peripheral nodes of the network. In addition, applying the spin glass model to empirical anatomical data of the human brain, we show that the positive effects on the functional repertoire attributed to the rich club phenomenon can be observed for the brain as well. We conclude that a rich club organization in network architectures may be crucial for the facilitation and integration of a diverse number of segregated functions.

Introduction

The human brain is composed of a large set of anatomically distinct regions and local clusters indicative of segregated neural information processing. The execution of higher order cognitive functions such as memory, perception, and attention demands the integration of this information via distributed computation. Computationally driven theories of cognition hypothesize that the brain may achieve integration of subsystems by flexibly arranging cortical areas into temporal functional networks in accordance with goal-related requirements (Baars, 2005; Deco et al., 2010; Ghosh et al., 2008). The exact nature as well as the size of the set of possible functional network configurations, referred to as the brain's functional repertoire, has been suggested to relate directly to the structural architecture of the brain (Deco et al., 2010, 2012; Senden et al., 2012). Network architectures that involve a scale free topology; meaning that the degree distribution follows a power law function indicating the existence of a small number of high-degree nodes, have been shown to be able to display a particularly diverse number of functional configurations (Deco et al., 2012).

In addition to a heavy tailed degree distribution the human brain has been shown to contain hubs which are not only individually 'rich' in connectivity but additionally show a dense level of interconnectivity (Colizza et al., 2006; Van den Heuvel and Sporns, 2011). This collective of highly interconnected hubs has been termed the 'rich club' analogously to the organization of social systems in which individuals rich in connections tend to form strongly interconnected clubs, taking a central position in the overall system (McAuley et al., 2007; Zhou and Mondragon, 2004). Similarly, neural rich clubs have been hypothesized to act as a central high-capacity backbone for global communication

* Corresponding author at: Department of Cognitive Neuroscience, Faculty of Psychology and Neuroscience, Maastricht University, Oxfordlaan 55, P.O. Box 616, 6200 MD Maastricht, The Netherlands.
E-mail address: mario.senden@maastrichtuniversity.nl (M. Senden).

http://dx.doi.org/10.1016/j.neuroimage.2014.03.066
1053-8119/

(Van den Heuvel et al., 2012) and integration (Van den Heuvel and Sporns, 2011) in the brain.

In this computational study we hypothesized that the presence of a rich club in an otherwise scale free type architecture further expands the functional repertoire of a system. To test this hypothesis a steady-state attractor model was applied to artificial network architectures as well as human experimental anatomical data to examine the influence of a network's architecture on its functional diversity. In addition, we studied the shape of the functional repertoire with a special focus on the comparison between scale free architectures that show rich club organization versus scale free architectures without rich club organization. Overall, our findings suggest that the presence of a central rich club on top of a scale free architecture may lead to an additional gain in the diversity of a network's functional repertoire, suggesting that a structural rich club in neural systems may further expand the brain's functional diversity. Interestingly, our findings further indicate that the presence of a rich club enhances the capability of the system to functionally integrate areas of low structural degree.

Methods

Artificial network architectures

Six types of network architectures were examined (Fig. 1): Regular (REG), Random (RAND), Small world (SW), Barabasi–Albert scale free including a rich club formation (SF-RC), Scale free without rich club formation (SF), and Scale free whose rich nodes are secluded from one another (SF-negRC). Each network contained exactly 24 nodes with each node (results of networks of $N = 30$ nodes are presented in the Supplemental materials), on average, making four bidirectional, unweighted connections to other nodes, resulting in a total of 96 connections (also referred to as edges) per network. Small networks were chosen due to the high computational demand of the spin glass model (see Supplemental materials). In what follows, the formation of these networks are described, starting with the REG, RAND and SW classes, followed by the three categories of SF networks.

Regular network (REG)

A single regular network was generated by ordering 24 nodes on a circular lattice and subsequently connecting each node to its two nearest neighbors on both sides.

Random networks (RAND)

A set of 100 random networks was generated using the algorithm described by Watts and Strogatz (1998) which rewires each connection in a regular network with a prefixed probability p. For random networks the probability of rewiring was set equal to one.

Small world networks (SW)

A set of 100 small world networks was generated using the rewiring algorithm described by Watts and Strogatz (1998) with a probability of rewiring set to 0.25, resulting in a network with a small world topology in which the majority of edges are between neighboring nodes, with a few connections forming short-cut connections between remote parts of the network.

Scale free networks

Scale free networks were generated by applying the Barabasi–Albert algorithm (Barabási and Albert, 1999) on random seed networks. This algorithm employs the principle of preferential attachment in which the probability that a newly added node will form a connection with an existing node is proportional to the degree of the existing node. As a result, the subset of seed nodes will end up as the most densely connected nodes (i.e. hubs) in the generated network. Three types of scale free networks were formed:

1. Scale free networks without a rich club (SF). A set of 100 scale free networks containing no rich club (SF) was generated by performing the Barabasi–Albert algorithm (Barabási and Albert, 1999) on a seed of intermediate density. The seed set had nine nodes each making four connections leading to the formation of a set of scale free networks in which the starting nodes show a high level of connectivity (i.e. form hubs) but no central rich club.

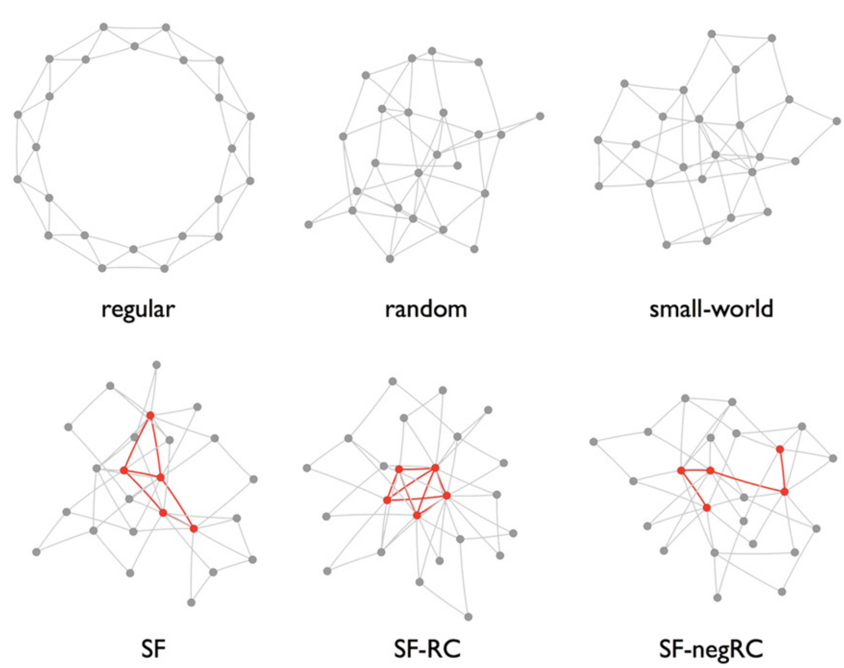

Fig. 1. Network architectures. The figure gives an illustrative representation of the artificial network architectures studied here. The upper row shows a regular (named the REG class, left), small world (SW, middle), and random (RAND, right) network. The lower row shows three scale free networks with different rich club organizations. Left is a typical scale free network without rich club organization (SF class). In the middle is the scale free network showing rich club organization (named the SF-RC class). Right is a scale free network showing negative rich organization (SF-negRC class). High degree hub nodes and hub-to-hub connections are shown in red.