Neuroplasticity explained by broad-scale networks and modularity?

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Abstract

The human brain is a formidably complex network, the seat of cognition and consciousness and many other remarkable features, including the capacities of growth, self-organisation, reorganisation and the ability to recover from significant damage. This combined dynamic capability is known as *plasticity*. Considerable neuro-reorganisation is a feature of the brain commonly thought to be restricted to childhood (the Kennard Principle); however, it is known to be a feature of adult brains as well. This paper provides a brief history of early theory and research, still valid today, on brain or neuroplasticity before discussing how current network theory and new brain mapping research on modularity can be synthesised to provide insight into this adaptive function from structure.

Key Words: Neuroplasticity, Network Theory, Modularity

Introduction

The human brain comprising one thousand trillion connections (Sporns et al, 2005) is a dynamic network from whose assembly emerges the higher cognitive functions and consciousness. Another striking feature of the brain is its plasticity, studies of hemespherectimised individuals or those with removal of significant functional brain areas show remarkable recovery (Battaro, 2000; Immordino-Yang, 2007, 2008; Li et al, 2009; Plaza, 2009). How is this possible? Network theory and new brain mapping research may provide some answers to this remarkable adaptive function from structure.

The brain is obviously a daunting ‘object’ of study, nonetheless, as with other complex systems mathematical and visual methods offer an approach to simplifying the system whist retaining the essence of the structure and function of that system.

Neuroplasticity can be defined as the brains lifelong capacity to form new connections in response to experience and to compensate for injury; a feature noted long ago by Paul Broca (1865). The rigorous study of this capacity began, however, with the work of Santiago Raymon y Cajal (1852- 1934).

The important first step in understanding how the brain achieves plasticity and resilience was discovering that the nervous system is a contiguous, dynamic network rather than a continuous, static grid.

Cajal

Cajal was the recipient of the first Nobel prize for Physiology which he shared in 1906 with Camillo Golgi (1843-1926). Golgi and Cajal are considered to be the founders of modern neuroanatomy and neuroscience. They shared the prize as Golgi provided the method of staining that allowed the mapping of individual cells and structures, whilst Cajal provided structural insight from his detailed histological studies.

Cajal and Golgi held completely different views of the brain (Cajal, 1906, 1928). Golgi argued that the brain was a continuous large syncytium[i] and that brain cells were fused and static. This was a reasonable assumption at the time, as microscopy did not have the resolution power to see synaptic junctions. The idea of a fused network, or 'reticular theory', was the working assumption of Golgi, which he maintained in the face of the ever accumulating evidence of the Cajal team against such a position.

Cajal, proposed that the brain was a network of individual brain cells, neurons, that were *dynamic*, that is they could extend and retract (plasticity). This is the *neuronal doctrine* named by Wilhelm Waldeyer in 1891 and remains the fundamental structural principle of the Central Nervous System. Cajal went on to propose the 'law of dynamic polarisation' whereby dendrites and the cell body receive signals before transmitting them via the axon to other neurons. With the power of the electron microscope and observations of synaptic junctions Cajal's theory was eventually empirically established. Cajal's work also helped in the foundation of brain hodology (pathways) and modern disconnection work (Geschwind, 1965).

Whilst observing that *neuroregeneration* is a feature of the Nervous System, Cajal and other pioneers (notably His and Kolliker) did not claim neurogenesis in the mammalian cortex, that is, the higher regions of the brain are non-renewable (Rakic, 2002). So if the cerebrum cannot replace cells, it must have a design that compensates for deletion, disconnection and degeneration. Insight into that design is provided by graph theory and in particular small world networks.

It's a small world after all.

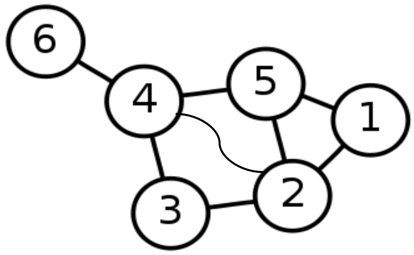
According to recent studies the brain exhibits a small-world network topology providing it with properties of economy, complexity and resilience (Achard et al, 2006; Basset and Bullmore, 2007; Honey and Sporns, 2008; Kwok, Jurica & Raffone 2007; Stam and Reijneveld, 2007).

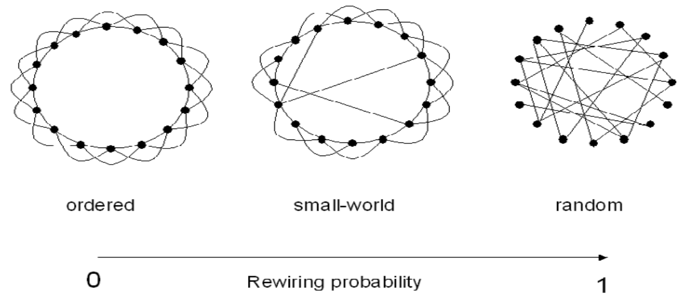
The mathematical commonalities found in a wide range of networks, physical, social and technological, stems from the publication of two papers. The first by Watts and Strogatz 'Collective Dynamics of Small World Networks' (1998) and the second by Barabasi and Albert, 'Emergence of Scaling in Random Networks' (1999).

This work extended graph theory (Erdös and Rényi, 1959), which is the mathematical, abstract representation of linked objects. The objects are called vertices (or nodes) the links are called edges and these simple mathematical concepts have proven enormously useful for the exploration of complex systems.

Figure1. First graph showing 6 vertices and 8 edges. Second graph depicts the transformation of a network from complete regularity (ordered) to small worldliness to randomness.

a) b)





Networks are characterized by path length and clustering, path length is the distance between nodes, clustering is the cliquishness between groups of nodes. Nodes can be measured in terms of their degree, that is the number of links in and out, nodes with a high degree are called hubs (a transport example would be Grand Central, New York). In figure 1a. node 4 has the highest degree, 6 the lowest. Degree can be measured in terms of *distribution*, for instance in a network like the world wide web, there are a small number of very popular sites and a large number of smaller sites, so it has a skewed degree distribution (known as scale free). Scale free networks, taken together with path length, clustering, hubs and skewed degree distribution describes the fundamental properties of most natural and technological nets.

What Watts and Strogatz found when exploring the properties of networks was that real world nets lie somewhere between complete regularity and total randomness (Figure. 1b). They started with a network comprising a ring of nodes and introduced shortcuts by rewiring a few nodes. These shortcuts dramatically altered the average path length whilst maintaining high clustering, which they called ‘small world’ after Milgrams’ famous six degrees of separation study.
Small world nets have an efficient communication structure whereby a few long distance connections pull disparate worlds together.

Small world robustness

The small world structure of the brain provides economical communication and importantly resilience to attack or damage. This is possible because small worlds are not vulnerable to the loss of individual nodes, or even hubs, nodes with high connectivity; this degree distribution is known as 'Broad Scale'. The work of the Cambridge Brain Mapping Unit using functional Magnetic Resonance Imaging (fMRI) and graph theory has shown that random and scale free networks[1] are more susceptible to failure than small world ones, following combined node deletion and hub destruction. Achard et al (2006) suggest that the 'small-world architecture of the brain may confer distinctive benefits in terms of robustness to both random elimination of nodes and selective attack on hubs', resulting in 'considerable fitness value in mitigating the loss of network functionality in the face of developmental aberration or disease' (p.6).

In addition to these network features, modularity is observed in the brain and indeed in many complex systems, but this is not the modularity of distinct neurological regions, but rather identifiable functional connective nets (communities), distributed throughout the brain.

Modularity

So another important topological feature of the brain relating to plasticity is modularity. A neural module in this conception is a 'group of nodes with dense intrinsic or intramodular connectivity and relatively sparse extrinsic or intermodular connectivity' (Bullmore et al, 2009, p.1130). Furthermore, networks can be considered as a hierarchy of modules within modules.

In a study mapping functional modules of the brain Meunier et al (2009) show changes in the topology of major brain modules between young and old persons. These functional modules were derived using algorithms to determine the strength of community structures in complex networks developed by Newman and Girvan (2004) and to produce resulting dendograms.

Essentially older brains show a reorganization and segregation into smaller modules with an accompanying attenuation of 'white matter density or integrity in major axonal tracts subserving some of the long distance connections' (p.722). Therefore, there would seem to be disconnections in the modular

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[1] Scale free means no meaningful average number of links (Achard et al, 2006)

networks associated with aging. In the network maps of the younger and older brains displayed in the appendix, there is a notable change in the 'frontal' module (blue map). Indeed, the connection coefficients between these modules, shows a 78% reduction in the older sample. A deeper probing and understanding of these disconnection processes unfolding over time would be a valuable contribution to understanding plasticity and learning across life.

Interestingly, the younger brains had an 'anatomically distributed' module with many connector nodes, not found in the older sample, though the older sample showed increased connector nodes in different modules. It is reasonable to argue that this organization of the brain contributes to the greater plasticity observed in the young, but also that this overall functional modularity continues to provide plasticity in adults. It is further worth considering that halving this modular network would still leave enough embedded information/function for the recovery seen in hemespherectimised children or in other cases of brain damage. Work on simulated lesions may provide future answers (Honey and Sporns, 2008).

Understanding the brain from a graph theoretical or current network perspective can help explain the brains plasticity as brains have a small world architecture and an evolving modularity, such that these network features can offer an explanation for some of the more remarkable ablation cases or for instance, in the case study by Plaza of a 27 year old man who recovered his speech after the removal of Broca's area (Plaza, 2009)).

Conclusion

Neuroplasticity is a function of the structure of the brain, an architecture that is a dynamic, resilient, modular, self healing, small world net. It is necessary to understand the fundamental underlying structure and function of the living developing brain and awareness of these fundamental issues in the wider community of psychologists, neuroscientists, developmentalists and educationalists should be promoted to gain new insights into cognitive development and decline across the lifespan. Clearly a great deal remains to be done, larger cross-sectional work, longitudinal research and biographical/case studies have yet to be carried out. Furthermore, little is yet known about the ‘mysterious dynamics *on* the system’ (Watts, 2003, p.161)

Nonetheless, even with the ‘vast ocean of truth’ undiscovered, the concepts and mathematical tools of graph theory and the technology to view living brain processes is allowing us to paddle in the shallows of the complex, dynamical processes that are the foundation of human development, cognition and behaviour.

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Endnote

[i] The brain cannot be a syncytium as it would not be able to function as it does; compare cardiac muscle which is a syncytium, one muscle cell contracts they all contract, such excessive, global sycnhronisation in the brain leads to seizure. It would, importantly, not allow the resilience exhibited by the brain, cut out a lobe and the brain can continue to function, removing a heart atrium would be extremely deleterious.

Appendix

Figure 2. Histograms of the number of nodes in modules for average young (a) and older (b) networks comprising 200 links each. Anatomical representations for average young (c) and older (d) population networks. From Meunier, D. et al. (2009) © NeuroImage Elseiver