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Beyond modularity: Fine-scale mechanisms and rules for brain network reconfiguration

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Abstract

The human brain is in constant flux, as distinct areas engage in transient communication to support basic behaviors as well as complex cognition. The collection of interactions between cortical and subcortical areas forms a functional brain network whose topology evolves with time. Despite the nontrivial dynamics that are germane to this networked system, experimental evidence demonstrates that functional interactions organize into putative brain systems that facilitate different facets of cognitive computation. We hypothesize that such dynamic functional networks are organized around a set of rules that constrain their spatial architecture – which brain regions may functionally interact – and their temporal architecture – how these interactions fluctuate over time. To objectively uncover these organizing principles, we apply an unsupervised machine learning approach called non-negative matrix factorization to time-evolving, resting state functional networks in 20 healthy subjects. This machine learning approach automatically groups temporally co-varying functional interactions into subgraphs that represent putative topological modes of dynamic functional architecture. We find that subgraphs are stratified based on both the underlying modular organization and the topographical distance of their strongest interactions: while many subgraphs are largely contained within modules, others span between modules and are expressed differently over time. The relationship between dynamic subgraphs and modular architecture is further highlighted by the ability of time-varying subgraph expression to explain inter-individual differences in module reorganization. Collectively, these results point to the critical role subgraphs play in constraining the topography and topology of functional brain networks. More broadly, this machine learning approach opens a new door for understanding the architecture of dynamic functional networks during both task and rest states, and for probing alterations of that architecture in disease.

Keywords: network neuroscience, non-negative matrix factorization, community detection, subgraph, cognitive control, functional connectivity

1. Introduction

More than just a sum of its parts, the brain performs computations and processes information by linking functionally specialized areas through complex patterns of anatomical wiring [2, 46, 126, 120]. Indeed, the underlying structural network forms the foundation of a wide repertoire of functional interactions between different regions [42, 113, 41]. Collectively, these interactions can be modeled as edges between nodes in a graph [6, 104, 27, 26, 66, 117] to probe the neurophysiological underpinnings of thought, perception, and action [118, 86]. Importantly, to actuate behavior and cognition through a changing landscape of environmental demands, these patterns of functional interactions must flexibly reconfigure [60, 28, 75, 83], presumably according to organizing principles that coordinate the dynamic engagement and disengagement of distinct sets of brain areas [10, 44, 95, 31].

A fundamental core of this dynamic architecture is thought to be *modularity* – the division of functionally engaged brain

regions into putative modules that may compartmentalize computation within discrete functional systems – such as motor, visual, auditory, or attention – without disturbing brain regions in other systems [92, 119]. Specifically, modules represent discrete clusters of a graph in which nodes of the same module are more strongly interconnected to one another than to nodes of different modules. The composition of a module may change with time as the edges in the network reconfigure over time. Reconfiguration of modules in brain networks is thought to support functional dynamics driving behavior and cognition, by compartmentalizing integrated and segregated neural processing of individual brain regions [18, 83]. Moreover, functional brain networks exhibit flexibility in their module composition as they adapt to cognitive demands associated with completing a task [22, 24, 83, 121], processing linguistic stimuli [44, 31], or learning a new skill [10, 13, 14]. Notably, individual differences in flexibility are correlated with individual differences in learning [10, 51], working memory performance [24], and cognitive flexibility [24], which is particularly interesting in light of its role as an intermediate phenotype in schizophrenia [22].

Yet, while flexibility appears to be an important attribute of functional brain networks, a fundamental understanding of

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