Brain Networks and Cognitive Architectures

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Most accounts of human cognitive architectures have focused on computational accounts of cognition while making little contact with the study of anatomical structures and physiological processes. A renewed convergence between neurobiology and cognition is well under way. A promising area arises from the overlap between systems/cognitive neuroscience on the one side and the discipline of network science on the other. Neuroscience increasingly adopts network tools and concepts to describe the operation of collections of brain regions. Beyond just providing illustrative metaphors, network science offers a theoretical framework for approaching brain structure and function as a multi-scale system composed of networks of neurons, circuits, nuclei, cortical areas, and systems of areas. This paper views large-scale networks at the level of areas and systems, mostly on the basis of data from human neuroimaging, and how this view of network structure and function has begun to illuminate our understanding of the biological basis of cognitive architectures.

Introduction

The term "cognitive architecture" used to refer to concepts that were entirely the domain of cognitive or computer scientists (see Box 1) whose efforts to elucidate the rules behind human cognition (Fodor and Pylyshyn, 1988) made little or no reference to the underlying biological substrate—the human brain. Times have changed. A new picture of cognitive architecture has begun to emerge, as amply documented by the contributions to this Special Issue. Most "cognitive architectures" now are thought of as sets of brain regions that contribute to the performance of some set of related tasks or a particular set of functions. Often these architectures are explicitly referred to as *networks*, for example, the default mode network (Raichle et al., 2001) and the attention networks (e.g., Corbetta and Shulman, 2002).

However, the meaning of the term "network" is highly variable. In many cases, network is informally applied to a simple collection of regions that is activated during a set of related fMRI imaging studies, without any explicit reference to connections between these regions. In contrast to this informal notion of networks as sets of regions stands the more formal definition of what constitutes a network, which is adopted in this article. A network is a set of pairwise relationships between the elements of a system—formally represented as a set of edges that link a set of nodes. Neurobiological networks come at many levels of scale from cell-specific metabolic or regulatory pathways inside of neurons to interactions between systems of cortical areas and subcortical nuclei (see Figure 1). At each level (neurons, neuronal circuits and populations, and systems), different kinds of networks with importantly different properties are present. At each of these levels, it is important not just to understand how the individual elements work but also to understand the sets of pairwise relations that put the elements into the context of the larger interconnected system (Sporns, 2011). With some exceptions, cognitive architectures mostly involve structures and mechanisms at this highest level of analysis (Sejnowski and Churchland, 1989). For this article, we would like to focus at these highest levels, with a view to understanding networks that relate to all or much of the brain. We would like to explore large-scale architectural principles and properties that encompass the more specific architectures discussed in other articles in this issue.

Approaching Large-Scale Brain Networks

The bulk of the article will entail looking at some of the concepts and results coming from taking an explicitly network perspective on brain organization in two related types of studies.

We first turn to work that has aimed to elucidate the anatomical networks upon which all functional activity unfolds. Anatomical networks provide the skeleton that constrains the passage of neuronal signaling and information that is crucial for shaping our thoughts, understanding, and actions.

A second major way in which many brain network studies have been studied is through correlated fluctuations of the fMRI BOLD signal (cf. Power et al., 2014). These studies often observe these correlations without any explicit task, forming so-called resting-state functional connectivity (RSFC). This work began with the important observation that, even at rest, fluctuations of the fMRI BOLD signal correlate in anatomically specific ways across the brain. For example, many regions that relate to motor function are strongly correlated with one another in the absence of any task. The organization of RSFC has been demonstrated to provide insight into common functional relationships between many brain regions beyond the motor system. The second

Box 1. Current Status of the Field

- The classic notion of "cognitive architecture" postulated the basic idea that human cognition is a computational process carried out as a series of operations on symbolic representations. This view explicitly embraced functionalism, which implies that cognition can be studied and understood without much (if any) reference to its biological basis.
- In parallel, understanding of the neural bases of human cognition was materially advanced through the mechanistic study of neurocognitive circuits in nonhuman primates and the application of noninvasive imaging technology in the human brain. An enduring achievement was the discovery of task-specific activations of specific neuronal populations and localized brain regions aided by the development of statistical tools for mass-univariate region-based analyses.
- Today, ROI-based analyses are increasingly complemented by an alternative perspective, based on the notion that cognitive function emerges from the dynamics of extended cortical and subcortical networks. Unlike classic "neural nets," these networks have a distinct anatomical basis in the brain's structural connectivity (the connectome) and manifest through coherent fluctuations in neural activity at rest as well as distributed patterns of activation in task states.
- Network approaches are appealing because they (1) transcend local and global function, as connectivity simultaneously accounts for regional differences (segregation) and interregional signaling and communication (integration); (2) can provide a common framework for describing both endogenously and exogenously driven neuronal activity and their mutual relations; and (3) can be applied across spatial scales, from neurons to regions, and even across different data domains, from genes to neural dynamics to social interactions.
- Current challenges for network approaches include the development of novel data acquisition and analytic methodologies that can cope with the ever-increasing volume and complexity of "big data." Mapping cognition to the brain will increasingly rely on sophisticated multivariate statistical algorithms involving clustering, module detection, and other dimension reduction approaches. In future, the growing application of "data-driven" machine learning or pattern recognition approaches could substantially benefit from added constraints coming from the rich tradition of cognitive anatomy.

main section of the article explores some basic observations and properties that these studies have provided.

In the final section we explore the relationship between structural and functional networks that we think is fundamental for understanding the biological mechanisms that underpin cognitive architectures (see Box 2). While recent work has uncovered some relationships between these two types of brain networks, many aspects of how structural connections constrain functional networks, and how these constraints play out on multiple timescales, remain incompletely understood. Integrative studies of networks across structure and function are an important goal for the future, and we end our article with charting some tentative footsteps down this path.

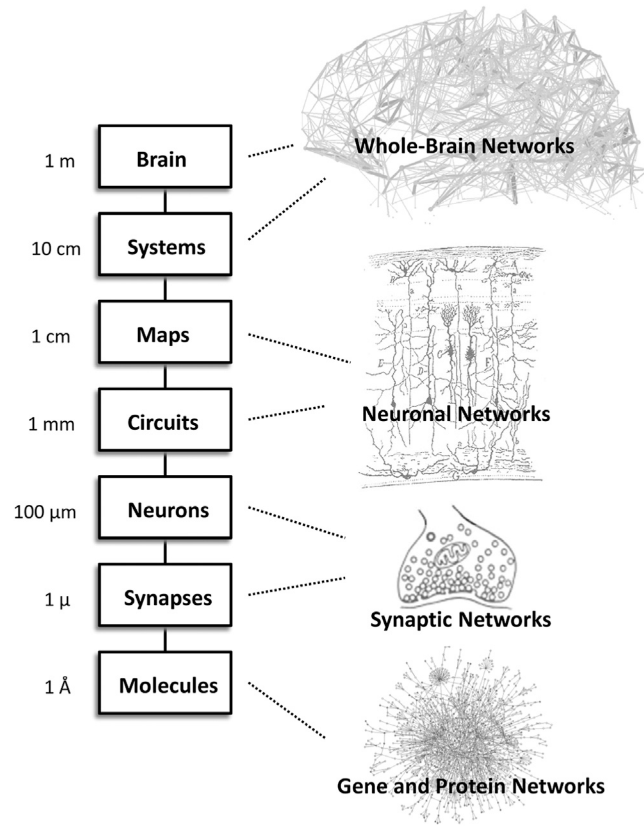

Figure 1. Schematic Representation of Levels of Structure within the Nervous System
The large-scale analyses discussed in the paper focus on the levels of areas/maps and systems, but network ideas clearly extend down to the level of neuronal circuits and populations, individual neurons and synapses, as well as genetic regulatory and protein interaction networks. Adapted from a similar illustration in Churchland and Sejnowski (1992) and Sejnowski and Churchland (1989).

Anatomical Networks

The search for anatomical principles of neurocognitive networks has a long history, extending at least as far back as the 19th century and marked by the development of new histological methods and new ideas about the localization of brain function. Deeply rooted in this tradition is the view that human cognition relies upon an intricately connected cortical architecture that underpins its various functional capacities. The fundamental idea that cognitive architecture has a structural foundation remains valid today.

Insights from Nonhuman Primates

Preceding the recent expansion of studies utilizing fMRI methodology in humans, the biological foundations of cognition were mainly explored from the vantage point of large-scale anatomy and cellular physiology in model organisms such as nonhuman primates. These classic approaches have led to the formulation