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# Understanding Cognition Through Large-Scale Cortical Networks


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*Abstract*

An emerging body of evidence from a number of fields is beginning to reveal general neural principles underlying cognition. The characteristic adaptability of cognitive function is seen to derive from large-scale networks in the cerebral cortex that are able to repeatedly change the state of coordination among their constituent areas on a subsecond time scale. Experimental and theoretical studies suggest that large-scale network dynamics operate in a metastable regime in which the interdependence of cortical areas is balanced between integrating and segregating activities. Cortical areas, through their coordination dynamics, are thought to rapidly resolve a large number of mutually imposed constraints, leading to consistent local states and a globally coherent state of cognition.



*Keywords*

cognitive neuroscience; cerebral cortex; neural networks; coordination dynamics; phase synchronization; constraint satisfaction


Do all of your thoughts arise in the same way in your brain? Is there a common neural mechanism for all cognitive functions? Until recently, definitive answers to such questions were not available. Now, advances in cognitive neuroscience are revealing common principles of neural organization and function that may underlie all cognitive function. Although understanding brain function at the cognitive level has lagged behind understanding at the cellular and molecular levels in the past quarter-century, cognitive neuroscience is beginning to shed light on some fundamental issues in psychology. This progress is due not only to the revolution in functional brain imaging, but also to important developments in neuroanatomy, neurophysiology, behavioral neurology, and theoretical neuroscience.

This confluence of approaches has brought about new insights into the difficult puzzle of how cognitive function is accomplished in brains. Current understanding emphasizes a balance between local processes (i.e., processes that occur within spatially discrete sets of neurons) and global processes (i.e., large-scale processes involving larger sets of interconnected neurons widely distributed across the brain). With respect to that critical organ of cognition, the cerebral cortex, a key insight has been that, although elementary cognitive operations reside in individual cortical areas, complex cognitive functions require the joint operation of multiple distributed areas acting in concert. The large-scale cortical network is conceived as a dynamic neurocognitive entity that incorporates both local and global function. This conception, representing a synthesis of historically opposed theories of neurocognitive function, provides a foundational principle for investigating the neural basis of thought.

## THE ANATOMICAL FRAMEWORK

Anatomical studies have been a driving force in the modern investigation of large-scale cortical networks. A deepening understanding of which cortical areas are connected has allowed the construction of detailed diagrams of large-scale cortical circuits (Felleman & Van Essen, 1991). The observed patterns of interconnectivity of cortical areas suggest that each area has a unique set of additional areas with which it is connected (i.e., its connection set). Most known connections, by far, are reciprocal, meaning that an area both sends output to and receives input from its connection set. These facts suggest that the activation of a cortical area will tend to engage other areas in its connection set, and that, by return pathways, those areas will tend to exert influences back on the first area. These interactions (referred to as reentrant processing), in concert with direct inputs and modulating influences from a variety of brain structures located beneath the cortex, are likely to exert profound effects on the local processes taking place in each cortical area (Tononi, Sporns, & Edelman, 1992). We can conclude that the large-scale connectional structure of the cortex supports complex patterns of interareal interaction that promote widespread influences among cortical areas.

## FUNCTIONAL RELATIONS

The involvement of large-scale cortical networks in cognition is suggested by numerous functional brain-mapping studies, employing functional magnetic resonance imaging, positron emission tomography, or single-photon emission computed tomography, which have demonstrated that multiple distributed cortical areas are coactivated during cognitive tasks. Detailed observations of brain-injured patients have further supported this conclusion (Mesulam, 1990). The fact that areas which are coactivated during cognitive function are likely to be reciprocally connected suggests that their activities do not simply take place concurrently, but are also interdependent because of reentrant processing. However, the aforementioned imaging techniques are only indirect indicators of neural activity and its interdependence. Direct evidence for the functional interdependence of multiple distributed cortical areas comes from studies that measure the phase synchronization[2] of electrical activity in the cortex (Bressler & Kelso, 2001; Varela, Lachaux, Rodriguez, & Martinerie, 2001). Interdependence is detected as a high level of phase synchronization of electrical waves generated by neuronal populations in different cortical areas. These waves are recorded either from within the skull as local field potential signals or from the scalp as electroencephalographic (EEG) signals. Phase-synchronization experiments have revealed specific patterns of cortical interdependence corresponding to identifiable cognitive states (Ding, Bressler, Yang, & Liang, 2000).

What is the functional significance of large-scale patterns of phase synchronization? To answer this question, we need to consider their relation to the local patterning of activity within individual cortical areas. High-density field potential recordings from sensory cortical areas have revealed coherent spatial activity patterns corresponding to an area's perceptual state (Ohl, Scheich, & Freeman, 2001). These patterns are produced by the internal dynamics of the local cortical area, and are given shape by the synaptic connections formed locally between neurons in the area during learning. The local patterning of activity in the individual area does not, however, occur in isolation. If connected areas impose constraining influences on one another through reentrant processing, the expression of information in a local area will depend heavily on its reentrant interactions with the areas of its connection set. Thus, the functional interdependence of distributed cortical areas should be reflected not only by their large-scale phase synchronization but also by the informational consistency of their local spatial activity patterns.

## THEORETICAL CONSIDERATIONS

Can local and large-scale influences be orchestrated in the cortex in such a way as to support cognitive function? The science of complex systems, which seeks to explain the cooperative behavior of systems having large numbers of interacting components, may provide guidance in addressing this question. An important topic of interest in this field is that of *coordination dynamics*, which refers to the manner in which the interdependence among the parts of a system changes with time (Kelso, 1994). Systems displaying a high degree of complexity (Tononi, Sporns, & Edelman, 1994) have been shown to have *metastable* coordination dynamics, characterized by a balanced interplay of integrating and segregating influences.

A characteristic feature of metastable systems is *intermittency*: The degree of coordination of their component parts changes over time, sometimes remaining low for a considerable time and then suddenly increasing. The cerebral cortex is observed to display intermittency in the coordination of its areas through changes in the large-scale phase synchronization just discussed (Bressler & Kelso, 2001). Distributed sets of cortical areas may remain uncoordinated for some time, and then, with a change in cognitive state, suddenly become coordinated through a rapid increase in phase synchronization. Metastability may allow the cortex to enter into many different states of coordination of its constituent areas without becoming trapped in any one state. This would provide the cortical system with the flexibility necessary to rapidly adapt at both large-scale and local levels to the changing contingencies required for cognitive function. This flexibility may be advantageous for cognition if it allows the cortex to carry out a variety of tasks simply by changing the coordination states of its networks.

## COGNITIVE IMPLICATIONS

It is reasonable to assume that large numbers of interacting cortical areas impose constraining influences on one another at each stage of cognitive processing. Because some influences are undoubtedly in conflict, whereas others are mutually consistent, a mechanism is needed to mutually satisfy these multiple constraints in order to produce a unified and coherent cognitive state (Thagard, 2000). To create a cognitive state that is in harmony with the current states of the external environment and body, this constraint-satisfaction mechanism should produce a rapid consensus among sets of cortical areas, allowing them to reach compatible internal states. Such a mechanism should be selective both at the large scale, by allowing specific large-scale networks of areas to coordinate their activity through phase synchronization, and at the local scale, by the concurrent expression of consistent spatial activity patterns in each of those distributed areas.

It is generally believed that cortical areas, because of their unique topological positions in the overall connectional structure of the cortex, process information in specialized cognitive domains. The specification of these domains may be general, such as visual, auditory, tactile, or motor, as well as more specific, as in the primary sound and speech-sound subdivisions of the auditory domain. The large-scale coordination of cortical areas during learning could explain the common human ability to associate information from different domains. If we assume the strengthening of synapses between neurons in different areas that are coordinated during perception (Squire & Alvarez, 1995), then the repeated coordination of mutually consistent patterns in a set of areas would cause the association of those patterns to become consolidated. Thus, to take a simple example, repeated coordination of higher-order visual areas representing faces and higher-order auditory areas representing names could lead to the consolidation of face-name associations. In like manner, the repeated coordination of cortical areas representing multiple cognitive domains would lead to the consolidation of even more complex cognitive associations.

The conjunction of consistent constraints impinging on a single cortical area has been described as a way to produce *context* for processing in that area (Phillips & Singer, 1997). From this perspective, the coordination of large-scale networks in variable configurations provides the potential for the dynamic creation of a wide range of local contexts for each cortical area's operations in the face of different external and internal environments. Likewise, the coordination of large-scale networks in reproducible configurations when environments are similar may create reproducible local contexts corresponding to those environments.

The basic mechanism of mutual constraint satisfaction leading to the consensual conjunction of consistent local activity patterns in a coordinated large-scale network has the capacity to support a diversity of cognitive functions. In visual perception, the mechanism may afford the flexible conjunction of different visual feature domains (e.g., color, shape, or motion) processed by the various visual cortical areas. It offers a means by which these areas could act together in a coordinated and efficient manner to reach a consistent interpretation of oftentimes ambiguous visual images. In motor production, basic control functions for force, direction, and velocity, as well as higher controls for sequencing and rhythm, are distributed in a variety of frontal cortical areas. In this realm, too, the flexible and consistent conjunction of local motor activity patterns, when coordinated within large-scale networks, would allow the dynamic control of motor output by multiple control functions acting in concert. For higher cognitive functions in general, mutual constraint satisfaction in coordinated large-scale networks may be a common mechanism for rapidly reaching a unified consensus among elementary cognitive operations represented in widely distributed cortical areas.

## LOOKING TO THE FUTURE

The theory of large-scale cortical networks draws on findings from a number of different disciplines to offer an integrated approach to understanding the neural basis of cognitive function. Clearly, though, this theory is still in a rudimentary stage of development, and future progress will depend on advances in these various disciplines. In the anatomical arena, the basic concept of "cortical area" is being subjected to intense scrutiny and will undoubtedly undergo continued elaboration for the foreseeable future. Furthermore, a great deal of effort is being directed toward better understanding the anatomical connection patterns of the whole cortex.

A number of corresponding advances are required on the physiological front. To test the relation between pattern-formation processes in different cortical areas, it will be necessary to analyze simultaneous high-density neural recordings from multiple areas in animals trained on a variety of cognitive tasks. It will also be necessary to investigate differences in frequency ranges between large-scale and local processing in the cortex. Coordination relations between cortical areas will need to be described in terms of the layers of gray matter that are involved. Insight into the relation between large-scale cortical networks and processes in noncortical brain areas is also a critical goal, and will require the analysis of simultaneous recordings from cortex and those other areas. Moreover, methods for measuring phase synchronization across the cortex of humans will need marked improvement, and the relation between phase synchronization and blood-flow changes will need to be explored.

As important as these issues are, continued growth in understanding the role of large-scale networks in cognition will additionally require advances in data-analysis techniques and artificial network modeling. One promising path is the development and application of improved methodologies for measuring causal influence in the cortex (Liang, Ding, Nakamura, & Bressler, 2000), and the correlation of the results with computational models of the flow of causal influence in large-scale artificial networks (Pastor et al., 2000). Progress is also being made in the construction of artificial network simulations that model pattern constraint through interactions between cortical areas. One current approach to this problem draws on formalisms of statistical inference to implement these constraints (Koechlin, Anton, & Burnod, 1999).

Cognition is central to all human endeavors. The identification of a common underlying neural mechanism and its deep theoretical elucidation are goals with enormous implications for society. The field of artificial intelligence clearly stands to benefit from a mechanistic understanding of cognition. Perhaps more important, the long-term success of treatments for debilitating cognitive impairments may depend just as much on progress at the large-scale level as at the molecular. What is heartening is that the prospect for realizing these goals has never before shown such promise.

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## Notes

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2. Phase synchronization is the tendency for waves of neural activity from different neurons, or populations of neurons, to be aligned in time. Phase synchronization is widely considered as a possible explanation for the perceptual grouping of features in the visual scene into discrete objects, a process called binding, but may also subserve the coordination of neural activity underlying a variety of cognitive functions.

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