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Operational principles of neurocognitive networks

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Abstract

Large-scale neural networks are thought to be an essential substrate for the implementation of cognitive function by the brain. If so, then a thorough understanding of cognition is not possible without knowledge of how the large-scale neural networks of cognition (neurocognitive networks) operate. Of necessity, such understanding requires insight into structural, functional, and dynamical aspects of network operation, the intimate interweaving of which may be responsible for the intricacies of cognition.

Knowledge of anatomical structure is basic to understanding how neurocognitive networks operate. Phylogenetically and ontogenetically determined patterns of synaptic connectivity form a structural network of brain areas, allowing communication between widely distributed collections of areas. The function of neurocognitive networks depends on selective activation of anatomically linked cortical and subcortical areas in a wide variety of configurations. Large-scale functional networks provide the cooperative processing which gives expression to cognitive function. The dynamics of neurocognitive network function relates to the evolving patterns of interacting brain areas that express cognitive function in real time.

This article considers the proposition that a basic similarity of the structural, functional, and dynamical features of all neurocognitive networks in the brain causes them to function according to common operational principles. The formation of neural context through the coordinated mutual constraint of multiple interacting cortical areas, is considered as a guiding principle underlying all cognitive functions. Increasing knowledge of the operational principles of neurocognitive networks is likely to promote the advancement of cognitive theories, and to seed strategies for the enhancement of cognitive abilities.

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1. Introduction

The gap between knowledge of the brain and of the mind can only be bridged with understanding of neural systems that perform cognitive operations. According to this perspective, the neurocognitive network is a critical concept for uniting neuroscience and cognitive science. Neurocognitive networks are integrated large-scale neural systems that execute the high-level brain functions of which cognition is comprised (Luria, 1962; Başar et al., 1975a, b; Goldman-Rakic, 1988; Mesulam, 1990; Fuster, 1995, 2003; Bressler, 1995, 1999, 2002, 2003a,b; Bullmore et al., 1996; Mountcastle, 1998; McIntosh, 2000; Nyberg et al., 2000; Hirsch et al., 2001; Başar and Karakaş,

2004). Although multitudinous in the variety of their expression, it is not unreasonable that these networks should follow common laws of operation, given the neuroanatomical and neurophysiological similarity that exists throughout the brain. The intent of this article is to consider what general principles might guide the operations of neurocognitive networks.

The approach to be followed is based on the tenet that there exist fundamental correspondences among the anatomical structure of neurocognitive networks, their functions, and the dynamic patterning of their active states (Arbib et al., 1997). The anatomical architecture of the network provides the basic substrate of interconnected brain regions that, by way of their interactions, are able to express particular functions, different functions depending on the specific subsets of connected regions that cooperate. The functions of the neurocognitive network are expressed in real time by the coordinated actions of cooperating areas, with the states of coordination changing dynamically (Bressler and Kelso, 2001).

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In this process, the active states of neurocognitive networks are selectively structured in three key dimensions (Fig. 1). First, they are spatially structured by the combined activation of discrete, local cortical and subcortical neuronal assemblies. Next, they are temporally structured by the changing combinatorial arrangement of active assemblies during the expression of cognitive functions. Finally they are coordinatively structured by the specifically patterned joint actions of activated assemblies. The presumption that neurocognitive networks do in fact implement cognitive function further implies that the expression of cognitive function occurs as structured states, with a structure corresponding to that of the active states of neurocognitive networks. Thus, by careful examination of the anatomical, functional, and dynamical aspects of neurocognitive networks, we anticipate the eventual emergence of a neural language for describing cognition.

2. Anatomical structure of neurocognitive networks

We consider the anatomical organization of neurocognitive networks to be of prime importance in shaping the cognitive operations of the brain. Neural networks may be described at various scales, from small assemblies of neurons to the whole brain. For the purpose of this review, we focus on the cerebral cortex as an essential anatomical component of neurocognitive networks, treating network organization in terms of the long-range connectivity of local cortical areas.

The cerebral cortex is deemed to be a structure of prime importance for human cognition, with its component areas specialized for many different functions. Parcellation of the cortex, though, is not obvious. Unlike many subcortical structures, in which neurons are packed into nuclei, the cortical sheet appears to the casual observer as a dense homogenous substratum with no obvious demarcation of its component areas. Yet, from decades of painstaking anatomical tracing studies, the anatomical structure of the cortex is known to have an elaborately parcellated nature. From a functional perspective, parcellation of the cerebral cortex is necessitated by evolution-

ary pressure: in the space-constrained skull, more computational efficiency is obtained by grouping together neurons with similar function and denser interactions, so that the overall number of interconnections is minimized (e.g., Murre and Sturdy, 1995; Chklovskii, 2000).

2.1. Local cortical area networks

Although the neuron is the primary cellular unit of cortical architecture, there is reason to believe that it is not the major operational effector of neurocognitive function (Bressler, 1995). In most circumstances, isolated cortical neurons are ineffective in triggering responses in target areas to which they project (Gabbott et al., 1987; Braitenberg and Schuz, 1991). It is likely that the joint action of a local assembly consisting of several tens to hundreds of neurons is minimally necessary to impact a distant local assembly (Bush and Sejnowski, 1994). The cortical minicolumn (Szentagothai, 1975; Mountcastle, 1978, 1997) is an anatomically distinct circuit of one–two hundred neurons (Fig. 2, left), oriented perpendicularly to the surface of the cortex, within which the autonomy of individual neurons is reduced (Buxhoeveden and Casanova, 2002) due to dense intrinsic connectivity. Thus, the minicolumn is a likely candidate as a structural component corresponding to a circumscribed neuronal assembly.

Perhaps 50–80 minicolumns are aggregated into a macrocolumn (Fig. 2, middle), forming a structure of interest for elementary cognitive operations (Mountcastle, 2003). In sensory areas, these columns have been identified as functional units (also called modules), because the tuning properties of their neurons are quite homogenous within, but manifest sharp transition between neighbors, as shown by normal or oblique microelectrode penetrations (Mountcastle, 1978). The existence of cortical macrocolumns has also received some anatomical confirmation, with connectivity between minicolumns provided by dense short-range horizontal connections (Mountcastle, 1997). The dense short-range interconnection of a set of macrocolumns in a local area of the

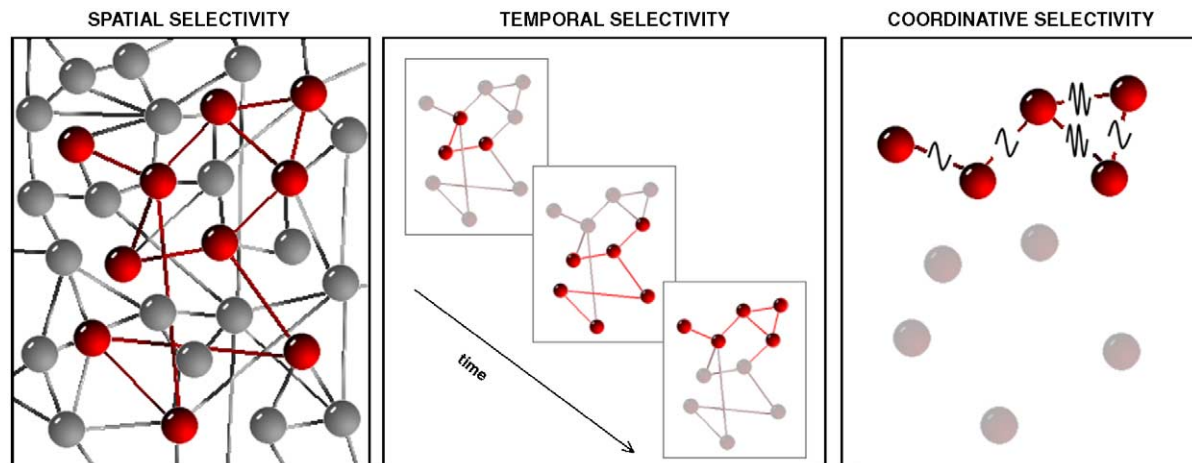


Fig. 1. Structure of the neurocognitive network. The neurocognitive network is configured by the joint activation of a set of local area networks (spatial selectivity). The configuration changes at successive instants of time (temporal selectivity). Specific patterns of coordination occur between co-active local area networks (coordinative selectivity).

cerebral cortex, with common input and output pathways, gives rise to a local cortical area network (Fig. 2, right). Connectivity between the neighboring macrocolumns decays with distance, but connectivity in primary visual cortex has been shown to increase again for specific target columns within the cortical area, forming patchy horizontal connections (Malach et al., 1993; Weliky and Katz, 1994).

Although originally defined by cytoarchitectonic methods as local neuronal populations distinguished by uniform laminar histology (Brodmann, 1909; von Economo and Koskinas, 1925; Zilles et al., 2002), definition of the local cortical area now depends as much on functional mapping as on structural mapping (see Mesulam, 1998 for a brief discussion). The extent of overlap between structural and functional maps in the cortex is an active topic of investigation, and depending on the desired granularity, a highly variable number of areas can be distinguished (Matelli and Luppino, 2004). For our purposes, the local cortical area network is taken to be a highly interconnected set of neighboring macrocolumns, sharing common input and output pathways, and showing a specialized low-level function. As such, the local cortical area network may be posited as a basic anatomical component of neurocognitive function.

2.2. Large-scale cortico–cortical connectivity

Charting the large-scale connectivity of the brain is an ongoing endeavor that will likely continue into the foreseeable future. One aspect of this connectivity is nonetheless clear: it is decidedly incomplete or sparse (i.e., all areas are not directly connected one to another). The sparseness of the brain's large-scale connectivity matrix allows the possibility of structural bottlenecks and preferred pathways which constrain the flow of activity in specific patterns, contributing critically to network functional expression and coordination dynamics. This sparsely connected anatomical structure may provide a critical edifice

within which the brain's cognitive functions are manifested (Sporns and Kötter, 2004).

Neuroanatomical studies of large-scale brain connectivity attempt to decipher patterns of long-range axonal projections. Two current approaches to the study of large-scale connectivity are active. One approach, with deep historical roots, focuses on a very small parcel of cortex (DeFelipe et al., 2002), and examines either its local or long-range connectivity. The methods used in this approach are especially suited for characterizing network connections, including determination of hierarchical level from the laminar profile of input and output connections (Rockland, 2004). Such studies typically sample only relatively small regions of tissue and numbers of fiber tracts.

A second approach is devoted to the systematic modeling of large-scale, or even whole-brain, connectivity. A large proportion of these studies concentrate on the interconnectivity of local area networks. The methods employed include meta-analysis of large collections of pathway tracing studies (Felleman and Van Essen, 1991; Scannell et al., 1995, 1999), visualization of connectivity matrices, hierarchical cluster analysis, structural equation modeling and path analysis (Scannell et al., 1995; Passingham et al., 2002), creation of probabilistic brain maps (Stephan et al., 2000), graph theoretic modeling (Sporns et al., 2000, 2004), and modeling of activity propagation (Kötter and Sommer, 2000). Such theoretical studies have revealed new characteristics of large-scale brain connectivity, such as scale-free (Eguíluz et al., 2005) and small-world (Chialvo, 2004; Sporns and Zwi, 2004) properties. Overall, this approach is especially suited to identifying and characterizing patterns of long-range connectivity, but sacrifices the fine details of connectivity.

Diffusion Tensor Imaging, a non-invasive method being developed to allow large-scale white-matter tractography (Le Bihan et al., 2001; Hagmann et al., 2003), also appears to have potential applications to the analysis of large-scale connectivity.

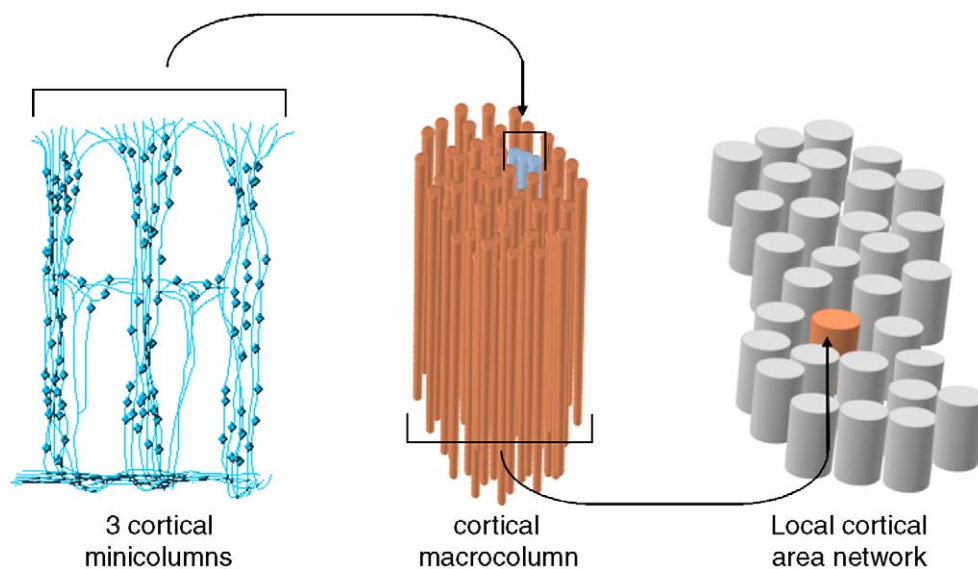


Fig. 2. Depiction of the local cortical area network and its components.

2.3. Experience-dependent modification of large-scale cortico–cortical connectivity

Developmental studies suggest that a selective strengthening of cortico–cortical pathways occurs, along with a decrease in the total number of synapses, as the anatomical connectivity of neurocognitive networks evolves with experience over the lifespan (see Fig. 3). Ontogenetic factors that shape network connectivity include neurogenesis and programmed neuronal death, growth and retraction of axonal branches (Cowan et al., 1984; O’Leary and Koester, 1993), and synaptogenesis and synaptic degeneration (Changeux and Danchin, 1976; Edelman, 1987; Changeux and Dehaene, 1989). Overall, large-scale neurocognitive network connectivity is suggested to undergo refinement over the lifespan by the selective sculpting of phylogenetically established pathways through processes that increase the selectivity of cortico–cortical synaptic connections (Fuster, 2000).

3. Functional expression of neurocognitive networks

The intricate anatomical connectivity of the cerebral cortex provides the basis for an enormous space of possible combinations of co-active areas. The guiding concept in this section is that the functional expression of a cognitive operation requires co-activation of a specific combination of interconnected local area networks. The co-activated local area networks represent a subset of the total set of possible networks in the cerebral cortex. The members of this subset act in concert as a neurocognitive network to express the cognitive operation, with each local cortical area network making its own specialized contribution.

In the present section, we first discuss local cortical area network specialization, and then consider the question of identifying the specific local networks that participate in a

neurocognitive network that is expressing a cognitive operation (spatial selectivity). This discussion will necessarily involve methodologies from neuropsychology and functional brain imaging that characterize cortical activity on a slow time scale of seconds to minutes. In Section 4, we will then consider how methods with higher (sub-second) temporal resolution are used to understand the dynamic evolution of the configuration of co-active areas (temporal selectivity) involved in cognitive function, and their specific coordination patterns (coordinative selectivity).

3.1. Local cortical area network function

The investigation of local area network function in the cerebral cortex has a long history in sensory and motor neurophysiology, traditionally relying on electrical recording of single neuron activity as single-unit spiking, and neuronal assembly activity as multi-unit spiking and local field potentials (Adrian, 1928; John et al., 1969; Mitzdorf, 1988; Shoham and Nagarajan, 2004). More recently, event-related optical imaging has provided complementary insights into local area network function, allowing spatial differentiation of local networks that may be interdigitated within the same area (Blasdel and Salama, 1986; Malach et al., 1993; Arieli et al., 1996; Villringer and Chance, 1997; Tsodyks et al., 1999). In sensory systems, much of this work has aimed to define preferred stimulus features for single neurons (Granit and Svaetichin, 1939; Galambos and Davis, 1943; Barlow, 1972; see also Galambos, 2006-this issue). In this approach, neurons are monitored in sensory cortical areas of animals exposed to a variety of sensory stimuli, and neuronal function is inferred from the stimulus features that cause the neuron to respond by an increase in spike rate. The function of a local network may then be extrapolated from the function of its constituent neurons.

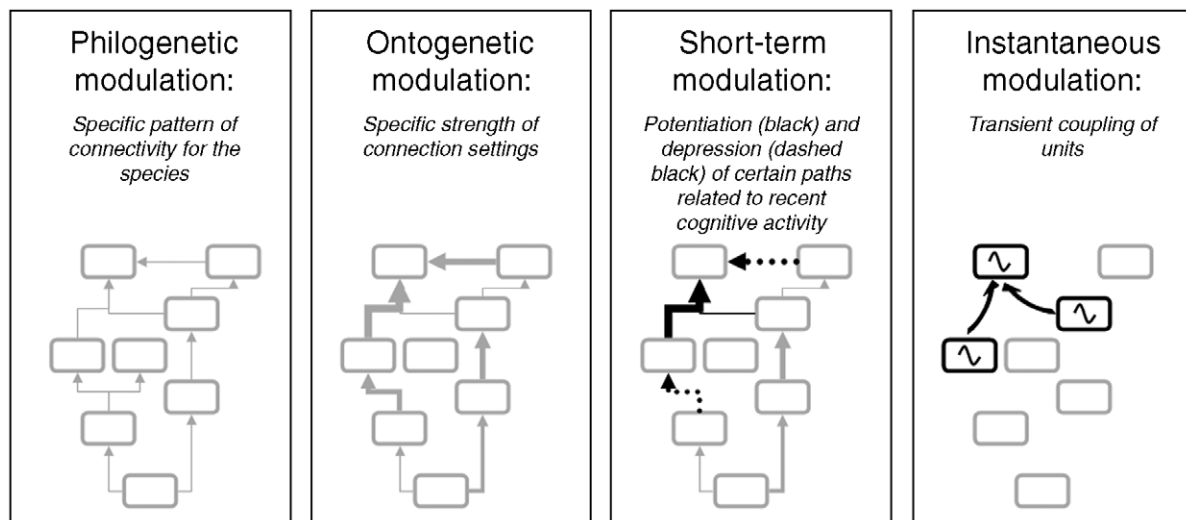


Fig. 3. Modulation of the neurocognitive network. The basic pattern of anatomical connectivity is determined by evolution of the species (phylogenetic modulation). This anatomical pattern undergoes maturational and experience-dependent modulation over the life span (ontogenetic modulation). The anatomical patterning may undergo synaptic modulation on a short time scale of seconds to minutes with respect to cognitive factors such as emotion, attention, and working memory (short-term modulation). Sub-second modulation occurs by the transient coordination of neuronal assembly activity (instantaneous modulation).

3.2. Large-scale cortical network function

The technique having the longest history in the study of large-scale cortical function is clinical analysis of the functional consequences of focal brain lesions in patients (Broca, 1861; Penfield and Milner, 1958; Luria, 1962, 1973; Lezak, 1995; Kolb, 1999; Young et al., 2000). Beginning in the nineteenth century, clinical studies were supplemented by studies of intentional lesions in animals. The goal of this form of analysis is to localize critical cortical areas involved in a particular cognitive task, owing to correspondences between structural damage and cognitive deficits. This approach has established that, in general, a local cortical area network shows *multifunctionality*: its contribution to cognitive operations consists of a specific set of functions rather than a single specific function. This finding leads to the overall conclusion that a one-to-one correspondence between cortical location and function does not exist.

Complex functional relations of neurocognitive networks are often revealed by focal lesions of the cerebral cortex. During the acute phase following a lesion, structure-function relationships are blurred by the phenomena of diaschisis, the functional silencing of intact tissue due to disconnection from the damaged tissue (Von Monakow, 1914). Diaschisis suggests that the proper functioning of local area networks is through interactions with other connected local area networks (Bressler, 2002; Passingham et al., 2002). In simulation studies (Young et al., 2000), a local network's vulnerability to dysfunction due to a remote lesion depends on its pattern of connectivity within the large-scale network: (a) local networks with relatively few connections have low vulnerability to lesions in other local networks to which they do not directly connect, but very high vulnerability to lesions in those to which they do directly connect; whereas (b) local networks with relatively many connections are less affected by lesions in local networks to which they directly connect, but are more affected by lesions in those to which they do not directly connect. These results suggest that the function of a local area network depends on its pattern of synaptic interconnectivity with other local networks.

From these considerations, we conclude that local function may only be interpreted in terms of large-scale functional expression, a conclusion also supported by studies demonstrating the functional degeneracy of local cortical networks, i.e., their ability to substitute for one another in the expression of a given cognitive operation (Wall, 1977; Atwood and Wojtowicz, 1999; Tononi et al., 1999; Price and Friston, 2002). While the correspondence between large-scale networks and integrated functions is relatively clear and consistent, a direct correspondence between local cortical area networks and elementary functions (also called “primitives” in the sensory domain) may not be possible. Accordingly, a given local cortical area network may express activities related to more than one function, and its integrated functional expression may only be achieved when it exerts its contribution in the presence of concurrent activity in interconnected areas within the large-scale network.

From our perspective, the importance of functional neuroimaging methods (fMRI, PET), which have revolutionized the study of large-scale cortical network function (Horwitz et al.,

1999, 2000; Taylor, 2001; Donaldson, 2004; Ramnani et al., 2004), is that they reveal the spatial organization of neurocognitive networks as maps of co-active local area networks. In contrast to the localizationist viewpoint (Bressler, 2003a), which regards locally circumscribed brain areas as having unitary functions, our perspective considers functional neuroimaging as disclosing the set of distributed areas that form a neurocognitive network. A principal result from the vast majority of imaging studies is that every cognitive process is supported by a widespread constellation of activated areas extending throughout the brain. Although this conclusion may often be obfuscated by the drastic restriction in field of view that ensues from excessive significance thresholding or region-of-interest selection, functional neuroimaging results generally support the existence of distributed neurocognitive networks in the brain (see Fuster, 2006-this issue).

A relatively new trend in functional neuroimaging analysis, that is entirely compatible with this view, is the investigation of “functional connectivity” in the brain (Friston, 1994; Bullmore et al., 1996; Horwitz et al., 1999; Horwitz, 2003; Fingelkurts et al., 2005), measuring statistical correlations between the levels of activation in different areas in relation to cognitive function (Gerstein et al., 1978; Aertsen et al., 1989; Bullmore et al., 2000; Harrison et al., 2003). Functional connectivity measurements have the potential to reveal the functional interdependence of neurocognitive networks. That is, they can show which brain areas are functionally correlated in the expression of a cognitive function, rather than being merely co-active on average. This approach is most effective for determining the functional connectivity of brain regions on a slow time course when it is applied to event-related fMRI recordings (Newman et al., 2002). Nonetheless, the relatively poor temporal resolution (seconds to minutes) of the hemodynamic and metabolic signals on which functional neuroimaging methods are based is a major shortcoming in the analysis of network timing relations, despite the great utility of these techniques for charting spatial relations. This poor temporal resolution causes the contributions of various brain areas to a cognitive operation to be cumulative over the time scale of seconds to minutes (Hernandez et al., 2002), meaning that sub-second changes in the coordination relations of neural activity in different brain areas are lost. Thus, the coordinative selectivity of neurocognitive networks cannot be effectively realized by network analysis based solely on the functional neuroimaging methods currently in existence. The investigation of coordination relations in neurocognitive networks on a finer time scale requires the analysis of magnetic or electric brain signals, which is the topic of the next section.

4. Dynamics of neurocognitive networks

We consider neurocognitive networks to be flexibly adaptive to the rapidly changing computational demands of cognitive processing (Bressler, 1995). This adaptivity requires that the neurocognitive network be able to organize and reorganize in different patterns of coordination as computationally required on a sub-second time scale. The large-scale anatomical connectivity of the cerebral cortex provides a richly intricate structure within

which the constituent local area networks have an enormous potential for coordination in a multitude of different patterns. The theory of coordination dynamics (Kelso, 1995; Bressler and Kelso, 2001) provides insight into the dynamic characteristics of such interacting complex neural systems.

Grossberg (2000) has appropriately emphasized that for a system to successfully adapt its behavior to an ever-changing environment, it must be endowed with the twin properties of stability and plasticity. Insight into this problem may be sought in the principles of self-organization (Haken, 1977; Kelso, 1995; Friston, 2000), which apply to a system of interacting units that form globally ordered patterns as a result of their mutual constraints. It has been suggested that the brain is a self-organizing system that is capable of balancing the contrasting requirements of stability and plasticity by operating in a state of *metastability* (Kelso, 1995; Friston, 1997; Bressler and Kelso, 2001; Fingelkurts and Fingelkurts, 2004). Metastability allows such a system to operate in an intermediate regime between complete stability, which would lack flexibility, and complete plasticity, which would lack useful organization (Atlan, 1979; Paillard, 1983). A metastable system can manifest a state that is quasi-stable, and it can also flexibly switch to another such state. In the terminology of nonlinear dynamics, the metastable system trajectory can visit the vicinity of quasi-stable attractors, but never settles into a stable attractor because stable attractors do not actually exist in the energy landscape (Bressler and Kelso, 2001).

It has been postulated that the quasi-stable attractor state of the neurocognitive network is a state of coordination in which a set of interconnected local area networks are able to coordinate their activities within a matter of milliseconds (Bressler, 1999, 2002, 2003a,b, 2004). According to this hypothesis, local area networks in a neurocognitive network impose locally patterned spatiotemporal constraints on one another by long-range interactions and thereby rapidly self-organize into large-scale patterns of coordinated activity. The imposed constraints provide a *neural context* (Watt and Phillips, 2000; McIntosh, 2004) for the local processing within each interacting local area network. The neurocognitive network “relaxes” into a quasi-stable attractor state as some of its local area networks reach consistent local spatiotemporal activity patterns. The quasi-stable coordination state that is reached involves the exclusion of non-consistent local area networks as well as the inclusion of consistent ones, and thereby enables the neurocognitive network to express informational coherence and incoherence relations (Thagard and Verbeurg, 1998).

By operating in a metastable regime, neurocognitive networks are further postulated to evolve through a progression of quasi-stable coordination states, each lasting on the order of a few hundred milliseconds or less, as cognitive processing progresses. Assuming that each such state of the network corresponds to a microstate of cognition (McClelland et al., 1986; Koenig et al., 2002), the evolution of states of the neurocognitive network thereby endows cognitive processing with the ability to progress through a series of microstates, eventually reaching a computational solution, a decision, or a behavioral goal.

A great deal of experimental evidence points to the phase synchronization of oscillatory neuronal assembly activity as a likely mechanism for the fast-time long-range coordination of cortical neuronal assembly activity (Bullock et al., 1995; Başar et al., 1999; Klimesch, 1999; Rodriguez et al., 1999; von Stein et al., 1999; Haig et al., 2000; Brown and Marsden, 2001; Keil et al., 2001; Tallon-Baudry et al., 2001; Bhattacharya and Petsche, 2002; Freeman and Rogers, 2002; Brovelli et al., 2004; Gross et al., 2004). The fact that this oscillatory activity exists at a wide range of oscillation frequencies has long motivated the suggestion that frequency depends on the recirculation time of activity in pathway loops, with lower frequencies corresponding to longer circulation times and loop distances (Bressler and Freeman, 1980; von Stein and Sarnthein, 2000; Başar et al., 2001; Swindale, 2003). A number of authors have proposed that synchronized oscillatory activity plays a central role in the selective coordination of neurocognitive networks (Pulvermüller et al., 1997; Karakaş et al., 2000; Gross et al., 2001; Engel et al., 2001; Varela et al., 2001; David et al., 2003; Schack et al., 2003; Ward, 2003; Buzsaki and Draguhn, 2004; Fingelkurts and Fingelkurts, 2004). The detection of metastable dynamics in the brain through analysis of synchronized oscillations is currently being actively explored (Bressler and Kelso, 2001; Bressler, 2003a; Freeman et al., 2003; Fingelkurts and Fingelkurts, 2004).

5. Coordination and cognition

We have argued here that the neural underpinning of cognition is best understood through the study of neurocognitive networks, which, following the organizational approach of Arbib et al. (1997), may be pursued through the joint consideration of neuroanatomical structure, neurophysiological function, and neuronal assembly dynamics of the cerebral cortex. When examined from this perspective, cognition is seen as a dynamic process that rapidly evolves through a series of informationally consistent coordination states. In each moment of cognitive processing, the cognitive microstate is defined by the selective coordination of local cortical area networks that are interacting by virtue of their interconnectivity within the large-scale anatomical structure of the cortex.

One implication of this outlook is that various forms of cognitive dysfunction may be regarded as disorders of neural coordination. The cognitive impairment that is typically evident during epileptic seizures (Kostopoulos, 2001) is perhaps the most obvious cognitive manifestation of neural discoordination, in this case a discoordination in the form of hypercoordination. However, there is also growing evidence for cognitive discoordination as a root cause in certain classes of schizophrenia (Andreasen, 1999; Haig et al., 2000; Phillips and Silverstein, 2003; Bressler, 2003a,b). The distortions of perception and reasoning that are associated with schizophrenia may result from discoordination in the form of hypocoordination.

A second implication is that attention and working memory, which are often treated as independent cognitive processes, may both be considered to be aspects of a common dynamic process that coordinates neurocognitive networks. Attention may relate

to the selectivity of that coordination process, in advance of and during sensory perception and motor action, whereas working memory may relate to the persistence of a state of coordination over time, even in the absence of overt perceptuomotor behavior. It is certainly the case that both selective attention and working memory critically involve the prefrontal cortex. This region, by virtue of its privileged anatomical connectivity with widely distributed sensory and motor areas, may serve to guide a common coordination process that is necessary for both attention and working memory.

The essential involvement of prefrontal cortex in the delay tasks which are commonly used to test working memory in humans and monkeys, and which cannot be performed without the direct involvement of selective attention, stems from the requirement in these tasks for the integration of a motor act with prior sensory information (Fuster, 2000). Assuming that the hallmark of the prefrontal cortex's executive function is indeed sensorimotor integration over time, then prefrontal involvement in both selective attention and working memory would naturally follow from its guiding role in the coordination of processing between sensory and motor cortical areas. It is noteworthy that, in light of the above proposed relation between neural context and neuro-cognitive network coordination, a vital aspect of prefrontal cortical function has been described as the maintenance of contextual representations in the brain (Braver and Barch, 2002). A general operational principle of neurocognitive networks may be that neural context throughout the cortex, and by implication the cognitive microstate itself, is created by the actions of prefrontal and other executive areas that coordinate their own activities as well as those of sensory and motor areas.

A final and related conclusion relates to the issue of how information in sensory and motor areas of the brain is integrated. Sensorimotor processing has often been conceptualized as a serial transfer of information from one area to another (Bullier and Nowak, 1995; Thorpe and Fabre-Thorpe, 2001). We recognize the need for seriality in cognitive processing, but from our perspective, serial processing is not a serial transfer of information between areas, but rather a serial succession of self-organized coordination states, under guidance of prefrontal cortex and other executive areas. Serial information transfer is conceptually appealing because it appears to offer the convenient flow of causal influence through the brain from sensory receptors to motor effectors. Nonetheless, we maintain that the high degree of reciprocal connectivity in the cerebral cortex mandates that every instant of sensorimotor processing involve the coordination of multiple sensory and motor areas, under guidance from executive coordinating areas such as the prefrontal cortex. Causal influences may indeed be exerted from one area to another within this framework (Pastor et al., 2000; Brovelli et al., 2004), but these are most clearly interpreted as constraints on the local processing in a receiving area (Bressler, 2004).

We believe that the interrelations of neural structure, function, and dynamics form a conceptual core for the elucidation of neurocognitive function. Encouraging developments

are currently taking place in cross-disciplinary research aimed at comprehending this issue (see [Neuroinformatics special issue, 2004](#)). We look forward to the development of more sophisticated recording and analysis tools to fuel future advances in understanding this most intriguing of scientific questions.

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