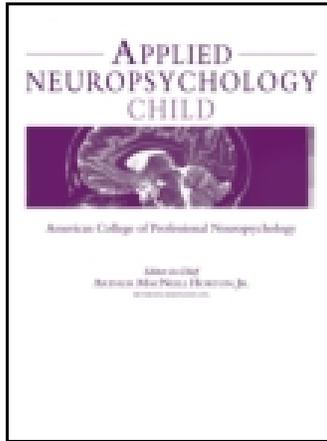


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Structure and Function of Large-Scale Brain Systems

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Structure and Function of Large-Scale Brain Systems

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This article introduces the functional neuroanatomy of large-scale brain systems. Both the structure and functions of these brain networks are presented. All human behavior is the result of interactions within and between these brain systems. This system of brain function completely changes our understanding of how cognition and behavior are organized within the brain, replacing the traditional lesion model. Understanding behavior within the context of brain network interactions has profound implications for modifying abstract constructs such as attention, learning, and memory. These constructs also must be understood within the framework of a paradigm shift, which emphasizes ongoing interactions within a dynamically changing environment.

Key words: attention, executive functions, large-scale brain systems, learning, memory

INTRODUCTION

Neuroscientific findings are rapidly emerging and have generated compelling evidence for a shift in our thinking concerning how cognition and behavior are organized within the brain (Herve, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013). The classical lesion model taught us how specific areas of the brain generated performances on neuropsychological tests and about the behavior that resulted when a particular area was damaged. Studies on patients with various circumscribed lesions eventually resulted in theories of hemispheric specialization and the roles that specific brain

regions might play in generating behavior. However, there is no single localizable brain area for the meaning of any event or fact, and there is no isolated brain region specialized for any particular activity (Bechara, Tranel, & Damasio, 2000). Therefore, the lesion model can no longer be applied as initially conceptualized. Information processing within the brain is both localized and distributed (Squire, 1987). The brain is never “at rest,” and this intrinsic, ongoing activity has been shown to be critically important in understanding how “normal” and pathological cognition and behavior are organized within neural networks (Raichle, 2011). Specialized structural and functional neuroimaging technologies, electrophysiological techniques, and neurochemical methodologies inform us that behavior is organized within the brain in a much different way than clinical neuropsychology first conceptualized. Isolated

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brain regions, or even collections of brain regions, do not generate specific behaviors. Instead, the human brain is characterized by distributed functional networks that undergo complex transformations across the life span (M. Cao, Wang, et al., 2014). Cognition and behavior emerge from these integrated neural systems (Rosazza & Minati, 2011).

The global organization of the brain is characterized by large-scale systems that support certain “general” functions, while the “small world” organization within these systems is responsible for communication within and between these large-scale networks to generate adaptive behavior. This has profound implications for understanding pediatric development, neurodevelopmental disorders, neuropsychological evaluation, symptom identification, and treatment (Chu-Shore, Kramer, Bianchi, Caviness, & Cash, 2011). The paradigm shift proposed in this four-part series has two broad components. First, cognition and behavior should be understood within the context of large-scale brain systems (LSBS). These functional brain networks have a profound impact upon how we understand constructs such as *attention*, *executive functioning*, and *learning and memory*, which represent the infrastructure of cognition. An awareness of how these large-scale brain networks develop and function is critically important to pediatric neuropsychology for the purpose of understanding what drives cognition and behavior at different ages. Second, this model warrants expansion to encompass the neurobiological reality that the brain evolved to meet and serve the needs of interactive behavior (Cisek & Kalaska, 2010). Neuropsychology has traditionally interpreted tests within a static type of model that emphasizes serial-order processing. The assumption is made that first we perceive, then we think, and then we respond—all of which represent discrete events. However, infants, children, adolescents, and adults are continuously interacting within a dynamically changing environment. A static and explicit paradigm is insufficient for understanding cognition and behavior.

Perceptions, ideas, and behaviors are retained within the same distributed brain networks within which they were initially processed. Constant interaction requires ongoing modification of our behavior (Shadmehr, Smith, & Krakauer, 2010). This includes an awareness of how well things are going (feedback control), evaluation of alternative activities as they might become appropriate from moment to moment, and judgments about “tradeoffs” between persisting with a behavior or switching to a different one. These ongoing processes can be either explicit or implicit. Many of these behaviors are automatic, while other behaviors require adjustment through episodes of cognitive control (Blais, Harris, Guerrero, & Bunge, 2010; Koziol, Budding, & Chidekel, 2010). This fact establishes an expanded

framework for test interpretation and encompasses implicit measures along with the numerous tests of explicit function already available. This series of manuscripts identifies and describes the structure and functions of LSBS. The concept of functional connectivity is introduced to understand how the human brain manages interactive behavior. Although clinical neuropsychology has always focused on corticocentric theories, the functions of large-scale cortical brain networks are fundamentally dependent upon interactions with subcortical structures (De La Fuente, Xia, Branch, & Li, 2013). Therefore, these interactive processes are also reviewed. Next, because the brain’s anatomical networks are profoundly remodeled between childhood and adulthood (Dennis et al., 2013), we describe what is known about the development of these brain systems and the patterns of functional connectivity that ultimately generate autonomous, adult behavior. An important neurodevelopmental principle that emerges concerns the changing landscape of subcortical–cortical interactions. In fact, this represents the major hallmark of the developing brain (Menon, 2013). Finally, we review how this “interim solution” of our understanding of brain function affects test interpretation, which emerges from neuroscientific principles that have informed us about how behavior is organized within the developing brain (Koziol & Budding, 2009). We demonstrate how currently available neuropsychological tests can be conceptualized and interpreted, and we illustrate what is missing from the traditional neuropsychological evaluation tool kit. Finally, we describe implicit test methodologies that are currently being developed for the purpose of a more comprehensive assessment that can be administered within a brief period of time (Koziol, 2014).

LARGE-SCALE BRAIN SYSTEMS

Although the human brain can be characterized as consisting of numerous systems and networks (M. Cao, Wang et al., 2014; Hwang, Hallquist, & Luna, 2012), Yeo and colleagues (2011) identified a seven-network parcellation of the human cortex and observed the remarkable replicability and consistency of these patterns within 1,000 healthy adult participants. This seven-network pattern represents a good starting point for understanding the infrastructure in which perception, thinking, and behavior are organized within the brain. These networks are the neuroanatomic substrates for understanding the distributed nature of neural processing within the brain and serve as points of reference for examining specific symptoms in all neurodevelopmental and neuropsychiatric disorders (Cortese et al., 2012; Menon, 2013). For example, although these brain

systems were identified by resting-state neuroimaging techniques, there is a very close correspondence of these networks with functional task activity patterns (Menon, 2010). Therefore, networks identified “at rest” are also systematically engaged during cognition, which implies that these brain systems are a fundamental substrate for the organization of complex brain–behavior relationships (Cole, Bassett, Power, Braver, & Petersen, 2014). The same LSBS can be identified in primates, infants, children, and young adults, although different levels of activity are evident at different ages, which makes good neurodevelopmental sense (Supekar, Musen, & Menon, 2009; Uddin, Supekar, & Menon, 2010; Whitfield-Gabrieli & Ford, 2012). Each LSBS is composed of several brain regions; each specific region is an essential “node” in the system. Knowing about the maturational pattern of these systems and how connections within these systems develop and unfold has profound implications for pediatric neuropsychology in the understanding of behavior and neurodevelopmental disorders and for the interpretation of neuropsychological test results throughout the lifespan (M. Cao, Shu, Cao, Wang, & He, 2014). These seven brain networks are illustrated in Figure 1.

The Default Network

When we are awake and alert, yet at rest, relaxing, or doing “nothing,” considerable organized activity is occurring within a set of brain regions called the default mode network (DMN; Sandrone, 2012). The idle mind truly never rests. This activity is believed to represent the physiological “baseline” of the brain, but its activity is suspended, or suppressed, during the performance of goal-directed cognitive tasks and behaviors (Castellanos & Proal, 2012). The DMN is anchored in two brain regions referred to as “hubs,” or centers of primary neural activity (a concept that will be described in the second article of this series). The anterior medial prefrontal cortex (aPFC) and the posterior cingulate cortex are the two central hubs. These regions are connected with two subsystems. The dorsomedial subsystem is activated when a person’s mind drifts toward self-referential, “autobiographical” thinking in the present; the medial temporal-lobe subsystem (MTL) is engaged when our minds drift toward thinking about the future, which makes good sense when considering that anticipation is an inherent design characteristic of the brain; as we think and reflect, the content is often characterized by how memories can

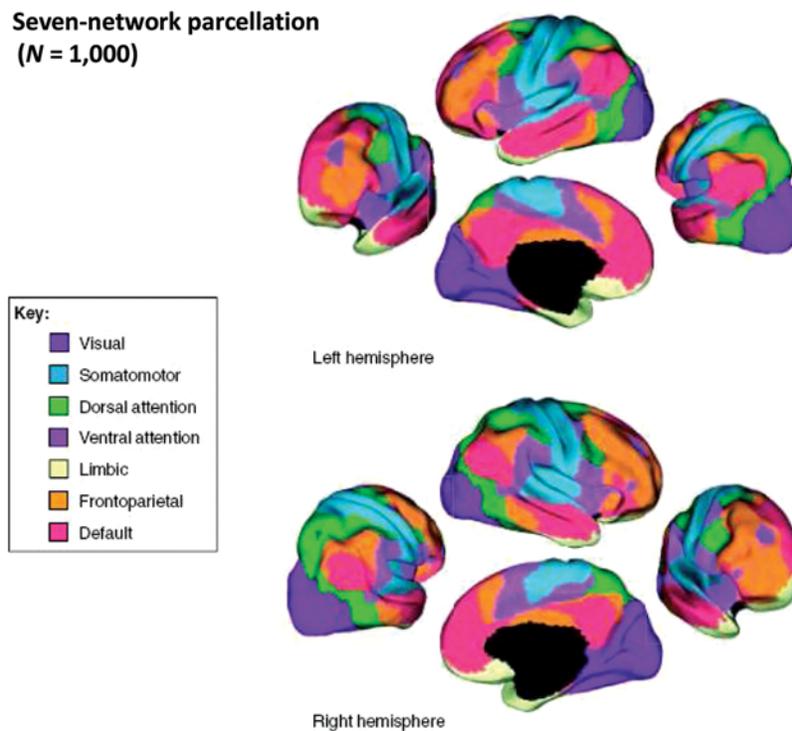


FIGURE 1 Coarse (seven-network) parcellation of the human cerebral cortex obtained through clustering of resting state-functional magnetic resonance imaging data of 1,000 individuals. At this resolution, the association cortex is distinguished from the primary sensorimotor cortex. The association networks converged on and extended networks previously described in the resting-state literature, including the dorsal attention, ventral attention, frontoparietal control, and default networks. *Source:* Castellanos & Proal (2012).

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be applied to some sort of future activity (Kinsbourne & Jordan, 2009).

So the DMN, in aggregate, is composed of several nodes that function as an integrated system that spontaneously generates all sorts of thinking. We think about the past and future; we make judgments about our feelings, behavior, and character; memories run through our minds; we think about our aspirations. Sometimes we think about other people or imagine what they are thinking. Experimental tasks that require self-reflection also activate the DMN; components of the DMN are activated in social cognition. Therefore, there is an association of the DMN with both an *intrinsic* and an *extrinsic focus of attention* (Habas et al., 2009; Whitfield-Gabrieli & Ford, 2012). Diminished regulation of DMN activity is observed in nearly all psychiatric disorders, from autism to schizophrenia. It is associated with the lapses in attention observed in attention-deficit hyperactivity disorder (ADHD) and the negative rumination of depressed people (Menon, 2011; Weissman, Roberts, Visscher, & Woldorff, 2006). Both increased and decreased activity (hyperactivation vs. hypoactivation), relative to normal controls, is seen in most neuropsychological disorders. So knowing about this “physiological baseline” of brain activity seems to provide a good starting point or framework for understanding *controlled attention* and *cognitive processing*, which has implications for understanding neurodevelopmental disorders. For example, aside from the dementias, nearly all disorders have a developmental origin in childhood or adolescence (Cicchetti & Cohen, 2006). There are no specific neuropsychological tests of the DMN, but when interpreting test performances, the activity of the DMN always needs to be considered in the mind of the examiner in terms of possible “background noise” potentially contributing to test score variability. The mind of the inattentive person obviously tends to drift.

The Visual Network

The visual network (VN) is defined by the occipital lobe, the lateral temporal cortex, and the superior parietal lobule. This network is the critical underpinning of the general attention network. It supports and interacts with the dorsal attention network (DAN) and ventral attention network (VAN) and plays a key role in sustaining attention and in suppressing attention to extraneous, irrelevant stimuli. Therefore, the VN represents an important node in the brain’s “action control” behavioral system.

The Ventral Attention Network

The VAN consists of the temporoparietal junction, the supramarginal gyrus, the frontal operculum, and the

anterior insula, which makes a critical contribution to the brain’s salience system (Menon, 2010). These same regions of the temporal/parietal lobes project to the striatum (Seger, 2009). The VAN identifies objects that are out there in the world and has traditionally been known as the “what” pathway (Milner & Goodale, 2008; Rauschecker, 2012). However, an important feature of this pathway concerns the fact that the primary reason for identifying objects concerns the worth of that object, what that object is used for, or what that object can do/how it can behave—or object salience, which might be understood in a very practical way as relevance. Therefore, this network specifies the “reward value” of objects and plays a very important role in behavioral praxis or potential “action.” This network, with its projections to the striatum, which is critical to the basal ganglia instrumental learning system, most often operates implicitly beyond our conscious awareness (Koziol & Budding, 2009; see chap. 4, pp. 95–124). It is active early on and throughout the course of development (McBride & Parker, 2014; Menon, 2013). Therefore, the functions of this network help us understand how toddlers and even infants “learn,” without conscious recollection and willful, intentional cognitive control. Learning occurs through *activity*, as is generally evident within an interactive paradigm for understanding human behavior, and this activity is reward-based (Haden et al., 2011; Sheth, Abuelem, Gale, & Eskandar, 2011).

The Dorsal Attention Network

The DAN is anchored in the intraparietal sulcus and the frontal eye fields. The primary role of the DAN is to change or shift the focus of attention and to control spatial attention, or where we orient attention to the external world. Because we are constantly adapting to a dynamically changing environment, this system plays a critical role in that interactive process. This network reorients attention so that the DAN is critical to executive control processes (Corbetta, Patel, & Shulman, 2008). Although the DAN has been referred to as the “where” pathway (Cisek & Kalaska, 2005, 2010), the function of the dorsal/parietal stream, through reciprocal connections with premotor regions, supports pragmatic, practical representations of the opportunities for action that those objects afford (Barsalou, 2008; Cisek & Kalaska, 2010). This network specifies the parameters for a person’s actions; it informs frontal systems about “how to do” something. This features the roles of the DAN in *explicit* executive control processes and in *implicit* procedural memory functions. We cannot have adaptive behavior, or successful environmental interactions with objects and people, without the DAN, which includes dorsal-frontal and parietal interactions. Frontal systems cannot direct behavior in a goal-directed way

without reciprocal frontal-parietal interactions (Cole et al., 2013; Jacob & Nieder, 2014; Mehnert et al., 2013). Therefore, the *functions of this network significantly change our understanding of the parietal lobes and go well beyond the parameters of what has traditionally been referred to as “visual-spatial” functioning.*

Integrating Networks, Auditory–Visual Interactions, and Action Control

Our knowledge of these networks and their interactions significantly modifies the theoretical construct of attention. One vital issue concerns the integration of ventral and dorsal systems. Object identification (which includes reward value) and knowing the location of these objects and how to use them (developmental praxis) are so critical to development that these two systems are integrated by the age of 9 months (Kaldy & Leslie, 2003). In addition, the integration of these systems is extremely important for the later development of semantic (fact) and episodic (autobiographical) memories, supported by the MTL (Lavenex & Lavenex, 2013). The VAN projects through the perirhinal cortex primarily to the lateral division of the entorhinal cortex; the DAN projects through the parahippocampal cortex to the medial division of the entorhinal cortex. These two streams of information processing mainly converge within the hippocampus (Dickerson & Eichenbaum, 2010). Studies have demonstrated that hippocampal neurons encode semantic facts, features of events, and the places where they occur (Eichenbaum, 2004). The integration of these systems supports the development of semantic and later episodic, autobiographical memories and places events and situations in context (Bauer, 2007; Pathman, Samson, Dugas, Cabeza, & Bauer, 2011; Ribordy, Jabes, Banta Lavenex, & Lavenex, 2013). These functions are obviously relevant for the operations of the DMN and the frontoparietal network (FPN). For example, whenever we plan a future behavior, we typically reflect upon the past and what we did before, and we make judgments about how effective that behavior was and the outcome it produced. The FPN, as will be discussed, is an underpinning for certain goal-directed behavior, particularly in novel problem-solving situations, as we draw upon past experiences to solve current problems.

Auditory processing follows the same organization as the visual system within the VAN and the DAN. The ventral auditory pathway “maps” sound to meaning; the dorsal auditory pathway, through connections with the parietal lobes and frontal eye fields, serves to orient visual attention toward spatial location (Arnott & Alain, 2011). This is extremely easy to understand by providing simple examples. Imagine yourself sitting in a room with the door closed; you hear a “familiar” pattern of footsteps. You can immediately identify that

person, without seeing that individual; you might even orient your attention toward the door, particularly if you were anticipating that person’s arrival. The auditory system serves these identification and location functions through the same VAN and DAN systems. The human is incredibly dependent upon vision. Vision and audition can serve different purposes dependent upon the time of day or lighting conditions. Under circumstances of darkness, when you hear a sound, the ventral stream provides information about identification and the dorsal stream provides information about location. These aspects of audition integrate information and orient attention, a form of “action planning” that guides you to an area of interest. In fact, functioning within the context of these examples likely evokes implicit visual images.

Auditory and visual systems interact so that the trajectory of eye movements influences spatial reasoning through an implicit eye movement–cognition link (Grant & Spivey, 2003; Thomas & Lleras, 2007). Primary visual cortex (V1 and V3 within the medial occipital lobes) as well as higher-level multimodal association areas receive inputs from both visual and auditory sensory systems. This neuroanatomic substrate provides the functional connectivity that supports implicit auditory–visual interactions, outside of conscious awareness, while at the same time supporting cognitive control (Banich & Compton, 2011; Johnson, Woodman, Braun, & Luck, 2007; Naatanen, Kujala, & Winkler, 2011; Salmi, Rinne, Degerman, & Alho, 2007). In fact, during the administration of the “auditory” digit span task, and most other “auditory attention” tasks, the medial occipital cortex is robustly activated (Gerton et al., 2004). Similarly, Castellanos and Proal (2012) reported that numerous neuroimaging studies have shown repeated differences in the medial occipital cortex in ADHD as compared with normal control participants across the life span. In functional studies, these anomalies have been associated with inhibitory and working memory failures and attentional lapses (Q. Cao et al., 2013; Massat et al., 2012). Simply put, the auditory versus visual dichotomy initially proposed when neuropsychology was in its infancy is false, incomplete, and potentially diagnostically misleading. Instead, the VN, VAN, and DAN interact to guide attention and in aggregate transform into an “action control” network (Njiokiktjien, 2010). All sensory systems are organized in parallel and appear to operate within these network guidance systems. Therefore, we can no longer interpret test data within a simple auditory–visual dichotomy.

The Limbic Network

Whatever we do, from the simplest to the most complex activity, always requires motivation. This motivation

can be the pursuit of an immediate reward or the immediate avoidance of a negative outcome. Alternatively, performing a goal-directed activity might include the achievement of a longer-term positive outcome or the avoidance of a negative outcome; the negative consequence or positive reward might be well down the road, in the future. Rewards can be very concrete, as in fulfilling a bodily need; it might be as tangible as receiving a paycheck. Reward can also be abstract, as in “feeling good” after making a positive contribution to a charitable organization. It might be receiving a “pat on the back” after a job well done, or the nontangible relief we sometimes feel after completing a demanding or even monotonous project. So the negative and positive outcomes we experience can be tangible or very abstract—a concept that has been termed “fictive reward” (Lohrenz, McCabe, Camerer, & Montague, 2007; Montague, King-Casas, & Cohen, 2006). Reward should be considered along this very broad spectrum; it is believed to be hierarchically organized (Mars, Sallet, Rushmore, & Yeung, 2011). However, all reward is governed by the limbic network (LN). The LN can be thought of as anchored within two “hub” systems. The primary contributors to these systems are the dopaminergic reward system and the amygdala. These two center hubs provide the reasons for why we do things. Both systems are directly linked to the limbic/paralimbic regions of the cerebral cortex through the basal ganglia. The basal forebrain is rich in dopamine connections and is considered an instrumental learning system; this system allows the brain to learn what to do for the purpose of achieving positive outcomes, and it also teaches the cerebral cortex what not to do to avoid negative outcomes (Nakanishi, Hikida, & Yawata, 2014). The amygdala, residing at the anterior tip of the body of the caudate of the basal ganglia, is fueled by the noradrenergic system. It influences levels of arousal and governs “fight or flight” reactions. In this way, it can also be a generator of symptoms of anxiety, which are also important in instrumental and reinforcement learning processes. However, the critical component of these two aspects of the LN concerns the fact that these processes influence all behavior through interactions with other LSBS. The “learning properties” of these systems are largely implicit, which is not to say that broadly defined “reward system” learning cannot be explicit. The most critical point concerns the fact that these systems, when activated or deactivated, play a primary role in what we attend to, what we ignore, and what we notice or do not notice implicitly. Ultimately, the LN generates the motivational valence for engaging in certain behaviors and avoiding other activities, which is essentially decision making.

In view of these system interactions, as we live and make adjustments to our behaviors within a constantly changing environment, theoretical constructs such as attention and executive functioning can no longer be considered processes that are completely under conscious cortical control. Attention and the implicit–explicit decision making inherent in executive functioning are dynamic processes, evident everywhere, in everything we say or do. Within a paradigm of practical, adaptive, continuous interactions with the world in which we live, the static parameters of the constructs of attention and executive functioning require significant modification; these theoretical construct modifications are imperative and necessary due to the neurobiological evidence that the brain evolved and developed to meet and serve the changing needs of interactive behaviors. All behaviors are neurobiologically situated to serve these interactive, adaptive needs. In addition, the integration of cognitive, activity, and reward systems reveals the artificial boundaries of “cognitive” versus “emotional” compartmentalization of functions. In fact, considering these LSBS interactions, in aggregate, potentially places neuropsychological evaluation near the center of the arena of understanding personality functioning.

The Somatomotor (Sensorimotor) Network

This network is defined by the primary motor cortex, the primary and secondary sensory cortices (anterior regions of the parietal lobes), the supplementary motor cortex, the ventral premotor cortex, the putamen, the thalamus, and the cerebellum (Castellanos & Proal, 2012). This neuroanatomy makes perfect logical sense. Frontal–parietal lobe interactions specify the parameters of action (Njiokiktjien, 2010). These interactions enable the development of motor programs. Corticostriatal interactions “chunk” together these sequences of movement (Graybiel, 1998) and “gate” or select behavioral “candidates” on the basis of instrumental learning processes (Cockburn & Frank, 2011). The sequencing of movement also occurs for thought; in the interest of editorial space considerations, cognitive sequences will be discussed in the concluding article of this series. The cerebellum refines these “programs” and adapts these behaviors across similar contexts through a process of sensorimotor prediction (Koziol, Budding, & Chidekel, 2012; Shadmehr et al., 2010). These refined programs are then projected back to the neocortex, which retains the most efficient representation of the sequence. Therefore, the frontal cortex retains what the cerebellum learns (Galea, Vazquez, Pasricha, de Xivry, & Celnik, 2011; Houk et al., 2007). This process generates the automated behaviors we frequently recruit for quick, spontaneous environmental interaction.

The Frontoparietal Network

The FPN is a cognitive and action control network. This network consists of the dorsolateral prefrontal cortex (DLPFC), the anterior cingulate cortex, the anterior prefrontal cortex, the lateral cerebellum, the anterior insula, the caudate nucleus, and the inferior parietal lobe. The FPN is commonly engaged during effortful cognitive task performance requiring information or rules to be held in mind, also known as “working memory,” to guide behavior. Although many behaviors are routine or automatic, a situation can change and require adjustment or the programming of a new behavior to solve a novel problem. The caudate appears to be particularly sensitive to context (Ashby & Ennis, 2006; Seger, 2008). When the external situational context changes, the caudate appears to activate the DLPFC for the purpose of consciously developing a new behavior. However, there is also evidence that in routine circumstances requiring minor adjustments, “executive” judgments can be made automatically, outside of conscious awareness (Seger & Cincotta, 2005, 2006). It is proposed that the basal ganglia actually “train” the prefrontal cortex (Antzoulatos & Miller, 2014).

Behavioral control is always characterized by the continuous adjustment to a changing environment. This involves the ongoing anticipation and adaptation of appropriate actions and the inhibition of inappropriate activities (Duque, Lew, Mazzocchio, Olivier, & Ivry, 2010). The level or degree of control varies as a function of internal and external factors setting the task context (Wardak, Ramanoël, Guipponi, Boulinguez, & Ben Hamed, 2012). The left-hemisphere FPN network is critical for guiding behavior according to current *cognitive context*. This network drives behavior according to the content of what one is thinking about for contextually dependent functioning. The right-hemisphere FPN is critical for cognitive selection driven by *the external environment* and for context-independent behavior; under these circumstances, the FPN processes cognitive task novelty and task orientation and generates novel problem-solving strategies. Therefore, one critically important feature of the FPN appears to be its inherent flexibility in rapidly recruiting and updating whatever brain systems are necessary for any particular context (Cole et al., 2013). This topic brings us to the concept of cognitive and behavioral “hubs,” which characterize the internal, “small world” organization of LSBS to be discussed in the next article in this series.

SUMMARY

Cognition and behavior are organized within the framework of seven reliably identified LSBS. These systems

interact to integrate perceptions, ideas or mental representations, and activities to serve the needs of interacting within a dynamically changing environment. The operations of these systems profoundly impact our understanding of theoretical constructs such as attention, learning and memory, and executive functioning. Neuropsychological test results and all cognitive/behavioral pathologies need to be understood within this foundational framework. In fact, this paradigm expands the role of neuropsychological evaluation by placing it within the realm of understanding personality functioning.

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