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Dynamic network interactions supporting internally-oriented cognition

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Recent advances in systems neuroscience have solidified the view that many cognitive processes are supported by dynamic interactions within and between large-scale brain networks. Here we synthesize this research, highlighting dynamic network interactions supporting a less explored aspect of cognition with important clinical relevance: internally-oriented cognition. We first present a brief overview of established resting-state networks, focusing on those supporting internally-oriented cognition, as well as those involved in dynamic control. We then discuss recent empirical work emphasizing that many cognitive tasks involving internally-oriented processes — such as mind-wandering, prospection, and creative thinking — rely on dynamic interactions within and between large-scale networks. Our aim is to provide a snapshot of emerging trends and future directions in an important aspect of human cognition.

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Introduction

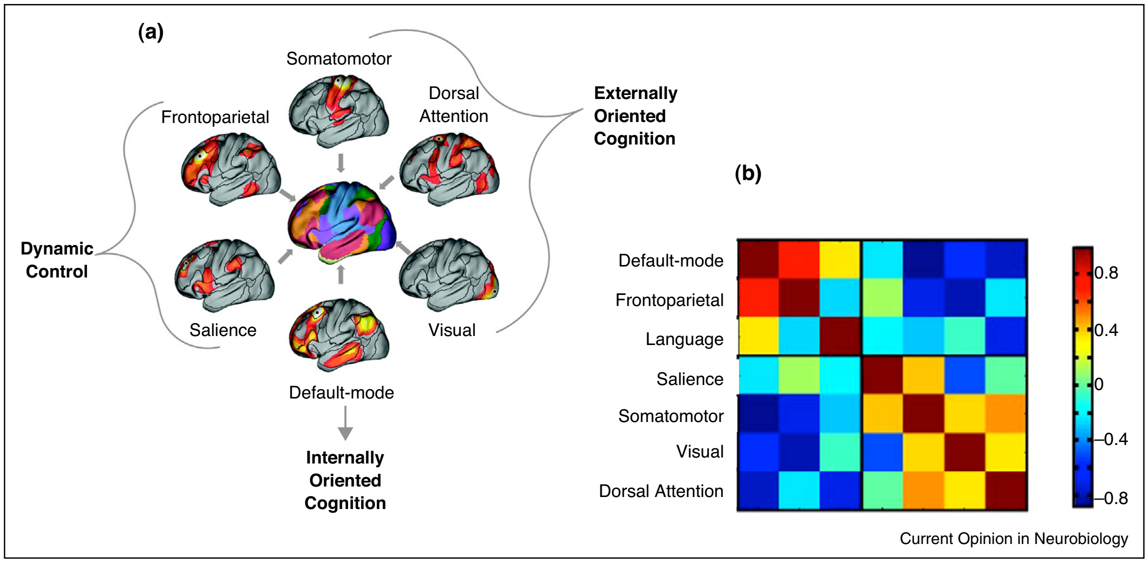
The last several decades of neuroscience research have witnessed a sea change in our understanding of systems neuroscience, from early conceptualizations of brain organization as a collection of isolated modular regions, to more recent views highlighting *dynamic interactions* among brain regions and large-scale brain systems (see [1•]). Much of this insight in recent years can be attributed to the development of *resting state functional connectivity MRI* (rs-fcMRI), a technique that measures correlated patterns of fMRI activity across brain regions during extended periods of awake rest [2•]. A basic principle of rs-fcMRI is that brain regions that share anatomical and/or functional properties exhibit similar patterns of fMRI activity fluctuations, and consequently cluster together into large-scale brain systems [2•,3] (Figure 1a,b). Indeed, many studies have shown convergence between brain systems identified from rs-fcMRI and patterns of anatomical connectivity as revealed from diffusion tensor imaging (DTI) [4] and anatomical tract tracing [5]. Although several investigations using rs-fcMRI have revealed separable resting-state networks (RSNs) that support distinct cognitive domains [6–8], more recent approaches highlight the flexible nature of the brain, with a growing appreciation that resting state networks interact with each other in a dynamic fashion on multiple time-scales [9••].

Here we synthesize research on brain network interactions supporting attention and cognition, and their dynamic regulation. Although most existing research has characterized networks supporting externally-oriented attention and cognition (e.g., [10]), we focus on a less established topic that has garnered considerable interest in recent years because of its relevance to mental health: internally-oriented attention and cognition [11], encompassing one's thoughts, memories, emotions, and other internal representations. We first present a brief overview of established resting-state networks, focusing on default-mode and limbic networks, as well as those involved in dynamic control of externally-oriented and internally-oriented cognition. Then we highlight recent empirical work emphasizing that many cognitive tasks involving aspects of internally-oriented cognition — such as unconstrained rest and mind-wandering, prospective planning and anxious apprehension, and creative thinking — rely on dynamic interactions within and between these large-scale networks. Our hope is that highlighting this interactive framework will help newcomers to the field of systems neuroscience gain a snapshot of emerging trends and future directions in an important aspect of human cognition.

Anatomy and function of large-scale brain networks

The idea that the brain is best characterized across multiple levels of analysis as an interactive map of connections is the major tenet of a field of inquiry known as *connectomics* [12]. At the systems level, structural and functional connectivity techniques have provided strong support for the interactive nature of the brain. Despite use of different subject samples, scanner sequences, seed regions, and analysis techniques across studies, a remarkably consistent set of large-scale networks has emerged in recent years. Below we summarize a common seven-network solution to resting

Figure 1



Large-scale resting-state networks and their between-network relationships. **(a)** Six common large-scale resting-state brain networks. Each outer map shows the functional connectivity of a small seed region marked by a dark circle (figure adapted with permission from [3,8]). *Note*: limbic network omitted from original figure. **(b)** A pairwise correlation matrix between a seven-cluster network solution similar to (a) reveals functional interactions between networks (figure adapted with permission from [13]). *Note*: the 'language network' overlaps strongly with default and limbic networks.

state connectivity approaches [6–8,13], and discuss each network's hypothesized functions in external and internal attention, and dynamic control.

Networks supporting externally-oriented cognition

Some of the most evolutionarily primitive and stable brain networks include those that support attention to, and interaction with, the external environment. These networks include sensory networks such as the *visual network* (including predominantly V1–V3) [14], which can be further parcellated into central and peripheral systems, and the s*omatomotor network* (including primary motor and premotor cortex, and primary sensory cortex) contributing to movement and touch [15]. The *dorsal attention network* (DAN) regulates sensory networks in a top-down manner, enabling deliberate attention to visual stimuli and spatial locations [16]. The DAN includes a posterior frontal region called the frontal eye fields, the superior parietal lobule, and the middle temporal (MT+) extrastriate area. These three large-scale networks are positively correlated at rest [13], and interact during many externally-oriented tasks (see [17]).

Networks supporting internally-oriented cognition

Although attention is often directed towards the external environment, humans spend a great deal of time turning their attention inwards, towards their thoughts, memories, emotions and other internal representations [18]. Networks supporting *internally-oriented cognition* are less well-characterized than those supporting externally-oriented cognition, and this area marks a rapidly growing avenue of research in recent years [19•]. Existing work points to the role of the brain's *default network* (DN; or *default mode network*) and the nearby *limbic network* in key aspects of internally-oriented cognition [11]. Although the DN was traditionally referred to as the 'task-negative network' because of its common deactivation during externally-directed tasks, recent analyses show that the DN is best characterized not by its opposition to a task, but by the self-generated mental content that it supports [20,21]. The DN includes cortical, subcortical and cerebellar regions that become engaged when cognition unfolds independent of current perceptual stimuli (such as during the 'resting state),' as well as when self-generated operations are spontaneously or deliberately performed on external stimuli [19•].

Resting state fcMRI and clustering approaches applied to DN activity indicate that the DN can be parcellated into at least three subsystems: a ventrally-positioned *medial temporal lobe* (MT) subsystem, a more dorsally-positioned *dorsal medial* (DM) subsystem, and a centrally-positioned *core* [22]. The MTL subsystem plays an important role in episodic retrieval and memory-based construction (including imagination and future thinking), and may allow spontaneous thoughts to emerge [6,23]. The DM subsystem becomes engaged during more abstract processes, such as when individuals meta-cognitively reflect on their thoughts and infer the mental states of other people [19•,24]. Both subsystems are highly interconnected with the DN CORE, a hub-like subsystem including the