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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

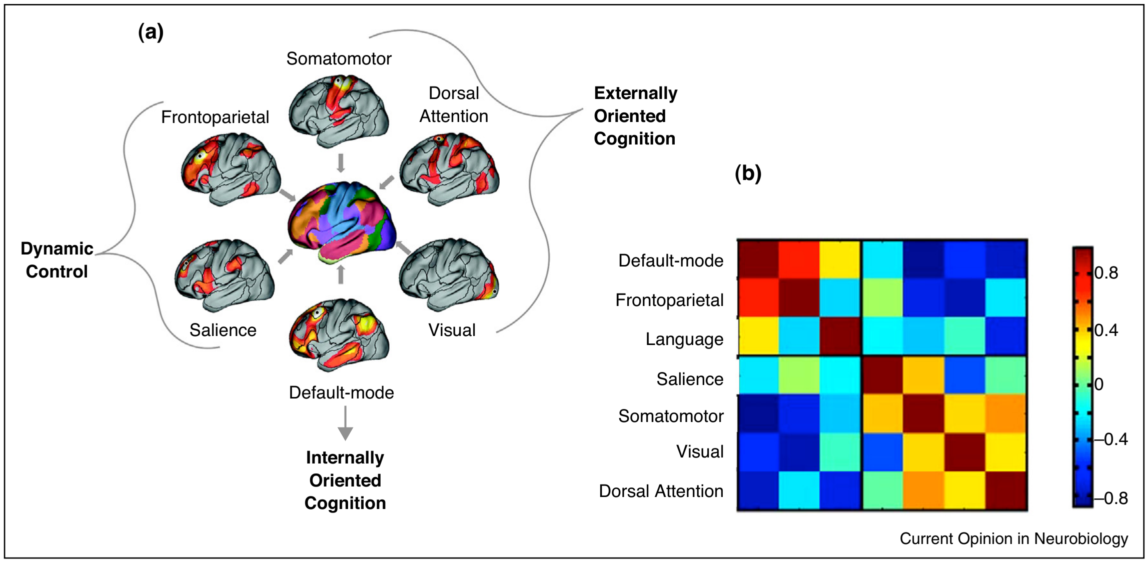
The last several decades of neuroscience research have witnessed a sea change in our understanding of systems neuroscience, from early conceptualizations of brain organization as a collection of isolated modular regions, to more recent views highlighting *dynamic interactions* among brain regions and 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 timescales [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 anterior MPFC, posterior cingulate, and dorsal angular gyrus that activates in response to a broad range of internal, often self-related tasks [19•]. These findings suggest a role of the DN CORE in broad self-generated functions, including computing the self-relevant nature of internal and external information.

The nearby *limbic network* includes regions such as subgenual anterior cingulate cortex and the amygdala that often couple with — and are sometimes considered part of — the DN [13,25]. This network activates when individuals engage in a wide range of emotional processes ranging from receipt of reward [26], to punishment [27], and activity in this network is dysfunctional in mood and anxiety disorders [28].

Networks supporting dynamic control of externally-oriented and internally-oriented cognition

The *salience network* (SN) and *frontoparietal control network (FPN)* interface with external and internal attention networks, and are considered important brain-wide hubs [29]. The salience network appears to partially overlap with the nearby ventral attention network, thought to play a role in stimulus-driven external attention [16]. The broader salience network also includes anterior insula and dorsal ACC regions often linked to salient emotions, leading some researchers to propose a broader role of the salience network in bottom-up attention to external and internal information [30•]. Information deemed to be perceptually or emotionally salient often influences subsequent cognitive processing, and initial studies suggest the salience network couples with the FPN when attention to salient information must be up-regulated in a top-down fashion [30•,31,32].

The FPN is widely considered to play a role in deliberate attentional control, and its connectivity to the DAN and DN varies dynamically in a task-dependent manner (see below). The FPN may be subdivided into central executive (including dorsal lateral PFC, anterior inferior parietal lobule, and dorsal ACC/pre-SMA) and cingulo-opercular (including anterior insula/frontal operculum and rostral lateral PFC) subsystems, which may support adaptive and stable forms of control [33].

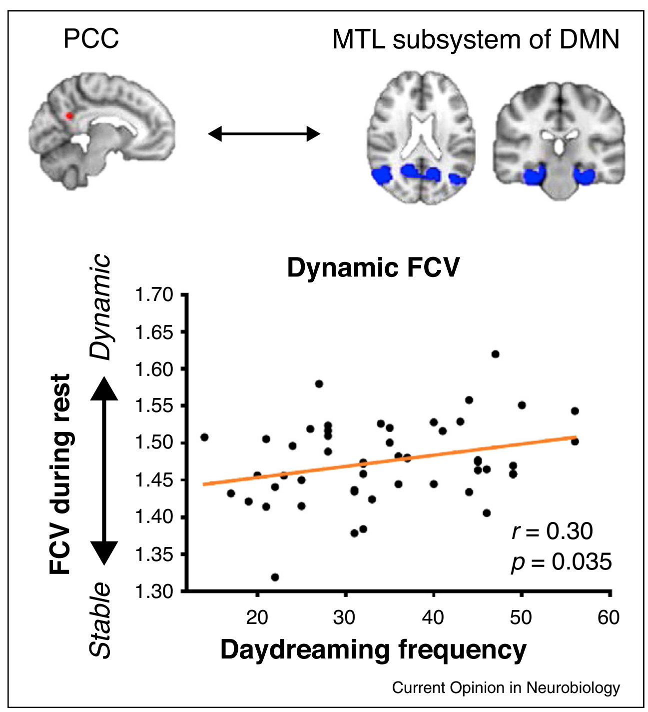
Large-scale network interactions during internally-guided tasks

Though the networks described above likely make distinct contributions to internally-oriented and externally-oriented cognition, the precise nature of those contributions can be difficult to pinpoint because large-scale networks can reconfigure and dynamically interact in a time-dependent and context-dependent manner [9••,34,35]. The dynamic properties of the brain are perhaps most elusive during internally-guided tasks, which encourage self-generated processes that often vary within and between individuals in ways that may not be easily detectible. Below we highlight initial evidence for dynamic network coupling during three internally-guided contexts: unconstrained periods of rest and mind-wandering, prospective planning and anxious apprehension, and creative thinking.

Unconstrained rest and mind-wandering

In the absence of constrained tasks, the mind has a tendency to wander about, from the sights and sounds of the external environment, to internal musings — some mundane, others significant in nature [11,36]. Adopting measures of dynamic connectivity such as sliding window correlations to extended periods of rest reveal remarkable variability in the correlation between regions over time [37]. Indeed, brain regions or networks that may be weakly or negatively correlated during one window of time may be strongly positively correlated during another [37]. Even static measures of resting state networks vary *within-subjects* with respect to the nature of the internal and external cognitive state [3,38] and *between-subjects* with respect to individual and group differences in level of consciousness [39], frequency of mind-wandering [40•,41], and content of thought [42–44]. These findings raise the possibility that the mental flexibility inherent to unconstrained states may partly shape the dynamics of large-scale networks at rest [45]. Supporting this hypothesis, individuals who mind-wander to a greater degree exhibit more dynamic variability in network correlations within the DN [40•] (Figure 2), while depressed individuals

Figure 2



Dynamic functional connectivity at rest relates to daydreaming. Evidence for a positive correlation between frequency of mind-wandering and dynamic variability in network correlations within the DN. *Source*: figure adapted with permission from [40•].

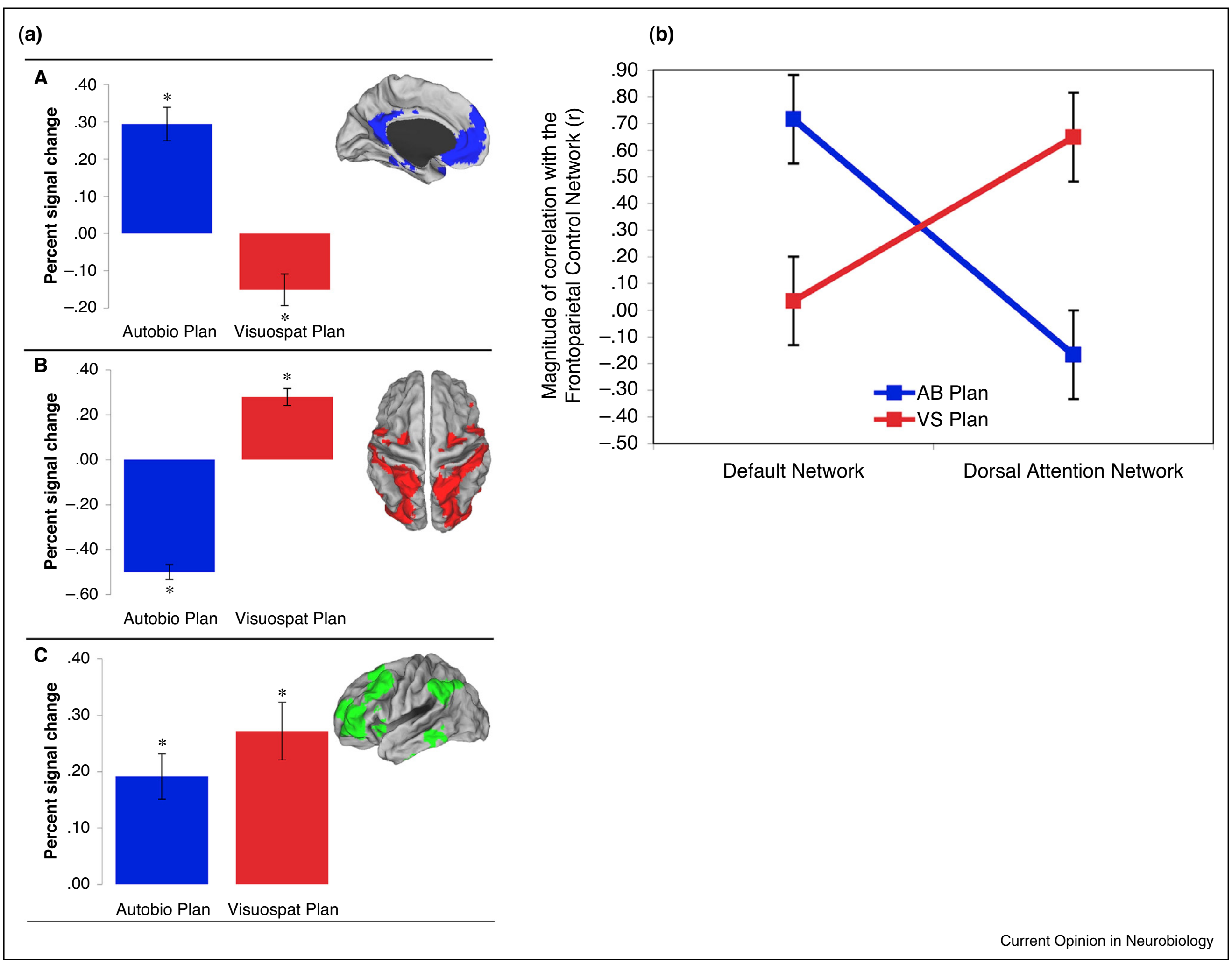
(particularly those with high levels of rumination) exhibit less dynamic variability amongst a similar set of DN regions [46••].

Although unconstrained tasks may maximize mind-wandering behavior, the mind also wanders to off-task topics during experimentally-constrained tasks [47]. Although strong links have been drawn between mind-wandering and activation in brain regions comprising the DN, mind-wandering also appears to consistently recruit other brain regions outside of the DN, particularly regions comprising the frontoparietal network, salience, and sensory cortices [48•]. Overt shifts in attention back to the task at hand can subsequently lead to reconfiguration of brain networks to support focused attention [49]. How the various large-scale networks involved in mind-wandering and reorienting of attention dynamically unfold remains an important unexplored question.

Prospective planning and anxious apprehension

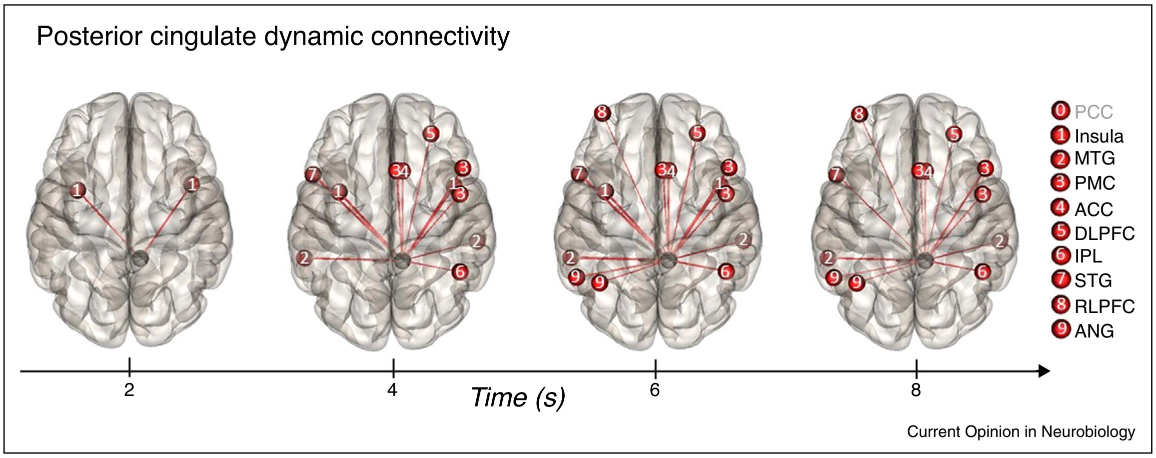
Many studies analyzing the content of the wandering mind observe a future-oriented, or *prospective*, bias to one's thoughts (reviewed in [19•]). However, while mind-wandering reflects spontaneous fluctuations in mental content, prospective thoughts can also be elicited using top-down mechanisms, and a growing task literature reveals that the brain networks supporting prospective thinking overlap with those supporting retrospective thinking (i.e. memory; [50]). There is some suggestion that brain networks evoked during prospective planning dynamically change within an imaginative future episode (i.e. when constructing versus elaborating on an imagined

Figure 3



Flexible involvement of frontoparietal control networks in audiobiogaphical and visuospatial planning. **(a)** Internally-oriented and externally-oriented planning tasks exhibit preferential activity within default and dorsal attention networks, but common involvement of the frontoparietal attention networks. **(b)** Evidence for positive coupling between the FPN and DN during autobiographical prospective planning (AB), and for negative coupling between the FPN and DAN during visuospatial prospective planning (VS).
Source: figure adapted with permission from [52].

Figure 4



The posterior cingulate cortex dynamically changes its functional coupling in a time-dependent manner. Early stages of performance on a divergent thinking task (generating possible solutions to an open-ended problem > naming object characteristics) shows increased coupling between DN and salience network regions, while later stages exhibit increased coupling between DN and FPN regions.
Source: figure adapted with permission from [57•].

scenario [51]), and across prospective task contexts (i.e. [52]). For example, whereas autobiographical planning is associated with positive coupling between the FPN and DN [52], coupling between these networks is replaced by FPN–DAN coupling when the prospective task is visuospatial in nature [52] (Figure 3).

Dynamic connectivity is also evident in different stages of prospective thinking: simulating the step-by-step processes required to reach a goal involves coupling between the DN and FPN, while simulating the events associated with achieving the goal involve coupling between the DN and limbic networks [53•]. Thus, growing evidence suggests the brain dynamically reconfigures its connectivity patterns dependent on the mental processes and contents of prospective thinking. Of note, while the above studies explore the dynamic underpinnings of imagining positive future outcomes such as achieving a goal, the brain also appears to reconfigure in a dynamic fashion when imagining negative outcomes, such as upcoming shock [54•], pain [55], or social evaluative threat [56].

Creative thinking

Like mind-wandering, creativity encourages flexible flow of thoughts, while requiring stable guidance to hone in on a creative idea, as is the case in prospective planning. Flexible flow of thoughts is especially evident in the initial stages of the creative process. In the context of a divergent thinking task, which involves generating several possible solutions to an open-ended problem, early stages (i.e., flexible flow of thoughts, detecting useful information potentially derived from long-term memory) involve increased coupling between DN and the salience network regions, while later stages (i.e., honing in, elaboration, and evaluation of the solution) exhibit increased coupling between DN and FPN regions [57•] (Figure 4). Similarly, idea elaboration [58] and poetry evaluation [59] are associated with increased coupling of DN and FPN regions. Likewise, people with high divergent thinking ability show increased resting state coupling between DN and left inferior frontal gyrus, a region of the FPN [60].

Dynamic connectivity between resting-state networks may also depend on the emotional content of the creative task: musical improvisation with emotional context involves coupling between the DN and FPN, while constraining musical performance to specific pitch sets (no emotional context) involves coupling between FPN and several motor control regions [61]. In this context, FPN may regulate top-down control over generative processes of the DN network during emotionally based improvisation.

Although generating creative solutions to open-ended problems is one of the most widely used assessments of creativity, semantic distance has also been considered the hallmark of creative cognition, where increased semantic distance is associated with increased coupling between regions of the DN and the FPN [62]. Thus compelling evidence from various assessments of creativity suggests creative thought, especially its later stages, may benefit from the dynamic cooperation of DN and FPN regions.

Summary

In recent years, parallel lines of research in resting state connectivity and task-related fMRI have emphasized the importance of a connectomics, or network-centered, approach to understanding brain function [63]. Our aim for this manuscript has been to synthesize this literature by focusing on the contributions of large-scale brain networks to internally-guided processes ranging from mind-wandering to creativity. We have shown that while it may be difficult to infer mental states from static patterns of connectivity, dynamic connectivity approaches offer great promise for tracking human cognition because our thoughts and attention often vary over time, shifting focus between the external world and our inner mental lives [45]. Human evolution appeared to have favored a flexible introspective mind, and incorporating the study of brain dynamics into future research in systems neuroscience may be the key to unlocking its mysterious contents.

Conflict of interest statement

Nothing declared.

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