The Default Network and Social Cognition

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Glossary

Default network A neurocognitive brain network linked to various modes of self-generated thought.

Mentalizing The cognitive process of inferring the thoughts, feelings, or beliefs of other people.

Resting-state functional connectivity (RSFC) A method for detecting large-scale brain networks from an analysis of low-frequency oscillations in blood oxygen level-dependent signal measured using functional magnetic resonance imaging while participants are at rest, or not actively engaged in a task.

A key component of social cognition is the ability to infer the thoughts and feelings of other people, a process termed mentalizing (Frith & Frith, 2003). Neuroimaging studies of mentalizing have revealed a network of regions including the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ), lateral temporal cortex, posterior cingulate cortex (PCC), and inferior frontal gyrus (Mar, 2011). An independent body of work examining correlated patterns of fMRI activity at rest has converged on an overlapping set of regions referred to as the 'default network' (Buckner, Andrews-Hanna, & Schacter, 2008). The default network is widely appreciated for its high levels of activity when external demands are low, suggesting a role in self-generated cognition decoupled from the physical world (Andrews-Hanna, 2012).

Given the similarity between the default and mentalizing networks, a central question has emerged in social neuroscience as to whether the core function of the default network is to mediate internal aspects of social cognition. Although mentalizing involves attention to external stimuli, it relies on self-generated cognition because humans do not have immediate perceptual access to other people's thoughts (Frith & Frith, 2003; Lieberman, 2007). However, the default network has also been linked to other internally oriented processes related to the self and memory, which can interact with social cognition or operate independently (Andrews-Hanna, Smallwood, & Spreng, 2014). Indeed, successful navigation of the social environment relies upon interactions between many self-generated processes that extend beyond mentalizing, including self-referential thought, conceptual processing, memory, and prediction. According to this perspective, the default network may function more broadly to support self-generated cognition, of which mentalizing may be a key component process.

The architecture of the default network, revealed by resting-state functional connectivity (RSFC) MRI, suggests a pattern of organization that may support multiple components of self-generated cognition (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Yeo et al., 2011). To assess the role of the default network in social cognition, we begin by delineating the network topology based on RSFC. We then explore the cognitive functions associated with this neuroanatomy in a large-scale meta-analysis and narrative review. This approach serves to organize the multiple functions of the default network and may provide unique insight into component processes and neural underpinnings of social cognition.

Delineating the Default Network

Analysis of low-frequency oscillations of blood oxygen level-dependent fMRI signal in the resting human brain can reveal distinct and dissociable functional–anatomical networks (Fox & Raichle, 2007). Using an unbiased whole-brain clustering approach to RSFC, the topology of the default network, and other large-scale brain networks, has recently been delineated (Figure 1(a); Yeo et al., 2011). The default network can be further broken down into 'core' regions and two distinct subsystems (Andrews-Hanna et al., 2010; Yeo et al., 2011). Core regions include the anterior mPFC (amPFC), PCC, bilateral angular gyrus, lateral temporal lobes, and superior frontal gyrus. The 'dorsomedial subsystem' comprises the dorsal mPFC (dmPFC), TPJ, lateral temporal cortex, temporal pole, and inferior frontal gyrus. However, the default network extends to a second subsystem, the 'medial temporal subsystem,' which includes the hippocampus, parahippocampal cortex, retrosplenial cortex, and posterior inferior parietal lobe. Core regions exhibit strong functional coherence with both subsystems, possibly allowing information to transfer between subsystems (Andrews-Hanna et al., 2010).

The functional–anatomical heterogeneity revealed by RSFC is consistent with patterns of white matter connectivity, derived from both diffusion tensor imaging in humans and analogous tracer studies using macaques, that show strong connections within subsystems and sparser connections between subsystems (see Andrews-Hanna et al., 2014, for a detailed review). In summary, the RSFC and anatomical properties of the default network suggest a heterogeneous brain system comprised of three separable components: (1) core regions, (2) a dorsomedial subsystem, and (3) a medial temporal subsystem. Next, we discuss the functions of the core components and the two subsystems with a meta-analysis and narrative review of the relevant neuroscience findings.

Meta-Analysis of Default Network Cognitive Function

The functions of the three components of the default network, derived from a whole-brain RSFC study (Figure 1(a); Yeo et al., 2011), were decoded using the NeuroSynth framework (originally reported by Andrews-Hanna et al., 2014). NeuroSynth is

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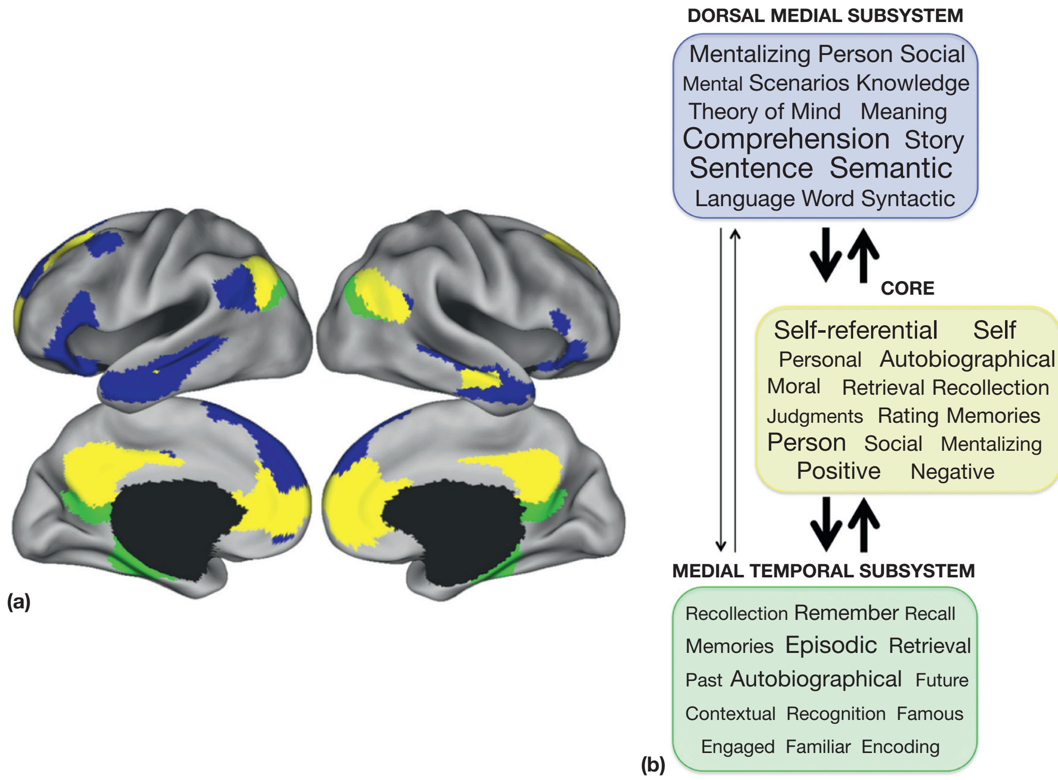

Figure 1 Default network components and cognition. (a) Topology of the default network revealed by resting-state functional connectivity MRI. Reproduced from Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., et al. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*, 1125–1165. Regions in yellow are core structures, regions in blue are the dorsomedial subsystem, and regions in green are the medial temporal subsystem. (b) Large-scale meta-analysis of terms activated within network components derived from NeuroSynth. The font size reflects the size of the correlation between the top meta-analytic maps for the three default network components (ranging from $r = 0.05$–0.35 in increments of 0.05). Adapted from Andrews-Hanna, J. R., Smallwood, J., & Spreng, R. N. (2014). The default network and self-generated thought: Component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*. doi:10.1111/nyas.12360, with permission.

the largest database of neuroimaging studies to date, with nearly 200 000 coordinates from over 5000 published articles (see Yarkoni, Poldrack, Nichols, Van Essen, and Wager (2011) for details and limitations of the framework). We took advantage of the database's 526 meta-analytic maps based on coordinates associated with articles using each of 526 cognitive terms/feature sets at high frequency (i.e., memory, attention, emotion, sensory, etc.) by computing the spatial similarity (using Pearson's correlation) between each meta-analytic map and the three default network components from Yeo et al. (2011). The 15 meta-analytic maps exhibiting the highest correlations were extracted, and the terms corresponding to each of these meta-analyses are shown in each colored box (Figure 1(b)).

The dorsal medial subsystem corresponded most strongly with meta-analytic maps pertaining to mentalizing and social cognition (i.e., mentalizing, social, person, theory of mind, mental, scenarios), as well as story comprehension and semantic/conceptual processing (i.e., comprehension, semantic, sentence, story, meaning, knowledge, language, word, syntactic). The medial temporal subsystem corresponded most strongly with meta-analytic maps pertaining to past and future autobiographical thought (i.e., autobiographical, past, future), episodic memory (i.e., episodic, memories, remember, recollection, recall) and contextual retrieval (i.e., contextual, retrieval). Finally, the core network associated with self-related processes (i.e., self-referential, self, autobiographical, personal), emotion/evaluation (i.e., positive, negative, moral), and social and mnemonic processes shared by the dorsal medial and medial temporal subsystem (i.e., social, person, mentalizing, recollection, retrieval, memories). These findings provide initial evidence of functional dissociation between the default network components and their interaction.

Dorsomedial Subsystem and Functions

Key structures within the dorsomedial subsystem, including the dmPFC and TPJ, are widely appreciated for their role in mentalizing (Frith & Frith, 2003; Lieberman, 2007; Mar, 2011; Saxe, 2006; Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008). The dmPFC is engaged during a broad range of social-processing tasks, including discriminating between the representations of distinct individuals (Hassabis et al., 2014). In contrast, the right TPJ has been suggested to play a particular role in reflecting on the beliefs of other people (e.g., Saxe, 2010). Inferior frontal and lateral temporal regions, extending anteriorly into the temporal poles, are also activated during many social tasks and likely contribute to semantic/conceptual aspects of mentalizing (Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009; Seghier, 2012). The dorsomedial subsystem often interacts with dorsal lateral prefrontal regions during social tasks that involve executive control (Lieberman, 2007), as when social information must be maintained in working memory (Meyer & Lieberman, 2012). Synthesizing these and our meta-analytic findings, the dorsomedial subsystem may contribute to social cognition by allowing individuals to access social conceptual knowledge and meta-cognitively reflect on such knowledge when reasoning about the minds of other people.

Medial Temporal Subsystem and Functions

The medial temporal subsystem has been predominantly examined for its role in memory but is now recognized more broadly for its role in mental simulation and imagination (Andrews-Hanna, 2012; Bar et al., 2007; Buckner et al., 2008; Hassabis & Maguire, 2007; Schacter et al., 2012). Results of the meta-analysis suggest that the medial temporal subsystem plays an important role in episodic recollection, contextual retrieval, and simulating one's personal future. Regions throughout this subsystem become engaged when individuals view objects with a strong contextual association (Bar, 2007) and/or use associative conceptual knowledge to guide decision-making (Kumaran, Summerfield, Hassabis, & Maguire, 2009). The medial temporal subsystem can function to integrate an individual into a 'situation model,' including a particular time, place, and context (Ranganath & Ritchey, 2012). Memories of the past and simulated future events are often populated by people, and co-occurring activity in the dorsomedial subsystem is often observed during these social aspects of autobiographical thought (Andrews-Hanna, Saxe, & Yarkoni, 2014; Rabin et al., 2010; Spreng & Grady, 2010; Szpunar, St. Jacques, Robbins, Wig, & Schacter, 2014). The medial temporal lobe subsystem allows for the tracking and updating of person knowledge well outside of the immediate perceptual environment, from minutes to years. Working with the dorsomedial subsystem, as well as core regions, the explicit simulation of social experiences, and memory for prior encounters that carry forth to inform current interactions, becomes possible.

Core Regions and Functions

The PCC is a functionally heterogeneous region (Leech, Braga, & Sharp, 2012; Leech, Kamourieh, Beckmann, & Sharp, 2011; Vogt, Vogt, & Laureys, 2006) and an important zone of integration. The PCC is thought to support bottom-up attention to behaviorally relevant sources of information drawn from memory and/or perception (Leech & Sharp, 2014) including the perception of social dynamics. Consistent with the meta-analytic results, the PCC activates across nearly all tasks that require self-generated thoughts, including self-referential processing, episodic or autobiographical memory, future thinking, mentalizing, spatial navigation, and conceptual processing (Binder et al., 2009; Brewer, Garrison, & Whitfield-Gabrieli, 2013; Qin & Northoff, 2011; Spreng, Mar, & Kim, 2009). Dorsal regions of PCC have been linked to monitoring behaviorally relevant stimuli and environmental changes (Leech et al., 2011; Pearson, Heilbronner, Barack, Hayden, & Platt, 2011) that would be important for social navigation. The anterior lateral temporal cortex and angular gyrus are also zones of integration within the default network that activate across a variety of tasks, ranging from mentalizing to semantic processing and memory retrieval (Mar, 2011; Ranganath & Ritchey, 2012; Seghier, 2012). The anterior lateral temporal cortex plays a key role in the representation of social information (Simmons, Reddish, Bellgowan, & Martin, 2010) and conceptual knowledge more broadly (Binder & Desai, 2011; Patterson, Nestor, & Rogers, 2007). The angular gyrus may also function as a cross modal hub, linking internal and perceptual sources of information with conceptual representations about events in spatiotemporal context (Binder & Desai, 2011; Seghier, 2012). The amPFC is most recognized for its role in self-related processing, including when individuals reference information to themselves, retrieve personal knowledge, recall autobiographical memories, consider their future goals or mental states, and simulate personal future events or social interactions (Andrews-Hanna, 2012; D'Argembeau, 2013; Denny, Kober, Wager, & Ochsner, 2012; Moran, Kelley, & Heatherton, 2013; Spreng et al., 2009). The amPFC becomes engaged when making decisions pertaining to other people we value, including our friends and relatives (Benoit, Gilbert, Volle, & Burgess, 2010; Krienen, Tu, & Buckner, 2010; Murray, Schaer, & Debbane, 2012), as well as those we deem similar (Mitchell, Macrae, & Banaji, 2006; but see Krienen et al., 2010). The amPFC is characterized by an extensive pattern of connectivity with the PCC as well as the dorsomedial and medial temporal subsystems (Andrews-Hanna et al., 2010). The core regions of the default network represent information relevant to the self and interact closely with the two subsystems that (1) allow information related to the self and other people to be reflected upon in a meta-cognitive manner and (2) construct associative information into coherent mental scenes.

Default Network in Context

Through its widespread connectivity with mnemonic, limbic, and semantic structures, the default network is well positioned to integrate salient external or internal information with one's current social context, affective experience, and prior knowledge. An emergent outcome of these associations might be the mental construction of personal meaning, which can subsequently frame and update existing representations. These dynamic representations could then guide purposeful behavior over longer timescales and mediate the complex process of social navigation.

A significant question remains as to whether the function of the default network, or even the dorsomedial subsystem in particular, is *specific* to social cognitive processes. Several regions of the default network are engaged during tasks involving narrative comprehension or inductive reasoning, although many of the stimuli employed in such tasks tend to be social in nature (Mar, 2011; Van Overwalle, 2011). Furthermore, regions within the dorsomedial subsystem also become engaged when individuals reflect on autobiographical memories (D'Argembeau et al., 2014) and nonsocial stimuli (Baetens et al., 2014), but a large proportion of autobiographical memories are social in nature (D'Argembeau et al., 2014), and reflection on social stimuli tends to activate the dorsomedial subsystem more than nonsocial stimuli (Baetens et al., 2014). A speculative hypothesis is that our evolutionary social nature may predispose us to prefer social over nonsocial information (Dunbar, 1998), leading to heightened activity for social material within a key network of regions important for more basic conceptual processes.

In summary, we find that the 'mentalizing network' is better characterized as the dorsomedial subsystem and core regions of the default network. Examining the relations among cognitive processes that activate the three default network components yields unique insight into processes whose neuroanatomy is densely interconnected. Specifically, social cognitive regions are more integrated with self- and memory-related brain regions than other neurocognitive networks, such as those facilitating motor control, perception, or executive functions. This observation is compelling because it suggests the function of memory may not be simply for remembering, but to form and update models of our experiences and use these models prospectively to navigate the complexities of the social world (Spreng & Mar, 2012). The default network may be critical for adaptive social cognition and is hypothesized to facilitate the integration of personal and interpersonal information and provide a means for personal experiences to become social conceptual knowledge (Spreng & Mar, 2012). Social dynamics are extraordinarily complex, unstructured, and difficult to predict. Successful navigation through the varied social landscape is essential to forming and maintaining the durable social bonds necessary for physical and mental health. The content of self-generated thoughts, mediated by the components of the default network, suggests that they serve a critical and adaptive purpose by allowing individuals to navigate this social world.

See also: **INTRODUCTION TO COGNITIVE NEUROSCIENCE**: Semantic Processing; The Medial Temporal Lobe and Episodic Memory; **INTRODUCTION TO METHODS AND MODELING**: Meta-Analyses in Functional Neuroimaging; Resting-State Functional Connectivity; Reverse Inference; **INTRODUCTION TO SOCIAL COGNITIVE NEUROSCIENCE**: Mentalizing; Person Knowledge and Attribution; Self-Knowledge; Strategic Mentalizing: The Neural Correlates of Strategic Choice; **INTRODUCTION TO SYSTEMS**: Large-Scale Functional Brain Organization.

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