Social by Default: Characterizing the Social Functions of the Resting Brain

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Abstract
Social-neuroscience research has identified a set of medial frontoparietal brain regions that reliably engage during social cognition. At the same time, cognitive-neuroscience research has shown that these regions comprise part of the default network, so named because they reliably activate during mental breaks by default. Although the anatomical similarity between the social brain and the default brain is well documented, why this overlap exists remains a mystery. Does the tendency to engage these regions by default during rest have particular social functions, and if so, what might these be? Here, it is suggested that the default network performs two critical social functions during rest: social priming and social consolidation. These constructs will be defined, recently published empirical findings that support them will be reviewed, and directions for future research on the topic will be proposed.

Keywords
default network, memory, rest, resting state, social cognition

The Social Brain
Social cognition refers to how people make sense of other people as well as themselves (Fiske & Taylor, 2008), and such processes are reliably associated with a specific network in the brain. The medial frontoparietal network, including medial prefrontal cortex (MPFC), precuneus/posterior cingulate (PC/PCC), and temporoparietal junction (TPJ; Fig. 1a), corresponds with high-level social cognition, such as mental-state and personality-trait attribution (Mitchell, Macrae, & Banaji, 2004; Saxe & Kanwisher, 2003; Spunt, Satpute, & Lieberman, 2011; Van Overwalle, 2009) and social-hierarchy and stereotype representation (Contreras, Banaji, & Mitchell, 2012; Parkinson, Kleinbaum, & Wheatley, 2017; Zerubavel, Bearman, Weber, & Ochsner, 2015). These findings are consistently replicated, and they also map onto real-world social outcomes. Individuals with an autism spectrum disorder, who struggle to understand...
others in daily life, show atypical function in medial frontoparietal network (Kennedy & Courchesne, 2008). In contrast, greater activation in these regions during social-cognition tasks is associated with superior communication skills (Falk, Morelli, Welborn, Dambacher, & Lieberman, 2013), empathy (Rameson, Morelli, & Lieberman, 2012; Zaki, Weber, Bolger, & Ochsner, 2009), and social integration (Krol, Meyer, Lieberman, & Bartz, 2018; Powers, Chavez, & Heatherton, 2016). Taken together, such findings indicate that when we are tasked with interpreting the social world, the medial frontoparietal network is critical.

Fig. 1. Neural-priming and consolidation results. The brain images (a) show regions associated with both social cognition and rest: temporoparietal junction (TPJ), precuneus/posterior cingulate cortex (PC/PCC), dorsomedial prefrontal cortex (DMPFC), anterior medial prefrontal cortex (AMPFC), and anterior temporal lobe (ATL). In Meyer and Lieberman’s (2018) study (b), participants rated their own personality traits (self), another person’s personality traits (e.g., Barack Obama’s), and a physical location’s traits (e.g., the Grand Canyon’s) while in the MRI scanner. Analyses of the interaction between participants’ pretrial resting-state activity and their reaction time suggest that both AMPFC and DMPFC prime self-referential processing, whereas only DMPFC primes nonself social processing (Obama condition). Lower values indicate greater priming, given that plotted values reflect how greater activity at a given rest period relates to faster (i.e., smaller) reaction time on the subsequent trial. AMPFC and DMPFC regions of interest (ROIs) were created by using the search terms “self” and “social” in Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011), a database that identifies brain regions previously associated with psychological processes. The bottom row (c) shows results from Meyer, Davachi, Ochsner, and Lieberman (2018). The graphs show the correlation between two sets of ROIs during resting-state scans that occurred during three different time windows (left) and when social trials were completed first and when nonsocial trials were completed first (right). Results showed that medial prefrontal cortex (MPFC) and TPJ increased connectivity during resting-state scans that occurred after social trials (labeled “after social rest”) and that this increase was sustained for individuals who completed social trials first. The MPFC and TPJ ROIs were created by a localizer scan in which participants quickly alternated between social and nonsocial impression formation. In addition (not shown here), greater connectivity between these regions, as well as with PC/PCC and ATL, during rest following social impression formation also correlated with participants’ subsequent social-memory performance measured outside of the MRI scanner, further implicating engagement of these regions during rest in social-memory consolidation.
The Default Brain

The medial frontoparietal network is also implicated in doing no particular task at all. Brain-imaging paradigms typically include rest periods between experimental conditions. For years, these baseline time points were not considered meaningful. However, in 1997, Shulman et al. demonstrated that the medial frontoparietal network systematically increases activity during these between-condition rest periods. The pattern emerges across a variety of paradigms—regardless of whether participants perform a visual search task, spatial attention task, or language task. Such findings are so robust that they led neuroscientists to label this network the default mode network, or default network, because it engages by default when participants rest in the scanner (Raichle et al., 2001).

Two findings in particular implicate the default network in the brain’s baseline physiological state. First, increased engagement of these regions occurs during brief rest (e.g., 7.5 s of rest between experimental trials; Spunt, Meyer, & Lieberman, 2015), indicating that this neural baseline emerges over relatively short time scales. Second, these regions sustain engagement over longer periods of rest as well. Default-network regions show strong functional connectivity (i.e., correlated time courses) during resting-state scans, when participants passively rest for approximately 4 to 11 min in the MRI scanner (Greicius, Krasnow, Reiss, & Menon, 2003). This latter finding suggests that the tendency for medial frontoparietal regions to engage during rest is not likely noise but rather an organized state of the brain.

Given that the social brain and the resting brain appear to be anatomically similar, a logical speculation is that the default network is doing something related to social cognition at rest. Indeed, this speculation has been made numerous times (Buckner & Carroll, 2007; Lieberman, 2013; Mitchell, 2006; Schilbach et al., 2008; Spreng et al., 2009). However, little to no empirical research has revealed precisely what that something is. Can we gain a more precise understanding of what the medial frontoparietal network contributes to social cognition during rest? The observation that the medial frontoparietal network comprises a neural baseline at both shorter term (e.g., a handful of seconds) and longer term (e.g., a handful of minutes) time scales may offer some clues.

Two Social Functions of the Resting Brain

Social priming

The observation that the brain reverts back to the medial frontoparietal network relatively quickly suggests that as soon as it does not need to attend to nonsocial external demands, it may be ready for social cognition. Thus, one function of activating the medial frontoparietal regions by default may be to prime subsequent social inferences; bouncing back to this network may keep the brain prepared to think about the self and others in any given moment. This idea borrows principles from semantic priming in cognitive psychology (Tulving, Schacter, & Stark, 1982). It is well known that if participants first see the word “doctor” on a computer screen, they will be quicker (i.e., respond with a faster reaction time) to categorize a semantically related word, such as “nurse,” relative to an unrelated word, such as “bread.” In the same way, default-network engagement at rest may function like the word “doctor” or as an endogenous prime that makes it easier for us to subsequently categorize the social world.

A recent study tested the social-priming hypothesis (Spunt et al., 2015). Participants alternated between brief periods of rest (6–9 s) and periods in which they judged a person’s mental state (i.e., a person’s intention), judged a person’s physical state (i.e., how a person was performing an action), or solved math problems. Trial-by-trial analysis examined how neural activity at the onset of each rest period modulated reaction time on the subsequent trial. Only the onset of the rest period was modeled to help ensure that the default tendency to engage these regions, rather than the content of thought engaged over the course of the 6-s to 9-s rest period, primed subsequent behavior. Such analyses reveal where in the brain greater default activity primes the following judgment (corresponding in this case to faster reaction time).

A striking pattern emerged: The degree of activity in one portion of the medial frontoparietal network—the dorsomedial prefrontal cortex (DMPFC)—at rest just prior to a mental-state reasoning trial was associated with a faster reaction time on that particular trial. The same was not true for rest periods prior to physical-state or math judgments: No portions of the brain demonstrated neural priming for these conditions. Critically, mental-state, physical-state, and math-problem trials were randomly presented, ruling out the possibility that during the brief rest, subjects mentally prepared for the kind of trial they knew would come next. Just as the word “doctor” helps us categorize the word “nurse,” keeping the DMPFC portion of the frontoparietal network active during rest may help us categorize behavior as intentionally motivated by minds.

The social-priming results align with functional MRI (fMRI) findings broadly implicating DMPFC in mental-state reasoning. Interestingly, although DMPFC is thought to play a general role in social cognition across a variety of social targets, an anterior portion of medial...
prefrontal cortex (AMPFC) is thought to engage more specifically when reflecting on the self (Denny et al., 2012; Lieberman, Straccia, Meyer, Du, & Tan, 2019). By extension, might AMPFC preferentially prime self-reflection? This question was posed in another recent neural-priming study (Meyer & Lieberman, 2018). As in the study described above, participants alternated between brief rest periods (6–9 s) and experimental trials. However, in this study, the trials required participants to rate their own personality traits (e.g., “Am I thoughtful?”), another person’s personality traits (e.g., “Is Barack Obama charming?”), and a physical location’s traits (e.g., “Is the Grand Canyon dry?”). Activity in DMPFC during pretrial rest primed both self- and other (Barack Obama) judgments. Meanwhile, the AMPFC pretrial rest activity preferentially primed self-judgments. Neither of these regions primed physical-location judgments, indicating that observed priming effects do not extend to all categories of semantic processing (see Fig. 1b). More broadly, results from these two neural-priming studies suggest there may be short-term, momentary social gains to activating the DMPFC and AMPFC portions of the medial frontoparietal network by default. In any given moment, this tendency may help us interpret ourselves and others on the fly.

**Social consolidation**

There also may be longer term social gains to engaging the default network spontaneously during rest. Numerous studies have found that regions of the medial frontoparietal network show strong functional connectivity during resting-state scans. At the same time, memory research has consistently found that rest is a time when new information is solidified in memory. Evidence for consolidation during rest spans from episodic replay in rodents and primates to associative learning in humans (Foster & Wilson, 2006; Hoffman & McNaughton, 2002; Kudrimoti, Barnes, & McNaughton, 1999; Tambini & Davachi, 2013). Given this literature, one function of coordinated engagement of the medial frontoparietal network during extended rest may be social consolidation, the solidification of newly acquired social information in memory.

This possibility was recently tested by interleaving resting-state scans with impression-formation tasks, in which participants formed impressions of new people (social) and impressions of new locations (nonsocial; Meyer, Davachi, Ochsner, & Lieberman, 2019). An initial resting-state scan occurred before participants began forming any impressions (baseline resting state). Then the order in which participants completed social and nonsocial impression-formation tasks was counterbalanced across participants, and both were interleaved with resting-state scans. After the scan session, participants completed a surprise memory test for the information they observed while forming their impressions. Consistent with prior research, results indicated that medial frontoparietal regions showed heightened functional connectivity during the baseline resting-state scan. More intriguing were three new findings. First, MPFC and bilateral TPJ showed significantly greater functional connectivity directly after forming social impressions (see Fig. 1c). Second, greater functional connectivity between these regions during the rest period after forming social impressions was associated with superior social-memory performance. These two findings suggest that functional connectivity between MPFC and TPJ regions during rest may facilitate our ability to effectively learn new social information.

The final finding from this study—an order effect—was even more provocative: If participants first formed social impressions, not only did they show increased functional connectivity between MPFC and TPJ during the subsequent rest but also this increase was sustained during the resting-state scan that followed the formation of nonsocial impressions (see Fig. 1c). In contrast, participants who first formed nonsocial impressions did not show increased MPFC–TPJ connectivity during rest directly following nonsocial impressions, perhaps because they had no new social information to consolidate yet. Instead, this group showed only increased MPFC–TPJ connectivity during the rest period directly following their second task—forming social impressions. Although speculative, such findings may indicate that because these regions show strong functional connectivity by default during rest, they may more easily sustain the postencoding increases in resting-state connectivity that promote consolidation. In other words, perhaps the tendency to engage MPFC and TPJ during extended rest maximizes our chances for social learning.

**Conclusion and Future Directions**

There has been a great deal of speculation about why brain regions associated with high-level social cognition also engage by default during rest (Buckner et al., 2008; Raichle et al., 2001; Schilbach et al., 2008; Spreng & Grady, 2010). However, prior to the research reviewed here, such speculations had not been empirically tested, and the precise functions of this overlap remain underspecified. Recent research suggests that engaging medial frontoparietal regions by default may perform both short-term social-priming and long-term social-learning functions.

These initial observations generate many more interesting questions. For example, do different portions of
the medial frontoparietal network prime and consolidate different types of information about ourselves and others? It is noteworthy that the medial frontoparietal network is also associated with autobiographical memory—though of course such memories are intrinsically linked to the self and can include social content. Future research using priming and consolidation paradigms with a richer sampling of conditions (e.g., trials parameterized on their social, self, and memory content) may disentangle the extent to which these functions are preferentially social cognitive in nature.

In relation to the social-consolidation findings, the approach presented here builds on recent neuroscience approaches to studying memory consolidation during brief rest (Foster & Wilson, 2006; Hoffman & McNaughton, 2002; Kudrimoti et al., 1999; Tambini & Davachi, 2013). Nonetheless, memory consolidation is often discussed as a longer term process, for example with memories strengthened over a night of sleep (Stickgold, 2005; Walker & Stickgold, 2004). Interestingly, the default network is also engaged during sleep but is more strongly engaged during earlier stages of sleep and decreases functional connectivity in later sleep stages (Horovitz et al., 2009; Samann et al., 2011). Future research on social-memory consolidation may reveal whether social memory is likewise strengthened during sleep, the role of the default network in this process, and whether earlier sleep stages may be important to social learning.

Other interesting questions surround the potential consequences of social priming and consolidation. Do these patterns facilitate prosocial behavior by enhancing our attention to the social world, or do they facilitate stereotyping, making it easier for us to identify and learn stereotype-consistent intentions in others? If medial frontoparietal regions tend to spontaneously engage during rest, does this mean the resting brain prioritizes learning about the self and others over other kinds of learning? And do known developmental changes in default-network resting-state connectivity (Fair et al., 2008; Supekar et al., 2010) correspond with developmental gains in self- and other-knowledge?

Humans are a highly social species. As children, we are dependent on caretakers for support. As adolescents, we navigate intricate social hierarchies. As adults, we cooperate in complex work environments. Across this spectrum, anticipating our own and others’ reactions and learning about the nuances of our social networks is imperative. The social-priming and consolidation findings reviewed here offer exciting new research directions geared toward understanding the role of rest in such social phenomena. More broadly, the findings reviewed here, in conjunction with future research on this topic, may clarify whether and how humans may be social by default.

Recommended Reading
Schilbach, L., Eickhoff, S. B., Rotarska-Jagiela, A., Fink, G. R., & Vogele, K. (2008). (See References). Reviews findings from social and cognitive neuroscience demonstrating the similarity between the resting brain and social brain and proposes that humans may engage in social cognition by default.

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Note
1. To examine neural priming, the researchers first statistically modeled neural activity during the task, as is done in standard task-based functional MRI (fMRI) analyses employing the general linear model. Second, they performed priming analyses on the residuals of the task-based model to minimize any influence of task-evoked effects.

References


