


Social cognitive network neuroscience

Anne C. Krendl  and Richard F. Betzel

Department of Psychological & Brain Sciences, Indiana University, Bloomington, IN 47405, USA

Correspondence should be addressed to Anne C. Krendl, Department of Psychological and Brain Sciences, Indiana University, 1101 E. 10th St., Bloomington, IN 47405, USA. E-mail: akrendl@indiana.edu.

Abstract

Over the past three decades, research from the field of social neuroscience has identified a constellation of brain regions that relate to social cognition. Although these studies have provided important insights into the specific neural regions underlying social behavior, they may overlook the broader neural context in which those regions and the interactions between them are embedded. Network neuroscience is an emerging discipline that focuses on modeling and analyzing brain networks—collections of interacting neural elements. Because human cognition requires integrating information across multiple brain regions and systems, we argue that a novel social cognitive network neuroscience approach—which leverages methods from the field of network neuroscience and graph theory—can advance our understanding of how brain systems give rise to social behavior. This review provides an overview of the field of network neuroscience, discusses studies that have leveraged this approach to advance social neuroscience research, highlights the potential contributions of social cognitive network neuroscience to understanding social behavior and provides suggested tools and resources for conducting network neuroscience research.

Key words: social cognitive network neuroscience; social neuroscience; network neuroscience; social network neuroscience

Over the past three decades, research from the field of social neuroscience has identified a myriad of brain regions that support social cognition—the process by which people understand, store and apply information about others (e.g. Mitchell, 2008; Adolphs, 2009; Kliemann and Adolphs, 2018). This research has provided fundamental insights into mapping discrete brain regions to specific social cognitive functions (e.g. theory of mind, face processing, stereotyping and prejudice). Recently, social neuroscience research has begun to leverage complex computational approaches, such as multivariate pattern analysis and psychophysiological interactions (PPIs), to better characterize functionality within brain regions (Weaverdyck et al., 2020; Parkinson, 2021) or between two brain regions (e.g. O'Reilly et al., 2012; Cassidy et al., 2016). However, these approaches may overlook the broader neural context in which individual brain regions are embedded.

The human brain is fundamentally a multiscale network. The average human brain contains 86 billion neurons with trillions of connections (Azevedo et al., 2009). These interconnections represent the anatomical scaffolding along which information is transferred throughout the brain and are therefore strongly related to the way the brain functions (McIntosh, 2000; Park and Friston, 2013; Smith et al., 2013). Human cognition requires integrating information across multiple brain regions (e.g. McIntosh, 2000), forming a distributed network composed of systems that support specialized brain function (Bassett and Sporns, 2017). Thus,

in addition to identifying the individual brain regions underlying social cognition, understanding their collective interactions and organization into systems may provide deeper insight into social behavior. The field of network neuroscience provides the mathematical framework for doing so, leveraging sophisticated tools for mapping the interactions within and among brain systems, modeling them as a network and understanding how those networks help to organize, segregate and integrate information (Bassett et al., 2018).

Network neuroscience has the potential to make important contributions to social neuroscience. Specifically, recent research suggests that examining brain function at a network level instead of at a region level may provide more comprehensive insight into how the brain gives rise to socially relevant behavior (see Tompson et al., 2018). Consistent with this assertion, although studies examining age deficits in social cognitive function (e.g. theory of mind and deception detection) have identified age differences in the extent to which specific brain regions are engaged during social cognition, these patterns of activation are not necessarily linked to behavior (Castle et al., 2012; Moran et al., 2012; Cassidy et al., 2016). For example, one study examining older adults' deficits in theory of mind found that they had weaker activation than young adults in the medial prefrontal cortex when performing theory of mind tasks, but it was unclear whether this related to their behavioral deficits (Moran et al., 2012). However, a recent study using a network neuroscience approach found

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that age-related deficits in connectivity mediated age deficits in theory of mind (Hughes *et al.*, 2019). Together, these studies suggest that a network neuroscience approach may provide novel insights into understanding social behavior. In this review, our goal is to provide an overview of the field of network neuroscience and suggest several strategies by which social neuroscience can capitalize on these approaches to better characterize the social brain.

What is network neuroscience?

Network neuroscience is the study of brain networks—mathematical abstractions of the brain in which cells, populations or regions are modeled as nodes and their pairwise interactions as connections or edges (Bullmore and Sporns, 2009, 2012; Sporns and Betzel, 2016). (See Table 1 for glossary). This definition of a network is consistent with historical definitions of networks (e.g. Friston, 1994), even those preceding functional magnetic resonance imaging (fMRI) research (e.g. Mesulam, 1998). However, it is distinct from its other uses in recent neuroimaging and cognitive neuroscience research, where the term ‘network’ has been used to refer to a collection of voxels whose activities increase from baseline during a task, spatial components obtained from independent component analysis or functionally defined systems (e.g. the default-mode network). In this review, however, we use the term ‘network’ to refer to examining the brain as a collection of nodes linked to one another by edges (for discussion, see Uddin *et al.*, 2019).

In network models of the brain, connections typically come in two different ‘flavors’: structural or functional. Structural connections represent the physical and material pathways between brain regions. At the macroscale (measurable with MRI), they correspond to interregional white-matter pathways. Functional connections, on the other hand, represent statistical associations

between the activity recorded from pairs of voxels, grayordinates or regions. Historically, they have been defined as ‘temporal correlations between spatially remote neurophysiological events’ (Friston, 1994, p. 57). In practice, functional connections are measured as a correlation, but could be estimated using a wide range of other measures (Friston, 1994; Honey *et al.*, 2007; Smith *et al.*, 2011).

The functional connections that comprise brain networks are typically measured during ‘resting-state’—a period typified by the absence of explicit task instruction in which participants are engaged in undirected thought (Greicius *et al.*, 2003; Meindl *et al.*, 2010). There are several important benefits to defining brain networks in this manner. First, resting-state connectivity is broadly related to the brain’s anatomical connections of white-matter fascicles (Hagmann *et al.*, 2008; Honey *et al.*, 2009), suggesting that there is an overlap between structural and functional connectivity (see also Suárez *et al.*, 2020; Tovar and Chavez, 2021). However, dynamic changes in functional connectivity throughout resting state suggest that, although functional connectivity may be constrained by structural connectivity, the two are dissociable (e.g. Buckner *et al.*, 2013). Second, although the brain consumes as much as 25% of the body’s metabolic energy (Herculano-Houzel, 2012), 60–80% of that energy is consumed during resting state, whereas only 0.5–1% of its energy is task-specific (Raichle and Mintun, 2006). Finally, task-based state connectivity patterns are highly correlated with resting-state connectivity (Smith *et al.*, 2009; Cole *et al.*, 2014; Hughes *et al.*, 2020), suggesting that resting-state connectivity may serve as a functional backbone, constraining task-evoked connectivity and offering more comprehensive insight into network reconfiguration (e.g. Damoiseaux *et al.*, 2006; see also Hughes *et al.*, 2019).

An important challenge to resting-state functional connectivity is that resting state, by definition, is an unconstrained period in which individuals’ minds are allowed to wander and are not constrained to a specific type, or even domain, of thought. As such, individual differences in functional connectivity patterns during resting state likely relate to differences in participants’ mental states during this task (Buckner *et al.*, 2013; Gonzalez-Castillo *et al.*, 2021). Indeed, a recent study found that functional connectivity measured during naturalistic viewing (e.g. movie-watching) yielded more accurate predictions of individuals’ cognition and emotion (as measured in separate tasks) than did their resting-state functional connectivity patterns (Finn and Bandettini, 2021). Moreover, this study found that although cognition was better predicted than emotion from either functional connectivity source, watching movies with social content gave the most accurate predictions for both cognition and emotion. The findings from this study raise important questions for future research about the suitability of resting-state vs passive movie-watching tasks for extracting functional connectivity patterns to relate to social behavior. In order to ascertain the most suitable approach for social cognitive network neuroscience research, future work should compare functional connectivity patterns from resting-state vs passive movie-watching and determine which best relates to explicit measures of targeted social behaviors.

In the following sections, we introduce some of the canonical findings from network neuroscience and discuss some of the technical challenges associated with the construction of brain networks from MRI data. Next, we review some of the ways that network neuroscience is being used to probe brain-behavior associations and for extending our understanding of ‘the social brain’. Finally, we conclude by discussing some of

Table 1. Glossary of terms

Term	Definition
Node	The smallest unit of interest in an analysis; may be a voxel (or grayordinate) or collection of spatially contiguous voxels grouped into a parcel
Edge	A measure of whether two nodes interact with one another or are connected, usually operationalized as a correlation. In general, can be weighted/binary or directed/undirected
Network	A collection of nodes interconnected to one another by edges. Also referred to as a graph
Module or community	Sub-networks of densely interconnected nodes embedded within a larger network
System	A special class of sub-network usually defined based on neuroscientific knowledge, e.g. groups of nodes known to be co-active across conditions. Often referred to by names that reference the cognitive functions, the system is supposed to subtend, e.g. somatomotor, visual and attention systems
Grayordinates	Gray matter vertices on a surface projection
Multilayer network	The connectivity between the same set of nodes may be across connectivity modality, time and individuals. Multilayer networks are a way of representing differential patterns of connectivity among those nodes using a single model

Box 1.

Although our discussion of network analysis focuses primarily on fMRI approaches, networks can be defined using multiple other neuroimaging tools [e.g. diffusion tensor imaging, structural data, EEG, MEG and functional near-infrared spectroscopy (fNIRS)]. Diffusion imaging measures the microscopic motion of water molecules to detect the presence of white-matter fascicles using 'tractography' algorithms. These algorithms provide maps of the gray matter starting and end points of myelinated fiber bundles. The result is a (usually sparse) network of interregional white-matter connectivity (Iturria-Medina *et al.*, 2007; Hagmann *et al.*, 2008; Hermundstad *et al.*, 2013). There exist a number of strategies for weighting edges. On one hand, one could simply weight edges based on the number of streamlines between two regions. This number can be inflated based on region (parcel) volume and surface area, so typically a correction is necessary. On the other hand, one could weight white-matter edges using biophysical measures, e.g. mean fractional anisotropy or mean diffusivity, which are related to fiber integrity.

Additionally, networks can be constructed from structural data (T1 or T2 images). One popular strategy for doing so is to generate 'structural covariance matrices' (Gong *et al.*, 2012; Evans, 2013). The weight of the edge between regions *i* and *j* is usually defined as the population-level covariance of *i* and *j*'s cortical thickness (or some other structural measure). Accordingly, structural covariance matrices are typically defined at the group level. However, recent studies have extended this approach to the level of individual subjects by computing the covariance (or correlation) between ensembles of morphological metrics defined regionally (e.g. Seidlitz *et al.*, 2018).

Apart from MRI data, networks can also be constructed from scalp and intracranial electroencephalography (sEEG and iEEG; e.g. Betzel *et al.*, 2019; Paban *et al.*, 2019; Scheid *et al.*, 2021), MEG (e.g. Jin *et al.*, 2011; Messaritaki *et al.*, 2021) and fNIRS (e.g. Niu *et al.*, 2013; Cai *et al.*, 2018) data. These methods record brain activity using electrical, magnetic and spectral properties. While some clinical conditions require placing recording electrodes directly onto the exposed cortical surface, more commonly EEG, MEG and fNIRS record signals on the scalp and generally offer poorer spatial resolution compared to fMRI. However, they acquire data at a frequency that is orders of magnitude faster than that of fMRI, making it possible (in principle) to detect and characterize changes in network structure with sub-second precision. Network nodes can be defined either as the sensors themselves, or, following source reconstruction, anatomically, which makes it possible to use familiar parcellation-based approaches for defining network nodes. The improved temporal resolution along with the oscillatory basis of EEG and MEG signals have contributed to the widespread use of phase-based measures of synchrony to define edge weights, e.g. phase-locking values. The spectral content of EEG and MEG is much broader than that of fMRI; it is common to define connectivity within specific canonical frequency ranges.

the latest methodological advances in network neuroscience and explore how they might be used within the context of social neuroscience.

Constructing brain networks from neuroimaging data

An important consideration in network neuroscience is how to construct brain networks from neuroimaging data. Although brain networks can be constructed using data collected from virtually any recording modality (see Box 1), here we will focus on fMRI data. Two of the greatest sources of variability across network studies using fMRI are (i) how to define regions of interest or

parcels that later become the nodes in the network and (ii) how to measure the presence/absence of a functional connection between two regions and its weight (the edges between the nodes) (e.g. Smith *et al.*, 2011; Eickhoff *et al.*, 2015; Arslan *et al.*, 2018; Pervaiz *et al.*, 2020).

Defining nodes

In principle, one could define nodes as the smallest possible unit of interest. In neuroimaging, this corresponds to voxels or surface vertices (grayordinates). However, voxel-wise networks are large (on the order of 10^5 number of nodes) and can present computational challenges. Additionally, many voxels and vertices connect similarly to the rest of the brain, suggesting that those voxels could be merged together without a loss of much information. There are numerous approaches to take to defining nodes, including functional specificity, topographic organization and connectivity (Felleman and Van Essen, 1991; Van Essen and Glasser, 2018). However, in practice, most studies elect to parcellate the cerebral cortex into, roughly, hundreds of non-overlapping parcels (e.g. regions of interest) by assigning every voxel/vertex to one parcel.

There are, of course, many strategies for generating these parcellations. Early studies took advantage of existing divisions of the brain into regions based on anatomical (e.g. Automated anatomical labeling; Rolls *et al.*, 2020) or cytoarchitectonic information (e.g. Brodmann areas; Sporns, 2011). While these parcellations continue to be used, they have been largely supplanted by data-driven approaches in which parcels are defined using functional connectivity data (Power *et al.*, 2011; Shen *et al.*, 2013; Gordon *et al.*, 2016; Schaefer *et al.*, 2018) and sometimes other microstructural properties (see Glasser *et al.*, 2016). The aim of these approaches is to generate functionally homogeneous parcels such that the voxels assigned to any given parcel exhibit similar patterns of connectivity with respect to the rest of the brain. Additionally, parcels are usually defined to be spatially contiguous and should be generalizable, so that when they are imposed on new brains, the resulting parcels are still functionally homogeneous. Homogeneity, as it is discussed here, does not refer to the blood-oxygen-level-dependent (BOLD) signal, but rather is assessed using similarity or distance-based metrics on measures such as functional or anatomical connectivity, cytoarchitectural properties or topography.

Recently, it has become clear that parcels generated from pooled, group-averaged functional connectivity may systematically distort individual features (Braga and Buckner, 2017; Gordon *et al.*, 2017; Gratton *et al.*, 2018), igniting new efforts to generate flexible parcellations that can adapt group-level parcels to individual brains (Chong *et al.*, 2017; Bijsterbosch *et al.*, 2018; Kong *et al.*, 2019; Mejia *et al.*, 2020) by leveraging data collection tools such as multi-echo fMRI (Lynch *et al.*, 2020). Using individual parcellations may be particularly beneficial for social cognitive network neuroscience research, given that its goal is to estimate individual differences in social behavior from brain networks (see Mwilambwe-Tshilobo *et al.*, 2019 for a relevant example).

In network analyses, parcels are treated as nodes. In general, the choice of parcellation will impact the properties of a network such that two different parcellations of the same brain can exhibit contradictory properties or provide misleading summaries of interregional connectivity (Wang *et al.*, 2009; Zalesky *et al.*, 2010). Since there is, generally, no ground truth by which to

assess the validity of any parcellation, it is difficult to unambiguously and objectively determine which parcellation is 'best'. Even measures of parcellation quality, e.g. the average homogeneity of parcels, can be biased by the number and size of parcels, with finer parcellations exhibiting greater levels of homogeneity (Gordon *et al.*, 2016). Further complicating this process is the fact that parcel boundaries vary across conditions (Salehi *et al.*, 2020) and time (Iraji *et al.*, 2019), thereby resulting in there not being a universally optimal parcellation.

To increase the reliability and replicability of their parcellations, some of the more widely cited parcellations are those that were generated (and validated) using large datasets (e.g. Power *et al.*, 2011; Yeo *et al.*, 2011; Schaefer *et al.*, 2018). For example, Yeo and colleagues (2011) used resting-state data collected from 1000 brains to identify network parcellations. They generated their initial network structure from a subset of 500 brains and replicated the structure across the second set of 500. Using this approach, they ultimately identified (and cross-validated) 17 putative systems that largely divide seven core cognitive domains—visual, somatomotor, default mode, limbic, dorsal attention, ventral attention and frontoparietal (Yeo *et al.*, 2011). At present, one of the most widely used atlases was developed by Schaefer and colleagues (2018) using a multi-modal approach and data from nearly 1500 participants. Similar to the approach by Yeo and colleagues, the data were divided in half to create a discovery and replication sample. Rather than a fixed number of nodes, this study resulted in a multiresolution network parcellation comprising between 100 and 1000 parcels (in increments of 100), each of which could be mapped to one of 17 validated brain systems, analogous to those in the Yeo atlas (Yeo *et al.*, 2011). Importantly, the parcels generated by Schaefer *et al.* were more functionally homogeneous compared to a set of comparable parcellations (for discussion, see Schaefer *et al.*, 2018), including the well-known Gordon atlas (Gordon *et al.*, 2016). Although these differences emphasize the importance of standardizing approaches, they also demonstrate that using a parcellation that was defined

in a rigorous manner may reduce the likelihood of spurious findings (for discussion, see Arslan *et al.*, 2018).

Since nodes vary across conditions (Salehi *et al.*, 2020), another approach is to define the nodes of interest through a task-based localizer (Chai *et al.*, 2016; Schmäzle *et al.*, 2017; Hughes *et al.*, 2019). Although such approaches are less common, they may provide a more targeted and hypothesis-driven method for modeling resting-state and especially task-based functional connectivity. For example, one study found that global vs specific task-defined parcellations had dissociable effects in predicting task performance on language tasks (Bansal *et al.*, 2018). Two recent social neuroscience studies have also used this approach. One compared functional connectivity within the default-mode system to connectivity derived from a task-based localizer (e.g. Hughes *et al.*, 2019) and found that only the latter predicted social behavior (theory of mind performance). Another study found that connectivity between nodes in a theory-defined 'mentalizing system' during a social exclusion task predicted aspects of adolescent males' friendship networks (Schmäzle *et al.*, 2017). An important future direction for social cognitive network neuroscience research will be to evaluate the effectiveness of using a data-driven vs theory-driven approach in predicting social behavior.

Defining edges

A second, but oftentimes less explored, source of variation in network organization is how one determines the presence or absence of a functional connection and its weight (the edges between pairs of nodes). In general, functional connectivity is defined as a measure of statistical dependence between activities recorded from distinct neural sources (Friston, 1994; Sporns, 2010; Figure 1A–C). In practice, however, resting-state functional connectivity is almost always calculated as a temporal correlation of activity, i.e. a Pearson correlation (Smith *et al.*, 2009). Note that in studies of task-evoked connectivity, additional preprocessing steps need

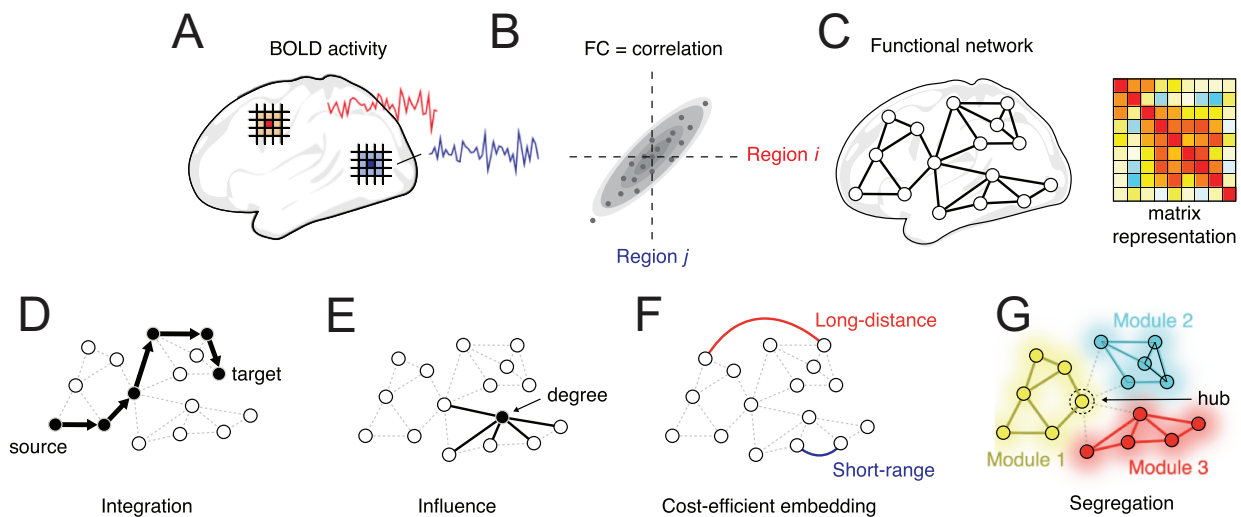


Fig. 1. Functional network construction and canonical properties of brain networks. Functional networks are constructed by extracting fMRI BOLD time courses from voxels, grayordinates or parcels (A) and computing their temporal correlation (B). Note that, in principle, other measures of statistical dependence can be substituted, e.g. that account for nonlinearities. This process is repeated for all pairs of neural elements, usually defined to be parcels. The result is a correlation matrix that is referred to as a 'functional network' (C). The network can be viewed in anatomical space by drawing a circle (node) at the spatial center of each parcel and linking connected nodes by lines (edges). The resulting network can be analyzed with tools from network neuroscience. These tools can (D) track the flow of information through the network by studying paths, (E) identify influential nodes based on the number of connections (a node's degree), (F) assess the contribution of the brain's spatial embedding on its network architecture (in general, brain networks prefer to form low-cost, short-range connections rather than costly long-distance connections) and (G) identify functionally specialized sub-networks known as modules or communities.

to be performed prior to computing the correlation. Specifically, activations driven by presentation should be regressed out so that they do not artifactually drive correlations (Cole et al., 2019).

In general, the definition of functional connectivity as a bivariate statistical relationship leaves open the possibility of measuring a functional interaction between brain regions using a myriad of other measures, many of which are applied widely to construct networks from magnetoencephalography (MEG)/electroencephalography (EEG) data and other imaging modalities besides fMRI (see Box 1). Although Pearson correlation has become the *de facto* measure of choice, there exist many alternatives, including some that are specific to task data. For instance, functional connectivity weights have previously been defined based on spectral coherence (Bassett et al., 2011)—correlations in the frequency domain—and mutual information (Garofalo et al., 2009). However, these measures are non-negative and tend to ‘rectify’ anticorrelations, e.g. nodes whose activities are perfectly anticorrelated have high levels of mutual information. Other studies, rather than reporting correlation coefficients, report regression coefficients—i.e. the β weights from linear regression models (Cole et al., 2021). Compared to Pearson correlation, which measures the extent to which two variables are linearly correlated, the regression coefficients reveal the slope of that relationship.

Other studies have used temporal precedence measures to establish pseudo-causal relationships between time series, e.g. Granger causality and transfer entropy (Smith et al., 2011; Holper et al., 2012; Maki-Marttunen et al., 2013; Ribeiro et al., 2021). Broadly, these measures test whether the past activity of one region helps predict the future of another region’s activity above and beyond what its own activity can predict. While temporal precedence measures like Granger causality and transfer entropy hold tremendous promise in revealing directed interactions between brain regions, their accurate estimation requires large amounts of data and, in the case of transfer entropy, necessitate the binarization of time series or force the user to make assumptions about the underlying distribution of brain activity. Finally, care must be taken in interpreting these measures. While their application to spike trains and cellular levels lead to straightforward interpretations, the slow and serially correlated fMRI BOLD signal (itself an indirect measure of population-level activity) may obscure true causal relationships.

In general, any bivariate measure of statistical dependence can be used to assess the presence, absence and/or weight of an edge. However, the decision to use a particular measure should be motivated by the experimental paradigm. For example, PPI, which assesses the effect of tasks influence the coupling strength between two regions (Friston et al., 1997; O’Reilly et al., 2012), should only be used for tasks, and for maintaining continuity with extant literature. Introducing a novel measure when an existing measure is capable of capturing the desired effect makes it challenging to compare the present results against those from previous studies and may have the unwanted effect of confusing readers.

As with node definition, how one defines a functional connection has implications for the organization of the inferred network. Different measures also have the capacity to summarize different modes of coupling between network nodes. For instance, the commonly used Pearson correlation assesses the linear relationship between the activities recorded from two nodes. However, if that relationship is nonlinear, the Pearson correlation might be misleading. In contrast, measures like mutual information may

be better suited for capturing generic, nonlinear relationships between nodes (Smith et al., 2011; Pervaiz et al., 2020).

Figure 2 provides an overview of the steps discussed in this section. In summary, social cognitive network neuroscience should carefully consider how to reduce variability in node selection and in how functional connectivity is calculated. One potential way to do this would be to build on existing models from the field of network neuroscience, such as using well-studied network parcellations (e.g. Schaefer et al., 2018). In addition to providing a clearer foundation upon which the field can evolve, such an approach would provide more domain-general insights into social neuroscience.

Organizing principles of human brain networks

Brain network analyses necessarily shift focus away from measuring activation in specific brain regions and instead emphasize on how different parts of the brain interact with one another as components of distributed networks. This increasingly global view allows for network neuroscientists to identify the overarching principles by which brains are organized and operate. Inspired by advances in other scientific disciplines (Watts and Strogatz, 1998), early work in network neuroscience focused on ‘small-worldness’ (Sporns and Zwi, 2004; Bassett and Bullmore, 2006), which refers to the propensity for nervous systems to simultaneously exhibit locally dense (interconnected) clusters and shorter-than-expected path length. These two characteristics are thought to support specialized information processing and rapid transmission of information, respectively (Figure 1D). Small-world organization has been observed in brain networks across phylogeny and at virtually every spatial scale, from synaptic contacts among single cells (Latora and Marchiori, 2001; Varshney et al., 2011) to large-scale brain networks (Iturria-Medina et al., 2008; Muldoon et al., 2016).

More recent studies have provided evidence that brain networks are organized around an exclusive set of hub regions—highly connected and highly central regions that occupy positions of influence within the brain (Hagmann et al., 2008; Power et al., 2013). Because of high levels of connectivity, these regions are capable of both delivering and receiving information to and from large portions of the brain, respectively (Figure 1E). Moreover, these putative hubs tend to be connected to one another, forming an integrative structure known as a ‘rich club’, which serves as a backbone for efficient information transfer (Zamora-López et al., 2010; van den Heuvel and Sporns, 2011). Once again, hubs and rich clubs are conserved across phylogeny (Harriger et al., 2012; de Reus and van den Heuvel, 2013; Towlson et al., 2013; Shih et al., 2015).

Other studies have suggested that embedding the brain in three-dimensional space serves as an overarching organizing principle (Stiso and Bassett, 2018; Figure 1F). All things equal, long-distance connections require proportionally more material and energy, of which the brain has limited amounts, than short-range connections. Consequently, brains need to balance the formation of functionally adaptive features like efficient processing paths, hubs and rich clubs with the material and metabolic cost of forming and supporting those features (Kaiser and Hilgetag, 2006; Samu et al., 2014). This trade-off restricts the types of features that brain networks can support simultaneously and gives rise to a heavy-tailed distribution of connection lengths that favors short (low-cost) connections (Ercsey-Ravasz et al., 2013; Betzel and Bassett, 2018).

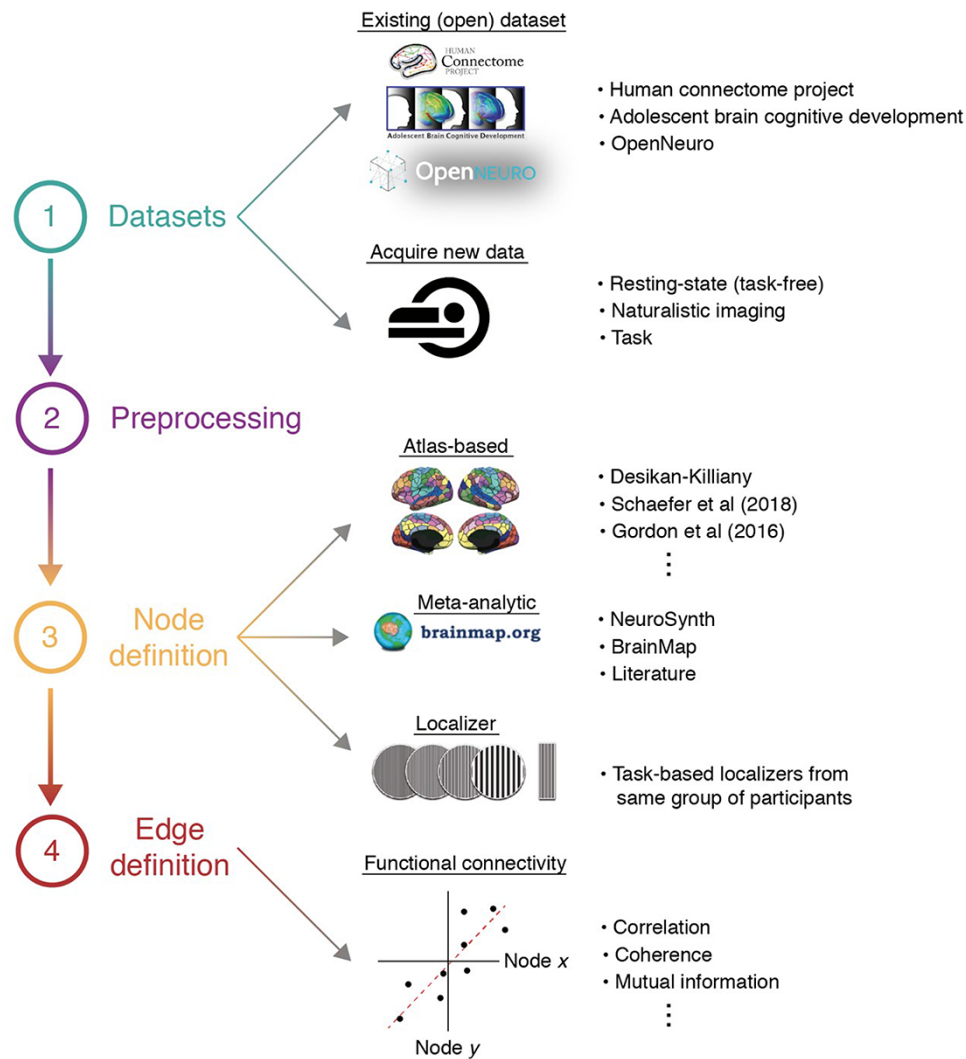


Fig. 2. Constructing brain networks from neuroimaging data. Graphical depiction of the suggested pipeline for constructing brain networks. Each step is associated with multiple user-defined parameters and options, whose strengths and weaknesses are discussed in detail in the review. Several choices (e.g. selecting the dataset to use in the first step) will largely be dictated by the research question. The steps are presented in sequential order but are not intended to be prescriptive. Rather, they are intended to offer a summary of the key steps discussed in this review and are presented for convenience and clarity. Constructing a network begins with data selection (Step 1). Traditionally this meant collecting data under different conditions (while performing a task, while passively listening/viewing audiovisual stimuli or in the absence of explicit task instruction). Recent initiatives, however, have made high-quality data publicly available, organized according to field-defined standards and processed via distributed computing. After data selection, data undergo basic preprocessing steps (Step 2; alignment, intensity normalization, nuisance regression, frame censoring, etc.). This procedure results in ‘cleaned’ voxel/vertex time series. In most network analyses, the dimensionality of these data is reduced via a parcellation step (Step 3), in which voxels/vertices are aggregated into parcels. Parcels may be determined a priori based on existing atlases, meta-analytic activation maps or using localizers to co-locate similar functional territories across individuals. The final step (Step 4) is to establish whether a connection exists between pairs of parcels (nodes). In human neuroimaging (especially of the resting brain), the convention is to estimate connection strength based on the extent to which two regions’ activity time courses are correlated with one another. Other measures (e.g. mutual information, spectral coherence and Granger causality) are discussed in the review.

Studying brain networks as sub-networks, modules and systems

One of the hallmark features of biological neural networks—and one that is increasingly becoming the focus of network science applications in neuroimaging and cognitive neuroscience—is their decomposability into cohesive sub-networks known as ‘modules’ or ‘communities’ (Power *et al.*, 2011; Sporns and Betzel, 2016; Yeo *et al.*, 2011; Figure 1G). Modular structure is evident at all spatial scales (Jarrell *et al.*, 2012; Betzel and Bassett, 2018), but it has been investigated in depth at the macroscale using human fMRI data. At rest, modules correspond closely to patterns of task-evoked activity and delineate well-known functional

systems (Smith *et al.*, 2009; Crossley *et al.*, 2013) and at multiple resolutions (Gordon *et al.*, 2020). The correspondence of module boundaries with well-established functional systems suggests that the brain’s modular structure helps support functionally specialized processing (Stevens and Spreng, 2014).

For example, partitions of functional brain networks identify modules corresponding to frontoparietal and both dorsal and ventral attention systems, which include collections of brain regions known to play central roles in control (for review, see Scolar *et al.*, 2015), top-down guided attention and processing of sensory or perceptual information, respectively (Corbetta and Shulman, 2002; Vossel *et al.*, 2014). The default-mode system, one of the

most widely studied collections of regions in the brain, has the unique property of being more active during resting than task states (see Raichle, 2015). Numerous animal studies have also identified a homologous default-mode system in non-human primates, rats and mice (Mantini et al., 2011; Lu et al., 2012; Stafford et al., 2014). Within humans, the default-mode system has been implicated in a myriad of functions, including receiving and conveying sensory information from the external world (for review, see Raichle, 2015), mind wandering (Andrews-Hanna et al., 2010) and, directly relevant in the current review, social cognition (e.g. Mars et al., 2012; Meyer, 2019).

Modules represent collections of densely connected brain regions that, on their own, are thought to support specific cognitive functions. Complex cognition, then, is thought to arise from interactions between these modules. Accordingly, relating functional connectivity strength within and between modules during resting and/or task states to behavior has been one of the most common applications of network neuroscience, with applications in personality neuroscience (Markett et al., 2018), cognitive neuroscience (Medaglia et al., 2015) and even social neuroscience (Schmälzle et al., 2017; Wasylyshyn et al., 2018; Hughes et al., 2019). This approach will be discussed in more detail in a later section.

There are several key takeaways from these sections. First, the field of network neuroscience studies brain networks, which models brain regions as nodes and their pairwise functional interactions as connections. Second, small-world organization, hubs and short path length are key organizing principles of networks. Third, sub-networks or modules support specific cognitive functions. These features are expressed to some extent in virtually all brains and are thought to be critical ‘ingredients’ for healthy brain function. An important future direction for social cognitive network neuroscience research will be to apply these principles to social behavior, specifically. This includes, but is not limited to, identifying how modules and their interactions give rise to social cognition and better understanding of the roles of hubs and rich clubs in social cognition, by mediating the flow of information between modules. In the next section, we explore how network neuroscience techniques have been applied to advance our understanding of social behavior.

Social cognitive network neuroscience and the default mode

The limited work applying a network neuroscience approach to understanding social behavior has focused primarily on within- and/or between-module functional connectivity patterns. One of the primary modules of interest in this research has been the default mode, which is generally viewed as comprising a core aspect of the social brain (Mars et al., 2012; Meyer, 2019). The default mode is typically defined as a set of brain regions that are more active when the brain is at rest than during a task (Raichle et al., 2001). An emerging body of research applying network neuroscience techniques to social behavior has shown that default-mode connectivity relates to numerous aspects of social behavior, including perceived social isolation (Spreng et al., 2020), theory of mind (Hughes et al., 2019), social rejection (Schmälzle et al., 2017; Wasylyshyn et al., 2018), conformity (Wasylyshyn et al., 2018), creativity (Beaty et al., 2019) and even real-world social outcomes (e.g. Falk and Bassett, 2017; Joo et al., 2017; Pillemer et al., 2017; Schmälzle et al., 2017; Hyon et al., 2020; Tompson et al., 2020).

A recent study examined whether functional connectivity differed as a function of being socially included or excluded

(Schmälzle et al., 2017). The study had adolescent males perform the Cyberball task (Williams and Jarvis, 2006), a widely used manipulation of social exclusion, and evaluated whether being socially excluded during the task was associated with increased within-network connectivity in networks related to mentalizing or social pain. Mentalizing and social pain were targets of interest in this study because prior work has shown that being socially excluded is painful (Rotge et al., 2015) and elicits greater activity from brain regions associated with mentalizing (inferring other people’s mental states; Powers et al., 2013). The parcellations in this study were operationalized in two ways: first, by using theory-driven approach that identified nodes associated with mentalizing and social pain using meta-analytic data from NeuroSynth (Yarkoni et al., 2011); and second, by using a data-driven whole-brain network parcellation approach. Both approaches used largely overlapping nodes: mentalizing consisted primarily of nodes within the default-mode system, whereas social pain comprised nodes from portions of the salience and cingulo-opercular systems. The results were consistent using both the theory- and data-driven approaches: when participants were socially excluded, they showed higher within-system connectivity in the mentalizing system than when they were included. No significant changes in connectivity were observed within the social pain system nor were there changes in between-system connectivity. Another study found that increased within-system connectivity in the mentalizing and social pain systems during social exclusion predicted adolescent males’ increased likelihood to subsequently comply with perceived social norms (e.g. be more or less risky while in a driving simulator; Wasylyshyn et al., 2018).

An interesting aspect of the finding by Wasylyshyn and colleagues (2018) is that it demonstrated that connectivity during the social exclusion task predicted behavior outside of the scanner. Similarly, a recent study found that resting-state functional connectivity was associated with theory of mind performance (Hughes et al., 2019). Specifically, Hughes and colleagues (2019) examined resting-state connectivity within a localizer-defined theory of mind system in the default mode for young adults (individuals between the ages of 18 and 25) and older adults (individuals over the age of 65). They found that age differences in resting-state connectivity within this system predicted older adults’ theory of mind deficits on a separate task. Importantly, overall age deficits in global default-mode connectivity did not predict older adults’ theory of mind deficits, suggesting that theory-driven approaches (e.g. focusing on a sub-system or a localizer-defined system) may provide more insight into social behavior in some cases than a strictly data-driven approach. An important implication of this study is that it suggests that resting-state functional connectivity may constrain social behavior. Related to this finding, Christov-Moore and colleagues (2020) examined whether resting-state connectivity predicted empathic concern, which is essential for everyday communication and survival in the social environment (Eisenberg and Strayer, 1987). The authors found that greater resting-state connectivity within the somatomotor system predicted greater empathic concern.

A burgeoning area of interest has been to use network neuroscience techniques to examine real-world social outcomes, including loneliness (Spreng et al., 2020), and the number and structure of individuals’ social relationships (e.g. Falk and Bassett, 2017; Schmälzle et al., 2017; Hyon et al., 2020). These studies have examined both resting-state (e.g. Spreng et al., 2020) and task-based connectivity (e.g. Schmälzle et al., 2017). With respect to the former, individuals with greater within-system resting-state default-mode connectivity had higher levels of loneliness

(perceived social isolation; Spreng *et al.*, 2020). This finding has important implications for social neuroscience research because longitudinal and cross-sectional studies have found that, even when controlling for other risk factors (e.g. socioeconomic status and cognitive and physical health), loneliness is associated with poorer mental, physical and cognitive health and higher mortality rates (Cornwell and Waite, 2009; Cacioppo *et al.*, 2010; Luo *et al.*, 2012; Perissinotto *et al.*, 2012; Kuiper *et al.*, 2015).

Several recent studies have also examined whether functional connectivity predicts aspects of individuals' personal social networks—the group of people with whom an individual is socially embedded (Joo *et al.*, 2017; Pillemer *et al.*, 2017; Schmälzle *et al.*, 2017; Tompson *et al.*, 2020). These studies primarily have examined connectivity as it relates to unique individual's social connections (Schmälzle *et al.*, 2017; Pillemer *et al.*, 2017; Hyon *et al.*, 2020; Tompson *et al.*, 2020; but see, Joo *et al.*, 2017). In some cases, these studies have been more qualitative, focused on identifying patterns of resting-state connectivity that predict features of an individual's social network (Joo *et al.*, 2017; Pillemer *et al.*, 2017). For example, one study with older adults found that their resting-state connectivity in a subcomponent of the default-mode system was positively related to the number of individuals in their network, whereas connectivity within the frontoparietal system was positively related to the number of network members with whom the older adult was close (e.g. was in contact with at least biweekly; Pillemer *et al.*, 2017).

Other studies, however, have used task-based connectivity to explore potential mechanisms underlying the relationship between functional connectivity and individuals' social networks (Schmälzle *et al.*, 2017; Tompson *et al.*, 2020). For example, Schmälzle and colleagues (2017) explored the possibility that changes in adolescents' functional connectivity in response to being socially excluded might relate to the structure of their social network. They found that having greater within-system connectivity in a subcomponent of the default-mode system during social exclusion predicted having less dense (e.g. fewer interconnections among friendships) social networks.

Another potential application of network neuroscience methods to understanding social behavior is to determine whether social intelligence may facilitate non-social cognitive performance. To do this, Tompson and colleagues (2020) examined whether greater engagement of 'social brain' networks offsets adolescent males' underdeveloped or underutilized inhibitory abilities to improve their cognitive performance. The two social brain systems of interest in this study were theory-defined self-referential and mentalizing brain systems. They also examined a theory-defined inhibition system. They found that adolescent males who performed better on a measure of inhibition (a go/no-go task) had stronger connectivity between the self-referential and response inhibition systems and weaker within-system connectivity in the self-referential system. Moreover, they found that the relationship between task performance and greater between-system connectivity was most pronounced for adolescents with less dense social networks. Together, these findings suggest that some aspects of social functioning may facilitate non-social cognitive function.

Although this section has focused primarily on the default-mode system, it is important to note that there are multiple other systems that play a key role in social cognition (e.g. Lamm *et al.*, 2011; Alcalá-López *et al.*, 2018; Redcay and Schilbach, 2019). A recent meta-analysis that classified regions comprising the "social brain connectome" (Alcalá-López *et al.*, 2018) provides a potential overview of different "social brain systems". Specifically,

the authors identified four main functional systems, including a visual-sensory system, composed of the fusiform gyrus and superior temporal sulcus, a limbic system, composed of the amygdala, hippocampus and nucleus accumbens, and two cognitive systems: one that included the anterior insula, middle cingulate cortex and inferior frontal gyrus, and a second that included the dorsal medial prefrontal cortex, posterior cingulate cortex, precuneus and temporoparietal junction. Future work should align the social brain systems with those commonly defined by network neuroscience work to bring parsimony between the two fields.

Together, these studies provide important insights into a myriad of potential applications of a social cognitive network neuroscience approach. Identifying the brain systems and interactions among systems that give rise to social behavior is an important future direction for social neuroscience research. A social cognitive network neuroscience approach that builds on extant research from the field of network neuroscience thus may provide a more comprehensive and accurate map of the 'social brain' (e.g. Charpentier and O'Doherty, 2018; Kliemann and Adolphs, 2018). We next review research from the fields of personality and cognitive neuroscience that uses network neuroscience techniques to study individual differences and cognition. Our goal is to highlight potential techniques or approaches that social cognitive network neuroscience research may leverage to study social behavior.

Using functional connections to characterize individual differences and behavior

To date, one of the most common approaches to applying network neuroscience techniques to personality neuroscience, cognitive neuroscience and social neuroscience research has been to measure functional connectivity strength within or between modules during resting and/or task states and relate it to behavior or performance (Medaglia *et al.*, 2015; Schmälzle *et al.*, 2017; Markett *et al.*, 2018; Wasylyshyn *et al.*, 2018; Hughes *et al.*, 2019). A basic premise of this approach is that weaker connectivity within a module (sometimes referred to as dysregulation) during resting state is considered a measure of relative dysfunction in that module (for review, see Ferreira and Busatto, 2013). However, increased between-module connectivity during task performance is generally considered to facilitate performance because it is thought to relate to the exchange of task-relevant information between systems (e.g. Cohen and D'Esposito, 2016; Rosenberg *et al.*, 2016; Bassett and Mattar, 2017). Studies examining fixed behaviors (e.g. personality traits) have tended to relate the behavior of interest to resting-state connectivity, whereas studies examining transient behaviors (e.g. attention) have tended to relate the behavior of interest to task-based connectivity.

Personality neuroscience research has frequently used measures of within-module resting-state functional connectivity to predict a myriad of individual differences in real-life function (Vaidya and Gordon, 2013; Dubois and Adolphs, 2016; Bassett and Sporns, 2017; Shen *et al.*, 2017; Markett *et al.*, 2018; Christov-Moore *et al.*, 2020), including intelligence (e.g. Song *et al.*, 2008; Cole *et al.*, 2012; Smith *et al.*, 2015), attention (Finn *et al.*, 2015), cognitive control (Marek *et al.*, 2015; Spielberg *et al.*, 2015) and working memory (Cohen and D'Esposito, 2016). Within-module resting-state functional connectivity patterns also predict other individual differences, including mind wandering (Wang *et al.*, 2018), lifestyle factors, including education, income and life satisfaction (Smith *et al.*, 2015), and socially relevant traits, such

as empathic concern (Christov-Moore *et al.*, 2020) and creativity (Beatty *et al.*, 2019). Challenges to interpreting relationships between resting-state functional connectivity and these myriad of individual differences arise due to the noteworthy heterogeneity in participants' mental states during resting state (e.g. Buckner *et al.*, 2013; Gonzalez-Castillo *et al.*, 2021). Indeed, a recent study found that functional connectivity patterns associated with passive movie-watching better predicted participants' cognition and emotion than did their functional connectivity patterns during resting state (Finn and Bandettini, 2021). Future work is thus needed to identify the optimal states in which to measure functional connectivity patterns.

Cognitive neuroscience research, however, has explored the extent to which task-based between-network connectivity facilitates performance (Medaglia *et al.*, 2015). The premise of this work is that greater between-network connectivity reflects the exchange of task-relevant information between systems (e.g. Cohen and D'Esposito, 2016; Rosenberg *et al.*, 2016; Bassett and Mattar, 2017). For example, Rosenberg and colleagues (2016) found that stronger functional connectivity between motor and visual systems during a sustained attention task predicted better performance than having stronger connectivity between temporal and parietal regions. Another study compared connectivity during resting state to connectivity during a motor and working memory task (Cohen and D'Esposito, 2016). They predicted that since the motor task likely engaged one system (e.g. somatomotor), but the working memory likely engaged multiple systems (e.g. visual, frontoparietal and somatomotor), greater between-system connectivity would facilitate working memory, but not motor, performance. Indeed, this is what the authors found.

Another approach to using functional connectivity strength as a measure of behavior or performance is to examine the extent to which connectivity flexibly reconfigures within and between modules during both rest (Betzel *et al.*, 2017) and task states (Bassett *et al.*, 2011; Cole *et al.*, 2013; Vatansever *et al.*, 2015; Shine *et al.*, 2016). For example, greater variations in flexible reconfiguration of connectivity during resting state predicts individual differences in positive affect (Betzel *et al.*, 2017). Moreover, although motor learning is accompanied by increased autonomy of visual and somatomotor systems (Bassett *et al.*, 2015), greater flexibility during a motor learning task predicts improved performance (Bassett *et al.*, 2011). Other work has shown that the frontoparietal system, which is involved in cognitive control (for review, see Scolari *et al.*, 2015), flexibly reconfigures connectivity to other systems to support ongoing task demands (Cole *et al.*, 2013). These studies suggest that although there is a great deal of overlap in system configuration between resting and task states (e.g. Cole *et al.*, 2014; Krienen *et al.*, 2014; Hughes *et al.*, 2020), there are important task-specific differences. Indeed, a recent study comparing functional connectivity patterns among a group of 18 healthy individuals during resting state and also during movie-watching found that connectivity patterns became more consistent across individuals when they were watching a movie (van der Meer *et al.*, 2020).

An important benefit of relating patterns of functional connectivity to behavior is that they have clear and measurable individual differences. Finn and colleagues (2015) examined whether functional connectivity patterns serve as 'fingerprints' to identify individuals (see also Miranda-Dominguez *et al.*, 2014). To do this, they examined whether individuals (among a pool of 126) could be correctly identified across scan sessions based solely on their functional connectivity patterns. In addition to finding that functional connectivity patterns were uniquely characteristic to

each individual, the authors found that resting-state connectivity in the medial frontal and frontoparietal systems were the most accurate in individual subject identification, with nearly 100% accuracy. In a related study by Miranda-Dominguez and colleagues (2014), the researchers identified unique 'fingerprints' (which they refer to as connectotypes) for humans and non-primates. An important contribution of these findings is that they suggest that functional connectivity 'fingerprints' may provide a gateway for studying individual differences. However, it is important to note that functional connectivity patterns may be conflated by inter-subject differences in node location (e.g. due to warping and distortion during preprocessing). Future work should examine this possibility.

Finally, a widely used application of functional connectivity patterns has been to identify potential biomarkers that may have clinical relevance, including for Alzheimer's disease (Wang *et al.*, 2006; Supekar *et al.*, 2008; Damoiseaux *et al.*, 2012), ASD (Hull *et al.*, 2017), schizophrenia (Garrity *et al.*, 2007; Lynall *et al.*, 2010; Venkataraman *et al.*, 2012) and depression (Fox *et al.*, 2013; Drysdale *et al.*, 2017). A widely targeted population for this work has been with cognitively normal older adults (Betzel *et al.*, 2014; Chan *et al.*, 2014; Wig, 2017; Spreng and Turner, 2019). In both healthy and pathological aging, older adults have weaker within-module connectivity coupled with stronger between-module connectivity during resting state (Wang *et al.*, 2006; Betzel *et al.*, 2014; Chan *et al.*, 2014; Spreng and Turner, 2019; Hughes *et al.*, 2020), which have been suggested to reflect decreased functional specialization of the systems over the lifespan (e.g. Betzel *et al.*, 2014; Wig, 2017; Spreng and Turner, 2019; Koen *et al.*, 2020).

A key module of interest in this work has been the default mode (for review see Broyd *et al.*, 2009; also, Badhwar *et al.*, 2017; Garrity *et al.*, 2007), which consists of medial and lateral parietal cortex, medial prefrontal cortex, and the medial and lateral temporal cortices (Raichle, 2015). Research on autism spectrum disorder (ASD), a development disorder widely associated with disrupted social function, has shown that ASD is associated with weaker resting-state default-mode system connectivity (Assaf *et al.*, 2010; Weng *et al.*, 2010; Gotts *et al.*, 2012; Hull *et al.*, 2017), the magnitude of which relates to the magnitude of individuals' social and communication impairments (e.g. Assaf *et al.*, 2010; Gotts *et al.*, 2012). Recent work in network neuroscience has defined three functionally distinct subdivisions of the default-mode system: two in the prefrontal cortex (the ventral medial and the dorsal medial prefrontal cortices) and one in the posterior cortex that is composed of the posterior cingulate cortex, precuneus and lateral parietal cortex (Figure 3; Raichle, 2015). Although Alzheimer's disease has been widely associated with disruptions in resting-state functional connectivity throughout the default-mode system (Greicius *et al.*, 2004; Koch *et al.*, 2012; Badhwar *et al.*, 2017), some evidence suggests that connectivity within the default-mode system subcomponents differs over the course of Alzheimer's disease (Damoiseaux *et al.*, 2012). Thus, although the preponderance of research on the default-mode system focuses on it as a whole system, future work may benefit from disentangling its unique subcomponents.

Given its unique role in social cognition (Mars *et al.*, 2012; Meyer, 2019), the default-mode system has already emerged as an important target for social cognitive network neuroscience research. In the next section, we will explore some key limitations in network neuroscience research that should be considered in the context of studying social behavior. We then consider future directions for the field of social cognitive network neuroscience.

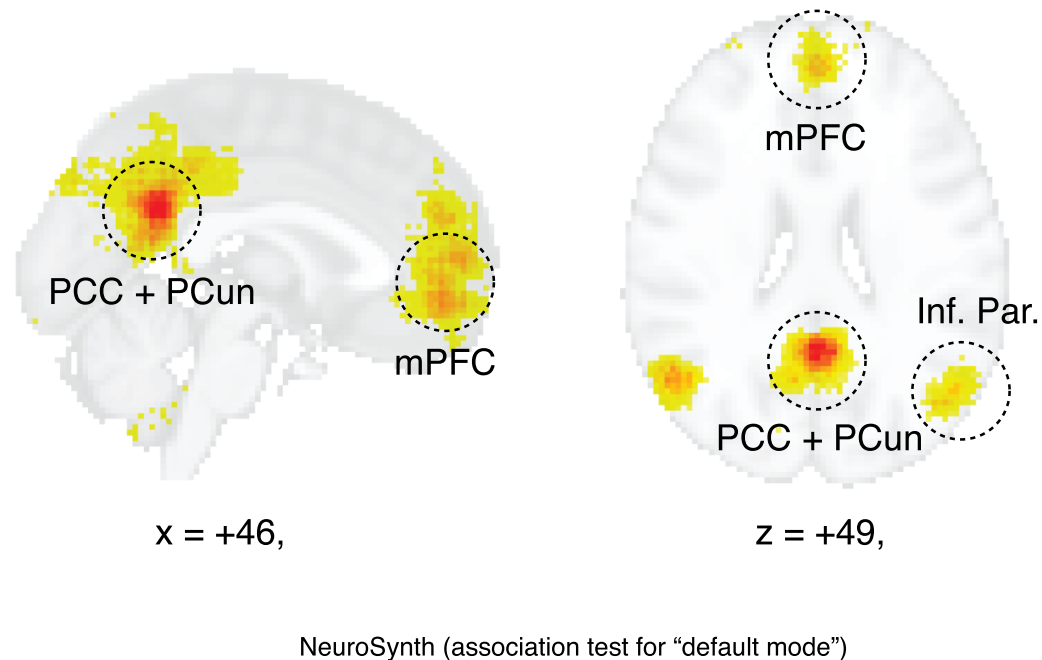


Fig. 3. Cortical components of the default-mode network. The activation map was obtained using NeuroSynth (Yarkoni *et al.*, 2011) and the term ‘default mode’.

Limitations

The goal of the current review was to highlight the potential impact of using a social cognitive network neuroscience approach to advance our understanding of social cognition. However, there are several limitations to this approach that should be considered. First, network neuroscience research lacks consistency in how nodes are defined in brain parcellations (e.g. Power *et al.*, 2011; Yeo *et al.*, 2011; Gordon *et al.*, 2016; Schaefer *et al.*, 2018). Variability among parcellations may contribute to spurious findings (for discussion, see Arslan *et al.*, 2018). Further complicating node selection is the fact that nodes vary across conditions, even for the same individuals (Salehi *et al.*, 2020). To increase reliability and replicability, social cognitive network neuroscience research should consider building on existing models from the field of network neuroscience. This could be accomplished by using well-studied network parcellations (e.g. Schaefer *et al.*, 2018) that were generated (and validated) from large datasets (see also, Power *et al.*, 2011; Yeo *et al.*, 2011).

Recent concerns have also emerged regarding reliability of functional connectivity across tasks and sessions. A recent meta-analysis examining test–retest reliability of functional connectivity found relatively poor reliability across scanning sessions (Noble *et al.*, 2019). However, an important caveat to these findings is that because reliability was measured using mean edge-level intraclass correlation coefficients, the meta-analysis was based on a small pool (about 12%) of studies examining test–retest reliability. Thus, these results should be interpreted with caution.

Finally, an important consideration in all neuroimaging research is the magnitude of the effects associated with the different analytical approaches. The effect sizes associated with functional connectivity and behavior remain largely unexplored (but see Seguin *et al.*, 2020), particularly as they might compare to region-specific activation and other measures of brain activity

(e.g. Tompson *et al.*, 2018). Although some research suggests that neuroimaging doubles the amount of variance explained in some behavior (e.g. health) relative to self-report measures alone (Falk *et al.*, 2011), meta-analyses have demonstrated that the effect sizes in cognitive neuroscience research are relatively low (Button *et al.*, 2013; Szucs and Ioannidis, 2017). This limitation is compounded by relatively small sample sizes in neuroimaging work (e.g. $N=20-30$; Cremers *et al.*, 2017), which have been consistently subject to criticism (Button *et al.*, 2013; David *et al.*, 2013; Szucs and Ioannidis, 2017; Clayson *et al.*, 2019). Although some research suggests that at least 50 subjects may be necessary to detect reliable effects in targeted (e.g. not whole-brain) analyses (Yarkoni, 2009), other work points to even higher sample sizes (e.g. $N = 80$) to detect reliable effects on social tasks (e.g. face processing; Bossier *et al.*, 2020). Thus, more work is needed to identify ideal sample sizes for social cognitive network neuroscience research.

A potential benefit of a social cognitive network neuroscience approach is that the availability of large datasets that measure a variety of domains of cognition, including social cognition (e.g. the Human Connectome Project; Van Essen *et al.*, 2013), provide opportunities to replicate findings within datasets (e.g. Bossier *et al.*, 2020). Moreover, they also facilitate replicability by other researchers, given the established infrastructure for accessing these data.

Future directions

Network neuroscience offers a set of tools for representing brains as networks of nodes and edges. This abstraction necessarily results in a loss of detail, but allows researchers to interrogate network data at different spatiotemporal scales using a rich and ever-growing suite of quantitative methods. To date, most social

Table 2. A summary of measures discussed in this review that concisely enumerate and articulate how to interpret different graph measures. This is not intended to be an exhaustive list, nor does it include mathematical descriptions of measures (for a more comprehensive list, see Rubinov and Sporns, 2010). We also direct the reader to the corresponding functions in the Brain Connectivity Toolbox (BCT; <https://sites.google.com/site/bctnet/>) that make these measurements. If that function does not exist in the BCT, we include links to an alternative source. We note that there may be other implementations of these same functions through other software packages and scientific programming languages (e.g. NetworkX in Python; <https://networkx.org/>)

Name	What it measures	Where can I find code?
Density	<ul style="list-style-type: none"> Of all possible connections, the number that exist 	density_und.m (BCT)
Community (module)	<ul style="list-style-type: none"> A group of network nodes Usually detected algorithmically using 'community detection' algorithms Usually 'assortative', so that nodes are more likely to connect to other members of the same community than to other communities 	Community_louvain.m (BCT)
Participation coefficient	<ul style="list-style-type: none"> The extent to which a node's connections are concentrated within a single community (or small number of communities) or distributed across many 	Participation_coef.m, Participation_coef_sign.m (BCT)
Modularity maximization	<ul style="list-style-type: none"> A heuristic for detecting communities in a network Communities are defined as groups of nodes whose density of connections to one another is maximally greater than what would be expected by chance Can be applied to signed/weighted networks Louvain algorithm is a popular optimization heuristic A heuristic for detecting communities in a network Communities are defined based on probabilistic trajectory of 'random walker' 	community_louvain.m (BCT)
Infomap	<ul style="list-style-type: none"> Communities are groups of nodes tend to 'trap' the flow of the walker The number of connections that a node makes Weighted analog is 'strength' Hubs tend to make many connections 	infomap (https://www.mapequation.org/)
Degree	<ul style="list-style-type: none"> Any one of a series of measures that describes how important a node (or edge) is to some process Betweenness centrality measures importance of a node/edge to shortest paths by counting how many shortest paths traverse a given node/edge Hubs tend to be highly central A group of highly connected nodes that are also connected to each other Detected based on 'rich club coefficient' Needs to be compared against a null connectivity model Estimate of (functional) connectivity using a subset of temporally contiguous time points, i.e. a window Window advanced a fixed number of frames and connectivity gets estimated again This process is repeated, thereby generating a time-varying sequence of networks 	Degrees_und.m, degrees_dir.m, strengths_und.m, strengths_dir.m, strengths_und_sign.m
Centrality	<ul style="list-style-type: none"> Betweenness centrality measures importance of a node/edge to shortest paths by counting how many shortest paths traverse a given node/edge Hubs tend to be highly central A group of highly connected nodes that are also connected to each other Detected based on 'rich club coefficient' Needs to be compared against a null connectivity model Estimate of (functional) connectivity using a subset of temporally contiguous time points, i.e. a window Window advanced a fixed number of frames and connectivity gets estimated again This process is repeated, thereby generating a time-varying sequence of networks 	Betweenness_bin.m, betweenness_wei.m
Rich club	<ul style="list-style-type: none"> Detected based on 'rich club coefficient' Needs to be compared against a null connectivity model Estimate of (functional) connectivity using a subset of temporally contiguous time points, i.e. a window Window advanced a fixed number of frames and connectivity gets estimated again This process is repeated, thereby generating a time-varying sequence of networks 	Rich_club_bd.m, rich_club_bu.m, rich_club_wd.m, rich_club_wu.m
Sliding-window time-varying connectivity	<ul style="list-style-type: none"> Estimate of (functional) connectivity using a subset of temporally contiguous time points, i.e. a window Window advanced a fixed number of frames and connectivity gets estimated again This process is repeated, thereby generating a time-varying sequence of networks 	
Multilayer network	<ul style="list-style-type: none"> Time-varying networks can be modeled as a multilayer network: the connectivity matrix at each instant is a layer A multilayer analog of the Louvain algorithm can be applied to multilayer networks to simultaneously detect communities in all layers 	Genlouvain.m, Community_louvain.m (http://netwiki.amath.unc.edu/GenLouvain)
Flexibility	<ul style="list-style-type: none"> How frequently a node changes its community assignment from one layer to the next Estimated from the output of the multilayer modularity maximization algorithm 	http://commdetect.weebly.com/

network neuroscience studies have focused on brain systems and modules, with particular emphasis being placed on the default mode and its interactions with other systems and the rest of the brain. However, network neuroscience offers a much more diverse and comprehensive set of tools to interrogate networks. In this section, we highlight several tools from network neuroscience that are (Table 2 provides links to code for these measures), at present, underutilized within the social neuroscience community. We further speculate on how these tools could be used to enhance our understanding of the role played by networks in shaping social cognition.

Modules and hubs

In the previous sections, we discussed brain systems—groups of brain regions that are cohesively connected internally but sparsely connected between one another. Oftentimes, the identities of these systems are treated as 'given'. For instance, one might define the default-mode system based on the parcel labels that accompany the Schaefer atlas (Schaefer et al., 2018). This approach is appropriate and reasonable, but only under the assumption that systems are identical across individuals. However, recent work has shown that the boundaries of brain systems vary systematically and reliably across individuals (Gordon et al.,

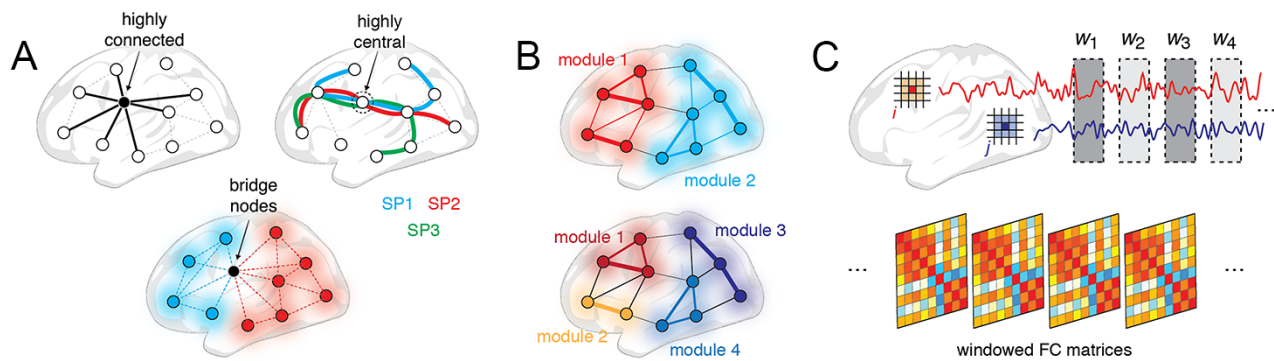


Fig. 4. Frontiers in social cognitive network neuroscience. Network neuroscience offers a suite of computational tools, many of which are not currently widely used in social neuroscience. Here, we identify several approaches that could be used to better understand the neural bases of social cognition. (A) The definition of a ‘hub’ in network neuroscience is imprecise. In practice, hubs could be defined in a number of ways. For instance, hubs could correspond to nodes that make many connections and occupy positions of influence. They can also be defined as nodes that are central or important to a process taking place on the network, e.g. the transmission of information over a network’s shortest paths. Hubs can also be defined as nodes whose connections straddle the boundary (e.g. are bridges) between communities. Exploring the variety of alternative hub definitions has the potential to enrich social neuroscience studies. (B) Another area of interest for future studies is the decomposition of modules into hierarchies and multiple scales. Large high-level modules correspond to groups of brain regions that share a broad set of functions (e.g. are domain general). Lower-level and smaller modules reflect increasing functional specialization (e.g. may be more domain specific). (C) A final topic that could be explored in future studies is the study of changes in network structure over short timescales. Many cognitive processes unfold over timescales of seconds. In contrast, fMRI resting-state scan sessions can last as long as 30 minutes. This incongruity of timescales makes it difficult to track fast changes in network structure associated with rapid fluctuations in cognitive state. Time-varying or ‘dynamic’ connectivity studies segment time points into windows and separately estimate connectivity for each window, resulting in a time series of dissimilar connectivity matrices.

2017), suggesting that to study brain systems meaningfully, we need to estimate them at the subject level. Such an approach could be particularly useful for social cognitive research targeting focal brain regions, such as the fusiform ‘face’ area (Kanwisher et al., 1997).

How does one go about doing this? One solution is to algorithmically discover a network’s systems using ‘community detection’ methods (Fortunato, 2010). In network neuroscience parlance, a ‘community’ or ‘module’ refers to a collection of nodes that exhibit similar connectivity profiles, usually such that nodes belonging to the same community are strongly connected to one another, a property called community assortativity (Sporns and Betzel, 2016; Betzel and Bassett, 2018). Community detection, then, refers to data-driven methods that attempt to identify the optimal partition of nodes into communities for a given individual. In network neuroscience, the two most popular methods are Infomap (Rosvall and Bergstrom, 2008), which identifies communities as groups of nodes that ‘trap’ the probabilistic flow of a random walker over the network, and modularity maximization (Newman and Girvan, 2004), which defines communities as groups of nodes whose internal density of connections is maximally greater than what would be expected by chance. With either of these simple heuristics, one can identify putative communities in a network without any prior knowledge—the community boundaries are informed by the network itself. Knowing a network’s community structure is useful—it allows for ‘coarse graining’, the discovery of functionally related regions, and can be applied meaningfully to both structural and functional networks.

Another way to leverage modules and communities is to use them to determine nodal roles, e.g. identifying hubs whose connections span module boundaries and therefore may play outsized roles in mediating inter-modular communication and information transfer (Figure 4A; Guimera and Amaral, 2005). Hub regions can be detected quantitatively using the participation coefficient measure, which has a value close to unity when a node’s connections are uniformly distributed across multiple

modules and zero when a node’s connections are concentrated within a single module. Interestingly, previous studies have found that hubs tend to be situated within transmodal cortex in higher-order cognitive networks (Power et al., 2013; Bertolero et al., 2015) and that damage to hub regions as a result of focal lesions corresponds to widespread cognitive deficits (Warren et al., 2014). Notably, however, there are other methods for identifying and defining hubs, including their more common definitions as highly connected and highly central regions (Figure 4A). Collectively, these dissimilar hub definitions offer a suite of measurements for classifying and categorizing brain regions based on their connectivity patterns.

One particularly intriguing hub that should be targeted in social cognitive network neuroscience is the insula. In social neuroscience research, the insula has been implicated in a variety of social cognitive functions, including several affective states (e.g. disgust and empathy), social decision-making (e.g. Singer et al., 2009) and even loneliness (Eisenberger and Cole, 2012). Network neuroscience has identified the insula as a hub that plays an important role in saliency, task switching, attention and control (Menon and Uddin, 2010). Focusing on the insula as a hub may provide novel insight into its broader role in social cognition.

Multiscale and hierarchical modules

Many brain systems exhibit known hierarchies and subdivisions, such that they are composed of systems within systems within systems, etc. (Figure 4B; Betzel and Bassett, 2018). Consider, for instance, the organization of the somatomotor system. At a coarse scale, it can be viewed as a singular system associated with representing sensory information and executing movements. However, its territories can be meaningfully subdivided based on the type of information that a given patch of cortex represents, with distinct subsystems associated differentially with one’s hands, feet, mouth, etc. These subsystems, in turn, can be even further subdivided according to individual digits. Clearly, the coarse grouping of these areas as a singular ‘somatomotor sys-

tem' label fails to resolve these fine-scale features. Even at rest there are questions surrounding the correct number of brain systems. For instance, some studies have characterized the brain in terms of a bipartition into large 'task-positive' and 'task-negative' communities (Golland *et al.*, 2008), while other studies have focused on finer subdivisions of canonical systems (Gordon *et al.*, 2020). But how might one access these details using data-driven and network science approaches? Is there a way to resolve different sized communities and modules and, from these different estimates, arrange them into a hierarchy of communities?

Fortunately, the data-driven methods described in the previous section are well-suited for addressing these questions. Both Infomap and modularity maximization include tunable parameters that effectively vary the size and number of detected communities (Reichardt and Bornholdt, 2006). These parameters can be fixed ahead of time to uncover either smaller or larger communities but can also be varied systematically as part of a 'parameter sweep' to discover communities across a range of sizes. At the coarsest level, this type of multiscale analysis yields a bipartition of the network into two communities. A parameter sweep will reveal communities of different sizes but will not, unfortunately, determine whether those communities are hierarchically related to one another. However, new methods like multiresolution consensus clustering (Jeub *et al.*, 2018) use a statistical criterion to arrange a multiscale ensemble of communities into a coherent hierarchy of communities within communities within communities.

Together, these two approaches offer a framework for flexibly examining brain network modules at different scales. Not only does this allow a user to carry out an analysis at one scale or another, but the hierarchy itself can be characterized in the form of different summary statistics, e.g. number of levels, which may vary with cognitive state or clinical condition. This approach may be an interesting complement or alternative to multivariate pattern analyses, which have been widely used in social neuroscience research in recent years (e.g. Weaverdyck *et al.*, 2020). That is, rather than focusing on patterns of activations within specific regions, this approach would allow researchers to explore patterns of connectivity within specific modules.

Dynamic and time-varying network analyses

Functional and structural connectivity represent static network maps of the brain. That is, their connections represent interaction weights between pairs of brain regions either at a specific moment in time or averaged over a longer period. However, brain networks are constantly in flux. Functional connections fluctuate over timescales of seconds and minutes (Hutchison *et al.*, 2013), possibly reflecting instantaneous changes in cognitive state or performing homeostatic function (Laumann and Snyder, 2021). Similarly, anatomical connections wax and wane over longer timescales with learning, development and aging. Clearly, then, the view of networks as static and temporally invariant objects cannot capture this rich temporal variation. Social neuroscience research has recently embraced a similar viewpoint, integrating techniques such as hyperscanning to measure neural synchrony between two individuals during social interactions (Misaki *et al.*, 2021).

To better characterize how a network changes over time, a growing number of studies have begun modeling time-varying or dynamic networks, usually in the context of functional connectivity (Lurie *et al.*, 2020). Estimating time-varying networks is usually

carried out using a sliding-window analysis, in which a functional network is estimated using a small subset of time points (those that fall within a temporally contiguous window of fixed length; Shakil *et al.*, 2016; Hindriks *et al.*, 2016; Leonardi and Van De Ville, 2015; see Figure 4C). The window is then advanced by some number of frames, and a new network is generated. This procedure is repeated until the window can be advanced no further, yielding a time series of networks, each corresponding to a different window in time. These networks can be analyzed to track time-varying changes in individual connections or even network properties, like modularity (Betzel *et al.*, 2016; Fukushima *et al.*, 2018), distribution of hubs and the segregation/integration of brain systems (Shine *et al.*, 2016).

Time-varying networks can be treated like static networks and analyzed independently of one another. However, they can also be analyzed collectively as part of a multilayer network (Vaiana and Muldoon, 2020). This allows researchers to take advantage of multilayer network analyses tools, including analogs of community detection methods, like modularity maximization (Mucha *et al.*, 2010). When applied to a multilayer network, this approach yields temporally resolved estimates of communities, allowing users to trivially track changes in community assignments and estimate the network measure of 'flexibility'—how frequently a node changes its community assignment from one time point to the next (Bassett *et al.*, 2011, 2013). In previous studies, flexibility has been linked with learning rate (Bassett *et al.*, 2011), affective state (Betzel *et al.*, 2017) and clinical status (Braun *et al.*, 2016), among others, suggesting that it serves as a powerful marker of behavior.

Time-varying network analysis, however, is not without limitations. Sliding-window analyses require that the user specify the window duration and the amount of overlap between successive windows. Care must be taken in selecting these parameters; short windows can exhibit aliasing effects, and overlap between windows means that the resulting networks are no longer independent from one another, which can have implications for their subsequent analysis. To circumvent these issues, several studies have developed 'point-wise' estimates of functional connectivity, thus obviating the need for a sliding window while still generating temporally resolved estimates of functional connectivity (Liu and Duyn, 2013; Shine *et al.*, 2015; Esfahlani *et al.*, 2020). These newer methods are relatively untested, but in principle allow users to address some of the issues associated with sliding-window analyses.

Summary

In this review, we have provided an overview of the field of network neuroscience with the goal of demonstrating how a social cognitive network neuroscience approach may advance our understanding of the social brain. In addition to providing more comprehensive insights into how the brain gives rise to social behavior, another potential contribution of social cognitive network neuroscience is that it may help address recent critiques arguing that social neuroscience research is too domain specific and overly simplifies our understanding of how the brain gives rise to social behavior (Barrett and Satpute, 2013; Spunt and Adolphs, 2017; Ramsey and Ward, 2020). These critiques build on prior work highlighting the overlap between seemingly unique cognitive processes (e.g. working memory and intelligence), noting, for instance, that working memory accounts for 40% of the variance in global fluid intelligence (Fukuda *et al.*, 2010). Extending these observations to the field of social neuroscience, the critiques

argue against the notion of a ‘social brain’, suggesting that social and non-social cognitive processes are likely largely overlapping (e.g. Ramsey and Ward, 2020). However, an important caveat to these critiques is that although specific brain regions may share social and non-social functions (e.g. Spunt and Adolphs, 2017; Ramsey and Ward, 2020), the manner in which brain regions communicate information may differ for social and non-social information. Thus, a potential contribution of social cognitive network neuroscience could be to determine whether the manner in which brain systems communicate information differs for social vs non-social information.

Finally, a social cognitive network neuroscience approach has several key benefits. First, it could provide novel insights into how, if at all, brain regions work together to give rise to social behavior. Second, it provides potential resources by which to minimize concerns about power and sample sizes in neuroscience research (e.g. Button et al., 2013; David et al., 2013; Szucs and Ioannidis, 2017; Clayson et al., 2019). Specifically, large, publicly available datasets (e.g. the Human Connectome Project; Van Essen et al., 2013) contain resting-state and task-based neuroimaging data from more than 1000 participants, as well as extensive behavioral measures. Large datasets provide opportunities to conceptually replicate findings (e.g. across different subsamples of the dataset; e.g. Bossier et al., 2020), as well as ease for replicability by other researchers, given the established infrastructure for accessing these data. Finally, it could allow us to determine whether a social cognitive network neuroscience approach potentially accounts for unique, or even more, variance in behavior than traditional social neuroscience approaches.

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Conflict of interest

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