

The neural representation of social networks

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The computational demands associated with navigating large, complexly bonded social groups are thought to have significantly shaped human brain evolution. Yet, research on social network representation and cognitive neuroscience have progressed largely independently. Thus, little is known about how the human brain encodes the structure of the social networks in which it is embedded. This review highlights recent work seeking to bridge this gap in understanding. While the majority of research linking social network analysis and neuroimaging has focused on relating neuroanatomy to social network size, researchers have begun to define the neural architecture that encodes social network structure, cognitive and behavioral consequences of encoding this information, and individual differences in how people represent the structure of their social world.

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Humans spend most of their lives in the company of others, maintaining large numbers of meaningful, enduring social bonds [1]. The computational demands associated with navigating such large, complexly bonded groups are thought to have shaped human brain evolution [1,2] (cf. [3,4]). Yet, research on social networks and neural information processing has largely been siloed. Thus, little is known about how individuals track, encode, and are influenced by the structure of their social networks. Researchers have begun to bridge this gap in understanding by integrating theory and methods from neuroscience, social network analysis (SNA), and psychology. Here, we review work at the nexus of these disciplines and discuss its potential to elucidate how

humans create, understand, and navigate distinctively large and complex social worlds.

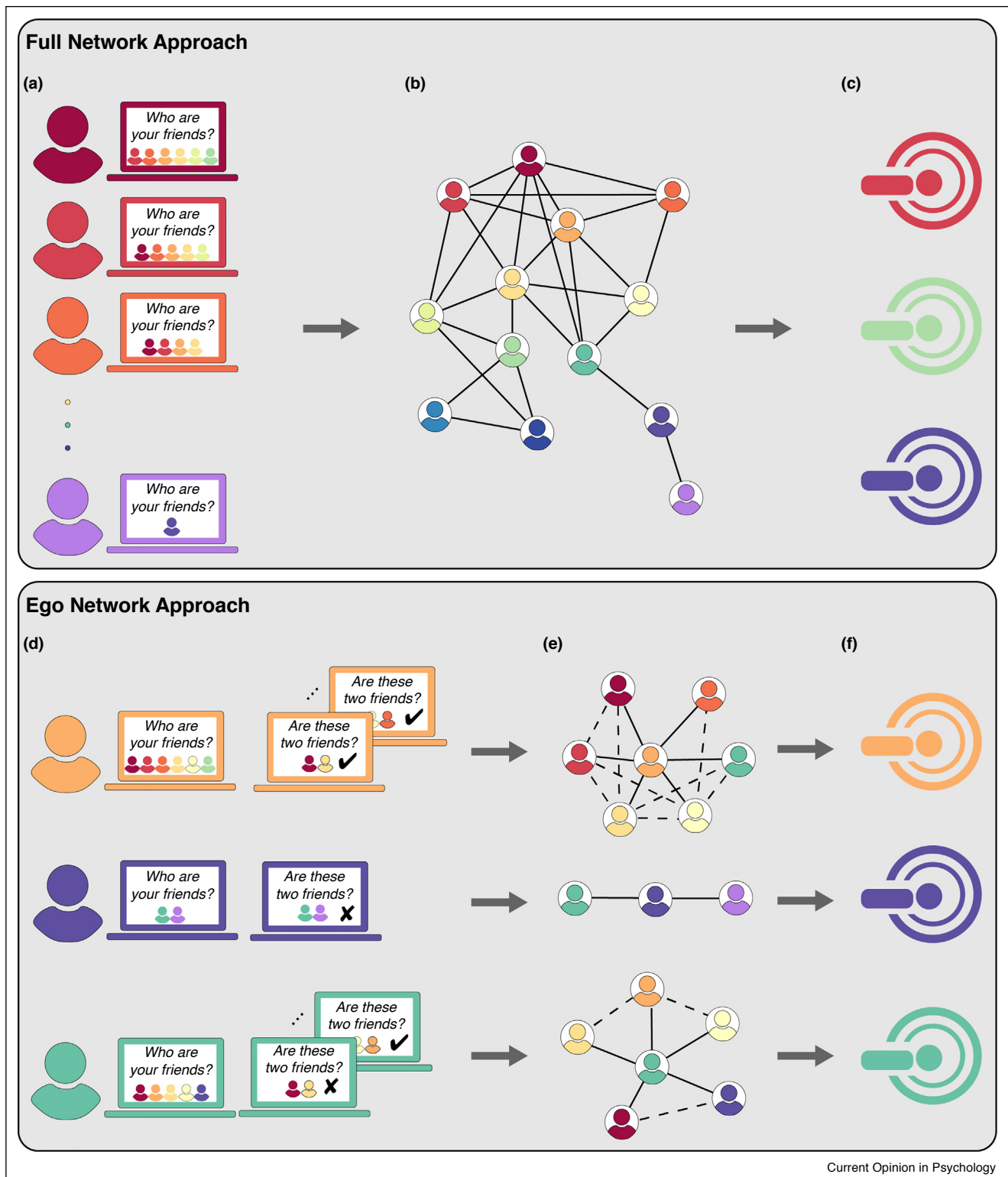
Neural encoding and cognitive consequences of direct social ties

Research on the neural encoding of social relationships has focused on direct ties (i.e., ties between oneself and others), often contrasting responses to familiar others' and strangers' faces. Whereas the core face processing system (fusiform and occipital face areas; posterior superior temporal cortex–STC), which supports visual analysis of faces, responds to faces generally [5], recruitment of the extended face processing system, which supports extraction of social meaning [6,7], is modulated by familiarity [8–10]. Familiar faces preferentially recruit regions involved in representing mental states, attitudes, and traits (e.g., temporo-parietal junction, medial prefrontal cortex–MPFC), affective processing (e.g., amygdala, insula), and retrieving biographical knowledge (e.g., anterior temporal lobe–ATL, precuneus) [6,8]. These results inspired suggestions that encountering familiar others automatically triggers processing of social knowledge and distinctive emotional responses (e.g., decreased vigilance). Behavioral findings support these conclusions: familiarity dampens stress elicited by the presence of others [11], and familiar others' mental states are detected more rapidly than those of strangers [12] and are especially impactful on one's own mental states [13]. Recent work has identified differences in neural responses to friends and kin [14], suggesting that future social neuroscience research should look beyond the coarse distinction between familiar others and strangers.

Are indirect relationships important to social thought and behavior?

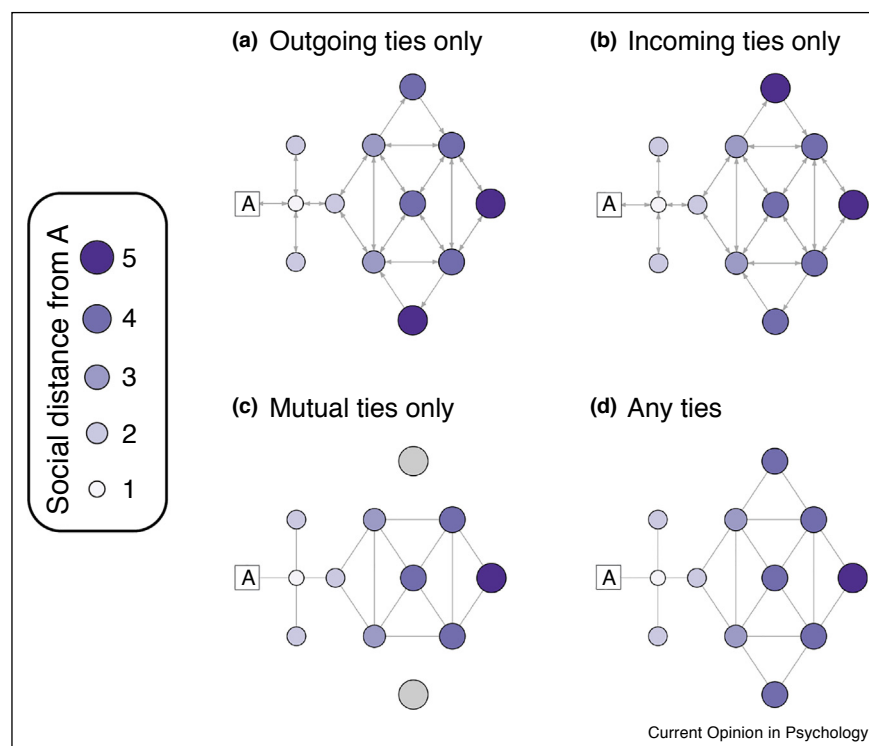
Another potentially relevant facet of relationship knowledge concerns indirect relationships (i.e., relationships between third parties), which affect behavior and evolutionary fitness [15–17]. There is growing interest in the extent to which social species, including humans, track and encode patterns of third-party relationships and use this information to shape behavior [18*]. Such research integrates theory and methods from neuroscience, psychology, and SNA [19], thereby affording increasingly comprehensive characterization of social structures and the individuals that comprise them [20]. Individuals' network positions can be characterized by reconstructing their social networks, then related to individual cognition by recruiting network members to participate in neuroimaging and behavioral experiments (Figure 1). Below, we briefly discuss three aspects of social network position likely relevant to social cognition and behavior. We then discuss research on how

Figure 1



Approaches to studying neural representations of social networks. Top panel (a–c): (a) In the full-network approach, social ties connecting all members in an entire bounded community are characterized and (b) used to reconstruct the full social network. (c) Social network structure and position information can then be related to neural information processing within individuals by recruiting subsets of members for functional neuroimaging studies [36^{••},66^{••},68]. Bottom panel (d–f): (d) In cases where full network characterization is not feasible, an ego network approach may be used in which participants identify their direct connections, and indicate their beliefs about ties between third parties, signified in the ego

Figure 2



Defining distance between individuals in a social network. The distance between two individuals in a social network is given by the smallest number of intermediary social ties necessary to connect them (i.e., geodesic distance or 'degrees of separation'). Node shade and size both correspond to distance from person A. Social distance can be defined in ways that take into account the directedness of social ties, such as in panel (a), where social distance is defined in terms of outgoing ties (i.e., the shortest directed path from person A to a given node) or in panel (b), where social distance is defined in terms of incoming ties (i.e., the shortest directed path from a given node to person A). Social distance can also be defined in an undirected manner — e.g., by only counting social ties that were mutually reported by the individuals involved (c), or by considering any social tie, irrespective of its direction and whether or not it was reciprocated (d). Note that in (c), two of the nodes (grey circles) are not connected because the edges connecting them to other nodes were not mutually reported (as shown in panels a and b). Thus, those two nodes are unreachable from person A through mutual ties and the social distance between A and those nodes is undefined. Different ways of defining social distance are differentially suited to studies linking this aspect of social network position to cognition and neural information processing within individuals.

these characteristics are understood and encoded, and potential downstream consequences of this encoding.

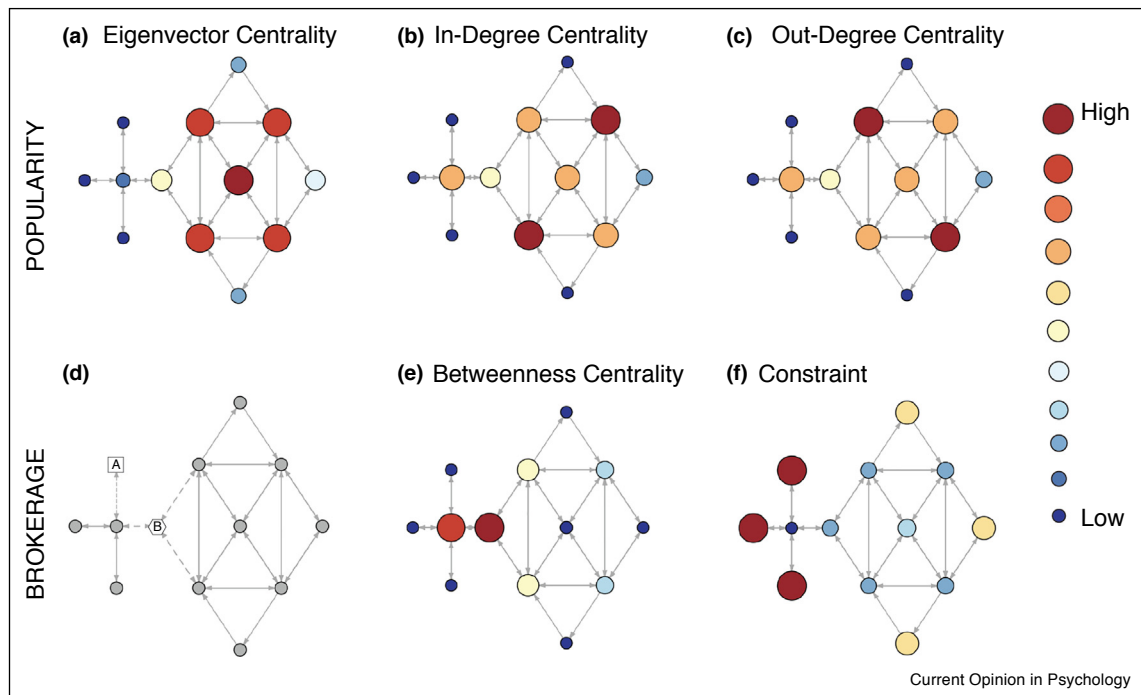
Social distance. Distance in social networks typically refers to the smallest number of ties required to connect individuals (Figure 2). While direct ties are most relevant, given the importance of reputation management for human behavior [21,22], individuals 'two degrees away' are important to identify and monitor, as negative interactions could damage relationships with mutual friends. Similarly, individuals may be more trusting of others who share mutual friends, given potential reputation costs of bad behavior.

Who is well-connected? Centrality refers to an individual's importance in a network. Several centrality

measures can be computed, including number of direct ties (degree centrality) and measures that account for indirect connections (e.g., eigenvector centrality—EVC; Figure 3). EVC captures the extent to which someone is well-connected to well-connected others [23], and is thought to signify the status associated with an individual's network position [23–25]. EVC impacts the costs and benefits of treating someone positively or negatively [24]; individuals connected to well-connected others may be protected from mistreatment because they are more likely to be defended by their direct connections, who themselves are more likely to be defended. Thus, potential reputation costs associated with mistreating low-EVC individuals are minimal, given the low likelihood of mutual friends, and their limited influence

(Figure 1 Legend Continued) networks shown in (e) by solid and dashed lines, respectively. (f) The neural representation of social network structure and position information can then be probed by having the same participants complete functional neuroimaging studies. Note that since the ego network approach tends to rely on a given participant's perception of third party ties, some participants may not agree. In this figure, this is true of the orange and green participants' perceptions of their friends' relationships.

Figure 3



Social network position characteristics. Upper panel (a–c): An individual's popularity or status in a social network is often defined in terms of eigenvector centrality, which measures how well-connected that individual is to well-connected others (a). In-degree (b) and out-degree centrality (c) are also measures of connectedness that only take into account an individual's direct social ties. In-degree centrality (b) is defined as the number of directed edges towards the individual (e.g., how many people say they are friends with the person), whereas out-degree centrality (c) is defined as the number of directed edges away from the individual (e.g., how many friends the person says they have). Lower panel (d–f): Because of the structure of their social ties, brokers have opportunities to connect otherwise unconnected sets of individuals in a network. In (d), if person A were removed, everyone else in the network would still be connected to one another; contrastingly, if person B were removed, there would be two completely unconnected groups. Correspondingly, person B has a much higher capacity for brokerage than person A. Two common ways of measuring brokerage are (e) betweenness centrality and (f) constraint (an inverse measure of brokerage). A person's betweenness centrality (e) is proportional to the frequency with which the shortest paths between other individuals in the network pass through them. A person's network constraint (f) corresponds to the degree to which their ties are concentrated within a single interconnected group of individuals.

on information flow [24]. Correspondingly, high-EVC individuals are more likely to be treated favorably and less likely to serve as scapegoats and targets of negative gossip [24,26,27].

Brokerage. Individuals who bridge between otherwise unconnected others are called brokers, and can coordinate behavior and translate information between groups [28,29] (Figure 3). Brokerage predicts professional success [28], arguably because it facilitates access to diverse information and resources [30,31]. Brokers can integrate ideas and information that would otherwise be 'stuck' within segregated groups and control the flow of information between these groups [32]. Thus, they can display different beliefs and characteristics to different partners and often serve as opinion leaders. Contrastingly, in 'closed' networks, characterized by low brokerage among members (Figure 3), reputation costs for bad behavior increase, fostering trust and cooperation [32].

Thus, everyday behaviors (e.g., determining how to seek or spread information, calibrating interpersonal trust) would benefit from tracking patterns of indirect relationships. Next, we consider what individuals know about the structure of their social networks.

Probing mental representations of social networks

There are two broad approaches to investigating mental representations of social networks. The first assesses individuals' ability to learn and remember artificial networks, which constituted some of the earliest work on this topic [33], and revealed schemata that facilitate, but sometimes distort, social network representations (e.g., a network containing two individuals with a mutual friend is easier to learn if those individuals are also friends [34]). Such schemata may serve as 'compression heuristics' that reduce large numbers of relationships into more cognitively manageable formats, allowing humans to track

exceptionally large numbers of social ties [34^{*}]. The second approach characterizes real-world networks, and typically compares participants' perceptions of network structure with ground truths defined by observed interactions or consensus perceptions [35]. People accurately report characteristics of familiar others' network positions, including EVC and brokerage, which requires accurately perceiving overall network topology, as well as individual relationships [36^{**}]. Thus, although there exist systematic biases in people's social network representations, humans represent their real-world social network structures, and where others sit in those networks, with considerable accuracy.

Neural encoding of social network position

Is social network position knowledge spontaneously retrieved whenever familiar individuals encounter one another, or only when situational goals demand it? A recent study characterized the network of students in an academic program, a subset of whom participated in a neuroimaging study where they passively viewed videos of several classmates [36^{**}]. When participants viewed each classmate, network position information (distance, EVC, brokerage) was encoded in distributed neural response patterns (Figure 4). These results cohere with evidence that humans spontaneously process other aspects of social information (e.g., intentions, traits) when encountering others to facilitate appropriate, beneficial social interactions [37,38]. The accuracy and automaticity with which people represent others' network positions points to its likely behavioral relevance: successfully navigating the social world may depend not only on tracking, encoding, and cultivating direct relationships, but also on monitoring information about others' bonds and potential social influence.

Largely distinct sets of brain regions appear to encode different social network position characteristics, illuminating how this information might influence mental processes engaged during social encounters.¹ For example, distance was encoded in right inferior parietal cortex and STC (Figure 4). Past work suggests that this region maps the physical space around oneself [39] and encodes social and spatial distances analogously [40]. When encountering familiar others, people may retrieve those individuals' proximity to themselves in a mental map of their social

network. 'Targets' brokerage was represented in lateral STC, while their EVC was encoded in areas of medial parietal cortex and MPFC associated with encoding traits and mental states, and regions involved in modulating visual attention (Figure 4). While caution should be exercised when engaging in reverse inference with such results, given the functional heterogeneity of the implicated brain regions, these findings suggest testable hypotheses regarding how different aspects of social network position impact social thought and behavior. For example, others' brokerage was encoded in regions implicated in extracting social meaning from movement dynamics [41], suggesting that brokerage may relate to expressivity or to how perceivers attend to one's expressions and gestures, possibilities that may be tested behaviorally. EVC being encoded in regions implicated in visual attention and interpreting mental states suggests that how well-connected someone is may impact attention to that individual and their apparent mental states, and thus, may have social cognitive consequences similar to more widely studied facets of social status (e.g., dominance [42]).

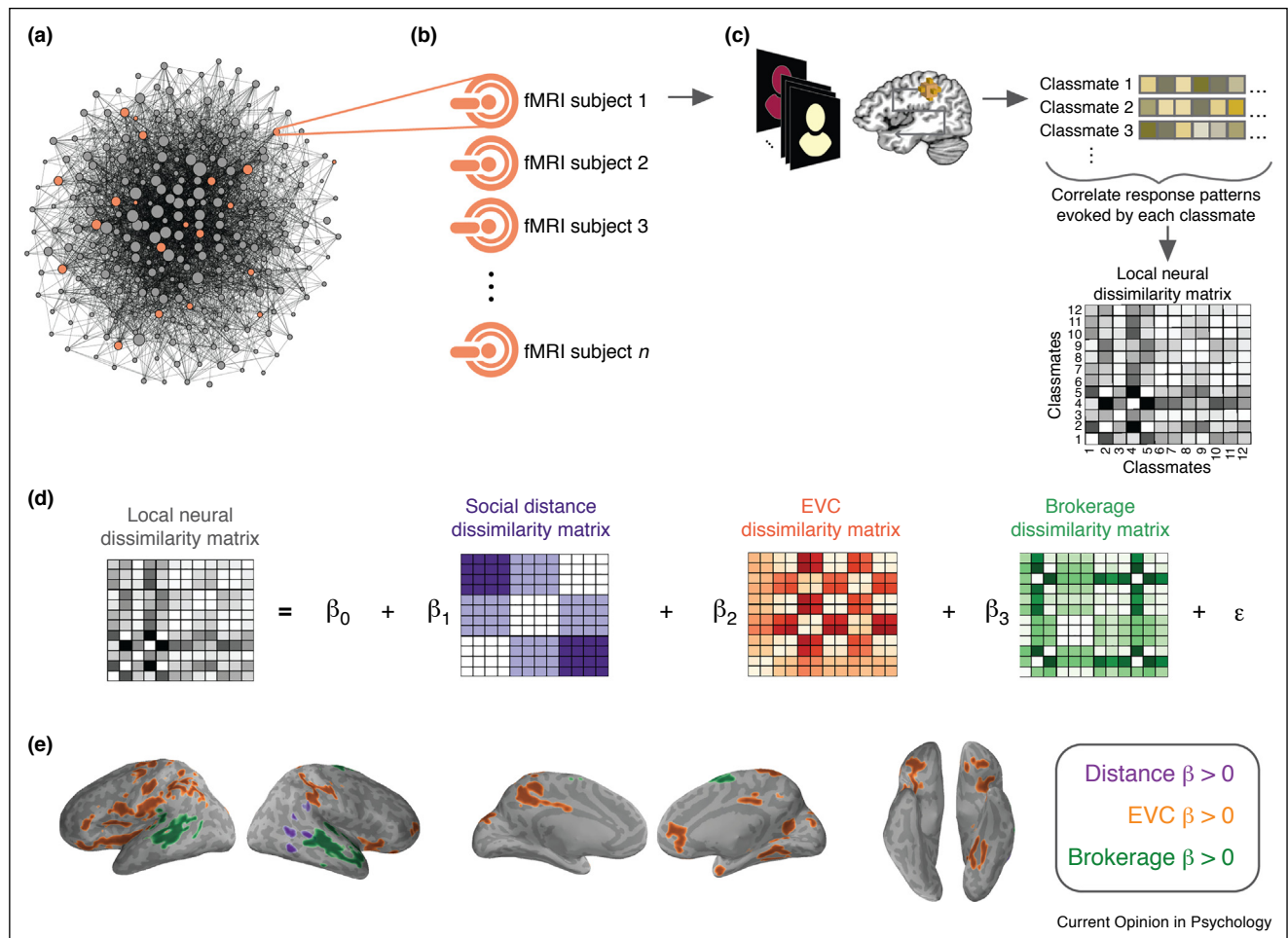
Social network centrality as a facet of social status. In all human societies, there exist differences in individuals' capacities to influence group decisions, resource allocation, and conflicts; individuals who have more influence on such phenomena are referred to as having higher social status [43]. Although recent research has investigated prestige (expertise-based respect) as a source of status, past research on the perception, antecedents, and consequences of status in humans has focused on dominance, perhaps due to the considerable literature on dominance hierarchies in other animals [44,45]. However, as the successful navigation of everyday life depends progressively more on affiliative relationships and reputation management, rather than threatening or avoiding violence [46,47], for contemporary humans, the influence and support conferred by social connections is likely an increasingly behaviorally relevant facet of social status.²

Integrating SNA and neuroimaging may be especially useful for advancing understanding of how different facets of status are tracked, encoded, and shape behavior. In other domains, relating mental phenomena to underlying neural substrates has advanced psychological theory by elucidating when processes that may subjectively

¹ It is often difficult to ascertain if the apparent neural encoding of stimulus characteristics reflects the *representation* of those characteristics themselves or spontaneously evoked, systematic effects of those representations on associated mental processes, even when using very basic (e.g., passive viewing) tasks. This interpretive issue for cognitive neuroscience research is not fully resolved [69]; a challenge for the field moving forward entails disentangling these accounts in order to advance our understanding of the psychological significance (e.g., representation of social concepts; effects on associated mental processes) of the apparent neural encoding of social information within and across task contexts.

² Although relationships between social network centrality and subjective evaluations of dominance and prestige have not, to our knowledge, been systematically characterized in experiments with adult samples, the related construct of likeability has received comparatively more attention, particularly in developmental samples (e.g., of young children) [45]. Research exploring relationships between status based on dominance, prestige, and likability and their behavioral consequences in adults suggests that these different facets of status have dissociable influences on social rank and attention, and that likability is positively associated with prestige but negatively associated with dominance [44].

Figure 4



Assessing the neural encoding of social network position: Example analyses and results. In a recent study [36**], (a) the full social network of an academic cohort was characterized; circles signify students and lines signify friendships between them. A subset of students (shown in orange) participated in an fMRI study where they viewed images of their classmates (b). (c) Neural response patterns evoked when viewing each of 12 classmates were extracted in local neighborhoods throughout the brain using a searchlight approach. In each local neighborhood (i.e., searchlight center), response patterns evoked by each classmate were correlated with one another to generate a local neural dissimilarity matrix that captures the extent to which the brain area distinguishes between the people whom the participant viewed. (d) Social network-based dissimilarity matrices can also be constructed that describe how the classmates whom the participant viewed in the scanner differ in terms of social distance from the participant (purple), EVC (orange) and brokerage (green). Each local neural similarity structure can then be modeled as a weighted sum of these social network-based similarity structures to assess if and where social network position information is carried in local neural response patterns. (e) Brain regions that reliably carry information about social distance, EVC, and brokerage across individuals are displayed in purple, orange, and green, respectively. Figure reproduced with permission from [36**]. EVC = eigenvector centrality; fMRI = functional magnetic resonance imaging.

seem similar are actually distinct (e.g., different forms of memory [48]) and when seemingly disparate phenomena reflect common processes (e.g., conceptual reasoning and spatial navigation [49]). Neuroimaging research testing if the encoding, antecedents, and consequences of status based on social network centrality and other factors (e.g., dominance) involves shared or distinct mechanisms promises to refine understanding of these phenomena. To what extent do findings about how status hierarchies are learned, updated, and shape behavior [50–55] generalize

to social network centrality? While researchers have yet to directly contrast the neural encoding of these different types of status, structural neuroimaging suggests distinct neuroanatomical correlates of social dominance and centrality [56].

Social network position and individual differences in social information processing

Most research integrating SNA and neuroscience has focused on brain structure [57–62]. Social network size

is associated with volume and grey matter density of brain regions implicated in diverse aspects of social and affective processing (e.g., amygdala, STC, orbitofrontal cortex–OFC, ATL) [57–60]. There are inconsistencies across studies regarding the neural structural correlates of social network size, perhaps due in part to inconsistencies in how ties are defined (e.g., recent socialization; Facebook ‘friendships’). The relationship between OFC volume and social network size is mediated by individual differences in social cognitive abilities (e.g., higher order reasoning about mental states [57]), consistent with the notion that associations between the size of social networks and social brain regions are related to the computational demands of maintaining large numbers of social relationships.

Recent work has explored how social network position characteristics relate to the recruitment of particular brain regions during social interactions. For example, one’s own brokerage is positively associated with recruitment of brain regions implicated in mentalizing when making recommendations to peers following peer feedback that differs from one’s own prior preferences [63**]. This may reflect a greater tendency for brokers, who are structurally poised to translate information between groups, to consider others’ perspectives. Interestingly, such neural differences did not manifest in behavioral outcomes (i.e., high-brokerage and low-brokerage individuals updated recommendations to align with peer feedback to similar degrees), highlighting the value of neuroimaging as a window into covert mental processes evoked during social interactions as they unfold, and how they may differ across individuals.

Social network position also affects how accurately individuals represent network structure. Low-centrality individuals have more accurate representations of network structure (who is connected to whom) [64], which may stem in part from how low-centrality versus high-centrality individuals distribute attention across group members: low-centrality individuals attend to others to an equivalently high degree, irrespective of those individuals’ centrality, and exhibit elevated responses in brain regions associated with valuation and motivational relevance (e.g., ventral MPFC, ventral striatum, amygdala) when viewing any group member. Contrastingly, high-centrality individuals attend comparatively less to low-centrality individuals, only exhibiting elevated valuation-related brain activity when viewing high-centrality others [65,66**]. These results may reflect the fact that the behaviors and mental states of high-status individuals are relevant to all group members, whereas low-status individuals are relatively less behaviorally relevant to high-status group members [66**,67].

Conclusions

Understanding how the human brain encodes and navigates the social world requires combining the study of

individual cognition with methods for characterizing patterns of social ties. Recent research integrating these lines of inquiry offers insight into the mental architecture that encodes the structure of our social environment, the impact of this structure on cognition and behavior, and individual differences in how we represent and are influenced by patterns of social relationships. Since social cognition and behavior are necessarily embedded within social networks, future research integrating these approaches promises to deepen understanding of how humans understand, shape, and are shaped by, our distinctively complex social worlds.

Conflict of interest statement

Nothing declared.

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● of special interest

●● of outstanding interest

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