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Abstract and Keywords

From its beginning, the study of networks has drawn on a variety of disciplinary perspectives. For much of its history, research on social networks has assumed that social networks behave like other similarly large, interconnected structures. However, the nodes that make up social networks—human beings—think and behave in flexible, complex, and often seemingly irrational ways. A deep understanding of social networks, therefore, requires not only analysis at the network level but also an understanding of how such networks shape and are shaped by the psychological processes of their members. In recent years, psychology has begun to make inroads into the network literature, but while neuroscience is an increasingly important area of psychology, research on the neuroscience of social networks remains scarce. This chapter reviews extant research pertaining to the neuroscience of social networks and sketches a research agenda to augment this already interdisciplinary field with insights from neuroscience.

Keywords: social networks, neuroscience, social brain, social relationships, fMRI

(p. 496) The Neuroscience of Social Networks

FROM its beginning, the study of networks has drawn on a variety of disciplinary perspectives. For much of its history, research on social networks has assumed that *social* networks behave like other similarly large, interconnected structures. However, the nodes that make up social networks—human beings—think and behave in flexible, complex, and often seemingly irrational ways. A deep understanding of social networks, therefore, requires not only analysis at the network level but also an understanding of how such networks shape and are shaped by the psychological processes of their members. In recent years, psychology has begun to make inroads into the network literature, but while neuroscience is an increasingly important area of psychology, research on the neuroscience of social networks remains scarce. In this chapter, we review the extant research pertaining to the neuroscience of social networks and sketch a research agenda to augment this already interdisciplinary field with insights from neuroscience.

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Fields Collide: The Social Brain Hypothesis

Research on the neuroscience of social networks traces its origins to the work of the anthropologist Robin Dunbar. Dunbar began with the observation that as the size of a group increases, the social complexity—that is, the number of potential dyadic ties within that group—increases exponentially. Combining field-based observations of social primates with neuroanatomical data, he noted a correlation between the average size of the brain's neocortex in a primate species and the sociality of that species (Figure 27.1).



Figure 27.1 Predicting human social group size from brain structure. (A) The relationship between mean social group size and neocortex ratio [i.e., (neocortex volume) / (total brain volume - neocortex volume)] in primates (white triangles = prosimians; black triangles = New and Old World Monkeys; white squares = apes; black square = modern humans; dashed lines depict, from left to right, separate regression lines for prosimians, monkeys, and apes). By extrapolating the relationship between group size and neocortex ratio in other primates to predict the average human social group based on the characteristic human neocortex ratio, Dunbar (1998) predicted an average social group size for humans of approximately 150 individuals. This number corresponds closely to the observed mean group size in modern humans (black square). Reproduced from (Dunbar, 2018). (B) Average social group sizes across three contemporary samples from the United States (black triangles), as well as traditional human societies from Africa, Asia, Australia, North America, and South America, including hunter-gatherer and horticultural communities. While hunter-gatherers tend to form small, relatively unstable, overnight camps of 30 to 50 individuals (white circles) and larger tribes of 500 to 2,500 individuals defined by a common cultural identity (white squares), they also consistently form clans or villages of approximately 150 individuals (black circles) whose members interact with one another regularly enough to form bonds based on direct and specific knowledge about each other (Dunbar, 1993). The predicted social group size (i.e., 150) extrapolated from the relationship shown in (A) is depicted by the solid black horizontal line; dashed horizontal lines indicate 95% confidence intervals. Reproduced from Dunbar (1998).

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(p. 497) Extrapolating from a regression model relating neocortical volume and social group size in primates, Dunbar (1993) predicted that humans should have an average social group size of 150 individuals (Figure 27.1). This number—now known as "Dunbar's number"—turns out to be a surprisingly common group size for humans. Dunbar found 150 to be the average clan size in traditional hunter-gatherer societies characterized by anthropologists (Dunbar, 1993). Similarly, although modern industrialized societies are much larger than 150 individuals, 150 appears to be the limit on the number of individuals (e.g., relatives, friends, acquaintances) with whom we maintain regular contact on at least an annual basis, and with whom we maintain defined social relationships (for a review, see Dunbar, 2008). In the corporate world, the company behind the Gore-Tex brand is well known for its policy of building plants to house 150 employees, with subsequent growth requiring the addition (p. 498) of a new building. "We've found again and again that things get clumsy at one hundred and fifty," founder Bill Gore said (quoted in Glad-well, 2000).

Dunbar's idea, known as the social brain hypothesis, posits that humans' exceptional intelligence and corresponding unusually large brains evolved to meet the pressures associated with surviving and reproducing in large, complexly bonded groups (Byrne & Whiten, 1988; Dunbar, 1993). In many other species, interactions with unrelated others are limited to aggressive and reproductive encounters. Even among the relatively small subset of species whose members live peacefully in groups alongside nonkin with whom they have no reproductive ties, social groups are often composed of fluid, anonymous aggregations (Dunbar & Shultz, 2010). Contrastingly, as humans, we spend our lives almost entirely in the company of unrelated others with whom we forge lasting, intense bonds of the sort typically reserved for reproductive relationships in most other species (Dunbar & Shultz, 2007). Successfully navigating groups composed of very intense and varied social relationships characterized by shifting loyalties and rivalries, coalition formation, tactical deception, and strategic betrayals requires a brain with considerable computing power, since each member must keep track of his or her own relationships with others, relationships between third parties, and how best to use this information to his or her own benefit.

A considerable body of neuroscience evidence has amassed in support of the social brain hypothesis by systematically relating social network size to brain size, and in particular, to the relative volume of neocortex (i.e., a component of the brain involved in higher-order mental functions, such as conscious thought and language), across species. In line with the notion that the cognitive demands of surviving and thriving in large, complexly bonded social groups selected for the unusually large human neocortex, average social group size is positively correlated with relative neocortical volume across primate species (Dunbar, 1993). The brain, in short, appears to have evolved to enable life in our social networks. If so, understanding how the structure and function of the brain affect—and are affected by—our networks is an important area for research.

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An Emerging New Field

Humans' distinctive sociality—enabled by our large neocortex—is thought to reflect an evolutionary advantage: coordinating with otherwise would-be strangers likely enhanced our ancestors' abilities to survive, thrive, and reproduce. However, while inhabiting large, complexly bonded social groups confers substantial benefits to individual group members, it is also extremely cognitively demanding: as group size increases, each group member must monitor and remember an ever-increasing amount of social information (e.g., Who is friends with whom? Who is in conflict with whom?) to maintain harmony and avoid conflict within the group. Thus, social complexity and human brain evolution are thought to be tightly linked (Dunbar & Shultz, 2007). Understanding this relationship— how the brain supports and constrains our sociality, and how our social networks impact brain structure and function—is the topic of an emerging new field at the intersection of neuroscience, anthropology, and sociology: the neuroscience of social networks. In this chapter, we explore this new field and how an understanding of the brain may shed light on how we shape and are shaped by the networks in which we are embedded.

(p. 499) By integrating approaches from the fields of neuroscience and social network analysis, we can begin to ask questions like: What kinds of social network information does the brain track and encode? How do situational factors shape the kinds of social network information that is encoded, and how does such information modulate subsequent thought and behavior? How do biological factors, such as brain structure, influence the kinds of social network positions that individuals occupy? And how do the network positions that we occupy affect subsequent brain development? Although we do not yet have complete answers to these questions, they are well within reach of the combined expertise of these fields.

Why the Brain?

A question often posed to neuroscientists studying social behavior is: *Why go to the brain at all*? That is, what explanatory power does a neuroscientific explanation provide over and above a behavioral one? The candid answer is that *right now*, neuroscientific explanations for social behavior are limited. The field of social neuroscience is in its infancy. However, even inchoate explanations are beginning to bear fruit and these explanations reveal two answers. The first is that a deep understanding of how people connect requires an understanding of the *tools* the brain uses to support that connectivity. Moreover, it requires an understanding of the limitations of that biological endowment. The second answer is that a behavioral approach requires behavior to observe. In contrast, brain activity offers a window into mental processing and can even predict behavior *before* it occurs, thereby providing both a predictive model of future behavior and the possibility of intervention. Furthermore, by decoding thought—even patterns of thought that exist under the threshold of conscious awareness (Soon et al., 2008)—neuroscience can reveal how

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people respond to the social world in ways that may not be directly reportable by the persons involved or that may lack overt behavioral corollaries.

For example, a recent functional magnetic resonance imaging (fMRI) study found that people whose social network positions afford more brokerage opportunities recruit brain regions that support considering others' points of view to a greater extent when updating their own opinions following exposure to divergent peer feedback (i.e., peers' opinions that disagreed with their own). Yet, no differences were identified between high- and lowbrokerage individuals in behavioral performance (i.e., the extent to which people changed their own opinions following divergent peer feedback) on the same task (O'Donnell et al., 2017). More generally, functional neuroimaging can provide an information-rich measure of diverse aspects of how people attend to, mentally respond to, and interpret the world around them. These characterizations can be compared across members of the same social networks, for example, to investigate homophily and social influence effects in a finer-grained manner than might otherwise be possible (Parkinson, Kleinbaum, & Wheatley, 2018). In addition, as discussed later in this chapter, characterizing neural response patterns evoked when people view personally familiar others can provide insight into what aspects of social knowledge people track and retrieve during social encounters (e.g., traits, characteristics of their social network position), and mapping out what brain systems encode such knowledge can inform testable hypotheses regarding impact on downstream thoughts and behaviors (Parkinson, Kleinbaum, & Wheatley, 2017; Zerubavel et al., 2015). Social (p. 500) neuroscience may be in its infancy, but its potential to add signal to models of human behavior should not be underestimated. Here, we provide examples of how this potential is currently being realized to advance our understanding of how individuals encode, shape, and are shaped by their social environment and suggest directions for future research.

How the Brain Encodes Social Relationships

In this section, we highlight psychological and neuroscientific research on how people think about, and are affected by, social relationships between themselves and others.

Differential Neural Responses to Friends and Strangers

The majority of psychological and neuroscientific research examining how individuals' real-world social relationships impact their thoughts, emotions, and behaviors has been limited to contrasting behavioral and neural responses to friends and strangers. This growing body of literature suggests marked differences in how the human brain responds to strangers and personally familiar others (Deaner, Shepherd, & Platt, 2007; Fareri et al., 2012; Gobbini et al., 2013; Visconti di Oleggio Castello et al., 2014). For example, merely viewing familiar faces (cf. strangers' faces) engages brain systems involved in affective processing and theory of mind (i.e., thinking about other people's thoughts), purportedly reflecting emotional responses and the activation of person knowledge (e.g., traits, intentions, attitudes), respectively (Gobbini & Haxby, 2007). The automatic activation of knowl-

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edge about familiar individuals when encountering them is thought to assist the perceiver in appropriately "shifting gears" depending on whom the perceiver has encountered (e.g., an old friend, an acquaintance, an employer). Thus, our brains automatically distinguish between familiar and unfamiliar others when encountering them, and differential neural responses to strangers and familiar others likely serve to facilitate effective, beneficial social interactions.

The Need to Move beyond "Friend versus Stranger"

Perhaps reflecting the logistical challenges of bringing real-world social relationships into the lab, very little research has extended the study of how personal relationships are represented in the brain and/or how they impact neural processing beyond the relatively crude distinction between familiar others and complete strangers. Therefore, with few exceptions (e.g., mother-infant bonds; Case, Repacholi, & Stevenson, 2006; Leibenluft et al., 2004; E. E. Nelson & Panksepp, 1998), extremely little is known about how the human brain encodes information about the nature and quality of our relationships with personally familiar others, or the neural mechanisms through which such information influences cognition and behavior. Yet, given that many of our everyday interactions take place with people who are already familiar to us (Sun et al., 2013), it seems likely that these interactions (p. 501) are influenced by more nuanced social relationship information than the simple distinction between those we have encountered before and those we have not. Better understanding how social relationship information, such as social closeness, is encoded in the brain, and how such information impacts downstream neural processing (and thus subsequent thoughts, emotions, and actions), is an important direction for future research.

The Neural Representation of Social Closeness

We recently sought to address this gap in understanding by investigating how the brain encodes social closeness (i.e., tie strength) between perceivers and individuals with whom they are familiar. We hypothesized that social closeness would be represented in the brain using neural mechanisms also involved in encoding proximity to oneself in other domains (e.g., spatial and temporal frames of reference). This prediction was rooted in the observation that converging theories from cognitive linguistics, neuroscience, and social psychology suggest that different domains of psychological distance (i.e., removal from one's own current, firsthand experience) are encoded similarly. Conceptual metaphor theory (Lakoff & Johnson, 2008) suggests that we use spatial language to describe social relationships (e.g., "close friend," "distant relative") because we mentally represent this information in spatial terms. Neuroscientists have suggested that over the course of evolution, mechanisms devoted to spatial processing may have been redeployed to "plot" information in increasingly abstract (e.g., social, temporal) frames of reference (Parkinson & Wheatley, 2013, 2015; Yamazaki, Hashimoto, & Iriki, 2009). Mounting evidence from social psychology supports these assertions and suggests an explanation for overlap in the language and brain areas used to represent spatial and social distance: the degree to which information is removed from our current experience in time or space or

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the extent to which it refers to someone else (i.e., social distance) carries a common psychological meaning with important implications for the perceiver: relevance to the self in the here and now, and thus, at what level of detail such information should be construed (Liberman & Trope, 2008; Vallacher & Wegner, 1985).

We scanned participants using fMRI as they viewed trials consisting of sequentially presented pairs of objects photographed at different egocentric distances (spatial distance trials), phrases referring to the immediate or more remote future (temporal distance trials), and names and photographs of familiar others and acquaintances (social distance trials). In each trial, participants saw two images sequentially and were asked to judge how much closer or farther, sooner or later, or more or less familiar the second image was relative to the first for spatial, temporal, and social distance trials, respectively (Figure 27.2). Thus, in effect, the progression of stimuli over time within each trial was analogous to "movement" either toward or away from the participant in a spatial, temporal, or social frame of reference. Using statistical pattern recognition techniques, we found that a region of parietal cortex with a long-established role in encoding spatial distance in humans and other animals also underpins mental representations of social and temporal distances. The pattern of activity in this region for nearer versus farther objects was similar to the pattern evoked by more familiar versus less familiar others and the pattern for sooner versus later time (Parkinson, Liu, & Wheatley, 2014), suggesting a common neural mechanism for distinguishing social, spatial, and temporal distances from the self.

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Figure 27.2 Evidence for shared neural mechanisms for representing spatial, temporal, and social closeness. (A-C) In an fMRI study, participants viewed sequentially presented stimuli such that stimulus change over time was analogous to "movement" either toward or away from the observer in spatial, temporal, or social frames of reference. (A) Spatial distance trials consisted of objects photographed at different egocentric distances. (B) Temporal distance trials consisted of phrases referring to the immediate or more remote future. (C) Social distance trials consisted of names and photographs of four friends and four acquaintances of the participant. Experimental stimuli contained individuals' actual first and last names rather than the words *friend* and *acquaintance* (D) In a large cluster within the right inferior parietal cortex, a brain region consistently implicated in spatial cognition, neural response patterns encoded relative distance from the self, irrespective of whether that distance was social, spatial, or temporal in nature. Adapted from Parkinson et al. (2014). Full color figures available on Oxford Handbooks Online.

(p. 502) This finding suggests that encoding social closeness to oneself (i.e., tie strength) relies on an evolutionarily ancient computation for representing distances from the self in the physical world. Our ability to track how *socially* close we are to an individual at any moment is possible in part because we represent the strength of a social bond as "distance from self." These findings also support speculation that brain circuitry originally devoted to spatial computations was "recycled" to perform analogous operations in increasingly abstract frames of reference (Parkinson & Wheatley, 2013, 2015; Yamazaki et al., 2009). More generally, the current results are consistent with suggestions that neural mechanisms supporting higher-order cognition may often be best understood in terms of the computations, rather than the domains of knowledge, that they involve (Mitchell, 2008). Although cognition is often studied according to common-sense categories, it would be inefficient for the brain to represent spatial, social, and temporal distances using entirely separate mechanisms if they carry a common psychological meaning, as suggested by strikingly similar effects on predictions, evaluations, and behavior (Liberman & Trope, 2008): proximity to the self in the here and now.

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(p. 503) By combining the characterization of individuals' real-world social relationships with neuroimaging methods, we can begin to understand how social relationship information, such as the strength of a social tie, is encoded in the brain. Using similar approaches, we are hopeful that future research will shed light on the neural mechanisms through which aspects of our direct social relationships modulate cognitive, emotional, and behavioral responses to other people (e.g., attention to social cues: Deaner et al., 2007; reactions to others' pain: Martin et al., 2015). Continued progress on this front will require that researchers continue to combine information about real-world social relationships (beyond the friend vs. stranger distinction) with methods for characterizing neural information processing.

The Neural Encoding of Indirect Social Relationships

In the following section, we consider how people think about and are affected by social relationships between others, and patterns thereof.

The Importance of Indirect Social Relationships to Everyday Human Thought and Behavior

One of the key insights of the social network perspective is that relationships between third parties shape behavior (Brent, 2015; Massen, Pašukonis, Schmidt, & Bugnyar, 2014; Massen, Szipl, Spreafico, & Bugnyar, 2014). Knowledge about third-party relationships (e.g., who is friends with whom) and patterns of social ties (e.g., who has many friends) can be useful for managing our own reputations and for tracking the reputations of others. For example, cooperation and trust between otherwise unfamiliar individuals are facilitated when those individuals share mutual friends (Ferrin, Dirks, & Shah, 2006), presumably because shared social ties heighten the potential reputation costs and benefits posed by an interaction (Coleman, 1988). Many everyday behaviors, such as predicting the potential consequences of a recent social misstep or determining how best to seek or spread a particular piece of information, depend on the ability to track and encode not only the states of our own relationships but also patterns of ties between third parties in our social groups.

Despite the apparent importance to individual cognition and behavior of relationships between third parties in our social networks (Krackhardt, 1990), extremely little is known about how, and under what circumstances, such information is encoded in the brain and how third-party relationship knowledge may come to influence cognition, emotions, and behavior during social interactions (Weaverdyck & Parkinson, 2018). Given that neuroscientists have historically paid very little attention to even *direct* social relationship information, beyond the friend versus stranger distinction, the dearth of research investigating the neural encoding and consequences for downstream neural processing of *indirect* social relationship information is perhaps not altogether surprising.

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(p. 504) The Neural Encoding of Social Network Position Characteristics

In a recent study, we sought to gain insight into how the human brain tracks and encodes patterns of social relationships—specifically, where others sit in one's real-world social network (Parkinson et al., 2017). We first characterized the friendship network of a grad-uate student cohort (N = 275) and recruited a subset of these students for an fMRI study. A customized stimulus set was created for each fMRI participant to ensure that he or she viewed individuals who varied in terms of at least two aspects of social network position that we predicted would be behaviorally relevant: geodesic distance from the participant and eigenvector centrality. Accordingly, each participant's stimulus set consisted of brief videos of the two highest and lowest eigenvector centrality individuals at geodesic distances of 1, 2, and 3 from him or her in the friendship network. During the fMRI study, participants were instructed to simply watch these videos and press a button if the same video was displayed twice in a row (to maintain their attention on the screen).

After exiting the scanner, participants saw the same classmates again and rated them in terms of perceived social closeness, eigenvector centrality, and brokerage. These subjective ratings were highly positively correlated with the individuals' actual proximity to the participant in the friendship network, eigenvector centrality, and brokerage, respectively, suggesting that participants had relatively accurate knowledge of familiar others' social network positions. In addition, the fMRI results suggested that this knowledge had been spontaneously retrieved in the students' brains when viewing one another, even in the absence of a related task. In other words, information about social distance from the participant, brokerage, and eigenvector centrality was reliably carried in distributed patterns of neural responses evoked when network members merely saw one another's faces.

Geodesic distance from the participant was encoded in the same region of parietal cortex that we previously found contained a common neural code for social, spatial, and temporal distances from oneself (Parkinson et al., 2014), consistent with suggestions that brain regions with an evolutionarily old role in encoding physical space may be redeployed to encode where other people sit in a mental map of "social space" (Parkinson & Wheatley, 2013, 2015). Brokerage information was encoded in brain areas (e.g., superior temporal and supplementary motor regions) widely implicated in action understanding. Future work will hopefully clarify if this pattern of results is attributable to brokers imbuing more social meaning into their gestures or commanding differential amounts of attention from perceivers to their actions and gestures (e.g., because of perceivers' knowledge of their brokerage status or of qualities related to this aspect of network position). Finally, eigenvector centrality in the friendship network was encoded in brain regions critical for inferring others' mental states and intentions (e.g., dorsomedial prefrontal cortex, posterior cingulate cortex) and visual attention (e.g., extrastriate visual cortex), and for assessing the value of stimuli (e.g., ventromedial frontal cortex). Interestingly, a related study that focused on identifying brain regions that track in-degree centrality reported a similar pattern of results, as described in more detail below.

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Zerubavel et al. (2015) investigated the neural mechanisms involved in tracking sociometric popularity, operationalized as in-degree centrality (i.e., the sum of liking ratings received from fellow group members). The authors first characterized the social networks of two (p. 505) student groups (i.e., 13-member on-campus clubs), then measured group members' brain activity while they viewed photographs of one another in an fMRI scanner. When high in-degree centrality individuals' photographs were shown, greater activity was observed in brain regions that have previously been implicated in tracking the value of rewards (e.g., ventromedial prefrontal cortex, ventral striatum), as well as in brain systems involved in understanding others' mental states (e.g., dorsomedial prefrontal cortex, the temporoparietal junction). Moreover, Zerubavel et al. (2015) found that activity in reward-related brain areas mediated the relationship between the sociometric popularity of the individual being viewed and the engagement of areas involved in social cognition (e.g., inferring others' mental states) in the perceiver's brain. These results suggest that brain systems involved in monitoring the value of stimuli in our surroundings may assign increased motivational relevance to highly popular individuals, which may in turn trigger the engagement of brain regions involved in understanding the mental states of those individuals.

Distinct but Analogous Facets of Social Status

Interestingly, the pattern of results described previously concerning the neural encoding of social network centrality closely mirrors what has been observed in studies of the neural encoding and cognitive consequences of dominance-based social status in our close primate relatives. For example, rhesus macaques ascribe value to viewing the faces of high-status (i.e., dominant) conspecifics and attend more to cues to dominant/high-ranking individuals' mental states (Deaner, Khera, & Platt, 2005; Klein & Platt, 2013; Shepherd, Deaner, & Platt, 2006). Thus, in humans, sociometric popularity appears to exert strikingly similar effects on neural and cognitive processing to those exerted by dominance-based social status in other primates.

More research is needed to better understand the neural mechanisms through which sociometric status is encoded and impacts the processing of other domains of information, as the vast majority of psychological and neuroscientific research on the perception, antecedents, and consequences of social status in humans has centered on the status conferred by physical dominance and, to a lesser degree, prestige (i.e., respect based on expertise; Cheng et al., 2013). Indeed, whereas sociological research has investigated the social status that individuals receive through their patterns of social connections and its influence on interpersonal interactions (e.g., Ellwardt, Labianca, & Wittek, 2012), the overwhelming majority of psychological and neuroscientific literature on social status has operationalized social status in terms of physical dominance and the associated capacity to inflict physical violence on others (Cheng et al., 2013). Given that for modern humans, success in everyday life is increasingly dependent on affiliative social relationships and reputation management (Tennie, Frith, & Frith, 2010) rather than the need to display or avoid physical violence (Pinker, 2011), the support and capacity for influence associated with an individual's social network position (e.g., being connected to other highly influen-

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tial individuals) is likely a highly behaviorally relevant facet of social status. Yet, the neural encoding and cognitive consequences of this aspect of social status are only beginning to be understood.

For humans, tracking and encoding relationships and interactions between third parties account for a large proportion of what we speak, and likely think, about every day. Roughly two-thirds of human conversations are centered on social topics about third parties (i.e., on (p. 506) gossip; Dunbar, 2004). Consistent with the suggested importance of patterns of third-party relationships to individual cognition and behavior, this preponderance of gossip is thought to allow information about interactions and relationships between third parties to percolate efficiently through social groups, allowing individuals' knowledge about other group members to extend well beyond what would be possible for them to observe firsthand (Dunbar, 2004; Mullins, Whitehouse, & Atkinson, 2013). Managing our own reputations and monitoring those of others not only figures prominently in modern human life but also has been suggested to be a pressure that drove the evolution of language (Knight, Studdert-Kennedy, & Hurford, 2000; Tennie et al., 2010). Thus, monitoring relationships and information flow between third parties appears to be central to the evolution, and everyday deployment, of human cognition. However, we are only beginning to map out the neural mechanisms involved in monitoring and encoding information about relationships between third parties (e.g., whether an individual is a friend, a friend of a friend, or further removed from oneself in social ties; structural characteristics of an individual's social network position, such as how well connected he or she is, or whether or not he or she presents a brokerage opportunity). Further research integrating approaches from cognitive neuroscience and social network analysis is needed to better understand these phenomena.

How the Brain Shapes and Constrains Social Networks

Until recently, research relating brain size to social network size had only examined this relationship *across* species. Researchers have now begun to relate brain structure to social network characteristics in humans. The first study of this kind found that social network size and complexity (as indexed by the Number of People in Social Network and Number of Embedded Networks subscales of the Social Network Index [SNI], respectively; Cohen et al., 1997) were correlated with the volume of the amygdala, a brain region involved in social and emotional processing (Bickart et al., 2011). Subsequent studies replicated and extended this work by demonstrating that amygdala volume is positively associated with the size of both face-to-face and online (i.e., Facebook) social networks (Kanai et al., 2012; Von Der Heide, Vyas, & Olson, 2014) and have highlighted positive associations between social network size and the volume of other brain regions within the frontal and temporal lobes that are implicated in social information processing (Kanai et al., 2012; Lewis et al., 2011; Powell et al., 2012; Von Der Heide et al., 2014). However, there remains some inconsistency across studies in the particular brain regions that have

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been associated with social network size in humans. This may be due in part to variability across studies in the indices of social network size that have been used (e.g., number of Facebook friends; number of people an individual has had social contact with during the past month; the SNI: Cohen et al., 1997; the Norbeck Social Support Questionnaire: Norbeck, Lindsey, & Carrieri, 1981). Although more work is needed to better understand exactly how and why various indices of social engagement are differentially related to brain structure, it is striking that studies using a wide range of methodologies and samples consistently find positive associations between social network size (i.e., ego degree) and the size of brain structures involved social cognition.

(p. 507) Notably, Lewis et al. (2011) found that the cortical volume of two regions of the medial prefrontal cortex was positively correlated with both social cognitive competence (indexed by the ability to engage in higher-order reasoning about mental states, e.g., "I believe that you suppose that she thinks ...") and social network size. Later work by the same group demonstrated that individual differences in social cognitive skills mediate the relationship between prefrontal cortical volume and social network size (Powell et al., 2012). These studies provide an important source of support for the social brain hypothesis: for evolution to work, there must be within-species variability upon which natural selection can operate, and if the social brain hypothesis is correct, then variability in neocortical volume should relate to both social cognitive competencies and social network size (e.g., neocortical volume) to social group size within and across species, these results strongly suggest that the human brain increased in size over the course of evolution to meet the cognitive demands of navigating large, complexly bonded social networks.

Does the Processing Capacity of the Human Brain Constrain Social Network Size?

Modern technologies, such as the internet, would seem to provide us with the tools necessary to forge and maintain social relationships on a far larger scale than would otherwise be possible. Yet, the same average social community size—150 individuals—that characterizes social networks in both modern industrial and hunter-gatherer societies (Hamilton et al., 2007; Hill & Dunbar, 2003; Roberts et al., 2009; Zhou et al., 2005) characterizes the number of relationships that people maintain online (e.g., on Facebook: Dunbar, 2016; on Twitter: Gonçalves, Perra, & Vespignani, 2011; via email communications: Haerter, Jamtveit, & Mathiesen, 2012). In addition, use of social networking sites does not appear to meaningfully impact face-to-face social network size (Christakis & Fowler, 2009) or feelings of emotional closeness to members of one's offline network (Pollet, Roberts, & Dunbar, 2011). Thus, even though modern technological innovations allow us to "friend" thousands of individuals, the number with whom we can manage significant relationships is constrained by limits on both our time and the processing capacity of our brains.

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Of course, an individual's social effort (e.g., time, emotional investment) is not distributed equally across his or her alters. There appear to be sharp, consistent breakpoints in an ego's level of investment in his or her alters, such that our social networks are composed of a series of layers, with each successive layer containing approximately three times the number of alters in the previous layer (i.e., 5, 15, 45, ~150), and with relationships in each successive layer characterized by decreasing levels of intimacy and frequency of interaction (Dunbar, 2008). Evidence for this hierarchical structure has been found across diverse cultural contexts (e.g., industrial and hunter-gatherer societies) and in both online and face-to-face networks (Dunbar et al., 2015; Dunbar & Spoors, 1995; Hamilton et al., 2007; Hill & Dunbar, 2003; Zhou et al., 2005). It is possible that universal and biologically predisposed limits on our social cognitive abilities constrain not only the size of our personal social (p. 508) networks but also the distribution of tie strength within them. For instance, for each individual with whom one maintains a strong social tie, one must maintain an exceptionally comprehensive set of memories (e.g., intimate details about that person and the relationships with oneself and others). Cross-cultural consistency in the number of relationships within each concentric "layer" of one's personal network may reflect limitations on the capacity to remember and manage specific relationship information (Sutcliffe et al., 2012; Zhou et al., 2005). In the same vein, it has even been suggested that the innermost circle of one's social network is limited to an average of five individuals because humans, on average, can only simultaneously represent the mental states of five individuals (Stiller & Dunbar, 2007). Alternatively, it is possible that human social networks evince a universal "layered" structure across cultures and contexts because of constraints on the amount of time required to forge and maintain a bond of a given strength. Furthering our understanding of precisely how the processing power of the human brain constrains the size and structure of the social networks that we inhabit is a promising avenue for future research.

How Social Networks Shape the Brain

An intriguing new line of research suggests that just as biologically predisposed characteristics of brain structure and function shape our social networks, our social networks themselves can alter our brains. Indeed, recent evidence of the brain's neuroplasticity has overturned the prior scientific consensus that the brain, once developed, remains largely static throughout adulthood (Pascual-Leone et al., 2005). The prevailing view now holds that brain structure and function remain changeable in response to experience throughout the life course. But very little research to date has examined how the brain adapts in response to the social networks within which we are embedded.

When relating brain structure to sociality in humans, it is often difficult to ascertain the direction of causality in the relationship between neural and social network variables: do people whose brains are already especially well suited to advanced social cognition go on to forge more social connections, or do the cognitive demands of managing a larger number of social relationships engender changes in the structure and function of brain regions involved in social cognition? The answer is very likely that both phenomena occur,

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given that many aspects of social network position appear to be heritable (Fowler, Dawes, & Christakis, 2009) and given the large and growing body of evidence for neuroplasticity (C. A. Nelson, 1999). However, because researchers lack control of human research participants' social context, until recently, there was no evidence that individuals' social networks can shape the structure and function of their brains.

Fortunately, laboratory studies of our close primate relatives provide one way to address this issue. In a landmark study, Sallet et al. (2011) assessed the relationship between social network size and brain structure in adult rhesus macaques that were randomly assigned to live in social groups of varying sizes in a research colony. Living in larger social groups caused the macaques to develop more gray matter (i.e., more neural cell bodies) in areas of the frontal and temporal lobes known to be involved in social and emotional processing (e.g., superior temporal sulcus, temporal pole, amygdala, rostral prefrontal cortex), and also caused increased functional coupling (i.e., connectivity) between these brain regions, as (p. 509) measured by correlations of fMRI time series across brain regions. In other words, manipulating social network size exerted a causal effect on the structure and functional response profile of brain regions involved in social and emotional processing.

Thus, the structure and function of brain regions implicated in navigating the social environment, rather than being fixed or purely genetically predetermined, appear to remain labile even into adulthood. Observational evidence in humans appears to be consistent with the results of the macaque research. One study showed that relative to bus drivers, who repeatedly drive a fixed route, London taxi drivers, who must learn several thousand streets to successfully navigate the city, have increased gray matter volume in a brain region involved in encoding mental maps of space, the posterior hippocampus, and the volume of this brain structure is positively correlated with years of taxi-driving experience (Maguire, Woollett, & Spiers, 2006). Thus, increased experience with mentally representing and reasoning about complex maps of space (i.e., engaging in expert navigation) increases gray matter volume in a brain region supporting spatial navigation. In the same way, inhabiting a complex social environment (e.g., being embedded in a larger social group) may demand a significant degree of expert social cognition, thereby shaping the structure and function of brain regions supporting the underlying mental processes.

In addition to their importance to furthering our understanding of the relationship between brain structure and the social environment, these findings have several practical implications. For example, many clinical disorders associated with alterations in social engagement (e.g., depression, autism) are also associated with neuroanatomical differences (e.g., cortical thinning) in brain regions involved in social cognition and emotion regulation (Hadjikhani et al., 2005). If the complexity of one's social environment exerts a causal effect on the structure of brain regions involved in social and emotional processing, then relationships between the structure of these brain regions and clinical disorders characterized by altered social interactions may at least partially reflect the consequences, rather than the causes, of concomitant alterations in social functioning.

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The finding that social network size shapes brain structure also has important implications for efforts to identify potential risk factors for, and protective factors against, cognitive decline in older adults. The same brain regions (e.g., prefrontal cortex) that increase in volume to support navigating large social networks (Sallet et al., 2011) also support more general high-level cognitive functions, such as working memory, planning, attention, and language. This has led some researchers to suggest that maintaining a high level of social engagement is analogous to "exercise" for these brain structures, which may provide some degree of protection against the functional impairments associated with normal aging and with the onset of neurodegenerative diseases (Wald, 2016). Consistent with such speculation, longitudinal studies have found evidence that maintaining an extensive social network protects older individuals against the development of dementia (Fratiglioni et al., 2000), and against memory loss more generally (Ertel, Glymour, & Berkman, 2008). Relatedly, while cognitive degeneration and old age typically entail decreased long-distance connectivity between brain regions, a recent study demonstrated that greater social network embeddedness is associated with higher levels of long-distance brain connectivity in older adults (Joo et al., 2017). The relationship between social engagement and cognitive function is not limited to older adults; recent evidence also points to associations between cognitive abilities (e.g., memory, executive functioning) and the size of one's social network among adults ranging in age from 35 to 85 (Seeman et al., 2011). In addition, a recent study found (p. 510) that older adults (i.e., 80 years of age on average) who participated in a social engagement intervention consisting of daily, 30-minute web-enabled face-to-face conversations improved on tests of memory and executive function over a six-week period (Dodge et al., 2015). Thus, mounting evidence suggests that social engagement, like cognitive and physical exercise, can aid individuals in staving off the cognitive decline associated with aging. Interestingly, socially focused interventions have been shown to have very high adherence rates (Dodge et al., 2015), possibly because individuals tend to view them as less effortful or aversive than interventions involving cognitive training or physical exercise. Given that social interactions tend to be relatively effortless and enjoyable, encouraging individuals to maintain social ties throughout the lifespan is a promising way to promote healthy brain aging.

Summary

Human cognition, behavior, success, hardship, and opportunity are all embedded within the social networks that we build and inhabit. Characteristics of our own relationships in these groups, such as their nature and intimacy, have wide-ranging effects on how we interact with one another. The relationships that shape our social behavior are not limited to our direct social ties, but also include the webs of contacts possessed by each of our interaction partners. Researchers are only beginning to understand how our brains track and encode information about the complex webs of social relationships that we inhabit and how this information is used to shape subsequent mental processing and behavior. We are also only in the early stages of understanding how the evolved structure and function of the human brain impacts how we construct and navigate our social networks and how the social networks we inhabit influence brain structure and function. An exciting

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new body of interdisciplinary research is beginning to shed light on questions central to our understanding of a fundamental facet of human nature: our sociality. Psychologists are realizing that a deep understanding of the mind requires understanding human connectedness. Conversely, social network analysis can benefit from understanding how brain function constrains and shapes that connectedness.

Research in cognitive neuroscience and psychology has provided considerable insight into the processes underlying individual human thought and action. Yet, this research has often stripped human perception and behavior of much of its social nature, either studying individuals in isolation or studying them in artificial social contexts. Although these paradigms can afford experimental control and robust results, their ability to enhance our understanding of real-world social behavior is in many ways limited. Contrastingly, parallel research on social networks consistently demonstrates that both direct and indirect social ties powerfully shape our behavior (Christakis & Fowler, 2009) and, increasingly, that the behavior of humans and other social animals is informed by our knowledge of third-party relationships and by the structure of the social networks we inhabit (e.g., Ellwardt et al., 2012; Ferrin et al., 2006; Fuong, Maldonado-Chaparro, & Blumstein, 2015). By combining these two separate fields, we can begin to understand how larger-scale, emergent social phenomena arise from the constraints and connectivity of individual minds.

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