HOW WE CONNECT: NEURAL MECHANISMS UNDERPINNING HUMAN SOCIAL NETWORKS

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Abstract

One of the most distinctive aspects of humans as a species is our propensity to form complex social networks made up of intense, non-reproductive bonds with non-kin. Navigating these networks presents a considerable cognitive challenge that is thought to have comprised a driving force in human brain evolution. Yet, little is known about how the human brain understands and influences the vast social networks in which it is embedded. This dissertation combines methodologies from cognitive neuroscience and social network research to investigate how social network structure is encoded in the brain and the cognitive consequences of this structure.

Study 1 investigates the neural encoding of social distance and its relationship to other domains of knowledge, and provides evidence for a shared neural code signaling distance from the self in social ties, space, and time. Study 2 tests for the spontaneous encoding of social relationship knowledge. The results of this study suggest that social network position characteristics based on direct relationships, bonds between third parties, and aspects of the broader network topology are accurately perceived and automatically encoded when familiar individuals encounter one another. In addition, participants who tend to regulate their behavior and self-presentation more to suit their current social context in everyday life spontaneously encoded more social information when encountering familiar others, consistent with the notion that automatically activating social knowledge serves to prepare perceivers for appropriate and beneficial interactions. Study 3 tested the hypothesis that human social networks exhibit assortativity in terms of how their members perceive, interpret, and respond to the environment. Consistent with this hypothesis, inter-subject similarities of neural responses during free viewing of naturalistic stimuli accurately predicted whether or not two individuals were friends, as well as the geodesic social distance between those individuals. Neural response similarity decreased with social distance up to three degrees of separation in the social network.

Human cognition is embedded within social networks. Although these fields of research have progressed largely independently, the current findings demonstrate that integrating the systematic study of real-world social relationships and cognitive neuroscience can provide insight into how we perceive and shape our social world.

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General Introduction

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 (Burt & Knez, 1995; Ferrin, Dirks, & Shah, 2006). In addition to the impact of both direct and indirect social ties on how our interactions unfold, our embeddedness within social networks interacts with individual human tendencies toward mimicry and conformity, causing norms and behaviors to percolate through social groups, and extending the reach of an individual's influence well beyond his or her immediate social environment (Christakis & Fowler, 2013).

In these and other ways, structural characteristics of the social groups that we inhabit combine synergistically with individual social cognitive processes to shape human behavior. Yet, research on the structure of social groups and research on individual social cognition have progressed largely independently. This dissertation combines theory and methodology from social psychology, cognitive neuroscience, and social network analysis in order to investigate how the human brain encodes information about real-world social relationships, and to probe the cognitive consequences of the positions that we inhabit in our social networks.

Background

The centrality of social relationships to human life

Whereas members of many other species have only aggressive and reproductive encounters with non-kin conspecifics, humans spend their lives almost entirely in the company of unrelated others. This feature of human social life is presumed to reflect an evolutionary advantage: Coordinating with otherwise would-be strangers enhanced our ancestors' abilities to survive, thrive, and reproduce (Brent, Chang, Gariépy, & Platt, 2014; Seyfarth & Cheney, 2012). Social bonds remain critical to health and happiness in contemporary society, comprising a dominant influence on our emotional lives (Baumeister & Leary, 1995; Cacioppo & Hawkley, 2003; Diener & Seligman, 2002; Jaremka, Gabriel, & Carvallo, 2011). For example, when asked to name the most positive and negative emotional events that they have ever experienced, people tend to cite events marking the strengthening or dissolution of social bonds, respectively (Jaremka et al., 2011).

Human sociality is also distinctive in terms of its complexity. Whereas members of many other intensely social species enact social behavior in fluid, anonymous aggregations, such as flocks, schools, herds or swarms, in human social groups, each individual tends to have large numbers of differentiated and enduring social relationships (Shultz & Dunbar, 2010). A growing body of evidence demonstrates that relationships in these groups – both our own social ties and those between third parties – have wide-ranging influences on human cognition and behavior.

The impact of direct social ties on human cognition and behavior

Differential responses to strangers and personally familiar others. A growing body of literature on social familiarity suggests marked differences in how humans respond to strangers and personally familiar others. Social familiarity appears to modulate reactions to others’ pain, including the vicarious experience of that pain (Martin et al., 2015), and to dampen emotional responses to disgust-eliciting material emanating from other people (e.g., bodily fluids), as indexed by physiological responses, behavior, and self-report (Curtis, Aunger, & Rabie, 2004; Peng, Chang, & Zhou, 2013). In addition, merely viewing familiar faces engages brain systems involved in affective processing and theory of mind, possibly reflecting emotional responses and the activation of person knowledge (e.g., traits, intentions, attitudes), respectively; the latter might assist the perceiver to appropriately “shift gears,” for instance, depending on if he has encountered an employer or a close friend (Gobbini & Haxby, 2007). In addition, familiar others’ faces are detected more rapidly than those of strangers (Gobbini et al., 2013), and visual cues to the direction of their attention (e.g., eye gaze, head angle) are both detected faster (Visconti di Oleggio Castello, Guntupalli, Yang, & Gobbini, 2014) and used more readily to direct one’s own attention (Deaner, Shepherd, & Platt, 2007) compared to cues to the direction of strangers’ attention. Thus, social familiarity has wide-ranging effects on how cognition and behavior unfold in everyday life.

Moving beyond “friend vs. stranger.” Perhaps reflecting the logistical challenges of bringing real-world social relationships into the lab, little psychological research has extended the study of how personal relationships impact human cognition and behavior beyond the distinction between familiar others and strangers. Psychological experiments on social behavior tend to involve the creation of anonymous or artificial social contexts (e.g., experimentally assigned roles; minimal groups paradigms); when psychology and neuroimaging experiments do take into account real-world social identities and relationships, they tend to only consider broad demographic categories and group affiliations (Huettel & Kranton, 2012). Therefore, with few exceptions (e.g., mother-infant bonds, Case, Repacholi, & Stevenson, 2006; Leibenluft, Gobbini, Harrison, & Haxby, 2004; Nelson & Panksepp, 1998), very little is known about how the human brain encodes information about the nature and quality of our relationships with personally familiar others, or how this information influences cognition and behavior. Yet, given that many of our interactions take place with people who are already familiar to us (Sun, Axhausen, Lee, & Huang, 2013), it seems likely that these interactions are influenced by more nuanced social relationship information than the simple distinction between those whom we have encountered before and those whom we have not.

Research documenting the behavior of other group-living primates suggests possible ways in which social relationship information, within the spectrum of personally familiar individuals, might impact human behavior. For example, when competing for access to valued resources, macaques show greater tolerance toward close associates than they do toward other (also personally familiar) group members (De Waal, 1991). In addition, macaques more readily respond to social cues emanating from individuals with whom they have a strong positive social bond compared with cues communicated by other (also personally familiar) group members (Micheletta & Waller, 2012). Better understanding how human cognition and behavior is influenced by the nature and intimacy of our relationships with personally familiar others comprises an important, but understudied, topic for future research.

The impact of indirect social ties on cognition and behavior

In addition to our direct social ties with others, humans are among the handful of species whose members track and encode third party relationships and routinely use this information to shape our behavior (Brent, 2015; Massen, Pašukonis, Schmidt, & Bugnyar, 2014; Massen, Szipl, Spreafico, & Bugnyar, 2014). Ties between third parties influence the reputation costs and benefits of our actions, and the degree to which individuals attain power and status within their social groups (Burt & Knez, 1995; Ellwardt, Labianca, & Wittek, 2012; Ferrin et al., 2006). In addition, due to our embeddedness within social networks and our fundamental tendencies to mimic the behaviors and "catch" the internal states of those around us (Chartrand & Bargh, 1999; Hatfield, Cacioppo, & Rapson, 1993), each individual's thoughts, feelings, and actions influence, and are influenced by, people outside of his or her immediate social context (Christakis & Fowler, 2013).

Indirect relationships and reputation management. Roughly two-thirds of human conversations are centered on gossip about third parties, which allows information about interactions and relationships between third parties to percolate efficiently and seemingly effortlessly throughout social groups, and causes individuals' knowledge about other group members to extend well beyond what is possible for them to observe first-hand (Couzin & Laidre, 2009; Mullins, Whitehouse, & Atkinson, 2013). Managing our own reputations and monitoring those of others figures prominently in modern human life, and has even been suggested as a pressure that drove the evolution of language (Knight, Studdert-Kennedy, & Hurford, 2000; Tennie, Frith, & Frith, 2010). Humans routinely use knowledge about third party relationships – e.g., who is friends with whom – and patterns of social ties – e.g., who has many friends – to manage our own reputations and track those of others. For example, cooperation and trust between otherwise unfamiliar individuals are facilitated when those individuals share a mutual friend (Burt & Knez, 1995; Ferrin et al., 2006), presumably because the shared social tie heightens the potential reputation costs and benefits posed by the interaction. Indeed, many everyday behaviors, like predicting the potential consequences of a recent social misstep, determining how to seek or spread a piece of information, and deciding whether or not to trust someone, all depend on the cognitive 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.

Indirect relationships and social status. In all human societies, there exist differences in individuals' capacities to influence group decisions, resource allocation, and the development and resolution of conflicts; individuals who have comparatively more influence on such phenomena are referred to as having higher social status (J. Berger, Cohen, & Zelditch, 1972). Given their heightened behavioral relevance to other group members, perceivers are compelled to attend to and monitor the actions and apparent internal states of high status individuals (Dalmaso, Galfano, Coricelli, & Castelli, 2014; Dalmaso, Pavan, Castelli, & Galfano, 2012; Deaner, Khera, & Platt, 2005; Shepherd, Deaner, & Platt, 2006). Most psychological and neuroscientific research on the perception, antecedents, and consequences of social status in humans has centered on status conferred by physical dominance and, to a lesser degree, prestige (i.e., respect based on expertise, Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013). However, as the successful navigation of everyday life depends increasingly on affiliative social relationships and reputation management (Tennie et al., 2010), rather than the need to display or avoid physical violence (Pinker, 2011), for modern humans, the influence and support conferred by an individual's social connections (e.g., being connected to influential individuals) is likely a highly behaviorally relevant facet of social status. Whereas status conferred by physical dominance and prestige can be inferred based on observing a given individual in isolation (e.g., facial width-to-height ratio or masculinity, Jones et al., 2010), understanding social status based on interpersonal connections demands that perceivers track and encode relationships between third parties. 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 et al., 2012), but 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 (Cheng et al., 2013).

Indirect relationships and interpersonal influence. A considerable body of psychological research has demonstrated that humans are strongly influenced by the thoughts, feelings, and actions of those around us. For example, aspects of humans' empathic abilities are thought to arise from very basic and evolutionarily ancient mechanisms for emotional contagion, through which we tend to adopt the perceived emotional states of others (de Waal, 2007; Hatfield et al., 1993). Similarly, people tend to unintentionally mimic the mannerisms and behaviors of their interaction partners (Chartrand & Bargh, 1999). Social psychologists have tended to study interpersonal influence within the context of an individual’s immediate environment, often employing experimental paradigms involving social interactions within dyads (i.e., networks consisting of two individuals).

A growing, complementary body of research on the spread of behaviors, attitudes, and emotions in human social networks demonstrates that the influence exerted and experienced by any given individual extends well beyond those with whom he or she interacts directly (Christakis & Fowler, 2009, 2013). Such research has employed longitudinal analyses and experimental manipulations of social networks to examine the spread of phenomena as diverse as cooperation, tastes in popular media, divorce, happiness, obesity, alcohol and drug use, sleeping behavior, and political mobilization through social groups (for a recent review, see Christakis & Fowler, 2013).

For a wide-ranging set of behaviors, attitudes, and emotions, interpersonal influence appears to spread throughout social networks, and this spread exhibits a striking empirical regularity that has been termed the “three degrees of influence rule” (Christakis & Fowler, 2009). Specifically, phenomena tend to spread up to three degrees of separation in human social networks, such that one’s behavior influences, and is influenced by, one’s friends, friends of one’s friends, and friends of one’s friends’ friends. For example, an individual’s risk of being obese increases by 45% if she has an obese friend, by 20% if she has a friend who has an obese friend, and by 10% if there is an obese individual three degrees away from her in a social network; beyond four degrees of separation, there ceases to be a statistically significant relationship between two individuals' probabilities of being obese (Christakis & Fowler, 2007). Thus, because humans tend to imitate and influence one another, and because we are connected to one another, our health, attitudes, cognitions, and emotions are also connected, and depend on the behaviors of people with whom we might never interact directly.

The current research

The research discussed above highlights the centrality of social relationships to human life. The intense and varied relationships that comprise human social networks exert wide-ranging effects on how the individuals within them think, feel, and behave. However, research on social networks and social cognition has largely been siloed. Psychologists and cognitive neuroscientists tend to investigate individual cognition without a deep understanding of how people are influenced by the larger, real life networks in which they are embedded: Social cognition experiments tend to create artificial, anonymous social contexts or consider only very limited social relationship information, such as group affiliation or distinctions between friends and strangers (Huettel & Kranton, 2012). On the other hand, social network researchers tend to investigate the structure and dynamics of networks, oftentimes without a deep understanding of the workings of the minds within them. Therefore, very little is known about how the human brain encodes information about personally familiar others' relationships with ourselves and with third parties, or how this information influences cognition and behavior.

This dissertation seeks to bridge this gap in understanding by investigating how the brain encodes social relationship information about familiar individuals (Study 1), by testing if social relationship knowledge is spontaneously encoded when encountering people whom we know (Study 2), and by testing if individuals tend to respond to their surroundings exceptionally similarly to others who are close to them in their real-world social networks (Study 3).

Study 1 investigates the neural mechanisms involved in encoding the strength of one's social tie with a personally familiar individual. More specifically, this experiment tests the prediction that a common neural mechanism is involved in computing distance from oneself in social ties, distance from one's current location in space, and temporal distance from the present. The existence of such an encoding would be consistent with suggestions that any kind of egocentric distance information has common implications for downstream processing and behavior (Trope & Liberman, 2010).

Study 2 combines social network analysis with multi-voxel pattern analysis of functional magnetic resonance imaging (fMRI) data to test if distances in social ties, as well as other potentially behaviorally relevant aspects of social network position, are spontaneously encoded when encountering personally familiar others, and explores the brain systems involved in this encoding. Taken together, Studies 1 and 2 seek to better understand the neural mechanisms involved in encoding social relationship information, and how this information may impact the mental processes that are automatically engaged when encountering others.

Study 3 combines social network analysis with the analysis of inter-subject correlations of fMRI data (Hasson, Malach, & Heeger, 2010) while viewing naturalistic, dynamic stimuli (e.g., film and television clips). The purpose of Study 3 is to test whether or not brain responses are more similar between individuals who are closer to one another in their social network than between individuals who are comparatively more distant from one another in the same social network. Similar neural responses suggest similar mental inferences, shared understanding, and common patterns of attentional allocation across individuals (Ames, Honey, Chow, Todorov, & Hasson, 2014; Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Hasson et al., 2010). Thus, assortativity in neural responses to naturalistic stimuli would suggest that our mental reactions to and interpretations of the world around us are more similar to those who are closer to us in our social networks.

There is a noted dearth of research examining how patterns of social network connections impact individual cognition (Burt, Kilduff, & Tasselli, 2013). By combining the systematic characterization of real-world social relationships with methods for assessing information processing within individual brains, the proposed research seeks to better understand interactions between human social networks and human cognition.

Study 1

A Common Cortical Metric for Social, Spatial, and Temporal Distance

Converging theories from cognitive linguistics, cognitive neuroscience, and social psychology suggest that different domains of psychological distance are encoded similarly. Conceptual Metaphor Theory (CMT, Lakoff & Johnson, 2008) suggests that we use spatial language to describe social and temporal relationships (e.g., “close friend,” “distant future”) 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., temporal, social) frames of reference (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 social, spatial, and temporal distance. The degree to which information is removed from our current experience in time, space or the extent to which it refers to someone else carries a common meaning with important implications for the perceiver: proximity for action, and thus, how concretely or abstractly it should be construed (Liberman & Trope, 2008; Vallacher & Wegner, 1985).

The common meaning shared across psychological distance domains is accessed automatically. Words characterizing shorter social and temporal distances are automatically associated with closer spatial locations, whereas words referring to increased social and temporal distances are associated with farther locations (Bar-Anan, Liberman, Trope, & Algom, 2007). Different domains of psychological distance also impact a range of mental phenomena similarly, from visual perception (Förster, Friedman, & Liberman, 2004) to humor (McGraw, Warren, Williams, & Leonard, 2012) and moral judgment (Eyal, Liberman, & Trope, 2008). Additionally, the capacity to mentally traverse different domains of distance follows a similar developmental trajectory (Suddendorf & Corballis, 2007). Thus, converging evidence is consistent with the possibility of a common mechanism for representing different domains of egocentric distance.

If different domains of egocentric distance are conflated at some level of processing, relatively near or far distances should be represented similarly at that level of processing, irrespective of domain. Previous fMRI studies suggest that judging and traversing spatial, social, and temporal distances recruit overlapping brain regions (Buckner & Carroll, 2007; Spreng, Mar, & Kim, 2009; Tamir & Mitchell, 2011; Yamakawa, Kanai, Matsumura, & Naito, 2009; Yamazaki et al., 2009). However, past studies have used univariate analyses that spatially smooth and average data to identify areas involved in tasks (Friston et al., 1995). Importantly, a common encoding cannot be inferred from independent univariate fMRI contrasts. Both a shared encoding mechanism and nearby but distinct codes would yield overlapping results (Peelen & Downing, 2007).

To determine if different domains of egocentric distance are represented by a common code, we used information-based searchlight mapping (Kriegeskorte, Goebel, & Bandettini, 2006), which provides a data-driven method of continuously mapping local information content throughout the brain using multi-voxel pattern analysis (Norman, Polyn, Detre, & Haxby, 2006). Cross-domain searchlights tested if decision boundaries that distinguish local response patterns based on distance within one domain generalize to other domains. Additionally, we combined representational similarity analysis

(Kriegeskorte, Mur, & Bandettini, 2008) with searchlight mapping to search for regions whose representational content reflect subjective ratings of psychological distance.

Methods

Participants

Fifteen participants (10 female, ages 20–28 years, mean age = 24.6 years) completed Study 1. All participants were right-handed, fluent in English and had normal or corrected-to-normal vision. Participants provided informed consent and the experiment was approved by the Dartmouth College Committee for the Protection of Human Subjects.

fMRI paradigm

While being scanned in a 3T Philips scanner, participants saw Spatial, Temporal, and Social distance trials, consisting of objects photographed at different egocentric distances (Figure 1A), words referring to the immediate or more remote future (Figure 1B), and names and photographs of familiar others and acquaintances (Figure 1C), respectively. In order to make distances meaningfully comparable across domains, participants were asked to compare each stimulus to a reference point or Anchor from the same distance domain. More specifically, each trial began with a briefly presented (500 ms) Anchor from the same stimulus domain as the Target stimulus that was presented for the majority of the trial (1500 ms). Participants were asked to think about how much closer or farther, more or less familiar, or sooner or later the Target was relative to the Anchor during Spatial, Social, and Temporal distance trials, respectively. Different trial types within a domain (e.g., Closer and Farther Spatial distance trials) contained the same stimuli in reverse order such that the direction (i.e., either toward or away from the self) of relative egocentric distance changes over time, but not the magnitude of these changes (e.g., 250 cm for Spatial distance trials), differed between trial types (e.g., Closer vs. Farther) within each distance domain (e.g., Spatial distance). Thus, in effect, the progression of stimuli over time within each trial was analogous to “movement” by an equivalent amount either toward or away from the participant in a spatial, temporal or social frame of reference.

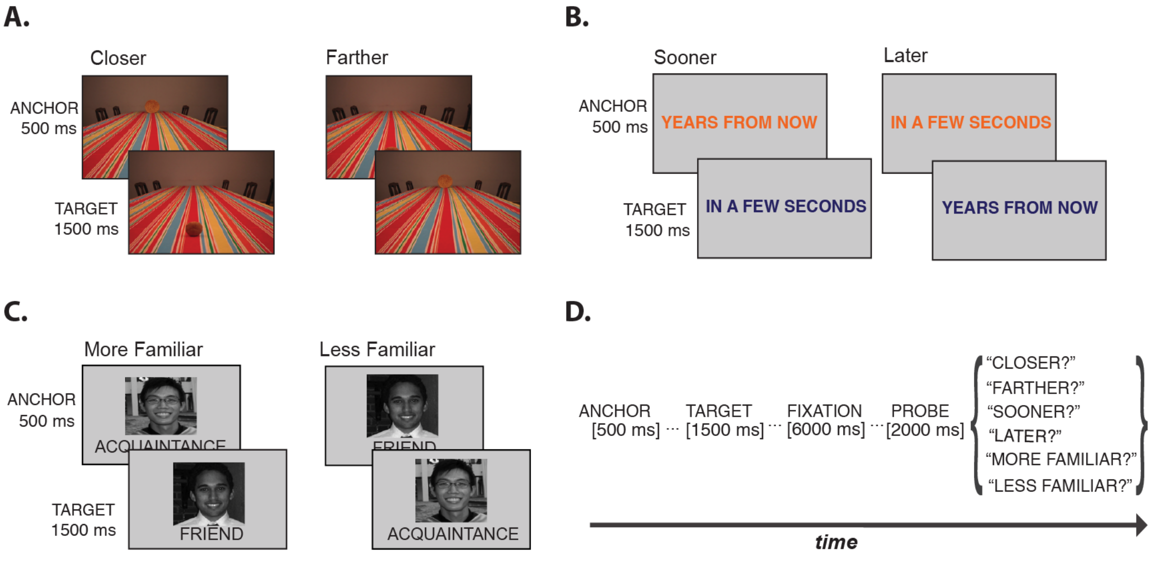


Figure 1. Experimental paradigm used in Study 1. (A-C) Examples of each trial type. Within each trial, stimulus change over time was analogous to “movement” either toward or away from the observer in a spatial, temporal or social frame of reference. **(A)** Spatial distance trials consisted of household objects photographed at different egocentric distances. **(B)** Temporal distance trials consisted of phrases referring to the immediate or more remote future. **(C)** Social distance stimuli consisted of the names and photographs of four friends and four acquaintances of each participant. Experimental stimuli contained individuals’ actual first and last names rather than the words “friend” and “acquaintance.” **(D)** Generic trial schematic. Within each domain, two possible probes varied randomly across trials (e.g., either “Sooner?” or “Later?” for Temporal distance trials). Participants responded “Yes” or “No” with a button press. Each trial was followed by an additional 6 s of fixation prior to the beginning of the next trial.

Trials were presented according to a slow event-related design. Each trial was followed by 6 s of fixation, then a probe (e.g., “Later?”) that was intended to ensure that participants were comparing the Anchor and Target stimuli in the intended manner (i.e., in terms of relative egocentric distance and not other aspects of the stimuli). Participants responded “Yes” or “No” to the probe with a Lumina response pad regarding, in this example (“Later?”), if the Target phrase referred to a point in time later in the future than the Anchor phrase. All probes were presented in black 96-point font. Each probe was followed by an additional 6 s of fixation before the beginning of the next trial. Participants used the left response button to indicate “Yes” and the right response button to indicate “No.” Within each domain, there were two possible probes that could follow each trial (i.e., either “Sooner?” or “Later?” for Temporal distance trials; either “More familiar?” or “Less familiar?” for Social distance trials; either “Closer?” or “Farther?” for Spatial distance trials). Probes were randomized across trials so that participants could not anticipate the correct response or formulate an appropriate motor plan until after each trial had ended. More specifically, for trials from each distance domain, because participants did not know which of the two possible probes would appear until several seconds after the trial had ended, they could not anticipate the correct button response (i.e., a left button press for “Yes” or a right button press for “No”) during trials. This approach also ensured that left and right response buttons were equally likely to signify relatively near and far egocentric distances within each tested distance domain throughout the experiment.

Each participant’s stimulus set consisted of pictures of four friends, four acquaintances, four relatively close objects and four relatively distant objects, as well as four verbal phrases referring to the immediate future and four verbal phrases referring to the more remote future. All four friend pictures preceded and followed all four acquaintance pictures an equal number of times during Social distance trials, all four photographs of close objects preceded and followed all four photographs of distant objects an equal number of times during Spatial distance trials, and all four phrases referring to the immediate future preceded and followed all four phrases referring to the remote future an equal number of times during Temporal distance trials. This yielded a total of 96 unique trials per participant. Each run consisted of 36 trials (six instances of each of six trial types: Closer, Farther, Sooner, Later, More familiar, Less familiar). Within runs, trials were presented in a pseudo-random order to approximate second-order counterbalancing of trial type (i.e., of Closer, Farther, Sooner, Later, More familiar, and Less familiar trials). Counterbalanced trial type orders were filled with specific trials by drawing randomly without replacement from lists of all trials belonging to each trial type, with each trial repeated three times. Thus, each unique trial was repeated three times over the course of eight functional runs.

Stimuli

Spatial distance stimuli. All stimuli and probes were presented against a light gray 1280 x 600 pixel background (Figure 1A). Spatial distance stimuli came from a pre-existing stimulus set depicting common household objects either 50 or 300 cm away amid a naturalistic background containing strong monocular depth cues (Berryhill & Olson, 2009). These stimuli were previously tested to ensure that viewers perceive them to be at the intended egocentric distances, and have previously been demonstrated to automatically elicit egocentric distance processing (Berryhill & Olson, 2009). Retinal subtense was approximately consistent across near and far pictures, as stimuli were drawn from four image pairs that depicted similar objects of different sizes (e.g., circular breads – a mini pita and a pizza shell), with the larger and smaller objects photographed at distances of 300 and 50 cm, respectively. The images used in the current study depicted spoons, round breads, beverage pitchers and round yellow fruits.

Temporal distance stimuli. Temporal distance stimuli consisted of verbal phrases referring to the immediate or more remote future. Previous work suggests that words describing relatively proximal and distal temporal entities are automatically processed in terms of egocentric psychological distance (Bar-Anan, Liberman, & Trope, 2006; Bar-Anan et al., 2007). To ensure readability of these quickly transitioning stimuli, the Anchor and Target phrases were presented in different font colors: the Anchor phrase was always presented in orange text, and the Target phrase was always presented in blue text (Figure 1B). Phrases were presented in 96-point font. Remote future phrases were: “A YEAR FROM NOW”; “DECADES FROM NOW”; “A MONTH FROM NOW”; “IN A FEW YEARS.” Immediate future phrases were: “IN A FEW SECONDS”; “MOMENTS FROM NOW”; “IN AN INSTANT”; “A MINUTE FROM NOW.” Wilcoxon rank-sum tests (function wilcox.test in R, R Core Development Team, 2013) indicated that word counts in immediate (median = 3.50) and remote (median = 4.00) future phrases did not significantly differ, $W = 10$, $p = 0.61$, $r = 0.18$. Letter counts also did not significantly differ between immediate (median = 13.50) and remote (median = 12.50) future phrases, $W = 6$, $p = 0.65$, $r = 0.16$. Additionally, the number of plural nouns was exactly matched between the two trial types (i.e., exactly two of the immediate future phrases and two of the remote future phrases contained one plural noun). The frequency of all phrases and their constituent words were obtained from the Corpus of Contemporary American English (COCA, Davies, 2010), a 450 million-word corpus of spoken English, fiction, newspapers, popular magazines and academic journals from 1990-2012. The frequencies of words used in the immediate (median = 1,106,896) and remote (median = 718,023) future phrases did not significantly differ, $W = 116.5$, $p = 0.61$, $r = 0.09$, nor did the frequencies of the exact immediate (median = 102) and remote (median = 291.5) future phrases used, $W = 10$, $p = 0.69$, $r = 0.14$.

Social distance stimuli. Prior to scanning, participants provided names and front-facing photographs of four people whom they know well and with whom they have a strong personal relationship, and of four people whom they know well but with whom they do not have a strong friendship or interpersonal connection. Familiar and unfamiliar others were matched for gender, race, age, and facial expression (which was either neutral or slightly positive). These photographs were cropped to include only the shoulders, neck and head, and grey-scaled. Photographs were presented at a size of 400 pixels x 400 pixels directly above the individual's full name in black 72-point font (Figure 1C).

Post-scan questionnaire

After scanning, 12 participants completed a paper-and-pencil questionnaire consisting of behavioral ratings of psychological distance between stimuli. Stimuli were grouped by domain (Social, Spatial, Temporal); domain order was counterbalanced across participants. All stimulus pairs were presented with the psychologically "closer" stimulus on the left of the psychologically “farther” stimulus. Participants rated the difference in psychological distance between the two stimuli on a seven-point scale between one (equally soon/close/familiar) and seven (the image/phrase on the left is a great deal sooner/closer/more familiar). Distance ratings for trials containing the same stimulus pairs in reverse order were assigned the same numerical ratings multiplied by negative one. One participant completed both this questionnaire and a questionnaire with stimuli presented in reverse order that asked for ratings between one (equally late/far/familiar) and seven (the image/phrase on the left is a great deal later/farther/less familiar). Ratings did not differ between the two versions of the questionnaire.

Image acquisition and pre-processing

Image acquisition. Participants were scanned at the Dartmouth Brain Imaging Center using a 3T Philips Achieva Intera scanner with a 32-channel head coil. An echo-planar sequence (35 ms TE; 2000 ms TR; 3.0 mm x 3 .0 mm x 3.0 mm resolution) was used to acquire functional images, with 291 dynamic scans per run, for a total acquisition time of 582 s per run. A high-resolution T1-weighted anatomical scan (8200 ms TR; 3.7 ms TE; 0.938 mm x 0.938 mm x 1.0 mm resolution) was acquired at the end of the scanning session. Foam padding was placed around subjects’ heads to minimize motion.

Image preprocessing. Functional data were preprocessed and parameter estimates (βs) were obtained for each of the six trial types in each run using AFNI (Cox, 1996). Data were time-shifted to correct for interleaved slice order, and each volume was spatially registered to the volume immediately preceding the high-resolution anatomical scan. Next, data were despiked to remove transient, extreme values in the signal not attributable to biological phenomena, and spatially smoothed using a 4-mm full-width at half-maximum (FWHM) Gaussian kernel. Each voxel time series was scaled to a mean amplitude of 100. Next, parameter estimates were extracted for each voxel using the general linear model (GLM). Stimulus events were defined as the 2 s trial period beginning with the onset of the 0.5 s presentation of the Anchor and ending at the conclusion of the 1.5 s presentation of the Target, and were convolved with the standard hemodynamic response function. The GLM included six predictors, one for each trial type, and six regressors of no interest (motion parameters), resulting in an estimate of each voxel's response to each trial type within each run for use in classification analyses. For representational similarity analysis and univariate analyses, deconvolution was performed on concatenated data from all eight runs. Gray matter segmentation of each participant's anatomical image was performed using FreeSurfer (Fischl, 2012). Gray matter masks were aligned to anatomical images following anatomical images' alignment to functional data, then resampled to the resolution of the functional data.

Data analysis

Classification analysis. The spatial variability of response patterns can reveal information that distinguishes between experimental conditions, even in the absence of overall mean activation differences (Peelen & Downing, 2007). Thus, compared to univariate analyses, multi-voxel pattern analysis can be more sensitive to differences between trial types within domains (e.g., Closer vs. Farther trials). Additionally, multi-voxel pattern analysis can provide a more stringent test of whether or not common cortical mechanisms encode egocentric distance across domains, as overlapping univariate contrasts could result from a shared computational process or from the elicitation of overlapping but functionally independent population responses (Peelen & Downing, 2007). Thus, cross-domain distance decoding based on distributed patterns of fMRI responses provides a useful means of testing whether or not response patterns within a given brain region similarly distinguish between relatively near and relatively far egocentric distances across distance domains.

Six spherical searchlights (radius = 3 voxels) were moved throughout each subject's gray matter-masked data that iteratively performed cross-domain distance decoding (Figure 2) on local fMRI response patterns using PyMVPA (Hanke et al., 2009). At each searchlight center (i.e., at each voxel), a linear support vector machine (SVM) learning algorithm was trained to discriminate local distributed patterns of fMRI responses to trials from one domain (e.g., Social distance) in terms of relative psychological distance (e.g., More vs. Less familiar) within data from seven of the eight functional runs, and was tested on local response patterns corresponding to trials from another distance domain (e.g., Temporal distance) from the left-out run. In the aforementioned example, classification would be considered correct if Sooner and Later trials were classified as More familiar and Less familiar trials, respectively. For each searchlight, this procedure was repeated eight times using each run's data for testing once. Classification accuracy was averaged across data folds within each searchlight, resulting in a percent accuracy score at each voxel for each participant for each searchlight. This procedure was repeated using all possible pairwise combinations of distance domains (Social, Spatial, Temporal) to train and test the pattern classifier, yielding six accuracy maps for each participant. Each accuracy map describes how well the decision boundary that best separates response patterns according to relative egocentric distance within one distance domain generalizes to a new distance domain within a 9-mm sphere centered on each voxel. For example, the accuracy map corresponding to using Spatial distance trials as training data and Temporal distance trials as testing data describes the proportion of the time that Sooner and Later trials (i.e., the testing data) fall on the same side of the decision boundary that best separates Closer and Farther trials (i.e., the training data) as Closer trials and Farther trials do, respectively (as illustrated in Figure 2).

Percent accuracy maps resulting from cross-domain distance decoding analyses were aligned to standard space (Talairach & Tournoux, 1988) and arcsine-transformed ($y = arcsine\sqrt{x}$, where x is proportion of classifications that were correct and y is the result of the transformation) before being tested against chance across participants, as this procedure approximates a normal and homoscedastic distribution given binary data summarized as proportions (e.g., proportion of correct/incorrect classifications, Freeman & Tukey, 1950; Zar, 2010). Each set of accuracy maps was then submitted to a two-tailed one-sample t-test against the arcsine-transform of 50% correct across participants. A conjunction analysis of these six t-statistic maps was performed using a threshold of $p < .05$, false discovery rate (FDR, Benjamini & Hochberg, 1995) corrected, for each map, in order to identify regions where psychological distance could be decoded across all distance domains.

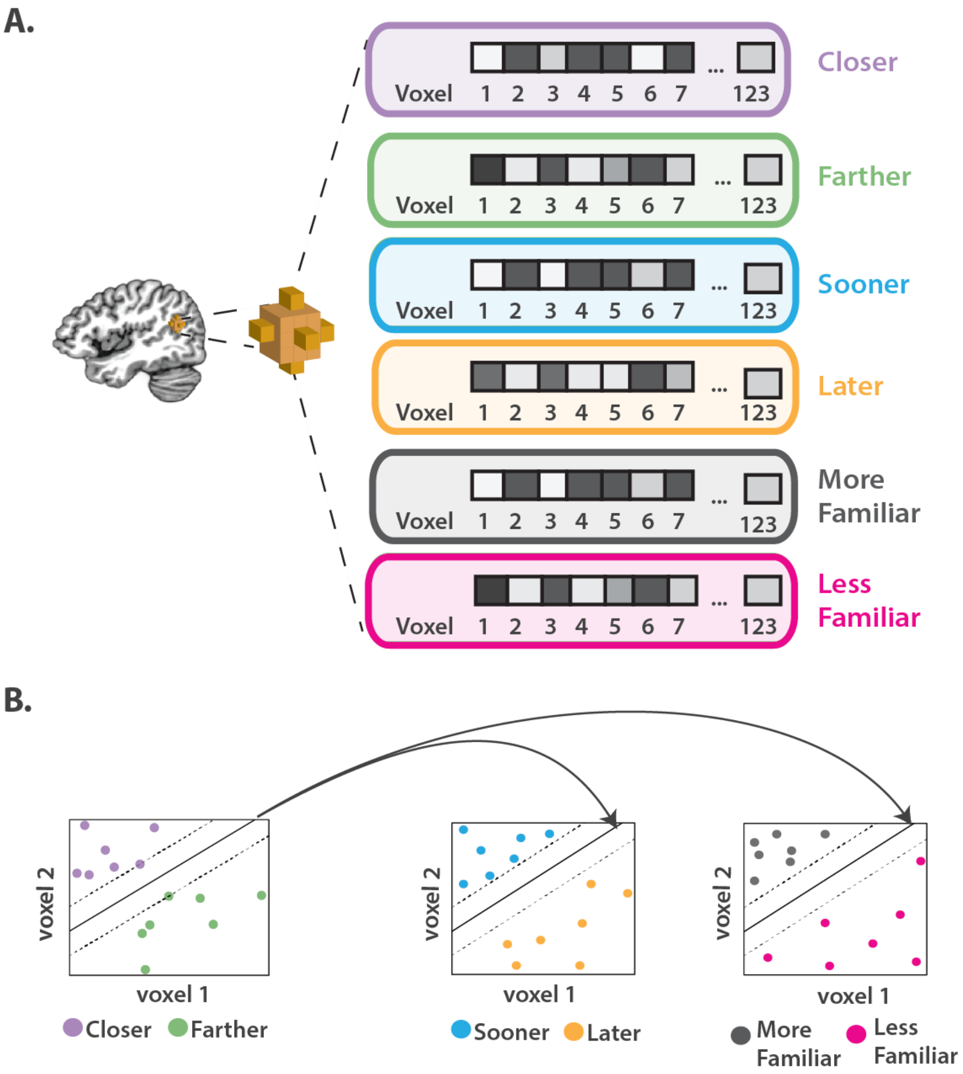


Figure 2. Classification searchlight analysis used in Study 1. (A) At each voxel, local response patterns corresponding to each condition were extracted (total searchlight area: 123 voxels). In schematic depictions of multi-voxel patterns, darker gray indicates greater fMRI responses. **(B)** A linear support vector machine learning algorithm was trained to distinguish trials from one distance domain based on the direction of the distance change, and tested on each of the remaining two distance domains independently. This procedure was repeated using all pairwise combinations of Social, Spatial and Temporal distance trials as training and testing data, resulting in six accuracy maps per participant. For ease of visualization, **(B)** depicts two-dimensional response patterns; response patterns in searchlights were 123-dimensional.

Importantly, the conjunction analysis requires above-chance distance decoding across all pairs of distance domains. It should be emphasized that for each classification searchlight, predictions were only considered correct if trials characterized by decreasing psychological distance in the test domain (e.g., More familiar trials) were classified as if they were trials characterized by decreasing psychological distance in the training domain (e.g., Sooner trials). Although distances characterizing Social and Spatial stimuli were inherently self-referential (e.g., 250 cm closer to or farther away from oneself; differences in social familiarity to oneself), Temporal distance stimuli could be compared in terms of the durations implied by the words in these phrases without reference to oneself. However, comparing stimuli in terms of magnitude without respect to distance from the self in the here and now would likely often result in erroneous predictions. For instance, More familiar (i.e., increasing familiarity) trials would be classified as if they were Later (i.e., increasing temporal "amount") trials, and vice versa, and Less familiar (i.e., decreasing familiarity) trials would be classified as if they were Sooner (i.e., decreasing temporal "amount") trials, and vice versa, which would all be considered inaccurate classifications. Thus, comparing "amounts" implied by stimuli without reference to the self would likely engender incorrect cross-domain classifications in many cases. Because the conjunction analysis requires above-chance distance decoding across all pairs of distance domains, this approach should identify areas that contain a domain-general encoding of egocentric distance.

Representational similarity analysis. A representational similarity searchlight (Kriegeskorte, 2008) was used to probe for the existence of brain regions where the similarity structure of local population responses reflected the similarity structure evinced in each participant's post-scan ratings of distance across domains (Figure 3). Following Kriegeskorte et al. (2008), at each searchlight center, a non-parametric test of representational relatedness was performed to evaluate the significance of the correlation between behavioral and neural representational dissimilarity matrices (RDMs). This procedure allows for each participant's cortex to be continuously mapped in terms of the relatedness of representations manifested in local fMRI responses and behavioral ratings. Thus, this approach provides a direct assessment of how well a participant's behavioral responses capture the information contained in the fMRI patterns within each searchlight sphere.

In general, representational similarity analysis permits the direct, quantitative comparison of data acquired using diverse methods (e.g., fMRI, behavioral questionnaires) in terms of the information that each dataset contains about a set of experimental conditions. This is possible because unlike voxel response patterns, the units of analysis used in representational similarity analysis (i.e., RDMs) are not intrinsically bound to the spatial layout of the original data. RDMs are indexed not by voxel or by time point, but by experimental condition. Each RDM contains a cell corresponding to the dissimilarity between each pair of experimental conditions (Figure 3). Representational similarity analysis is uniquely concerned with the relationships between experimental conditions, as its units of analysis (i.e., RDMs) only contain information about the dissimilarities between responses to different experimental conditions. An RDM can be constructed that captures the degree to which all pairs of experimental conditions can be distinguished from one another by fMRI data or by behavioral responses. Thus, it is possible to directly compare the informational content of fMRI and behavioral data by assessing correlations between RDMs generated from fMRI data and those generated from behavioral responses (Kriegeskorte et al., 2008).

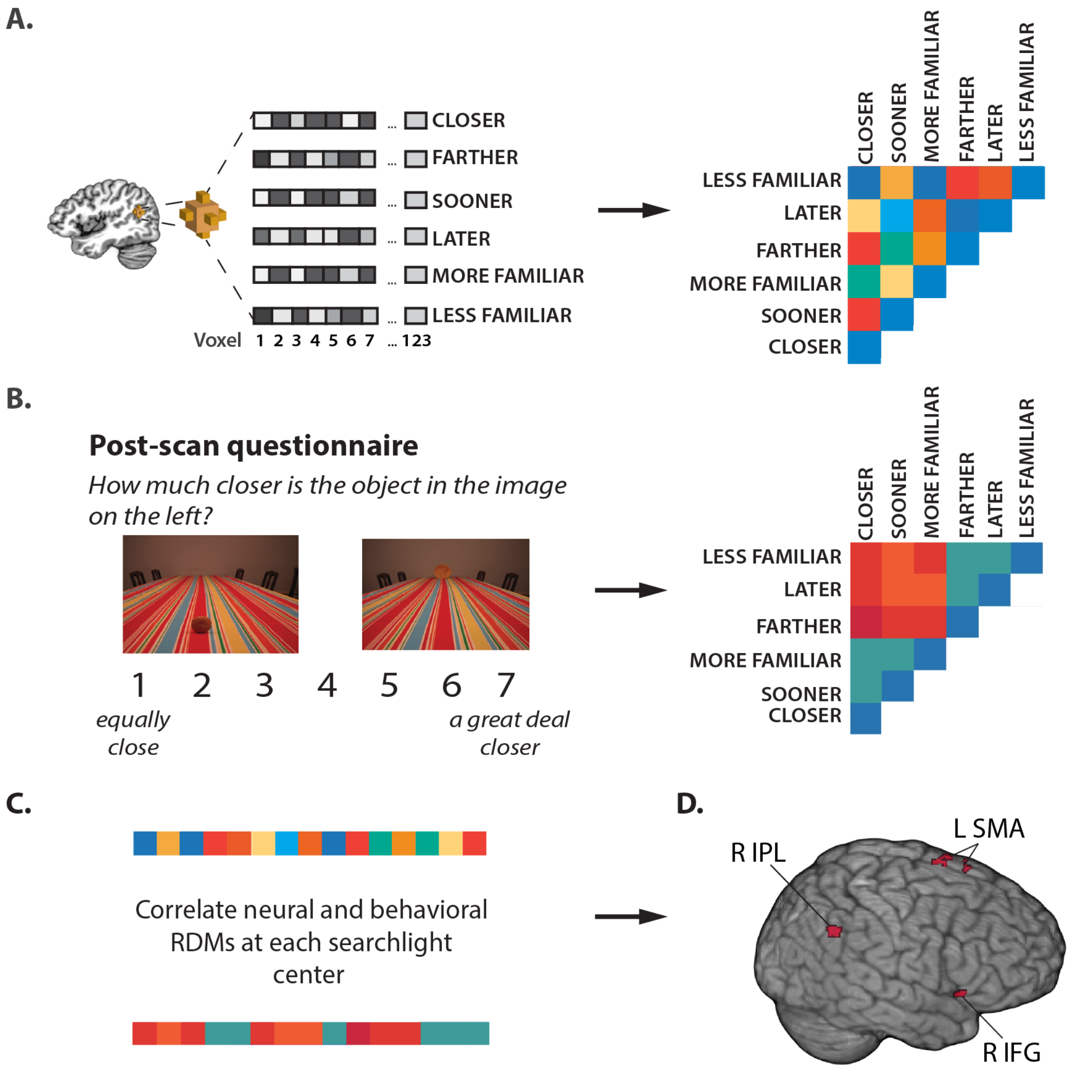


Figure 3. Representational similarity analysis and results from Study 1. (A-C) Analysis steps. (A) At each voxel, a neural RDM was generated based on pairwise correlation distances between local neural response patterns to each condition. In schematic depictions of multi-voxel patterns, darker gray indicates greater fMRI responses. In RDMs, warmer and cooler colors indicate higher and lower dissimilarities, respectively. **(B)** Behavioral RDMs were constructed for each subject using Euclidean distances between post-scan distance ratings and **(C)** correlated with local neural RDMs at each voxel. **(D) Results.** The largest cluster where local neural and behavioral RDMs were significantly related was in the right inferior parietal lobule (R IPL). Behavioral and neural RDMs were also related in the right inferior frontal gyrus (R IFG) and left supplementary motor area (L SMA).

Because the current study has six experimental conditions, each neural and behavioral RDM has 15 unique parameters. Thus, RDMs provide a relatively information-rich summary of the information carried in behavioral and fMRI responses.

Other methods of relating fMRI data to behavior are often qualitative or involve relating neurometric and psychometric functions, which tend to contain fewer parameters (Kriegeskorte et al., 2008). At the same time, constructing an RDM is a useful dimensionality reduction step, as the number of features in the original fMRI data far exceeds the number of unique elements in each RDM. Thus, after constructing RDMs, data are usefully condensed in comparison to their original form. Additionally, rather than assuming that all distance domains were perceived equivalently, this data analytic approach preserves differences in behavioral ratings between domains. Similarly, because RDMs are generated separately for each participant, idiosyncratic differences in relative psychological distance ratings for each participant are preserved.

Representational similarity analysis was implemented using Python (particularly PyMVPA, Hanke et al., 2009; and SciPy, Oliphant, 2007) For each participant, a 6 x 6 behavioral RDM was computed by first averaging behavioral ratings within each trial type, then calculating the Euclidean distances between all possible pairs of these mean trial type ratings (see Figures 3 and 4). Next, a similarity searchlight (radius = 3 voxels) was carried out by iteratively computing a neural RDM corresponding to the pairwise Pearson correlation distances between local multi-voxel patterns of parameter estimates corresponding to the six trial types at each voxel in each subject’s gray matter-masked data (Figure 3A). Custom code was written in Python and PyMVPA in order to compare the off-diagonal elements of the lower triangular halves of the neural and behavioral RDMs at each voxel for each participant (Figure 3C) using the Spearman rank coefficient, which was used because it does not assume a linear match between neural and behavioral RDMs (Kriegeskorte et al., 2008). This procedure yielded a statistical map of Spearman rank coefficients characterizing the relationship between local neural and behavioral RDMs, mapped to the center of each searchlight sphere for each participant.

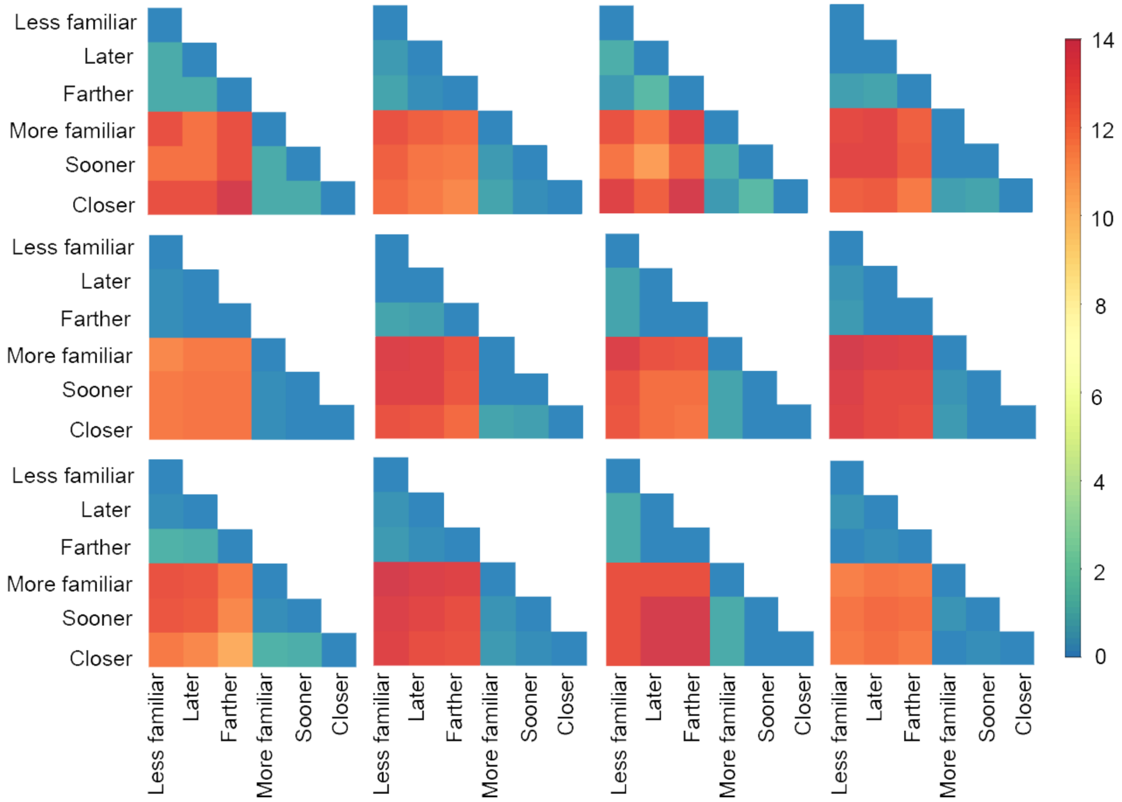


Figure 4. RDMs generated from post-scan behavioral distance ratings for each participant. After scanning, 12 participants rated each pair of stimuli seen in the scanner in terms of relative temporal soon-ness, social familiarity, and physical closeness on a 1-7 scale. The Euclidean distance between each participant's average behavioral rating for each category were used to construct behavioral dissimilarity matrices for his or her similarity searchlight analysis.

At each searchlight center, the statistical significance of the relationship between the behavioral and local neural RDMs was evaluated using permutation testing. A distribution of Spearman rank coefficients corresponding to the null hypothesis that no relationship exists between the neural and behavioral RDMs was obtained by randomly shuffling the domain labels on the behavioral RDM 1,000 times, then computing the correlation between the neural RDM and each of the 1,000 randomly generated permutations of the behavioral RDM. Next, the inverse of the cumulative normal distribution was calculated in order to convert the resultant *p*-values into *z*-scores (Connolly et al., 2012). *Z*-statistic maps describing the relationship between the similarity structure of each participant's behavioral ratings of distance for each trial type and the similarity structure of local distributed fMRI response patterns corresponding to each trial type were aligned to standard space (Talairach & Tournoux, 1988) and submitted to a group analysis (one-sample *t*-test against a *z*-score of zero) in AFNI (Cox, 1996).

Conventional univariate analysis. A standard univariate analysis using the GLM was performed in AFNI (Cox, 1996) to determine if the multi-voxel pattern analysis results merely reflected differences in the overall average magnitude of responses to Closer, Sooner, and More familiar trials, as compared to Farther, Later and Less familiar trials, respectively. Voxel-wise parameter estimates generated from concatenated data from all eight runs were submitted to three paired *t*-tests (Sooner vs. Later; Closer vs. Farther; More familiar vs. Less familiar) using the AFNI program 3dttest++. In order to determine if any brain areas could distinguish between Closer and Farther trials, Sooner and Later trials, and More familiar and Less familiar trials based solely on the overall magnitude of local voxel responses, a conjunction analysis was performed on the statistical maps resulting from each of these three *t*-tests, using a threshold of $p < .05$, FDR-corrected, for each test.

Results

Behavioral results

Results of post-scan written questionnaires confirmed that participants perceived stimuli pairs from trials in all domains to differ substantially in terms of relative egocentric psychological distance. Mean ratings of perceived egocentric distance differences on a scale from one (equally soon/close/familiar) to seven (one image/phrase is a great deal sooner/closer/more familiar) were 6.21 ($SD = 0.70$), 6.29 ($SD = 0.82$), and 6.52 ($SD = 0.62$) for Closer, Sooner, and More familiar trials, respectively. One sample *t*-tests indicated that distance ratings for stimulus pairs from each domain significantly differed from one (equally soon/close/familiar), all *p*'s < .00001. A one-way analysis of variance (ANOVA) indicated that perceived relative psychological distance did not significantly differ across the three tested domains of psychological distance, $F(2,22) = 1.94$, $p = 0.17$, $\eta^2_G = .09$. Additionally, response accuracies to probes during scanning were high, suggesting that participants were able to attend to and compare the Anchors and Targets in the intended manner during scanning. Run accuracies ranged from 95.83% to 100% ($M = 97.97\%$; $SD = 1.34\%$).

Classification results

Clusters (cluster size >10 voxels) where relative egocentric distance could be decoded across all possible pairwise combinations of distance domains are presented in Table 1 and Figure 5. All voxels in each of these clusters were associated with significantly above-chance classification across participants for each of the six group analyses ($p < .05$, FDR-corrected, each test). Specifically, relative egocentric distance could be decoded across all distance domains above chance across participants in searchlights centered on voxels in a large (273-voxel) cluster in the right inferior parietal lobule (IPL) extending into the posterior superior temporal gyrus (STG; Figure 3). Cross-domain distance decoding was also possible in smaller clusters throughout the right IPL, spanning both the supramarginal (SMG) and angular gyri (AG), as well as in one cluster in medial occipital cortex, as summarized in Table 1.

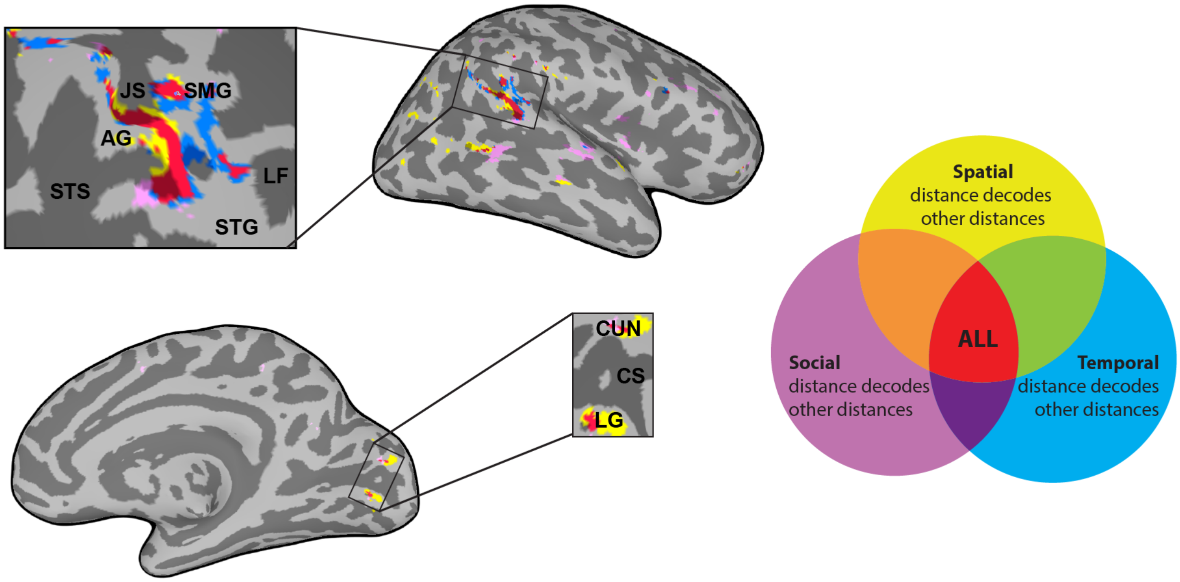


Figure 5. Classification searchlight results from Study 1. Accuracy maps from all classification searchlight analyses (i.e., six classification searchlight analyses using all pairwise combinations of Social, Spatial and Temporal distance categories as training and testing data) were tested against chance across participants. Red indicates the conjunction of significant results ($p < .05$, FDR-corrected, each test) across all six tests. The largest significant cluster was located in right IPL, encompassing both the AG and SMG, and extending into the posterior temporal lobe, followed by a cluster in medial occipital cortex. Results are projected on the right hemisphere of the AFNI TT_N27 template surface. CUN = cuneus; CS = calcarine sulcus; JS = intermediate sulcus of Jensen; LF = lateral fissure; LG = lingual gyrus; STS = superior temporal sulcus.

Table 1. Regions where changes in psychological distance could be decoded from local patterns of brain activity across all distance domains in Study 1

Hemi	**Location**	**BA**	**Number of voxels**	**COG *X***	**COG *y***	**COG *z***	**Average peak % accuracy**
R	IPL (AG), STG	39, 22	273	61	-39	9	62.33
L, R	LG, CUN	18	200	0	-77	5	66.12
R	IPL (SMG)	40	70	59	-46	21	65.18
R	IPL (SMG)	40	29	62	35	31	61.30
R	IPL (AG)	39	24	54	-59	26	62.19
R	IPL (SMG)	40	21	60	-38	26	66.01
R	STG, IPL (SMG)	42, 40	15	61	-28	16	60.49

All presented results are significant at an FDR-corrected threshold of $p < .05$ (two-tailed) for each of six statistical tests (corresponding to significance tests for accuracy maps derived from using all possible pairs of the three tested distance domains for training and testing data). To obtain average peak accuracy values, a mask of each of these clusters was applied to average accuracy maps for each of the six tests, and peak percent accuracies were averaged across tests for each cluster. Hemi = hemisphere; BA = Brodmann's Area; COG = center of gravity; R = right; L = left; IPL = inferior parietal lobule; AG = angular gyrus; STG = superior temporal gyrus; LG = lingual gyrus; CUN = cuneus; MTG = middle temporal gyrus; FG = fusiform gyrus; SMG = supramarginal gyrus. All coordinates in Talairach space.

Representational similarity analysis results

Representational content within a large cluster in the right IPL was significantly related to behavioral distance ratings, suggesting that population codes within searchlights centered in this area contain representations that reflect subjective perceptions of egocentric distance. As summarized in Table 2 and Figure 3, the local neural similarity structure in smaller clusters within the right inferior frontal gyrus (IFG) and throughout the left supplementary motor area (SMA) were also significantly related to the similarity structures evinced in participants' behavioral ratings of distance, suggesting that information contained in local population codes within these regions may also be related to judgments of relative egocentric social, spatial and temporal distance. Further details regarding all significant clusters ($p < .05$, FDR-corrected; cluster size >10 voxels) from this analysis are described in Table 2.

Table 2. Clusters where behavioral and local neural RDMs were correlated across participants in Study 1.

Hemi	**Location**	**BA**	**Number of voxels**	**COG x**	**COG y**	**COG z**	**Peak x**	**Peak y**	**Peak z**
R	IPL (AG, SMG)	39, 40	113	47	-54	36	48	-55	36
L	SMA	6	43	-17	-3	60	-18	-2	59
R	IFG	47	35	23	15	-11	23	16	-11
L	SMA	6	16	-7	13	60	-8	12	59
L	SMA	6	13	-17	2	63	-17	1	63

All presented results are significant at an FDR-corrected threshold of $p < .05$ (two-tailed). RDM = representational dissimilarity matrix; Hemi = hemisphere; BA = Brodmann's area; COG = center of gravity; R = right; L = left; IPL = inferior parietal lobule; SMA = supplementary motor area; IFG = inferior frontal gyrus. All coordinates in Talairach space.

Univariate results

No voxels survived an FDR-corrected threshold of $p < .05$ in any of the three *t*-tests comparing trials based on distance within each distance domain (i.e., Sooner vs. Later; More Familiar vs. Less Familiar; Closer vs. Farther). Even using a dramatically reduced voxelwise threshold of $p < .01$, uncorrected, for each test, no regions emerged as significant in the conjunction analysis, suggesting that no regions could distinguish distances in all three distance domains tested here in terms of average activity level. This suggests, at least at the current level of observation, using the current experimental paradigm, that the local distributed patterns, rather than average magnitude, of fMRI responses contain information that distinguishes between different relative egocentric distances across social, spatial, and temporal distance domains.

Discussion

The current results suggest that the human brain contains a parsimonious encoding of relative egocentric distance that generalizes to social, spatial, and temporal frames of reference. In several clusters throughout the right IPL, a classifier trained to distinguish trials based on relative egocentric distance within any single domain could distinguish trials within any other domain according to distance above chance across participants. Additionally, the similarity structure of population codes in this region reflected subjective proximity ratings.

What purpose would a domain-general encoding of relative egocentric distance serve? According to Construal Level Theory (CLT, Trope & Liberman, 2010), distance in any domain signifies a common meaning: distance from current first-hand experience. Whereas information relevant to our present experience elicits detailed, concrete representations, humans tend to think about information removed from our current experience using decontextualized, abstract representations (Liberman & Trope, 2008). Recently, Tamir and Mitchell (2011) found fMRI evidence consistent with behavioral findings that different distance domains impact our thoughts and actions analogously. Whereas the current study examined how egocentric distance itself is represented, Tamir and Mitchell (2011) examined how contemplating events from distal or proximal perspectives influences the richness of mental simulations. When participants evaluated their opinions and enjoyment of activities in proximal or distal scenarios, fMRI response magnitudes in areas associated with mental simulation were influenced similarly by different distance domains. Thus, evidence from social psychology and neuroimaging demonstrates analogous effects of different distance domains on cognition and behavior, consistent with suggestions that this information implies a common psychological meaning (Liberman & Trope, 2008). The current results provide evidence for a parsimonious representation of this shared meaning in the brain.

Walsh (2003) suggested that, on the scale of action execution, space, time, and quantity are encoded by a common metric that was repurposed for other magnitudes. Fittingly, areas involved in reaching and eye movements, the horizontal aspect of the intraparietal sulcus (hIPS, Cantlon, Platt, & Brannon, 2009; Dehaene, Piazza, Pinel, & Cohen, 2003; Eger et al., 2009) and superior parietal lobule (SPL, Knops, Thirion, Hubbard, Michel, & Dehaene, 2009), are implicated in representing and processing number. To characterize the contribution of domain-general magnitude representations to psychological distance processing, future studies should examine egocentric distance representations without attempting to minimize magnitude-related effects, and directly compare such representations to those of other magnitudes. We predict that representations of magnitudes characterizing egocentric distances would be found in the hIPS, which encodes other magnitudes (e.g., numerosity, Eger et al., 2009); egocentric distances may be encoded similarly to other magnitudes in this region. Contrastingly, representations more specific to egocentric distance may be found in the right IPL and posterior STG (i.e., the right temporoparietal junction, RTPJ), where cross-domain distance decoding was possible in the current study. The RTPJ encodes egocentric space (Schindler & Bartels, 2013), and is thought to support self-other distinctions (Decety & Sommerville, 2003). Lesions to this region produce deficits in representing space (Karnath & Rorden, 2012) and events along a mental time line (Saj, Fuhrman, Vuilleumier, & Boroditsky, 2014). The current results suggest that the RTPJ represents egocentric spatial, temporal, and social distances according to a parsimonious coding scheme. Future work should investigate how distance representations in the RTPJ relate to other signals of behavioral relevance and salience (Corbetta, Patel, & Shulman, 2008). A close relationship between these variables is suggested by mounting behavioral evidence for interactions between motivational relevance and egocentric distance perception (Cole, Balcetis, & Dunning, 2013; Vagnoni, Lourenco, & Longo, 2012).

CLT suggests that psychologically proximal information promotes attention to concrete, contextual details, whereas distal information evokes decontextualized, abstract representations (Liberman & Trope, 2008). These modes of cognition are subserved by distinct, competing brain networks: The default mode network (DMN) is associated with internally-directed thought involving memory (Buckner & Carroll, 2007; Mason et al., 2007), whereas the dorsal attention network (DAN) supports attention to the external environment (Fox et al., 2005). A third network, the frontoparietal control network (FPCN, Vincent, Kahn, Snyder, Raichle, & Buckner, 2008), including the RTPJ (Corbetta et al., 2008), flexibly couples with the DMN and DAN to arbitrate between internally and externally directed cognition (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). The egocentric distance code found here may direct attention to details of the external environment or decontextualized internal representations by influencing connectivity of the FPCN with the DAN and DMN. In the same way that the SPL may encode “movements” along the mental number line and saccades similarly because its connectivity and structure support operations relevant both for computing eye movements and arithmetic (Knops et al., 2009), anatomical characteristics of the IPL may render it suitable for representing various kinds of egocentric distance analogously. Future work should test this speculation by comparing network dynamics while participants interact with their current surroundings or mentally traverse psychological distances.

Cross-domain distance decoding was also possible in medial occipital cortex. As this region is associated with mental imagery during relative spatial distance comparisons (Thompson, Slotnick, Burrage, & Kosslyn, 2009), it is possible that participants performed analogous mental imagery in social and temporal frames of reference. This result could also arise from communication between areas of an occipito-parietal circuit that integrates visual information into egocentric spatial representations (Kravitz, Saleem, Baker, & Mishkin, 2011), or top-down modulation of population responses in visual cortex to enhance attention to particular spatial locations, since close temporal and social distances are automatically associated with proximal locations (Bar-Anan et al., 2007).

The largest significant clusters in both classification and similarity analyses were in the right IPL. Smaller clusters where local information content reflected subjective distance ratings occurred in the left SMA and right IFG. These areas are involved in retrieving spatial locations from memory (Baumann, Chan, & Mattingley, 2010), and may be similarly involved in accessing temporal and social frames of reference. These results may also relate to the relevance of psychological distance to action. Left frontal activity is associated with personal relevance, approach motivation, and attentional narrowing (Harmon-Jones & Gable, 2009; Harmon-Jones, Lueck, Fearn, & Harmon-Jones, 2006), which are associated with diminished psychological distance (Harmon-Jones, Price, & Gable, 2012). Close objects are likely to be personally relevant and elicit immediate action, and thus, may evoke similar SMA activation patterns.

These findings provide preliminary support for speculation that IPL circuitry originally devoted to sensorimotor transformations (Walsh, 2003) and representing one's body in space (Lenggenhager, Smith, & Blanke, 2006) was "recycled" to operate analogously on increasingly abstract contents as this region expanded during evolution (Yamazaki et al., 2009). Such speculations are analogous to cognitive linguists' suggestions that we may speak about abstract relationships in physical terms (e.g., "inner circle") because we think of them in those terms (Lakoff & Johnson, 2008). Consistent with representations of spatial distance scaffolding those of more abstract distances, compelling behavioral evidence demonstrates that task-irrelevant spatial information has an asymmetrically large impact on temporal processing (Casasanto & Boroditsky, 2008; Casasanto, Fotakopoulou, & Boroditsky, 2010; Merritt, Casasanto, & Brannon, 2010). Future studies extending this approach to neuroimaging will be instrumental in characterizing relationships between neural representations of different domains of distance.

Interestingly, CMT posits that several aspects of physical experience ("source domains," e.g., elevation) scaffold representations of more abstract concepts ("target domains," e.g., valence). Taken together, the range of metaphors described by CMT and the present results might suggest that any source and target domains would be represented similarly. We hypothesize that this would be true only to the extent that source and target domains share implications for processing and behavior. Relationships between domains of psychological distance are distinguished from those between other source and target domains because any domain of psychological distance confers a chronically accessible, automatically processed common meaning (Bar-Anan et al., 2006,

2007) that impacts perception, cognition and behavior similarly (Liberman & Trope, 2008). Neural representations of other source and target domains may be less consistently and reciprocally associated (Quadflieg et al., 2011).

In sum, the results of Study 1 provide the first evidence for a common cortical code for relative egocentric spatial, temporal and social distances. A wealth of behavioral evidence demonstrates that considering information at near or far psychological distances confers a “switch” from concrete, low-level mental construal to more abstracted, decontextualized representations (Liberman & Trope, 2008). The domain-general population code documented here is well-situated to provide a mechanism for this “switch,” as the RTPJ belongs to the FPCN, which can couple with the DMN or DAN to promote internally or externally directed cognition, respectively (Corbetta et al., 2008; Spreng et al., 2010). These findings also support speculation that IPL circuitry originally devoted to spatial computations was “recycled” to perform analogous operations in increasingly abstract frames of reference (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 commonsense categories, it would be inefficient for the brain to represent spatial, social, and temporal distances entirely separately 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.

Study 2

Spontaneous Neural Encoding of Social Network Position

Relationships are intrinsic to human behavior. Everyday interactions are shaped not only by our own relationships with others, but also by knowledge of bonds between third parties and by the structure of the broader social networks in which we are all embedded. Well-connected individuals can effectively threaten or bolster one's reputation (Ellwardt et al., 2012), those who bridge otherwise disparate groups of people can efficiently seek and spread novel information (Burt et al., 2013), and knowledge that one shares mutual friends with a conversational partner inform what one shares with that person, as well as trust decisions (Burt & Knez, 1995). Social intelligence rests, in part, on a calculus that inheres in an understanding of social network structure (Brent, 2015; Seyfarth & Cheney, 2015).

Is knowledge about familiar individuals' positions in our social networks automatically activated when we encounter them, or only when our explicit goals require it? It is possible that information about patterns of social ties is processed only when the task at hand demands reasoning about others' social connections (e.g., when determining how to best go about obtaining a particular piece of information; when forecasting the likely social repercussions of a recent embarrassment). Although we can call to mind a wealth of knowledge about familiar others if prompted, it is unlikely that all of this information is registered each time that we meet them. On the other hand, given its established importance to many aspects of behavior and to impressions of others' status and competence (Brent, 2015; Ellwardt et al., 2012; Podolny, 2001), it would be useful for the brain to activate knowledge about familiar individuals' social network positions upon encountering them. Indeed, humans automatically register a great deal of information about other people when we come across them, such as their apparent intentions, personality traits, emotional states, age, gender, and even coalitional allegiances (e.g., Kurzban, Tooby, & Cosmides, 2001; Todorov, Gobbini, Evans, & Haxby, 2007; Uleman, Newman, & Moskowitz, 1996). This automatic processing of person knowledge is thought to prepare perceivers for appropriate and beneficial social interactions (Gobbini & Haxby, 2007). Automatically registering familiar others' positions in one's social network would be similarly useful in aiding the perceiver to predict the social repercussions of potential courses of action, and, more broadly, to successfully negotiate his or her social world. Thus, in Study 2, we sought to test whether or not information about familiar others' social network positions is encoded automatically upon encountering them.

In order to probe for the spontaneous neural encoding of social network position, we combined social network analysis with representational similarity analysis of multi-voxel response patterns in fMRI data. As noted in Study 1, representational similarity analysis involves distilling fMRI response patterns into representational similarity structures indexed by experimental condition, which capture the information carried in a given brain region's response patterns about a set of stimuli. In so doing, representational similarity analysis affords the direct, quantitative evaluation of the degree to which the informational content of neural response patterns reflects the informational content of data acquired using other modalities of measurement or of computational models (Kriegeskorte et al., 2008). Social network analysis treats social groups as systems of actors connected by relationships (Wasserman & Faust, 1994). This approach emphasizes the embeddedness of human behavior within networks of relationships and the value of interpersonal connections (Burt et al., 2013). By studying topological characteristics of systems of human relationships, it is possible to study phenomena above and beyond what would be observable by targeting individuals in isolation or dyads (Christakis & Fowler, 2009), and beyond what would be possible by constructing artificial social contexts (e.g., artificial coalitions or groups) in the lab.

We characterized the social network of a cohort of 277 Masters of Business Administration (MBA) students at a private university in the northeastern United States and collected psychometric data about students using self-report questionnaires (see Methods for further details). A subset of these individuals completed an fMRI study in which they viewed individually tailored stimulus sets consisting of brief videos of 12 of their classmates. Each individual in each fMRI participant's stimulus set was characterized according to three potentially behaviorally relevant metrics derived from the social network data: geodesic distance from the participant in the network (i.e., the smallest number of intermediary social ties required to connect the participant and the target individual), eigenvector centrality (i.e., the degree to which an individual is well-connected to well-connected others), and network constraint (i.e., the degree to which an individual connects others who would not otherwise be connected), which are described in greater detail below. After scanning, participants were asked about their subjective perceptions of each social network analysis-derived metric of interest for each individual in their stimulus set. This allowed us to test the accuracy of participants' explicit perceptions of others' social network positions, and to evaluate how well participants' explicit perceptions of their social networks matched the data used to construct their stimulus sets.

Social network position characteristics

Social distance. In Study 2, social distance refers to the smallest number of intermediary social ties required to connect two individuals (i.e., “degrees of separation” or the geodesic distance between individuals). For clarity, all individuals in a given social network are referred to as nodes; the focal node relative to whom social ties are being characterized is referred to as “ego,” and individuals to whom ego is connected are termed “alters.” By definition, a given ego’s alters have a distance of one from ego, and the nodes to whom the alters are connected (but who are not directly connected to the ego themselves) have a distance of two from ego (i.e., the alters’ alters). The alters of those individuals have a distance of three from the ego, and so on (Wasserman & Faust, 1994).

Relationships between third parties inform the behavior of humans and other group-living primates (Cheney, 2011). Given the importance of reputation management for human behavior (Coleman, 1988; Tennie et al., 2010), individuals who are “two degrees away” from oneself in a social network may be important to identify and monitor given that negative interactions could damage one’s relationship with a mutual friend; similarly, individuals may be more likely to trust others who share friends in common, given the potential reputation cost of bad behavior (Burt et al., 2013; Coleman, 1988). On the other hand, individuals who are three or more degrees away from oneself in a social network may be less relevant to one’s own thoughts and behavior.

Recent research has made substantial progress in identifying how the neural and behavioral correlates of responses to personally familiar faces differ from those of strangers (Deaner et al., 2007; Fareri, Niznikiewicz, Lee, & Delgado, 2012; Gobbini et al., 2013; Visconti di Oleggio Castello et al., 2014). However, given that many of our everyday interactions tend to unfold in the company of personally familiar others, such as coworkers, friends, acquaintances, family members, and “familiar strangers” (Sun et al., 2013), more nuanced distinctions than those between friends and strangers likely influence human social behavior. In the current study, all individuals in participants’ stimulus sets were personally familiar to the participants, allowing for the investigation of differences in processing caused by relatively graded differences in social distance.

Eigenvector centrality. Eigenvector centrality (Bonacich, 1987) belongs to a family of prestige-based centrality metrics that take into account not only how many connections a given individual has, but also the relative statuses or centralities characterizing each of those connections. Prestige-based centrality metrics are particularly useful when characterizing social status, given that being named as a social tie by a popular individual should increase one’s own sociometric popularity more compared with being named by a less popular individual (Bonacich & Lloyd, 2001). Thus, eigenvectors of adjacency matrices can provide useful estimates of social status (see Methods for further details, Bonacich & Lloyd, 2001; Bonacich, 2007). High eigenvector centrality implies that an individual who is well-connected to well-connected others, and low eigenvector centrality implies that an individual has few friends who tend to be unpopular.

Eigenvector centrality has previously been used to assess social status in friendship networks, and is thought to influence the costs and benefits of treating another individual positively or negatively (Ellwardt et al., 2012). For example, individuals embedded within networks of supportive social ties with well-connected others may be protected from mistreatment because they are more likely to be defended by others, who themselves are more likely to be defended. On the other hand, there is a relatively lower risk associated with developing an acrimonious relationship with a low eigenvector centrality individual, given the low likelihood of sharing a mutual relationship that may be compromised by betraying a low eigenvector centrality individual, and given that low eigenvector centrality individuals have little influence on the spread of information (i.e., potential reputation costs are minimal) and other resources in the network (Ellwardt et al., 2012).

Although the majority of past psychological and neuroimaging research on social status has focused on physical dominance (Cheng et al., 2013), for humans and other group-living primates, social power is relatively less contingent on individual strength and self-serving physical aggression, and relatively more dependent on group dynamics and affiliative relationship maintenance (de Waal, 2000; Keltner, Van Kleef, Chen, & Kraus, 2008). Given that overt physical violence is relatively rare in contemporary human groups compared to in other species (Pinker, 2011), and that social support and reputation management are central to everyday human life (Tennie et al., 2010), one's social status in terms of social network position is likely an especially important determinant of social status for humans.

Network constraint. Individuals who connect others who would not otherwise be connected to one another are referred to as occupying network positions low in constraint, and have the capacity to serve as “brokers” of resources (e.g., information) in the network. Because of the structure of their local social ties, brokers can coordinate behavior and translate information across structural holes in the network (Burt et al., 2013). Information tends to become “sticky” and tacit within groups, as individuals embedded within a densely interconnected area of the network come to share implicit understandings and systems of communicating, thinking, and behaving (Burt et al., 2013; Burt, 1992). Low constraint individuals can broker the flow of information between such groups and put together ideas and information that would otherwise be “stuck” within unconnected groups. As a result, these individuals tend to develop more creative ideas that tend to be more positively received, and to serve as opinion leaders who exert a disproportionate influence on the flow of ideas and resources throughout the network (Burt et al., 2013; Burt, 2005). Low constraint individuals also have the opportunity to display different beliefs and characteristics to different individuals (Burt et al., 2013). On the other hand, operating within “closed” networks, characterized by high constraint, introduces reputation costs for bad behavior. Correspondingly, high constraint can foster increased trust and cooperation (Burt et al., 2013; Burt, 2005). Thus, many aspects of others’ behavior (e.g., decisions about how to effectively go about seeking or sharing information; trusting another individual) would benefit from encoding this aspect of social network position.

Is social network position spontaneously encoded?

To test for the spontaneous encoding of social network position information, we used the recently introduced GLM decomposition searchlight approach (Chikazoe, Lee, Kriegeskorte, & Anderson, 2014). Local neural RDMs, which capture the information contained in local multi-voxel patterns about a set of experimental conditions (i.e., the individuals in a participant's stimulus set, Kriegeskorte et al., 2008), were iteratively extracted within 9-mm radius spheres centered at each point in each participant's brain. Within each participant, each local neural RDM was modeled as a weighted combination of distance matrices that had been created based on properties of the social network positions of the individuals in that particular participant's stimulus set. Using this technique, participants' brains were mapped in terms of the degree to which the information contained in multi-voxel patterns of brain activity evoked in response to familiar others could be explained by those individuals' positions in their social network.

Next, to explore the degree to which social network information explains variance in our spontaneous responses to familiar individuals that could not be explained by aspects of those individuals in isolation (e.g., by personality traits), we performed two additional GLM decomposition searchlight analyses. First, we mapped participants' brains in terms of the degree to which local neural information content could be explained by a weighted combination of distance matrices based on both social network position information and Big Five personality traits (John & Srivastava, 1999). Second, we performed an analogous analysis in which only distance matrices based on personality traits were used as predictor variables. To probe for brain regions where social network position information explains information about our responses to familiar others over and above what could be explained by personality traits alone, we compared the variance accounted for by the eight-predictor (personality traits and social network position characteristics) and five-predictor (personality traits only) models described above.

Individual differences in social tuning

Finally, as a preliminary test of the hypothesis that the purpose of automatically activating person knowledge (e.g., knowledge about someone's social network position) when encountering other people is to inform subsequent social interactions, we tested if individuals who adjust their behavior more to suit their current social context (i.e., high self-monitors, Snyder & Gangestad, 1986) automatically represent more person-specific social knowledge when perceiving familiar others. Individuals who are low self-monitors tend to act and express themselves according to their own current internal states, irrespective of their audience. These individuals tend to endorse statements such as, "I have trouble changing my behavior to suit different people and different situations" (Snyder & Gangestad, 1986). High self-monitors, on the other hand, tend to closely monitor their social context and regulate their behavior accordingly. Individuals who are high self-monitors tend to endorse phrases such as, "In different situations and with different people, I often act like very different persons" (Snyder & Gangestad, 1986). We tested if high self-monitors' neural responses to familiar others contained more information about the personalities and social network positions of these individuals.

The current study provides the first test of whether or not humans spontaneously encode structural information about the patterns of ties in their real-world social networks. Furthermore, this investigation explores the degree to which social network position explains information about our responses to other people that cannot be explained by aspects of those individuals in isolation (e.g., their personality traits). Finally, this study tests if certain individuals spontaneously encode more person knowledge than others. We predicted that if humans spontaneously encode social network position and other person knowledge (e.g., personality traits) in order to inform our subsequent thoughts and behavior, then this information should be carried in neural responses to familiar others. Furthermore, we predicted that individuals who tend to titrate their behavior more to suit their current social context (i.e., high self-monitors) would spontaneously encode more person knowledge about familiar others when encountering them.

Methods

Part 1: Social network characterization and psychometric questionnaires

Participants. Participants in Part 1 of Study 2 were 275 first-year MBA students at a private university in the northeastern United States who participated as part of their coursework on leadership (91 females and 184 males). The total class size was 277 students; two students failed to complete the online questionnaires, so a 99.3% response rate was obtained for Part 1 of Study 2. All participants provided informed consent in accordance with the standards of the Dartmouth Committee for the Protection of Human Subjects.

Part 1a: Social network characterization

Method. In order to characterize the social network of all first-year students, an online social network survey was administered. Participants followed an e-mailed link to the study website where they responded to a survey designed to assess their position in the social network of first-year students in their academic program. The survey question was adapted from Burt (1992) and has been previously used in the modified form used here (Feiler & Kleinbaum, 2015; Kleinbaum, Jordan, & Audia, 2015). It read*, "Consider the people with whom you like to spend your free time. Since you arrived at [institution name], who are the classmates you have been with most often for informal social activities, such as going out to lunch, dinner, drinks, films, visiting one another's homes, and so on?"*

A roster-based name generator was used to avoid inadequate or biased recall. Classmates' names were listed in four columns, with one column corresponding to each section of students in the MBA program. Students' names were listed alphabetically within section. Participants indicated the presence of a social tie with an individual by placing a checkmark next to his or her name. Participants could indicate any number of social ties, and had no time limit for responding to this question.

Data analysis. Social network analysis was performed using the R package igraph (Csardi & Nepusz, 2006; R Core Development Team, 2013). Three social network-derived metrics were extracted for each node: network constraint, eigenvector centrality and geodesic distance from other individuals. These metrics are described in greater detail below.

Network constraint. The network constraint of actor i is given by the following equation, where P_{ij} corresponds to the proportion of i's direct social ties accounted for by his or her tie to actor j. The inner summation approximates the indirect constraint imposed on *i* by other actors, *q*, who are socially connected to both *i* and *j* (i.e. mutual friends of *i* and *j*):

$$\boldsymbol{Constraint_i = \sum_{j=1}^{n} (P_{ij} + \sum_{q=1}^{n} P_{iq} P_{qj})^2}$$

In the current study, an unweighted, undirected graph was used to estimate network constraint. More specifically, the presence of any social tie, irrespective of its direction (e.g., an undirected edge would connect *i* and *j* if *i* named *j* as a social tie, if *j* named *i* as a social tie, or if both *i* and *j* named each other as social ties) was used to compute the network constraint of each node.

Eigenvector centrality. A graph consisting of vertices connected by edges can be characterized by an adjacency matrix *A*, populated by elements such that $a_{ij} = 1$ if vertices *i* and *j* are directly connected, and $a_{ij} = 0$ if these vertices are not connected. The eigenvector centrality of each vertex is given by the eigenvector of *A* in which all elements are positive. The requirement that all elements of the eigenvector must be positive results in a unique eigenvector solution (i.e., that corresponding to the greatest eigenvalue). In the current study, when computing eigenvector centrality, the directionality of the graph was preserved; in the event of asymmetric relationships, only incoming, rather than outgoing, ties were used to calculate a given vertex's eigenvector centrality. For example, if actor *j* names actor *i* as a friend, but actor *i* does not name *j* as a friend, then this relationship will contribute to actor *i*'s eigenvector centrality, but not to that of actor *j*.

Social distance. Social distance was operationalized as the smallest number of intermediary social ties required to connect two individuals in the network (i.e., geodesic distance). Individuals who a given participant named as friends have a distance of one from that participant. Individuals whom a participant's friends named as friends (but who were not named as friends by the participant) have a distance of two from the participant. Individuals who were named as friends by classmates at a distance of two from the participant (but who were not named as friends by the participant or his/her friends) have a distance of three from the participant, and so on.

Part 1b: Psychometric questionnaires

Method. The same set of students who completed the online network questionnaire subsequently completed the Big Five Inventory (John & Srivastava, 1999) to assess their personality characteristics. The Big Five Inventory is a 44-item questionnaire that assesses openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism. For each item, participants rated on a five-point scale the degree to which they agreed or disagreed with statements about themselves. In addition, participants completed the Self-Monitoring Scale (Snyder & Gangestad, 1986) to assess trait self-monitoring. This instrument is comprised of 18 statements that participants label as true or false about themselves. Sample items include, "In different situations and with different people, I often act like very different persons," "I have trouble changing my behavior to suit different people and different situations" (reverse-scored), and "At parties and social gatherings, I do not attempt to do or say things that others will like" (reverse-scored). Both questionnaires were completed online following the completion of the social network questionnaire.

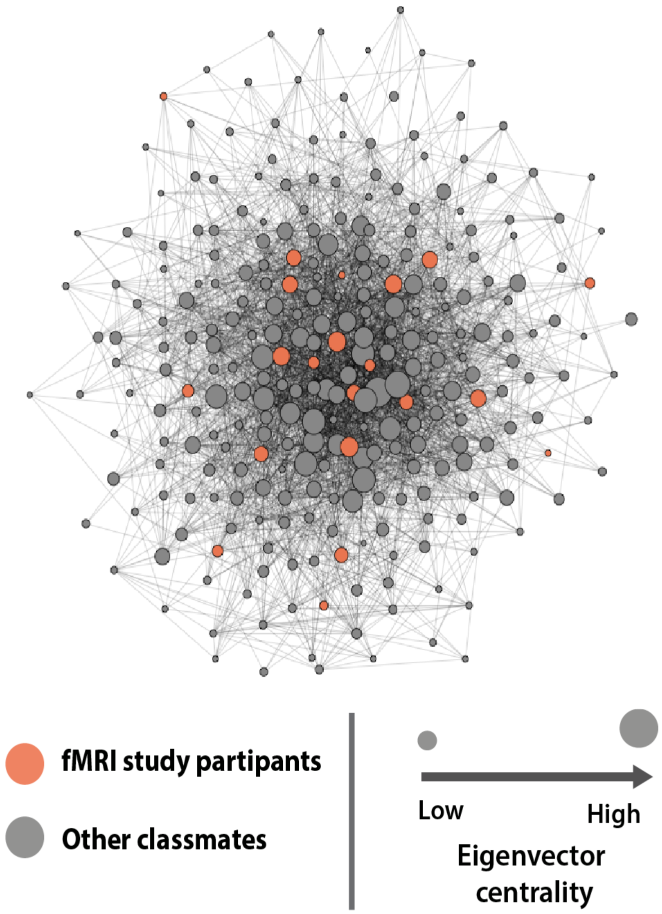


Figure 6. Characterization of the social network used in Study 2. The social network of a first-year cohort of MBA students was reconstructed based on responses to online questionnaires administered to all members of the class (*N* = 275; 99.3% response rate). Nodes indicate students; lines indicate reported social ties between them. For ease of visualization, only mutually reported social ties are illustrated. A subset of these students participated in an fMRI study. Orange nodes indicate fMRI study participants; gray nodes denote other members of the graduate program. Node size is proportional to eigenvector centrality.

Part 2: Neuroimaging study

Participants. A subset of individuals who had completed Part 1 of the study participated in a subsequent neuroimaging experiment (Figure 6). Participants were informed during class about the opportunity to participate in an fMRI study in which they would view pictures of faces. They were informed that they would receive $20 per hour as compensation for their time, as well as anatomical images of their brains. All participants were right-handed, fluent in English and had normal or corrected-to-normal vision. Participants provided informed consent in accordance with the policies of the Dartmouth College Committee for the Protection of Human Subjects. Twenty-four participants (12 females) completed the neuroimaging component of the study. One participant was excluded due to image artifact, and two were excluded because they scored less than 65% correct on the one-back memory task used in the scanner; this threshold was based on what has been used previously in similar studies (e.g., Said, Moore, Engell, & Haxby, 2010). Consequently, we analyzed data from 21 participants (10 females, aged 25-33, *M* = 27.95, *SD* = 2.16).

Image acquisition. Participants were scanned at the Dartmouth Brain Imaging Center using a 3T Philips Achieva Intera scanner with a 32-channel head coil. An echo-planar sequence (35 ms TE; 2000 ms TR; 3.0 mm x 3 .0 x 3.0 mm resolution; 80 x 80 matrix size; 240 x 240 mm FOV; 35 interleaved transverse slices with no gap; 3.0 mm slice thickness) was used to acquire functional images. Functional runs consisted of 180 dynamic scans, for a total acquisition time of 360 s per run. A high-resolution T1-weighted anatomical scan was also acquired for each participant (8.2 s TR; 3.7 ms TE; 240 x 187 FOV; 0.938 mm x 0.938 mm x 1.0 mm resolution) at the end of the scanning session. Foam padding was placed around subjects' heads to minimize head motion.

Stimuli. For each fMRI study participant, a customized stimulus set was constructed. These stimulus sets consisted of short videos of four individuals at each of three geodesic distances (i.e., one, two, and three) from the participant in the social network of first-year MBA students. At each social distance, the two highest and lowest eigenvector centrality individuals were chosen for inclusion in the stimulus set (see Figure 7).

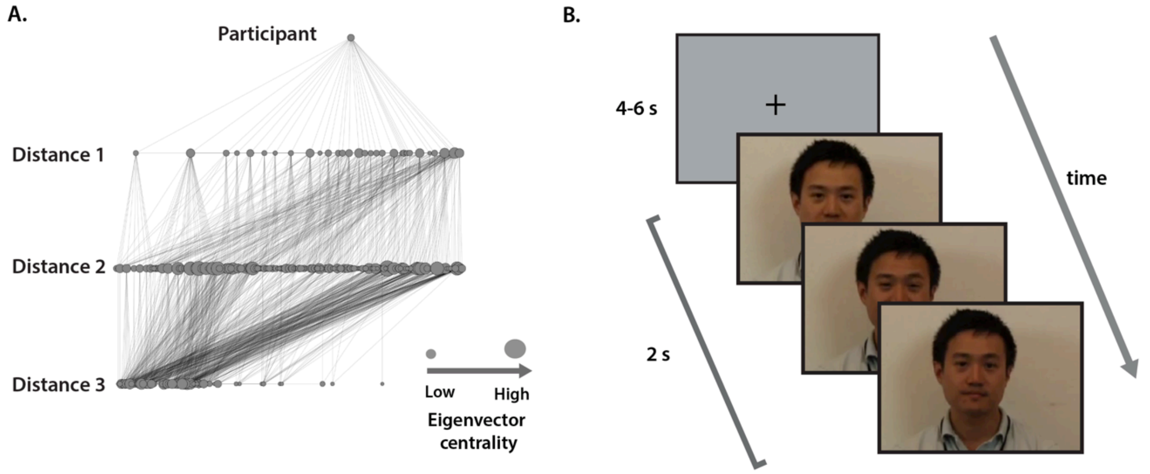


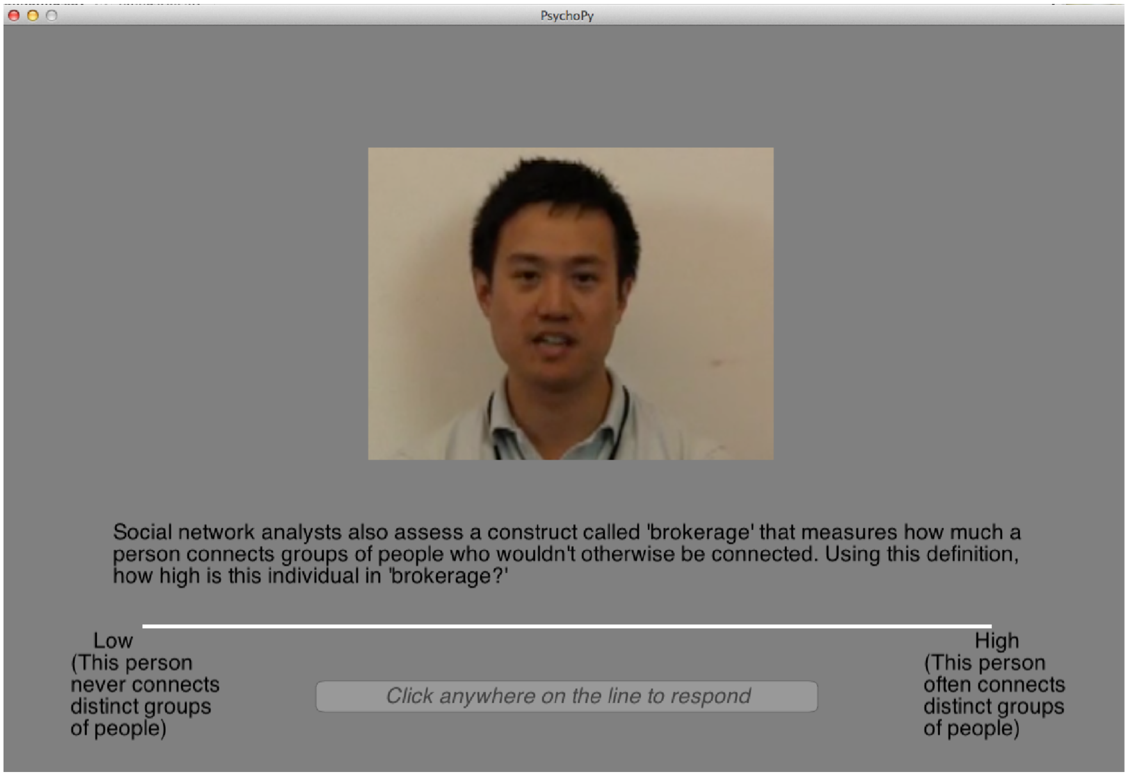
Figure 7. Stimulus set construction and paradigm for neuroimaging component of Study 2. (A) The geodesic distance between each fMRI study participant and every other student in the network was characterized. An alternative visualization of the network is shown in which nodes are organized into horizontal layers according to distance from a particular participant. Each participant's stimulus set was comprised of 12 of his or her classmates: the two lowest and two highest eigenvector centrality individuals at distances of one, two, and three from the participant in the network (e.g., the classmates signified by the two smallest and two largest nodes within each layer in **(A)**). **(B)** During the fMRI study, participants viewed brief (2 s) videos of the 12 individuals in their stimulus sets separated by 4-6 s of fixation. In order to maintain attention, a one-back task was used (i.e., participants were instructed to use a button press to indicate when an identical video was presented twice in a row).

The short videos used as stimuli consisted of individuals introducing themselves to the camera (e.g., "Hi may name is [first name], and you can call me [first name or nick name]"). A video of this kind was made involving each student at the beginning of the academic year as a resource for other students and faculty. Videos were truncated to 2 s in duration, beginning with when the subject began to say the word, "Hi," and were presented without sound. Prior to entering the fMRI scanner, participants were shown each video with sound to familiarize themselves with the stimuli.

fMRI paradigm. The fMRI study consisted of 10 runs and followed a rapid event-related design with an inter-trial interval consisting of 4 s of fixation (Figure 7C). Four null events, each consisting of an additional 2 s of fixation, were randomly inserted into each run. In each run, four repetitions of 14 event categories (12 identities; one null event; one catch trial) were pseudo-randomized such that there were no consecutive repeats of the same category. Horizontal mirroring was randomly applied to half of the presentations of each stimulus within each run in order to reduce similarities within identities due to local low-level visual features. Catch trials involved seeing the same stimulus at the same mirroring level as the immediately previous stimulus (or two trials back if a catch trial followed a null event). Participants were instructed to indicate with a button press when an identical video was presented twice in a row (i.e., when they experienced a catch trial).

Post-scan questionnaire. After scanning, participants were asked about their subjective perceptions of each social network metric of interest for each individual in their stimulus set, as well as questions that assessed tie strength**.** This allowed us to assess how well our participants' explicit perceptions of social network structure matched the data used to construct their stimulus sets.

Participants performed the post-scan questionnaire on a 13" MacBook laptop. Participants first viewed an instruction screen that read, *"Now you will see the same people who you saw in the scanner. You will be asked questions about each person. These questions relate only to this person's interactions within the [institution name] MBA cohort. We understand that people have many social circles that they participate in (perhaps including family, friends outside of [the institution], other contacts, etc.). For*



Social network analysts also assess a construct called 'brokerage' that measures how much a person connects groups of people who wouldn't otherwise be connected. Using this definition, how high is this individual in 'brokerage?'

Figure 8 Post-scan questionnaire used in Study 2. Following scanning, participants responded to questions about their subjective perception of each aspect of social network position of interest for each individual in their stimulus set. A screenshot of the question corresponding to network constraint (reverse-scored) is shown.

these questions, please just consider interactions within the MBA cohort. You will be presented with a continuous rating scale for each question. You can choose any point along the continuum to respond. Press any key to continue." During the survey, videos of the 12 individuals from the participant's stimulus set were presented in a random order. Participants responded to all questions about a given individual sequentially, and the same video that had played in the scanner repeated on a loop (without sound) above the question text and response scale (Figure 8).

Participants were presented with questions concerning lay definitions of eigenvector centrality (*"In social network analysis, scientists assess a construct that measures how many friends a person has, and how many friends a person's friends have.*

How would you rate this person on this construct?" Responses ranged from *"Low (few friends who have few friends)"* to *"High (many friends who have many friends)"*), and constraint (*"Social network analysts also assess a construct called 'brokerage' that measures how much a person connects groups of people who wouldn't otherwise be connected. Using this definition, how high is this individual in 'brokerage'?"* Responses ranged from "*Low (this person never connects distinct groups of people*" to "*High (This person often connects distinct groups of people)*"). Responses to the item assessing brokerage were reverse scored in order to estimate perceived network constraint.

Participants were also presented with the name generator that had originally been used to construct the network ("*Consider the people with whom you like to spend your free time. During the last month, is this one of the classmates who you have been with most often for informal friendship activities, such as going out to lunch, dinner, drinks, films, visiting one another's homes, and so on?*" Responses ranged on a continuum from "*None of my social activities in the past month have included this person*" to "*All of my social activities in the past month have included this person*"), as well as questions designed to assess tie strength ("*How close are you with this person?*" Responses ranged from "*Distant*" to "*Less than close*" to "*Close*" to "*Especially Close*") and frequency of interactions ("*On average, how often do you talk to this person (any social or business discussion)*?" Responses ranged from "*Less often*" to "*Monthly*" to "*Weekly*" to "*Daily*").

fMRI data preprocessing. For fMRI data analysis, data were preprocessed and average voxel-wise hemodynamic responses to each identity were estimated using AFNI (Cox, 1996). Pre-processing steps included applying AFNI's 3dDespike function to remove transient, extreme values in the signal not attributable to biological phenomena, slice timing correction to correct for interleaved slice acquisition order within volumes, registration of all volumes to the last volume of the final run using a six-parameter 3-D motion correction algorithm, spatial smoothing using a 4-mm FWHM Gaussian kernel, and scaling each voxel time series to have a mean amplitude of 100. Additionally, prior to regression, consecutive volumes in which the Euclidean norm of the derivatives of the motion parameters exceeded 0.3 mm were excluded from further analysis, as were volumes in which more than 10% of brain voxels were identified as outliers by the AFNI program 3dToutcount.

Parameter estimates were extracted for each voxel using a GLM that consisted of gamma-variate convolved regressors for each of 13 predictors (one for each of the 12 identities in each participant's stimulus set, and one for catch trials), as well as 12 regressors for each of the six demeaned motion parameters extracted during volume registration (roll, pitch, yaw, and displacement in the superior, left, and posterior directions) and their derivatives, and three regressors for linear, quadratic, and cubic signal drifts within each run. This procedure allowed for the removal of variance caused by regressors of no interest, and resulted in an estimate of the response of each voxel to each trial type.

Data analysis

GLM decomposition searchlight. Using PyMVPA (Hanke et al., 2009) and SciPy (Oliphant, 2007), a GLM decomposition searchlight (Chikazoe et al., 2014) was performed within each participant's data. A sphere (radius = 3 voxels) was moved throughout each participant's brain. At each point in the brain, the local distributed patterns of neural responses to each person in a stimulus set were extracted within a sphere centered on that point, and the correlation distance between them was calculated, in order to construct a local neural RDM (Figure 9A-C). Each local neural RDM was then decomposed into a weighted combination of predictor RDMs using ordinary least squares regression (Figure 9D). There were three predictor RDMs, one corresponding to each social network position metric of interest (social distance, eigenvector centrality, network constraint). Predictor RDMs were constructed by taking the Euclidean distances between the relevant social network position metrics for all possible pairs of identities within each participant's stimulus set. Each predictor RDM for each participant was then *z*-scored. Next, for each RDM (e.g., the eigenvector centrality-based RDM for a given participant), the variance accounted for by the remaining two predictor RDMs (e.g., the social distance and network constraint-based RDMs for that participant) was removed using an ordinary least squares regression. Thus, the resultant predictor RDMs were made orthogonal to one another prior to performing the GLM decomposition searchlight.

At each searchlight center (i.e., at each voxel in the brain), the GLM decomposition procedure yielded a β value corresponding to each social network derived metric of interest, as well as an R^2 value corresponding to how much the information content of local neural response patterns can be explained by the social network positions of the individuals comprising a given participant's stimulus set.

Group analysis. Each subject's maps of regression coefficients and R^2 values were transformed to standard space (Talairach & Tournoux, 1988) using AFNI (Cox, 1996). To identify areas containing information about each specific aspect of social network position, the regression coefficients for each social network position-derived RDM were tested against zero across participants using one-tailed one-sample *t*-tests.

Correction for multiple comparisons was carried out using 3dClustSim in AFNI, which implements 1,000 Monte Carlo simulations to compute the cluster extent thresholds and voxel-wise significance thresholds necessary to establish a given family-wise false positive rate. This procedure requires first computing the spatial structure of the noise. The spatial structure of the noise in the statistical maps derived from the GLM decomposition searchlight was estimated using a procedure adapted from previous work involving information-based brain mapping (Linden, Oosterhof, Klein, & Downing, 2012). For each set of statistical maps of interest (i.e., for β maps for each predictor variables), statistical maps were averaged across participants. Given that the signal of interest is carried in the group average map, subtracting the group average map from each individual's map yields maps of residual information scores unrelated to the signal of interest. Thus, for each set of statistical maps of interest, the group average map was subtracted from the corresponding statistical map of each individual to obtain maps of the inherent correlation in the information content of neighboring voxels. Next, 3dFWHMx was used to estimate the spatial smoothness in each residual map in the x, y, and z directions. These resulting estimated kernel widths were averaged across subjects and predictors, and then input into 3dClustSim to compute the minimum cluster size for family-wise error (FWE) correction. In order to achieve FWE rate of 0.5% (i.e., $p < .005$, FWE-corrected), a cluster extent threshold of 242 voxels and a voxel-wise significance threshold of $p < .05$ was used.

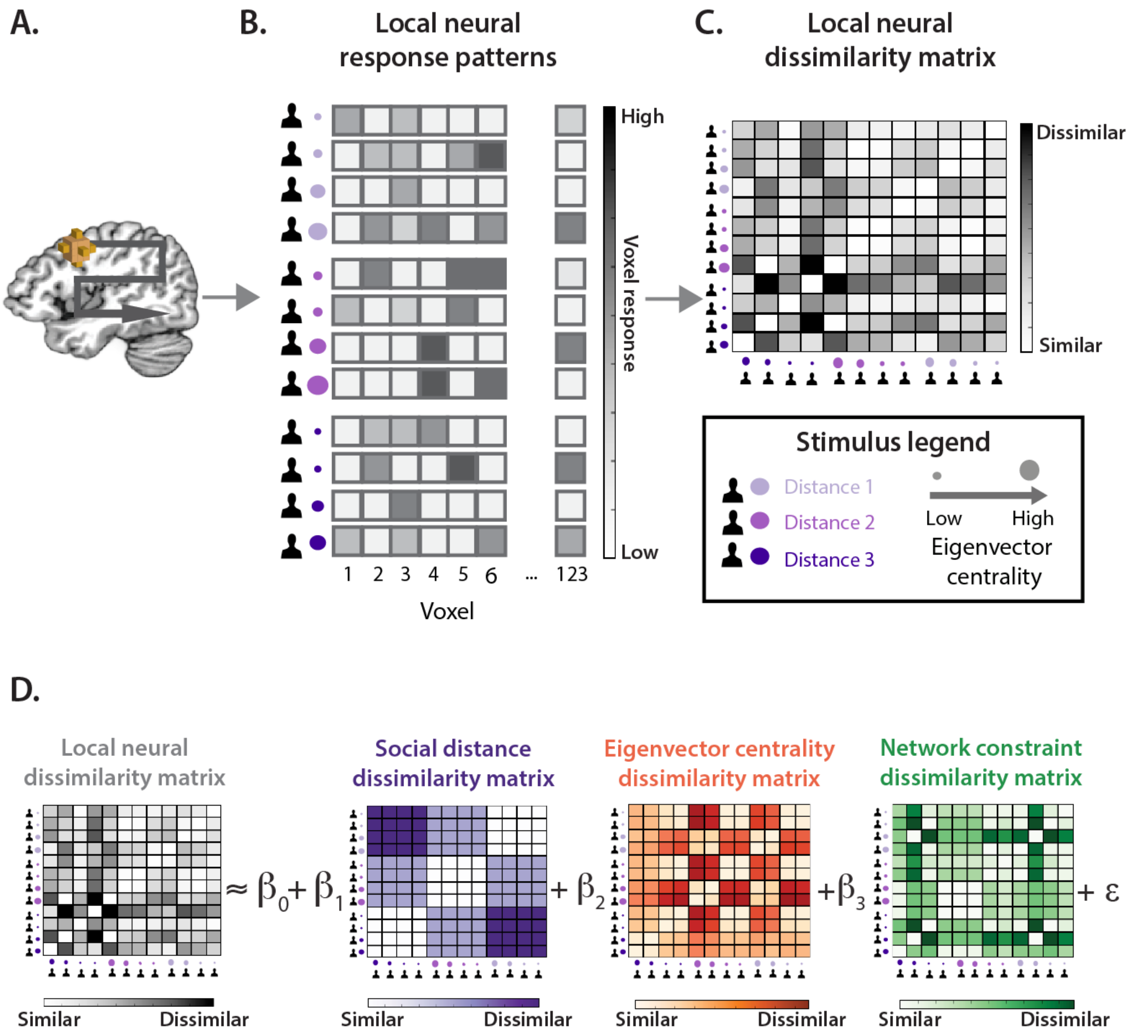


Figure 9. GLM decomposition searchlight used in Study 2. (A) A spherical searchlight was moved throughout each participant's brain. **(B)** At each point in the brain, distributed patterns of neural responses to each individual in the participant's stimulus were extracted within a 9-mm radius sphere centered on that point. **(C)** At each searchlight center, a neural RDM was generated based on pairwise correlation distances between local neural response patterns to each classmate in the participant's stimulus set. **(D)** Each local neural RDM was modeled as a weighted combination of RDMs constructed based on the pairwise Euclidean distances between individuals in each participant's stimulus set in terms of social distance, eigenvector centrality, and network constraint.

GLM decomposition searchlight (eight- and five-predictor models). Analogous data analytic procedures to those described above were used in order to carry out the eight- and five-predictor GLM decomposition searchlights. For these analyses, predictor variables in the ordinary least squares regression carried out at each searchlight center were RDMs based on the personality traits of the classmates in each participant's stimulus set (for the five-predictor model) and on the personality traits and social network positions of those individuals (for the eight-predictor model). As with the three-predictor model, RDMs were created based on the Euclidean distance between each pair of 12 individuals in the stimulus set in terms of each of these variables (i.e., personality trait scores; social network position metrics), and RDMs were normalized and orthogonalized to one another prior to analysis.

In order to explore where in the brain social network position explains variance in our spontaneous reactions to encountering others that could not be explained by aspects of those individuals in isolation (i.e., by their personality traits), the difference between the variance accounted for by the eight-predictor (social network position and personality) and five-predictor (personality-only) models was computed at each voxel for each participant.

Testing for individual differences in social tuning. In order to test if and in what brain regions individuals who are high self-monitors (and thus, tend to regulate their behavior to suit their current social context) spontaneously encode more person knowledge, perceivers' self-monitoring scores were correlated with their voxel-wise R^2 values from the eight-predictor model (i.e., with the degree to which local neural responses contain information about the personality traits and social network positions of the individuals being viewed) using the AFNI program 3dRegAna. As with the GLM decomposition searchlight, results were corrected for multiple comparisons across space using FWE-correction at a threshold of $p < .005$, one-tailed.

Results

Population coding of social network position

The GLM decomposition searchlight, in which predictor variables were RDMs based on the social distance, eigenvector centrality, and network constraint of individuals in a given participant's stimulus set, and the dependent variable was the local neural RDM for that participant (Figure 9D), accounted for between 0 and 39.6% of the variance in local neural RDMs, as illustrated in Figure 10. Areas where social network position information explained the local neural information content particularly well included the lateral superior temporal cortex, amygdala, striatum, and SMA. Distinct and distributed sets of brain regions were implicated in encoding different properties of social network position (see Figure 10 and Tables A1-A3 in Appendix 1 for a full summary of the results of this analysis).

The largest cluster in which local neural RDMs were significantly related to social distance-based RDMs was centered in the RTPJ. This cluster encompassed both the SMG and AG of the IPL, and extended inferiorly throughout the posterior lateral temporal cortex, including ventral temporal cortex (i.e., the fusiform gyrus, FG). Similar results spanning a more limited spatial extent were observed in the left hemisphere. Information about social distance was also carried in multi-voxel response patterns in the temporal poles (TP) and FG bilaterally, as well as the medial prefrontal cortex (MPFC). The largest cluster in which the eigenvector centrality of the individuals in participants' stimulus sets predicted the information content of local neural response patterns was located in early visual cortex (EVC). Eigenvector centrality-based RDMs were significantly related to neural RDMs in the ventromedial and ventrolateral prefrontal cortex (VMPFC; VLPFC) and the STG. The information contained in local multi-voxel response patterns to participants' classmates in large clusters in the right and left lateral superior temporal cortex was significantly related to the network constraint of those individuals. Network constraint also predicted the information content of population responses in the striatum, as well as in the orbitofrontal cortex (OFC), FG and SMA bilaterally. See Figure 10 and Tables A1-A3 in Appendix 1 for a summary of where local neural response patterns contained information about particular characteristics of the social network positions of the individuals being viewed.

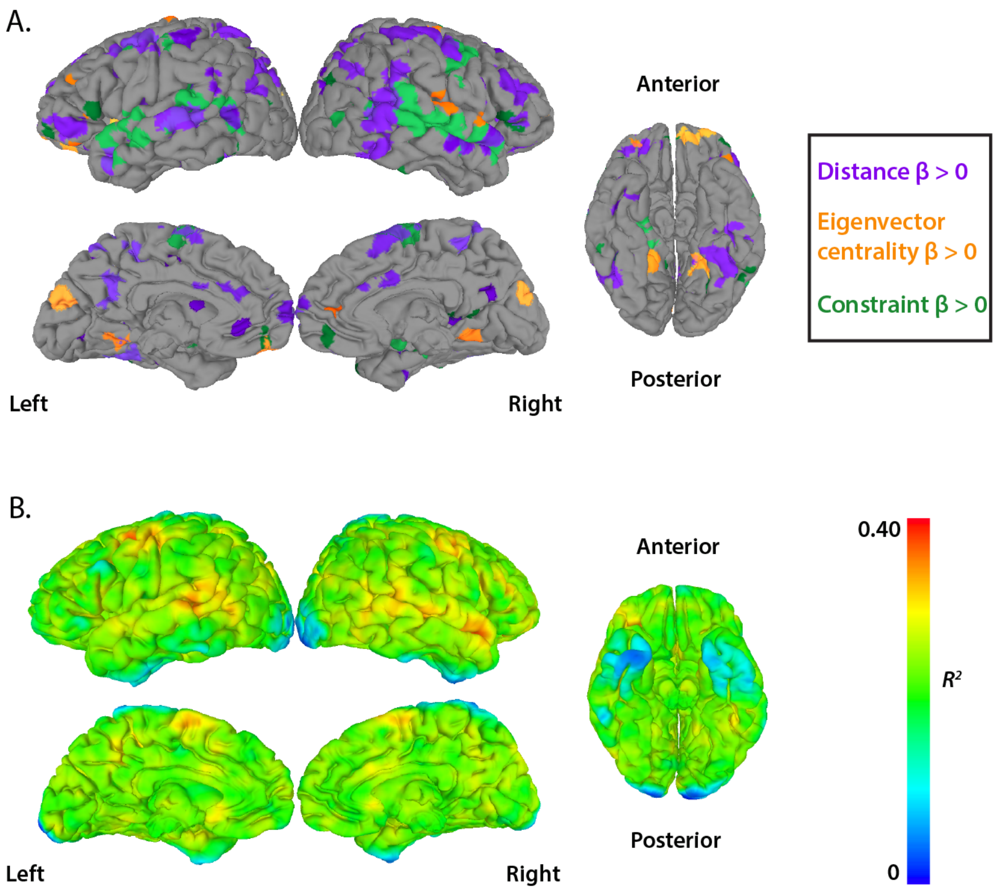


Figure 10. Population coding of social network position in Study 2. (A) Distinct brain regions encode different properties of peers' social network positions (social distance = purple; eigenvector centrality = orange; network constraint = green). Beta values indicate the extent to which the information contained in local multi-voxel response patterns to participants' classmates could be predicted based on properties of those individuals' social network positions; $p < .005$, FWE-corrected. **(B)** The R^2 value corresponding to the GLM decomposition performed at each searchlight center indicates the extent to which the information contained in local multi-voxel response patterns can be explained by the social network positions of the classmates being viewed

Population coding of personality and social network position

Next, an eight-predictor GLM-decomposition searchlight was performed, in which the predictor variables were RDMs based on the three social network position characteristics described above, as well as the "Big Five" personality traits describing the individuals in a given participants' stimulus set (i.e., openness, conscientiousness, extraversion, agreeableness, neuroticism), and the dependent variable was the local neural similarity structure for that participant. Results indicated that on average, personality and social network position information together accounted for up to 57.9% of the variance in the information content of local neural population responses to familiar others (Figure 11A). Brain areas where the local information content could be particularly well explained by the personality and social network position of the person being viewed included the left and right lateral superior temporal cortex, FG and parahippocampal gyrus, as well as aspects of the left and right dorsal and ventral striatum, dorsolateral prefrontal cortex, and supplementary and premotor cortices.

In order to explore if and where the social network positions of the individuals being viewed explained participants' neural responses to them, above and beyond what could be explained based only on aspects of those individuals in isolation (i.e., their personality traits), the variance in the local neural information content explained at each voxel by the eight-predictor model described above was compared to that explained by a five-predictor (personality trait-based) model. Social network position appeared to explain variance in participants' population responses, beyond what could be explained based only on personality traits, in the right and left FG, lateral superior temporal cortex, and aspects of the dorsal and ventral striatum, as well as in the right IPL, amygdala and OFC. In these brain areas, social network position information appears to explain aspects of responses to others that could not be accounted for based only on information about those individuals in isolation.

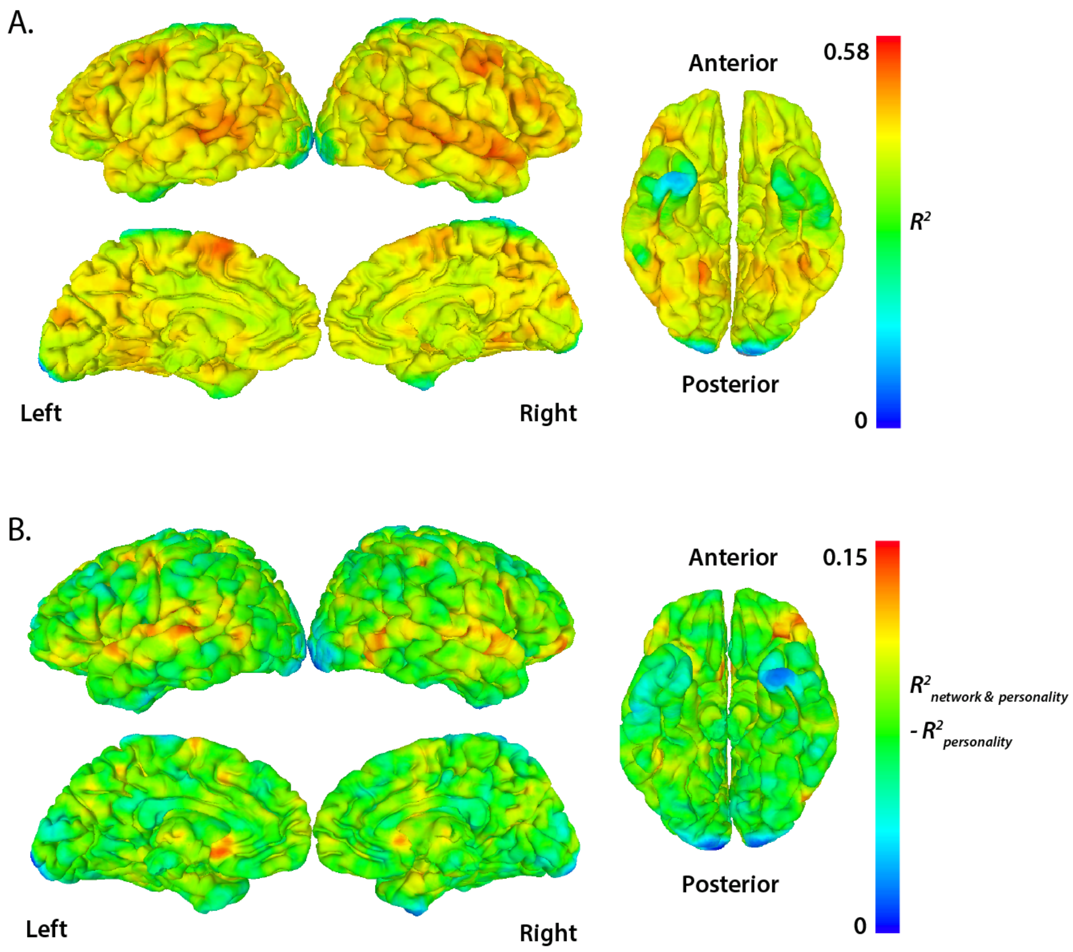


Figure 11. Population coding of personality and social network position in Study 2. (A) Variance explained by eight-predictor model. A second eight-predictor GLM decomposition searchlight was performed that included model dissimilarity structures based on both social network position properties (social distance; eigenvector centrality; network constraint) and personality traits (openness; conscientiousness; extraversion; agreeableness; neuroticism) of individuals in each participant's stimulus set. The R^2 value corresponding to the GLM decomposition procedure performed at each voxel indicates the extent to which the information contained in local multi-voxel response patterns can be explained by these aspects of person knowledge (i.e., the social network position and personality traits of the individual being viewed). Illustrated R^2 values have been averaged across participants. **(B) Difference between variance explained by eight- and five-predictor models.** In order to probe for brain regions where social network position information explains variance in local neural information content that could not be explained by personality, at each voxel, the variance in the local neural RDM accounted for the eight-predictor model (personality and social network position) was compared to the variance in local neural RDM that would be accounted for by considering personality traits alone, without regard to the social network data. Differences between the eight- and five-predictor model R^2 values have been averaged across participants.

Individual differences in social tuning

The degree to which a local neural similarity structure can be explained by a model consisting of a weighted combination of predictor similarity structures (e.g., similarity structures based on social network position characteristics, Figure 9D) indicates the degree to which local neural response patterns contain information about the stimulus set that is also contained in the measures used to construct the predictor similarity structures. Thus, in a given participant's data, brain regions where the R^2 of the eight-predictor GLM decomposition searchlight are particularly low comprise areas where the information contained in that participant's responses to the individuals in his or her stimulus set is not well explained by the personality traits and social network positions of those individuals. On the other hand, brain regions characterized by very high R^2 values comprise areas where the information contained in that participant's neural response patterns to the individuals in his or her stimulus set is well explained by their personality traits and social network positions. In other words, if a brain region in a given participant is characterized by a high R^2 value, then it contains information about the personality traits and social network positions of the individuals whom that participant viewed in the scanner.

If the purpose of spontaneously encoding person knowledge when encountering personally familiar individuals is to inform the perceiver's thoughts and behaviors in preparation for effective and beneficial social interactions, then the extent to which an individual spontaneously encodes person knowledge should be positively related to the extent to which that individual tends to moderate his or her behavior to suit current company. Consistent with this notion, a positive correlation between fMRI participants' self-monitoring scores and the extent to which their neural responses contained information about the personality traits and social network positions of the individuals whom they viewed was observed in brain areas previously implicated in creating and maintaining models of others' personalities. More specifically, the largest significant cluster (see Figure 12; Table A4 in Appendix 1) in which the perceiver's self-monitoring score was positively associated with the amount of information that local neural patterns contained person knowledge was in the MFPC. Self-monitoring was also positively related to the extent to which the information contained in fMRI responses in the OFC, striatum, SPL, FG, and EVC could be explained based on the personalities and social network positions of the people being viewed.

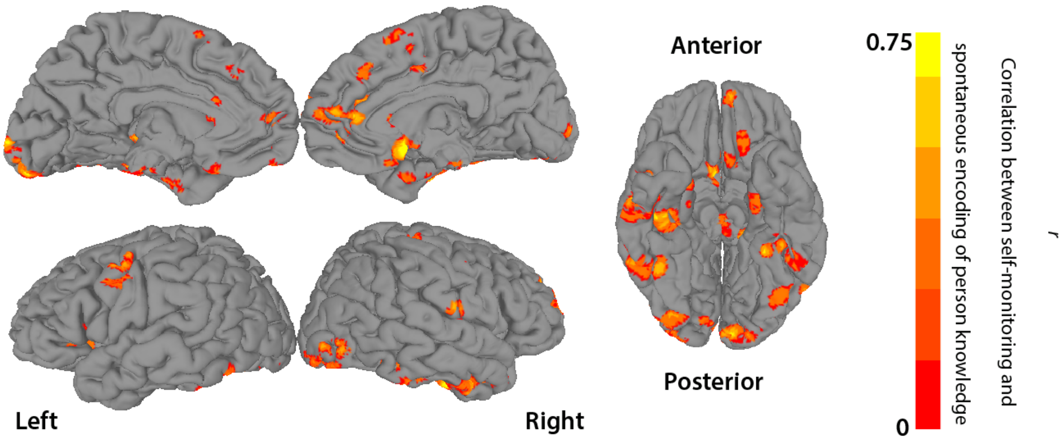


Figure 12. High self-monitors spontaneously encode more person knowledge (Study 2). A regression analysis was performed to test if the extent to which an individual reports adjusting his or her behavior to suit the current social context predicts the extent to which that individual automatically encodes social knowledge about familiar others when encountering them. Warm colors depict brain regions where local neural RDMs contained more social information (i.e., personality traits and social network position properties of the peers being viewed) among individuals higher in self-monitoring, $p < .005$, FWE-corrected.

Explicit perceptions of network structure

After scanning, participants completed a self-report questionnaire designed to assess their perceptions of aspects of the social network positions (i.e., eigenvector centrality; network constraint; social distance from the participant in terms of perceived closeness, perceived frequency of discussion and perceived proportion of social time spent together) of the individuals in their stimulus sets. Before comparing data from these questionnaires to the actual values of eigenvector centrality, network constraint, and social distance, self-report data were standardized across identities within each question for each participant. In addition, to alleviate skew in the network data, eigenvector centralities and network constraint values were log-transformed prior to analysis.

Participants' estimates of the constraint characterizing the network positions of the individuals in their stimulus set were significantly positively correlated with the actual network constraint scores of those individuals, $r = 0.56$, $p < .00001$ (Figure 13). Similarly, participants' estimates of the eigenvector centralities of the individuals in their stimulus set were significantly related to the actual eigenvector centralities of those individuals, $r = 0.74$, $p < .00001$ (Figure 13). In order to test if perceived social closeness between the participant and the individuals in his or her stimulus set varied according to the geodesic distance between the participant and those individuals in the social network, a one-way ANOVA was implemented with geodesic distance and perceived closeness as the independent and dependent variables, respectively. Perceived social closeness differed according to social distance, $F(2,40) = 547.60$, $p < .00001$. Analogous analyses indicated that perceived frequency of discussions also varied according to social distance, $F(2,40) = 346.83$, $p < .00001$, as did the proportion of his or her social time that the participant spent with the individual, $F(2,40) = 257.58$, $p < .00001$. Results of post-hoc pairwise tests, Bonferroni-corrected to control for family-wise type I error across comparisons, indicated that all groups (i.e., individuals at geodesic distances of one, two, and three from participants in the social network) differed significantly from one another in terms of perceived closeness, perceived proportion of social time spent together, and perceived frequency of discussion, such that participants reported feeling closer to, spending a greater proportion of their social time with, and having more frequent discussions with individuals who were closer to them in the social network (all p's $< .05$; Figure 13).

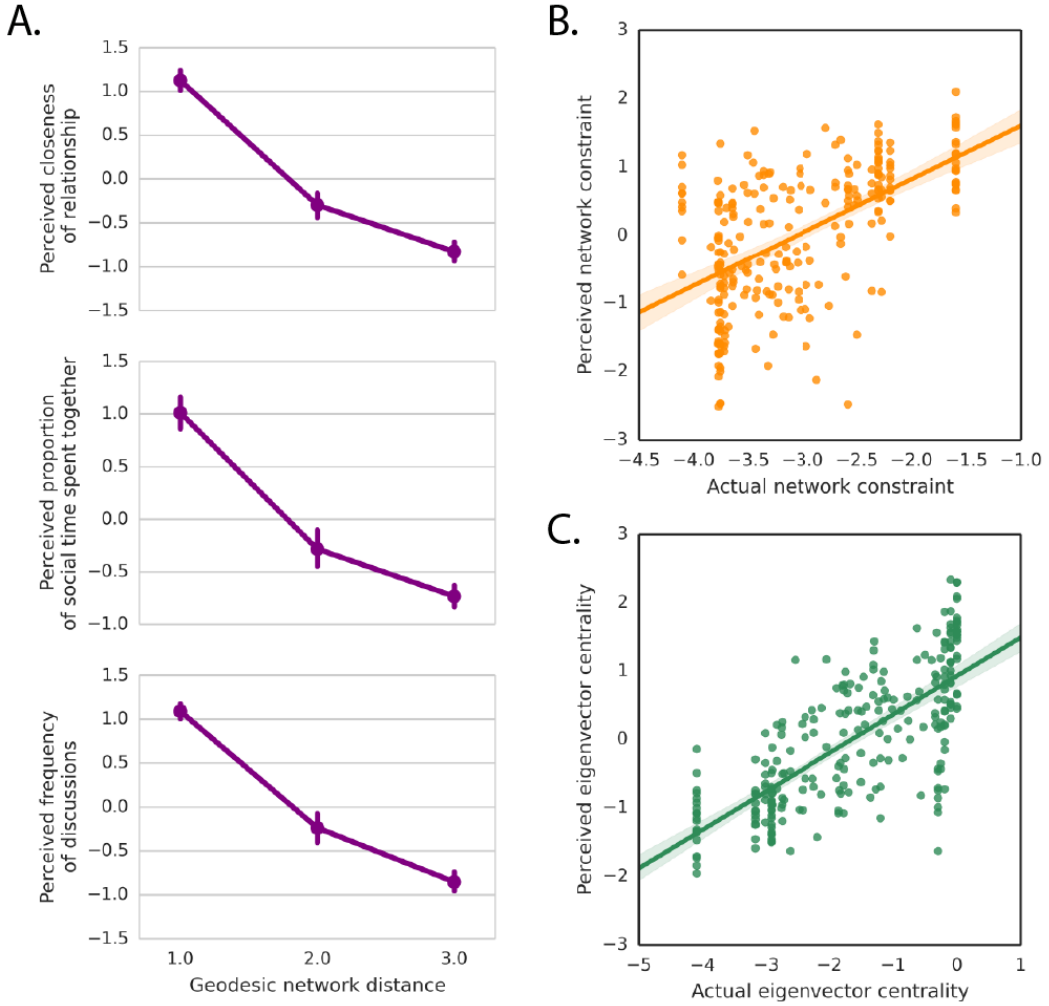


Figure 13. Associations between perceived and actual social network position characteristics in Study 2. (A) Neuroimaging study participants' subjective ratings of social closeness, proportion of social time spent together, and frequency of discussions with the individuals in their stimulus sets varied according to geodesic network distance from them in the network. Error bars indicate 95% CI. **(B)** Participants' estimates of the network constraint of individuals in their stimulus sets were associated with the actual constraint of those individuals' positions in the social network, $r = 0.56$, $p < .000005$. **(C)** Participants' estimates of the eigenvector centrality of the individuals in their stimulus sets were also closely related to those individuals' actual eigenvector centralities, $r = 0.74$, $p < .000001$. Shaded regions in **(B)** and **(C)** indicate 95% C.I. of the ordinary least squares fit to the data. As described in the main text, self-report data was obtained after scanning and was *z*-scored within variable within participant; network constraint and eigenvector centrality were log-transformed prior to plotting and analysis to alleviate skew.

Discussion

In contrast to many other highly social species that enact social behavior by forming loose, anonymous aggregations (e.g., flocks, herds), humans form relatively stable, structured social groups consisting of many long-term, differentiated, non-reproductive bonds with non-kin (Shultz & Dunbar, 2010). The cognitive demands of navigating these groups (e.g., understanding the prospective implications of one’s own and others’ behavior) are thought to have been a driving force in human brain evolution (Dunbar & Shultz, 2007). A growing body of literature that integrates approaches from social network analysis and psychology suggests that humans and other highly social animals monitor not only direct relationships with others, but also patterns of social ties between third parties, and that this knowledge is used to inform individual behavior (Brent et al., 2014; Brent, 2015; Burt & Knez, 1995; Cheney & Seyfarth, 1986; Ellwardt et al., 2012; Fuong, Maldonado-Chaparro, & Blumstein, 2015; Massen, Pašukonis, et al., 2014; Massen, Szipl, et al., 2014; Slocombe & Zuberbühler, 2007). The findings presented in Study 2 confirm that humans possess a strikingly accurate understanding of the social network positions of familiar others, and demonstrate for the first time that this knowledge is activated spontaneously upon viewing those individuals. Furthermore, these results indicate that individuals who tend to regulate their behavior and self-presentation more to suit their current social context tend to spontaneously encode more knowledge about familiar individuals when encountering them.

Spontaneous neural encoding of social network position

The task used in the fMRI study (i.e., a one-back memory task) did not require subjects to retrieve social relationship or personality knowledge about the individuals being viewed. Nevertheless, up to 40% of the information content of local neural responses to personally familiar others could be explained merely by characteristics of those individuals' positions in the perceiver's social network (Figure 10B). Remarkably, when personality traits and social network position characteristics were included in the model, up to 58% of the information content of neural responses to personally familiar individuals could be explained (Figure 11A). These findings are consistent with behavioral evidence that humans spontaneously activate knowledge about other people's personality traits and attitudes when perceiving them so that this knowledge can usefully inform our thoughts and behavior (Andersen, Reznik, & Manzella, 1996; Bargh, Chen, & Burrows, 1996; Todorov & Uleman, 2002). The current study provides the first evidence that humans automatically activate knowledge about other people's positions in our social networks when viewing them. This spontaneous encoding of social network position is consistent with psychologists' mounting appreciation for the importance of both direct and indirect relationship knowledge to everyday cognition and behavior.

Brain areas where the local neural information content could be particularly well explained by social knowledge about the individuals being viewed included regions that have previously been suggested to support the retrieval of person knowledge when viewing familiar individuals, such as the TP and posterior superior temporal cortex (Gobbini & Haxby, 2007). Information about particular aspects of social network position was carried in diverse and distributed sets of brain regions (Figure 10A).

Although we hesitate to engage in a significant amount of speculative reverse inference, preliminary interpretations of the localization of these results are discussed briefly below. In addition, we discuss how these results might inform and constrain testable hypotheses regarding how relative social network position impacts human perception, cognition, and behavior.

Spontaneous neural encoding of social distance. The largest cluster in which the local neural information content could be significantly explained by egocentric social distance was centered in the RTPJ. This finding is consistent with the results of Study 1, which demonstrated that egocentric social distances are represented in multi-voxel response patterns in the RTPJ when participants are asked to explicitly judge egocentric social distances (Parkinson, Liu, & Wheatley, 2014). The current findings suggest that neural population codes in the RTPJ automatically encode social distances from oneself, even in the absence of a related task.

Information about social distance was also carried in multi-voxel response patterns in brain areas previously implicated in encoding facial identity (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Nestor, Plaut, & Behrmann, 2011), such as the TP and FG bilaterally, as well as areas that have been implicated in encoding other aspects of person knowledge (e.g., personality traits), such as the MPFC (Hassabis et al., 2014; Ma et al., 2014). The fact that population responses in areas previously implicated in encoding personality trait information and identity also encode social distance suggest that distance from oneself in terms of social ties comprises a dimension of social meaning along which our mental representations of other people are organized.

More generally, these results suggest that egocentric social distance obligatorily influences our responses to familiar others. Although a rich body of literature has investigated how neural and behavioral responses to other people differ when those individuals are strangers rather than friends (Deaner et al., 2007; Fareri & Delgado, 2014; Martin et al., 2015; Meyer et al., 2013; Visconti di Oleggio Castello et al., 2014), far less is known about the impact of social distance on cognition and behavior within the spectrum of individuals who are already familiar to us, even though these are the individuals with whom we tend to have regular, repeated social interactions. In the current study, all individuals in participants' stimulus sets were personally familiar to them. Information about participants' social distance from these individuals was encoded in several brain regions, including areas that have previously been implicated in encoding self-relevance, modeling other minds, modulating attention, and retrieving memories (Adolphs, 2009; Amodio & Frith, 2006; Gobbini & Haxby, 2007; Hassabis et al., 2014; Parkinson et al., 2014). Given the functional heterogeneity of many of these regions, it is not possible to discern precisely which of the mental processes that these regions underlie are impacted by social distance between the perceiver and familiar others. Nonetheless, the current results suggest that social distances between ourselves and familiar others may have wide-ranging effects on our thoughts and behavior. Given that this information appears to be encoded automatically, future research should investigate how distances in social ties from other members of our social networks (e.g., whether someone is a friend, a friend-of-a-friend, or farther removed from us in terms of social ties) impact specific processes such as emotional contagion, mentalizing, social attention, and assessments of trustworthiness.

Spontaneous neural encoding of network constraint. Large clusters spanning both the right and left lateral superior temporal cortex carried information about the network constraint of the individuals being viewed (Table A3). Although the lateral superior temporal sulcus (STS) is consistently associated with biological motion processing (Grossman, Battelli, & Pascual-Leone, 2005; Grossman & Blake, 2002), subsequent analyses of experimental stimuli indicated that individual differences in video subjects' network constraint were not associated with differences in the amount that those individuals moved in their videos (see Appendix 1; Figure A1). Thus, the fact that information about the network constraint of the individuals being viewed is encoded in the right and left STS appears not to be attributable to low-level differences in the amount of motion present in the videos used in the experiment.

It is possible that a perceiver's knowledge of the network constraint of an individual, or of dispositions that tend to co-vary with this aspect of social network position, impacts how the perceiver attends to that individual's movements. For example, brokers may be perceived as differentially charismatic or interesting (e.g., because they often serve as sources of novel information or opportunities, Burt et al., 2013), and thus, may command differential amounts of top-down attention to their expressions, movements, and gestures. Alternatively, brokers may differ in the amount of social meaning carried in their facial and bodily movements. Two individuals' videos could contain equivalently large amounts of movement, but differ in terms of implied vocal expressivity, which the STS also encodes (Grandjean et al., 2005), or in terms of the degree of social information conveyed in those movements. For instance, one person could fidget aimlessly while another uses movement to express themselves coherently.

The latter interpretation is consistent with previous evidence that the STS responds to the social meaning, rather than amount, of movement in dynamic displays (Wheatley, Milleville, & Martin, 2007). Future studies could arbitrate between these competing hypotheses by testing if strangers are able to differentiate between individuals who occupy high- and low-constraint network positions, and perhaps even infer this social network position information, based on their observed movements. If so, this would suggest that network constraint is encoded in the STS because this aspect of social network position is apparent in people's movements – i.e., in how individuals carry themselves. If not, this would be consistent with the interpretation that perceivers' knowledge of an individual's network constraint, or of qualities related to this aspect of social network position, influences how perceivers attend to that individual's expressions, gestures, and bodily movements.

Spontaneous neural encoding of eigenvector centrality. The largest cluster that carried a significant amount of information about the degree to which the individual being viewed was well connected to well connected others (i.e., his or her eigenvector centrality) was located in EVC. This result is unlikely to be due to low-level visual differences in the stimuli, as each fMRI participant had a unique stimulus set, and because videos corresponding to each individual in each stimulus set were horizontally mirrored on half of trials. Given that population codes in EVC are impacted by attention and by participants' expectations (Jehee, Brady, & Tong, 2011; Kok, Jehee, & de Lange, 2012), this finding may reflect the effects of social status in terms of social ties on visual attention. Information about other kinds of social status (e.g., physiognomic cues to dominance) impacts the allocation of visual attention in humans and in other group-living primates: We tend to preferentially orient toward high-status individuals and to the loci of their attention, presumably in order to obtain behaviorally relevant information about our surroundings (Dalmaso et al., 2012; Klein, Shepherd, & Platt, 2009; Shepherd et al., 2006). Given that information about eigenvector centrality is carried in neural response patterns in EVC, future research should test if visual attention is also preferentially allocated to individuals who are more central to one's social network.

Eigenvector centrality-based RDMs were significantly related to neural RDMs in brain areas that have been previously implicated in encoding social status in terms of physical dominance, prestige, and morality, such as the VMPFC, VLPFC, and STG (Cloutier, Ambady, Meagher, & Gabrieli, 2012; Cloutier & Gyurovski, 2014; Marsh, Blair, Jones, Soliman, & Blair, 2009). Given that these regions are functionally quite heterogeneous, future work should explore how the representation of social status in terms of social network position in these regions relates to the representation of other kinds of social status (e.g., status based on physical dominance or prestige) and other domains of information, as well as to these regions' more general functions.

The current findings indicate that an individual's social status in terms of social ties influences how others respond to that individual. High eigenvector centrality individuals tend to be people whose approval is particularly beneficial, and with whom negative interactions could be particularly socially costly (Ellwardt et al., 2012). Cognitive resources may be devoted to identifying and monitoring these individuals because of their relatively high behavioral relevance and value as social partners. Given that we appear to automatically encode the eigenvector centralities of familiar others upon encountering them, future research should test the specific cognitive and behavioral consequences of this aspect of social network position.

Individual differences in social tuning

The results of our main analyses suggest that individuals spontaneously encode information about the social network positions and personality traits of familiar individuals when viewing them (Figure 10). If it is the case that spontaneously encoding person knowledge serves to inform subsequent behavior, then individuals who tend to regulate their behavior more to suit their current audience should encode more of this information when encountering familiar others. In line with this prediction, the MPFC, a brain region with a long-established role in making inferences about others' personality traits (Harris, Todorov, & Fiske, 2005; Ma et al., 2014; Mitchell, Cloutier, Banaji, & Macrae, 2006; Wagner, Haxby, & Heatherton, 2012), and that has recently been shown to contribute to the creation and maintenance of personality models via information carried in its distributed response patterns (Hassabis et al., 2014), encoded more information about the personality traits and social network positions of the individuals whom participants were viewing to the extent that participants themselves were high self-monitors. The MFPC contained the largest cluster in which participants' self-monitoring scores were significantly positively related to the degree to which local neural response patterns encoded person knowledge (Table A4).

Self-monitoring was also positively related to the extent to which the eight-predictor model explained the informational content of clusters within brain areas implicated in affective/reward processing (e.g., OFC; ventral striatum), attention (e.g., SPL), and encoding person identity (e.g., FG). Thus, the cognitive and emotional processes carried out in these brain regions may also be more systematically impacted by one's current social context to the extent that one is a high self-monitor.

Conclusions

Social network position characteristics comprise largely heritable dispositions that influence how we interact with one another in day-to-day life, success in contemporary society, and even reproductive fitness (Aral & Alstyne, 2011; Brent et al., 2014; Brent, 2015; Burt et al., 2013; Fowler, Dawes, & Christakis, 2009; Scott & Judge, 2009). The current results indicate that we can accurately infer characteristics of familiar individuals' social network positions, and that we process this information automatically when encountering people whom we know. Furthermore, consistent with the suggestion that spontaneously encoding person knowledge serves to inform behavior (Gobbini & Haxby, 2007), participants who reported regulating their self-presentation and behavior more to suit current company in everyday life encoded more social information about their classmates upon viewing them. The results of Study 2 underline the importance and utility of integrating an understanding of the social networks that we inhabit into the study of social perception. Our everyday interactions are influenced not only by information that would be available to any perceiver, such as an individual's apparent emotional state or group membership, but also by that individual's relationship to us and by patterns of relationships between third parties within our social networks. Thus, adopting an interdisciplinary approach that combines theory and methods from social psychology, neuroscience, and social network analysis is likely to enrich our understanding of how humans negotiate the intricacies of everyday social interactions.

Study 3

Minds of a Feather: Inter-subject Similarities of Neural Responses to Naturalistic Stimuli Predict Social Network Proximity

In 1545, William Turner wrote "*Byrdes of on kynde and color flok and flye allwayes together*," reflecting the ancient truism that people resemble their friends (Titelman, 1996). Research has borne out this intuition: Social ties are forged within the same age groups, genders, ethnicities, and many other demographic categories at higher than expected rates (McPherson, Smith-Lovin, & Cook, 2001). This assortativity in friendship networks is referred to as homophily and has been demonstrated across diverse contexts and geographic locations, including online social networks (Apicella, Marlowe, Fowler, & Christakis, 2012; Fu, Nowak, Christakis, & Fowler, 2012; Lewis, Gonzalez, & Kaufman, 2012; McPherson et al., 2001). Indeed, consistent evidence suggests that homophily is an ancient organizing principle of human sociality. Despite pressures within the kinds of social groups in which humans evolved to divide labor and otherwise organize complementary needs and roles, social ties in small hunter-gatherer bands instead reflect *similarities* of age, weight, body fat, handgrip strength, and cooperative behavioral tendencies (Apicella et al., 2012). Significant examples of heterophily – i.e., the tendency to associate with others who are dissimilar from oneself – are markedly rarer in such groups. Consistent with its ancient history, homophily also characterizes the social networks of our close primate relatives (Massen & Koski, 2014); similarity has been suggested to confer advantages for cohesion, collective action, and empathy (Apicella et al., 2012; Massen & Koski, 2014). When humans *do* forge ties with individuals who are dissimilar from themselves, these relationships tend to be instrumental, task-oriented (e.g., professional collaborations involving people with complementary skill sets, Moody, 2004), and short-lived, often dissolving after the individuals involved have achieved their shared goal (Rivera, Soderstrom, & Uzzi, 2010). Thus, human social networks tend to be overwhelmingly homophilous (Rivera et al., 2010).

Despite robust evidence that homophily organizes human social networks, significant lacunae remain in our understanding of how homophily arises and functions in these networks (Fu et al., 2012; Massen & Koski, 2014). Prior studies of homophily have been concerned largely with physical traits and demographic variables (e.g. age, gender, class). Importantly, additional research has demonstrated that homophily extends beyond overt, demographic cues, to behaviors associated with mental states such as empathy and aspects of personality. For example, behavioral tendencies (e.g., public goods games donations) associated with altruistic behavior are more similar among individuals who are friends compared with those who are not (Apicella et al., 2012), consistent with suggestions from evolutionary game theory that altruistic behavior only benefits individuals if their interaction partners also behave altruistically (Gilchrist, 2007; Smith, 1984). Remarkably, social network proximity is as important as genetic relatedness and more important than geographic proximity in predicting the similarity of two individuals' cooperative behavioral tendencies (Apicella et al., 2012). Thus, social network proximity can be a powerful predictor of behavioral similarity.

Recent work has just begun to move beyond externally evident demographic attributes. In addition to the cooperative behavioral tendencies described above, some personality traits may also exhibit social assortativity. Two of the "Big Five" personality traits – extraversion (Feiler & Kleinbaum, 2015; Selfhout et al., 2010) and openness to experience (Selfhout et al., 2010) – appear to be more similar among friends than among individuals who are not friends with one another. However, the remaining Big Five traits do not predict friendship formation well (Selfhout, Denissen, Branje, & Meeus, 2009). Similarities in conscientiousness and neuroticism are not associated with friendship formation (Selfhout et al., 2010), and evidence for more similar levels of trait agreeableness among friends has been found in some studies (Selfhout et al., 2010), but not in others (Feiler & Kleinbaum, 2015).

It is possible that certain personality traits exhibit assortativity because people who are similar to one another in terms of such traits choose to enter into similar situations. Thus, similar individuals may have a disproportionately large number of opportunities to interact and connect with one another (Blau & Schwartz, 1984). For example, similarities in individuals' levels of openness to experience may be reflected in similarities in those individuals' vocational choices (Holland, Johnston, Hughey, & Asama, 1991). Additionally, individuals who exhibit high levels of extraversion may seek out more social gatherings, whereas more introverted individuals may choose to interact in more intimate settings (Feiler & Kleinbaum, 2015). Individuals who find themselves in the same vocations and social settings would, of course, have more opportunities to develop friendships with one another. Thus, homophily may result simply from more frequent interaction opportunities among similar individuals. Indeed, sociologists have documented precisely such "induced homophily" (McPherson & Smith-Lovin, 1987) resulting from endogenous selection into residential neighborhoods (Blau & Schwartz,

1984) or work organizations (Bielby & Baron, 1986) whose members are disproportionately similar.

While the extant research has focused predominately on demographic variables and has recently begun to examine personality, it is also possible that people cluster along these dimensions because they reflect commonalities in perceiving, thinking about, and reacting to the world. Similarity in how individuals perceive, interpret and respond to their environment increases the predictability of one another's thoughts and behavior during social interactions (C. R. Berger & Calabrese, 1975), since knowledge about oneself is a more valid source of information about similar others than about dissimilar others. This increased predictability during social interaction, in turn, allows for less effortful and more confident communication, thus fostering more enjoyable social interactions, and increasing the likelihood of developing friendships (C. R. Berger & Calabrese, 1975). In the same vein, interacting with individuals who share similar values, opinions, and interests may be rewarding because it reinforces one's own values, opinions, and interests, thus producing an implicit positive affective response, promoting attraction to similar others, and increasing the likelihood of developing friendships with individuals who see the world similarly to ourselves (Clore & Byrne, 1974). If friends are indeed exceptionally similar to one another in terms of how they perceive, interpret, and react to their environment, then social network proximity should be associated with similarity of cognitive processes as they unfold in real time. Whether or not humans tend to associate with others who perceive, interpret, and respond to the world similarly has yet to be tested directly.

In Study 3, we sought to test if neural responses while viewing naturalistic stimuli are more similar among friends than among individuals who are farther removed from one another in a real-world social network. Measuring neural activity while people view naturalistic stimuli (e.g., movies, natural scenes) offers an unobtrusive window into individuals' unconstrained thought processes as they unfold (Cantlon & Li, 2013). Inter-subject correlations of neural response time series during natural viewing of dynamic stimuli are associated with similarities in participants' interpretation and understanding of the stimuli that they experience (Ames et al., 2014; Cantlon & Li, 2013; Hasson et al., 2009, 2012). Thus, inter-subject similarities of neural response time series data offer insight into the similarity of individuals' thought processes as they experience the world around them.

We first characterized the social network of an entire cohort of MBA students (a different cohort than was used in Study 2). A subset of these individuals subsequently participated in an fMRI study. During the fMRI study, each participant watched the same collection of video clips. We predicted that inter-subject similarities among friends would be higher than inter-subject similarities among individuals who are two or more degrees removed from one another in the social network. Further, we tested if similarities of neural responses can be used to predict the social distance between members of this social network.

Methods

Part 1: Social network characterization and demographic data collection

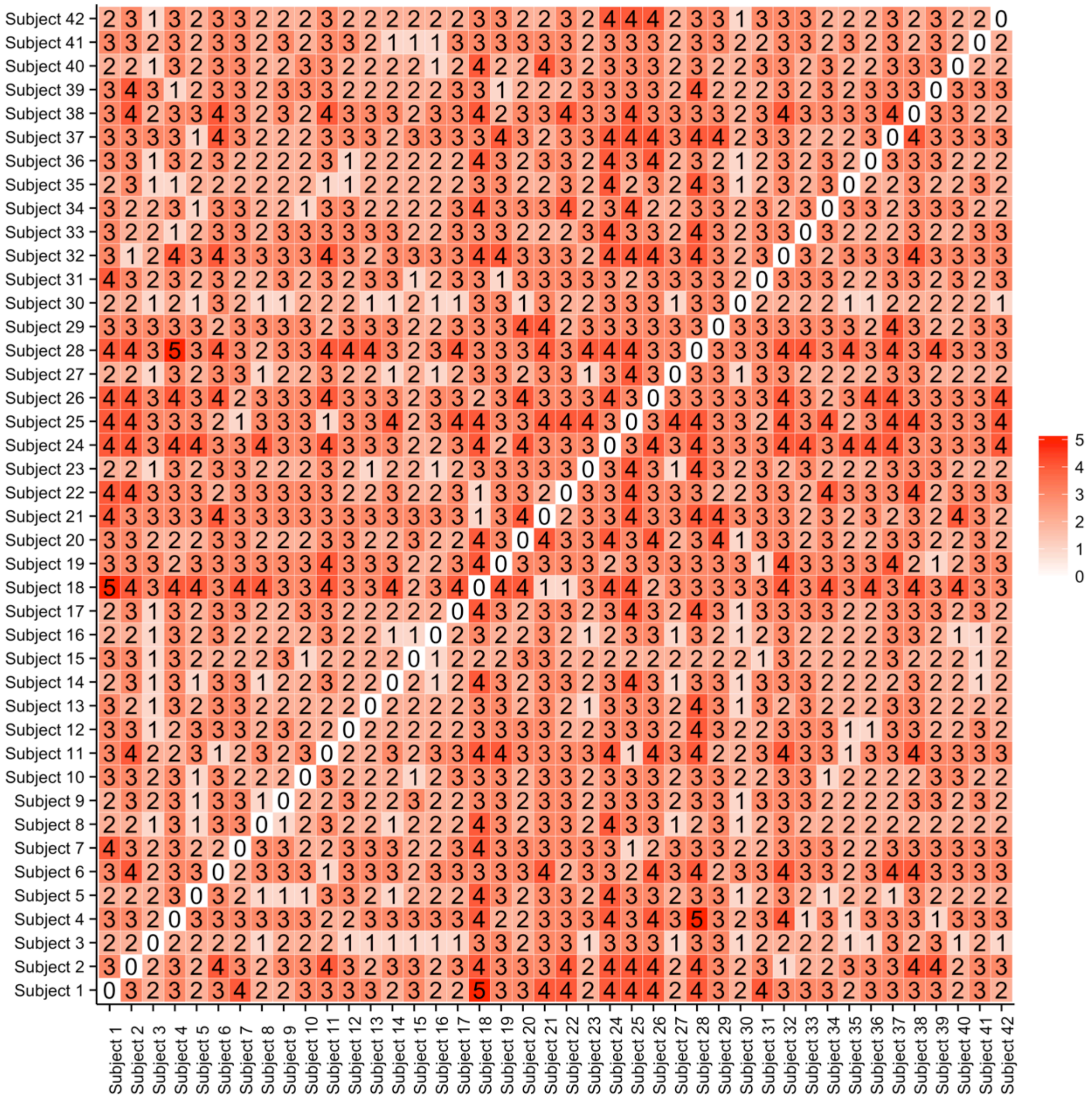
Participants. Participants in Part 1 of the study were 279 first-year MBA students (89 females) at a private university in the northeastern United States who participated as part of their coursework on leadership. The total class size was 279 students; a 100% response rate was obtained for Part 1 of the study. All participants provided informed consent in accordance with the standards of the Dartmouth Committee for the Protection of Human Subjects.

Figure 14. Social network characterization (Study 3). The social network of an entire first-year cohort of MBA students was reconstructed based on responses to an online questionnaire administered to all members of the class (*N* = 279; 100% response rate). Nodes indicate students; lines indicate reported social ties between them. Only mutually reported social ties are illustrated. A subset of these students participated in an fMRI study. Orange nodes indicate fMRI study participants; gray nodes denote other members of the graduate program.

Method. In order to characterize the social network of all first-year MBA students, the same online social network survey was used that was used in Study 2. Participants followed an e-mailed link to the study website where they responded to a survey designed to assess their position in the social network of first-year students in their academic program. The survey question was nearly identical to that used in Study 2 (*"Consider the people with whom you like to spend your free time. Since you arrived at* *[institution name], who are the classmates you have been with most often for informal social activities, such as going out to lunch, dinner, drinks, films, visiting one another's homes, exercising together, and so on?"*), and there were no significant changes in how the social network survey was administered in Study 3 relative to Study 2. The social network of the cohort of MBA students who participated in Study 3 is illustrated in Figure 14.

In addition, demographic data about each subject's gender, ethnic identity, and country of citizenship were obtained from the school's registrar. Personally identifying information was removed from these data; participants' demographic, social network, and neuroimaging data were linked only by anonymous ID numbers.

Data analysis. Social network analysis was performed using the R package igraph (Csardi & Nepusz, 2006; R Core Development Team, 2013). An unweighted, undirected graph consisting only of reciprocal (i.e., mutually reported) social ties was used to estimate social distances between individuals. For example, an undirected edge would connect two actors *i* and *j* only if *i* and *j* each nominated the other as a friend. If *i* nominated *j*, but *j* did not nominate *i,* or vice versa, these actors were not considered friends for the purposes of this study. Social distance was operationalized as the smallest number of intermediary, mutual social ties required to connect two individuals in the network (i.e., geodesic distance). Pairs of individuals who both named one another as friends were assigned a social distance of one. An individual would be assigned a distance of two from a given participant if he or she had a mutually reported friendship with that participant's friend, but not with the participant him or herself, and so on. Social distances between all pairs of fMRI study participants are provided in Figure 15.



	Subject 1	Subject 2	Subject 3	Subject 4	Subject 5	Subject 6	Subject 7	Subject 8	Subject 9	Subject 10	Subject 11	Subject 12	Subject 13	Subject 14	Subject 15	Subject 16	Subject 17	Subject 18	Subject 19	Subject 20	Subject 21	Subject 22	Subject 23	Subject 24	Subject 25	Subject 26	Subject 27	Subject 28	Subject 29	Subject 30	Subject 31	Subject 32	Subject 33	Subject 34	Subject 35	Subject 36	Subject 37	Subject 38	Subject 39	Subject 40	Subject 41	Subject 42
Subject 42	2	3	1	3	2	3	3	2	2	2	3	2	2	2	2	2	2	3	3	2	2	3	2	4	4	4	2	3	3	1	3	3	3	2	2	2	3	2	3	2	2	0
Subject 41	3	3	2	3	2	3	3	2	3	2	3	3	2	1	1	1	3	3	3	3	3	3	2	3	3	3	2	3	3	2	2	3	3	2	3	2	3	2	3	2	0	2
Subject 40	2	2	1	3	2	3	3	2	2	3	3	2	2	2	2	1	2	4	2	2	4	3	2	3	3	3	2	3	2	2	3	3	2	3	2	2	3	3	3	0	2	2
Subject 39	3	4	3	1	2	3	3	2	3	3	3	2	2	2	2	2	3	3	1	2	2	2	3	3	3	3	2	4	2	2	2	3	2	3	2	3	3	3	0	3	3	3
Subject 38	3	4	2	3	3	4	3	2	3	2	4	3	3	3	2	3	3	4	2	3	3	4	3	3	4	3	3	3	3	2	3	4	3	3	3	3	4	0	3	3	2	2
Subject 37	3	3	3	3	1	4	3	2	2	2	3	3	3	2	3	3	3	3	4	3	2	3	3	4	4	4	3	4	4	2	3	3	2	2	2	3	0	4	3	3	3	3
Subject 36	3	3	1	3	2	3	2	2	2	2	3	1	2	2	2	2	2	4	3	2	3	3	2	4	3	4	2	3	2	1	2	3	2	3	2	0	3	3	3	2	2	2
Subject 35	2	3	1	1	2	2	2	2	2	2	1	1	2	2	2	2	2	3	3	2	2	3	2	4	2	3	2	4	3	1	2	3	2	3	0	2	2	3	2	2	3	2
Subject 34	3	2	2	3	1	3	3	2	2	1	3	3	2	2	2	2	3	4	3	3	3	4	2	3	4	2	2	3	3	2	3	2	3	0	3	3	2	3	3	3	2	2
Subject 33	3	2	2	1	2	3	3	2	3	3	3	3	3	3	2	2	3	3	3	2	2	2	3	4	3	3	2	4	3	2	3	3	0	3	2	2	2	3	2	2	3	3
Subject 32	3	1	2	4	3	4	3	3	3	3	4	3	2	3	3	3	3	4	4	3	3	3	2	4	4	4	3	4	3	2	3	0	3	2	3	3	3	4	3	3	3	3
Subject 31	4	3	2	3	2	3	2	2	3	2	3	2	3	3	1	2	3	3	1	3	3	3	3	3	2	3	3	3	3	2	0	3	3	3	2	2	3	3	2	3	2	3
Subject 30	2	2	1	2	1	3	2	1	1	2	2	2	1	1	2	1	1	3	3	1	3	2	2	3	3	3	1	3	3	0	2	2	2	2	1	1	2	2	2	2	2	1
Subject 29	3	3	3	3	3	2	3	3	3	3	2	3	3	3	2	2	3	3	3	4	4	2	3	3	3	3	3	3	0	3	3	3	3	3	3	2	4	3	2	2	3	3
Subject 28	4	4	3	5	3	4	3	2	3	3	4	4	4	3	2	3	4	3	3	3	4	3	4	4	4	3	3	0	3	3	3	4	4	3	4	3	4	3	4	3	3	3
Subject 27	2	2	1	3	2	3	3	1	2	2	3	2	2	1	2	1	2	3	3	2	3	3	1	3	4	3	0	3	3	1	3	3	2	2	2	2	3	3	2	2	2	2
Subject 26	4	4	3	4	3	4	2	3	3	3	4	3	3	3	2	3	3	2	3	4	3	3	3	4	3	0	3	3	3	3	3	4	3	2	3	4	4	3	3	3	3	4
Subject 25	4	4	3	3	3	2	1	3	3	3	1	3	3	4	2	3	4	4	3	3	4	4	4	3	0	3	4	4	3	3	2	4	3	4	2	3	4	4	3	3	3	4
Subject 24	4	4	3	4	4	3	3	4	3	3	4	3	3	3	2	2	3	4	2	4	3	3	3	0	3	4	3	4	3	3	3	4	4	3	4	4	4	3	3	3	3	4
Subject 23	2	2	1	3	2	3	3	2	2	2	3	2	1	2	2	1	2	3	3	3	3	3	0	3	4	3	1	4	3	2	3	2	3	2	2	2	3	3	3	2	2	2
Subject 22	4	4	3	3	3	2	3	3	3	3	3	2	2	3	2	2	3	1	3	3	2	0	3	3	4	3	3	3	2	2	3	3	2	4	3	3	3	4	2	3	3	3
Subject 21	4	3	3	3	3	4	3	3	3	3	3	3	3	3	3	3	3	1	3	4	0	2	3	3	4	3	3	4	4	3	3	3	2	3	2	3	2	3	2	4	3	2
Subject 20	3	3	2	2	2	3	3	2	2	2	3	3	2	2	3	2	2	4	3	0	4	3	3	4	3	4	2	3	4	1	3	3	2	3	2	2	3	3	2	2	3	2
Subject 19	3	3	3	2	3	3	3	3	3	3	4	3	3	3	2	2	3	4	0	3	3	3	3	2	3	3	3	3	3	3	1	4	3	3	3	3	4	2	1	2	3	3
Subject 18	5	4	3	4	4	3	4	4	3	3	4	3	3	4	2	3	4	0	4	4	1	1	3	4	4	2	3	3	3	3	3	4	3	4	3	4	3	4	3	4	3	3
Subject 17	2	3	1	3	2	3	3	2	2	3	3	2	2	2	2	2	0	4	3	2	3	3	2	3	4	3	2	4	3	1	3	3	3	3	2	2	3	3	3	2	3	2
Subject 16	2	2	1	3	2	3	2	2	2	2	3	2	2	1	1	0	2	3	2	2	3	2	1	2	3	3	1	3	2	1	2	3	2	2	2	2	3	3	2	1	1	2
Subject 15	3	3	1	3	2	2	2	2	3	1	2	2	2	2	0	1	2	2	2	3	3	2	2	2	2	2	2	2	2	2	1	3	2	2	2	2	3	2	2	2	1	2
Subject 14	2	3	1	3	1	3	3	1	2	2	3	2	2	0	2	1	2	4	3	2	3	3	2	3	4	3	1	3	3	1	3	3	3	2	2	2	2	3	2	2	1	2
Subject 13	3	2	1	3	2	3	3	2	2	2	2	2	0	2	2	2	2	3	3	2	3	2	1	3	3	3	2	4	3	1	3	2	3	2	2	2	3	3	2	2	2	2
Subject 12	3	3	1	2	3	3	3	2	3	2	2	0	2	2	2	2	2	3	3	3	3	2	2	3	3	3	2	4	3	2	2	3	3	3	1	1	3	3	2	2	3	2
Subject 11	3	4	2	2	3	1	2	3	2	3	0	2	2	3	2	3	3	4	4	3	3	3	3	4	1	4	3	4	2	2	3	4	3	3	1	3	3	4	3	3	3	3
Subject 10	3	3	2	3	1	3	2	2	2	0	3	2	2	2	1	2	3	3	3	2	3	3	2	3	3	3	2	3	3	2	2	3	3	1	2	2	2	2	3	3	2	2
Subject 9	2	3	2	3	1	3	3	1	0	2	2	3	2	2	3	2	2	3	3	2	3	3	2	3	3	3	2	3	3	1	3	3	3	2	2	2	2	3	3	2	3	2
Subject 8	2	2	1	3	1	3	3	0	1	2	3	2	2	1	2	2	2	4	3	2	3	3	2	4	3	3	1	2	3	1	2	3	2	2	2	2	2	2	2	2	2	2
Subject 7	4	3	2	3	2	2	0	3	3	2	2	3	3	3	2	2	3	4	3	3	3	3	3	3	1	2	3	3	3	2	2	3	3	3	2	2	3	3	3	3	3	3
Subject 6	3	4	2	3	3	0	2	3	3	3	1	3	3	3	2	3	3	3	3	3	4	2	3	3	2	4	3	4	2	3	3	4	3	3	2	3	4	4	3	3	3	3
Subject 5	2	2	2	3	0	3	2	1	1	1	3	3	2	1	2	2	2	4	3	2	3	3	2	4	3	3	2	3	3	1	2	3	2	1	2	2	1	3	2	2	2	2
Subject 4	3	3	2	0	3	3	3	3	3	3	2	2	3	3	3	3	3	4	2	2	3	3	3	4	3	4	3	5	3	2	3	4	1	3	1	3	3	3	1	3	3	3
Subject 3	2	2	0	2	2	2	2	1	2	2	2	1	1	1	1	1	1	3	3	2	3	3	1	3	3	3	1	3	3	1	2	2	2	2	1	1	3	2	3	1	2	1
Subject 2	3	0	2	3	2	4	3	2	3	3	4	3	2	3	3	2	3	4	3	3	3	4	2	4	4	4	2	4	3	2	3	1	2	2	3	3	3	4	4	2	3	3
Subject 1	0	3	2	3	2	3	4	2	2	3	3	3	3	2	3	2	2	5	3	3	4	4	2	4	4	4	2	4	3	2	4	3	3	3	2	3	3	3	3	2	3	2

Figure 15. Social distances between all pairs of fMRI study participants in Study 3. This symmetric distance matrix illustrates social distances between all pairs of fMRI study participants in Study 3. Social distance was operationalized as the geodesic distance between participants based on mutually reported social ties in the entire social network of first-year MBA students.

Part 2. Neuroimaging Study

Participants. Forty-two subjects (12 female; 3 left-handed) aged 25 to 32 (M = 27.98; SD = 1.72) who had completed Part 1 of the study completed a subsequent neuroimaging study. Students were informed during class about the opportunity to participate in an fMRI study involving viewing visual stimuli. They were informed that they would receive $20 per hour as compensation for their time, as well as anatomical images of their brains. All participants were fluent in English and had normal or corrected-to-normal vision. Participants provided informed consent in accordance with the policies of the Dartmouth College Committee for the Protection of Human Subjects.

Image acquisition. Participants were scanned at the Dartmouth Brain Imaging Center using a 3T Philips Achieva Intera scanner with a 32-channel head coil. An echo-planar sequence (35 ms TE; 2000 ms TR; 3.0 mm x 3 .0 x 3.0 mm resolution; 80 x 80 matrix size; 240 x 240 mm FOV; 35 interleaved transverse slices with no gap; 3.0 mm slice thickness) was used to acquire functional images. Stimuli were presented over the course of six functional runs. Functional runs consisted of 204, 276, 194, 147, 189, and 108 dynamic scans, for a total functional data acquisition time of approximately 33.7 minutes, excluding time between functional runs. A high-resolution T1-weighted anatomical scan was also acquired for each participant (8.2 s TR; 3.7 ms TE; 240 x 187 FOV; 0.938 mm x 0.938 mm x 1.0 mm resolution) at the end of the scanning session. Foam padding was placed around subjects' heads to minimize head motion.

fMRI paradigm. Prior to being scanned, participants were informed that they would be watching a series of brief videos while in the scanner. Participants were informed that these videos would be brief and would vary in content, and that the experience of participating in the study would be analogous to passively watching television while someone else "channel surfed." Videos were presented in the same order to all participants in order to avoid inducing inter-subject response variability that would be attributable simply to differences in the manner in which clips were presented in the experiment (e.g., if a serious video happened to be preceded by a comedic clip for some participants and not others). Given that the current study aimed to test if participants' positions relative to one another in their social networks are associated with neural response similarity, rather than to contrast responses to particular stimuli, the benefits of using a single trial order for all subjects were judged to outweigh potential costs. After the scanning session had concluded, the experimenter interviewed each participant to determine if he or she had previously seen any of the video clips used in the experiment.

All participants experienced the same stimuli in the same order, and were provided with the same instructions. Therefore, differences in the similarities of participants' neural response time courses likely stem from factors such as differences in participants' dispositions, moods, cognitive styles, pre-existing assumptions, expectations, values, views, and interests, as well differences in the pre-existing knowledge structures into which incoming stimuli are integrated.

Stimuli. Stimuli consisted of 14 videos presented with sound over the course of six fMRI runs. Videos ranged in duration from 91 s to 305 s (Table 3). Three principal criteria were used to select video clips as stimuli. First, we sought to select stimuli that participants in our sample would be relatively unlikely to have seen before. This was done in order to avoid inducing differences in inter-subject correlations due to simple familiarity with the stimuli, given that friends may be more likely to have seen the same videos prior to the experiment compared with pairs of individuals who are not friends with one another.

Second, we sought to select engaging stimuli. We reasoned that insufficiently engaging stimuli would be likely to evoke mind wandering, which would likely involve idiosyncratic thoughts unrelated to the experiment, and thus would introduce unwanted noise into estimates of inter-subject correlations and their relationships to social distance. In contrast, stimuli that effectively engage an audience do so by directing and constraining viewers' thoughts and associated neural activity. As such, professionally directed movies and television shows elicit more reliable responses within and across participants than unedited video footage or series of static photographs (Hasson et al., 2010). Professionally directed videos are engineered to engage viewers' attention and drive their inferences by inducing particular reactions and interpretations at specific times, and thus, are well-suited for experiments seeking to induce a shared series of cognitive states across participants (Hasson et al., 2012).

Third, we sought to select stimuli that, while engaging, would also introduce meaningful variability in inter-subject correlations. We reasoned that for the purposes of the current study, *uninformative* inter-subject variability in neural response time series data would arise largely from using stimuli that failed to effectively engage participants, and thus, failed to constrain their thoughts and attention. In contrast, *meaningful* inter-subject variability in neural response time series data would arise from using stimuli that produced diverging inferences and patterns of attentional allocation in different sets of viewers. We sought to select stimuli that minimized *uninformative* inter-subject variability by engaging participants' attention, but at the same time, promoted *meaningful* inter-subject variability by evoking divergent reactions across participants. For example, videos were chosen that might be interpreted as sweet by some participants, but cloying or "sappy" by others (e.g., a sentimental music video), that would appeal to different styles of humor (e.g., physical comedy, wry humor, "cringe" comedy, sophomoric or “lowbrow” humor), and that presented one or both sides of an argument that participants might resonate with or respond to with criticism (e.g., a debate about whether college football should be banned). Brief descriptions of all 14 videos are presented in Table 3.

Table 3. Summary of video clips shown in Study 3

Clip		**Description**	**Duration (s)**
1	‘An Astronaut’s View of Earth’	An astronaut discusses viewing Earth from space, and in particular, witnessing the effects of climate change from space. He then urges viewers to mobilize to address this issue.	223
2	Google Glass review	A journalist wears a Google Glass headset for a day and weighs the pros and cons of being an ‘early adopter’ of this technology.	88
3	‘Crossfire’	Two journalists debate the appropriateness of President Obama’s use of humor in a speech; excerpts from the speech are shown.	89
4	‘All I Want’	A sentimental music video depicting a social outcast with a facial deformity seeking companionship.	305
5	Wedding film	A homemade film depicting scenes from two men’s wedding ceremony and subsequent celebration with family and friends.	120
6	Scientific demonstration	An astronaut at the International Space Station demonstrates and explains what happens when one wrings out a waterlogged washcloth in space.	118
7	‘Food Inc.’	An excerpt from a documentary discussing how the fast food industry influences food production and farming practices in the United States.	178
8	‘We Can Be Heroes’	An excerpt from a ‘mockumentary’-style series in which a man discusses why he nominated himself for the title of ‘Australian of the Year.’	202
9	‘Ban College Football’	Journalists and athletes debate whether or not football should be banned as a college sport.	195
10	Soccer match	Highlights from a soccer match.	91
11	Baby sloth sanctuary	A documentary about caring for baby sloths at a sanctuary in Costa Rica.	200
12	‘Ew!’	A comedy skit in which grown men play teenage girls disgusted by things around them.	169
13	‘Life’s Too Short’	An example of ‘cringe comedy’ in which a dramatic actor is depicted unsuccessfully trying his hand at improvisational comedy.	106
14	‘America’s Funniest Home Videos’	A series of homemade video clips depicting examples of unintentional physical comedy arising from accidents.	101

Data Analysis

Cortical reconstruction and volumetric segmentation of anatomical data.

Anatomical regions were delineated by applying the FreeSurfer anatomical parcellation algorithm (Fischl, 2012) to each subject's high resolution anatomical scan (Figure 16A). Briefly, this process includes removal of non-brain tissue, automated segmentation of the cerebral cortex, subcortical white matter, brainstem, cerebellum, and deep gray matter volumetric structures (e.g., amygdala, hippocampus, putamen), generation of a model of each subject's cerebral cortical surface, and automated parcellation of each subject's cortical surface model into anatomical units based on his or her cortical folding patterns. The Desikan-Killiany cortical atlas (Desikan et al., 2006) as implemented in FreeSurfer 5.3 (Fischl, 2012) was used to assign anatomical labels to each subject's cortical surface model. This gyral-based atlas defines a gyrus as tissue between two adjacent sulci. As such, a particular gyral label in this atlas (e.g., left inferior temporal gyrus) corresponds to both the associated gyrus and the adjacent banks of its limiting sulci. This procedure yielded 34 atlas labels for each hemisphere, as well as six labels corresponding to sub-cortical structures within each hemisphere. Thus, in total, 80 anatomical regions of interest (ROIs) were defined for each subject (for a full list of these regions, please refer to Table A5 in Appendix 2).

Preprocessing of fMRI data. Preprocessing of fMRI time series data was performed using AFNI (Cox, 1996). For each run, functional data were despiked using the AFNI program 3dDespike to remove transient, extreme signal fluctuations not attributable to biological phenomena. Next, each subject's functional scans were aligned to his or her anatomical scan using a six-parameter rigid body least squares transformation. Motion parameters from this volume registration step were saved for later removal from the signal time series as regressors of no interest. The first two volumes of each run were discarded in order to avoid including data potentially characterized by large signal changes prior to tissue reaching a steady state of radiofrequency excitation. Each voxel's time series was scaled to its mean within each run.

In addition to motion parameters extracted during volume registration, time series from voxels corresponding to white matter and ventricles were extracted for later inclusion as regressors of no interest, as signal fluctuations in white matter and cerebrospinal fluid largely reflect noise due to participant motion, instrument instabilities, and physiological artifacts, such as cardiac and respiratory effects, (Dagli, Ingeholm, & Haxby, 1999; Windischberger et al., 2002). White matter and ventricle masks were extracted based on each subject's FreeSurfer segmentation file. These masks were eroded to avoid inclusion of grey matter voxels by excluding any voxels with one or more non-white matter neighbors from the white matter mask, and any voxels with two or more non-ventricle voxels neighbors from the ventricle mask. A relatively less conservative erosion threshold was applied to the ventricle masks to ensure that all subjects' ventricle masks contained voxels; these thresholds were chosen based on the recommendations provided by afni_restproc.py. Data were spatially smoothed separately within gray matter and non-gray matter masks using a 4-mm FWHM Gaussian smoothing kernel. The average time series from each run was extracted from the ventricle mask for use as a global regressor of no interest. In addition, a local regressor of no interest was computed for each voxel by taking the average time series of white matter voxels within a 15-mm radius of that voxel. The temporal derivatives of each regressor of no interest (i.e., motion parameters extracted during volume registration, average ventricle signal, local white matter signal) were computed for use as additional regressors of no interest. Next, a third order polynomial was removed from all regressors of no interest to avoid the inclusion of competing polynomial terms during the subsequent regression.

Finally, nuisance signals (i.e., motion parameters, average ventricle signal, local white matter signal, their derivatives) and a third order polynomial were regressed out of the preprocessed time series of each voxel for each run for each subject. The goal of this procedure was to remove signal changes dues to subject motion, physiological artifacts (e.g., respiration and cardiac effects), and instrument instabilities in order to provide a better estimate of signal fluctuations due to neural processing. For each subject, these pre-processed time series data were concatenated across all six experimental runs. The average pre-processed time series from each of the 80 anatomical regions of interest was extracted for each subject (i.e., data were averaged across all voxels within a given ROI at each time point for each subject).

Due to coverage issues, five subjects were missing data for one or more ROI. Specifically, two subjects were missing data for a single ROI, one subject was missing data for two ROIs, one subject was missing data for six ROIs, and one subject was missing data for 21 ROIs. Missing data was concentrated primarily in the temporal lobes. A complete summary of the number of missing data points for each ROI is provided in Table A6 of Appendix 2.

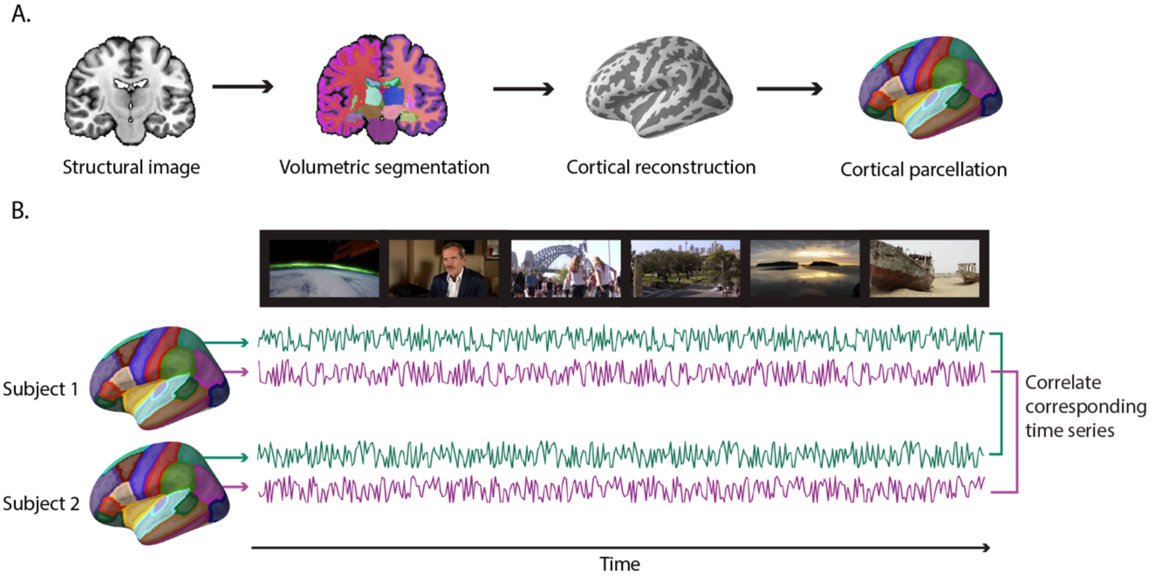


Figure 16. Computing inter-subject time series correlations. (A) Eighty anatomical regions of interest (ROIs) were derived for each participant using the Freesurfer image analysis suite. Segmentation of cerebral cortex, subcortical white matter, and deep gray matter volumetric structures (e.g., hippocampus, amygdala, putamen) was performed on the high-resolution scan of each participant's brain volume. Next, a cortical surface model was reconstructed and parcellated into anatomical units based on cortical folding patterns and neuroanatomical convention. An inflated cortical surface model is shown; dark gray indicates sulcal regions; light gray indicates gyral regions. In the image on the far right, cortical parcellation units are shown overlaid onto an inflated model of the cortical surface. **(B)** For each participant, the average response time series within each ROI was extracted during natural viewing of a collection of video clips during the fMRI study. Next, the correlation distance between the time series extacted from each pair of corresponding ROIs was computed for each unique pair of participants.

Extracting inter-subject similarities of fMRI response time series. Given that there were 42 participants in the fMRI component of the study, there were 861 unique dyads of fMRI participants. For each of these 861 dyads, the Pearson correlation distance between the time series of their fMRI responses was computed for each of 80 anatomical regions of interest (Figure 16B). For 1,259 of these 68,880 total data points (i.e., 861 subject pairs x 80 anatomical ROIs), at least one subject in the dyad lacked data for the corresponding ROI (see Table A6 for a complete summary of missing data). In such cases, the correlation distance value for this dyad was replaced with the average correlation distance value for that ROI from all remaining dyads. The resulting distance vectors for each of the 80 anatomical ROIs were normalized to have a mean of zero and a standard deviation of one. These normalized correlation distance values were then multiplied by negative one in order to obtain an estimate of the similarity of responses between pairs of individuals for each ROI.

Results

Social distances between fMRI participants

Of these 861 dyads of fMRI participants, 63 (7.32%) were characterized by a social distance of one (i.e., they were friends), 286 (33.22%) were characterized by a social distance of two (i.e., they were friends of one another's friends), 412 (47.86%) were characterized by a social distance of three, 98 (11.38%) were characterized by a social distance of four, and two (0.23%) were characterized by a social distance of five. Given that there were only two dyads characterized by a social distance of five, data from dyads characterized by social distances of four and five were collapsed into a single category ('4+') for statistical analyses.

Prior familiarity with stimuli

The majority of participants (29 of 42) had not seen any of the video clips used in the fMRI study prior to participating (*M* = 0.41; *SD* = 0.70). For the majority of videos used as experimental stimuli (i.e., nine out of 14), there were no dyads whose members had both seen the clip prior to scanning. Of the remaining video clips, two had previously been seen by two participants (i.e., by both members of a single dyad, or 0.12% of all dyads), two had been seen previously seen by three participants (i.e., by both members of three dyads, or 0.35% of dyads), and one clip had been seen previously by four participants (i.e., by both members of six dyads; 0.70% of the 861 total dyads). Please refer to Table A6 for a complete summary of participants' reported familiarity with the 14 video clips used as experimental stimuli.

Is similarity of fMRI responses related to social distance?

Are friends more similar to one another than average? We first tested whether inter-subject neural time series similarities between friends exceeded average inter-subject time series similarities. For this analysis, inter-subject similarities were averaged within brain regions at each level of social distance. A one-sample *t*-test indicated that the average similarity of friends' neural response time series ($M = 0.158$; 95% CI: [0.13, 0.19]) significantly exceeded the average, $t(79) = 9.68$, $p = 4.69 \times 10^{-15}$, $r = 0.74$; this effect size exceeds the conventional threshold (i.e., $r > 0.50$) to be considered a large effect (Cohen, 1992).

Inter-subject similarities of indirectly connected dyads. In addition to testing for higher than average inter-subject similarities across brain regions among friends, we also explored inter-subject time series similarities within dyads belonging to the remaining social distance categories. Neural responses of dyads characterized by a social distance of two were more similar to one another than average, $t(79) = 7.75$, $p = 2.63 \times 10^{-11}$, $r = 0.66$.

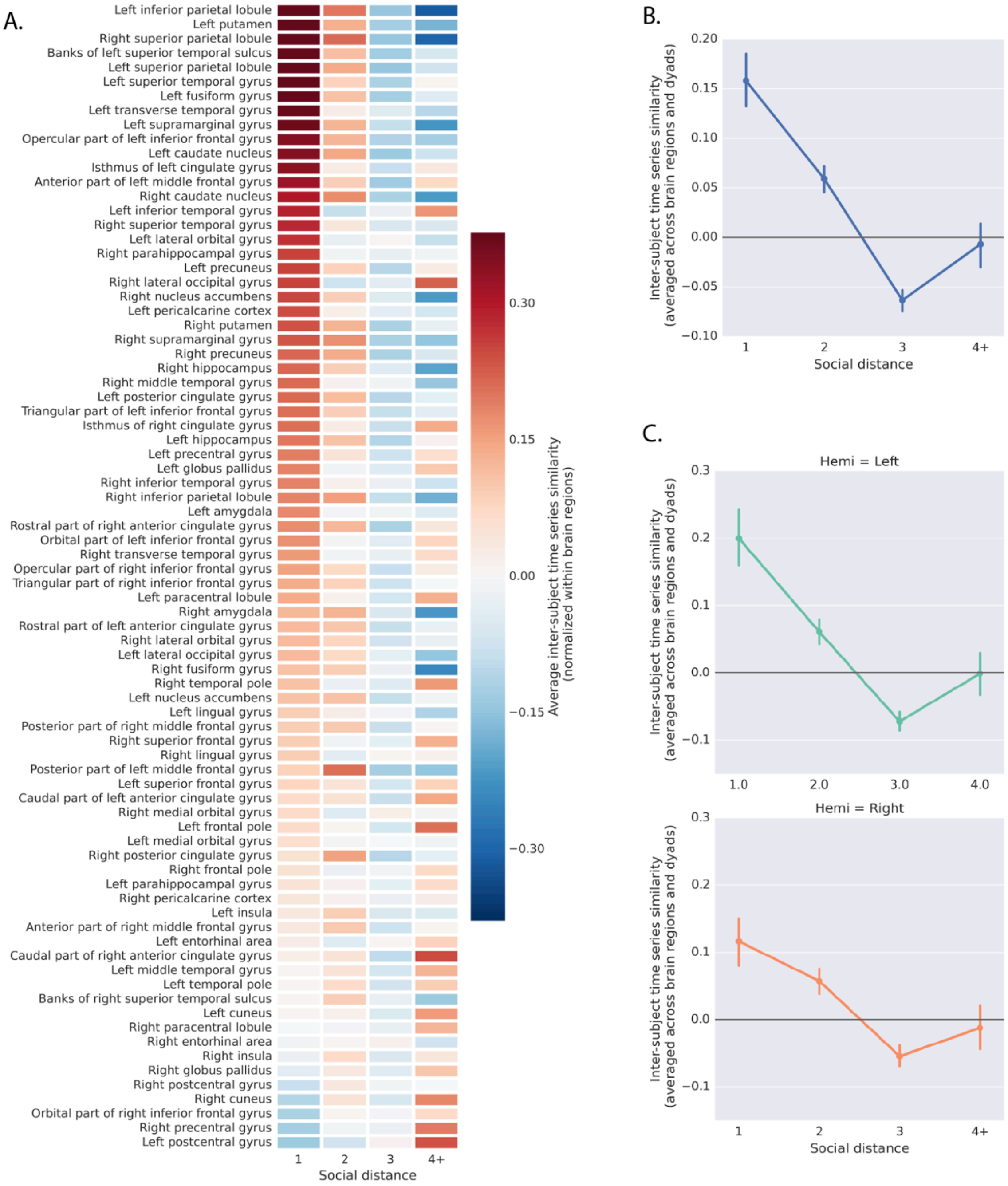


Figure 17. Inter-subject similarities by social distance. (A) Inter-subject similarities for each ROI at each level of social distance. For each of the 80 anatomical ROIs, an 861-element vector of inter-subject correlation distances was obtained. Inter-subject correlation distances were normalized within brain region, then averaged across dyads within each level of social distance, and multiplied by negative one to convert distance values to similarities. Warmer colors indicate higher inter-subject similarity; cooler colors indicate lower inter-subject similarity. **(B) Inter-subject similarities averaged across ROIs within each level of social distance.** Neural response time series of dyads comprised of students one or two “degrees away” from one another in the network were

more similar than average, whereas those of dyads comprised of students three "degrees away" from one another were less similar than average. Neural responses of dyads comprised of students four or more "degrees away" from one another in the network did not significantly differ from zero (i.e., the average). **(C)** The same pattern of results was observed in the left and right hemispheres. Error bars reflect 95% confidence intervals.

Contrastingly, fMRI response time series of dyads characterized by a social distance of three were significantly less similar to one another than average, $t(79) = 12.88$, $p = 4.24 \times 10^{-21}$, $r = 0.82$. Interestingly, inter-subject fMRI response similarities among dyads characterized by a social distance of four or more did not significantly differ from the mean, $t(79) = 0.48$, $p = .63$, $r = 0.05$. The same pattern of results was obtained when using non-parametric statistical tests (i.e., topological clustering), which better account for the non-independence of dyads (see Appendix 2 for further details). Means and 95% confidence intervals of inter-subject similarities at each level of social distance, as well as mean inter-subject similarities for each ROI at each level of social distance are displayed in Figure 17. In addition, for the levels of social distance for which inter-subject similarities differed from the mean, average inter-subject similarities for each brain region are shown overlaid on an inflated cortical surface model in Figure 18. See Figure A5 in Appendix 2 for a similar figure that includes data from all distance categories, as well as medial views of the brain.

Does inter-subject similarity decrease with social distance? We also tested whether inter-subject time series similarities varied as a function of social distance. A one-way ANOVA was conducted with social distance (four levels: 1, 2, 3, 4+) as the independent variable and inter-subject neural response similarity, averaged within each ROI at each level of social distance, as the dependent variable. This analysis revealed a large and significant effect of social distance on inter-subject fMRI response time series similarities, $F(3, 316) = 65.52$, $p = 5.72 \times 10^{-33}$, $\omega^2 = 0.38$; this value of ω^2 is consistent with social distance having a large effect on inter-subject similarities (Kirk, 1996).

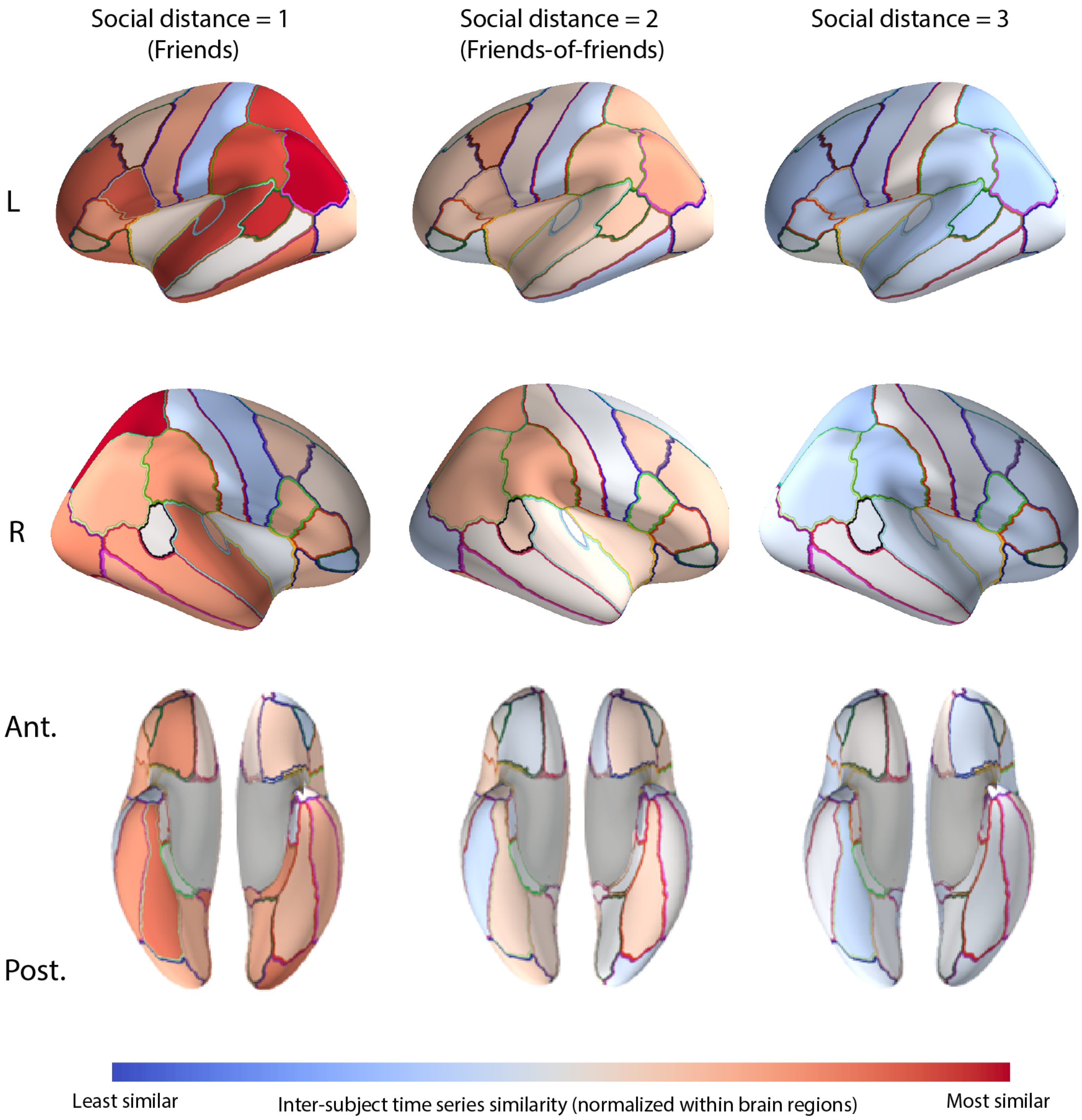


Figure 18. Inter-subject time series similarities by social distance overlaid on a cortical surface model. Average normalized inter-subject time series similarities are shown overlaid on an inflated model of the cortical surface for each of the social distance categories for which inter-subject time series similarities differed significantly from the mean. Ant. = anterior; P = posterior; L = left; R = right.

Post-hoc pairwise comparisons revealed that inter-subject similarities of dyads comprised of friends were greater than those of dyads from each of the remaining social distance categories. Specifically, dyads comprised of friends were characterized by higher inter-subject similarities than dyads comprised of friends-of-friends (i.e., by a social distance of two), $t(158) = 5.49$, $p = 1.56 \times 10^{-7}$, $r = 0.40$, as well as dyads characterized by a social distance of three, $t(158) = 12.99$, $p = 1.07 \times 10^{-26}$, $r = 0.72$, and dyads characterized by a social distance of four or more, $t(158) = 7.60$, $p = 2.42 \times 10^{-9}$, $r = 0.52$. Thus, the neural responses of friends were significantly more similar to one another than dyads within every other social distance category.

Similarly, dyads characterized by a social distance of two were more similar to one another than dyads characterized by a social distance of three, $t(158) = 13.51$, $p = 3.97 \times 10^{-28}$, $r = 0.73$, and were also more similar than dyads characterized by a social distance of four or more, $t(158) = 4.08$, $p = 7.26 \times 10^{-5}$, $r = 0.31$. Unexpectedly, dyads characterized by a social distance of four or more were more similar to one another compared with dyads characterized by a social distance of three, $t(158) = 3.76$, $p = .0002$, $r = 0.29$. See Figure 17.

Effects of brain region. We did not have specific predictions about which brain regions might drive how inter-subject fMRI response time series similarities vary with social distance. However, an exploratory analysis was performed to test for possible interactions between social distance and brain region: a two-way ANOVA with social distance (four levels: 1, 2, 3, 4+) and brain region (80 levels; see Table A5) as independent variables and inter-subject neural response similarity as the dependent variable. This analysis again revealed a significant main effect of social distance, F(3, 68,560) = 113.61, $p = 2.19 \times 10^{-73}$, and no main effect of brain region, $F(79, 68{,}560) = 7.54 \times 10^{-25}$, $p = 1$. An interaction between social distance and brain region $F(237, 68{,}560) = 1.71$, $p = 6.56 \times 10^{-11}$ was observed. The average inter-subject similarities for each of the 80 anatomical ROIs at each of the four social distance levels (1, 2, 3, 4+) are shown in Figure 17. Regions that appeared to be particularly highly similar for friend dyads included the bilateral SPL, brain areas in vicinity of the left and right temporoparietal junction (e.g., IPL; SMG; AG; STG; banks of the left STS), components of the dorsal and ventral striatum (e.g., nucleus accumbens, putamen, caudate nucleus), regions of the limbic system (e.g., left and right hippocampus; left amygdala), and EVC. Please refer to Figure 17A for a full summary of inter-subject similarities in each of the 80 anatomical ROIs at each level of social distance.

In addition, please see

Controlling for demographic variables. Analyses were repeated after controlling for potentially confounding demographic variables. The goal of this endeavor was not to control for all variables on which participants might be homophilous, but rather, to remove the effects of variables that exhibit assortativity in social networks *and* that could impact brain structure and functional organization. Failing to control for variables that meet both of these criteria could artificially inflate estimates of inter-subject neural response similarities for dyads comprised of friends. Details regarding these analyses and the corresponding results are included in Appendix 2; results were nearly identical to those reported in the main text.

Predicting friendship based on neural similarities

We also tested if it is possible to predict whether or not two individuals are friends based on the similarities of their fMRI response time series. If so, it should be possible to build a predictive model of friendship status by training an algorithm to recognize patterns of neural similarities associated with friendship from a subset of dyads' data. This model should correctly generalize to predicting the friendship statuses of new dyads based on those dyads' patterns of neural similarities.

Accordingly, 80-element vectors of neural similarities were extracted for the 63 dyads of fMRI participants characterized by a social distance of one. Data from a random subset of 63 dyads comprised of individuals who were not friends with one another was also extracted. Only a subset of the 798 dyads characterized by a social distance of two or more were included in the classification analysis because using an unbalanced dataset could lead a classifier to preferentially assign new examples the most frequently occurring category label in order to minimize prediction error. This dataset, comprised of data from 63 friends and a random subset of 63 non-friend dyads (n = 126), was randomly partitioned into training (n = 100) and validation (n = 26) datasets such that an equal number of examples of each label (i.e., friends, non-friend dyads) was present in each subset of the data.

A grid search procedure was implemented in scikit-learn (Pedregosa et al., 2011) to select the hyper-parameters (i.e., linear or radial basis function kernel; a C parameter of 1, 10, 100 or 1000; a γ parameter of 0.001 or 0.0001) of an SVM learning algorithm that would best separate items in the training dataset according to friendship status. More specifically, the training dataset was subdivided into 10 data folds, and the combination of hyper-parameters that performed most accurately across folds was selected as the best estimator. The best estimator within the training set was an SVM classifier with a C parameter of 10, a γ parameter of 0.001, and a radial basis function kernel.

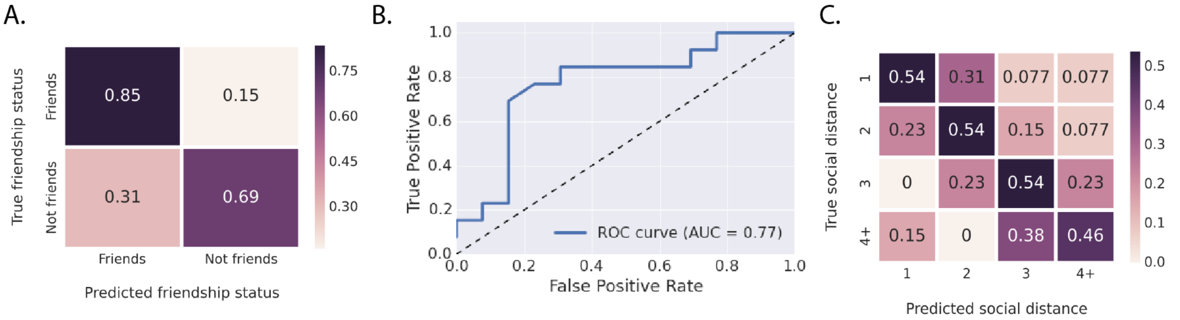


Figure 19. Predicting friendship status and social distance based on inter-subject neural similarities. (A) Confusion matrix summarizing classifier performance during cross-validation for a classifier trained to predict friendship status based on patterns of inter-subject neural similarities. Numbers and cell colors indicate how often the classifier predicted that friend and non-friend dyads belonged to each friendship status category. Chance performance would be 0.50 for this two-way classification problem. **(B)** Receiver-operating characteristic curve and corresponding area under the curve value (0.77) summarizing the classifier's true positive rate (e.g., the probability of correctly labeling friends as friends) and its false positive rate (e.g., the probability of incorrectly categorizing non-friend dyads as friends) across varying decision boundaries. The dashed line indicates the performance that would be obtained by random guessing. Points above the diagonal reflect good classification results (i.e., better than random guessing), and points below the diagonal reflect poor classification (i.e., worse than random guessing). **(C)** Confusion matrix summarizing cross-validated prediction performance of a classifier trained to predict the geodesic distance between members of a dyad in their social network based on their patterns of neural response time series similarities. Chance performance would be 0.25 in this four-way classification problem.

Following hyper-parameter tuning, this classifier was trained on the entire training dataset to predict the friendship status of dyads based on corresponding patterns of inter-subject neural time course similarities. Finally, the predictive performance of this classifier was tested on data from the previously left-out validation dataset, which was comprised of data from dyads to which the model had not previously been exposed. As shown in Figure 19A, the classifier was able to correctly predict the friendship status of dyads who were friends in 85% of cases, as well as the friendship status of non-friend dyads in 69% of cases. Further, patterns of specificity and sensitivity, as illustrated in the receiver-operating characteristic curve (Figure 19B) were consistent with good classification performance.

Predicting social distance based on neural similarities.

Next, we tested if it was possible to infer more nuanced social distance information based on patterns of neural response similarities. Analogous data analytic procedures to those described above were used for this multi-class prediction problem. Again, given that the smallest social distance category was that consisting of friends (n = 63), a random subset of 63 dyads from each of the remaining social distance categories was used for this analysis, which thus involved a total of 252 dyads. These 252 dyads were randomly partitioned into training (n = 200) and validation (n = 52) datasets such that an equal number of examples of each label (i.e., friends, dyads characterized by a social distance of two, dyads characterized by a social distance of three, dyads characterized by a social distance of four or more) were present in both subsets of data.

The same grid search procedure used for the two-way classification problem outlined above was used for four-way classification, and the same set of hyper-parameters performed best in the training data. Following hyper-parameter tuning, the classifier was trained on the entire training dataset to predict the social distance characterizing a dyad based on corresponding patterns of inter-subject neural time course similarity. Finally, the predictive performance of this classifier was tested on data from the validation dataset, which was comprised of data from dyads to which the model had not previously been exposed. As shown in Figure 19C, the classifier tended to predict the correct labels for dyads in all distance categories.

Discussion

The results reported here suggest that people tend to be friends with individuals who respond similarly to the world around them. Neural responses during unconstrained viewing of complex, real-world stimuli were significantly more similar among friends than average. Moreover, inter-subject similarities among friends were significantly greater than inter-subject similarities among individuals at every other possible social distance from one another in the social network. In addition, predictive models trained to discern friendship status and social distance based solely on patterns of inter-subject neural response similarity were able to accurately generalize to novel data, correctly predicting the friendship statuses and social distances of new pairs of individuals based only on those dyads' patterns of fMRI response similarities. Further, all results survived after controlling for demographic variables, such as age, gender, nationality, and ethnicity (see Appendix 2).

Much previous research has shown that humans tend to associate with others who are similar to themselves in terms of a wide range of characteristics, including demographic information (e.g., age, gender, ethnicity, McPherson et al., 2001), certain personality traits and behavioral tendencies (Feiler & Kleinbaum, 2015; Selfhout et al., 2010), and even aspects of our genotypes (Christakis & Fowler, 2014; Fowler, Settle, & Christakis, 2011). The current findings extend this research by demonstrating that covert mental responses to the environment, as indexed by neural processes evoked naturalistically during undirected viewing of videos, are exceptionally similar among friends.

Associations between inter-subject similarity and social distance

Friends' neural responses are exceptionally similar. Dyads comprised of friends were characterized by greater fMRI time series similarities than average, as illustrated in Figures 17 and 18. This effect was both large and significant. Moreover, friends were significantly more similar to one another than dyads in every other social distance category that existed in this sample, consistent with exceptional similarities of fMRI response time series among friends. These effects survived after accounting for demographic variables such as gender, age, ethnicity, and nationality (see Appendi-x 2).

Similarity decreases with increasing social distance up to three degrees away in the social network. In addition to heightened similarity among friends compared with dyads in all other social distance categories, dyads characterized by a social distance of two were more similar to one another than those characterized by a social distance of three or more (see Figures 17 and 18). Thus, overall neural similarity appeared to decrease with social distance up to a distance of three degrees in the social network.

Inter-subject similarities among dyads characterized by a social distance of four or more. Interestingly, dyads characterized by social distances of four or more were less similar to one another compared with dyads characterized by a social distance of one or two, but did not significantly differ from the mean, and unexpectedly, were *more* similar to one another compared with dyads characterized by a social distance of three (Figure 17).

There are at least two broad reasons why the pattern of results observed up to a distance of three (i.e., decreasing similarity with increasing social distance) may have "broken down" at distances equal to or exceeding four. First, it is possible that individuals at distances greater than three from one another in the network simply do not encounter one another frequently enough in order to have the opportunity to befriend one another. Therefore, the collection of dyads characterized by a social distance of four or more may include both dyads that would be compatible and incompatible as friends. Individuals at such a large social distance from one another may simply fail to come into contact with one another sufficiently often for assortativity to occur.

A second, not mutually exclusive, possibility is related to the "three degrees of influence rule" that governs the spread of a wide range of phenomena in human social networks (Christakis & Fowler, 2013). For example, experiments on human cooperative behavior have shown that one's social influence on other individuals' contributions in public goods games extends up to three degrees of geodesic distance from oneself in a social network; relatively highly variable effects at a distance of four were observed that did not significantly differ from zero (Fowler & Christakis, 2010). Large-scale observational studies have also found that wide-ranging phenomena spread up to approximately three degrees of geodesic distance in social networks, such as obesity, happiness, depression, loneliness, alcohol consumption, and smoking (Christakis & Fowler, 2009, 2013). Social influence may occur through several mechanisms, such as shifting social norms based on the observed behavior of others (Christakis & Fowler, 2007), unconscious conformity processes (Cialdini & Goldstein, 2004) that foster similar ways of thinking and behaving among friends, and innate mimicry processes, including those that engender emotional contagion across diverse contexts (Coviello et al., 2014; de Waal, 2007; Kramer, Guillory, & Hancock, 2014). Humans' embeddedness within social networks causes these social influence effects to reverberate outward in social ties, and thus, to extend beyond those individuals with whom we interact with directly (Christakis & Fowler, 2009). The apparent limit of social contagion processes at a social distance of three that has been observed in many studies may be due to multiple factors, including social influence effects decaying with social distance to the extent that the they are undetectable at social distances exceeding three, as well as the relative instability of long chains of social ties (Christakis & Fowler, 2013).

In the current sample, few dyads were characterized by a social distance of four or more (*n* = 100) compared with the other categories of non-friend dyads (i.e., *n* = 286 for distance 2 dyads; *n* = 412 for distance 3 dyads), and the diameter of the network (i.e., the maximum social distance between individuals) was only five. These data clearly suggest that the similarity of participants' neural response time series decreases with increasing social distance up to a distance of three. However, further research using social networks characterized by wider diameters, and that includes more dyads characterized by relatively remote social distances, is needed to better understand how the observed inter-subject similarities of distance 3 and 4 dyads relate to inter-subject similarities in the population more generally (i.e., including individuals at very remote social distances from one another). For example, if the pattern of results observed here (Figure 17B) held true in such studies, and inter-subject similarities at distances beyond four did not increase or decrease relative to distance 3 and 4 dyads, this might suggest that similarities in cognitive responding spread up to a social distance of two. Alternatively, such studies may find a different pattern of results for distance 4 dyads (given that there were relatively few distance 4 dyads in the current study), such that members of these dyads would be less similar to one another compared with members of distance 3 dyads; if this research also revealed inter-subject similarities to be relatively stable as social distances extended beyond four, this would be consistent with cognitive responses being characterized by three "degrees of influence" (if such similarities are due to social influence effects rather than homophily). That said, different aspects of mental processing might be characterized by differing degrees of spread in social networks, given the diversity of variables (e.g., pre-existing values, interests, and knowledge; emotional reactions) that mental processing of naturalistic stimuli likely reflects and encompasses.

Due to diverse phenomena spreading across network ties, beyond individuals who are indirectly connected to one another, characteristics of how we perceive, interpret and respond to the world may be influenced by, and in turn, may influence, the ways in which scores of other people, including those who we do not interact with directly, perceive and interpret the world around them. As discussed in the Future Directions section, subsequent investigations employing longitudinal designs will be useful in arbitrating between explanations of the observed effects based on homophily and social influence.

Spatial localization of results. We hesitate to make strong assumptions about similarities in the specific mental processes that underlie the results observed here, given that the anatomical ROIs used were often quite large and likely highly functionally heterogeneous. Figure 17A presents average normalized inter-subject similarity values for each ROI for each social distance category, with rows sorted vertically by descending inter-subject similarity among friends. These results are also shown overlaid onto an inflated cortical surface model in Figures 18 and A4.

As illustrated in Figures 17 and 18, brain areas in which time courses appeared to be highly similar among friends included regions thought to support wide-ranging aspects of mental processing, such as areas involved in low- and high-levels of auditory and visual processing (e.g. bilateral superior temporal cortex; bilateral lateral occipital cortex; right lingual gyrus; left pericalcarine cortex; bilateral inferior temporal cortex), areas involved in attentional allocation (e.g., bilateral SPL), sub-cortical areas implicated in motivation, learning, and affective processing (e.g., right nucleus accumbens, bilateral putamen and caudate nucleus), and areas in the posterior midline (e.g., precuneus, posterior cingulate cortex) and in the vicinity of the temporoparietal junction (e.g., AG; SMG; IPL; superior temporal cortex) that have been implicated in constructing and maintaining contextual models of situations, discerning others' mental states, processing the narrative contents of stories, and sense-making more generally (Kastner & Ungerleider, 2000; Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013; Mar, 2011; Mitchell, 2009; Poremba et al., 2003; Robbins & Everitt, 1996; Shomstein, 2012; Volkow et al., 2006; Wise, 2004). Many of these regions have previously been demonstrated to become tightly coupled when participants are similarly emotionally engaged (Nummenmaa et al., 2012, 2014) or captivated (e.g. by powerful political speeches, Schmälzle, Häcker, Honey, & Hasson, 2015), provided with shared contexts for understanding a situation (Ames et al., 2014), or adopt similar psychological perspectives (Lahnakoski et al., 2014). Thus, the current findings suggest that friends may be more similar to one another in these aspects of our responses to our surroundings.

It should be noted that the spatial pattern of results observed here is undoubtedly influenced by the choice of stimuli used, and the processing demands associated with those stimuli. For example, the majority of videos depicted a single individual speaking directly to the camera (e.g., in the context of a documentary interview, a televised debate, a scientific demonstration, and an excerpt of television news); few depicted social interactions unfolding over time. This may explain why some brain areas, such as the MPFC, which have been shown to be involved in observing and interpreting social interactions between other individuals (Mitchell, 2009), did not appear to be markedly coupled between participants in the current study, or to differ in coupling as a function of social distance. This is illustrated in Figure A6, which depicts the un-normalized inter-subject similarities for each ROI for each social distance category. Future targeted investigations using carefully selected stimulus sets should be undertaken in order to elucidate the degree to which individual differences in particular kinds of mental processing are characterized by assortativity within human social networks.

Benefits of the current approach

There are several reasons why our method of assessing inter-subject similarity may have been particularly effective for predicting friendship status, as well as of more nuanced social distance information. First, time courses of fMRI responses evoked during naturalistic stimulation offer a particularly information-rich window into participants' thought processes as they unfold over time (Cantlon & Li, 2013). In contrast to neuroimaging analysis techniques centered on characterizing the peak amplitudes of brain regions' responses to particular stimuli, the current analyses take into account both small and large signal variations, as well as temporal characteristics of these fluctuations. For example, time courses of neural activity while participants viewed comedic video clips presumably indexed whether or not participants detected intended examples of humor, the degree to which participants found those stimuli amusing, and the time points at which these humor detection and appreciation processes occurred.

In addition to the informational richness of this neural measure itself, the current paradigm also benefits from using complex, real world videos as stimuli. Compared with the more tightly controlled and ‘stripped down’ stimuli often used to study cognition, such stimuli are likely to evoke a greater proportion of the manifold cognitive and emotional processes that characterize everyday mental life, and offer increased ecological validity (Hasson et al., 2010). Further, such videos are purposefully designed to tightly constrain the attention and interpretations of their viewers, thereby minimizing noise due to idiosyncratic thoughts/mind-wandering (Hasson et al., 2010). Thus, engaging, naturalistic stimuli elicit reliable data that capture the broad assortment of mental processes evoked in everyday life, and measuring time courses of participants’ neural responses to such stimuli provides an information-rich window into these mental processes as they transpire.

In addition, the particular method of assessing inter-subject similarities of fMRI response time courses implemented here, in which response time series were extracted from subject-specific segmentations of the cerebral cortex and deep gray matter structures, eliminates possible spatial distortion of functional data that can be imposed by warping participants to a common anatomical template. Moreover, in each subject’s data, brain activity was averaged across voxels within each of the anatomical ROIs used (see

Figure 17A or Table A5 for a list of all ROIs) at each time point, thus reducing high spatial frequency noise in the data.

We did not directly compare the results obtained in the current study to those that might be obtained by using behavioral measures, such as explicit questions about participants' reactions to experimental stimuli, or self-report measures of personality traits or other individual difference variables. Therefore, we cannot ascertain if comparable results could have been achieved without the use of neuroimaging. That said, we suggest that the paradigm used here offers several advantages compared with other methods of assessing similarities in how individuals respond to their environment.

First, as previously mentioned, the current paradigm and data analytic approach likely recruits a relatively large proportion of the emotional and cognitive processes that characterize everyday mental life, and does so unobtrusively in a relatively ecologically valid manner. The unobtrusive nature of the current paradigm is beneficial not only because it allows participants' mental processes to unfold without interruption; it also allows for such processes (or more precisely, the neural processes underlying them) to be measured contemporaneously, as they transpire, rather than asking participants to reflect on those processes after they occur and report on those reflections to experimenters. Indeed, a large body of social psychological literature has demonstrated that our ability to accurately introspect about our own mental processes is often limited (Wilson & Nisbett, 1978). We appear to lack any conscious access to many aspects of mental processing (Wilson, 2002), limiting the efficacy of self-report measures for capturing many aspects of cognition and perception. In contrast, neural measures have the advantage of capturing aspects of mental processing to which we lack conscious access, but that nevertheless impact behavior (e.g., Soon, Brass, Heinze, & Haynes, 2008). Similarly, compared with self-report, the validity of responses obtained using the current paradigm is less likely to be threatened by participants' attempts to present themselves in a socially desirable manner, which can distort experimental results in a variety of ways (King & Bruner, 2000). Therefore, the data obtained using the current paradigm is less likely to be contaminated by several factors that can diminish the validity of self-report data.

In addition, measuring fMRI responses from all of cortex simultaneously confers the benefit of concurrently measuring brain activity associated with diverse aspects of mental processing. Rather than being limited to a few targeted questions, using data recorded from the entire brain during natural viewing allows for neural processing to be captured associated with whatever emotional (e.g., amusement, disgust, sadness, desire, fear) and cognitive (e.g., attention to different aspects of the stimulus; interpretations of a video as they are informed by participants' pre-existing assumptions, knowledge, and values; waxing and waning levels of overall attentional engagement) responses happen to be elicited, at whatever time points those responses happen to be recruited. Even if it were possible to assess the same information using self-report questionnaires, it would presumably be necessary to use an extremely large battery of questions in order to do so.

Future directions

Is similarity of neural responses a cause or consequence of friendship? Do we become friends with people who respond to the environment similarly, or do we come to respond to the world similarly to our friends? Given its cross-sectional nature, the current study cannot address this question directly. Thus, future longitudinal studies should measure whether inter-subject neural response similarities predict subsequent friendship formation among members of evolving social networks.

We anticipate that such studies will find that the exceptional similarity of neural responses among friends reflects both homophily and social influence processes. A large body of research demonstrates that people in our immediate environment influence how we think, feel, and behave (Cialdini & Goldstein, 2004; de Waal, 2007). At the same time, similar people may tend to become connected at higher rates because they find themselves in common situations (McPherson & Smith-Lovin, 1987). Similarly, pre-existing similarities in how individuals tend to perceive, interpret, and respond to their environment can enhance social interactions and increase the probability of developing a friendship via positive affective processes and by increasing the ease and clarity of communication (C. R. Berger & Calabrese, 1975; Clore & Byrne, 1974). Future research should extend the current findings by adopting longitudinal experimental designs that afford insight into the extent to which the results observed here reflect homophily and social influence processes. Notably, the same forces – i.e., assortativity, social influence, or both – that produce ‘in-groups’ among friends within a given area of the network necessitate the creation of relatively distinct ‘out-groups’ in different areas of the network. Therefore, the brain regions that are particularly similar among friends are particularly dissimilar among dyads characterized by more remote distances in the social network (Figure 17).

In addition, the current paradigm involved undirected viewing of continuous, complex, real-world stimuli. Although naturalistic neuroimaging paradigms confer the advantages of relatively high ecological validity, increased signal reliability, and recruitment of a large proportion of the suite of mental processes that arise outside of experimental settings (Cantlon & Li, 2013; Hasson et al., 2010), a more specific understanding of precisely which cognitive and emotional processes underlie the effects observed here might be achieved by complementary follow-up studies involving behavioral measures and more constrained experimental paradigms. In addition, a single sequence of stimuli was used for the current study in order to provide a common context throughout all time points in the experiment for all participants. Future studies may wish to adopt experimental designs that allow for drawing inferences about exactly what kinds of stimuli (e.g., comedic content, political content) are particularly important for predicting patterns of real-world social ties.

Conclusions

These results suggest that friends are exceptionally similar to one another in terms of how they perceive, interpret and react to the world around them, as reflected in unobtrusive measurements of cognitive processes as they unfold over time. Proximity in terms of social ties in a real-world social network was strongly associated with similarity in the magnitude and timing of the recruitment of neural processes related to attending to, perceiving, and interpreting auditory and visual information, emotional responding, and sense-making. In addition, these results suggest that the similarity of our real-time mental responses to the world around us decreases with increasing social distance up to a social distance of three degrees in our social networks.

These data also demonstrate that it is possible to predict whether or not two individuals are friends, as well as more nuanced social distance information (i.e., geodesic distance in a real-life social network) based only on the similarity of temporal patterns in their neural responses during free viewing of complex, real-world scenes. Time courses of individuals' neural responses to continuous, naturalistic stimuli provide signatures of those individuals' interpretations of and reactions to the experimental stimuli, which are presumably shaped by characteristics of those individuals' dispositions, pre-existing knowledge, views, opinions, interests, and values. These signatures can be used to identify individuals who are likely to be friends, as well as individuals who are likely to be indirectly connected via mutual friends, in a real-world social network.

General Discussion

Summary

The studies comprising this dissertation combined methodologies for studying information processing within individual brains with characterizations of individuals' real-world social contexts. These results provide insight into the neural mechanisms involved in encoding social relationship knowledge, and emphasize the importance of integrating a richer understanding of our social networks into the study of person perception. Furthermore, the current findings suggest that evolution may have honed the human brain to automatically process information about the social networks that surround us in order to beneficially inform our behavior. Finally, these results demonstrate that we process the world around us exceptionally similarly to our friends, and that this similarity decreases with increasing social distance up to three degrees of separation in our social network. Key findings from each study are summarized below.

Study 1 characterized distributed patterns of brain activity while participants viewed stimuli depicting relatively near and far egocentric distances in social ties, time, and space. Using statistical pattern recognition techniques, we found that a region of parietal cortex thought to have an evolutionarily ancient role in encoding egocentric spatial distance (Parkinson & Wheatley, 2015) encodes information according to its relevance to (i.e., distance from) the perceiver not only in space, but also in social ties and in time. Further, representations in this region appeared to be organized not by distance domain (e.g., social vs. spatial), but by relative distance from the perceiver (i.e., near vs. far), and reflected participants' own judgments of social familiarity, spatial distance, and temporal soon-ness, suggesting a parsimony of human brain function such that information about these different facets of relevance to the self are at least partially encoded using shared computational mechanisms. With respect to the aims of the current dissertation, these results provide new insight into the neural mechanisms involved in encoding a particular aspect of social relationship knowledge: social distance.

Study 2 demonstrated that social distance is spontaneously encoded when perceiving people whom we know. The results of Study 2 converged with those of Study 1 in that the same region of the right anterior IPL was found to carry information about egocentric social distance in its distributed neural population responses. This was the case even though social distance was operationalized differently in Studies 1 and 2, and even though participants were not instructed to evaluate or attend to social distance in Study 2. This particular result is consistent with suggestions that psychological distance comprises a fundamental aspect of meaning that is processed automatically, even when it is unrelated to the task at hand (Trope & Liberman, 2010).

In addition to social distance, aspects of relationship knowledge that depend on tracking and encoding information about the broader structure of our social networks (e.g., who tends to bridge different groups, who is well-connected to well-connected others) were accurately perceived and automatically encoded when participants in Study 2 viewed familiar individuals. In the MPFC, neural encoding of social information was particularly accurate for those participants who identified as being sensitive to social cues (i.e., high self-monitors). This finding is consistent with the MPFC playing a role in modeling other people's personality traits and mental states (Hassabis et al., 2014; Ma et al., 2014; Wagner et al., 2012). Taken together, the results of Study 2 suggest social relationship knowledge – both about our direct social ties and about relationships between third parties – comprises an important component of person perception, and that encoding this knowledge serves to appropriately shape the perceiver's behavior to suit his or her social context.

The results of Study 3 suggest that humans tend to be surrounded by others whose spontaneous and covert mental responses to the environment are exceptionally similar to their own. Further, inter-subject similarity of neural responses decreased up to distances of three degrees in participants' social network. Beyond three degrees of separation, inter-subject neural similarities were not significantly different than average. These results survived after controlling for the effects of inter-subject similarities in age, gender, nationality, and ethnicity. In addition, it was possible to predict both the friendship status and social distance characterizing a dyad (i.e., if two individuals are friends, friends of one another's friends, or more remote from each other in their social network) based only on that dyad's patterns of neural similarity to one another.

Findings from Study 3 extend a large body of research showing that humans tend to be surrounded by others who are similar to themselves, both because we are attracted to people who resemble ourselves (McPherson et al., 2001), and because we tend to be influenced by those around us. This interpersonal influence results both from aspects of our psychology as individuals (e.g., tendencies toward mimicry and conformity, Chartrand & Bargh, 1999; Cialdini & Goldstein, 2004; Hatfield et al., 1993), and from our embeddedness within densely interconnected social networks, which extends the reach of our influence as individuals well beyond the people with whom we interact directly (Christakis & Fowler, 2013).

Future Directions

Disentangling social contagion and homophily. In particular, future research is needed to disentangle whether the results observed in Study 3 are reflective of homophily (i.e., people befriending others who are similar to themselves), interpersonal influence (i.e., people becoming increasingly similar to their friends), or some combination of these factors. Given the wide array of variables on which people are homophilous – e.g., gender, age, race, political attitudes, religiosity, certain aspects of personality (McPherson et al., 2001) – it is likely that the effects observed here are in part due to the human tendency to befriend similar others. At the same time, given that neural processes give rise to all of our thoughts, feelings, and actions, and thus must underlie the myriad attitudes, affective states, and behavioral tendencies that have been shown to exhibit social contagion, it is also likely that the effects observed here are in part reflective of the fundamental human tendency to take on the ways of thinking, feeling, and behaving evinced by those around us (Chartrand & Bargh, 1999; Cialdini & Goldstein, 2004; Hatfield et al., 1993). Future studies employing longitudinal designs are required to clarify the degree to which exceptionally high inter-subject similarities among friends are the product of social contagion, and the degree to which these similarities reflect the human tendency to associate with people who are already similar to ourselves.

Integrating third-party relationships into social cognition and neuroscience studies. Sociologists have long appreciated the manifold ways in which relationships between third parties influence human behavior. This appreciation has led to entire sub-fields of inquiry on such topics as the "social capital" afforded by particularly advantageous social network positions (Burt, 2001; Coleman, 1988). However, psychologists and neuroscientists studying individual cognition and behavior have, for the most part, only recently begun to consider how third party relationships, and individuals' understandings thereof, influence social cognition and behavior (Brent, 2015; Fuong et al., 2015). The results of Study 2 suggest that characteristics of social ties between third parties (e.g., who is a friend of our friend), and structural aspects of their positions in our social networks (e.g., who tends to connect otherwise disparate groups of people) are processed automatically, and thus, are likely to shape subsequent aspects of cognition and behavior. Given these results, future studies should probe precisely how nuanced information about others' positions in our social networks influences our cognitive and neural responses to those individuals.

For example, does one's social status, as conferred by patterns of social ties, moderate the degree to which other individuals monitor one's behavior and apparent internal states, as has been found to the case with other facets of social status, like status conferred by cues to physical dominance (Deaner et al., 2005; Jones et al., 2010; Shepherd et al., 2006)? The fact that information about familiar others' eigenvector centrality was carried in neural population codes in brain regions known to be modulated by visual attention suggests that this might be the case. Future research should test if visual attention is preferentially allocated to individuals who are more central to one's social network, as well as if perceivers preferentially attend to the apparent mental states of such individuals (e.g., using gaze-following paradigms).

Cultivating close social relationships benefits from maintaining accurate knowledge not only of our friends, but also knowledge of who the friends of our friends are, and who the enemies of our friends are. An additional direction for future research involves examining how other kinds of social relationships – such as whether third parties respect one another, are loyal to one another, or are rivals with one another – are processed, and if this information automatically influences neural processing, cognition, and behavior. The results of Study 2 suggest that our knowledge of patterns of affiliative relationships, including those between third parties, and including information that relies on mentally representing topographical characteristics of a friendship network, is both accurate and activated automatically upon encountering familiar others. Do we also accurately perceive networks of enemies, and networks based on who respects whom, or who is loyal to whom? Additionally, how does knowledge of these relationships interact with knowledge of affiliative ties? Although friendship comprises a hallmark of human behavior, it cannot explain all of human sociality – In fact, the notion that humans' large brains evolved to meet the cognitive demands of inhabiting complexly bonded social groups is alternatively referred to as the "social brain hypothesis" and the "Machiavellian intelligence hypothesis" (Dunbar, 2003). A full understanding of how humans shape and navigate our social worlds will require a consideration of the many kinds of relationships that characterize the human social landscape.

Conclusions

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 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 (Gallotti & Frith, 2013; Huettel & Kranton, 2012). 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 that we inhabit (Brent, 2015; Burt & Knez, 1995; Ellwardt et al., 2012; Ferrin et al., 2006; Fuong et al., 2015).

The studies presented here all combined the study of individual cognition with the characterization of patterns of real-world relationships. In so doing, these studies sought to examine how human minds perceive, and perhaps, are shaped by, the webs of social relationships in which we are embedded. Given that our cognition and behavior are necessarily embedded within our social networks, future research should continue to take an integrative approach in order to better understand how human minds understand and build our social worlds.

Appendix 1: Supplementary Information for Study 2

Supplementary results tables for Study 2

Table A1. Brain regions where local neural information content was associated with the social distance from the participant of the individuals being viewed in Study 2.

Hemi	Size (Number of voxels)	COG *X*	COG *y*	COG *z*	Peak *X*	Peak *Y*	Peak *z*	Location
R	13370	49.7	-46.4	6.5	63.0	-42.0	30.0	SMG, AG, pSTG, pSTS, pMTG, pITS, pITG, FG
L	9572	-39.8	-9.7	36.6	-43.0	-14.0	41.0	Precentral gyrus, pIns
L	8715	-50.2	-34.5	-5.1	-45.0	-26.0	-5.0	FG, PHG, pITG, pITS, pMTG
R	7734	39.0	31.6	8.8	51.0	35.0	22.0	MPFC, OFC
R	4140	42.6	-23.2	50.0	39.0	-37.0	53.0	Postcental gyrus, IPL,
L	2781	-22.6	-57.8	58.6	-18.0	-56.0	63.0	Precuneus, SPL
L	2550	-22.0	43.8	23.7	-16.0	44.0	25.0	DMPFC, DLPFC
L	1818	-7.5	-38.4	50.6	-8.0	-39.0	51.0	MCC, precuneus, paracentral lobule
L	1580	-26.9	-80.2	35.1	-25.0	-81.0	37.0	Cuneus, Precuneus
L	1507	-19.9	-65.7	-33.5	-20.0	-67.0	-31.0	Cerebellum
L	1319	-39.5	31.1	-1.8	-47.0	34.0	-1.0	IFG, MFG
R	1192	24.9	-70.4	48.5	22.0	-71.0	52.0	SPL, precuneus,
L	954	-9.1	-50.3	31.5	-7.0	-51.0	32.0	AG, IPL, Precuneus
L	917	-28.9	-58.1	33.7	-35.0	-51.0	34.0	Precuneus, PCC, AG
R	827	58.7	9.2	-9.7	59.0	9.0	-12.0	TP, aSTS, aSTG
R	773	15.5	66.4	2.3	13.0	67.0	0.0	MPFC
L	647	-47.8	6.1	-18.6	-53.0	7.0	-16.0	TP, aSTS, aMTG
R	537	10.9	4.4	28.0	9.0	4.0	28.0	MCC
R	520	12.0	-56.3	22.0	12.0	-56.0	20.0	Precuneus, PCC
R	508	10.2	9.1	53.3	12.0	11.0	54.0	SFG
R	495	43.2	-66.1	31.3	48.0	-66.0	33.0	AG
R	476	4.5	2.5	63.4	6.0	3.0	61.0	SFG
L	466	-7.8	26.5	23.1	-7.0	23.0	24.0	ACC
L	416	-8.1	63.6	4.9	-10.0	65.0	1.0	MPFC
R	390	33.1	-2.7	-20.6	30.0	-3.0	-18.0	PHG
L	348	-50.4	-11.4	9.3	-51.0	-11.0	6.0	STG, postcentral gyrus
L	342	-40.1	-73.0	21.3	-42.0	-70.0	24.0	MTG
L	338	-22.7	-41.7	2.5	-22.0	-43.0	4.0	PHG
R	317	17.3	-38.3	3.4	14.0	-38.0	4.0	PHG

R	305	28.4	-43.7	25.2	31.0	-43.0	26.0	Precuneus
L	290	-8.6	31.8	1.6	-10.0	30.0	1.0	ACC
L	288	-45.9	-33.6	51.2	-45.0	-34.0	53.0	IPL
R	284	1.5	63.4	13.6	-2.0	61.0	14.0	MPFC
L	250	-54.3	-60.5	5.3	-56.0	-59.0	4.0	pMTG

Hemi = hemisphere; COG = center of gravity; L = left; R = right; p = posterior; a = anterior; AG = angular gyrus; SMG = supramarginal gyrus; IPL = inferior parietal lobule; STG = superior temporal gyrus; ITG = inferior temporal gyrus; FG = fusiform gyrus; MPFC = medial prefrontal cortex; MTG = middle temporal gyrus; ACC = anterior cingulate cortex; PHG = parahippocampal gyrus; SFG = superior frontal gyrus; PCC = posterior cingulate cortex; TP = temporal pole; MCC = mid-cingulate cortex; ITS = inferior temporal sulcus. All reported results are significant at a statistical threshold of $p < .005$, FWE-corrected.

Table A2. Brain regions where local neural information content was associated with the eigenvector centrality of the individuals being viewed in Study 2.

Hemi.	**Size (Number of voxels)**	**COG *x***	**COG *y***	**COG *z***	**Peak *X***	**Peak *y***	**Peak *z***	**Location**
L, R	5925	0.6	-81.0	17.0	1.0	-79.0	20.0	EVC
L	3576	-30.6	2.3	-2.6	-31.0	3.0	-3.0	Ins., striatum, claustrum
L	2646	-17.7	50.0	-11.6	-24.0	54.0	-9.0	OFC, VMPFC
L	1413	-17.1	-54.1	-5.4	-10.0	-54.0	-5.0	PHG
R	1413	19.7	-49.1	-4.1	19.0	-51.0	-3.0	PHG
R	965	30.0	48.6	-2.3	29.0	45.0	-5.0	VMPFC
R	897	27.1	-13.5	60.2	29.0	-15.0	63.0	Pre-central gyrus
R	712	27.5	21.1	-1.3	27.0	21.0	0.0	aIns., IFG
R	661	64.1	-20.0	12.1	63.0	-22.0	17.0	STG
R	564	13.5	45.2	9.3	13.0	44.0	9.0	MPFC
L	487	-37.6	34.0	24.6	-44.0	34.0	27.0	DLPFC
L	479	-36.5	25.4	6.8	-36.0	27.0	8.0	aIns., IFG
L	394	-19.3	-46.8	43.3	-16.0	-50.0	43.0	Precuneus
R	371	39.5	7.7	0.3	37.0	9.0	0.0	Ins.
L	300	-39.9	30.8	-8.2	-41.0	32.0	-11.0	VLPFC
L	275	-19.5	-19.6	68.2	-18.0	-19.0	68.0	Pre-central gyrus

Hemi = hemisphere; COG = center of gravity; L = left; R = right; a = anterior; p = posterior; EVC = early visual cortex; OFC = orbital frontal cortex; PHG = parahippocampal gyrus; STG = superior temporal gyrus; MPFC = medial prefrontal cortex; DLPFC = dorsolateral prefrontal cortex; MFG = middle frontal gyrus; IFG = inferior frontal gyrus; Ins. = insula; VLPFC = ventrolateral prefrontal cortex; VMPFC = ventromedial prefrontal cortex. All reported results are significant at a statistical threshold of $p < .005$, FWE-corrected.

Table A3. Brain regions where local neural information content was associated with the network constraint of the individuals being viewed in Study 2.

Hemi.	**Size (Number of voxels)**	**COG *x***	**COG *y***	**COG *z***	**Peak *X***	**Peak *Y***	**Peak *z***	**Location**
R	27658	49.7	-18.8	-1.2	44.0	-25.0	8.0	STS, STG, IPL, PHG
L	18265	-51.9	-29.8	4.0	-55.0	-36.0	1.0	STS, STG
R	14790	28.4	-7.8	47.7	9.0	11.0	61.0	Pre-central gyrus, SMA
L	6803	-41.9	-7.3	44.2	-44.0	1.0	48.0	Pre-central gyrus, SMA
R	3691	44.9	-58.1	8.0	45.0	-50.0	12.0	pSTS, pMTG
L	1783	-22.0	-1.2	-2.5	-23.0	-3.0	-3.0	Striatum
L	1017	-22.5	-30.3	45.3	-20.0	-31.0	43.0	Precentral gyrus, central sulcus
R	846	37.0	-37.2	-29.7	32.0	-36.0	-30.0	Cerebellum
L	833	-35.4	-65.0	5.3	-33.0	-64.0	5.0	ESC
R	824	1.3	48.0	-6.8	3.0	49.0	-8.0	OFC
R	732	32.4	-78.8	27.7	32.0	-79.0	29.0	ESC
L	621	-50.9	-60.4	-19.9	-51.0	-65.0	-20.0	FG
R	591	52.0	21.4	3.6	52.0	23.0	4.0	IFG
R	523	13.7	-43.0	8.5	15.0	-46.0	9.0	PCC
L	467	-24.0	-65.4	-3.5	-23.0	-63.0	-1.0	FG, LG
L	397	-27.5	-79.6	39.1	-28.0	-79.0	38.0	Precuneus
L	383	-41.7	47.2	-4.1	-44.0	47.0	1.0	OFC
R	355	48.1	-42.2	-14.5	51.0	-40.0	-18.0	FG
L	328	-44.4	-17.5	19.6	-45.0	-17.0	19.0	pIns.
L	281	-53.2	16.4	8.1	-52.0	15.0	10.0	IFG

Hemi = hemisphere; COG = center of gravity; L = left; R = right; a = anterior; p = posterior; STS = superior temporal sulcus; STG = superior temporal gyrus; IPL = inferior parietal lobule; PHG = parahippocampal gyrus; SMA = supplementary motor area; MTG = middle temporal cortex; ESC = extrastriate cortex; OFC = orbital frontal cortex; FG = fusiform gyrus; IFG = inferior frontal gyrus; PCC = posterior cingulate cortex; LG = lingual gyrus; Ins. = insula. All reported results are significant at a statistical threshold of $p < .005$, FWE-corrected.

Table A4. Brain regions exhibiting a positive relationship between perceivers' self-monitoring scores and the degree to which local neural response patterns contained information about the personalities and social network positions of the individuals being viewed (Study 2).

Hemi.	**Size (Number of voxels)**	**COG** *x*	**COG** *y*	**COG** *z*	**Peak** *X*	**Peak** *y*	**Peak** *z*	**Location**
R	4649	16.0	46.8	12.3	7.0	36.0	12.0	MPFC
R	4562	40.8	-12.2	-22.4	39.0	-15.0	-27.0	FG, PHG
L	2814	-0.8	-87.9	-11.4	5.0	-87.0	-16.0	EVC
L	2135	-33.0	-36.8	-22.8	-26.0	-39.0	-18.0	FG
L	2083	-3.4	17.8	-7.8	8.0	10.0	-5.0	Ventral striatum
L	1630	-47.9	-8.4	39.0	-51.0	-7.0	34.0	Pre-central gyrus
--	1586	3.2	-17.1	-24.1	-2.0	-20.0	-26.0	Brainstem
R	1491	46.4	-45.9	-19.5	53.0	-43.0	-21.0	FG
L	1458	-24.6	-15.1	5.3	-28.0	-11.0	9.0	Dorsal striatum
L	1267	-11.1	19.0	13.8	-18.0	21.0	13.0	Dorsal striatum
R	1218	12.0	-0.2	46.3	11.0	-3.0	42.0	MCC
L	1112	-41.2	-52.8	59.0	-43.0	-59.0	54.0	SPL
R	1036	46.3	-78.9	-4.0	46.0	-79.0	-6.0	EVC
R	1021	33.3	-83.1	-15.4	34.0	-77.0	-15.0	FG
L	932	-39.8	17.7	5.1	-42.0	19.0	6.0	AIns.
R	708	23.4	52.8	-16.3	18.0	53.0	-18.0	OFC
R	684	38.3	-45.2	-5.3	45.0	-37.0	-9.0	FG, PHG
L	661	-31.6	-67.4	-16.8	-35.0	-65.0	-16.0	FG
L	611	-16.9	-10.6	-26.0	-15.0	-14.0	-26.0	PHG
R	401	44.9	-11.3	35.0	44.0	-10.0	33.0	Pre-central gyrus
L	345	-47.6	-25.6	60.8	-47.0	-20.0	62.0	Post-central gyrus
R	337	21.4	1.3	-26.9	23.0	1.0	-27.0	PHG
L	335	-26.4	-11.3	43.4	-26.0	-12.0	42.0	MFG
R	324	2.3	32.1	36.2	2.0	32.0	34.0	DMPFC
R	259	19.5	21.2	13.2	21.0	25.0	10.0	Caudate
L	258	-7.3	51.7	-10.0	-7.0	52.0	-12.0	VMPFC
L	254	-49.8	-61.8	-17.7	-51.0	-61.0	-15.0	FG
R	249	62.9	-18.7	17.0	64.0	-20.0	20.0	IPL
R	245	28.3	43.7	30.7	27.0	43.0	31.0	DLPFC

Hemi = hemisphere; COG = center of gravity; L = left; R = right; a = anterior; p = posterior; MPFC = medial prefrontal cortex; FG = fusiform gyrus; PHG = parahippocampal gyrus; EVC = early visual cortex; MCC = mid-cingulate cortex; Ins. = insula; OFC = orbitofrontal cortex; MFG = middle frontal gyrus; DMPFC = dorsomedial prefrontal cortex; VMPFC = ventromedial prefrontal cortex; IPL = inferior parietal lobule; DLPFC = dorsolateral prefrontal cortex. All reported results are significant at a statistical threshold of $p < .005$, FWE-corrected.

Optical flow analysis of stimuli used in Study 2

To quantify the amount of movement within each video clip used in Study 2, the average optical flow (i.e., the pattern of apparent motion between consecutive video frames) was computed for each video that was shown in the fMRI study. Given that the videos used as stimuli were recorded by a stable camera against a plain, static background, optical flow estimates for these videos capture of the amount that each individual moved his or her facial features and head in the video clip. Farneback's algorithm for motion estimation (Farnebäck, 2003) as implemented in OpenCV (Bradski, 2000) was used to estimate the average magnitude of optical flow in each video. This method extracts a pixel-wise motion vector for each pair of sequential frames in which each pixel is characterized by a magnitude and a direction. To estimate the magnitude of motion within each frame pair, the magnitude values (without respect to direction) were summed across pixels. To compute the mean magnitude of optical flow for a given video, the motion magnitude estimates were averaged across frames within that video.

In order to test whether or not individual differences in network constraint were related to movement in the videos used as stimuli, the correlation between network constraint and average motion magnitude was assessed among the 88 individuals whose videos were used as stimuli in the fMRI study. Given that distributions of both variables were highly skewed, data were log-transformed prior to analysis. The results of this procedure suggest that in the stimuli used in the current study, network constraint and amount of movement were not significantly correlated, r = -0.12, p = 0.28 (see Figure A1).

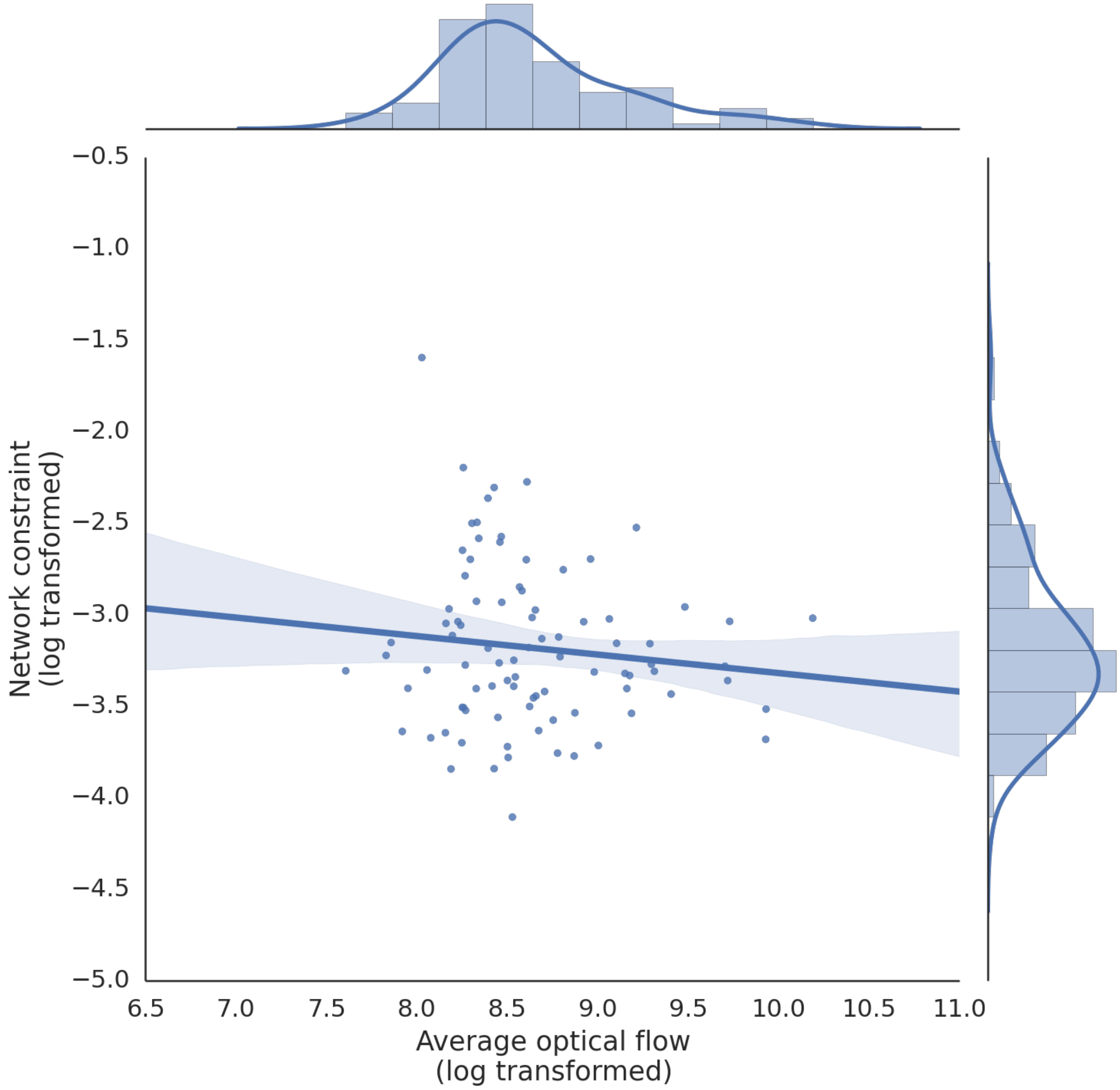


Figure A1. The amount of movement of the 88 individuals whose videos were used as stimuli was not significantly related to the constraint characterizing those individuals' positions in the social network of first-year MBA students, *r* = -0.12, *p* = 0.28.

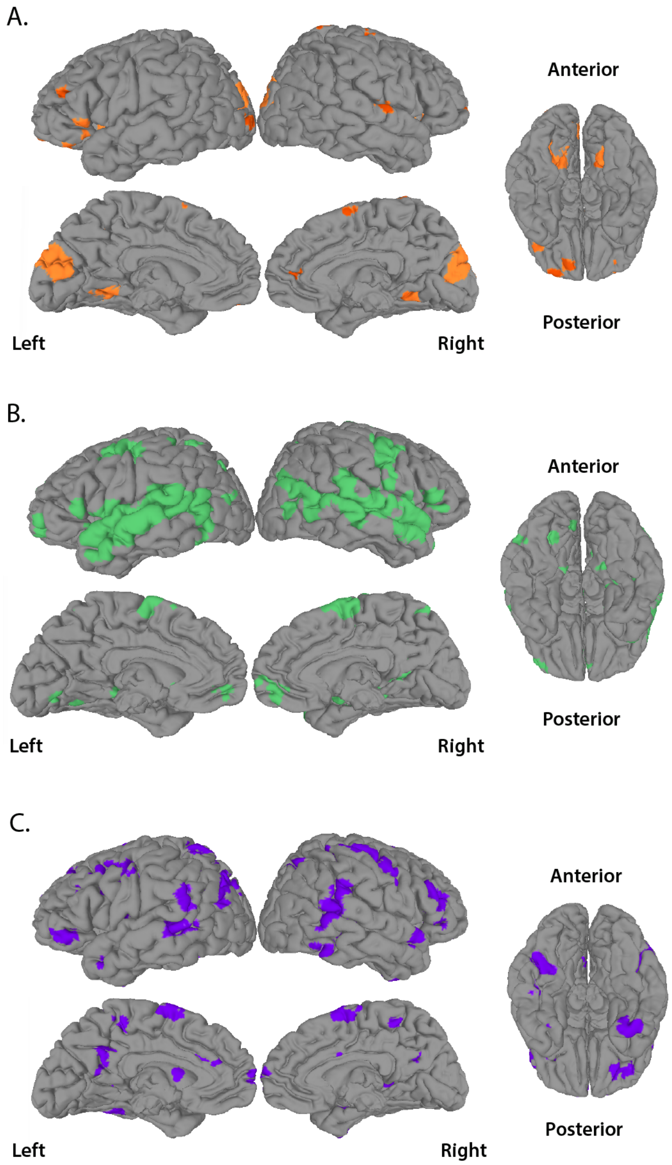


Figure A2. Assessing the neural encoding of each aspect of social network position in isolation. For each participant, at each point in the brain, the strength of the association between the information content of local neural response patterns and each social network metric of interest was computed based on the Spearman rank correlation coefficient between the local neural RDM and each social network-based RDM. Brain areas where local neural RDMs were significantly related to RDMs based on eigenvector centrality **(A)**, network constraint **(B)**, and social distance **(C)** closely mirrored the results obtained from the GLM decomposition searchlight described in the main text. All presented results survive a statistical threshold of *p* < .005, FWE-corrected.

Appendix 2: Supplementary Information for Study 3

Demographic data of participants in Study 3

Data concerning participants' age, gender, and handedness are presented in the main text. Data regarding participants' self-reported nationality and ethnicity are presented below.

Nationality. Twenty-seven fMRI participants were American citizens and 15 were not. Of the 15 individuals who were non-US citizens, four participants were citizens of the People's Republic of China, three were citizens of Brazil, and one participant was a citizen of each of: Austria, Colombia, Italy, Mexico, Nigeria, Singapore, the Ukraine and the United Kingdom.

Ethnicity. Of the 42 fMRI study participants, 17 identified as White/non-Hispanic, 11 did not respond to this question, one identified as Native American, three identified as Hispanic/Latino, one identified as Black/non-Hispanic, eight identified as Asian/Asian American/Pacific Islander, and one identified as African American/Latino.

Results of Study 3 after accounting for inter-subject similarities in demographic variables

Given that people of similar ages and of the same gender are more likely to be friends with one another than people of different ages and genders (O'Malley & Christakis, 2011), and that these variables have been reported to be associated with differences brain anatomy and functional organization (Good et al., 2001; Tamnes et al., 2010; Vink, Derks, Hoogendam, Hillegers, & Kahn, 2014), homophily in terms of age and gender could lead to inflated estimates of similarity of neural response time courses among friends, irrespective of how individuals interpreted and attended to experimental stimuli. Similarly, given that people of similar cultural and linguistic backgrounds are more likely to be friends (McPherson et al., 2001), and that one's first language impacts the neural processing of content in other languages (Kim, Relkin, Lee, & Hirsch, 1997), homophily in terms of cultural/linguistic background could lead to inflated estimates of the impact of social distance on neural information processing. Therefore, we repeated our main analyses after removing variance in inter-subject neural time series correlation distances that could be accounted for by differences in age, gender and cultural background.

Additionally, handedness (left-handed or right-handed) is sometimes associated with differences in localization of brain function (Willems, Van der Haegen, Fisher, & Francks, 2014). Although handedness does not tend to be significantly more similar among friends than non-friends (O'Malley & Christakis, 2011), similarities and differences in handedness could comprise a potential source of noise in inter-subject neural time course correlations. Therefore, variance in inter-subject neural time series correlation distances that could be accounted for by differences in handedness were also removed prior to further analyses.

Participants' age, handedness, and gender were recorded on the day of each subject's participation in the fMRI study. Although we did not have a direct measure of cultural/linguistic background, information on country of citizenship and ethnicity was available from the university registrar. In order to compare each of the 861 dyads of fMRI participants in terms of categorical variables of no interest (i.e., handedness, gender, ethnicity, nationality), each dyad was assigned a one for the relevant variable (e.g., gender) if they differed in terms of that variable (e.g., a pair in which one participant was male and one participant was female), and a zero otherwise. For the continuous variable (i.e., age), each dyad was assigned the absolute value of their age difference. Each set of inter-subject distances was normalized prior to further analysis such that inter-subject distances for each demographic variable had a mean of zero and a standard deviation of one.

For each of the 80 anatomical ROIs, an ordinary least squares regression was performed in which the dependent variable was the 861-element vector of inter-subject correlation distances for that ROI, and the predictor variables were vectors of normalized inter-subject distances for each of the five effects of no interest described above (i.e., age, gender, handedness, ethnicity, nationality). The residuals obtained from these regressions provide vectors of inter-subject differences in neural time series for each ROI, after regressing out potential confounds (i.e., age, gender, cultural/linguistic background) and sources of noise (i.e., handedness). The resulting distance vectors for each of the 80 anatomical ROIs were normalized to have a mean of zero and a standard deviation of one. These normalized correlation distance values were then multiplied by negative one in order to obtain an estimate of the similarity of responses between pairs of individuals for each ROI, after accounting for inter-subject similarities in variables of no interest (i.e., handedness, age, gender, ethnicity, nationality).

Is similarity of fMRI responses related to social distance?

Are friends more similar to one another than average? Inter-subject similarities (after controlling for differences in demographic variables) were averaged within brain regions at each level of social distance. A one-sample *t*-test indicated that the average similarity of friends' neural response time series ($M = 0.141$; 95% CI: [0.11, 0.17]) significantly exceeded the average, $t(79) = 9.50$, $p = 1.02 \times 10^{-14}$, $r = 0.73$; this effect size exceeds the conventional threshold (i.e., $r > 0.50$) to be considered a large effect (Cohen, 1992).

Inter-subject similarities of indirectly connected dyads. After controlling for inter-subject differences in demographic variables, neural responses of dyads characterized by a social distance of two were more similar to one another than average, $t(79) = 6.65$, $p = 3.53 \times 10^{-9}$, $r = 0.60$, and fMRI response time series of dyads characterized by a social distance of three were significantly less similar to one another than average, $t(79) = 12.77$, $p = 6.82 \times 10^{-21}$, $r = 0.82$. Interestingly, inter-subject fMRI response similarities among dyads characterized by a social distance of four or more did not significantly differ from the mean, $t(79) = 1.10$, $p = 0.27$, $r = 0.12$. Means and 95% confidence intervals of inter-subject similarities at each level of social distance, as well as mean inter-subject similarities for each ROI at each level of social distance after controlling for variables of no interest are displayed in Figure A3. In addition, for the levels of social distance for which inter-subject similarities differed from the mean, average inter-subject similarities for each brain region, after controlling for inter-subject similarities in demographic variables, are shown overlaid on an inflated cortical surface model in Figure A4.

Does inter-subject similarity decrease with social distance? A one-way ANOVA was conducted with social distance (four levels: 1, 2, 3, 4+) as the independent variable and inter-subject neural response similarity (after controlling for similarities in demographic variables), averaged within each ROI at each level of social distance, as the dependent variable. This analysis revealed a large and significant effect of social distance on inter-subject fMRI response time series similarities, even after controlling for inter-subject similarities in demographic variables, $F(3, 316) = 57.86$, $p = 7.72 \text{ x } 10^{-30}$, $\omega^2 = 0.35$; this value of ω^2 is consistent with social distance having a large effect on inter-subject similarities (Kirk, 1996).

Post-hoc pairwise comparisons revealed that inter-subject similarities of dyads comprised of friends were greater than those of dyads from each of the remaining social distance categories. Specifically, dyads comprised of friends were characterized by higher inter-subject similarities than dyads comprised of friends-of-friends (i.e., by a social distance of two), $t(158) = 5.99$, $p = 1.34 \text{ x } 10^{-8}$, $r = 0.43$, as well as dyads characterized by a social distance of three, $t(158) = 12.71$, $p = 6.29 \text{ x } 10^{-26}$, $r = 0.71$, and dyads characterized by a social distance of four or more, $t(158) = 6.35$, $p = 2.21 \text{ x } 10^{-9}$, $r = 0.45$. Thus, even after controlling for inter-subject similarities in demographic variables, the neural responses of friends were significantly more similar to one another than dyads within every other social distance category.

Similarly, dyads characterized by a social distance of two were more similar to one another than dyads characterized by a social distance of three, $t(158) = 12.58$, $p = 1.38 \text{ x } 10^{-25}$, $r = 0.71$. However, this pattern of results (i.e., inter-subject similarity decreasing with social distance) did not hold true for dyads characterized by a social distance of four or more. Such dyads, whose members' fMRI response time series were not significantly more or less similar to one another compared with the average inter-subject similarity, as indicated above, were not significantly more or less similar to one another than dyads characterized by a social distance of two, $t(158) = 1.96$, $p = .05$, $r = 0.15$ (given that these post-hoc pairwise comparisons would need to meet a Bonferroni-corrected significance threshold of $p < .0083$ in order to be considered statistically significant). In addition, unexpectedly, dyads characterized by a social distance of four or more were more similar to one another compared with dyads characterized by a social distance of three, $t(158) = 5.01$, $p = 1.42 \times 10^{-6}$, $r = 0.37$. See Figure A3.

Effects of brain region. As in the analyses presented in the main text, an exploratory analysis was performed to test for possible interactions between social distance and brain region in a two-way ANOVA with social distance (four levels: 1, 2, 3, 4+) and brain region (80 levels; see Table A5) as independent variables and inter-subject neural response similarity, after controlling for inter-subject similarities in demographic variables, as the dependent variable. This analysis again revealed a significant main effect of social distance, $F(3, 68{,}560) = 83.15$, $p = 1.07 \times 10^{-53}$, and no main effect of brain region, $F(79, 68{,}560) = 4.19 \times 10^{-25}$, $p = 1$. An interaction between social distance and brain region $F(237, 68{,}560) = 1.39$, $p = 6.51 \times 10^{-5}$ was observed. The average inter-subject similarities, after controlling for inter-subject similarities in demographic variables, for each of the 80 anatomical ROIs at each of the four social distance levels (1, 2, 3, 4+) are shown in Figure A3.

Results of Study 3 using permutation testing

Permutation testing of the data from Study 3 were performed to supplement the analyses described in the main text. We adopted the topological clustering methods employed by Christakis and Fowler (2013) to test if there was a greater degree of clustering of particular neural response patterns than would be expected based on chance (i.e., if there was exceptionally high neural similarity among connected individuals). This method entailed iteratively computing the neural similarity between all individuals in the network in 1,000 randomly generated datasets in which the topology of the social network and the prevalence of particular neural response patterns were held constant while the assignment of neural data to individuals was randomly shuffled.

More specifically, a distribution of Pearson correlation coefficients corresponding to the null hypothesis that no relationship exists between social distance and neural similarity was obtained by randomly shuffling the neural time series data among participants 1,000 times, then computing the average neural similarity (averaged across brain regions and dyads) within each social distance category for each of the 1,000 randomly generated permutations of the dataset. Each participant's neural time series data consists of an 80 (brain regions) x 1,010 (time points) matrix – i.e., a set of 80 time series, each consisting of 1,010 time points. These neural time series datasets were randomly shuffled among the 42 fMRI study participants 1,000 times while keeping the social network data characterizing these participants constant. For each of the 1,000 permutations, 68,880 Pearson correlation coefficients corresponding to each of the 80 brain regions for each of 861 dyads were computed, then averaged across brain regions and dyads within each social distance category. The magnitude of the average neural similarity for each social distance category within each of the randomly permuted datasets was compared to that of the original, non-permuted data.

Results of these permutation tests revealed a similar pattern of results to those described in the main text. Distance 1 dyads' neural response time series were, on average, exceptionally more similar to one another than would be expected based on chance, *p* = .036. There was a slight non-significant trend such that distance 2 dyads were more similar to one another than would be expected based on chance, *p* = .12. Distance 3 dyads were exceptionally *less* similar to one another than would be expected based on chance, *p* = .01. Distance 4 dyads were neither more or less similar to one another than would be expected based on chance, *p* = .47.

The rationale for performing the permutation analyses described above was two-fold. First, because the structure of the social network is preserved throughout all 1,000 permutations of the data, this method better accounts for the fact that the 861 dyads are not independent of one another (i.e., the same individual participates in multiple dyads, but does not participate in all 861 dyads) compared with the analyses described in the main text. Second, this method provides an estimate of the degree of neural similarity that would be expected within dyads corresponding to each social distance category based on chance alone. Therefore, this method provides an indication of whether the average degree of neural similarity observed for each social distance category is greater or less than what would be expected based on chance. For example, as hypothesized, members of distance 1 dyads were significantly more similar to one another than would be expected based on chance, members of distance 3 dyads were more *dissimilar* to one another than would be expected based on chance, and members of distance 4 dyads were neither more or less similar to one another than would be expected based on chance.

Results of Study 3 using an undirected graph that includes unreciprocated ties

The same pattern of results as that which is described in the main text was observed when both reciprocal and non-reciprocal ties were included in the graph characterizing the social network of first-year MBA students. When including both reciprocal and non-reciprocal ties in the graph, the diameter of the network decreased from 5 to 3. This network, in which an unreciprocated nomination is taken to comprise a social tie between two individuals, includes 171 distance 1 dyads, 644 distance 2 dyads, and 46 distance 3 dyads. As in the main analyses, the distance 1 dyads were significantly more similar to one another than average, $t(79) = 8.59$, $p = 6.15 \times 10^{-13}$, $r = 0.70$. The fMRI response time series of dyads characterized by a social distance of two were significantly less similar to one another than average, $t(79) = 3.25$, $p = 6.82 \times 10^{-4}$, $r = 0.39$, as were those of dyads characterized by a social distance of three, $t(79) = 8.92$, $p = 1.39 \times 10^{-13}$, $r = 0.71$.

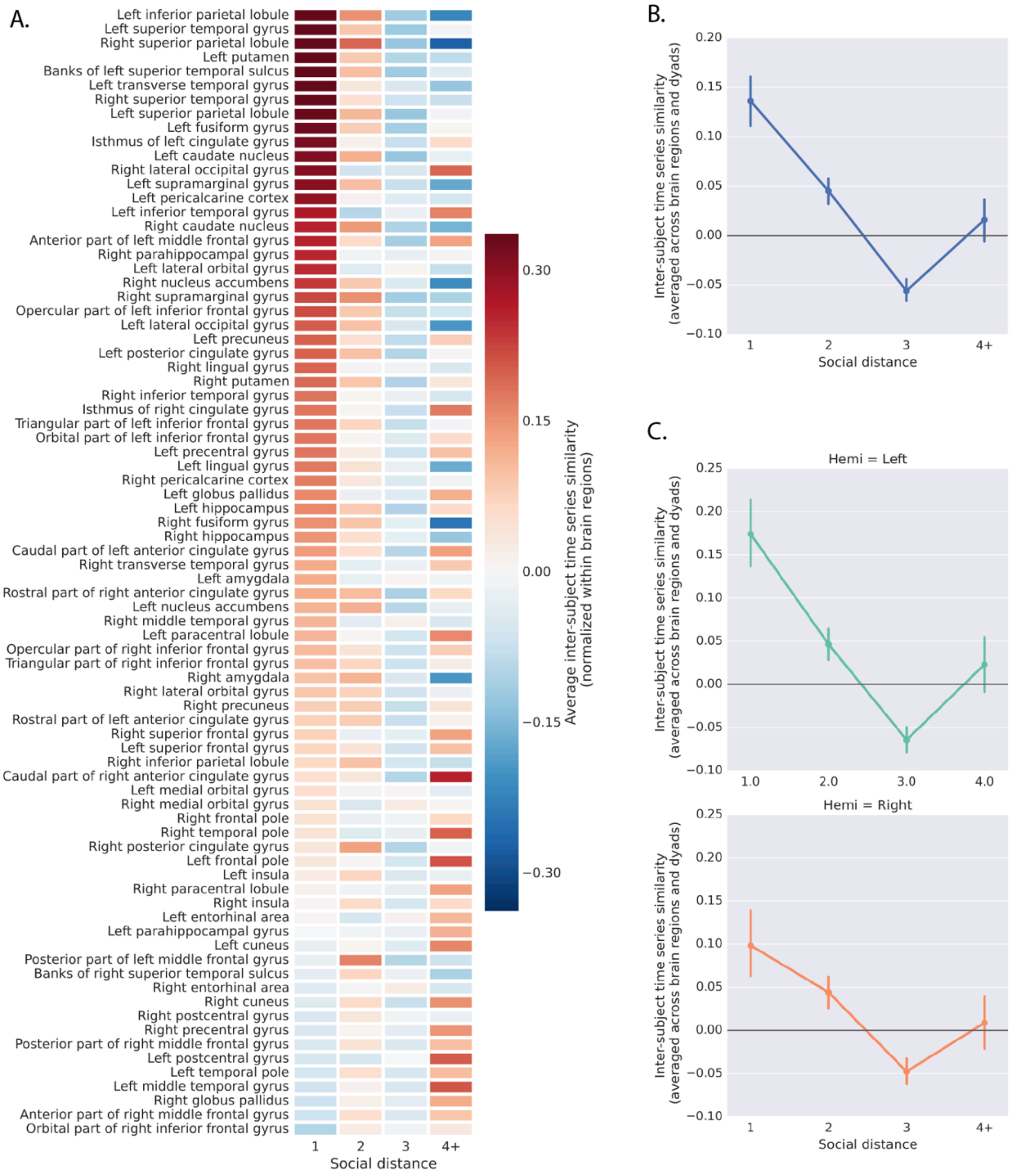


Figure A3. Inter-subject similarities by social distance after controlling for the effects of gender, age, nationality, ethnicity, and handedness. (A) Inter-subject similarities for each ROI at each level of social distance. For each of the 80 anatomical ROIs, an 861-element vector of inter-subject correlation distances was obtained. After removing the effects of inter-subject differences in age, gender, ethnicity, handedness, and nationality, inter-subject correlation distances were normalized within brain region, averaged across dyads within each level of social distance, and multiplied by negative one to convert distance values to similarities. Warmer colors indicate higher inter-subject similarity; cooler colors indicate lower inter-subject similarity. **(B) Inter-subject similarities averaged across ROIs within each level of social distance.** Neural response time series of dyads comprised of students one or two “degrees away” from one another in the network were more similar than average, whereas those of dyads comprised of students three “degrees away” from one another were less similar than average. Neural responses of dyads comprised of students four or more “degrees away” from one another in the network did not significantly differ from zero (i.e., the average). **(C)** The same pattern of results was observed in the left and right hemispheres. Error bars reflect 95% confidence intervals.

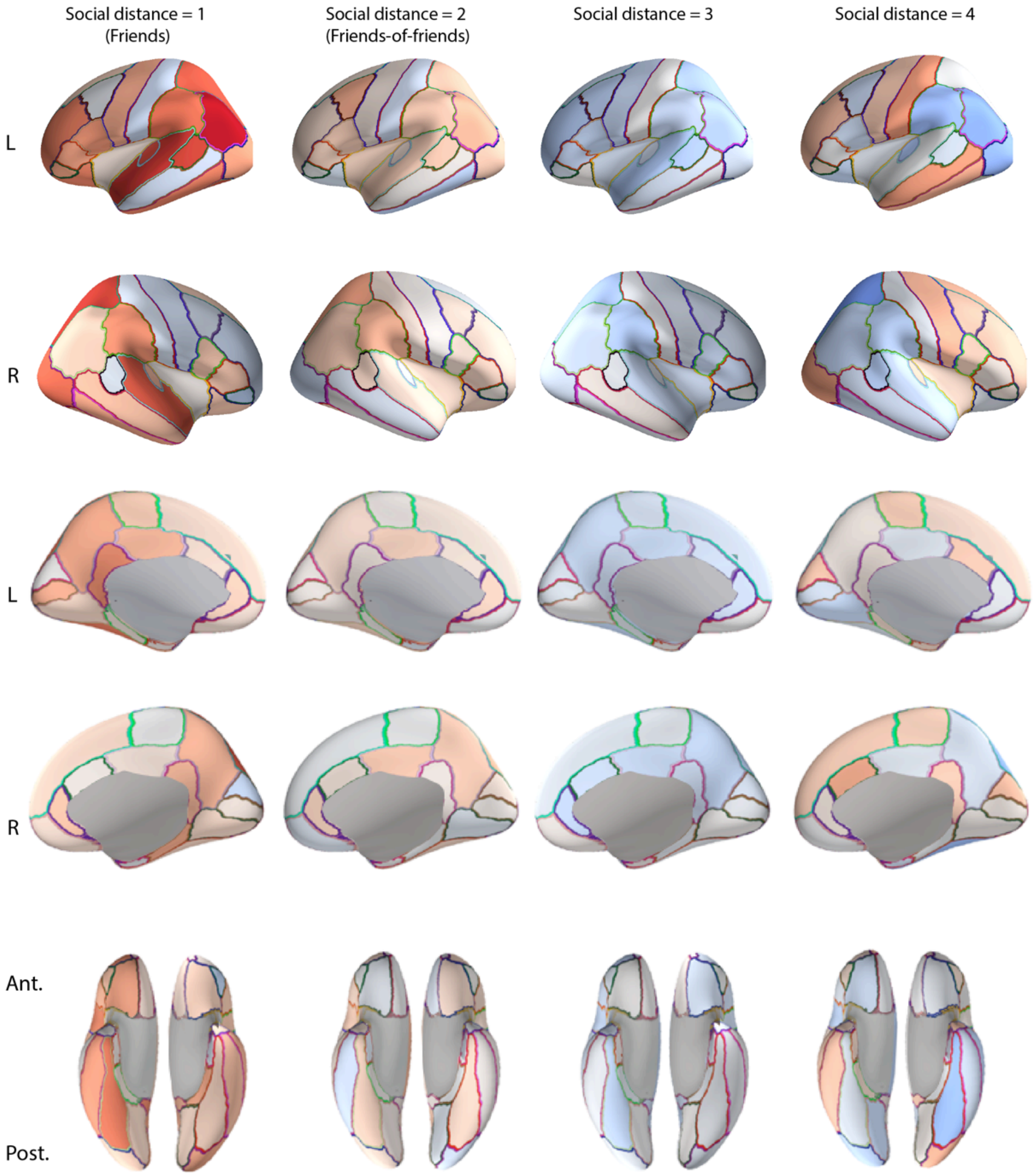


Figure A4. Inter-subject time series similarities by social distance, after controlling for the effects of gender, age, nationality, ethnicity, and handedness, overlaid on a cortical surface model. Average normalized inter-subject time series similarities, after removing the effects of inter-subject similarities in demographic variables (i.e., age, gender, ethnicity, nationality, handedness), are shown overlaid on an inflated model of the cortical surface for each of the social distance categories. The top two, middle two, and bottom two rows depict lateral, medial, and ventral views of the brain, respectively. Ant. = anterior; Post. = posterior; L = left; R = right.

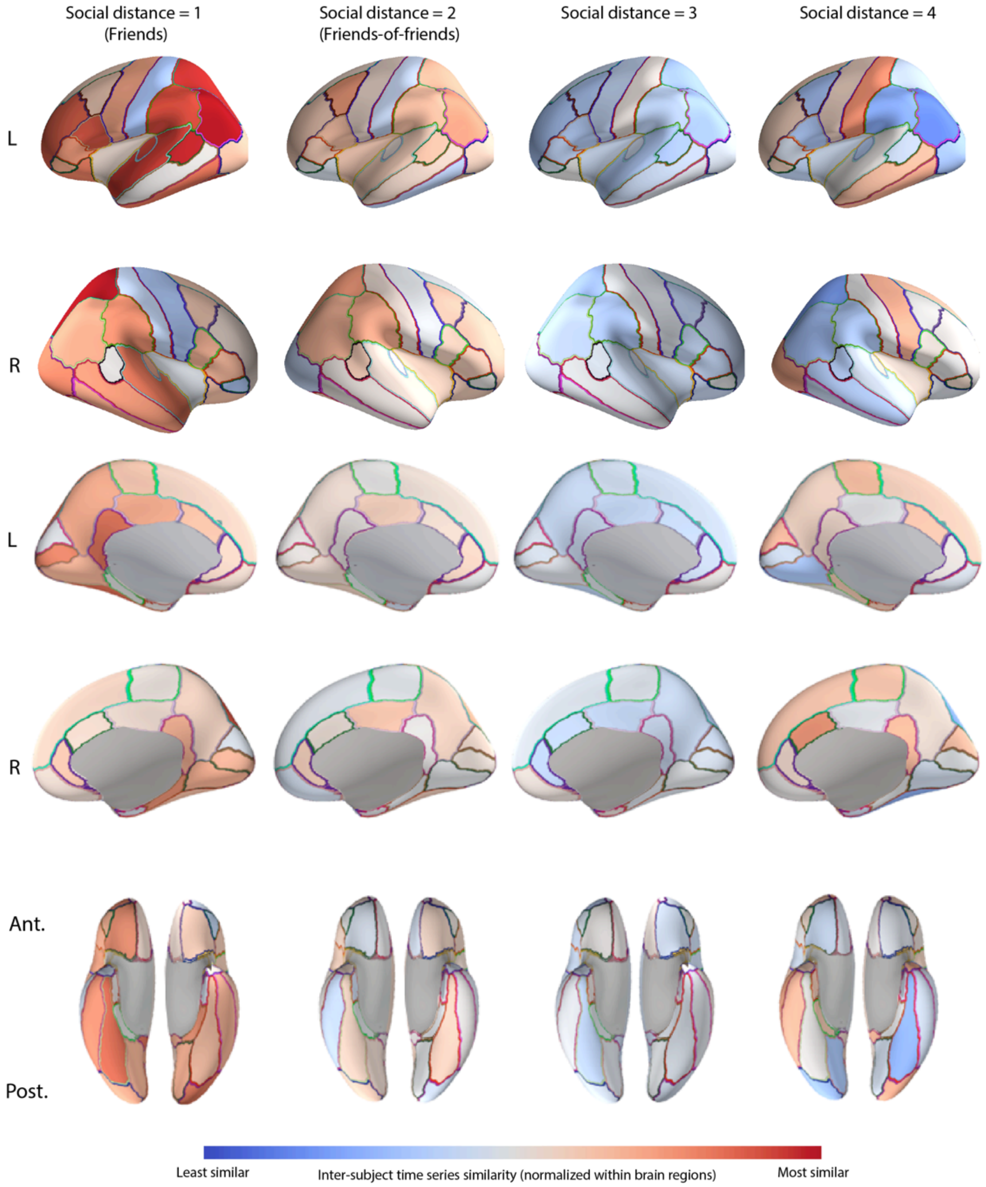


Figure A5. Inter-subject time series similarities by social distance for all distance categories, overlaid on a cortical surface model. Average normalized inter-subject time series similarities (prior to the removal of any covariates) are shown overlaid on an inflated model of the cortical surface for each of the social distance categories. The top two, middle two, and bottom two rows depict lateral, medial, and ventral views of the brain, respectively. Ant. = anterior; Post. = posterior; L = left; R = right.

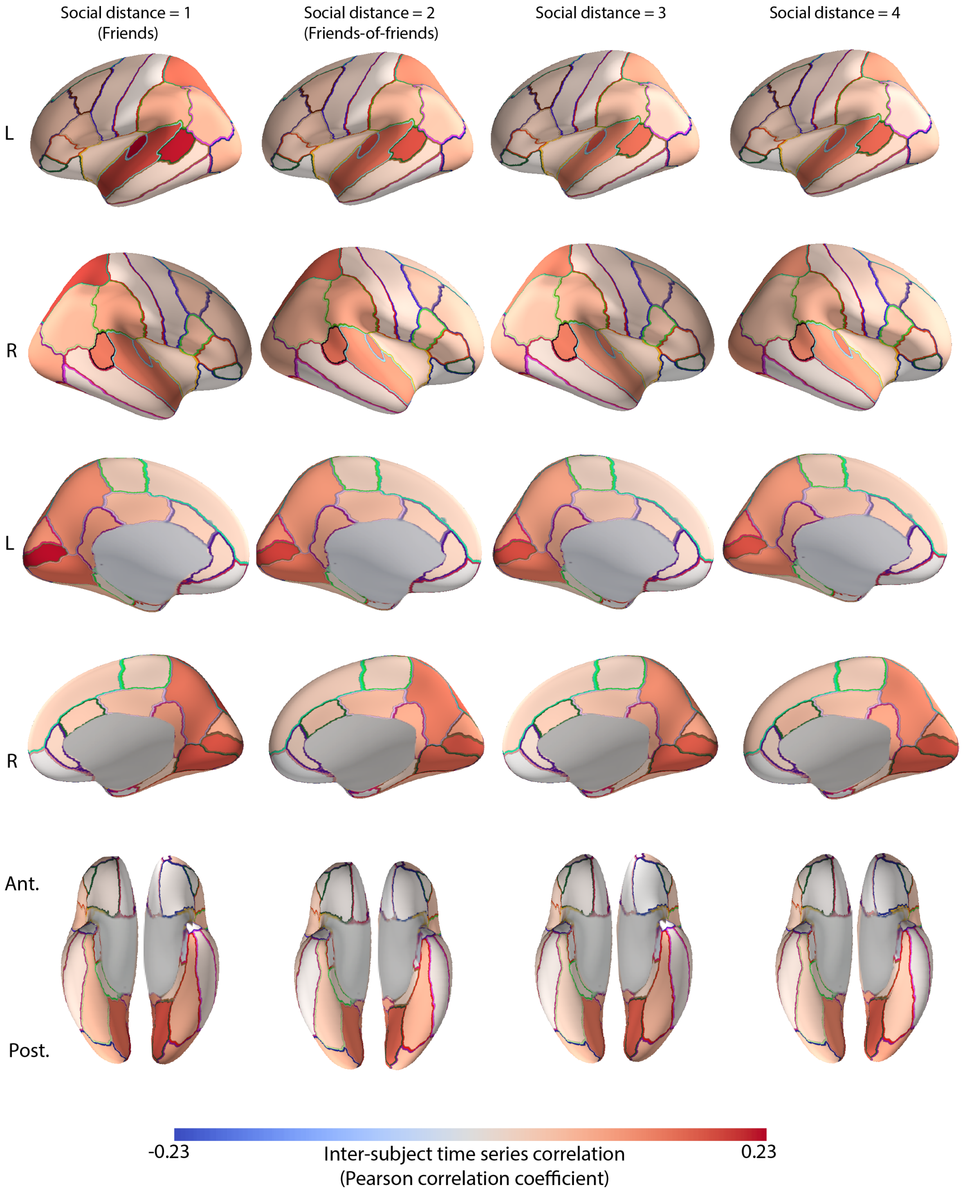


Figure A6. Un-normalized inter-subject time series similarities by social distance for all distance categories, overlaid on a cortical surface model. Average inter-subject time series similarities (prior to the removal of any covariates) are shown overlaid on an inflated model of the cortical surface for each of the social distance categories. The top two, middle two, and bottom two rows depict lateral, medial, and ventral views of the brain, respectively. Overlay colors indicate average Pearson correlations of time series corresponding to each brain region. Warmer colors indicate increased similarity. Ant. = anterior; Post. = posterior; L = left; R = right.

Table A5. Frequency of missing data for each anatomical ROI in Study 3

	Number of subjects missing data (/42)	
	Left	**Right**
Temporal lobe – medial aspect		
Entorhinal area	3	3
Parahippocampal gyrus	1	2
Temporal pole	2	2
Fusiform gyrus	2	2
Temporal pole – lateral aspect		
Superior temporal gyrus	0	0
Middle temporal gyrus	1	0
Inferior temporal gyrus	1	2
Transverse temporal gyrus	0	0
Banks of the superior temporal sulcus	1	0
Frontal lobe		
Superior frontal gyrus	0	0
Posterior middle frontal gyrus	0	0
Anterior middle frontal gyrus	0	0
Inferior frontal gyrus, *pars opercularis*	0	0
Inferior frontal gyrus, *pars triangularis*	0	0
Inferior frontal gyrus, *pars orbitalis*	0	0
Lateral orbital gyrus	0	0
Medial orbital gyrus	0	0
Frontal pole	0	0
Precentral gyrus	0	0
Paracentral lobule	0	0
Parietal lobe		
Postcentral gyrus	0	0
Supramarginal gyrus	0	0
Superior parietal cortex	0	0
Inferior parietal cortex	0	0
Precuneus	0	0
Occipital Lobe		
Lingual gyrus	1	1
Pericalcarine cortex	1	1
Cuneus	0	0
Lateral occipital gyrus	1	1
Cingulate cortex		
Rostral anterior cingulate gyrus	0	0
Caudal anterior cingulate gyrus	0	0
Posterior cingulate gyrus	0	0
Isthmus of the cingulate gyrus	0	0
Insula and subcortical structures		
Insula	0	0
Amygdala	1	0
Caudate nucleus	0	0
Hippocampus	1	1
Globus pallidus	0	0

Putamen	0	0
Nucleus accumbens	0	0

Table A6. Summary of participants' prior familiarity with the video clips used in Study 3

Clip	Title	Number of fMRI participants who had seen clip before (/42)	Number of dyads of fMRI participants who had both seen clip before (/861)
1	'An Astronaut's View of Earth'	0	0
2	Google Glass review	1	0
3	'Crossfire'	0	0
4	'All I Want'	2	1
5	Wedding film	0	0
6	Scientific demonstration	3	3
7	'Food Inc.'	0	0
8	'We Can Be Heroes'	1	0
9	'Ban College Football'	0	0
10	Soccer match	1	0
11	Baby sloth sanctuary	2	1
12	'Ew!'	3	3
13	'Life's Too Short'	4	6
14	'America's Funniest Home Videos'	0	0

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