Brain Coding of Social Network Structure

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Humans have large social networks, with hundreds of interacting individuals. How does the brain represent the complex connectivity structure of these networks? Here we used social media (Facebook) data to objectively map participants' real-life social networks. We then used representational similarity analysis (RSA) of functional magnetic resonance imaging (fMRI) activity patterns to investigate the neural coding of these social networks as participants reflected on each individual. We found coding of social network distances in the default-mode network (medial prefrontal, medial parietal, and lateral parietal cortices). When using partial correlation RSA to control for other factors that can be correlated to social distance (personal affiliation, personality traits, and visual appearance, as subjectively rated by the participants), we found that social network distance information was uniquely coded in the retrosplenial complex, a region involved in spatial processing. In contrast, information on individuals' personal affiliation to the participants and personality traits was found in the medial parietal and prefrontal cortices, respectively. These findings demonstrate a cortical division between representations of non-self-referenced (allocentric) social network structure, self-referenced (egocentric) social distance, and trait-based social knowledge.

Key words: default-mode network; Facebook; fMRI; social distance; social media; social networks

Significance Statement

Each of us has a social network composed of hundreds of individuals, with different characteristics and different relations among them. How does our brain represent this complexity? To find out, we mapped participants' social connections using Facebook data and then asked them to think about individuals from their network while undergoing functional MRI scanning. We found that the position of individuals within the social network, as well as their affiliation to the participant, are mapped in the retrosplenial complex, a region involved in spatial processing. Individuals' personality traits were coded in another region, the medial prefrontal cortex. Our findings demonstrate a neural dissociation among different aspects of social knowledge and suggest a link between spatial and social cognitive mapping.

Introduction

Social interactions and connections form a major part of human life (Dunbar, 2018). To successfully operate in a social world, people need to represent information about hundreds of individuals comprising their social network, that is, their relations with each other (allocentric social network structure), the relation of each

individual to themselves (egocentric personal affiliation), and individuals' unique features (such as their personality traits). Although the brain systems related to personal affiliation and personality trait coding have been investigated (Maddock et al., 2001; Shah et al., 2001; Mitchell et al., 2006; Jenkins et al., 2008; Jenkins and Mitchell, 2011; Hassabis et al., 2014; Parkinson et al., 2014, 2017; Włodarski and Dunbar, 2016; Tamir et al., 2016; Thornton et al., 2019), it is less clear how people store information on the non-self-referenced (allocentric) structure of their social network. This information can be important for proper social interaction and decision making, independently of personal affiliation knowledge (e.g., if one feels close to two people but they dislike each other). Interestingly, the two types of social proximity information—personal affiliation and social network structure/distances—may be equated to egocentric and allocentric processing in the spatial domain (where items are located with respect to one's current location vs the structure of the map regardless of one's location in it), in line with previous studies suggesting that social networks and spatial environments share similar neurocognitive representations (Parkinson and Wheatley, 2013; Peer et al., 2015; Epstein et al., 2017).

Received Oct. 13, 2020; revised Feb. 18, 2021; accepted Apr. 5, 2021.

Author contributions: M.P. and S.A. designed research; M.P., M.H., B.T., and S.A. performed research; M.P., M.H., B.T., and S.A. analyzed data; M.P. and S.A. wrote the paper.

This work was supported by the Israeli Science Foundation (Grant No. 1306/18). M.P. was supported by a Fulbright postdoctoral fellowship from the United States–Israel Educational Foundation, a Zuckerman STEM Leadership Program fellowship, and the Eva, Luis, and Sergio Lamas Scholarship Fund. We thank Assaf Yohalashet, Lee Ashkenazi, Dr. Yuval Porat, and Prof. Leon Deouell from the Edmond & Lily Safra Center for Brain Sciences neuroimaging unit; Rachel Fried, Catherine Nadar, Dr. Iva Brunec, Dr. Nicholas Diamond, Dr. Shachar Maidenbaum, Dr. Yoed Kenett, Dr. Zvi N. Roth, and Prof. Russell Epstein (University of Pennsylvania) and Prof. Daniel L. Schacter (Harvard University) for helpful suggestions and discussions.

The authors declare no competing financial interests.

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<https://doi.org/10.1523/JNEUROSCI.2641-20.2021>

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Several neuroimaging lines of research may shed light on how the brain codes different aspects of social knowledge (Anzellotti and Young, 2020). Investigations of social representations have demonstrated that activity levels in the medial parietal, lateral parietal, medial temporal, and medial prefrontal cortex reflect individuals' personal affiliation to the participant (Maddock et al., 2001; Shah et al., 2001; Parkinson et al., 2014, 2017; Tavares et al., 2015; Włodarski and Dunbar, 2016), overall social network size (Kanai et al., 2012; Bickart et al., 2012; Powell et al., 2012; Von Der Heide et al., 2014; Meshi et al., 2015; Hampton et al., 2016), and others' personality traits (Mitchell et al., 2006; Jenkins et al., 2008; Jenkins and Mitchell, 2011; Hassabis et al., 2014). These regions are part of the brain's default-mode network, known to be active during self-referential processing and internal mentation (Buckner et al., 2008; Buckner and DiNicola, 2019), including mentation about others (e.g., theory of mind; Saxe and Kanwisher, 2003; Buckner and Carroll, 2007; Thornton et al., 2019).

More recent studies have directly investigated aspects of the brain coding of social network structure. Studies of how the brain represents social hierarchy and power (using fictional individuals) demonstrated involvement of the hippocampus, amygdala, medial prefrontal, and posterior cingulate cortices (Kumaran et al., 2012, 2016; Tavares et al., 2015). Another recent study mapped real-life social distances among people in a specific class of students, identifying coding of personal affiliation to the participant and measures of individuals' centrality in the social network (eigenvector centrality and brokerage) across regions of the lateral temporal, medial and lateral parietal, and medial prefrontal cortex (Parkinson et al., 2017). However, the following several questions remain unanswered: (1) How does the brain represent the allocentric structure of social networks (i.e., the social network distances between other individuals)? (2) Is this representation independent of other factors, such as egocentric affiliation to the self, or similarity among individuals along different features? and (3) How does the brain represent the structure of real-world, large-scale social networks, that may contain individuals from different groups and social contexts? To answer these questions, we used real-life social media data and multivoxel functional magnetic resonance imaging (fMRI) activity analyses to identify how the brain represents different aspects of social knowledge.

Materials and Methods

Experiment and analysis overview

To investigate the neural coding of social information, we extracted mutual friendship information from participants' social media profiles. We used this objective information to calculate the social network distance between all individuals in each participant's network and reconstruct the network's structure, independently of these individuals' affiliation to the participant. We used a social network distance measure (proportion of individuals' mutual friends relative to all friends) that captures individuals' distance from each other in terms of their social network location, that is, are they in the same part of the network or belong to the same social group, regardless of the strength of personal or emotional connection among them. Note that although social-media-based connectivity may be biased with respect to reality (e.g., influenced by individuals' frequency of social media usage), the use of a distance measure based on the overall pattern of connections in the network mitigates these biases and results in reasonable approximations of real-world perceived social distance (see below, Calculation of dissimilarity matrices). We then recorded functional MRI activity while participants thought about each individual. To encourage thinking about different individuals, in each trial the name of one individual was presented, and the participant was

Figure 1. Experimental design. The paradigm was designed to make participants think about individuals they know. To this end, participants were presented with a question, followed by names of 24 individuals from their personal social network, and were asked to respond to the same question on each of the individuals using a 1–4 rating scale. There were 12 questions, 4 about personal affiliation (e.g., How much do you like this person?), 4 about personality traits (e.g., How smart is this person?), and 4 about visual appearance (e.g., How tall is this person?). Each question was presented for 10 s, followed by a randomly ordered sequence of all 24 names, each presented for 4 s with an interval of 4 s between names. The same 24 unique individual names were used for all questions.

asked to answer a question about this individual by providing a rating regarding personal affiliation, personality traits, or visual appearance; Fig. 1). Although these questions served mainly to encourage thinking about each individual, they also provided subjective ratings that enabled calculating the similarity between these individuals in terms of their subjectively perceived characteristics. Importantly, participants were not explicitly asked at any stage about relations among individuals along any social dimension. Finally, we used representational similarity analysis (RSA) of multivoxel activity patterns to identify brain regions representing unique information on different aspects of social knowledge—social network distance, personal affiliation, personality traits, and visual appearance. The use of RSA relies on the assumption that if a brain region codes information on a specific dimension (here, social network distance), it will display similar activity patterns when participants think of individuals who are close along this dimension. By concurrently investigating the similarity among individuals along multiple social dimensions, our study enables dissociating the unique aspects that make up relational social knowledge.

Participants

Eighteen healthy participants (9 male, 9 female, all students at Hebrew University of Jerusalem, mean age $\pm$ SEM 25.8 ± 3.4 years) participated in the study. The number of participants was selected based on sample sizes used in studies of multivoxel pattern representations of spatial distances between landmarks (Morgan et al., 2011; Marchette et al., 2014; Sulpizio et al., 2014; Nielson et al., 2015; Deuker et al., 2016; Huffman and Ekstrom, 2019). Participants were required to have a Facebook social media account. All participants provided written informed

consent, and the study was approved by the ethics committee of the Hadassah Hebrew University Medical Center.

Experimental stimuli. Participants were asked to provide the full names of 24 of their Facebook social media platform friends, from 4 different social groups in their life (6 individuals from each group). All 24 names had to be distinct from each other. Examples of social groups provided by the participants are family members, friends from a trip abroad, high school friends, national service friends, friends from work, friends from the university, and friends from a youth movement. The request to provide names from four distinct social groups was to sample multiple parts of each participant's social network while still maintaining within-group variability (although this design prevented investigations of individuals who are part of multiple social groups).

Extraction of social network data

Social network connectivity information was extracted using the Lost Circles Chrome Extension, a tool that maps which of the participant's friends on Facebook are connected with each other (mutual friends), thus enabling reconstruction of their social network. Each participant installed and ran the Lost Circles extension, and the resulting data file was converted to a binary connectivity matrix among all individuals in the participant's social network. Participants' social network comprised on average 571 ± 379 individuals (mean $\pm$ SD, smallest network size = 99, largest network size = 1279). No other data about Facebook interactions among individuals was collected. The experimenters did not have access to participants' Facebook accounts at any point.

Experimental paradigm

During the experiment, participants were asked to respond to 12 questions about each of the 24 individuals whose names they provided while undergoing fMRI scanning (Fig. 1). The following four questions were related to personal affiliation: How much do you trust this person? How much do you like this person? How well do you know this person? and How often do you see this person? The following four questions were related to personality traits: How funny is this person? How charismatic is this person? How smart is this person? and How ambitious is this person? The following final four questions were related to visual appearance: How pretty is this person? How dark is this person's skin? How tall is this person? and How muscular is this person? The questions were designed to encourage deep elaboration of each individual in turn but in addition provided data (participants' subjective ratings) for control analyses of factors influencing brain activity beyond social network structure.

The experiment consisted of six experimental runs. Each run started with 4 s of fixation, followed by two question phases yielding a total of 12 questions across the experiment. Each question phase started with the presentation of one of the 12 questions for 10 s, followed by 4 s of fixation. After each question, the 24 names provided by the participant were presented sequentially, each shown for 4 s followed by 4 s of fixation before the next name (This fixed interstimulus interval was selected to create maximal separation among the experimental stimuli while fitting the experiment within a 1 h time frame; Dimsdale-Zucker and Ranganath, 2018). Participants were required to answer the preceding question for all the 24 names using a 4-button response box, leading to a rating of 1 to 4 for each response. Question order was randomized across participants, and the order of the 24 presented names was randomized across questions.

Calculation of dissimilarity matrices

For each participant, four 24×24 dissimilarity matrices were computed between each of the 24 participant-provided individual names, using the following metrics.

Social network distance. The network distance between each pair of individuals was computed as one minus the proportion of friends they share out of the total number of their friends (Granovetter, 1973; Bapna et al., 2017). Intuitively, individuals with many mutual friends will occupy the same region of the social graph (or same social group), whereas individuals with few mutual friends will occupy different graph regions. Therefore, this measure maps distances between individuals in

the social space (whether they occupy the same region of the social network), regardless of the strength of connection between them. This social network distance measure controls for individuals' popularity (overall number of friends) and diminishes the effects of shortcuts between graph regions, as opposed to path length measures. To test the relation of this measure to interindividual friendship strength, four participants ranked the friendship strength for all 276 pairs of 24 individuals they provided on a scale of 1–10; the average correlation between the friendship ratings and the Facebook-based computed social network distance was $r = 0.86$ (minimum 0.84, maximum 0.88; all correlations significant at $p < 0.0001$), indicating that Facebook-derived connectivity-based distances are a reasonable proxy for perceived real-world connection strength. Note that this social network distance measure is computed based on the Facebook connectivity data in contrast to the following measures that were computed based on participants' responses during the experiment. See below the section "Analysis of alternative distance measures" for other investigated social distance measures.

Dissimilarity in personal affiliation to the participant. This is calculated as the Euclidean distance between the participant's responses to the four personal affiliation questions. For example, if a participant gave the same answers for two individuals regarding how much she/he trusts them, how frequently they meet, and so on, these individuals will have a high similarity value.

Dissimilarity in personality. This is calculated as the Euclidean distance between answers to the four personality traits questions.

Dissimilarity in visual appearance. This is calculated as the Euclidean distance between answers to the four visual appearance questions.

Three participants had one name each that could not be identified in their Facebook network (one participant provided a name that did not appear in the Facebook friends list, and two participants had two different individuals in their network with the same first and last name). For these participants, the missing names were removed from all connectivity matrices, and the resulting 23×23 dissimilarity matrices were used in all further analysis.

MRI acquisition

Participants were scanned in a Skyra 3T MRI (Siemens) at the Edmond & Lily Safra Center neuroimaging unit. Blood oxygenation level-dependent (BOLD) contrast was obtained with an echo-planar imaging sequence [repetition time (TR), 2 s; echo time (TE), 30 ms; flip angle, 75°; field of view, 192 mm; matrix size, 64×64 ; functional voxel size, $3 \times 3 \times 3$ mm; 37 slices, axial slice orientation according to participants' anterior to posterior commissure axis, descending slice acquisition order, 0.3 mm gap; 213 TRs per run]. In addition, T1-weighted anatomic images ($1 \times 1 \times 1$ mm, 160 slices) were acquired for each participant using an MPRAGE protocol [TR, 2300 ms; TE, 2.98 ms; flip angle, 9°; field of view, 256 mm].

MRI processing

Data from fMRI were processed and analyzed using BrainVoyager 20.6 (Brain Innovation; RRID:SCR_013057), NeuroElf version 1.1 (RRID:SCR_014147), and in-house MATLAB scripts (MathWorks, version 2018a; RRID:SCR_001622). Preprocessing of functional scans included slice timing correction (cubic spline interpolation), 3D motion correction by realignment to the first run image (trilinear detection and sinc interpolation), high-pass filtering (up to 0.005 Hz), smoothing (full-width at half-maximum = 2 mm), exclusion of voxels below intensity values of 100, and coregistration to the anatomic T1 images (using the original first image of the functional run before smoothing and filtering). Anatomical brain images were corrected for signal inhomogeneity and skull-stripped. All images were subsequently normalized to Montreal Neurologic Institute (MNI) space ($3 \times 3 \times 3$ mm functional resolution, trilinear interpolation). Correct coregistration and normalization of each run was visually verified.

Estimation of cortical responses to each stimulus

A general linear model (GLM) analysis was applied. Each modeled predictor corresponded to one of the 24 individuals and included all

experimental trials where this individual's name was shown, regardless of the question asked in this trial. Predictors were convolved with a canonical hemodynamic response function, and the model was fitted to the BOLD time course at each voxel. Twenty-four motion parameters were added to the GLM to eliminate motion-related noise; these parameters consisted of the six translation and rotation parameters, their temporal derivatives, and the squared values of the six parameters and their derivatives (Friston et al., 1996; Charest et al., 2018). The resulting GLM β values were converted to t values using BrainVoyager contrasts (1 for each predictor and 0 for all other predictors; Misaki et al., 2010). Finally, the t values corresponding to each individual name were averaged across experimental runs to obtain a single pattern for each individual name (Dimsdale-Zucker and Ranganath, 2018).

Representational similarity analysis searchlight

To investigate the brain's representation of different social factors, neural pattern similarities were compared with the different behavioral dissimilarity matrices using a whole-brain representational similarity analysis (RSA) searchlight approach (Kriegeskorte et al., 2008). Analyses were performed using CoSMo Multivariate Pattern Analysis (CoSMoMVPA; Oosterhof et al., 2016) and in-house MATLAB scripts. A spherical searchlight was run by defining a sphere with a radius of three voxels that was moved across the brain. In each sphere location, the t values for each of the 24 individual names were extracted from all voxels included in the sphere. Next, the mean activity pattern across all 24 conditions was subtracted from all activity patterns to eliminate global effects (Diedrichsen and Kriegeskorte, 2017). Subsequently, for each searchlight sphere location, a 24×24 neural dissimilarity matrix was computed between the 24 individual-specific activity patterns using Pearson's correlation. The neural dissimilarity matrix was then compared with each of the four behavioral dissimilarity matrices (Facebook-derived social network distance, personal affiliation, personality traits, and visual appearance dissimilarity matrices) using Spearman's correlation (Nili et al., 2014), resulting in a whole-brain correlation map for each matrix. Group analysis was performed for each matrix's correlation map using permutation testing (10,000 iterations) with threshold-free cluster enhancement, as implemented in the CoSMoMVPA toolbox (Smith and Nichols, 2009; Stelzer et al., 2013). A conjunction analysis was performed by identifying the voxels passing the significance threshold for all social measures for which significant representation was found (social network distance, personal affiliation, and personality).

To identify the independent contribution of each social dissimilarity matrix, a similar RSA searchlight was performed for each of the four dissimilarity matrices (social network distance, personal affiliation, personality traits, and visual appearance dissimilarity matrices), using a partial correlation approach as implemented in CoSMoMVPA (regressing out from each matrix the contribution of the other three matrices to control for their shared variance; Parkinson et al., 2017). Group-level results were again computed using permutation testing with threshold-free cluster enhancement. The anatomical labels of peak searchlight coordinates were determined by the Atlas of Intrinsic Connectivity of Homotopic Areas (Joliot et al., 2015).

Overlap of RSA searchlight results with resting-state networks

Overlap was calculated between the significant voxels in the RSA searchlight group analysis result and each of the seven major resting-state networks as identified by Yeo et al., 2011 (<https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation>). The overlap was calculated as the number of significant searchlight voxels included in each network divided by the overall number of significant searchlight voxels. The significance of the overlap with each network was computed by permuting the voxel labels for the seven networks 1000 times and looking at the number of permutations reaching the same degree of overlap or higher.

RSA analysis in regions of interest

Functional regions of interest (ROI) masks of scene-selective regions in each hemisphere (regions that respond preferentially to scene viewing compared with other types of visual stimuli—retrosplenial complex (RSC), parahippocampal place area (PPA), and occipital place area

(OPA))—were obtained from a previous publication (Julian et al., 2012; <http://web.mit.edu/bcs/nklab/GSS.shtml>). These masks represent group activation clusters from 30 participants who watched visual images with a contrast of scenes > objects. Additional functional ROIs for regions active during social and spatial proximity judgments were defined from the results of our previous study (Peer et al., 2015; contrasts—social judgments vs lexical control and spatial judgments vs lexical control, random-effects group analysis results). An anatomic hippocampal region of interest was extracted from the Automatic Anatomical Labeling atlas (Tzourio-Mazoyer et al., 2002). In each of these predefined ROIs, the partial correlation RSA analysis described above was performed for each participant separately (using the activity pattern across all ROI voxels). Significance in each ROI was computed using a one-sample two-tailed t test across participants [with multiple comparisons correction for the number of ROIs using the false discovery rate (FDR) Benjamini-Hochberg method as implemented in MATLAB]. Within each ROI, significant differences between social factors were additionally calculated using repeated-measures ANOVA, with *post hoc* testing performed using paired-samples two-tailed t tests with FDR correction. Finally, an additional analysis of the correlation to each social factor matrix (without partial correlation) was performed in the ROIs identified using the partial-correlation searchlight for each social factor.

Analysis of alternative distance measures

In addition to the main Facebook social network distance measure described above (proportion of mutual friends), we also attempted to test other measures of social network distance: the overall number of mutual friends two individuals have, the shortest path length between individuals (calculated with the Brain Connectivity Toolbox; Rubinov and Sporns, 2010), the existence of a direct connection between individuals (binary measure), and the communicability between individuals as reflected by the connectivity matrix exponential (Estrada and Hatano, 2008). All measures were normalized to the range of 0–1 (normalizing by maximum value) and were converted to dissimilarity matrices by subtracting from 1. The RSA searchlight approach described above was repeated with each of these matrices. In addition, we examined the specific effects of direct connectivity and social group membership on the neural representations by performing a partial correlation of the original dissimilarity matrix (proportion of mutual friends) and partialling out either the direct connectivity matrix or the social groups matrix (a matrix with 1 if participants determined that the individuals belong to the same social group or 0 otherwise) in the regions of interest found to represent social information (left and right RSC, social orientation and spatial orientation regions).

Estimation of individual-specific pattern consistency in ROIs across questions and within social groups

Following the main RSA analysis, we tested whether individual-specific patterns are consistent across questions (in each participant separately) and between individuals belonging to the same social group to measure whether the observed effects relate to question-specific or group-specific contextual factors instead of reflecting each individual's unique position in the social network. This analysis was performed in the ROIs found to code for social network distance information (left and right RSC, social and spatial orientation regions). To measure question-specific patterns, the multivoxel pattern of t values corresponding to each of the 24 individuals was extracted from each ROI for each experimental question separately. Each individual-specific pattern was then correlated to all other individuals' patterns across each possible pair of questions, resulting in 66 interquestion correlation matrices. For each of these matrices, the mean of the matrix diagonal (depicting how similar is each individual's pattern to the pattern of the same individual in a different question) was computed, and the mean of the nondiagonal elements (representing similarity of the individual's pattern to other individuals' patterns) was then subtracted from it. If a pattern is consistent across questions, the subtraction result should be positive. The resulting values were averaged across all question pairs for each participant, and a one-tailed dependent-samples t test was performed on the average subtraction values in each ROI

Figure 2. The default-mode network represents social network distance information. **A**, Demonstration of the representational similarity searchlight procedure on social media network distance between individuals. **B**, Analysis results. Pattern similarity across regions of the default-mode network was associated with distance between individuals in each participant's personal social network, as derived from the social media connectivity data. The black outline delineates the default-mode network, as defined in Yeo et al., 2011. All p values < 0.01 , Monte Carlo permutation test, threshold-free cluster enhancement correction for multiple comparisons.

across participants to test for consistent coding of individuals' identity across questions.

To test for social group effects, a similar analysis was performed across questions, with subtraction of the mean of the interquestion correlation matrix diagonal elements from the mean of the matrix cells corresponding to individuals' pattern correlations to other individuals in their social group (as defined by the participants during stimulus selection). The result of the one-tailed dependent-samples t test of these values indicates if ROI patterns contain information on individuals' identity beyond their shared membership in a social group.

Analyzing question type effects

To test whether information on each social dimension is represented in neural activity patterns even when participants are not being asked about these dimensions, we repeated the partial correlation analysis of the three social dimensions to which the questions referred (personal affiliation, personality traits, and visual appearance). For each social factor, the analysis was performed by using data only from the eight questions that were not related to the social dimension of interest. This analysis was performed in the regions of interest where coding of these dimensions was identified in the original partial correlation RSA searchlight analysis.

Data visualization

Volume results were converted to surface representations and displayed using Connectome Workbench (Marcus et al., 2011).

Data availability

All the preprocessing codes, analysis codes, and resulting statistical maps are available at https://github.com/CompuNeuroPsychiatryLabEinKerem/publications_data/tree/master/social_networks.

Results

The default-mode network represents information on social network distance between personally familiar individuals

Social network distance between individuals was computed using their objective friendship patterns as extracted from social media, independent of their affiliation to the participants. Representational similarity searchlight analysis was then used to compare social network distances to the similarity in neural patterns when participants think of these individuals. This analysis revealed coding of social network distances in regions within the

medial and lateral parietal and frontal cortices (Fig. 2). Comparison of the regions coding social network distances to large-scale resting-state networks (Yeo et al., 2011) reveals that these regions correspond to the default-mode network (Dice's coefficient for default-mode network overlap = 0.79, $p < 0.001$, permutation test; no other resting-state network had significant overlap with social network distance coding regions). In addition, several regions in the lateral prefrontal cortex outside the default-mode network (left and right superior frontal gyrus, left precentral gyrus, and right inferior frontal gyrus) also represented social network distances (Fig. 2).

Partial dissociation between coding of social network distances, personal affiliation, and personality traits in the parietal and frontal cortices

The correspondence between neural pattern similarity and social network distance could be related to other factors that are correlated with social network distance, such as personal affiliation to the participant and similarity in personality traits (Table 1). To dissociate these factors, we constructed similarity matrices for individuals' personal affiliation to the participant, personality traits, and visual appearance, based on participants' subjective ratings. Representational similarity searchlight using these matrices revealed that similarity in personal affiliation and personality traits (but not visual appearance) is also correlated to neural pattern similarity within the default-mode network in accordance with their shared variance with social network distance (Table 1; Fig. 3). To measure the independent contribution of each factor (similarity in activity explained by the unique variance of each factor, excluding the effect of the common variance), we performed an RSA searchlight using a partial correlation approach (Fig. 4; Table 2). We found that after controlling for the aforementioned factors, the only region representing information on social network distances is the posterior part of the medial parietal lobe in the precuneus and parieto-occipital sulcus. An adjacent and partially overlapping region within the medial parietal lobe, and an additional region in the lateral parietal lobe, represented information on personal affiliation to the participant. Finally, information on similarity in individuals' personality traits was found in the medial prefrontal lobe (Fig. 4). No region represented information on similarity in visual appearance. Direct correlation analysis of the original dissimilarity matrices in the regions identified by the RSA searchlight indicated that neural similarity patterns in each of these regions were maximally correlated with the social factor by which the region was identified (Fig. 5).

The individual-specific activity patterns were extracted from fMRI responses while participants answered questions on these individuals, including questions related to the social aspects of interest (personal affiliation, personality traits). To check if this had an effect on the results, we tested whether information on personal affiliation and personality traits can be decoded from brain activity in regions identified in the partial correlation analysis, when excluding the fMRI data recorded during response to questions about these factors. Personal affiliation was represented in the personal affiliation coding regions when excluding the personal affiliation questions' data ($t_{(16)} = 3.19$; $p = 0.006$),

Table 1. Correlation between dissimilarity matrices

	Social network distance (proportion of mutual friends)	Similarity in personal affiliation ratings	Similarity in personality traits ratings	Similarity in visual appearance ratings
Social network distance (proportion of mutual friends)	1.00	0.13	0.08	0.03
Similarity in personal affiliation ratings	0.13	1.00	0.18	0.08
Similarity in personality traits ratings	0.08	0.18	1.00	0.08
Similarity in visual appearance ratings	0.03	0.08	0.08	1.00

Average of within-participant Pearson's correlation values (r) between the different dissimilarity matrices representing different aspects of social knowledge. The distance among individuals in the social network was found to be correlated to the similarity of responses to questions about personal affiliation, personality traits, and visual appearance. All correlations between dissimilarity matrices are significantly larger than 0 except between the social network distance and the responses to visual appearance questions (all $p < 0.05$, 1-sample 1-tailed t test across participants, FDR corrected for multiple comparisons).

but personality traits were not represented in the personality coding regions when excluding questions about personality traits ($t_{(16)} = 1.37$; $p = 0.19$). This may indicate that information on individuals' personal affiliation to the participant is represented in the parietal lobe even when participants are not actively thinking about this attribute. In contrast, personality traits information can be decoded from medial prefrontal activity patterns only when participants are explicitly asked about these traits.

Social network distance information is found in scene-selective and spatial processing regions

The identified medial parietal region coding for social network distances appears to overlap with the RSC, a region involved in scene processing (Epstein et al., 2007; Epstein, 2008). The social network coding region also appears to overlap with regions we identified in a previous study (Peer et al., 2015), which are active when participants make egocentric proximity comparisons to different places (spatial orientation region) and to different people (social orientation region). To measure whether these regions indeed represent social network information, we performed the partial-correlation RSA in each of these independently defined regions of interest, for each social factor of interest (social network distance, personal affiliation, personality traits, and visual appearance). We found significant coding of social network distance between individuals in the left and right retrosplenial complex, as well as within the spatial and social orientation regions (Fig. 6; $t_{(16)} = 4.52, 3.32, 3.63, 4.71$; $p = 0.002, 0.01, 0.008, 0.002$, respectively; no effects were found in the left and right PPA, left and right OPA, or left and right hippocampus, $t_{(16)} = 1.73, -0.22, -0.28, 0.80, 1.81, -0.75$, respectively; all p values > 0.05 , FDR corrected for multiple comparisons). Coding of personal affiliation to the participant was also found in the social orientation region (Fig. 6; $t_{(16)} = 3.66$; $p = 0.02$; no effects found in the left and right RSC, left and right PPA, left and right OPA, left and right hippocampus, and spatial orientation region, $t_{(16)} = 1.85, 2.62, 0.12, 1.20, 0.58, 1.84, 1.39, 1.69, 2.03$, respectively; all p values > 0.05 ,

Figure 3. The default-mode network represents information on similarity between personally familiar individuals across multiple aspects of social knowledge. Similarity between activity patterns related to thinking about different familiar individuals was compared with the similarity between these individuals in different social aspects using a representational similarity searchlight analysis (sphere radius = 3 voxels). **A–D**, Pattern similarity across regions of the default-mode network was associated with distance between individuals in the participants' personal social networks, as derived from social media (Facebook) connectivity data (**A**; similar to Fig. 2); similar ratings of personal affiliation to the participant (**B**); and similar ratings of personality traits (**C**); but not with similar ratings of visual appearance (**D**). **E**, A conjunction analysis revealed that social network distance, personal affiliation, and personality traits are all coded in similar voxels that lie within the default-mode network (black outline) and in an additional lateral prefrontal (precentral gyrus) cluster. All p values < 0.01 , Monte Carlo permutation test, threshold-free cluster enhancement correction for multiple comparisons.

FDR corrected for multiple comparisons). Comparisons between the coding of the different social factors in each ROI revealed significant differences in the social and spatial orientation regions (repeated-measures ANOVA, $F_{(16)} = 4.26, 3.96$; $p = 0.01, 0.01$, respectively), but *post hoc* tests found a significant difference only between social network distance and visual appearance coding in the spatial orientation region and not between the other

Figure 4. Partial dissociation between representations of social network distances, personal affiliation, and personality traits. **A**, Similarity matrices for individuals’ social network distance, personal affiliation to the participant, personality traits, and visual appearance were used in a representational similarity searchlight with a partial correlation approach (regressing the contribution of other matrices from the matrix of interest), to identify the independent variance explained by each factor. **B**, Along the medial wall, activity pattern similarity in the medial parietal lobe represented information on the social network distance between individuals and their personal affiliation to the participant, whereas pattern similarity in the medial prefrontal cortex was correlated to similarity between individuals in their perceived personality traits. No regions were found to significantly contain information on similarity in visual appearance. Representational similarity searchlight, spherical radius = 3 voxels, $p < 0.01$, Monte Carlo permutation test, threshold-free cluster enhancement correction for multiple comparisons.

Table 2. Peak MNI coordinates of the clusters identified in the partial correlation searchlight

	X (MNI)	Y (MNI)	Z (MNI)	Statistical value at peak voxel	Number of voxels in cluster	Anatomical label
Social network distance	11	−51	11	2.41	44	Precuneus
	−5	−37	31	2.58	77	Precuneus
	−9	−52	10	2.82	192	Precuneus
Personal affiliation	−53	−67	30	2.77	187	Superior temporal sulcus
	−49	−17	59	2.69	154	Central sulcus
	−4	−55	27	2.56	300	Precuneus
Personality traits	−11	44	25	2.69	357	Superior medial frontal gyrus

Only clusters of 5 voxels or larger were considered. Anatomical labels were determined by the Atlas of Intrinsic Connectivity of Homotopic Areas (Joliot et al., 2015).

factors ($t_{(16)} = 3.20$, $p = 0.03$, paired-samples t tests with FDR correction). No significant representation of personality traits or visual appearance was found in any ROI (personality traits, $t_{(16)} = 3.18, 1.01, 2.35, 1.59, 2.22, 2.19, 0.50, 1.23, 2.67, 2.26$; visual appearance, $t_{(16)} = 0.55, 0.56, 0.16, -0.13, 0.09, -1.88, 0.92, 1.16, 0.20, -0.10$, for left and right RSC, left and right PPA, left and right OPA, left and right hippocampus, social and spatial orientation regions, respectively; all p values > 0.05). These findings indicate that the retrosplenial complex, as identified by an independent localizer for spatial scene selectivity (Julian et al., 2012), contains information on social network distances between individuals.

Neural patterns code individual-specific knowledge and not social group or question-related context information
One potential alternative explanation for the coding of social network distance as observed here is that contextual factors are encoded rather than social distances. According to this explanation, when participants answer questions about different individuals, they evoke specific contexts, locations, or episodic

memories that tend to be more similar for more socially close individuals. This hypothesis predicts that different questions will evoke different shared contexts, leading to differences in individuals’ representation across questions; in addition, patterns for individuals in the same social group should be similar, instead of being unique to each individual. To test these two predictions, we first measured whether patterns corresponding to each individual are consistent across questions. Such consistency would suggest that more than just question-related context is represented. We found that individual-specific patterns were consistent across questions in all the social network distance coding ROIs ($t_{(17)} = 4.44, 4.33, 6.40, 5.21$; $p = 0.0002, 0.0002, 0.00001, 0.00007$, for left and right RSC, social orientation and spatial orientation regions, respectively, FDR corrected for multiple comparisons). In addition, we measured pattern consistency for each individual compared with patterns of others from the individual’s social group to test for the existence of information on each individual beyond shared group-related factors. We found that individual-specific patterns reflected individual identity and not group identity ($t_{(17)} = 4.52, 4.69, 6.77, 5.39$; $p = 0.0001, 0.0001, 0.000007, 0.00005$, for left and right RSC, social orientation and

Figure 5. Coding of different social factors in ROIs identified with the partial-correlation RSA searchlight. ROIs for each graph are regions that code unique information on social network distance, personal affiliation, and personality traits, as identified in the partial-correlation searchlight (Fig. 4); y-axis values represent correlation (Pearson's r) to each social factor matrix in these ROIs, averaged across participants. Repeated-measures ANOVA across participants demonstrated the existence of significant difference between the different factors in each ROI (all ANOVA p values < 0.05). Black lines represent significant interfactor differences (*post hoc* dependent-sample two-tailed t tests, FDR corrected across comparisons). Red lines indicate the partial correlation coefficients in the same ROIs.

spatial orientation regions respectively, FDR corrected for multiple comparisons). These analyses demonstrate that the observed activity patterns represent individuals' identities and their social relations, beyond what can be explained only by question-specific or group-specific contextual factors.

Representation of social distances in the default-mode network is robust across multiple social distance measures

In the previously described analyses, we have used a specific measure of social distance—the proportion of mutual friends between each two individuals. To verify that the results do not depend on the use of this specific social distance measure, the RSA searchlight procedure was repeated using other social network distance measures: shortest path length, total number of mutual friends, direct connectivity, and communicability. All measures except communicability yielded similar results to the main analysis (Fig. 7), demonstrating that the coding of social network distances in the default-mode network is robust across distance measures.

Because these different distance measures are correlated to each other, we next attempted to find whether the results actually reflect the social network distance as measured by the main experimental measure (percentage of common friends). We first tested whether the results could be explained only by direct connectivity between individuals. To this aim, we repeated the partial correlation approach in the regions of interest found to represent social information (partialling out the effects of direct connectivity from those of the main social network distance measure). In the left and right RSC, social network distance coding was not found after controlling for direct connectivity ($t_{(17)} = 1.09, 1.31$; $p = 0.15, 0.10$), indicating that the RSC representation

may be explained by direct connectivity alone. In contrast, the social and spatial orientation regions represented social network distance even when controlling for direct connectivity ($t_{(17)} = 2.23, 2.17$; $p = 0.02, 0.02$), demonstrating that in these regions second-order connections explained more variance than could be explained by direct connectivity alone. We also used the same approach to test the effects of social group membership; when controlling for social group membership, we found no significant coding of social network distance in either of the four regions of interest ($t_{(17)} = -0.63, -0.03, 0.10, 0.69$; $p = 0.73, 0.51, 0.46, 0.25$, for the left and right RSC and social and spatial orientation regions, respectively). Therefore, although individual-specific patterns reflect more than simple social group membership (as described in the previous section), relations across the network may be represented at the resolution of social groups and not individual connections. Because our experimental procedure divided individuals into groups (which therefore explains a significant amount of data variance), and our social network distance measure (proportion of mutual friends) emphasized this grouping, we cannot disentangle social-grouping effects from those of individual connectivity.

Discussion

Our study revealed several novel findings. When participants thought about familiar individuals, activity patterns in the default-mode network reflected the social network distances between these individuals, their personal affiliation to the participant, and the similarity in their personality traits. When dissociating these social dimensions, social network distance coding was identified in the medial parietal lobe, personal affiliation was represented in the medial and lateral parietal cortex, and

Figure 6. Social network distances are coded in spatial and scene processing regions. Representational similarity analysis was performed in regions of interest defined using scene viewing (retrosplenial complex; Julian et al., 2012) and spatial or social self-proximity judgments (spatial and social orientation regions; Peer et al., 2015). The analysis of coding of each factor (social network distance, personal affiliation, personality traits, and visual appearance) was performed with a partial correlation approach (controlling for the variance explained by the matrices corresponding to the other factors), as in Figure 4. Significant coding of social network distance between individuals was found in the right and left RSC, and in the spatial and social orientation regions. Significant coding of personal affiliation was also found in the social orientation region ($*p < 0.05$, $**p < 0.01$, all p values FDR corrected for multiple comparisons across regions); y -axis values are Pearson's r correlation values; error bars represent SEM.

personality traits were represented in the medial prefrontal cortex. Finally, the region coding for social network distances overlapped with the retrosplenial complex, a scene-selective region, suggesting similar processing of spatial and social relations.

Our findings suggest that knowledge about familiar others can be partially dissociated into at least three components—social network organization, personal affiliation to others, and personality traits. All of these are processed in different regions of the default-mode network, a system involved in processing

social and self-referential information (Buckner et al., 2008). Previous studies have observed personal-affiliation-related activity in the medial and lateral parietal cortex (Gusnard et al., 2001; Maddock et al., 2001; Shah et al., 2001; Parkinson et al., 2014, 2017; Peer et al., 2015; Tavares et al., 2015; Włodarski and Dunbar, 2016), and activity during personality traits judgments in the medial prefrontal cortex (Mitchell et al., 2006; Hassabis et al., 2014; Chavez and Heatherton, 2015; Tamir et al., 2016). Our results extend these findings to show representation of social

network distances in the parietal cortex, with partial dissociation from affiliation and personality. Notably, social network distance and personal affiliation representations were evoked spontaneously, even when participants were not explicitly asked about these relations, whereas personality traits could only be decoded when participants explicitly judged those traits. This distinction between explicit and implicit social thinking may be further investigated in future studies. Finally, our findings reflect a distinction between parietal coding of social network relations and prefrontal coding of personality traits. This finding is in line with a recent proposal that these brain regions encode different types of relational knowledge—graph-like relations in the parietal cortex (e.g., social network structure) versus continuous features in the prefrontal cortex (e.g., personality traits; Peer et al., 2021).

Our study revealed social network distance representations in the RSC. The RSC is involved in scene processing, as well as coding of spatial location, heading direction and navigational goals (Epstein et al., 2007; Marchette et al., 2014; Brown et al., 2016), and integration of egocentric and allocentric information (Byrne et al., 2007; Arzy and Schacter, 2019). In a recent study, we also found that medial parietal regions anterior to RSC also engage in spatial processing (at different scales; Peer et al., 2019). In addition, the RSC/medial parietal cortex is also active during social and temporal judgments (Peer et al., 2015) and represents nonspatial relations among social group categories (Leshinskaya et al., 2017) and events in time (Baldassano et al., 2017; Stawarczyk et al., 2021; Foudil et al., 2020). These findings strengthen the idea that brain systems involved in spatial processing (including the RSC) have a domain-general role in mapping knowledge across space, time, and the social domain (Parkinson and Wheatley, 2013, 2015; Parkinson et al., 2014; Tavares et al., 2015; Peer et al., 2015, 2021; Epstein et al., 2017; Behrens et al., 2018; Bellmund et al., 2018; Schafer and Schiller, 2018; Arzy and Schacter, 2019). These findings contrast with previous studies (including our own) that have emphasized a differentiation between spatial and social processing in the posterior and anterior medial parietal cortex, respectively (Peer et al., 2015; Silson et al., 2016, 2019a,b; Steel et al., 2020), and a corresponding division between posterior and anterior default-mode network components (Braga and Buckner, 2017; Braga et al., 2019). One possibility is that medial parietal subdivisions are not driven by domain but by other factors related to domain and task (e.g., the level of abstractness of the represented relations (Margulies et al., 2016; Peer et al., 2019)). Task differences among the studies may also play a role; in tasks that require attention to social features, differences in these features may drive the variance in the observed activity, in contrast to tasks that require attention to the

Social network distance effects – different distance measures

Figure 7. Information on social network structure obtained using different social distance measures. Representational similarity searchlight on social media network connections between individuals. Voxels with significant representational similarity are displayed for each social distance measure ($p < 0.01$, Monte Carlo permutation test, threshold-free cluster enhancement correction for multiple comparisons). Social distance matrices for each measure, from 1 sample participant, are presented to the left of each fMRI result (all matrices normalized to the range 0–1). **A**, Proportion of mutual friends (the main measure used in the article, similar to Fig. 2; Granovetter, 1973). **B**, Total number of mutual friends. **C**, Direct connectivity among individuals (binary coding). **D**, shortest network path length. **E**, Graph communicability (Estrada and Hatano, 2008). Results are similar between different measures of social distance, except for the communicability measure, which does not show any significant coding across the brain, indicating that pattern similarity reflects distance between individuals in the social network instead of ease of information transfer across the network.

difference between domains. Furthermore, posterior–anterior functional differences may be continuous and may appear as distinct regions because of statistical thresholding (Margulies et al., 2016; Huntenburg et al., 2018; Buckner and DiNicola, 2019; Peer et al., 2019). Future studies may shed more light on the factors influencing medial parietal lobe selectivity to different domains. Finally, we did not find social coding in the hippocampus, despite its known role in coding spatial, social, and abstract relations (Schapiro et al., 2012; Tavares et al., 2015; Deuker et al., 2016). This null finding may be because the hippocampus primarily represents newly learned relations in contrast to lifelong social relations whose memory is consolidated over time (Norman and O'Reilly, 2003; Winocur et al., 2007), or because the hippocampus is affected by susceptibility artifacts and signal distortions (Olman et al., 2009; Peer et al., 2016), and we acquired the data using axial slices, which are not optimal for its imaging (Weiskopf et al., 2006). Further research may reveal the hippocampal role in representation of real-world social network structure.

Our study used information from social media to map real-life relations between individuals. Previous studies on social relations mostly introduced participants to imaginary characters (Mitchell et al., 2006; Kumaran et al., 2012; Hassabis et al., 2014; Tavares et al., 2015) or used a small subset of familiar individuals (Jenkins et al., 2008). Studies using social media information have mostly investigated correlates of social network size (Kanai et al., 2012; Bickart et al., 2012; Hampton et al., 2016), with an exception of a study that mapped real-life relations in a student group and revealed representations of individuals' social network centrality and personal affiliation to the participants (Parkinson et al., 2017). Here, we extended these investigations to study relations between individuals from different social groups and contexts who are personally known for a prolonged period of time. The combination of social media data, which enables mapping thousands of social connections and avoiding subjective-report biases, together with multivariate pattern analysis, provides a valuable tool for investigating real-life social representations (Meshi et al., 2015). Although previous studies have shown that social media connectivity (including mutual friendship information) generally corresponds to real-life interpersonal friendship (Ellison et al., 2007; Subrahmanyam et al., 2008; Gilbert and Karahalios, 2009), this approach can introduce platform-related biases (e.g., because of different patterns of social media use in different individuals). To mitigate these biases, we took several measures. First, we mapped online connectivity between individuals and not information on their interactions, thus posing minimal platform engagement requirements and limiting the effects of social media usage patterns. Second, we used an aggregate measure of social network distance based on the total number of mutual friends, mitigating the effect of missing or extra connections. Finally, we mapped the relations between 24 individuals, reducing the impact of single individuals whose connectivity is distorted with respect to reality. These measures led to high correspondence between social-media-based distance and participants' perceived strength of relationship between individuals, as tested in a subset of participants (mean $r = 0.86$; see above, Materials and Methods). However, individuals' social connectivity strength, which may form an important part of mental social network representations, was not directly tested. Future studies using other measures (such as self-rated friendship strength, or characterization of social media interaction through posts and chat data) may yield further insights on the coding of social relations.

Our study has several limitations. First, we asked participants to provide names of individuals from different social groups, and therefore group membership explains a large amount of variability in the dissimilarity matrices and cannot be completely disambiguated from specific connections between individuals. Second, to avoid analysis circularity, ROIs were defined using masks from separate studies; therefore, these regions may not precisely correspond to each individual's functional regions. Third, our partial correlation analysis disentangled the unique variance explained by different social factors, but additional variance may be shared among matrices; therefore, the identified regions may represent not one but multiple social factors (although we did find preferential processing of each social factor in its identified region). Finally, social connectivity in real life is associated with other shared contextual factors in addition to friendship, such as participation in similar activities or meeting in similar places or situations. To mitigate these effects, our participants were asked 12 different questions about each individual, limiting the evoked shared context. We also found that neural patterns represent

individual-specific patterns and not question- or group-specific contexts. However, we cannot completely rule out an interaction of nonsocial contextual factors with the coding of social network distances, and additional experiments may provide insights into the unique processes involved in each of these aspects.

In conclusion, we have demonstrated dissociable coding of different aspects of knowledge about personally familiar others in different regions of the default-mode network, including regions involved in the coding of spatial cognitive maps. Our findings support the notion that the brain uses similar systems to process relational knowledge across cognitive domains, and the revealed subdivisions may apply to relational coding in other, more abstract cognitive domains.

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