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10   The neural representational space of social memory
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41   **Abstract:** Social functioning involves learning about the social networks in which we

42   live and interact; knowing not just our friends, but also who is friends with our friends.

43   Here we utilized a novel incidental learning paradigm and representational similarity

44   analysis (RSA), a functional MRI multivariate pattern analysis technique, to examine the

45   relationship between learning social networks and the brain's response to the faces

46   within the networks. We found that accuracy of learning face pair relationships through

47   observation is correlated with neural similarity patterns to those pairs in the left

48   temporoparietal junction (TPJ), the left fusiform gyrus, and the subcallosal ventromedial

49   prefrontal cortex (vmPFC), all areas previously implicated in social cognition. This

50   model was also significant in portions of the cerebellum and thalamus. These results

51   show that the similarity of neural patterns represent how accurately we understand the

52   closeness of any two faces within a network, regardless of their true relationship. Our

53   findings indicate that these areas of the brain not only process knowledge and

54   understanding of others, but also support learning relations between individuals in

55   groups.

56
57   **Significance Statement:** Knowledge of the relationships between people is an

58   important skill that helps us interact in a highly social world. While much is known about

59   how the human brain represents the identity, goals, and intentions of others, less is

60   known about how we represent knowledge about social relationships between others. In

61   this study, we used functional neuroimaging to demonstrate that patterns in human

62   brain activity represent memory for recently learned social connections.

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65   Social relationships guide and support much of human behavior. Not only do we

66   form strong lifelong family bonds, we also interact with others in work, education, and

67   leisure settings and create lasting non-kin relationships. For many species, including

68   humans, non-kin based social networks can have important consequences for health

69   and fitness (Cheney, 2011; Tung et al., 2015). Benefits of social relationships can come

70   both from direct connections (our friends) as well as second-order or indirect

71   connections (friends of our friends) (Brent, 2015; Seyfarth & Cheney, 2015). A

72   considerable amount of research has revealed the cognitive and neural mechanisms

73   underlying the representation of social faces, voices, and bodies (Allison, Puce, &

74   McCarthy, 2000; Arsenault & Buchsbaum, 2015). There is also a good understanding of

75   the neural basis of social knowledge about other individuals (Koski, Xie, & Olson, 2015;

76   Wang et al., 2017), how we represent ingroup versus outgroup members (Van Bavel &

77   Cunningham, 2012; Shkurko, 2013), and how we represent the mental states of others

78   (Contreras, Schirmer, Banaji, & Mitchell, 2013; Saxe & Kanwishwer, 2003).

79   Less well understood is how we represent knowledge about indirect social

80   connections. Memory for who knows whom is important for navigating social

81   relationships, including knowing who to approach for information, support, and other

82   resources. Individual differences in sociality have been linked to neural and behavioral

83   measures of social perception (Baron-Cohen et al., 1999; Dziura & Thompson, 2014;

84   Kanai, Bahrami, Roylance, & Rees, 2012), and there are differences in how well people

85   can remember social networks (Brewer, 2000; Casciaro, 1998; Freeman, Romney, &

86   Freeman, 1987). However, the underlying neural processes involved in learning

87   complex social network relationships has not been thoroughly examined. Human social

88 organization is dynamic, as the composition of groups and the ties within them change

89 over an individual's lifetime (Couzin, 2006). Prior literature indicates several brain areas

90 likely to be important for representing information about social networks. Perception of

91 changes in relationship ties and tie strength has been linked to activity in the bilateral

92 posterior superior temporal sulcus (pSTS) and temporoparietal junction (TPJ) (Bault,

93 Pelloux, Fahrenfort, Ridderinkhof, & Van Winden, 2015). Retrieval of social knowledge,

94 including consideration of kin group cohesion, involves medial and lateral prefrontal

95 cortex (mPFC; lPFC) (Rüsch et al., 2014; Satpute, Badre, & Ochsner, 2014). Learning

96 and representing information about social hierarchy, an important component to many

97 social networks, recruits amygdala, hippocampus, and ventral mPFC (Kumaran, Melo,

98 & Duzel, 2012). A recent study by Parkinson and colleagues (2017) revealed that the

99 similarity of local patterns of fMRI responses in ventral mPFC and lPFC, as well as

100 lateral temporal cortex and TPJ, to viewing videos of individuals from participants' real

101 world social network, conveyed information about network position of the members.

102 These findings suggest that information about social network relationships is

103 represented in patterns of fMRI responses associated with viewing individuals from

104 one's network.

105   In this study, we examined the memory and neural representation of connections

106 between members of two novel social networks, using fMRI and representational

107 similarity analysis (RSA). Artificial networks were used in order to experimentally control

108 the closeness of network members and assess the role of the memory for relationship

109 strength in fMRI responses. We examined if the pattern similarity of fMRI responses to

110 any two faces from a learned social network reflected the tie strength (closeness) of

111   those two individuals within the network: that is, does the similarity of the pattern of

112   response to two network members increase as a function of the closeness of those

113   members? We also examined if the memory for tie strength between network members

114   was related to the similarity of the fMRI voxel pattern response to the faces of members.

115   To understand the contribution of the frequency of face pairing during network learning

116   to memory and neural representations, we compared a network in which centrality

117   differed between members (i.e. some members had more connections than others) to a

118   network with no individual centrality.

119

120   **Materials and Methods**

121   **Participants**

122   22 healthy individuals (10 females; age range = 18-34; mean age = 23; ethnicity

123   = 64% White, 18% Hispanic/Latino, 18% Asian) participated in a 1.5 hour learning

124   session immediately followed by a 1.5 hour fMRI scanning session. Behavioral data

125   from a total of 31 individuals was collected, but seven subjects did not meet the learning

126   criteria from the behavioral task, one subject was unable to be scanned, and one

127   subject's fMRI data was incomplete. All participants were right handed (self-reported)

128   with normal or corrected-to-normal vision. Participants provided written informed

129   consent in accordance with the Declaration of Helsinki and the Human Subjects Review

130   Board at George Mason University and were compensated for their time.

131

132   **Experimental Design and Statistical Analysis**

133   **Stimuli**

134   Task stimuli consisted of 24 faces of varying ethnicities, equally divided by

135   gender. Faces were all in color and facial expressions were all smiling. These stimuli

136   were downloaded from the Park Aging Mind Laboratory Database at UT Dallas (Minear

137   & Park, 2004) and were chosen to be as realistic to a college campus as possible,

138   ensuring the perception of real people who might interact and be friends with each

139   other.

140

141   **Task Design**

142   Participants completed a two-alternative forced choice task to become familiar

143   with the structure of two six-person social networks (**Figure 1**). Pairs of faces

144   represented connections within each network, with the frequency of pairing indicating

145   relationship strength. Each network had an equal number of male and female faces of

146   varying ethnicities. Network properties differed between the two in that although each

147   network had an equal number of connections of each strength level, there were

148   differences among the individual members (faces) in each network. The faces in

149   network 1 had varying numbers of connections and therefore each had a different

150   average closeness to the rest of the network, whereas the faces in network 2 had an

151   equal number of connections and an equal average closeness to all other faces in the

152   network. This meant that in network 1 the centrality of members was varied (variable-

153   centrality network), while in network 2 centrality was equated across members (fixed-

154   centrality network). This also meant that the frequency of presentation of each face

155   differed in network 1, but was equivalent in network 2. Each trial consisted of a face pair

156   presented for 4 seconds accompanied by a question, and participants were asked to

157   make a comparison between the faces and decide which person better fit the question.

158   Questions consisted of behavioral and personality characteristics taken from various

159   personality surveys included in the International Personality Item Pool

160   (http://ipip.ori.org/). Half of the questions asked which person was more likely to exhibit

161   a characteristic, and half asked which person was less likely (example: "Who is more

162   likely to be easily intimidated?"). Network learning took place in alternating blocks,

163   where the subjects viewed 36 randomly presented trials of one network followed by 36

164   trials of the second network. Participants completed 720 trials in total (360 per network),

165   with the weakest network connections being presented a total of 20 times and the

166   strongest a total of 80 times.

167   After completing the paired face viewing portion, participants were explicitly

168   tested on their knowledge of the network connections. They were told that the faces

169   represented college students living in a dorm together, the faces that they saw paired

170   together previously represented friend connections, and the more often they were

171   presented together, the closer in friendship the pair was. They were asked to group all

172   of the faces into two separate halls, as a check to make sure that they could distinguish

173   between the faces in different networks. They were then presented with all possible

174   within-network face pairs twice and asked to rate their relationship on a scale of 0 (do

175   not know each other) to 4 (know each other very well). They were not asked about

176   cross-network face relationships. This explicit testing period was included to ensure that

177   participants learned the structure of the networks to an appropriate level before being

178   scanned. Participants who were within 2 standard deviations of pilot data (hit rate =

179   0.85, SD = 0.14; false alarm rate = 0.35, SD = 0.15) were included in further analysis.

180   Both parts of the behavioral task (learning and recall) were presented to the participant

181   using PsychoPy version 1.842 software (http://www.psychopy.org/).

182   The fMRI task stimuli included the same 12 faces from the behavioral task as

183   well as 12 novel faces as a control. Faces were presented one at a time for one second

184   on a black background with a 4.5 second inter-stimulus interval (black screen with a

185   white fixation dot), and participants completed a 1-back task to ensure they were

186   attentive. The task consisted of four runs of 9.6 minutes each, resulting in each face

187   being presented a total of 16 times (not counting repeats, which were included in

188   analysis as a separate regressor). Following the face task, participants underwent an

189   unrelated dynamic localizer session. Localizer stimuli consisted of 18 second blocks

190   each of faces, body parts, outdoor scenes, moving objects, and scrambled objects. The

191   fMRI experiment was presented to the participant using Neurobehavioral Systems

192   Presentation version 16.3 (https://www.neurobs.com).

193

194   **fMRI data acquisition, preprocessing, and analysis**

195   fMRI data were collected with a Siemens Allegra 3T scanner and a quadrature

196   birdcage head coil at the Department of Psychology at George Mason University. Visual

197   stimuli were displayed on a rear projection screen and viewed by participants on a head

198   coil-mounted mirror. Blood oxygenation level dependent (BOLD) data were acquired

199   using gradient-echo, echoplanar imaging scans: 40 axial slices (3-mm slice thickness),

200   repetition time (TR)/echo time (TE) = 2350/30 ms, flip angle = 70, 64 x 64 matrix, field of

201   view = 192 mm. 245 volumes were collected in each run. At the end of the fMRI

202   scanning session, one T1 whole-head anatomical structural scan was acquired using a

203   three-dimensional, magnetization-prepared, rapid-acquisition gradient echo (MPRAGE)

204   pulse sequence. The following parameters were used for these scans: 160 1-mm slices,

205   256 x 256 matrix, field of view = 260 mm, TR/TE = 2300/3.37 ms. Functional data were

206   analyzed using FSL (version 5.0.8) fMRI Expert Analysis Tool (fsl.fmrib.ox.ac.uk) and

207   Matlab (version R2012a) software (http://www.mathworks.com). Preprocessing included

208   brain extraction, high-pass filtering at 96 s, slice-timing correction, motion correction,

209   and smoothing with a 6 mm FWHM kernel. Runs with > 1 mm of motion were run

210   through the BrainWavelet Despiking program in Matlab (Patel et al., 2014). For first-

211   level analysis, linear regression was conducted at each voxel, using generalized least

212   squares with a voxel-wise, temporally and spatially regularized autocorrelation model,

213   drift fit with Gaussian-weighted running line smoother. For second-level analysis, linear

214   regression was conducted at each voxel, using ordinary least squares.

215

216   **Regions of Interest (ROI) and Mask Creation**

217   Localizer data preprocessing steps were identical except the functional data was

218   registered only to each subject's specific structural image. Face-selective regions of

219   interest (ROIs) were created from subtracting the combined object, scrambled object,

220   and scene conditions from the face condition. These regions included bilateral posterior

221   STS and fusiform face area (FFA). Activity was thresholded at $Z > 3.7$ ($p < 0.0001$) for

222   most ROIs, although this threshold was relaxed to $Z > 3$ ($p < 0.001$) in one subject, $Z >$

223   2.3 ($p < 0.01$) in four subjects, and $Z > 1.65$ ($p < 0.05$) in three subjects because of

224   lower overall BOLD activity. These masks were projected back into native functional

225   space for further analysis. Finally, an anatomical mask of areas involved in memory for

226   faces (encompassing the bilateral pSTS, extrastriate body area (EBA), ventral

227   temporal/fusiform gyrus, precuneus/posterior cingulate cortex (PC/PCC), and

228   hippocampus) was created from the Harvard-Oxford Cortical Structural Atlas in FSL.

229

230   **Univariate Analysis**

231   Each subject's functional data was registered to his or her anatomical scan and

232   then registered to the MNI standard template. The regressors used in the generalized

233   linear modeling (GLM) analysis were Network 1 v. rest, Network 2 v. rest, Control v.

234   rest, and Response Trials v. rest. Contrasts used were Network 1 v. Control, Network 2

235   v. Control, Both Networks v. Control, Control v. Both Networks, Network 1 v. Network 2,

236   and Network 2 v. Network 1. Group nonparametric 1-sample (conditions v. rest) and 2-

237   sample (condition A v. condition B) t-tests (5000 permutations) including threshold-free

238   cluster enhancement and variance smoothing of 8 mm were conducted with

239   fslrandomise within the mask created from anatomically-defined regions selective for

240   face processing and memory.

241

242   **Representational Similarity Analysis**

243   Representational similarity analysis (RSA) is a form of multivariate pattern

244   analysis that compares the distance between stimuli in neural representational space

245   (Kriegeskorte, Mur, & Bandettini, 2008), and correlates this neural information with

246   external patterns of information. In this way it can be utilized to assess different models

247   or patterns of cognition above and beyond univariate analysis, or even more traditional

248   multivariate pattern classification techniques (Haxby, Connolly, & Guntupalli, 2014). For

249   initial analysis of task data, no registration to structural or functional data was carried

250   out, and the smoothing kernel used was 4 mm FWHM. All other preprocessing

251   parameters mirrored the univariate whole-brain analysis. The GLM included separate

252   regressors for each of the 24 faces and repeats. Resulting z-statistics were grouped by

253   network for further analysis. Four separate dissimilarity matrices (DMs) were created for

254   each network (for examples, see **Figure 5**): true network structure (created from tie

255   strength), perception of network structure (taken from each subject's behavioral recall

256   data after learning the networks), group average of perceived structure (where each

257   face pair's perceived strength was averaged across subjects), and recall accuracy

258   (measured by calculating the absolute distance between the true strength of each face

259   pair and the average strength of the pair reported in the recall phase). The

260   CoSMoMVPA toolbox in Matlab was used for RSA calculations (Oosterhof, Connolly, &

261   Haxby, 2016).

262   Separate whole-brain searchlights using Spearman correlations (size = 50

263   voxels) were conducted on the average z-statistics for the faces within each network for

264   each DM.   The ensuing correlation maps were transformed into standard space for

265   group analysis. No significant group differences were found across the two networks (in

266   group nonparametric paired-sample t-tests with 5000 permutations), so the correlation

267   maps in individual subject space were then averaged across networks within subjects

268   and transformed again to standard space for across-network group analysis. Group

269   nonparametric 1-sample t-tests (5000 permutations) including threshold-free cluster

270   enhancement and variance smoothing of 8 mm were conducted with fslrandomise.

271   Resulting t-statistic maps were visualized in the MNI volume as well as transformed to

272   the PALS-B12 standard atlas in Caret (http://www.nitrc.org/projects/caret/) for surface

273   data visualization (Van Essen, 2005). RSA was also carried out within each localizer-

274   defined ROI and the resulting correlations within each region were averaged across

275   subjects.

276

277   **Results**

278   **Behavioral task**

279   Participants became familiar with the structure of two six-person social networks

280   by viewing two faces presented simultaneously (**See Figure 1**). A paired set of faces

281   represented a connection within the network, with the frequency of pairing indicating

282   relationship strength. Analysis of social network recall data was conducted in Microsoft

283   Excel (version 2016) and R Version 3.3.2 (https://www.r-project.org/). Subjects correctly

284   identified relationship ties significantly greater than chance across both networks (t(21)

285   = 8.08, p = 7.004e-08). **Table 1** shows the average hit rate, false alarm rate, sensitivity

286   (d′), and the correlation between true and reported perceived strength for ties and

287   relationship strength across subjects. Paired sample two-tailed t-tests revealed no

288   significant differences between recall measures for the two networks. There were also

289   no significant age or gender effects for any of the measures. When averaged together

290   across subjects, group perceived relationship strength was highly correlated with the

291   true network structure (r = 0.896, p < 0.00001). In order to assess whether our

292   behavioral task was comparable to previous forms of social network learning and recall,

293   we calculated performance measures used by Brashears (2013). Accuracy refers to the

294   number of ties correctly recalled divided by the number of total ties reported, coverage

295   refers to the number of ties correctly recalled divided by the total tie number in the

296   network, and performance refers to the product of accuracy and coverage. T-tests

297   revealed no significant differences between accuracy or performance measures in our

298   task and those of Brashears (accuracy: t(21) = 0.98, p = 0.34; performance: t(21) =

299   0.58, p = 0.56), and we actually saw an increase in coverage (t(21) = 3.58, p = 0.002),

300   although our networks were smaller, so participants did not need to remember as many

301   ties.

302   When exploring network recall, it is important to not only look at the correctly

303   identified ties, but also at the pattern of mistakes made. Specifically, we wanted to see

304   whether there are systematic biases that could be predicted by the level of relationship

305   strength of the friend pairs. We assessed recall by relationship strength by looking at

306   the relative direction of the errors made (i.e. how much subjects overestimated or

307   underestimated the strength of the connection). A linear mixed effects regression model

308   (fixed effect = strength; random effects = subject, residual) revealed that relationship

309   strength affected recall error compared to a null model ($\chi^2(1)$ = 226.9, p < 2.2e-16). This

310   pattern shows that overall, weak ties were reported to be stronger than they actually

311   were whereas strong ties were reported to be less strong (**Figure 2a**). This reflects a

312   general tendency to assume a mid-level relationship between observed people when

313   the relationship is not explicitly known or is unable to be recalled. This central tendency

314   effect seems to be robust, as it was also observed in a separate subject sample (N =

315   23, 17 females, mean age = 19.6 (sd = 2.4)) learning a larger social network (N= 9) and

316   a larger possible range of relationship tie strengths to choose from (0-6) ($\chi^2(1)$ = 362.84,

317   p < 2.2e-16) (**Figure 2b**). In order to be able to compare network memory performance

318   to the neural patterns in response to each face in the network, we converted the relative

319   error for each subject to absolute error, which gives a measure of distance from the true

320   network structure, regardless of the direction of that error. The absolute error measure

321   for each subject for each network was then used as a dissimilarity model for RSA to

322   elucidate what neural patterns underlie these errors.

323

324   **fMRI Results**

325   During fMRI scanning, participants viewed the original faces from the social

326   network behavioral session, as well as 12 novel faces and were asked to press a button

327   when they saw a face repeated to guarantee attention. We first conducted a GLM

328   comparing the 12 familiar faces from the two networks to unfamiliar control faces.

329   **Figure 3** shows that an area of the left fusiform gyrus was more active when viewing

330   unfamiliar faces, whereas the posterior cingulate gyrus/precuneus was more active

331   when viewing familiar faces (p < 0.05, FWE-corrected with threshold-free cluster

332   enhancement within an anatomical mask composed of areas previously shown to be

333   relevant for face perception and memory; see **Table 2** for cluster information). While

334   perception for different categories of faces is highly dependent on task demands, our

335   findings are consistent with some previous literature examining recognition of familiar

336   faces (Natu & O'Toole, 2011). The fusiform gyrus has been shown to activate

337   significantly less to famous faces than to strangers in the left hemisphere (Gobbini,

338   Leibenluft, Santiago, & Haxby, 2004), and the posterior cingulate/precuneus area is

339   consistently activated more to personally familiar faces when compared to strangers

340   (Gobbini et al., 2004; Pierce, Haist, Sedaghat, & Courchesne, 2004; Sugiura et al.,

341   2001). There were no univariate differences between responses to faces across the two

342   networks.

343

344   **Representational Similarity Analysis**

345   To examine whether information related to social network recall is represented in

346   the brain, we carried out RSA searchlight analysis on several DMs representing

347   different types of information about the networks. The first compared neural pattern

348   similarity to social tie strength, with more similar neural responses to any pair of faces

349   representing a closer relationship between those faces. Neural pattern similarity that

350   reflects this network structure would indicate that the brain carries information about the

351   true relationship between individuals, regardless of whether people recall those

352   relationships accurately. We did not find a significant correlation between these

353   measures in our analyses. As the network properties differed between network 1 and 2

354   (see Methods section for details), we compared the two networks and found no

355   significant differences.

356   While the pattern similarity to viewing faces was not significantly associated with

357   social tie strength, it was significantly associated with the subjects' memory for that tie

358   strength. We assessed this by measuring each subject's absolute distance from each

359   true network structure and the 1-correlation distance between the neural response to

360   each face viewed in the scanner. An association between these two measures would

361   indicate that the more accurately a subject perceives the true relationship tie strength

362   between a pair of faces, the more similar their neural pattern response is to those two

363   faces. In other words, this association does not rely on the actual connection strength of

364   the relationships themselves, but the subject's memory of that connection, reflecting a

365   second-order knowledge or understanding of a social relationship. Neural pattern

366   similarity in the left TPJ, the left fusiform gyrus, the subcallosal cingulate cortex, the

367   cerebellum, the left thalamus, and a small portion of the left lateral occipital lobe was

368   significantly correlated with the recall accuracy model, suggesting that neural

369   populations within these areas are important for accurate perception of social

370   relationship strength (**Figure 4**). **Table 3** reports MNI coordinates, cluster size, and

371   peak voxel activity of results. As with tie strength similarity, we compared the two

372   networks to each other separately and found no significant differences. This indicates

373   that the significant findings are not due simply to frequency of the face pairs being

374   presented, as this differed between the two networks.

375   We also conducted RSA searchlights using two other dissimilarity matrix models:

376   recalled structure as measured by behavioral judgments, and the group average of

377   those behavioral judgments (**Figure 5**). Neural pattern similarity that reflects behavioral

378   recall would indicate that the brain carries information about an individual's perception

379   of relationships, regardless of how accurate those perceptions are. This perceived

380   structure at the group average level can show general trends in how relationships are

381   viewed by groups. However, neither model reached significance in the whole-brain

382   searchlight analysis. Finally, we utilized a separate functional localizer to create regions

383   of interest selective for face processing in the STS and fusiform gyrus, and conducted

384   RSA correlations across each ROI for every subject. No selected regions yielded

385   significant results.

386

Discussion

387

388   In this study, we used fMRI and RSA to examine the neural representational

389   space of friendship connections of members of a social network. Indirect connections

390   (i.e., the friends of our friends) play an important role in assessing our own place in our

391   social world. This could include knowledge about social hierarchy which may affect how

392   we act around different network members, or knowledge about which people are more

393   well-connected and might therefore be better to approach for acquiring resources. We

394   examined if the strength of ties between pairs of network members was represented in

395   human brain via the similarity of fMRI responses associated with viewing the faces of

396   those members. We did not find support for this proposal. Instead, our results show that

397   several brain regions, including the TPJ, subcallosal vmPFC, fusiform gyrus,

398   cerebellum, and thalamus, represent memory or knowledge about tie strength, rather

399   than tie strength itself, in the similarity of neural patterns between face pairs. That is,

400   these areas code memory for relationship strength regardless of what that connection

401   is, or even whether there is a connection at all, within a social network. The more

402   accurately a participant recalled the tie strength for a pair of faces (regardless of the

403   closeness of ties), the more similar the pattern of fMRI responses was to viewing those

404   two faces.

405   Our results indicated that the relationship between memory for tie strength and

406   neural pattern similarity was not due to factors such as the frequency at which different

407   faces were paired with others during the learning of the network, as we found no

408   differences in memory performance or RSA results between a network in which some

409   faces were paired more often with others (variable-centrality network) and one in which

410 all faces had the same number of connections to other network members (fixed-

411 centrality network). In addition, participants saw each individual face the same number

412 of times as they learned one of the two networks and there were no significant

413 behavioral or neural differences between the two networks, and therefore our results

414 are not driven by the familiarity of one face over any other. Instead, our results indicate

415 that information about pairs of network members, such as how close they are, is coded

416 in TPJ and vmPFC via the similarity of neural responses.

417   Both the TPJ and vmPFC have been consistently linked with complex facets of

418 social understanding, such as tracking the popularity of real-world social network

419 members (Zerubavel, Bearman, Weber, & Ochsner, 2015). The TPJ, dorsomedial PFC,

420 and ventrolateral PFC are engaged when participants recall different facets of socially

421 relevant knowledge (Satpute et al., 2014). The left TPJ is selectively modulated by

422 vasopressin, a neuropeptide linked to a number of complex social behaviors, during

423 social recognition (Zink et al., 2011) and lesions to the left TPJ lead to specific deficits in

424 social reasoning (Samson, Apperly, Chiavarino, & Humphreys, 2004). The vmPFC

425 shows increased activation when thinking about friends compared to kin (Wlodarski &

426 Dunbar, 2016), and the subgenual cingulate cortex is involved in tracking individual

427 differences in perceptions of cohesiveness in kin groups (Rüsch et al., 2014). Our

428 findings are in line with this previous literature showing the importance of these areas in

429 forming and maintaining social relationships. They further indicate that these areas are

430 not only important in the knowledge and understanding of other individuals, but they

431 also support learning relations between individuals in groups. The fusiform gyrus is also

432 heavily involved in social perception, particularly in response to face stimuli (Kanwisher,

433   McDermott, & Chun, 1997). While early models of face perception suggested a strict

434   feed-forward mechanism for distinguishing, identifying, and gaining socially-relevant

435   information from faces, recent proposals indicate a more interactive process between

436   different neural regions when engaging in higher-order social face perception (Atkinson

437   & Adolphs, 2011). Our data indicates that patches of the fusiform gyrus do not simply

438   perceive and distinguish facial features (from each other as well as non-face stimuli),

439   but are also involved in learning more abstract social relationships between faces.

440   A large meta-analysis of fMRI studies has revealed that areas of the cerebellum

441   are activated in several features of social cognition, with increases in activity occurring

442   with increasing social abstraction levels in the cognitive tasks (Overwalle, Baetens,

443   Marien, & Vandekerckhove, 2014). The authors suggest this cerebellar activity is due to

444   a general increase in cognitive task demands, in line with the theory of the cerebellum

445   as a cognitive process modulator (Andreasen & Pierson, 2008). Our finding that the

446   cerebellum is involved in accurate knowledge of abstract learned relationships between

447   others is consistent with this. Furthermore, we found that the thalamus is also involved

448   in this process. The thalamus has a large number of connections to other areas of the

449   brain, and has been shown to have specific emotional and socially-relevant associations

450   (Christoffel et al., 2015; Feng et al., 2016; Ioannidis et al., 2013). It also has high

451   functional connectivity to the hippocampus (Stein et al., 2000), and may be a critical link

452   in the formation of episodic memories, regardless of the sociality of those memories

453   (Aggleton et al., 2010).

454   The findings of the present study complement a recent paper by Parkinson and

455   colleagues (2017), who reported that neural pattern similarity in ventral mPFC and

456   IPFC, TPJ and lateral temporal cortex, as well as other regions, to viewing videos of

457   individuals from a participants' social network was associated with network

458   characteristics of those viewed, including centrality within the network, social distance

459   from the participant, and the 'brokerage' of an individual (the extent to which they

460   connected other, low contact network members to others in the network). Parkinson and

461   colleagues took advantage of the one, real-world social network in which all of the

462   participants and those who were used as stimuli were embedded. In contrast, we used

463   an artificial social network in which all network members were initially unfamiliar to the

464   participants, and thus only examined relationships between the network members, and

465   not those between network members and our participants. Together, the more

466   naturalistic, field-work informed approach of Parkinson and colleagues and the

467   laboratory-based approach of as ours, in which factors such as familiarity and the

468   statistics of connections were experimentally controlled, both reveal that social network

469   information is represented in brain regions implicated in social cognition through the

470   similarity of local patterns of neural responses to viewing individual network members.

471   While most of our subjects were able to accurately report relationship ties, there

472   were individual differences between ability to recall relationship strength (measured by

473   the correlation between the true structure and the reported structure of the networks).

474   Previous literature does indicate that there are individual differences in social recall.

475   Individuals tend to report group and relationship averages or norms more accurately

476   than individual interactions, but more experienced observers show more accurate recall,

477   especially when group structure is transitive (Freeman & Romney, 1987; Freeman,

478   1992; Kumbasar, Romney, & Batchelder, 1994). It has been suggested that humans

479 use cognitive heuristics such as triadic closure in order to remember social ties (De

480 Soto, 1960; Freeman, 1992; Brashears, 2013; Brashears & Quintaine, 2015).

481 Overestimation of symmetric ties for less central network members, and

482 underestimation of more central network members, has also been reported previously

483 (Krackhardt, 1987). There are also differences in the ability to perceive and remember

484 non-social patterns, but evidence suggests that learning, remembering, and storing

485 social information might be distinct from traditional learning and memory systems

486 (Okuyama, Kitamura, Roy, Itohara, & Tonegawa, 2016; Meyer, Taylor, & Lieberman,

487 2015; Tendler & Wagner, 2015). Further experiments could explore this type of task

488 explicitly, as prior social network learning studies informed participants that they would

489 be tested on connections (Brashears, 2013; De Soto, 1960).

490   The way in which people learn and remember social connections between

491 individuals in groups has a considerable impact on everyday life. We are not only able

492 to perceive and understand the social signals of other individuals, but we can also

493 perceive and understand information about social connections or relationships in which

494 we are not directly involved. Our results show that representations of these indirect

495 connections are coded in the pattern of neural responses associated with viewing

496 related individuals. This is a critically important skill because the accuracy with which we

497 perceive and remember subtle connections and relationships seen in our surroundings

498 helps us move more freely and easily in our highly social world.

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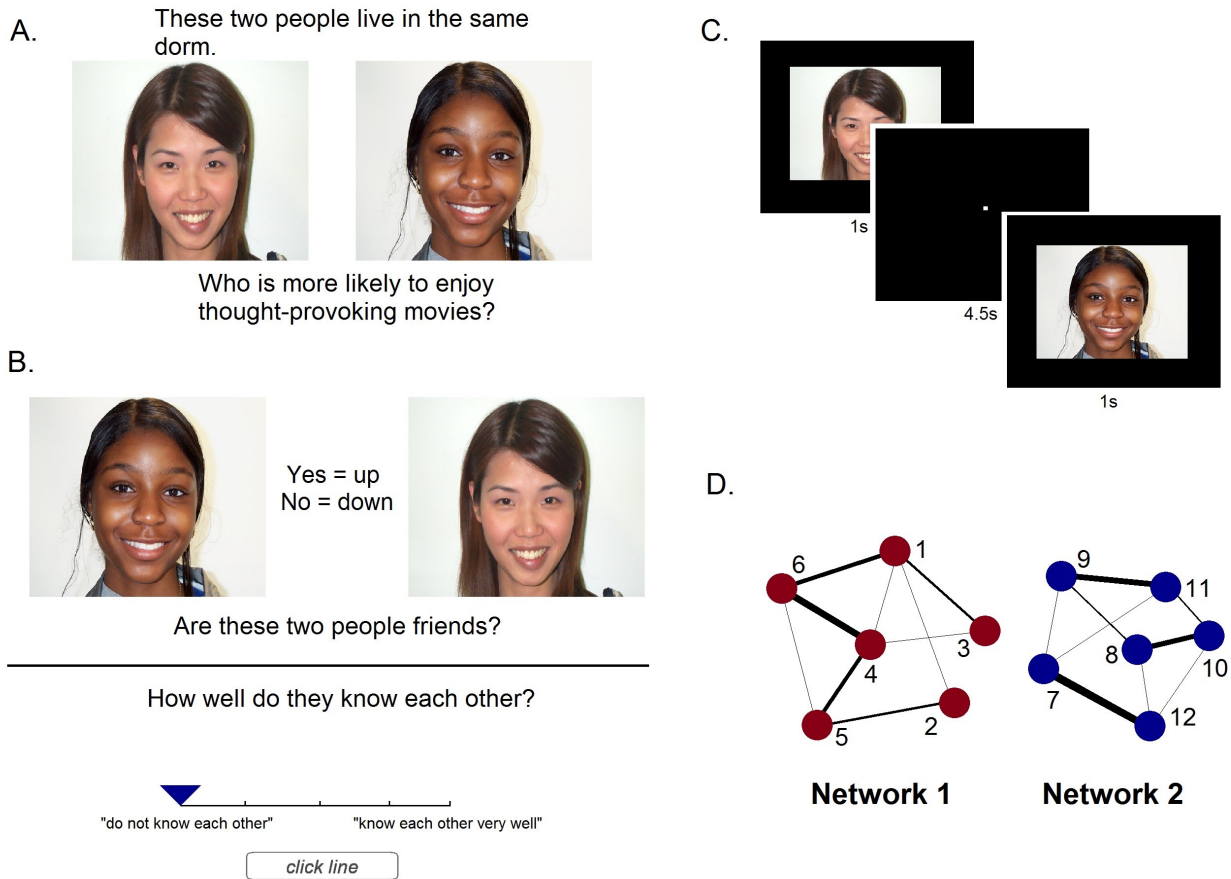
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682   **Figure 1.** A. Example trial of the paired presentation of a social network tie, where subjects
683   were asked to judge between the two faces on an unrelated characteristic. B. Example trial of
684   the recall task, where subjects were asked to report whether a pair of faces was connected, and
685   how well they know each other (0-4 scale). C. fMRI task, where each face was presented
686   individually for 1 second (4.5 second inter-stimulus interval). D. Structure of the two social
687   networks. Each node represents a different face and line thickness represents connection
688   strength. All ties are non-directed (reciprocal).
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	Network 1	Network 2	Both Networks	t-value (p)
Hit Rate	**0.82**	**0.83**	**0.83**	**-0.13 (0.89)**
SD	*0.14*	*0.11*	*0.09*	
False Alarm Rate	**0.39**	**0.47**	**0.43**	**-1.23 (0.23)**
SD	*0.21*	*0.24*	*0.19*	
d'	**1.3**	**1.2**	**1.2**	**0.70 (0.49)**
SD	*0.71*	*0.86*	*0.6*	
Strength Correlation (r)	**0.58**	**0.53**	**0.54**	**0.82 (0.42)**
SD	*0.25*	*0.21*	*0.21*	

696

697   **Table 1.** Accuracy of recalling network relationships after incidental learning. Hit rate, false
698   alarm rate, and d' represent the accuracy of recalling the true connections within the networks.
699   Strength correlation refers to the correlation between the matrix of true relationship strength of
700   the faces in the networks and the behavioral judgments of strength, and is therefore a measure
701   of accuracy of recalling relationship strength. T-values and p-values for paired sample two-tailed
702   t-tests between the two networks are reported at the right of the table. Bold indicates primary
703   data, and italics indicate the standard deviation of the data.
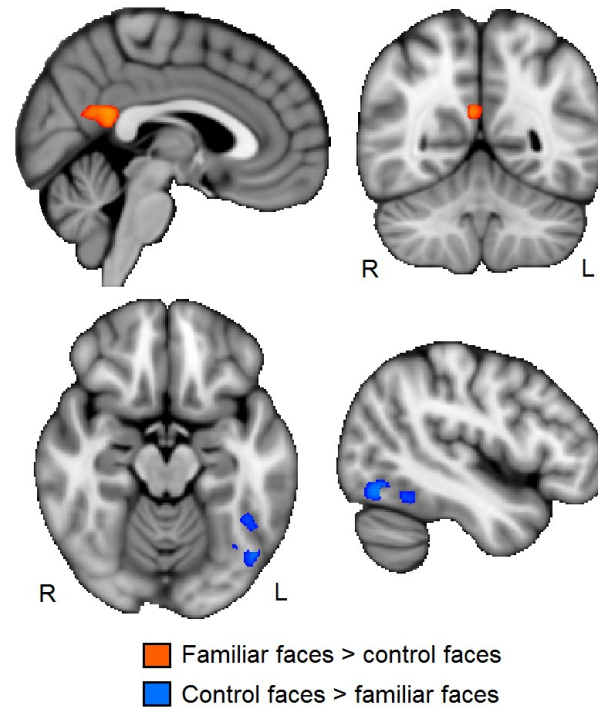
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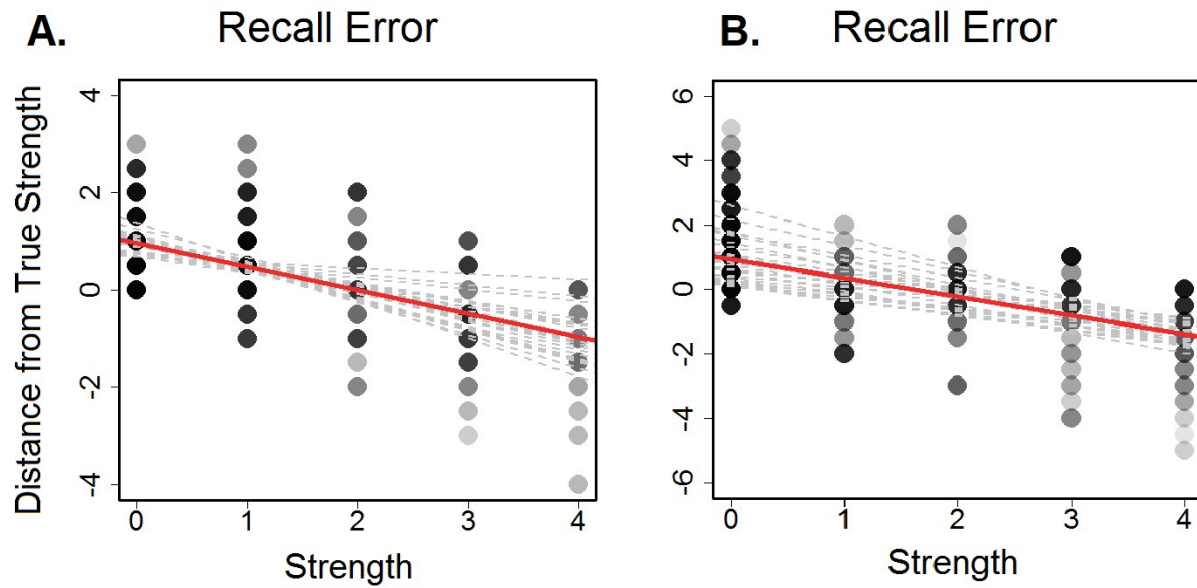
Figure 2. A. Each subject's error by pair strength level (0 = unconnected, 4 = close friends) from the primary dataset. Positive values = overestimation of strength and negative values = underestimation of strength. Gray lines show individual subject regression lines. The red line shows the group regression line. B. Subject error by pair strength level (0 = unconnected, 6 = close friends) from the secondary dataset with a larger social network (N = 9). Positive values = overestimation of strength and negative values = underestimation of strength. Gray lines show individual subject regression lines. The red line shows the group regression line.

Figure 3. Results from group analysis of z-statistic maps of familiar (network 1 and 2) faces vs. control faces (p < 0.05, FWE-corrected with threshold-free cluster enhancement within an anatomical mask composed of areas previously shown to be relevant for face perception and memory).

Cluster	Peak Value (t)	Voxels	x	y	z
Familiar > Control					
Posterior cingulate/precuneus	4.44	152	6	-48	20
Posterior cingulate/precuneus	3.62	7	2	-36	30
Posterior cingulate/precuneus	3.37	6	-4	-60	32
Control > Familiar					
L fusiform gyrus	4.01	248	-44	-68	-14
L fusiform gyrus	4.11	30	-38	-90	-8
L fusiform gyrus	4.19	11	-24	-30	-26

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737 **Table 2**. Coordinates, cluster size, and peak activity for the group-level clusters from the

738 univariate familiar vs. control face analysis.
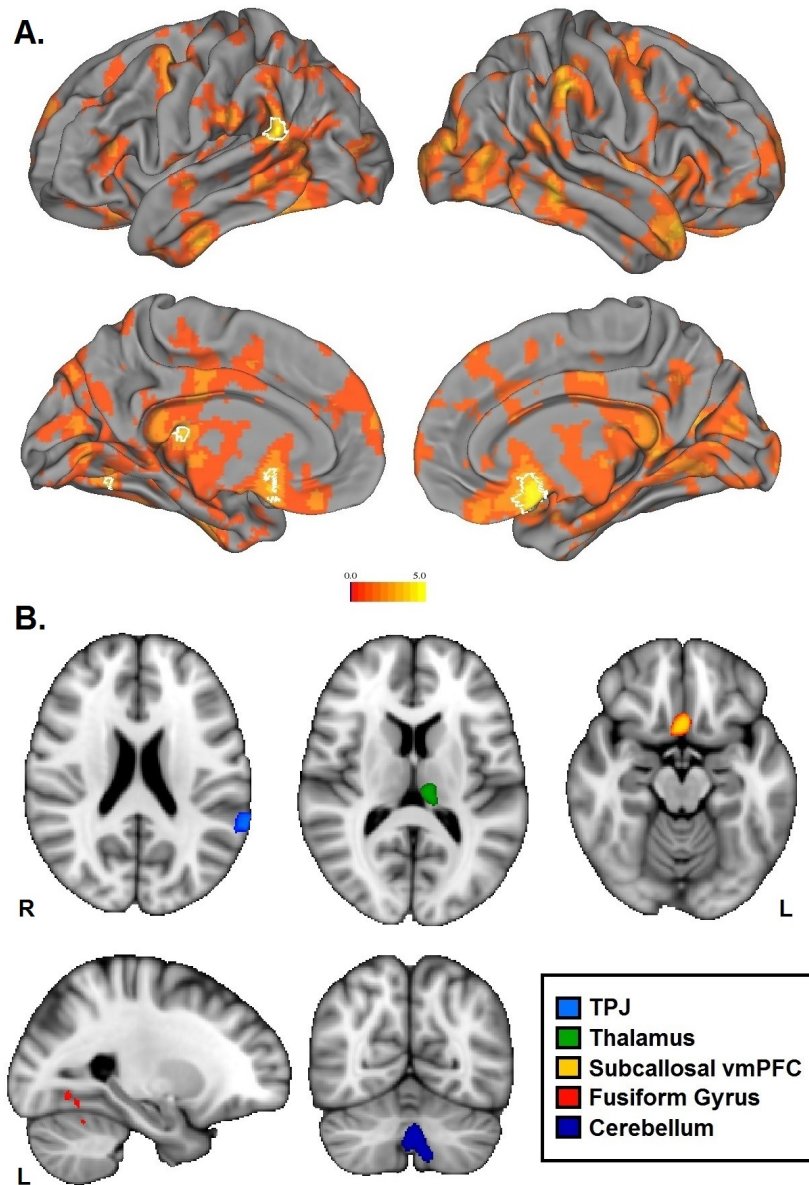
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741   **Figure 4**. Results from group-level nonparametric 1-sample t-test on the correlation maps from

742   RSA searchlight on the recall accuracy model. A. t-statistic map of all positive t-values projected

743   onto the surface, where white borders delineate significant clusters from the group analysis (p <

744   0.05, FWE-corrected with threshold-free cluster enhancement). B. The same significant clusters

745   projected in the volume.

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Cluster	Peak Value (t)	Voxels	x	y	z
Cerebellum	3.92	730	0	-64	-38
Subcallosal vmPFC	5.6	274	2	14	-16
Thalamus	4.14	132	-10	-28	10
TPJ	4.31	117	-64	-48	18
Fusiform Gyrus	3.28	11	-26	-60	-12
Fusiform Gyrus	3.5	5	-24	-66	-8
Fusiform Gyrus	3.37	5	-26	-56	26
Lateral Occipital	3.65	3	-52	-56	2
Lateral Occipital	3.66	3	-56	-70	-2

749

750   **Table 3.** Coordinates, cluster size, and peak activity for the group-level significant clusters from
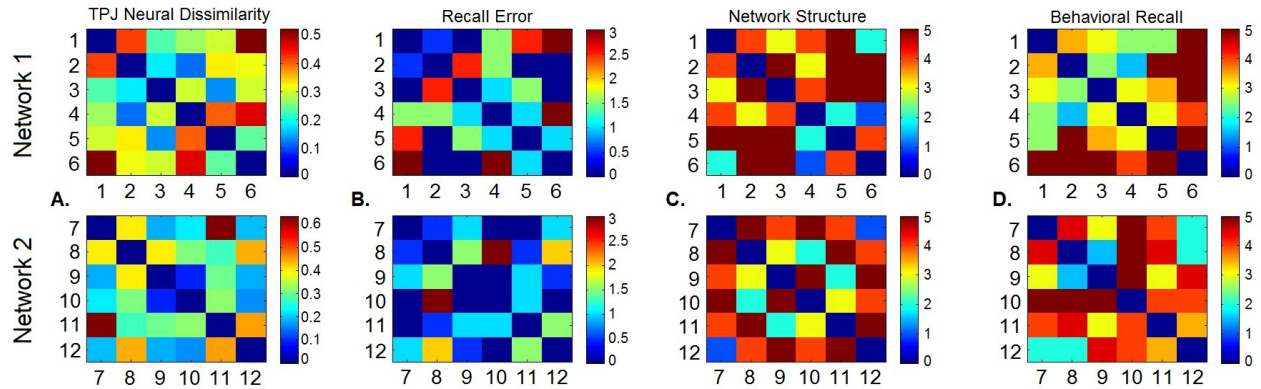
751   the recall error model.

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Figure 5. Dissimilarity matrices between face pairs for a sample subject. A. Neural dissimilarity in an example region in the temporoparietal junction. B. Recall error DM (0 = perfectly accurate recall). C. True network structure DM (0 = unconnected). D. Behavioral recall of face pair strength (0 = unconnected).