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Evidence That Default Network Connectivity During Rest Consolidates Social Information

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Abstract

Brain regions engaged during social inference, medial prefrontal cortex (MPFC) and tempoparietal junction (TPJ), are also known to spontaneously engage during rest. While this overlap is well known, the social cognitive function of engaging these regions during rest remains unclear. Building on past research suggesting that new information is committed to memory during rest, we explored whether one function of MPFC and TPJ engagement during rest may be to consolidate new social information. MPFC and TPJ regions significantly increased connectivity during rest after encoding new social information (relative to baseline and post nonsocial encoding rest periods). Moreover, greater connectivity between rTPJ and MPFC, as well as other portions of the default network (vMPFC, anterior temporal lobe, and middle temporal gyrus) during post social encoding rest corresponded with superior social recognition and social associative memory. The tendency to engage MPFC and TPJ during rest may tune people towards social learning.

Key words: default network, memory consolidation, MPFC, social cognition, TPJ

Over the past few decades a lingering question has pervaded neuroscience research: why do the same brain regions that support social cognition also spontaneously engage during rest? Social neuroscience research consistently finds that 2 brain regions—the medial prefrontal cortex (MPFC, Brodman area 9/10) and tempoparietal junction (TPJ)—play a critical role in understanding people (Mitchell et al. 2004; Saxe 2006; Van Overwalle and Baetens 2009; Lieberman 2010; Denny et al. 2012). MPFC and TPJ have been associated with encoding social information and forming impressions of people's personalities (Mitchell et al. 2004), as well as inferring mental states and intentions (Saxe and Kanwisher 2003; Ochsner et al. 2005; Frith and Frith 2006; Spunt and Lieberman 2012; Tamir et al. 2016).

Meanwhile, cognitive neuroscience research consistently finds that MPFC and TPJ are also part of a brain network that spontaneously engages during rest. For example, these regions increase activity when participants pause from performing experimental tasks (Shulman et al. 1997; Binder et al. 1999; Mazoyer et al. 2001; Raichle et al. 2001) and their spontaneous fluctuations during rest are reliably correlated (Greicius et al. 2003; Fox et al. 2005; Fransson 2005; Damoiseaux et al. 2006; Vincent et al. 2007). This pattern is so robust that it led neuroscientists to label this set of brain regions the "default network" (Raichle et al. 2001; Buckner et al. 2008) because they are reliably active by default, in the absence of other instructions.

While to date several review papers and meta-analyses have highlighted the anatomical overlap between the brain regions that support social cognition and those that engage by default during rest (Buckner and Carroll 2007; Spreng et al. 2009; Andrews-Hanna et al. 2014), the psychological functions

of engaging these regions during rest remain mysterious. One suggestion has been that the spontaneous engagement of these regions during rest may facilitate subsequent social inference. If they are already engaged by default prior to social interaction, this may facilitate their use during social interaction (Spunt et al. 2015). Here, we suggest a second function, focusing on the function of these regions after social inference. Specifically, MPFC and TPJ engagement during rest may consolidate newly acquired social information.

This consolidation hypothesis stems from memory research, which finds that recent experiences may be consolidated during post encoding rest. Initial evidence linking rest with memory consolidation emerged from findings in rodents showing that patterns of hippocampal neural firing "replay" during postexperience sleep and rest periods (Kudrimoti et al. 1999; Hoffman and McNaughton 2002; Lee and Wilson 2002; Foster and Wilson 2006). Recent work has extended these findings to humans, demonstrating that hippocampal–cortical connectivity and cortical–cortical brain activity patterns persist into postencoding rest periods and correlate with later associative memory (Peigneux et al. 2006; Stevens et al. 2010; Tambini et al. 2010; Deuker et al. 2013; Staresina et al. 2013; Tompary et al. 2015; Murty et al. 2017). While this past work suggests that the brain continues to process and consolidate new information during rest, no studies have examined whether functional connectivity between MPFC and TPJ during rest may facilitate social memory consolidation.

One impediment to studying social consolidation during rest is that past social neuroscience paradigms measure neural activity during experimental tasks, rendering tests for consolidation during rest untenable. Building off of past memory consolidation research, we developed a novel social consolidation paradigm in which participants alternated between extended periods of rest and active social and nonsocial encoding. We were therefore able to test, for the first time, the hypothesis that MPFC and TPJ default network regions commit new social information to memory during rest.

Methods

Participants

Nineteen individuals from the University of California-Los Angeles (UCLA) community participated in the study (11 females; mean age = 22.33 years, standard deviation [SD] = 4 years). Participants provided informed consent in accordance with the UCLA Institutional Review Board and received $100 in compensation.

Procedure

During their brain scan session, participants completed social encoding and nonsocial encoding tasks (task order counterbalanced across participants). Each encoding task comprised 2 runs of fMRI data acquisition. Participants also completed resting state scans before encoding (baseline rest) and after each set of encoding tasks, as well as a structural scan. Participants' final scan was a localizer task designed to pinpoint regions of neural activity associated with social and nonsocial processing. After their scan session, participants were escorted to a quiet testing room outside of the scanner where they completed a questionnaire assessing their thoughts during their rest scans and a surprise memory test. Figure 1A presents an overview of the experiment.

Encoding Tasks

For a given social encoding trial, participants first observed a photograph of a person, their job title (e.g., "doctor") and 2 traits that had been used to describe that person in the past (e.g., "educated, sincere"; see Fig. 1B). Participants encoded this information for 5 s, during which time they were instructed to form an impression of the person, based on all of the information available to them. Participants next rated the person's warmth (5 s) and competence (5 s) using a 1–100 scale. Warmth and competence are well-known dimensions guiding social impression formation (Fiske et al. 2007) and were included to facilitate impression formation processes in our subjects. Participants next saw a crosshair on the screen (5 s) and then completed 2 match-to-sample trials (to facilitate overall task engagement).

Nonsocial (i.e., place) encoding trials followed the same format as social encoding trials. Participants first observed a photograph of a location, the country where the photograph was taken (e.g., "Brazil"), and 2 traits that had been used to describe the location in the past (e.g., "breezy, sunny"). Participants were instructed to form an impression of the location (5 s) and subsequently rate the location on warmth (in terms of temperature; 5 s) and pleasantness (5 s) using a 1–100 scale. Participants encoded 60 social trials and 60 nonsocial trials (30 per run). To increase believability and external validity, naturalistic photographs of people and places were acquired from an online database of stock photos (depositphotos.com). Each photograph was paired with a unique job title/country and set of traits. No people were shown in any of the nonsocial encoding trials.

Localizer Task

During the localizer task, participants alternated between blocks of social and nonsocial impression formation. For the social trials, participants were shown a photograph of a person and one of their family roles (e.g., "sister") and 2 traits that have been used to describe the person in the past. For nonsocial trials, participants were shown a photograph of a location and the corresponding state (in the United States of America) where it is located (e.g., "Virginia") and 2 traits that have been used to describe the place in the past. As in the nonsocial encoding task, no people were shown in any of the nonsocial localizer trials. Each stimulus was shown for 5 s, with 4 stimuli shown per block. Prior to each block, participants read a cue (2 s) indicating which block type they would complete next. Participants completed 3 blocks of each stimulus type. For each impression formation trial, participants were instructed to form an impression of the person/place given all of the information provided. To enhance overall task engagement, participants also completed 6 blocks (20 s each) of match-to-sample trials and 6 blocks of rest (10 s each). All localizer task photographs were distinct from those used in the experimental encoding tasks.

Resting State Scans

Participants' scan session began with a baseline resting state scan and separate resting state scans following social encoding and nonsocial encoding. Following past work (Tambini et al. 2010), each rest scan was 8.4 min in duration. Participants were not shown a stimulus during rest scans and were instructed to relax, think about whatever they wanted, and to stay awake.
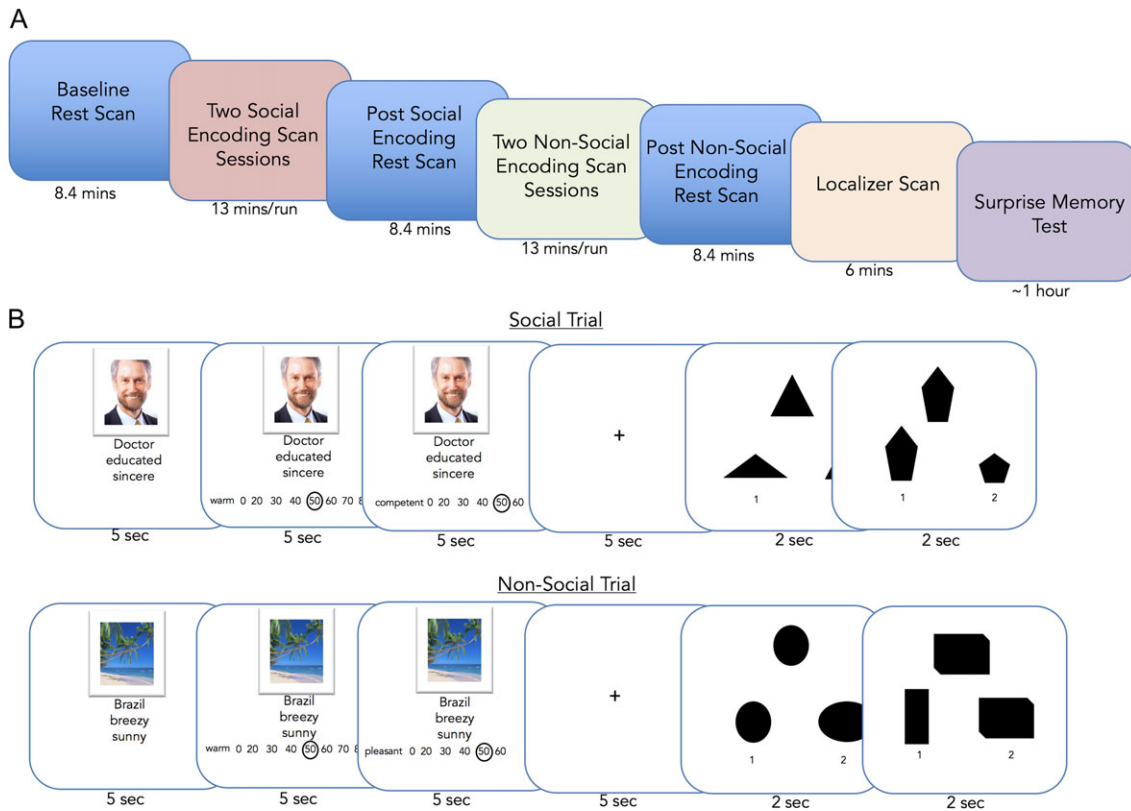
Figure 1. (A) Experimental paradigm. Rest scans were interleaved between social and nonsocial encoding scans. Encoding scan order was counterbalanced across participants. After completing the last rest scan, participants completed the social and nonsocial localizer scans. After the scanning session participants completed a surprise memory test in a quiet testing room. (B) Encoding trial structure for social encoding trials and nonsocial encoding trials.

Post Scanning Assessments

Directly after their scan, participants went into a quiet testing room to complete a computerized questionnaire and surprise memory test. For the questionnaire, participants first wrote what they thought about during their rest scans. Next, they rated on a 1–7 scale the extent to which the contents of their thoughts varied between periods of baseline rest, post social rest, and post nonsocial rest.

Participants next completed a surprise memory test. Following previous work (Tambini et al. 2010), participants answered memory questions blocked on content (people vs. places) in the same content order (people first, places second or places first, people second) in which they encoded people and places during their scan. Within these blocks, the presentation order of people and place trials was randomized across participants. For the social memory test, participants were randomly shown the 60 faces they encoded during scanning and 60 similar lure faces not previously presented during encoding. For each face, participants decided whether or not they remembered seeing the face during their scan. If participants indicated that they had seen the face, they were next asked 2 separate associative memory questions. First, they were asked to indicate the appropriate job title paired with the face and second, the set of traits that were presented with the face. For each association question, 3 viable options were listed, as well as the option "I don't remember" in order to reduce guessing. The location memory test was analogous to the person memory test. Participants were randomly shown the 60 encoded locations as well as 60 similar lure locations. For each location they indicated if they had seen the photograph during their scan and if so, which country and set of traits accompanied the location.

A trial was considered a successful associative memory trial only if both the job (or country) and trait set were both correctly identified. Social (and nonsocial) associative memory scores were computed by dividing the overall number of correctly recognized faces (or places) by the number of correct paired associations. For example, a social trial was considered correctly associated in memory if a face was matched with both the correct job title and traits. Likewise, a nonsocial trial was considered correctly associated in memory if a place was matched with the correct corresponding country and traits. We next multiplied these ratios by 100 so that scores reflect a percentage of associative hits. This method allows us to partial out associative memory from recognition memory, with scores reflecting the percentage of correctly associated information.

Brain Imaging Data Acquisition

Brain imaging data were collected at the UCLA Ahmanson-Lovelace Brain Mapping Center with a 64-channel coil. Functional magnetic resonance images (fMRI) were acquired with an anterior-to-posterior phase encoding using the following parameters: voxel size = 2 × 2 × 2, repetition time (TR) = 72 ms, echo time (TE) = 37 ms, field of view (FoV) = 208 mm, slice thickness = 2 mm. Each subject also underwent a high resolution T-1 weighted structural scan (magnetization-prepared rapid-acquisition gradient echo [MPRAGE]; voxel size = 1.1 × 1.1 × 1.2 mm^3). Encoding stimuli were projected to participants through LCD goggles and their responses

during encoding tasks were recorded with a button-box. Scan sessions lasted ~1.5 h.

Brain Imaging Data Analysis

Brain imaging data were analyzed with Statistical Parametric Mapping (SPM) software (SPM8; Wellcome Department of Cognitive Neurology, London, England). Functional image volume pre-processing included realignment, normalization into Montreal Neurological Institute (MNI) space, and spatial smoothing with a 6-mm full-width, half-maximum Gaussian kernel. Following past work, resting state data were high pass filtered with a 111 s cutoff in order to remove low frequencies below 0.009 Hz and low pass filtered to keep frequencies between 0.01 and 0.1 Hz (Fox et al. 2005, 2006; Tambini et al. 2010). For each subject, nuisance variables were created for the 6 motion parameters from realignment and their temporal derivatives, as well as activation from white matter and cerebral spinal fluid (CSF). Next, a general linear model was created for each subject that included each subject's nuisance variables as regressors. Residual images from this analysis—which comprise neural activity during rest, controlling for activation attributable to motion, CSF, and white matter—were saved and used for all subsequent resting state analyses.

Encoding and localizer task volumes were preprocessed in the same way as the resting state scans, however, we applied the standard 128 s high-pass filter to our task fMRI data. A general linear model was created (separately for encoding and localizer tasks) for each participant with a regressor for each experimental condition, as well as nuisance variables (6 motion parameters, CSF, and white matter). For the localizer task, first-level contrasts were created for each subject that compared social versus nonsocial impression formation and nonsocial versus social impression formation. These localizer task contrasts were submitted to second-level analyses to identify regions-of-interest (ROIs). Neural activity for the localizer comparisons was considered significant if it passed a statistical threshold of $P < 0.005$, 86 voxels. This joint voxelwise and cluster-size threshold corresponds to a false-positive discovery rate of 5% across the whole brain as estimated by a Monte Carlo simulation (10 000 iterations) implemented using 3dClustSim in AFNI (Cox 1996). It is noteworthy that this version of AFNI (17.1.10) does not have the potential problems raised by Eklund et al. (2016). Comparisons of social versus nonsocial impression formation identified clusters of activation in rTPJ, lTPJ, and MPFC whereas the nonsocial versus social impression formation comparison identified clusters of activation in left ventrolateral prefrontal cortex (lVLPFC), and right and left parahippocampal place area (rPPA, lPPA). To confirm that these ROIs discriminate social from nonsocial encoding in the experimental encoding tasks, mean activation in these ROIs was extracted from social and nonsocial experimental encoding tasks and submitted to statistical tests in SPSS software (Version 23).

Past work implicates the hippocampus in memory and hippocampal–cortical functional connectivity has been shown to facilitate memory consolidation during rest (Peigneux et al. 2006; Tambini et al. 2010; Deuker et al. 2013; Staresina et al. 2013; Tompary et al. 2015; Murty et al. 2017). Thus, we also performed exploratory analyses to examine the possibility that the hippocampus communicates with MPFC and TPJ to facilitate social memory consolidation. In particular, given that the hippocampus may play a more domain-general role in memory consolidation during rest, we were interested in examining whether this region differentially couples with cortical regions associated with social and nonsocial (place) processing, depending on the content of the previously encoded material. To this end, we created first level models for each subjects' encoding data that compared neural activity for all trials (social and nonsocial) that were correctly recognized (vs. not recognized) in the surprise memory test, which revealed a cluster in the right hippocampus [$x = 34$ $y = -8$ $z = -20$]. To ensure this region was limited to the hippocampus, we constrained it to voxels within a structural hippocampus ROI generated in PickAtlas (Fig. 5A).

For each participant, timecourse data from the localizer and hippocampal ROIs was also extracted from each resting state scan. We next computed, separately for each resting state scan and each participant, the simple Pearson correlation (r) between timecourses for the social ROI pairs (rTPJ–MPFC, lTPJ–MPFC, and rTPJ–lTPJ,) and nonsocial ROI pairs (rPPA–lVLPFC; lPPA–lVLPFC; rPPA–lPPA), as well as the hippocampal ROI pairs (e.g., hippocampus–MPFC, hippocampus–lVLPFC). Correlation values were next fisher-z transformed to allow for statistical comparisons between resting state scans. One outlier more than 2 SD outside of the group rTPJ–MPFC connectivity mean during post location rest was removed from analyses. Results are similar with and without the outlier.

Voxelwise resting state functional connectivity analysis was also performed using the CONN Toolbox in SPM8 (Whitfield-Gabrieli and Nieto-Castanon 2012) to allow for regression analyses examining whether voxels within TPJ increase connectivity with other brain regions as a function of social memory performance. For each subject, a first level analysis, seeded with the rTPJ ROI, was computed for each resting state scan. The rTPJ was selected as the seed because it was the only region that showed increased connectivity with each of the other social cognition ROIs during post social encoding rest (i.e., "post social rest"; see Results). These first level analyses were then taken to SPM8, where we performed voxelwise regression analysis to examine how connectivity strength varied as a function of memory performance. We also performed regression analyses using the same steps, but seeded in the nonsocial rPPA and lPPA localizer ROIs, as well as the hippocampus ROI. Regression analyses were probed with the threshold of $P < 0.005$, 86 voxels, as determined by Monte Carlo simulation (10 000 iterations) using 3dClustSim in AFNI (version 17.1.10).

Results

Memory Performance

Our paradigm allows for the separate computation of 1) social recognition memory (percentage of correctly identified people [hit rate] vs. falsely recognized people [false alarm rate]) and 2) social associative memory (of the correctly identified people, the percentage of trials that participants also correctly associated the traits and jobs). The same scores can also be computed for nonsocial recognition memory and nonsocial associative memory. Participants showed greater social memory performance for both recognition and associative memory (mean person recognition [hit rate – false alarm rate] = 35%, SD = 14%; mean place recognition [hits rate – false alarm rate] = 25%, SD = 16%, P = 0.016; mean social associative memory = 57%, SD = 22%; mean nonsocial associative memory = 37%, SD = 18%, P = 0.0002).

Neural Manipulation Checks

Before examining our primary hypotheses, we first wanted to confirm that the ROIs from our localizer tasks indeed discriminate

social from nonsocial cognition in our experimental encoding tasks. In line with this goal, average neural activation within our social cognition localizer ROIs (rTPJ, lTPJ, MPFC) was significantly greater during social (vs. nonsocial) encoding tasks, whereas average neural activity in our nonsocial localizer ROIs (rPPA, lPPA, lVLPFC) was significantly greater during nonsocial (vs. social) encoding tasks (P's < 0.01; Fig. 2B, Supplementary Table S1). It is also worth mentioning that these regions emerged in whole-brain comparisons of the social and nonsocial encoding tasks (Supplementary Fig. S1; Supplementary Table S2).

Second, given that part of the social consolidation hypothesis stems from past research finding that MPFC and TPJ regions show stronger engagement during rest relative to other brain regions, we tested whether MPFC and TPJ showed greater functional connectivity during baseline rest than lVLPFC and PPA. Consistent with past work showing that MPFC and TPJ regions engage during rest by default, mean baseline resting state connectivity, collapsed across each MPFC and TPJ ROI pair (i.e., MPFC–rTPJ; MPFC–lTPJ; rTPJ–lTPJ; mean = 0.60, SD = 0.22), was significantly greater than connectivity collapsed across each lVLPFC and PPA pair (lVLPFC–lPPA; lVLPFC–rPPA; lPPA–rPPA; mean = 0.31, SD = 0.18, t[18] = 4.67, P < 0.0001).

Psychological Manipulation Checks

We also wanted to verify that any observed differences in resting state functional connectivity did not reflect variation in the kinds of explicit thinking that participants engaged in during rest scans. Specifically, we wanted to confirm that participants did not, for example, preferentially rehearse aspects of the social stimuli during their subsequent postsocial encoding rest period. After their scan session, participants completed a questionnaire in which they were asked to describe their thoughts during each resting state scan, as well as rate the extent to which their thoughts varied during each pair of rest periods (post social rest vs. baseline rest; post nonsocial rest vs. baseline rest; post social rest vs. post nonsocial rest). No subjects

reported thinking about any of the stimuli during their rest scans and their ratings of whether their thoughts differed between pairs of rest scans were not significantly different from one another (P's > 0.546). Although these self-reports are retrospective, they are consistent with the possibility that any observed differences in functional connectivity between rest scans do not reflect different forms of explicit thinking during these idle periods. Consistent with past research on the resting brain (Ruby et al. 2013), a number of participants reported thinking about themselves and their own social lives during their rest scans, despite not reporting thinking about the social stimuli presented in the social encoding task.

Post Social Encoding Resting State Connectivity

Our primary hypothesis is that one function of TPJ and MPFC activity during rest may be to consolidate newly acquired social information. If this were the case, then we would expect increased connectivity between these regions during rest that occurs after social encoding, relative to periods of rest that occur 1) before social encoding or 2) after nonsocial encoding. To test this hypothesis, we computed a linear contrast that directly compared post social rest to baseline rest and post nonsocial rest. Post social rest showed greater functional connectivity relative to the other 2 rest periods for rTPJ–lTPJ connectivity (t[51] = 2.33, P = 0.012), rTPJ–MPFC connectivity (t[51] = 1.79, P = 0.040), and marginally for lTPJ–MPFC connectivity (t[51] = 1.43, P = 0.079). Follow-up paired sample t-tests showed that rTPJ–lTPJ connectivity was significantly stronger for post social rest versus baseline rest (t[18] = 2.39, P = 0.014), as well as post social rest versus post nonsocial rest (t[18] = 2.35, P = 0.016). RTPJ–MPFC connectivity was greater for post social rest versus baseline rest (t[18] = 1.79, P = 0.045), but not post social rest versus post nonsocial rest (t[17] = 0.42, P = 0.341; Fig. 3A).

One reason for the lack of a significant difference in rTPJ–MPFC connectivity between post social and nonsocial rest periods could be the presence of an order effect. Specifically, it is
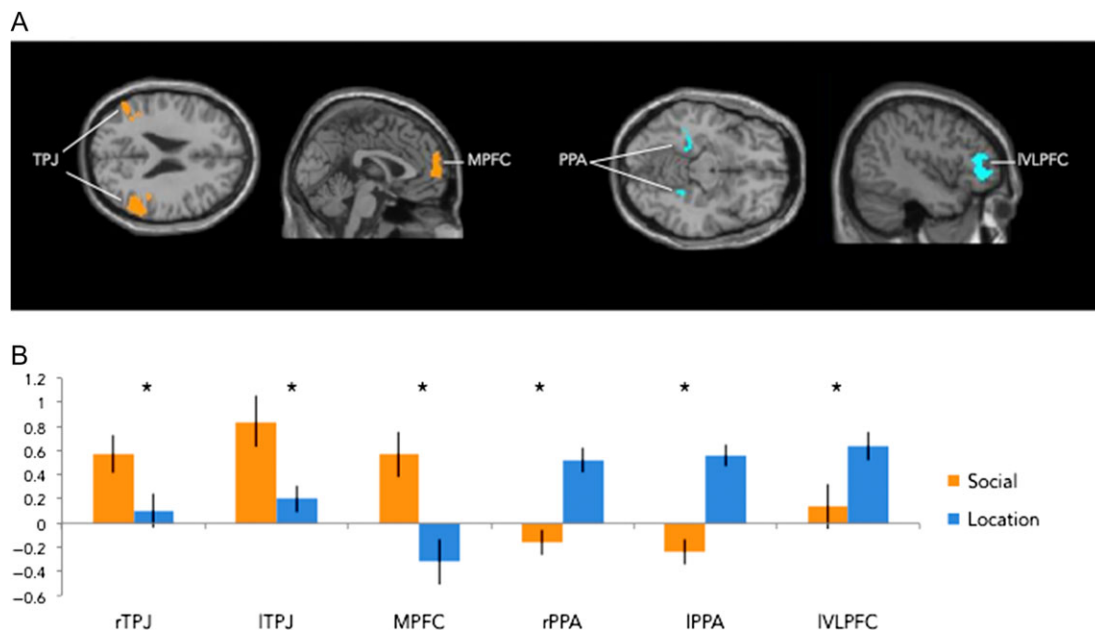

Figure 2. (A) Localizer regions-of-interest (ROIs). ROIs associated with the social cognition task (person impression formation) are displayed in orange (MPFC, rTPJ, lTPJ). ROIs associated with the nonsocial cognition task (location impression formation) are displayed in blue (lVLPFC, rPPA, lPPA). (B) Regions-of-interest (ROIs) from the localizer scan show preferential increases in activation for social and nonsocial experimental encoding tasks.
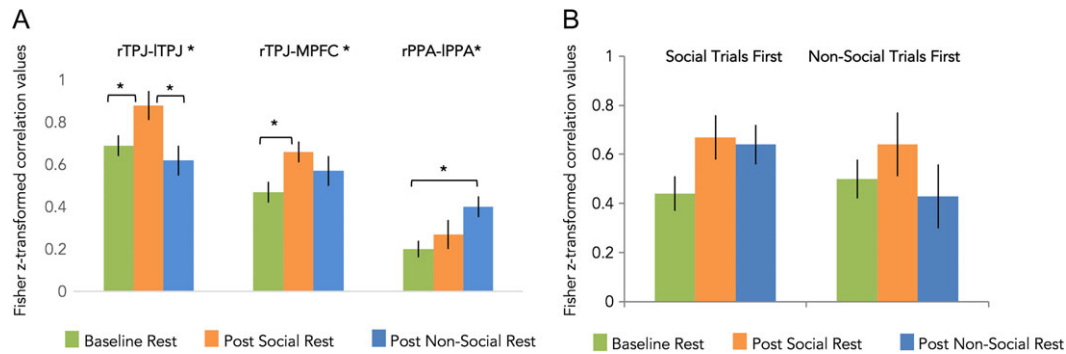
Figure 3. (A) Resting state functional connectivity between rTPJ–lTPJ, rTPJ–MPFC, and lPPA–rPPA plotted separately for each rest period. (B) rTPJ–MPFC resting state functional connectivity plotted separately for participants who completed social encoding first or location encoding first.

possible that if the post social rest precedes the post nonsocial rest, then rTPJ–MPFC connectivity would continue to consolidate the social information in the post nonsocial rest period. Consistent with this possibility, this order effect was observed for rTPJ–MPFC connectivity ($t[51] = 1.88$, $P = 0.033$). As can be seen in Figure 3B, participants who first encoded nonsocial information showed the expected pattern of results: similar levels of rTPJ–MPFC connectivity after nonsocial encoding and baseline and heightened connectivity only during post social rest. However, participants who previously completed social encoding kept rTPJ–MPFC regions highly connected not only during post social rest, but also during post nonsocial rest.

The results suggest that rTPJ–MPFC and bilateral TPJ communication may preferentially consolidate social information during rest. There are 2 alternative interpretations, however, to this possibility. First, it is possible that all brain regions increase communication after encoding information about people, rather than TPJ and MPFC regions more specifically. Second, it is possible that greater rTPJ–MPFC and/or bilateral TPJ show greater postencoding resting state connectivity for tasks that are better subsequently remembered. Indeed, participants showed superior recognition and associative social memory than nonsocial memory performance (P's < 0.02). To rule out these alternative possibilities, we examined resting state connectivity patterns in our nonsocial ROIs (rPPA, lPPA, and lVLPFC). If nonsocial ROIs show increased connectivity during post nonsocial encoding rest, as has been shown in prior work (Peigneux et al. 2006; Tambini et al. 2010; Deuker et al. 2013; Staresina et al. 2013; Tompary et al. 2015; Murty et al. 2017), it would suggest a double dissociation between brain regions associated with social and nonsocial consolidation during rest. Consistent with this suggestion, rPPA and lPPA showed significantly greater functional coupling during post nonsocial encoding rest when compared with 1) baseline and 2) post social encoding rest ($t[51] = 1.79$, $P = 0.040$). Follow-up t-tests revealed that rPPA–lPPA coupling was significantly greater during post nonsocial encoding rest versus baseline rest ($t[18] = 2.03$, $P = 0.029$ Fig. 3A) though not relative to post social rest ($t[18] = 1.18$, $P = 0.127$). Importantly, connectivity between bilateral PPA was not significantly greater during post social encoding rest versus baseline rest ($t[18] = 0.91$, $P = 0.187$), suggesting that not all brain regions significantly increase connectivity following social encoding. Unlike the rTPJ–MPFC connectivity, there was no order effect observed for the rPPA–lPPA coupling ($t[51] = 0.82$, $P = 0.21$). PPA regions were also not significantly coupled with lVLPFC during post nonsocial encoding rest (P's > 0.30).

Post Social Encoding Resting State Connectivity and Social Memory

If TPJ–MPFC communication during rest helps consolidate social information, then connectivity between these regions after social encoding should also correspond with superior memory for newly acquired social information. Whole-brain regression analyses revealed clusters whose coupling with the rTPJ seed increased as a function of social memory advantage (Fig. 4A). RTPJ was selected as a seed region for these whole-brain connectivity analyses because this was the only region that showed significant connectivity with both the MPFC and lTPJ. Greater person recognition memory (hit rate – false alarm rate) corresponded with greater connectivity between rTPJ and a cluster in MPFC ($x = 0$ $y = 46$ $z = 0$, $k = 91$) as well as ventromedial prefrontal cortex (vMPFC; $x = 6$ $y = 52$ $z = -12$, $k = 139$), anterior temporal lobe (aTL; $x = -52$ $y = -12$ $z = -24$, $k = 329$), and posterior temporal gyrus (pTG; $x = -50$ $y = -42$ $z = -4$, $k = 131$) during post social encoding rest. Performing the same analyses for baseline and post nonsocial encoding rest revealed no clusters of activation.

We next examined whether greater social associative memory showed greater coupling between rTPJ and other portions of the brain during post social encoding rest. Greater social associative memory corresponded with greater rTPJ connectivity with clusters in temporal pole ($x = -56$ $y = 2$ $z = -4$, $k = 174$), posterior cingulate ($x = 8$ $y = -56$ $z = 18$, $k = 205$), and fusiform gyrus ($x = -20$ $y = -44$ $z = -14$, $k = 224$). It is noteworthy that a cluster in MPFC also emerged in this analysis at a less strict cluster threshold ($x = 2$ $y = 64$ $z = 4$, $k = 26$). Performing the same analyses for baseline and post nonsocial encoding rest periods revealed no clusters of activity. Interestingly, whole-brain regression analyses testing for neural activity during social encoding related to subsequent social memory revealed a single cluster in supplementary motor area extending into middle cingulate ($x = -4$ $y = 12$ $z = 54$, $t = 4.25$, $k = 115$) associated with social associative memory, and lateral prefrontal cortex ($x = -24$ $y = 46$ $z = 10$, $t = 5.48$, $k = 143$) and posterior cingulate ($x = -12$ $y = -44$ $z = 46$, $t = 4.26$, $k = 97$) were associated with person recognition (hits-false alarms). Thus, while MPFC and TPJ appear to be important for social consolidation during rest, their role during social encoding may be less critical for committing new social information to memory.

Post Nonsocial Encoding Resting State Connectivity and Nonsocial Memory

Testing which regions of the brain show increased connectivity with PPA as a function of nonsocial associative memory
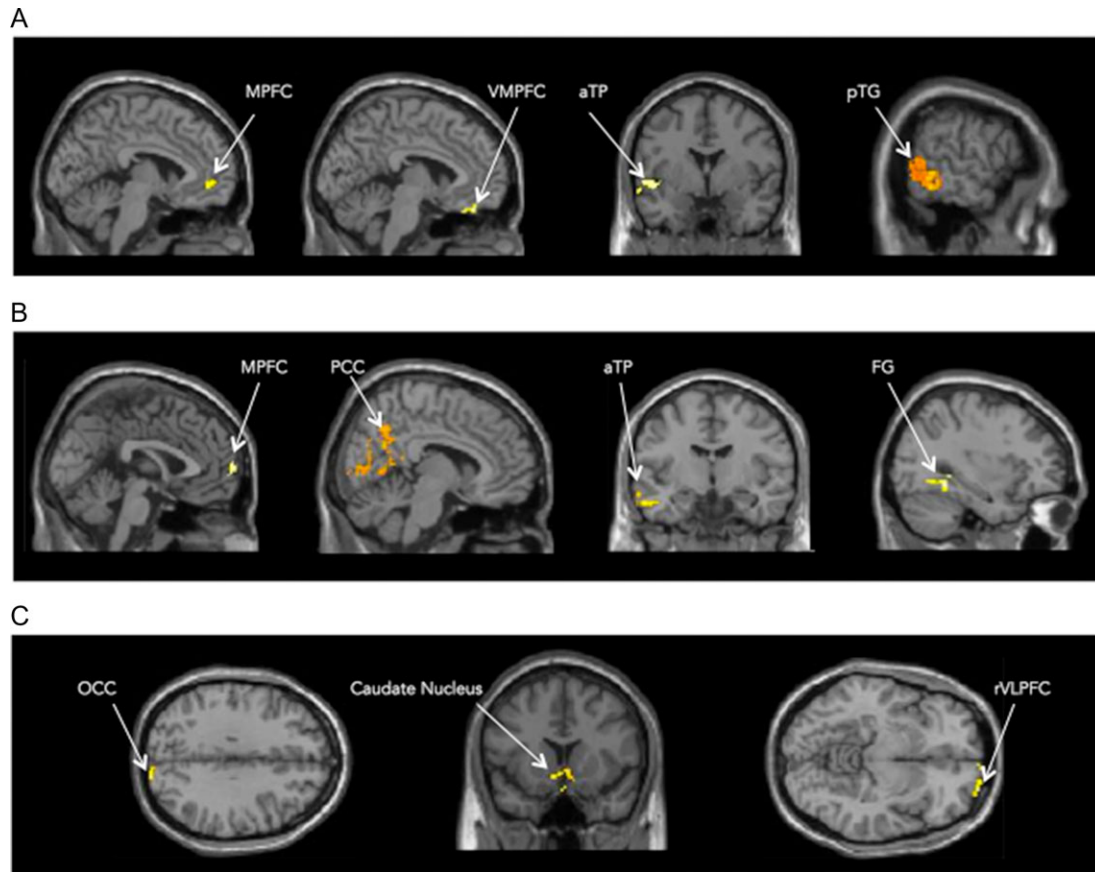
Figure 4. Whole-brain functional connectivity analyses seeded in rTPJ during postsocial encoding rest. (A) Regions showing greater connectivity with rTPJ during post social encoding rest as a function of social recognition memory. (B) Regions showing greater connectivity with rTPJ during post social encoding rest as a function of social associative memory. (C) Regions showing greater connectivity with lPPA during post nonsocial encoding rest as a function of nonsocial associative memory. Abbreviations stand for the following brain regions: MPFC = medial prefrontal cortex, vMPFC = ventromedial prefrontal cortex, TP = temporal pole, pTG = posterior temporal gyrus, PCC = posterior cingulate cortex, FG = fusiform gyrus, OCC = Occipital Cortex, rVLPFC = right ventrolateral prefrontal cortex. Note that the MPFC cluster that emerged in the social associative memory regression survives at a lower extent threshold ($k = 26$).

revealed that our lPPA seed increased connectivity with rVLPFC ($x = 28$ $y = 66$ $z = −12$, $k = 77$), caudate nucleus ($x = 6$ $y = 18$ $z = −6$), $k = 136$, and lateral occipital lobe ($x = 16$ $y = −94$ $z = 32$, $k = 150$; Fig. 4C). No clusters of activity increased with our ROIs as a function of place recognition memory (hit rate – false alarm rate). Performing the same analyses for baseline and post social rest periods revealed no clusters of activity. Similarly, whole-brain regression analyses of nonsocial memory recognition and associative memory revealed no clusters significantly associated with nonsocial encoding.

Post Encoding Resting State Connectivity with the Hippocampus

Finally, we explored whether the hippocampus, a region implicated in memory consolidation (Peigneux et al. 2006; Tambini et al. 2010; Deuker et al. 2013; Staresina et al. 2013; Tompary et al. 2015; Murty et al. 2017), may differentially couple with brain regions associated with social and nonsocial processing, depending on the content of the previously encoded material. The right hippocampal ROI associated with both social and nonsocial recognition (Fig. 5A) demonstrated heightened connectivity with the MPFC during post social rest (vs. baseline and post nonsocial rest; $t[18] = 2.194$, $P = 0.021$, Fig. 5B). Follow-

up t-tests confirmed that coupling between this hippocampal ROI and MPFC was significantly greater during post social rest versus baseline rest ($t[18] = 2.504$, $P = 0.011$) and versus post nonsocial rest ($t[18] = 2.145$, $P = 0.023$).

Whole-brain regression analyses seeded in the right hippocampal ROI further revealed that this region increases connectivity with a dorsal cluster in MPFC ($x = 10$ $y = 58$ $z = 24$, $k = 120$; Supplementary Table S3) as a function of greater person recognition memory (hit rate – false alarm rate). An MPFC cluster also showed increased connectivity with the hippocampus during post social rest as a function of social associative memory at a less strict statistical threshold ($x = −8$ $y = 58$ $z = −2$, $k = 324$, $P < 0.05$; Fig. 5C).

Although this hippocampal ROI did not, on average, increase connectivity with the nonsocial localizer ROIs during post nonsocial rest (P's > 0.22), whole brain regression analyses seeded in the hippocampal ROI demonstrated that greater connectivity during post nonsocial rest between hippocampus and lVLPFC ($x = −24$ $y = 68$ $z = 2$, $k = 101$) and caudate nucleus ($x = 6$ $y = 18$ $z = −6$, $k = 136$) corresponds with superior nonsocial associative memory performance (Fig. 5D). A cluster in dorsal anterior cingulate cortex (dACC; Fig. 5D) emerged at a lower statistical threshold ($x = −4$ $y = −40$ $z = 16$, $k = 29$, $P < 0.01$) when nonsocial recognition memory (hit rate – false alarm rate) scores were regressed on post nonsocial rest.
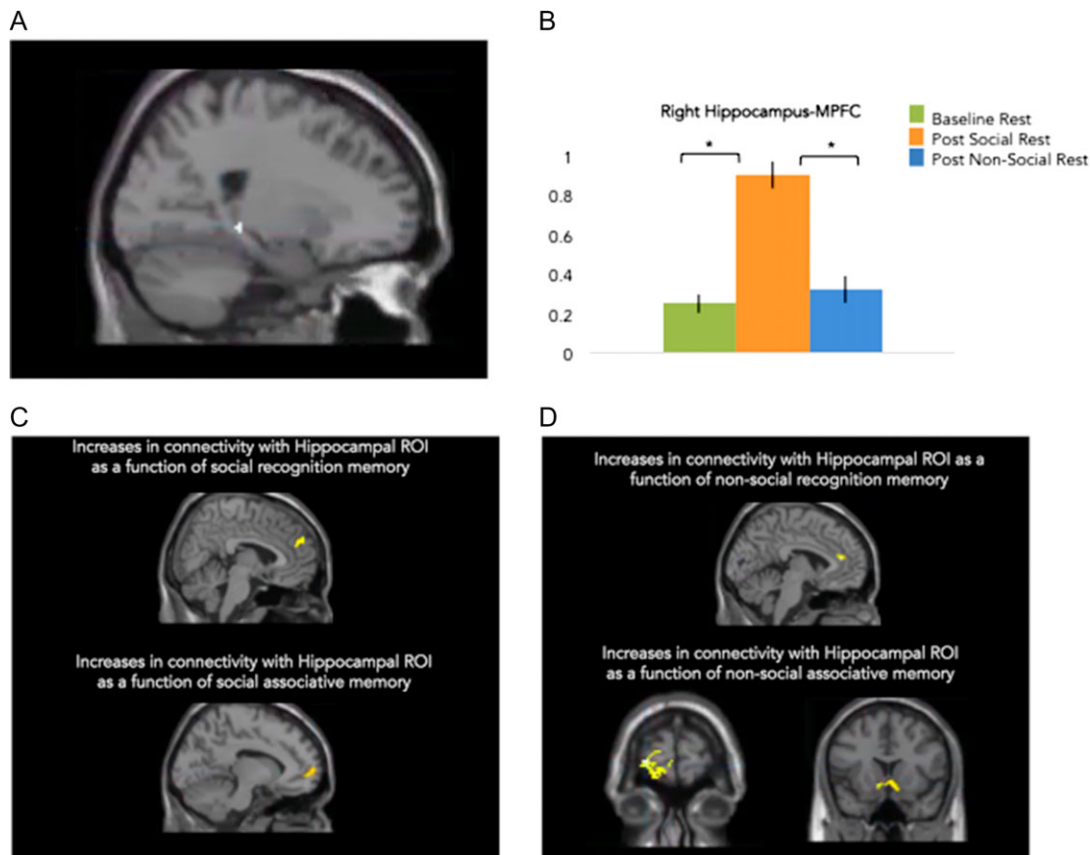
Figure 5. Brain regions that increase functional connectivity with the hippocampus during post encoding rest. (A) Hippocampus region of interest (ROI) created from the encoding contrast comparing successful recognition memory (hit rate − false alarm rate) for both social and nonsocial encoding trials. (B) The hippocampus ROI increases functional connectivity with the MPFC ROI during post social encoding rest relative to each of the other rest periods. (C) Greater increases in functional connectivity between the hippocampus ROI and MPFC corresponds with better social memory performance. (D) Greater increases in functional connectivity between the hippocampus ROI and dACC, lVLPFC, and caudate corresponds with better nonsocial memory performance.

Discussion

Why do the same brain regions that support social cognition also engage by default during rest? Results from the present study suggest that one function of MPFC and TPJ engagement during rest may be to commit new social information to memory. During rest periods that followed the encoding of social information, MPFC and TPJ default network regions showed increased functional connectivity. Connectivity between these regions, as well as other portions of the default network (aTL, precuneus and middle temporal gyrus) during post social encoding rest also corresponded with better social memory performance on a surprise memory test conducted outside of the scanner. In fact, participants who encoded social information directly after a baseline rest scan showed heightened MPFC–rTPJ connectivity not only during rest that directly followed social encoding, but also during rest that followed a subsequent, nonsocial task.

To date, the dominant approach to understanding default network function has been to make side-by-side anatomical comparisons between patterns of brain activity during rest and the psychological processes that also activate these regions during experimental tasks (Buckner and Carroll 2007; Spreng et al. 2009; Andrews-Hanna et al. 2014). Although this approach has been critical to hypothesis generation, highlighting common patterns of neural activity during rest and psychological

tasks does not directly test the psychological functions these regions may perform during rest. Engaging portions of the default network during live social interactions, when actively decoding the people around us, and later engaging these regions when relaxing after the social interaction, may both facilitate social functioning. Nonetheless, these brain regions may perform different operations during these two time points. Consistent with this suggestion, we observed that connectivity between MPFC and TPJ during rest might be critical in translating new social information into lasting associations in memory.

Such observations lead to new hypotheses regarding the function of resting state connectivity between other portions of the default network. For example, within the default network, a more anterior portion of MPFC shows strong functional connectivity with the precuneus/posterior cingulate cortex (PC/PCC) during rest (Andrews-Hanna et al. 2010), and both of these regions have been associated with thinking about the self in the past, present, and future (Gusnard et al. 2001; Kelley et al. 2002; Ochsner et al. 2004; Spreng et al. 2009; Spreng and Grady 2010). While the more posterior portion of MPFC observed in the current study may work with the TPJ to consolidate information about other people during rest, it is possible that aMPFC–PC/PCC connectivity may support a similar consolidation process for the self. As people transition between social roles and receive feedback from their peers, they might update

their self-knowledge, a process that may be facilitated by resting state connectivity between aMPFC and PC/PCC.

Our results also offer the first empirical insight into the mechanisms that support social consolidation. Extant social neuroscience paradigms tend to focus on the moment of social reasoning, finding that MPFC and TPJ support mental state and trait inference (Saxe and Kanwisher 2003; Mitchell et al. 2004, 2005; Ochsner et al. 2005; Frith and Frith 2006; Saxe 2006; Van Overwalle and Baetens 2009; Spunt et al. 2011; Denny et al. 2012). Yet, how in vivo social reflection translates into lasting social knowledge previously remained unexplored. Our results suggest that committing social information to memory, specifically consolidating information about people's identities, personalities and social roles, is underpinned, in part, by default network connectivity during rest. These findings dovetail nicely with recent research showing one portion of the default network—the aTL—is critical for retrieving recently associated biographical information (e.g., job, age, or hometown) with a person's identity (Wang et al. 2017). We similarly observed that greater connectivity between rTPJ and aTP during post social encoding rest corresponded with superior social associative memory performance (i.e., correctly remembering the personality traits and job shown with a face during encoding) measured outside of the scanner. Future work may further probe the ways in which aTL works with other portions of the default network during rest to possibly create a storehouse of person knowledge.

Interestingly, for participants who completed social encoding first, MPFC–rTPJ connectivity increased not only during rest that immediately followed social encoding, but also during rest that followed nonsocial encoding. In contrast, a previous study that used a structurally similar paradigm to the one used in the present study did not observe stimulus encoding order effects—participants showed significantly increased connectivity between brain regions associated with stimulus encoding during rest that immediately followed encoding (Tambini and Davachi 2013). This previous study and the present study employed encoding and resting state scans of similar duration, suggesting this difference is not likely due to timing differences. Instead, one possibility is that the difference reflects the importance of social learning and the functional properties of default network regions. Future research may confirm whether, perhaps because they engage during rest by default, MPFC and rTPJ regions are well suited to consolidate new social information across extended periods of time, facilitating social learning.

The results additionally complement and extend past research on systems level memory in general, and social memory, in particular. Consistent with theories of systems level memory consolidation (McClelland et al. 1995), which suggest that the hippocampus interacts with neocortex to create a memory representations distributed throughout the brain, we observed that the hippocampus exhibited connectivity with different neocortical regions during post encoding rest periods. Specifically, social memory performance was associated with greater functional connectivity between the hippocampus and MPFC during post social rest. In contrast, greater nonsocial (place) memory was associated with greater functional connectivity between the hippocampus and VLPFC, caudate, and to a lesser extent dACC during post nonsocial rest.

In the context of past research on social memory, animal and human research suggests that the hippocampus and MPFC, as well as the amygdala, play critical roles in social recognition (Kogan et al. 2001; Olson et al. 2007; Hitti and Siegelbaum 2014; Garrido et al. 2016). For example, in mice, the identity of a previous cagemate is consolidated by the hippocampus, MPFC, and amygdala (Tanimizu et al. 2017). In humans, face recognition is associated with dorsal MPFC (dMPFC; Mitchell et al. 2004), and we likewise observed that connectivity between the hippocampus and dMPFC during post social rest corresponded with superior face recognition. As in past work examining face recognition with a similar social encoding paradigm (Mitchell et al. 2004), we did not observe the amygdala in any of our social memory analyses. However, past work implicating the amygdala in social recognition typically measures responses to either familiar others or highly emotional facial expressions. In contrast, participants in our study encoded strangers demonstrating relatively neutral facial expressions. Relatedly, a recent study found that encoding highly emotional social and nonsocial images corresponded with increased amygdala-hippocampal connectivity during post encoding rest periods (Tambini et al. 2017). Future work may reveal whether the amygdala communicates with the hippocampus and/or MPFC to consolidate more emotionally arousing social information and/or information about the people in our own personal lives.

It is worth noting that some of the past associative memory paradigms examining consolidation during rest have also included human faces in the encoded stimuli. For example, Tambini et al. (2010), instructed participants to associate faces with everyday objects (e.g., a beach ball) and scenes (e.g., a beach) and found that enhanced connectivity between neural regions outside of the canonical default network, such as fusiform face area (FFA), PPA, and lateral occipital complex, increased during post encoding rest. Critically, however, by associating faces with objects and scenes, participants in this past work were likely engaging fewer social inference processes than participants in our study—who were instructed to form an impression of the targets and rate them in terms of their warmth and competence. Indeed, FFA appears to switch its connectivity to MPFC during sleep when consolidating face associations, if the face was previously encoded along social dimensions. Specifically, when participants first form impressions of faces that they subsequently associate with a location on the screen, greater connectivity between FFA and MPFC during subsequent sleep corresponds with greater face-screen location association (van Dongen et al. 2011). Thus, in our view, it is the social cognitive processing of stimuli (e.g., forming a social impression) that is likely critical for the increase in connectivity between the MPFC and TPJ post social encoding observed in our study. Future research can test this more explicitly, for example, by instructing participants to anthropomorphize nonsocial objects during encoding and examining whether MPFC and TPJ increase connectivity during subsequent rest and facilitates subsequent memory.

Limitations

The present results are not without limitations. First, participants performed significantly better on the social versus nonsocial memory test. Thus, an alternative explanation for our findings is that MPFC and TPJ increase connectivity during post encoding rest to consolidate more easily learned information. However, we think this is unlikely to be the case, since previous research finds that more easily remembered face–object associations corresponds with greater connectivity between cortical regions associated with stimulus encoding (e.g., FFA and lateral occipital cortex), not MPFC and TPJ. Second, while existing research finds that MPFC and TPJ regions engage both during social encoding and rest, it is possible that different underlying

neural patterns within these regions are more or less associated with these two mental events. Future research that employs multivoxel pattern analyses to rest and social encoding periods, as well as high resolution imaging, may reveal the extent to which similar or different neural populations within MPFC and TPJ support social encoding and consolidation during rest.

Conclusion

Neuroscientists have wondered for two decades why the default network is surprisingly active at rest. Our results take a step towards answering this question. Taken together, our results suggest that during rest MPFC and TPJ connectivity with one another, as well as other portions of the default network, may serve to consolidate newly acquired social information. Given the importance of learning about the social world in order to navigate it successfully, the brain may have evolved a propensity toward social learning whenever humans pause from external demands.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

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