Task-related and resting-state fMRI identify distinct networks that preferentially support remembering the past and imagining the future

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ABSTRACT

The relation between episodic memory and episodic future thought (EFT) remains an active target of research. A growing literature suggests that similar cognitive processes and neural substrates tend to support these acts. However, direct comparisons of whole-brain activity reveal clear differences, with numerous regions more active when engaging in EFT than when remembering, and a smaller collection of regions displaying the opposite pattern of activity. Although various network labels have been applied to prior neuroimaging results, to date no formal resting-state functional connectivity analysis has been conducted. In the current experiment, 48 subjects remembered events from their past and engaged in EFT. Resting-state data were collected from all subjects. Task results replicated recent findings, with more activity during EFT in regions across frontal and parietal cortex, and with more activity during remembering in a smaller number of predominantly parahippocampal and retrosplenial regions. Resting-state connectivity analysis, based on seed locations defined using the fMRI task data, indicated that regions preferentially activated during EFT fell primarily within the default mode network, while those more active during remembering fell primarily within the contextual association network. These results suggest that despite their general similarity, the functional network membership of regions showing task differences is dissociable. We discuss our results in light of several hypotheses that attempt to relate remembering and EFT, and suggest that the data speak to differences in the relative contributions of episodic and semantic memory, as well as controlled and automatic processing, during the acts of remembering or engaging in EFT.

1. Introduction

Over the past several decades, cognitive psychologists and neuroscientists have studied the degree to which the processes involved in remembering events from one's personal past (episodic memory; Tulving, 1972) are related to those involved in imagining personal events that might occur in one's future (termed "episodic future thought" (EFT); Atance and O'Neill, 2001). Since 2007, the fMRI literature has reported a largely overlapping collection of brain regions that appears to support both the reconstruction of past events and the novel construction of hypothetical future scenarios (Addis et al., 2007, 2009; Hassabis et al., 2007; Szpunar et al., 2007, 2009; see also Benoit and Schacter, 2015). This is consistent with behavioral reports suggesting that remembering and imagining share many phenomenological similarities (Tulving, 1985; D'Argembeau and Van der Linden, 2004; Szpunar and McDermott, 2008; Arnold et al., 2011; McDermott et al., 2016).

Despite the numerous similarities between remembering and EFT, differences in neural activity between the two tasks have also been widely observed. For example, regions such as the superior frontal gyrus (SFG), angular gyrus (AG), and medial prefrontal cortex (mPFC), tend to respond more strongly when participants are engaging in EFT than when they are remembering (Benoit and Schacter, 2015). These regions are associated with the brain's default mode network (DMN, Shulman et al., 1997; Raichle et al., 2001). With less frequency, cortical regions showing the opposite pattern of activity have been identified within parahippocampal cortex (PHC) and the retrosplenial complex (RSC; including retrosplenial cortex and extending posteriorly into the parieto-occipital sulcus) (Addis et al., 2009; Gilmore et al., 2016). Both PHC and RSC have been associated with a "contextual association network," (CAN) which is sensitive to how strongly associated a particular object or concept is with a given (typically spatial) context (e.g.,

Bar and Aminoff, 2003; Aminoff et al., 2007).

It therefore appears that regions within the DMN preferentially support EFT, whereas regions within the CAN support the remembering of past events. However, this hypothesis relies upon observations from task-related fMRI experiments. A more direct test would—within a single set of participants—use both task-related fMRI and resting-state functional connectivity (RSFC) MRI. This would allow for network-level properties of task-defined regions to be characterized. The DMN and CAN have been identified separately in multiple different research groups in large-scale RSFC analyses (e.g., Doucet et al., 2011; Power et al., 2011; Yeo et al., 2011; Shirer et al., 2012) as well as in analyses of highly-sampled individual subjects (Laumann et al., 2015). It therefore seems reasonable to hypothesize that the apparent distinction in network memberships of regions preferentially activated by remembering or EFT could be corroborated using RSFC within a single group of subjects.

There were two goals in the present study. One was to replicate findings that remembering activates the CAN more strongly than EFT. Additionally, we sought to directly assess the network membership of regions differentially active during remembering or EFT using RSFC. In order to accomplish both of these goals, subjects underwent fMRI while retrieving episodic memories from their pasts or imagining events in their personal futures. Resting-state scans were collected for each subject prior to the start of the experimental task. If remembering and EFT are preferentially supported by distinct networks, then they would be expected to exhibit distinct patterns of connectivity during rest. In particular, regions showing greater activity during remembering should produce correlation maps strongly reflective of the CAN, whereas regions showing the opposite pattern should exhibit resting state correlations with the DMN. Across a cohort of 48 subjects, we replicated the differences observed previously in PHC and RSC, and also found a clear segregation of connectivity patterns for regions associated with remembering or with EFT.

2. Materials and methods

2.1. Subjects

All subjects were recruited from Washington University in St. Louis and the surrounding area, and were right-handed, neurologically healthy, native English speakers, with normal or corrected-to-normal vision. Informed consent was obtained from all subjects in accordance with standard Washington University human research practices. Subjects were paid $25/h for their participation.

Fifty-seven subjects were recruited for the present experiment. Of these, 3 were excluded for excessive movement, 1 for failing to comply with task instructions, and 5 for failing to reach performance criteria (as determined by a post-scan questionnaire, described below). The remaining 48 subjects[1] included 25 females and had a mean age of 21.9 years (range: 18–36). Due to within-scan movement, one scan was excluded from each of three different subjects.

2.2. Stimuli

Task stimuli consisted of 144 words and short phrases, identical to those reported by Gilmore et al. (2016). These stimuli depicted common objects (e.g., bicycle), locations (e.g., post office), and

[1] The present experiment was actually run as two separate experiments (N = 24 in each). Data from the first cohort suggested that differences might have been present during the task orientation cue period (see below). We therefore doubled the number of trials per subject and tested another 24 individuals, at which point it became clear that orientation cue differences were minimally present (discussed in Supplemental materials, see also Supplemental Fig. 1, Supplemental Table 1). As the only difference between groups was the number of experimental task scans (3 vs. 6), the data from all 48 subjects were combined in the present report.

activities (e.g., ordering dessert), and ranged from 6 to 25 characters in length (mean length = 13.2 ± 4.5 characters). Stimulus presentation was counterbalanced such that a given word was equally likely to appear in each condition across subjects. All stimuli, including the fixation crosshair shown between task trials and during the resting-state scan, were presented in 48-point Arial font.

2.3. Task design

Subjects were asked on a trial-by-trial basis to envision a specific scenario in response to one of three different types of task orientation cues (Fig. 1A). These orientation cues directed subjects to either remember a specific event that occurred in their own past (REMEMBER), imagine a specific event that might occur in their own personal futures (FUTURE), or imagine President Barack Obama participating in a specific event (OTHER). The OTHER condition was not of primary interest in this report, but comparisons between it and the REMEMBER and FUTURE conditions are presented in Supplemental materials (Supplemental Fig. 7). Subjects saw each orientation cue for 2.5 s (1 TR), during which time they were to turn their attention to thinking about events in their past, their future, or about President Obama, as indicated by each orientation cue. Cues were presented in the center of the screen, and subjects were shown 10 of each type of cue per scan.

On 80% of the trials (24/scan), the orientation cue was followed by an event probe (i.e., a short word or phrase meant to help them form a given scenario mentally, e.g., LOTTERY). This probe was presented for 10 s (4 TRs), and replaced the orientation cue in the middle of the screen. Trials in which the orientation cue was followed by the event probe are referred to as compound trials; trials ending after the orientation cue are partial trials. During the event probe subjects were instructed to remember or imagine, as appropriate, an event related to the word or phrase being presented. Subjects were told that each envisioned event should be unique (i.e., should not be repeated), should be specific in time and place, and should be thought about for the full duration of a trial. Fixation crosses appeared in the center of the screen at the end of each trial for a variable period of 2.5–7.5 s to introduce temporal jitter. Subjects were instructed that upon seeing a fixation cross, they should clear their mind, relax, and await presentation of the next orientation cue.

The remaining 20% of the experimental trials (6/scan run) were partial trials (Ollinger et al., 2001a, 2001b). In these trials, subjects saw the orientation cues as usual, but no event probe was presented. Instead, a fixation crosshair immediately followed the orientation cue. The partial trials allowed for separation of the blood oxygen level-dependent (BOLD) response associated with orientation cue presentation from that associated with event probe presentation. This manipulation enabled us to focus on activity related to the task of interest (i.e., remembering or imagining) without contamination from possible trial-orientation signals. A ratio of 20% partial trials to 80% compound trials provides enough observations to model each event type, without making partial trials so frequent that they will be anticipated by subjects (for validation, see Ollinger et al., 2001a).

Prior to the start of the episodic task, a resting-state scan of approximately 8 min duration was collected for every subject, in which they passively fixated on a crosshair in the middle of the screen. In addition, after completing the episodic task but prior to exiting the scanner, all subjects completed a separate task that will not be focused on in this report. For half of the subjects (n = 24; those contributing three experimental scan runs) this was an unrelated recognition memory task, which lasted approximately 20 min. For the remaining half, this separate task was another 8-min resting scan. To equate as well as possible the contribution of all 48 subjects to the resting-state analyses, only data from the first rest scan are included in the current report.

After exiting the scanner, all subjects provided phenomenological ratings for each event they had thought about in the scanner.
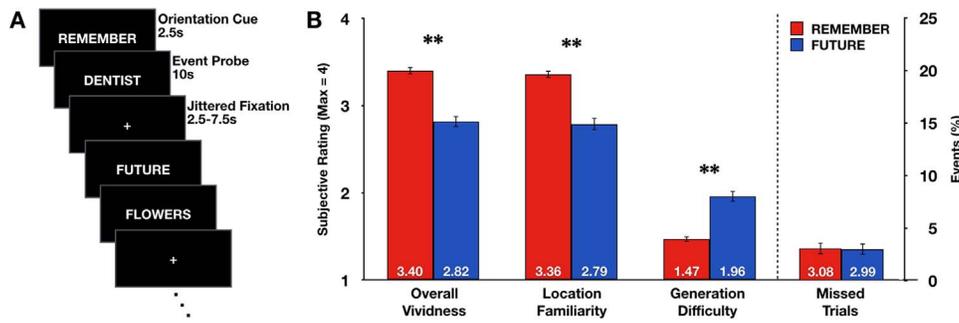
Fig. 1. Experimental design and behavioral results. (A) Subjects were presented with orientation cues for 2.5 s, followed by event probes for 10 s. A centrally located crosshair was presented for 2.5–7.5 s of jittered fixation following each trial. (B). Phenomenological report data taken from the post-scan questionnaire. Remembered events (red bars) were rated as more vivid, as having occurred in more familiar locations, and as being less difficult to generate than imagined future events (blue bars). No differences between conditions were observed in the number of events subjects missed through failing to generate an event. Error bars represent *SEM*. **p < .001.

Specifically, they rated on a 1–4 scale how vivid each event had been (1 = not at all vivid; 4 = extremely vivid), how familiar the location of the event had been (1 = not at all familiar; 4 = extremely familiar), and how difficult it had been for each event to come to mind (1 = not at all difficult; 4 = extremely difficult). During this time, subjects were also asked to identify any event probes for which no specific event had come to mind. Such trials were scored as "missed trials" and these did not contribute to a subject's phenomenological rating average. Subjects who reported missing more than 10% of trials were excluded from any analyses we report here. Differences in phenomenology ratings between conditions are reported using paired-samples *t*-tests. Effect sizes are reported using Cohen's *d*, and are adjusted to account for the correlation between paired samples (Cohen, 1988).

2.4. fMRI data acquisition

Foam pads and a thermoplastic mask (fastened to the head coil) helped stabilize head position. For 5 subjects, no masks were available. For these subjects, foam pads and medical tape helped subjects remain still. These subjects did not display abnormal amounts of movement as compared with other subjects. All images were obtained with a Siemens MAGNETOM Tim Trio 3.0 T Scanner (Erlangen, Germany) using a Siemens 12-channel Matrix head coil. A T1-weighted sagittal MPRAGE structural image was obtained for each subject (TE = 3.08 ms, TR (partition) = 2.4 s, TI = 1000 ms, flip angle = 8°, 176 slices with 1 × 1 × 1 mm voxels; Mugler and Brookerman, 1990). A T2-weighted turbo spin echo structural image (TE = 84 ms, TR = 6.8 s, 32 slices with 2 × 1 × 4 mm voxels) in the same anatomical plane as the BOLD images was also obtained to improve alignment to an atlas. Gradient field maps were collected to estimate inhomogeneities in the magnetic field for each subject. An auto-align pulse sequence protocol provided in the Siemens software was used to align the acquisition slices of the functional scans parallel to the anterior commissure-posterior commissure (AC-PC) plane. Slices collected were therefore parallel to the slices in the Talairach atlas (Talairach and Tournoux, 1988). Functional imaging was performed using a BOLD contrast sensitive gradient echo-planar sequence (TE = 27 ms, flip angle = 90°, in-plane resolution = 4 × 4 mm). Whole brain EPI volumes (MR frames) of 32 interleaved, 4 mm-thick axial slices were obtained every 2.5 s. The first 4 functional images of each scan were discarded to allow for T1 equilibration effects.

MRI-compatible headphones dampened scanner noise and enabled communication with subjects. An Apple iMac computer (Apple, Cupertino, CA) running PsyScope software (Cohen et al., 1993) was used for display of visual stimuli. An MRI compatible fiber optic key-press device recorded the subjects' in-scanner responses. An LCD projector (Sharp model PG-C20XU) was used to project stimuli onto a MRI-compatible rear-projection screen (CinePlex) at the head of the bore, which the subjects viewed through a mirror attached to the coil (field of view = 21° of visual angle).

2.5. Data preprocessing

Imaging data from each subject were pre-processed to remove noise

and artifacts using a standard lab protocol, including temporal re-alignment using sinc interpolation of all slices to the temporal midpoint of the first slice to account for differences in slice time acquisition; correction for movement within and across scans using a rigid-body rotation and translation algorithm (Snyder, 1996); gradient field map correction using FSL's FUGUE (http://fsl.fMRIb.ox.ac.uk); and whole brain voxelwise normalization to a common mode intensity of 1000 to allow for comparisons across subjects (Ojemann et al., 1997). Functional data were then resampled into 3 mm isotropic voxels and transformed into stereotaxic atlas space. This involved aligning each subject's T1-weighted image to a custom atlas-transformed (Lancaster et al., 1995) target T1-weighted template (711-2C) using a series of affine transforms (Michelon et al., 2003).

2.6. GLM-based fMRI data analysis

Task scans for each subject consisted of 185 frames (189 before discarding the first 4 frames of each scan) and were concatenated into a single time series for each subject (totaling 555 or 1110 frames, adjusted accordingly for subjects with specific scans excluded). Data from the concatenated scans were analyzed using a general linear model (GLM; Friston et al., 1994; Miezin et al., 2000), in which the data for each time point in each voxel are treated as the sum of all effects present at that time point. The time course of activity for effects in each condition was modeled as a set of delta functions following the onset of each coded event (Ollinger et al., 2001a, 2001b). This approach assumes that all events associated with a specific condition evoke the same BOLD response, but makes no assumptions about the shape of that response. Regressors reflect distinct task conditions as well as effects of non-interest, the specifics of which are discussed below.

2.7. GLM coding

For each subject the GLM was coded with 6 separate task regressors: orientation cue components for the REMEMBER, FUTURE, and OTHER conditions, and event probe components for these conditions. Trialwise behavioral covariates (vividness, familiarity, and difficulty) derived from the post-scan questionnaire were not included in the analysis reported here. Our conclusions did not change in models in which these covariates were included. Partial trials were modeled only as orientation cues of the appropriate event type, and compound trials included regressors for both orientation cues and event probes. Specifically, the orientation cue was modeled at the onset of the trial, and the event probe was modeled as beginning 1 TR later, consistent with how trials were presented to subjects. Two additional regressors of non-interest were included for each run: a trend term to account for linear changes in signal and a constant term to model the baseline signal. Consistent with prior partial trial experiments, both partial trial and compound trial orientation cues for each condition were treated as a single trial type in the model, and were combined in this way because subjects had no way of determining in advance whether or not a given cue was going to be followed by an event probe (for related discussion, see Wheeler et al., 2006).

The orientation cue regressors were modeled over 11 time points, and the event probe regressors were modeled over 10 time points. The incorporation of temporal jitter between trials, combined with the partial trials, provided a sufficient number of independent equations to separately model the BOLD response for orientation cue and event probe timecourses for each condition (Ollinger et al., 2001a, 2001b). The separate modeling was intended to let us examine activity that could specifically be attributed to remembering and imagining per se, and event cue activity is not considered further in this report.

Image processing was performed using in-house software (FIDL) written in IDL (Research Systems, Inc.). All atlas coordinates were converted from 711-2C to MNI152 space using software written by Avi Snyder and are reported in MNI152 space throughout this report. For display purposes, statistical maps were projected onto a partially inflated surface representation of the human brain using Connectome Workbench software (Marcus et al., 2011).

2.8. t-test parameters & ROI definition

We conducted a voxelwise *t*-test (paired samples, two-tailed) of the REMEMBER and FUTURE event probe conditions. Activity estimates used in the comparison were determined by aggregating activity across the 4th and 5th time points (7.5–12.5 s) following the event probe. These time points were chosen based on peak response periods identified in prior studies (Szpunar et al., 2007, 2009; Addis et al., 2009; Gilmore et al., 2016). The resulting image (presented in Fig. 2) was smoothed using a spherical Gaussian kernel with a 6 mm FWHM and corrected for multiple comparisons to achieve a whole-brain family-

wise error rate of $p < .05$. This correction process was based on prior Monte Carlo simulations (McAvoy et al., 2001) and retained voxels with a $z > 2.5$ that were contiguous with at least 34 other such voxels. Overlaid upon this statistical image were the DMN and CAN boundaries as defined by the Yeo et al. (2011) 17-network parcellation (network numbers 16 and 15, respectively).

An automated peak-finding algorithm (peak_4dfp) written by Avi Snyder located the local maxima for each cluster in the group *t*-test image. If multiple peaks were identified within a 10 mm radius of one another, these were averaged together in a subsequent processing step. ROIs were then created by centering a 10 mm sphere, masked by the multiple comparison corrected image, about the coordinates identified by the algorithm (Table 1). Peaks located in CSF were excluded from analysis.

2.9. Resting-state functional connectivity analysis

Resting-state scans consisted of 189 frames in total (the first 5 frames of which were excluded). Initial preprocessing was conducted in the same manner as the task-evoked data described above.

Following this initial preprocessing, data were prepared for functional connectivity analysis using techniques described by Power et al. (2013). Briefly, these steps included a multiple regression of ventricular signal, white matter signal, and global gray matter signal as well as 6 detrended head motion realignment parameters and their temporal derivatives; a band-pass filtering ($.009 < f < .08$ Hz); and spatial smoothing using a 6 mm FWHM kernel. Ventricle, white matter, and gray matter masks were created using Freesurfer (http://surfer.nmr.
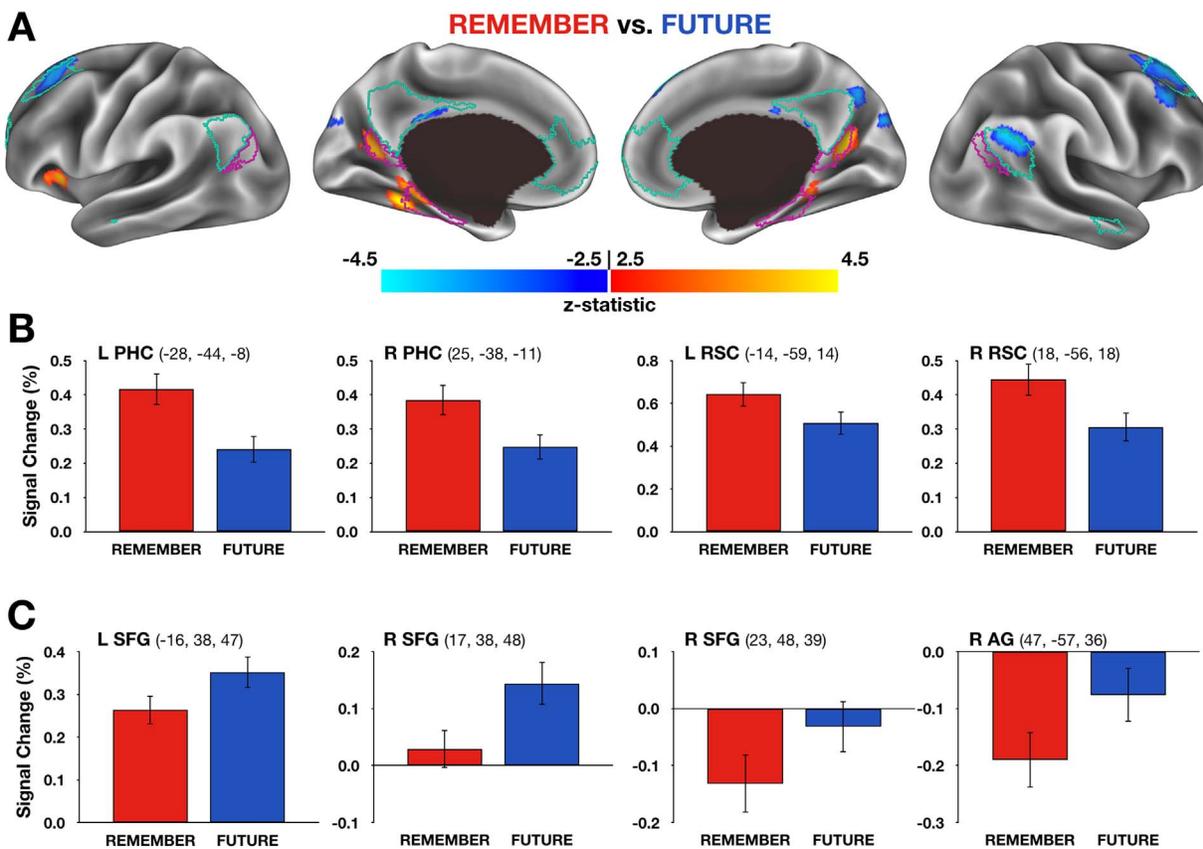

Fig. 2. Voxelwise results of different task conditions during remembering and imagining. (A) A *t*-test (paired samples, two-tailed) identified voxels whose activity differed between the two conditions. Warm colors were more active in the REMEMBER condition, and cool colors were more active in the FUTURE condition. REMEMBER > FUTURE regions fall primarily within regions of PHC and RSC, while regions showing FUTURE > REMEMBER activity are more widespread, including regions of the SFG, MFG, and AG. Borders from the default mode network and contextual association network (taken from Yeo et al. (2011) 17-network parcellation) are overlaid on the voxelwise image in light blue and magenta, respectively. (B) Example response magnitudes derived from local maxima identified in the voxelwise analysis that show REMEMBER > FUTURE effects in red and blue colors, respectively. (C) Response magnitudes derived from local maxima showing FUTURE > REMEMBER effects. Statistical maps are shown on a partially inflated surface rendering of the human cortex using Connectome Workbench software (Marcus et al., 2011). Coordinates are listed in MNI152 space. Error bars denote *SEM*.

Table 1

Regions exhibiting different activity during remembering the past and engaging in episodic future thought (*t*-test of REMEMBER – FUTURE conditions, aggregating activity over time points 4 + 5).

Region	Peak MNI coordinate (x, y, z)			z-statistic
Future > Remember				
Right superior frontal gyrus	23	48	39	3.02
Right superior frontal gyrus	17	38	48	3.88
Left superior frontal gyrus	−16	38	47	3.12
Left middle frontal gyrus	−28	28	45	2.84
Right middle frontal gyrus	36	22	45	3.33
Right middle frontal gyrus	27	19	55	2.75
Mid-cingulate cortex	0	−26	25	3.18
Left cerebellum	−44	−49	−28	4.37
Left cerebellum	−27	−67	−33	3.00
Right angular gyrus	47	−57	36	4.04
Right cerebellum	34	−64	−33	3.44
Right precuneus	8	−71	42	3.45
Left cuneus	−1	−79	34	2.64
Left cuneus	−8	−90	31	3.35
Right cuneus	7	−85	30	3.87
Remember > Future				
Left anterior insula/frontal operculum	−33	34	−6	3.22
Left anterior insula/frontal operculum	−33	22	−1	4.04
Left anterior parahippocampal cortex	−16	−35	−13	3.85
Left posterior parahippocampal cortex	−28	−44	−8	5.14
Right parahippocampal cortex	25	−38	−11	3.47
Right retrosplenial complex	18	−56	18	4.22
Left retrosplenial complex	−14	−59	14	4.36

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Data were motion scrubbed (Power et al., 2012, 2014) to remove spurious correlations that were a result of subject head motion and not neuronal activity. This involved calculating frame-by-frame changes in head position and signal change, and frames exceeding relative position changes of .2 mm or signal changes of .25% were excluded. The two frames preceding and following each motion scrubbed frame were also excluded. Missing values in the time series created by the motion scrubbing were replaced by interpolating across the missing epochs. Only subjects retaining more than 130 of the original 184 possible frames (i.e., those with over 70% frame retention) were included in the RSFC analysis. Of the 48 subjects in this experiment, 42 were retained based on this requirement.

Seed correlation maps were then defined from the 19 cortical peaks identified in the episodic task analysis. Seeds were centered around peak coordinates in the REMEMBER – FUTURE contrast (showing significant differences in either direction), and were 10 mm diameter spheres, created in the same manner as task ROIs (described previously). Signal within each ROI was averaged across all included voxels and then correlated with every other voxel within the Freesurfer-defined gray matter mask, on a subject-by-subject basis. The subject-level correlation maps were converted to a *z*-map using Fisher's *r*-to-*z* transform, and averaged across subjects to produce a single group connectivity map for each seed region.

Spatial correlations were then computed in a pairwise fashion for all 19 seed maps, after which they were subjected to a hierarchical clustering analysis. The distances between each correlation map were computed by taking a 1-*r* calculation, using a shortest distance clustering algorithm in Matlab R2013b's (The MathWorks, Natick, MA) *linkage* function. Five distinct clusters emerged from this analysis, each containing between two and seven regions (Fig. 3A). A cophenetic correlation coefficient was calculated for the final dendrogram to evaluate the degree to which the clustering represented the underlying similarities among the seed maps. Correlation maps for each seed location are presented in Supplemental Figs. 3–6, and are organized by

cluster.

A summary connectivity map for each cluster was then created by averaging the maps from all ROIs within each cluster (Fig. 3B). We again took the DMN and CAN borders from the Yeo et al. (2011) 17-network parcellation and overlaid these on binarized forms of the two largest identified clusters (clusters 3 and 4) (Fig. 4A and B). We likewise placed the borders on a conjunction image of the two clusters based on their *z* > 2.5 thresholded connectivity maps (Fig. 4C).

3. Results

3.1. Behavioral data are consistent with those reported previously

After exiting the scanner, all subjects provided ratings for each event they had remembered or imagined (summarized in Fig. 1B). Overall, ratings were consistent with those obtained previously (e.g., D'Argembeau and Van der Linden, 2004; Arnold et al., 2011; Gilmore et al., 2016). Events in the REMEMBER condition were more vivid, occurred in more familiar locations, and were less difficult to generate than events in the FUTURE condition (minimum obtained *t*-value across all comparisons: $t(47) = 10.57$, $d = 2.75$, $p < .001$; obtained for the subjective difficulty rating). Importantly, subjects failed to generate very few events (~ 3% per condition), and this number did not differ between conditions, $t(47) = .13$, $d = .02$, $p = .90$.

3.2. Voxelwise analysis of REMEMBER and FUTURE conditions replicates previous experimental results

We conducted a whole-brain *t*-test (paired-samples, two-tailed) of activity associated with the REMEMBER and FUTURE event conditions. Results of this analysis are presented in Fig. 2 and Table 1. Regions showing significant FUTURE > REMEMBER activity included bilateral regions of the SFG, middle frontal gyri (MFG), right AG, bilateral cuneus (CUN), right precuneus (PCU), a section along the mid-cingulate/posterior cingulate cortex (MCC/PCC), and several regions of the cerebellum. This general pattern is consistent with results of prior studies (Addis et al., 2007, 2009; Szpunar et al., 2007, 2009; Weiler et al., 2010; Gilmore et al., 2016).

Regions showing REMEMBER > FUTURE activity were located bilaterally in PHC and RSC, as well as in the left anterior insula/frontal operculum (aI/fO). This activation pattern largely recapitulates the results of a recent similar contrast (Gilmore et al., 2016). To better quantify the apparent similarity, we calculated the Euclidian distance between corresponding voxelwise peaks in the two datasets. The peaks within left and right PHC and right dorsal RSC were an average distance of approximately 6 mm from those in our previous report, supporting the consistency of PHC and RSC region location across experiments. To further determine the consistency of REMEMBER > FUTURE responses—which are less commonly observed than FUTURE > REMEMBER effects in the literature—targeted ROI analyses of regions identified by Gilmore et al. (2016) were conducted and results are displayed in Supplemental Fig. 2. Three of the five ROIs carried forward showed significant REMEMBER > FUTURE effects, and the non-significant regions nevertheless displayed differences in the correct direction. In sum, the voxelwise REMEMBER – FUTURE contrast is consistent with that expected based on prior literature.

To better characterize the activity patterns underlying the statistical image presented in Fig. 2A, we created ROIs around voxels showing peak differences and plotted several magnitude estimates for the two conditions of interest. Regions with REMEMBER > FUTURE activity were fairly consistent in the pattern of differences observed (Fig. 2B), but the response properties of regions showing FUTURE > REMEMBER activity were variable, and included regions showing patterns ranging from deactivations to activations (Fig. 2C).

The spatial patterns associated with the REMEMBER and FUTURE conditions were reminiscent of the CAN and DMN, respectively. For
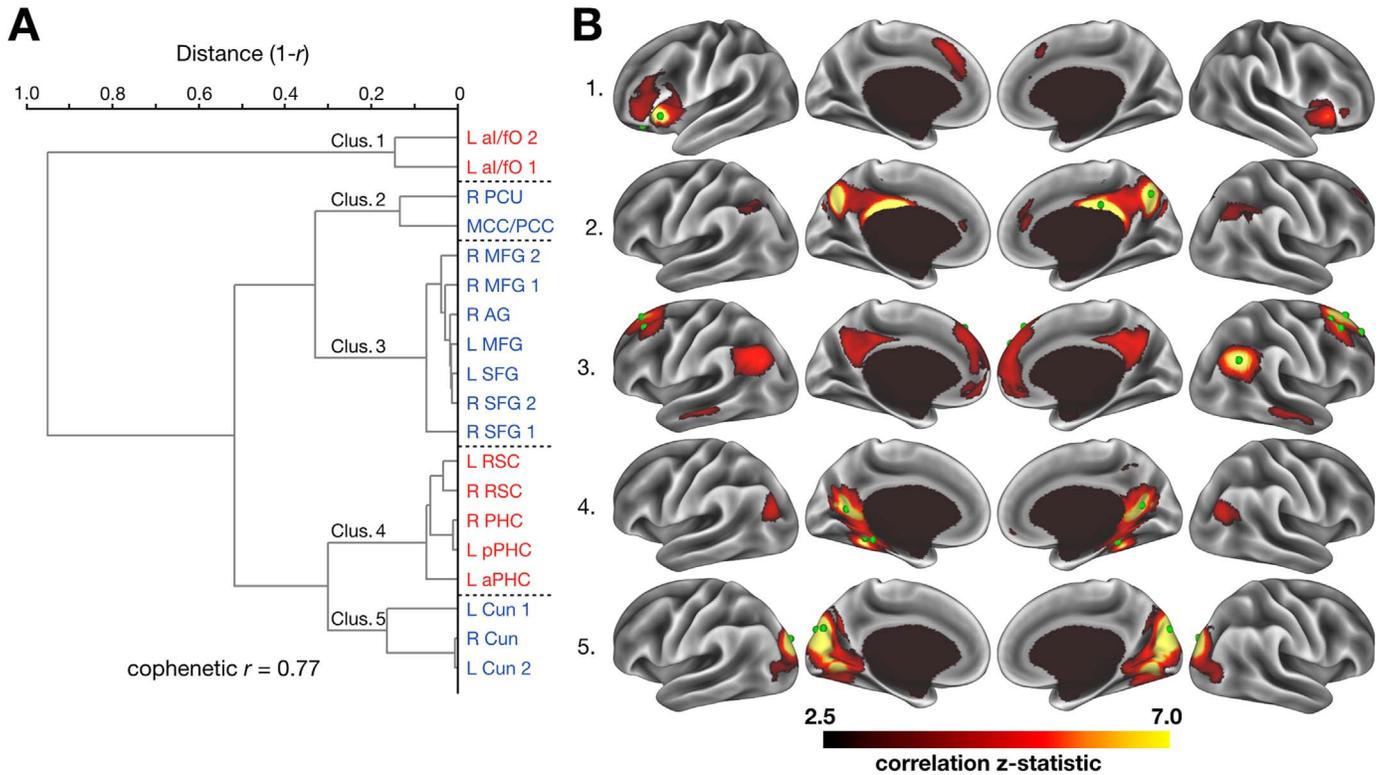
Fig. 3. Multiple distinct connectivity maps emerge from task-defined seed regions. (A) A hierarchical clustering analysis grouped seed regions into 5 clusters based on their connectivity profiles. Regions exhibiting FUTURE > REMEMBER effects during the episodic task are listed in blue, and REMEMBER > FUTURE regions are listed in red. (B) Thresholded average connectivity maps for each cluster suggest different functional network memberships. Seed locations are shown as green spheres.
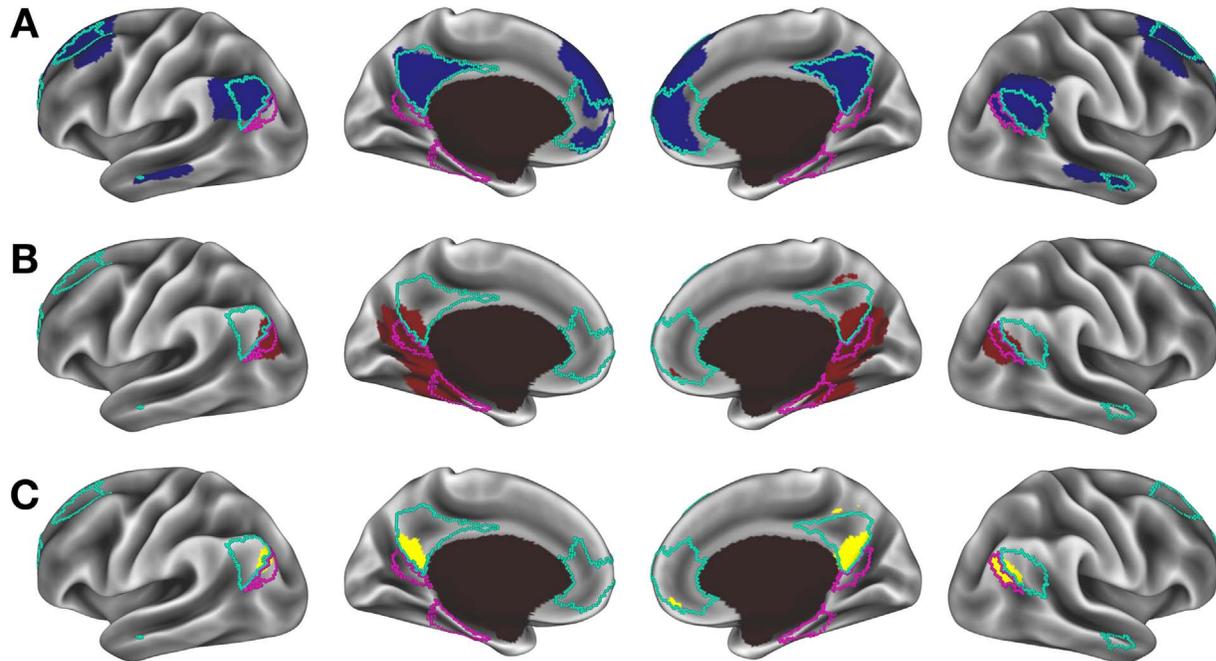

Fig. 4. Binarized connectivity maps for Cluster 3 and Cluster 4 recapitulate the DMN and CAN. (A) The average Cluster 3 connectivity map recapitulates the DMN, as estimated using the Yeo et al. (2011) 17-network parcellation. Borders of the DMN are shown in light blue. Connectivity overlap included midline regions and the left AG even though source seeds were only located in SFG, MFG, and the right AG. (B) The average Cluster 4 connectivity map recapitulates the CAN (borders shown in magenta). (C) The overlap of the two binarized connectivity maps (yellow) falls predominantly in the DMN, including mPFC, PCC, and bilateral components of the AG. With the exception of right AG virtually no overlap occurs within the CAN.

comparative purposes, independently-derived network boundaries (defined using the Yeo et al. (2011) 17-network parcellation scheme) were projected over the contrast map (Fig. 2A). One can observe that the bilateral SFG and right AG FUTURE > REMEMBER regions fell generally within (extending slightly beyond) the DMN. However, the MCC/PCC and right PCU regions appeared to straddle—yet fall outside of—the DMN's boundaries. Turning now to clusters showing RE-MEMBER > FUTURE effects, the RSC activations were well captured by the CAN boundaries, and the PHC activation fell within and extended beyond this network's boundaries. The aI/fO and CUN regions were

clearly outside of the displayed borders. Collectively, these observations provided evidence that many regions preferentially activated when remembering or engaging in EFT are segregated by network membership, consistent with similar proposals in the past which have relied on task-based analysis (Addis et al., 2009). The possibility of distinct networks preferentially being associated with remembering and EFT was explored more directly using RSFC.

3.3. Resting-state functional connectivity analysis demonstrates distinct network memberships for regions showing REMEMBER > FUTURE and FUTURE > REMEMBER activity

We conducted seed-based RSFC analysis for cortical regions showing REMEMBER > FUTURE or FUTURE > REMEMBER effects. Seeds were 10 mm diameter spheres centered around peaks identified from the voxelwise REMEMBER – FUTURE analysis. The 19 seeds were used as a basis for creating voxelwise correlation maps for each seed location (see Supplemental Figs. 3–6 for the correlation maps for each seed location).

The correlation maps for each seed location were subjected to a hierarchical clustering analysis to determine the structure of their interrelations. We found the seed maps to be segregated into five clusters (Fig. 3A). Cluster 1 consisted of the two aI/fO regions; Cluster 2 the MCC/PCC and PCU regions; Cluster 3 the SFG and MFG regions, along with the right AG; Cluster 4 the RSC and PHC regions; and Cluster 5 the CUN regions. The cophenetic correlation of the obtained dendrogram was high (cophentic $r = .77$) which suggested that the clustering solution accurately represented the underlying similarities and differences among seed correlation maps.

For each cluster, we averaged the correlation maps generated from each seed in order to create a "summary" connectivity map (Fig. 3B). As predicted by the clustering, each map appeared to capture largely distinct expanses of cortex. Clusters 3 and 4, in addition to being the largest two clusters, again bore a strong resemblance to the DMN and CAN, respectively.

Consequently, we projected the borders of the DMN and CAN from the Yeo et al. (2011) 17-network parcellation onto binarized Cluster 3 and Cluster 4 maps. We observed strong agreement between the Cluster 3 map and the DMN boundaries, including medial components such as the PCC and mPFC as well as left AG (Fig. 4A). The Cluster 4 map likewise recapitulated the CAN (Fig. 4B). When the overlap of voxels contained within Clusters 3 and 4 was directly calculated, it fell overwhelmingly within the DMN (Fig. 4C), including regions of the PCC and mPFC. This was less evident in the AG overlap regions, which covered the border between the two networks and contained voxels within each (particularly in right AG).

4. Discussion

In this work, task-based fMRI and RSFC MRI were combined to interrogate the network membership of regions preferentially activated by remembering the past or envisioning the future. We obtained two main results. First, we replicated recent experimental findings that regions in PHC and RSC exhibited significantly greater BOLD activity during remembering than EFT (Gilmore et al., 2016). In addition, RSFC analysis of regions identified in the episodic task revealed that FUTURE > REMEMBER and REMEMBER > FUTURE effects can be segregated into distinct clusters that capture distinct resting-state networks. We consider the broader implications of these results.

4.1. REMEMBER > FUTURE results are consistent with those observed previously

Numerous regions across the cortex show significantly greater activity when one is engaging in EFT than when one is remembering autobiographical events (for a recent meta-analysis, see Benoit and

Schacter, 2015), and this pattern was repeated in the current dataset. However, the reverse pattern has been observed far less frequently, so this study was an important means of replicating results reported by Gilmore et al. (2016). In a time when the reproducibility of psychological and biomedical research is often called into question (e.g., Ioannidis, 2005; Open Science Collaboration, 2015), and which has been referred to as a period of "replication crisis" (Pashler and Harris, 2015), additional testing of infrequent findings is a clear priority. In the current experiment, we collected data from a relatively large sample of 48 subjects, and replicated the REMEMBER > FUTURE pattern previously observed in CAN regions. This result was observable in both the voxelwise contrast results (Fig. 2) as well as direct comparisons in *a priori* ROIs that were taken from the Gilmore et al. (2016) dataset (Supplemental Fig. 2).

The current experiment shared some features with the one reported in Gilmore et al. (2016), such as the specific event probes provided to subjects, task trial durations, and control condition. As the goal was both replication and extension of the prior findings, there were also several differences: most notably, the current experiment featured a partial trial design that separated the temporal orientation cues (e.g., "REMEMBER" or "IMAGINE") from the event probes by 1 MR frame (2.5 s). This allowed us to model orientation-related activity separately from activity related to remembering or EFT per se, and one might have expected this to impact the results we observed when REMEMBER and FUTURE conditions were directly compared. However, this was not the case. The consistency of observations across the datasets therefore speaks to a robustness of PHC and RSC regions to the particulars of an experimental task, and provides confidence that the effects are not driven by initial attentional effects that may be unrelated to the actual processes of interest (i.e., of remembering or engaging in EFT).

REMEMBER > FUTURE effects were also observed in left aI/fO. A similar region was observed by Gilmore et al. (2016), again suggesting that effects in this direction are replicable across experimental designs. Given the strong association of aI/fO with the cingulo-opercular control network (e.g., Dosenbach et al., 2007; Nelson et al., 2010), one might hypothesize that aI/fO emerges from the contrast due to differences in task set parameters required during remembering as compared to during EFT. Clarification of the functional significance of activations in this region should be addressed in future work.

4.2. Distinct networks preferentially support remembering and EFT

An important aspect of this research was its utilization of RSFC in addition to more traditional task-based analysis. Task-defined ROIs were used as seed locations to generate resting-state correlation maps before being subjected to a hierarchical clustering. Five clusters were identified, with three clusters (2, 3, and 5) emerging from regions exhibiting a FUTURE > REMEMBER effect in the memory task, and the remaining two clusters (1 and 4) exhibiting a REMEMBER > FUTURE effect. Clusters 3 and 4 were the largest, and appeared to capture the DMN and CAN respectively (Fig. 4A and B). These will be discussed in more detail below. Additional clusters captured recognizable aspects of other networks. Cluster 1 appeared to capture a portion of the cingulo-opercular control network. Cluster 2 captured the parietal memory network (Gilmore et al., 2015). Cluster 5 appeared to capture a component of the visual system that has previously been associated with the peripheral visual field (cf. network 2 in the 17-network parcellation of Yeo et al. (2011)).

4.2.1. The default mode network supports the synthesis of disparate event details

Several hypotheses have been forwarded to describe why certain regions may be more active during EFT than during remembering. The most commonly invoked is the Constructive Episodic Simulation Hypothesis, which stresses the importance of recombining details from episodic memories into coherent events (Schacter and Addis, 2007;

Schacter et al., 2012). By this account, the greater activity associated with EFT is a product of the way in which events are mentally constructed: imagined events require the assembly of multiple disparate details from multiple disparate memories, whereas remembered events require retrieval from a single episodic trace. Thus, imagined events place greater demands on retrieval and post-retrieval processes that support the organization of the various details into a single coherent scenario.

An alternative but not mutually exclusive possibility is that differences within the DMN reflect differences in the personal relevance of different event types. We did not collect ratings of personal relevance for events in this experiment, but prior work has suggested that future events tend to be more emotional and significant (D'Argembeau and Van der Linden, 2004, 2006; Addis et al., 2007; McDermott et al., 2016) than are remembered past events. To the extent that differences in emotionality and personal significance may be responsible for some of the FUTURE > REMEMBER activity observed in DMN regions in the current experiment, this explanation would also be consistent with results reported by Andrews-Hanna et al. (2010), who found activity across numerous DMN regions to correlate linearly with the emotionality or personal significance of stimuli when judged by a group of independent raters.

4.2.2. Differences in the CAN reflect differences in the contextual strength of events

We have hypothesized previously (McDermott and Gilmore, 2015; Gilmore et al., 2016) that differences in the nature of constructed scenes are responsible for different patterns of activity in PHC and RSC regions. Articulated in the Contextual Association Hypothesis, we posited that remembered events are typically more contextually rich than are imagined future events, given that the former occurred by definition in a single context whereas the latter must be newly generated by drawing from multiple contextual sources. This results in more vivid, clearly organized "backdrops" for events that are remembered as compared to imagined (Fig. 1; see also Johnson et al., 1988; D'Argembeau and Van der Linden, 2004; Szpunar, 2010; Arnold et al., 2011). In addition to producing phenomenological differences, the strength of associations between details within an event is also reflected in the REMEMBER > FUTURE pattern we observed in PHC and RSC. In effect, we argue that the same processes responsible for producing differences in activity between weakly and strongly contextualized (Bar and Aminoff, 2003; Aminoff et al., 2007) and more or less permanent objects (Auger et al., 2012) also result in the CAN's sensitivity to the mnemonic status of an event. Further, given that differences are observed when passively viewing stimuli (Bar et al., 2008), activity evoked within CAN regions is likely generated in a largely automatic manner, and likely reflects semantic knowledge of the world (for related discussion, see Binder et al., 2009; Schacter et al., 2012). An updated depiction of the contextual association hypothesis and how we believe remembering and EFT may differ is presented in Fig. 5.

4.2.3. Understanding network differences in view of different construal levels

A common framework for understand how events are mentally represented is Construal Level Theory (CLT; Liberman et al., 2002; Trope and Liberman, 2010). Within this framework, events that are more "psychologically distant" (e.g., those viewed as more hypothetical, as farther away in time, or as involving people or places with which one is less familiar) are "construed" at a more abstract level than those events perceived to be less "distant." To the extent that imagined future scenarios are construed as more psychologically distant, the results of the present study appear to support predictions from CLT, and this is particularly notable in the phenomenological reports: remembered events were more vividly experienced (suggesting they were less abstractly depicted), and occurred in more familiar places (which could imply less psychological distance) than were imagined future events (Fig. 1B).

4.3. A possible distinction between automatic and controlled processing in remembering and imagining

In the preceding sections of the discussion, we suggested that activity within the DMN may reflect difficulty in assimilating different details into a single event (echoing ideas forwarded in the Constructive Episodic Simulation Hypothesis), whereas activity within the CAN is reflective of contextual-associative strength (as stated in the Contextual Association Hypothesis). One can observe that the Constructive Episodic Simulation Hypothesis emphasizes *controlled* processing, by asserting that imagining requires more top-down processing than remembering. In contrast, the Contextual Association Hypothesis emphasizes differences in *automatic* processing. That is, differences observed in PHC and RSC activity are thought to be driven by differences in the "background" features of remembered or imagined events, which tend to be richer for remembered events.
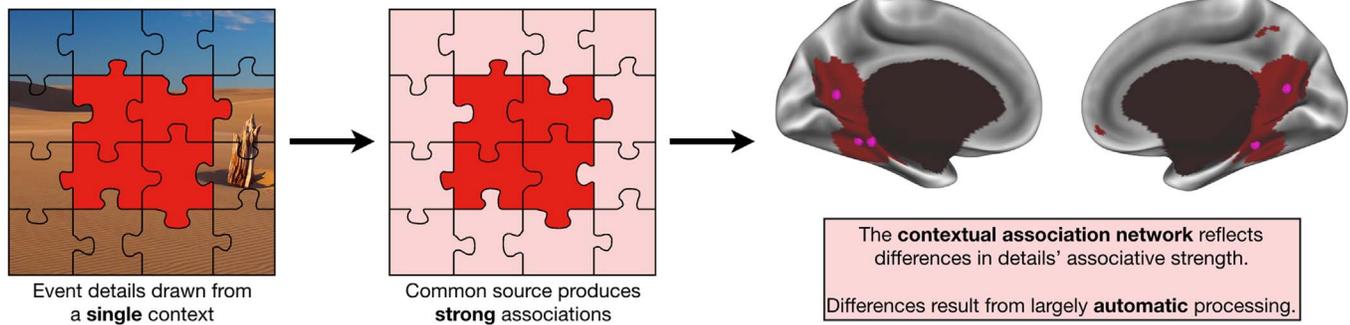
Distinctions between the automatic and controlled nature of retrieval processes as they relate to remembering and imagining have been remarked upon previously (Anderson, 2012; see also Schacter et al., 2012), and may be useful in separating different network contributions to remembering and EFT. Future research that is cognizant of network (and subnetwork) memberships appears to be a promising avenue by which we can better understand how functional networks support (or do not support) our ability to use information from our pasts to imagine hypothetical events in our future.

4.4. The parietal memory network, but not the frontoparietal control network, is more active during EFT than during remembering

Results of the FUTURE > REMEMBER contrast identified several regions outside of the DMN, including regions in MCC/PCC and the PCU. As was recently noted by Benoit and Schacter (2015), both of these regions are among those most reliably associated with FUTURE > REMEMBER patterns of activity. However, as was also noted by Benoit and Schacter, the network memberships of these regions can be somewhat ambiguous; in coarse network solutions such as the 7-network parcellation offered by Yeo et al. (2011), these regions appear to straddle both the DMN and frontoparietal control network (FPCN). However, in finer-grained solutions these regions form a separable network consisting of MCC/PCC, PCU, and a region of the posterior inferior parietal lobule/dorsal AG (Doucet et al., 2011; Power et al., 2011; Yeo et al., 2011; Shirer et al., 2012). Similarly, in the current experiment the correlation maps of the MCC/PCC and PCU regions formed a separate cluster that also included portions of the dorsal AG (Fig. 3, Supplemental Fig. 3). This small network has only recently been described and was given the label of the "parietal memory network" ("PMN;" Gilmore et al., 2015). None of the other clusters that emerged resembled the FPCN (Fig. 3), despite the general agreement between locations of FUTURE > REMEMBER effects in non-DMN regions in the Benoit and Schacter (2015) meta-analysis and the current dataset. Consequently, we cannot endorse a strong association between the FPCN and EFT.

Why might the PMN exhibit greater activity during EFT than during remembering? Preliminary evidence suggests the PMN to be important for orienting to the novelty or familiarity of a visual stimulus (Gilmore et al., 2015; for related evidence see Rosen et al., 2016). Typically, regions within the PMN deactivate in the presence of novel stimuli and activate above baseline levels for familiar stimuli (Nelson et al., 2013). Further, the degree to which a stimulus captures one's attention seems to lead to greater deflections from baseline in PMN regions (O'Connor et al., 2010; Jaeger et al., 2013). One might therefore speculate that remembered and imagined events may differentially capture one's attention as a result of the differences in their phenomenological qualities. Features such as personal significance and emotionality—both of which are typically greater for future events—may drive some of the difference in activity, through differences in the degree of attentional

Remembered Events

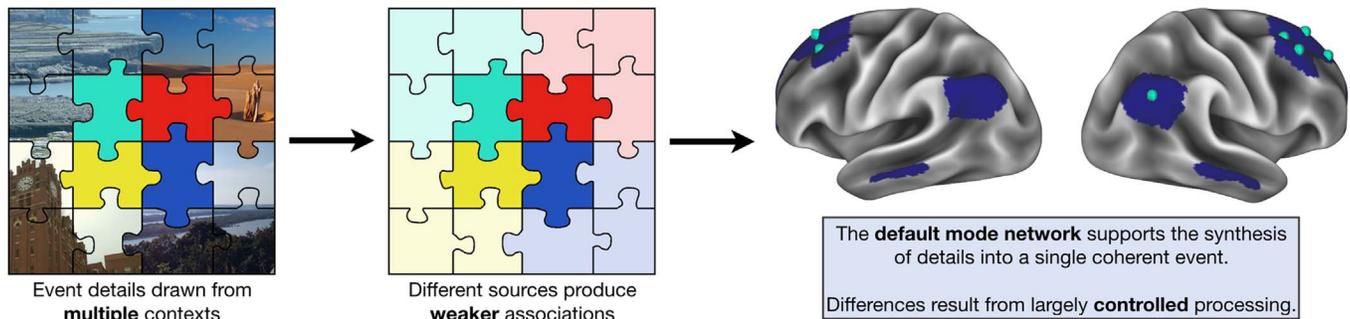Event details drawn from
a **single** context

Common source produces
strong associations

The **contextual association network** reflects differences in details' associative strength.

Differences result from largely **automatic** processing.

Imagined Events

Event details drawn from
multiple contexts

Different sources produce
weaker associations

The **default mode network** supports the synthesis of details into a single coherent event.

Differences result from largely **controlled** processing.

Fig. 5. Schematic depiction of the contextual association hypothesis. Remembered and imagined events differ in the number of sources utilized in their creation. Multiple sources are required for imagined future events, which increases the relative difficulty of detail synthesis. This increase is reflected in greater activity across numerous default mode network regions. The difference in information sources also leads to differences in the strength of association among event details, with the components of remembered events being more strongly associated. The contextual association network becomes more activated during remembering than episodic future thought as a result of stronger associations.

capture associated with mental imagery. We stress however that we lack the data to examine this possibility at present. Future work will need to focus on exactly what processes are causing this network to emerge in studies of episodic memory and EFT, especially given the consistency of PMN regions in showing a FUTURE > REMEMBER pattern of activity. It will also be important for future research to more carefully separate DMN, PMN, and FPCN regions within experimental task data, as conflation of these networks will lead to confusion regarding the functional contributions of each.

4.5. Concluding remarks

The present study combined task-based fMRI and RSFC approaches to clarify the network membership of regions associated with remembering and EFT. We replicated previous fMRI findings suggesting that remembering and EFT evoke preferential activity in distinct sets of regions, and demonstrated using RSFC analysis that the segregation of these activities appeared largely to adhere to known network boundaries. This distinction provides novel insight into the functional properties of several networks and highlights the utility of using task-based fMRI data to guide questions about the large-scale network organization within the human brain.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2017.06.016.

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