



Research report

Intrinsic medial temporal lobe connectivity relates to individual differences in episodic autobiographical remembering



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ABSTRACT

People vary in how they remember the past: some recall richly detailed episodes; others more readily access the semantic features of events. The neural correlates of such trait-like differences in episodic and semantic remembering are unknown. We found that self-reported individual differences in how one recalls the past were related to predictable intrinsic connectivity patterns of the medial temporal lobe (MTL) memory system. A pattern of MTL connectivity to posterior brain regions supporting visual-perceptual processing (occipital/parietal cortices) was related to the endorsement of episodic memory-based remembering (recalling spatiotemporal event information), whereas MTL connectivity to inferior and middle prefrontal cortical regions was related to the endorsement of semantic memory-based remembering (recalling facts). These findings suggest that the tendency to engage in episodic autobiographical remembering is associated with accessing and constructing detailed images of a past event in memory, while the tendency to engage in semantic autobiographical remembering is associated with organizing and integrating higher-order conceptual information. More broadly, these findings suggest that differences in how people naturally use memory are instantiated through distinct patterns of MTL functional connectivity.

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1. Introduction

Remembering in a naturalistic context is different than remembering laboratory-based stimuli, both in terms of behavior (Conway, 1991) and patterns of brain activity (McDermott, Szpunar, & Christ, 2009). The neural processes that underlie individual differences in performance on standard memory laboratory tasks have been well studied (Alkire, Haier, Fallon, & Cahill, 1998; King, de Chastelaine, Elward, Wang, & Rugg, 2015; Wang et al., 2010). Despite a growing interest in how memory occurs in naturalistic contexts, due in part to the discovery of the brain's default mode network (DMN; Fox & Raichle, 2007; Raichle & Snyder, 2007) and its connection to autobiographical information (Philippi, Tranel, Duff, & Rudrauf, 2015; Spreng & Grady, 2010), less is known about the neural correlates of individual differences in the way people naturally remember.

Identifying trait-like differences in mnemonic style is critical for understanding how information about the past is accessed and constructed, as the manner in which people retrieve past events shapes one's subjective experience and constrains the content of what is recalled (Klein, 2015). For example, the fluent recovery of sensory details from specific events, such as vividly recollecting the soft baguette and creamy cheese from a dinner eaten on a recent trip to Paris, promotes a rich experience of recollection. Conversely, reflecting on the knowledge that one enjoyed Paris and was impressed by the food focuses recall at an implicational level as opposed to reliving or simulating event details. These modes of remembering, which parallel episodic and semantic long-term memory (Tulving, 2002), can be conceptualized and assessed as orthogonal traits reflecting stable individual differences in subjective mnemonic experiences (Palombo, Williams, Abdi, & Levine, 2013). In the present study, we tested the hypothesis that these traits, reflecting how individuals access and experience past personal information, are related to the intrinsic connections of memory-specific brain regions within the DMN.

This hypothesis is built upon a model in which autobiographical memories are accessed from a hierarchical knowledge structure, from life time periods to general events to event-specific knowledge (Conway & Loveday, 2015; Conway, Meares, & Standart, 2004; Conway & Pleydell-Pearce, 2000). We suggest that the tendency for robust episodic remembering (vividly recalling specific event details) entails accessing this hierarchy in a fundamentally different way (i.e., more specific or directed retrieval) than the tendency to access information at more abstract, higher levels in the hierarchy. Individual differences in this tendency to access information via direct or higher-level abstracted routes will be reflected in intrinsic patterns of brain connectivity that correspond to medial temporal lobe (MTL) neural networks that support episodic versus semantic processes, respectively.

We based our hypothesis on two sets of findings. First, individual differences on a variety of cognitive factors, including those measured via subjective reports, have been linked to variations in on-task functional networks (Kirchhoff & Buckner, 2006; Miller, Donovan, Bennett, Aminoff, & Mayer, 2012; Miller et al., 2002) and in resting-state networks (Fox &

Raichle, 2007) for domains ranging from perception to cognitive style (Baldassarre et al., 2012; Hao et al., 2013; King et al., 2015; Koyama et al., 2011; Seeley et al., 2007; Wang et al., 2010; Xu et al., 2014). Thus, intrinsic connectivity is a viable marker for variability in skills, experience, and subjective ability, and can provide valuable insight into the link between cognition and the brain (Stevens & Spreng, 2014).

Second, individual differences in memory performance, as measured by laboratory tests, are reflected in the activity and connectivity of the MTL (e.g., Alkire et al., 1998; King et al., 2015; Shapira-Lichter, Oren, Jacob, Gruberger, & Hendler, 2013; Wang et al., 2010), a hub for mnemonic processing within the DMN (Buckner, Andrews-Hanna, & Schacter, 2008; Rugg & Vilberg, 2013) and autobiographical memory network (Spreng, Mar, & Kim, 2009). We used these studies to make predictions about the relationship between MTL connectivity and how individuals access memory content for naturalistic experiences.

To measure individual differences in mnemonic traits, we used the Survey of Autobiographical Memory (the SAM; Palombo et al., 2013), a well-validated self-report measurement of the tendency to engage in distinct forms of remembering (see the Method sections for measures of SAM validity). The SAM provides composite scores that relate to the tendency to access and experience autobiographical knowledge via episodic or semantic routes, which we related to patterns of MTL connectivity obtained from the resting-state scans in 66 individuals. If episodic remembering is underscored by the reinstatement or simulation of past events in terms of contextual details or event specific information (Conway & Pleydell-Pearce, 2000), then episodic SAM scores should be associated with intrinsic MTL connections to posterior brain regions that support the recovery and integration of sensory-perceptual details (Greenberg, Eacott, Brechin, & Rubin, 2005; Greenberg & Rubin, 2003). We tested the specificity of this association by including the SAM semantic scale, which reflects the tendency to recall events in terms of their abstract implications and facts. Since semantic remembering does not rely on imagery or vivid recollective processing to the same extent as episodic remembering, we predicted that MTL connectivity to posterior perceptual brain areas would be preferentially associated with our measure of trait episodic remembering. In contrast, we anticipated that differences in semantic remembering would relate to MTL connections to regions involved in conceptual integration and monitoring, such as the inferior frontal and temporal cortices (Achim & Lepage, 2005; Burianova & Grady, 2007).

2. Materials and methods

2.1. Participants

Sixty-nine healthy adults (average age = 24 years, SD = 4.7, range = 18–41 years; average education = 16 years, SD = 2.8, range = 12–27 years; 16 male; 56 right-handed; 3 removed due to excessive movement or incomplete SAM questionnaire) participated in two related studies of memory ($N_1 = 27$, $N_2 = 39$), from which the resting state brain scans (collected prior to any task) are combined here. All participants were free

from significant physical or mental illnesses, gave informed consent in accordance with the institutional ethical guidelines, and received compensation for their participation.

2.2. Mnemonic traits

Self-reported mnemonic traits were measured in a separate test session with the SAM (Palombo et al., 2013). The SAM contains 102 items. Participants rated the extent to which an item (statement) described their overall memory ability on a 5-point Likert scale. Weighted sums of the items produced factor scores for self-reported autobiographical episodic memory (42 items), semantic memory (24 items), spatial memory (20 items), and future thinking (16 items) abilities, with a mean of 100 and a standard deviation of 15 (n.b., a shorter [26-item] version of the SAM is available). The present analysis focused on episodic and semantic memory factor scores (in the tested sample, episodic scores: average = 99, SD = 15, range = 79–128; semantic scores: average = 101, SD = 13, range = 82–127). Whereas the episodic memory component of the SAM includes questions that target one's ability to remember specific event and contextual details (e.g., "When I remember events, in general I can recall people, what they looked like, or what they were wearing"; "When I remember events, in general I can recall objects that were in the environment"), the semantic memory component includes questions that target one's ability to recall facts or knowledge about oneself, events, and the world (e.g., "I can learn and repeat facts easily even if I don't remember where I learned them from"; "After I have met someone once, I easily remember his or her name").

The SAM episodic and semantic subscales relate to other measures of autobiographical memory in predictable ways. In the original study, SAM episodic scores (but not semantic scores), were reduced in participants with a history of depression, which is associated with reduced episodic autobiographical memory (also see Soderlund et al., 2014; Williams et al., 2007), and SAM episodic scores were related to a laboratory measure of scene recollection (an indicator of episodic memory processing), but not familiarity (Palombo et al., 2013).

We recently collected additional data concerning the discriminant validity of the SAM episodic scores in cases of highly superior autobiographical memory (HSAM), whereby individuals have a selective and extreme ability to remember past autobiographical events (LePort et al., 2012), and cases of severely deficient autobiographical memory (SDAM), which refers to healthy individuals who have severe deficits in recalling episodic elements of autobiographical events (Palombo, Alain, Soderlund, Khuu, & Levine, 2015). Those with HSAM and SDAM differed significantly from matched control participants and each other on the SAM episodic subscale, but not on the SAM semantic subscale (see [Supplementary material, Figure S2](#)). This suggests that SAM episodic but not semantic scores are capturing the ability to subjectively remember past events in detail. Importantly, neither HSAM nor SDAM cases showed differences from matched controls on most standardized memory tests (LePort et al., 2012; Palombo et al., 2015), underscoring the fact that such tests are insensitive to the constructs captured by the SAM subscales.

In the current sample, we ruled out a number of mitigating factors that could be influencing episodic and semantic scores. Given that memory age affects the manner in which episodic and semantic processes are implemented, we tested how the fluency with which recent or remote events come to mind relates to SAM scores. Following a common resting state scan protocol, participants completed one of two autobiographical memory retrieval tasks (see [Supplementary materials](#)). Study 1 participants recalled any personal event memory that came to mind in response to viewing 20 randomly pictured objects (for details, see Sheldon & Levine, 2015 or the [Supplementary information](#) section). Study 2 participants retrieved autobiographical memories from pre-determined time periods so were not included in this analysis). We used the dates of the memories that were naturally retrieved to these cues and classified them as either recent (within the past 6 months) or remote (over 6 months), thus giving an indication of a preference for recovering recent or remote memories. A regression analysis for SAM episodic scores featuring the number of recent and remote memories as predictors was not significant [$F(2,23) = .39$, $p = .27$], nor was a model of SAM semantic scores using the same predictors [$F(2,23) = .86$, $p = .44$]. Thus, variance in endorsing episodic or semantic traits on the SAM could not be accounted for by a tendency to retrieve recent or remote memories. Using the full sample, we also found that neither age nor education were significantly related to episodic [$r(64) = .22$, $p > .05$, $r(64) = .05$, $p = .67$, respectively] or semantic scores [$r(64) = .21$, $p > .05$, $r(64) = .03$, $p = .80$, respectively].

In accordance with this SAM episodic/semantic dissociation, episodic scores but not semantic scores in the present study correlated with ratings of vividness, a hallmark of episodic recollection (Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Moscovitch et al., 2005), which participants made during an in-scanner episodic autobiographical recall task completed after the resting state scan [episodic: $r(64) = .33$, $p = .007$; semantic: $r(64) = .07$, $p = .59$]. The correlations between vividness and episodic and semantic scores were unchanged after statistically adjusting for age and education: [episodic: $r(64) = .37$, $p < .05$; semantic: $r(64) = .03$, $p = .81$]. We further confirmed the selective relation between episodic scores and vividness with a regression analysis that showed a significant model [$F(2,63) = 2.62$, $p = .026$] in which episodic scores were a predictor of vividness ratings [$b = .24$, $t(65) = 2.73$, $p = .008$] but semantic scores were not [$b = -.005$, $t(65) = -.483$, $p = .63$].

To summarize, data from the original SAM study (Palombo et al., 2013) and data reported here support the validity of the SAM (particularly the episodic and semantic scores) both in relation to external criteria (objective and subjective measures of recollection) and in relation to differentiating groups (depression and HSAM vs. SDAM). These data support the use of the SAM as a valid measure of trait episodic and semantic remembering. The SAM episodic and semantic scores are interpreted as orthogonal mnemonic traits or dimensions rather than categorical classifiers of individuals according to their memory style. Thus, one can score either high or low on both episodic and semantic SAM scales.

2.3. Resting state connectivity

2.3.1. Scan acquisition

Participants were scanned in the context of two separate studies using the same 3 Tesla Siemens full-body MRI machine located at the Rotman Research Institute at Baycrest Health Sciences. In one study, 27 participants were scanned with a standard 12-channel array head coil; in another study, 39 participants were scanned using a 32-channel array head coil. While combining scans using different head coils introduces noise, this was justified by the increased power afforded from a larger sample size. To adjust for this noise, we coded for study and included this as a nuisance regressor in second level analyses.

Anatomical scans were acquired via a T1-weighted volumetric MRI (TR = 2000 msec, TE = 2.63 msec, 160 axial slices, 1.0 mm thick, FOV = 256 mm). For the resting state scan, 32 axial slices with T2*-weighted EPI pulse sequence were obtained (TE/TR = 30/2000 msec, flip angle = 70°, FOV = 200 × 200 mm, 64 × 64 acquisition matrix, 3.1 × 3.1 × 4.5 mm³ voxels) with no spacing. These scans were acquired over 6.5 min, after anatomical localizer and structural scans, and before any experimental tasks or manipulations were performed inside or outside the scanner. During the resting state scan, participants were presented with a black fixation cross presented on a white screen and asked to keep their eyes open while focusing on this cross and allow their mind to wander. All participants completed task-based functional runs that were part of separate studies (see [Supplemental materials](#)).

2.3.2. Data processing

The MRI data were reconstructed and pre-processed using AFNI (Cox, 1996). The first ten images acquired for the functional run were discarded. Images were reconstructed and corrected for physiological movement related to heart rate and respiration. Slice-time was corrected to the first slice and motion was corrected using a 3-D Fourier transform interpolation with a functional volume that minimized the amount of motion to approximately 1.5 mm. The data were transformed into voxels of 4 × 4 × 4 mm³, normalized to a MNI EPI template, and smoothed with an 8 mm isotropic Gaussian filter. Following smoothing, nuisance covariates were regressed out of each participant's dataset, including the 6 motion parameters, mean white matter signal, cerebrospinal fluid (CSF) signal, and the global Blood-Oxygen-Level Dependent (BOLD) signal, a step that effectively and importantly reduces the impact of inter-individual variations between the resting state measure and motion (Gotts et al., 2013; Yan et al., 2013). The aforementioned functional signal nuisance covariates were extracted using predefined whole brain, white matter, and CSF masks obtained through the REST toolbox (Song Xiaowei, <http://restfmri.net/forum/index.php>). Following covariate removal, data were linearly de-trended and passed through a band-pass filter to include only data between .01 and .08 Hz.

2.3.3. Functional connectivity analysis

Seed-based connectivity analyses were carried out by assessing the correlation between BOLD responses in seed regions with the rest of the brain. We determined how these

correlations related to individual differences in SAM episodic and semantic scores.

There are multiple ways to approach resting state analysis. Because we had specific hypotheses regarding MTL connectivity, our primary analyses took an anatomical region of interest (ROI)-based approach (Greicius, Krasnow, Reiss, & Menon, 2003). The brain was segregated into distinct regions via the Automated Anatomic Labeling (AAL) template regions (Tzourio-Mazoyer et al., 2002). The mean time series was extracted for each of these regions, and temporal correlations were calculated between the voxels in the ROI and the rest of the brain. Our main analysis was driven by interest in the MTL connections of the DMN that are most strongly associated with mnemonic processing; thus, we used the parahippocampal gyrus (PHG; bilateral) as our MTL seed. The PHG is functionally and structurally connected to the DMN (Ward et al., 2013) and is associated with the particular type of memory context reinstatement which is of interest in this study (Diana, Yonelinas, & Ranganath, 2013). Left and right seed regions were created using the predefined parahippocampal regions derived from the AAL atlas.

We also assessed MTL connectivity using a functional ROI derived from the peak activity in the left and right MTL during an autobiographical retrieval task that a subset of participants (Study 1, N = 27; see [Supplementary materials](#)) performed after the resting state scan (Sheldon & Levine, 2015). They were asked to think about the details of the event for a 24 sec retrieval period. 10 mm³ spheres surrounding the voxel that was most active and representative of the left and right MTL at coordinates x, y, z = -24, -32, -18 and = 28, -36, -14, respectively, were combined to form the bilateral MTL functional ROI. To assess connectivity, we applied this seed to the full sample (N = 66). Finally, we examined connectivity using anatomically defined cortical seed regions that associated with the types of processes that we predicted relate to episodic and semantic remembering, specifically the left medial prefrontal cortex (MPFC) and left precuneus (Buckner et al., 2008).

In separate analyses for each seed region, the vectors of average time course data were used as regressors of whole brain activity, generating a brain map of seed-region connectivity for each participant. These maps were z-scored and entered into group level factorial analysis using SPM8 (University College London, UK; <http://www.fil.ion.ucl.ac.uk/spm/software/spm8>). At this group level, mean-centered SAM episodic and semantic scores were entered as covariates in the regression model, allowing for evaluation of the relationship between memory trait and seed-region connectivity across the brain for each seed ROI. We entered study and sex as second level regressors in each model. We extracted regions that had significantly increased connectivity for episodic scores compared to semantic scores or significantly decreased connectivity for semantic compared to episodic scores (1 -1); regions that had significantly increased connectivity for semantic compared with episodic scores or significantly decreased connectivity for episodic compared to semantic scores (-1 1) were also extracted. 3dCLUSTSIM was used to control for multiple voxel-wise comparisons by providing a cluster (k) extent (via Monte Carlo simulation

technique using 100000 simulations) equivalent to $p < .01$ across the whole brain, minimizing the frequency of false positives. Applying this correction, we set all resulting maps to a voxel-wise threshold of $p < .005$ and a cluster extent threshold of 30. The PickAtlas software toolbox with the AAL toolbox was used to determine peak coordinates of the resulting clusters (Maldjian, Laurienti, Kraft, & Burdette, 2003).

3. Results

3.1. MTL connectivity

3.1.1. PHG anatomical seed

We employed a multiple regression model to contrast patterns of connectivity to an anatomically defined MTL seed associated with episodic and semantic scores (Fig. 1, top right; Supplemental Figure S1 for the overall pattern of connectivity). Connectivity effects between the MTL seed and posterior regions were more strongly and positively associated with episodic scores than with semantic scores. This pattern included a peak in the left occipital lobe, the calcarine gyrus, and the posterior cingulate. A separate pattern of MTL connectivity that included bilateral middle and inferior prefrontal cortical clusters was more strongly associated with semantic than episodic scores (Fig. 1; Table 1).

Table 1 – Peak regions (global peaks of each significant cluster and local peaks that were >8 mm apart) of medial temporal lobe (MTL) connectivity correlating with Survey of Autobiographical Memory (SAM) episodic versus semantic scores using anatomical MTL seed (Fig. 1). The peaks of the clusters are reported in MNI coordinates (x, y, z). BA = Brodmann area. CS = cluster size. Peak = peak T score of the cluster.

Peak regions	BA	X	Y	Z	CS	Peak
<i>Episodic > Semantic</i>						
Left calcarine	30	-8	-60	6	278	3.91
Right posterior cingulate	31	16	-48	34		3.86
Left middle occipital gyrus		-20	-72	18		3.84
<i>Semantic > Episodic</i>						
Right middle frontal gyrus	10	44	48	10	61	4.68
Right inferior frontal gyrus	9	44	40	30		4.00
Left middle frontal gyrus	10	-44	44	10	64	4.02
Left inferior frontal gyrus	47	-32	32	-6		3.67
Left middle frontal gyrus		-28	56	14		3.43

We plotted the z-transformed difference between episodic and semantic scores for each participant against the signal extracted from the peak cluster with the highest signal from each of these contrasts (left calcarine for the episodic > semantic contrast; right middle/inferior frontal gyrus for the semantic > episodic contrast). This was done to illustrate the relation between episodic scores and MTL

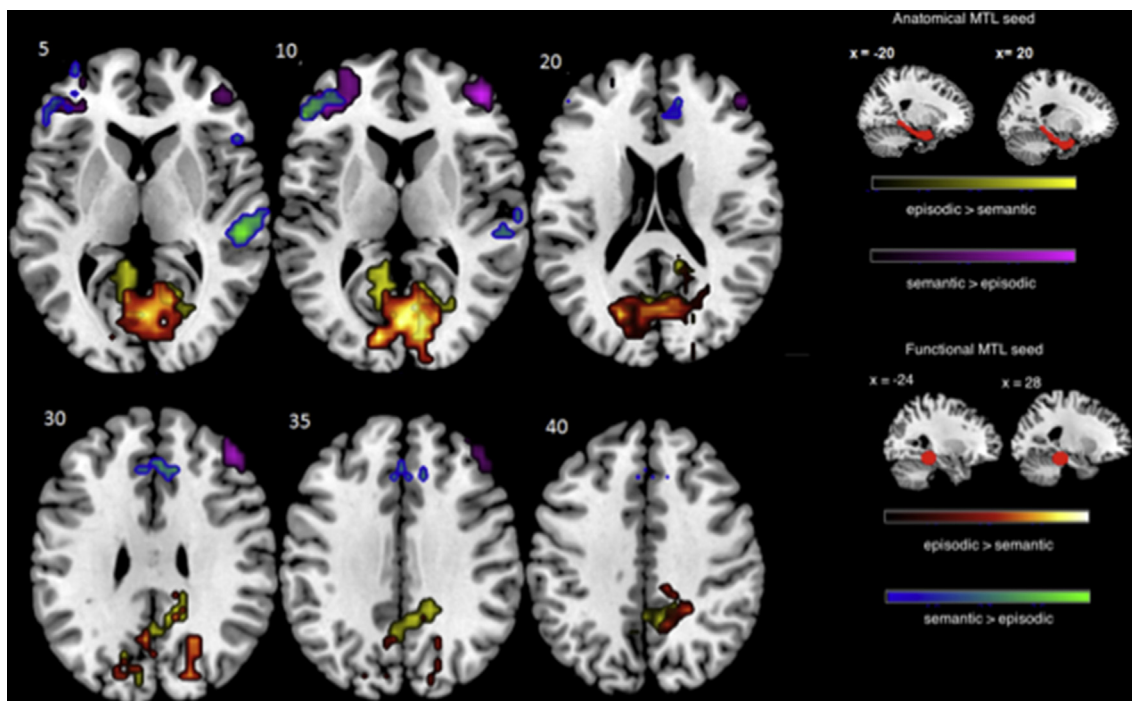


Fig. 1 – The relation between Survey of Autobiographical Memory (SAM) scores and medial temporal lobe (MTL) connectivity using the anatomical seed (top right) and functional seed (bottom right). Results for the anatomical and functional seeds are overlaid on the brain templates in the left. The MTL connectivity pattern that was positively associated with episodic scores in comparison to semantic scores is depicted in warm colors (yellow for the anatomical seed and orange for the functional seed). This pattern was distinct from the MTL connectivity pattern that was positively associated with semantic scores in comparison to episodic scores, depicted in cool colors (purple for the anatomical seed and blue/green for the functional seed). The threshold was set to $p < .005$, $k = 30$.

connectivity patterns while controlling for inter-individual differences in overall item endorsement (Fig. 2). The significant positive relationship between the difference scores (episodic minus semantic) and MTL connectivity to the left calcarine as well as the significant negative relationship between the difference scores and MTL connectivity to the right middle/inferior frontal gyrus illustrate the direction of the relation between episodic scores and MTL connectivity at the individual subject level. Fig. 2 also shows that outliers did not influence our findings.

We extracted parameter estimates from the individual contrasts for the connectivity maps that were positively associated with each predictor of interest (i.e., episodic and semantic score covariates) to describe the nature of the relationship between episodic and semantic scores and MTL connectivity. Participants' z-scored connectivity maps were entered into group level factorial analysis using SPM8 (University College London, UK; <http://www.fil.ion.ucl.ac.uk/spm/software/spm8>) with mean-centered episodic or semantic scores entered as separate covariates in the regression model. Single sample t-tests (0 1 or 1 0) evaluated the relationship between SAM scores and seed region connectivity (using the anatomical seed; Table S1). Beta values were extracted from the global maxima of the connectivity maps for each analysis (i.e., episodic and semantic scores; these peaks were identical to those identified in the above regression analysis). The pattern that was positively associated with episodic scores had peak cortical activity in the medial parietal lobe (left precuneus; MNI $x, y, z = -4, -60, 30$) and had a positive beta value when not taking memory covariates into consideration (beta = .04, SE = .02). The beta values associated with the episodic and semantic relation to MTL-covariates of precuneus connectivity were nearly equivalent in magnitude but in opposite directions (episodic beta = .007, SE = .002; semantic beta = -.007, SE = .002). Thus, the positive coupling

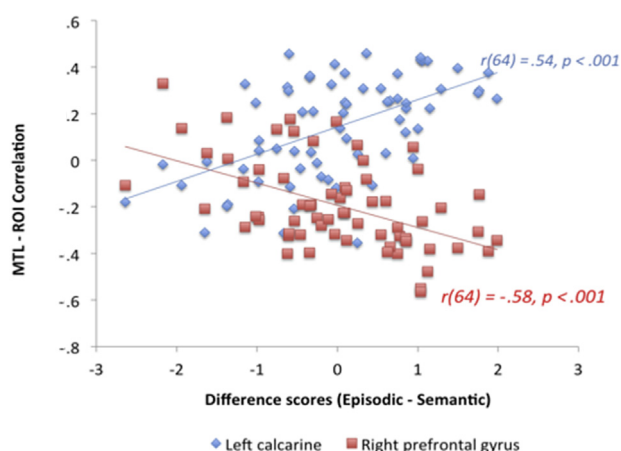


Fig. 2 – The relation between Survey of Autobiographical Memory (SAM) episodic minus semantic (within-subject) difference scores and medial temporal lobe (MTL) to region of interest (ROI) connectivity using the main clusters extracted from the connectivity maps presented in Fig. 1. Scatterplots and correlation coefficients are presented for descriptive purposes only in order to display the nature of the brain-behavior relationship at the single subject level.

between the MTL seed and these posterior brain regions was enhanced with increasing episodic scores, but was reduced with increasing semantic scores. The pattern that was positively associated with semantic scores showed a peak in the right prefrontal cortex (MNI $x, y, z = 44, 48, 10$), demonstrating a negative beta value irrespective of memory scores (beta = -.13, SE = .02), suggesting an inverse relationship between the MTL and this region at rest. Higher semantic scores were associated with a weakening of this reciprocal relationship (beta = .009, SE = .002), whereas higher episodic scores were associated with a stronger reciprocal relationship (beta = -.006, SE = .002).

3.1.2. General intelligence differences

To ensure that SAM scores were not influenced by different levels of general intelligence, we regressed out scores from the Wechsler Abbreviated Scale of Intelligence (WASI) Matrix Reasoning (average score = 30; maximum score = 35; SD = 1.7), a standardized test that reflects non-verbal reasoning available for a subset of participants ($N = 27$), then repeated the regression analysis reported above. The Matrix Reasoning score was used instead of a verbal component of the WASI (i.e., Vocabulary) given that vocabulary knowledge is a component of semantic memory. In this sample, matrix reasoning scores approached a significant correlation with episodic SAM scores [$r(25) = .37, p = .06$] but did not correlate with semantic SAM scores [$r(25) = .17, p = .40$]. Although the results with this smaller sample did not mirror all of the main findings, the key findings of episodic scores associated with MTL connectivity to midline posterior regions (right precuneus and lingual gyrus, left middle occipital gyrus), and semantic scores associated with MTL connectivity to the bilateral inferior frontal gyri and the bilateral inferior temporal gyri held (see Supplemental Table S2) were observed.

3.1.3. MTL functional seed

There is some concern over the variance associated with using anatomical ROIs (for a discussion, see Zalesky et al., 2010); thus, we confirmed our findings using a functionally defined bilateral MTL ROI (see Methods; Figure S1, right panel, for overall connectivity pattern). The posterior/anterior dissociation between episodic and semantic scores and MTL connectivity was similar to that reported above for the anatomically-defined seed (Fig. 1, Table 2); episodic scores were associated with expansive parietal and occipital connectivity. Semantic scores were significantly associated with left inferior prefrontal cortical activity and also with regions in the right superior and middle temporal lobe.

3.2. Anterior and posterior cortical connectivity

To explore the relationship of SAM scores and connectivity with non-MTL seeds that align with our hypothesis, connectivity to anatomically-defined left MPFC and left precuneus seeds was examined (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010).

Both seeds yielded a consistent DMN/autobiographical memory network pattern irrespective of SAM scores. For the precuneus seed, episodic scores were positively associated with a connectivity pattern that included activity in the right

Table 2 – Peak regions (global peaks of each significant cluster and local peaks that were >8 mm apart) of medial temporal lobe (MTL) connectivity correlating with Survey of Autobiographical Memory (SAM) episodic versus semantic scores using a functionally-defined bilateral MTL seed (Fig. 1). The peaks of the clusters are reported in MNI coordinates (x, y, z). BA = Brodmann area. CS = cluster size. Peak = peak T score of the cluster.

Peak regions	BA	X	Y	Z	CS	Peak
<i>Episodic > Semantic</i>						
Right calcarine	30	8	-68	10	432	4.43
Left calcarine		0	-76	10		4.27
Right calcarine		12	-76	10		4.20
Brainstem		12	-28	-38	35	3.89
		4	-28	-46		3.49
		-8	-40	-50		3.38
<i>Semantic > Episodic</i>						
Right superior temporal gyrus	56	-28	6	43	4.43	
	48	-16	-2		3.30	
Right middle temporal gyrus	56	-24	-6		2.92	
Left inferior frontal gyrus		-40	40	-6	141	4.18
		-52	36	10		3.92
		-52	20	-2		3.84
Right anterior cingulate	32	8	36	26	33	3.90
Left superior medial frontal gyrus		0	32	34		3.13
Right superior temporal pole	38	52	16	-10	62	3.87
Right inferior frontal gyrus	47	52	20	2		3.76
Right inferior orbitofrontal cortex	48	36	-10			3.06

Table 3 – Peak regions (global peaks of each significant cluster and local peaks that were >8 mm apart) of left precuneus connectivity correlating with Survey of Autobiographical Memory (SAM) episodic versus semantic scores using anatomical seeds. The peaks of the clusters are reported in MNI coordinates (x, y, z). BA = Brodmann area. CS = cluster size. Peak = peak T score of the cluster.

Left precuneus						
Peak regions	BA	X	Y	Z	CS	Peak
<i>Episodic > Semantic</i>						
Right thalamus (extends into hippocampus)	50	16	-28	6	36	5.15
Right precuneus	30	12	-44	6		3.27
Left cingulate		-12	-28	34	62	4.21
		16	-40	34		3.71
Left middle cingulate gyrus		0	-36	46		3.63
Left postcentral gyrus	43	-56	-8	22	32	3.72
Left superior temporal lobe	13	-56	-12	10		3.39
Left insula	13	-40	-12	14		3.02
Right middle occipital lobe	39	44	-64	26	33	3.69
		36	-68	26		3.61
<i>Semantic > Episodic</i>						
Right brainstem		12	-20	-42	85	4.39
		-4	-16	-38		4.18
		8	-28	-46		3.95
Left inferior frontal gyrus	11	-44	48	-14	58	3.93
Left middle frontal gyrus		-36	60	10		3.76
		-36	60	-6		3.55
	8	-40	28	46	37	3.83
		-36	24	54		3.39
	9	-52	20	38		3.06

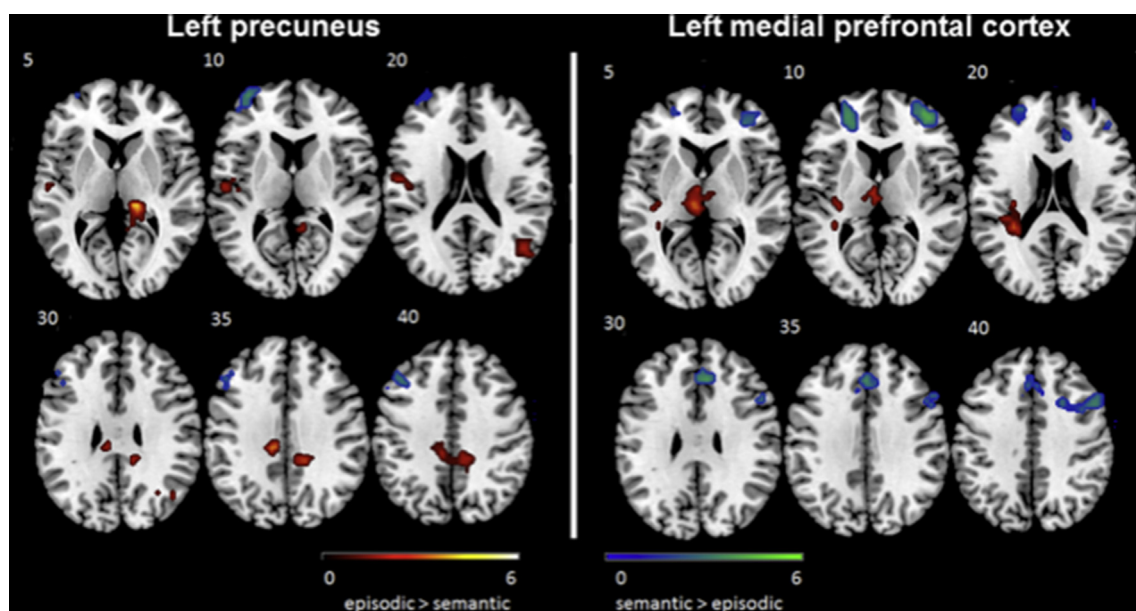


Fig. 3 – The relation between Survey of Autobiographical Memory (SAM) scores and anatomically defined cortical seeds, the precuneus (left), and the medial prefrontal cortex (MPFC; right). For both analyses, the connectivity pattern that was positively associated with episodic scores in comparison to semantic scores is depicted in orange and the pattern that was positively associated with semantic scores in comparison to episodic scores is depicted in blue. The threshold was set to $p < .005$, $k = 30$.

thalamus and MTL (right parahippocampus and hippocampus), and semantic scores were associated with a connectivity pattern that included distinct regions (brainstem, left middle frontal gyrus). MPFC activity was positively related to activity in the left insula and inferior temporal gyrus extending into the MTL, in association with episodic scores. Semantic scores were associated with MPFC connectivity to the middle frontal gyrus bilaterally (Fig. 3; Tables 3 and 4).

4. Discussion

Autobiographical memory is characterized by the subjective experience of recollection that accompanies the content of the retrieved memory. While previous reports have shown that individual differences in the content of a retrieved memory, as measured by objective laboratory-based memory tasks, relate to distinct patterns of neural connectivity (Alkire et al., 1998; King et al., 2015; Shapira-Lichter et al., 2013; Wang et al., 2010), we report for the first time that individual variations in the subjective experience of remembering (i.e., differences in naturalistic mnemonic trait characteristics) also correspond to stable differences in functional patterns of activity.

Using a validated self-report questionnaire (the SAM), we found that trait differences in autobiographical remembering were related to intrinsic neural connectivity patterns in the MTL mnemonic subsystem of the well-established DMN. Episodic SAM scores were related to MTL functional connectivity to posterior regions of the brain, particularly to those

regions involved in sensory-perceptual and visual processing. These functional connectivity data were consistent with our hypothesis that a tendency towards episodic remembering, indicating an ability to remember specific event details from the past, is associated with the tendency to access, recover, and reinstate rich images and perceptual details (Daselaar, Porat, Huijbers, & Pennartz, 2010; Fuentemilla, Barnes, Duzel, & Levine, 2014). Furthermore, this relation was specific to episodic remembering. The endorsement of trait semantic remembering (i.e., remembering factual information) was related to a distinct pattern of MTL connectivity that included prefrontal cortical regions (Badre & D'Esposito, 2007; Badre & Wagner, 2002).

Thus, our findings extend reports that connectivity measures relate to individual differences in memory from laboratory performance (e.g., King et al., 2015) to individual differences in naturalistic and subjective remembering. Since we assessed these abilities outside the scanner, our findings are held to reflect general mnemonic traits, not mental states induced during the scanning session. We are confident that our choice of trait measurement (the SAM) provides an accurate description of naturalistic memory. In our own sample, we validated the dissociation of SAM scores by relating episodic and semantic scores to the experience of recollection measured on a separate autobiographical task (vividness ratings of autobiographical recall; see Methods). Furthermore, SAM episodic and semantic scores are related to distinct memory performance profiles across groups known to have distinct autobiographical memory experiences (e.g., depression, HSAM, SDAM). We acknowledge that self-ratings reflect a subjective evaluation that may include non-mnemonic factors. Yet this does not detract from the importance of delineating stable brain networks associated with these trait mnemonics.

The observation that functional connections of the MTL were more strongly associated with episodic than semantic remembering aligns with described patterns of on-task connectivity associated with laboratory measures of episodic memory retrieval. For example, online measurements of posterior DMN activity have been associated with episodic retrieval during a word generation task (Shapira-Lichter et al., 2013). The pattern we report using offline measures of trait memory emphasizes the validity of trait memory characteristics in terms of the contribution of DMN subcomponents to both the content and experience of memory retrieval.

The patterns we report were observed when we used an anatomical MTL seed as well as a functionally derived seed from a separate autobiographical task and when we took differences in general intellectual abilities into account. The distinction in MTL connectivity between episodic and semantic remembering held in spite of a positive relation [$r(64) = .39, p = .002$] between SAM episodic and semantic scores in our sample. This indicates that SAM episodic scores reflect orthogonal tendencies to engage in episodic and semantic routes to memory, as opposed to a binary classification of individuals as “episodic” or “semantic.”

The reported connectivity patterns support novel hypotheses and models of individual differences in general mnemonic traits or characteristics. Specifically, the link between high SAM episodic scores, endorsing the ability to engage in

Table 4 – Peak regions (global peaks of each significant cluster and local peaks that were >8 mm apart) of left medial prefrontal cortex (MPFC) connectivity correlating with Survey of Autobiographical Memory (SAM) episodic versus semantic scores using anatomical seeds. The peaks of the clusters are reported in MNI coordinates (x, y, z). BA = Brodmann area. CS = cluster size. Peak = peak T score of the cluster.

Left MPFC						
Peak regions	BA	X	Y	Z	CS	Peak
<i>Episodic > Semantic</i>						
Left insula	13	-32	-36	18	65	4.52
Sub-gyral		-40	-24	-2		4.06
Left insula	13	-32	-24	14		3.81
Left thalamus: Medial dorsal nucleus		-8	-20	6	42	4.2
Left thalamus		-4	-8	6		3.87
Left fusiform gyrus	20	-32	-4	-46	32	3.92
<i>Semantic > Episodic</i>						
Right middle frontal gyrus	10	36	52	10	48	4.38
Right middle frontal gyrus	10	40	44	26		3.12
Left middle frontal gyrus		-28	56	14	47	4
Right middle cingulate gyrus		8	32	30	47	3.9
Left superior medial frontal gyrus		0	32	34		3.84
Right superior medial frontal gyrus		8	24	42		2.86
Right middle frontal gyrus		40	12	46	72	3.89
Right precentral gyrus		52	12	38		3.52
Right inferior medial frontal gyrus	9	56	20	38		3.42

general episodic remembering, and stronger MTL connectivity to medial and posterior brain regions that support visual perceptual processing (i.e., the occipital cortex and precuneus), reflects the preferential use of reconstructive and integrative processes associated with visual imagery when thinking about the past. Based on the contemporary view that the same processes that support experiencing the past support event memory and event simulations in general (Maguire & Mullally, 2013; Rubin & Umanath, 2015; Schacter & Addis, 2009), we further predict that endorsing episodic remembering processes that promote the fluent and vivid recollection of perceptual details would hold for any form of specific and selective event simulation. In short, individuals with a strong episodic remembering trait have a strong sense of reliving and re-experiencing events in general.

Endorsing semantic remembering was associated with a distinct pattern of MTL connectivity that included bilateral inferior prefrontal cortical regions. We speculate that the connectivity between the MTL and prefrontal cortical regions is related to the reliance on processes that support the organization of information (Badre & D'Esposito, 2007; Badre & Wagner, 2002), a relationship that is generally reciprocally negative at rest (in the present sample). This finding is reminiscent of enhanced memory-related activation of prefrontal regions associated with aging (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Geerligs, Renken, Saliassi, Maurits, & Lorist, 2014) and is suggestive of a neural context that is similar to tendencies in older adults who retrieve an excess of semantic details and a paucity of episodic details when extemporaneously describing past events and imagined future events (Addis, Wong, & Schacter, 2008; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). Although it is not clear which of the multiple factors associated with accessing semantic information from the past (e.g., general or factual information, or personal semantic information) is being captured by high SAM semantic scores, [a topic our group has discussed in a previous review (Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012)], the behavioral and neural dissociation from episodic remembering tells us that there are clearly different ways to remember and that these differences have a reliable neural basis.

Lastly, we found that the connectivity of two common cortical areas involved in event remembering also revealed different relationships to SAM episodic scores that were complementary to those reported with the MTL seeds. Connectivity between the MPFC, an anterior hub of the DMN, and posterior regions, including the left MTL and left occipitotemporal lobe, was distinctly associated with episodic scores. This suggests that medial aspects of the frontal lobe that are commonly associated with mentalizing are simultaneously engaged with posterior cortical regions associated with mnemonic and perceptual processes in individuals reporting high episodic, but not necessarily semantic, remembering (Denny, Kober, Wager, & Ochsner, 2012). Similar findings were noted for the precuneus seed analysis in which connectivity to the right MTL positively covaried with episodic scores.

Our findings call for the incorporation of trait-based mnemonic characteristics that measure the subjective experience of remembering into models of memory. These concepts are represented in existing models, such as Conway's model of

autobiographical knowledge (Conway & Loveday, 2015; Conway et al., 2004; Conway & Pleydell-Pearce, 2000), which proposes that one can access autobiographical knowledge from different level of abstraction, from lifetime periods to generalized events to the specific episodic elements of a past event (Conway & Pleydell-Pearce, 2000). Our findings suggest that those endorsing high episodic remembering take a direct route to remembering, bypassing higher-order abstracted knowledge in favor of accessing a memory via the episodic elements, or specific sensory-perceptual information. This is reflected by the intrinsic MTL functional connections to the precuneus and visual cortical regions that intrinsically support reinstating perceptual details from event memories (Daselaar et al., 2010; Fuentemilla et al., 2014). Strong trait measures of semantic remembering reflect a tendency towards integrating higher-order facts and information when retrieving memories or thinking about events, or taking a generative approach to remembering, which is supported by MTL connectivity to areas implicated in task integration or monitoring (Badre & D'Esposito, 2007; Badre & Wagner, 2002).

The present study highlights that there is a distinction between what is retrieved in autobiographical memory versus how that content is accessed, reconstructed, and subjectively experienced in consciousness (Klein, 2015). There are stable dimensions in this latter process, operationalized as mnemonic traits and individual differences in these traits have a neural basis. It is suggested that future studies articulate how differences in brain and behavior in relation to the subjective experience of memory should best be incorporated into the understanding of remembering.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2015.11.005>.

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