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The relationship between episodic detail generation and anterotemporal, posteromedial, and hippocampal white matter tracts

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Abstract

Episodic details populate autobiographical memories with vivid representations of people, objects, and event happenings, and they link events to a specific time and place. Episodic detail generation is believed to be a function of medial temporal lobe (MTL)-cortical interaction, but much remains unclear about how this retrieval process unfolds. In the present study, we combined an autobiographical interview and diffusion magnetic resonance imaging to investigate the relationships of two types of episodic detail, namely details about entities of an event (people and objects) or “event elements” and details about spatiotemporal context, to the integrity of anterotemporal (uncinate fasciculus; UF) and posteromedial (cingulum bundle; CB) cortical pathways. We also measured the relationships of these detail types to the fornix, and the relationship between non-episodic details and these tracts. We found that only episodic detail generation was significantly related to cortical and hippocampal pathways. Notably, the UF was more strongly related to event element details than it was to spatiotemporal context details. In contrast, CB was significantly and similarly related to the generation of event element and spatiotemporal context details (when not controlling for age and global diffusion). The fornix was also significantly related to both types of episodic detail, although the relationship to spatiotemporal context was particularly robust. These findings support the idea that anterotemporal cortical regions are related to the retrieval of episodic details about the entities that are incorporated into autobiographical events. Our findings also align with the notion that posteromedial and hippocampal-cortical involvement support the retrieval of episodic details.

Keywords

Autobiographical memory; hippocampus; episodic memory; diffusion

1. Introduction

Episodic autobiographical memories are recollected to remind us who we are, share stories with and remember others, and reflect on valuable examples for decision making (Conway, 2005; Nelson, 2003; Grilli & Verfaellie, 2015; Gupta et al., 2009). One feature that defines episodic autobiographical memories is their vivid representations of a specific event, incorporating high resolution episodic details about people, objects, space, and time (Levine et al., 2002). The ability to reconstruct unique events with episodic details varies considerably across individuals (Palombo, Sheldon, & Levine, 2018a), tends to decline with age (Levine et al., 2002; St. Jacques & Levine, 2007), and may be essential for some adaptive functions of autobiographical memory, such as future thinking and decision-making (Gaesser & Schacter, 2014; Sheldon et al., 2011).

1.1 Medial temporal lobe-cortical involvement in episodic detail generation

The ability to reconstruct a vivid, coherent representation of a unique event requires that episodic details are simultaneously retrieved and integrated. According to several theories, episodic details are at least partly stored in distributed cortical regions, with their integration made possible by hippocampal-cortical interaction (Eichenbaum, Yonelinas, & Ranganath, 2007; Moscovitch, Cabeza, Winocur, & Nadel, 2016; Ranganath & Ritchey, 2012). Proposed functions of the hippocampus include the ability to (re)construct a scene that can scaffold episodic detail generation (Maguire & Mullaley, 2013), engage in relational retrieval of episodic details across small (e.g., person) and large (e.g., scene) event scales (Roberts et al., 2017; Schacter & Addis, 2007), and separate events with overlapping details (Palombo et al., 2018b; Yassa et al., 2011). Despite lingering questions about the key computational process(es) of the hippocampus, studies on amnesia (Race et al., 2011; Rosenbaum et al., 2008), task-based functional neuroimaging (Addis et al., 2007; Martinelli et al., 2013; McCormick et al., 2015; Ryan et al., 2001; Svoboda et al., 2006), and high resolution structural and diffusion neuroimaging of hippocampal neuroanatomical properties (Hodgetts et al., 2017; Palombo et al., 2018b) indicate that episodic detail generation depends on this neural region.

Less is known, however, about the contributions of other medial temporal lobe (MTL)/cortical regions to episodic detail generation. This is despite considerable functional neuroimaging evidence for widespread MTL-cortical involvement in episodic autobiographical memory retrieval, including medial prefrontal, anterotemporal, and medial/lateral parietal lobe regions (Martinelli et al., 2013; Svoboda et al., 2006). There also is support for causal roles with some of these regions; a few studies have shown that lesions and transcranial magnetic stimulation of the parietal lobes and medial prefrontal cortex are linked to disrupted episodic detail generation, albeit to a milder degree than what is commonly associated with hippocampal amnesia (Berryhill et al., 2007; Bertossi et al., 2016; Davidson et al., 2008; Irish et al., 2004; Philippi et al., 2015; Thakral et al., 2017). Indeed, it is thought that many cortical areas may work together to form networks for autobiographical memory retrieval (Andrews-Hanna et al., 2014; McCormick et al., 2015; Svoboda et al., 2006). Yet, whether certain cortical regions or networks are functionally specialized for particular types of episodic detail retrieval remains unclear (Burke et al.,

2018; Ramanan et al., 2018; Reagh & Ranganath, 2018; Sheldon et al., 2019). The goal of the present study therefore was to help close this gap in knowledge by focusing on understanding how cortical networks support episodic details of unique events.

1.2 Applying diffusion MRI to understand cortical contributions

Recent work has shown that high angular resolution diffusion-weighted imaging (diffusion MRI) of white matter tracts may be a useful method for shedding light on the contributions of MTL-cortical networks to episodic detail generation (Irish et al., 2014; Hodgetts et al., 2017). For instance, in a sample of young adults, Hodgetts and colleagues (Hodgetts et al., 2017) found that normal variation in the microstructural integrity of the fornix, the major input/output pathway of the hippocampus, corresponded with typical individual differences in episodic detail generation, but not semantic detail generation. Of particular relevance, these findings demonstrate that this method is sensitive and specific to the proposed function of hippocampal-cortical interaction in detail generation. Irish and colleagues (Irish et al., 2014) further highlight that in the context of dementia, diffusion MRI can reveal relationships between episodic detail generation and proficiency of information processing between distributed cortical regions outside of the hippocampus. Diffusion MRI therefore has promise for uncovering cortical network contributions to normal variation in the generation of memory details.

1.3 The posteromedial anterotemporal framework as a model for investigating episodic detail generation with diffusion MRI

In regard to the application of diffusion MRI to understand cortical contributions to episodic detail generation, one theoretical model proposes that there are two key pathways through which episodic content is funneled to the hippocampus (Ranganath & Ritchey, 2012; Ranganath, 2010; Ritchey et al., 2015). According to this posteromedial anterotemporal (PMAT) framework, the hippocampus sits atop a neuroanatomically principled hierarchy of information processing in which anterotemporal and posteromedial cortical regions connect to non-hippocampal MTL regions, namely perirhinal cortex and parahippocampal cortex respectively, which in turn connect to the hippocampus (for an illustration of the PMAT framework, see Figure 1, which is adapted from Ritchey et al., 2015). Of particular importance for diffusion MRI, there are two prominent white matter tracts connecting these two MTL-cortical networks. One is the uncinate fasciculus (UF). This tract connects regions of the anterotemporal network, including the lateral orbitofrontal cortex, anterior lateral temporal lobe, temporal pole, amygdala, and the perirhinal cortex, and is integrated in the temporal stem, which also incorporates the anterior commissure, the inferior frontal occipital fasciculus, and the anterior optic tract (Von Der Heide et al., 2013). The other tract is the cingulum bundle (CB), a pathway that connects the posteromedial network, including the precuneus, retrosplenial cortex, posterior cingulate, inferior lateral parietal lobe, medial prefrontal cortex, and the parahippocampal cortex. Together, these white matter pathways maintain inputs/outputs to the broader cortical network that has been implicated in episodic memory, and therefore may have central roles in episodic detail generation (Irish et al., 2014).

While UF and CB may share a common role in episodic detail generation, the PMAT framework takes into consideration the putative cognitive functions of the anterotemporal and posteromedial networks and suggests that these tracts may be weighted towards the retrieval of different types of episodic content. That is, according to this framework, the UF/ anterotemporal network, by connecting regions implicated in item/conceptual processing, may be particularly important for the retrieval of entities/core event information that can be enriched with episodic details, including visual, socioemotional, and action/conversation-based qualities. In comparison, the CB/posteromedial network, by connecting regions involved in space and broader contextual processing, may be particularly important for details that ground events in space and time, and capture the temporal unfolding of an event. By extension, this view also aligns with the notion that hippocampal involvement may be essential for integrating details about entities with the spatiotemporal features of a unique event (i.e. binding items in contexts), because these two types of detail may be kept somewhat, albeit not entirely (Burke et al., 2018), separate prior to the hippocampus (Eichenbaum et al., 2007; Reagh & Ranganath, 2018).

1.4 Present study

To shed light on the extent to which episodic detail generation aligns with the PMAT framework, we investigated the relationship of episodic detail generation to white matter microstructural integrity of the UF and the CB via diffusion MRI. We utilized data from a sample of middle-aged and older adults who within six months completed an Autobiographical Interview (Levine et al., 2002) and an fMRI scan with diffusion tensor imaging (DTI) as part of a project on memory and aging. To determine whether the UF and CB are more prominently related to certain types of episodic details, we calculated two composite scores using a modified Autobiographical Interview approach (Levine et al., 2002). The first we referred to as an “event elements” content score, which included details about the actions/conversations of entities, their thoughts/emotions, and their perceptual qualities (i.e., people and other objects). We viewed this composite as reflective of the types of content proposed by the PMAT framework to be particularly relevant to MTL-cortical regions connected by the UF. The second we referred to as the “spatiotemporal context” content score. This score included place/scene and time episodic context details and details about the temporal sequencing or causal relationships of mini-events within a single episode. We took this spatiotemporal score as reflective of the details that according to the PMAT framework, would be particularly relevant to MTL-cortical regions connected by the CB. We focused on the parahippocampal portion of the CB, because it is the segment that connects the multiple posteromedial regions implicated in the representation of spatiotemporal context (Bubb et al., 2018; Ekstrom et al., 2017; Reagh & Ranganath, 2018).

In addition to cortical pathways, we also sought to build on the work of Hodgetts and colleagues (Hodgetts et al., 2017) and our understanding of fornix involvement in autobiographical memory. Hodgetts and colleagues, using the original Autobiographical Interview scoring protocol (Levine et al., 2002), found that fornix integrity was significantly related to episodic detail generation, with spatiotemporal details being the strongest predictor of this relationship. They interpreted these findings as important for understanding information processing in the “extended hippocampal system,” suggesting a key role for

spatiotemporal context. Given that we used a modified version of the Autobiographical Interview scoring approach and created a composite for details about event entities, we investigated whether we would find similar results to those of Hodgetts and colleagues. Such an analysis could shed light on the sensitivity of this white matter pathway to the generation of different types of episodic detail.

To contextualize the episodic detail findings, we also examined the relationship between our three tracts of interest (i.e., UF, CB, and fornix) and non-episodic details, using the validated “external” composite from the Autobiographical Interview (Levine et al., 2002). Notably, the external composite includes semantic details, mention of other events beyond the target unique event, as well as other narrative/language based features, such as editorializing. Examining the relationship of non-episodic details to these MTL-cortical tracts can provide further clarity regarding the functional weighting of these neural pathways to episodic content for a specific event.

Based on the notion that distributed cortical regions support the retrieval of episodic details, and UF and CB are two prominent cortical pathways to the MTL, we hypothesized that the generation of episodic details would be related to the integrity of these pathways. In accordance with the PMAT framework, we predicted that the UF would be more strongly related to event element details than spatiotemporal context details, whereas the CB would be more strongly related to spatiotemporal context details relative to event element details. In regard to the fornix, we predicted an association with spatiotemporal context details, replicating and extending the findings of Hodgetts and colleagues to our modified scoring approach. Additionally, we predicted that details about event elements would be associated with fornix integrity, reflecting this white matter pathway’s connection to the hippocampus, which is believed to be essential for integrating all types of episodic detail into events.

2. Methods

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. Recruitment and experimental testing was a collaborative effort between two labs (LR and MDG) and procedures administered for this study took place in the context of other experimental cognitive testing that was not relevant to the present study. No part of the study procedures or analyses were preregistered prior to the research being undertaken. Analyzed data and code are archived here: [https://osf.io/cuka4/?view_only=379345a8fed4932bb79d902b7d59767]. For ethical reasons, we have not archived individual MRI scans or the participants’ ages at time of study, as we did not obtain consent from these research participants to publicly share such data. These data can be requested from the senior author through a data sharing contract. This research protocol was approved by the institutional review board at University of Arizona.

2.1 Participants

Participants were drawn from a recently completed wave of memory testing and MRI scanning. Twenty-nine cognitively normal middle-aged and older adults completed both

episodic autobiographical memory testing and an MRI scan within 6 months and therefore were included in this study (21 women and 8 men; mean age = 68 years, range = 52–81 years, mean level of education = 17 years, range = 14–20 years). Three individuals were in their 50s, 6 were 60–64, 7 were 65–69, 7 were 70–74, 5 were 75–80, and 1 was over 80. For eight of these individuals, episodic autobiographical memory data scored using a different protocol have been previously reported (Grilli et al., 2018a). All participants were right-handed. Participants were screened for and absent of abnormal cognitive decline, prior significant head injury, drug or alcohol abuse, psychiatric disorder, and the use of anti-depressive, antipsychotic, and sleep medication, and any metal in their body. These inclusion/exclusion criteria were established prior to data analysis.

2.2 Procedure

2.2.1 Autobiographical memories.—The autobiographical memories used for the present study were from three relatively recent time periods: 5 years ago to 1 year ago, 1 year ago to 1 week ago, and last week, not including the day of experiment. Similar to the original Autobiographical Interview, participants were given five minutes to freely describe each memory. They were required to describe unique events, and they were encouraged to focus on the episodic details. A general probe was given if participants naturally ended their description before five minutes, but no specific probing was provided in this free recall session. For the eight participants reported in Grilli and colleagues (Grilli et al., 2018a), three more remote memories were also collected (i.e., from childhood to later adulthood). However, to be consistent with the other participants, only the three more recent memories from the free recall/general probe were used. Participants' responses were audio recorded and transcribed.

Events generated in this Autobiographical Interview were scored using an adaptation of the internal and external detail approach of the Autobiographical Interview protocol (Levine et al., 2002). Two internal/episodic detail subtype labels were taken from the original Autobiographical Interview protocol and our guidelines for scoring these details closely aligned with the original Autobiographical Interview. These were time details and thought/emotion details. We also used the perceptual detail label but in our case we focused on details about entities of an event (objects and people). Perceptual and other details about the spatial relations of entities in an event and place details (from the original Autobiographical Interview) were combined in a place/scene detail subtype. We did not use the “event” detail subtype label from the original Autobiographical Interview. Rather, we essentially split this category into two details. One focused on action or conversation/language features of entities. The other detail type focused on temporal sequencing, meaning descriptions of temporally-based causal relationships. The guidelines used to score each detail subtype and examples are presented in Figure 2.

As noted, two composite scores were created. The first composite, which we refer to as the “event elements” content score, includes details about action/conversation-based features of entities, their thoughts/emotions, and their perceptual qualities. The second composite, which we refer to as the “spatiotemporal context” content score, includes details about place/scene, time, and temporal sequencing. We acknowledge that the real-world does not come

with obvious labels for entities versus spatiotemporal context (Reagh & Ranganath, 2018), but we viewed our composites as reasonable separations of event features that are commonly associated with either items or scene/context qualities.

The remaining details were scored as external using the guidelines of the original Autobiographical Interview protocol. Details were scored as external if they were a semantic detail (i.e., a personal fact or general knowledge of things), meta-comments about the experimental task or one's current state of mind (e.g., "I'm trying to remember..."), repetitions of previous statements, and reference to other events not related to the unique event being described.

Consistent with established procedures (Grilli, Wank, & Verfaellie, 2018b; Verfaellie, Bousquet, & Keane), a primary scorer assessed all of the memories, and inter-rater reliability was calculated based on a random selection of approximately 30 percent of the memories from this study, which were assessed by a secondary scorer also trained on the scoring protocol. The primary scorer demonstrated excellent inter-rater reliability with a secondary scorer for total episodic details, event element details, and spatiotemporal context details (Cronbach's α 's > .94). Inter-rater reliability also was good for external details (Cronbach's α = .84).

2.2.2 Image acquisition.—MRI images were collected at the University of Arizona on a Siemens 3.0 Tesla Skyra Scanner equipped with a 32-channel head coil. Total scan time was 1 hour. High angular resolution diffusion-weighted images (DWI) were collected in 60 axial sections (2 mm sections, no skip, TR = 10,000 ms, TE = 80 ms, matrix = 128×128 , FOV = 254×254 mm²), with 64 directions and 6 b-zeroes.

2.2.3 DTI processing and analysis.—Diffusion-weighted images were preprocessed with the Functional Software Library (FSL) package (<http://www.fmrib.ox.ac.uk/fsl>). Images were realigned, linear eddy current distortions were removed, non-brain tissue was removed, and eigen vectors and values were calculated (Smith, S.M. 2002). Images were converted into tensors using DTI-tk (Zhang et al., 2010). Advanced Normalization Tools (ANTs) was then used to calculate a symmetric diffeomorphic transformation from each participant's native space to the John Hopkins University 2 mm FA Template, relying on Syn (0.25). Tracts were defined using John Hopkins probabilistic white matter tractography atlas, which defined structures probabilistically by averaging the results of deterministic tractography on 28 normal subjects (mean age 29, M:17, F:11) (Wakana et al. 2004; Hua et al. 2008). The three tracts of primary interest for the present study included the fornix (body and columns), UF, and CB (see Figure 3). As a secondary analysis, we also examined the inferior longitudinal fasciculus (ILF), in an attempt to replicate and extend one of the main findings of Hodgetts and colleagues, namely a selective association between ILF MD and semantic details. All template-defined tracts were converted into regions of interest and warped into native space using the inverse of the diffeomorphic transforms for each participant. The John Hopkins atlas divides the anterior and parahippocampal portions of the CB at the axial level of the splenium of the corpus callosum. The anterior portion originates at the splenium and terminates anteriorly at the genu of the corpus callosum. The parahippocampal portion runs along the ventral aspect of the hippocampus, originating at the splenium and terminating in a

plane anterior to the pons (Wakana et al., 2007). As noted, we focused on the parahippocampal portion of the CB.

Fractional anisotropy (FA) and mean diffusivity (MD) were calculated in each tract and from each participant's global white matter mask. FA is a measure of the directionality of water diffusion independent of rate, with higher FA values believed to represent better microstructural (e.g. myelination) and macrostructural (e.g. coherence of fiber orientation) white matter tract integrity. White matter integrity can also be assessed based on the magnitude of water flow along primary (axial diffusivity) and perpendicular (radial diffusivity) directions. The average of these diffusivity rates (mean diffusivity; MD) provides an indication of the rate of water flow.

2.2.4 Statistical analysis.—In accordance with the analysis plan of Hodgetts and colleagues (Hodgetts et al., 2017), we used a combination of null hypothesis significance testing and Bayesian analyses to evaluate and interpret our results. Duplicating the plan of Hodgetts and colleagues, given our strong theoretical motivation and recent evidence (Hodgetts et al., 2017), directional Pearson correlations were conducted between measures of autobiographical memory (i.e., event element details, spatiotemporal context details, and external details) and tract-specific measures of white matter integrity (FA and MD) in the UF (bilateral), CB (bilateral), and fornix. We first ran bivariate correlations between tracts and details. As noted, the three types of details examined were event element, spatiotemporal context, and external. We also followed-up by examining relationships involving semantic details specifically. Given the age and age range of our sample, we then followed up with partial correlations controlling for age and global diffusion. All correlations were run in SPSS. Also aligning with Hodgetts and colleagues, for significance testing, these correlations were Bonferroni-corrected by dividing $\alpha = .05$ by the number of statistical comparisons for each DTI metric (i.e., $\alpha = .05/2 = .025$).

A Bayesian Pearson directional correlation equivalent model was used for estimation analysis. We used JASP to conduct and evaluate the robustness of these analyses (JASP Team, 2018). We focused our Bayesian analyses on the bivariate correlations, and for these relationships we report the Bayes Factors and the 95% highest density intervals (HDI), which are the smallest ranges covering 95% of the estimated parameter values in the posterior distribution. We used the default uniform beta prior, but a sensitivity analysis revealed that the Bayes Factors were minimally affected by stretching the beta distribution.

All visualizations of the data were created in R (R Core Team, 2018).

2.2.5 Power analysis.—Our sample was slightly larger than Hodgetts and colleagues (Hodgetts et al., 2017, $n = 27$) and similar to Palombo and colleagues (Palombo et al., 2018b, $n = 30$), both of which investigated the relationships between episodic detail generation and structural integrity. An a priori power analysis was conducted using Gpower (Faul, Erdfelder, Buchner & Lang, 2009) to determine the minimum number of participants needed assuming we could detect large effects, which were found in both Hodgetts and colleagues (Hodgetts et al., 2017) and Palombo and colleagues (Palombo et al., 2018b). A

one-tailed significance test, with power = 0.8, alpha = .025, and $r = .50$ equated to a minimum of 26 participants.

3. Results

3.1 Episodic detail qualities and non-episodic content generation

Participants generated an average of 30.3 event element details (range = 6.3 to 56; $SD = 12.9$) and 8.4 spatiotemporal context details (range = 2.7 to 16.3; $SD = 3.8$) per memory. They also generated on average 16.1 external details (range = 5–31.3, $SD = 6.1$) per memory.

3.2 Relationships between episodic and non-episodic details and white matter tracts

For illustrative purposes, Figures 4–6 show the bivariate Pearson correlations for each detail type and white matter tract. Notably, for FA a positive association is indicative of better integrity being related to greater generation of that type of detail. In contrast, for MD a negative association is indicative of better integrity being associated with greater generation of that type of detail. Visualization of the posterior distributions for our primary Bayes analyses (sections 3.3 through 3.5) are reported in the Supplemental Materials.

3.3. Anterotemporal network: UF

In regard to FA, we found significant and substantial evidence for a positive relationship to event element details ($r = .44$, $p = .008$, $BF_{+0} = 7.36$, $HDI = .10$ to $.68$). In comparison, UF FA was not significantly related to spatiotemporal context details, with the evidence substantially in favor of there being no relationship ($r = -.02$, $p = .46$, $BF_{+0} = .21$, $HDI = .01$ to $.39$). Similarly, UF FA was not significantly related to external details, with substantial evidence in favor of no relationship ($r = -.07$, $p = .38$, $BF_{+0} = .18$, $HDI = .01$ to $.36$). For MD, UF was significantly related to event element details ($r = -.39$, $p = .02$, $BF_{-0} = 3.63$, $HDI = -.64$ to $-.07$) but not spatiotemporal context details ($r = .01$, $p = .47$, $BF_{-0} = .22$, $HDI = -.39$ to $-.01$), or external details ($r = .25$, $p = .10$, $BF_{-0} = .11$, $HDI = -.27$ to $-.003$). Whereas the evidence was substantial for their being a relationship with event element details, it was substantial for no relationship with spatiotemporal context details or external details. Notably, focusing on semantic details, instead of the external detail composite, did not meaningfully alter the outcomes for the UF.

3.4 Posteromedial network: CB

For the parahippocampal segment of the CB, the evidence for a relationship between FA and event element details was not significant, although the Bayes Factor suggests anecdotal evidence for a positive relationship ($r = .30$, $p = .05$, $BF_{+0} = 1.48$, $HDI = .03$ to $.59$). The relationship between FA and spatiotemporal context details was similar ($r = .27$, $p = .08$, $BF_{+0} = 1.07$, $HDI = .02$ to $.56$). In comparison, the relationship to external details was weaker, with substantial evidence in favor of no relationship ($r = -.09$, $p = .33$, $BF_{+0} = .17$, $HDI = .004$ to $.35$). For MD, there was evidence that better integrity of the parahippocampal segment of the CB was significantly related to greater generation of event element ($r = -.54$, $p = .001$, $BF_{-0} = 38.79$, $HDI = -.74$ to $-.21$) and spatiotemporal context details ($r = -.39$, $p = .02$, $BF_{-0} = 3.44$, $HDI = -.64$ to $-.06$), with the evidence ranging from strong (for event

elements) to substantial (for spatiotemporal context). In contrast, again the relationship to external details was not significant, with anecdotal evidence for no relationship, ($r = -.26$, $p = .09$, $BF_{+0} = .999$, $HDI = -.55$ to $-.02$). Notably, focusing on semantic details, instead of the external detail composite, did not meaningfully alter the outcomes for the CB.

3.5 Hippocampal-cortical pathway: Fornix

In regard to the fornix, we found significant and credible evidence for a relationship with event element and spatiotemporal context details. Specifically, better integrity of the fornix, as measured by FA, was associated with greater generation of both event element details ($r = .40$, $p = .02$, $BF_{+0} = 4.01$, $HDI = .07$ to $.65$) and spatiotemporal context details ($r = .52$, $p = .002$, $BF_{+0} = 25.92$, $HDI = .18$ to $.73$). Here, the evidence for relationships ranged from substantial (for event elements) to strong (for spatiotemporal context). In comparison, for external details, the relationship was not significant and anecdotally in favor of the null ($r = .20$, $p = .15$, $BF_{+0} = .67$, $HDI = .02$ to $.52$). The relationship between fornix MD and event element details was anecdotal and not significant ($r = -.32$, $p = .05$, $BF_{-0} = 1.68$, $HDI = -.59$ to $-.04$), as was the relationship with spatiotemporal details ($r = -.34$, $p = .04$, $BF_{-0} = 2.08$, $HDI = -.61$ to $-.04$). The correlation between fornix MD and external details also was not significant, but here there was anecdotal evidence for no relationship ($r = -.15$, $p = .22$, $BF_{-0} = .47$, $HDI = -.48$ to $-.01$).

3.6 Controlling for global diffusion and age

When we controlled for age and global diffusion, the relationship between event element details and UF FA remained significant ($r = .39$, $p = .02$). Similarly, the relationship between spatiotemporal context details and fornix FA remained significant ($r = .38$, $p = .02$). In contrast, the relationships between CB MD and both episodic detail composites were no longer significant (event element: $r = -.07$, $p = .37$; spatiotemporal context: $r = -.20$, $p = .15$). Similarly, the relationship between event element details and the fornix was no longer significant (FA: $r = .05$, $p = .40$) as was the relationship between UF MD and event element details ($r = .10$, $p = .30$). Finally, none of the bivariate correlations that were not significant switched to being significant when controlling for age and global diffusion, with one external detail exception noted below. Specifically, for the remaining partial correlations and event element details: CB FA ($r = .02$, $p = .46$) and fornix MD ($r = .17$, $p = .20$). For the remaining partial correlations and spatiotemporal context details: UF FA ($r = -.24$, $p = .12$), UF MD ($r = .36$, $p = .03$), CB FA ($r = .12$, $p = .27$), and fornix MD ($r = -.13$, $p = .25$). For the partial correlations between external details: UF FA ($r = -.08$, $p = .36$), UF MD ($r = .53$, $p = .002$), CB FA ($r = -.13$, $p = .25$), CB MD ($r = -.23$, $p = .13$), Fornix FA ($r = .24$, $p = .12$), and fornix MD ($r = -.10$, $p = .30$). We note that the one significant finding for external details is in the opposite direction of what would be predicted if greater UF integrity was associated with more generation of such content.

Controlling for global diffusion and age had a greater impact on our significant MD findings relative to FA, and in particular washed out our CB findings. To better understand why, we examined the bivariate relationships between our significant MD findings and age, as well as with global MD (two-tailed, $\alpha = .05$). Age was significantly related to CB MD ($r = .41$, $p = .03$) but not with UF MD ($r = .26$, $p = .17$). In contrast, global MD was highly correlated

with CB MD ($r = .76, p < .001$) and UF MD ($r = .72, p < .001$). This suggests that CB MD integrity was closely related to broader age-related diffusion effects in our participants. For comparison, we note that UF FA, while significantly correlated with global FA ($r = .65, p < .001$) was not significantly related to age ($r = -.05, p = .80$). Fornix FA was significantly related to age ($r = -.53, p = .003$) but not global FA ($r = .23, p = .24$).

3.7 Steiger Z-tests

3.7.1 Comparing episodic detail types for each tract—Our null hypothesis significance testing and Bayesian analyses indicated that UF FA might be significantly more strongly related to event element details relative to spatiotemporal context details. To explore this further, we conducted Steiger Z-tests (two-tailed) on these correlations using <http://quantpsy.org/corrtest/corrtest2.htm> (Lee & Preacher, 2013). To more completely address our predictions, we also conducted Steiger Z-tests for other tracts/metrics for which at least one episodic detail composite was significant, comparing the magnitude of the relationship to each of our two detail types. We applied an FDR-correction ($q = .05$) and adjusted p-values are reported. For UF FA, the relationship to event element details was significantly greater than the relationship to spatiotemporal details (bivariate: $z = 2.66, p = .01$; partial: $z = 3.19, p = .02$), and the bivariate relationship between UF MD and event element details was significantly greater than that of spatiotemporal context details ($z = 2.27, p = .046$). For CB MD, the bivariate relationship to spatiotemporal context details did not differ from that of event element details ($z = 1.0, p = .38$). For fornix FA, the relationship to spatiotemporal context details did not significantly differ from the relationship to event element details (bivariate: $z = .78, p = .44$; partial: $z = 1.66, p = .14$).

3.7.2 Comparing anterotemporal and posteromedial tracts—We also ran Steiger Z-tests (two-tailed) to examine whether UF was significantly more strongly related to event element details relative to CB and vice versa for spatiotemporal context details, using the same approach and FDR-correction ($q = .05$). UF FA was not significantly more strongly related to event element details relative to CB FA (bivariate: $z = .81, p = .42$; partial: $z = 1.39, p = .33$). The bivariate relationship between CB MD and spatiotemporal context details also was not significantly different from that of UF MD ($z = 2.09, p = .15$), nor was the comparison of the bivariate relationship between CB MD and event element versus UF MD ($z = .91, p = .42$).

3.7.3 Comparing episodic detail generation and non-episodic content—Finally, we examined whether UF, CB, or fornix were significantly more strongly related to episodic details relative to non-episodic (external) details. Again, we focused on metrics for which an episodic detail relationship was significant (no external detail relationships were significant) and we used an FDR-correction ($q = .05$) with corrected p values reported. For UF, we focused on event element details, given that these details were more strongly related this tract relative to spatiotemporal context details. For CB MD and fornix FA, we collapsed across episodic detail subtypes, as event element and spatiotemporal context details did not significantly differ in their relationship to these tracts. We also focused on bivariate relationships, given that controlling for age and global diffusion did not alter any of the previous Z-tests. These comparisons revealed that UF was significantly more strongly

related to episodic (event element) details relative to external details (FA: $z = 2.22$, $p = .05$; MD: $z = 2.8$, $p = .02$). Although effect sizes were modestly in favor of episodic details, CB MD was not significantly more strongly related to episodic details relative to external details ($z = 1.4$, $p = .22$), and fornix FA was not significantly more strongly related to episodic details relative to external details ($z = 1.2$, $p = .23$).

3.8 Comparing to Hodgetts and colleagues' findings—Hodgetts and colleagues (Hodgetts et al., 2017) found that fornix FA integrity was related to total episodic detail generation, which was driven by place and time details, but not semantic detail generation. To build more directly on these findings, we investigated the relationship between fornix FA and a) total episodic details and total semantic details (a subtype of the external detail category) and b) our episodic detail subtypes.

Similar to Hodgetts and colleagues, we found that fornix FA was significantly and strongly associated with total episodic detail generation, regardless of whether we included temporal sequence details (with sequence details: $r = .47$, $p = .005$, $BF_{+0} = 10.0$, $HDI = .12$ to $.69$; without sequence details: $r = .47$, $p = .005$, $BF_{+0} = 10.14$, $HDI = .12$ to $.69$). Indeed, our bivariate relationships were remarkably similar in magnitude to Hodgetts and colleagues (i.e., .46 vs. .47). However, controlling for age and global diffusion, which was not done in Hodgetts and colleagues given their younger, more age-homogenous sample, resulted in our relationships no longer being significant (with sequence details: $r = .15$, $p = .22$ and without sequence details: $r = .17$, $p = .20$). Also similar to Hodgetts and colleagues (Hodgetts et al., 2017) we found that semantic details were not significantly correlated with fornix FA, with the evidence anecdotally in favor of the null ($r = .20$, $p = .14$, $BF_{+0} = .67$, $HDI = .02$ to $.52$). Controlling for age and global diffusion did not alter this relationship ($r = .20$, $p = .16$). Unlike Hodgetts and colleagues, however, we did not find that the bivariate relationship between fornix and episodic details was greater than that of fornix and semantic details (with sequence details: $z = 1.1$, $p = .14$; without sequence details: $z = 1.1$, $p = .14$). For comparison, the magnitude of the difference was $z = 1.85$ in Hodgetts and colleagues.

In regard to episodic detail subtypes, similar to Hodgetts and colleagues, we found significant and substantial to strong relationships between fornix FA and place/scene details ($r = .56$, $p = .001$, $BF_{+0} = 53.86$, $HDI = .23$ to $.75$) and time details ($r = .44$, $p = .01$, $BF_{+0} = 6.72$, $HDI = .10$ to $.67$). In our sample there also was a significant and strong relationship with perceptual details ($r = .49$, $p = .004$, $BF_{+0} = 13.85$, $HDI = .14$ to $.71$). Fornix FA was not significantly related to action/conversation details ($r = .31$, $p = .05$, $BF_{+0} = 1.52$, $HDI = .03$ to $.59$), thought/emotion details ($r = -.01$, $p = .47$, $BF_{+0} = .22$, $HDI = .01$ to $.39$), or sequence details ($r = .07$, $p = .37$, $BF_{+0} = .31$, $HDI = .01$ to $.43$). Controlling for age and global diffusion weakened all of these effects. However, the relationship to place/scene details remained significant ($r = .50$, $p = .004$). The remaining, non-significant correlations were: time ($r = .35$, $p = .04$), perceptual ($r = .32$, $p = .05$), action/conversation ($r = -.09$, $p = .32$), thought/emotion ($r = -.17$, $p = .20$), and sequence ($r = -.09$, $p = .33$). Notably, Hodgetts and colleagues combined place and time details in their analyses. When we did the same, we found a very strong relationship to fornix FA ($r = .61$, $p < .001$, $BF_{+0} = 166.5$, $HDI = .29$ to $.78$), which remained strong after controlling for age and global diffusion ($r = .54$, $p = .002$). Notably, the relationship between fornix FA and this spatiotemporal composite was

significantly stronger than the relationship between fornix FA and semantic details (bivariate: $z = 2.2$, $p = .03$; partial: $z = 2.1$, $p = .03$). While the difference in effects for spatiotemporal context details and external details also was large, the outcomes were not significant (bivariate: $z = 1.9$, $p = .06$; partial: $z = 1.3$, $p = .18$).

Hodgetts and colleagues (Hodgetts et al., 2017) also found that ILF MD was significantly related to semantic details, but not to episodic details, although the difference in magnitude of the relationships was not significantly different. As this effect was more pronounced for left ILF ($r = -.48$) than right ($r = -.31$), we focused on left ILF MD for the current analysis. In our sample, however, left ILF MD was not significantly related to semantic details, with the evidence substantially favoring no relationship ($r = -.02$, $p = .91$, $BF_0 = .25$, $HDI = -.41$ to $-.01$). Controlling for age and global diffusion did not alter this outcome ($r = .13$, $p = .27$). Surprisingly, left ILF MD was significantly related to episodic details (with sequence details: $r = -.40$, $p = .02$, $BF_0 = 4.27$, $HDI = -.65$ to $-.07$; without sequence details: $r = -.39$, $p = .02$, $BF_0 = 3.62$, $HDI = -.64$ to $-.06$). However, controlling for age and global diffusion washed out these relationships (with sequence details: $r = .01$, $p = .47$; without sequence details: $r = -.04$, $p = .42$), suggesting that the latter effects are largely driven by age-related microstructural changes.

3.9 Exploratory analyses

Given that we did not find evidence for greater involvement of the parahippocampal CB in the generation of spatiotemporal context details over event element details, we conducted exploratory analyses with the anterior segment of the CB (FA/MD). Indeed, although our focus on the parahippocampal segment of the CB was motivated by the PMAT framework and evidence correlating diffusion MRI with episodic memory, the anterior segment does connect medial prefrontal and posterior cortical regions and thus may contribute to episodic detail generation, especially spatiotemporal context. Nonetheless, we found that none of these correlations were significant. They are reported in the Supplemental Materials.

4. Discussion

4.1 Anterotemporal and posteromedial contributions to episodic detail generation

In regard to the anterotemporal network, several pieces of evidence indicated that UF was linked with episodic detail generation, most strongly event element details. Specifically, better integrity of the UF, as measured by both FA and MD, was significantly related to greater generation of event elements, and this relationship was significantly stronger than the relationship of UF integrity to spatiotemporal context details. Also, whereas there was substantial evidence for a positive relationship between UF FA/MD and event element details, there was substantial evidence in favor of no relationship between UF FA/MD and spatiotemporal context details. Yet, we also must emphasize that the relationship between the UF and event element details was not significantly greater than the relationship between the CB and this detail type, suggesting that the retrieval of such content is likely supported to varying degrees by distributed neocortical regions, possibly through interaction between regions of this broader network. Nonetheless, overall, these findings support the notion that the anterotemporal network is related to the retrieval of episodic details about entities – more

so than spatiotemporal details. We suggest that this may reflect the role of this network in representing specific features of known entities that when incorporated into a unique event, add to and evoke episodic specificity of the unfolding experience.

Prior neuropsychological work has suggested a link between episodic detail generation and the UF (Irish et al., 2004; Levine et al., 1998; Levine et al., 2009). For instance, Levine and colleagues found that M.L., who had considerable damage to the right UF (along with diffuse axonal injury), had severe retrograde amnesia for autobiographical events, accompanied by disrupted subjective reports for anterograde memories. In the second of these studies (Levine et al., 2009), Levine and colleagues used the original Autobiographical Interview and revealed that episodic detail generation for anterograde memories was reduced in M.L., albeit not significantly, with the greatest reduction evident for thought/emotion details (an event element detail subtype in our scoring protocol). Irish and colleagues further found that in a group that included individuals with dementia, left UF FA was related to total episodic detail generation for remote autobiographical memories (Irish et al., 2014). Our results build on this work by showing that diffusion MRI can identify a relationship between normal variation in UF integrity and individual differences in different types of episodic detail.

For the posteromedial network, the relationship between episodic detail generation and the CB was somewhat mixed. On the one hand, we observed relationships that were significant, and substantial in terms of Bayesian hypothesis testing, between the parahippocampal portion of the CB and *both* event element details and spatiotemporal context details. On the other hand, this evidence was no longer significant when we controlled for age and global diffusion. We also did not reveal clear support of this particular white matter pathway being most strongly involved in the retrieval of spatiotemporal context details, nor was the link between the CB and spatiotemporal details greater than that of the UF. Overall, our findings only partially support our proposed correlational separation of event element and spatiotemporal context details. That is, although the UF was more strongly related to event element details relative to spatiotemporal context details, the connection between the CB and episodic detail generation was not weighted more heavily toward spatiotemporal context details relative to event element details.

In regard to non-episodic or “external” details, we did not find any significant relationships with UF or CB, and our Bayesian analyses indicated that our findings were generally substantially in favor of the null (i.e., no relationship). Also, when directly compared, the relationship between UF and event element details was significantly stronger than the relationship between this tract and external details. Notably, although the significance and Bayesian analyses also signaled a stronger link between CB and episodic over non-episodic details, the magnitude of the difference was not significant. Taken together, whereas the UF findings bolster the connection to event element details, the CB findings add to the overall mixed results for this tract. That is, while some evidence favors a more prominent role for the CB in episodic relative to external content, the degree of separation is unclear.

There are several reasons why we may not have identified a stronger link between the CB and spatiotemporal context details. First, the contributions of posteromedial white matter

pathways to autobiographical retrieval may not be as specialized for spatiotemporal context details as might be expected according to the PMAT framework. Notably, prior neuropsychological and fMRI evidence has raised the possibility that the involvement of posteromedial regions in the retrieval of perceptual details (autobiographical and lab-based “real world” stimuli) may not be scene specific (Ahmed et al., 2018; St.-Laurent et al., 2016). Similarly, Ramanan and colleagues recently proposed that the angular gyrus may be important for recalling multimodal, perceptual/contextual details for core elements of an episodic memory (Ramanan et al., 2018). Second, given that our participants were middle-aged to older, the lack of specialization of the CB may be an age-related outcome. There is evidence that older adults often approach memory tasks with different strategies and neural resources (Memel & Ryan, 2018; King, de Chastelaine, & Rugg, 2018; Reuter-Lorenz & Cappell, 2008; Davis, Dennis, Daselaar, Fleck & Cabeza, 2008; Naveh-Benjamin, Brav & Levy, 2007). Third, posteromedial regions may have complex pathways for communication with the MTL, as highlighted by recent theoretical work on the role of the functional organization of posterior cortical memory retrieval mechanisms (Burke et al., 2018; Ramanan et al., 2018). From this view, the combination of our diffusion methodology and focus on the entire parahippocampal segment of the CB may have limited our ability to detect subregions of the CB, or other pathways, that are primarily geared toward the generation of spatiotemporal context details. A fourth possibility is that our separation of episodic details into event element and spatiotemporal context is not precise enough to reveal the functional specialization of the CB in episodic remembering. Notably, our adapted Autobiographical Interview approach is novel and assumes that relatively process pure metrics of item- and spatiotemporal-related content can be filtered from narratives. This approach will need to be independently replicated to have more confidence in not only the CB results but also the other tract-specific findings. A fifth consideration is that the generation of spatiotemporal context details is more closely tied to the hippocampus – an idea that we consider further in section 4.2.

4.2 Comparison to Hodgetts and colleagues’ (2017) findings

Replicating the findings from Hodgetts and colleagues (Hodgetts et al., 2017), we found a significant and substantial relationship between fornix FA and spatiotemporal context details. This was evident with our novel composite, as well as the place and time composite examined by Hodgetts and colleagues. We also observed significant relationships when we examined place/scene details and time details separately. Notably, after controlling for age and global diffusion, the relationship between time details and fornix FA was no longer significant, but there remained a strong and significant relationship to place/scene details, and to the combined spatiotemporal context score (whether done as Hodgetts and colleagues did, or with temporal sequence details). This replication of Hodgetts and colleagues not only adds confidence to our results, but also they add credibility to the idea that an important function of hippocampal-cortical interaction is to tag events with space and time reference points, which Hodgetts and colleagues suggest forms the “context” of an autobiographical event. An emphasis on place/scene details also fits with evidence that the fornix is key for navigation (Ekstrom et al., 2017; Jankowski et al., 2013) and scene discrimination (Postans et al., 2014).

What is less clear is if the importance of the fornix reflects the hippocampus' role as an integrator of spatiotemporal details funneled from cortical regions to the MTL, direct cortical interaction via fornix circuitry with the mamillary bodies, anterior thalamic nucleus, and medial prefrontal cortex, or both mechanisms. We note that episodic autobiographical memories are rarely unidimensional in space and time, but rather often evoke spatial footprints and time stamps varying in scale from small (e.g., area of a room) to large (e.g., the event was from childhood). The types of details that we included in our spatiotemporal context score reflect the multidimensional nature of space and time of events with some perhaps being weighted more towards navigational properties (e.g., place/scene) and others more towards event or content context (e.g., time and temporal sequencing). We suggest that this may indicate that the fornix is an important pathway for bringing together these two types of episodic features. Notably, according to one theory of the functional organization of the long axis of the hippocampus, this neural region may be ideally suited for combining spatiotemporal details across small to large scales of event resolution (Poppenk, Encensmoen, Moscovitch & Nadel, 2013; Collin, Milivojevic & Doeller, 2015; Moscovitch, Cabeza, Winocur & Nadel, 2016).

Although we found a strong link between spatiotemporal context detail and the fornix, we also found evidence of a significant relationship between this white matter pathway and event element details. On the one hand, the latter relationship was no longer significant when we controlled for age and global diffusion. Also, for Bayesian hypothesis testing, the evidence for a relationship between fornix FA and spatiotemporal context details was more substantial relative to that of event element details. On the other hand, the magnitude of the relationship between the fornix and spatiotemporal details was not significantly greater than the relationship to event element details. Relatedly, we also found a significant bivariate relationship between fornix FA and perceptual details, which is consistent with neuropsychological and fMRI results from St-Laurent and colleagues (St-Laurent et al., 2014; 2016) showing a link between the hippocampus and the retrieval of perceptual details, broadly defined. Taken together, these findings can be interpreted as evidence that the fornix is important for retrieving spatiotemporal information, while also playing a role in the retrieval of other types of episodic content, perhaps because in episodic memories, multiple entities are imbedded in scenes. Broadly, this perspective fits with models that place the hippocampus at the top of a hierarchy of information integration (Eichenbaum et al., 2007; Moscovitch et al., 2016; Ranganath & Ritchey, 2012).

Similar to the UF and CB analyses, we did not find significant correlations between the fornix and external details, with our evidence consistently favoring no relationship between this detail type and tract (from a Bayesian perspective). We further showed that the relationship between the fornix and spatiotemporal context details (using the Hodgetts composite) was significantly stronger than the relationship between this tract and semantic details, consistent with the findings of Hodgetts and colleagues (Hodgetts et al., 2017). We found similar outcomes when we considered external details more broadly, although we acknowledge that in this case the magnitudes of the relationships did not significantly differ. In sum, these findings appear to largely confirm those of Hodgetts and colleagues (Hodgetts et al., 2017).

In contrast to the findings of Hodgetts and colleagues (Hodgetts et al., 2017), however, we did not identify a significant association between ILF MD and semantic details (although we did replicate the lack of a significant relationship with episodic details after controlling for age and global diffusion). As a major pathway between the occipital lobe and anterior temporal lobe, ILF is thought to facilitate the integration of unimodal information from the occipitotemporal fusiform gyrus into amodal semantic representations in the anterior temporal lobes (Lambon Ralph et al., 2017). The findings from Hodgetts and colleagues align with this neurocognitive model, whereas on the surface, ours do not. We speculate that the age of our sample might have contributed to our semantic detail-ILF results. Notably, recent work by Strikwerda-Brown and colleagues (Strikwerda-Brown et al., 2017) indicates that the semantic/external detail subtypes from the Autobiographical Interview blur the boundaries between episodic and semantic information. In light of these findings, one possibility is that young and older adults generate different types of external details while describing unique events, with younger adults focusing on more abstract semantics that align with the functional specialization of the ILF. Further fractionation of semantic details based on spatiotemporal proximity (near vs. far) and personal relevance (personal semantics vs. general semantics), as recommended by the recent literature on autobiographical memory (Strikwerda-Brown et al., 2017; Grilli & Verfaellie, 2014; 2016) may help elucidate the types of semantics generated by young and cognitively normal older adults, and the neural underpinning of these distinct semantic details.

4.3 Future directions

In the present study, we capitalized on an available data set that included cognitively normal middle-aged and older adults. However, the age of our sample comes with several caveats. As noted, the extent to which our CB findings, which departed from the PMAT framework, are an age-related effect remains unclear. Effects of age on diffusion metrics are also important to consider. Our MD findings were universally weakened by controlling for age and global diffusion, and this washed out effects for the CB. The divergence of findings for FA and MD is not too surprising. Although the precise neural mechanisms of FA and MD remain unclear (Winston, 2012), they do estimate structural integrity in different ways, and FA may more closely reflect axonal directional organization and coherence (Billiet et al., 2015). Also, age-related change to FA and MD may not entirely overlap spatially (Sexton et al., 2014). The significant correlations between CB MD and age/global diffusion, combined with our modest sample size, could account for why our MD results did not hold after controlling for age-related variables. While the effects remained in the predicted direction, this should be interpreted cautiously. They do, nonetheless, motivate further investigation in a larger group, and perhaps a younger sample, as this could add clarity to the relationships between FA/MD and episodic detail generation.

While the separation of episodic details into event element and spatiotemporal context details is a novel feature of our study, it also highlights the need for further validation. For instance, convergence in other clinical and non-clinical populations and using complementary cognitive neuroscience methods would bolster the notion that episodic content can be reliably divided into details related to items versus spatiotemporal context. More broadly, much could be gained from applying this scoring approach in the context of

narratives that contain more information describing place/scene and time features of autobiographical events. Critically, in our sample, fewer details were classified as spatiotemporal in nature. We cannot rule out the possibility that this contributed to the mixed CB findings specifically, or other outcomes more broadly, although the limited range appears not to have compromised the ability to detect a relationship with the fornix. It is possible that young adults generate more spatiotemporal details, or perhaps in future research, it would be useful to guide participants to focus on describing the spatiotemporal context of unique events.

Consistent with prior studies using the Autobiographical Interview approach, in the present study we emphasized scoring the content of self-generated narratives, and we modified the original Autobiographical Interview scoring protocol to extract additional data from such memory reports. As is the case with most autobiographical memory research, we could not evaluate the veracity of our participants' memory reports. This likely introduces some error in our findings and raises the possibility that our detail and white matter tract relationships more broadly reflect individual differences in mental event construction as opposed to memory retrieval specifically. Indeed, the cognitive and neural overlap between remembering and imagining suggests this is a strong possibility (Schacter, 2012; Schacter & Addis, 2007). Relatedly, it would be interesting to investigate whether our diffusion-episodic detail relationships hold when narrative construction of an event does not require memory retrieval or event construction per se. This question has been explored in MTL amnesia comparing past and future retrieval to picture description, with some evidence that the hippocampus may be necessary for the generative retrieval of episodic details, but not the perception and generation of readily available episode details of pictures (Race et al., 2011). Also, the lack of significant relationships between external details and our white matter tracts of interest cast additional doubt on the notion that these pathways serve broader roles in verbosity. However, we acknowledge that much remains unknown about the extent to which language, socioemotional, and personality factors influence how memories are orally narrated. This will be important to address, especially when narrative report scoring protocols require fine-grained separation of detail types. A future study could evaluate the relationship between cortical white matter tracts and a range of oral reports, as well as measure personality, language functioning, and the socioemotional context of memory sharing, as doing so could tease apart the contributions of memory versus other cognitive processes to such narratives.

We also want to emphasize that our UF findings need to be considered in light of work by Irish and colleagues, who have shown that episodic remembering for recent events is relatively spared in individuals with semantic dementia (Irish et al., 2012a; 2012b). Although we did not ask our participants to give a precise date for their memories, they may have tended to draw on events that have begun to undergo a semanticization process (while we acknowledge that this seems unlikely for the most recent memory). Also, the UF has the potential to be the functional confluence of multiple anterior temporal lobe regions, perhaps most notably the perirhinal cortex. Therefore, it will be important to investigate further whether the relationship between the UF and episodic memory retrieval, especially for entity specific details, varies as a function of memory remoteness, and lesion studies could help

piece together a more complete view of the functional specialization of anterotemporal regions.

4.4 Summary

The present study adds to recent work showing that high-resolution MRI of healthy individuals can provide a more refined view of the hippocampal-cortical system that supports individual differences in episodic detail generation (Hodgetts et al., 2017; Palombo et al., 2018b). Our findings also support the notion that episodic detail retrieval is a function of a hierarchical, neuroanatomically guided framework of information processing that centers on, but extends beyond, the hippocampus. We suggest that future work should continue to use individual differences in the quality of constructive thought to test the boundaries between hippocampal and cortical involvement in episodic autobiographical memory and other forms of mental time travel.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Depiction of the PMAT framework with relevant white matter pathways. The anterotemporal system includes the perirhinal cortex (PRC), anterior ventral temporal cortex (aVTC), amygdala (AMYG), and lateral orbitofrontal cortex (IOFC). The posteromedial system includes parahippocampal cortex (PHC), retrosplenial cortex (RSC), posterior cingulate (PCC), angular gyrus (AnG), precuneus (Prec), anterior thalamus and mammillary bodies (aThal), and medial prefrontal cortex (mPFC). Hippocampus (HC) and ventromedial prefrontal cortex (vmPFC) are posited as sites of integration.

<i>Episodic Detail type</i>	<i>Definition</i>	<i>Examples</i>
<u>Event Element Details</u>		
Action or conversation/ language-based	Mention of the presence of or actions/language of a person (or other animal/object)	"Tom was there." "She laughed" "He dropped the plate" "I said to him '...'"
Thoughts/feelings	Description of a thought or feeling of self or another person/entity	"I remember feeling very pleased." "He was annoyed"
Perceptual (entity)	Visual or other sensory description of a person or object	"The car was a bright orange color" "It was cold to the touch"
<u>Spatiotemporal Context Details</u>		
Place/Scene	Description of the location of an event or event entity	"We were in the car" "The dog was to my right"
Time	Details about the timing of an event	"It was in the spring" "In the morning..."
Temporal Sequencing	Details capturing the passage of time or temporally-based causal relationships of things	"Right after that..." "And then he..."

Figure 2.
Description of modified episodic detail scoring protocol.

Figure 3. Primary regions of interest depicted on a standard white matter template (Fornix in red, UF in blue, and CB in green).

Figure 4.
Correlations between the bilateral uncinatus fasciculus (UF) (FA and MD) and event element details, spatiotemporal context details, and external details.

Figure 5.
Correlations between the cingulum bundle (CB) (FA and MD) and event element details, spatiotemporal context details, and external details.

Figure 6.
Correlations between the fornix (FA and MD) and event element detail, spatiotemporal context details, and external details.