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## Fornix white matter microstructure differentially predicts false recollection rates in older and younger adults

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ABSTRACT

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# Healthy aging is accompanied by increased false remembering in addition to reduced successful remembering in older adults. Neuroimaging studies implicate age-related differences in the involvement of medial temporal lobe and fronto-parietal regions in mediating highly confident false recollection. However, no studies have directly examined the relationship between white matter microstructure and false recollection in younger and older adults. Using diffusion-weighted imaging and probabilistic tractography, we examined how white matter microstructure within tracts connecting the hippocampus and the fronto-parietal retrieval network contribute to false recollection rates in healthy younger and older adults. We found only white matter microstructure within the fornix contribute to false recollection rates, and this relationship was specific to older adults. Fornix white matter microstructure did not contribute to true recollection rate, nor did common white matter contribute to false recollection, suggesting fornix microstructure is explicitly associated with highly confident false memories in our sample of older adults. These findings underlie the importance of examining microstructural correlates associated with false recollection in younger and older adults.

#### 1. Introduction

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Aging is accompanied by declines in successful remembering as well as increases in false memories, or memories for events that never truly occurred (Koutstaal and Schacter, 1997; Norman and Schacter, 1997; Tun et al., 1998). Age-related memory impairment is equally impacted by increases in false remembering as it is by declines in successful remembering (McCabe et al., 2009). Within the context of memory, older adults exhibit the most considerable impairment in recollection-based memory errors (Anderson et al., 2008; Bastin and Van der Linden, 2003; Dennis et al., 2014; McCabe et al., 2009). Age-related deficits in recollection are accompanied by deficits in neural activation within the recollection network, including reduced activity in the hippocampus, visual cortex and frontoparietal cortex (Ally et al., 2008; Daselaar et al., 2006; Dennis et al., 2014; Duarte et al., 2010; Zheng et al., 2019). Concerning the core recollection region, the hippocampus, altered hippocampal recruitment in older adults may stem from an age-related shift away from pattern separation (the differentiation of overlapping representations into distinct representations) towards pattern completion (the reactivation of representations in the response of degraded cues) (Yassa et al., 2011). Such shifts are observed alongside increased activity in CA3 and dentate gyrus in older compared to younger adults and suggest that older adults are less able to distinguish between overlapping memory representations such as target items and related lure items (Yassa et al., 2011). This, in turn, is proposed to lead to increases in false recollection in older adults.

Further examining the neural basis of false recollection, Dennis et al. (2014) found that older adults elicited significantly higher rates of false recollection compared to younger adults, but without increased neural recruitment among older adults. Instead, older adults exhibited reduced activity in regions throughout the episodic retrieval network, including prefrontal, parahippocampal gyrus, and occipitoparietal cortex, suggesting an age-related deficit in reconstructive processes contributing to increases in false recollection (Dennis et al., 2014). Additionally, older adults display reduced hippocampal activation compared to younger adults while attempting to correctly reject lures during recollection

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processes (Tsukiura et al., 2014). Other research has also shown that activity in fronto-parietal regions mediates recollection-based false memories (Kim and Cabeza, 2007; Okado and Stark, 2003; Slotnick and Schacter, 2004; Webb et al., 2016). Supporting this, meta-analyses of retrieval activation have identified consistent neural activation associated with recollection in left superior parietal and dorsolateral and anterior prefrontal cortex (PFC; (Kim, 2013; Spaniol et al., 2009). Similarly, a meta-analysis of false memory studies from our group has also implicated the fronto-parietal network in false retrieval (Kurkela and Dennis, 2016). Understanding the collaborative role of hippocampal and fronto-parietal retrieval network regions is therefore critical in understanding the neural basis of age-related increases in false recollection.

While studies investigating the neural basis of age-related memory decline have focused primarily on differences in neural activation between younger and older adults, a handful of studies have also looked to the role of white matter microstructure in mediating memory processes. Notably, several studies show that age-related declines in recollection are associated with individual differences in white matter integrity of the fornix, a white matter tract connecting the medial temporal lobe (MTL) and medial diencephalon (Nestor et al., 2007; Pagani et al., 2008; Rudebeck et al., 2009; Tsivilis et al., 2008; Vann et al., 2009). For example, higher microstructural integrity in the fornix tail was found to be associated with significantly better recollection memory than familiarity memory (Rudebeck et al., 2009). No significant correlation between fornix microstructure and familiarity memory was observed across two non-mnemonic tasks, suggesting that this may be a distinct MTL-diencephalon pathway underlying recollection-specific processing. Supporting this distinction, Easton et al. (2009) investigated the effects of lesions to the fornix on disruption of recollection in rodents. Results showed that animals with fornix lesions had recollection impairments, but no such impairment was observed for judgments of familiarity in the same animals. While the relationship between white matter microstructure and true recollection processes is emerging, little work has examined the relationship between such microstructural measures and false recollection.

To our knowledge, only one study has examined the relationship between white matter microstructure and false memories. Specifically, Fuentemilla et al. (2009) examined false recollection rates using diffusion tensor imaging and the Deese-Roediger-McDermott (DRM) paradigm in a sample of younger adults. They found individual differences in false memories were positively related to fractional anisotropy (FA; thought to reflect the efficiency of neuronal connections) within the superior longitudinal fasciculus (SLF), which connects prefrontal regions to posterior regions. The authors attributed this decline in FA to increased neural activation of related lures, or items similar to original studied items. Critically, however, no studies have examined how the relationship between white matter microstructure in memory-relevant tracts and false recollection rates may be affected in older adults who typically exhibit both increases in false memories and declines in white matter microstructure (McCabe et al., 2009; Pagani et al., 2008).

Inspired by these findings, we sought to extend the examination of false memory rates and white matter microstructure to older adults, with a specific emphasis on examining the relationship between false recollection and white matter microstructure within the retrieval network in a sample of healthy younger and older adults. Based on previous research, we posited that we would observe age-related differences in the relationship between false recollection and white matter microstructure in the fornix and tracts connecting the fronto-parietal retrieval network, including the SLF. Additionally, recent studies have demonstrated that white matter properties common among multiple tracts, as opposed to specific tracts, maintain relationships with behavior in aging (Johnson et al., 2015; Webb et al., 2019). To account for this, we also examined potential age-related differences in the relationship between common white matter microstructure and false recollection.

#### 2. Materials and methods

#### 2.1. Participants

Participants in the current analysis were drawn from two prior false memory studies in the lab in which DTI data was collected, but not previously analyzed (Dennis et al., 2014; Webb and Dennis, 2018). In the case where an individual participated in both studies (n = 1), behavioral and DTI data from their second participation was used. One participant was excluded from analysis for failure to track all tracts of interest (see 2.5 Probabilistic Tractography Procedures). In total, 44 younger adults (M = 22.29; SD = 3.15, range = 18–29) and 44 older adults (M = 73.98; SD = 6.11, range = 62–85) were included in the following analyses. In accord with previously reported fMRI analyses of these datasets, all participants were screened for history of neurological disorders and psychiatric illness, dementia, and contraindications to magnetic resonance imaging. All participants provided written informed consent and received monetary compensation for their participation. The Institutional Review Board at the Pennsylvania State University approved all procedures.

#### 2.2. False memory tasks

Behavioral data were collected from two long-term episodic memory tasks used to investigate age-related differences in neural activation associated with visually-based false memories (for a full description of task designs and procedures, see Dennis et al., 2014; Webb and Dennis, 2018). Briefly, both encoding tasks included incidental encoding of objects (Dennis et al., 2014) and objects within scenes (Webb and Dennis, 2018)(see Supplemental Fig. 1a and ca&c for an overview of each task's encoding format). Objects in both tasks were related to either a category (e.g., "cats"; "balloons"; Dennis et al., 2014) or schematic theme (e.g., "Christmas"; "Bathroom"; Webb and Dennis, 2018). During memory retrieval, participants were presented with target objects previously viewed during study, lure objects related to the encoded categories or schemas, and unrelated lure objects (See Supplemental Fig. 1b and d). Participants were asked to indicate their memory for each object using the same 'Remember/Know/New' paradigm in both tasks. Participants were instructed to respond with 'Remember' if they recalled specific details of the presented stimulus (e.g., color, shape, or their thoughts of the stimulus during encoding). Participants were instructed to respond with 'Know' if the stimulus appeared familiar, but they could not recollect specific details of its previous presentation. Participants were instructed to respond with 'New' if they believed the stimulus was not present during encoding. Behavioral responses were sorted according to signal detection theory metrics: hits, false alarms, correct rejections, and misses (Green and Swets, 1966). Given our goal of relating false recollection with white matter microstructure, we calculated the false alarm rate associated with 'Recollection' responses to related lures in each of the 2 contributing studies. We then z-scored the false recollection rates within each study. A two-sample t-test across studies indicated that there was no difference in the mean or distribution of scores between studies (see 3.1 Behavioral Results). Thus, data from both studies were combined. A similar procedure was undertaken for true recollection and false familiarity (by taking response rates to 'Know' responses).

#### 2.3. Image acquisition

All imaging data were collected on a 3T Siemens Magnetom Prisma Fit Scanner at the Pennsylvania State University's Social, Life, and Engineering Sciences Imaging Center (SLEIC). Diffusion MR scans were acquired for each participant using a twelve channel headcoil and parameters did not differ between Dennis et al. (2014) and Webb et al. (2018) (TR = 6,700 ms; TE = 93 ms; flip angle = 90°; Field of View = 240 mm; matrix =  $128 \times 128$ ; voxel size =  $1.9 \times 1.9 \times 3.0$  mm; 48 axial slices; 20 diffusion-weighted directions;  $b = 1,000 \text{ s/mm}^2$ ; 1 non-diffusion-weighted reference image).

High-resolution T1 images were collected using MPRAGE sequences for both the studies by Dennis et al. (2014) and Webb and Dennis (2018), and acquisition parameters were similar between the two studies. In Dennis et al. (2014) structural images were collected using a 2,300 ms TR, 3.41 ms TE, 230 mm field of view,  $256^2$  matrix, 160 axial slices, and 0.9 mm slice thickness for each participant. In Webb et al. (2018), structural images were collected using a 1,650 ms TR, 2.03 ms TE, 256 mm field of view,  $256^2$  matrix, 160 axial slices, and 1.0 mm slice thickness for each participant.

#### 2.4. Diffusion-weighted imaging (DWI) pre-processing

FSL 5.0 (Smith et al., 2004) and FMRIB's Diffusion Toolbox (FDT (Behrens et al., 2003); were used for image pre-processing. Raw images were brain extracted, eddy current corrected, and motion-corrected using affine transformation to the B0 image. All images were visually inspected for artifacts such as susceptibility and fat saturation artifacts (Yeh et al., 2012), and none were observed. We used FSL's FNIRT (Andersson et al., 2007) to transform images from native diffusion space to MNI template space to obtain inverse parameters. To create FA images, FSL's DTIFIT (Behrens et al., 2003) was used to fit a tensor model within each voxel.

#### 2.5. Probabilistic Tractography Procedures

Based on our a priori predictions and in line with past research demarcating the episodic retrieval network (Spaniol et al., 2009), we identified five tracts-of-interest that have been shown to support this network. These tracts included (see Fig. 1): the fornix, the forceps minor, the superior longitudinal fasciculus (SLF), the inferior longitudinal fasciculus (ILF), and the dorsal cingulum bundle.

Due to the curved nature of the fornix tract, making it challenging to track traditionally with spherical target regions, we followed tracking procedures validated by Brown et al. (2016) for fornix tracking. The hippocampus was selected as a seed and target region from the Harvard-Oxford Subcortical Atlas and thresholded at 50. The fornix 'crus/stria terminalis' was used as a waypoint, and the 'fornix body' was used as a seed and target region, both were chosen from the ICBM-DTI-81 white matter labels. Also, to create a more morphologically accurate exclusion mask for fornix tracking, we dilated the fornix template resulting from Brown's 2016 study (publicly available in FSL) and inverted the dilated mask. Fornix seed regions and target regions, waypoints, and the exclusion mask began in FMRIB58 FA 1 mm space and were nonlinearly warped into each participant's native diffusion space for tractography with FSL's FNIRT function and parameters obtained during preprocessing.

To define the latter four tracts, we selected seed regions adjacent to white matter tracts using seed voxels generated from a meta-analysis examining neural activation underlying successful episodic memory recollection at retrieval (Spaniol et al., 2009). This allowed us to identify white matter tracts based on regions functionally relevant to episodic retrieval performance. Specifically, we selected activation coordinates across all regions based on significant clusters of univariate activity for objective recollection found in Spaniol et al. (2009). Regions are provided according to each tract of interest and all coordinates are reported in Montreal Neurological Institute (MNI) space: forceps minor: left frontal pole (-36, 48, 2), right frontal pole (36, 52, 8); left dorsal cingulum bundle: left anterior cingulate cortex (-14, 36, 32), left posterior cingulate cortex (-20, -38, 36); right dorsal cingulum bundle: right anterior cingulate cortex (14, 36, 32), right posterior cingulate cortex (20, -38, 36); left ILF: left occipital cortex (-20, -84, 0), left temporal cortex (-42, -2, -26); right ILF: right occipital cortex (20, -84, 0), right temporal cortex (42, -2, -26); left SLF: left dorsolateral PFC (-50, 22, 26), left inferior parietal sulcus (-36, -58, 46); right SLF: right dorsolateral PFC (44, 38, 30), right inferior parietal sulcus (34, -66, 44). We then generated seed and target region masks by dilating a sphere around the peak coordinates by a 6 mm kernel. To maintain homologous tracts across hemispheres, for any non-homologous tracts of interest, we flipped the peak coordinate across the x-axis. To prevent cross-hemispheric and thalamic streamlines, we included the sagittal midline (x = 0) and subcortical regions in exclusion masks for all tracts of interest, except the fornix and the forceps minor. For purposes of realigning tractography seeds from MNI template space to participants' native space, we performed nonlinear transformations using FSL's FNIRT. Seed regions, target regions, and exclusion masks for the forceps minor, SLF, ILF, and dorsal cingulum bundle began in MNI space and were nonlinearly warped into each participant's native diffusion space using nonlinear transformation parameters.

Probabilistic tractography followed procedures used by Brown et al. (2016) and Rizio and Diaz (2016). To prepare for FSL's PROBTRACKX2, we used BEDPOSTX (Behrens et al., 2003), which creates a probabilistic diffusion distribution with a two-fiber model in each voxel. PROB-TRACKX2 (Behrens et al., 2003) was then carried out in seed-mask mode within each participant's native diffusion space using seed and target region masks for each tract of interest. Target region masks were also used as waypoints using the 'AND' condition. To facilitate the generation of proportionalized tract images in the final tractography step, streamline images (fdt\_paths) were kept in raw streamline count units by disabling pathlength correction. All other flags and parameters for PROBTRACKX2 were set at default settings. Tractography was run separately for all tracts. To reduce noise in tracking a given tract, we first ran PROBTRACKX2 from the seed region to the target region. We then reran PROBTRACKX2, setting the target region as the seed region and the seed as the target. To create proportionalized images within participants, for each tract, we divided the non-pathlength corrected fdt\_paths image by its respective waytotal (number of successful streamlines) and thresholded at 5%. To produce finalized tracts-of-interest within each participant for subsequent FA extraction



**Fig. 1.** Tracts of interest. Group-average probabilistic maps of tracts of interest are depicted on the MNI T1 1 mm template: fornix (yellow), forceps minor (pink), SLF (blue), ILF (red), dorsal cingulum bundle (green). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

we binarized and convolved the two proportionalized tract images (See Fig. 1 for group-average examples of each tract of interest).

#### 2.6. Diffusion extraction parameters

For quality assurance, every convolved tract was visually inspected following tractography within each participant's native diffusion space via custom visualizations created with FSL's slicer and overlay utilities (png images available on OSF). For participants who did not have a visible or complete tract, target regions and seed regions were shifted axially one region mask radius (4 voxels) towards the tract of interest and re-tracked. This procedure worked for all but one participant who was excluded from statistical analysis for repeated failure to successfully track all tracts of interest. FA values were then extracted from within the convolved tracts. To minimize partial volume effects, we excluded voxels with FA values < 0.2. FA values from homologous tracts were averaged across hemispheres to create a single FA measure per tract for homologous tracts.

#### 2.7. Statistical analyses

We wished to examine if common white matter microstructural variance, rather than a specific tract of interest, predicted recollection false alarms. We conducted a principal component analysis (PCA) on the FA of all five tracts of interest, with one factor to reflect general white matter microstructure. We included this factor as a nuisance predictor in subsequent regression analyses.

We first examined potential age and study differences in false recollection rates with a 2 (age group: younger adult; older adult) by 2 (study group: Dennis et al., 2014; Webb et al., 2018) ANOVA. To examine the relationship between white matter microstructure in specific tracts of interest and false memory rates in our sample of younger and older adults, we first conducted a multiple linear regression with false recollection rates as the outcome variable. Predictors in the first regression model included age group (younger adult, older adult) and study (Dennis et al., 2014; Webb et al., 2018) as categorical variables and the white matter factor, FA from each tract as well as each tract FA by age interaction term as predictor variables.

In our second regression, we examined if any behavioral relationship with white matter microstructure in specific tracts of interest reflected a bias to respond 'old'. To do so, we conducted a multiple linear regression with recollection hits as the outcome variable. Predictors in the regression included age group (younger adult, older adult) and study (Dennis et al., 2014; Webb et al., 2018) as categorical variables and the white matter factor, FA from each tract, as well as each tract FA by age interaction term as predictor variables.

All statistical models were completed using RStudio (http://www.rst udio.com/) and the following packages: knitr (Xie, 2019), dplyr (Wickham et al., 2018), tidyverse (Wickham, 2017), foreign (R Core Team, 2017a), and stats ((R Core Team, 2017b).

#### 3. Results

#### 3.1. Behavioral Results

We conducted a 2 (age group: younger adult; older adult) by 2 (study group: Dennis et al., 2014; Webb et al., 2018) ANOVA to investigate potential age and study differences in false recollection. We observed a significant age deficit in false recollection rates (F[1,83] = 4.09, p < .05) as well as a significant age by study interaction (F[1,83] = 5.84, p < .05). Follow-up t-tests revealed a significant age reduction in false recollection rates in the study by Dennis et al. (2014) (t[25.15] = -3.26, p < .01), but not by Webb et al. (2018) (t[50.22] = 0.30, p > .05). Critically, we observed no significant differences in false recollection rates between the two studies (F[1,83] = 0.04, p > .05). Thus, data were collapsed across studies in subsequent analyses.

#### 3.2. Tract FA and memory performance

In our first regression model, where every tract FA and age by tract moderator term were used to predict false recollection, only the fornix FA by age group interaction term significantly predicted recollection false alarms (b = -22.18, t(72) = -2.55, p < .05). Age group, study, the white matter factor, all other tract-specific FA, and all other interaction terms failed to predict recollection false alarms (all p's > .05; Table 1.). The negative parameter estimate for the fornix FA by age interaction term reflected a negative relationship between fornix FA and recollection false alarm rates in older adults (b = -17.68, t(40) = -2.56, p < .05) and a numerically positive, but non-significant, relationship in younger adults (b = 2.02, t(41) = 1.99, p > .05). See Fig. 2 for depictions of the relationships between tract FA and recollection false alarms for all tracts of interest.

To address the possibility that the observed relationship between fornix FA and false memory does not reflect a valid error in memory decision-making, but rather a bias to respond that stimuli have been seen previously, we replicated the first regression using true recollection as the outcome variable. Neither age group, study, white matter factor, any tract FA terms, nor any of the age by tract FA interaction terms significantly predicted recollection hit rates (all p's > .05). This suggests the contribution of fornix FA in our study is specific to false memories rather than a bias for reporting 'old'.

At the suggestion of a reviewer, we performed a mediation analysis to further examine the role of fornix FA in the context of recollection false memories. Specifically, age group was the independent variable (X), fornix FA was the mediator (M), and recollection false alarms were the outcome variable (Y). Mediation was performed using regression and bootstrapping to examine whether fornix FA accounted for the relationship between age group and false recollection rates. Controlling for study and the white matter factor, we found that fornix FA did not mediate the relationship between age group and false recollection rates ([.-.0054, .0106]). Such results suggest that fornix FA may not represent the pathway through which age-associated increases in false recollection emerge over the adult lifespan. Rather, taken together with the significant age x fornix FA and false recollection depends upon age.

#### 4. Discussion

#### 4.1. White matter microstructure and false recollection

The current study sought to examine the relationship between white matter microstructure within memory-relevant tracts and false recollection rates in younger and older adults. Among our five tracts of interest, we found a negative relationship between microstructure of the fornix and false recollection in aging, such that fornix white matter

Table 1						
Relationship	between	false	recollection	and	tract	FA.

Predictor	β	t	р
Intercept	5.89e5	1.02	0.32
Study	.266	1.07	0.29
Age Group	1.83	.38	0.71
White Matter Factor	4.0e4	1.02	0.31
SLF FA	-4.05e5	-1.02	0.31
ILF FA	2.86e5	-1.02	0.31
Forceps Minor FA	-1.93e4	-1.02	0.31
Dorsal Cingulum Bundle FA	-3.3e5	-1.02	0.31
Fornix FA	-2.82e5	$^{-1.2}$	0.31
Age Group x SLF FA	-3.70	-0.37	0.71
Age Group x ILF FA	9.33	1.23	0.22
Age Group x Forceps Minor FA	1.10	0.45	0.65
Age Group x Dorsal Cingulum Bundle FA	2.04	0.25	0.80
Age Group x Fornix FA*	-22.18	-2.55	0.01

\*Effects significant at p < .05.



Fig. 2. Plots depicting the relationships between tract FA and false recollection. Age group moderated the relationship between fornix FA and recollection false alarms such that fornix FA negatively predicted recollection false alarms in older adults, but not younger adults.

microstructure negatively predicted false recollection rates in older, but not younger, adults. This relationship also did not reflect a bias for identifying retrieval items as 'old', as fornix white matter microstructure also did not predict true recollection rates in our older adult sample. Additionally, common white matter microstructure among our tracts of interest did not contribute to false recollection in our sample.

The relationship between fornix white matter microstructure and false recollection among older adults furthers our understanding regarding functional recruitment and connectivity of the retrieval network underlying episodic retrieval. Specifically, past research has shown that the MTL and PFC activate collaboratively as part of a recollection network (Aggleton and Brown, 1999; Geib et al., 2017; King et al., 2015; Rugg and Vilberg, 2013; Shimamura, 1994; Spaniol et al., 2009), and that connectivity between the MTL and PFC is altered in older adults (Sander M. Daselaar et al., 2006; Dennis et al., 2008; Grady et al., 2003; Sala-Llonch et al., 2014). Older adults, compared to younger adults, display reduced hippocampal activity associated with true recollection (Daselaar et al., 2006) as well as impaired monitoring during recollection-based retrieval (Buschert et al., 2010). Age-related reductions in prefrontal and hippocampal activation associated with monitoring of item-specific details have also been observed during retrieval of false memories (Dennis et al., 2008, 2014; Fandakova et al., 2014; Paige et al., 2016) and is posited to contribute to increased false memories in older adults.

Given the coupling between the PFC and MTL as part of the retrieval process, it stands that the white matter connections among such regions are also a critical component of their functional relationship. While transmission of information among regions implicated in higher-order retrieval processes may be related to microstructural differences associated with successful remembering (Charlton et al., 2010; Gorbach et al., 2017; Lockhart et al., 2012; Metzler-Baddeley et al., 2011), reduced microstructural integrity of a tract connecting the MTL, a region associated with basic computations of stimuli information, appears critical in the formation of recollection-based false memories in later adulthood. Recent reports suggest global or common white matter microstructure contributes to cognition in older adults (Johnson et al., 2015; Webb et al., 2019); however, our findings support the notion that specific white matter microstructure variance maintains a relationship with false recollection. Further, inconsistent age-related differences in hippocampal activation during false memory processing (Dennis et al., 2015; Devitt and Schacter, 2016) may be attributed to individual differences in fornix white matter microstructure associated with false recollection among older adults.

It should be noted that the observed relationship between fornix white matter microstructure was specific to false recollection rates, and not true recollection, a bias for responding 'old' in our older adults. While previous studies have found fornix microstructure positively relates to true remembering in younger adults (Douet and Chang, 2015; Mielke et al., 2009; Sexton et al., 2010; Zhuang et al., 2013), the current study adds to a growing literature demonstrating that, in older adults, fornix white matter microstructure underlies recollection processes. Notably, Rudebeck et al. (2009) showed that fornix white matter microstructure predicted true recollection rates, but not familiarity rates among younger adults, and Metzler-Baddeley et al. (2011) found fornix white matter microstructure predicted true recall, but not recognition, in older adults. Similarly, in our sample, neither fornix FA, nor an age by fornix FA interaction contributed to false familiarity rates (all p's > 0.05; See Supplemental Table 1). Additionally, animal studies show that lesions to the fornix in rats results in impaired true recollection, but not familiarity (Bussey et al., 2000; Easton et al., 2009; Shaw and Aggleton, 1993). It should also be noted that the studies by Rudebeck et al. (2009), Metzler-Baddeley et al. (2011), and Easton et al. (2009) did not examine the relationship between false recollection or false recall and fornix microstructure, so it is unknown whether their findings would extend to false recollection as well. Amnesia case studies also point towards disruptions in fornix integrity underlying recollection, yet not familiarity, processing (Tsivilis et al., 2008; Vann et al., 2009). Our results add to this literature, demonstrating that reduced white matter microstructure in the fornix of older adults is related specifically to increases in false recollection, but not false familiarity. The present finding of false versus true recollection associated with fornix microstructure in older adults also supports the notion that distinct diencephalon pathways contribute to subtle differences among memory response processes during retrieval that emerges in later adulthood.

Interestingly, our study did not find a relationship between false memories and white matter microstructure within the SLF, as Fuentemilla et al. (2009) reported in their investigation in younger adults. This may be due to subtle differences in retrieval processes examined between the two studies. While we examined recollection and familiarity of rich visual stimuli using a Remember/Know/New paradigm, Fuentemilla et al. (2009) investigated recall and yes/no recognition processes associated with a verbal DRM paradigm. As younger adults have been found to utilize fronto-parietal regions during high confidence as opposed to low confidence false memories (Kim and Cabeza, 2007), our results, in tandem with Fuentemilla et al. (2009), suggest a shift may occur in later adulthood as hippocampal processing differences become more prominent between younger and older adults. Further, diverging results may reflect differences in stimuli used, and thus the nature of false memories examined. It may be that the SLF plays a more significant role in semantic false memories influence by frontal and parietal regions while fornix microstructure underlies MTL failures in recollection for perceptual details. This theory is supported by a recent meta-analysis from our lab showing that verbal, but not pictorial false memories, are mediated by common neural activation in the parietal and prefrontal cortex (Kurkela and Dennis, 2016).

Finally, at the helpful suggestion of a reviewer we assessed the potentially causal role of fornix FA in the context of age and false recollection rates. We found that fornix FA did not mediate the relationship between age and highly confident false memories. Our finding that age significantly moderated the association between fornix FA and false recollection suggests that a link between the state of the diencephalon pathway and highly confident false memories may be late emerging in the adult lifespan (i.e. present in older adults, but not in younger adults). It is well-established that this pathway is affected by aging and age-associated neurodegenerative disease, and is associated with long-term memory alterations. Our current findings extend these observations to highly confident false memories, which we expect to contribute uniquely to older adults' quality of life and activities of daily living.

#### 4.2. Limitations and future directions

While the current study contributes to our understanding of the relationship between white matter microstructure and false memories in later adulthood, certain limitations that should be considered. First, given the correlational nature of our analyses, future studies are needed to determine the causal role of white matter microstructure and increases in false recollection in older adults. Second, we chose five tracts of interest predicted to contribute to false recollection rate differences based on regions of common neural activation observed during episodic memory retrieval (Spaniol et al., 2009). Future studies should also examine how other white matter tracts connecting portions of the limbic system, such as the parahippocampal cingulum or uncinate fasciculus, may relate to false memories. Further, in the current study we utilized a tractography approach that has been shown to be informative and reliable in elucidating white matter microstructure properties underlying cognition and aging (Brown et al., 2016; Rizio and Diaz, 2016). Moving forward, more advanced methods, such as Neurite Orientation Dispersion and Density Imaging (NODDI), may offer more detailed information regarding the neurite factors contributing to FA and its relationship to false recollection among older adults. Finally, recent investigations have found that cognitive and exercise interventions improve fornix white matter microstructure in older adults (Antonenko et al., 2016; Burzynska et al., 2017). Thus, additional studies should examine whether increased fornix microstructural integrity relates to training-induced reductions in false memory.

#### 4.3. Conclusions

Here we presented novel findings that white matter microstructure within the fornix, a primary output tract of the MTL, negatively predicted false recollection rates in older adults. Moreover, the microstructure within this tract did not contribute to an 'old' response bias, suggesting that its influence in aging may be specific to false recollection in older adults. White matter microstructure common among tracts implicated in recollection processes also did not contribute to false recollection. While previous investigations of false memories highlight the influence of differences in neural activation between younger and older adults, our results highlight the importance of examining agerelated differences in white matter microstructure underlying agerelated increases in false memories.

#### Credit author statement

Jordan D. Chamberlain: Methodology, Conceptualization, Software, Validation, Formal analysis, Writing - Original Draft, Writing -

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#### Declaration of competing interest

The authors declare no competing financial interests.

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#### Appendix A. Supplementary data

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