Curious connections: white matter pathways supporting individual differences in epistemic and perceptual curiosity

Abbreviated title: Curious connections

Ashvanti Valji[1], Alisa Priemysheva[1], Carl J. Hodgetts[1], Alison G. Costigan[1], Greg D. Parker[2,1], Kim S. Graham[1], Andrew D. Lawrence[1], Matthias J. Gruber[1]

[1]Cardiff University Brain Research Imaging Centre (CUBRIC), School of Psychology, Cardiff University, Cardiff, United Kingdom, CF24 4HQ.

[2]Experimental MRI Centre (EMRIC), School of Bioscience, Cardiff University, Cardiff, United Kingdom, CF10 3AX.

Corresponding Authors:

Ashvanti Valji, ValjiA@cardiff.ac.uk;

Matthias J. Gruber, GruberM@cardiff.ac.uk;

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Abstract

Across the lifespan, curiosity motivates us to learn, yet curiosity varies strikingly between individuals. Such individual differences have been shown for two distinct dimensions of curiosity: *epistemic curiosity* (EC), the desire to acquire knowledge about facts, and *perceptual curiosity* (PC), the desire for sensory information. It is not known, however, whether both dimensions of curiosity depend on different brain networks and whether inter-individual differences in curiosity depend on variation in anatomical connectivity within these networks. Here, we investigated the neuroanatomical connections underpinning individual variation in trait curiosity. Fifty-one female participants underwent a two-shell diffusion MRI sequence and completed questionnaires measuring EC and PC. Using deterministic spherical deconvolution tractography we extracted microstructural metrics (fractional anisotropy (FA) and mean diffusivity (MD)) from two key white matter tracts: the fornix (implicated in novelty processing, exploration, information seeking and episodic memory) and the inferior longitudinal fasciculus (ILF) (implicated in semantic learning and memory). In line with our predictions, we found that EC – but not PC – correlated with ILF microstructure. Fornix microstructure, in contrast, correlated with both EC and PC with posterior hippocampal fornix fibres - associated with posterior hippocampal network connectivity - linked to PC specifically. These findings suggest that differences in distinct dimensions of curiosity map systematically onto specific white matter tracts underlying well characterized brain networks. Furthermore, the results pave the way to study the anatomical substrates of inter-individual differences in dimensions of trait curiosity that motivate the learning of distinct forms of knowledge and skills.

Significance statement

Despite recent interest in curiosity states and the broad spectrum of variation in stable tendencies to experience or express curiosity, the biological correlates of trait curiosity are unknown. Here, we found that specific types of curiosity correlate with microstructure of specific white matter tracts in the brain - the inferior longitudinal fasciculus and the fornix. Our findings on the relationship between specific aspects of curiosity and anatomical connections underlying well characterized brain networks highlight the specificity of trait curiosity. Furthermore, our findings pave the way to further understand inter-individual differences in curiosity and which aspects of curiosity benefit language, memory and other cognitive processes cultivating a deeper knowledge and skill set.

Introduction

Curiosity is described as the desire for new information that motivates seeking out and acquiring knowledge (Loewenstein, 1994; Litman, 2005). The momentary experience of curiosity can be seen as a motivational state that facilitates knowledge acquisition (Silvia & Kashdan, 2009; Gottlieb and Oudeyer, 2018). Consistent with this idea, studies have shown that states of high curiosity enhance long-term memory (Kang et al., 2009; Gruber et al., 2014; McGillivray et al., 2015; Marvin and Shohamy, 2016; Stare et al., 2018; Galli et al., 2018). Furthermore, recent neuroimaging evidence suggests that state curiosity enhances memory via increased activation in the mesolimbic dopaminergic circuit including the hippocampus (Gruber et al., 2014; Kang et al., 2009). Notably, the positive effects of state curiosity on memory have been found to greatly vary between individuals in that individual variations observed in the midbrain and hippocampus activity predict the magnitude of memory enhancements (Gruber et al., 2014).

Over the last decades, between-person differences in curiosity as a personality trait (i.e. tendencies to experience and express curiosity) have been well characterized. Based on Berlyne's (1954) suggestion that different types of curiosity are aroused by opportunities for new knowledge or sensory stimulation, trait curiosity has been split into two broad facets: curiosity as engagement with semantic knowledge - *epistemic curiosity* (EC); or as engagement with sensory stimuli - *perceptual curiosity* (PC). Building on Loewenstein's (1994) model of aversive curiosity, Litman and colleagues further proposed that these two aspects of curiosity can be further separated into diversive/interest-based and specific/deprivation-based curiosity. Diversive/interest curiosity is linked to positive affect and is thought to energize and direct exploration with the ultimate goal of stimulating one's interest and reduce boredom. In contrast, specific/deprivation curiosity is accompanied by a negative, frustrated feeling of information deprivation and uncertainty, associated with a specific knowledge gap, that people are motivated to eliminate (Berlyne, 1966; Litman, 2005, 2008, Litman and Spielberger, 2003; Litman and Jimerson, 2004).

The neuroanatomical substrates underpinning individual differences in trait curiosity are unknown. Studies investigating higher-order personality traits subsuming curiosity, however, provide a fruitful starting point to investigate the neuroanatomical connections underlying trait curiosity (DeYoung, 2014; Woo et al., 2014). For example, Privado et al. (2017) found an association between 'openness to experience' and microstructure of the inferior longitudinal fasciculus (ILF), a ventral, temporo-occipital association tract implicated in semantic memory (Herbet et al., 2018; Hodgetts et al., 2015, 2017). Additionally, Cohen et al. (2009) showed that individual differences in novelty seeking were associated with microstructure of the fornix, a key pathway that connects the hippocampus - involved in novelty detection, exploration, information seeking and episodic memory (O'Keefe and Nadel, 1978; Kumaran and Maguire, 2009; Murray et al., 2017; Voss et al., 2017) - to the thalamus, ventral striatum, amygdala and prefrontal cortex (Saunders and Aggleton, 2007; Aggleton et al. 2015).

Here, we used multi-shell diffusion MRI and spherical deconvolution tractography to investigate whether individual differences in ILF and fornix microstructure would be associated with individual differences in trait curiosity. Given the importance of ILF to semantic cognition (Hodgetts et al., 2017; Ripollés et al., 2017; Herbet et al., 2018), we predicted an association between ILF microstructure and EC but not PC. In contrast, given that hippocampal circuitry supports novelty detection, exploratory behaviour and information seeking in many domains (O'Keefe and Nadel, 1978; Kumaran and Maguire, 2009; Murray et al., 2017; Voss et al., 2017) we predicted an association between fornix microstructure and *both* EC and PC. Further, given evidence of a posterior (fine-grained) to anterior (gist-based) gradient of representational specialization along the long-axis of the hippocampus (Ranganath and Ritchey, 2012; Poppenk et al. 2013; Strange et al., 2014; Murray et al., 2017), we predicted that fornical fibres associated with posterior and anterior hippocampus (Christiansen et al., 2017; Saunders and Aggleton, 2007) would be more strongly associated with PC and EC, respectively.

Materials and Methods

Participants

Fifty-one healthy female adult undergraduate students, with a mean age of 20 years (SD ± 1, range = 19-24) participated. They provided written consent prior to participating in the study, which was approved by the Cardiff University Research Ethics Committee, and received a remuneration of approximately £25 for their participation.

Trait curiosity measures

Participants completed the *Epistemic Curiosity Scale (EC)* (Litman, 2008) and the *Perceptual Curiosity Scale (PC)* (Collins et al., 2004), along with other self-report measures not relevant to the current study. The EC scale consists of five interest EC items and five deprivation EC items with participants answering on a scale ranging from 1 (*almost never*) to 4 (*almost always*). The interest EC items are associated with behaviours that stimulate positive affect, or involve learning something completely new (e.g. “I enjoy learning about subjects that are unfamiliar to me”). In contrast, deprivation EC items describe behaviours that reduce negative feelings of information deprivation and uncertainty (e.g. “I can spend hours on a single problem because I just can’t rest without knowing the answer”). The PC scale (Collins et al., 2004) comprised of twelve items (6 diversive PC items and 6 specific PC items) and again participants respond on a scale that ranged from 1 (*almost never*) to 4 (*almost always*). The diversive PC items describe exploratory behaviours in which one seeks out new places and a broad range of sensory stimulation (e.g. “I like to discover new places to go”), whereas specific PC describes exploration of novel, specific and sensorially stimulating stimuli (e.g. “When I hear a strange sound, I usually try to find out what caused it”). The Cronbach’s alpha coefficients for the scales were all >= .70 suggesting good internal consistency.

Imaging acquisition

Imaging data were obtained at CUBRIC, Cardiff University on a 3 Tesla MRI scanner (Siemens Magnetom Prisma) with a 32-channel head coil. T1-weighted structural 3D images were acquired using an MPRAGE sequence (orientation = sagittal; TR = 2250ms; TE = 3.06ms; TI = 900ms; flip angle = 9°; FOV = 256mm²; slice thickness = 1mm; voxel size = 1mm³; number of slices = 224; bandwidth = 230Hz/pixel; total acquisition time = 7 minutes 36 seconds).

Diffusion weighted images were acquired using a multi-shell sequence (orientation = transversal/axial; TR = 9400ms; TE = 67.0ms; FOV = 256mm²; slice thickness = 2mm; voxel size = 2mm³; number of slices = 80). Diffusion gradients were applied in (i) 30 isotropic directions by using a diffusion-weighted factor b=1200sec/mm², (ii) in 60 isotropic directions by using a diffusion-weighted factor b=2400sec/mm², and (iii) a volume without diffusion gradients (b=0sec/mm²) (bandwidth = 1954Hz/pixel; total acquisition time = 15 minutes 51 seconds).

Diffusion MRI pre-processing

T1-weighted structural images were subjected to a 'brain-tissue only' mask using FSL's Brain Extraction Tool (RRID:SCR_002823; Smith, 2002). Using ExploreDTI (RRID:SCR_001643; v4.8.3; Leemans et al., 2009) each b-value image was then co-registered to the T1 structural image. Subsequently, all b-value images were corrected for head motion and eddy currents within ExploreDTI. Tensor fitting was conducted on the b-1200 data given the tensor model assumes hindered (Gaussian) diffusion, and at lower b-values more of the signal is due to hindered rather than restricted diffusion (Jones et al., 2013). To correct for voxel-wise partial volume artefacts arising from free water contamination, the two-compartment 'Free Water Elimination' (FWE) procedure was applied to the current b-1200 data – this improves reconstruction of white matter tracts near the

139 ventricles such as the fornix (Pasternak et al., 2009, 2014), yielding whole brain voxel-wise
140 free-water corrected FA and MD tissue maps. Following FWE, corrected diffusion tensor-
141 derived structural metrics were computed. Fractional anisotropy (FA), reflects the extent to
142 which diffusion within biological tissue is anisotropic (constrained along a single axis). MD
143 (10^{-3} mm^2 s^{-1}) reflects overall degree of diffusivity (Vettel et al., 2017). The resulting free
144 water corrected FA and MD maps were inputs for the tractography analysis.
145
146 *Tractography*
147 As higher b-values allow for better fibre orientation estimations (Vettel et al., 2017), we
148 performed tractography on the b-2400 data using damped Richardson-Lucy spherical
149 deconvolution (dRL-SD). Spherical deconvolution provides a direct estimate of the
150 underlying distribution of fibre orientations in the brain and when applied to tractography
151 leads to accurate reconstructions of the major white matter pathway, and an improved ability
152 to describe complex white matter anatomy (Dell'Acqua and Tournier, 2018). The algorithm
153 extracted peaks in the fibre orientation density function (fODF) at the centre of each voxel,
154 where streamlines along the orientation of the fODF peaks were reconstructed using a step
155 size of 0.5mm. Streamline tracts were terminated if the direction of the pathway changed
156 through an angle greater than 45° or if the fODF threshold fell below 0.05.

157 In ExploreDTI, manual tractography was carried out using AND, NOT, and SEED
158 ROI gates on colour-coded FA maps to extract specific white matter tracts. AND gates
159 (**Figure 1** - green) were used to extract fibres that passed through the gate, NOT gates
160 (**Figure 1** - red) were used to exclude any fibres that passed through the gate, and finally
161 SEED gates (**Figure 1** - blue) were used as a starting point to extract fibres that passed
162 through this gate and then to include only those fibres that then passed through any added
163 AND gates. Manual tractography was carried out on a minimum of 15 subjects in order to
164 calculate a tract model to perform automated tractography on all 51 data sets (Explore DTI;
165 Parker et al., 2013). This procedure enables the construction of white matter tracts in space

166 in which streamlines belonging to particular anatomical features of interest consistently
167 project to distinct sub-regions, allowing the reconstruction of streamline data by observing
168 their projected positions (Parker et al., 2013). After running the automated tractography
169 software each tract was visually inspected, and any erroneous fibres were pruned using
170 additional NOT gates. These tract masks from the b=2400 data were then intersected with
171 the b=1200 free-water corrected FA and MD maps to derive free-water corrected tract-
172 specific measures of FA and MD values for statistical analysis.

173

174 *Inferior Longitudinal Fasciculus tractography*. The ILF (**Figure 1B**) was reconstructed using
175 a two-ROI approach in each hemisphere (Wakana et al., 2007). In the mid-saggital slice of
176 the brain, the coronal crosshair was placed posterior to the corpus callosum. In the coronal
177 plane a SEED gate was drawn around the entire cortex of interest. Next in the coronal view,
178 the last slice where the temporal lobe was separate from the frontal lobe was identified and
179 one AND gate was drawn around the temporal lobe. Any stray fibres not consistent with the
180 ILF pathway were removed with NOT gates. FA and MD of the right and left ILF were
181 summed and averaged to provide a bilateral measure for the main analyses.

182

183 *Fornix tractography*. The fornix (**Figure 1A**) was traced in line with the landmarks described
184 in Catani and Thiebaut de Schotten (2008). In the mid saggital slice of the brain, the coronal
185 crosshair was placed at the anterior commissure and moved approximately 6 voxels
186 posterior in the brain. In the coronal plane, one AND gate was drawn around the fornix
187 bundle where the anterior pillars enter the body of the fornix. Finally, NOT gates were drawn
188 around any protruding areas that were not part of the fornix.

189

190 *Anterior and posterior hippocampal fornix tractography*. In addition, we employed a method
191 adapted from prior work to reconstruct the anterior and posterior hippocampal fornix fibres
192 (Christiansen et al., 2017). Both anterior and posterior hippocampal fornix reconstructions

193 required the AND and NOT gates that were applied during whole fornix tractography. Some
194 NOT gates were augmented to enable better extraction of the anterior and posterior
195 hippocampal streamlines of the fornix. A standard landmark for the anterior-posterior
196 hippocampal boundary was proposed to be a small bundle of grey matter that outlines the
197 most anterior extent of the parahippocampal gyrus that is called uncal apex or uncus
198 (Poppenk et al., 2013). This landmark was identified for each hemisphere separately when
199 carrying out manual tractography of the anterior and posterior hippocampal fornix. In order to
200 perform this, the uncus was first localised at its anterior part and traced to its posterior
201 boundary. The first coronal slice in which the uncus was not visible anymore was used as
202 the landmark in order distinguish between fibres that project into anterior (head of the
203 hippocampus) and posterior hippocampus (body and tail of the hippocampus) (**Figure 1C**).

204 After the left and right hemispheric landmarks were identified, one NOT gate on each
205 hemisphere was drawn around the hippocampus to set boundaries for posterior
206 hippocampal fornix tracts, removing fibres that pass through these NOT gates (**Figure 1D**).
207 After the posterior hippocampal fornix was identified, the same coordinates of the anterior-
208 posterior hippocampal boundary landmark for each hemisphere were used to replace the
209 NOT gates with AND gates for the left and right anterior hippocampal fornix reconstruction
210 (**Figure 1E**). The posterior, left, and right anterior hippocampal fornix were saved as
211 separate tracts to aid subsequent automated tractography (**Figure 2**). Note that diffusion
212 tensor metrics of the whole fornix and those averaged across anterior and posterior
213 hippocampal fornix segments were highly correlated (FA, $r(51) = 0.940$, $p < 0.001$; MD, $r(51)$
214 $= 0.942$, $p < 0.001$) indicating that the anterior and posterior hippocampal fornix
215 reconstructions matched the whole fornix reconstructions.

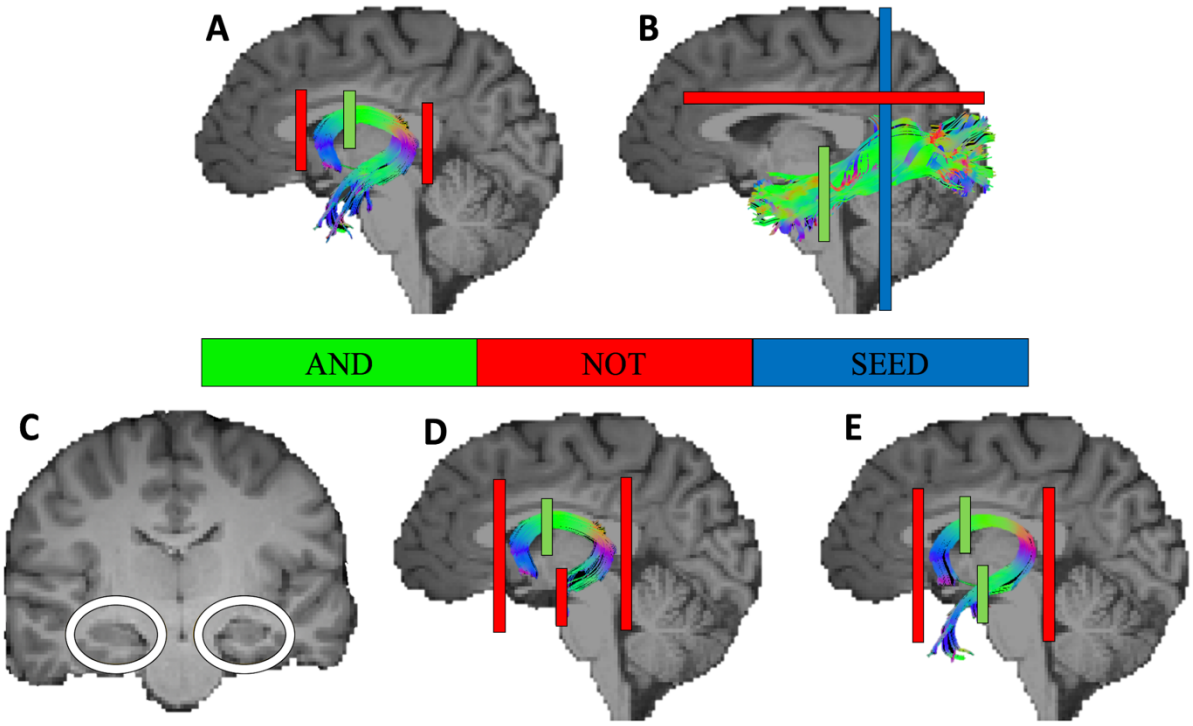

Figure 1. Automated tractography reconstructions of the fornix, its anterior and posterior hippocampal fornix fibres and the inferior longitudinal fasciculus (ILF). AND (green), NOT (red), and SEED (blue) ROI gates for each of the tracts are displayed on the sagittal midline plane. (**A**) Fornix tractography using AND and NOT gates. (**B**) Left ILF tractography using SEED, AND and NOT gates. (**C**) Location of AND and NOT gates for tractography of the anterior and posterior hippocampal fornix, respectively. (**D**) Posterior hippocampal fornix tractography using one additional NOT gate placed between the head and the body of the hippocampus to only include fornical fibres that connect with posterior hippocampus (i.e., hippocampal body and tail). (**E**) Anterior hippocampal fornix tractography using one additional AND gate placed between the head and body of the hippocampus (i.e., identical location as NOT gate in (D)) to include fibres that pass through this ROI gate to the anterior hippocampus.

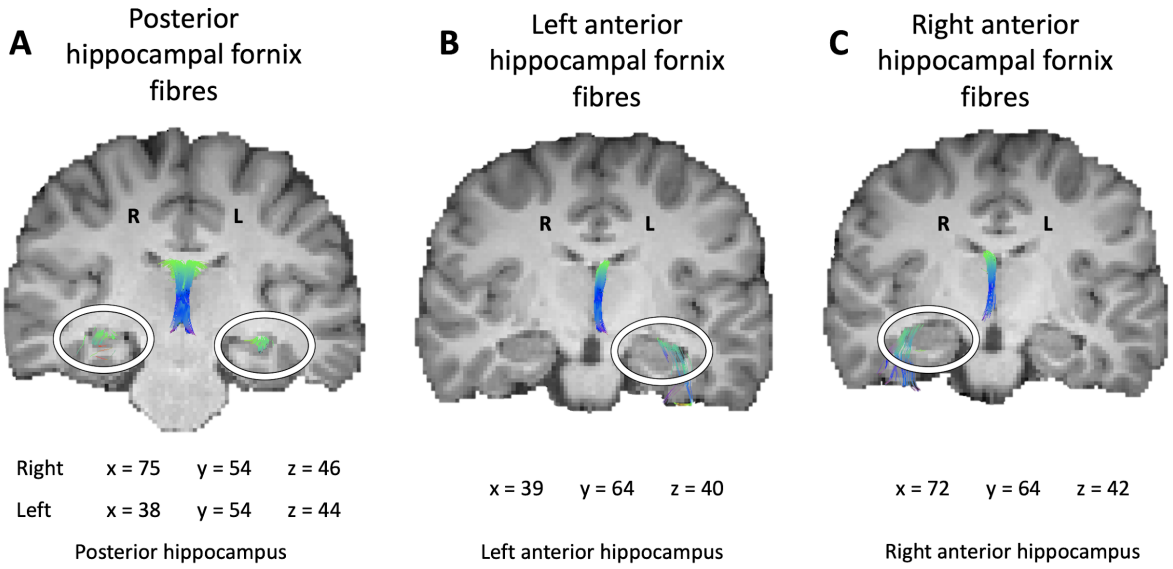

Figure 2. Automated tractography reconstructions of anterior and posterior hippocampal fornix fibres on coronal slices. Tractography of the fornix fibres projecting to the posterior hippocampus (**A**). Tractography of fornix fibres projecting to the left anterior hippocampus (**B**). Tractography of the fornix fibres projecting to the right anterior hippocampus (**C**).

Experimental Design and Statistical analyses

For the questionnaire data, in the event of missing responses (2 participants failed to give a response to one PC item), the mean value of the remaining items that were answered in the full scale was calculated which then replaced the missing item score. For each curiosity subscale (i.e., the two subscales of PC and EC), we calculated a total score for each participant. Participants' data with diffusion tensor metrics +/– 3SD beyond the group mean were considered as outliers and removed from respective analyses. This resulted in one participant's data being removed from all analyses involving ILF MD and a different participant's data being removed from analyses including bilaterally averaged ILF FA.

To test for associations between curiosity trait scores and microstructure of our selected anatomical tracts, we conducted directional *Pearson's* correlations using MATLAB

247 (RRID:SCR_001622). Since higher FA and lower MD is typically associated with higher
248 microstructural integrity (Vettel et al., 2017), we predicted a positive correlation between
249 levels of curiosity and FA and a negative correlation with MD.

250 To determine whether the *Pearson's* correlation coefficient *r* was statistically
251 significant, we performed non-parametric permutation tests that randomly permute the real
252 data between participants. Permutation tests were conducted separately for the two
253 microstructure metrics (i.e., FA and MD) and for the EC and PC scales. Importantly, we
254 corrected for multiple comparisons across the subscales within a curiosity scale (e.g.,
255 diversive- and specific PC). The steps were as follows: First, we performed *Pearson's*
256 correlations on the real data (i.e., correlations between the scores of the two curiosity
257 subscales and the microstructure measure (e.g., diversive PC with ILF MD and specific PC
258 with ILF MD)). Thereby, we obtained the empirical correlation coefficients reflecting the
259 relationship between the two curiosity subscales and a specific microstructure measure.
260 Second, within each curiosity subscale, we shuffled the curiosity scores across participants,
261 which resulted in pairs containing a curiosity score and a microstructure value that is
262 randomly assigned across participants. On these shuffled data, we then calculated surrogate
263 *Pearson's* coefficients for the two curiosity subscale scores and the microstructure metric,
264 and saved the maximum surrogate *Pearson's r* across the two correlations (i.e., subscale-
265 microstructure$_{max}$) (Groppe, Urbach and Kutas, 2011). Third, the second step was repeated
266 5000 times. Based on the 5000 permutations, we created a null distribution of all surrogate
267 subscale-microstructure$_{max}$ coefficient values and determined the alpha cut-off point
268 ($p < 0.05$; one-sided; i.e., 4750th data point of the surrogate null distribution) in order to test
269 the statistical significance of the real *Pearson's* coefficients reflecting the relationship
270 between the two subscales and the microstructure measure. This approach allowed us to
271 correct for multiple comparisons across the two subscales within each curiosity scale. In
272 follow-up analyses for specific curiosity subscales (e.g., interest EC subscale), we also
273 performed follow-up permutation tests that corrected for multiple comparisons across both

274 hemispheres (e.g., left and right ILF MD). The 95% confidence intervals (CI) for each
275 correlation was derived using a bootstrapping method based on 1000 iterations.
276

277 **Results**

278 *Epistemic curiosity – but not perceptual curiosity – correlates with ILF microstructure*

279 *ILF FA.* We conducted a series of permutation tests that investigated the relationships
280 between curiosity trait scores and microstructure in *a-priori* selected anatomical tracts. For
281 each permutation test, we corrected for multiple comparisons for the two subscales
282 separately within the EC and PC scale. The first permutation test targeted ILF FA and EC.
283 We found that bilaterally averaged ILF FA did not significantly correlate with either subscale
284 of EC (deprivation EC, $r(50) = 0.143$, $p_{corr} = 0.243$, 95% CI [-0.105, 0.364]; interest EC, $r(50)$
285 $= 0.191$, $p_{corr} = 0.151$, 95% CI [-0.0734, 0.440]). A further permutation test was conducted on
286 bilaterally averaged ILF FA with the two subscales of PC, where again neither subscale
287 significantly correlated with bilateral ILF FA (specific PC, $r(50) = 0.109$, $p_{corr} = 0.329$, 95% CI
288 [-0.229, 0.427]; diversive PC, $r(50) = 0.207$; $p_{corr} = 0.122$, 95% CI [-0.109, 0.453]).
289

290 *ILF MD.* Targeting ILF MD, a permutation test revealed a significant negative correlation
291 between ILF MD and deprivation EC ($r(50) = -0.388$, $p_{corr} = 0.004$, 95% CI [-0.572, -0.124],
292 **Figure 3A**) and a significant negative correlation between ILF MD and interest EC ($r(50)$ =
293 -0.289, $p_{corr} = 0.038$, 95% CI [-0.489, 0.007], **Figure 3B**). In contrast, bilateral ILF MD was
294 not significantly correlated with any subscale of PC (specific PC, $r(50) = -0.134$, $p_{corr} = 0.267$,
295 95% CI [-0.392, 0.157]); diversive PC ($r(50) = 0.020$, $p_{corr} = 0.710$, 95% CI [-0.260, 0.271]).
296

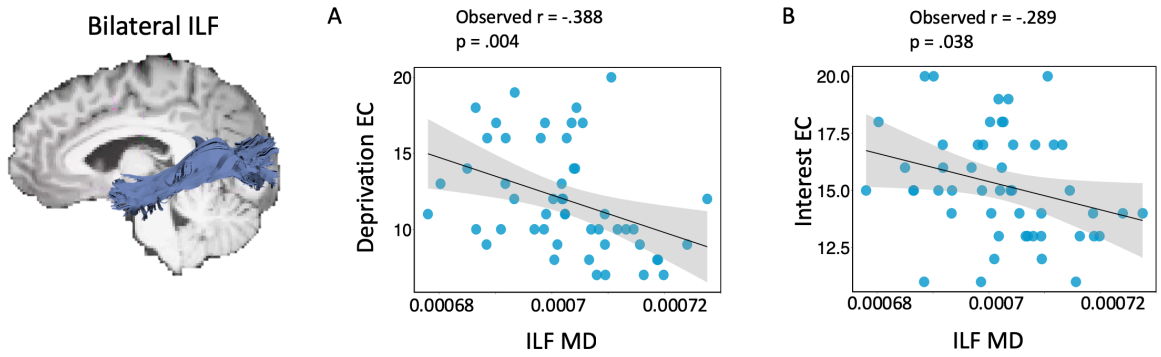

Figure 3. Inferior longitudinal fasciculus microstructure only shows relationship with epistemic curiosity. These results were obtained from non-parametric permutation tests that corrected for multiple comparisons across the two subscales within the Epistemic Curiosity scale (EC). A significant relationship was found between MD of the inferior longitudinal fasciculus (ILF) with deprivation- and interest EC (**A**, **B**, respectively). The line of best fit is shown on each scatter plot with 50 data points.

Neuropsychological evidence suggests that semantic knowledge is represented bilaterally in the anterior temporal lobes (ATL) but may show subtle inter-hemispheric (left > right) gradations for verbal stimuli (Rice et al., 2015). Therefore, we asked whether the significant correlation between bilateral ILF MD and both EC subscales were driven specifically by the left as opposed to the right ILF. Separate permutation tests were conducted for each subscale of EC with left ILF MD and right ILF MD as the two variables of interest (i.e., correcting for multiple comparisons across the two hemispheres). The first permutation test on deprivation EC found that both left and right ILF MD significantly correlated with deprivation EC (left ILF: $r(50) = -0.341$, $p_{corr} = 0.016$, 95% CI [-0.566, -0.078]; right ILF: $r(50) = -0.358$, $p_{corr} = 0.012$, 95% CI [-0.564, -0.106]). The second permutation test investigating whether interest EC correlates with left and right ILF MD indicated a numerical negative relationship for both tracts but neither reached significance with the adopted multiple comparisons correction (left ILF: $r(50) = -0.254$, $p_{corr} = 0.066$, 95% CI [-0.491, 0.086]); right ILF: $r(50) = -0.267$, $p_{corr} = 0.051$, 95% CI [-0.472, -0.056]).

Interest epistemic curiosity correlates with fornix microstructure

Fornix FA. Regarding fornix FA, permutation tests revealed a significant positive correlation between interest EC and fornix FA ($r(51) = 0.281$, $p_{corr} = 0.039$, 95% CI [-0.008, 0.491], **Figure 4**). In contrast, deprivation EC showed no significant correlation with fornix FA ($r(51) = 0.155$, $p_{corr} = 0.214$, 95% CI [-0.120, 0.422]). A second permutation test was conducted on fornix FA with the two subscales of PC, diversive and specific, but neither subscale significantly correlated with fornix FA (specific PC, $r(51) = 0.111$, $p_{corr} = 0.328$, 95% CI [-0.266, 0.4252]; diversive PC, $r(51) = 0.064$, $p_{corr} = 0.466$, 95% CI [-0.204, 0.351]).

Fornix MD. Despite the earlier findings of a significant positive correlation between interest EC and fornix FA, permutation tests revealed no significant negative correlation between fornix MD and interest EC ($r(51) = -0.110$, $p_{corr} = 0.332$, 95% CI [-0.372, 0.171]) or deprivation EC ($r(51) = -0.029$, $p_{corr} = 0.574$, 95% CI [-0.314, 0.296]). The second permutation test, investigating the association between fornix MD and the two subscales of PC, also showed that neither specific nor diversive PC significantly correlated with fornix MD (specific PC, $r(51) = -0.250$, $p_{corr} = 0.070$, 95% CI [-0.499, 0.054]; diversive PC, ($r(51) = -0.159$; $p_{corr} = 0.214$, 95% CI [-0.398, 0.113]).

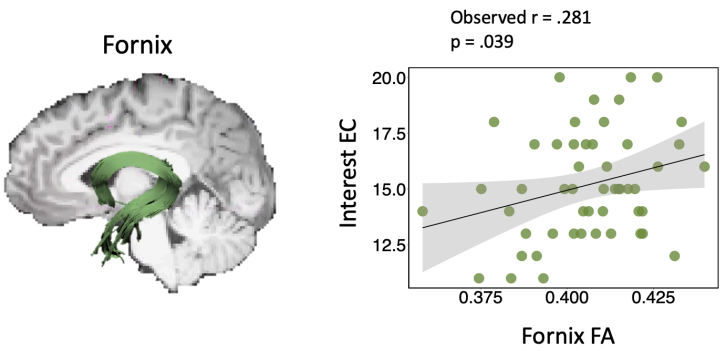

Figure 4. Fornix microstructure shows relationship with interest epistemic curiosity. These results obtained from non-parametric permutation tests correcting for multiple

346 comparisons across subscales within the Epistemic Curiosity scales (EC). A significant
347 relationship was found between fractional anisotropy (FA) of the whole fornix and interest
348 EC. The line of best fit is shown on the scatterplot with 51 data points.
349

350 *Specific perceptual curiosity shows relationship with posterior hippocampal fornix*

351 Recent accounts postulate a posterior-anterior gradient of representational granularity along
352 the long axis of the hippocampus, linked to a gradient in anatomical connectivity (Aggleton,
353 2012; Strange et al., 2014), from 'fine' perceptual detail to 'course' or gist-like
354 representations (Poppenk et al., 2013; Robin and Moscovitch, 2017; Sheldon et al., 2019).
355 This account suggests that a correlation might be evident between posterior hippocampal
356 fornix and PC, and anterior hippocampal fornix and EC, respectively. To test this account,
357 we explored the relationship between *specific* PC (i.e., associated with a detailed perceptual
358 knowledge gap) and anterior/posterior hippocampal fornix MD, given that the correlation
359 between specific PC and whole fornix MD did not reach significance in the preliminary
360 analyses. Conversely, to pinpoint how EC is associated with the anterior/posterior
361 hippocampal fornix FA, we focussed our analyses on *interest* EC for which we had found a
362 positive correlation with whole fornix FA.

363 A first permutation test (corrected for multiple comparisons) targeted the three
364 individual fornix segmentations (i.e., left anterior, right anterior, bilateral posterior
365 hippocampal fornix). (Note the anterior hippocampal fornical fibres form the lateral fornix but
366 posterior hippocampal fornical fibres form the medial fornix which cannot easily be
367 separated into separate hemispheres). We found that specific PC significantly correlated
368 with posterior hippocampal fornix MD ($r(51) = -0.277$, $p_{corr} = 0.047$, 95% CI [-0.528,0.056],
369 **Figure 5**), but it did not correlate significantly with left or right anterior hippocampal fornix
370 MD (left: ($r(51 = -0.189$, $p_{corr} = 0.176$, 95% CI [-0.451,0.062]); right: ($r(51) = -0.028$, p_{corr} =

371 0.610, 95% CI [-0.289,0.264]). This finding suggests that specific PC might mainly be
372 supported by fornical fibres that have connections to the posterior hippocampus.

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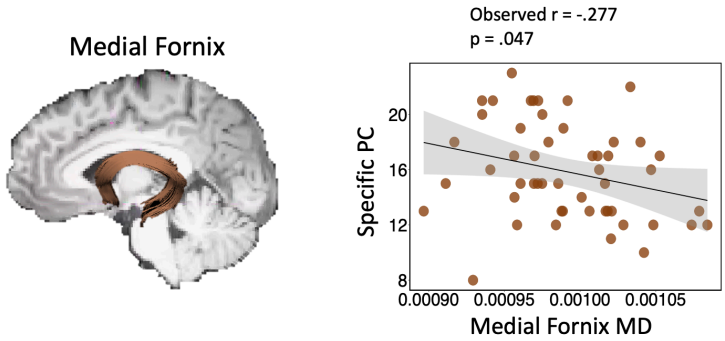

380 **Figure 5. Posterior hippocampal fornix microstructure shows relationship with**
381 **aspects of perceptual curiosity.** Results obtained from non-parametric permutation tests
382 correcting for multiple comparisons across subscales within the Perceptual Curiosity scales
383 (PC). A significant relationship was found between MD of the posterior hippocampal fornix
384 (i.e., fornix fibres that project specifically into posterior hippocampus) and specific PC. The
385 line of best fit is shown on the scatterplot with 51 data points.

386

387 In contrast, although we found that interest EC significantly correlates with *whole*
388 fornix FA, the three distinct fornix segmentations did not reveal significant correlations with
389 interest EC (left anterior hippocampal fornix FA, $r(51) = 0.269$, $p_{corr} = 0.065$, 95% CI [-0.029,
390 0.521]; right anterior hippocampal fornix FA ($r(51) = 0.080$, $p_{corr} = 0.479$, 95% CI [-0.161,
391 0.307]); posterior hippocampal fornix FA, $r(51) = 0.272$, $p_{corr} = 0.062$, 95% CI [-0.009,
392 0.479]).

393 In summary, we found that two individual subscales that tap into epistemic and
394 perceptual curiosity traits showed significant correlations with fornix microstructure. In
395 particular, we found that whole fornix FA significantly correlated with interest EC whereas
396 posterior hippocampal fornix microstructure significantly correlated with specific PC.

Discussion

Curiosity motivates us to seek out information and it facilitates knowledge acquisition (Loewenstein, 1994; Litman, 2005; Silvia and Kashdan, 2009; Gottlieb and Oudeyer, 2018). While a fledgling line of research has shown that curiosity states - the momentary experience of curiosity - enhance hippocampus-dependent memory (for a review, see Gruber et al., 2019), there is also a broad spectrum of variation in *stable* tendencies to experience or express curiosity. Here, we found that ILF microstructure correlated with both interest and deprivation EC traits, but not with PC traits. Additionally, fornix microstructure was associated with interest - but not deprivation - EC, and specific - but not diversive - PC. In particular, while microstructure of the whole fornix correlated with interest EC, specific PC correlated with the posterior hippocampal fornix. These findings support the notion that curiosity is a multifaceted motivational construct and that distinct aspects of curiosity map onto specific white matter tracts underlying well-characterized brain networks.

Epistemic curiosity and ILF

The ILF, which connects ventral aspects of ATL, occipito-temporal, and occipital cortex (Herbet et al., 2018), appears critical for bidirectional interactions between an ATL-based bilateral semantic 'hub' and representations supported by occipital and middle/posterior temporal regions (Patterson et al., 2007; Lambon Ralph et al., 2017; Chen et al., 2017). In addition to demonstrations of altered ILF microstructure in semantic dementia (Agosta et al., 2010), recent studies report associations between ILF microstructure and individual differences in semantic learning (Ripollés et al., 2017) and memory (Hodgetts et al., 2017). Here, we found that participants with reduced diffusivity (i.e., lower MD values) in the ILF showed higher trait scores in both dimensions of EC. Critically, we found that the ILF supported both the general exploration of semantic information motivated by positive affect (EC as a feeling-of-interest) but also the search for specific information in order to close a knowledge gap (EC as an aversive feeling-of-deprivation) (Litman, 2005, 2008;

Loewenstein, 1994; Lauriola et al., 2015). One explanation for this may be that perhaps the more that we learn, the more we are attuned to the gaps in our knowledge, and attending to these gaps is tension-producing and enjoyable at the same time (Loewenstein, 1994). In addition, the association between EC and ILF microstructure is in line with the literature on the higher-order personality trait 'openness to experience', of which curiosity is one facet (Woo et al., 2014). Privado et al. (2017) demonstrated that ILF microstructure was associated with levels of trait 'openness'. Our findings extend this work by pinpointing that the exploration and specific search for semantic information might be one critical factor that carries the association between 'openness' and ILF microstructure.

Curiosity and Fornix

The hippocampus is a medial temporal lobe structure supporting the encoding and recall of long-term memory (Burgess et al., 2002; Davachi, 2006; Eichenbaum et al., 2007; Murray et al., 2018). Given that the hippocampus has been implicated in a number of processes critical to curiosity, including exploration, reward seeking and novelty detection (O'Keefe and Nadel, 1978; Murray et al., 2017; Kumaran and Maguire, 2009; Voss et al 2017), we investigated the relationship between curiosity and the fornix - the principal tract linking the hippocampus with sites beyond the temporal lobe (Postans et al., 2014; Rudebeck et al., 2009). Regarding the relationship between curiosity and fornix microstructure, we performed analyses targeting the microstructure of the whole fornix, but also the anterior and posterior hippocampal fornix segments that correspond to the functional subdivisions of the anterior and posterior hippocampus, respectively (Christiansen et al., 2017; Saunders and Aggleton, 2007). Given current theoretical ideas, the anterior and posterior hippocampal fornix fibres may reflect functional subdivisions of the anterior and posterior hippocampus reflecting gist-based (schematic) and detailed (episodic) information, respectively (Robin and Moscovitch, 2017; Poppenk et al., 2013; Sheldon et al., 2019). Therefore, the present study investigated whether the functional subdivisions of the fornix, connecting to the anterior and posterior hippocampus, may potentially map onto diversive/interest and specific/deprivation curiosity,

respectively. Consistent with this hypothesis, we found that the posterior hippocampal fornix (but not the anterior hippocampal fornix) showed a relationship with specific PC which is described as the desire to reduce uncertainty by searching for a specific novel perceptual information.

In contrast, we found that interest EC positively correlated with microstructure of the whole fornix. Interest EC is described as the desire for diversive exploration and information seeking which is accompanied by positive affect (Litman, 2008). Given these ideas on the functional relevance of interest EC and theoretical ideas and evidence about anterior hippocampal functions, we would have expected that interest EC would show a relationship with anterior hippocampal fornix (i.e., which is strongly connected to anterior hippocampus). The anterior hippocampus has, however, also been proposed to support gist-based and schematic information (Poppenk et al., 2013; Robin and Moscovitch, 2017). Although interest EC reflects the general, explorative search for semantic information, interest EC also triggers search for detailed information rather than gist-based information. Therefore, interest EC might also depend on more posterior hippocampal regions in which detailed 'cognitive maps' of the environment, as a means to obtain information, are formed and transition in a graded fashion along the long axis to more gist-based global-contextual 'cognitive maps' (Aggleton, 2012; Graham et al., 2010; Murray et al., 2018; Poppenk et al., 2013; Strange et al., 2014). In line with this idea of a hippocampal gradient, we found that interest EC did not reach significance for correlations with the left anterior and the posterior hippocampal fornix, but was found to significantly correlate with the whole fornix reflecting the idea that perhaps interest EC depends on fornix fibres that stretch along the whole of the long axis of the hippocampus aligned to EC's dependence on integrative conceptual and detailed maps.

Our study involved questionnaires to tap into distinct curiosity traits. Other recent studies that investigated individual differences in curiosity utilized measures of eye-movement as an objective indicator of visual exploration. For instance, Baranes and colleagues (2015), found curiosity-based enhancement of anticipatory gaze correlated with trait curiosity, and Risko et al. (2012) used a scene-viewing task to demonstrate that participants' PC trait score predicted the degree to which they explored the scenes. These studies using eye-movements to investigate curiosity-based exploration and our present findings on fornix microstructure highlight how individual differences in curiosity play a critical part in the degree of exploration of one's environment.

Limitations and future directions

First, our correlation analyses cannot establish causality of one variable over the other. Longitudinal studies would be needed to determine the causality of these relationships to investigate whether trait curiosity shapes white matter connections, vice versa, or whether both reinforce each other in a bidirectional manner. For instance, recent work on adaptive myelination suggests that change in myelination through activity-dependent adaptation of an initially hard-wired process is in response to experiences and contributes to learning (Bechler et al., 2018). Second, interpreting the biological relevance of diffusion metrics from white matter tracts, such as FA and MD, can be challenging. Whilst FA and MD are believed to be inversely related where typically a high FA and low MD suggest greater white matter microstructure (Vettel et al., 2017), we found that for the majority of microstructure-curiosity correlations that only one of the two diffusion metrics significantly correlated with curiosity. These dissociations could be due to the structure of the selected white matter tracts. For example, evidence suggests that FA has been found to be less consistent along a given tract (Yeatman et al., 2012) and other studies also found similar variability in FA and MD measures of the fornix and ILF (e.g., Hodgetts et al., 2017). Inconsistences between FA and MD measures could also be due to a number of biological properties such as axon diameter

and density, myelination and the arrangement of fibres in a given voxel (Beaulieu, 2002). For instance, high FA has been found to reflect high myelin density and structured histological orientation whereas high values of MD is more likely to reflect low myelin density and diffuse histological orientation (Seehaus et al., 2015). This emphasizes the need to use more sophisticated methods in future studies, such as Neurite Orientation Dispersion and Density Imaging, a white matter index which is more informative about brain cellular microstructure than FA and MD alone.

Conclusion

The present study found inter-individual variation in the microstructure of the fornix related to interest EC and inter-individual variation in the microstructure of the ILF related to both interest and deprivation EC. Furthermore, posterior hippocampal fornix microstructure was associated with specific PC. In conclusion, our findings on the relationship between curiosity traits and anatomical connections underlying well characterized brain networks provide a foundation for future studies to examine the relationship between curiosity traits, curiosity states and their neuroanatomical substrates. Our findings pave the way to further understand inter-individual differences in curiosity and which aspects of curiosity benefit language, memory and other cognitive processes cultivating a deeper knowledge and skill set.

522 **Author contributions**

523 A.V., K.S.G., A.D.L. and M.J.G. contributed to the conception and design of the experiment.
524 A.V. and A.C. contributed to data acquisition. All authors contributed to data analysis and
525 interpretation. A.V. and M.J.G. drafted the manuscript and together with C.J.H., K.S.G. and
526 A.D.L. revised the manuscript. A.D.L. and M.J.G. jointly supervised this work.

527

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700 **Figure Legends**

701

702 **Figure 1. Automated tractography reconstructions of the fornix, its anterior and**
703 **posterior hippocampal fornix fibres and the inferior longitudinal fasciculus (ILF).** AND
704 (green), NOT (red), and SEED (blue) ROI gates for each of the tracts are displayed on the
705 sagittal midline plane. (**A**) Fornix tractography using AND and NOT gates. (**B**) Left ILF
706 tractography using SEED, AND and NOT gates. (**C**) Location of AND and NOT gates for
707 tractography of the anterior and posterior hippocampal fornix, respectively. (**D**) Posterior
708 hippocampal fornix tractography using one additional NOT gate placed between the head
709 and the body of the hippocampus to only include fornical fibres that connect with posterior
710 hippocampus (i.e., hippocampal body and tail). (**E**) Anterior hippocampal fornix tractography
711 using one additional AND gate placed between the head and body of the hippocampus (i.e.,
712 identical location as NOT gate in (D)) to include fibres that pass through this ROI gate to the
713 anterior hippocampus.

714

715 **Figure 2. Automated tractography reconstructions of anterior and posterior**
716 **hippocampal fornix fibres on coronal slices.** Tractography of the fornix fibres projecting
717 to the posterior hippocampus (**A**). Tractography of fornix fibres projecting to the left anterior
718 hippocampus (**B**). Tractography of the fornix fibres projecting to the right anterior
719 hippocampus (**C**).

720

721 **Figure 3. Inferior longitudinal fasciculus microstructure only shows relationship with**
722 **epistemic curiosity.** These results were obtained from non-parametric permutation tests
723 that corrected for multiple comparisons across the two subscales within the Epistemic
724 Curiosity scale (EC). A significant relationship was found between MD of the inferior
725 longitudinal fasciculus (ILF) with deprivation- and interest EC (**A**, **B**, respectively). The line of
726 best fit is shown on each scatter plot with 50 data points.

Figure 4. Fornix microstructure shows relationship with interest epistemic curiosity. These results obtained from non-parametric permutation tests correcting for multiple comparisons across subscales within the Epistemic Curiosity scales (EC). A significant relationship was found between fractional anisotropy (FA) of the whole fornix and interest EC. The line of best fit is shown on the scatterplot with 51 data points.

Figure 5. Posterior hippocampal fornix microstructure shows relationship with aspects of perceptual curiosity. These results obtained from non-parametric permutation tests correcting for multiple comparisons across subscales within the Perceptual Curiosity scales (PC). A significant relationship was found between MD of the posterior hippocampal fornix (i.e., fornix fibres that project specifically into posterior hippocampus) and specific PC The line of best fit is shown on the scatterplot with 51 data points.