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*Research Articles: Behavioral/Cognitive*

## **Differentiable processing of objects, associations and scenes within the hippocampus**

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DOI: 10.1523/JNEUROSCI.0263-18.2018

Received: 30 January 2018

Revised: 11 June 2018

Accepted: 29 June 2018

Published: 6 August 2018

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**Author contributions:** M.A.D., P.Z., C.M., and E.A.M. designed research; M.A.D. performed research; M.A.D., P.Z., C.M., and E.A.M. analyzed data; M.A.D., C.M., and E.A.M. wrote the paper.

**Conflict of Interest:** The authors declare no competing financial interests.

This work was supported by a Wellcome Principal Research Fellowship to E.A.M. (101759/Z/13/Z) and the Centre by a Centre Award from Wellcome (203147/Z/16/Z). The authors are grateful to David Bradbury for technical assistance.

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**Cite as:** J. Neurosci ; 10.1523/JNEUROSCI.0263-18.2018

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1 Behavioral/Cognitive

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**Abbreviated title:** Multiple processing circuits in the hippocampus

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31

**Number of pages:** 40

32

**Number of figures:** 4

33

**Number of tables:** 3

34

**Abstract word count:** 250

35

**Introduction word count:** 643

36

**Discussion word count:** 1500

37

38

39

40

**Acknowledgements:** This work was supported by a Wellcome Principal Research Fellowship to  
E.A.M. (101759/Z/13/Z) and the Centre by a Centre Award from Wellcome (203147/Z/16/Z). The  
authors are grateful to David Bradbury for technical assistance.

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The authors declare no competing financial interests and no conflicts of interest.

45

46 **Abstract**

47 The hippocampus is known to be important for a range of cognitive functions including episodic  
48 memory, spatial navigation and future-thinking. Wide agreement on the exact nature of its  
49 contribution has proved elusive, with some theories emphasising associative processes and another  
50 proposing that scene construction is its primary role. To directly compare these accounts of  
51 hippocampal function in human males and females, we devised a novel mental imagery paradigm  
52 where different tasks were closely matched for associative processing and mental construction, but  
53 either did or did not evoke scene representations, and we combined this with high resolution  
54 functional MRI. The results were striking in showing that differentiable parts of the hippocampus,  
55 along with distinct cortical regions, were recruited for scene construction or non-scene-evoking  
56 associative processing. The contrasting patterns of neural engagement could not be accounted for  
57 by differences in eye movements, mnemonic processing or the phenomenology of mental imagery.  
58 These results inform conceptual debates in the field by showing that the hippocampus does not  
59 seem to favour one type of process over another; it is not a story of exclusivity. Rather, there may be  
60 different circuits within the hippocampus, each associated with different cortical inputs, which  
61 become engaged depending on the nature of the stimuli and the task at hand. Overall, our findings  
62 emphasise the importance of considering the hippocampus as a heterogeneous structure, and that a  
63 focus on characterising how specific portions of the hippocampus interact with other brain regions  
64 may promote a better understanding of its role in cognition.

65

66

67 **Significance statement**

68 The hippocampus is known to be important for a range of cognitive functions including episodic  
69 memory, spatial navigation and future-thinking. Wide agreement on the exact nature of its  
70 contribution has proved elusive. Here we used a novel mental imagery paradigm and high resolution  
71 fMRI to compare accounts of hippocampal function that emphasise associative processes with a  
72 theory that proposes scene construction as a primary role. The results were striking in showing that  
73 differentiable parts of the hippocampus, along with distinct cortical regions, were recruited for  
74 scene construction or non-scene-evoking associative processing. We conclude that a greater  
75 emphasis on characterising how specific portions of the hippocampus interact with other brain  
76 regions may promote a better understanding of its role in cognition.

77

78

79 **Abbreviations**

80	ENT	Entorhinal cortex
81	EVC	Early visual cortices
82	PCC	Posterior cingulate cortex
83	PHC	Posterior parahippocampal cortex
84	PRC	Perirhinal cortex
85	RSC	Retrosplenial cortex

86

87 **Introduction**

88 There is long-standing agreement that the hippocampus is essential for supporting memory,  
89 especially long-term episodic or autobiographical memory (Scoville and Milner, 1957; Squire, 1992;  
90 Clark and Maguire, 2016) and for facilitating spatial navigation (O'Keefe and Nadel, 1978). More  
91 recently, the hippocampus has been linked with other roles including scene perception (Graham et  
92 al., 2010), short-term memory (Hartley et al., 2007; Hannula and Ranganath, 2008), constructing  
93 mental representations of scenes (Maguire and Mullally, 2013; Zeidman and Maguire, 2016),  
94 imagining the future (Schacter et al., 2012; Hassabis et al., 2007), decision-making (McCormick et al.,  
95 2016; Mullally and Maguire, 2014) and mind-wandering (Karapanagiotidis et al., 2017; McCormick et  
96 al., 2018). In addition, accumulating evidence suggests that different hippocampal subfields are  
97 preferentially recruited during specific cognitive processes (see examples in Berron et al., 2016;  
98 Dimsdale-Zucker et al., 2018; Eldridge et al., 2005; Guzman et al., 2016; Hodgetts et al., 2017;  
99 Zeidman et al., 2015a).

100

101 Numerous theories attempt to describe how the hippocampus may support such a seemingly  
102 diverse range of functions, including the relational theory and scene construction theory. The  
103 relational theory proposes that the hippocampus is required for the binding of arbitrary relations  
104 among individual elements within an experience or associating items within a context regardless of  
105 whether or not these associations are couched within a spatial framework (Konkel and Cohen, 2009;

106 Cohen and Eichenbaum, 1993). This view has much in common with other theories that place  
107 associative processing at the heart of hippocampal function, namely, the binding of item and context  
108 model (Ranganath, 2010), the domain dichotomy model (Mayes et al., 2010), the configural theory  
109 (Rudy and Sutherland, 1995), the constructive episodic simulation hypothesis (Roberts et al., 2017)  
110 and the high resolution binding hypothesis (Yonelinas, 2013).

111

112 In contrast, the scene construction theory posits that a prime function of the hippocampus is to  
113 construct internal models of the world in the form of spatially coherent scenes. Summerfield et al.  
114 (2010) and Mullally and Maguire (2013) found that three objects and a three-dimensional (3D) space  
115 are sufficient to form the subjective experience of a scene during mental imagery. This is the  
116 operational definition of a scene that we use here. Recently, scene construction has been linked  
117 with a specific part of the hippocampus – the anterior medial portion that encompasses the  
118 presubiculum and parasubiculum (pre/parasubiculum; Zeidman et al., 2015a; Zeidman et al., 2015b;  
119 Zeidman and Maguire, 2016; Hodgetts et al., 2016; Maass et al., 2014; Dalton and Maguire, 2017).

120

121 Our goal in the current study was to directly compare the relational/associative and scene  
122 construction theories. We devised a novel mental imagery task in which participants engaged in  
123 mental construction of objects, non-scene arrays (three objects and a 2D space) and scenes (three  
124 objects and a 3D space). These tasks were matched for associative processing but, importantly, only  
125 the latter evoked the mental experience of a scene representation. This paradigm, therefore, made  
126 it possible to examine whether hippocampal recruitment was modulated by the associative  
127 processing that was required for both array and scene construction, or whether the hippocampus  
128 was preferentially engaged by scenes. Findings either way would provide novel evidence to inform  
129 conceptual debates in the field.

130

131 Given previous findings linking the anterior medial hippocampus with scene processing, we  
132 predicted that this area would be activated by our scene construction task. We also evaluated the  
133 recent relevant prediction, based on anatomical considerations, that the objects task might  
134 preferentially activate prosubiculum/CA1 due to direct links with the perirhinal cortex (PRC; Dalton  
135 and Maguire, 2017; Insausti and Munoz, 2001). More widely, we predicted that retrosplenial (RSC),  
136 posterior cingulate (PCC) and posterior parahippocampal (PHC) cortices would be particularly active  
137 during the scene construction task given their known links with scene processing (Epstein, 2008),  
138 while the object and array construction tasks would engage PRC, given its acknowledged role in  
139 object processing (Nelson et al., 2016; Olarte-Sanchez et al., 2015; Buckley and Gaffan, 1998).

140

## 141 **Materials and Methods**

### 142 **Participants**

143 Thirty healthy, right handed participants took part in the study (20 females, mean age 24 years, SD  
144 4.12). All had normal or corrected to normal vision and gave written informed consent in accordance  
145 with the University College London research ethics committee.

146

### 147 **Tasks and stimuli**

148 The fMRI experiment comprised six separate mental construction tasks: 'Imagine Fixation', 'Imagine  
149 Objects', 'Imagine 2D Grid', 'Imagine 3D Grid', 'Construct Array' and 'Construct Scene' (Fig. 1A-F). For  
150 each task, participants engaged in mental construction with their eyes open while looking at a blank  
151 white screen.

152

153 For the 'Imagine Fixation' task, participants were asked to imagine a black 'plus' sign in the centre of  
154 a blank white screen (Fig. 1A). While imagining the plus sign, participants were auditorily presented  
155 with three nonsense phrases (see Fig. 1G, left panel, for examples of the nonsense phrases), which  
156 compromised non-imageable abstract words, spoken one at a time. These were included in order to

157 mirror the auditory input in the object tasks (see below) while precluding mental imagery.  
158 Participants were instructed not to try and interpret the nonsense phrases in any way. This 'Imagine  
159 Fixation' task was essentially a rest condition providing participants with a break from the more  
160 challenging imagination tasks described below.

161

162 For the 'Imagine Objects' task, participants were auditorily presented with three object descriptions  
163 (see Fig. 1G, right panel, for examples of object descriptions) one after another and instructed, when  
164 hearing the first object description, to imagine the object alone in the centre of the blank white  
165 screen (Fig. 1B). When hearing the second object description, they were asked to imagine the  
166 second object in place of the first in the centre of the screen and when hearing the third object  
167 description, to imagine it in place of the second object. During pre-scan training, participants were  
168 instructed and trained to imagine each object in complete isolation.

169

170 For the 'Imagine 2D Grid' task, participants were asked to create a mental image of a regular, flat 2D  
171 grid covering roughly the bottom two thirds of the blank screen (Fig. 1C). For the 'Imagine 3D Grid'  
172 task, participants were asked to create a mental image of a 3D grid covering roughly the bottom two  
173 thirds of the blank screen (see Fig. 1D). While imagining the grids, participants were auditorily  
174 presented with three nonsense phrases, spoken one at a time. The important difference between  
175 these tasks is that the 3D grid induces a sense of depth and 3D space.

176

177 For the 'Construct Array' task, participants were instructed to first imagine the 2D grid on the  
178 bottom two thirds of the screen. While doing this, participants were auditorily presented with three  
179 object descriptions one after another which they imagined on the 2D grid. More specifically,  
180 participants were asked, when hearing the first object description, to imagine the object in an  
181 arbitrary location on the 2D grid. When hearing the second object description, participants were  
182 asked to imagine it on another arbitrarily chosen location on the 2D grid while maintaining the

183 image of the first object in its original location. When hearing the third object description,  
184 participants were asked to imagine it on another part of the 2D grid while maintaining the image of  
185 the first two objects in their original positions. We explicitly told participants that the final product of  
186 their mental imagery was to be three objects in random locations on a flat 2D grid (Fig. 1E).

187

188 For the ‘Construct Scene’ task, participants were instructed to first imagine a 3D grid on the bottom  
189 two thirds of the screen. While doing this, they were auditorily presented with three object  
190 descriptions one at a time which they were asked to imagine on the 3D grid. Specifically, participants  
191 were asked, when hearing the first object description, to imagine the object in any location on the  
192 3D grid. When hearing the second object description, participants were asked to imagine it on  
193 another location on the 3D grid while maintaining the image of the first object in its original position.  
194 When hearing the third object description, participants were asked to imagine it on another part of  
195 the 3D grid while maintaining the image of the first two objects in their original locations. The final  
196 product of their mental imagery was to be 3 objects in a simple 3D scene (Fig. 1F).

197

198 For tasks which required object imagery (‘Imagine Objects’, ‘Construct Array’ and ‘Construct Scene’)  
199 we emphasised the importance of engaging imagination rather than memory for each object. We  
200 asked participants to imagine a unique version of each object based on the descriptions alone and,  
201 as far as possible, not to recall specific objects that they were familiar with, any personal memories  
202 involving the objects or any places that they might associate with the described objects. We also  
203 asked participants not to imagine any movement, even if objects had movable parts, but to create  
204 static images of each object in their mind’s eye.

205

206 For the Imagine 2D Grid and Imagine 3D Grid tasks, participants were instructed to keep their  
207 ‘viewpoint’ of the grid fixed and static and not to imagine either the grid moving or themselves  
208 moving along the grid. In contrast to the 2D grid, mental imagery of the 3D grid induces a sense of



209 depth and participants were additionally asked not to imagine moving 'into' the 3D space in any  
210 way.

211

212 For the Construct Array and Construct Scene tasks, participants were asked that for each trial, they  
213 keep the objects separate from each other so that no objects physically touched and no objects  
214 interacted. We asked participants not to add any additional elements but to create the arrays and  
215 scenes using only the objects provided. Participants were asked to utilise the full extent of the grids  
216 to place the objects and to continue imagining the objects on the grids for the duration of the  
217 imagination period. Also, having imagined all three objects on the grid, participants were asked not  
218 to mentally 'rearrange' the objects. Rather, they were asked to leave them where they were initially  
219 placed in their mind's eye. We asked participants to keep their viewpoint fixed and central and not  
220 to imagine themselves or any objects moving in any way. For the Construct Array task, we  
221 emphasised the importance of not linking the objects together into a scene but to arbitrarily place  
222 the objects in random locations.

223

224 Separate audio files were recorded for each object description and nonsense phrase. These were  
225 recorded in a sound proof room and spoken by a male voice in an even tone. Prior to the  
226 experiment, a separate group of participants ( $n = 10$ ) rated each object description on whether it  
227 was space defining (SD) or space ambiguous (SA) (Mullally and Maguire, 2011, 2013) and also  
228 provided ratings of object permanence (Auger et al., 2012; Mullally and Maguire, 2011). Object  
229 descriptions and nonsense phrases were further rated for imageability. The auditory stimuli for each  
230 task were all three words in length and carefully matched on a range of specific features.

231

232 In relation to the object descriptions, the Imagine Objects, Construct Array and Construct Scene  
233 tasks were matched according to the number of SD and SA objects ( $F_{(2,215)} = 0.128$ ,  $p = 0.880$ ), ratings  
234 of object permanence ( $F_{(2,215)} = 0.106$ ,  $p = 0.899$ ), syllable number ( $F_{(2,215)} = 0.234$ ,  $p = 0.792$ ) and

235 utterance length ( $F_{(2,215)} = 0.014$ ,  $p = 0.986$ ). In addition, the order of presentation of SD/SA items  
236 was balanced across all trials. Object triplets were arranged so that objects within each triplet had  
237 no obvious semantic or contextual associations.

238

239 In relation to nonsense phrases, syllable number ( $F_{(2,215)} = 1.953$ ,  $p = 0.144$ ) and utterance length  
240 ( $F_{(2,215)} = 0.591$ ,  $p = 0.555$ ) were matched across the Imagine Fixation, Imagine 2D Grid and Imagine  
241 3D Grid tasks. In addition, syllable number ( $F_{(5,431)} = 0.925$ ,  $p = 0.464$ ) and utterance length ( $F_{(5,431)} =$   
242  $0.658$ ,  $p = 0.656$ ) were matched across all tasks, and the nonsense phrases were rated as  
243 significantly less imageable than the object descriptions ( $t_{(1,49)} = 81.261$ ,  $p < 0.001$ ).

244

245 In summary, the two tasks of primary interest were the 'Construct Array' and 'Construct Scene'  
246 tasks. As described above, these tasks involved participants hearing three object descriptions and  
247 imagining them on either an imagined 2D or 3D space. With all else being equal in the stimuli, this  
248 simple manipulation of space gave rise to mental representations of non-scene arrays (objects and  
249 2D space) and scenes (objects and 3D space). We also included tasks that examined the  
250 representation of three objects without a spatial context where the objects were imagined one after  
251 another in the same location on the centre of the screen, and the representation of either 2D or 3D  
252 space alone without objects. Overall, this novel paradigm allowed us to separately examine the  
253 neural correlates of constructing mental representations of objects alone (with no spatial context),  
254 two types of space (2D and 3D space alone with no objects) and two different combinations of  
255 objects and space where only one gave rise to scene representations. Importantly, no visual stimuli  
256 were presented during the imagination phase of any task (Fig. 1H). Therefore, between-task  
257 differences in neural recruitment could not be influenced by differences in visual input.

258

259

260

261 **Pre-scan training**

262 Participants were trained before scanning to ensure task compliance. After listening to the  
263 instructions, participants engaged in four practice trials of each task while sitting at a desktop  
264 computer in a darkened room. They rated the vividness of mental imagery for each trial on a scale of  
265 1 (not vivid at all)...5 (extremely vivid). If they gave a rating of 3 or below on any practice trial, they  
266 repeated the practice session. When participants rated 4 or above on all practice trials and indicated  
267 that they could vividly engage in the mental imagery relevant to each task, they were transferred to  
268 the scanner for the experiment.

269

270 **fMRI task**

271 Each trial of the experiment (Fig. 1H) was comprised of a visual cue (2 seconds) which informed of  
272 the task, followed by a 1-4 second jitter and then the imagination phase of ~15 seconds. During the  
273 imagination phase, participants engaged in the mental imagery pertinent to each task while hearing  
274 three auditory phrases (either objects or nonsense, depending on the task, Fig. 1G) delivered via MR  
275 compatible headphones (Sensimetrics model S14). The length of each auditory phrase was  
276 approximately 2s followed by a 1s gap between the presentation of each phrase. After hearing the  
277 third auditory phrase, participants had approximately 7s to finalise and maintain the mental image  
278 they had created. They were required to do this with their eyes open while looking at a blank white  
279 screen. They then rated the vividness of their mental image on a 1 (not vivid at all)...5 (extremely  
280 vivid) scale (max 2 seconds). Finally, an inter-trial interval of 2 seconds preceded the cue for the next  
281 trial. Twenty four trials were presented for each condition (144 trials in total) in a pseudo-  
282 randomised order across 4 separate blocks. Each block lasted approximately 15 minutes and blocks  
283 were separated by a brief rest period. It was emphasised to participants that the main objective of  
284 the experiment was to create vivid mental images in their imagination. However, to ensure  
285 participants were attending throughout, we included an additional 12 catch trials (2 per task) across

286 the experiment where participants had to press a button if, within a nonsense or object triplet, they  
287 heard a repeated phrase.

288

### 289 **In-scan eye tracking**

290 As a further measure of task compliance, we utilised in-scan eye tracking to ensure participants were  
291 performing each task according to the instructions. For the Imagine Fixation and Imagine Objects  
292 tasks, participants were asked to focus their eyes on the centre of the screen where they imagined  
293 the plus sign or objects to be. When imagining the 2D and 3D grids, they were asked to move their  
294 eyes around where they imagined the grids to be on the screen. For the Construct Array and  
295 Construct Scene tasks, participants were required to imagine each of three objects against the  
296 imagined 2D or 3D grid respectively. Eye tracking data were acquired using an Eyelink 1000 Plus (SR  
297 Research) eye tracker. The right eye was used for calibration, recording and analyses. During the  
298 imagination phase, the x and y coordinates of all fixations were recorded. Visualisation of fixation  
299 locations was performed with Eyelink Data Viewer (SR Research). Eye tracking data from 8  
300 participants were unavailable due to technical issues, leaving 22 data sets in the eye-tracking  
301 analyses.

302

### 303 **Post-scan surprise memory tests**

304 After completing the experiment and leaving the scanner, participants were taken to a testing room  
305 and given surprise item and associative yes/no recognition memory tests. Participants first  
306 performed an item memory test, where they were auditorily presented with all 216 object  
307 descriptions heard during the Imagine Object, Construct Array and Construct Scene tasks (72 objects  
308 per task) and an additional 72 lure items which were not heard during the experiment. Object  
309 descriptions were randomised across tasks and were presented one at a time. For each object  
310 description participants were asked to respond 'yes' if they thought the object description was heard  
311 during the scanning experiment and 'no' if they thought it was not.

312

313 Participants then performed a more difficult associative memory test. For this, participants were  
314 auditorily presented with 72 sets of object triplets (24 sets from each of the Imagine Object,  
315 Construct Array and Construct Scene tasks). Forty eight of these object triplets (16 from each of the  
316 three tasks) had been presented together during the experiment (intact triplets). Twenty four of the  
317 object triplets (8 from each of the three tasks) contained object descriptions that were presented  
318 during the experiment, but not together in a triplet (recombined triplets). For each object triplet,  
319 participants were asked to respond 'yes' if they thought the objects were heard together during the  
320 fMRI experiment and 'no' if they were not. For both memory tasks, participants also gave a  
321 confidence rating on a 1-5 scale for each decision and timing was self-paced (up to a maximum of 5  
322 seconds each) for both the choices and confidence ratings. Note that we do not include the data  
323 from the confidence ratings from the associative memory test as they were, perhaps unsurprisingly,  
324 dominated by 'guessing' ratings. Memory test data from 7 participants were unavailable due to  
325 technical issues.

326

#### 327 **Post-scan debriefing**

328 Following the memory tests, participants were probed on how they approached each task, and  
329 performed a number of ratings as described in the Results section and Table 3.

330

#### 331 **Data acquisition and pre-processing**

332 Structural and functional MRI data were acquired using a 3T Siemens Trio scanner (Siemens,  
333 Erlangen, Germany) with a 32-channel head coil within a partial volume centred on the temporal  
334 lobe and included the entire extent of the temporal lobe and all of our other regions of interest.  
335 Structural images were collected using a single-slab 3D T2-weighted turbo spin echo sequence with  
336 variable flip angles (SPACE) (Mugler et al., 2000) in combination with parallel imaging, to  
337 simultaneously achieve a high image resolution of  $\sim 500 \mu\text{m}$ , high sampling efficiency and short scan

338 time while maintaining a sufficient signal-to-noise ratio (SNR). After excitation of a single axial slab  
339 the image was read out with the following parameters: resolution =  $0.52 \times 0.52 \times 0.5 \text{ mm}^3$ , matrix =  
340  $384 \times 328$ , partitions = 104, partition thickness = 0.5 mm, partition oversampling = 15.4%, field of  
341 view =  $200 \times 171 \text{ mm}^2$ , TE = 353 ms, TR = 3200 ms, GRAPPA x 2 in phase-encoding (PE) direction,  
342 bandwidth = 434 Hz/pixel, echo spacing = 4.98 ms, turbo factor in PE direction = 177, echo train  
343 duration = 881, averages = 1.9. For reduction of signal bias due to, for example, spatial variation in  
344 coil sensitivity profiles, the images were normalized using a prescan, and a weak intensity filter was  
345 applied as implemented by the scanner's manufacturer. To improve the SNR of the anatomical  
346 image, three scans were acquired for each participant, coregistered and averaged. Additionally, a  
347 whole brain 3D FLASH structural scan was acquired with a resolution of  $1 \times 1 \times 1 \text{ mm}$ .

348

349 Functional data were acquired using a 3D echo planar imaging (EPI) sequence which has been  
350 demonstrated to yield improved BOLD sensitivity compared to 2D EPI acquisitions (Lutti et al., 2013).  
351 Image resolution was  $1.5\text{mm}^3$  isotropic and the field-of-view was 192mm in-plane. Forty slices were  
352 acquired with 20% oversampling to avoid wrap-around artefacts due to imperfect slab excitation  
353 profile. The echo time (TE) was 37.30 ms and the volume repetition time (TR) was 3.65s. Parallel  
354 imaging with GRAPPA image reconstruction (Griswold et al., 2002) acceleration factor 2 along the  
355 phase-encoding direction was used to minimise image distortions and yield optimal BOLD sensitivity.  
356 The dummy volumes necessary to reach steady state and the GRAPPA reconstruction kernel were  
357 acquired prior to the acquisition of the image data as described in Lutti et al. (2013). Correction of  
358 the distortions in the EPI images was implemented using B0-field maps obtained from double-echo  
359 FLASH acquisitions (matrix size  $64 \times 64$ ; 64 slices; spatial resolution  $3\text{mm}^3$ ; short TE=10 ms; long  
360 TE=12.46 ms; TR=1020 ms) and processed using the FieldMap toolbox in SPM (Hutton et al., 2002).

361

362 Preprocessing of structural and fMRI data was conducted using SPM12 (Wellcome Centre for Human  
363 Neuroimaging, University College London). All images were first bias corrected, to compensate for

364 image inhomogeneity associated with the 32 channel head coil (Van Leemput et al., 1999).  
365 Fieldmaps were collected and used to generate voxel displacement maps. EPIs for each session were  
366 then realigned to the first image and unwarped using the voxel displacement maps calculated above.  
367 The three high-resolution structural images were averaged to reduce noise, and co-registered to the  
368 whole brain structural FLASH scan. EPIs were also co-registered to the whole brain structural scan  
369 and spatially smoothed using a Gaussian smoothing kernel of 4 x 4 x 4 mm full-width at half  
370 maximum.

371

#### 372 **Statistical analyses: behavioural data**

373 Data from eye tracking, in-scan vividness ratings, post-scan memory tests and debrief ratings were  
374 analysed using repeated measures ANOVAs (SPSS 17.0, Chicago: SPSS inc.) with a significance  
375 threshold of  $p < 0.05$ . Where Mauchly's test indicated that the assumption of sphericity had been  
376 violated, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

377

#### 378 **Statistical analyses: fMRI data**

379 We used non-rotated task Partial Least Squares (PLS) for data analysis which is a multivariate  
380 method for extracting distributed signal changes related to varying task demands (Krishnan et al.,  
381 2011; McIntosh and Lobaugh, 2004). Data for each condition were included in a block design analysis  
382 and we conducted separate analyses for each of our contrasts of interest. Significance for each  
383 contrast was independently determined using a permutation test with 1000 permutations. We  
384 considered latent variables less than  $p = 0.05$  as significant. The reliability of voxel saliences was  
385 assessed by means of a bootstrap estimation of the standard error (McIntosh and Lobaugh, 2004).  
386 Bootstrapping is a sampling technique in which subjects are randomly selected into the analysis with  
387 replacement from the entire group of subjects. For each new sample, the entire PLS analysis is re-  
388 calculated. In the present study, this sampling and analysis procedure was carried out 500 times,  
389 resulting in estimates of the standard error of the salience at each voxel. No corrections for multiple

390 comparisons are necessary because the voxel saliences are calculated in a single mathematical step  
391 on the whole volume. We considered clusters of 10 or more voxels in which the bootstrap ratio was  
392 greater than 1.96 (approximately equivalent to  $p < 0.05$ ) to represent reliable voxels. In the current  
393 analyses, we specified a 14.6 second temporal window for each event (i.e. 4 TRs) to include the  
394 active phase of mental construction. Importantly, for each significant contrast reported in the main  
395 text, confidence intervals did not cross the 0 line suggesting that each condition contributed to the  
396 pattern.

397

398 We used a large region of interest that included the whole medial temporal lobe (MTL) –  
399 hippocampus, entorhinal cortex (ENT), PRC, as well as PHC, RSC and PCC which have been implicated  
400 in scene processing. The mask also extended posteriorly to encompass regions of the early visual  
401 cortices (EVC) including the precuneus (only inferior portions due to the partial volume), the  
402 calcarine sulcus, the lingual gyrus and portions of the posterior fusiform cortex, given these regions  
403 have previously been implicated in different elements of mental imagery (de Gelder et al., 2016;  
404 Lambert et al., 2002; Klein et al., 2000).

405

## 406 **Results**

407 Our main focus was on contrasts involving the Construct Scene task (the full results of all the task  
408 comparisons are provided in Table 1). The contrast of primary interest was the Construct Scene task  
409 with the closely matched Construct Array task. As described above, these two conditions were well  
410 matched, requiring mental construction and associative processing of objects and space. The only  
411 difference between them was the scene construction task required objects to be imagined on a 3D  
412 grid that gave rise to a scene-like representation (compare the panels in Fig. 1E and F). Directly  
413 contrasting these tasks, therefore, allowed us to investigate brain regions that underpin scene  
414 construction while controlling for content, mental constructive and associative processes.

415



416 **fMRI task comparisons**

417 Comparison of the Construct Scene task with the Construct Array task revealed that, in line with our  
418 prediction, a circumscribed region of the anterior medial hippocampus (peak voxel at  $y = -24$ )  
419 encompassing the pre/parasubiculum was preferentially recruited, bilaterally, during scene  
420 construction along with the PHC, RSC and PCC (Fig. 2B, Fig. 3). Interestingly, the opposite contrast  
421 showed that array, more than scene, construction engaged bilateral ENT, PRC, EVC and the left  
422 posterior hippocampus which was part of a larger cluster of activity which encompassed the anterior  
423 lingual gyrus and portions of the EVC. This contrast also revealed activation of the left ENT abutting  
424 the anterior medial hippocampus (peak voxel at  $y = -12$ ) that was more anterior to the  
425 pre/parasubiculum engaged by scene construction (Fig. 2B, Fig. 3).

426

427 The contrast of Construct Scene with Imagine Objects provided further support that bilateral  
428 pre/parasubiculum along with the PHC, RSC and PCC were specifically associated with scene  
429 construction (Fig. 3, Table 1,). The reverse contrast showed that the mental construction of objects,  
430 more so than scenes, was associated with bilateral PRC and ENT. The right anterior lateral  
431 hippocampus, encompassing prosubiculum/CA1, and a left ENT activation that abutted the anterior  
432 medial hippocampus were also engaged. This area was more anterior (peak voxel at  $y = -10.5$ ) to  
433 that associated with scene construction (Fig. 2B, Fig. 3).

434

435 The contrast of Construct Scenes with the Imagine 3D Grid revealed increased engagement of an  
436 anterior medial portion of the hippocampus in the approximate location of the uncus (peak voxel at  
437  $y = -9$ ) and bilateral PRC. The reverse contrast showed that the mental construction of 3D grids,  
438 more so than scenes, was associated with bilateral ENT and posterior portions of EVC. Imagine 3D  
439 Grid did not evoke increased hippocampal activation compared to Imagine 2D Grid, suggesting that  
440 3D space alone was insufficient to engage the hippocampus.

441

442 To summarise (see Fig. 3), our experimental design allowed us to parse the hippocampus and related  
443 areas dependent on the process that was being engaged. Circumscribed portions of the bilateral  
444 pre/parasubiculum (around  $y = -24$ ) were specifically recruited during scene construction. By  
445 contrast, a more anterior portion of the ENT that abutted the anterior medial hippocampus was  
446 engaged during both array and object construction. Of note, these activated regions were clearly  
447 distinct (explicit smoothing = 4mm; Euclidean distance between peak voxels of the Construct Scene  
448 versus Construct Array contrasts 11.89mm; Construct Array versus Imagine Object contrasts  
449 13.64mm). The construction of mental images of arrays was also associated with increased activity  
450 in the posterior hippocampus as part of a larger cluster which encompassed the lingual gyrus and  
451 EVC. Object construction engaged anterior lateral hippocampus in the region of prosubiculum/CA1.  
452 Outside of the hippocampus, compared to array construction, the PHC, RSC and PCC were  
453 preferentially recruited during scene construction. In contrast, compared to scene construction,  
454 array construction was associated with more posterior portions of the EVC, while both array and  
455 object construction were more strongly associated with the ENT and PRC.

456

457 But could other factors have influenced the results? We conducted a range of further analyses to  
458 investigate.

459

#### 460 **Did participants truly engage with the tasks?**

461 The construction of mental imagery cannot be directly measured. We therefore used a combination  
462 of methods to assess task attentiveness and compliance. First, we included catch trials where  
463 participants had to press a button if, during any trial, they heard a repeated phrase. On average, 94%  
464 (SD = 0.09) of catch trials were correctly identified indicating that participants remained attentive  
465 throughout the experiment.

466

467 Second, we utilised in-scan eye tracking to ensure participants were performing each task according  
468 to the instructions. Visualisation of fixations confirmed that participants engaged in each task  
469 according to our instructions (see examples in Fig. 4A). To formally determine the extent of eye  
470 movements, we measured the variance of all fixations in the horizontal axis during the construction  
471 phase of each trial (Fig. 4B). We predicted that if participants performed the mental imagery tasks as  
472 expected, there would be less variance in fixation location during the centre-focussed Imagine  
473 Fixation and Imagine Objects tasks and a more dispersed pattern of fixations across the other tasks.  
474 The results of a repeated measures ANOVA revealed a significant difference in the variance of  
475 fixations between tasks ( $F_{(2,28,47.77)} = 26.22, p < 0.001$ ). In line with our prediction, post hoc analyses  
476 revealed significantly less variance during the Imagine Fixation task compared to the other tasks  
477 (compared to the Imagine 2D Grid  $t_{(21)} = 6.286, p < 0.001$ ; Imagine 3D Grid  $t_{(21)} = 5.296, p < 0.001$ ;  
478 Construct Array  $t_{(21)} = 6.247, p = 0.001$ ; Construct Scene  $t_{(21)} = 5.839, p < 0.001$ ). Significantly less  
479 variance was also observed in the Imagine Objects task compared to the other tasks (Imagine 2D  
480 Grid  $t_{(21)} = 6.241, p < 0.001$ ; Imagine 3D Grid  $t_{(21)} = 4.949, p < 0.001$ ; Construct Array  $t_{(21)} = 6.266, p <$   
481  $0.001$ ; Construct Scene  $t_{(21)} = 5.336, p < 0.001$ ). There was no difference between the Imagine  
482 Fixation and Imagine Objects tasks ( $t_{(21)} = 1.702, p = 0.806$ ). Variance during the Imagine 2D Grid  
483 task was significantly less than during the Imagine 3D Grid task ( $t_{(21)} = 3.819, p = 0.015$ ). No other  
484 significant between-task differences were observed, including between the Construct Scene and  
485 Construct Array tasks ( $t_{(21)} = 1.897, p = 0.884$ ).

486

487 Taken together, these measures provide quantitative evidence that participants paid attention  
488 during the experiment and engaged in mental imagery construction in accordance with task  
489 instructions.

490

491 After scanning, we also asked participants to draw how they had imagined the arrays and scenes  
492 during the fMRI tasks. Examples are shown in Fig. 4C and also indicate that participants complied

493 with task requirements. The drawings also show that, despite both being composed of three objects  
494 related to a space, there was a clear representational difference between the arrays and the scenes.  
495 Further informative measures were obtained during post-scan testing and debriefing, and these are  
496 described in following sections.

497

#### 498 **Did other eye movement features contribute to between-task differences?**

499 To investigate the possibility that between-task differences in neural recruitment may be explained  
500 by other eye movement features, we investigated the number of fixations, fixation durations, the  
501 number of saccades, saccade amplitudes and scan paths, with a specific focus on our tasks of  
502 interest, Construct Array and Construct Scene. There were no differences in terms of the number of  
503 fixations ( $t_{(21)} = 0.144$ ,  $p = 1.00$ ), fixation durations ( $t_{(21)} = 0.423$ ,  $p = 1.00$ ), the number of saccades  
504 ( $t_{(21)} = 0.033$ ,  $p = 1.00$ ) or saccade amplitudes ( $t_{(21)} = 1.822$ ,  $p = 0.726$ ).

505

506 To examine scan paths, we split the screen into three equal areas of interest (AOI), left, middle and  
507 right, and plotted the scan path for each trial. Two variables were measured in order to provide an  
508 index of the spatial distribution of scanning - the number of fixations and the dwell time within each  
509 AOI. Analyses showed that there was a task by AOI interaction for number of fixations ( $F_{(1.249,26.237)} =$   
510  $5.989$ ,  $p = 0.016$ ), with Construct Array associated with more fixations to the right of the screen  
511 ( $t_{(21)} = 2.251$ ,  $p = 0.035$ ,  $d = 0.16$ ), Construct Scenes with more fixations in the middle ( $t_{(21)} = 2.175$ ,  $p$   
512  $= 0.041$ ,  $d = 0.24$ ), with no difference for the left side of the screen ( $t_{(21)} = 1.784$ ,  $p = 0.089$ ). Neither  
513 of these effects survived Bonferroni correction, and the effect sizes (Cohen's  $d$ ) were small. There  
514 was also a task by AOI interaction for dwell time ( $F_{(1.329,27.918)} = 4.0$ ,  $p = 0.045$ ), with Construct Scene  
515 associated with a longer dwell time in the middle ( $t_{(21)} = 2.369$ ,  $p = 0.027$ ,  $d = 0.19$ ), with no  
516 difference for the left of the screen ( $t_{(21)} = 0.772$ ,  $p = 0.449$ ) or the right of the screen ( $t_{(21)} = 1.840$ ,  $p$   
517  $= 0.080$ ). This effect did not survive Bonferroni correction, and the effect size was small.

518

519 Overall, therefore, the Construct Array and Construct Scene tasks were generally well matched,  
520 making it unlikely that between-task differences in neural recruitment were related to eye  
521 movements.

522

### 523 **Was hippocampal recruitment related to mnemonic processing?**

524 Once out of the scanner after completing the experiment, participants were given two surprise  
525 memory tests (see Materials and Methods). Given the large number of stimuli, and the fact that  
526 there was no explicit instruction to encode information – rather the emphasis was on mental  
527 construction, and memory was never mentioned – our expectation was that performance would be  
528 poor, even at chance, on the memory tests. We felt it was necessary, however, to conduct these  
529 tests in case successful encoding differed across tasks, and this could have explained differences in  
530 the brain areas that were engaged. Scores (Means, SD) are shown in Table 2.

531

532 For the item memory test, participants performed above chance at recalling stimuli that were from  
533 the Imagine Objects ( $t_{(22)} = 13.491$ ,  $p < 0.001$ ), Construct Array ( $t_{(22)} = 9.268$ ,  $p < 0.001$ ) and Construct  
534 Scene ( $t_{(22)} = 8.514$ ,  $p < 0.001$ ) tasks, and were above chance at identifying novel items ( $t_{(22)} = 13.710$ ,  
535  $p < 0.001$ ). The good performance on this test (with task means between 70-83% correct – see Table  
536 2) is a further indication that the participants paid attention, encoded information and were  
537 engaged by the tasks. A repeated measures ANOVA revealed a significant between-task effect on the  
538 item memory test ( $F_{(1,77, 38.98)} = 9.524$ ,  $p < 0.001$ ). Post hoc analyses showed that participants were  
539 better at recognising object descriptions which were presented in the Imagine Objects task than  
540 objects presented in the Construct Array ( $t_{(22)} = 4.829$ ,  $p < 0.001$ ) and Construct Scene ( $t_{(22)} = 7.210$ ,  $p$   
541  $< 0.001$ ) tasks. Participants were also better at recognising novel items than objects presented in the  
542 Construct Scene task ( $t_{(22)} = -3.382$ ,  $p = 0.016$ ). Notably, there was no significant difference between  
543 the Construct Array and Construct Scene tasks ( $t_{(22)} = 2.707$ ,  $p = 0.075$ ).

544

545 On the very challenging associative memory task, as we expected, participants did not perform  
546 above chance on the recognition of intact triplets that were from the Imagine Objects ( $t_{(22)} = 0.368$ ,  $p$   
547  $= 0.717$ ), Construct Array ( $t_{(22)} = 1.177$ ,  $p = 0.252$ ) and Construct Scene ( $t_{(22)} = 0.682$ ,  $p = 0.503$ ) tasks.  
548 A repeated measures ANOVA showed that there were no significant differences between the tasks  
549 for either the recognition of intact object triplets ( $F_{(2,44)} = 0.870$ ,  $p = 0.426$ ), or correct rejection of  
550 recombined object triplets ( $F_{(2,44)} = 1.651$ ,  $p = 0.204$ ). This included no significant difference between  
551 Construct Array and Construct Scene tasks (intact triplets:  $t_{(22)} = 1.047$ ,  $p = 0.667$ ; recombined  
552 triplets:  $t_{(22)} = 1.124$ ,  $p = 0.616$ ).

553

554 Overall, these results revealed no significant differences in memory performance in particular  
555 between our two tasks of interest, Construct Array and Construct Scene. Therefore, the differences  
556 we observed in neural recruitment during fMRI cannot be accounted for by differences in encoding  
557 success. Of note, it was not appropriate to run a subsequent memory analysis on the fMRI data using  
558 the individual object stimuli. This is because the three object descriptions that comprised one trial  
559 were presented in quick succession and it was not possible with fMRI to reliably tease apart signals  
560 relating to the specific items within a trial. Considering associative memory for the triplets, given  
561 that performance was not above chance in the subsequent surprise memory test, and that  
562 participants expressed low confidence about their memory decisions, using these data to interpret  
563 the fMRI data would be ill-advised. Moreover, in the associative memory test, two thirds of the  
564 triplets were tested intact, but one third of triplets were recombined in order to act as lures.  
565 Therefore, any subsequent memory fMRI analysis would likely be underpowered.

566

#### 567 **Can imagery vividness account for hippocampal engagement?**

568 During fMRI scanning, participants rated the vividness of mental imagery on each trial (see Materials  
569 and Methods; Fig. 1H; means (SDs) on Table 3). Results of the repeated measures ANOVA revealed a  
570 significant between-tasks difference in vividness ratings ( $F_{(2,70, 78.26)} = 11.60$ ,  $p < 0.001$ ). Post hoc

571 analyses showed that mental imagery during the Imagine Objects task was rated as more vivid than  
572 during the Imagine Fixation ( $t_{(29)} = 4.095$ ,  $p = 0.005$ ), Imagine 2D Grid ( $t_{(29)} = 5.586$ ,  $p < 0.001$ ),  
573 Imagine 3D Grid ( $t_{(29)} = 4.195$ ,  $p = 0.004$ ), Construct Array ( $t_{(29)} = 4.506$ ,  $p < 0.001$ ) and Construct  
574 Scene ( $t_{(29)} = 3.265$ ,  $p = 0.041$ ) tasks. Imagery during the Construct Array task was rated significantly  
575 more vivid than during the Imagine 2D Grid task ( $t_{(29)} = 3.398$ ,  $p = 0.029$ ). Imagery during the  
576 Construct Scene task was rated significantly more vivid than during the Imagine 2D Grid ( $t_{(29)} =$   
577  $4.116$ ,  $p = 0.004$ ) and Imagine 3D Grid ( $t_{(29)} = 3.224$ ,  $p = 0.046$ ) tasks. Importantly, no significant  
578 difference was observed between the Construct Array and Construct Scene tasks ( $t_{(29)} = 2.116$ ,  $p =$   
579  $0.483$ ).

580

581 **Can perceived task difficulty or subjective differences in mental imagery account for hippocampal**  
582 **recruitment?**

583 In the debriefing session after scanning, and once the surprise memory tests were completed,  
584 participants were asked about their experience of performing each task (see means (SDs) on Table  
585 3). Participants reported that they could perform the tasks with ease with no between-task  
586 differences for perceived task difficulty ( $F_{(3,37,97.85)} = 2.396$ ,  $p = 0.066$ ; including no difference  
587 between the Construct Array and Construct Scene tasks,  $t_{(29)} = 0.524$ ,  $p = 1.00$ ). Significant between-  
588 task differences were observed for the rating of mind-wandering ( $F_{(3,46,100.39)} = 3.638$ ,  $p = 0.011$ ). Post  
589 hoc analyses showed that compared to the Imagine Objects task, participants were more prone to  
590 engage in mind-wandering during the Imagine Fixation ( $t_{(29)} = 3.465$ ,  $p = 0.025$ ) task. This makes  
591 sense considering the fixation task was included as a rest condition for participants. There was no  
592 significant difference between Construct Array and Construct Scene tasks ( $t_{(29)} = 0.436$ ,  $p = 1.00$ ).  
593 Significant differences were also observed on the rating of detail of mental imagery ( $F_{(3,47, 100.70)} =$   
594  $3.510$ ,  $p = 0.014$ ). Post hoc analyses showed that mental imagery during the Construct Scene task  
595 was significantly more detailed than during the 'Imagine 2D Grid' task ( $t_{(29)} = 3.093$ ,  $p = 0.043$ ). No

596 other significant between-task differences were observed, including between Construct Array and  
597 Construct Scene tasks ( $t_{(29)} = 1.884$ ,  $p = 0.514$ ).

598

599 Participants further confirmed (Table 3) that, during the Construct Scene task, they were successful  
600 at creating a scene in their minds eye. In contrast, participants reported a clear sense of imagining  
601 objects on a 2D grid during the Construct Array task and stated that they rarely felt a need to repress  
602 mental imagery of scenes during this task. Direct comparison showed that, as expected, the  
603 Construct Scene task was rated as subjectively more 3D than the Construct Array task which was  
604 rated as more 2D ( $t_{(29)} = 11.988$ ,  $p < 0.001$ ). There were no significant differences between the tasks  
605 (including between Construct Array and Construct Scenes tasks) on several other subjective  
606 measures: the creation of narratives about the stimuli ( $F_{(2,15,62.43)} = 0.597$ ,  $p = 0.565$ ; Construct Array  
607 versus Construct Scene  $t_{(29)} = 1.00$ ,  $p = 0.981$ ), the fixedness of the viewpoint ( $F_{(1,96,56.75)} = 0.139$ ,  $p =$   
608  $0.867$ ; Construct Array versus Construct Scene  $t_{(29)} = 0.441$ ,  $p = 0.999$ ) and the inclusion of  
609 extraneous objects or other details ( $F_{(2,58)} = 0.957$ ,  $p = 0.390$ ; Construct Array versus Construct Scene  
610  $t_{(29)} = 1.055$ ,  $p = 0.657$ ).

611

612 In summary, subjective measures indicated that the participants performed the task with ease, and  
613 adhered to the instructions. As might be expected, there were some minor differences, for example  
614 increased mind-wandering during the Imagine Fixation task but, importantly, no significant  
615 differences between the Construct Array and Construct Scene tasks.

616

### 617 **Results summary**

618 The results of the fMRI analyses revealed that when other associative and mental constructive  
619 processes were taken into account, a specific region of the anterior medial hippocampus –  
620 corresponding to the location of the pre/parasubiculum – was engaged during scene construction  
621 along with other regions which have previously been linked to scene processing including the PHC,



622 RSC and PCC. In contrast, array construction was more strongly associated with the ENT, PRC,  
623 posterior portions of EVC and activation within the left posterior hippocampus and left ENT abutting  
624 the anterior medial hippocampus. Importantly, this latter activation was in a location more anterior  
625 to the cluster observed during scene construction. Interestingly, the Imagine Objects task resulted in  
626 activation of the anterior lateral hippocampus. The differing patterns of neural recruitment between  
627 the very tightly matched Construct Array and Construct Scene tasks could not be accounted for by  
628 differences in eye movements, mnemonic processing or the phenomenology of mental imagery.

629

### 630 **Discussion**

631 The aim of this study was to compare accounts that place associative processes at the heart of  
632 hippocampal function with the theory that proposes scene construction as one of its primary roles.  
633 Using closely matched tasks during high resolution fMRI we found that, as predicted, the  
634 pre/parasubiculum in the anterior medial hippocampus was preferentially engaged by the  
635 construction of scenes (three objects and a 3D space). However, it was also evident that different  
636 regions *within* the hippocampus were engaged by the construction of arrays (three objects and a 2D  
637 space) that did not evoke scene representations. In this case, the posterior hippocampus and an  
638 ENT region that abutted the anterior hippocampus were recruited. Even the imagination of object  
639 triplets that had no spatial context activated this latter region along with an anterior portion of the  
640 lateral hippocampus in the approximate location of prosubiculum/CA1. Overall, these results show  
641 that one possible reason for ongoing debates about how the hippocampus operates may be because  
642 it does not only process space or associations or scenes. Instead, there may be multiple processing  
643 circuits within the hippocampus that become engaged depending on task demands.

644

645 Our primary contrast of interest was array construction compared with scene construction. These  
646 tasks were closely matched on stimulus content and mental constructive and associative processes.  
647 Attention, eye movements, encoding success and perceived difficulty did not differ between them.

648 Phenomenologically, the vividness and detail of their imagery were also matched. Nevertheless, in  
649 line with our prediction and previous reports, a circumscribed portion of the pre/parasubiculum in  
650 the anterior medial hippocampus was preferentially involved in scene construction (Zeidman and  
651 Maguire, 2016; Zeidman et al., 2015a; Zeidman et al., 2015b; Hodgetts et al., 2016; Maas et al.,  
652 2014). Importantly, our findings reveal for the first time that this region is preferentially recruited,  
653 not for mental construction per se, not for imagining a 3D space alone, but specifically for mental  
654 construction of scenes that are couched within a naturalistic 3D spatial framework.

655

656 Drawing on the latest anatomical evidence, Dalton and Maguire (2017) recently noted that the  
657 pre/parasubiculum is a primary target of the parieto-medial temporal processing pathway and may  
658 receive integrated information from foveal and peripheral visual inputs (Kravitz et al., 2011). Thus, it  
659 has privileged access to holistic representations of the environment and so could be  
660 neuroanatomically determined to preferentially process scenes. Indeed, Dalton and Maguire (2017)  
661 suggest the pre/parasubiculum may be the hippocampal ‘hub’ for scene-based cognition. The PHC,  
662 RSC and PCC are also implicated in the anatomical scene processing network connecting with the  
663 pre/parasubiculum. Aligning with this evidence and their known links with scene processing  
664 (Epstein, 2008), we found that these brain areas were more engaged during scene compared to  
665 array construction.

666

667 By contrast, array construction engaged a different set of brain areas, namely, the ENT, PRC and  
668 posterior portions of EVC, with the left ENT/PRC cluster extending to abut the anterior medial  
669 hippocampus and the EVC cluster extending anteriorly along the lingual gyrus into the left posterior  
670 hippocampus. Where the activity involved the ENT and abutted the hippocampus, the location  
671 bordered the pre/parasubiculum much more anteriorly than that for scene construction. Therefore,  
672 naturalistic 3D scene representations may engage a circumscribed portion of the anterior  
673 pre/parasubiculum in unison with the PHC, RSC and PCC. By contrast, more general or abstracted

674 forms of spatial imagery, such as objects on a 2D space (see also Constantinescu et al., 2016), might  
675 recruit a more anterior portion of ENT abutting the very anterior pre/parasubiculum. The different  
676 parts of the hippocampus and distinct cortical regions engaged by scenes and arrays, despite the  
677 close matching of the tasks, precludes the view that scenes are merely being enabled by processing  
678 sets of associations similar to those underpinning array construction. What we document here are  
679 separable mental construction processes giving rise to distinct types of representation in and around  
680 the hippocampus.

681

682 Considering the posterior hippocampal activation during array construction, this area has been  
683 implicated in a broad range of cognitive processes (Strange et al., 2014; Poppenk et al., 2013;  
684 Zeidman and Maguire, 2016), including spatial memory (Maguire et al., 2006; Moser and Moser,  
685 1998) and mnemonic processing of items in a 2D space (de Rover et al., 2011). While our results  
686 reflect involvement of the posterior hippocampus in mental imagery of objects in a 2D rather than  
687 3D space, it is unlikely that the posterior hippocampus is only involved in this form of mental  
688 imagery. The anatomy of the most posterior portion of the human hippocampus is particularly  
689 complex (Dalton et al., 2017), with much still to learn. Ultra-high resolution MRI investigations at the  
690 level of subfields are required to further inform our understanding of posterior hippocampal  
691 contributions to specific cognitive processes.

692

693 The Construct Objects task was not designed to be a close match for the array and scene tasks, but  
694 was included to inform about the brain areas engaged during object construction and object only  
695 associations, where spatial context was irrelevant. Of note, vividness of the imagery and memory  
696 for the objects in this task was significantly better than those in the array and scene construction  
697 tasks. Therefore, any fMRI results should be interpreted with this in mind. PRC recruitment during  
698 object imagery would be predicted, and indeed was found, considering the strong association  
699 between the PRC and object-centred cognition (Murray et al., 2007). Overall, the object task

700 engaged very similar areas to those recruited for array construction, namely, the PRC, ENT abutting  
701 the very anterior medial left hippocampus. This may reflect a generic area for non-scene based  
702 associative processing. Where object construction differed from both array and scene tasks was in  
703 the activation of the right anterior lateral hippocampus in the region that aligns with the location of  
704 the prosubiculum/CA1. This finding is concordant with the prediction of Dalton and Maguire (2017),  
705 based on neuroanatomical considerations, where PRC, ENT and prosubiculum/CA1 are heavily  
706 interconnected (Li et al., 2017; Insausti and Munoz, 2001). Therefore, as with the array and scene  
707 construction tasks, the mental construction of isolated objects engaged a differentiable portion of  
708 the hippocampus.

709

710 Our results show that for associations between objects, between objects and 2D space or objects  
711 and 3D space, the hippocampus does not seem to favour one type of representation over another; it  
712 is not a story of exclusivity. Rather, there may be different circuits within the hippocampus, each  
713 associated with different cortical inputs, which become engaged depending on the nature of the  
714 stimuli and the task at hand. This may explain why it has been so difficult to reconcile hippocampal  
715 theories that have generally focused on one type of process or representation. Our results may also  
716 explain why disparate patterns of cognitive preservation and impairment are reported in patients  
717 with bilateral hippocampal lesions. For any individual, damage may affect particular subregions  
718 within the hippocampus more than others. These subtle case-by-case differences in the microscopic  
719 topography of damage and sparing may impact on cognition in different ways that as yet remain  
720 undetectable by current MRI technology.

721

722 While some theoretical accounts have posited that distinct areas within the MTL may preferentially  
723 process specific types of representation (Graham et al., 2010; Barense et al., 2005), perhaps  
724 surprisingly, such representational differences have not typically been extended to processing *within*  
725 the hippocampus. Non-human primate tract tracing studies have shown clear differences in how

726 different cortical and subcortical brain regions interact not only with specific hippocampal subfields  
727 (Ding et al., 2000; Rockland and Van Hoesen, 1999; DeVito, 1980) but also disproportionately  
728 interact with specific portions of subfields along the longitudinal (anterior–posterior) and transverse  
729 (distal–proximal) axes of the hippocampus (Insausti and Munoz, 2001). In recent years, functional  
730 differentiation down the long axis of the hippocampus (reviewed in Poppenk et al., 2013; Nadel et  
731 al., 2013; Strange et al., 2014; Zeidman and Maguire, 2016) and subfield-specific hypotheses  
732 (Guzman et al., 2016; Berron et al., 2017; Libby et al., 2012) have received increasing attention. Our  
733 results further emphasise the importance of considering the hippocampus as a heterogeneous  
734 structure, and that a focus on characterising how specific portions of the hippocampus interact with  
735 other brain regions may promote a better understanding of its role in cognition.

736

737 It remains possible that other factors may have affected our results. For example, it could be that  
738 participants engaged in more size transformation of objects, or visualisation of objects in a more  
739 distant space, during the Construct Scene task. We are, however, unaware of any evidence for MTL  
740 involvement in these processes (Larsen et al., 2000). Future work is needed to precisely characterise  
741 the different information processing streams within the human hippocampus, both anatomically and  
742 functionally. Presumably these circuits are linked, but how and to what extent will also be important  
743 questions to address. In humans, little is known about intrahippocampal functional connectivity or  
744 even connectivity between specific hippocampal subfields and the rest of the brain. Use of ultra-high  
745 resolution (f)MRI is clearly warranted to help move beyond an ‘either/or’ view of the hippocampus  
746 to a more nuanced understanding of its multifaceted contributions to cognition.

747

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955 **Figure 1. Experimental design.** (A-F) Representations of how participants engaged in mental imagery  
956 during each task, with the text cues on the left of each panel. Note that participants looked at a  
957 blank white screen during the imagination phases. The images depicted on the right of each panel  
958 are based on what participants said they imagined during the task. (G) Examples of object  
959 descriptions and nonsense phrases. (H) Example of the time line of a single trial.

960

961 **Figure 2. Results of the fMRI analysis.** (A) Left panel, a representation of the oblique angle cutting  
962 through the hippocampus that we use to present the results in the other panels. Middle panel,  
963 shows the averaged structural MR image of the participants exposing the length of the  
964 hippocampus. Right panel, depicts the regions of particular interest. (B) From left to right, the results  
965 for the contrast of Construct Scene > Construct Array, Construct Array > Construct Scene, Imagine  
966 Object > Construct Scene and all of the results combined. PCC = posterior cingulate cortex; results  
967 are thresholded at  $p < 0.05$ .

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969 **Figure 3. Summary of the main hippocampal activations.** (A) The location of the left posterior  
970 hippocampal activation for the Construct Array > Construct Scene contrast (left, top panel). The right  
971 anterior medial hippocampal activation – pre/parasubiculum – observed for the contrast of  
972 Construct Scene > Construct Array (left, second panel from top). The entorhinal region abutting the  
973 much more anterior pre/parasubiculum that was recruited for both Construct Array (left, third panel  
974 from top) and Imagine Objects (left, bottom panel) tasks more so than Construct Scenes. The right  
975 anterior lateral hippocampal activation – prosubiculum/CA1 – for the contrast of Imagine Objects >  
976 Construct Scene (left, bottom panel). The right panels show representative schematics of the  
977 locations of the hippocampal subregions. (B) Schematic representation of the hippocampus (white)  
978 and entorhinal cortex (grey) in the axial plane. The location of each of the coronal plane images  
979 presented in (A) is shown along with representations of the extent of each cluster.

980

981 **Figure 4. Eye movements and examples of post-scan drawings.** (A) Representative examples of  
982 fixation locations (cyan circles) during the imagination phase of a single trial of each task are overlaid  
983 on a blank white screen on which participants focused their imagination (left panel). A visual  
984 representation of what participants were asked to imagine on the screen is shown to the right of  
985 each panel. Note the central focus of fixations for the Imagine Fixation and Imagine Objects tasks,

986 the more dispersed pattern over the bottom two thirds of the screen for the Imagine 2D Grid and  
987 Imagine 3D Grid tasks and the three clusters for both the Construct Array and Construct Scene tasks  
988 representing the locations of the imagined objects. (B) The mean variance ( $\pm 1$  SEM) of fixations on  
989 the x coordinate during the imagination phase of each task is shown. (C) Representative examples of  
990 post-scan drawings for the Construct Array (left) and Construct Scene (right) tasks.

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**Table 1. Results of the fMRI task comparisons.**

	Contrast	Brain Regions	Hemisphere (L/R)	MNI peak coordinate			BSR	Number of voxels
<b>Construct scene</b>	Construct Scene > Construct Array (p = 0.004)	Anterior medial hippocampus – pre/parasubiculum	R	22.5	-24	-16.5	3.7655	56
		Anterior calcarine sulcus (encompassing anterior lingual gyrus / posterior cingulate cortex / retrosplenial cortex / inferior precuneus)	L	-10.5	-51	6	3.3724	81
		Anterior calcarine sulcus (encompassing anterior lingual gyrus / posterior cingulate cortex / retrosplenial cortex / inferior precuneus)	R	9.0	-55.5	12.0	3.2213	102
		Posterior PHC	R	28.5	-43.5	-10.5	2.8698	36
		Anterior medial hippocampus – pre/parasubiculum	L	-21.0	-21.0	-19.5	2.8138	45
		Posterior fusiform cortex	R	28.5	-33.0	-18.0	2.4450	20
	Construct Scene > Imagine Objects (p = 0.015)	Anterior lingual gyrus (encompassing inferior precuneus / posterior cingulate cortex / retrosplenial cortex and extending posteriorly to encompass posterior lingual gyrus / posterior calcarine sulcus)	R / L	10.5	-55.5	7.5	4.8465	3041
		Posterior PHC	L	-30.0	-42.0	-10.5	4.0339	249
		Posterior hippocampus	R	18.0	-37.5	1.5	3.9468	55
		Posterior PHC (extending anteriorly to encompassing anterior medial hippocampus – pre/parasubiculum)	R	28.5	-42.0	-12.0	3.7299	360
		Anterior PHC (perirhinal cortex)	L	-33.0	-24.0	-34.5	3.6459	29
		Retrosplenial cortex / posterior cingulate cortex	L	-7.5	-39.0	6.0	3.0623	16
		Anterior medial hippocampus – pre/parasubiculum	L	-25.5	-24.0	-16.5	2.9320	52
		Posterior fusiform cortex	R	21.0	-60.0	-12.0	2.2978	14
	Construct Scene > Imagine 3D Grid (p = 0.005)	Anterior lingual gyrus (encompassing anterior calcarine sulcus / inferior precuneus / posterior cingulate cortex / retrosplenial cortex)	R	9	-54	9	6.0388	341
		Inferior precuneus (encompassing posterior cingulate cortex / retrosplenial cortex / anterior calcarine sulcus / anterior lingual gyrus)	L	-4.5	-55.5	10.5	5.7412	314
		Posterior PHC	L	-24	-37.5	-19.5	5.5618	723
		Posterior PHC	R	25.5	-34.5	-21	4.6426	488
		Anterior PHC (perirhinal cortex)	L	-31.5	-6	-36	3.6334	89
		Anterior medial hippocampus – uncus	L	-12	-9	-25.5	3.3703	10
Anterior PHC (perirhinal cortex)		R	30	-3	-40.5	3.3075	110	
Anterior medial hippocampus – uncus		R	22.5	-7.5	-25.5	2.6372	26	

<b>Construct array</b>	Construct Array > Construct Scene (p = 0.004)	Anterior lingual gyrus (extending anteriorly to encompass posterior hippocampus and extending posteriorly to encompass posterior lingual gyrus / posterior calcarine sulcus)	L / R	-16.5	-51.0	-4.5	4.9728	3479
		Anterior PHC (perirhinal cortex / entorhinal cortex)	L	-28.5	-1.5	-39.0	3.8068	181
		Anterior PHC (perirhinal cortex / entorhinal cortex)	R	28.5	3.0	-43.5	3.6093	440
		Anterior PHC (Entorhinal cortex / abutting the anterior medial hippocampus)	L	-19.5	-12.0	-27.0	3.1719	119
		Anterior PHC (Entorhinal cortex)	L	-19.5	4.5	-36.0	2.7904	27
		Anterior lingual gyrus	R	4.5	-63.0	4.5	2.5501	10
	Construct Array > Imagine Objects (p = 0.005)	Posterior calcarine sulcus (encompassing posterior lingual gyrus extending anteriorly to encompass anterior lingual gyrus / posterior PHC / posterior hippocampus)	R / L	10.5	-81.0	4.5	6.4355	6992
		Anterior PHC (perirhinal cortex)	R	24.0	1.5	-39.0	3.6467	47
		Posterior PHC	R	34.5	-36.0	-13.5	2.4383	10
		Anterior PHC (entorhinal cortex)	L	-21.0	-16.5	-30.0	2.3777	16
		Anterior PHC (perirhinal cortex)	L	-28.5	-4.5	-37.5	2.3342	17
		Middle lateral hippocampus – CA1	L	-34.5	-25.5	-16.5	2.3212	15
	Construct Array > Imagine 2D Grid (p < 0.001)	Posterior PHC (extending anteriorly to encompass entorhinal cortex / perirhinal cortex)	L	-30	-27	-24	5.3247	1014
		Posterior PHC (extending anteriorly to encompass entorhinal cortex / perirhinal cortex)	R	31.5	-24	-22.5	4.5307	522
		Inferior precuneus (encompassing anterior calcarine sulcus / posterior cingulate cortex / retrosplenial cortex / posterior hippocampus)	L	-6	-52.5	12	4.1098	488
Posterior hippocampus (encompassing inferior precuneus / posterior cingulate cortex / retrosplenial cortex)		R	15	-39	3	4.0605	279	
Anterior PHC (perirhinal cortex)		R	22.5	0	-49.5	3.3109	73	
Anterior lingual gyrus		L	-24	-54	-3	2.7134	21	
<b>Imagine objects</b>	Imagine Objects > Construct Scene (p = 0.015)	Anterior PHC (entorhinal cortex / perirhinal cortex)	R	21.0	-9.0	-33.0	3.4047	241
		Anterior lateral hippocampus – CA1	R	33.0	-10.5	-27.0	3.3312	11
		Anterior PHC (perirhinal cortex)	L	-25.5	-3.0	-39.0	3.2742	34
		Anterior PHC (entorhinal cortex / abutting the anterior medial hippocampus)	L	-18.0	-10.5	-27.0	3.2310	126
	Imagine Objects > Construct Array (p = 0.005)	Anterior lateral hippocampus – CA1	R	30.0	-13.5	-21.0	3.0863	42

<b>Imagine 3D grid</b>	Imagine 3D Grid > Construct Scene ( $p = 0.005$ )	Posterior lingual gyrus (encompassing posterior calcarine sulcus extending anteriorly to anterior lingual gyrus)	L / R	-10.5	-78	-10.5	5.2507	3088
		Posterior fusiform cortex	R	27	-55.5	-18	3.4263	33
		Anterior calcarine sulcus	L	-22.5	-66	9	3.3149	24
		Anterior lingual gyrus	R	27	-52.5	-6	3.1481	134
		Anterior lingual gyrus	L	-22.5	-45	-1.5	3.102	14
		Anterior lingual gyrus	L	-33	-54	-6	3.0345	13
		Anterior PHC (entorhinal cortex)	R	15	-6	-31.5	2.8463	73
		Anterior PHC (entorhinal cortex)	L	-18	-4.5	-31.5	2.4347	27
		Imagine 3D Grid > Imagine 2D Grid ( $p = 0.191$ )	No significant between-task differences	-	-	-	-	-
<b>Imagine 2D grid</b>	Imagine 2D Grid > Construct Array ( $p < 0.001$ )	Posterior lingual gyrus (encompassing posterior calcarine sulcus extending anteriorly to anterior lingual gyrus / anterior calcarine sulcus)	L / R	-16.5	-72	-10.5	5.38	2134
		Anterior calcarine sulcus	R	22.5	-61.5	10.5	3.9023	45
		Posterior calcarine sulcus		0	-90	-4.5	3.4177	20
		Anterior hippocampus	R	28.5	-19.5	-15	2.6862	36
		Anterior lingual gyrus	R	24	-46.5	-10.5	2.6018	27
		Anterior calcarine sulcus	L	-21	-66	6	2.3526	22
		Imagine 2D Grid > Imagine 3D grid ( $p = 0.191$ )	No significant between-task differences	-	-	-	-	-

997 PHC = parahippocampal cortex; L = Left; R = Right; BSR = Boot Strap Ratio (reliability of voxel saliences);  $BSR > 1.96 = p < 0.05$ ;  $> 2.58 = p < 0.01$ ;  $> 3.29 = p < 0.001$ .  
 998 Note that  $p$  values in the 'Contrast' column relate to condition differences following permutation testing of the latent variables.  
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1002 **Table 2. Item and associative memory test performance (% correct).**  
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	<b>Task</b>	<b>Mean <math>\pm</math> standard deviation</b>
<b>Item memory</b>	Imagine Object	82.85 $\pm$ 11.68
	Construct Array	76.03 $\pm$ 13.47
	Construct Scene	71.07 $\pm$ 11.87
	Identifying Novel Items	81.94 $\pm$ 11.17
<b>Associative memory intact triplets</b>	Imagine Object	51.09 $\pm$ 14.18
	Construct Array	55.16 $\pm$ 21.04
	Construct Scene	51.90 $\pm$ 13.38
<b>Associative memory recombined triplets</b>	Imagine Object	46.20 $\pm$ 17.45
	Construct Array	54.35 $\pm$ 19.44
	Construct Scene	48.91 $\pm$ 19.91

1004

1005 Table 3. Subjective measures.  
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Question	Rating (Yes/No or 1-5 Likert scale)		Tasks of relevance	Mean ± SD
<b>How vivid was your imagination of the xxxx?</b> (From the trial-by-trial vividness ratings during scanning)	1 = not vivid at all	...5 = extremely vivid	Imagine Fixation Imagine Object Imagine 2D grid Imagine 3D grid Construct Array Construct Scene	3.77 ± 0.65 4.16 ± 0.53 3.69 ± 0.62 3.84 ± 0.57 3.96 ± 0.52 4.03 ± 0.53
<b>How difficult was it to imagine the xxxx?</b>	1 = very easy	...5 = very difficult	Imagine Fixation Imagine Object Imagine 2D grid Imagine 3D grid Construct Array Construct Scene	2.58 ± 1.22 2.01 ± 0.75 2.65 ± 1.09 2.13 ± 0.88 2.35 ± 0.76 2.43 ± 0.85
<b>How often did you engage in off-task thoughts (mind-wander) during this task?</b>	1 = never	...5 = always	Imagine Fixation Imagine Object Imagine 2D grid Imagine 3D grid Construct Array Construct Scene	2.22 ± 0.80 1.77 ± 0.57 2.30 ± 0.99 1.87 ± 0.67 1.88 ± 0.65 1.95 ± 0.83
<b>In general, how detailed do you think your images of the xxxx were?</b>	1 = Hardly any details at all	...5 = Extremely richly detailed	Imagine Object Imagine 2D grid Imagine 3D grid Construct Array Construct Scene	3.27 ± 0.45 2.97 ± 0.81 3.22 ± 0.67 3.27 ± 0.69 3.45 ± 0.62
<b>In general, did you feel that you successfully imagined the objects in a scene?</b>	1 = never successful	...5 = always successful	Construct Scene	3.77 ± 0.84
<b>Did you feel that you imagined the objects in a scene at all and had to try to repress this?</b>	1 = never had to repress	...5 = always repressed	Construct Array	1.28 ± 0.69
<b>On a scale of 1-5, how 2D/3D was your mental imagery during this task?</b>	1 = completely 2D	...5 = completely 3D	Construct Array Construct Scene	1.90 ± 0.84 4.10 ± 0.82



Did you make up any stories or scenarios related to the xxx?	0 = No 1 = Yes		Imagine Object	0.02 ± 0.09	
			Imagine 2D grid	0.07 ± 0.25	
			Imagine 3D grid	0.02 ± 0.09	
			Construct Array	0.03 ± 0.18	
Did you keep your viewpoint fixed?	0 = No 1 = Yes		Construct Scene	0.07 ± 0.25	
			Imagine 2D grid	0.98 ± 0.09	
			Imagine 3D grid	0.97 ± 0.18	
			Construct Array	0.97 ± 0.18	
To what extent did you imagine other objects or details in addition to the given objects? Did you...?	1 = think of objects with other details the entire time	. . . 5 = not think of other objects or details at all	Construct Scene	0.98 ± 0.09	
			Imagine Object	4.07 ± 0.83	
				Construct Array	4.23 ± 0.73
				Construct Scene	4.08 ± 0.77

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