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Characterising the hippocampal response to perception, construction and complexity

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ABSTRACT

The precise role played by the hippocampus in supporting cognitive functions such as episodic memory and future thinking is debated, but there is general agreement that it involves constructing representations comprised of numerous elements. Visual scenes have been deployed extensively in cognitive neuroscience because they are paradigmatic multi-element stimuli. However, questions remain about the specificity and nature of the hippocampal response to scenes. Here, we devised a paradigm in which we had participants search pairs of images for either colour (perceptual) or layout (spatial constructive) differences. Importantly, images depicted either naturalistic scenes or phase-scrambled versions of the same scenes, and were either simple or complex. Using this paradigm during functional MRI scanning, we addressed three questions: 1. Is the hippocampus recruited specifically during scene processing? 2. If the hippocampus is more active in response to scenes, does the cognitive process (perception or construction) being engaged influence its activation? 3. If the hippocampus is upregulated during scene processing, does the complexity of the scenes affect its response? We found that, compared to phase-scrambled versions of the scenes, the hippocampus was more responsive to scene stimuli. Moreover, a clear anatomical distinction was evident, with scene perception engaging the posterior hippocampus and scene construction recruiting the anterior hippocampus. The complexity of the scenes did not influence hippocampal activity. These findings seem to align with perspectives that propose the hippocampus is especially attuned to scenes, and its involvement occurs irrespective of the cognitive process or the complexity of the scenes.

Key words

hippocampus, scene perception, scene construction, longitudinal hippocampal axis, visual complexity

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1. Introduction

The hippocampus makes a crucial contribution to episodic memory (Scoville & Milner, 1957), spatial navigation (O'Keefe & Dostrovsky, 1971), and a range of other cognitive domains including imagining the future (Addis, Wong, & Schacter, 2007; Hassabis, Kumaran, Vann, & Maguire, 2007), mind-wandering (Karapanagiotidis, Bernhardt, Jefferies, & Smallwood, 2016; McCormick, Rosenthal, Miller, & Maguire, 2018) and dreaming (Spano et al., 2020). Theoretical accounts differ on precisely how the hippocampus supports these diverse cognitive functions. Nevertheless, across perspectives there is a common thread, namely that its contribution involves constructing representations composed of numerous elements (Cohen & Eichenbaum, 1993; Lee et al., 2005; Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019; Hassabis & Maguire, 2007; Schacter & Addis, 2007). Visual scenes are paradigmatic multi-element stimuli and consequently have been deployed extensively to test hippocampal function in perceptual, associative, recognition, recall and imagination tasks (Aly, Ranganath, & Yonelinas, 2013; Barry, Chadwick, & Maguire, 2018; Lee, Brodersen, & Rudebeck, 2013; McCormick, Rosenthal, Miller, & Maguire, 2017). A scene is defined as a naturalistic three-dimensional spatially-coherent representation of the world typically populated by objects and viewed from an egocentric perspective (Dalton, Zeidman, McCormick, & Maguire, 2018).

Patients with hippocampal damage show scene-related perceptual, imagination and mnemonic impairments (Lee et al., 2005; Hassabis, Kumaran, Vann, & Maguire, 2007; Mullally, Intraub, & Maguire, 2012; Aly, Ranganath, & Yonelinas, 2013), and functional MRI (fMRI) studies have consistently reported hippocampal engagement during scene processing as part of a wider set of brain areas that includes ventromedial prefrontal cortex (vmPFC), parahippocampal, retrosplenial and parietal cortices (Robin, Buchsbaum, & Moscovitch, 2018; Zeidman, Mullally, & Maguire, 2015). It is unclear precisely why the hippocampus responds to scenes, and theoretical perspectives differ in the emphasis they place on specific features of scenes and

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their processing in order to explain hippocampal engagement, and to make inferences about its function. However, there are several gaps in our knowledge of scene processing which, if filled, may help to clarify the role of the hippocampus. Here we sought to increase our understanding by asking three questions using functional MRI (fMRI).

First, is the hippocampus especially attuned to scenes? Some accounts argue that scenes and spatial contexts merely exemplify relational processing where elements are bound together, and it is this fundamental associative processing that the hippocampus provides (Aly et al., 2013; Eichenbaum, 2006; Eichenbaum & Cohen, 2014; Erez, Cusack, Kendall, & Barense, 2016; Lee et al., 2005; Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019). A contrasting perspective proposes that the hippocampus is specifically concerned with constructing scene representations, and more so than other types of multi-feature representations (Hassabis & Maguire, 2007; Maguire & Mullally, 2013). It is challenging to compare these differing views in a controlled way. One approach, devised by Dalton et al. (2018), had participants gradually build scene imagery from three successive auditorily-presented object descriptions and an imagined 3D space during fMRI. This was contrasted with constructing mental images of non-scene arrays that were composed of three objects and an imagined 2D space. The scene and array stimuli were, therefore, highly matched in terms of content and the associative and constructive processes they evoked. Constructing scenes compared to arrays was associated with increased activity in the anterior medial hippocampus, suggesting that this part of the hippocampus may be especially tuned to scene processing (Zeidman & Maguire, 2016).

However, these simple scene representations are far removed from the naturalistic scenes that we experience in the real world. But if we want to examine naturalistic scenes, then it is still important to compare them to similar non-scene stimuli. One possibility, which we pursued here, is to create phase-scrambled versions of scenes (Yoonessi & Kingdom, 2008). The

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resulting images possess the same spatial frequency and colour scheme as the original scenes, but their phase is randomized such that any meaning is removed from the image. By combining the scenes and their phase-scrambled versions with the manipulation of a key feature of interest (complexity – more on this later), and matched cognitive task requirements, we predicted that, in line with Dalton et al. (2018), naturalistic scene stimuli would preferentially engage the anterior medial hippocampus.

If the hippocampus were more involved in scene processing, the second question we asked is whether the cognitive process engaged at the time would influence hippocampal recruitment. Lee et al. (2005; see also Lee et al., 2013; Barense, Henson, Lee, & Graham, 2010) used an odd-one-out paradigm where patients with bilateral hippocampal damage were shown three scenes from different viewpoints and were unable to select the one scene that was different from the two others. The authors interpreted this result as a scene perception deficit since all scenes were visible throughout each trial. However, it has been argued that this odd-one-out task also requires the construction of internal models of the scenes which are needed to mentally rotate the scenes in order to compare them to one another (Zeidman & Maguire, 2016). Consequently, findings such as these could reflect a hippocampal role in scene perception and/or the construction of scene imagery.

Zeidman et al. (2015) examined this issue further by having participants view visual scenes or construct scenes in their imagination, where there was the potential to be asked subsequently to hold the perceived or imagined scene in working memory. They found that perceiving scenes was associated with extensive activation in posterior hippocampus and the anterior medial hippocampus, whereas scene construction engaged the anterior medial hippocampus. This suggests that while posterior hippocampus might be particularly engaged during scene perception, anterior medial hippocampus might play a role in constructing representations of

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scenes, whether perceived or imagined, when there is a need to retain them in memory. While it is difficult to separate perception and construction completely, here we sought to disentangle perception and construction processes, where visual input was identical, and there was no memory requirement.

Extending previous experimental designs (Aly et al., 2013; Lee et al., 2013), on each trial participants had to examine two images that were displayed side by side and judge whether or not the two images were the same or subtly different. Images could have either a colour (perceptual) or layout (constructive) difference. We reasoned, based on pilot testing, that a very subtle change in global colour between two images would engage participants in comparing the perceptual qualities of images to one another, while minimising the processing of layout within the image. For the constructive task, we manipulated the spatial relationships between elements within an image (see Aly et al., 2013 for a similar approach). Here, we expected that participants would focus on mentally constructing the spatial layout of one image in order to compare it to the other image. Participants were cued before each image pair whether they should focus on the colour or layout of the images. Importantly, most of the image pairs, and those that were the focus of data analysis, were identical; therefore, participants focused on colour or layout differences in the absence of visual differences. This manipulation allowed us to counterbalance the stimuli across participants so that half of the participants searched a particular image pair for colour differences and the other half of the participants searched the same pair for layout differences. We predicted that our scene perception task, with no need for scene construction, would engage the posterior hippocampus, while the scene construction task would recruit the anterior hippocampus.

If the hippocampus were more involved in scene processing, the third question we asked was whether its engagement would be affected by the complexity of the scenes. We used Snodgrass

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and Vanderwart's (1980) definition of visual complexity as the amount of detail or intricacy in an image (see also Donderi, 2006 for a review). Thus, for example, simple scenes have a very limited number of conjunctions in the image (e.g., a deserted beach, a sky with a single bird). By contrast, complex scenes have many conjunctions (e.g., a crowded supermarket, an amusement park). Complexity is central to several perspectives on hippocampal function with high complexity, increased level of detail, number of associations or conjunctions, held to be linked to hippocampal engagement (Barense et al., 2010; Eichenbaum & Cohen, 2014; Graham, Barense, & Lee, 2010; Lee, Yeung, & Barense, 2012; Yonelinas, 2013). Therefore, the prediction of these accounts would be that complex scenes would activate the hippocampus more than simple scenes. By contrast if, as we predict here, the hippocampus is particularly attuned to scene processing (Hassabis & Maguire, 2007; Maguire & Mullally, 2013), then any scene, simple or complex, should recruit the hippocampus.

Overall, therefore, this study had a 2x2x2 factorial design which enabled us to examine the main effects of three factors and their interactions: 1. Image type (naturalistic scenes or phase-scrambled images); 2. Cognitive process (perception or construction); and 3. Complexity (simple or complex images). To reiterate, data analysis focused on the trials where the image pairs were identical (which were the majority of trials), with stimuli counterbalanced across participants. We employed two approaches, one data driven and the other involving pre-specified contrasts. While our main focus was on the hippocampus, we examined the whole brain in order to contextualise and further inform the research questions. In addition, we recorded eye-tracking data during scanning, performed a post-scan surprise memory task to examine potential effects of incidental encoding, collected complexity ratings for the stimuli, and asked participants about the cognitive strategies they used to perform the tasks. While we had clear hypotheses, as outlined above, our paradigm also permitted evaluation of other perspectives, given the clearly contrasting predicted outcomes.

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2. Materials and methods

2.1. *Participants*

Twenty healthy, right-handed participants (8 males, mean age 27.6 years, SD 5.5, range 21-38 years) participated in the study. None had a history of neurological or psychiatric disorders. Given the pictorial nature of the stimuli, we excluded individuals engaging (as professionals, students or hobbyists) in any intensive art or design-related activities. Colour-blind individuals were also excluded as one of the tasks involved detecting subtle colour differences. All participants gave informed written consent in accordance with the University College London research ethics committee.

2.2. *Stimuli and conditions*

Five hundred and six pairs of images were used in this study (26 in a pre-scan practice session, 320 during scanning, and 160 as lures in a post-scan surprise memory test). Images were all in colour, and adjusted in Adobe Photoshop CS6 to an image size of 300 dpi and cropped to the same square size (450 x 450 pixels). Given our three main factors (image type, cognitive process and complexity), there were eight main conditions: 1. Simple scene perception, 2. Complex scene perception, 3. Simple scrambled perception, 4. Complex scrambled perception, 5. Simple scene construction, 6. Complex scene construction, 7. Simple scrambled construction, 8. Complex scrambled construction. In addition, we included a number of image pairs that were of medium complexity. Their function was to act as distractors for the participants so that overall the stimuli seemed to reflect a range of complexity rather than two extremes. This resulted in four more conditions: 9. Middle scene perception, 10. Middle scrambled perception, 11. Middle scene construction, and 12. Middle scrambled construction, although the fMRI data from these middle complexity conditions were not considered as they comprised fewer stimuli

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than the main eight conditions. Lastly, there was also a low-level baseline task that involved viewing a fixation cross and counting from one onwards until the next cue. This was designed to allow participants to disengage from the other cognitively challenging tasks. For each of the main eight conditions, there were 25 target stimuli (that is, those with no difference between the two images in a pair) and 8 catch images (those with a difference between the two images in a pair). For each of the four middle complexity conditions, there were 10 target trials and 3 catch trials. There were 25 low-level baseline trials.

2.3. *Image manipulations*

Although we only analysed target trials in which the two images in a pair were identical and the participants identified them correctly as such, the manipulation of the catch trials was crucial to ensure that participants would engage in different cognitive processes, i.e., perceptual versus constructive processes. We, therefore, carefully created the catch trials, whereby naturalistic and scrambled as well as simple and complex images underwent the same manipulations (see Fig. 1).

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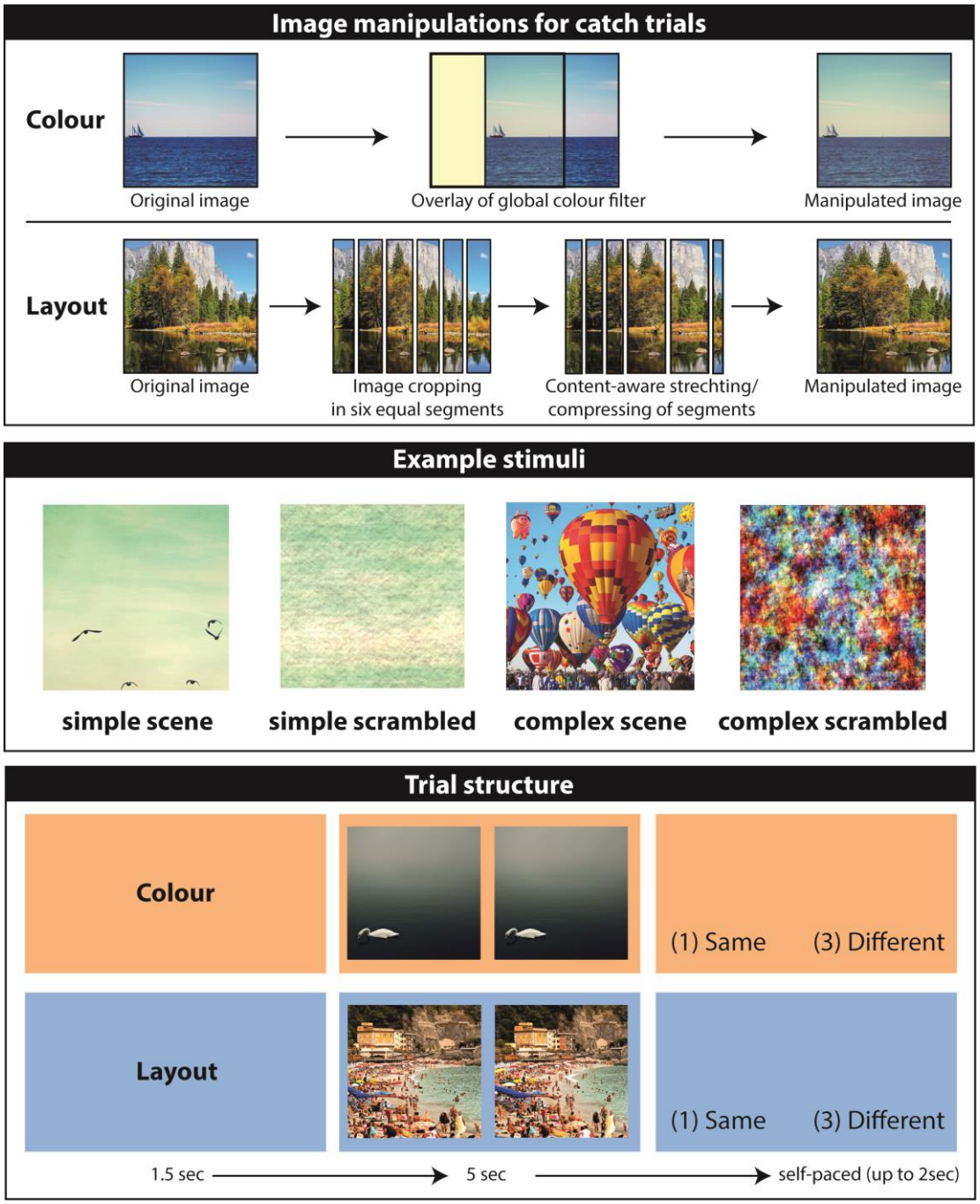

Fig 1 - Image manipulations and experimental design. The upper panel illustrates the main image manipulations that were made in order to create the catch trials for the perception (colour differences) and construction (layout differences) tasks. The middle panel shows example scene and scrambled stimuli. Simple scenes had only a few details whereas complex scenes had lots of details. The scrambled versions of these scenes led to simple scrambled and complex scrambled images. The lower panels illustrate example trials, first where the participant received a cue (orange background) for 1.5sec indicating that, on this trial, they should search the upcoming image pair for a colour difference. After the cue, the image pair was displayed for 5 sec, after which there was up to 2 sec in which to make a decision. There is no difference between the images in this example. Below this is an example of a layout trial, in this case, a catch trial where there is a layout difference between the scene images.

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2.3.1. *Perception catch trials*

For the catch trials in the perception task, we manipulated the global colour balance of one image of a pair. For this effect, we selected one image and used Adobe Photoshop's colour balance feature on the entire image to change the balance very slightly to either red, green or blue. Hence, when displayed, one image was shown with its original colour balance next to the altered image, creating a catch trial in which the images were different. Pilot testing (including in the MRI scanner) ensured that the colour changes were detectable but sufficiently subtle to engage the participants for the trial duration. Furthermore, the analyses reported in this study were based solely on pairs in which there were no differences between the images of a pair, yet all participants reported that they kept searching the images for colour differences for the entire trial length.

2.3.2. *Construction catch trials*

For the catch trials in the construction task, we manipulated the spatial relationship between features of one image of a pair. Of note, we chose not to employ the fisheye distortion used by Aly et al. (2013) because we found that this could on occasion result in objects or lines (e.g., people, horizons), bending unnaturally. Instead, for each construction catch trial, we divided the catch image into six identical strips either vertically or horizontally. We then stretched or pinched each strip into a new dimension using Adobe Photoshop's content-aware stretching feature which preserves lines or naturally occurring objects. Thus, whereas each strip originally occupied 1/6 of the original image, in a manipulated catch trial image, the first strip could occupy 2/6 and the sixth strip only 1/12 of the resulting image. Together, this procedure allowed us to selectively manipulate the spatial configuration of the images in a natural and global manner (i.e., the detection of errors could not be achieved by single features). At display, one image was shown with its original spatial layout next to the altered image, creating a catch trial in which the spatial layout of the images was different.

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2.3.3. *Phase scrambling*

In order to examine whether hippocampal engagement was scene-specific or not, we created phase scrambled images from the stimuli used in the scene conditions using Matlab (2014a, Mathworks), adapting a script from www.visionscience.com. This technique produced images with the same spatial frequency and colour scheme as the original scene images but because the phase was random, any meaning was removed from the images (Yoonessi and Kingdom, 2008).

2.3.4. *Complexity*

We selected scene images that were freely available from the internet and which had varying degrees of visual complexity, basing our selection on Snodgrass and Vanderwart's (1980) definition of visual complexity as the amount of detail or intricacy in an image (see also Donderi, 2006 for a review). Simple scenes had a very limited number of conjunctions in the image, whereas complex scenes had many conjunctions (more than 100). Importantly, the complexity of the images did not alter significantly when simple scenes were converted into simple scrambled images and complex scenes were converted into complex scrambled images. Our categorisation of complexity was used in the fMRI analyses. Of note, these complexity classifications were endorsed in pilot testing, and by the fMRI study participants (see more on this later).

2.4. *Tasks and procedure*

Before scanning, participants had a short introduction and practice session. They were told that on each trial they would see a pair of images on the screen. They were instructed to look carefully at each pair because some of them would show two images that were identical whereas for others, the images would be slightly different, and that the main question they would have to answer after viewing each pair was whether the two images were the same or different.

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Participants were further told that a pair could differ in two ways, either in terms of the colour or the layout, and there would be cues to inform them about the type of difference they would encounter in the upcoming trial. Participants were then shown an example of a pair of scene images with one image being slightly different in colour. They were alerted to the fact that the colour change was not specific to a single object in the image but rather would affect the whole image. The participants were then shown an example of a pair of scene images with one image containing layout differences. They were told to focus specifically on the spatial relationships between features of the images and that, in the case of the example, the layout differed subtly between the two images. Participants were then shown examples of pairs with scrambled images and it was explained that in some cases, just as with the scenes, they would be asked to detect either colour or layout differences in scrambled image pairs. It was stressed to the participants that in all cases it was important to follow the cue and only look for colour differences if the cue had indicated that it was a colour trial, and only for layout differences if the cue had indicated that it was a layout trial. Moreover, they were told they should follow these instructions regardless of whether the trial involved a pair of scenes or scrambled images.

To help focus on the different cognitive tasks, pairs of images were also surrounded by an orange frame for colour trials or a blue frame for layout trials. Importantly, we counterbalanced target images (pairs of images that were identical) across participants, so that for any one image pair 12 participants looked for colour differences and 8 for layout differences. Participants were further instructed to indicate with a button press after each pair whether they thought the pair had been the same (key 1) or different (key 3). Lastly, participants were informed that occasionally a fixation cross would appear on the screen and they were asked to empty their minds from any images and instead to count from one onwards until the next cue appeared on the screen (the low-level baseline condition).

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Following these instructions, participants completed a practice session on a computer. There were 2 blocks with 13 trials each and involved stimuli that were not used in the experiment proper. The experiment was run using Cogent 2000 version 125 (Wellcome Centre for Human Neuroimaging, UCL, London, UK). Each trial started with the cue (either "Colour" or "Layout") being displayed for 1.5 sec. Next, a pair of images was presented for 5 sec after which the decision question "Same (1) or (3) Different" appeared on the screen. Participants then responded in a self-paced manner (up to a maximum of 2 sec) by pressing the first button on the MRI button box if they thought the current pair was identical, and the third button if they thought the pair was different. After each trial of the practice session, the experimenter would give verbal feedback and if there were any mistakes, the experimenter would bring up the relevant image pair on the computer screen again after completion of the practice session for closer inspection.

After the practice session, participants were set up in the scanner, and the main experiment began. The experiment proper was completed in four blocks with 80 trials each. The trials were presented in pseudo-randomised order so that no more than two trials of the same condition were presented consecutively. The timings of the main experiment were identical to the practice session (Fig. 1). Completion of the practice and main experiment took approximately 120 minutes.

2.5. *Eye-tracking during fMRI scanning*

To examine whether and how patterns of eye movements changed depending on the image type, cognitive process or image complexity, we acquired eye-tracking data during the fMRI experiment. We used an MRI compatible Eyelink 1000 Plus (SR Research) eye-tracker during scanning and Eyelink Data Viewer (SR Research) to extract fixation durations and fixation

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counts. The right eye was used for a 9-point grid calibration, recording and analyses. During the visual exploration of the image pairs, we recorded x and y coordinates of all fixations at a sampling rate of 1000Hz.

2.6. *MR image acquisition*

Structural and functional MRI data were acquired using a 3T Magnetom Trio scanner (Siemens Healthcare, Erlangen, Germany). The structural images were collected using a T1-weighted fast low angle shot (FLASH) sequence with 1 mm isotropic resolution (Weiskopf et al., 2013). Functional T2*-weighted images were acquired over four sessions each lasting ~15 minutes. The sequence was optimised to minimise signal dropout in the ventromedial prefrontal cortex (vmPCF) and medial temporal lobes using a slice tilt of -30 degree and a z-shim of -0.4 (Weiskopf et al., 2006). The volume TR was 3.36 sec, with a TE of 30 ms and echo spacing of 0.5 ms. Per volume, 48 slices were collected in transverse orientation, resulting in a matrix size of 64 x74 and a 3 mm isotropic voxel size. Following the first functional session, we also acquired a fieldmap with the following parameters: short TE=10 ms, long TE=12.46 ms, polarity of phase-encode blips=-1, applied Jacobian modulation=no, total EPI readout time=37 ms, in an ascending slice order.

2.7. *Post-scan surprise memory test and complexity ratings*

After the scan, participants underwent a surprise memory test. In addition, we asked participants to rate the complexity of each image. Visual complexity was explained to the participants as the level of detailedness or intricacy of an image, and an example scale of simple and complex scenes and scrambled images was provided. On a computer screen, one at a time, they saw the 320 images (scenes and scrambled) from the fMRI experiment plus 160 lures (40 simple scenes, 40 complex scenes, 40 simple scrambled, and 40 complex scrambled images). On each trial, participants responded in a self-paced manner but with a maximum of 5 sec response time to

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each of three questions: 1. Recognition memory: "(1) Old or (3) New"; 2. Confidence: "1=very sure, 2=somewhat sure, and 3=not at all sure"; and 3. Complexity: "(1) very simple, (2) simple, (3) middle simple, (4) middle complex, (5) complex, (6) very complex".

2.8. *Strategies*

In a debriefing session, we asked participants to describe what strategies they had used during the experiment to search for colour or layout differences in simple and complex, scene and scrambled images. We also asked whether participants had seen any of the images before, but none had.

2.9. *Data analysis*

2.9.1. *Behavioural*

Behavioural data collected during the fMRI scan and during the post-scan memory test were assessed using separate 2x2x2 repeated measures analysis of variance (3way-RM-ANOVA) with factor 1 being the image type with two levels (scenes, scrambled images), factor 2 being the cognitive process (perception, construction), and factor 3 being image complexity with two levels (simple, complex). Where 3way-RM-ANOVAs yielded significant effects (at $p<0.05$), we report the main and interaction effects. We examined significant effects further using Sidak's multiple comparisons test and report significant results if $p<0.05$.

2.9.2. *MRI pre-processing*

All MRI pre-processing was performed using SPM12 (Statistical Parametric Mapping 12; Wellcome Centre for Human Neuroimaging, London, UK). The anatomical images were segmented into grey matter, white matter and CSF maps and normalized to the Montreal Neurological Institute (MNI) template. The first five functional images were discarded to allow for signal equilibrium. Functional data were then realigned and unwarped (including distortion

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correction with fieldmaps) and coregistered to the anatomical image. Forward deformation fields from the anatomical image were then used to normalise the functional images into MNI space. Finally, functional images were smoothed with an 8x8x8mm kernel FWHM.

2.9.3. *Partial least squares (PLS) analyses*

We used PLS to analyse the fMRI data. This is a multivariate, correlational technique that allowed us to examine associations between brain activity and the experimental conditions in two ways – in a contrast free, data driven manner, and also using pre-specified contrasts (Krishnan et al., 2011; McIntosh et al., 2004; McIntosh and Lobaugh, 2004). Detailed descriptions of PLS can be found elsewhere (Krishnan et al., 2011). In brief, PLS uses singular value decomposition to extract ranked latent variables (LVs) from the covariance matrix of brain activity and conditions in a data driven manner. These LVs express patterns of brain activity associated with each condition. Statistical significance of the LVs was assessed using permutation testing. In this procedure, each participant's data was randomly reassigned (without replacement) to different experimental conditions, and a null distribution was derived from 500 permutated solutions. We considered LV as significant if $p < 0.05$. Furthermore, we assessed the reliability of each voxel that contributed to a specific LV's activity pattern using a bootstrapped estimation of the standard error (bootstrap ratio, BSR). For each bootstrapped solution (100 in total), participants were sampled randomly with replacement and a new analysis was performed. In the current study, we considered clusters of 50 or more voxels with BSRs greater than 2 (approximately equal to a $p < 0.05$) to represent reliable patterns of activation.

In a first pass, we used a mean-centred version of PLS for block fMRI data which maximises the correlation between brain data and experimental conditions in a data driven way.

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Importantly, this approach allowed us to examine the fMRI data without specifying a priori contrasts.

In a second pass, we used the non-rotated version of PLS for block fMRI data to specify contrasts that would test our hypotheses. While there is the potential to examine many different contrasts with this data set, we restricted our multiple comparisons to three contrast-driven PLS analyses that corresponded to our three research questions: 1. Is the hippocampus specifically engaged in scene processing? To test this, we contrasted brain activity correlated with all scene trials (regardless of cognitive process and complexity) versus all scrambled images (regardless of cognitive process and complexity). 2. If the hippocampus is specifically engaged in scene processing, does the cognitive process matter? Here, we contrasted simple and complex scene perception versus simple and complex scene construction. 3. If the hippocampus is specifically engaged in scene processing, does the complexity of the scenes matter? Here, we contrasted all simple scenes versus complex scenes (regardless of the cognitive process). To account for the multiple PLS analyses, we corrected the p-value of the LV's using Bonferroni's multiple comparison correction for four LV's, resulting in a statistical threshold of $p<0.017$.

2.9.4. *Signal intensity extraction*

In order to examine the broader scene processing network, we extracted signal intensities of specific brain regions within the scene processing network, namely the vmPFC (MNI: 2 50 -22), anterior (-32 -2 -22) and posterior (-28 -36 4) hippocampus and occipito-temporal cortex (-6 -92 -4). These coordinates were chosen based on the highest boot strap ratios within these regions of interest of the contrast driven PLS #1 (i.e., scenes versus scrambled images). Signal extraction was performed within the PLS toolbox using a sphere around the MNI coordinates of 3 adjacent voxels.

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3. Results

3.1. *In-scanner behavioural measures*

In general, participants performed the in-scanner task (same or different) with high accuracy (mean of the corrected hit rate over all conditions=90.6, SD=8.8, see Table 1 for more details). The 3way-RM-ANOVA yielded a significant main effect of complexity ($F(1,152)=16.5$, $p=0.001$), as well as interaction effect of image type and complexity ($F(1,152)=9.1$, $p=0.007$), and an interaction effect of cognitive process and complexity ($F(1,152)=6.5$, $p=0.02$). However, the three way interaction between image type, cognitive process, and complexity was not significant ($F(1,152)=0.2$, $p=0.64$). Post hoc statistics revealed that these effects were driven by a lower accuracy for simple scenes than complex scenes during the colour detection task ($t(152)=3.5$, $p=0.005$). Importantly, there was no main effect of cognitive process ($F(1,152)=1.4$, $p=0.71$), nor was there an image type by cognitive process interaction ($F(1,152)=3.6$, $p=0.07$), indicating that there were no systematic differences in behavioural performance that would impact the interpretation of the fMRI data regarding our research questions. We also examined reaction times and found that there were no significant differences across conditions (all F's$(1,152)<2.6$, p's>0.11).

Table 1: Summary of in-scanner accuracy and eye-movement measures.

Image category	Accuracy		RT		Fixation duration		Fixation counts	
Simple scene perception	83.4	*12.4*	0.7	*0.1*	298.5	*60.7*	27.7	*4.0*
Complex scene perception	95.5	*5.7*	0.7	*0.1*	280.9	*51.3*	29.2	*4.3*
Simple scrambled perception	89.2	*10.0*	0.7	*0.2*	311.7	*75.4*	26.4	*4.6*
Complex scrambled perception	95.6	*5.0*	0.7	0.1	294.1	*72.8*	26.2	*4.0*
Simple scene construction	87.6	*12.3*	0.8	0.1	287.1	*61.0*	28.8	*3.9*
Complex scene construction	93.2	*7.2*	0.8	0.2	279.6	*72.6*	30.8	*4.5*
Simple scrambled construction	89.4	*10.5*	0.7	0.1	289.7	*57.9*	28.0	*4.2*
Complex scrambled construction	91.1	*7.0*	0.8	0.1	278.0	*54.6*	28.3	*3.9*

Means are shown for all eight conditions of interest with standard deviations displayed in a smaller font and in italics. In-scanner accuracy of task performance is expressed as a percentage of corrected hit rate, and reaction times (RT) in seconds. Also shown are the means and standard deviations for the in-scanner eye-tracking - fixation duration (in msec) and fixation counts.

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3.2. *In-scanner eye-tracking*

Next, we examined eye-movements while participants were searching for colour or layout differences in simple and complex scene and scrambled images. Eye-tracking was not possible for two participants due to technical difficulties, so the following analyses are based upon data from 18 participants. We focussed on two eye-tracking measures, fixation duration and fixation counts (see Table 1 for more details).

3.2.1. *Fixation duration*

The 3way-RM-ANOVA yielded a significant main effect of cognitive process ($F(1,136)=7.1$, $p=0.02$) and of complexity ($F(1,136)=23.0$, $p=0.001$). Post hoc analyses revealed that in general participants spent longer fixating during the perception than during the construction tasks (simple scrambled perception versus simple scrambled construction: $t(17)=4.1$, $p<0.02$; complex scene perception versus complex scene construction: $t(17)=4.5$, $p=0.01$), and on simple compared to complex images (simple scene perception versus complex scene perception: $t(17)=4.0$, $p<0.02$; simple scrambled perception versus complex scrambled perception: $t(17)=4.1$, $p<0.02$).

3.2.2. *Fixation counts*

We observed a different pattern for fixation counts. Here, the 3way-RM-ANOVA yielded significant main effects for all three factors, image type ($F(1,136)=53.5$, $p=0.001$), cognitive process ($F(1,136)=27.7$, $p=0.001$), and complexity ($F(1,136)=29.6$, $p=0.001$). In addition, we found an interaction effect of image type and complexity ($F(1,136)=16.9$, $p=0.001$). Post hoc analyses revealed that searching images for layout differences resulted in more fixation counts than searching images for colour differences (simple scrambled perception versus simple scrambled construction: $t(17)=4.2$, $p=0.01$; complex scrambled perception versus complex scrambled construction: $t(17)=4.3$, $p=0.002$). This effect was more pronounced for scenes than

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scrambled images (simple scrambled perception versus simple scene perception: t(17)=4.7, p=0.003; complex scrambled perception versus complex scene perception: t(17)=9.6, p<0.0001; complex scrambled construction versus complex scene construction: t(17)=6.9, p=0.0001), and more pronounced for complex compared to simple scenes (simple scene perception versus complex scene perception: t(17)=4.0, p=0.01; simple scene construction versus complex scene construction: t(17)=4.3, p=0.007). Overall, these results indicate that participants had more fixation counts for complex scene construction.

3.3. *Post-scan surprise memory test and complexity ratings*

3.3.1. *Memory accuracy*

Due to the large number of different images and the short encoding time, recognition memory was, unsurprisingly, poor and barely exceeded chance level (mean over all conditions=60.7, SD=17.9, see Table 2 for further details). The 3way-RM-ANOVA across all conditions yielded a significant main effect of complexity (F(1, 152)=19.0, p=0.001) and an interaction effect of image type and complexity (F(1, 152)=21.4, p=0.001). Simple scrambled images for both perception (t(17)=4.7, p=0.004) and construction (t(17)=5.2, p=0.001) tasks were less well remembered than the complex scrambled images for both perception and construction. This result did not come as a surprise since simple scrambled images were particularly featureless. Importantly, there was no main effect of cognitive process (F(1,152)=0.4, p=0.52), indicating that there were no systematic differences in encoding success between perception and construction that could have impacted the interpretation of the fMRI data in relation to our research questions.

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Table 2: Summary of post-scan behavioural measures.

Image category	Recognition memory		Confidence		Complexity	
Simple scene perception	55.1	*17.3*	1.7	*0.3*	2.2	*0.4*
Complex scene perception	60.3	*21.8*	1.6	*0.3*	4.1	*0.5*
Simple scrambled perception	49.9	*14.5*	2.2	*0.6*	2.6	*0.5*
Complex scrambled perception	72.3	*17.2*	2.1	*0.7*	4.2	*0.6*
Simple scene construction	68.2	*20.1*	1.7	*0.3*	2.0	*0.4*
Complex scene construction	65.5	*23.8*	1.6	*0.3*	4.2	*0.5*
Simple scrambled construction	45.9	*16.0*	2.1	*0.6*	2.5	*0.4*
Complex scrambled construction	68.6	*12.9*	2.1	*0.7*	4.2	*0.9*

Means are shown for all eight conditions of interest with standard deviations displayed in a smaller font and in italics. Incidental encoding was evaluated using percentage of corrected hit rates of recognition memory, as well as confidence ratings (1=very sure to 3=not sure at all). The means and standard deviations of participants' complexity ratings (1=very simple to 6=very complex) are also shown (see also Fig. 2).

3.3.2. *Memory confidence ratings*

In general, participants were not confident about whether or not they had seen a particular image in the scanner, showing that they had insight into their poor memory performance on the surprise memory test (mean over all conditions=2.0, SD=0.5, see Table 2 for further details). The 3way-RM-ANOVA across all conditions yielded a main effect of image type ($F(1,152)=17.7$, $p<0.001$), with participants, unsurprisingly, less confident about their memory judgements for scrambled images compared to scenes (simple scrambled perception versus simple scene perception: $t(17)=3.2$, $p=0.02$; complex scrambled perception versus complex scene perception: $t(17)=3.4$, $p=0.01$; complex scrambled construction versus complex scene construction: $t(17)=3.6$, $p=0.005$).

3.3.3. *Complexity ratings*

To examine whether participants' ratings of complexity (shown in Fig. 2) accorded with our designations, we calculated the mean complexity rating for each of our designated conditions but now based on the participants' ratings, and entered these into a 3way-RM-ANOVA. This yielded a significant main effect of complexity ($F(1,152)=428.8$, $p<0.0001$). Post hoc analyses

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revealed significant differences between all simple and complex stimuli (simple scrambled perception versus complex scrambled perception: t(17)=10.6, p<0.0001; simple scene perception versus complex scene perception: t(17)=9.1, p<0.0001; simple scrambled construction versus complex scrambled construction: t(17)=12.1, p<0.0001; simple scene construction versus complex scene construction: t(17)=9.7, p<0.0001). Therefore, the participants' ratings accorded well with our classification of complexity which was mirrored across image types and cognitive processes.

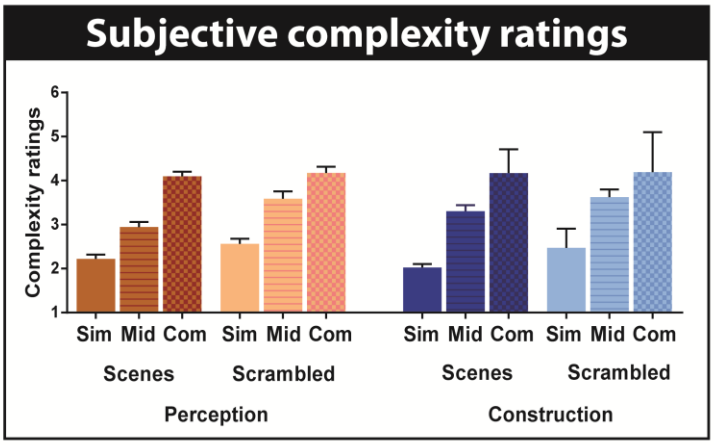

Fig 2 - Participants' stimulus complexity ratings. The means and standard errors of the complexity ratings made by the participants (1=very simple to 6= very complex) are shown for all conditions. Sim=simple, mid=middle, com=complex.

3.4. *Strategies*

Also after scanning, we asked participants about how they had decided whether two images were the same or different. Generally, participants reported different strategies for the two cognitive processes, perception and construction, but did not report different strategies based on the image type or complexity.

For the perception task, participants indicated that they mostly focused on selected parts of the images without paying much attention to the content of the image. For example, they would

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compare corners, brightly lit or especially dark areas between the images. Participants indicated that they followed this strategy whether the images were simple or complex, or scenes or scrambled images. In contrast, for the construction task, participants reported examining and mentally constructing the spatial relationships within one image and then comparing these relationships to the second image. Again, participants described the same constructive strategy for simple and complex images, and for scenes and scrambled images.

3.5. *Data driven mean-centred PLS*

The fMRI data driven PLS included all eight conditions of interest and revealed three significant LV's (Fig. 3). As noted previously, this approach allowed us to examine the fMRI data without specifying a priori contrasts, enabling us to explore the dominant patterns of activity in the brain elicited by the tasks. Below we unpack each LV in turn.

3.5.1. LV1 – scene construction

The first significant LV (LV1, $p<0.0001$, explaining 50% of the variance, Fig. 3A, see Table S1 for all the brain regions that were engaged and their MNI coordinates), identified a contrast between the two conditions that we argued might be most dependent upon scene construction (i.e., simple scene construction and complex scene construction) and the other conditions. The correlated brain pattern included a widespread network that is typically engaged during the construction of scene imagery, such as bilateral anterior medial hippocampus, parahippocampal gyrus, fusiform gyrus, vmPFC, bilateral precuneus and inferior parietal lobules as well as occipital cortices. Together, this finding suggests that scene construction is a dominant cognitive process associated with a distributed brain network.

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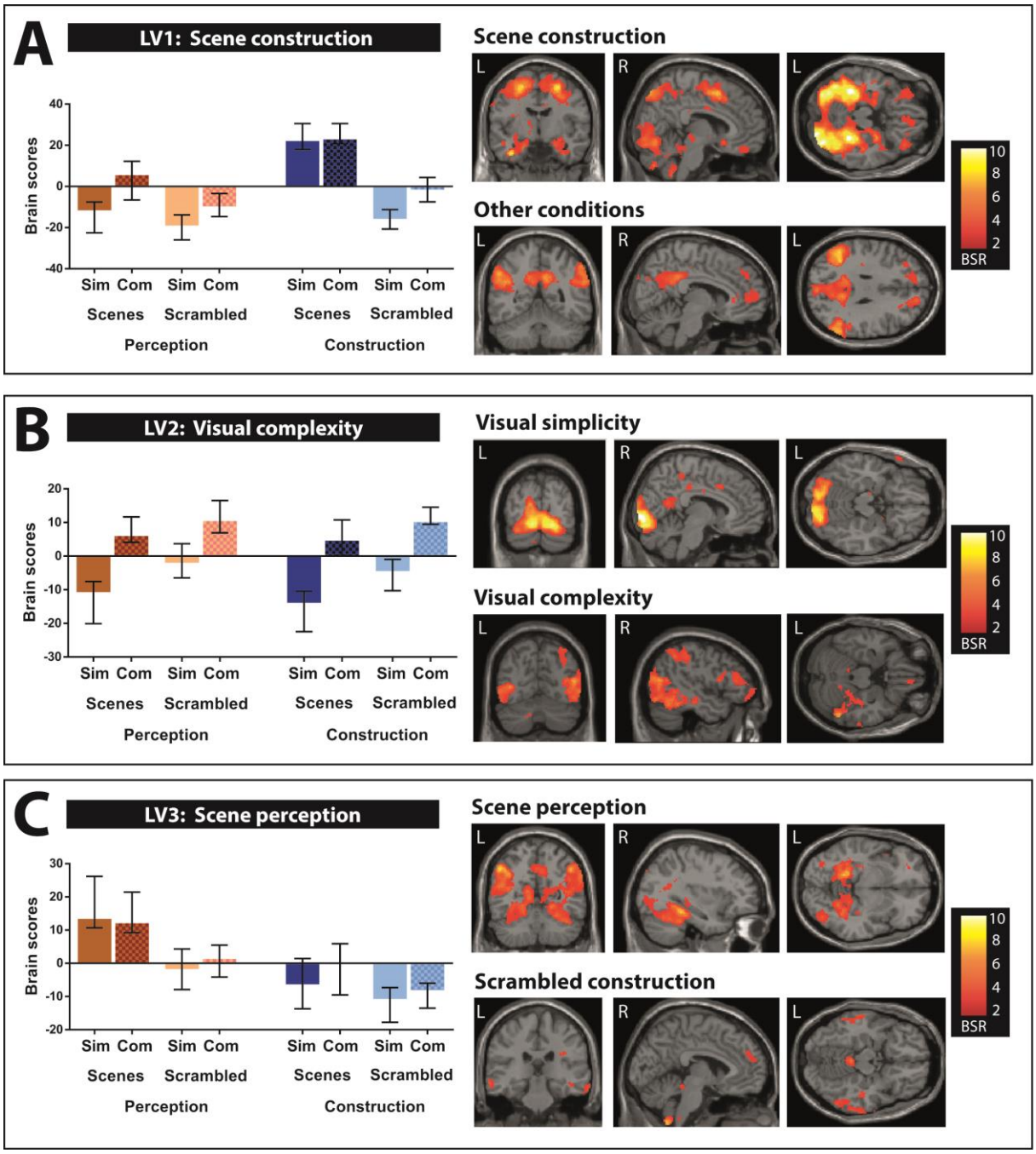

Fig 3 - Summary of the significant latent variables (LVs) detected by the data driven PLS. Bar graphs depict means and confidence intervals for all conditions. Sim=simple, com=complex. Activations are displayed on a T1-weighted MRI scan (MNI template); L=left, R=right, BSR=boot strap ratio. (A) LV1 explained 50% of the variance. This pattern contrasted simple and complex scene construction against all other conditions. (B) LV2 explained 15% of the variance. This pattern contrasted most simple images against complex images, regardless whether they were scenes or scrambled images, or whether participants were engaged in a perceptual or constructive task. (C) LV3 also explained 15% of the variance. This pattern highlighted simple and complex scene perception. See also Tables S1-S3 for full details.

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3.5.2. LV2 – main effect of complexity

The second significant LV (LV2, p<0.0001, explaining 15% of the variance, Fig. 3B, see Table S2 for all the brain regions that were engaged and their MNI coordinates) reflected the main effect of complexity. Interestingly, we found distinct patterns associated with simple and complex images. While simple images seemed to engage more medial posterior brain regions (e.g., medial occipital cortices), complex images engaged more lateral posterior brain regions (e.g., lateral occipital, temporal and parietal cortices). An exception to this rule was the medial subgenual vmPFC which was more activate for complex than simple images. Of note, hippocampal activity was not modulated by image complexity. Overall, this LV suggests that complexity as a general image feature engages mostly posterior visual brain regions. Nevertheless, one has to interpret this result with caution since this main effect reflects a combination of multiple, very different conditions. In our follow-up contrast driven PLS analyses, we specified more tailored contrasts to examine the effect of stimulus-specific complexity.

3.5.3. LV3 – scene perception

The third significant LV (LV3, p<0.02, explaining 15% of the variance, Fig. 3C, see Table S3 for the relevant brain regions and their MNI coordinates) identified a contrast between conditions depending upon scene perception (i.e., simple scene perception and complex scene perception) and constructing scrambled images (i.e., simple scrambled construction and complex scrambled construction). While searching scrambled images for layout differences involved mainly lateral temporal, parietal and dorsomedial prefrontal cortices, the associated brain pattern for scene perception involved the posterior hippocampi, as well as several brain regions along the ventral visual pathway, such as the fusiform gyrus, parahippocampal gyrus and the inferior temporal gyrus. Of note, a number of regions previously found to be associated with scene construction, such as the anterior medial hippocampi and the vmPFC, were absent

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for this scene perception related brain activity pattern. Again, this LV resulted from a data driven method, hence the interpretation of contrasting scene perception against scrambled construction is not immediately clear. Therefore, in a second pass, we conducted non-rotated PLS analyses where scene perception and scene construction were directly contrasted.

3.6. *Contrast driven non-rotated PLS*

We had three specific research questions which we focussed on in the analyses described below: 1. Is the hippocampus specifically engaged in scene processing in this experiment?; 2. If hippocampal engagement is specific to scene processing, does the cognitive process (i.e., perception or construction) matter?; and 3. If the hippocampus is responsive during scene processing, does the complexity of the scenes matter?

3.6.1. Contrast driven PLS #1: Is the hippocampus specifically engaged in scene processing?

To answer this question, we contrasted all four conditions involving scene processing (simple scene perception, complex scene perception, simple scene construction, and complex scene construction) against the other four conditions of scrambled images (simple scrambled perception, complex scrambled perception, simple scrambled construction, and complex scrambled construction). The PLS revealed a significant LV ($p<0.0001$, Fig. 4A, see Table S4 for the relevant brain regions and their MNI coordinates) separating all scene conditions from all scrambled conditions. Confirming our hypotheses, the brain pattern associated with scene processing included bilateral hippocampi (both anterior and posterior segments), as well as the usual scene processing network along the ventral visual pathway. In addition, the subgenual vmPFC also showed greater activation during scene processing than for the scrambled conditions. In contrast, processing of scrambled images was associated with a much more restricted pattern of brain activity that included engagement of the precuneus and the anterior cingulate cortex.

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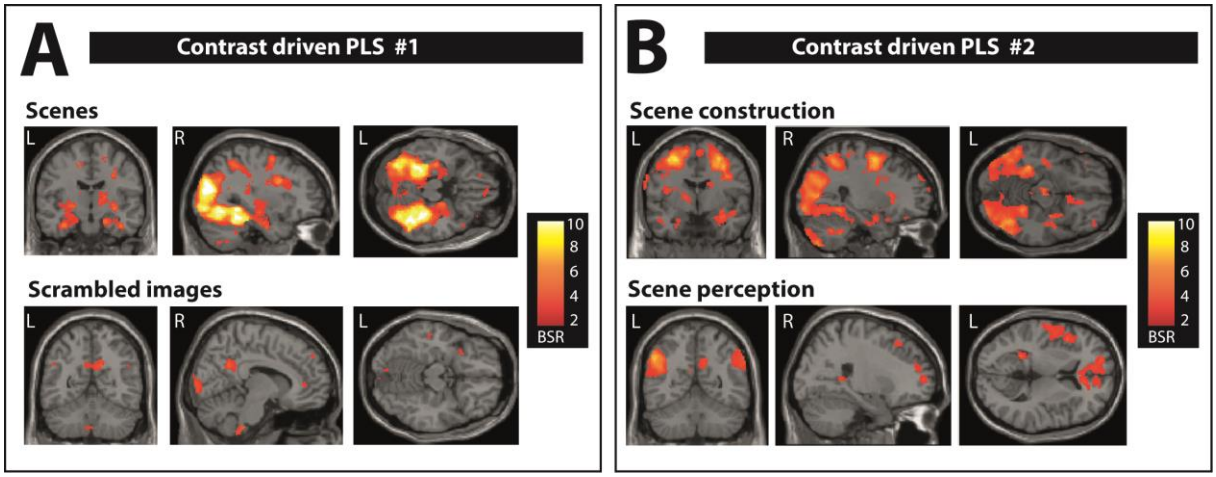

Fig 4 - Brain activity patterns associated with the contrast driven PLS. Activations are displayed on a T1-weighted MRI scan (MNI template); L=left, R=right, BSR=boot strap ratio. (A) The brain activity pattern associated with simple and complex scene perception and construction, shown in the upper panel, reflected the well-known scene processing network including widespread, increased activity in the vmPFC, bilateral hippocampus and along the ventral visual stream. This is in contrast to the brain pattern associated with simple and complex scrambled perception and construction, shown in the lower panel, which included lateral and medial parietal cortices and anterior cingulate cortex. (B) The brain activity pattern associated with simple and complex scene construction, shown in the upper panel, included increased activity along the ventral visual stream, bilateral anterior medial hippocampus and vmPFC. The brain pattern associated with simple and complex scene perception, shown in the lower panel, included medial and lateral parietal cortices and anterior cingulate cortex. In addition, we observed increased bilateral posterior hippocampal activity for scene perception.

3.6.2. Contrast driven PLS #2: If the hippocampus is specifically engaged in scene processing, does the cognitive process matter?

Given that in the first contrast we identified greater hippocampal involvement in scene processing compared to scrambled images, we next asked whether the brain activity patterns, including hippocampal engagement, was specific to scene construction. We, therefore, contrasted conditions involving scene construction (simple scene construction and complex scene construction) against scene perception (simple scene perception and complex scene perception). The resulting LV was highly significant ($p<0.0001$, all conditions contributing, Fig. 4B, see Table S5 for all relevant brain regions and their MNI coordinates). The hippocampus was engaged during both scene construction and scene perception tasks.

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Interestingly, there was a clear dissociation between its anterior and posterior segments in terms of their responsiveness to the different types of scene processing. Whereas scene perception engaged the posterior hippocampus, scene construction engaged bilateral anterior hippocampus. Furthermore, while scene perception engaged the precuneus and angular gyrus, as well as anterior cingulate cortex, scene construction was associated with several brain regions along the ventral visual pathway and superior parietal lobule. In addition, the subgenual vmPFC was also more activated during scene construction compared to scene perception.

3.6.3. Contrast driven PLS #3: If the hippocampus is specifically engaged in scene processing, does the complexity of the scenes matter?

Here, we contrasted simple (simple scene perception and simple scene construction) versus complex scenes (complex scene perception and complex scene construction). However, this PLS analysis did not reveal a significant LV ($p=0.06$ with the Bonferroni cut-off being $p<0.017$, and with confidence intervals for both complex scenes conditions crossing zero).

3.6.4. Regional signal intensities

As alluded to previously, scene processing is supported by a brain wide network including the vmPFC, anterior and posterior hippocampus and the occipito-temporal cortices. Since the contrast-driven PLS #1 (scenes versus scrambled images) revealed this network, we investigated specific contributions of these brain areas to scene processing (Fig. 5). We did this by extracting signal intensities from the brain regions along this network which had the highest bootstrap ratios in the contrast driven PLS #1 analyses. Activity in vmPFC (x y z: 2 50 -22) had a multifaceted pattern, reflecting a preference for scenes, especially scene construction, whilst also keeping track of the visual complexity of all stimuli. The anterior (-32 -2 -22) and posterior (-28 -36 4) hippocampus had distinct patterns of activity that were more clear-cut, with the

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former engaged by scene construction, and the latter by scene perception. Activity within the occipito-temporal cortex (-6 -92 -4) reflected predominantly visual complexity.

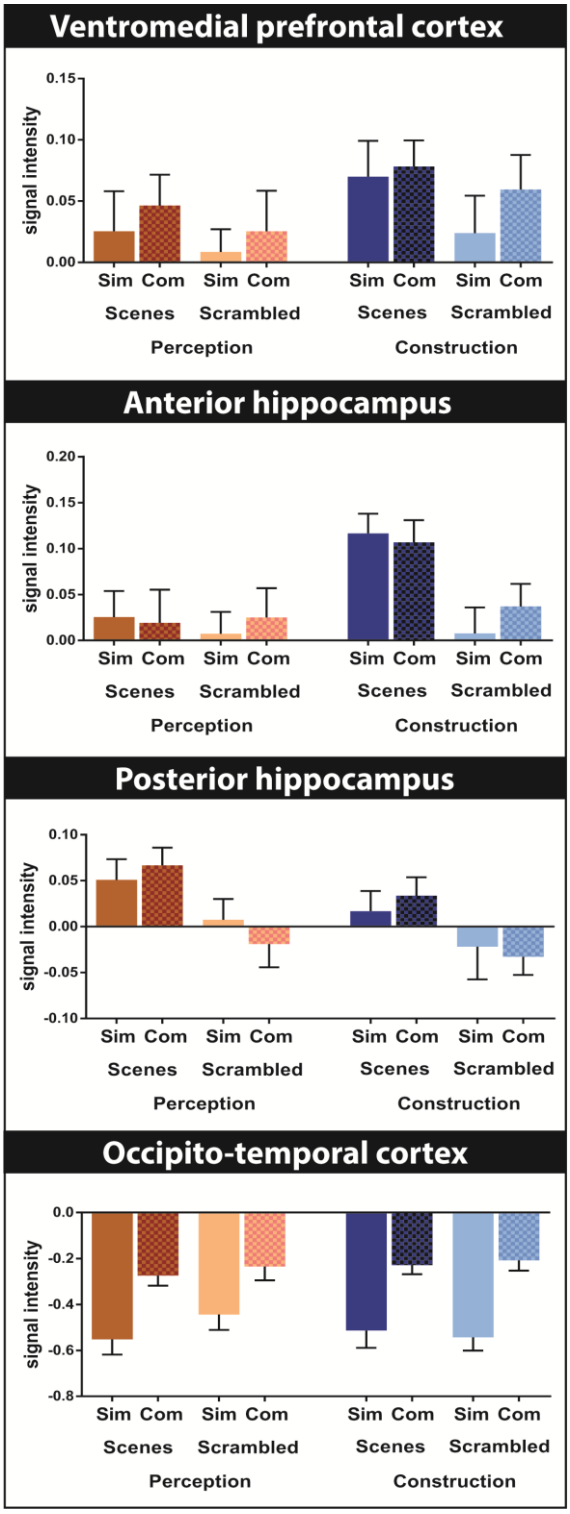

Fig 5 - Extracted signal intensities from brain regions within the scene processing network. Bar graphs depict means and standard errors of the eight conditions for the vmPFC, anterior and posterior hippocampus and occipito-temporal cortex. Sim=simple, com=complex. These regions were chosen based on the highest bootstrap ratio in the associated contrast driven PLS #1 analysis. Activity in vmPFC had a multifaceted pattern, reflecting a preference for scenes, especially scene construction, whilst also keeping track of the visual complexity of all stimuli. The anterior and posterior hippocampus had distinct patterns of activity that were more clear-cut, with the former engaged by scene construction, and the latter by scene perception. Activity within the visual cortex reflected predominantly visual complexity.

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4. Discussion

In this study we sought to deepen our understanding of hippocampal processing by addressing three questions: 1. Is the hippocampus recruited specifically during scene processing? 2. If the hippocampus is active in response to scenes, does the cognitive process being engaged influence its activation? 3. If the hippocampus is upregulated during scene processing, does the complexity of the scenes affect its response? We found that, compared to phase-scrambled versions of the scenes, the hippocampus was more responsive to scene stimuli. Moreover, there was a clear distinction in terms of which parts of the hippocampus were engaged, with scene perception associated with the posterior hippocampus and scene construction with the anterior hippocampus. The complexity of the scenes did not influence hippocampal activity. We discuss each of these results in turn.

4.1. *The hippocampus is upregulated during scene processing*

The hippocampi (anterior and posterior segments) were more engaged for scenes than scrambled images. This echoes previous work using highly simplified representations of scenes and non-scene arrays which also showed preferential activation of the hippocampus for scenes (Dalton et al., 2018), and aligns in particular with accounts of hippocampal function that propose the hippocampus is especially attuned to scene processing (Hassabis & Maguire, 2007; Maguire & Mullally, 2013). We acknowledge that it is challenging to devise non-scene stimuli for comparison with naturalistic scenes. Here, we contrasted the scenes with images that were phase-scrambled versions of the same scenes, thus preserving the spatial frequency and colours. The scenes and scrambled stimuli were rated comparably by participants in terms of the various levels of complexity. There was no main effect of image type for the same/different judgements during scanning, or in eye movement fixation duration. The pattern of memory performance in the surprise post-scan test was similar, in particular for complex scenes and complex scrambled stimuli. Moreover, the strategies participants reported using during the tasks did not differ as a

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function of stimulus type. Nevertheless, despite all of these similarities, the hippocampus was engaged preferentially for scenes.

It is perhaps not surprising that scenes are particularly stimulating for the hippocampus, as they mirror how people experience and perceive the world. In addition, scenes are a highly efficient means of packaging information. Clark et al. (2019) recently reported that the ability to construct scene imagery explained the relationships between episodic memory, imagining the future and spatial navigation task performance. The prominence of scenes was further emphasised in another study involving the same sample, where the explicit strategies people used to perform episodic memory recall, future thinking and spatial navigation tasks was assessed (Clark, Monk, & Maguire, preprint). In each case, the use of scene visual imagery strategies was significantly higher than for all other types of strategies (see also Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010). The apparent utility and prevalence of scene processing has led to the suggestion that scene imagery may be the currency of cognition (Maguire & Mullally, 2013).

4.2 *A hippocampal distinction between scene perception and scene construction*

Given that scenes activated the hippocampus more than scrambled versions of the same scenes, we next considered whether the cognitive process being engaged during the scene tasks influenced hippocampal recruitment. During scene perception, participants searched pairs of scenes for potential colour differences whereas during scene construction they searched pairs of scenes for potential layout differences. The scene perception and scene construction tasks were well-matched in a number of respects. Importantly, we counterbalanced images across participants so that all analyses dissociating perception and construction processes were conducted on the same images. The accuracy during scanning where participants correctly identified pairs of images as being identical did not differ between perception and construction

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trials. In addition, recognition memory assessed during a surprise memory task after scanning was similar for both tasks, indicating that there was no disparity in terms of incidental encoding. Despite these similarities, there were differences in the hippocampal response to perception and construction.

A striking result of the data driven mean centred PLS (LV1) was a clear anterior medial hippocampus preference for the two conditions thought to weigh most heavily on scene construction, namely the tasks involving the processing of simple and complex scene layouts. This finding accords with the numerous previous reports associating scene construction with the anterior hippocampus (reviewed in Zeidman & Maguire, 2016; see also Zeidman et al., 2015a,b; Dalton et al., 2018; Dalton & Maguire, 2017). By contrast, another data driven LV, this time involving the posterior hippocampus, was associated with the perception of scenes, simple and complex, with no evidence of the anterior hippocampus in this brain pattern. A direct contrast between scene construction and scene perception confirmed that the two processes involved different hippocampal segments, anterior and posterior respectively. These findings are in line with research stressing functional dissociations along the anterior-posterior axis of the hippocampus during scene construction and scene perception (e.g., Zeidman et al., 2015a; Zeidman and Maguire, 2016), and more generally (Poppenk, Evensmoen, Moscovitch, & Nadel, 2013; Sekeres, Winocur, & Moscovitch, 2018; Strange, Witter, Lein, & Moser, 2014).

The medial hippocampus is well suited to scene-based cognition given its anatomical (Dalton & Maguire, 2017) and functional (Dalton et al., 2019a,b) connectivity with regions in the parieto-medial temporal pathway. While the resolution of the current fMRI data do not permit hippocampal subfield analyses, it is important to acknowledge that subfields might further differentiate between perceptual and constructive processes, as well as scenes and other types of stimuli. For example, recent high-resolution fMRI studies indicate that the anterior medial

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portion of the subiculum or pre-/parasubiculum may be specifically engaged during scene construction (Zeidman et al., 2015b; Hodgetts et al., 2017; Dalton et al., 2018). In contrast, several previous fMRI studies showed that posterior hippocampal activity was associated with tasks involving perceptual discrimination between visually similar scenes (Aly et al., 2013; Barense et al., 2010; Lee, Buckley, et al., 2005; Lee, Bussey, et al., 2005). The posterior hippocampus has strong anatomical and functional connections with the ventral visual stream and early visual cortices (Chadwick, Mullally, & Maguire, 2013; Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008). Therefore, it may be that the posterior hippocampus is involved in guiding ongoing scene perception while the anterior hippocampus supports online construction into a coherent mental model of the world.

Interestingly, eye-tracking data recorded during scanning revealed a difference between the perception and construction tasks. Whereas the perception conditions were associated with longer fixation durations, the constructive conditions had more fixation counts. This effect was most pronounced during the perception and construction of scenes, especially complex scenes. These results generally align with extant studies linking rapid visual sampling to the construction of mental events (El Haj & Lenoble, 2017; Hannula & Ranganath, 2009; Liu, Shen, Olsen, & Ryan, 2017). Of note, since there were no recognition memory differences between perception and construction trials, our eye-tracking results speak against a proposal that exploratory visual sampling is purely memory-guided (Voss, Bridge, Cohen, & Walker, 2017). Rather, our findings seem to indicate that the pattern of eye-movements relates an interaction between the dominant cognitive process and the image type (naturalistic versus scrambled, complex versus simple) during a particular task.

We also asked participants directly about their cognitive strategies during the perception and construction tasks. All participants reported distinct cognitive approaches to searching image

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pairs for colour versus layout differences. They indicated that they mostly focused on selected parts of the images without paying much attention to the content of the image during perception trials. For example, they would compare corners, brightly lit or especially dark areas between the images. In contrast, for the construction task, participants reported examining and mentally constructing the spatial relationships within one image and then comparing these relationships to the second image. Of interest, participants reported using the same strategies for the different image types (i.e., naturalistic or scrambled images, complex or simple).

Overall, therefore, our results suggest that both cognitive processes, scene perception and scene construction, engage the hippocampus, but with long-axis differences in the portion most involved. The next question we addressed was whether or not the complexity of scenes affected hippocampal recruitment.

4.3. *No effect of scene complexity on hippocampal engagement*

In the current study, we operationalised visual complexity in terms of the amount of detail or intricacy of an image (Snodgrass & Vanderwart, 1980; see also Donderi, 2006), and the participants showed high agreement with our designations of simple, middle and complex images. A number of current hippocampal theories argue that visual complexity (or the number of associations or conjunctions), is an important driver of hippocampal activity (Eichenbaum & Cohen, 2014; Lee et al., 2012; Yonelinas, 2013). Thus, more complex images should evoke greater hippocampal response compared to simpler images. This is in contrast to another perspective that suggests a primary function of the hippocampus is to construct scene imagery, irrespective of whether the scenes are simple or complex (Hassabis & Maguire, 2007; Maguire & Mullally, 2013). Complexity might also be relevant for another issue, namely the assertion by Poppenk, Evensmoen, Moscovitch, & Nadel (2013; see also Brunec et al., 2018) that representations in the hippocampus vary from fine to coarse grained in a posterior to anterior

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direction. This leads to the prediction that complex scenes should engage the posterior hippocampus.

However, the data driven and contrast driven analyses showed that hippocampal activity was not influenced by scene complexity. This finding accords with the view that the hippocampus processes scenes regardless of whether they are simple or complex (Hassabis & Maguire, 2007; Maguire & Mullally, 2013). Instead, complexity as a general image feature engaged mostly posterior visual brain regions.

4.4. *Beyond the hippocampus*

The main focus of the current study was the hippocampus. Nevertheless, our analyses revealed that the hippocampus was part of a wider set of activated brain areas, among which the vmPFC had the most interesting profile. While it was recruited to a greater extent during construction compared to perception, it also seemed to be more responsive to scenes than scrambled images and to complex than simple stimuli. We speculate that this result might suggest that the vmPFC is a hierarchically superordinate structure that keeps track of scene processing (for a related idea see Robin & Moscovitch, 2017; Sekeres et al., 2018). In fact, we have suggested that the vmPFC may initiate scene construction processes in the hippocampus (Ciaramelli, De Luca, Monk, McCormick, & Maguire, 2019; McCormick, Ciaramelli, De Luca, & Maguire, 2018). In support of this proposal, recent magnetoencephalography studies have found vmPFC activity preceded and then drove that of the hippocampus during both scene imagination (Barry, Barnes, Clark, & Maguire, 2019) and the recall of autobiographical memories (McCormick et al., 2020).

4.5. *Conclusions*

In this study we sought to probe hippocampal function by manipulating three factors. We found evidence that the hippocampus was engaged by naturalistic scenes compared to scrambled

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images. Furthermore the posterior hippocampus was activated to a greater extent during scene perception and the anterior hippocampus during scene construction, regardless of the complexity of scenes. In-scanner task performance and incidental encoding could not explain these findings. Overall, these results seem to fit best with the view that the hippocampus may be attuned to processing scenes, be they simple or complex (Hassabis & Maguire, 2007; Maguire & Mullally, 2013). This conclusion could be investigated further in future studies by testing patients with bilateral hippocampal damage, whereby the prediction would be that they should be impaired on tasks involving scenes, be they simple or complex, but unimpaired on tasks involving scrambled stimuli.

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CRediT authorship contribution statement
Cornelia McCormick: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Marshall A. Dalton:** Conceptualization, Writing - review & editing. **Peter Zeidman:** Conceptualization, Writing - review & editing. **Eleanor A. Maguire:** Conceptualization, Methodology, Funding acquisition, Supervision, Formal analysis, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest
None.

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Supplementary Materials

Table S1: Peak coordinates of the data driven PLS LV1

Region	side	MNI coordinates			BSR
		X	Y	Z	
Scene construction					
Middle occipital gyrus	left	-40	-84	0	14.60
Parahippocampal gyrus*	left	-30	-30	-20	9.96
Precuneus*	left	-8	-64	58	5.14
Inferior partietal lobule*	left	-52	-38	48	4.23
Middle occipital gyrus	right	36	-82	-6	14.3
Fusiform gyrus*	right	30	-44	-16	12.5
Precuneus*	right	14	-44	42	2.92
Inferior parietal lobule*	right	50	-44	50	2.67
Inferior frontal gyrus	right	46	10	28	7.84
Hippocampus (anterior)*	right	28	-2	-28	5.23
Hippocampus (anterior)*	left	-28	-4	-18	5.02
Cerebellum	left	-14	-46	-48	4.87
Cerebellum	right	20	-42	-46	4.60
Insula	right	30	22	6	4.06
Middle cingulate gyrus	right	8	-2	32	4.00
Middle frontal gyrus	right	38	62	10	3.98
Inferior frontal gyrus	left	-40	36	-18	3.42
Ventromedial prefrontal cortex	left	-4	36	-18	3.33
All other conditions					
Angular gyrus	left	-48	-56	34	5.06
Anterior cingulate gyrus	right	4	32	0	4.64
Angular gyrus	right	54	-60	36	4.55
Brainstem	left	-8	-38	-48	4.27
Cerebellum	right	18	-80	-30	4.21
Precuneus	left	-10	-54	28	3.97
Superior frontal gyrus	left	-12	36	48	3.26
Middle temporal gyrus	left	-64	-24	-10	3.11
Middle temporal gyrus	right	60	-20	-18	2.88
Middle cingulate gyrus		0	-22	40	2.58

X,Y, and Z coordinates in MNI space, BSR=Bootstrap ratio, *=regions included in larger clusters

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Table S2: Peak coordinates of the data driven PLS LV2

Region	side	MNI coordinates			BSR
		X	Y	Z	
Visual simplicity					
Calcarine gyrus	left	-6	-92	-4	12.42
Postcentral gyrus	left	-54	-6	48	4.63
Middle cingulate gyrus	left	-6	14	40	4.21
Precuneus	left	-10	-56	20	3.95
Middle frontal gyrus	left	-4	-22	54	3.90
Caudate	right	10	2	6	3.81
Thalamus	left	-16	-16	-2	3.65
Cuneus	left	-16	-70	26	3.30
Middle cingulate gyrus	left	-12	-28	38	3.20
Precuneus	left	-10	-38	54	3.11
Visual complexity					
Inferior temporal gyrus	right	52	-54	-18	6.20
Inferior occipital gyrus*	right	36	-82	-6	5.41
Inferior frontal gyrus	right	32	32	10	5.64
Cerebellum	left	-20	-64	-34	5.56
Middle temporal gyrus	left	-60	-56	-2	5.06
Inferior temporal gyrus	left	-50	-72	-10	4.86
Inferior occipital gyrus*	left	-38	-82	-4	3.21
Inferior parietal lobule	right	54	-30	48	4.62
Ventromedial prefrontal cortex	right	16	42	-18	4.21
Pallidum	left	-26	-12	-4	3.79
Fusiform gyrus	right	28	-4	-36	3.66
Middle frontal gyrus	right	32	6	54	3.49
Cerebellum	left	-4	-56	-58	3.46
Superior frontal gyrus	right	8	28	38	3.36
Middle frontal gyrus	right	40	60	0	3.20
Middle frontal gyrus	left	-36	56	-4	3.08
Cerebellum	left	-8	-58	-8	2.84
Supramarginal gyrus	left	-62	-20	24	2.71
Inferior parietal lobule	left	-38	-46	52	2.59

X,Y, and Z coordinates in MNI space, BSR=Bootstrap ratio, *=regions included in larger clusters

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Table S3: Peak coordinates of the data driven PLS LV3

Region	side	MNI coordinates			BSR
		X	Y	Z	
Scene perception					
Fusiform gyrus	right	24	-36	-16	8.44
Parahippocampal gyrus	left	-22	-42	-10	7.58
Angular gyrus	left	-38	-60	38	6.91
Inferior frontal gyrus	right	46	36	4	4.82
Posterior cingulate gyrus	left	-2	-36	40	4.65
Hippocampus (posterior)*	left	-36	-28	-14	4.55
Supramarginal gyrus	left	-58	-20	20	4.06
Postcentral gyrus	left	-52	-18	54	3.65
Inferior temporal gyrus	right	34	0	-38	3.42
Inferior frontal gyrus	right	58	12	10	3.20
Hippocampus (posterior)*	right	32	-32	-4	2.47
Scrambled construction					
Dorsomedial prefrontal cortex	right	12	38	22	6.52
Superior parietal lobule	right	16	-70	58	5.30
Cerebellum	right	36	-68	-46	5.06
Middle cingulate cortex	left	-8	14	44	4.80
Inferior frontal gyrus	right	54	10	24	4.79
Brainstem	left	-4	-18	-12	4.46
Middle temporal gyrus	right	50	-24	-16	4.11
Middle frontal gyrus	left	-36	-2	44	4.11
Superior parietal lobule	left	-18	-56	60	3.96
Cerebellum	left	-14	-46	-58	3.73
Cerebellum	right	6	-58	-52	3.72
Inferior parietal lobule	right	40	-38	52	3.35
Caudate	right	10	6	8	3.12
Postcentral gyrus	right	66	0	30	2.60

X,Y, and Z coordinates in MNI space, BSR=Bootstrap ratio, *=regions included in larger clusters

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Table S4: Peak coordinates of the contrast driven PLS - scenes versus scrambled images

Region	side	MNI coordinates			BSR
		X	Y	Z	
Naturalistic scenes					
Middle occipital gyrus	left	-38	-78	16	19.02
Superior frontal gyrus	left	-24	12	58	6.80
Fusiform gyrus	right	32	-2	-36	6.03
Precentral gyrus	right	40	2	56	5.44
Middle frontal gyrus	right	52	48	-6	4.57
Hippocampus (anterior)*	right	18	-8	-22	4.27
Hippocampus (posterior)*	right	23	-36	2	3.28
Brainstem	left	-8	-34	-36	3.64
Ventromedial prefrontal cortex	right	2	50	-22	3.63
Middle cingulate gyrus	right	8	-2	32	3.58
Middle frontal gyrus	left	-46	50	-4	3.46
Globus Pallidus	left	-14	-2	4	3.42
Cerebrellum	left	-30	-68	-50	3.19
Rolandic operculum	left	-50	-22	18	3.01
Superior temporal pole	right	50	20	-16	2.89
Hippocampus (anterior)*	left	-24	-10	-20	2.71
Hippocampus (posterior)*	left	-18	-31	-2	2.67
Middle frontal gyrus	right	26	36	-14	2.52
Scrambled images					
Precuneus	left	-14	-54	30	4.31
Anterior cingulate gyrus	right	2	30	0	3.82
Cerebellum	right	2	-60	-48	3.71
Calcarine gyrus	left	-12	-92	4	3.49
Middle frontal gyrus	right	26	48	36	3.36
Middle temporal gyrus	right	52	-28	-10	3.34
Middle cingulate gyrus	left	-2	-24	30	2.99
Superior frontal gyrus	right	12	42	22	2.91
Superior frontal gyrus	left	-6	60	8	2.32

X,Y, and Z coordinates in MNI space, BSR=Bootstrap ratio, *=regions included in larger clusters

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Table S5: Peak coordinates of the contrast driven PLS - scene construction versus scene perception

Region	side	MNI coordinates			BSR
		X	Y	Z	
Scene construction					
Superior parietal lobule	right	16	-74	58	8.16
Precentral gyrus	right	32	0	54	7.97
Cerebellum	right	36	-70	-46	6.33
Fusiform gyrus	left	-42	-60	-14	5.73
Hippocampus (anterior)	left	-32	-2	-22	5.08
Superior frontal gyrus	right	6	62	36	4.89
Cerebellum	left	-30	-46	-38	4.16
Ventromedial prefrontal cortex	left	-8	44	-22	4.08
Hippocampus	right	24	-8	-24	3.81
Middle frontal gyrus	left	-38	36	-16	3.54
Inferior frontal gyrus	right	30	46	-18	3.04
Scene perception					
Angular gyrus	left	-48	-60	42	6.60
Anterior cingulate gyrus	right	2	32	2	4.45
Superior fronal gyrus	right	18	30	38	3.91
Angular gyrus	right	54	-54	50	3.89
Precuneus	right	14	-50	34	3.72
Hippocampus (posterior)	left	-28	-36	4	3.67
Hippocampus (body)	left	-34	-18	-14	3.57
Insula	left	-48	12	6	3.57
Superior fronal gyrus	left	-12	28	58	3.33
Middle temporal gyrus	left	-60	-22	-6	2.77
Middle frontal gyrus	left	-32	22	44	2.75

X,Y, and Z coordinates in MNI space, BSR=Bootstrap ratio, *= in the text referred to as ventromedial prefrontal cortex (vmPFC).