

Differential contribution of anterior and posterior midline regions during mental simulation of counterfactual and perspective shifts in autobiographical memories

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ABSTRACT

Retrieving autobiographical memories induces a natural tendency to mentally simulate alternate versions of past events, either by reconstructing the perceptual details of the originally experienced perspective or the conceptual information of what actually occurred. Here we examined whether the episodic system recruited during imaginative experiences functionally dissociates depending on the nature of this reconstruction. Using fMRI, we evaluated differential patterns of neural activity and hippocampal connectivity when twenty-nine participants naturally recalled past negative events, shifted visual perspective, or imagined better or worse outcomes than what actually occurred. We found that counterfactual thoughts were distinguished by neural recruitment in dorsomedial prefrontal cortex, whereas shifts in visual perspective were uniquely supported by the precuneus. Additionally, connectivity with the anterior hippocampus changed depending upon the mental simulation that was performed – with enhanced hippocampal connectivity with medial prefrontal cortex for counterfactual simulations and precuneus for shifted visual perspectives. Together, our findings provide a novel assessment of differences between these common methods of mental simulation and a more detailed account for the neural network underlying episodic retrieval and reconstruction.

1. Introduction

Episodic autobiographical memories (AMs) involve the reconstruction of mental simulations from past experiences. Often, the dynamic nature of this reconstruction modifies the content of AMs by mentally manipulating the way in which a memory is retrieved. For instance, though AMs are frequently retrieved from the same “own eyes” perspective in which they were originally experienced, we can also shift perspectives and adopt an observer’s point of view (Nigro and Neisser, 1983). Actively shifting from an own eyes to observer perspective increases natural recall from the observer perspective (St. Jacques et al., 2017), reduces accuracy for what actually occurred (Marcotti & St. Jacques, 2018), and can mollify mnemonic and emotional elements of the experienced event (Wallace-Hadrill and Kamboj, 2016). AMs can also be manipulated upon retrieval by mentally simulating alternative ways in which past personal events could have occurred but did not – a common psychological phenomenon known as *episodic counterfactual thinking* –

CFT (De Brigard and Parikh, 2019; Roese and Epstude, 2017). Extant evidence has shown that directional CFT (imagining better or worse outcomes) typically elicits emotional responses, such as regret, relief, or simply an increase in the emotional intensity associated with the original event (McMullen, 1997; Roese, 1997). Just as with perspective shifts, recent findings suggest that engaging in CFT during AM retrieval modifies phenomenological characteristics of AMs (De Brigard, Hanna, St. Jacques and Schacter, 2019), and might contribute to regulating their emotional properties (De Brigard and Hanna, 2015; De Brigard and Parikh, 2019). Yet, while these different forms of episodic reconstruction contribute to how we think about our past, an understanding for how they are supported by the brain remains to be further developed (St. Jacques, 2019; Van Hoeck et al., 2015). Investigations in this area have been growing in recent years, and continued study can help us better appreciate how memories are shaped and changed over time, especially since visual perspective shifts and CFT are common means by which humans naturally reevaluate past emotional events. In the present study,

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we set forth to specifically evaluate differences in neural activation and connectivity depending on the focus of a mental simulation – that is, whether the simulation is more conceptually driven in manipulating an event outcome or more perceptually driven in shifting visual perspective.

The shared reconstructive nature of these mental simulations is evident in recent neuroimaging findings showing commonalities between brain regions engaged in AM retrieval and those engaged during perspective-shift (St. Jacques et al., 2017) and CFT (De Brigard et al., 2013a). Indeed, a recent study revealed common engagement of the episodic memory system when AMs were mentally simulated as alternative versions and from alternative visual perspectives (St. Jacques et al., 2018). In this study, participants were asked to repeatedly shift their visual perspective or to simulate an alternative way a past personal event could have occurred but without changing its affective outcome. A fMRI adaptation paradigm revealed that both types of mental simulation recruited similar frontoparietal regions. Such commonalities could be accounted for by the *constructive episodic simulation hypothesis* (Schacter and Addis, 2007), according to which mental simulations place greater demands on the same episodic system that enables AM reconstruction, primarily comprising the default mode network (DMN), which reflects the constructive demands necessary for this process (Benoit and Schacter, 2015; Schacter et al., 2007). By recruiting the episodic memory network, both visual perspective shift and CFT are considered as imaginative processes that flexibly recombine and modify past events to simulate novel scenes.

While the constructive episodic simulation hypothesis suggests a general shared network supporting this mental simulation of past events, the precise neural mechanisms underlying the generation of diverse reconstructive episodic simulations remains unclear, particularly those that directly manipulate event outcomes to be better or worse than they actually were. For instance, in their evaluation of both perspective shifts and alternative simulations, St. Jacques et al. (2018) only focused on simulations of alternate events which could have still led to the same affective outcome. This kind of mental simulation, whereby only the antecedent is modified but the consequent (i.e., outcome) is kept fixed, is known in the psychological literature as *semifactual* thoughts (Barker, 1991), and are usually captured by “even if” statements – e.g., if a picnic was ruined because of rain, one might think *even if it had not rained, the picnic would still have been ruined because of the strong wind*. By contrast, directional CFT changes both the antecedent and the outcome of the event, as expressed by conditional statements following “if only” or “what if” clauses (e.g. *if only it had not rained, the picnic would not have been ruined*). Counterfactual simulations involving these directional changes likely place greater demands on episodic reconstruction via the conceptual recombination of event details and evaluation of affective outcome, which might have different effects compared to semifactual thoughts. Accordingly, when reading statements of novel scenarios, the use of directional CFT or semifactual thinking has been shown to differentially influence affective and causal judgements – only the simulation of alternative outcomes via CFT increases the negative emotional reaction and perceived causal relationship between an antecedent event and the true outcome, when compared to not thinking about any alternative (McCloy and Byrne, 2002). Given these differences, an evaluation of how directional CFT preferentially engages unique patterns of neural activation would be an important extension to the findings from St. Jacques et al. (2018). By recruiting constructive processes to generate alternate episodic events and outcomes, the creation of a novel contextual scene via better or worse CFT might engage distinct neural processes separable from the creation of a novel spatial viewpoint via visual perspective shift, although this dissociation in episodic reconstruction remains to be tested.

The notion that the brain uniquely supports these different types of mental simulations has been proposed in several studies. Accumulating evidence suggests a high degree of functional dissociation in components of the DMN, emphasizing that successful remembering of the past requires the functional integration of anterior and posterior subsystems

that support separate constructive processes in autobiographical recall (Andrews-Hanna et al., 2010; Xu et al., 2016). Recently, this divide in neural engagement has been suggested to reflect different forms of remembering – that is, a posterior hippocampal-cortical system supports the simulation of perceptual details (e.g. spatial representations), and an anterior hippocampal-prefrontal system facilitates emotion and knowledge-based conceptual processing (Sheldon et al., 2019). This anterior-posterior split in perceptual or conceptual construction might also extend to episodic reconstructions during perspective shifts and CFT. Accordingly, spatial manipulation of AMs via perspective shifts have been shown to engage posterior parietal regions, mainly the precuneus (St. Jacques et al., 2018), whereas constructing a counterfactual outcome recruits prefrontal regions that support an abstract modification of event details and evaluation of event outcomes (Alexander and Brown, 2011; Van Hoeck et al., 2015). That these different forms of reconstruction seem to promote dissociable patterns of neural recruitment would suggest the need for an updated account of how mental simulations are supported in the brain, although more empirical evidence is needed to warrant this claim.

Further, it is currently unknown whether the anterior-posterior dissociation in brain regions contributing to episodic reconstruction is supported by differential patterns of hippocampal connectivity, an important hypothesis put forth by Sheldon et al. (2019). Assessments of hippocampal functional connectivity are surprisingly scarce in neuroimaging studies evaluating mental simulations of past events, despite the centrality of this region to memory and mental simulation models, as well as observations of functional dissociation in anterior and posterior hippocampal regions related to mental scene construction (Addis and Schacter, 2012; McCormick et al., 2015; Zeidman and Maguire, 2016). Hippocampal connectivity with the PFC aids the creation of imagined future events (Campbell et al., 2018) and is sensitive to whether CFT is self, other, or object-based (De Brigard et al., 2015). Engagement of the medial temporal lobe network has also been shown to differentiate between episodic scene construction from an own eyes and observer perspective (St. Jacques et al., 2013), and recent evidence suggests that hippocampal connectivity differentially supports the initial construction of AM retrieval from multiple visual perspectives (Irie & St. Jacques, 2018). The prevailing neural account for the hippocampus and episodic simulation suggests a component process model whereby the posterior hippocampus supports accessing episodic details and the anterior hippocampus supports the recombination of event details (Addis and Schacter, 2012; Thakral et al., 2017a,b). However, despite evidence suggesting that hippocampal subregions uniquely contribute to imaginative processes, no study has explicitly compared how hippocampal connectivity might further dissociate neural support for episodic simulations that reconstruct AMs via perspective shifts versus CFT. Given that differential patterns of large-scale connectivity profiles for anterior and posterior hippocampal regions arise from increasingly coarse and global representations in the anterior region (Poppenk et al., 2013), we expect that this long-axis specialization has important contributions to our understanding of how the brain supports different types of mental simulations.

Therefore, the present functional magnetic resonance imaging (fMRI) study investigated functional dissociations in neural activity and hippocampo-neocortical connectivity during the generation of three types of episodic-based mental simulations: worse (downward) CFT, better (upward) CFT, and perspective-shifts. By evaluating preferential neural recruitment and connectivity within the constructive episodic simulation system, we hope to better refine the contribution of subsystem specialization to mental reconstruction and, more broadly, enhance our understanding of memory processing in the brain (Schacter et al., 2012). Thus, this approach can further elucidate components within the mental simulation network that are uniquely associated with reconstructing specific properties in memory for a past, episodic event. To achieve this goal, the present study was divided into three separate experimental sessions. At the first session, participants recollected AMs and provided

cues to use in a scanning session a week later, where the memories were either naturally recalled or mentally reconstructed with thoughts of better counterfactual outcomes, worse counterfactual outcomes, or a novel observer perspective. Participants then returned the following day for the final session in order to rate the memories on a variety of phenomenological characteristics.

Importantly, the current investigation differs in several key ways from the only other neuroimaging study on episodic reconstruction that included both perspective shifts and thoughts of alternative events (St. Jacques et al., 2018). Here participants were instructed to explicitly generate one of two novel directional counterfactuals that changed the outcome of a past autobiographical event (i.e., upward or downward), as opposed to imagining an undirected alternative way in which the remembered event could have occurred. Further, consistent with the literature on spontaneous counterfactual generation (Roese and Epstude, 2017), and in order to control the affective nature of the AMs simulated, participants in our study were asked to only recall AMs of past negative events. Thus, the present study significantly extends the findings from St. Jacques et al. (2018), while still providing the opportunity to corroborate some of their key results. Based on a review of the neuroimaging literature in this area, we hypothesized an anterior-posterior dissociation in neural support depending on whether episodic reconstruction is conceptually or perceptually-based, which we tested with a combination of whole-brain univariate and multivariate analytical techniques. Specifically, we predicted that perspective shift uniquely recruits posterior parietal cortex and CFT preferentially engages lateral and medial prefrontal regions, reflecting a divide in the recruitment of core DMN regions. Further, we expected hippocampal-cortical connections to demonstrate a similar dissociation, which we tested separately for anterior and posterior hippocampal seeds given increasing demonstrations of a functional divide that also exists within the hippocampus for autobiographical memory retrieval (Sheldon et al., 2019; Thakral et al., 2017a,b; Zeidman and Maguire, 2016). With these approaches, the present study provides a comprehensive evaluation of neural activation and connectivity that supports different forms of remembering and reconstruction of the past, ultimately expanding our understanding for

memory processing in the brain.

2. Materials and methods

2.1. Participants

Thirty-four participants volunteered for the study and completed informed consent in accordance with the University Health System Institutional Review Board guidelines and received \$10/h for time outside of the fMRI scanner and \$20/h for time in the scanner. All participants were right-handed, had normal or corrected-to-normal vision, and no history of a neurological disorder. Five participants withdrew from the study early (two did not want to complete session 1 due to length, one did not feel comfortable in the scanner, and two more due to technical issues and impossibility of rescheduling), resulting in a final sample size of $N = 29$ (14 male, 15 female; mean age = 23.7 years) for all analyses. On average, these participants scored low in trait anxiety on the State-Trait Anxiety Inventory Form Y-2 (Spielberger, 1983), with an average score of 34.7 ($SD = 9.1$).

2.2. Experimental procedures

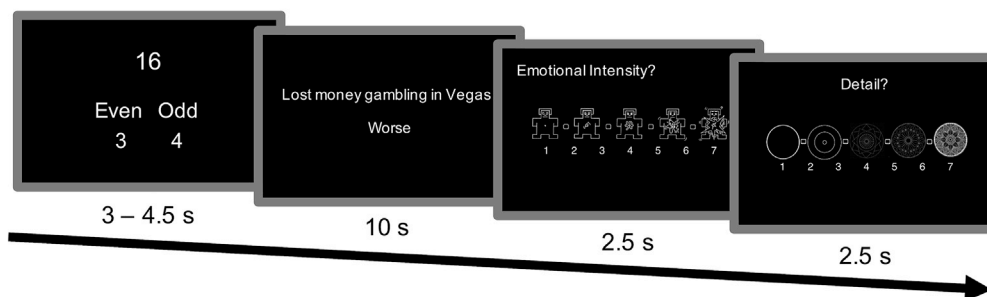
The study consisted of three separate sessions (Fig. 1). During session 1 (which on average took 3 h and 37 min), participants generated 120 negative and predominately own eyes AMs with help from a list of possible scenarios. Negative AMs were chosen since they are more likely to promote CFT (Roese, 1997), and we defined them as events associated with negative valence at the time in which they occurred. Participants were instructed to limit their memories to the past seven years and to provide subjective ratings of valence (the degree of positive or negative affect felt while remembering the event), arousal (the intensity of the emotion experienced while remembering the event), detail (how detailed they can reimagine the event), regret (how much regret they have for their role in the event), perceived control (the degree to which they felt they had control over the remembered event), own eyes perspective, observer perspective, and frequency of retrieval (on 7-point scales from 1

Session 1 – Record 120 negative autobiographical memories that are predominately retrieved from the first-person, own eyes perspective.

- Create memory titles to use as cues during sessions 2 and 3
- Provide ratings for memory characteristics

Session 2 (~1 week later, during fMRI) – For each memory either:

- Imagine a **worse** outcome
- Imagine a **better** outcome
- Mentally shift to an **observer** perspective
- Naturally **remember** the memory



Session 3 (next day) – rate all memories on the same scales used during session 1.

Fig. 1. Experimental design. During session 2, each simulation trial was separated by an active fixation period of rating numbers as even (press button 3) or odd (press button 4). Participants were provided with 10 s to recall the autobiographical memory and then engage in the instructed simulation. Participants indicated with a button press when an image of the memory first came to mind. After these 10 s, participants provided ratings of emotional intensity and detail for the simulation before moving to the next trial.

= negative/calm/vague/low to 7 = positive/excited/clear/high). Each memory was also assigned a short title by the participant in order to cue them during fMRI at session 2. These memories were pseudo-randomly sorted into five groups (24 memories per group) in order to ensure that the conditions during session 2 retrieval did not significantly differ in average initial ratings for valence, arousal, detail, or regret.

Participants returned about one week later for session 2 ($M = 6.8$ days, $SD = 0.6$), which took place in a fMRI scanner. During scanning, participants were cued on their memories and instructed to either simply retrieve the memory (“remember”), simulate an upward counterfactual of the memory (“better”), simulate a downward counterfactual of the memory (“worse”), or shift perspective to that of an observer (“observer”). Specifically, in the remember condition participants were told to place themselves back in the memory and relive the event exactly as they remember it occurring. For the counterfactual conditions, participants were instructed to simulate a better outcome to the event (e.g. by thinking about “if only this event had happened”) or to simulate a worse outcome to the event (e.g. by thinking about “at least this event didn’t happen”). Finally, in the observer condition participants were told to place themselves back in the memory as an observer, watching themselves in the event from an external witness point of view but not changing anything about what occurred. Participants were given time to practice these conditions and the timing of the task by using events from that day, such as eating breakfast or meeting the experimenter. Participants were allowed to ask questions about the task after the practice session, and the experimenter ensured that the instructions were understood prior to scanning.

The memories used for these conditions were pulled from the different lists that were generated in session 1. Thus, a total of 96 memories were shown during session 2 and the remaining list of 24 memories was saved for session 3 as a measure of baseline memory retrieval. Participants were given 10 s to retrieve and mentally manipulate the memory, followed by 2.5 s to rate the emotional intensity of the simulation and 2.5 s to rate the detail of the mental simulation. These ratings used the same scales as session 1 and the order of the ratings was counterbalanced. For each memory, participants were instructed to first indicate when they formed an initial image of the event, and then to engage with the condition associated with that memory, which was written at the bottom of the screen as “worse”, “better”, “observer”, or “remember”. Trials were separated by an active baseline odd/even numerical decision task that was variable in length (3–4.5 s). Each presentation screen was further separated by a variable fixation period (0.5–1.5 s). The order of the trials was pseudo-randomized for each participant, such that no condition was repeated more than two times in a row. Each run consisted of 24 memories, with 6 memories randomly assigned to the Remember, Better, Worse, or Observer conditions. The full scan time consisted of four runs, resulting in a total of 24 memories for each condition. Due to technical issues, one participant received an uneven number of conditions for one of the runs, and so this run was removed from behavioral and neural analyses. All other participants completed all four runs.

The following day participants returned for session 3, outside of the scanner. They were asked to naturally retrieve the 96 memories that were seen during session 2 and the additional 24 memories that were generated during session 1 but not seen during session 2. For each memory, participants again provided subjective ratings of valence, arousal, detail, regret, perceived control, own eyes and observer perspectives. Memory cues and ratings were presented in sessions 2 and 3 using Psychtoolbox (www.psychtoolbox.com), a MATLAB-based software package (Mathworks).

2.3. Statistical analysis of behavioral data

All subjects included in the analyses completed all three sessions and all experimental conditions. To investigate differential change in phenomenological characteristics across time as a function of condition,

a 2 (Session: First, Third) \times 5 (Condition: Better, Worse, Observer, Remember, Baseline) repeated measures ANOVA was conducted for each rating, using IBM SPSS Statistics software. A one-way repeated measures ANOVA was also used to assess differences in online ratings of arousal and detail during session 2, based on condition.

2.4. fMRI data acquisition and preprocessing

Neuroimaging data was acquired at the Duke University Brain Imaging and Analysis Center with a 3T General Electric MR750 scanner and 8-channel head coil. A 3D fast SPGR pulse sequence was used to acquire high-resolution T1-weighted structural scans ($TR = 8.16$ ms; $TE = 3.18$ ms; image matrix = 256^2 ; voxel size = $1 \times 1 \times 1$ mm), while a SENSE™ spiral-in sequence parallel to the AC-PC line was used to collect whole-brain functional scans ($TR = 2$ s; $TE = 30$ ms; image matrix = 64^2 ; $FOV = 240^2$; voxel size = $3.75 \times 3.75 \times 4$ mm, 36 slices with interleaved acquisition, flip angle = 60°). The first four timepoints in each functional scan were discarded to ensure scanner stabilization. Participants provided ratings using two 4-button MR-compatible response boxes in each hand.

Preprocessing of fMRI data was performed using fMRIprep v1.1.4 (Esteban et al., 2019a,b; RRID:SCR_016216), which is based on Nipype 1.1.1 (Gorgolewski et al., 2017, 2011; RRID:SCR_002502). Many internal operations of fMRIprep use Nilearn 0.4.2 (Abraham et al., 2014; RRID:SCR_001362), mostly within the functional processing workflow. The following description of the anatomical and functional preprocessing steps is provided by fMRIprep with each subject’s preprocessed report.

2.4.1. Anatomical data preprocessing

The T1-weighted (T1w) image was corrected for intensity non-uniformity (INU) using N4BiasFieldCorrection (Tustison et al., 2010; ANTs 2.2.0), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped using antsBrainExtraction.sh (ANTs 2.2.0), using OASIS as target template. Spatial normalization to the ICBM 152 Nonlinear Asymmetrical template version 2009c (Fonov et al., 2009; RRID:SCR_008796) was performed through nonlinear registration with antsRegistration (ANTs 2.2.0, RRID:SCR_004757; Avants et al., 2008), using brain-extracted versions of both T1w volume and template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast (FSL 5.0.9, RRID:SCR_002823; Zhang et al., 2001).

2.4.2. Functional data preprocessing

The following preprocessing was performed for each of the 4 BOLD runs for each subject. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIprep. Head-motion parameters with respect to the BOLD reference were estimated before any spatiotemporal filtering using mcflirt (FSL 5.0.9; Jenkinson et al., 2002). BOLD runs were slice-time corrected using 3dTshift from AFNI (RRID:SCR_005927). The BOLD time-series (including slice-timing correction) were resampled onto their original, native space by applying a single, composite transform to correct for head-motion and susceptibility distortions. The BOLD reference was then co-registered to the T1w reference using flirt (FSL 5.0.9, Jenkinson and Smith, 2001) with the boundary-based registration (Greve and Fischl, 2009) cost-function. Co-registration was configured with nine degrees of freedom to account for distortions remaining in the BOLD reference. Automatic removal of motion artifacts using independent component analysis (ICA-AROMA, Pruim et al., 2015) was performed on the preprocessed BOLD on MNI space time-series after a spatial smoothing with an isotropic, Gaussian kernel of 6 mm full-width half-maximum. Corresponding “non-aggressively” denoised runs were produced after such smoothing. The BOLD time-series were resampled to MNI152N-Lin2009cAsym standard space, generating a preprocessed BOLD run in MNI152N-Lin2009cAsym space. Four confounding time-series were

calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and two region-wise global signals. FD and DVARS were calculated for each functional run, both using their implementations in Nipype (following Power et al., 2014). The two global signals were extracted within the CSF and WM masks. All resamplings were performed with a single interpolation step by composing all the pertinent transformations. Gridded (volumetric) resamplings were performed using antsApplyTransforms (ANTs), and configured with Lanczos interpolation to minimize the smoothing effects of other kernels (Lanczos, 1964). Non-gridded (surface) resamplings were performed using mri_vol2surf (FreeSurfer). Prior to analysis, the nonaggressively AROMA denoised outputs from fMRIPrep were skull-stripped using FSL's brain extraction tool (BET) and high-pass filtered at 100s.

2.5. fMRI analysis

2.5.1. Mean-centered partial least squares (PLS) analysis

All imaging analyses used the final preprocessed data that was non-aggressively AROMA denoised through fMRIPrep, skull-stripped, and temporally filtered. The PLS analysis was conducted using software provided by the Rotman Research Institute (www.rotman-baycrest.on.ca) following procedures for a mean-centered analysis (McIntosh and Lobaugh, 2004). The brain region threshold was set at a threshold of 0.05 and data was normalized to the first scan. The mean-centered analysis was conducted on a 12 s temporal window (6 TRs) beginning at the onset of each memory cue. Statistical significance was tested using 500 permutations and bootstrap resampling with 500 repetitions, with salience maps determined from a bootstrap ratio (BSR) threshold of 3.2 (approximate $p = .0014$). Clusters are reported if they were larger than 15 voxels.

2.5.2. Univariate analysis

Univariate general linear model (GLM) analyses were conducted using FSL's FEAT (v5.0.9; Woolrich et al., 2004; Woolrich et al., 2001). First-level GLMs were created for each subject and for each run, based on task regressors for each experimental condition (Worse, Better, Observer, and Remember), as well as the onset and durations for the initial memory formation period (indicated by the participants for each trial), arousal ratings, and detail ratings. Thus, the timing of each condition in the GLM was based on when the participants first brought an image of the memory to mind. The first-level GLMs also included confound regressors for CSF, WM, DVARS, and FD, while any timepoint with a FD above 0.6 mm was censored. The regressors were convolved with a double-gamma hemodynamic response function, and primary contrasts were specified as each simulation condition (Worse, Better, and Observer) compared to the regular retrieval condition (Remember).

Psychophysiological interactions (PPI) analyses were conducted using bilateral anterior (ventral) and posterior (dorsal) hippocampal ROIs. These ROIs were defined anatomically in the Wake Forest University PickAtlas software (Maldjian et al., 2003) using the AAL library definition of the hippocampus, with the anterior and posterior portions of the hippocampus split at $y = -24$ mm in MNI space (Åhs et al., 2015; Poppenk et al., 2013). In these first-level models, the interaction of conditions with the anterior or posterior hippocampal timeseries was specified in addition to the average activation for those conditions.

The four runs were combined within each subject at second-level analyses using a fixed-effects approach. The resulting average responses for each subject were then used as input to the third-level group analysis, which utilized FMRIB's local analysis of mixed effects (FLAME 1 + 2). A single-group average (one-sample t -test) design was used to determine the average response for each contrast originally defined at the first-level (e.g. *observer > remember*), while a single-group paired difference (paired t -test) design was used to compare these first-level contrasts to one another (e.g. *observer > remember > worse > remember*). The group results were assessed at a cluster-forming threshold of $z = 2.3$ and a cluster significance threshold of $p = .05$. This

combination of FLAME 1 + 2 with cluster forming and significance thresholds provides an effective control against inflated false positive findings in fMRI studies (Eklund et al., 2016). In order to ensure differences were due to greater activation in the contrast of interest, the results for each double subtraction (paired difference between contrasts) were further masked by the respective maps passing significance for the single subtraction (e.g. *observer > remember > worse > remember* masked by *observer > remember*).

2.6. Research data

Due to the personal nature of the reported autobiographical memories, some of the data generated in this study cannot be made publicly available. However, all non-sensitive material is currently available at <https://github.com/IMC-Lab>. Requests for additional materials can be sent directly to the corresponding author. Depending on the nature of the request, Data Use Agreements may be required to protect the privacy of the participants.

3. Results

3.1. Autobiographical memory ratings

Average ratings of valence, arousal, detail, regret, control, own eyes perspective, and observer perspective recorded during sessions 1 and 3 are presented in Table 1. In separate 2 (Session: First, Third) \times 5 (Condition: Better, Worse, Observer, Remember, Baseline) repeated measures ANOVAs for each rating, main effects of session were observed in ratings of detail ($F_{1,28} = 12.903$, $p = .001$, $\eta_p^2 = 0.315$), own eyes perspective ($F_{1,28} = 20.993$, $p < .001$, $\eta_p^2 = 0.428$), and observer perspective ($F_{1,28} = 64.545$, $p < .001$, $\eta_p^2 = 0.697$), indicating that across all conditions memories generally decreased in ratings of detail and own eyes perspective, while increased in ratings of observer perspective. Though a significant main effect of condition was also found for ratings of observer perspective ($F_{4,112} = 3.466$, $p = .010$, $\eta_p^2 = 0.110$), these main effects of session and condition were qualified by a Session \times Condition interaction ($F_{4,112} = 2.784$, $p = .03$, $\eta_p^2 = 0.09$). Dunnett's post-hoc t -tests revealed that only the observer condition demonstrated a greater increase in ratings of observer perspective when compared to baseline memories ($t_{28} = 2.604$, $p = .015$, Cohen's $d = 0.484$).

During session 2 fMRI, participants provided ratings of arousal and detail for each retrieval trial. A main effect of condition was observed for arousal ($F_{3,84} = 12.986$, $p < .001$, $\eta_p^2 = 0.317$), and post-hoc Bonferroni-adjusted t -tests revealed that generating worse counterfactuals elicited higher arousal when compared to generating better counterfactuals ($t_{28} = 4.526$, $p = .001$, Cohen's $d = 0.841$), shifting to observer perspective ($t_{28} = 4.715$, $p < .001$, Cohen's $d = 0.875$), or simply remembering the memory ($t_{28} = 4.100$, $p = .002$, Cohen's $d = 0.761$). A main effect of condition was also observed for detail ($F_{3,84} = 5.956$, $p = .003$, $\eta_p^2 = 0.175$), such that remembering a memory was associated with greater detail than generating worse ($t_{28} = 3.736$, $p = .005$, Cohen's $d = 0.694$) or better ($t_{28} = 2.899$, $p = .043$, Cohen's $d = 0.538$) counterfactuals, or shifting visual perspective ($t_{28} = 4.399$, $p = .001$, Cohen's $d = 0.817$).

3.2. Mean-centered partial least squares (PLS) analysis

The mean-centered PLS analysis incorporating all conditions (Worse, Better, Observer, and Remember) identified a significant latent variable (LV1; $p = .002$) that accounted for 41.66% of the crossblock covariance (Fig. 2A). LV1 revealed a pattern of activation differentiating brain activity associated with worse and better counterfactual conditions versus the observer perspective and remember conditions. The temporal change in brain scores further showed that this separation was greatest at lag 5 (8–10 s), toward the end of the simulation period. The bootstrap ratio map for lag 5 (Fig. 2B) revealed clusters associated with positive saliences (i.e., observer and remember conditions) in precuneus, bilateral

Table 1

Ratings for autobiographical memory and mental simulation characteristics, with calculated difference scores from session 1 to session 3. *** $p < .001$, ** $p < .01$, * $p < .05$ (Bonferroni-adjusted within each rating).

	Session 1		Session 3		S3-S1	Cohen's d
	Mean	SD	Mean	SD		
Valence						
Worse	2.95	0.65	3.00	0.74	0.05	0.11
Better	2.93	0.72	3.02	0.77	0.09	0.17
Observer	3.02	0.71	3.12	0.73	0.10	0.19
Remember	2.96	0.67	3.09	0.75	0.14	0.23
Baseline	2.98	0.66	3.06	0.81	0.07	0.14
Arousal						
Worse	3.02	0.99	3.24	1.22	0.22	0.30
Better	3.04	1.15	3.27	1.22	0.24	0.31
Observer	2.97	1.08	3.17	1.09	0.20	0.29
Remember	2.96	1.09	3.18	1.20	0.21	0.31
Baseline	3.00	1.05	3.37	1.18	0.36	0.51
Detail						
Worse	5.18	0.88	4.68	0.93	-0.50***	0.85
Better	5.14	0.88	4.72	0.99	-0.42*	0.62
Observer	5.12	0.90	4.75	0.97	-0.37*	0.54
Remember	5.11	0.92	4.78	0.93	-0.33	0.46
Baseline	5.18	0.79	4.73	0.93	-0.45**	0.71
Regret						
Worse	3.53	1.02	3.45	0.94	-0.08	0.12
Better	3.48	0.97	3.53	0.97	0.06	0.09
Observer	3.56	0.94	3.41	0.78	-0.15	0.26
Remember	3.49	0.93	3.36	0.95	-0.13	0.21
Baseline	3.56	0.98	3.52	0.99	-0.05	0.07
Control						
Worse	3.84	0.83	3.70	0.84	-0.14	0.24
Better	3.80	0.89	3.66	0.88	-0.14	0.21
Observer	3.78	0.80	3.64	0.84	-0.14	0.25
Remember	3.82	0.91	3.71	0.93	-0.11	0.17
Baseline	3.92	0.81	3.77	0.84	-0.15	0.25
Own Eyes Perspective						
Worse	5.95	0.94	5.40	0.92	-0.56**	0.73
Better	5.99	0.96	5.37	0.85	-0.62***	0.87
Observer	5.94	0.85	5.39	0.82	-0.55***	0.80
Remember	5.92	0.94	5.36	0.83	-0.56**	0.76
Baseline	5.99	0.86	5.42	0.88	-0.57**	0.82
Observer Perspective						
Worse	1.98	0.93	2.87	1.10	0.88***	1.47
Better	1.98	0.88	2.83	1.15	0.85***	1.30
Observer	2.03	0.95	3.05	1.13	1.01***	1.61
Remember	2.02	0.94	2.89	1.12	0.87***	1.44
Baseline	2.04	0.99	2.80	1.13	0.76***	1.05
Session 2			Session 2			
	Mean	SD		Mean	SD	
Arousal			Detail			
Worse ^a	4.02	1.09	Worse ^a	4.52	0.83	
Better ^b	3.49	0.88	Better ^a	4.51	0.77	
Observer ^b	3.36	0.84	Observer ^a	4.45	0.74	
Remember ^b	3.62	0.89	Remember ^b	4.76	0.75	

Note: unique letter labels represent significant differences between conditions ($p < .05$, corrected).

angular gyrus, and lateral prefrontal cortex (PFC), whereas those associated with negative saliences (i.e., worse and better counterfactual conditions) were primarily in dorsomedial PFC. The full cluster report for lag 5 of LV1 is provided in Table 2.

3.3. Univariate analysis

3.3.1. Whole-brain activation

To complement the findings from the PLS analysis, a univariate analysis was conducted to directly evaluate differences in whole-brain activation between the conditions, based on when participants indicated that they had initially recalled the event and started the simulation ($M = 4.58$ s, $SD = 2.06$). First, for each simulation condition (worse counterfactual, better counterfactual, and observer perspective) we

subtracted out activation related to naturally remembering a memory. Across all conditions, greater activation was observed in clusters encompassing posterior parietal and lateral occipital cortex, middle/inferior temporal gyrus, PFC, and cerebellum when compared to natural recall (Table 3), demonstrating the additional constructive demands when imagining a novel visual scene or counterfactual scenario.

We then compared these effects between simulations – that is, after accounting for neural activation related to the remember condition, we tested for significant differences in whole-brain activation. When the simulation conditions were contrasted with one another, shifting to an observer perspective elicited greater activity in the precuneus, middle frontal gyrus, and lateral occipital cortex when compared to both counterfactual conditions, whereas the counterfactual conditions generally displayed greater engagement of dorsomedial PFC, primarily in the medial superior frontal gyrus, as well as crus I/II of the cerebellum (Fig. 3). Worse counterfactuals also demonstrated greater activation in left inferior frontal gyrus, when compared to perspective shift. No significant differences in univariate activation were observed between the counterfactual conditions.

3.3.2. Functional connectivity

Given a recent proposal of differential network engagement dependent upon anterior and posterior hippocampal connections (Sheldon et al., 2019), we conducted PPI analyses to evaluate whether differences in whole-brain connectivity with anterior and posterior hippocampal seeds is also observed between methods of mental reconstruction (Fig. 4). Compared to naturally recalling a memory, generating CFT and shifting visual perspective displayed similar increases in posterior hippocampal connectivity with clusters encompassing rostral anterior cingulate and ventromedial PFC. Generating worse counterfactuals also demonstrated increased coupling with the left thalamus, whereas generating better counterfactuals showed greater coupling with the left caudate nucleus.

Assessments of anterior hippocampal connectivity revealed more differentiation between the contrasts. Shifting perspective compared to natural recall was more likely to elicit increased hippocampal connectivity with precuneus and lateral occipital cortex, whereas the counterfactual conditions displayed greater connectivity with lateral frontopolar and medial prefrontal regions. All conditions also displayed enhanced coupling with superior temporal gyrus. These connectivity profiles were observed independently with each simulation condition compared to natural recall, though no significant effects were found when the simulation contrasts were compared in a double subtraction at the whole-brain level. The full cluster report for the PPI analyses is provided in Table 4. Exploratory amygdala connectivity analyses confirmed that signal from the amygdala was not solely driving the reported anterior hippocampus connectivity differences between the simulation and remember conditions (Supplementary Figure 1; Supplementary Table 1).

Given that PPI analyses can lack power in event-related designs (O'Reilly et al., 2012), we further tested for significant differences in anterior hippocampal connectivity when directly contrasting simulation conditions without also subtracting out the remember condition. This analysis revealed that the observer condition showed greater coupling with the precuneus when compared to both counterfactual conditions (Supplementary Figure 2A; Supplementary Table 2). Differences were also found between the two CFT conditions, such that generating worse counterfactuals exhibited enhanced connectivity of the anterior hippocampus with the left frontopolar cortex, right inferior parietal lobule, and right middle/inferior frontal gyrus, when compared to generating better counterfactuals (Supplementary Figure 2B).

4. Discussion

The current study investigated differences in neural activity for three closely related kinds of AM-based episodic simulation: upward CFT, downward CFT, and perspective-shift. To explore such differences, a data-driven multivariate analysis as well as univariate GLM and

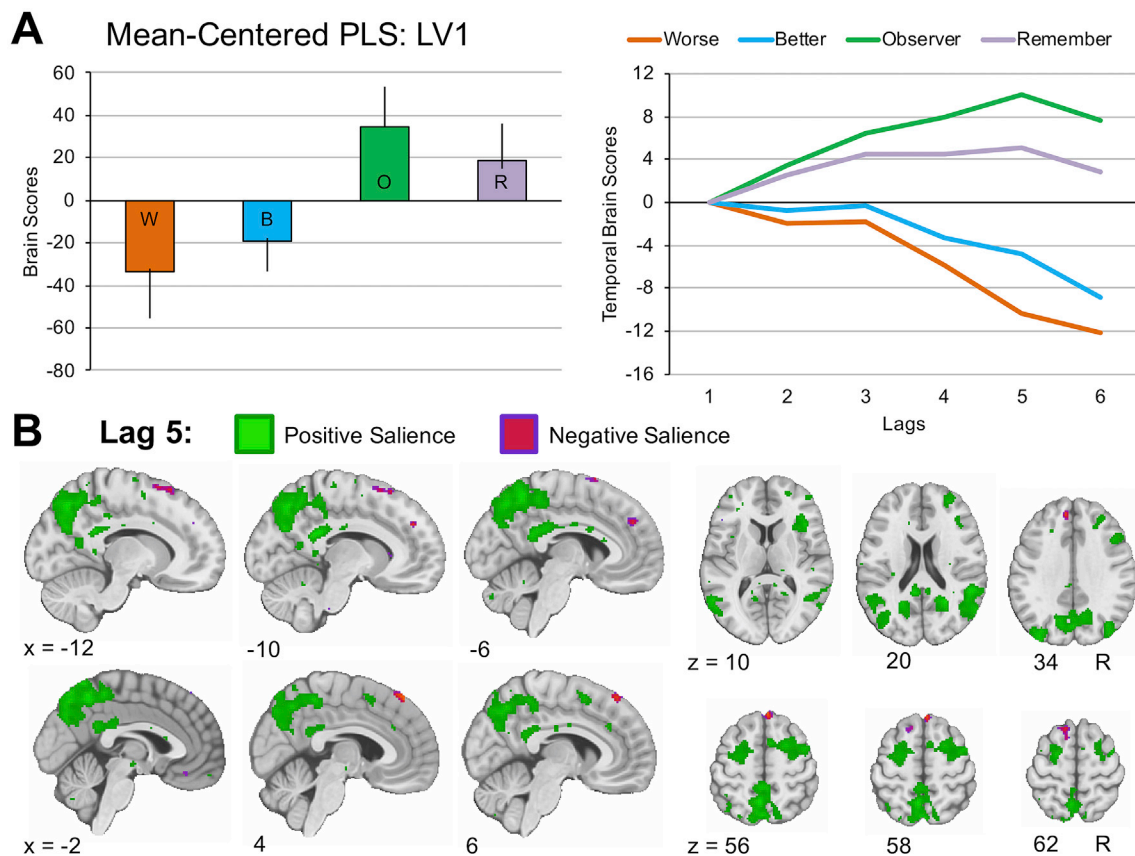


Fig. 2. Mean-centered PLS analysis. (A) Brain scores for LV1, which shows separation of the perspective shift and natural recall conditions from the counterfactual conditions. (B) Salience map for LV1 of the PLS analysis, focused on lag 5 (8–10s) which demonstrated the greatest differentiation in brain scores across the conditions. Positive saliences associate with the observer and natural recall conditions (e.g. precuneus and lateral posterior parietal/occipital cortex), while negative saliences associate with the counterfactual conditions (dorsomedial prefrontal cortex).

functional connectivity approaches were employed on fMRI data acquired during the generation of these mental simulations. Our results converge on a functional differentiation between neural regions associated with CFT versus own eyes and observer perspective recall of AM. Specific differences between conditions, as well as dissociable patterns of cortical connectivity with anterior and posterior hippocampus were also identified.

While the primary focus of the current investigation was on this neural separation, we also evaluated whether ratings of memory characteristics might be differentially influenced by the type of mental simulation performed. As expected, ratings of arousal were highest for generating worse CFT (Stanley et al., 2017), which may have been specific to the simulated experience by amplifying negative emotional intensity associated with what really happened (McMullen, 1997). Assessments of change in phenomenological characteristics of the memories revealed a long-term influence of perspective shift, such that only the observer condition promoted enhanced natural recall from the observer perspective, when compared to baseline memories. This effect was found when just a single perspective shift was induced for each memory in the observer condition, demonstrating the strength of this simulation in restructuring how past events are naturally remembered (St. Jacques et al., 2017).

In regard to the neural findings, we expected a functional dissociation for regions that preferentially support modifying perceptual features of an AM-based episodic simulation, such as visual perspective, versus those that support conceptual or abstract changes, such as outcomes. Consistent with this prediction, the mean-centered PLS analysis resulted in a significant LV revealing neural activity in dmPFC preferentially associated with CFT, relative to conditions that did not involve changing event

outcomes (i.e., perspective shift and natural recall). This distinct separation in neural recruitment validates claims of the medial PFC's specialized support for the flexible recombination of past events to construct alternate scenarios (Van Hoeck et al., 2015). In contrast, differentiation of the non-CFT conditions was primarily driven by neural patterns in posterior parietal and lateral regions of the episodic retrieval system (Benoit and Schacter, 2015; Burianova et al., 2010), with the observer condition contributing primarily to this separation likely due to increased recombination demands (St. Jacques et al., 2018).

To assess neural activity specifically related to memory modification, we further evaluated enhanced neural recruitment for each experimental condition contrasted with natural recall, and focused exclusively on the simulation period after initial AM search. These contrasts revealed enhanced recruitment for all simulation conditions in regions often implicated in episodic retrieval, such as medial PFC, lateral parietal and temporal regions (Benoit and Schacter, 2015; Burianova et al., 2010), as well as lateral frontal regions typically implicated in cognitive control and emotional reappraisal functions (Buhle et al., 2014). In particular, the left angular gyrus was one of the most consistently found regions showing greater activation in all the simulation conditions, highlighting its contribution to multiple forms of episodic reconstruction. In fact, a recent transcranial magnetic stimulation study showed that temporary disruption of activity specifically to the left angular gyrus has causal effects on memory and simulation experiences (Thakral et al., 2017a,b). Our findings of enhanced recruitment within this region during the manipulation of an autobiographical event thus supports the notion that the angular gyrus is recruited for the multimodal integration of contextual information when simulating novel scenarios or perspectives (Ramanan et al., 2018).

Table 2

Cluster report for the mean-centered PLS analysis. Clusters are reported if they pass a BSR threshold of 3.2, a minimum size threshold of 15 voxels, and a distance between cluster peaks of at least 10 mm.

Region	Hemi	x	y	z	BSR	Cluster Size
Positive Salience						
Angular Gyrus	R	50	-54	16	9.30	1453
	R	38	-54	40	4.51	82
Lateral Occipital Cortex	L	-38	-84	30	7.78	1587
Precuneus	L	-4	-56	54	7.50	4474
	R	26	-56	22	6.99	268
Posterior Cingulate Cortex	L	-10	-44	24	7.23	529
	L	-12	-44	6	4.16	24
	R	8	-16	30	4.14	26
Lateral Superior Frontal Gyrus	R	22	4	52	6.21	1087
	L	-22	-4	62	5.61	732
Cerebellum Crus II	R	40	-66	-48	5.86	24
Inferior Frontal Gyrus	R	42	22	10	5.61	255
	L	-56	20	28	3.72	24
Superior Temporal Gyrus	L	-48	-16	6	5.34	343
	R	56	-2	-16	4.17	83
Middle Frontal Gyrus	R	44	22	30	5.21	448
Insula	R	38	4	-12	5.20	36
Dorsal Anterior Cingulate Cortex	R	12	24	40	4.97	46
	R	10	34	30	4.49	56
	L	-6	6	26	4.50	22
	L	-14	24	24	4.08	16
Superior Parietal Lobule	L	-40	-48	50	4.96	494
	L	-14	-50	68	3.70	16
Frontal Pole	R	28	52	22	4.88	432
	R	34	42	4	4.38	18
	R	44	52	12	4.14	81
	L	-40	50	8	3.99	46
	L	-36	42	30	3.95	38
	R	26	44	-16	3.86	16
	L	-52	40	8	3.80	31
Brainstem	R	14	-20	-32	4.34	20
	R	0	-14	-10	3.83	20
Temporal Fusiform Cortex	L	-34	-40	-18	4.24	93
	R	34	-36	-14	4.23	19
Putamen	R	16	8	-12	4.08	40
Precentral Gyrus	L	-8	-28	68	3.96	15
Hippocampus (Posterior)	R	28	-36	-2	3.95	38
Thalamus	R	18	-28	12	3.85	16
Frontal Operculum Cortex	L	-42	10	6	3.81	17
Supramarginal Gyrus	R	56	-40	42	3.81	19
Postcentral Gyrus	L	-64	-14	16	3.72	19
Negative Salience						
Dorsomedial Prefrontal Cortex (Medial SFG)	R	4	40	56	-5.52	76
	L	-8	44	32	-5.06	38
	L	-12	24	62	-4.34	86
	L	-6	10	72	-4.26	19

Our primary interests, however, concerned how this enhanced recruitment differed by condition, in an attempt to replicate and extend the PLS findings. For the CFT conditions we again found preferential recruitment of dmPFC, as well as greater IFG activation for worse CFT. The increased engagement of prefrontal regions with CFT in both the PLS and univariate analyses suggests the relevance of this neural recruitment in mentally undoing autobiographical events and this region's centrality to evaluative processing during the conceptual construction of a novel mental representation (Sheldon et al., 2019). Of note, our findings also highlight consistently enhanced cerebellar crus I/II activation for CFT, although this region has received comparably less attention in models of CFT despite its unique association with nonmotor cognitive performance measures (Klein et al., 2016; Salmi et al., 2010) and coupling with the DMN (Buckner et al., 2011).

Compared to both CFT conditions, we found preferential engagement of precuneus, lateral occipital cortex, and middle frontal gyrus during the observer condition, supporting the parietal window hypothesis which

Table 3

Cluster report of max z-statistics for the primary univariate contrasts of interest (each simulation compared to natural recall). Due to contrast masking, coordinates for the double subtractions are only reported if they were also present in the single subtraction.

Region	Hemi	x	y	z	Z	Cluster Size
Worse > Remember						
Medial Superior Frontal Gyrus	L	-17	34	58	5.8	6630
(W > R) > (O > R)		-13	28	60	5.46	3845
Inferior Frontal Gyrus	L	-57	20	4	5.22	2892
(W > R) > (O > R)		-55	20	16	3.82	918
Angular Gyrus	L	-61	-55	36	5.1	1837
Inferior Temporal Gyrus	L	-55	-7	-39	4.85	1815
Cerebellum Crus I/II	R	32	-77	-37	5.63	1736
(W > R) > (O > R)		24	-77	-21	3.95	1464
Lateral Occipital Cortex	R	62	-63	34	4.35	450
Orbital Frontal Cortex	R	44	28	-11	3.29	373
Cerebellum Crus I/II	L	-29	-75	-35	3.88	362
Better > Remember						
Medial Superior Frontal Gyrus/Frontal Pole	L	-17	56	36	6.02	6757
(B > R) > (O > R)		-13	28	60	4.54	3948
Orbital Frontal Cortex	L	-51	32	-15	4.71	3909
Lateral Occipital Cortex	L	-59	-63	32	6	1680
Cerebellum Crus I/II	R	34	-77	-39	4.26	1141
Lateral Occipital Cortex	R	60	-67	30	5.37	954
Middle Temporal Gyrus	R	64	-11	-25	4.06	535
Cerebellum Crus I/II	L	-37	-83	-35	4.23	531
(B > R) > (O > R)		-45	-79	-35	3.33	362
Frontal Pole	R	46	40	-21	3.46	334
Observer > Remember						
Precuneus/Lateral Occipital Cortex	L	-1	-67	54	6.27	10014
(O > R) > (W > R)		-5	-61	60	6.01	14293
(O > R) > (B > R)		-9	-73	58	5.85	14743
Middle Frontal/Precentral Gyrus	L	-37	-1	56	4.46	3698
(O > R) > (W > R)		-27	-5	50	4.21	885
(O > R) > (B > R)		-27	-5	54	4.99	1263
(O > R) > (B > R)		-39	24	22	3.87	1106
Lateral Occipital Cortex	R	46	-79	36	4.83	3477
(O > R) > (W > R)		52	-63	16	4.87	10765
(O > R) > (B > R)		52	-59	12	4.68	4050
Middle Frontal Gyrus	R	44	18	40	4.08	929
(O > R) > (B > R)		56	38	28	3.55	1254
(O > R) > (B > R)		26	-5	62	4.58	1781
Cerebellum Crus I/II	R	14	-77	-27	4.01	749
Middle Temporal Gyrus	L	-55	-9	-25	3.82	499
Paracingulate Gyrus	L	-9	24	46	4.2	469
Cerebellum Crus II	R	44	-43	-45	3.98	334
Frontal Pole	R	46	40	40	3.39	323
Frontal Pole	R	60	38	-13	4.62	313

suggests that the posterior parietal cortex is uniquely engaged when updating and manipulating spatial information in memory (Byrne et al., 2007). In particular, the precuneus finding corroborates recent demonstrations of a causal role for the precuneus in AM retrieval and perspective shifts (Hebscher et al., 2019), as well as a structural relationship between precuneus volume and individual differences in perspective-taking (Freton et al., 2014; Hebscher et al., 2018).

Taken together, this pattern of results demonstrates, for the first time, distinct differences in neural recruitment of two core DMN regions – medial PFC and precuneus – depending on whether a simulation experience conferred new visual properties to a memory or actively modified the outcome of an AM. We thus provide empirical support for a recent neurocognitive model on the constructive nature of episodic memory (Sheldon et al., 2019), whereby perceptual remembering recruits a posterior medial-temporal subsystem supporting multimodal sensory integration and spatial processing while conceptual remembering engages a

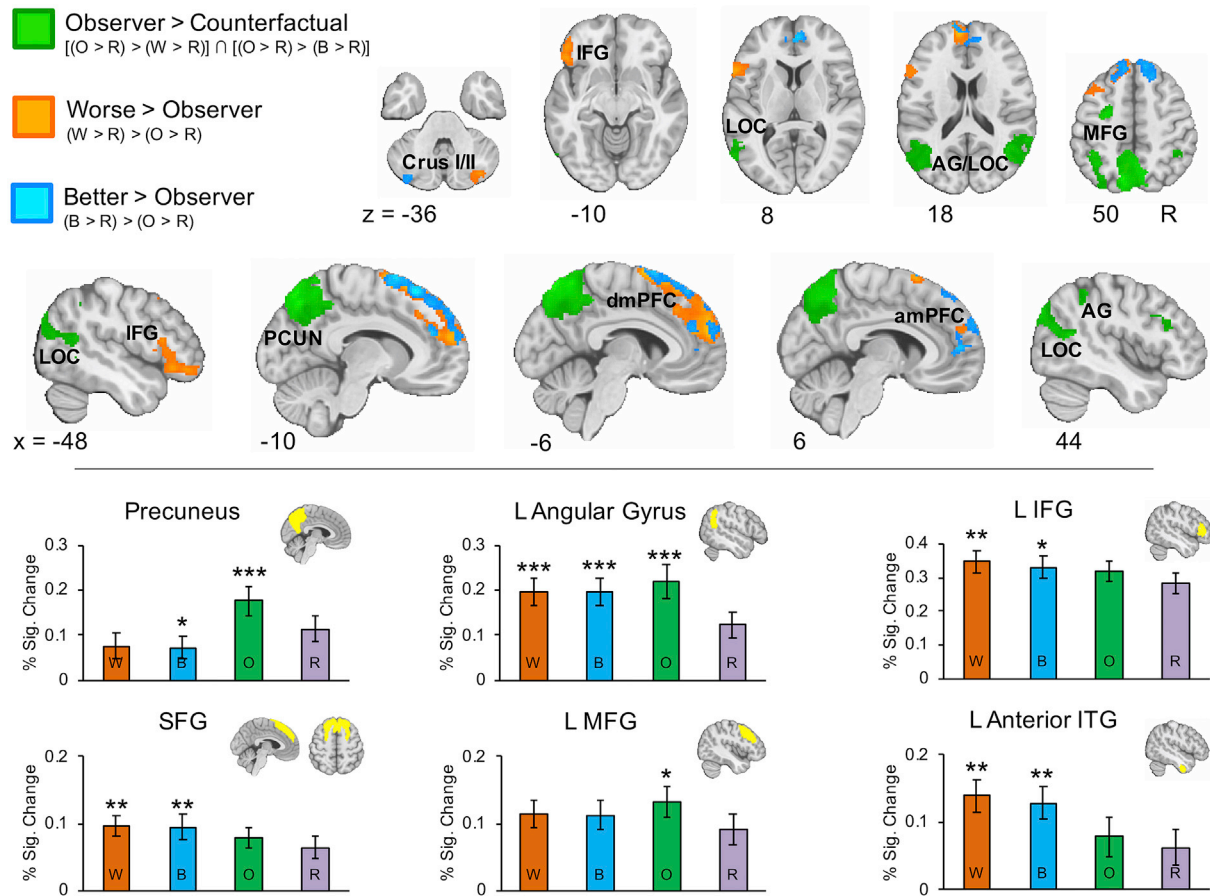


Fig. 3. Whole-brain univariate analysis. Results from the univariate analysis assessing activation differences between the simulation conditions, after subtracting out activation related to the natural recall (remember) condition. Statistical maps represent the group result after mixed effects analysis ($z > 2.3$, cluster-corrected $p < .05$). The observer condition elicited greater activation in precuneus, MFG, and clusters spanning lateral occipital and inferior parietal cortices, whereas the counterfactual conditions generally associated with greater activation in medial prefrontal regions. Graphs represent the average percent signal change for each condition in regions commonly implicated in episodic retrieval and mental scene construction, based on masks provided by the Harvard-Oxford Cortical and Subcortical atlases (set at a 30% probability threshold). Significance markers indicate a significant difference for a simulation condition when compared to the remember condition. Error bars indicate standard error of mean. IFG, inferior frontal gyrus; LOC, lateral occipital cortex; AG, angular gyrus; SFG, superior frontal gyrus; MFG, middle frontal gyrus; PCUN, precuneus; dmPFC, dorsomedial prefrontal cortex; amPFC, anterior medial prefrontal cortex; ITG, inferior temporal gyrus. *** $p < .001$, ** $p < .01$, * $p < .05$, Bonferroni-adjusted.

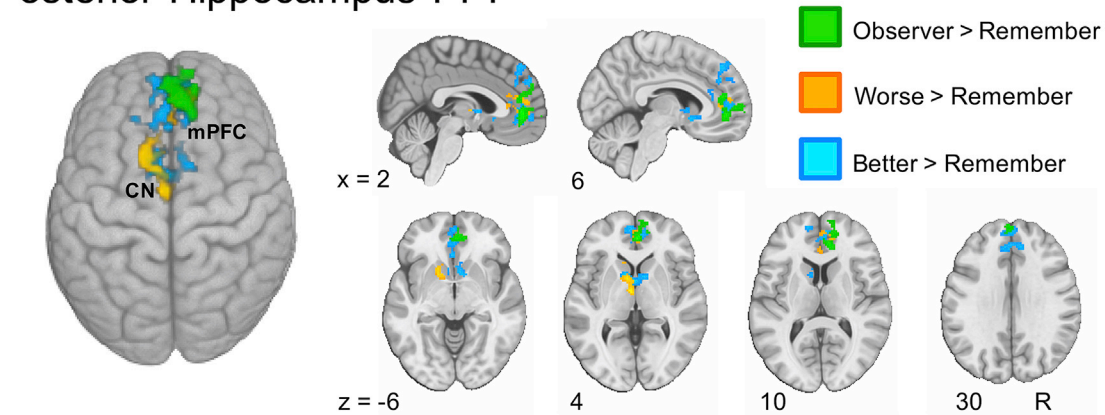
more anterior dorsal-medial subsystem supporting schema processing and emotion-based evaluation. Though a previous investigation demonstrated common engagement of medial PFC when shifting perspective and simulating alternative event details (St. Jacques et al., 2018), here we instructed participants to actively change event outcomes for better or worse during CFT, therefore placing greater demand on prefrontal neural mechanisms that guide outcome evaluation (Alexander and Brown, 2011) and promoting greater separation in neural support for the initial generation of novel perceptual or conceptual manipulations.

Of note, the PLS analysis did identify clusters in frontopolar cortex uniquely associated with the remember and own eyes conditions, while the univariate analyses revealed enhanced recruitment of frontopolar regions for both CFT and perspective shift when compared to naturally remembering a memory. Together, these findings provide a more nuanced interpretation of the anterior-posterior dissociation observed in the preferential recruitment of dmPFC and precuneus between these conditions, as it posits a more universal recruitment of anterior PFC during higher-order cognition pertaining to event knowledge (Krueger et al., 2009) and evaluation of internally generated information (Baird et al., 2013; Christoff and Gabrieli, 2000). Thus, while anterior PFC might be commonly engaged across these mental simulations as part of the initial construction of a novel mental scene, dmPFC and precuneus seem to be differentially recruited based on whether perceptual or

conceptual properties are manipulated. Further, while the activation associated with CFT did encompass rostral anterior cingulate cortex – the primary medial PFC region that contributes to the DMN (Buckner et al., 2008) – we also note that the majority of the neural activation associated with CFT was actually localized to more posterior dmPFC. This region is commonly referred to as the *dorsal nexus* for interactions among default, cognitive control, and affective networks (Sheline et al., 2010) and therefore still validates the integrative cognitive demand placed on counterfactual thought via the use of affective evaluation and flexible recombination of past events (Van Hoock et al., 2015). We thus interpret this increased dmPFC engagement as reflecting the increased demands that are placed on outcome evaluation during counterfactual thought, and not purely memory retrieval, given that we find with two separate analytical approaches the preferential recruitment of this region when compared to both natural recall and visual perspective shift.

Moreover, while more strongly activated in the CFT conditions, the left IFG was also recruited for the observer and remember conditions. Given our use of negative autobiographical memories as stimuli, as well as specific shifts in valence during the CFT conditions, this finding supports a recent proposal according to which left frontal control regions coupled with the DMN support the generation of endogenous emotions (Engen et al., 2017). However, the increase in percent signal change in left IFG when moving from the remember to observer to CFT conditions

Posterior Hippocampus PPI



Anterior Hippocampus PPI

Fig. 4. Differential patterns of posterior and anterior hippocampal connectivity between conditions. The posterior hippocampus consistently demonstrated increased connectivity across all conditions with mPFC, whereas the anterior hippocampus presented with an anterior-posterior divide in enhanced cortical connectivity between the counterfactual and perspective shift conditions. Both hippocampal regions showed increased connectivity with dorsal striatal regions, including the CN and putamen, across the simulation conditions. CN, caudate nucleus; vmPFC, ventromedial prefrontal cortex; FPC, frontopolar cortex; DS, dorsal striatum; PG, precentral gyrus; SG, supramarginal gyrus; STG, superior temporal gyrus; IC, intracalcarine cortex; LOC, lateral occipital cortex; PCUN, precuneus.

seems to further reflect increasing demands on constructing a novel affective outcome to the event and integrating multiple sources of information to achieve this goal (Van Hoeck et al., 2015).

To complement these whole-brain analyses, we also conducted a series of functional connectivity assessments to evaluate whether dissociations between mental reconstruction and natural recall of AMs is further reflected in cortical engagement with the hippocampus. Accordingly, these analyses were conducted separately for anterior and posterior portions of the hippocampus to reflect the differential engagement of these regions with cortical networks (Sheldon et al., 2019). Our PPI analyses revealed that the posterior hippocampus displays remarkably similar patterns of enhanced connectivity with medial PFC for all simulation conditions when compared to natural recall, suggesting a more general association of posterior hippocampal connectivity with AM reconstruction and confirming recently proposed network models of feedback loops between the vmPFC and hippocampus that supports building a mental scene (Campbell et al., 2018; McCormick et al., 2018).

In contrast, the anterior hippocampus showed greater heterogeneity in connectivity differences between simulation conditions, though overlap was observed in the superior temporal gyrus. The CFT conditions demonstrated enhanced coupling with medial and lateral PFC regions, although slightly more inferior (better CFT) and lateral (worse CFT) when compared to the medial PFC clusters identified in the whole-brain activation analysis, while the observer condition elicited increased coupling with posterior parietal and lateral occipital cortex, including the precuneus, which was also reminiscent of the effects observed with the

PLS and whole-brain univariate analyses. This finding aligns with a similar functional connection between anterior hippocampal and posterior medial regions that was recently found during the initial construction of observer compared to own eyes perspectives during remembering (Irie & St. Jacques, 2018). However, here we further demonstrate a distinction between anterior and posterior cortical connections depending on the perceptual or conceptual focus of the mental reconstruction, but only for the anterior hippocampus. The unique contribution of the anterior hippocampus to the recall and imagination of episodic scenes has been recently suggested (Thakral et al., 2017a,b; Zeidman and Maguire, 2016), but here our findings specifically suggest differential connections depending on the type of mental reconstruction performed.

Interestingly, both anterior and posterior hippocampal connectivity assessments also provided evidence for dorsal striatal contributions to mental reconstruction. Scimeca and Badre (2012) originally proposed a specific role of the striatum in memory by implementing cognitive control to guide retrieval processes, while we provide some of the first evidence specifically linking regions within the dorsal striatum to reconstructive processes in both CFT and perspective shift, implicating a wider role beyond just affective outcome evaluation (Van Hoeck et al., 2015). Thus, given the scarcity of hippocampal connectivity assessments in the mental simulation literature, the PPI findings presented here provide a much-needed inspection of hippocampo-cortical coupling that illustrates differences in episodic reconstruction beyond just whole-brain patterns of activity or univariate activation levels.

Table 4

Cluster report of max z-statistics for the functional connectivity analyses with anterior and posterior hippocampal seeds.

Region	Hemi	x	y	z	Z	Cluster Size
<i>Anterior Hippocampus</i>						
Worse > Remember						
Superior Temporal (Heschl) Gyrus	R	46	−23	10	3.81	415
Insula	L	−31	−1	14	3.23	395
Frontal Pole	L	−31	60	12	4.1	315
Better > Remember						
Superior Temporal (Heschl) Gyrus	R	48	−17	8	4	580
Ventromedial Prefrontal Cortex	L	−3	40	−17	3.7	526
Intracalcarine Cortex	R	6	−65	16	3.1	296
Observer > Remember						
Supramarginal Gyrus	L	−63	−35	50	3.72	730
Lateral Occipital Cortex	R	58	−69	20	3.82	511
Precentral Gyrus	L	−51	4	22	3.69	489
Lateral Occipital Cortex	L	−55	−77	26	4	436
Putamen	L	−29	−1	14	3.71	416
Temporal Pole	R	60	6	−3	3.89	393
Superior Temporal (Heschl) Gyrus	L	−45	−27	8	3.36	314
Lateral Occipital Cortex/ Precuneus	R	14	−75	52	3.97	296
<i>Posterior Hippocampus</i>						
Worse > Remember						
Thalamus	L	−7	−9	−1	3.58	312
Anterior Cingulate Cortex	R	4	44	14	3.1	281
Better > Remember						
Ventromedial Prefrontal Cortex	R	2	46	2	3.69	1225
Caudate	L	−9	6	2	3.94	350
Observer > Remember						
Ventromedial Prefrontal Cortex	R	4	48	−1	3.77	654

5. Limitations and future directions

While the present study offers a novel evaluation of the differential neural support for reconstructive mental simulations, we note that the experimental design is limited in control over participant engagement and subjective experience during the task, a common limitation for AM studies. As such, there is a possibility that the current findings are confounded by processes related to these variables, such as task difficulty. However, online ratings of detail did not significantly differ between the CFT and perspective shift conditions, suggesting that participants were generally successful at constructing novel mental scenes in relatively equal vividness. Moreover, our neural findings demonstrate a unique activation profile for each simulation condition when compared to natural recall, reflecting the distinct processes engaged by CFT and perspective shifts. Finally, while extant findings show that ease of simulation is susceptible to certain kinds of manipulation (e.g., repetition; De Brigard et al., 2013b; De Brigard et al., 2017), we have yet to find consistent differences across conditions, which suggests that the ease of the initial simulation is highly dependent on the content of the autobiographical memory retrieved.

Our findings also suggest several directions for further investigation into the behavioral and neural effects of episodic reconstruction. A general increase in observer perspective was found for all conditions, suggesting that training in perspective shifts might have induced a natural increase in using alternative perspectives at retrieval, which may also have contributed to a general decrease for detail across the

simulation conditions (Marcotti & St. Jacques, 2018). This finding highlights the need to consider how perspective shifts might interact with other mental simulations, such as CFT, in scene reconstruction and long-term changes in memory (St. Jacques, 2019). Moreover, repeatedly inducing counterfactual and perspective shifts for the same memory may aid to promote more discernible differences in the long-term effects of these simulation experiences. Such an approach might be better able to identify dissociable neural support for generating better and worse counterfactuals. From a neural perspective, an interesting avenue would also be to consider how memory activation changes from before to after these simulation experiences, and whether neural recapitulation during natural recall of an event is influenced by the degree to which an individual previously engaged with perspective shifts or CFT during mental manipulation.

Given recent demonstrations that affective status can influence the experience, lasting consequences, and ability to engage in mental imagery (Holmes et al., 2016), future work in this area should evaluate whether the online experience of these simulations and subsequent effects differ depending on anxious or depressive traits, especially since both CFT and perspective shift have been suggested as means of regulating or changing emotional response to negative experiences (De Brigard and Hanna, 2015; Wallace-Hadrill and Kamboj, 2016). Accordingly, we also note that the present findings are based only on the retrieval of negative autobiographical memories, whereas the experience of simulating counterfactuals has been shown to differ depending on the valence of the remembered event (Stanley et al., 2017). Thus, recruitment of the constructive episodic system might further dissociate depending on the type of event that the mental simulation is manipulating, which we were unable to address.

6. Conclusion

When retrieving an autobiographical experience from memory we tend to manipulate different elements of how the event was initially perceived. Here we have shown that just a single experience with these simulations promotes differential online and offline effects, and places unique demands on neural recruitment depending on the constructive nature of the simulation. The functional dissociation between perceptual or conceptual manipulation of past events is also highlighted in differential patterns of anterior hippocampal connectivity and, taken together, provides an updated account for the neural support of episodic memory reconstruction.

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Declaration of competing interest

The authors declare no competing financial interests.

CRediT authorship contribution statement

Leonard Faul: Conceptualization, Methodology, Software, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Peggy L. St. Jacques:** Conceptualization, Methodology, Writing - review & editing. **Jacqueline T. DeRosa:** Investigation, Project administration. **Natasha Parikh:** Conceptualization, Methodology, Software, Writing - review & editing. **Felipe De Brigard:** Conceptualization, Methodology, Writing - original draft.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2020.116843>.

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