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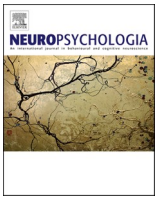

Peering into the future: Eye movements predict neural repetition effects during episodic simulation

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ABSTRACT

Imagining future scenarios involves recombining different elements of past experiences into a coherent event, a process broadly supported by the brain's default network. Prior work suggests that distinct brain regions may contribute to the inclusion of different simulation features. Here we examine how activity in these brain regions relates to the vividness of future simulations. Thirty-four healthy young adults imagined future events with familiar people and locations in a two-part study involving a repetition suppression paradigm. First, participants imagined events while their eyes were tracked during a behavioral session. Immediately after, participants imagined events during MRI scanning. The events to be imagined were manipulated such that some were identical to those imagined in the behavioral session while others involved new locations, new people, or both. In this way, we could examine how self-report ratings and eye movements predict brain activity during simulation along with specific simulation features. Vividness ratings were negatively correlated with eye movements, in contrast to an often-observed positive relationship with past recollection. Moreover, fewer eye movements predicted greater involvement of the hippocampus during simulation, an effect specific to location features. Our findings suggest that eye movements may facilitate scene construction for future thinking, lending support to frameworks that spatial information forms the foundation of episodic simulation.

1. Introduction

An adaptive feature of episodic retrieval processes is the ability to recombine elements of past experiences into something novel. This idea forms a central tenet of the constructive episodic simulation hypothesis (Schacter and Addis, 2007, 2020), which emphasizes the role of recombination in future thinking. Over the past decade, considerable evidence has accumulated showing that several processes beyond future thinking draw on constructive episodic retrieval and simulation including counterfactual thinking, decision-making, prosocial interactions, creativity, navigation, and dreaming (Arnold et al., 2016; De Brigard et al., 2013; Gaesser and Fowler, 2020; Madore et al., 2019; Schacter et al., 2017; Schacter and Addis, 2007; van Genugten et al., 2022; Wamsley, 2022). Episodic simulation, in all its forms, robustly engages a core set of brain regions collectively referred to as the default network (e.g., Addis et al., 2007). Prior work has shown that different brain regions may uniquely support the recombination of different features (e.g., locations and people) during simulation (Cooper and Ritchey, 2022; Szpunar et al., 2014). An open question is whether and how these separable patterns of brain function contribute to the experience of simulation vividness.

Often measured with self-report ratings, the vividness, or mental clarity, of imagination tends to scale with episodic memory performance. For example, autobiographical memories that are rated as more vivid are recounted with more specific episodic detail (e.g., Folville et al., 2022; but see Clark and Maguire, 2020; Lockrow et al., 2023). Parallel findings have been demonstrated with imagined future events, although ratings are overall relatively lower (D'Argembeau & Van Der Linden, 2004; Gamboz et al., 2010; Grysman et al., 2013; Morton and MacLeod, 2023). As such, self-report ratings are inherently tied to the content of simulation. Visual imagery, which has been found to uniquely predict the amount of episodic detail during autobiographical memory retrieval and future thinking (Aydin, 2018), may elicit the sensation of vividness during simulation (D'Argembeau and Van der Linden, 2006).

Eye movements may provide more objective information about vividness than self-report ratings. The eyes spontaneously move in a systematic way when individuals imagine a visual scene, even when looking at a blank screen. This 'looking at nothing' effect is thought to

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reflect the eyes recapitulating the spatial locations of previously encountered objects (Brandt and Stark, 1997), and has been observed to facilitate memory retrieval and subjective feelings of vividness (e.g., Johansson et al., 2022; Johansson and Johansson, 2014; Laeng and Teodorescu, 2002; Olsen et al., 2014; Wynn et al., 2022). Indeed, the oculomotor system is well positioned to integrate visually rich details into an imagined, episodic simulation. Its posterior extent within the visual system and anterior extent within the oculomotor control system directly abut the posterior cingulate and medial prefrontal hubs of the default network (Conti and Irish, 2021; Ryan et al., 2020; Shen et al., 2016). Findings from non-human primates suggest anatomical connections between these systems (Shen et al., 2016), while work with humans often demonstrates activation in posterior parietal and occipital cortices during personal memory and imagination tasks (e.g., Beaty et al., 2018). Concretely, eye movements predict individual differences in imagery (Chiquet et al., 2022; Johansson et al., 2011): Individuals who score higher on object imagery scales make fewer fixations when imagining previously encountered objects. While not an objective index of vividness, per se, physiological eye movement may convey different information about the quality of imagination than self-report ratings.

There is less consensus about the relationship between eye movements and episodic processing. Armson et al. (2021) took participants on a staged campus tour and later had them recall the tour while monitoring their eyes. The authors found that more fixations were related to greater episodic detail recalled, which was mediated by greater self-report ratings of episodic memory. In contrast, Sheldon et al. (2019) had participants imagine future personal scenarios while their eyes were tracked and found that *fewer* fixations contributed to the construction of more episodic details. While seemingly in conflict with one another, these results may point to eye movements as a means by which to distinguish past from future imagination. More germane to the present study is how eye movements and vividness during simulation predict simulation-related activity in regions of the default network.

In light of prior evidence that separable patterns of brain activity support the inclusion of different details during episodic simulation (Szpunar et al., 2014), it is plausible that different features drive eye movements and self-reported vividness. Szpunar et al. (2014) found that simulation of location features was associated with activity in medial prefrontal cortex, posterior cingulate cortex, angular gyrus, and areas within the medial temporal lobe, whereas simulation of person features was associated with activity in medial prefrontal cortex. Vividness was not assessed. The scene construction hypothesis suggests that spatial scenes are integral to episodic processes, whether information is retrieved from the past or used to simulate the future (Hassabis and Maguire, 2007; Maguire and Mullally, 2013). According to this view, spatial details should preferentially impact vividness. Both remembered and imagined events involving familiar locations—locations that an individual has personally encountered— tend to be rated as more vivid than those in unfamiliar locations (see Robin, 2018 for review). Eye movements also facilitate memory performance during associative recall when objects are paired with scenes compared to faces (Robin and Olsen, 2019). However, other work suggests that person details are more (D'Argembeau and Mathy, 2011) or as important (Jeunehomme and D'Argembeau, 2017) to vividness as spatial details. Vividness is also enhanced by person familiarity (Robin et al., 2016). It is possible that eye movements reflect spatial relationships between the features of an imagined event to re-instantiate a spatiotemporal context (Brandt and Stark, 1997; Wynn et al., 2019), rather than a single scene feature. It is yet unresolved whether vividness and eye movements are preferentially sensitive to certain features of simulation.

Here we integrated eye-tracking into a repetition suppression paradigm to examine how simulation vividness, measured both subjectively (i.e., self-reported vividness ratings) and objectively (i.e., eye movements), predicts brain activity related to future simulation, focusing on three key aims. Our first aim was to test the relationship between vividness ratings and eye movements, as measured by fixations. We anticipated a negative relationship, as in prior work with future simulation (Sheldon et al., 2019). Our second aim was to test whether vividness ratings and/or eye movements could predict the magnitude of repetition suppression in the brain. A third exploratory aim was to determine whether this relationship would pertain to specific features of simulation. To this end, we employed a recombination technique to separately examine brain activity related to person and location features of simulation. Given the negative relationship between fixations and future-oriented episodic detail, one might expect a parallel relationship between fixations and repetition suppression in the default network, and the opposite relationship for self-reported vividness. If scenes are integral to the experience of simulation vividness, location features may drive this effect. If supported, these findings will shed light on the shared and distinct roles of self-reported vividness ratings and eye movements in future simulation and how they may give rise to separable features during construction.

2. Materials & methods

2.1. Participants

Thirty-four healthy young adults between the ages of 18–32 (14 male, 18 female, 2 nonbinary; $M = 23.11$ years, $SD = 4.41$ years) were included in the study. Participants were recruited from Harvard University and the greater Boston area to take part in a 2-3-h study on imagination through online and flier advertisements. Compensation was course credit or cash payment. Initial screening involved a phone call to rule out use of psychoactive medications, history of disorders known to impact cognition (e.g., mood disorders), and standard MRI contraindications (i.e., metal in the body). All participants were right-handed with normal or corrected-to-normal vision. Seven additional participants were excluded for excessive in-scanner motion (n = 5), discomfort in the scanner (n = 1), and scanner presentation errors (n = 1). All participants provided written informed consent in compliance with the Harvard University Institutional Review Board.

2.2. Simulation paradigm and procedure

Prior to the experimental session, participants generated a list of 72 familiar people and 72 familiar locations on their personal computers. Participants were allowed to use their phone contacts and/or social media to help them. A familiar person included anyone that participants personally knew and could visually bring to mind. Familiar locations included specific, relatively small areas of space that the participants had personally visited. For houses and larger buildings, each room was considered a different location if the visual image was distinct. For larger outside locations, participants were instructed to focus in on a specific area where they could imagine the immediate surroundings, which could include a landmark. All people and locations were limited to 3–4 words. No other constraints were placed on participants (e.g., number of relatives listed, when the location was last visited). Participants sent the completed lists to the researchers and feedback was provided when necessary (e.g., repeats, too many words). Prior to the session, people and locations were randomly combined to generate person-location pairs for the experimental session. This recombination technique has been used in similar fMRI (e.g., Szpunar et al., 2014) and behavioral studies of future simulation (e.g., Wiebels et al., 2020).

Upon arrival, participants were first trained on the simulation task with generic person-location pairs of famous people and places. Participants were allowed to repeat the practice task as many times as needed. On every trial of the simulation task, participants saw a person-location pair from their lists presented on screen. After 2 seconds, the text disappeared and a black screen was presented for 10 seconds. During this time, participants were asked to imagine a plausible future event unfolding while keeping their eyes open and on screen. Specifically, participants were instructed to imagine being in the location and

interacting with the person (actively or passively). Critically, participants were instructed not to recall past experiences for these events. The trial ended with a vividness rating on a 4-point Likert scale ("How vivid was your imagined event?" 1: not at all vivid, 4: very vivid) before the next trial began. Trials were separated by a manual drift correction with a central disk.

The simulation task was divided into two parts: a session with eye-tracking outside of the scanner and a MRI session. The pre-scan session was broken down into two runs of the task (Exposure 1 and Exposure 2), each with 48 unique person-location pairings. Trials in each Exposure run were identical except for the order of presentation. In other words, participants saw each of the unique 48 pairs twice. Trials during the MRI session were broken down into 5 different conditions: 1) *Repeat*, or person-location pairs that were seen twice before scanning (Exposure 3); 2) *New Location*, where the person was previously encountered in the pre-scan session but was now paired with a new location from the participant's list; 3) *New Person*, where the location was previously encountered in the pre-scan session but was now paired with a new person from the participant's list; 4) *Recombine*, where both the person and location were previously encountered in the pre-scan session but in different pairings, and 5) *Novel*, where a completely new person-location pair was presented from the participant's lists. As eye-tracking was not collected during scanning, trials were separated by a jittered inter-trial interval of 2.5–10 s with a central fixation cross. Each run of the MRI session consisted of 20 trials, 4 trials per condition. Three MRI runs were collected, resulting in 60 total trials, 12 per condition.

The simulation paradigm was used to test for repetition effects on the component features of event simulation (as in Szpunar et al., 2014). By pairing the exposure runs with eye-tracking and vividness ratings, we could also test whether vividness ratings and/or eye movements from the initial simulation predicted repetition effects by the third simulation. Fig. 1 depicts the experimental procedure and key dependent variables.

2.3. Data acquisition and processing

2.3.1. Eye-tracking & behavioral data

During the pre-scan session, the task was presented in Experiment Builder (SR Research Ltd., Mississaugua, Canada) on a 24-inch monitor (1366 x 768 pixel resolution) positioned 70 cm away from participants. A chin rest was used to mitigate participant head motion. Monocular eye movements were recorded with a remote Eyelink 1000 Plus eye tracker (SR Research Ltd., Mississaugua, Canada) at 1000Hz sampling rate. A 9-point calibration was performed before the start of the task and manual drift correction with a central disk (>5°) was performed before the start of each trial to maximize data quality.

In an effort to speak to the opposite findings for past recollection and future simulation, our eye movement measure of interest was fixation count, which was calculated as part of the eye-tracking output. Eyelink defines saccades greater than 0.5° of visual angle as having a velocity threshold of 30°/sec, an acceleration threshold of 8000°/sec, and an onset threshold of 0.15°. Blinks are defined as periods where saccade signal is missing for 3 or more consecutive samples. All other samples are classified as fixations. The number of fixations on each trial is tallied to yield a fixation count. Fixation counts were extracted from an interest period of 10 seconds when the black screen was up. Fixation counts on each trial as well as vividness and vividness response times (RT) were extracted for each participant.

2.3.2. Neuroimaging

Neuroimaging data were collected on a 3T Siemens Magnetom Prisma (Siemens Helathineers, Erlangen, Germany) with a 32-channel head coil. Anatomical images were T1-weighted volumetric multi-echo magnetization prepared rapid gradient echo sequence with inversion recovery (TR = 2.2s; TE = 1.69; FA = 7°; 1 mm isotropic voxels; FOV = 256mmx256mm; 176 slices; total time = 6m12s). Three task-based functional runs were collected with a multi-band single-echo EPI sequence with 2D readout (TR = 2s; TE = 30ms; FA = 80°; 1.7 mm isotropic voxels; FOV = 124mmx124mm; multiband acceleration factor = 3; 231 vol; total time = 8m10s). Duo pads were used to help stabilize participants' heads. The task was presented in Experiment Builder (SR Research Ltd., Mississaugua, Canada) and back-projected with a mirror mounted on the head coil. A multi-button response box was used for vividness ratings. Participants wore MRI-safe glasses when needed.

Anatomical and functional images were preprocessed with fMRIprep.

2.3.2.1. Anatomical preprocessing. A total of 1 T1-weighted (T1w)

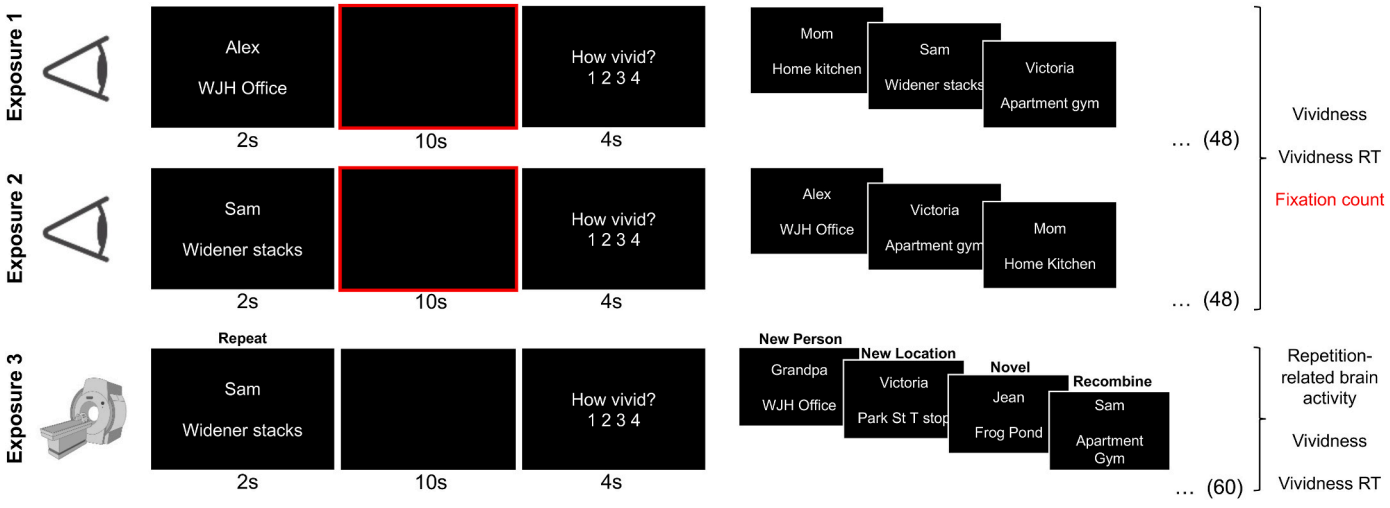

Fig. 1. Experimental Paradigm. A recombination paradigm was used to create participant-specific cues for simulation. On each trial, participants imagined future events involving the cued person and place for several seconds before rating the vividness of the imagined event. The first part of the session, Exposure 1 and Exposure 2, was conducted outside of the scanner and with eye-tracking. Trials from Exposure 1 and Exposure 2 were identical, except that they were presented in different orders. These trials included the first and second simulations of the same event. Following these trials, Exposure 3 was conducted inside the scanner. It contained exact repeats, which served as the third simulation of an event, along with New Person and New Location variations. Dependent variables of interest from Exposure 1 and Exposure 2 were vividness, RT for the vividness rating, and fixation counts. Variables of interest from Exposure 3 were repetition-related brain activity, vividness, and vividness RT.

images were found within the input BIDS dataset. The T1-weighted (T1w) image was corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al., 2010), distributed with ANTs 2.3.3 (Avants et al., 2008), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a *Nipype* implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid, white matter and gray matter was performed on the brain-extracted T1w using fast (FSL, Zhang et al., 2001). Brain surfaces were reconstructed using recon-all (FreeSurfer 7.2.0, Dale et al., 1999), and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (Klein et al., 2017). Volume-based spatial normalization to one standard space (MNI) was performed through nonlinear registration with antsRegistration (ANTs 2.3.3), using brain-extracted versions of both T1w reference and the T1w template. The following templates were selected for spatial normalization: *Custom young-old population MNI-space MRI anatomical template.*

2.3.2.2. Functional preprocessing. For each of the 3 BOLD runs found per participant, the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated by aligning and averaging 1 single-band reference (SBRefs). Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 6.0.5.1, Jenkinson et al., 2002). BOLD runs were slice-time corrected to 0.955s (0.5 of slice acquisition range 0s–1.91s) using 3dTshift from AFNI (Cox and Hyde, 1997). The BOLD time-series (including slice-timing correction when applied) were resampled into their original, native space by applying the transforms to correct for head-motion. These resampled BOLD time-series will be referred to as preprocessed BOLD in original space, or just preprocessed BOLD. The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer) which implements boundary-based registration (Greve and Fischl, 2009). Co-registration was configured with six degrees of freedom. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions, Power et al., 2014) and Jenkinson (relative root mean square displacement between affines, Jenkinson et al., 2002). FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by Power et al., 2014). The three global signals are extracted within the cerebrospinal fluid, the white matter, and the whole-brain masks. The head-motion estimates calculated in the correction step were placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (Satterthwaite et al., 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. Additional nuisance timeseries are calculated by means of principal components analysis of the signal found within a thin band (crown) of voxels around the edge of the brain, as proposed by (Patriat et al., 2017). The BOLD time-series were resampled into standard space, generating spatially-normalized, preprocessed BOLD runs in MNI space. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Automatic removal of motion artifacts using independent component analysis (ICA-AROMA, Pruim et al., 2015) was performed on the preprocessed BOLD data in MNI space time-series. The "aggressive" noise-regressors were collected and placed in the corresponding confounds file. Critically, no denoising was performed at this step. The preprocessed BOLD data in MNI space were then smoothed at 4 mm FWHM in SPM12.

As in the exposure session, vividness and vividness RT were extracted from each trial of the MRI session.

2.4. Analysis

2.4.1. Eye-tracking & behavioral data

Our measures of interest from the pre-scan Exposure runs were vividness and fixation counts (see Fig. 1). Average rating, RT, and fixation count per Exposure run were calculated for each participant. Vividness ratings from the Exposure runs were not recorded for 7 participants due to a technical error early in the experiment. Analyses with vividness ratings and RT include 27 participants, while all others include the full sample of 34 participants.

A series of one-way repeated measures ANCOVAs were conducted to test for repetition effects on vividness ratings, vividness rating RT, and fixation counts. ANCOVAs on vividness ratings and RT also included Repeat trials from the MRI session (Exposure 3). Notably, these analyses included 48 trials for Exposure 1, 48 trials for Exposure 2, and 12 trials for Exposure 3 (see Supplemental Material for analyses using only the repeated trials across Exposures). Two additional two-way repeated measures ANCOVAs were run on all trials from the MRI session only to test for condition and run effects on vividness ratings and RT. Gender and education were included as covariates of noninterest in all ANCOVAS. For variables demonstrating a significant change between the first and second Exposure runs, a difference score was calculated as the score from Exposure 2 minus the score from Exposure 1.

Our first aim was to examine the relationship between eye movements and vividness during initial future simulation. Spearman's ρ correlations were conducted between vividness ratings and RT or fixation counts to account for the ordinal nature of vividness ratings. We report Spearman's ρ correlations with 95% confidence intervals at an alpha of 0.05 and $p < 0.05$. Correlations were repeated for change scores. All correlations are reported with gender and education partialed out.

2.4.2. Neuroimaging

Functional data were fed into SPM12 to estimate general linear models (GLM) with a slow, event-related design assuming a canonical hemodynamic response function. For each participant, each run was modeled separately and consisted of cue onsets with a 12-second duration (cue + simulation) and vividness rating onsets with 4-second durations. Regressors of non-interest included the 6 rigid-body motion parameters as well as the timeseries of motion components flagged in AROMA ($M = 18.91, SD = 6.76$). Two participants only had two runs of data: one chose to end the experiment early, one arrived late.

Fixed participant effects were brought to the group level, where a series of planned contrasts were tested to identify regions showing repetition effects of simulation (as in Szpunar et al., 2014). Specifically, repetition suppression effects identified regions involved in constructing simulated events, the locations in which the events took place, and the people involved. These contrasts included Novel > Repeat, New Location > Repeat (exclusively masked by New Person > Repeat), and New Person > Repeat (exclusively masked by New Location > Repeat). Exclusive masks were used to inspect activity unique to construction of location and person features, and to control for potential variations in binding operations and effort. The conjunction between New Location > Repeat and New Person > Repeat was also examined to identify shared activity for the construction of location and person features. Repetition enhancement effects identified regions related to elaboration of simulated events, the locations in which the events took place, and the people involved. These contrasts included Repeat > Novel, Repeat > New Location, and Repeat > New Person. The conjunction between Repeat > New Location and Repeat > New Person was also examined. For completeness, we also examined Novelty (Novel > Repeat masked

by New Person + New Location > Repeat) to explore suppression-related activity for social scenarios in general, and Recombine > Repeat to explore activity repetition suppression related to binding processes (see Supplementary Material). All contrasts included each participant's total number of AROMA noise components (M = 55.23, SD = 17.31) as a covariate to control for the variable number of nuisance regressors included at the participant level. Exclusive masks were thresholded at $p < 0.05$. Contrasts were thresholded at an uncorrected $p < 0.001$ with an extent of 20 contiguous voxels. Only results passing a cluster-level $p < 0.001$ (equivalent to a T = 3.22) are reported.

2.4.3. Brain-behavior relationships

Our second and third aims were to test whether vividness ratings and/or eye movements during an initial simulation could predict repetition effects during a third simulation, and to explore whether a relationship would pertain to specific features of simulation. To this end, beta values were extracted from each contrast for clusters significantly active at $p < 0.001$. For the conjunctions, beta coefficients were extracted for each of the included contrasts. Partial correlations were conducted between beta values and the following variables from the Exposure runs: average vividness from Exposure 1, average change in vividness across Exposure runs, average fixation count from Exposure 1, and average change in fixation count across Exposure runs (see also Supplemental Material). Relationships with average vividness ratings from Exposure 3 were also tested for completeness. As in the random effects imaging analyses, total number of AROMA noise components were partialled out, along with gender and education. We report Spearman's ρ correlations with 95% confidence intervals at an alpha of 0.05 and a Bonferroni adjustment of $p < 0.013$ based on 4 tests for each cluster.

3. Results

3.1. Eye-tracking and behavior

We first tested for repetition effects on vividness ratings, vividness rating RT, and fixation counts. For each subject, 48 trials for Exposure 1, 48 trials for Exposure 2, and 12 trials for Exposure 3 were included. We orient the reader to Supplemental Material for re-analysis with the 12 trials repeated across sessions in participants with data from all Exposures.

A one-way repeated measures ANCOVA on vividness ratings revealed a significant main effect of repetition ($F(2,2962) = 8.07$, $p < 0.001$, $\eta p^2 = 0.01$; Fig. 2A, left panel), such that second and third simulations were rated as more vivid than the first simulation ($T_{12}(2932) = -2.70$, $p < 0.05$, Cohen's $d = 0.10$; $T_{13}(2574) = -3.69$, $p < 0.001$, Cohen's $d = 0.14$). Vividness between second and third simulations was not significantly different ($T_{23}(2571) = -1.96$, $p = 0.12$).

The corresponding ANCOVA on vividness RT also showed an effect of repetition ($F(2,2962) = 10.04$, $p < 0.001$, $\eta p^2 = 0.001$; Fig. 2B, left

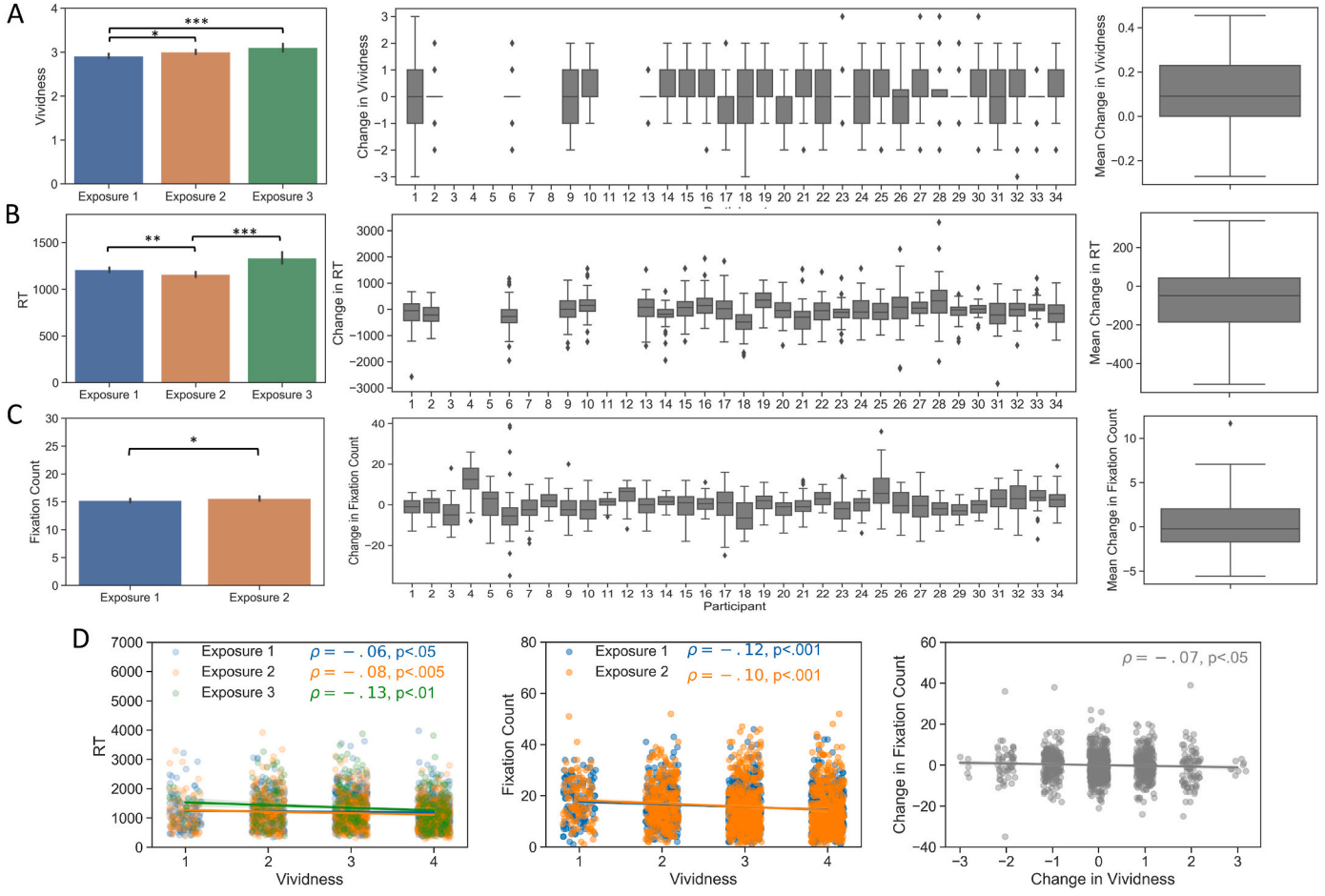

Fig. 2. Repetition effects on behavioral variables and relationships between them. (A–C) Vividness, RT, and fixation counts displayed as a function of repetition (left), as change scores between Exposure 1 and Exposure 2 (middle), and as mean change scores across the full sample (right). Change scores were calculated as the score from Exposure 2 minus the score from Exposure 1. (D) Scatterplots with trendlines depict associations between the variables, colored by repetition where appropriate. Partial correlation coefficients overlay the non-residualized data. Spearman's rho correlations were conducted controlling for gender and education. Statistical analyses on vividness include 27 participants, all others include 34. Trial numbers included in analysis varied between Exposures 1–2 and Exposure 3: Exposure 1 consisted of 48 trials, Exposure 2 consisted of 48 trials, and Exposure 3 consisted of 12 trials. *p < 0.05, **p < 0.01, ***p < 0.001.

panel). Ratings were made faster on the second simulation compared to the first ($T_{12}(2932) = 3.00, p < 0.01$, Cohen's $d = 0.11$), but were made slower on the third simulation compared to the second ($T_{23}(2571) = -4.10, p < 0.001$, Cohen's $d = 0.15$). No difference in RT was observed between the first and third simulations ($T_{13}(2574) = -2.22, p = 0.068$). Vividness ratings were negatively correlated with RT during each simulation (first: $\rho(1279) = -0.06, p < 0.05$, [-0.12,-0.01]; second: $\rho(1290) = -0.08, p < 0.005$, [-0.13,-0.02]; third: $\rho(386) = -0.13, p < 0.01$, [-0.23,-0.03]; Fig. 2D, left panel). It is likely that RT was slower during the third simulation due to the short delay needed to transition participants into the scanner.

The ANCOVA testing for differences in fixation count showed a main effect of repetition ($F(1,3260) = 4.56, p < 0.05, \eta p^2 = 0.001$; Fig. 2C, left panel), where fixation count was slightly higher during the second simulation compared to the first ($T(3260) = -2.134$, $p < 0.05$, Cohen's $d = 0.08$). This effect was likely due to one participant who uniquely demonstrated more overall fixations during the second simulation, as can be appreciated by an outlying value for change in fixations (Fig. 2C, right panel). Indeed, no difference in fixation count was observed across sessions when this participant was removed from the analysis ($F(1,3164) = 0.02, p = 0.884, \eta p^2 < 0.00$). We opted to keep the participant in subsequent analyses, but use Spearman's correlations, which are more robust to outliers.

Our first aim was to test for a relationship between eye movements and vividness during an initial future simulation. Higher vividness ratings were related to fewer fixations during initial simulation ($\rho(1279) = -0.12$, $p < 0.001$, [-0.17, −0.06]; Fig. 2D, middle panel). The relationship remained when controlling for RT ($\rho(1278) = -0.11$, $p < 0.001$, [-0.17,-0.06]). The same negative relationship was present during the second simulation ($\rho(1290) = -0.10, p < 0.001$, [-0.15,-0.04]), and persisted when controlling for RT ($\rho(1289) = -0.11$, $p < 0.001$, [-0.16,-0.06]). These results are broadly in line with findings showing that more detailed simulation relates to fewer, longer fixations (Sheldon et al., 2019). Average scores of vividness, RT, and fixation counts per Exposure session were calculated for subsequent brain-behavior correlations. No average scores were related (all p values > 0.3).

We next tested whether vividness, RT, and fixation count repetition effects were related. Change scores of each variable were calculated trial-wise for each participant and averaged to yield one score per participant (Fig. 2A–C, middle and right panels). Although vividness and RT were negatively correlated during each simulation separately, change in vividness was not related to change in RT ($\rho(1281) = -0.03, p = 0.274$, [-0.09,0.02]). Change in vividness was significantly related to change in fixation count, such that a more positive change in vividness was related to a more negative change in fixation count across simulations ($\rho(1277) = -0.07, p < 0.05$, [-0.12,-0.01]; Fig. 2D, right panel). The relationship remained when controlling for change in RT ($\rho(1276) = -0.06, p < 0.05$, [-0.11,-0.01]).

ANCOVAs were also conducted on all trials from the MRI session to test for condition and run effects on vividness ratings and RT (Supplementary Fig. 2). A main effect of condition ($F(4,1928) = 10.35, p < 0.001, \eta p^2 = 0.021$) demonstrated that Repeat trials were rated as more vivid than trials from all other conditions (all $Ts(1928) <= -0.59$ to $-4.50, p < 0.001$, Cohen's $d = 0.21$-0.25). That is, events that were simulated a third time were more vivid than all other simulations (Novel, New Person, New Place, Recombine). An effect of run number ($F(2,1928) = 1.67, p = 0.189, \eta p^2 = 0.002$) and the interaction between condition and run number ($F(8,1928) = 1.18, p = 3.103, \eta p^2 = 0.005$) were not significant. Condition also had a small but significant effect on RT ($F(4,1928) = 3.05, p < 0.05, \eta p^2 = 0.006$), where Repeat trials were rated faster than New Person trials only ($T(1928) = 2.959, p < 0.05$, Cohen's $d = 0.13$). Run number ($F(2,1928) = 0.95, p = 0.387, \eta p^2 = 0.001$) and the interaction between condition and run number ($F(8,1928) = 0.59, p = 0.791, \eta p^2 = 0.002$) had no effect on RT.

3.2. Neuroimaging

We next report on brain-based repetition effects from all 34 participants before summarizing brain-behavior relationships that address aims 2 and 3. To foreshadow, the imaging findings largely replicate Szpunar et al. (2014). Results from contrasts outside the scope of this paper can be found in Supplemental Material.

3.2.1. Repetition suppression effects

Initial compared to repeated simulation (Novel > Repeat) involved the recruitment of midline and lateral regions associated with the default network (Fig. 3A, warm colors), including posterior cingulate cortex, medial prefrontal cortex, dorsal prefrontal cortex, and posterior parietal cortex. Large bilateral hippocampus and cerebellar clusters were also observed. Full results are listed in Table 1. Initial, relative to repeated, simulation of locations (New Location > Repeat, masked by New Person > Repeat) uniquely engaged a small set of regions bilaterally (Fig. 4A): hippocampus, posterior cingulate cortex, and posterior parietal cortex (Table 2). No unique clusters were found for initial compared to repeated simulation of people (New Person > Repeat masked by New Location > Repeat). However, a conjunction analysis testing for shared, rather than unique, activation for first simulation of location and person features revealed that both features engaged posterior cingulate cortex, ventromedial prefrontal cortex, and dorsal prefrontal cortex during initial (compared to repeated) simulation (Supplementary Fig. 3A, warmer colors; Table S1). These results remained after masking out effects of potential new person and location binding processes with Recombine > Repeat (see Supplementary Fig. 3). Together these results suggest common neural engagement of different features during initial simulation as well as engagement unique to spatial construction.

3.2.2. Repetition enhancement effects

Repeated, relative to novel, simulations (Repeat > Novel) engaged mostly parietal regions including inferior and posterior parietal cortex, postcentral gyrus, and precuneus (Fig. 3A, cooler colors; Table 1). No clusters were uniquely related to repeated compared to initial simulation of locations or people (Repeat > New Location, Repeat > New People). However, the conjunction analysis revealed shared engagement of regions in bilateral inferior parietal cortex and precuneus (Supplementary Fig. 3A, cooler colors; Table S1). These findings suggest that neural repetition enhancement during simulation may not be specific to different constructive features.

3.3. Brain-behavior relationships

Our second aim was to test whether eye movements and/or vividness during initial simulation outside the MRI scanner predicted neural activation during a third simulation. Beta coefficients from significant clusters in the reported contrasts were extracted and correlated with average vividness from Exposure 1, average fixation count from Exposure 1, average change in vividness, and average change in fixation count.

Average fixation count, but not average vividness, was significantly correlated with activity in bilateral hippocampus during initial relative to repeated simulation (Fig. 3B, left panel). Specifically, fewer fixations on average during the first simulation predicted greater activity in these regions for Novel > Repeat (Left hippocampus: $\rho(29) = -0.534, p < 0.001$, [-0.74,-0.24]; Right hippocampus: $\rho(29) = -0.449, p < 0.01$, [-0.68,-0.13]). A more positive overall change in fixation count from Exposure 1 to Exposure 2 also predicted more activity in middle temporal cortex for Novel > Repeat ($\rho(29) = 0.563, p < 0.001$, [0.28,0.76]; Fig. 3B right panel). The relationship remained when dropping the participant with an outlying change score ($\rho(28) = 0.540, p < 0.001$, [0.24,0.75]). No other correlations for Novel > Repeat or Repeat > Novel survived correction for multiple comparisons (see Table 1 for full

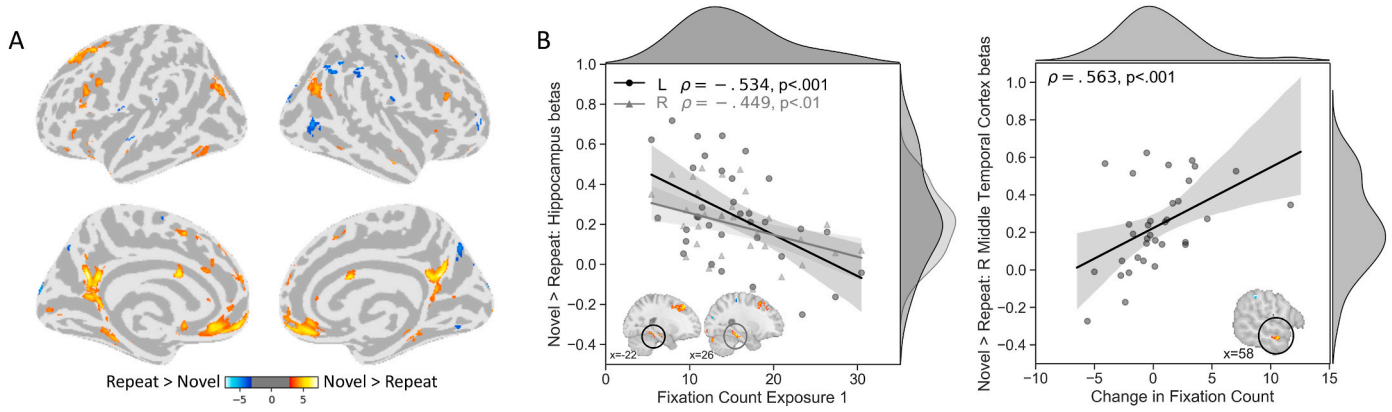

Fig. 3. Overall repetition effects and relationships to behavior. (A) Novel > Repeat and Repeat > Novel results projected on the surface and thresholded at T = 3 for visualization purposes. Beta coefficients from significant clusters were extracted and correlated with behavioral variables from Exposure 1 and change scores (see Methods). (B) Scatterplots with distributions and trendlines depict significant associations. Partial correlation coefficients are overlaid over the non-residualized data. Spearman's ρ correlations were conducted controlling for total AROMA noise components, gender, and education. Volumes containing the relevant clusters are also shown. 34 participants were included in this analysis. L = left, R = right.

listing).

Our third exploratory aim was to determine whether the detected brain-behavior relationships were driven by specific features of simulation (i.e., locations and/or people).

Correlations were run with beta coefficients from significant clusters in contrasts that revealed unique repetition-related brain activity for each feature. As no significant clusters were observed for New Person > Repeat (masked by New Location > Repeat), correlations were only run for coefficients from New Location > Repeat (masked by New Person > Repeat). Average fixation count during first simulation significantly predicted brain activity in the right hippocampus in New Location > Repeat ($\rho(29) = -0.465, p < 0.01, [-0.69, -0.15]$; Fig. 4B). No other correlations survived correction for multiple comparisons (see Table 2 for full listing).

Correlations were then repeated with beta coefficients from significant clusters in the conjunction between New Location > Repeat and New Person > Repeat as well as the conjunction between Repeat > New Location and Repeat > New Person. This analysis revealed whether brain-behavior relationships in the shared repetition-related activity were driven by one feature more than another. The only relationship that survived multiple comparisons correction was that between posterior parietal cortex activity for Repeat > New Location and average change in vividness (Supplementary Fig. 3B, Table S1). A more positive overall change in vividness between first and second simulations was related to less repetition enhancement of locations in posterior parietal cortex ($\rho(22) = -0.50, p < 0.01, [-0.74, -0.15]$). This relationship remained when controlling for change in RT ($\rho(21) = -0.53, p < 0.01, [-0.76, -0.18]$).

4. Discussion

4.1. More vivid simulations involve fewer eye movements

With respect to our first aim, we found that vividness ratings, but not eye movements, showed repetition effects. In other words, participants subjectively rated imagined scenarios as more vivid the second time, but objective fixation change was negligible. Intuitively, one might expect a mental image to be more vivid with repetition as construction demands decrease. Indeed, vividness ratings have been shown to go up after repeated simulation (De Brigard et al., 2013; Devitt et al., 2020; Wiebels et al., 2020). However, Gurguryan et al. (2021) found no change in self-reported vividness between the first and fifth retrieval of an autobiographical memory. This finding may point to a key difference in the reconstruction of a memory versus the construction of an imagined event. While remembered details may change over long periods of time (Fivush and Grysman, 2023), participants likely conjure up the same features—features cemented to an actual event—during each retrieval within a short timeframe, such as a study session. Conversely, features of an imagined future scenario may increasingly integrate into the event as it continues to crystallize with each repetition. Similarly, eye movements contain information about one's familiarity with a stimulus. Fixation counts generally decrease when a stimulus is old and increase when it is new, serving as an implicit mnemonic measure (Althoff et al., 1999; Ryan et al., 2007; Smith et al., 2006). Here, fixation counts were comparable across the first and second simulations, which may further suggest that participants were continuing to build the event in their minds.

More vivid simulations were accompanied by fewer fixations during initial as well as repeated simulation. Moreover, the more vivid simulations became with repetition, the fewer fixations participants made. These results add to a mixed literature on the relationship between eye movements and episodic processes. Armson et al. (2021) reported a positive association between fixations and episodic details, mediated by self-appraisal of better episodic memory abilities, during recall of a staged event. Corroborating the findings here, Sheldon et al. (2019; replicated in Wynn et al., 2022) reported the opposite: a negative relationship between fixation rate and episodic detail when individuals simulate future events and scenes. As alluded to above, one way to reconcile these seemingly opposite findings is that the eyes may behave differently during past and future construction.

There is robust evidence that past recollection evokes more episodic detail and higher subjective vividness than future simulation (Addis et al., 2010; D'Argembeau & Van Der Linden, 2004; Gamboz et al., 2010; Grysman et al., 2013; see also Schacter et al., 2012), but differential patterns of eye movements for past and future further suggests that vividness might transpire in different ways. Greater visual imagery during past, compared to future, thinking has also been related to more fixations (El Haj and Lenoble, 2018; Rasmussen and Berntsen, 2013). This finding has been interpreted as evidence that the visual system re-activates stored memory representations. In other words, eye movements during imagery are not random. Rather, they may re-instantiate the original spatial locations and relational associations of memory details (Brandt and Stark, 1997; Ferreira et al., 2008; Wynn et al., 2019). Higher fixations during recollection of ingrained memories may therefore be a consequence of adaptive memory retrieval. Indeed, associative memory performance with scenes exceeds that with either faces or objects, in part due to more fixations on scene trials (Robin and Olsen, 2019). With respect to future events, it has been suggested that fewer

Table 1
Repetition effects of future simulation and relationships to vividness and fixation count.

Region	Group-level Contrasts					Correlations with Exposure 1–2 Behavior: ρ (p) [CI]				Correlations with Exposure 3 Behavior: ρ (p) [CI]
	x	y	z	k	t	Vividness (exp1)	Change in Vividness (exp2 - exp1)	Fixation Count (exp1)	Change in Fixation Count (exp2 - exp1)	Vividness (exp3)
Novel > Repeat										
Posterior cingulate cortex	1	−58	20	1613	7.38	0.040 (0.844) [-0.35, 0.41]	0.193 (0.335) [-0.20,0.53]	−0.355 (0.039) [-0.62,-0.02]	0.220 (0.212) [-0.13,0.52]	0.008 (0.964) [-0.33,0.35]
Cerebellum	−9	−83	−36	127	7.25	−0.005 (0.982) [-0.38,0.38]	−0.006 (0.976) [-0.39,0.37]	−0.077 (0.663) [-0.41,0.27]	0.155 (0.381) [-0.19,0.47]	0.016 (0.927) [-0.32,0.35]
Ventromedial prefrontal cortex	3	49	−9	1393	6.84	0.216 (0.280) [-0.18,0.55]	0.231 (0.246) [-0.16,0.56]	−0.106 (0.550) [-0.43,0.24]	0.259 (0.140) [-0.09,0.55]	0.235 (0.180) [-0.11,0.53]
Anterior cingulate cortex	−1	8	27	67	6.53	0.430 (0.025) [0.06,0.7]	0.221 (0.268) [-0.17, 0.55]	−0.064 (0.720) [-0.39,0.28]	0.100 (0.573) [-0.25,0.42]	0.393 (0.022) [0.06,0.65]
Dorsal prefrontal cortex	−23	32	50	546	6.12	0.036 (0.858) [-0.35,0.41]	0.071 (0.726) [-0.32,0.44]	−0.235 (0.181) [-0.53,0.11]	0.233 (0.184) [-0.11,0.53]	0.012 (0.945) [-0.33,0.35]
Middle temporal cortex	59	−5	−16	72	6.02	0.012 (0.952) [-0.37,0.39]	0.089 (0.661) [-0.30,0.45]	−0.057 (0.748) [-0.39,0.29]	**0.563 (0.001) [0.28,0.76]**	0.176 (0.320) [-0.17,0.49]
Hippocampus	26	−34	−16	241	6.01	0.104 (0.606) [-0.29,0.47]	−0.037 (0.854) [-0.41,0.35]	**−0.449 (0.008) [-0.68,-0.13]**	0.234 (0.182) [-0.11,0.53]	0.084 (0.637) [-0.26,0.41]
Cerebellum	8	−80	−33	329	5.84	−0.418 (0.030) [-0.69,-0.04]	−0.098 (0.626) [-0.46,0.29]	−0.120 (0.500) [-0.44,0.23]	0.139 (0.432) [-0.21,0.46]	−0.412 (0.015) [-0.66,.-0.09]
Posterior parietal cortex	43	−65	27	426	5.55	0.263 (0.186) [-0.13,0.58]	0.180 (0.369) [-0.21,0.52]	−0.405 (0.017) [-0.65,-0.08]	0.219 (0.213) [-0.13,0.52]	0.174 (0.325) [-0.17,0.48]
Cerebellum	6	−60	−46	184	5.53	0.162 (0.420) [-0.23,0.51]	0.166 (0.408) [-0.23,0.51]	−0.312 (0.072) [-0.59,0.03]	−0.107 (0.548) [-0.43,0.24]	0.048 (0.790) [-0.30,0.38]
Posterior parietal cortex	−43	−73	30	351	5.52	0.223 (0.264) [-0.17,0.56]	0.184 (0.357) [-0.21,0.53]	−0.239 (0.173) [-0.53,0.11]	0.200 (0.256) [-0.15,0.50]	0.160 (0.366) [-0.19,0.47]
Hippocampus	−30	−37	−14	211	5.48	0.324 (0.099) [-0.06,0.63]	0.084 (0.676) [-0.31,0.45]	**−0.534 (0.001) [-0.74,-0.24]**	0.155 (0.382) [-0.19,0.47]	0.109 (0.540) [-0.24,0.43]
Dorsomedial prefrontal cortex	−2	10	49	149	5.41	0.036 (0.858) [-0.35,0.41]	0.104 (0.604) [-0.29,0.47]	0.059 (0.742) [-0.29,0.39]	0.240 (0.171) [-0.11,0.54]	0.087 (0.625) [-0.26,0.41]
Occipital cortex	20	−100	−4	92	4.79	0.019 (0.925) [-0.36,0.40]	0.316 (0.109) [-0.07, 0.62]	−0.137 (0.440) [-0.45,0.21]	0.062 (0.726) [-0.28,0.39]	−0.019 (0.913) [-0.36,0.32]
Medial prefrontal cortex	−1	56	22	217	4.76	0.143 (0.477) [-0.25,0.50]	0.163 (0.417) [-0.23,0.51]	−0.158 (0.374) [-0.47,0.19]	0.138 (0.438) [-0.21,0.45]	0.100 (0.572) [-0.25,0.42]
Insula	−40	25	−4	86	4.61	0.020 (0.921) [-0.36,0.40]	−0.062 (0.758) [-0.43,0.33]	0.176 (0.318) [-0.17,0.49]	0.177 (0.316) [-0.17,0.49]	0.060 (0.735) [-0.28,0.39]
Dorsomedial prefrontal cortex	−8	27	25	65	4.57	−0.049 (0.809) [-0.42,0.34]	0.216 (0.279) [-0.18,0.55]	−0.148 (0.402) [-0.46,0.20]	0.378 (0.027) [0.05,0.64]	−0.058 (0.744) [-0.39,0.29]
Dorsolateral prefrontal cortex	−52	20	23	116	4.56	−0.015 (0.942) [-0.39,0.37]	−0.002 (0.993) [-0.38,0.38]	0.065 (0.714) [-0.28,0.39]	0.197 (0.265) [-0.15,0.50]	0.053 (0.766) [-0.29,0.38]
Dorsal prefrontal cortex	26	19	52	113	4.53	0.142 (0.481) [-0.25,0.50]	0.180 (0.369) [-0.21,0.52]	−0.417 (0.014) [-0.66,-0.09]	0.231 (0.188) [-0.12,0.53]	0.117 (0.508) [-0.23,0.44]
Posterior temporal cortex	−50	−61	−12	103	4.52	0.308 (0.118) [-0.08,0.62]	0.258 (0.193) [-0.14,0.58]	−0.045 (0.799) [-0.38,0.30]	−0.010 (0.956) [-0.35,0.33]	0.150 (0.397) [-0.20,0.46]
Repeat > Novel										
Posterior parietal cortex	−8	−95	13	104	5.76	0.116 (0.565) [-0.28,0.48]	−0.059 (0.769) [-0.43,0.33]	−0.369 (0.032) [-0.63,-0.04]	0.018 (0.921) [-0.32,0.35]	−0.145 (0.414) [-0.46,0.20]
Posterior temporal cortex	43	−68	5	54	5.74	−0.092 (0.647) [-0.45,0.30]	0.121 (0.548) [-0.27,0.48]	0.077 (0.667) [-0.27,0.40]	0.366 (0.033) [0.03,0.63]	−0.031 (0.863) [-0.37,0.31]
Inferior parietal cortex	54	−58	44	201	5.05	0.075 (0.710) [-0.31,0.44]	0.002 (0.993) [-0.38,0.38]	0.072 (0.687) [-0.27,0.40]	−0.236 (0.180) [-0.53,0.11]	0.168 (0.343) [-0.18,0.48]
Inferior parietal cortex	40	−48	42	57	4.85	0.208 (0.297) [-0.19,0.55]	0.021 (0.918) [-0.36,0.40]	0.049 (0.783) [-0.29,0.38]	0.054 (0.762) [-0.29,0.39]	0.172 (0.332) [-0.18,0.48]
Dorsolateral prefrontal cortex	43	53	3	69	4.65	−0.137 (0.494) [-0.49,0.26]	−0.242 (0.224) [-0.57,0.15]	0.286 (0.101) [-0.06,0.57]	−0.192 (0.277) [-0.50,0.16]	−0.027 (0.878) [-0.36,0.31]
Precuneus	13	−72	40	133	4.44	0.049 (0.782) [-0.29,0.38]	−0.065 (0.748) [-0.43,0.32]	0.008 (0.969) [-0.37,0.39]	0.149 (0.399) [-0.20,0.46]	0.023 (0.896) [-0.32,0.36]
Postcentral gyrus	62	−37	44	116	4.25	0.217 (0.276) [-0.18,0.55]	−0.213 (0.286) [-0.55,0.18]	0.048 (0.786) [-0.29, 0.38]	−0.205 (0.246) [-0.51,0.14]	0.136 (0.442) [-0.21,0.045]

Note. Group-level results were thresholded at an uncorrected cluster-level $p < 0.001$ and $k = 20$. Partial Spearman ρ correlation coefficients are reported controlling for total AROMA components, gender, and education. Bold denotes significance after Bonferroni correction for 4 tests. Exp1 = Exposure 1; Exp2 = Exposure 2; Exp3 = Exposure 3.

fixations are made as compared to retrieved events since visual imagery and memory retrieval demands are low (El Haj and Lenoble, 2018). That said, constraining eye movements during future thinking negatively impacts the episodic detail conveyed and visual imagery experienced (de Vito et al., 2015a, 2015b; Gautier et al., 2022). The negative relationship during 'free' simulation observed here may merely reflect less reliance on the retrieval of spatial relationships, perhaps suggesting that other episodic features drive vivid simulation of future events (Zaman et al., 2023). It is also possible that high familiarity with the people and place cues made it easy to simulate future events, whereas a more difficult task may require more eye movements (see also section 4.4; Johansson et al., 2011; Wynn et al., 2019). As vividness ratings were never at ceiling, task difficulty, or the lack thereof, cannot fully explain the negative relationship observed between subjective vividness and

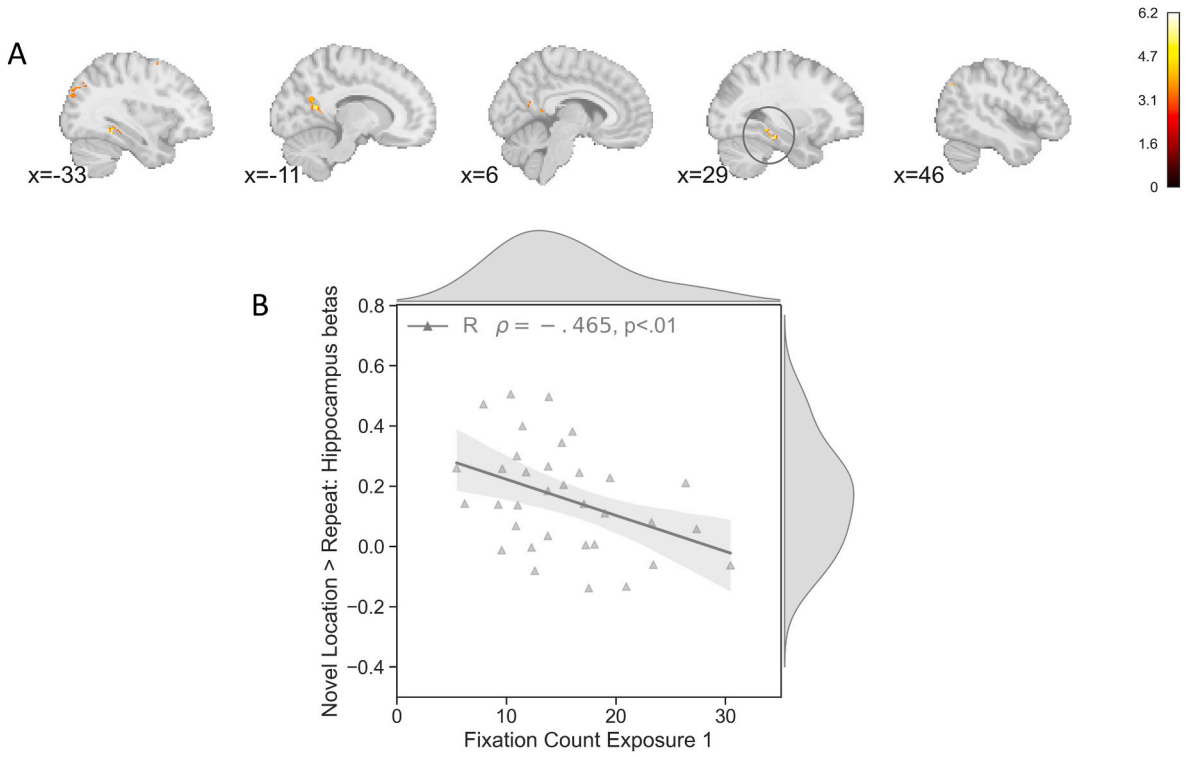

Fig. 4. Repetition suppression unique to locations. (A) New Location > Repeat masked by New Person > Repeat results shown in the volume and thresholded at T = 3 for visualization purposes. (B) The scatterplot with distributions and trendline depicts the only significant association. Partial correlation coefficients are overlaid over the non-residualized data. Spearman's ρ correlations were conducted controlling for total AROMA noise components, gender, and education. Volumes containing the relevant clusters are also shown. 34 participants were included in this analysis. R = right.

Table 2
Repetition effects of future simulation: Location.

Region	Group-level Contrasts					Correlations with Exposure 1–2 Behavior: ρ (p) [CI]				Correlations with Exposure 3 Behavior: ρ (p) [CI]
	x	y	z	k	t	Vividness (exp1)	Change in Vividness (exp2 - exp1)	Fixation Count (exp1)	Change in Fixation Count (exp2 - exp1)	Vividness (exp3)
New Location > Repeat masked by New Person > Repeat										
Hippocampus	30	−31	−19	122	6.25	0.189 (0.344) [-0.21,0.53]	−0.016 (0.937) [-0.39,0.37]	**−0.465 (0.006) [-0.69,-0.15]**	0.187 (0.291) [-0.16,0.49]	0.110 (0.537) [-0.24,0.43]
Posterior cingulate cortex	−11	−58	13	116	6.03	−0.009 (0.964) [-0.39,0.37]	0.139 (0.491) [-0.25,0.49]	−0.371 (0.031) [-0.63,-0.04]	0.075 (0.675) [-0.27,0.40]	−0.053 (0.767) [-0.38,0.29]
Posterior cingulate cortex	18	−51	16	177	5.50	−0.004 (0.983) [-0.38,0.38]	0.271 (0.171) [-0.12,0.59]	−0.253 (0.148) [-0.54,0.09]	0.088 (0.619) [-0.26,0.41]	0.055 (0.758) [-0.29,0.39]
Hippocampus	−33	−44	−11	85	5.53	0.114 (0.571) [-0.28,0.47]	0.109 (0.587) [-0.28,0.47]	−0.413 (0.015) [-0.66,-0.09]	0.169 (0.339) [-0.18,0.48]	0.087 (0.626) [-0.26,0.41]
Posterior parietal cortex	38	−82	35	252	5.29	0.195 (0.330) [-0.20,0.54]	0.244 (0.221) [-0.15,0.57]	−0.329 (0.058) [-0.60,0.01]	0.198 (0.260) [-0.15,0.50]	0.113 (0.524) [-0.23,0.43]
Posterior parietal cortex	−37	−77	33	105	4.26	0.389 (0.045) [0.01,0.67]	0.148 (0.462) [-0.25,0.50]	−0.327 (0.059) [-0.60,0.01]	0.001 (0.994) [-0.34,0.34]	0.297 (0.088) [-0.05,0.58]

Note. The contrast of New Person > Repeat was thresholded at $p < 0.05$ and used as an explicit mask for New Location > Repeat. Group-level results were thresholded at an uncorrected cluster-level $p < 0.001$ and $k = 20$. Partial Spearman ρ correlation coefficients are reported controlling for total AROMA components, gender, and education. Bold denotes significance after Bonferroni correction for 4 tests. Exp1 = Exposure 1; Exp2 = Exposure 2; Exp3 = Exposure 3.

fixations.

4.2. Neural repetition effects of simulation: feature invariance and specificity

A distributed set of brain regions serve as general purpose processors during task repetition, but a distinct set of regions in the default network appear to be involved in repeated episodic processing. A meta-analysis of 137 repetition suppression neuroimaging studies found that suppression-related activity converged in regions within lateral prefrontal cortex and ventral temporal cortex for word, scene, face, and object stimuli (Kim, 2017). Even with an internally oriented simulation paradigm, here we found that the same regions exhibited repetition suppression. While these regions were active across tasks, perhaps stemming from low-level attention toward a cue, suppression-related activity is otherwise highly task specific. Here, repetition suppression

of simulated events was overwhelmingly observed in regions affiliated with the default network. Large suppression-related activations included medial prefrontal cortex, posterior cingulate cortex, hippocampus, and dorsal prefrontal cortex, regions which all fall squarely within the default network (Andrews-Hanna et al., 2014; Buckner and DiNicola, 2019; Raichle et al., 1996). Comparable patterns of activity have been reported in studies of autobiographical memory, counterfactual thinking, and future simulation (Gurguryan et al., 2021; St. Jacques et al., 2017; Szpunar et al., 2014; van Mulukom et al., 2013), suggesting that this pattern is characteristic of episodic processes.

Within the default network, some structures may display feature invariance, playing a role in episodic processing more generally, while others may display feature sensitivity, coming online with the inclusion of certain details. The conjunction between location- and person-specific suppression revealed that large swaths of medial prefrontal cortex, posterior cingulate cortex, dorsal prefrontal cortex, and cerebellum are involved in the simulation of both types of details. The results persisted when controlling for binding-related effects of recombination, ruling out the possibility that shared activity is relegated to new construction demands. Indeed, medial prefrontal and posterior cingulate cortices, in particular serve as hubs in the core default network, displaying high functional connectivity with other regions throughout the network at rest and during different episodic tasks (Andrews-Hanna et al., 2010). Meanwhile subnetworks of the default network show evidence of differential task involvement, which may extend to differential features of recollection and imagination. As in Szpunar et al. (2014), suppression unique to locations was observed in bilateral posterior cingulate cortex, posterior parietal cortex, and hippocampus, regions that all come online during recollection and imagination of spatiotemporal details (Madore et al., 2016; Ritchey and Cooper, 2020). No unique activation was observed for people.

One interpretation of these results is that location features initiate simulation and crystallize sooner than person features to evoke repetition effects. This idea is broadly in line with the scene construction hypothesis, which posits that hippocampal-mediated instantiation of scenes forms the foundation of self-projection into the past, future, and navigational contexts (Hassabis and Maguire, 2007; Maguire and Mullally, 2013). If locations are used to create a scene, constructing new locations may unduly heighten constructive demands (Wiebels et al., 2020). As such, the brain activity observed here may have also been driven by the need to invoke a new context rather than location-related suppression. Future work that staggers cues for different features would help to determine the temporal importance of different features and how they uniquely contribute to subjective vividness (Benoit et al., 2014).

Unlike suppression, neural repetition enhancement may be task-agnostic. In the same meta-analysis of repetition effects, enhancement-related activity was common across different external attention tasks (Kim, 2017). Within the domain of episodic processing, task-general effects of stimulus familiarity have been localized to the parietal memory network (Gilmore et al., 2015; Gilmore et al., 2019a; but see also Gilmore et al., 2019b). This finding suggests that enhancement may happen at a coarser level, less impacted by specific features. Our results showed that activity related to repetition enhancement traversed default, ventral attention, and frontoparietal control networks. The largest clusters were observed across the parietal lobe—namely, inferior parietal cortex, precuneus, posterior parietal cortex, and postcentral gyrus—in a manner consistent with the parietal memory network (Gilmore et al., 2015). The conjunction results demonstrated that enhancement activation was common for people and location features of simulation in bilateral inferior parietal cortex and precuneus. Notably, the inferior parietal clusters spanned angular gyrus, a region involved in a variety of episodic processes including vividness appraisal (Thakral et al., 2017; Zou and Kwok, 2022). As gist-level information appears to drive the subjective experience of vividness (Cooper and Ritchey, 2022), the angular gyrus, a locus of multimodal integration and general event information required for simulation (e.g., Gilboa and Marlatte, 2017; Kuhnke et al., 2023; Tibon et al., 2019), may play a role in enhancing the clarity of a simulation as a whole (i.e., by way of repetition) to evoke the impression of vividness (for related discussion, see Schacter and Thakral, 2024).

4.3. Eye movements and vividness ratings differentially predict neural repetition effects of simulated locations

In pursuit of our second aim, we found that average fixation counts during initial simulation predicted repetition suppression during a third simulation. Specifically, making fewer average fixations during first simulation was related to more overall repetition suppression in bilateral hippocampus, paralleling the negative relationship between fixations and vividness. This finding expands on work implicating the hippocampus in looking behavior during memory retrieval (Hannula et al., 2012; Hannula and Ranganath, 2009; Liu et al., 2017; Ryals et al., 2015; Ryan et al., 2000), and suggests a role in future simulation as well (for a contrasting pattern of results, see Liu et al., 2017).

Hippocampal suppression during future simulation was likely driven by location features. The identical relationship between average fixation count during first simulation and suppression in the hippocampus was found when looking at suppression unique to locations, but only the relationship with right hippocampus survived correction for multiple comparisons. In other words, eye movements may set the imagined scene in a hippocampally-mediated way, although the exact nature of this relationship remains to be determined. While we cannot rule out the involvement of person features, our findings support assertions that eye movements during internally generated thought are not random (Brandt and Stark, 1997) and track spatiotemporal information (Wynn et al., 2019), even when entirely constructed. In fact, participants spontaneously initiate simulation with a spatial context even when cued with non-spatial features (Robin et al., 2016). High scene construction demands, in particular, engage the hippocampus (Palombo et al., 2018). This interpretation would lend further support to the scene construction hypothesis (Hassabis and Maguire, 2007; Maguire and Mullally, 2013), in that the eyes may help location information to materialize in mind prior to person information. An open question is whether fixation-related hippocampal suppression for locations facilitates more vivid simulation. Here, vividness ratings did not predict suppression. It is possible that a more direct relationship would have been observed with visual imagery, which may later give rise to a sense of vividness. As vividness and fixation counts were negatively correlated, the extension to hippocampal suppression is plausible. Alternatively, vividness ratings may be driven by more abstract gist-level information rather than any one feature of simulation (Cooper and Ritchey, 2022).

Finally, average change in vividness between first and second simulations predicted repetition enhancement, and this result too was driven by location features. Specifically, a more positive average change in vividness with repetition was associated with less enhancement in the right posterior parietal cortex, a cluster that emerged as a common region of enhancement for both locations and people. Said differently, enhancement was not unique to locations in posterior parietal cortex, but a relationship to vividness was driven by locations. The opposite relationship with left posterior parietal cortex and people approached significance but did not survive multiple comparisons correction. Both clusters encompassed angular gyrus. While repetition enhancement in angular gyrus may be feature agnostic, as discussed above, relationships to relative vividness may be driven by increasing clarity of separable imagined features. Though location and person vividness ratings during recollection and simulation tend to positively correlate (Thakral et al., 2017), suggesting a reliance on similar episodic content, it is possible that these details are constructed on different time scales. Person details may be more semantically embedded, such that individuals may first access abstract, personal semantic information related to people before constructing more specific episodic details about them. Location details, which are inherently more episodic, may surface more quickly. That

vividness was associated with repetition enhancement and not suppression may indicate that objective measures, such as eye movements, are more directly tied to objective aspects of simulation (i.e., repetition suppression) and subjective measures to subjective aspects of simulation (i.e., enhancement).

4.4. Limitations

Our primary aims were to examine the relationship between eye movements and vividness during future simulation and their associations with neural repetition effects, but several limitations are worth noting. Although participants generated their own lists of locations and people in the present study, intra-individual differences in the familiarity of different cues may have impacted vividness ratings. Indeed, familiarity boosts vividness for locations, people, and other non-spatial features of remembering and imagining (see Robin, 2018 for review). It is also possible that locations are frequented more often and for longer time periods, making them categorically more familiar, and therefore vivid, than people. Because no familiarity or difficulty ratings were collected, we cannot rule out the influence of familiarity in our results. Our examination was also limited by a relatively small number of simulations that were repeated for a third time during MRI scanning, rendering us unable to inspect trial-by-trial variability. The use of averages, both in the neural and behavioral data, may have thus obscured some effects. Finally, MRI scanning did not include eye-tracking and so a direct comparison of fixation counts across conditions isolating different simulation features could not be made. While interpretation of the results as scene construction demands are speculative, future work leveraging MRI-compatible eye-tracking and longer recombination paradigms in the scanner will help to further flesh out the interplay between brain activity, fixations, and vividness of future simulation and its component features.

4.5. Conclusions

The present study leveraged a repetition suppression paradigm with eye-tracking to investigate how eye movements and subjective vividness ratings predict neural repetition effects during future simulation. Eye movements were negatively related to vividness during future simulation, distinct from the relationship often reported for memory. In line with previous reports, repetition suppression was prominent in core regions of the default network, while repetition enhancement was observed in the parietal memory network. Average eye movements from first simulation predicted subsequent repetition suppression in the hippocampus, an effect driven by location features. Our findings lend support to the scene construction hypothesis, underscoring how eye movements may set the scene to initiate simulation.

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Conflict of interest disclosure

The authors declare no conflicts of interest.

Ethics approval statement

The present study was approved by and carried out in accordance with the Institution Review Board at Harvard University.

CRediT authorship contribution statement

Roni Setton: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Jordana S. Wynn:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Daniel L. Schacter:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2024.108852.

References

Addis, D.R., Musicaro, R., Pan, L., Schacter, D.L., 2010. Episodic simulation of past and future events in older adults: evidence from an experimental recombination task. Psychol. Aging 25 (2), 369–376. https://doi.org/10.1037/a0017280.

Addis, D.R., Wong, A.T., Schacter, D.L., 2007. Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. Neuropsychologia 45 (7), 1363–1377.

Althoff, R.R., Cohen, N.J., Hershey, J., Azen, R., Moric, M., Wasserman, S., Ryan, J., Romine, L., Zelinsky, G., Selco, S., Poldrack, R., Wszalek, T., Church, B., 1999. Eye-movement-based memory effect: a Reprocessing effect in face Perception. In: Journal of Experimental Psychology: Learning, Memory, and Cognition, vol. 25. Issue 4.

Andrews-Hanna, J.R., Reidler, J.S., Sepulcre, J., Poulin, R., Buckner, R.L., 2010. Functional-anatomic fractionation of the brain's default network. Neuron 65 (4), 550–562. https://doi.org/10.1016/j.neuron.2010.02.005.

Andrews-Hanna, J.R., Smallwood, J., Spreng, R.N., 2014. The default network and self-generated thought: component processes, dynamic control, and clinical relevance. Ann. N. Y. Acad. Sci. 1316 (1), 29–52. https://doi.org/10.1111/nyas.12360.

Armson, M.J., Diamond, N.B., Levesque, L., Ryan, J.D., Levine, B., 2021. Vividness of recollection is supported by eye movements in individuals with high, but not low trait autobiographical memory. Cognition 206. https://doi.org/10.1016/j.cognition.2020.104487.

Arnold, A.E.G.F., Iaria, G., Ekstrom, A.D., 2016. Mental simulation of routes during navigation involves adaptive temporal compression. Cognition 157, 14–23. https://doi.org/10.1016/j.cognition.2016.08.009.

Avants, B.B., Epstein, C.L., Grossman, M., Gee, J.C., 2008. Symmetric diffeomorphic image registration with cross-correlation: evaluating automated labeling of elderly and neurodegenerative brain. Med. Image Anal. 12 (1), 26–41. https://doi.org/10.1016/j.media.2007.06.004.

Aydin, C., 2018. The differential contributions of visual imagery constructs on autobiographical thinking. Memory 26 (2), 189–200. https://doi.org/10.1080/09658211.2017.1340483.

Beaty, R.E., Thakral, P.P., Madore, K.P., Benedek, M., Schacter, D.L., 2018. Core network contributions to remembering the past, imagining the future, and thinking creatively. J. Cognit. Neurosci. 30 (12), 1939–1951. https://doi.org/10.1162/jocn_a_01327.

Benoit, R.G., Szpunar, K.K., Schacter, D.L., 2014. Ventromedial prefrontal cortex supports affective future simulation by integrating distributed knowledge. Proc. Natl. Acad. Sci. U.S.A. 111 (46), 16550–16555. https://doi.org/10.1073/pnas.1419274111.

Brandt, S.A., Stark, L.W., 1997. Spontaneous eye movements during visual imagery reflect the content of the visual scene. J. Cognit. Neurosci. 9 (1), 27–38. http://direct.mit.edu/jocn/article-pdf/9/1/27/1932720/jocn.1997.9.1.27.pdf?casa_token=bW1_BW4vMqUAAAAA:LQvBrZ1B51d7GUSMhjAwU4jE2xQafnu8mau56AgOTJi-MtleOvO_7VoibvNnSVl1Hg.

Buckner, R.L., DiNicola, L.M., 2019. The brain's default network: updated anatomy, physiology and evolving insights. Nat. Rev. Neurosci. 20 (Issue 10), 593–608. https://doi.org/10.1038/s41583-019-0212-7. Nature Research.

Chiquet, S., Martarelli, C.S., Mast, F.W., 2022. Imagery-related eye movements in 3D space depend on individual differences in visual object imagery. Sci. Rep. 12 (1) https://doi.org/10.1038/s41598-022-18080-4.

Clark, I.A., Maguire, E.A., 2020. Do questionnaires reflect their purported cognitive functions? Cognition 195. https://doi.org/10.1101/583690.

Conti, F., Irish, M., 2021. Harnessing visual imagery and oculomotor behaviour to understand prospection. In: Trends in Cognitive Sciences, vol. 25. Elsevier Ltd, pp. 272–283. https://doi.org/10.1016/j.tics.2021.01.009. Issue 4.

Cooper, R.A., Ritchey, M., 2022. Patterns of episodic content and specificity predicting subjective memory vividness. Mem. Cognit. 50 (8), 1629–1643. https://doi.org/10.3758/s13421-022-01291-5.

Cox, R.W., Hyde, J.S., 1997. Software toolsfor analysis and visualization of FMRI data. NMR Biomed. 10 (4–5), 171–178.

Dale, A.M., Fischl, B., Sereno, M.I., 1999. Cortical surface-based analysis I. Segmentation and surface reconstruction. http://www.idealibrary.com.

D'Argembeau, A., Mathy, A., 2011. Tracking the construction of episodic future thoughts. J. Exp. Psychol. Gen. 140 (2), 258–271. https://doi.org/10.1037/a0022581.

D'Argembeau, A., Van Der Linden, M., 2004. Phenomenal characteristics associated with projecting oneself back into the past and forward into the future: influence of

valence and temporal distance. Conscious. Cognit. 13 (4), 844–858. https://doi.org/10.1016/j.concog.2004.07.007.
D'Argembeau, A., Van der Linden, M., 2006. Individual differences in the phenomenology of mental time travel: the effect of vivid visual imagery and emotion regulation strategies. Conscious. Cognit. 15 (2), 342–350. https://doi.org/10.1016/j.concog.2005.09.001.
De Brigard, F., Addis, D.R., Ford, J.H., Schacter, D.L., Giovanello, K.S., 2013. Remembering what could have happened: neural correlates of episodic counterfactual thinking. Neuropsychologia 51 (12), 2401–2414. https://doi.org/10.1016/j.neuropsychologia.2013.01.015.
de Vito, S., Buonocore, A., Bonnefon, J.F., Della Sala, S., 2015a. Eye movements disrupt episodic future thinking. Memory 23 (6), 796–805. https://doi.org/10.1080/09658211.2014.927888.
de Vito, S., Buonocore, A., Bonnefon, J.F., Della Sala, S., 2015b. Eye movements disrupt episodic future thinking. Memory 23 (6), 796–805. https://doi.org/10.1080/09658211.2014.927888.
Devitt, A.L., Thakral, P.P., Szpunar, K., Addis, D.R., Schacter, D.L., 2020. Age-related changes in repetition suppression of neural activity during emotional future simulation. Neurobiol. Aging 94, 287–297. https://doi.org/10.1016/j.neurobiolaging.2020.06.016.
El Haj, M., Lenoble, Q., 2018. Eying the future: eye movement in past and future thinking. Cortex 105, 97–103. https://doi.org/10.1016/j.cortex.2017.05.024.
Ferreira, F., Apel, J., Henderson, J.M., 2008. Taking a new look at looking at nothing. Trends Cognit. Sci. 12 (11), 405–410. https://doi.org/10.1016/j.tics.2008.07.007.
Fivush, R., Grysman, A., 2023. Accuracy and reconstruction in autobiographical memory: (Re)consolidating neuroscience and sociocultural developmental approaches. In: Wiley Interdisciplinary Reviews: Cognitive Science, vol. 14. John Wiley and Sons Inc. https://doi.org/10.1002/wcs.1620. Issue 3.
Folville, A., Simons, J.S., D'Argembeau, A., Bastin, C., 2022. I remember it like it was yesterday: age-related differences in the subjective experience of remembering. In: Psychonomic Bulletin and Review, vol. 29. Springer, pp. 1223–1245. https://doi.org/10.3758/s13423-021-02048-y. Issue 4.
Gaesser, B., Fowler, Z., 2020. Episodic simulation of prosocial interaction: investigating the roles of memory and imagination in facilitating a willingness to help others. Psychology of Consciousness: Theory Research, and Practice 7 (4), 376–387. https://doi.org/10.1037/cns0000232.
Gamboz, N., Brandimonte, M.A., De Vito, S., 2010. The role of past in the simulation of autobiographical future episodes. Exp. Psychol. 57 (6), 419–428. https://doi.org/10.1027/1618-3169/a000052.
Gautier, J., Sastoque, L.G., Chapelet, G., Boutoleau-Bretonnière, C., El Haj, M., 2022. "Look at the future": maintained fixation impoverishes future thinking. Conscious. Cognit. 105 https://doi.org/10.1016/j.concog.2022.103398.
Gilboa, A., Marlatte, H., 2017. Neurobiology of schemas and schema-mediated memory. Trends Cognit. Sci. 21 (8), 618–631. https://doi.org/10.1016/j.tics.2017.04.013.
Gilmore, A.W., Kalinowski, S.E., Milleville, S.C., Gotts, S.J., Martin, A., 2019a. Identifying task-general effects of stimulus familiarity in the parietal memory network. Neuropsychologia 124, 31–43. https://doi.org/10.1016/j.neuropsychologia.2018.12.023.
Gilmore, A.W., Nelson, S.M., Laumann, T.O., Gordon, E.M., Berg, J.J., Greene, D.J., Gratton, C., Nguyen, A.L., Ortega, M., Hoyt, C.R., Coalson, R.S., Schlaggar, B.L., Petersen, S.E., Dosenbach, N.U.F., McDermott, K.B., 2019b. High-fidelity mapping of repetition-related changes in the parietal memory network. Neuroimage 199, 427–439. https://doi.org/10.1016/j.neuroimage.2019.06.011.
Gilmore, A.W., Nelson, S.M., McDermott, K.B., 2015. A parietal memory network revealed by multiple MRI methods. In: Trends in Cognitive Sciences, vol. 19. Elsevier Ltd, pp. 534–543. https://doi.org/10.1016/j.tics.2015.07.004. Issue 9.
Greve, D.N., Fischl, B., 2009. Accurate and robust brain image alignment using boundary-based registration. Neuroimage 48 (1), 63–72. https://doi.org/10.1016/j.neuroimage.2009.06.060.
Grysman, A., Prabhakar, J., Anglin, S.M., Hudson, J.A., 2013. The time travelling self: comparing self and other in narratives of past and future events. Conscious. Cognit. 22 (3), 742–755. https://doi.org/10.1016/j.concog.2013.04.010.
Gurguryan, L., Rioux, M., Sheldon, S., 2021. Reduced anterior hippocampal and ventromedial prefrontal activity when repeatedly retrieving autobiographical memories. Hippocampus 31 (8), 869–880. https://doi.org/10.1002/hipo.23330.
Hannula, D.E., Baym, C.L., Warren, D.E., Cohen, N.J., 2012. The eyes know: eye movements as a veridical index of memory. Psychol. Sci. 23 (3), 278–287. https://doi.org/10.1177/0956797611429799.
Hannula, D.E., Ranganath, C., 2009. The eyes have it: hippocampal activity predicts expression of memory in eye movements. Neuron 63 (5), 592–599. https://doi.org/10.1016/j.neuron.2009.08.025.
Hassabis, D., Maguire, E.A., 2007. Deconstructing episodic memory with construction. Trends Cognit. Sci. 11 (7), 299–306. https://doi.org/10.1016/j.tics.2007.05.001.
Jenkinson, M., Bannister, P., Brady, M., Smith, S., 2002. Improved optimization for the robust and accurate linear registration and motion correction of brain images. Neuroimage 17 (2), 825–841. https://doi.org/10.1006/nimg.2002.1132.
Jeunehomme, O., D'Argembeau, A., 2017. Accessibility and characteristics of memories of the future. Memory 25 (5), 666–676. https://doi.org/10.1080/09658211.2016.1205096.
Johansson, R., Holsanova, J., Homqvist, K., 2011. The dispersion of eye movements during visual imagery is related to individual differences in spatial imagery ability. Proceedings of the Annual Meeting of the Cognitive Science Society 33, 1200–1205.
Johansson, R., Johansson, M., 2014. Look here, eye movements play a functional role in memory retrieval. Psychol. Sci. 25 (1), 236–242. https://doi.org/10.1177/0956797613498260.
Johansson, R., Nyström, M., Dewhurst, R., Johansson, M., 2022. Eye-movement replay supports episodic remembering. Proc. Biol. Sci. 289 https://doi.org/10.1098/rspb.2022.0964, 1977.
Kim, H., 2017. Brain regions that show repetition suppression and enhancement: a meta-analysis of 137 neuroimaging experiments. Hum. Brain Mapp. 38 (4), 1894–1913. https://doi.org/10.1002/hbm.23492.
Klein, A., Ghosh, S.S., Bao, F.S., Giard, J., Häme, Y., Stavsky, E., Lee, N., Rossa, B., Reuter, M., Chaibub Neto, E., Keshavan, A., 2017. Mindboggling morphometry of human brains. PLoS Comput. Biol. 13 (2) https://doi.org/10.1371/journal.pcbi.1005350.
Kuhnke, P., Chapman, C.A., Cheung, V.K.M., Turker, S., Graessner, A., Martin, S., Williams, K.A., Hartwigsen, G., 2023. The role of the angular gyrus in semantic cognition: a synthesis of five functional neuroimaging studies. Brain Struct. Funct. 228 (1), 273–291. https://doi.org/10.1007/s00429-022-02493-y.
Laeng, B., Teodorescu, D.-S., 2002. Eye scanpaths during visual imagery reenact those of perception of the same visual scene Cognitive Science 26, 207–231, 2002. http://www.elsevier.com/locate/cogsci.
Liu, Z.X., Shen, K., Olsen, R.K., Ryan, J.D., 2017. Visual sampling predicts hippocampal activity. J. Neurosci. 37 (3), 599–609. https://doi.org/10.1523/JNEUROSCI.2610-16.2016.
Lockrow, A.W., Setton, R., Spreng, K.A.P., Sheldon, S., Turner, G.R., Spreng, R.N., 2023. Taking stock of the past: a psychometric evaluation of the Autobiographical Interview. Behav. Res. Methods. https://doi.org/10.3758/s13428-023-02080-x.
Madore, K.P., Szpunar, K.K., Addis, D.R., Schacter, D.L., 2016. Episodic specificity induction impacts activity in a core brain network during construction of imagined future experiences. Proc. Natl. Acad. Sci. U.S.A. 113 (38), 10696–10701. https://doi.org/10.1073/pnas.1612278113.
Madore, K.P., Thakral, P.P., Beaty, R.E., Addis, D.R., Schacter, D.L., 2019. Neural mechanisms of episodic retrieval support divergent creative thinking. Cerebr. Cortex 29 (1), 150–166. https://doi.org/10.1093/cercor/bhx312.
Maguire, E.A., Mullally, S.L., 2013. The hippocampus: a manifesto for change. J. Exp. Psychol. Gen. 142 (4), 1180–1189. https://doi.org/10.1037/a0033650.
Morton, C., MacLeod, A.K., 2023. Vividness of imagery and affective response to episodic memories and episodic future thoughts: a systematic review and meta-analysis. In: Memory. Routledge. https://doi.org/10.1080/09658211.2023.2224609.
Olsen, R.K., Chiew, M., Buchsbaum, B.R., Ryan, J.D., 2014. The relationship between delay period eye movements and visuospatial memory. J. Vis. 14 (1) https://doi.org/10.1167/14.1.8.
Palombo, D.J., Hayes, S.M., Peterson, K.M., Keane, M.M., Verfaellie, M., 2018. Medial temporal lobe contributions to episodic future thinking: scene construction or future projection? Cerebr. Cortex 28 (2), 447–458. https://doi.org/10.1093/cercor/bhw381.
Patriat, R., Reynolds, R.C., Birn, R.M., 2017. An improved model of motion-related signal changes in fMRI. Neuroimage 144, 74–82. https://doi.org/10.1016/j.neuroimage.2016.08.051.
Power, J.D., Mitra, A., Laumann, T.O., Snyder, A.Z., Schlaggar, B.L., Petersen, S.E., 2014. Methods to detect, characterize, and remove motion artifact in resting state fMRI. Neuroimage 84, 320–341. https://doi.org/10.1016/j.neuroimage.2013.08.048.
Pruim, R.H.R., Mennes, M., van Rooij, D., Llera, A., Buitelaar, J.K., Beckmann, C.F., 2015. ICA-AROMA: a robust ICA-based strategy for removing motion artifacts from fMRI data. Neuroimage 112, 267–277. https://doi.org/10.1016/j.neuroimage.2015.02.064.
Raichle, M.E., Macleod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 1996. A default mode of brain function. In: National Academy of Sciences. www.pnas.org.
Rasmussen, A.S., Berntsen, D., 2013. The reality of the past versus the ideality of the future: emotional valence and functional differences between past and future mental time travel. Mem. Cognit. 41 (2), 187–200. https://doi.org/10.3758/s13421-012-0260-y.
Ritchey, M., Cooper, R.A., 2020. Deconstructing the posterior medial episodic network. In: Trends in Cognitive Sciences, vol. 24. Elsevier Ltd, pp. 451–465. https://doi.org/10.1016/j.tics.2020.03.006. Issue 6.
Robin, J., 2018. Spatial scaffold effects in event memory and imagination. In: Wiley Interdisciplinary Reviews: Cognitive Science, vol. 9. Wiley-Blackwell. https://doi.org/10.1002/wcs.1462. Issue 4.
Robin, J., Olsen, R.K., 2019. Scenes facilitate associative memory and integration. Learn. Mem. 26 (7), 252–261. https://doi.org/10.1101/lm.049486.119.
Robin, J., Wynn, J., Moscovitch, M., 2016. The spatial scaffold: the effects of spatial context on memory for events. J. Exp. Psychol. Learn. Mem. Cognit. 42 (2), 308–315. https://doi.org/10.1037/xlm0000167.supp.
Ryals, A.J., Wang, J.X., Polnaszek, K.L., Voss, J.L., 2015. Hippocampal contribution to implicit configuration memory expressed via eye movements during scene exploration. Hippocampus 25 (9), 1028–1041. https://doi.org/10.1002/hipo.22425.
Ryan, J.D., Althoff, R.R., Whitlow, S., Cohen, N.J., 2000. Amnesia is a deficit in relational memory. Psychol. Sci. 11 (6).
Ryan, J.D., Hannula, D.E., Cohen, N.J., 2007. The obligatory effects of memory on eye movements. Memory 15 (5), 508–525. https://doi.org/10.1080/09658210701391022.
Ryan, J.D., Shen, K., Liu, Z.X., 2020. The intersection between the oculomotor and hippocampal memory systems: empirical developments and clinical implications. In: Annals of the New York Academy of Sciences, vol. 1464. Blackwell Publishing Inc, pp. 115–141. https://doi.org/10.1111/nyas.14256. Issue 1.
Satterthwaite, T.D., Elliott, M.A., Gerraty, R.T., Ruparel, K., Loughead, J., Calkins, M.E., Eickhoff, S.B., Hakonarson, H., Gur, R.C., Gur, R.E., Wolf, D.H., 2013. An improved framework for confound regression and filtering for control of motion artifact in the

preprocessing of resting-state functional connectivity data. Neuroimage 64 (1), 240–256. https://doi.org/10.1016/j.neuroimage.2012.08.052.
Schacter, D.L., Addis, D.R., 2007. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. Phil. Trans. Biol. Sci. 362 (1481), 773–786. https://doi.org/10.1098/rstb.2007.2087.
Schacter, D.L., Addis, D.R., 2020. Memory and imagination: perspectives on constructive episodic simulation. In: The Cambridge Handbook of the Imagination. Cambridge University Press, pp. 111–131. https://doi.org/10.1017/9781108580298.008.
Schacter, D.L., Addis, D.R., Hassabis, D., Martin, V.C., Nathan, R., Szpunar, K.K., 2012. The future of memory: remembering, imagining, and the brain. Neuron 76 (4), 1–32. https://doi.org/10.1016/j.neuron.2012.11.001. The.
Schacter, D.L., Benoit, R.G., Szpunar, K.K., 2017. Episodic future thinking: mechanisms and functions. In: Current Opinion in Behavioral Sciences, vol. 17. Elsevier Ltd, pp. 41–50. https://doi.org/10.1016/j.cobeha.2017.06.002.
Schacter, D.L., Thakral, P.P., 2024. Constructive memory and conscious experience. J. Cognit. Neurosci.
Sheldon, S., Cool, K., El-Asmar, N., 2019. The processes involved in mentally constructing event- and scene-based autobiographical representations. J. Cognit. Psychol. 31 (3), 261–275. https://doi.org/10.1080/20445911.2019.1614004.
Shen, K., Bezgin, G., Selvam, R., McIntosh, A.R., Ryan, J.D., 2016. An anatomical interface between memory and oculomotor systems. J. Cognit. Neurosci. 28 (11), 1772–1783. https://doi.org/10.1162/jocn_a_01007.
Smith, C.N., Hopkins, R.O., Squire, L.R., 2006. Experience-dependent eye movements, awareness, and hippocampus-dependent memory. J. Neurosci. 26 (44), 11304–11312. https://doi.org/10.1523/JNEUROSCI.3071-06.2006.
St Jacques, P.L., Szpunar, K.K., Schacter, D.L., 2017. Shifting visual perspective during retrieval shapes autobiographical memories. Neuroimage 148, 103–114. https://doi.org/10.1016/j.neuroimage.2016.12.028.
Szpunar, K.K., Jacques, P.L.S., Robbins, C.A., Wig, G.S., Schacter, D.L., 2014. Repetition-related reductions in neural activity reveal component processes of mental simulation. Soc. Cognit. Affect Neurosci. 9 (5), 712–722. https://doi.org/10.1093/scan/nst035.
Thakral, P.P., Madore, K.P., Schacter, D.L., 2017. A role for the left angular gyrus in episodic simulation and memory. J. Neurosci. 37 (34), 8142–8149. https://doi.org/10.1523/jneurosci.1319-17.2017.
Tibon, R., Fuhrmann, D., Levy, D.A., Simons, J.S., Henson, R.N., 2019. Multimodal integration and vividness in the angular gyrus during episodic encoding and retrieval. J. Neurosci. 39 (22), 4365–4374. https://doi.org/10.1523/JNEUROSCI.2102-18.2018.
Tustison, N.J., Avants, B.B., Cook, P.A., Zheng, Y., Egan, A., Yushkevich, P.A., Gee, J.C., 2010. N4ITK: improved N3 bias correction. IEEE Trans. Med. Imag. 29 (6), 1310–1320. https://doi.org/10.1109/TMI.2010.2046908.
van Genugten, R.D.I., Beaty, R.E., Madore, K.P., Schacter, D.L., 2022. Does episodic retrieval contribute to creative writing? An exploratory study. Creativ. Res. J. 34 (2), 145–158. https://doi.org/10.1080/10400419.2021.1976451.
van Mulukom, V., Schacter, D.L., Corballis, M.C., Addis, D.R., 2013. Re-imagining the future: repetition decreases hippocampal involvement in future simulation. PLoS One 8 (7). https://doi.org/10.1371/journal.pone.0069596.
Wamsley, E.J., 2022. Constructive episodic simulation in dreams. PLoS One 17 (3 March). https://doi.org/10.1371/journal.pone.0264574.
Wiebels, K., Addis, D.R., Moreau, D., van Mulukom, V., Onderdijk, K.E., Roberts, R.P., 2020. Relational processing demands and the role of spatial context in the construction of episodic simulations. J. Exp. Psychol. Learn. Mem. Cogn. https://doi.org/10.1037/xlm0000831.
Wynn, J.S., Shen, K., Ryan, J.D., 2019. Eye movements actively reinstate spatiotemporal mnemonic content. Vision 3 (2). https://doi.org/10.3390/vision3020021.
Wynn, J.S., Van Genugten, R.D.I., Sheldon, S., Schacter, D.L., 2022. Schema-related eye movements support episodic simulation. Conscious. Cognit. 100 https://doi.org/10.1016/j.concog.2022.103302.
Zaman, A., Setton, R., Catmur, C., Russell, C., 2023. What is Autonoetic Consciousness? Examining what underlies subjective experience in memory and future thinking. https://doi.org/10.31234/osf.io/qp6hj.
Zhang, Y., Brady, M., Smith, S., 2001. Segmentation of brain MR images through a hidden markov random field model and the expectation-maximization algorithm. IEEE Trans. Med. Imag. 20 (Issue 1).
Zou, F., Kwok, S.C., 2022. Distinct generation of subjective vividness and confidence during naturalistic memory retrieval in angular gyrus. J. Cognit. Neurosci. 34 (6), 988–1000. https://doi.org/10.1162/jocn_a_01838.