Same Same, But Different: Brain Areas Underlying the Learning from Repetitive Episodic Prediction Errors

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ABSTRACT

■ Prediction errors (PEs) function as learning signals. It is yet unclear how varying compared to repetitive PEs affect episodic memory in brain and behavior. The current study investigated cerebral and behavioral effects of experiencing either multiple alternative versions ("varying") or one single alternative version ("repetitive") of a previously encoded episode. Participants encoded a set of episodes ("originals") by watching videos showing toy stories. During scanning, participants either experienced originals, one single or multiple alternative versions of the previously encoded episodes. Participants' memory performance was tested through recall of original objects. Varying and repetitive PEs revealed typical brain responses to the detection of mismatching information including inferior frontal and posterior parietal regions, as well as hippocampus, which is further linked to memory reactivation, and the amygdala, known for modulating memory consolidation. Furthermore, experiencing varying and repetitive PEs triggered distinct brain areas as revealed by direct contrast. Among others, experiencing varying versions triggered activity in the caudate, a region that has been associated with PEs. In contrast, repetitive PEs activated brain areas that resembled more those for retrieval of originally encoded episodes. Thus, ACC and posterior cingulate cortex activation seemed to serve both reactivating old and integrating new but similar information in episodic memory. Consistent with neural findings, participants recalled original objects less accurately when only presented with the same, but not varying, PE during fMRI. The current findings suggest that repeated PEs interact more strongly with a recalled original episodic memory than varying PEs. ■

INTRODUCTION

Retrieval can put a memory into a vulnerable state that allows for the integration of new information. This process opens a window to updated memories and returning them into a stable state over time (Lee, Nader, & Schiller, 2017). A driving factor of this remarkable plasticity of memory is probably prediction errors (PEs), that is, the difference between our expectations and our actual experience (Sinclair & Barense, 2019; Fernández, Boccia, & Pedreira, 2016; Exton-McGuinness, Lee, & Reichelt, 2015; Kim, Lewis-Peacock, Norman, & Turk-Browne, 2014). These PEs allow the brain to update internal models of the world with new information to maintain accurate and functional predictions (Friston, 2002). Recurrent exposure to different PEs results in repeatedly violating adapted predictions as ever-changing information occur, whereas repeated exposure to the same PE results in greater familiarity with alternative information over time, successfully updating expectations and recall of PE-related input (Frank & Kafkas, 2021). Whereas reconsolidating memories is a slow process over an extended period, adapting predictions and respective internal models of the world appears to be a rather dynamic, real-time process (Friston, 2002). In this way, PEs may fuel two types of processes: (i) adapting predictions during expectation violation and (ii) updating stored memories in the long run. As our memory is constantly destabilized and restabilized, it is necessary to understand how the brain processes different types of competing information to maintain long-term valid predictions in the face of persistent change (Lee, 2009).

In the current study, we aimed to separate the neural signatures of episodic prediction violation from those of episodic prediction adaptation. To this end, we manipulated episodic cues to induce either varying PEs, that is, multiple changes over time, or one single, repetitive PE. The basic idea was that the former condition should produce multiple predictions for an episode competing during reexperience of violated episodes, whereas the latter allows updated mnemonic predictions and, thus, facilitates subsequent memory modification in the long run (Brodt et al., 2016; Exton-McGuinness et al., 2015; Schiffer, Ahlheim, Ulrichs, & Schubotz, 2013).

We adapted an episode-modification paradigm from our previous studies (Jainta et al., 2022). Participants encoded episodes from videos of short action stories in the laboratory. The subsequent day, they returned to an fMRI session in which we presented both the original videos and slightly modified versions of the first day's episodes. These modifications were generated by substituting one of the objects shown in the video repeatedly with the same (repetitive [*rep*]) or with different objects over time (varying [*var*]). On Day 3, we tested memory performance by assessing correct recall rates of originally encoded objects.

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Regarding learning through PEs in episodic memory, the hippocampus (HC) has been suggested to be a core structure (Horner & Doeller, 2017; Stachenfeld, Botvinick, & Gershman, 2017) that processes mnemonic PEs (Bein, Duncan, & Davachi, 2020; Long, Lee, & Kuhl, 2016; Schiffer, Ahlheim, Wurm, & Schubotz, 2012), especially when the experience is in some way related to expectation and not entirely novel (Chen, Olsen, Preston, Glover, & Wagner, 2011; Duncan, Curtis, & Davachi, 2009; Kumaran & Maguire, 2007). Thus, HC is more active for competing than for novel events. Therefore, we expected HC would be activated by both repeated experience of repetitive and of varying alternative versions. In addition, we expected a stronger effect for hippocampal activity during experience of multiple alternative versions compared to repeated presentation of a single alternative (*var* vs. *rep*) as the PE should decrease by repetitions for single alternatives.

Beyond HC, we expected episodic mismatches to come with increased activity in the inferior frontal sulcus (IFS; including Brodmann's area [BA] 44 and BA 45), the parahippocampal gyrus, the fusiform gyrus, intraparietal sulcus (IPS), and occipitotemporal cortex (Siestrup et al., 2022, 2023). Because the *rep* condition was designed to facilitate learning from PE whereas varying PE would lead to a prolonged phase of uncertainty, repetitive and varying PEs were expected to differently modulate activity in this neocortical network too. We expected that same network to be enhanced for varying (vs. repetitive) PEs because of the repeatedly refreshed PE. In contrast, as we expected that the PE-related information of a single alternative version would lead to updating predictions regarding the repeatedly presented alternative, contrasting repetitive with varying PEs was expected to reveal brain regions that are typical for successful episodic retrieval, including the medial frontal cortex and precuneus (PCUN)/posterior cingulate cortex (pCC; Rugg & Vilberg, 2013; Schiffer et al., 2013). Notably, these cortical midline regions and a further one in the mid-cingulate cortex (mCC) were also more active for viewing originally encoded as compared to novel stories in several of our previous studies (Siestrup & Schubotz, 2023; Jainta et al., 2022). Moreover, medial frontal cortex, mCC, and pCC were found to increase in activity for repeated presentations of modified stories in another study (Siestrup et al., 2022), but only when resulting in false memories in a post-fMRI survey. Therefore, these cortical midline areas were expected to become engaged by repetitive (vs. varying) presentations of a specifically modified story in case this manipulation would lead to changes in episodic memory.

In our previous studies, we had found that recurrent experience of the same expectation violation of originally encoded episodes led to higher acceptance for modified versions (false alarms) and slightly lower acceptance of originals (misses; Jainta et al., 2022; Siestrup et al., 2022). We expected to see a replication of the effect that recall of originals is less accurate after being presented with a modified compared to a previously encoded version. However, the extent to which competing alternative episodes impair later retrieval of existing memories has been proposed to depend on two factors: (i) the coexistence of multiple alternatives for a single episode (Lee et al., 2017) and (ii) the memory strength of an alternative (Fernández et al., 2016). Hence, we could expect both varying and repetitive PEs to lead to impairments of memory performance.

METHODS

Participants

Forty-two right-handed participants participated in one encoding session, one fMRI scan, and one post-fMRI memory test session. Five participants were excluded from the analyses: four because of excessive body movement during scanning and one who did not complete the fMRI session. Therefore, 37 participants (23 women, 14 men) were included in the statistical analysis (age: $M = 22.22$ years, $SD = 2.26$ years, range = 18–28 years). In our previous work, this sample size yielded stable results by using an equivalent number of participants as well as experimental and statistical designs (Siestrup, Jainta, Cheng, & Schubotz, 2023; Jainta et al., 2022). Within the final data set, no person reported a history of neurological or psychiatric disorders or substance abuse. With regard to scores in the Edinburgh Handedness Inventory (Oldfield, 1971), all participants were right-handed, although scores varied from +60 to +100. The study protocol was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee of the University of Münster. Each participant gave written informed consent and received either course credits or reimbursement for their participation.

Stimuli

The stimulus material consisted of 96 videos (mean duration = 12.75 sec, $SD = 1.81$ sec, range = 8.64–16.08 sec) containing abstract action stories played with PLAYMOBIL toys. Videos showed only hands and forearms of an actress and the toys, including characters, animals, man-made objects, vehicles, plants, and tools. These action stories were composed of six to nine action steps ($M = 7.68$, $SD = 0.7$) and four to seven separable toys ($M = 5.77$, $SD = 0.79$). The final set of stories was based on two previous studies of our laboratory (Siestrup et al., 2023; Jainta et al., 2022).

Within the total set of videos, 90 videos consisted of 18 stories each existing in five different versions, that is, one original and four modified versions (for an example, please see Figure 1A). Modified versions could involve a change of the color or shape of an object, or an object could be replaced by a new object. In each video, only two objects of the original story were manipulated for alternative versions. Modifications never occurred during

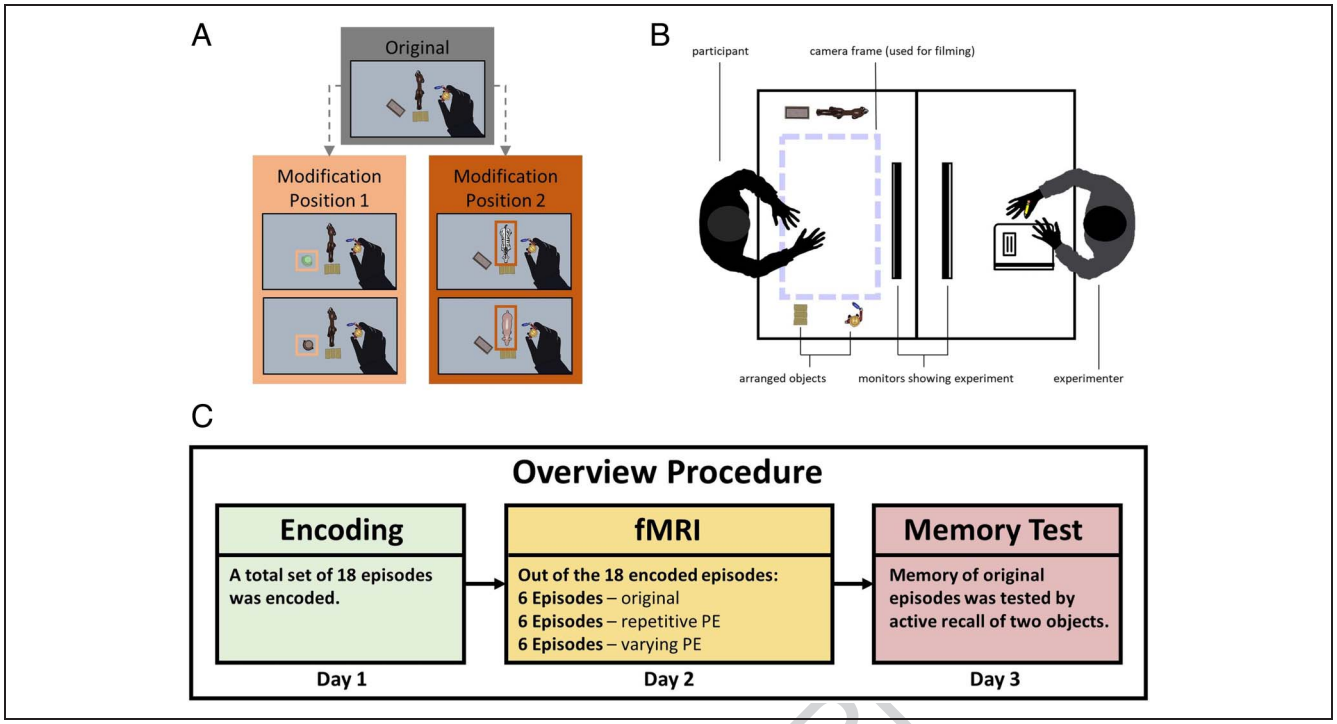

Figure 1. (A) Sample video frames for the original and four different modified versions for the episode "brushing the horse." In Position 1 (left column), the brown horse trough was replaced by either a green (top) or brown (bottom) bucket. In Position 2 (right column), the brown horse was replaced by either a black/white striped zebra (top) or a pink pig (bottom). Each violation only contained one replacement, meaning that at either Position 1 or Position 2, one object was replaced. (B) Original episodes were encoded at the same setup where the episodic videos were initially filmed. During the encoding session, videos were presented simultaneously to the participant and experimenter. The experimenter listened carefully to the participant's description and took notes on attempts and mistakes made. Objects used in each video were placed around the camera frame (dashed lines) to facilitate understanding of the episode and visual recognition of object features. The schematic overview was adapted from the study of Jainta and colleagues (2022). (C) Overview of the experimental procedure. All participants completed encoding (Day 1), cued retrieval during fMRI (Day 2), and a post-fMRI memory test (Day 3). On Day 1, participants encoded 18 episodes. On Day 2, six of the encoded episodes were presented in their original; six, in a single alternative version (repetitive); and six, in multiple alternative versions. For the memory test on Day 3, only the first two action steps of each episode were presented to trigger memory retrieval. Object recall was tested for the original object, encoded on Day 1.

the first or last two action steps of a story to ensure reactivation of the original story during the experiment. Four further videos served as novel videos (hereafter referred to as "novels" or *nov*) and were presented for the first time during the fMRI session. The remaining two videos were only used for practice in the training and memory test session and did not appear in the scanning session.

Videos were filmed using a digital single-lens reflex camera (Nikon D5300). The camera was mounted above the center of the table and faced straight down. Although we presented half of the videos from a first-person perspective and half from a third-person perspective, this factor was irrelevant for the present study. Therefore, to balance perspective effects, video perspective remained the same throughout all sessions, and it was counterbalanced for all conditions and aggregated for all behavioral and functional analyses. During filming, all toy-based actions were performed on a matte white paper background by an actress wearing a black pullover and black rubber gloves. Videos had a resolution of 1920 × 1080 pixels and 25 frames per second. All videos were edited using Adobe Premiere Pro CC (Version 12.1.2, Adobe Systems Software) to ensure that each video started with seven frames showing only a white background and seven frames showing the final scene. Throughout the study, videos were presented using the stimulus presentation software Presentation (Version 20.3 02.25.19, NeuroBehavioral Systems) at a visual angle of approximately 7.3° × 13°.

Procedure

Encoding

On the first of three consecutive days, participants took part in a "training session" (approximately 1.5 hr), which we refer to as encoding session and took place at the same setup we used for filming (for a schematic overview, see Figure 1B). During encoding, participants were instructed to watch a set of short videos played with PLAYMOBIL toys and describe them after watching.

To ensure that participants understood the task and description rules correctly, the session started with two practice trials. After the first practice video was presented and an ideal description example was given by the

experimenter, the second practice video was presented, and the participant had to give a detailed description of that practice story.

Subsequently, participants watched each video five times during encoding before verbally describing the respective action story. The number of video presentations needed to correctly understand and describe each story was based on our previous studies (Siestrup et al., 2023; Jainta et al., 2022). After half of the videos, we included a short break to let participants rest for a few minutes. For description, participants had to follow specific rules to ensure correct understanding and interpretation of the stories. To facilitate interpretation and object descriptions, toys for each story were placed on the table, but not interacted with by participants during encoding. Each action step had to be described in the correct order and by describing each object that was placed in the scene or manipulated during the action step. To describe an object correctly, participants had to tell the experimenter the correct name and main color of an object (e.g., "red table"). As characters usually include many different details, we instructed participants to name the color of the hair and the figure's role in each scene. In case characters wore a hat, the hat and its color had to be given instead of the hair color (e.g., "the pirate with a black hat"). All objects characters carried in their hands had do be described additionally (e.g., "the pirate with a black hat and a silver pistol in their hand"). In case participants made a mistake during description, the experimenter interrupted them immediately, pointed out the error, and asked them to restart. As the experimenter corrected them verbally, participants started the new description attempt without rewatching the video. The number of attempts to describe a story was not limited. In this way, we ensured participants' attention and understanding of each story. On average, participants needed 1.44 attempts per story and made 0.69 mistakes per story.

fMRI Session

The fMRI took place 1 day after the encoding session, and the experiment lasted approximately 52 min. During scanning, participants were presented with either original or modified videos reminiscent of the previously encoded episodes. Six episodes were only presented in the original version (hereafter referred to as "originals" or *ori*); six, only in one single modified version (repetitive version or *rep*); and six, in different modified versions (varying versions or *var*). Episodes were assigned to each condition in a counterbalanced manner between participants; that is, each video was presented equally often in each condition. Throughout the course of the experiment, each episode assigned to the *ori* or *rep* condition was presented eight times in the same version. As varying versions contained four different versions of a single story, each alternative video was presented twice, once in the first half of the experiment and once in the second half. Four videos served as novel stories (*nov*), each of them repeated four times during the fMRI session.

The fMRI experiment was composed of 244 trials, consisting of 144 video trials showing episodes similar to the ones encoded, 32 video trials showing novels, 24 null events in which only a fixation cross was presented for 7–10 sec, and 44 question trials of which half were to be accepted and the other half were to be rejected. The experiment was divided into eight blocks, each containing 18 videos of previously encountered episodes, four novels, three null events, and five to six question trials. Thus, 25% of the videos were followed by a short description of the episodes' scenery (e.g., "Under water?") to ensure that participants attentively watched and recognized the action videos. In addition, trials were variably jittered (0, 500, 1000, and 1500 msec) and ended with a fixation cross (2 sec after videos or 1 sec after questions). The trial order was pseudorandomized to balance the order of presentation of the conditions within each block and balance transition probabilities between conditions. For a schematic overview of trials during fMRI, please see Figure 2.

Memory Test

One day after the fMRI session, participants came back to the behavioral laboratory to conduct a memory test. Participants were not informed in advance that their memory performance would be tested on Day 3 but rather that they would return for a computer task in which they would again be presented with videos showing PLAYMOBIL stories.

The memory test took approximately 25 min. Participants were instructed to watch short videos showing only the first two action steps of PLAYMOBIL stories on a computer. To ensure that participants understood the task correctly, the session started with two practice trials including the practice videos from the encoding session. After each video, participants had to answer two questions using key responses and two questions asking for verbal recall of objects. Verbal responses were written down by the experimenter.

First, participants had to rate whether they remembered the cued episode presented from the encoding session. Responses were given on a 4-point Likert scale (1 = *no*, 2 = *rather no*, 3 = *rather yes*, 4 = *yes*) using four marked keys on the computer's keyboard.

Second, participants were asked how vivid their memory is. Here, participants were instructed to rate vividness based on how detailed their mental image of the episode is as well as how strong their feeling of mentally moving their arms in accordance with the presented videos is. Responses were measured on a 6-point Likert scale from 1 = *not vivid at all* to 6 = *very vivid*. Participants had to press one of six marked keys on the computer's keyboard. There was no time restriction for responses, but extreme

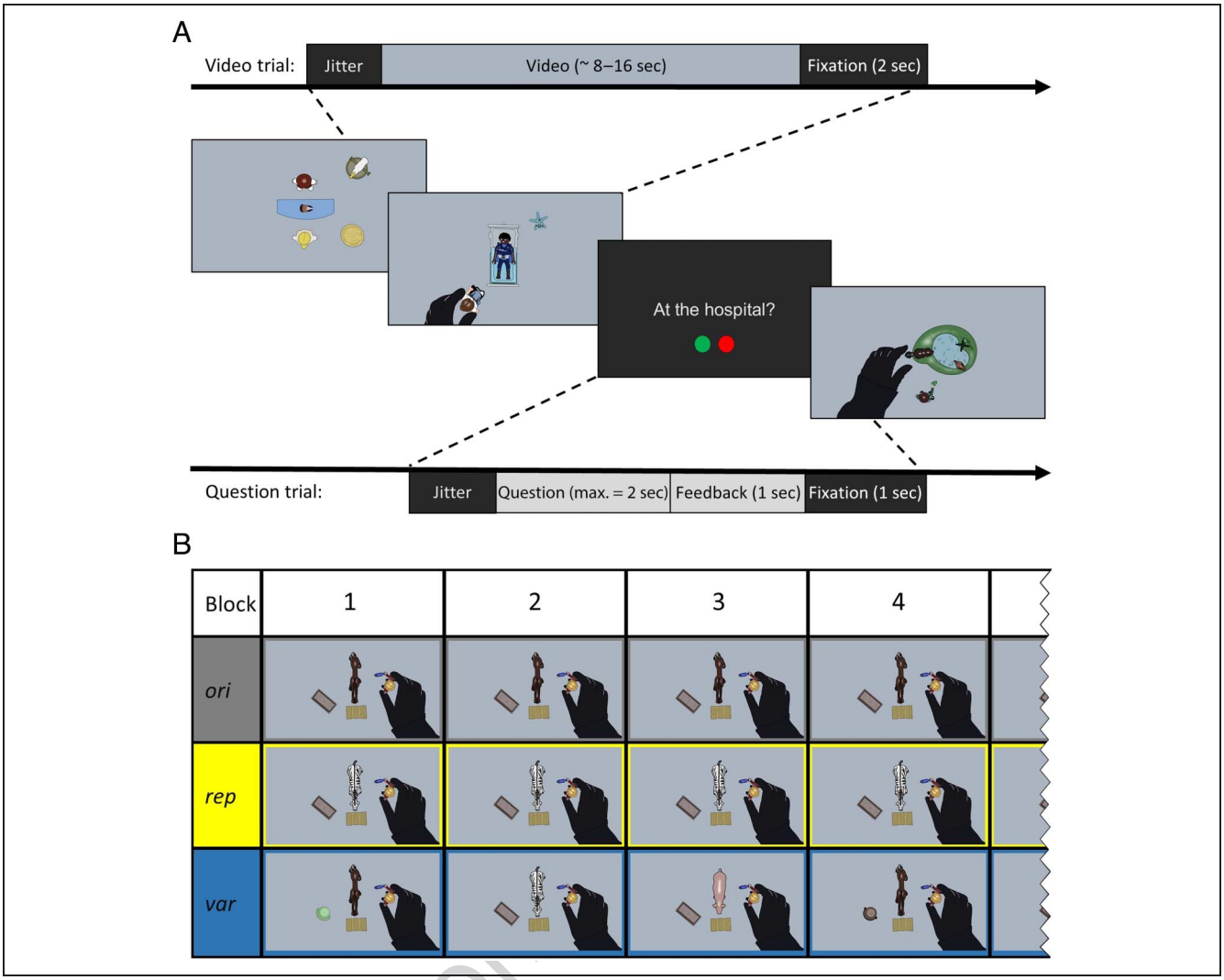

Figure 2. Schematic diagram of task during fMRI session. Video trials consisted of a variable jitter (0, 0.5, 1, or 1.5 sec of fixation), a video showing an episode (~8–16 sec), and an ISI (2 sec of fixation). (B) Schematic overview of different video versions for a single episode (here, "brushing the horse") when presented during scanning. The top row (white) shows the number of each respective block during fMRI. Originals (dark gray) were always presented in the same version as previously encoded. When presented with a repetitive PE (yellow), participants repeatedly experienced a single alternative version. For varying PEs (blue), participants watched multiple alternative versions of an encoded episode. Here, no alternative version was presented twice in a row. Please note that only four of eight video presentations are depicted here.

outliers were removed as described in the following section.

Third, participants were presented with a screenshot showing a later action step of the corresponding episode in which the first of the two potentially violated objects appeared. This object was masked using a black box showing the number "1" indicating Position 1. Then, participants were asked to answer which object was placed in the episode at Position 1. After verbally responding, participants had to press the space bar to continue with the next screenshot. The second screenshot showed the action steps in which the second potentially violated object was presented for the first time. To avoid feedback on previous responses, the object from the previous screenshot remained masked, but this time without an indexing number. The newly added black box contained the number "2" indicating Position 2, and participants were asked to name the object that was placed at that particular position. Participants were instructed to describe recalled objects and characters following the rules from the encoding session. Thus, after two practice trials, participants had to respond to 22 videos, that is, 18 originally encoded and four of the novel videos.

fMRI Acquisition and Preprocessing

MRI scans were performed on a 3-T Siemens MAGNETOM Prisma MR tomograph using a 20-channel head coil and took place 1 day after the encoding session. Participants laid down in a supine position, with their index and middle fingers positioned on the two buttons on the response box. Using form-fitting cushions, we minimized head and arm movements by tightly fixating participants' heads and arms. In addition, participants were provided with

earplugs and headphones to attenuate scanner noise. For stimuli presentation, the experiment was projected on a screen behind the fMRI machine that participants saw through an individually adjusted mirror on the head coil.

First, high-resolution anatomical images (T1 weighted) were created with a 3-D multiplanar rapidly acquired gradient-echo sequence (192 slices, thickness = 1 mm, repetition time = 2130 msec, echo time = 2.28 msec, flip angle = 8°, field of view = 256 × 256 mm^2). Whole-brain functional images were acquired in interleaved order along the AC–PC plane using a gradient-echo EPI sequence to measure BOLD contrast (33 slices, thickness = 3 mm, repetition time = 2000 msec, echo time = 30 msec, flip angle = 90°, field of view = 192 × 192 mm^2).

Brain image preprocessing and statistical analyses were conducted using SPM12 (Wellcome Trust) implemented in MATLAB (Version R2021b, The MathWorks Inc.). For functional images, we applied slice time correction to the middle slice to correct for differences in slice acquisition time, movement correction and realignment to the mean image, and coregistration of functional and structural scans. Furthermore, we normalized functional and structural images into standard Montreal Neurological Institute space and performed spatial smoothing using a Gaussian kernel of FWHM of 8 mm. A 128-sec high-pass temporal filter was applied.

Statistical Data Analysis

Behavioral Data Analysis

The behavioral data from the fMRI session and the memory test were analyzed using RStudio (Version 1.3.1073; R Core Team, 2020). Behavioral performance during fMRI was assessed by correct response rates and RTs on correctly answered question trials. For the memory test, the average ratings and RTs were analyzed using a repeated-measures analysis of variance (rmANOVA). Regarding RTs, we only selected correct answers based on the familiarity question. In the next step, the participants were sequentially presented with two images in which an object's position was hidden behind a black box. Here, participants had to verbally recall the respective object from the training session. The mean recall rates (achieved score/maximum score) and mean RTs were evaluated using an rmANOVA. For mean RTs, we only used trials in which participants made no mistake in recalling the object's attributes (name and color). For mean recall rates, we investigated differences in memory performance for previously encoded videos after experiencing an original version, a repetitive object change, or a varying object change during fMRI.

To investigate mean recall rates (achieved score/maximum score) and mean RTs, Bayesian hierarchical generalized models brms (Bürkner, 2017) and rStan (https://mc-stan.org/) were used. Two models were calculated. In these models, the recall rate (Equation 1) and RTs (Equation 2) were predicted by the type of modification and sequential position of the object. Furthermore, three random intercepts were assumed for trial, video, and participant. Because in both models, the output was not normally distributed, by checking the Cullen and Frey graph, appropriate generalized models were employed instead of normal linear ones. More specifically, a beta-binomial model for recall rate and a shifted log-normal model for RTs were used.

$$\begin{aligned} \textit{Recall Rate}\ (\textit{trials}|4) \sim\ & \textit{Modification} \times \textit{Position} \\ & + (1|\textit{Trial}) + (1|\textit{Video}) + (1|\textit{ID}) \end{aligned} \tag{1}$$

$$\begin{aligned} \textit{RT} \sim\ & \textit{Modification} \times \textit{Position} + (1|\textit{Trial}) \\ & + (1|\textit{Video}) + (1|\textit{ID}) \end{aligned} \tag{2}$$

For both models, uninformative priors were selected, as suggested by previous studies (Dienes & Mclatchie, 2018; Bürkner, 2017). For recall rates, we used *N* (0, 2.5) as uninformative priors for β coefficients, *student_t* (3, 0, 2.5) for intercept, *student_t* (3, 0, 2.5) for sigma, and *uniform* priors for ndt. For RTs, we applied *N* (0, 0.5) as uninformative priors for β coefficients, *student_t* (3, 8.7, 2.5) for intercept, *student_t* (3, 0, 2.5) for sigma, and *gamma* (0.01, 0.01) for phi. Both models were calculated with four chains, each having 5000 iterations with 2000 warmups. Both models converged with Rhat = 1.00 (i.e., the potential scale reduction factor on split chains). Furthermore, all parameters were sampled sufficiently, as all tail and bulk effective sample sizes were over 2000.

Hypotheses were tested using the hypothesis package included in brms (Bürkner, 2017). On the basis of recent literature, we considered Bayes factor (BF) > 3 and BF < $\frac{1}{3}$ as significant evidence for accepting and rejecting the tested hypothesis, respectively (van Doorn et al., 2021). One-sided hypotheses (denoted by BF_{+0}, BF_{-0}) were the comparison of the posterior probability of hypotheses against their alternative; two-sided tests (denoted by BF_{01}) were the comparison between hypotheses and their alternative computed via the Savage–Dickey density ratio method.

Before conducting the analyses, data distribution was tested by using the Shapiro–Wilk test and excluded outliers as defined by values higher than the 75% quartile +3 × interquartile range or lower than the 25% quartile −3 × interquartile range. In cases where data were normally distributed or could be logarithmically transformed to fit normal distribution (RTs), we used parametric rmANOVA. When data were not normally distributed, we opted for a nonparametric rmANOVA based on aligned rank data (package *ARTool*; Wobbrock, Findlater, Gergle, & Higgins, 2011) and calculated post hoc pairwise comparisons using the Wilcoxon signed-rank test.

For all rmANOVAs and respective post hoc testing, the significance level was set to $p < .05$. To address multiple comparisons, *p* values were adjusted according to the

Bonferroni–Holm correction (Holm, 1979). As descriptive statistics, we report mean values and *SEM*s.

fMRI Design Specifications

For the statistical analysis of the fMRI data with SPM12, we used the general linear model (GLM) for serially autocorrelated observations based on least-squares estimation (Worsley & Friston, 1995; Friston et al., 1994). The GLM convolved 15 regressors with a canonical hemodynamic response function. We included six regressors containing three predictors (*ori, var, rep*) and three parametric modulators (*par_ori, par_var, par_rep*) for the experimental conditions. Parametric modulators were included to model brain activity of repeated presentation over time. The 32 novel trials were modeled as one regressor as well (*nov*). All video trials were modeled as epochs containing the full video duration and onsets time-locked to the beginning of the video. In addition, two regressors modeled the 24 null events and the 44 question trials. Null events were modeled as epochs (7–10 sec), and questions were modeled as events. Six regressors of no interest were included for the participant-specific motion parameters obtained from realignment.

On the first level of the analysis, gray matter masking was implemented using the smoothed individual normalized gray matter image (8-mm FWHM). To create binary masks, smoothed images were thresholded at 0.2 using ImCalc in SPM12. For the second-level group analysis, one-sample *t* tests were performed to evaluate brain activation patterns across participants. We applied a threshold of $p < .001$ on the whole-brain level to identify significant effects. To control for false-positive results, we applied false discovery rate (FDR) correction at $p < .001$ to resulting *t* maps.

Our GLM aimed to examine the effects of varying and repetitive mnemonic PEs. Therefore, we calculated the first-level *t* contrasts *var* > *ori* and *rep* > *ori* to analyze brain activity in response to the specific PE types. To investigate shared effects of both modification types, we further calculated a conjunction of modification types (*var* > *ori*) ∩ (*rep* > *ori*). To gain a more detailed view of specific brain responses because of the respective modification type, we further calculated the direct contrasts *var* > *rep* and *rep* > *var*. Regarding the attenuation effects of repeated video presentation over time, we calculated the contrasts for parametric modulators against implicit baseline (*par_ori, par_var, par_rep*) to identify brain regions in which the BOLD response decreased with the number of presentations. To demonstrate successful retrieval of encoded episodes and replicate our previous findings, we calculated first-level *t* contrasts for each episodic condition versus novels (*ori* > *nov*).

In addition, we explored hippocampal activity for cued memory retrieval of original and violated episodic memories, that is, repetitive and varying PEs. Regarding recent research (Bein et al., 2020), we were interested in the specific contributions of cornu ammonis (CA) subregions (CA1 and CA3) during reexperience of repetitive and varying PEs. To this end, anatomical ROIs of the left and right HC were imported from the Julich-Brain Cytoarchitectonic Atlas (Amunts, Mohlberg, Bludau, & Zilles, 2020). To account for potential overlaps in ROIs, a threshold of 0.2 was implemented in ImCalc, and final ROIs were created using the MarsBaR toolbox (Brett, Anton, Valabregue, & Poline, 2002) in SPM12. Following Bein and colleagues (2020), CA3 ROI included probabilistic maps of the CA2 subregion and the dentate gyrus. We extracted mean beta values for left and right hippocampal subfields for the regressors *ori, var*, and *rep.* To extract mean beta values, we used the MarsBaR toolbox (Brett et al., 2002). For statistical analysis, we used a three-way rmANOVA with the factors $\text{Modification}_{\text{fMRI}}$ (*var, rep, ori*), Hemisphere (left, right), and Subfield (CA1, CA3). Post hoc comparisons were conducted with pairwise *t* tests (two-tailed), a significance level of $\alpha = .05$, and Bonferroni–Holm corrected for multiple comparisons (Holm, 1979).

RESULTS

Behavioral Results of the fMRI Session (Cover Task)

During the scanning phase, participants had to answer questions about the content of the video. Questions did not address information that could be modified because of the change of an object. After excluding trials in which no response was given (1.23%), the average RT was 922 msec (± 16 msec), whereas the average error rate was low (0.058 ± 0.006), indicating that participants attentively observed and recognized the action stories.

To analyze behavioral performance during fMRI, we conducted a nonparametric rmANOVA on error rates with the factor $\text{Condition}_{\text{fMRI}}$ (*ori, var, rep, nov*). We found a significant main effect of Condition, $F(3, 108) = 11.3$, $p < .001$, $\eta_p^2 = .24$. Bonferroni–Holm corrected post hoc analyses with Wilcoxon pairwise tests (two-tailed) revealed significant differences between *ori* ($M_{ori} = .033 \pm .008$) and *nov* ($M_{nov} = .13 \pm .019$; $Z = -3.9$, $p < .001$) as well as between *var* ($M_{var} = .067 \pm .012$) and *nov* ($M_{nov} = .13 \pm .019$; $Z = -2.7$, $p = .002$). In addition, there was a trend for the comparison between *rep* ($M_{rep} = .078 \pm .012$) and *nov* ($M_{nov} = .13 \pm .019$; $Z = -2.6$, $p = .02$). All together indicate that episodes were better recognized than novels. Furthermore, we found a significant difference between *ori* ($M_{ori} = .033 \pm .008$) and *rep* ($M_{rep} = .078 \pm .012$; $Z = -3.09$, $p = .002$) and a trend for the comparison between *ori* ($M_{ori} = .033 \pm .008$) and *var* ($M_{var} = .067 \pm .012$; $Z = -2.1$, $p = .036$), suggesting that participants performed best when videos showed original content from the training session.

With regard to RTs on correct responses, we found a significant main effect of $\text{Condition}_{\text{fMRI}}$, $F(3, 108) = 4.612$, $p = .004$, $\eta_p^2 = .114$. Bonferroni–Holm corrected post hoc analyses with pairwise comparisons (two-tailed) revealed a

significant difference between *var* (M_{var} = 893 ± 31 msec) and *nov* (M_{nov} = 961 ± 35 msec), $t(36) = -3.48, p = .001$, and a trend between *ori* (M_{ori} = 916 ± 30 msec) and *var* (M_{var} = 893 ± 31 msec), $t(36) = 2.19, p = .03$.

fMRI Results

Effects of Varying and Repetitive Expectation Violation

To identify specific brain regions related to varying PEs and repetitive PEs, we first calculated whole-brain contrasts for modified versus original videos (*var* > *ori, rep* > *ori*).

When comparing varying versions with original episodes (*var* > *ori*), recurrent experience of PEs activated dorsal premotor cortex (PMd), inferior frontal junction, IFS, and inferior frontal gyrus (IFG) including BA (BA 45), lateral occipital cortex, and caudate. Superior parietal lobe (SPL), PCUN, and STS showed increased activity in the right hemisphere.

For repetitive PEs versus baseline episodic retrieval (*rep* > *ori*), we found increased activity in bilateral PMd, IFS (extending into IFG), SMA, superior occipital lobe, HC, and amygdala, whereas unilateral activation was observed in right SPL, right anterior PCUN, right somatosensory cortex, left inferior parietal lobe (IPL), and left middle occipital lobe.

To detect shared brain activation in varying PEs and repetitive PEs, a conjunction of *var* > *ori* and *rep* > *ori* contrasts was calculated. Modified compared to original videos triggered bilaterally enhanced brain activation in PMd, IFS, IFG, SPL, IPS, HC, and amygdala as well as unilaterally right superior frontal sulcus, right anterior PCUN, and right posterior PCUN (Table 1, Figure 3).

To characterize differences between varying and repetitive PEs, we further calculated direct contrasts between the two types of PEs (*var* > *rep, rep* > *var*). In versions containing varying versus repetitive PEs (*var* > *rep*), significant brain activation included lateral occipital cortex, left SPL, left IPS, left IFG (BA 44), and right middle frontal gyrus extending into IFG (BA 45; Table 2, Figure 4C).

The reversed contrast (*rep* > *var*) revealed increased activity in ventral PM cortex, pregenual ACC (pgACC), pCC, and cuneus in both hemispheres. Unilaterally, we found increased brain activity in right anterior dorsolateral pFC (dlPFC), right subgenual ACC, right pCC, right posterior STS, right lingual gyrus, and right mid-insula (Table 3, Figure 4A).

Parametric Effects of Episode Repetition

In line with our main research question, we investigated the effects of repeated presentation of one single alternative version (*rep*) or multiple alternative versions (*var*) of a reactivated episode. To analyze parametric decrease during repeated exposure to PEs over time, we first calculated the contrasts for parametric modulators against implicit baseline (*par_ori, par_var, par_rep)* on the whole-brain level. Please note that as effects of parametric modulators did not survive FDR correction at $p < .001$, we applied an FDR correction at the significance level of < .05. For original videos (*par_ori*), we found a parametric decrease in bilateral ventral posterior PCUN (left: $x = -9, y = -64, z = 38, Z = 4.79$; right: $x = 15, y = -61, z = 35, Z = 4.53$), whereas for varying videos (*par_var*), a decrease was located in left ventral posterior PCUN (level: $x = -3, y = -67, z = 41, Z = 4.79$) and left IPL ($x = -42, y = -67, z = 50, Z = 3.98$). With regard to repetitive PEs (*par_rep*), we found significant attenuation in bilateral PCUN (left: $x = -9, y = -64, z = 38, Z = 4.13$; right: $x = 12, y = -67, z = 41, Z = 4.13$), bilateral IPL (left: $x = -39, y = -58, z = 47, Z = 4.21$; right: $x = 45, y = -58, z = 53, Z = 4.79$), left thalamus ($x = -3, y = -13, z = 2, Z = 4.24$), and right posterior mCC (pmCC; $x = 3, y = -31, z = 32, Z = 4.08$).

Explorative ROI Analysis

Furthermore, we used anatomical ROIs to investigate the specific contributions of hippocampal subfields during reexperience of originals and violated episodes. As recent literature (Bein et al., 2020) highlighted the role of hippocampal subfields in successful predictions and during experience of mnemonic PEs, we explored potential effects of small regions in our paradigm. Specifically, we tested whether CA1 and CA3 led to distinct brain responses during experience of repetitive and varying PEs. To further account for effects based on lateralization, we performed a three-way rmANOVA with the factors $\text{Modification}_{\text{fMRI}}$ (*var, rep, ori*), Hemisphere (left, right), and Subfield (CA1, CA3). During cued retrieval of episodes, we found significant main effects of $\text{Modification}_{\text{fMRI}}$, $F(2, 72) = 19.73, p < .001, \eta_p^2 = .354$, and Hemisphere, $F(1, 36) = 13.69, p < .001, \eta_p^2 = .276$. The main effect of Subfield was not significant, $F(1, 36) = 0.51, p = .48, \eta_p^2 = .014$. Post hoc two-sided testing revealed that originals (M = .007 ± .007) triggered significantly less activation of the hippocampal subfields compared to varying PEs (M = .033 ± .007), $t(36) = -4.69, p < .001$, Cohen's $d = .31$, and repetitive PEs (M = .035 ± .007), $t(36) = -5.08, p < .001, d$ = .33. Repetitive and varying PEs did not trigger distinct activation in HC, $t(36) = 0.45, p = .06, d = .02$. In addition, HC in the left hemisphere (M = .046 ± .005) was more strongly activated than in the right hemisphere (M = .005 ± .005), $t(36) = 4.32, p < .001, d = .5$. After correcting for multiple comparisons, we found a marginally significant interaction between the factors Modification and Subfield, $F(2, 72) = 3.54, p = .03, \eta_p^2 = .09$. Regarding activation of CA1, repetitive PEs (M = .036 ± .01), $t(36) = 5.07, p < .001, d = .35$, and varying PEs ($M$ = .035 ± .01), $t(36) = 4.8, p < .001, d$ = .33, each triggered stronger activation than originals in CA1 (M = .007 ± .01). Compared to originals (M = .008 ± .01), we found CA3 to be more activated during reexperience of both repetitive PEs (M = .034 ±.01), $t(36) = 5.04, p < .001$,

Table 1. Peak Activation of Second-level Whole-brain Analysis for Shared Brain Activity of Prediction Violation

			MNI Coordinates			
Area	*H*	*Cluster Extent*	*x*	*y*	*z*	*Z*
(*var* > *ori*) ∩ (*rep* > *ori*)						
SMA/pre-SMA	L	110	−3	14	50	4.90
	R	l.m.	3	8	59	4.54
PMd	R	380	45	−4	56	4.94
IFS	R	l.m.	42	23	23	4.42
		l.m.				
IFG (BA 45)	R	l.m.	54	26	23	4.14
Superior frontal sulcus	R	l.m.	24	5	50	3.97
IPS	L	2094	−24	−82	38	5.72
	R	l.m.	33	−82	29	5.21
SPL	R	l.m.	15	−79	47	5.51
	L	l.m.	−24	−67	41	5.43
pSTS	R	l.m.	57	−46	17	4.78
Dorsal posterior precuneus	R	19	9	−70	47	4.35
Anterior precuneus	R	17	9	−52	50	4.60
PCUN	L	l.m.	−6	−64	50	4.62
Superior frontal sulcus	L	694	−48	11	29	5.33
PMd	L	l.m.	−36	2	59	4.94
IFS	L	l.m.	−45	29	20	4.73
LOC	L	260	−54	−58	−10	5.70
Fusiform gyrus	L	l.m.	−30	−63	−13	4.07
OFC	R	86	36	29	−10	5.20
	L	51	−36	26	−13	4.76
Anterior dorsal insula	L	l.m.	−27	26	2	4.56
HC	L	42	−33	−22	−13	4.99
Amygdala	L	l.m.	−33	−7	−13	4.22
	R	66	30	−4	−19	4.84
HC	R	l.m.	36	−28	−13	4.49
Cerebellum	L	44	−9	−76	−16	4.84

FDR corrected at $p < .001$. L = left; R = right; H = hemisphere; MNI = Montreal Neurological Institute; l.m. = local maximum.

$d = .32$, and varying PEs ($M = .032 \pm .01$), $t(36) = 4.52$, $p < .001$, $d = .29$. We did not find any further two-way or three-way interactions.

Replication of Former Findings—Effects of Episodic Memory Retrieval

With regard to replicating results from our previous studies and demonstrating successful episodic retrieval, we contrasted original and new videos (*ori* > *nov*). Episodic retrieval triggered significant brain activation bilaterally in pgACC, BA 10, pmCC, IPL, and unilaterally in left posterior PCUN (Table 4, Figure 4B).

Memory Test Results

To investigate the effects of varying and repetitive PEs on behavioral memory performance, we concentrated our analysis of ratings, RTs, and original object recall on videos that have been encoded during the training session.

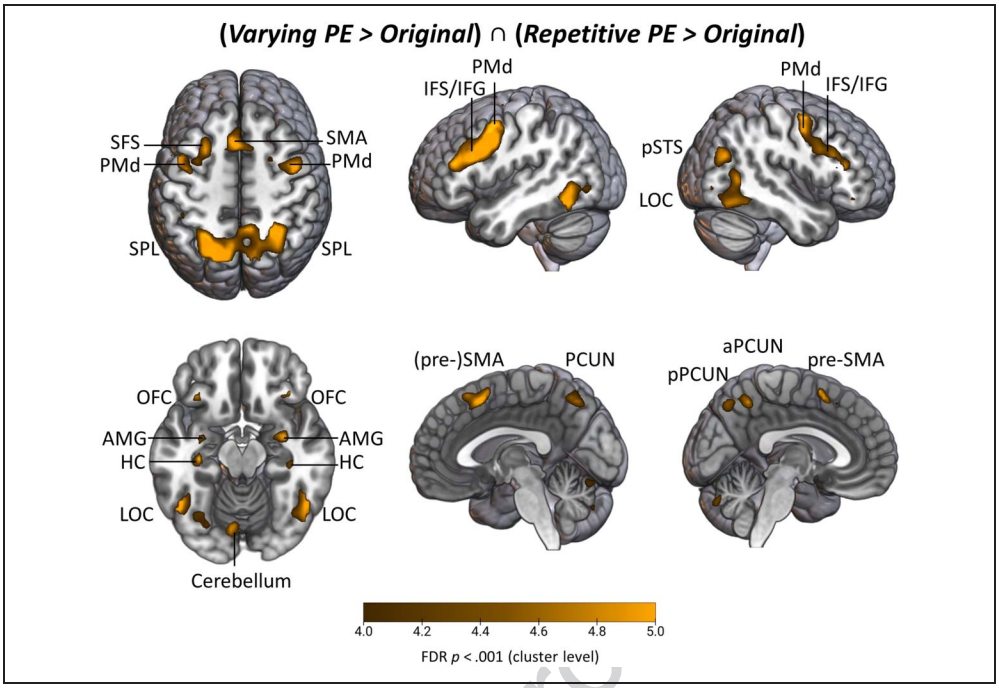

Figure 3. Shared brain activation to repetitive and varying episodic PEs. FDR-corrected t map ($p < .001$) for the (Varying PE > Original) ∩ (Repetitive PE > Original) contrast. SFS = superior frontal sulcus; PTL = parietal temporal lobe; LOC = lateral occipital cortex; AMG = amygdala; p/aPCUN = posterior/anterior PCUN.

Table 2. Peak Activations of Second-level Whole-brain Analysis of Varying Compared to Repetitive PEs

			MNI Coordinates			
Area	*H*	*Cluster Extent*	*x*	*y*	*z*	*Z*
(*var* > *rep*)						
SPL	L	178	−27	−67	56	5.06
IPS	L	l.m.	−27	−55	44	4.63
SPL	R	481	33	−55	41	6.18
Occipitotemporal cortex	R	l.m.	39	−73	20	5.10
Inferior frontal junction	R	369	39	5	32	6.02
MFG, i.e., IFG (BA 45)	R	l.m.	51	29	26	5.52
PMd	R	l.m.	36	−1	53	5.07
MFG	R	l.m.	39	8	62	4.86
Inferior frontal junction	L	50	−42	5	32	4.90
IFS/IFG (BA 44)	R	22	51	23	23	5.25
Fusiform gyrus	R	385	36	−52	−10	6.32
Inferior occipital lobe	R	l.m.	36	−64	−7	5.86
Lateral occipital cortex	R	l.m.	48	−73	−10	4.48
Fusiform gyrus	L	374	−39	−52	−10	5.87
Lateral occipital cortex	L	l.m.	−42	−67	−7	5.52
Cerebellum	L	111	−9	−73	−25	5.37
	R	18	3	−55	−37	4.39

FDR corrected at $p < .001$. MFG = middle frontal gyrus.

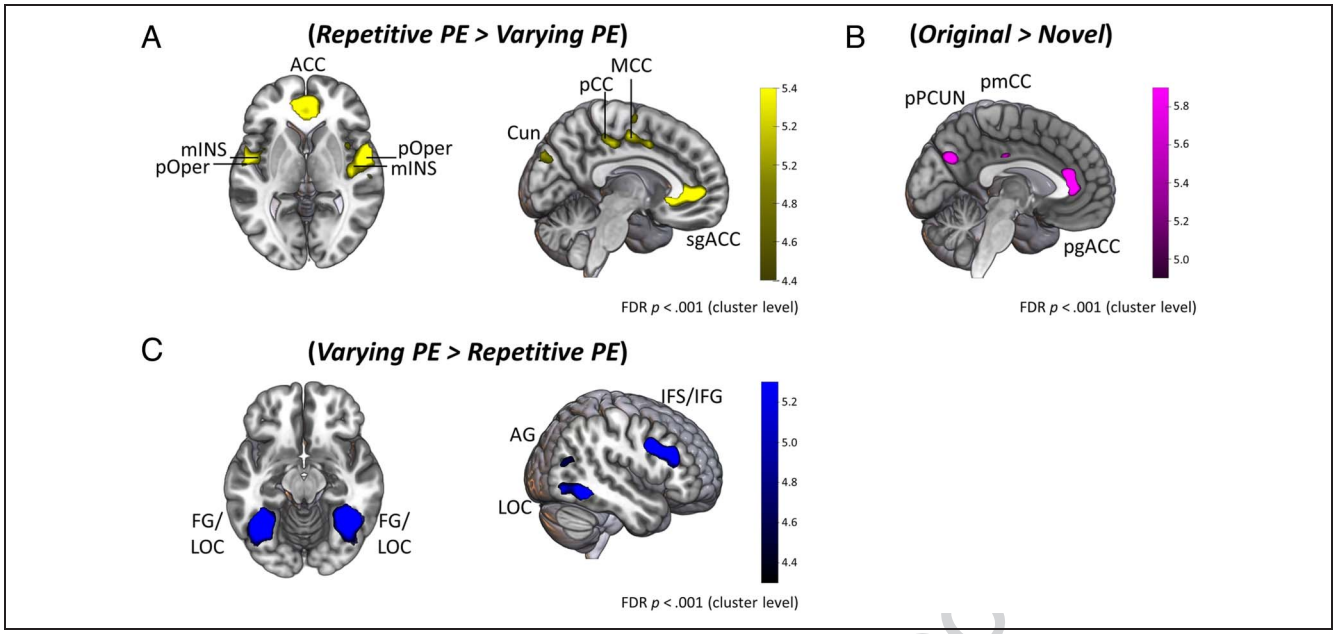

Figure 4. Distinct whole-brain activation for different types of cued episodes. (A) FDR-corrected t map ($p < .001$) for the Repetitive PE > Varying PE contrast. (B) FDR-corrected t map ($p < .001$) for the Original > Novel contrast. (C) FDR-corrected t map ($p < .001$) for the Varying > Repetitive contrast. mINS = mid-insula; pOper = parietal operculum; Cun = cuneus; pPCUN = posterior PCUN; FG = fusiform gyrus; LOC = lateral occipital cortex; AG = angular gyrus.

Table 3. Peak Activations of Second-level Whole-brain Analysis of Repetitive Compared to Varying PEs

			MNI Coordinates			
Area	*H*	*Cluster Extent*	*x*	*y*	*z*	*Z*
(*rep* > *var*)						
PMd	L	16	−33	−13	71	4.79
M1	L	63	−39	−22	53	4.57
SMA/mCC	L/R	185	0	−10	47	5.25
pCCd	R	26	9	−28	44	4.51
Anterior dlPFC	R	27	36	44	32	5.08
Cuneus	R	76	9	−91	32	4.36
	L	l.m.	−3	−85	26	4.34
Parietal operculum	L	385	−60	−28	20	5.43
PMv	L	l.m.	−54	−4	8	5.08
Mid-insula	L	l.m.	−36	5	11	4.89
PMv	R	497	54	−1	5	5.48
Parietal operculum	R	l.m.	60	−22	20	4.77
Mid-insula	R	l.m.	36	8	11	5.16
ACC	L	382	−12	38	−4	5.61
Subgenual ACC	R	l.m.	3	20	−4	5.43
Pregenual ACC	R	l.m.	6	44	−1	5.29
	L	l.m.	−3	32	8	5.18

FDR corrected at $p < .001$. PM(d/v) = (dorsal/ventral) premotor cortex; M1, primary motor cortex; pCCd, dorsal posterior cingulate cortex; dlPFC, dorsolateral pFC; SMG, supramarginal gyrus; pSTS, posterior STS.

Table 4. Peak Activations of Second-level Whole-brain Analysis of Originals Compared to Novels

Area	H	Cluster Extent	MNI Coordinates			Z
			x	y	z	
(*ori* > *nov*)						
Pregenual ACC (BA 24)	L	200	−6	35	8	7.03
	R	l.m.	9	35	2	6.38
BA 10	L + R	l.m.	0	47	8	4.59
Ventral posterior PCUN	L	95	−9	−64	29	5.88
Angular gyrus	L	28	−51	−58	50	5.29
	R	16	54	−58	47	5.11
pmCC (BA 23)	L + R	24	0	−22	35	5.20

FDR corrected at $p < .001$.

Object modifications never occurred in the first two action steps of an episode to ensure episodic memory retrieval during fMRI. We decided to not include novels in the analysis as they were presented the first time during the fMRI session, which made it more difficult for participants to correctly encode object details compared to the training session, biasing potential effects rather through visual than mnemonic accessibility. Furthermore, we showed in our previous studies (Siestrup et al., 2023; Jainta et al., 2022) that memory performance for encoded episodes was more accurate than that for novels.

Memory Performance on Original Object Recall

For recall rate, the results of the model (Equation 1) showed that memory performance was less accurate when presented with the same PE compared to reexperience of originals (H_-: *rep* < 0; mean = −0.43 [−0.74, −0.11], *EE* = 0.19, *pp* = .99, BF_{-0} = 70.86). However, for the experience of varying PEs compared to originals, the models did not show substantial evidence for accepting the tested hypothesis (H_-: *var* < 0; mean = −0.11 [−0.43, 0.21], *EE* = 0.21, *pp* = .71, BF_{-0} = 2.48). When directly comparing the same and varying PEs, the same PEs resulted in less accurate retrieval of originally encoded versions (H_-: *rep* – *var* < 0; mean = −0.31 [−0.63, 0.00], *EE* = 0.19, *pp* = .95, BF_{-0} = 19.34).

For the model of RTs (Equation 2), we found substantial evidence that repeated presentation of the same PE resulted in slower retrievals than originals (H_+: *rep* > 0; mean = 0.09 [0.01, 0.16], *EE* = 0.05, *pp* = .97, BF_{+0} = 35.59). Again, for repeated presentation with videos showing varying PEs, we did not find substantial evidence for the tested hypothesis (H_+: *var* > 0; mean = −0.01 [−0.07, 0.08], *EE* = 0.04, *pp* = .56, BF_{+0} = 1.28). Reexperiencing the same PE during scanning further led to slower retrieval during the memory test when compared to varying PEs (H_+: *rep* – *var* > 0; mean = 0.08 [0, 0.15], *EE* = 0.05, *pp* = .96, BF_{+0} = 21.9).

To account for the potential effects of object position within each episode, we included Position as a predictor in our models (Equations 1 and 2). Regarding original object retrieval, we found substantial evidence that less accurate recalls occurred for objects located in Position 2 compared to Position 1 (H_-: Pos2 < 0; mean = −0.34 [−0.65, −0.03], *EE* = 0.19, *pp* = .97, BF_{-0} = 27.92). Furthermore, we found substantial evidence that object retrieval from Positions 1 and 2 was similarly accurate for the recurrent presentation of the same PE during fMRI compared to the originals (H_0: *rep*:Pos2 = 0; mean = −0.28 [−0.22, 0.79], *EE* = 0.26, *pp* = .85, BF_{01} = 5.45). In addition, we found substantial evidence for the similarly accurate object retrieval from Positions 1 and 2 after reexperiencing repetitive compared to varying PEs in the scanner (H_0: *rep*:Pos2 – *var*:Pos2 = 0; mean = −0.23 [−0.75, 0.29], *EE* = 0.27, *pp* = .91, BF_{01} = 9.57). Regarding RTs, our models provided substantial evidence that objects from Position 2 were recalled slower than objects from Position 1 (H_+: Pos2 > 0; mean = 0.09 [0.02, 0.16], *EE* = 0.04, *pp* = .98, BF_{+0} = 48.79). In addition, interactions revealed substantial evidence that recurrent presentation of the same PE during fMRI compared to originals was retrieved with the same speed for Positions 1 and 2 (H_0: *rep*:Pos2 = 0; mean = −0.01 [−0.13, 0.11], *EE* = 0.06, *pp* = .88, BF_{01} = 7.64). We also found substantial evidence that reexperience of varying PEs (vs. originals) during scanning led to the same recall speed of original objects in the memory test (H_0: *var*:Pos2 = 0; mean = 0.07 [−0.05, 0.2], *EE* = 0.06, *pp* = .81, BF_{01} = 4.15). Furthermore, repeated experience of the same and varying PEs led to a similar object retrieval speed in Positions 1 and 2 (H_0: *rep*:Pos2 – *var*:Pos2 = 0; mean = −0.08 [−0.21, 0.04], *EE* = 0.0, *pp* = .83, BF_{01} = 5.06).

Familiarity and Vividness

First, we inspected familiarity ratings with regard to whether participants accurately identified an episode as known from the training session. We analyzed ratings

using a nonparametric one-way rmANOVA with the factor $\text{Modification}_{\text{fMRI}}$ (*ori, var, rep*). We did not find a significant main effect of familiarity, $F(2, 72) = 0.28, p = .76$, $\eta_p^2 = .008$, indicating that participants were able to recognize an encoded episode as belonging to the training session. Regarding corresponding RTs on correct responses, 7.02% of the trials were excluded as extreme outliers. The main effect did not reach significance, $F(2, 72) = 0.27, p = .76$, $\eta_p^2 = .007$.

Second, a nonparametric rmANOVA with the factor $\text{Modification}_{\text{fMRI}}$ (*ori, var, rep*) was conducted to analyze participants' vividness ratings and corresponding RTs on videos correctly assigned to the training session. We did not find a significant main effect of $\text{Modification}_{\text{fMRI}}$, $F(2, 72) = 0.28, p = .76, \eta_p^2 = .01$, suggesting that episodes were equally vivid irrespective of prediction violation during scanning. For RTs related to the question of vividness, we found a trend for the main effect of $\text{Modification}_{\text{fMRI}}$, $F(2, 72) = 2.68, p = .075, \eta_p^2 = .069$. Descriptively, participants showed fastest responses when presented with a repetitive PE (M_{rep} = 2099 ± 83 msec) and slowest responses for varying PEs (M_{var} = 2297 ± 88 msec).

DISCUSSION

Episodic memories are prone to change, which helps to integrate new information into existing memories and thus maintain long-term valid assumptions and expectations. In the current fMRI study, we aimed to disentangle the neural networks underlying the reexperience of multiple and single alternatives competing with existing episodic memories. We triggered memory reactivation by presenting either multiple alternative versions of an originally encoded episode (varying PE) or only one single alternative version repeatedly (repetitive PE). Although both conditions revealed brain activity that is typical for the detection of unexpected information in observed actions, we could identify distinct contributions of these and further areas to the processing of varying and repetitive changes. As expected, the BOLD results showed that both episodic PEs were associated with brain areas involved in memory reactivation and recognition of mismatches but also elicited specific brain activity in each case. This difference was supported by substantial evidence at the behavioral level: In contrast to the experience of multiple alternatives, repeated exposure to the same alternative version of an episode enabled expectancy adaptation and potentially impeded subsequent recall of the original version. The results contribute to the distinction between the neural signatures of violation of episodic predictions and those of adaptation to episodic predictions.

Brain Responses to Varying Episodic PEs

PEs drive the updating of encoded memories while having the greatest impact during the first encounter (Fernández et al., 2016; Exton-McGuinness et al., 2015). During varying PEs, participants never experienced an alternative version of an encoded episode twice in a row. As a result, there was no opportunity to correctly adjust predictions in response to continuous changes in content. Looking at the direct contrast between varying and repetitive alternatives, and at their conjunction, thus isolates the effect of PE, initializing the updating of episodic memory based on the amount of interference over time.

Starting with the conjunction of both conditions, episodic PEs were reflected in increased BOLD response in the HC, which is related to episodic memory reactivation (Jeong, Chung, & Kim, 2015), mismatch detection (Kumaran & Maguire, 2006), associative learning, and generating predictions (Chen et al., 2011). Previous studies also found HC involvement in episodic PEs, although only subthreshold possibly because of less frequent PE repetitions (Siestrup et al., 2022, 2023; Jainta et al., 2022). In contrast to previous studies (Bein et al., 2020; Duncan, Tompary, & Davachi, 2014), hippocampal subregions were not indicative of differentiating between varying and repetitive PEs in the present study (cf. Limitations). Remarkably, amygdala was coactivated with HC. Studies in rodents and humans suggest that the amygdala modulates memory consolidation and plasticity processes in the HC (Roesler, Parent, LaLumiere, & McIntyre, 2021). This modulation has been mostly investigated in the context of highly relevant, that is, emotionally loaded or stressful, contexts (Roozendaal, McEwen, & Chattarji, 2009; Phelps, 2004). In the present study, we did not use emotionally valanced stimuli but videos showing episodes that included typical everyday actions (e.g., relaxing at the pool) or fictional settings (e.g., knights at a tavern). We speculate that the amygdala modulated hippocampal-mediated responses to induced PE because these were accompanied by some increased arousal, that is, a small but consistent stress response. Note also that the amygdala was also reported for declarative memory recall of emotionally neutral objects (Inman et al., 2018).

Hippocampal and amygdala activity was accompanied by engagement of the ventrolateral pFC, an area that is most reliably involved in expectation-violating information in observed actions (Siestrup et al., 2022; El-Sourani, Trempler, Wurm, Fink, & Schubotz, 2020; Wurm & Schubotz, 2012; Schiffer & Schubotz, 2011). Similarly, posterior parietal regions (SPL, IPS) have been reported for PE highlighting the discrimination of original memories and alternative episodes (Cabeza et al., 2011; Uncapher & Wagner, 2009; Ciaramelli, Grady, & Moscovitch, 2008), especially also in the context of remembering the positions of objects in space (Harrison, Jolicoeur, & Marois, 2010). These regions and, most prominently, the bilateral fusiform gyrus were even more engaged for varying than for repeated single episode manipulations. Therefore, they most likely reflect the dissimilarity of multiple episodic PEs, as compared to always having the same expectation violation in the *rep* condition. In our experiment,

this dissimilarity existed at the level of object information, the processing of which is related to superior parietal (Uncapher & Wagner, 2009) and fusiform (Weiner & Zilles, 2016) areas. Varying PEs moreover engaged caudate nucleus significantly more than originals and also compared to repeated single PE when corrected with an FDR of 0.05. Caudate has been reported for signaling PE in different types of non-reward-based learning paradigms (Schiffer & Schubotz, 2011; Den Ouden, Daunizeau, Roiser, Friston, & Stephan, 2010; Badgaiyan, Fischman, & Alpert, 2007). Hence, persistent caudate activity may highlight an unstable state in which learning the latest version (here, exchanged object) does not increase predictive success.

Interestingly, the here-found brain network including HC, amygdala, and caudate has been associated with reflecting the experience of "unexpected uncertainty" during sequential learning (Soltani & Izquierdo, 2019; Yu & Dayan, 2005). Unexpected uncertainty refers to the encounter of unexpected changes in the environment, that is, a variation of unpredictable mismatches between predictions and perceptual input. In contrast, expected uncertainty reflects the level of predictable changes arising from revised predictions regarding prior knowledge. Presenting participants with varying versions may have led to recurrent unexpected uncertainty during cued episodic memory retrieval. Thus, recurrent violation of top–down predictions was in conflict with prediction adaption. Whereas expected uncertainty is suggested to enhance subsequent learning, random variation under constant probabilities does not (Courville, Daw, & Touretzky, 2006). Here, we argue that unpredictable changes prevented episodic memory updating in a way that the original episode was still accessible during subsequent memory testing.

Learning from Repeated Same Episodic PEs

To investigate the effects of updating episodic predictions through repetitive PEs, we analyzed recurrent experience of single alternative versions in contrast to varying versions and to originals. It is suggested that new information presented at episodic memory retrieval allows for incorporation of new information over time as an adaptive learning process (Lee et al., 2017). We found substantial evidence that originally encoded objects were recalled less accurate after being presented with a repetitive PE. In contrast, although varying PEs yielded strong and distinct brain responses, they did not result in interference strong enough to hamper subsequent recall of the original episode. Experiencing multiple alternative episodes rather may have facilitated change monitoring, maintaining the initial memory and leading to retrieval performance comparable with originals. For the *rep* condition, however, an alternative version of the episode could be learned after repeated presentation and later led to a reduction in recall performance in the memory of the original episode, possibly because of competition. These findings support the view that memory strength of the newly established memory trace seems to be a crucial boundary condition for memory updating (Fernández et al., 2016).

The substantial evidence for the behavioral effect of repeating PEs compared to varying PEs was reflected at the brain level. Thus, the repetitive versus varying PEs contrast showed largely the same activation pattern as the contrast between original and novel videos. In accordance with our previous study (Siestrup & Schubotz, 2023; Jainta et al., 2022), activity in cortical midline structures including the pgACC and the pmCC as well as in somatosensory and insula areas signaled successful retrieval of encoded episodic compared to novel information (Konishi, Wheeler, Donaldson, & Buckner, 2000). This network suggests that because of repeated presentations of the same modified episodes, participants integrated a new episode variant into their internal model.

Considering a recent meta-analysis (Palomero-Gallagher et al., 2019), the here-found pgACC area is functionally connected to mCC and pCC (Palomero-Gallagher et al., 2019). Via connections to parietal cortex and HC, pCC was suggested to contribute to action-outcome learning (Rolls, 2019) and self-referential processing (Northoff et al., 2006). The here-found coactivation of pgACC and pCC highlights the observation that pgACC's activity is triggered by matching similar experiences and/or challenging well-learned episodes with new but similar information. In previous studies, we consistently found pgACC when contrasting originally encoded with new episodic information (Siestrup et al., 2023; Jainta et al., 2022). Of particular interest to our findings is that, in a previous study (Siestrup & Schubotz, 2023), pgACC activation was increased in response to episodic modification in a PE condition characterized by strong memory modification effects in the post-fMRI memory test. Notably, in our other study (Siestrup et al., 2022), pgACC, mCC, pCC, and hippocampal activity increased over time for later false memories, pointing to a process related to new memory encoding. Although in the present study, we did not test memory on modified versions and hence false alarms could not be examined, we did find a decreased recall of episodes that were presented repeatedly modified during the fMRI session. Furthermore, when two slightly diverging episodes had been encoded, pgACC was found to be more activated for biased versus balanced episodic expectations (Schiffer et al., 2013). Together, these findings fit very well to the proposed pgACC's role in deciding for one option over others (Klein-Flügge, Bongioanni, & Rushworth, 2022). We therefore conclude that, in the present study, pgACC together with mCC and pCC reflect that, in case of repetitive as in contrast to varying PEs, robust second, alternative versions of the corresponding original episodes were established. With this in mind, it seems particularly interesting to further investigate the role of pgACC in episodic memory plasticity in future studies.

Limitations

We explored distinct contributions of hippocampal subregions CA1 and CA3. Despite the significant BOLD response in HC during experience of PEs, activity in hippocampal subfields did not differ between repetitive and varying PEs during memory retrieval. This contrasts with previous findings suggesting increased CA1 activity during predictive success and decreased CA1 activity during experience of multiple PEs at a time compared to CA3 (Bein et al., 2020). As we did not replicate this activity pattern, we assume that hippocampal subfield activity may be indicative of the amount of experienced interference at a time rather than over time. Furthermore, discrepancies in PE-related brain activity may further arise from different types of employed PEs, that is, interrupting episodic retrieval (Sinclair, Manalili, Brunec, Adcock, & Barense, 2021) or using static (Bein et al., 2020) or dynamic sceneries with almost identical content (Siestrup et al., 2023; Jainta et al., 2022). Further research is needed to understand the complexity of hippocampal responses to PEs.

As a caveat, we did not show direct evidence of brain–behavior interaction in the current study. Although we focused on investigating the neural differences during experience of repetitive and varying PEs, we acknowledge the limitation of not directly linking these neural findings to behavioral outcomes. This highlights the need to directly demonstrate the interaction between brain activity patterns and behavioral outcomes in future studies.

In addition, future studies should test whether balancing the number of presentations of each episode regarding repetitive and varying PEs, that is, presenting each varying version eight times, will lead to stronger impairment of memory performance after recurrent experience of varying versions. It is possible that potential effects of varying PEs on subsequent memory retrieval may depend on the encoding strength of alternative information. Therefore, this approach could shed further light on how potential boundary conditions could affect the updating of episodic memory through PEs.

Conclusion

Our study sheds light on the shared and distinct effects of varying and repetitive mnemonic PEs during episodic memory retrieval. Whether through varying or repetitive PEs, HC and amygdala, along with a number of neocortical areas, were involved in processing new information that occurred during episodic retrieval. This new information was linked to the originally encoded episode only if this PE was repeated in an identical way. In this case, our findings extend the role of cortical midline activity beyond mismatch monitoring in episodic memory to possibly having an impact on expectation adaptation through episodic memory reactivation. Further research is needed to understand the multifaceted functions of cortical midline activity in episodic memory reactivation and updating.

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Data Availability Statement

The data sets generated for this study are available on request to the corresponding author.

Author Contributions

Benjamin Jainta: Conceptualization; Formal analysis; Investigation; Methodology; Visualization; Writing—Original draft preparation; Writing—Review & editing. Anoushiravan Zahedi: Formal analysis; Writing—Review & editing. Ricarda I. Schubotz: Conceptualization; Funding acquisition; Methodology; Resources; Supervision; Writing—Original draft preparation; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. In the current article, we report its proportions of citations (successfully categorized DOIs = .797) by gender category to be as follows: M/M = .347, W/M = .245, M/W = .224, and W/W = .184.

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