Aging and the encoding of changes in events: The role of neural activity pattern reinstatement

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When encountering unexpected event changes, memories of relevant past experiences must be updated to form new representations. Current models of memory updating propose that people must first generate memory-based predictions to detect and register that features of the environment have changed, then encode the new event features and integrate them with relevant memories of past experiences to form configural memory representations. Each of these steps may be impaired in older adults. Using functional MRI, we investigated these mechanisms in healthy young and older adults. In the scanner, participants first watched a movie depicting everyday activities in a day of an actor's life. They next watched a second nearly identical movie in which some scenes ended differently. Crucially, before watching the last part of each activity, the second movie stopped, and participants were asked to mentally replay how the activity previously ended. Three days later, participants were asked to recall the activities. Neural activity pattern reinstatement in medial temporal lobe (MTL) during the replay phase of the second movie was associated with detecting changes and with better memory for the original activity features. Reinstatements in posterior medial cortex (PMC) additionally predicted better memory for changed features. Compared to young adults, older adults showed a reduced ability to detect and remember changes and weaker associations between reinstatement and memory performance. These findings suggest that PMC and MTL contribute to change processing by reinstating previous event features, and that older adults are less able to use reinstatement to update memory for changed features.

representational similarity analysis | cognitive aging | event cognition | episodic memory | change comprehension

Why do humans and other animals remember? One important reason is that features of past experiences can guide current behavior. Recent proposals suggest that a critical function of event memory (1)—also referred to as episodic memory (2)—is to guide anticipation of upcoming events (3, 4). In most cases, using event representations of past experiences facilitates predictions in similar new situations. However, when events unexpectedly change, memory-based predictions are subject to errors. Such errors impose a short-term cost but may have long-term benefits for detecting and registering that features of the environment have changed, as well as for encoding the new event features and integrating them with relevant memories of past experiences to form configural memory representations (5). Thus, memory systems must update representations when things change.

Memory updating upon change detection has been found to depend crucially on interactions between the hippocampus, the surrounding medial temporal lobes (MTL), and the rest of the cortex (6, 7). Memory updating comprises several computational operations with different neural correlates and behavioral signatures (8, 9). These include pattern completion, which is the prediction function that activates relevant prior memories and knowledge based on environmental cues; pattern separation and

differentiation, which keep features of the two experiences separate; and integration, which captures the relationships between different features of similar events. In order to integrate memory representations of events that are similar but include discrepant features, the brain needs to register the discrepancy and use it to prompt new learning. Models of memory updating propose that, when things change, pattern completion leads to prediction errors that can drive new learning, including integration processes to form configural memory representations (5, 10).

These accounts have been supported by behavioral and neuroimaging studies of the learning of word pairs and sequences of words or pictures (8, 9, 11, 12). However, compared to simple laboratory materials, real-world memory updating depends crucially on additional constraints and demands (13). Naturalistic event comprehension relies on a large set of processes working in concert, including object recognition, interpretation of biological motion, spatial orienting, and theory of mind. Event comprehension is also constrained by specific knowledge about particular classes of events and how the world works. For example, when eating a banana, one peels it before eating it. Thus, natural events exhibit correlations across features and time that are more complex than stimuli conventionally used in laboratory settings. Memory systems that capitalize on this richer structure can predict more effectively, but prediction errors and updating of naturalistic activity may function quite differently than the updating of stimuli with simpler temporal and correlational structures. It is therefore important to characterize memory updating in the context of complex, naturalistic activity.

Memory-based prediction and updating may be selectively impaired in older adults. Compared to young adults, older adults are less able to use episodic memory to make explicit judgments about previous events and to predictively guide action (14), and they are particularly prone to error when confronted with events

that include overlapping features (15). Such patterns could result from changes to any of several components of memory updating. Behavioral experiments using movie stimuli suggest that, when older adults encounter an event that begins similarly to a previous event but ends differently, they are less able than young adults to perform the memory updating necessary for effective formation of configural memory representations (5). In these studies, older and young adults watched movies that included pairs of events that began identically but could end in one of two ways. For example, the actor might unroll a yoga mat and then perform either stretches or abdominal crunches. For both young and older viewers, the ability to detect change and to remember it later along with the original activity feature was associated with better memory for the changed features. Older adults detected and remembered fewer event changes, and this was associated with greater memory disruption when a change occurred. These results suggest that, when change is experienced, prediction based on episodic retrieval can drive new learning through the formation of configural memory representations. These results further suggest that this mechanism is less functional in older adults, but the behavioral data alone leave uncertainty about where this breakdown occurs.

Neuroimaging data indicate that patterns of brain activity present while encoding new information are reinstated when this information is recollected, both for simple laboratory materials (e.g., refs. 16 and 17) and for more complex stimuli such as movies of everyday activities (18, 19). This effect is usually the strongest in the posterior areas of the default network (DN) (20), more specifically part of the posteromedial cortex (PMC) that includes the posterior cingulate cortex (PCC) and retrosplenial cortex (Rsp), and in the medial temporal lobe (MTL), including the parahippocampal cortex (PHC) and hippocampus. These regions are sometimes referred to as the posterior medial system (21) or contextual association network (22) due to their strong involvement in long-term memory recollection, particularly when episodic representations of everyday events must be remembered from visual cues (13, 23).

The hippocampus shows large metabolic alterations and volume loss in aging (24), making functional change in the MTL a potential source of age-related differences in the episodic memory processes that enable the formation of configural memory representations. In addition, the PMC undergoes substantial metabolic and structural change in aging (25), with the integrity of its functioning related to better cognitive abilities in older adults (26). These considerations make the MTL and PMC strong candidates for supporting the reinstatement of event features when encountering a new event that is similar to a previous one. However, there is no evidence to date establishing whether the reinstatement of brain activity patterns facilitates the processing of changes in naturalistic events, nor is there evidence regarding how pattern reinstatement in these regions differs between older and young adults.

In the present study, we aimed to directly assess the role of retrieving episode-specific event features when encoding a new event that was similar to an earlier event. To do so, we used functional MRI (fMRI) in combination with representational similarity analysis (RSA) (27) to assess whether the reinstatement of brain activity patterns associated with past events can facilitate the processing of changes during the perception of new events in older and young adults. We used a task adapted from ref. 5. During fMRI scanning, healthy young and older adult participants viewed two movies of discrete everyday activities, described as two days of an actor's life (hereafter referred to as day 1 and day 2). Together, the activities formed a narrative of the actor's day. Each activity was made up of two segments: an initial "cue" segment that was always the same on day 1 and day 2 and an ending "postdivergence" segment that either repeated or changed on day 2 (Fig. 1). The day 1 movie consisted of 45 activities. The day 2 movie depicted activities that were either repeated exactly (15 activities) or began the same but ended differently (30 activities). We stopped each day 2 movie after the initial cue segment (i.e., before any change) and asked participants to mentally replay the activity ending seen in the day 1 movie. After this "reinstatement" phase, participants viewed the ending of the day 2 activity. When the day 2 movie stopped after each activity ending, participants were asked if they remembered what happened in the day 1 movie and whether the day 2 activity ending included a repeated or changed feature (a measure of change detection). We then used RSA to determine the similarity of brain activity patterns in PMC and MTL between the day 1 viewing and day 2 reinstatement of activity endings by computing a reinstatement score for each activity and participant.
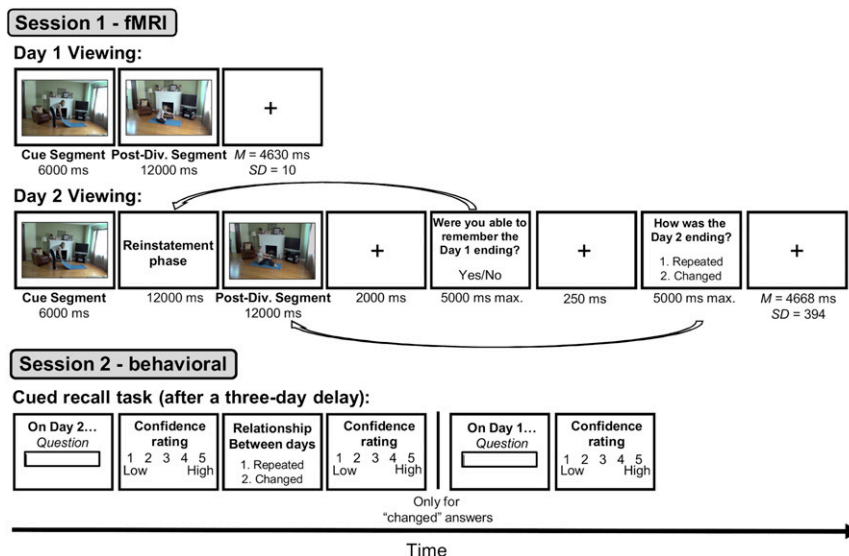
Fig. 1. Trial structure of the tasks. A more detailed description of the materials and procedure is provided in *Materials, Design, and Procedure* in the main manuscript and *SI Appendix*, sections 1.2 and 1.3. Post-Div., postdivergence.

Three days later, participants were given an unscanned cued recall test for the features of activities viewed in the day 2 movie (Fig. 1). In this memory test, participants were first asked about a feature of the activity (e.g., "What did the actor do on the exercise mat?") and then were asked whether that activity repeated or changed from day 1 to day 2. If they reported that the activity had changed, they were asked to recall the day 1 feature (*SI Appendix*, section 1.9, provides information on recall scoring).

We hypothesized that stronger day 2 reinstatement of day 1 MTL and PMC activity patterns would be associated with better change detection, better subsequent recall of the changed features, and better subsequent recollection that a change had occurred (including what the changed feature had been in the day 1 movie). Furthermore, given the decline of MTL and PMC functional integrity with aging, we expected that these associations between reinstatement and change detection, memory for changed activity features, and memory for change itself would be stronger for young than older adults and that this difference might be partly explained by diminished ability in older adults to retrieve event memories in the service of creating configural memory representations.

Results

All analyses of memory performance and neural pattern reinstatement effects were computed using linear mixed-effects models with subjects and activities as random effects. Logistic models were used when the dependent variable was binary (*SI Appendix*, section 1.8, provides more details).

Memory Performance and Change Classifications.

During day 2 viewing in the scanner, participants were asked after each activity whether they had successfully reinstated the day 1 activity ending and whether its day 2 ending was the same as on day 1 or had changed (Fig. 1). The reported rates of reinstatement success were higher for older than young adults, but older adults were less accurate at detecting when activities had changed. In young but not older adults, self-reported reinstatement predicted change detection accuracy. These results suggest that older adults were overconfident compared to young adults and less able to use subjective features of reinstatement to detect changes (*SI Appendix*, section 2.1.1, provides a detailed statistical report).

We examined performance in the unscanned cued recall task to determine whether remembering change and the original day 1 activity was associated with better memory for the changed day 2 features and whether this was affected by age. Participants attempted to recall event features from the day 2 movie and then were asked whether that event had changed from day 1 to day 2. When participants indicated that an event had changed, they were asked to recall the day 1 feature. Change could therefore be remembered with recall of day 1 features (change recollected), remembered without recall of day 1 features (change remembered but not recollected), or not remembered at all.

Models including fixed effects of age group and activity type indicated that older adults recalled fewer day 2 features than young adults [$\chi^2(1) = 9.61$, $P = 0.002$] and that this effect of age did not differ between repeated and changed activity types [$\chi^2(1) = 0.37$, $P = 0.54$; Fig. 2]. To examine the association between change recollection and day 2 recall, we fitted another model with fixed effects of age group and activity type but with levels for changed activities corresponding to each type of memory for change. Both age groups recalled changed activities less accurately than repeated activities when change was not remembered at all or remembered but not recollected (smallest z ratio = −7.64, $P < 0.001$). However, when participants recollected change, recall was higher than for repeated activities (z ratio = 5.95, $P < 0.001$). The estimated probabilities of change recollection were lower for older ($b = 0.27$, 95% CI = [0.19, 0.36]) than young ($b = 0.38$, 95% CI = [0.29, 0.48]) adults
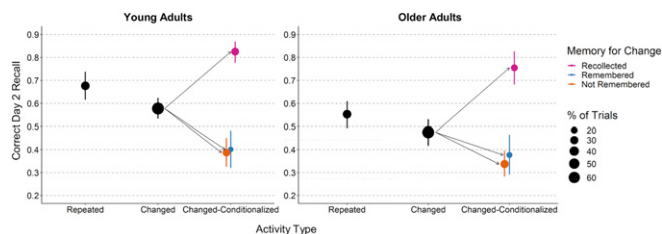
Fig. 2. Mean probabilities of correct day 2 recall. Error bars are bootstrap 95% CIs. Change could be remembered with recall of day 1 features (recollected; purple points), remembered without recall of day 1 features (remembered; blue points), or not remembered at all (not remembered; orange points). Point areas for conditional cells reflect the relative proportions of observations in each cell.

[$\chi^2(1) = 4.70$, $P = 0.03$]. Thus, both age groups showed enhanced recall of day 2 features when change was recollected, but older adults experienced this benefit on fewer trials.

For both young and older adults, self-reported successful reinstatement of day 1 features was associated with better recall of the changed day 2 features. However, this effect was not significant after controlling for variation in change recollection, indicating that self-reported successful reinstatements predicted better recall of changed day 2 features because those reinstatements also predicted better memory for change and recall of the day 1 activity feature at test (*SI Appendix*, section 2.1.1). When participants could not recall changed activity features, they were likely to erroneously intrude features from the corresponding activities viewed on day 1. Analyses of such day 1 intrusion rates generally mirrored the rates of correct day 2 recall (*SI Appendix*, section 2.1.2).

Representational Similarity Measures of Neural Memory Reinstatement.

To assay the neural reinstatement of activity-specific day 1 features following cue segments on day 2, we compared neural activity patterns in the MTL and PMC during day 1 viewing to the patterns from attempted reinstatement of day 1 activities. Patterns were analyzed at the level of parcels in the 17 networks/300 parcels cortex parcellation map from ref. 28, focusing on PMC and MTL parcels (*SI Appendix*, Fig. S1).

To extract patterns for each day 1 postdivergence segment and day 2 reinstatement attempt for each participant, we averaged the BOLD signal for each voxel over the 9th to 14th scans (11.97 to 18.62 s) after the beginning of the cue segment for each activity; this interval encompasses the fMRI response to the day 1 postdivergence segment/day 2 reinstatement phase, accounting for shift due to hemodynamic lag. We then computed reinstatement Z-scores that quantified the degree to which reinstatement activation patterns are more similar to their matching day 1 activity encoding activation pattern than to the others (18, 19) (Fig. 3). Reinstatement Z-scores for each parcel within each ROI were averaged, resulting in two scores for each activity for each participant, one for the MTL and one for the PMC.

Reinstatement Z-scores were mostly positive, indicating that participants were able to reinstate activity-specific neural activation patterns (Fig. 4A). Linear models with no fixed effect and reinstatement Z-scores as dependent variables indicated that the intercept was significantly above zero for both the PMC ($b = 0.17$, 95% CI = [0.12, 0.23], t-value = 6.49, $P < 0.001$) and MTL ($b = 0.14$, 95% CI = [0.08, 0.20], t-value = 4.77, $P < 0.001$). Similar models with age group added as a fixed effect revealed no age differences [PMC, $\chi^2(1) = 0.07$, $P = 0.79$; MTL, $\chi^2(1) = 2.01$, $P = 0.16$]. Follow-up analyses on the individual parcels within the cortex parcellation map (28) indicated significant reinstatement effects in many parcels for both age groups (*SI Appendix*, Fig. S2). Only one parcel within the two ROIs showed
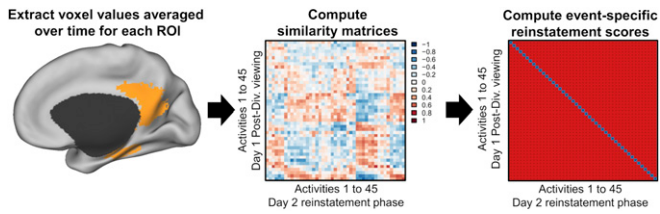
Fig. 3. Multivariate voxel analyses. After averaging voxel values over time in the parcels of interest during the day 1 postdivergence segments and day 2 reinstatement phases for each activity and participant, we correlated voxel values in the parcels of interest for each activity during day 1 viewing with the corresponding voxel values for all of the activities during day 2 reinstatement. The resulting correlation coefficients can be plotted in similarity matrices as illustrated. We then computed event-specific reinstatement scores by calculating the differences between each of the on-diagonal values indicated in blue and the off-diagonal values indicated in red. To calculate the distribution of this measure under the null hypothesis of no reinstatement, we randomly permuted the labels of the day 2 activities (i.e., the columns in the middle) 1,000 times and recomputed the correlation difference for each random permutation. The final reinstatement Z-score was the ranking of the actual (unpermuted) difference score relative to its null distribution, transformed to a Z-score.

a significant age difference in the reinstatement effect (left MTL parcel 144; *SI Appendix,* Table S1).

We then fitted models with between- and within-participant reinstatement Z-scores for changed activities, as well as age group, as fixed effects. Between-participant reinstatement Z-scores were mean reinstatement Z-scores for the changed activities of each participant across all changed activities for that participant. These allowed us to examine whether participants who reinstated day 1 neural activity patterns more strongly also recall day 2 features more accurately. Note that the grand mean (i.e., the mean of the mean reinstatement Z-scores) was subtracted from all observations for plotting. Within-participant reinstatement Z-scores were computed by centering reinstatement Z-scores for the changed activities within each participant (i.e., the mean of reinstatement Z-scores from all changed activities of that participant was subtracted from the reinstatement Z-score of each changed activity). These allowed us to examine whether day 2 activities with higher reinstatement Z-scores (independent of the mean reinstatement of the participants) were associated with better subsequent memory for day 2 features. In addition, because reinstatement Z-scores across parcels were only moderately correlated (*SI Appendix,* Table S2), we performed similar analyses but examined the effect of each individual PMC and MTL parcel on day 2 recall performance above and beyond the effects of all of the other parcels in the ROI. This procedure allowed us to examine whether reinstatement in specific parts of the PMC or MTL (such as the hippocampus) predicted behavioral performance. For brevity, only summarized results of these latter analyses are presented below (*SI Appendix,* sections 2.2.2 and 2.2.3, provide a more detailed statistical report).

Between-participant differences in reinstatement Z-scores were related to memory performance and subjective experience. We first examined whether RSA reinstatement Z-scores were correlated with self-reported reinstatement success across participants (Fig. 4 *B, Left*). Participants with higher mean PMC reinstatement Z-scores rated more of their neural reinstatements as successful [$\chi^2(1) = 5.44, P = 0.02$]. Although this effect did not interact with age group [$\chi^2(1) = 0.89, P = 0.35$], it was driven by specific PMC parcels in young but not older adults (*SI Appendix,* section 2.2.2). There was also a significant effect of mean reinstatement Z-score
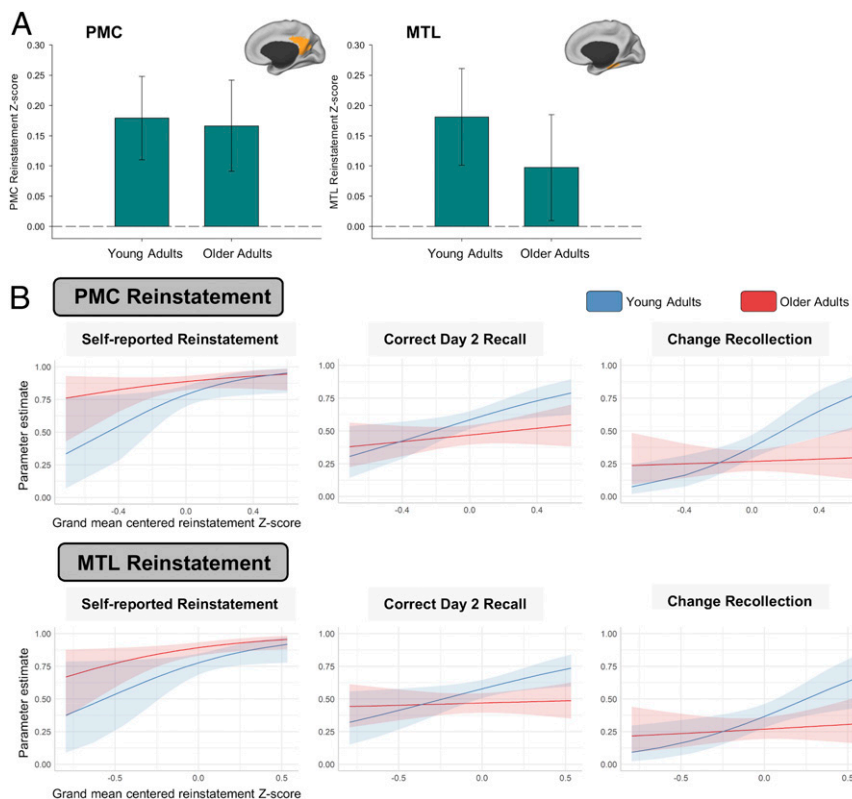
Fig. 4. (*A*) Parameter estimates for mean reinstatement Z-scores in the PMC and MTL by age group. The error bars are 95% CIs. (*B*) Parameter estimates for the between-participant associations between mean PMC/MTL reinstatement Z-scores and behavioral memory measures. The shaded regions are 95% CIs.

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for the MTL [$\chi^2(1) = 9.02$, $P = 0.003$] that did not interact with age group [$\chi^2(1) = 0.10$, $P = 0.75$] and was not driven by specific parcels. Further, mean PMC and MTL reinstatement Z-scores were correlated with the accuracy of change detection judgments in young but not older adults. Reinstatement in different PMC parcels both positively and negatively predicted change detection in each age group, with more parcels being negatively than positively associated with change detection for older adults (*SI Appendix*, sections 2.2.1 and 2.2.2), suggesting that older adults were less able to use reinstated activities to detect changed features.

We next correlated the mean reinstatement Z-scores for changed activities with correct day 2 recall performance (Fig. 4 *B*, *Middle*). Participants with higher PMC mean reinstatement Z-score had more accurate recall of day 2 features [$\chi^2(1) = 5.43$, $P = 0.02$], and this effect did not interact with age group [$\chi^2(1) = 1.85$, $P = 0.17$]. For the MTL, between-participant mean reinstatement Z-scores did not predict day 2 recall [$\chi^2(1) = 2.62$, $P = 0.10$], and reinstatement Z-scores did not interact with age group either [$\chi^2(1) = 2.78$, $P = 0.09$]. Examining the effects of individual parcels revealed that these between-participant effects were not driven by specific PMC or MTL parcels. Analyses of day 1 intrusions during day 2 recall of changed activities are provided in *SI Appendix*, sections 2.2.1 and 2.2.2.

Third, we examined whether reinstatement Z-scores predicted change recollection (Fig. 4 *B*, *Right*). Given that day 2 recall performance was comparable when change was remembered without day 1 recall and when change was not remembered at all (Fig. 2), we collapsed these cells here and in subsequent analyses into the category "change not recollected." Consistent with day 2 recall, mean between-participant PMC reinstatement was positively associated with change recollection [$\chi^2(1) = 4.44$, $P = 0.04$], but the effect was qualified by an interaction with age group [$\chi^2(1) = 4.71$, $P = 0.03$]. There was a significant positive association for young adults [$\chi^2(1) = 8.05$, $P = 0.005$] but not for older adults [$\chi^2(1) = 0.09$, $P = 0.76$]. Analyses of individual-parcel Z-scores revealed that the effect was driven by specific parcels in the young adults only (*SI Appendix*, section 2.2.2). There was a significant effect of mean reinstatement Z-score in the MTL [$\chi^2(1) = 4.05$, $P = 0.04$] that did not interact with age group [$\chi^2(1) = 3.01$, $P = 0.08$], indicating that participants with higher mean MTL reinstatement Z-scores had a better change recollection accuracy.

Finally, because between-participant differences in mean PMC reinstatement Z-scores for young adults were positively related to both day 2 recall of changed features and to change recollection, we examined whether the association between reinstatement Z-scores and day 2 recall accuracy for the changed activities could be explained by change recollection. This model included change recollection accuracy and mean between-participant PMC reinstatement Z-score as fixed effects (*SI Appendix*, Fig. S3, shows the associations between mean reinstatement Z-scores and day 2 recall and the unique contribution of change recollection to day 2 recall). With both reinstatement Z-scores and change recollection in the model as fixed effects, PMC reinstatement no longer predicted day 2 recall [$\chi^2(1) = 1.69$, $P = 0.19$]. However, change recollection was still positively associated with day 2 recall [$\chi^2(1) = 147.40$, $P < 0.001$]. The interaction between reinstatement Z-scores and change recollection accuracy was not significant [$\chi^2(1) = 2.10$, $P = 0.15$]. This is consistent with the possibility that the association between reinstating day 1 activities during day 2 viewing and subsequent day 2 recall is mediated by recollecting that the activity had changed. However, the present design does not allow for strong causal conclusions about this potential mediation.

Within-participant differences in reinstatement Z-scores were related to memory performance. Between-participant analyses informed how individual differences in reinstatement Z-scores were related to

behavioral performance. To assay whether activity-to-activity variation in reinstatement within a person was related to subsequent memory, we conducted a second set of analyses. First, regarding day 2 recall, neither the effect of mean reinstatement Z-scores in the PMC and MTL nor the interaction with age group was significant [largest $\chi^2(1) = 2.23$, $P = 0.14$; *SI Appendix*, Fig. S4]. However, analyses of individual parcels revealed that reinstatement Z-scores in two PMC parcels were positively associated with day 2 recall, whereas one other parcel showed the opposite effect, and no interaction with age group (*SI Appendix*, section 2.2.3). There was no significant effect of individual parcel reinstatement, nor was there an interaction with age group, in the MTL. No significant effects were found for either the mean PMC or MTL or individual-parcel reinstatement Z-scores regarding change recollection, self-reported reinstatement success, change detection accuracy, or day 1 intrusions onto day 2 recall [largest $\chi^2(1) = 3.01$, $P = 0.08$], with the exception of the interaction between age group and mean PMC reinstatement Z-score for change detection accuracy [$\chi^2(1) = 4.63$, $P = 0.03$]. Reinstatement Z-scores were not related to change detection accuracy in the young adults [$\chi^2(1) = 0.08$, $P = 0.77$], but greater mean PMC reinstatement predicted poorer change detection in the older adults [$\chi^2(1) = 4.87$, $P = 0.03$]. Thus, apart from day 2 recall of changed activities, there was no evidence for a beneficial within-participant relationship between neural pattern reinstatement and behavioral memory performance in either age group.

Mass Univariate Analyses. To further investigate age differences in the processing of changed day 2 activities during viewing, we performed mass univariate fMRI analyses using general linear models, as described in *SI Appendix*, section 1.6. Many models of memory updating propose that novelty detection and prediction error are critical components of memory updating when encountering changes (5, 7, 10). Consequently, we specifically examined the difference in the neural response between viewing of changed and repeated activity endings (the postdivergence segments). Across all participants, we found more activity for changed than repeated endings in clusters mainly located in the lateral prefrontal cortex and, at a lower threshold, in the bilateral anterior hippocampus (*SI Appendix*, Figs. S5 and S6). A two-sample *t* test showed that this neural response did not differ between age groups (no cluster was activated above threshold). In addition, neural activity was not parametrically modulated by reinstatement Z-scores during the changed activity epochs in any brain region for either age group (again, no cluster was activated above threshold).

To further assess the proposal that hippocampal responses to novelty are a critical component of memory updating when experiencing changes in events (e.g., ref. 10), we next examined whether between-participant differences in hippocampal response intensity while viewing changed versus repeated activity endings predicted reinstatement Z-scores and behavioral measures. Results showed no association between hippocampal response intensity and either PMC or MTL reinstatement Z-scores. At the behavioral level, hippocampal responses were only positively associated with change detection during day 2 viewing. No interaction with age group was significant (detailed in *SI Appendix*, section 2.3).

Finally, an unexpected finding of the RSA analyses was that reinstatement Z-scores did not differ across age groups. To examine whether there might still have been age-related differences in how participants initially perceived the activities, we used a pattern classifier, which showed that the voxelwise distribution of activation in the PMC and MTL differed between young and older adults (*SI Appendix*, sections 1.7 and 2.4). Thus, although young and older adults did not differ in their neural reinstatement of day 1 activities during the day 2 reinstatement

phases (Fig. 4A), the neural activity patterns during day 1 viewing still differed between the two groups.

Discussion

In this study, attempting to reinstate features of a relevant previous event during comprehension of a new one was associated with widespread reinstatement of fMRI activity patterns corresponding to anticipated features of the event. As hypothesized, reinstatement was associated with better subsequent memory for changed event features in the PMC. This was true for the PMC as a whole at the between-participant level and for a subset of PMC parcels at the within-participant level. When participants attempted to recall changed event features, the ability to recall what the feature had changed to was associated with being able to recollect that the feature had changed and to report what it had been previously. In addition, the positive association between neural pattern reinstatement in the PMC and memory for changed activity features was statistically explained in the young adults by their ability to recollect the original activity feature and the fact that the activity had changed. A similar pattern was seen for subjective judgments about whether participants had successfully reinstated activity features before viewing each activity's ending. In the MTL, between-participant differences in reinstatement for the ROI as a whole significantly predicted better change detection and memory for the original activity features, and the intensity of the neural response in the anterior hippocampus while viewing changed events predicted better change detection and recognition performance. However, reinstatement in the MTL was not related to better recall of the changed event features.

Neural measures of pattern reinstatement in the PMC as a whole were associated with more accurate recollection of the new information presented after the end of the reinstatement phase, information that conflicted with the previously encoded (and reinstated) features. This finding is consistent with previous studies showing that, during recollection, reinstatement of the brain activity pattern present in posterior DN areas while watching movies can predict memory for the movie content up to 1 wk later (18, 19), and with evidence for neural pattern reinstatement when rehearsing learned associations to pictures (9). The present results indicate that such reinstatement is related to the encoding of novel, unexpected event features. One possibility is that reinstatement leads to predictions, which in turn lead to a prediction error signal when events change, and then to memory updating (11). In a previous study using sequences of pictures, updating manifested as selective forgetting, or pruning, of previously encoded features (11), whereas here, memory updating was associated with better memory for previous as well as new event features. We attribute this difference to the formation of a configural representation composed of the original activity features, the changed features, and their temporal relations (5). Consistent with this idea, both neural and behavioral measures of reinstatement before encoding the change were associated with being able to recollect how the activity had changed, and neither self-reported nor neural pattern reinstatement remained significant predictors of memory accuracy for the changed features after controlling for change recollection accuracy. Forming a configural representation is related to integration of separate experiences into a common context, which is also associated with cortical reinstatement (9). It can be contrasted with differentiation, in which overlapping features are selectively deleted; differentiation acts to make experiences more distinctive rather than to merge them into a complex (29).

The PMC may play a key a role in supporting the event model representations from which predictions are generated. The PMC is part of the DN, and it was initially thought to be primarily involved in generating internal mentation, which stands in opposition with attention to the external world (30). However, there is now substantial evidence that the PMC also supports externally directed attention and event comprehension when task performance and the processing of perceptual inputs can benefit from relevant information stored in memory (31). In addition, recent studies have revealed that the transitions between activity patterns within the PMC while watching movies follow time scales ranging from seconds to minutes, closely matching how people segment movie content into distinct events (32). This supports the view that event model representations might be the means by which PMC facilitates interactions with the external world. Interestingly, at the level of individual parcels, reinstatement in some PMC parcels negatively predicted memory accuracy for the changed features, change detection performance, and self-reported reinstatement success. This suggests that the PMC might not be unitary regarding the role of its subregions in cognition, which aligns with recent speculations that some subregions might be more involved in processing perceptual inputs than memory representations (25).

As for the MTL, there is extensive evidence that this region is involved in the relational binding of information stored in memory and how it relates to perceptual inputs in order to form associative memory representations of everyday experiences (33, 34). Consistent with these findings, research has shown that peaks of activity in the hippocampus at the transition between perceived events can predict neural reinstatement in the PMC during recall (32, 35). Pattern reinstatement within the MTL in the present study might therefore reflect the relational binding of information stored in memory—whose retrieval is triggered by the cue segment—in order to form the event model that is supported by the PMC. This fits well with our results showing MTL involvement in detecting change and remembering original event features. However, MTL reinstatement did not predict memory for the changed features, suggesting that the formation of configural memory traces of everyday events relies more strongly on the contribution of cortical areas, among which PMC might play a prominent role.

Older adults were less likely than their younger counterparts to detect change and to recall the original activity features during the cued recall task. A possible explanation for this finding is that older adults are less able to use retrieved activity features when encoding changed features to form an updated configural representation that includes both features and their relationship. Previous studies of age-related deficits in change comprehension (5) and in associative memory (36) are consistent with this idea. A possible explanation for our findings is suggested by behavioral studies showing that the individuation of events during perception is impaired in older people (37): the event representations formed by older adults during the original viewing of the activities may have been less detailed than those of young adults. The finding that the spatial pattern of activation during movie viewing differed across groups is consistent with this possibility. As a result, they may have been less successful in forming configural representations when confronted with changed activities, and thus less successful in encoding and remembering changes. Although speculative, this proposal might explain why self-reported reinstatement accuracy in older adults did not predict better change detection during day 2 viewing and was not associated with fewer day 1 intrusions (*SI Appendix*, section 2.1.2) or accurate detection of changed activity features on day 2 (*SI Appendix*, section 3.2), as was the case for young adults. Further studies examining the quality of encoding during the initial viewing, for instance by asking participants to verbalize their experience while watching the day 1 movie and then relating these verbal reports to neural activity patterns, would test this possibility.

In any functional neuroimaging study comparing young and older adults, it is important to consider potential sources of artifact; these include group differences in neurovascular coupling,

head motion, and how the tasks are approached (38). Here, the fact that older adults showed robust overall neural reinstatement renders their significantly weaker relationships between neural reinstatement and behavioral memory measures particularly striking. Another caveat was that participants were instructed to reinstate previous activity features while day 2 activities were paused. Cognitive age differences are often larger when under time pressure and when self-initiated processing is required (39); therefore, the time to deliberately reflect in our study may have attenuated age differences. To generalize to naturalistic comprehension, it will be important to use converging measures that do not depend on strategic, interruptive task instructions.

In conclusion, the present results showed that the reinstatement of previously generated responses in the PMC and MTL predicted better memory for reinstated activity features and change detection, and that PMC reinstatement facilitated the encoding of related but changed activity features. This latter finding is particularly striking because the changed features conflicted with the just-retrieved features of the previous activity. We propose that retrieving activity features facilitates encoding precisely because it enables the system to register discrepancy between the predicted and encountered features. That discrepancy can drive formation of a configural representation that includes the old features, the new ones, and their relationship. This process was impaired in older adults; further, the pattern of impairment suggests that deficits in encoding a detailed memory representation of the original event might reduce older adults' ability to encode a configural representation of the changed event that includes its relationship to the previous event.

Method

The full stimulus sets for the materials used in the present experiments, anonymized data files, coded data, and R Markdown files (version 1.13; 2019) containing the analysis scripts are available on the Open Science Framework (https://osf.io/v3dqg/).

Participants. This study was approved by the Institutional Review Board of Washington University in St. Louis. All participants gave their written informed consent before participating in the study. Participants were recruited from the Washington University School of Medicine Research Participant Registry, flyers posted on campus, and word of mouth. Potential participants were initially contacted by phone for a prescreening interview. The sample included 62 healthy right-handed participants: 34 young adults (mean age, 22.85 y; SD = 2.71; range, 18 to 27 y; 22 female) and 28 older adults (mean age, 69.86 y; SD = 5.01; range, 65 to 84 y; 20 female). All older adults had a Mini-Mental State Examination (MMSE) score of 27 or above (M = 29.25, SD = 0.87; range, 27 to 30) (40). More details about recruitment and exclusion criteria are provided in *SI Appendix*, section 1.1.

Materials, Design, and Procedure. The materials were movies of a female actor performing daily activities on two fictive days in her life, which were described to participants as "day 1" and "day 2" (5). There were 45 activities, each of which was filmed in two versions (A and B) that differed on a thematically central feature (e.g., doing stretching or sit-ups on a yoga mat; Fig. 1). Each activity began with a 6,000-ms initial cue segment that was consistent across versions, followed by a 12,000-ms postdivergence segment (A or B). The version of the activity that participants saw in the day 1 movie (A or B) and whether the activity repeated or changed in the day 2 movie were both counterbalanced across participants.

Participants viewed the day 1 and day 2 movies during fMRI scanning and then returned after 3 d for the memory tests (Fig. 1). Activities in the day 1 movie appeared as continuous 18,000-ms clips that were each followed by a fixation interval. After a delay of ∼10 min, during which field map and anatomical images were collected, participants then watched the day 2 movie. All day 2 activities were paused for 12,000 ms between the cue and postdivergence segments (repeated or changed), during which participants were asked to mentally replay the day 1 ending. They were then asked whether they successfully replayed the day 1 features when the movie was stopped, and whether the activity features had changed. Finally, we collected a second set of field map images and a high-resolution T2-weighted image, taking ∼6 min. During session 2 (outside the scanner), we first tested participants' memory of the previously viewed activities using a cued recall task (Fig. 1). The recall cues for each activity appeared in the same order as the activities during each movie. We then administered a recognition test (*SI Appendix*, section 3). Finally, all participants completed a vocabulary test (41), after which older adults completed the MMSE (40). The 3-d retention interval was chosen based on pilot testing to avoid floor and ceiling effects on the memory measures. More methodological detail is provided in *SI Appendix*, sections 1.2 and 1.3.

fMRI Data Analyses. Because we had strong a priori hypotheses regarding the brain regions that would be relevant in the RSA, we employed an ROI-based analytic strategy. Specifically, we selected the PMC and MTL parcels of the DN subsystems from the 17 networks/300 parcels cortex parcellation map (28), to which we added ROIs of the left and right hippocampus. Following spatial preprocessing and prior to the RSA, data were normalized and detrended using second-order polynomials, spatially smoothed with a Gaussian kernel of 3-mm full-width at half maximum, and Z-scored. To summarize the activity within each voxel during the period of interest in each run, we performed temporal compression by averaging the 9th to 14th scans (11.97 to 18.62 s) after the beginning of each activity. This temporal compression procedure resulted in one brain image for each activity, run, and participant. (*SI Appendix*, section 1.5, provides additional details on image preprocessing for the RSA, and *SI Appendix*, section 1.6, provides a description of the mass univariate analyses.) We then compared the similarity of the brain activity patterns in each parcel between the two runs. Finally, we computed reinstatement Z-scores that quantified the degree to which reinstatement activation patterns are more similar to their matching day 1 activity encoding activation pattern than to the others (18, 19) (Fig. 3).

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