Encoding and retrieval eye movements mediate age differences in pattern completion

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Abstract

Older adults often mistake new information as ‘old’, yet, the mechanisms underlying this response bias remain unclear. Typically, false alarms by older adults are thought to reflect pattern completion – the retrieval of a previously encoded stimulus in response to partial input. However, other work suggests that age-related retrieval errors can be accounted for by deficient encoding processes. In the present study, we used eye movement (EM) monitoring to quantify older adults’ pattern completion bias as a function of EMs during both encoding and partially cued retrieval. Analysis of EMs revealed reduced encoding-related differentiation (i.e., more similar EMs across encoded images) and increased retrieval-related reinstatement (i.e., more similar EMs across encoding and retrieval) by older relative to younger adults, with both encoding and retrieval EMs predicting false alarms. These findings indicate that age-related changes in both encoding and retrieval processes, indexed by EMs, underlie older adults’ increased vulnerability to memory errors.

Keywords: memory, eye movements, aging, pattern completion

Healthy aging is accompanied by a host of cognitive changes, one of the most striking of which is a decline in the ability to differentiate among similar items, contexts, and events ¹⁻⁶. For example, whereas a young adult might easily recall the details of a recent party, an older adult might only recall the gist of that event, strung together from years of similar party experiences. One of the candidate mechanisms purported to underlie this change is *pattern separation*, a neurocomputational process whereby similar inputs are orthogonalized into distinct mnemonic representations ⁷⁻¹⁰. Relative to younger adults, older adults show a decline in pattern separation along with a shift towards *pattern completion*, a complementary process by which specific mnemonic representations are retrieved from incomplete input ^{10,11}. This bias has largely been inferred from behavioral evidence demonstrating that older adults are more likely than younger adults to incorrectly endorse a similar lure stimulus as ‘old’ e.g., ¹²⁻¹⁸. From a neurobiological standpoint, however, this effect can be attributed to age-related changes in the dentate gyrus (DG) and CA3 subregions of the hippocampus that bias older adults to respond to novel input by reactivating a similar existing representation (pattern completing) rather than forming a new representation based on unique features (pattern separating) e.g., ¹⁹⁻²¹.

Although evidence indicates that both hippocampal function and response tendencies change with age, behavioral studies leave open the question of whether lure false alarms by older adults are indeed the result of retrieval of the originally encoded similar item (i.e., that pattern completion has occurred). Alternatively, lure false alarms by older adults might reflect a more conservative response criterion, or impairments in encoding processes leading to impoverished memory representations. Thus, to address these questions more directly, the present study used eye movement (EM) monitoring in conjunction with behavioral responses to investigate how

age-related changes in encoding and retrieval processes contribute to older adults' pattern completion bias.

EMs provide a high resolution, indirect, and online measure of relational memory^{22,23}, and as such can avoid the stereotype threat that occurs when older adults are aware that their memory is being tested²⁴, see also, ²⁵. EMs have also been linked to neural processes involved in memory encoding and retrieval. For example, several studies have shown that visual sampling at encoding predicts subsequent memory success e.g., ^{26–29}, and is correlated with activity in the hippocampus³⁰, while other work has demonstrated that EMs support memory retrieval. Specifically, during retrieval, EMs shift to regions of the screen associated with salient regions of the to-be-retrieved image, even when it is not visually present e.g., ^{31–37}, and this EM-based reinstatement is correlated with both neural^{38,39} and behavioral e.g., ^{27,31,40,41} measures of memory success for review, see ^{23,42}.

EM-based reinstatement has been hypothesized to play an especially important role in memory maintenance and retrieval in older adults for review, see ²³. For example, a recent study from Wynn et al.⁴³ showed that when holding multiple items in memory over a delay, older adults shifted their gaze between regions of the screen previously occupied by those items to a greater extent than did younger adults, and this EM-based reinstatement was positively correlated with age-equivalent performance on a subsequent change detection task see also, ⁴¹. Extending this work, Vieweg and colleagues⁴⁴ found that older adults were more likely than younger adults to incorrectly identify test images on a recognition memory test (e.g., office identified as library) and that when they did so, their gaze patterns reflected their response (library) rather than the actual image (office). Together, these findings suggest that older adults spontaneously recruit EMs during memory retention and retrieval. However, whereas the relationship between EMs

and memory retrieval is preserved, and even enhanced with age, other work suggests that the ability to use gaze fixations to bind visual features during memory encoding may be disrupted. Specifically, whereas older adults make more fixations than younger adults during encoding ^{e.g., 45,46, for review, see 47}, only younger adults show a relationship between gaze fixations and hippocampal activity ⁴⁸.

Given that encoding and retrieval processes show dramatic changes as a function of age, and that EMs can reveal changes in these processes that may not be accessible to behavioral responses ^{for review, see 22,49}, the present study used EM monitoring to model age-related changes in lure discrimination as a function of changes in encoding and retrieval processes. In particular, we were interested in whether older adults' increased frequency of lure false alarms reflects a bias towards pattern completion- that is, retrieval of a previously encoded similar image- as indexed by EM-based reinstatement, and whether this response bias can be accounted for by age-related encoding inefficiencies, indexed by gaze fixations ^{see also, 27,28}.

The present study used a mnemonic discrimination task that has been shown to elicit functional gaze reinstatement (i.e., gaze reinstatement that predicts memory accuracy) in younger adults ⁵⁰. Younger and older adults repeatedly studied complex naturalistic images and were subsequently tested on degraded recognition probes. Test probes were presented briefly (<750ms) either in full or with 20-80% of the image obscured by randomly placed grey squares, and were followed by a 3s stimulus-free delay (posttest interval) prior to the recognition response. To quantify EM-based reinstatement of encoded representations, we derived two measures of encoding-retrieval EM similarity to capture reinstatement of encoding-related image features (image reinstatement), and reinstatement of encoding-related EMs (gaze reinstatement). To index encoding success, we measured the cumulative number of gaze fixations across

encoding, a measure that has been previously linked to subsequent memory^{e.g., 29,30}. Finally, we measured the similarity between EMs across identical repetitions of the same image (repetitive similarity), and across dissimilar images (idiosyncratic)⁵¹ to capture the updating (i.e., by viewing different regions of an image across repetitions) and differentiation (i.e., by viewing different regions across unique images) of mnemonic representations formed at encoding, respectively.

Based on previous evidence of an age-related bias towards pattern completion^{e.g., 12–18}, we predicted that older adults would show an increase in false alarms to lure items relative to younger adults. Moreover, we hypothesized that this bias would be accompanied by an increase in EM-based reinstatement (image and gaze) during retrieval and in cumulative gaze fixations, repetitive similarity, and idiosyncratic similarity during encoding for older adults relative to younger adults. Critically, by comparing multiple measures of encoding- and retrieval-related EMs across different test conditions and age groups, we can elucidate the component processes that underlie behavioral pattern completion, and memory errors more broadly, across the adult lifespan.

Methods

Participants

Participants were 64 young adults (YA; 43 female) aged 19–35 ($M = 23.66$, $SD = 3.85$) and 42 older adults (OA; 30 female) aged 62–88 ($M = 73.56$, $SD = 6.87$). All participants had normal or corrected-to-normal vision. Participants were recruited through the Rotman Research Institute's participant database. Data from the younger adults were reported previously in Wynn, Ryan, & Buchsbaum, 2020⁵⁰. All participants provided informed consent before participating in the experiment in accordance with the ethical guidelines of the Rotman Research Institute's

Research Ethics Board and were compensated at a rate of \$10/hr for their participation. Prior to the experiment, older adults completed the Montreal Cognitive Assessment (MoCA⁵²), a brief standardized neuropsychological test developed to screen for cognitive impairment ($M = 27.35$ ($\geq 26 = \text{pass}$), $SD = 2.26$). Twelve participants were excluded from analysis on the basis of missing data ($n = 2$ YA), below chance (50%) average performance (overall % correct; $n = 2$ YA, 3 OA), average gaze reinstatement greater than 3.5 SD from the mean ($n = 1$ YA), and failure to follow instructions ($n = 2$ YA, 4 OA). Data from the remaining 57 younger adults and 35 older adults were analyzed.

Apparatus

Stimuli were presented on a on a 1024 x 768 resolution, 19-inch Dell M991 monitor. Monocular EMs were recorded using a head mounted EyeLink II eyetracking system at 500 Hz sampling rate (SR Research Ltd., Mississauga, Canada). Eye movement calibration was accomplished using a 9-point calibration procedure, which was performed prior to the experiment. Drift correction ($>5^\circ$) was performed between trials. Saccades and blinks were defined by EyeLink as saccades greater than 0.5° of visual angle and the period in which saccade signal was missing for three or more consecutive samples, respectively. All remaining samples were classified as fixations.

Stimuli

Stimuli consisted, or 120 sets (A-B) of unique, but similar 800 x 600 pixel images (240 images total). All images were displayed against a black background. During the study phase, all images were presented in full. During the test phase, images were presented either in full or were degraded such that 20%, 40%, 60%, or 80% of the image was occluded by randomly placed 100 x 100 pixel grey squares, see Fig 1. The duration of image presentation was also manipulated,

with test images presented for 250, 500, or 750ms. Images were randomly assigned to one of 4 study/test blocks and counterbalanced across duration, degradation, and probe type (old, new). Of the 30 images presented during each study block, participants viewed 15 again as test probes (“old”). Lures from the alternate set of similar images were presented as test probes for the remaining 15 studied images.

Procedure

Fig 1. Experimental procedure. During the study period, each image was presented for 3000ms. A 2000ms fixation cross (not shown here) appeared between trials, to allow for online drift correction. Study images were presented 4 times each. During the test phase, each test probe was presented for 250, 500, or 750ms, either in full (0% degradation), or with 20%, 40%, 60%, or 80% of the image obscured by 100 x 100pixel grey squares. Test probes could be identical (old) or similar (lure) to a studied image. Following the test probe, a visual mask was presented for 50ms, after which a grey square was presented for 3000ms, during which time participants were instructed to visualize the presented image. Participants were given 3000ms to indicate whether the presented image was “old” (presented at study) or “new” (i.e., lure: similar, but not identical to an image presented at study). A 2000-6000ms fixation cross (not shown here) appeared between trials, to allow for online drift correction. Note that all images and the grey post-test interval square were presented at 800 x 600pixels on a black background; the images have been expanded here for visualization.

The current study used the same stimuli and procedure as was previously reported in Wynn, Ryan, & Buchsbaum, 2020⁵⁰. Before the start of the experiment, participants completed 6 practice trials to familiarize themselves with the experimental paradigm. During the experiment, participants completed 4 blocks of a modified mnemonic similarity task (Fig 1). During each block, participants studied, and were subsequently tested on, a set of 30 novel images. During the study phase, participants viewed each of the 30 images for 3s. Image presentation was repeated such that each study image was viewed 4 times over the course of the study phase. Image presentation order was randomized within each repetition. A 2s fixation cross was presented in between trials to allow for online drift correction. During the test phase, participants were tested on their memory for each of the 30 studied images. Test images were either old (presented during the study phase) or new (not presented during the study phase). Importantly, all new images were lures, meaning that they were similar, but not identical, to a previously studied image. Test images were presented for 250, 500, or 750ms. In addition, test images were manipulated such that the image could either be presented in full (0% degradation) or with 20%, 40%, 60%, or 80% of the image occluded by randomly placed 100 x 100 pixel grey squares. Following the presentation of each test image, a visual mask was presented for 50ms to prevent sensory persistence. Participants were then presented with an empty grey square (the same size as the images: 800 x 600 pixels) for 3s. Participants were instructed to visualize the presented image over the 3s post-test interval, after which they were asked whether the presented test image was old (viewed at study) or new (not viewed at study). Participants responses via key press. A 2-6s fixation cross was presented in between test trials to allow for online drift correction.

Eye Movement Analyses

Encoding Eye Movements

Fig 2. Illustration of the two measures of encoding EM similarity. Repetitive similarity is computed by correlating the heat maps generated from the same image viewed across four study presentations. Idiosyncratic similarity is computed by correlating the heat maps generated from different images. All density maps are smoothed and duration weighted.

To index encoding success, we calculated the cumulative number of gaze fixations summed across four repeated presentations (3s each) of each image. This measure has previously been correlated with memory accuracy ^{e.g., 26–29}, and hippocampal activity ³⁰. We additionally computed two measures of encoding similarity (Fig 2) using the R eyesim package (<https://github.com/bbuchsbbaum/eyesim>), see SI Appendix for further details. To index the extent to which participants updated their memories across encoding to form complete representations of each image, we computed the similarity between EMs elicited by the same image across four identical repetitions (*repetitive similarity*). Furthermore, to quantify the extent

to which participants formed differentiated memory traces for each image, we additionally computed the similarity between EMs across unique images (*idiosyncratic similarity*). High repetitive and idiosyncratic similarity scores would thus reflect viewing that does not change (update) across repetitions and does not differentiate among dissimilar images. Further details regarding these measures are provided in the SI Appendix.

Retrieval Eye Movements

Fig 3. Illustration of the three measures of EM-based reinstatement. The heat maps reflect fixation density, with warm values indicating areas of high fixation density. Probe reinstatement is computed by correlating the heat map generated from the test probe weighted by the fixations of all participants (S All) viewing the same image during study and a single participant (S1) subsequently reinstating that image (or a similar lure) during the post-test interval. Image reinstatement is computed by correlating the heat map generated from the cumulative fixations of all participants (S All) viewing a single image over four study presentations and a single participant (S1) subsequently retrieving that image (or a similar lure) during the post-test interval. Gaze reinstatement is computed by correlating the heat map generated from the cumulative fixations of a single participant (S1) viewing a single image over four study presentations and subsequently retrieving that image (or a similar lure) during the post-test interval. All density maps are smoothed and duration weighted. Figure re-presented from Wynn, Ryan, & Buchsbaum (2020) ⁵⁰.

Following the analysis procedure described in Wynn, Ryan, & Buchsbaum (2020)⁵⁰, we computed three separate measures of EM-based retrieval-related reinstatement (Fig 3). Although we were primarily interested in EM-based reinstatement of information from long term memory, our first measure, *probe reinstatement*, was aimed at quantifying the extent to which EMs during the post-test interval reflect reinstatement of the just-presented test image. To quantify the extent to which EMs during the post-test reinstate the previously encoded same (in the case of old test probes) or similar (in the case of lure test probes) image, we computed *image reinstatement* by correlating within-participant retrieval gaze patterns with across-participant encoding gaze patterns. Based on the theory that EMs both encode and are themselves embedded in mnemonic representations^{53,54}, we additionally computed *gaze reinstatement* to quantify the extent to which EMs during the post-test interval reinstate the previously encoded same or similar image *and* the corresponding encoding operations (i.e., EMs). This measure was computed by correlating within-participant retrieval gaze patterns with within-participant encoding gaze patterns. Importantly, whereas a high image or gaze reinstatement score for an old image indicates reinstatement of the same image, a high score for a lure image indicates reinstatement of the similar lure image.

All reinstatement scores (including repetitive and idiosyncratic similarity) were computed by correlating duration-weighted fixation density maps using Fisher-transformed Pearson correlations (details regarding density map computation can be found in the SI Appendix). To ensure that reinstatement scores were driven by memory and not by generic viewing patterns (e.g., center bias), each within-participant density map was additionally correlated with 50 other randomly selected across-participant density maps. The values resulting from this permutation were then averaged to obtain a control (across image) reinstatement score, which was then

subtracted from the corresponding raw reinstatement score, yielding a final difference score. Thus, all reported reinstatement scores (with the exception of the idiosyncratic measure, which reflects only the permuted similarity score) control for image-invariant viewing tendencies, including the tendency to fixate the center of the screen.

Data Analysis

To investigate factors contributing to performance on the recognition task, we ran a generalized linear mixed effects model (GLMM; glmer of package lme4)⁵⁵ with a bobyqa optimizer on trial-level accuracy (correct, incorrect, with a binomial distribution and logistic link function), with age (younger adult, older adult), probe type (old, lure), degradation (0%, 20%, 40%, 60%, 80%) and duration (250ms, 500ms, 750ms) as independent variables. Duration and degradation were z-scored and age and probe type were recoded as 0 (older adult, old) and 1 (younger adult, lure) to allow for simple effects analysis of significant interactions. Random intercepts were included for participant and item.

To investigate age differences in EMs during encoding, we ran t-tests (and Wilcoxon signed-rank tests where data were non-normally distributed) on the cumulative number of gaze fixations, repetitive similarity (i.e., similarity between gaze patterns across identical study repetitions), and idiosyncratic similarity (i.e., similarity between gaze patterns across images), with age as an independent variable. All measures were averaged across the four presentations of each image. To examine age differences in EMs during retrieval, we ran ANOVAs on gaze reinstatement, image reinstatement, and probe reinstatement, with age and probe type as independent variables.

Finally, to investigate the relationship between eye movements and mnemonic performance, we ran two additional GLMMs modeling accuracy as a function of age, probe type, and EMs during encoding and retrieval, respectively, using the same parameters as the GLMM reported above.

All models were built using a backward selection approach, starting with a maximal model which included fixed effects for all variables and their interactions, as well as random intercepts for participant and item. Models were compared using likelihood ratio tests with $\alpha = 0.05$, such that non-significant fixed effects were removed from the model in a stepwise fashion until no further model changes resulted in a significant likelihood ratio test. Results of the final best fit models arrived at via model comparison are reported, with significance values approximated with the lmerTest R package ⁵⁶. Visualizations of GLMM data were created using the ‘open-visualizations’ repository on GitHub ⁵⁷.

Results

Behavioral Results

Fig 4. Left: mean accuracy (overall % correct) by degradation, duration, and age (younger adult (YA), older adult (OA)); Right: mean accuracy by degradation, probe type, and age. Error bars represent 95% confidence intervals.

Table 1.					
Fixed Effects					
	β	95% CI	SE	z	p
(Intercept)	2.15	1.94, 2.36	0.11	20.53	<.001 ***
Duration	0.22	0.14, 0.29	0.04	5.53	<.001 ***
Degradation	-0.92	-1.08, -0.76	0.08	-11.50	<.001 ***
Age	0.15	-0.09, 0.40	0.13	1.17	>.05
Probe Type	-2.13	-2.30, -1.94	0.09	-23.39	<.001 ***
Duration x Degradation	-0.08	-0.15, 0.00	0.04	-2.04	0.041 *
Duration x Age	-0.05	-0.15, 0.05	0.05	-0.87	>.05
Degradation x Age	0.40	0.22, 0.59	0.09	4.26	<.001 ***
Degradation x Probe Type	0.59	0.41, 0.77	0.09	6.62	<.001 ***
Age x Probe Type	0.78	0.57, 1.02	0.11	6.86	<.001 ***
Duration x Degradation x Age	0.12	0.02, 0.22	0.05	2.38	0.017 *
Degradation x Age x Probe Type	-0.53	-0.75, -0.31	0.11	-4.70	<.001 ***
Total observations = 10998					
	Variance		SD		
Random Effect for Participant (Intercept)	0.15		0.39		
Random Effect for Item (Intercept)	0.37		0.61		
Model equation: Accuracy ~ Duration X Degradation X Age + Degradation X Probe Type X Age + (1 Participant) + (1 Image)					

Results of the final best fit model of accuracy arrived at via model comparison (Table 1) revealed significant effects of duration and degradation in older adults (Fig 4A), reflecting improved performance with increasing test probe duration and visual input (i.e., decreasing degradation). The effect of degradation was significantly attenuated in younger adults for old images (degradation X age; Fig 4B), suggesting that highly degraded test probes had a greater negative effect on the performance of older adults than that of younger adults. Significant interactions of duration X degradation and duration X degradation X age further indicated that whereas older adults showed a slightly enhanced effect of test probe degradation at longer test probe durations, younger adults showed a reduced effect (Fig 4A). That is, younger, but not older adults, were able to exploit longer test probe durations to reduce the negative effect of test probe degradation on performance. In older adults, the effect of degradation was significantly attenuated for lure images (degradation X probe type; Fig 4B), reflecting a possible criterion

shift at high levels of test probe degradation. This effect (degradation X age X probe type; Fig 4B) was reduced, and even slightly reversed, in younger adults, such that the effect of degradation on accuracy was slightly increased for lure images relative to old images (for which performance was at ceiling at low levels of degradation). Finally, we observed a significant effect of probe type in older adults, reflecting greater performance for old images compared to lure images, and this effect was significantly attenuated in younger adults (age X probe type; Fig 4B). Consistent with the well-established age-related bias towards pattern completion, this finding indicates that older adults were disproportionately impaired at rejecting lure images relative to younger adults. Indeed, a Welch t -test on mean response bias scores (mean accuracy for old images - mean accuracy for lure images) revealed a significant effect of age ($t(53.88) = 3.19, p = .002, d = 0.75$), with older adults showing a more positive response bias than younger adults ($M_{OA} = 34.2, M_{YA} = 18.73$).

Eye Movement Results

Given that older adults' behavior was consistent with an age-related shift towards pattern completion, we next sought to investigate whether this response bias was accompanied by changes in encoding- and/or retrieval-related EMs. To this end, we assessed age differences across 3 measures of encoding-related EMs, intended to capture different processes (e.g., relational binding and differentiation) that might contribute to successful encoding, and 3 measures of retrieval-related EMs that have been previously linked to retrieval success.

Eye Movements at Encoding

Cumulative Gaze Fixations

Prior work has indicated that older adults make more gaze fixations than younger adults during encoding^{e.g., 45,46}. In line with this work, we observed a significant difference in

cumulative gaze fixations between younger and older adults ($M_{OA} = 35.24$, $M_{YA} = 31.57$; $W = 1359$, $z = 2.90$, $p = .004$) indicating that older adults made significantly more fixations during encoding than younger adults.

Repetitive Similarity

To further investigate how younger and older adults encode images across identical repetitions, we computed the similarity between gaze patterns elicited by the same image across four study presentations. Compared with younger adults, older adults were more similar in their gaze patterns across identical repetitions of the same image ($M_{OA} = 0.24$, $M_{YA} = 0.21$; $t(90) = 2.67$, $p = .009$, $d = 0.57$). That is, whereas younger adults varied their scanning patterns, presumably to update their memory representations, older adults continued to view the same regions across repeated presentations of the same image.

Idiosyncratic Similarity

As a final measure of encoding, we computed the similarity between gaze patterns across unique images to index the distinctiveness of mnemonic representations formed at encoding. As with the repetitive similarity measure, older adults executed more similar gaze patterns across dissimilar images compared with younger adults ($M_{OA} = 0.08$, $M_{YA} = 0.07$; $W = 1266$, $z = 2.16$, $p = .031$), reflecting a decrease in EM-based differentiation.

Eye Movements at Retrieval

Given that younger and older adults differed significantly in the manner in which they viewed images at encoding, we subsequently tested whether retrieval-related reinstatement of the test probe image (probe reinstatement), reinstatement of the originally encoded image (image reinstatement), and reinstatement of the originally encoded image along with the corresponding EMs (gaze reinstatement) differed as a function of age (younger, older) and probe type (old,

lure). To ensure that our reinstatement measures captured image-specific reinstatement, that is, reinstatement of the corresponding encoding or test probe image that is greater than reinstatement of other images, we compared raw similarity values (within-participant, within-image) to permuted similarity values (within-participant, across-image) for each age group. Reinstatement scores are reported as the difference between raw and permuted similarity values, such that positive scores indicate reinstatement of the same image that is greater than chance (i.e., reinstatement of other images).

Probe Reinstatement

Probe reinstatement (raw probe reinstatement) was significantly greater than chance (permuted probe reinstatement) in both younger ($t(56) = 12.96, p < .001, d = 0.84$) and older adults ($t(34) = 14.73, p < .001, d = 1.76$). Moreover, results of the ANOVA on probe reinstatement revealed a significant main effect of age ($M_{OA} = 0.05, M_{YA} = 0.04; F(1,90) = 14.24, p < .001, \eta^2 = .14$), reflecting greater probe reinstatement by older adults relative to younger adults. The main effect of probe type ($F(1,90) = 0.59, p > .5$) and the interaction of age X probe type ($F(1,90) = 2.01, p = .16$) were not significant.

Image Reinstatement

Both younger and older adults showed evidence of image reinstatement that was significantly greater than chance (YA: $t(56) = 13.79, p < .001, d = 0.53$; OA: $t(34) = 13.41, p < .001, d = 1.08$). Image reinstatement was significantly greater in older adults relative to younger adults ($M_{OA} = 0.04, M_{YA} = 0.03; F(1,90) = 11.13, p = .001, \eta^2 = .11$), but did not differ significantly as a function of probe type ($F(1,90) = 1.96, p = .165$; probe type X age: $F(1,90) = 1.41, p = .238$).

Gaze Reinstatement

As with probe and image reinstatement, gaze reinstatement was significantly greater than chance in both age groups (YA: $t(56) = 3.17, p = .002, d = 0.41$; OA: $t(34) = 4.3, p < .001, d = 0.84$). Gaze reinstatement significantly differentiated old images from repeated images ($F(1,90) = 27.63, p < .001, \eta^2 = .235$), with significantly greater gaze reinstatement for repeated images ($M_{Repeated} = 0.04, M_{Lure} = 0.02$). Notably, although older adults had numerically higher gaze reinstatement values than younger adults ($M_{OA} = 0.04, M_{YA} = 0.03$), this difference was not significant ($F(1,90) = 0.56, p > .05$), nor was the interaction of age X probe type ($F(1,90) = 0.94, p > .05$).

Relationship Between Eye Movements and Behavior

To investigate the relationship between encoding-related EMs and accuracy, we first ran a GLMM on accuracy including all measures of encoding-related EMs (cumulative gaze fixations, repetitive similarity, idiosyncratic similarity). Duration and degradation were excluded from the model in order to reduce model complexity and allow for model convergence. Model comparison progressed in a backward fashion, beginning with all 3-way interactions of each EM measure with probe type and age. Results of the final model arrived at via model comparison are reported below.

Fig 4. Effects of encoding EMs on accuracy (hit, miss, correct rejection, false alarm) for younger adults (YA) and older adults (OA). Top row: within and between participant effects of cumulative gaze fixations, probe type, and age on accuracy. Bottom row: left: within and between participant effects of repetitive similarity and probe type on accuracy; right: within and between participant effects of idiosyncratic similarity and probe type on accuracy

Table 2.					
Fixed Effects					
	β		SE	z	p
(Intercept)	1.96	1.77, 2.16	0.10	19.80	<.001 ***
Cumulative Gaze Fixations	-0.04	-0.20, 0.13	0.08	-0.44	0.660
Probe Type	-2.00	-2.19, -1.84	0.09	-22.71	<.001 ***
Age	0.33	0.09, 0.56	0.12	2.78	0.005 **
Repetitive Similarity	-0.14	-0.23, -0.56	0.04	-3.22	0.001 **
Idiosyncratic Similarity	0.07	-0.02, 0.17	0.05	1.57	0.117
Cumulative Gaze Fixations X Probe Type	0.19	0.01, 0.37	0.09	2.09	0.036 *
Cumulative Gaze Fixations X Age	0.22	0.02, 0.43	0.10	2.17	0.03 *
Probe Type X Age	0.69	0.47, 0.92	0.11	6.10	<.001 ***
Probe Type X Repetitive Similarity	0.23	0.12, 0.33	0.05	4.31	<.001 ***
Probe Type X Idiosyncratic Similarity	-0.22	-0.34, -0.12	0.06	-4.06	<.001 ***
Cumulative Gaze Fixations X Probe Type X Age	-0.27	-0.50, -0.04	0.11	-2.32	0.02 *
Total Observations = 10998					
	<i>Variance</i>		<i>SD</i>		
Random Effect for Participant (Intercept)	0.13		0.36		
Random Effect for Item (Intercept)	0.57		0.75		
Model equation: Accuracy ~ Cumulative Gaze Fixations X Probe Type X Age + Repetitive Similarity X Probe Type + Repetitive Similarity X Age + Idiosyncratic Similarity X Probe Type + (1 Participant) + (1 Image)					

Results of the model (Table 2, Fig 4) revealed a non-significant effect of cumulative gaze fixations for older adults for old images, and this effect significantly increased as a function of age, indicating that the number of EMs executed during image encoding predicted subsequent recognition hits in younger adults, but not in older adults. The effect of cumulative gaze fixations was also increased as a function of probe type, reflecting an association between encoding EMs and correct rejections in older adults, and this effect was slightly attenuated as a function of age. There was additionally a significant negative effect of repetitive similarity on accuracy for old images, and this effect was significantly weakened and even reversed for lure images, suggesting that re-fixating the same regions across identical repetitions increased the likelihood of calling a

test probe ‘new’. Finally, there was a non-significant effect of idiosyncratic similarity on accuracy for old images and this effect was significantly reduced for lure images, demonstrating that similar gaze patterns across dissimilar images predicted false alarms to lure images. Together these findings suggest that changes in encoding-related EMs as a function of age, including an increased number of fixations, and increased consistency in gaze patterns both within and across images might contribute to the increased frequency of false alarms by older adults.

To investigate the relationship between retrieval-related EMs and accuracy, we ran an additional GLMM on accuracy including all 3 measures of retrieval-related reinstatement (probe reinstatement, image reinstatement, gaze reinstatement). Model comparison progressed in a backwards fashion. To ensure that the effects of retrieval-related EMs on accuracy were independent of the effects of encoding-related eye movements, we subsequently added each of cumulative gaze fixations, repetitive similarity, and idiosyncratic similarity to the final model in a stepwise fashion. Only cumulative gaze fixations significantly improved the fit of the model ($\chi^2 = 9.57, p = .002$; repetitive similarity: $\chi^2 = .05, p > .05$; idiosyncratic similarity: $\chi^2 = 1.52, p > .05$). Neither the addition of cumulative gaze fixations X age ($\chi^2 = 0.2, p > .05$) nor cumulative gaze fixations X probe type ($\chi^2 = 0.71, p > .05$) further improved the model fit. Results of the final model are reported below.

Fig 5. Effects of retrieval EMs on accuracy (hit, miss, correct rejection, false alarm) for younger adults (YA) and older adults (OA). Top row: within and between participant effects of gaze reinstatement, probe type, and age on accuracy. Middle row: within and between participant effects of image reinstatement, probe type, and age on accuracy. Bottom row: within and between participant effects of probe reinstatement and probe type on accuracy.

Table 3.					
Fixed Effects					
	β	95% CI	SE	z	p
(Intercept)	1.88	1.70, 2.07	0.09	19.87	<.001 ***
Gaze Reinstatement	-0.08	-0.23, 0.07	0.08	-1.03	0.304
Age	0.38	0.15, 0.61	0.12	3.29	<.001 ***
Probe Type	-1.92	-2.08, -1.76	0.08	-23.65	<.001 ***
Image Reinstatement	0.05	-0.11, 0.21	0.08	0.59	0.554
Probe Reinstatement	0.08	-0.02, 0.18	0.05	1.48	0.139
Cumulative Encoding Fixations	0.11	0.04, 0.18	0.04	3.12	0.002 **
Gaze Reinstatement X Age	0.17	-0.04, 0.38	0.11	1.61	0.107
Gaze Reinstatement X Probe Type	0.04	-0.15,0.22	0.10	0.40	0.689
Probe Type X Age	0.63	0.42, 0.84	0.11	5.97	<.001 ***
Image Reinstatement X Age	-0.20	-0.41, 0.00	0.10	-1.95	0.051
Image Reinstatement X Probe Type	-0.31	-0.50, -0.12	0.10	-3.17	0.001 ***
Probe Reinstatement X Probe Type	0.17	0.05, 0.29	0.06	2.74	0.006 **
Gaze Reinstatement X Age X Probe Type	-0.32	-0.56, -0.07	0.12	-2.54	0.011 *
Image Reinstatement X Age X Probe Type	0.30	0.06, 0.54	0.12	2.46	0.014 *
Total Observations = 10756					
	Variance		SD		
Random Effect for Participant (Intercept)	0.13		0.36		
Random Effect for Item (Intercept)	0.50		0.71		
Model equation: Accuracy ~ Gaze Reinstatement X Age X Probe Type + Image Reinstatement X Age X Probe Type + Probe Reinstatement X Probe Type + Cumulative Gaze Fixations + (1 Participant) + (1 Image)					

Results of the model (Table 3, Fig 5) revealed a significant effect of cumulative gaze fixations on accuracy, suggesting that greater exploration of images at encoding was associated with better subsequent mnemonic performance. Critically, the addition of cumulative gaze fixations to the model did not abolish the effects of retrieval-related reinstatement on performance, indicating that these effects were independent. Reinstatement of the test probe, though not predictive of accuracy for old images, had a significant effect on lure accuracy (correct > incorrect). Image reinstatement similarly had a non-significant effect on accuracy for old images. Notably, the effect of image reinstatement in older adults was significantly reduced for lure images (incorrect > correct), indicating that reinstatement of a previously encoded similar image was associated with lure false alarms in older adults. This effect was significantly

weakened in younger adults. Finally, we observed a non-significant effect of gaze reinstatement on accuracy for old images, and this effect did not change significantly for lure images in older adults. For younger adults, however, the effect of gaze reinstatement on accuracy changed significantly for lure images (false alarms > correct rejections). Thus, whereas image reinstatement was associated with increased rates of lure false alarms in older adults, gaze reinstatement was associated with increased rates of lure false alarms in younger adults ^{see also, 50}. In other words, whereas reinstating a previously encoded image is sufficient to elicit a false memory in older adults, the same response in younger adults is contingent on the erroneous retrieval of a previously encoded image via the accompanying pattern of EMs. Together these findings suggest that both the nature of reinstated representations and their relationship with behavioral performance differ as a function of age.

Discussion

Converging evidence indicates that cognitive aging can be characterized by a deficit in the ability to recollect previously learned associations or relations from memory ¹⁻⁶. But, what does such a “recollection deficit” entail? Behavioral studies have provided evidence that explicit measures like recognition and recall accuracy decline with age ⁵⁸⁻⁶⁰. However, although these behavioral responses allow us to measure the information that older adults can consciously access and use, the use of representations that may not be available to conscious introspection has remained unclear. In the present study, we used EM monitoring to compare both the intentional responses and incidental gaze patterns of younger and older adults during a recognition memory task ^{see also, 22}. Specifically, we investigated whether the well-established age-related bias towards pattern completion, indexed by an increased tendency to falsely endorse

lure stimuli as ‘old’ e.g., ^{12–18} is mediated by increased reinstatement of previously encoded stimuli during retrieval, and/or deficient processing of stimuli during encoding, both indexed by EMs.

In line with previous work ^{12–18,44}, older adults in the present study showed a response bias consistent with pattern completion. Relative to younger adults, older adults made more false alarms to lure stimuli, despite age-equivalent recognition performance for old images. Analysis of EM behavior further indicated that when cued with a partially-occluded image, both younger and older adults reinstated a specific, previously encoded image representation (i.e., gaze and image reinstatement) even in the absence of visual input, and this reinstatement was greater than would be expected by chance (i.e., reinstatement of other images). Consistent with findings from the pattern completion and EM literatures, these results indicate that both the response and gaze patterns of younger and older adults during partially cued retrieval reflect the contents of memory.

Previous research has suggested that the relationship between EMs and memory retrieval, including pattern completion, might be accounted for by EMs at encoding ^{27,28}. In the present study, older adults made a greater cumulative number of gaze fixations (i.e., across repeated presentations of the same image) than younger adults. Critically, however, gaze fixations were only predictive of recognition hits in younger adults. In line with recent findings from Liu et al. ⁴⁸ in which visual sampling was associated with encoding-related hippocampal activity and repetition-related suppression of hippocampal activity in younger adults, but less so in older adults, these findings suggest that older adults may be less effective than younger adults at using EMs to bind visual information into lasting memory representations. Instead, cumulative gaze fixations predicted correct rejection of lure images in older adults, suggesting that the mnemonic

representations built up by older adults may contain sufficient information to protect against interference effects related to similar lures.

In addition to making more fixations, older adults in the present study executed more similar gaze patterns across identical repetitions of the same image, and this effect was related to poorer subsequent memory performance. Thus, whereas younger adults continuously updated their memory representations by scanning different image regions on each presentation, older adults continued to view the same regions, either in an attempt to strengthen weak representations or re-encode forgotten details, resulting in less complete memory representations. Likewise, whereas younger adults' EMs differentiated among distinct images, older adults tended to view similar regions across images, leading to higher idiosyncratic similarity, which was negatively predictive of accuracy. These findings are consistent with evidence of dedifferentiation whereby older adults show less distinct neural activity patterns across different stimulus categories ^{e.g., 61,62}, and individual stimuli ^{e.g., 63}, and further suggest that altered viewing patterns at encoding contribute to subsequent memory deficits in older adults.

To elucidate the role of retrieval processes in older adults' mnemonic decisions, we compared probe, image, and gaze reinstatement, as well as the degree to which these measures predicted performance, across age groups. Reinstatement of the test probe image during the retrieval interval was greater in older adults compared with younger adults, particularly when the test probe image was old. Moreover, probe reinstatement was associated with the correct rejection of lure images in both groups, suggesting that EM's facilitate the comparison of presented visual input with stored memory representations ⁶⁴. Consistent with previous findings of increased EM-based reinstatement by older adults relative to younger adults ^{43, see also, 41}, older adults showed greater image reinstatement than younger adults and equivalent gaze

reinstatement, suggesting that older adults retain access to both salient features of encoded images and the EMs made to them. However, whereas reinstatement of encoding-related gaze patterns by younger adults was associated with lure false alarms, in older adults, false endorsement of lure images as ‘old’ was associated with increased reinstatement of previously encoded image content without the accompanying EMs, via image reinstatement. Extending findings of behavioral pattern completion, these results suggest that increased reinstatement of encoded image content underlies older adults’ increased tendency to falsely endorse lure images as ‘old’. Moreover, this effect could not be attributed to age-differences in encoding, suggesting that encoding and retrieval processes independently affect response behavior. Thus, although both younger and older adults use EMs to support the retrieval of previously encoded representations, the nature of those representations and the manner in which they support behavioral pattern completion differ with age. Below, we discuss these findings in the context of theories of cognitive aging.

Converging evidence suggests that memory retrieval is supported primarily by recollection-based processes in younger adults and by familiarity-based processes in older adults e.g., 65-67. Whereas recollection involves the slow and controlled retrieval of a prior stimulus or event, including contextual information such as when or how it was encoded, the faster and more automatic process of familiarity is typically divorced from such contextual experiences ^{for review,} see 66. Although behavioral studies support this distinction in the manner by which younger and older adults retrieve memories, they struggle to separate the content of those memories from the experience ^{see also,} 68. Accordingly, it has remained unclear whether the ‘recollection deficits’ experienced by older adults and expressed in their behavioral responses, like the increased tendency to falsely identify lure stimuli as ‘old’, reflect a change in the encoding of mnemonic

representations, the content retrieved from those representations, or in the processes by which those representations are retrieved.

In the present study, younger and older adults did not differ in the extent of retrieval-related reinstatement, but did show different patterns of association between reinstatement and performance, supporting a distinction between information that is retrieved and information that is used to guide explicit memory decisions. These findings suggest that older adults may have access to both the content (image reinstatement) and experience (gaze reinstatement) of a previously encoded event, but the latter is either not available, or not used to support behavioral pattern completion performance. It should be noted that we employ the term ‘experience’ here to dissociate reinstatement of encoding-related operations (i.e., EMs) from reinstatement of encoded content only; however, further research is required to support the broader assertion that EMs are related to the phenomenological experience of memory ^{see also, 69}.

Although the present results suggest that encoded image representations are stored in memory and reinstated by older adults during retrieval (as reflected by age invariant gaze reinstatement scores), it is possible that these representations are fundamentally flawed. Indeed, age differences in encoding EMs suggest that the binding of image features across encoding into complete and distinct representations is impaired in older adults, and therefore these representations may not serve the purpose of guiding explicit memory responses in older adults as they do in younger adults. This inability to leverage the reinstated experience of encoding to support performance is in line with evidence of age-related deficits in controlled retrieval ^{e.g., 70-73,} ^{for review, see 74} and suggests that the contribution of familiarity-based processes to older adults’ memory-based judgments may reflect a fundamental change in the quality or amount of detail within stored representations that then precludes the use of the recollection process, rather than

an inability to enact recollective processes itself. Indeed, other work has indicated that although older adults are more likely than younger adults to false alarm to lures, they show equivalently greater priming for old relative to lure items, suggesting that they can make use of perceptual details acquired during encoding when tested incidentally ⁷⁵. Thus, although recollective content may not be consciously accessible to older adults to support memory performance, including lure discrimination, it may be reasonably sufficient to influence EMs or performance on incidental retrieval tasks.

In conclusion, the results of the present study provide novel evidence that age differences in both encoding and retrieval processes underlie older adults' memory errors. Specifically, viewing patterns at encoding indicate that the mnemonic representations formed by older adults are less complete and distinct than those formed by younger adults. Moreover, EMs at retrieval provide further evidence that although both younger and older adults spontaneously reinstate the content (i.e., image reinstatement) and experience (i.e., gaze reinstatement) of encoding, only the content is used to support lure discrimination in older adults. Extending previous work, these findings indicate that pattern completion in younger and older adults may fundamentally differ not just in strength, but also in the content of the representations they retrieve and the manner by which those representations affect performance. Finally, the present findings are the first to show that age-related changes in encoding (i.e., cumulative gaze fixations), retrieval (i.e., gaze and image reinstatement), and comparison (i.e., probe reinstatement) processes independently contribute to age differences in pattern completion.

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