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 monitoring to quantify age-related changes in behavioral pattern completion as a function of eye movements during both encoding and partially cued retrieval. Consistent with an age-related encoding deficit, older adults executed more gaze fixations and more similar eye movements across repeated image presentations than younger adults, and such effects were predictive of subsequent recognition memory. Analysis of eye movements at retrieval further indicated that in response to partial lure cues, older adults reactivated the similar studied image, indexed by the similarity between encoding and retrieval gaze patterns, and did so more than younger adults. Critically, reactivation of encoded image content via eye movements was associated with lure false alarms in older adults, providing direct evidence for a pattern completion bias. Together, these findings suggest that age-related changes in both encoding and retrieval processes, indexed by eye movements, underlie older adults' increased vulnerability to memory errors.

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 (Chalfonte & Johnson, 1996; Grady, 2012; Grady & Ryan, 2017; Mitchell, Raye, Johnson, & Greene, 2006; Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008). 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 (Hunsaker & Kesner, 2013; Marr, 1971; McClelland, O'Reilly, & McNaughton, 1995; Yassa & Stark, 2011). Relative to younger adults, older adults appear to show a shift from pattern separation to *pattern completion*, a complementary process by which specific mnemonic representations are retrieved from incomplete input (Rolls, 2013; Yassa & Stark, 2011). This shift 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', or to pattern complete rather

than pattern separate (e.g. Ly, Murray, & Yassa, 2013; Pidgeon & Morcom, 2014; Reagh et al., 2016; Stark, Stevenson, Wu, Rutledge, & Stark, 2015; Stark, Yassa, Lacy, & Stark, 2013; Stark, Yassa, & Stark, 2010; Toner, Pirogovsky, Kirwan, & Gilbert, 2009). Specifically, as a result of age-related changes in the dentate gyrus (DG) and CA3 sub-regions of the hippocampus, older adults are more likely than younger adults to reactivate a similar existing representation (pattern completion) in response to novel input than to form a new representation based on unique features (pattern separation) (e.g. Wilson, Gallagher, Eichenbaum, & Tanila, 2006; Wilson, Ikonen, Gallagher, Eichenbaum, & Tanila, 2005; Yassa et al., 2011).

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 may reflect a more liberal response criterion (i.e., greater tendency to call items new) (Fraundorf, Hourihan, Peters, & Benjamin, 2019), or impairments in encoding processes leading to impoverished

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memory representations (Sander, Fandakova, & Werkle-Bergner, 2021). Thus, to address this question more directly, the present study used eye movement monitoring in conjunction with behavioral responses to investigate how age-related changes in encoding and retrieval processes contribute to lure false alarms by older adults. In particular, we used encoding- retrieval eye movement similarity to infer whether lure false alarms are associated with retrieval of a previously encoded similar item (i.e., pattern completion).

Eye movements provide a high resolution, indirect, and online measure of relational memory, and can provide insights into the content and processes of memory retrieval (for review, see Hannula, Althoff, Warren, Riggs, & Cohen, 2010; Ryan & Shen, 2020; Wynn, Shen, & Ryan, 2019), while avoiding the stereotype threat that occurs when older adults are aware that their memory is being tested (Rahhal, Hasher, & Colcombe, 2001), (see also Hannula, Ryan, Tranel, & Cohen, 2007). Importantly, eye movements can reveal changes in cognitive processes that either may not influence, or be necessarily accessible for, traditional behavioral responses (for review, see Hannula et al., 2010; Ryan & Shen, 2020; Wynn et al., 2019). For instance, eye movements shift to regions of a screen associated with salient regions of a to-be-retrieved image, even when it is not visually present (e.g. Bochynska & Laeng, 2015; Foulsham & Kingstone, 2013; Johansson & Johansson, 2013; Laeng, Bloem, D'Ascenzo, & Tommasi, 2014; Laeng & Teodorescu, 2002; Scholz, Mehlhorn, & Kreye, 2016), suggesting that the requisite information has indeed been retrieved from memory. Such eye movement-based reinstatement can occur early during viewing and is correlated with both neural (Bone et al., 2018; Ryals, Wang, Polnaszek, & Voss, 2015) and behavioral (e.g. Damiano & Walther, 2019; Holm & Mäntylä, 2007; Olsen, Chiew, Buchsbaum, & Ryan, 2014; Wynn et al., 2016), measures of memory success (for review, see Ferreira, Apel, & Henderson, 2008; Wynn et al., 2019). Eye movement-based reinstatement has been hypothesized to play an especially important role in memory retrieval in older adults (for review, see Wynn et al., 2019). For example, a recent study from Wynn, Olsen, Binns, Buchsbaum, & Ryan (2018) 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 gaze pattern was positively correlated with age-equivalent performance on a subsequent change detection task (see also Wynn et al., 2016).

Given that older adults spontaneously recruit eye movement-based reinstatement to support memory maintenance and retrieval, we might expect them to utilize the same mechanism to support the retrieval of a specific memory representation given a partial input cue (i. e., pattern completion). Seemingly in line with this proposal, a recent study by Vieweg and colleagues (Vieweg, Riemer, Berron, & Wolbers, 2018) in which younger and older adults were required to identify degraded test images as belonging to one of six previously presented scene categories, found that incorrectly identified test images (e.g., office identified as library) elicited gaze patterns similar to the gaze patterns elicited by correctly identified test images from the same response category (e.g., library identified as library). Notably, this gaze pattern similarity was correlated with a participant-level measure of behavioral pattern completion bias (i.e., better performance for learned stimuli compared to new stimuli) in older adults, which the authors interpreted as evidence for pattern completion.

From a neurocomputational standpoint, pattern completion entails the retrieval of a previously encoded representation from incomplete (i. e., partial or degraded) input. By contrast, the Vieweg study compared two measures of retrieval eye movements. As such, the observed gaze patterns, while providing interesting insights into the response patterns of older adults, cannot speak to whether the incorrect responses made by older adults reflect erroneous retrieval of a different, previously encoded scene. Instead, strong evidence for the occurrence of behavioral pattern completion would be found in eye movement patterns at retrieval that recapitulate the specific eye movement patterns that had occurred during encoding for a different, albeit similar, stimulus, in response to the presentation of a partial cue. Moreover, these gaze patterns should be observed in the absence of visual stimulation, such that eye movements can be divorced from bottom-up feature guidance, particularly for older adults who rely heavily on environmental support (for review, see Lindenberger & Mayr, 2014).

Thus, it remains an open question whether, and to what extent, older adults' memory errors are attributable to erroneous retrieval of previously encoded representations. Although the discussed evidence would seem to suggest that older adults are able to recapitulate a previously encoded representation, age-related deficits in mnemonic discrimination (i.e., false alarms) may not solely be due to processes enacted at retrieval. Specifically, a complementary line of research suggests that the ability to use gaze fixations to bind visual features during memory encoding may be disrupted in aging. Indeed, several studies have shown that visual sampling at encoding predicts subsequent memory success (e. g. Armson, Diamond, Levesque, Ryan, & Levine, 2019; Damiano & Walther, 2019; Molitor, Ko, Hussey, & Ally, 2014; Olsen et al., 2016), and is correlated with activity in the hippocampus (Liu, Shen, Olsen, & Ryan, 2017). However, although older adults make more fixations than younger adults during encoding (e.g. Firestone, Turk-Browne, & Ryan, 2007; Heisz & Ryan, 2011), (for review, see Açık, Sarwary, Schultze-Kraft, Onat, & König, 2010), only younger adults show a relationship between gaze fixations and hippocampal activity (Liu, Shen, Olsen, & Ryan, 2018). Thus, to elucidate the role of eye movements in memory retrieval in older adults, it is important to also quantify, and control for, the role of eye movements, and age differences in eye movements, during memory encoding.

In the present study, we used eye movement monitoring to model age-related changes in lure discrimination as a function of changes in both encoding and retrieval processes. In particular, we were interested in whether older adults' increased frequency of lure false alarms reflects a proposed shift towards pattern completion- that is, retrieval of a previously encoded similar image- as indexed by eye movement-based reinstatement, and whether this response bias can be accounted for by age-related changes in encoding, indexed by gaze fixations (see also Damiano & Walther, 2019; Molitor et al., 2014). To this end, we 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 (Wynn, Ryan, & Buchsbaum, 2020). Younger and older adults repeatedly engaged in free viewing of complex naturalistic images and were later tested on incomplete (briefly presented and/or degraded) recognition probes. To investigate whether false alarms by older adults indeed reflect pattern completion, as operationalized by both behavioral and neurocomputational models, the present study used recognition probes consisting of partial old and lure test images. Test probes were immediately followed by a short stimulus-free delay (post-test interval), during which participants were instructed to retrieve the presented image from memory before making a recognition response. Finally, to further explore whether pattern completion is mediated by the integrity of the retrieval cue (i.e., the amount of presented visual input), test probes were manipulated such that they varied in both the degree of image degradation and duration of presentation.

To quantify eye movement-based reinstatement of encoded representations, we derived two measures of encoding-retrieval similarity using eye movements extracted from the encoding (Fig. 2) and post-test intervals (Fig. 3). To capture reinstatement of generally salient image features that were present at encoding, we correlated participant-specific retrieval gaze patterns with image-specific encoding gaze patterns, aggregated across all participants (image reinstatement). To capture reinstatement of both salient image features *and* the operations (i.e., eye movements) by which they were encoded, we additionally correlated participant-specific retrieval gaze patterns with encoding gaze patterns from the same participant (gaze reinstatement). To evaluate age-related changes in encoding, we measured the cumulative number of gaze fixations (i.e., gaze fixations that are summed across

repetitions of an image), a measure that has been previously linked to subsequent memory (e.g. Liu et al., 2017; Olsen et al., 2016). To capture the updating of mnemonic representations across repetitions (i.e., by viewing different regions of an image on each successive viewing), we measured the similarity between eye movements across identical repetitions of the same image (repetitive similarity). Finally, to index the differentiation of mnemonic representations formed at encoding (i.e., by viewing different regions across unique images), we measured the similarity between gaze patterns across dissimilar images (idiosyncratic similarity) (see also Privitera & Stark, 2000).

Based on previous findings suggesting that aging is associated with a shift from pattern separation to pattern completion (e.g. Ly et al., 2013; Pidgeon & Morcom, 2014; Reagh et al., 2016; Stark et al., 2010; Stark et al., 2013; Stark et al., 2015; Toner et al., 2009), we predicted that older adults would show an increase in false alarms to lure items relative to younger adults. Moreover, we hypothesized that this response bias would be accompanied, and predicted by, an increase in eye movement-based reinstatement (image and gaze), indicating that older adults reactivate similar studied representations in response to partial novel input (i.e., pattern completing), and that such reactivation underlies lure false alarms. Critically however, this response bias may not be solely attributable to cognitive processes engaged at retrieval. Thus, we also predicted that age-related changes in encoding processes, as indexed by eye movements - specifically an increased number of fixations, and increased similarity within and between images - would be associated with increased lure false alarms in older adults. Together, these findings would indicate that older adults' proposed pattern completion bias can be attributed to both a decrease in the quality of encoded representations and erroneous reactivation of those representations at retrieval. Thus, by comparing multiple measures of encoding and retrieval eye movements across different test conditions and age groups, we can not only provide critical evidence of pattern completion but can also elucidate the component cognitive processes (e.g., encoding and retrieval) that underlie changes in behavioral pattern completion, and memory errors more broadly, across the adult lifespan.

1. Methods

1.1. 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 ($M = 73.56$, $SD = 6.87$).[1] 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 et al. (2020). 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 $10/h for their participation. Prior to the experiment, older adults completed the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), a brief standardized neuropsychological test developed to screen for cognitive impairment ($M = 27.35$, $SD = 2.26$[2]). 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.

1.2. Apparatus

Stimuli were presented on a on a 1024×768 resolution, 19-in. Dell M991 monitor. Monocular eye movements 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 nine-point calibration procedure, which was performed prior to the experiment. Drift correction ($>5°$) 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.

1.3. Stimuli

Stimuli consisted of 120 sets (A-B) of unique, but similar 800×600 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 100×100 pixel grey squares, see Fig. 1. The duration of image presentation was also manipulated, with test images presented for 250, 500, or 750 ms. Images were randomly assigned to one of four study/test blocks and counterbalanced across duration, degradation, and probe type (old, lure). 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.

1.4. Procedure

The current study used the same stimuli and procedure as was previously reported in Wynn et al. (2020). Before the start of the experiment, participants completed six practice trials to familiarize themselves with the experimental paradigm. During the experiment, participants completed four 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 3 s. Image presentation was repeated such that each study image was viewed four times over the course of the study phase. Image presentation order was randomized within each repetition. A 2 s 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 750 ms. 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 100×100 pixel grey squares. Following the presentation of each test image, a visual mask was presented for 50 ms to prevent sensory persistence. Participants were then presented with an empty grey square (the same size as the images: 800×600 pixels) for 3 s. Participants were instructed to visualize the presented image over the 3 s 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 2–6 s fixation cross was presented in between test trials to allow for online drift correction.

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[1] Given the novel analyses employed here, we had originally sought to recruit a large sample of younger adults see (Wynn et al., 2020). In previous studies, we have observed effects of age on eye movement behavior using sample sizes of approximately 20 per group (e.g. Wynn et al., 2016; Wynn et al., 2018),. We increased the number of older adults here to more closely match the number of younger adults recruited for the original study (Wynn et al., 2020).

[2] The reported mean and standard deviation include all older adult participants ($n = 42$). Of these participants, 4 failed the MoCA using the standard cutoff of 26, and 2 failed using the recommended cutoff of 23 (Carson, Leach, & Murphy, 2018). All included participants had scores ≥ 23.
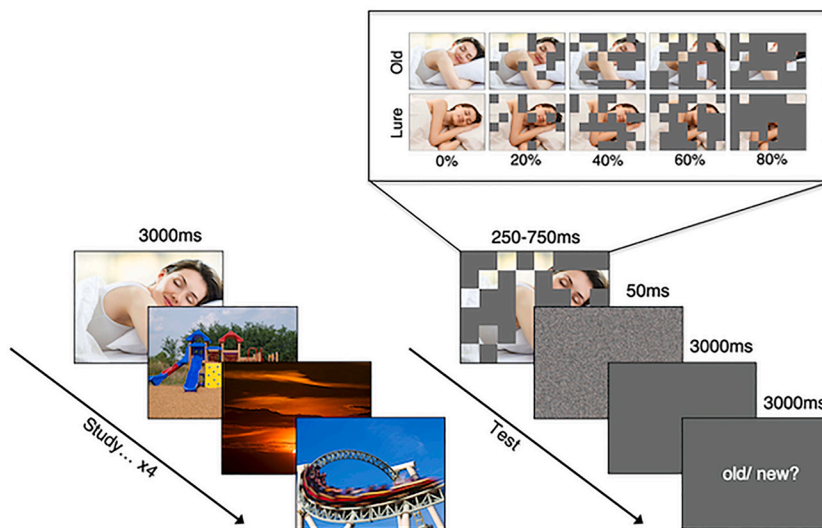
Fig. 1. Experimental procedure. During the study period, each image was presented for 3000 ms. A 2000 ms fixation cross (not shown here) appeared between trials, to allow for online drift correction. Study images were presented four times each. During the test phase, each test probe was presented for 250, 500, or 750 ms, either in full (0% degradation), or with 20%, 40%, 60%, or 80% of the image obscured by 100×100 pixel 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 50 ms, after which a grey square was presented for 3000 ms, during which time participants were instructed to visualize the presented image. Participants were given 3000 ms 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 2000-6000 ms 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 800×600 pixels on a black background; the images have been expanded here for visualization.

1.5. Eye movement analyses

1.5.1. Encoding eye movements

To index encoding success, we calculated the cumulative number of gaze fixations summed across four repeated presentations (3 s each) of each image. This measure has previously been correlated with memory accuracy (e.g. Armson et al., 2019; Damiano & Walther, 2019; Molitor et al., 2014; Olsen et al., 2016), and hippocampal activity (Liu et al., 2017). We additionally computed two measures of encoding similarity (Fig. 2) using the R eyesim package (https://github.com/bbuchsbaum/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 eye movements elicited by the same image across four identical repetitions *(repetitive similarity)*. To quantify the extent to which participants formed differentiated memory traces for each image, we additionally computed the similarity between eye movements 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.

1.5.2. Retrieval eye movements

Following the analysis procedure described in Wynn et al. (2020), we computed three separate measures of eye movement-based retrieval-related reinstatement (Fig. 3). Although we were primarily interested in eye movement-based reinstatement of information from long term memory, our first measure, *probe reinstatement,* was aimed at quantifying the extent to which eye movements during the post-test interval reflect reinstatement of the just-presented test image. To quantify the extent to which eye movements during the post-test interval 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, meant to capture generally salient regions of the encoded image. To further quantify the extent to which eye movements during the post-test interval reinstate eye movements made during encoding, we additionally computed *gaze reinstatement* by correlating within-participant retrieval gaze patterns with within-participant encoding gaze patterns, meant to capture both generally salient regions of the encoded image *and* the corresponding operations (i.e., eye movements) by which it was encoded. Critically, this measure allows us to evaluate the claim that eye movements both encode and are themselves embedded in mnemonic representations (i.e., that fixations are

stored in memory along with the features to which they were directed), such that their recapitulation is important, if not necessary, for successful retrieval (Noton & Stark, 1971a; Noton & Stark, 1971b). 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 studied image. Further details regarding these measures can be found in the SI Appendix.

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, within-image density map was additionally correlated with 50 other randomly selected within-participant, across-image density maps. The values resulting from this permutation were then averaged to obtain a control reinstatement score, which was then subtracted from the corresponding raw reinstatement score, yielding a final difference score (see SI Appendix for repetitive and idiosyncratic similarity controls). Thus, all reported reinstatement scores (including repetitive and idiosyncratic similarity) control for image-invariant (or participant-invariant, where appropriate) viewing tendencies, including the tendency to fixate the center of the screen.

1.6. 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) (Bates, Mächler, Bolker, & Walker, 2015) with a bound optimization by quadratic approximation (bobyqa) optimizer[3] (to optimally balance speed and convergence) 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 (250 ms, 500 ms, 750 ms) 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 eye movements during encoding,

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[3] By default, the lme4 package conducts parameter optimization for GLMMs through a combination of Nelder-Mead and Bound Optimization by Quadratic Approximation (bobyqa) methods.
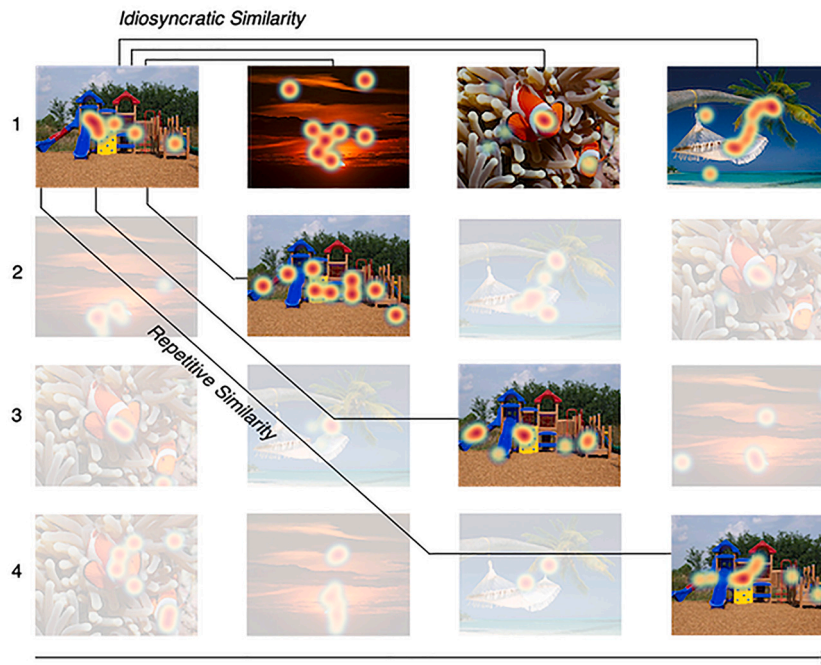
Fig. 2. Illustration of the two measures of encoding eye movement similarity. The heat maps reflect fixation density, with warm values indicating areas of high fixation density. Repetitive similarity is computed by correlating the density maps generated from the same image viewed across 4 blocks (repetitions). Idiosyncratic similarity is computed by correlating the density maps generated from different images across the same block. All density maps are smoothed and duration weighted.

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 eye movements during retrieval, we ran linear mixed effects models (LMEM) on gaze reinstatement, image reinstatement, and probe reinstatement, with all interactions of age, probe type, duration, and degradation as fixed effects and participant and item as random effects (intercepts). To allow for simple effects analysis of significant interactions, duration and degradation were z-scored and age and probe type were recoded as 0 (older adult, old) and 1

(younger adult, lure).

Finally, to investigate the relationship between eye movements and mnemonic performance, we ran two GLMMs modeling accuracy as a function of age, probe type, and eye movements during encoding (cumulative gaze fixations, repetitive similarity, idiosyncratic similarity) and retrieval (probe reinstatement, image reinstatement, gaze reinstatement), using the same parameters as the models reported above. All eye movement measures were z-scored.

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
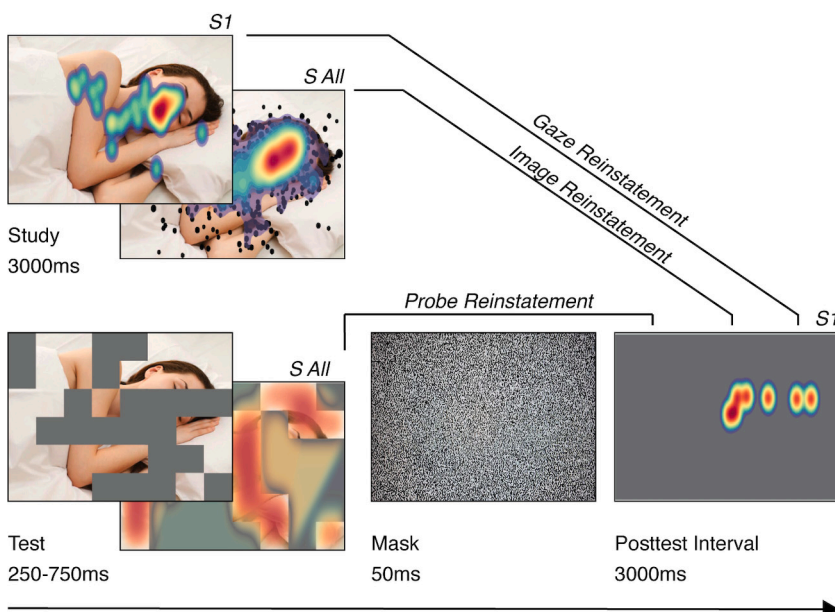

Fig. 3. Illustration of the three measures of retrieval eye movement reinstatement. The heat maps reflect fixation density, with warm values indicating areas of high fixation density. Probe reinstatement is computed by correlating the density map generated from the visible portions (pixels) of the test 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 density map generated from the cumulative fixations of all participants (S All) viewing a single image over 4 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 density map generated from the cumulative fixations of a single participant (S1) viewing a single image over 4 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 et al. (2020).

Table 1
Behavioral accuracy model.

Fixed effects					
	β	95% CI	SE	z	p
(Intercept)	2.15	1.94, 2.36	0.11	20.53	<0.001***
Duration	0.22	0.14, 0.29	0.04	5.53	<0.001***
Degradation	·−0.92	−1.08, −0.76	0.08	−11.50	<0.001***
Age	0.15	−0.09, 0.40	0.13	1.17	>0.05
Probe type	−2.13	−2.30, −1.94	0.09	−23.39	<0.001***
Duration × Degradation	−0.08	−0.15, 0.00	0.04	−2.04	0.041*
Duration × Age	−0.05	−0.15, 0.05	0.05	−0.87	>0.05
Degradation × Age	0.40	0.22, 0.59	0.09	4.26	<0.001***
Degradation × Probe type	0.59	0.41, 0.77	0.09	6.62	<0.001***
Age × Probe type	0.78	0.57, 1.02	0.11	6.86	<0.001***
Duration × Degradation × Age	0.12	0.02, 0.22	0.05	2.38	0.017*
Degradation × Age × Probe type	−0.53	−0.75, −0.31	0.11	−4.70	<0.001***
Total observations = 10,998					
		Variance		SD	
Random effect for Participant (Intercept)		0.15		0.39	
Random effect for Item (Intercept)		0.37		0.61	
Model equation: Accuracy ~ Duration × Degradation × Age + Degradation × Probe type × Age + (1 | Participant) + (1 | Image)					

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 (Kuznetsova, Brockhoff, & Christensen, 2017).

1.6.1. Supplementary materials

Raw fixation data are available on GitHub: https://github.com/bbuchsbaum/Wynn_etal_Cognition_2021

2. Results

2.1. Behavioral results

Results of the final best fit model of accuracy arrived at via model comparison (Table 1) revealed 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 × probe type; Fig. 4 right). Consistent with the proposed 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). The model additionally revealed significant effects of duration and degradation in older adults (Fig. 4 left), 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 × age; Fig. 4 right), suggesting that when test probes were highly degraded, older adults were more likely than younger adults to call an old image 'new'. Likewise, attenuation of the degradation effect for lure images in older adults (degradation × probe type; Fig. 4 right) and enhancement of the effect in younger adults (degradation × age × probe type; Fig. 4 right) suggest that when test probes were highly degraded, older adults were more likely than younger adults to call a lure image 'new'. Together, these findings suggest that pattern completion in older adults may be precluded or made more difficult by insufficient visual input. That is, when faced with a significantly degraded cue, older adults may fail to pattern complete and therefore do not successfully retrieve the encoded image. Similarly, inability to either initiate or carry out pattern completion in response to highly degraded cues may in turn result in older adults responding 'new' based on a dearth of visual evidence rather than comparison of presented visual

input with reactivated memory representations. Finally, significant interactions of duration × degradation and duration × degradation × age further indicate that whereas the effect of test probe degradation was slightly enhanced in older adults at longer test probe durations, younger adults showed a reduced effect (Fig. 4 left). 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.

2.2. Eye movement results

Given that older adults' response behavior was consistent with a proposed age-related shift towards pattern completion, we next sought to investigate whether this response bias was accompanied by changes in encoding and/or retrieval eye movements. To this end, we assessed age differences across three measures of encoding eye movements (cumulative gaze fixations, repetitive similarity, idiosyncratic similarity), intended to capture different processes (e.g., updating and differentiation) that might contribute to successful encoding, and three measures of retrieval eye movements (probe reinstatement, image reinstatement, gaze reinstatement) that have been previously linked to retrieval success.

2.2.1. Eye movements at encoding

2.2.1.1. Cumulative gaze fixations. Prior work has indicated that older adults make more gaze fixations than younger adults during encoding (e. g. Firestone et al., 2007; Heisz & Ryan, 2011). In line with this work, we observed a significant difference in cumulative gaze fixations (across four repeated study presentations) between younger and older adults (M_{OA} = 35.24, M_{YA} = 31.57; W = 1359, z = 2.90, p = .004; Fig. 5A) indicating that older adults made significantly more fixations during encoding than younger adults. A table of the mean number of fixations for each phase of the experiment (study, test probe, post-test interval) can be found in the Table S1.

2.2.1.2. 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. Repetitive similarity (similarity between participant-specific density maps for the same image across four repeated study presentations) was significantly greater than chance (similarity between participant-specific density maps and 50 randomly selected other participant density maps, see SI Appendix) in both younger (t (56) = 26.31, p < .001, d = 3.48) and older adults (t (34) = 5.28, p < .001, d = 0.89); for all subsequent analyses repetitive
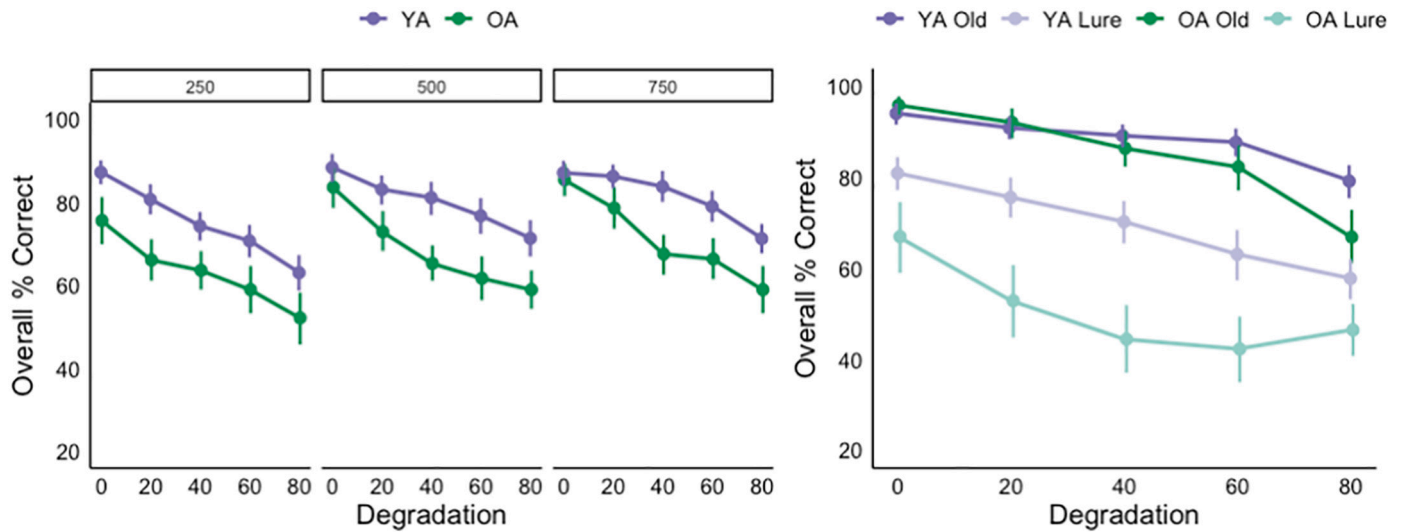
Fig. 4. Left: mean accuracy (overall % correct) by degradation, duration, and age (younger adult (YA), older adult (OA)); Right: mean accuracy by degradation, probe type, and age. Error bars represent 95% confidence intervals.

similarity is reported as the difference score. Compared with younger adults, older adults were more similar in their gaze patterns across identical repetitions of the same image ($M_{OA} = 0.24$, $M_{YA} = 0.21$; $t(90) = 2.67$, $p = .009$, $d = 0.57$; Fig. 5B). 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.

2.2.1.3. Idiosyncratic similarity. As a final measure of encoding, we computed the similarity between gaze patterns across unique images to index the distinctiveness of formed mnemonic representations, with greater idiosyncratic similarity reflecting less differentiated representations. Idiosyncratic similarity (similarity between participant-specific density maps for all encoded images) was significantly greater than chance (similarity between participant-specific density maps and 50 randomly selected other participant density maps, see SI Appendix) in both younger ($t(56) = 3.59$, $p < .001$, $d = 0.48$) and older adults ($t(34)$

= 4.94, $p < .001$, $d = 0.84$); for all subsequent analyses idiosyncratic similarity is reported as the difference score. Although older adults had numerically higher idiosyncratic similarity scores than younger adults ($M_{OA} = 0.019$, $M_{YA} = 0.014$; Fig. 5C), the groups did not differ significantly ($W = 1176$, $z = 1.43$, $p = .15$).

2.2.1.4. Relationship between encoding eye movements and behavior. To investigate the relationship between encoding eye movements and subsequent recognition accuracy, we ran a GLMM on accuracy including all measures of encoding eye movements (cumulative gaze fixations, repetitive similarity, idiosyncratic similarity). Model comparison progressed in a backward fashion, beginning with all three-way interactions of each eye movement measure with probe type and age. Results of the final model arrived at via model comparison are reported below.

Results of the encoding model (Table 2) revealed a significant positive effect of cumulative gaze fixations on accuracy for lure images in older adults (correct rejections > false alarms; cumulative gaze fixations
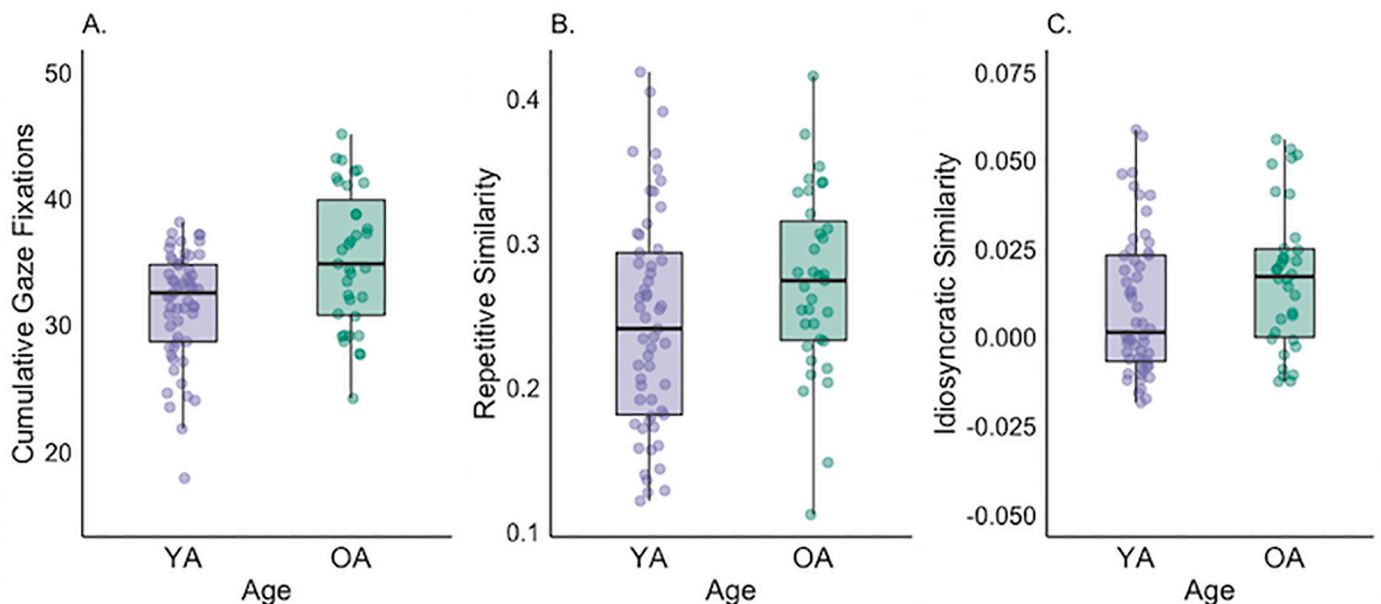

Fig. 5. Age differences (YA = younger adult, OA = older adult) in (A) Cumulative gaze fixations, (B) repetitive similarity, and (C) idiosyncratic similarity during encoding.

Table 2
Encoding eye movements accuracy model.

Fixed effects					
	β	95% CI	SE	z	p
(Intercept)	1.96	1.76, 2.15	0.10	19.87	<0.001***
Cumulative gaze fixations	−0.03	−0.19, 0.12	0.08	−0.40	0.690
Probe type	−2.00	−1.82, −2.16	0.09	−22.75	<0.001***
Age	0.34	0.10, 0.56	0.12	2.83	0.005**
Repetitive similarity	−0.15	−0.06, −0.23	0.04	−3.36	<0.001***
Idiosyncratic similarity	0.08	−0.01, 0.16	0.05	1.57	0.116
Cumulative gaze fixations × Probe type	0.18	0.00, 0.35	0.09	2.01	0.045*
Cumulative gaze fixations × Age	0.22	0.02, 0.42	0.10	2.16	0.030*
Probe type × Age	0.68	0.46, 0.90	0.11	6.10	<0.001***
Probe type × Repetitive similarity	0.24	0.13, 0.33	0.05	4.53	<0.001***
Probe type × Idiosyncratic similarity	−0.30	−0.19, −0.41	0.05	−5.60	<0.001***
Cumulative gaze fixations × Probe type × Age	−0.26	−0.03, −0.48	0.11	−2.27	0.023*
Total observations = 10,756					
		Variance		SD	
Random effect for Participant (Intercept)		0.13		0.36	
Random effect for Item (Intercept)		0.57		0.75	

Model equation: Accuracy ~ Cumulative gaze fixations × Probe type × Age + Repetitive similarity × Probe type + Repetitive similarity × Age + Idiosyncratic similarity × Probe type + (1 | Participant) + (1 | Image)

× probe type) and for old images in younger adults (hits > misses; cumulative gaze fixations × age). Conversely, repetitive similarity was significantly negatively associated with accuracy for old images (misses > hits), and this effect was reversed for lure images (correct rejections > false alarms; probe type × repetitive similarity), suggesting that re-fixating the same regions across identical repetitions increased the likelihood of calling a test probe 'new', regardless of its actual mnemonic status. Finally, idiosyncratic similarity was significantly negatively associated with accuracy for lure images (false alarms > correct rejections; probe type × idiosyncratic similarity), indicating that similarity of gaze patterns across dissimilar images was associated with false endorsement of lure images as old. Together, these findings suggest that changes in encoding eye movements as a function of age may contribute to changes in behavioral pattern completion.

2.2.2. Eye movements at retrieval

The results of the analyses on encoding eye movements suggest that younger and older adults differ significantly in the manner in which they view images during encoding, with encoding gaze patterns predicting subsequent memory. However, the critical test of pattern completion is whether older adults show greater reinstatement of encoded representations than younger adults during retrieval, and whether this reinstatement predicts lure false alarms. 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 first compared raw similarity values (within-participant, within-image) to permuted similarity values (within-participant, across-image) for each age group. For all subsequent analyses, 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). To index age differences in eye movements during retrieval, we ran LMEMs on 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 eye movements (gaze reinstatement) with fixed effects for age (younger, older), probe type (old, lure), duration (250 ms, 500 ms, 750 ms), and degradation (0%, 20%, 40%, 60%, 80%) and random intercepts for participant and item. Only results of the final best fit model achieved via backwards model comparison are reported.

2.2.2.1. Probe reinstatement.
Probe reinstatement was significantly greater than chance in both younger (t (56) = 12.96, p < .001, d = 0.84)

and older adults (t (34) = 14.73, p < .001, d = 1.76). Results of the LMEM on probe reinstatement (Table 3) revealed a significant effect of age, indicating that relative to younger adults, older adults showed greater evidence of reinstating the test probe during the stimulus free, post-test interval. The LMEM also revealed significant effects of duration and degradation, with probe reinstatement decreasing with increased test probe duration and degradation, and these effects were compounded for older adults, but not younger adults.

2.2.2.2. 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). Results of the LMEM on image reinstatement revealed significant effects of duration and age, indicating that image reinstatement was significantly decreased with increased test probe duration and was significantly greater in older adults relative to younger adults (Table 4). Thus, like probe reinstatement, older adults showed greater retrieval-related reactivation of previously encoded image features than younger adults.

2.2.2.3. 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). Results of the LMEM further indicated that gaze reinstatement significantly differentiated old images from repeated images, with significantly greater gaze reinstatement for repeated images. 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. Together, these findings indicate that both younger and older adults reinstate encoding gaze patterns (reflecting both salient image features and the operations by which they were encoded), and do so more for old images compared to lure images (Table 5).

2.2.2.4. Relationship between retrieval eye movements and behavior.
To investigate the relationship between retrieval eye movements and subsequent recognition accuracy, we ran an a GLMM on accuracy including all three measures of retrieval-related reinstatement (probe reinstatement, image reinstatement, gaze reinstatement), with model comparison progressing in a backwards fashion. Since duration and degradation did not interact with either age or probe type to predict image or gaze reinstatement (and to reduce model complexity and allow for model convergence), they were excluded from the model. To ensure that the effects of retrieval eye movements on accuracy were independent of the effects of encoding 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 ($\chi^2 = 9.57, p = .002$) and idiosyncratic similarity ($\chi^2 = 10.53, p = .001$) significantly improved the fit of the model (repetitive similarity: $\chi^2 = 0.39, p > .05$). The addition of idiosyncratic similarity × probe type further improved the model fit ($\chi^2 = 20.53, p < .001$), while additions of idiosyncratic similarity × age ($\chi^2 = 1.69, p > .05$), cumulative gaze fixations × age ($\chi^2 = 0.2, p > .05$), and cumulative gaze fixations × probe type ($\chi^2 = 0.71, p > .05$) did not. Results of the final model are reported below.

Results of the retrieval model (Table 6, Fig. 6) revealed a significant effect of probe reinstatement on lure accuracy (probe reinstatement × probe type; Fig. 6A), with greater reinstatement of the test probe for correct rejections relative to false alarms. On the contrary, image reinstatement had a significant negative effect on lure accuracy in older adults (false alarms > correct rejections; image reinstatement × probe type; Fig. 6B), indicating that reinstatement of a previously encoded similar image was associated with false endorsement of lure images as 'old' in older adults. This effect was significantly attenuated in younger adults (image reinstatement × age × probe type). Finally, although we observed a non-significant effect of gaze reinstatement on accuracy for old images, and for lure images in older adults (gaze reinstatement × probe type), there was a significant negative effect of gaze reinstatement on lure accuracy for younger adults (false alarms > correct rejections; gaze reinstatement × age × probe type; Fig. 6C). 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 Wynn et al., 2020). In other words, whereas reinstating the salient features of a previously encoded image (image reinstatement) is sufficient to elicit a false memory in older adults, the same response in younger adults is contingent on the erroneous retrieval of previously encoded image features via the accompanying pattern of eye movements (gaze reinstatement). Together, these findings suggest that both the nature of reinstated representations and their relationship with behavioral performance differ as a function of age. Moreover, these effects were not abolished by the addition of cumulative gaze fixations or idiosyncratic similarity to the model, suggesting that encoding and retrieval processes independently contribute to response behavior. Extending the reinstatement results, cumulative gaze fixations was positively associated with recognition success, while idiosyncratic similarity was negatively associated with recognition success for lures.

Table 3
Probe reinstatement model.

Fixed effects					
	β	95% CI	SE	t	p
(Intercept)	0.06	0.04, 0.06	0.006	8.72	<0.001***
Age	−0.02	−0.02, −0.01	0.004	−4.65	<0.001***
Duration	−0.01	−0.01, 0	0.002	−4.51	<0.001***
Degradation	−0.06	−0.06, −0.04	0.006	−9.73	<0.001***
Probe type	−0.00	−0.01, 0.00	0.003	−1.07	0.28
Age × Duration	0.00	−0.00, 0.01	0.003	0.64	0.53
Age × Degradation	−0.00	−0.01, 0.00	0.003	−0.76	0.45
Duration × Degradation	−0.01	−0.01, −0.00	0.002	−2.79	0.01*
Age × Duration × Degradation	0.01	0.00, 0.01	0.003	2.06	0.04*
Total observations = 10,998					
		Variance		SD	
Random effect for Participant (Intercept)		0.0001		0.011	
Random effect for Item (Intercept)		0.017		0.132	
Model equation: Probe reinstatement ~ Age × Duration × Degradation + Probe type + (1 | Participant) + (1 | Image)					

Table 4
Image reinstatement model.

Fixed effects					
	β	95% CI	SE	t	p
(Intercept)	0.04	0.03, 0.05	0.005	7.72	<0.001***
Duration	−0.004	−0.00, −0.01	0.001	−3.54	<0.001***
Age	−0.013	−0.01, −0.02	0.004	−3.64	<0.001***
Total observations = 10,998					
		Variance		SD	
Random effect for Participant (Intercept)		0.0001		0.01	
Random effect for Item (Intercept)		0.013		0.116	
Model equation: Image reinstatement ~ Duration + Age + (1 | Participant) + (1 | Image)					

Table 5
Gaze reinstatement model.

Fixed effects					
	β	95% CI	SE	t	p
(Intercept)	0.05	0.03, 0.06	0.008	5.98	<0.001***
Probe type	−0.02	−0.02, −0.03	0.003	−6.46	<0.001***
Total observations = 10,998					
		Variance		SD	
Random effect for Participant (Intercept)		0.004		0.063	
Random effect for Item (Intercept)		0.005		0.071	
Model equation: Gaze reinstatement ~ Probe type + (1 | Participant) + (1 | Image)					

Table 6
Retrieval eye movements accuracy model.

Fixed effects					
	β	95% CI	SE	z	p
(Intercept)	1.89	1.7, 2.07	0.09	19.93	<0.001***
Gaze reinstatement	−0.11	−0.26, 0.04	0.08	−1.41	0.159
Age	0.38	0.14, 0.60	0.12	3.24	0.001**
Probe type	−1.91	−2.07, −1.75	0.08	−23.44	<0.001***
Image reinstatement	0.06	−0.1, 0.22	0.08	0.73	0.466
Probe reinstatement	0.08	−0.02, 0.18	0.05	1.53	0.126
Idiosyncratic similarity	0.06	−0.03, 0.15	0.05	1.19	0.235
Cumulative gaze fixations	0.10	0.02, 0.16	0.04	2.75	0.006**
Gaze reinstatement × Age	0.15	−0.05, 0.35	0.10	1.42	0.155
Gaze reinstatement × Probe type	0.10	−0.08, 0.28	0.09	1.02	0.309
Probe type × Age	0.62	0.41, 0.82	0.11	5.85	<0.001***
Image reinstatement × Age	−0.20	−0.4, 0.00	0.10	−1.90	0.057
Image reinstatement × Probe type	−0.32	−0.12, −0.51	0.10	−3.26	0.001**
Probe reinstatement × Probe type	0.17	0.04, 0.28	0.06	2.68	0.007**
Idiosyncratic similarity × Probe type	−0.25	−0.14, −0.35	0.06	−4.49	<0.001***
Gaze reinstatement × Age × Probe type	−0.27	−0.03, −0.51	0.12	−2.24	0.025*
Image reinstatement × Age × Probe type	0.29	0.04, 0.52	0.12	2.34	0.019*
Total observations = 10,756					
		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 × Age × Probe type + Image reinstatement × Age × Probe type + Probe reinstatement × Probe type + Idiosyncratic similarity × Probe type + Cumulative gaze fixations + (1 | Participant) + (1 | Image)

Notably, although image reinstatement by older adults was negatively predictive of lure accuracy, it was not significantly predictive of accuracy for old images. Our prior work with younger adults see (Wynn et al., 2020), however, demonstrated that gaze reinstatement was associated with both lure false alarms and correct recognition of old images, but only (1) when those images were particularly difficult to differentiate from their similar lures, and (2) early in the retrieval interval. Thus, to investigate whether these effects extend to older adults, we ran (1) a GLMM on old image accuracy using image reinstatement, probe type, and image difficulty (greater or less than the median old image recognition accuracy = 66.67%), as predictors, and (2) a LMEM on density value with accuracy, reinstatement measure (probe, gaze, image), and time as predictors. Both models were run on older adults only for younger adults, see (Wynn et al., 2020) and included participant and item as random effects, see SI Appendix for further details.

Consistent with our previous work (Wynn et al., 2020), results of the best fit accuracy model (see Table S2) revealed a marginally significant effect of image reinstatement (p = .077) on older adults' recognition

memory for old images, only when those images were difficult (i.e., below the median accuracy). Image reinstatement was also significantly negatively predictive of older adults' accuracy for lure images (p = .007), and this effect did not interact with image difficulty. Thus, these results suggest that like younger adults, older adults may utilize eye movements (in this case, image reinstatement) to support recognition of old images that are particularly difficult to discriminate. Although a visual inspection of the temporal analysis results (see Fig. S1) showed greater image reinstatement for hits relative to misses, the LMEM (see Table S3) did not reveal any significant effects of image reinstatement on older adults' recognition accuracy for old images either early in the post-test interval or over time.

3. 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 (Chalfonte & Johnson, 1996; Grady,
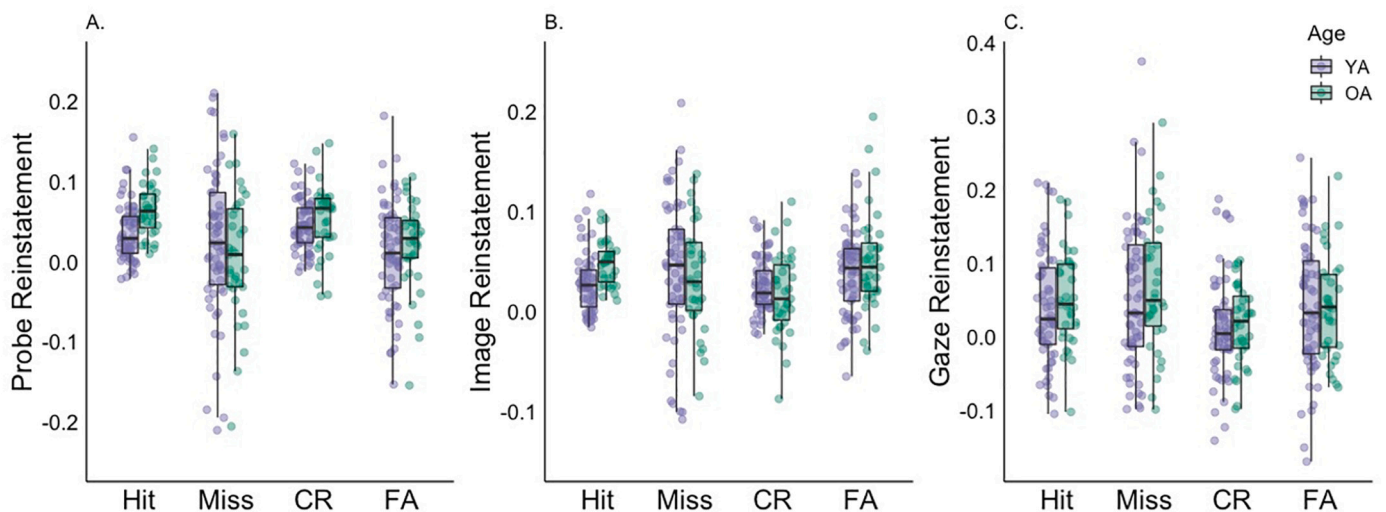

Fig. 6. Age differences (YA = younger adult, OA = older adult) in (A) probe reinstatement, (B) image reinstatement, and (C) gaze reinstatement as a function of probe type and accuracy (hits, misses, correct rejections, false alarms).

2012; Grady & Ryan, 2017; Mitchell et al., 2006; Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008). But what does such a 'recollection deficit' entail? Behavioral studies have provided evidence that explicit measures like recognition and recall accuracy decline with age (Craik & McDowd, 1987; Fraundorf et al., 2019; Rhodes, Greene, & Naveh-Benjamin, 2019). 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 elusive. Likewise, it has remained unclear how age-related changes in, and interactions between, encoding and retrieval processes culminate in age-related differences in behavioral responses. In the present study, we used eye movement monitoring to compare both the intentional responses and incidental gaze patterns of younger and older adults during a recognition memory task (see also Wynn et al., 2019). Specifically, we investigated whether older adults' proposed bias towards pattern completion, operationalized behaviorally by an increased tendency to falsely endorse lure stimuli as 'old' (e.g. Ly et al., 2013; Pidgeon & Morcom, 2014; Reagh et al., 2016; Stark et al., 2010; Stark et al., 2013; Stark et al., 2015; Toner et al., 2009), is mediated by increased reinstatement of previously encoded stimuli during retrieval, and/or deficient processing of stimuli during encoding, both indexed by eye movements.

In line with previous work (Ly et al., 2013; Pidgeon & Morcom, 2014; Reagh et al., 2016; Stark et al., 2010; Stark et al., 2013; Stark et al., 2015; Toner et al., 2009; Vieweg et al., 2018), older adults made more false alarms to lure stimuli relative to younger adults, despite largely age-equivalent recognition performance for old images. This response bias is consistent with a proposed age-related shift from pattern separation to pattern completion. Lending critical supporting evidence to this behavioral bias, analysis of eye movement behavior indicated that when cued with an incomplete 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). Thus, extending findings from the pattern completion and eye movement literatures, these results indicate that reactivation of a similar previously encoded representation from partial input (i.e., pattern completion), indexed via eye movements, underlies age-related memory errors.

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. Moreover, probe reinstatement was associated with the correct rejection of lure images in both groups, suggesting that eye movements facilitate the comparison of presented visual input with stored memory representations (see also Ryan & Cohen, 2004) Consistent with previous findings of increased eye movement-based reinstatement by older adults relative to younger adults (Wynn et al., 2018), (see also Wynn et al., 2016), 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 eye movements made to them.

Although the present accuracy model did not reveal significant effects of gaze or image reinstatement on recognition of old images (see also Wynn et al., 2020), previous analysis of the younger adult data see (Wynn et al., 2020) showed that gaze reinstatement supported recognition of old images when those images were particularly difficult to discriminate, and early in the retrieval interval (Wynn et al., 2020). Extending those results, we found that image reinstatement was marginally predictive of recognition accuracy for old images in older adults, only when those images were difficult (i.e., below the median recognition accuracy), while our temporal analysis did not reveal any significant results. Together, these findings suggest that eye movement-based reinstatement may support memory for studied images, but this

relationship is perhaps more nuanced than the relationship between reinstatement and lure performance. Indeed, previous work suggests that gaze reinstatement may be preferentially recruited when mnemonic task demands exceed available cognitive resources (e.g. Wynn et al., 2018), (for review, see Wynn et al., 2019). Although further research will be required to illuminate the relationship between reinstatement and task difficulty in older adults, the present results suggest that for older adults, like younger adults, engagement of eye movement-based mnemonic facilitation may vary based on task/cognitive demands.

Given that older adults' pattern completion bias is typically inferred based on lure false alarms, we were particularly interested in gaze patterns following presentation of incomplete lure test probes. Critically, 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 reinstatement of previously encoded image content, via image reinstatement. These findings suggest that reactivation of a previously encoded similar image in response to a lure test probe is detrimental to memory performance. With regard to age differences in pattern completion, the present results further suggest that increased reinstatement of encoded image content underlies older adults' increased tendency to falsely endorse lure images as 'old'. Importantly, 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 eye movements to support the retrieval of previously encoded representations, the manner in which such eye movement reinstatement supports behavioral pattern completion differs 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 see (Prull, Dawes, Martin, Rosenberg, & Light, 2006; Spencer & Raz, 1995; Yonelinas & The, 2002). 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 Yonelinas & The, 2002). 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 Cowell, Barense, & Sadil, 2019). 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 gaze reinstatement, and in fact, older adults exhibited greater image reinstatement than younger adults. However, younger and older adults did show different patterns of association between gaze and image 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., eye movements) from reinstatement of encoded content only; however, further research is required to support the broader assertion that eye movements are related to the phenomenological experience of memory (see also Ryan, Shen, & Liu, 2019).

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 eye movements enacted during the study phase suggest that mnemonic encoding processes may be altered with age. First, although older adults made more fixations than younger adults, gaze fixations predicted recognition hits in younger adults only. Considered together with recent findings from Liu et al. (2018) in which gaze fixations were 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 eye movements to bind visual information into lasting memory representations. Here, instead, cumulative gaze fixations predicted correct rejection of lure images in older adults, suggesting that the mnemonic representations built up by older adults may at least contain sufficient information to protect against interference effects related to similar lures. Second, older adults in the present study executed more similar gaze patterns across identical repetitions of the same image *(repetitive similarity)*, 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 repeatedly viewed the same regions, possibly in an attempt to strengthen weak representations or re-encode forgotten details, resulting in less complete memory representations.

The described alterations in viewing patterns for older adults during the study phase may reflect encoding deficits that subsequently lead to weakened, or lower-quality, mnemonic representations see (Fraundorf et al., 2019). Accordingly, 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 representations, or even the experience of encoding, to support performance is in line with evidence of age-related deficits in controlled retrieval (e.g. Amer, Giovanello, Grady, & Hasher, 2018; Cohn, Emrich, & Moscovitch, 2008; Dew & Giovanello, 2010; Jennings & Jacoby, 1993; Koutstaal, 2003), (for review, see Light, Prull, La Voie, & Healy, 2000). Furthermore, these fingings suggest 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. While this deficit may explain our results, it is perhaps not the only explanation, and indeed other work has suggested that information revealed by eye movements may be divorced from decision processes (Ryan & Shen, 2020). Thus, although recollective content may not be consciously accessible to, or used by, older adults to support memory performance, including lure discrimination, it may be reasonably sufficient to influence eye movements.

In conclusion, the results of the present study provide concurrent evidence of both reactivation (via eye movements) and behavioral pattern completion (via behavioral responses) in response to degraded lure test probes. Together, these two lines of evidence make a strong case for an age-related bias towards pattern completion. In other words, older adults make memory errors because they incorrectly recall a similar item from memory in response to degraded or partial input. The present results additionally 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 bound mnemonic representations formed by older adults are less complete than those formed by younger adults. Eye movements 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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2021.104746.

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