Fixation Reinstatement Supports Visuospatial Memory in Older Adults

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Research using eye movement monitoring suggests that recapitulating the pattern of eye movements made during stimulus encoding at subsequent retrieval supports memory by reinstating the spatial layout of the encoded stimulus. In the present study, the authors investigated whether recapitulation of encoding fixations during a poststudy, stimulus-free delay period—an effect that has been previously linked to memory maintenance in younger adults—can support mnemonic performance in older adults. Older adults showed greater delay-period fixation reinstatement than younger adults, and this reinstatement supported age-equivalent performance on a subsequent visuospatial-memory-based change detection task, whereas in younger adults, the performance-enhancing effects of fixation reinstatement increased with task difficulty. Taken together, these results suggest that fixation reinstatement might reflect a compensatory response to increased cognitive load. The present findings provide novel evidence of compensatory fixation reinstatement in older adults and demonstrate the utility of eye movement monitoring for aging and memory research.

Public Significance Statement

Eye movements can be used to boost memory. Here, we show that when asked to remember the locations of objects within a scene, older adults will spontaneously rehearse the locations by looking with their eyes at the spaces that had been previously occupied by those objects. This gaze pattern supports subsequent memory performance. This study enhances our understanding of the role eye movements play in memory and establishes eye-movement monitoring as a useful method in aging research.

Keywords: memory, aging, compensation, eye movements, eyetracking

Over the past several decades, an extensive literature has emerged linking eye movements and memory (for review, see Hannula et al., 2010). Research using eye-movement-monitoring suggests that younger adults reinstate encoding-related eye movements during memory maintenance (Olsen, Chiew, Buchsbaum, & Ryan, 2014) and retrieval (Foulsham & Kingstone, 2013; Laeng & Teodorescu, 2002; Noton & Stark, 1971; Spivey & Geng, 2001), and that this reinstatement supports memory performance (Olsen et al., 2014; Ryals, Wang, Polnaszek, & Voss, 2015; Wynn et al., 2016). Studies with memory-impaired populations provide further evidence that some gaze patterns are affected by damage to the hippocampus (Dragan et al., 2017; Ryan, Althoff, Whitlow, & Cohen, 2000), a key node in the neuroanatomically connected oculomotor and memory networks (Shen, Bezgin, Selvam, McIntosh, & Ryan, 2016). Taken together, these findings have led some researchers to hypothesize that eye movements play a functionally supportive role in memory retrieval (Johansson & Johansson, 2014; Ferreira, Apel, & Henderson, 2008). If this is the case, fixation reinstatement could provide a critical boost to memory in older adults, a population with documented deficits in relational memory and hippocampal function (for review, see Old & Naveh-Benjamin, 2008; Park et al., 2002). However, to date there has been little research investigating the relationship between fixation reinstatement and memory across the adult life span.

In a recent study, Olsen and colleagues (2014) showed that spontaneous reinstatement of encoding-related eye movements during a poststudy, stimulus-free delay period correlated with accuracy on a subsequent change detection task when the relations among the studied objects were manipulated. Indeed, several studies have shown that looking back to locations that were previously occupied by studied objects (i.e., "looking at nothing") benefits memory in younger adults (Laeng, Bloem, D'Ascenzo, & Tommasi, 2014; Laeng & Teodorescu, 2002; Spivey & Geng, 2001), whereas restricting viewing impairs performance (Johansson, Holsanova, Dewhurst, & Holmqvist, 2012; Johansson & Johansson, 2014; Laeng & Teodorescu, 2002; Pearson, Ball, & Smith, 2014). It has been suggested that looking at nothing facilitates memory retrieval by reinstating the spatial index of the encoded image and its associated visual, linguistic, and conceptual features (Ferreira et al., 2008). In line with this proposal, a recent study using combined eyetracking-neuroimaging showed that both neural and eye movement activity patterns were reinstated during visualization and were correlated with each other (Bone at al., 2016). Although these findings advance a direct link between fixation reinstatement and internal memory representations, it remains unclear

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whether, and how, fixation reinstatement supports memory retrieval when internal representations are compromised, as may be the case in older adults.

Relative to younger adults, older adults show impaired memory for the relations among objects and objects and their surrounding contexts (for review, see Old & Naveh-Benjamin, 2008), and these impairments extend to measures of eye movements. Across a range of tasks, perceptual and mnemonic deficits in older adults are indicated by lower amplitude saccades (reflecting a smaller useful field of view; see Açık, Sarwary, Schultze-Kraft, Onat, & König, 2010), and decreased preference for viewing novel versus repeated objects, compared to younger adults (Whitehead et al., 2016). Yet, other studies suggest that older adults' gaze patterns can be used to improve memory as successfully as younger adults. For example, both younger and older adults direct preferential viewing to studied material following intentional instructions to do so, and this gaze pattern predicts subsequent performance (Shih, Meadmore, & Liversedge, 2012). Younger and older adults also show similar benefits for active viewing over passive viewing (object recognition; Brandstatt & Voss, 2014) and for free viewing over constrained viewing (face recognition; Chan, Kamino, Binns, & Ryan, 2011), further suggesting that despite declining memory, older adults might maintain access to the performance-enhancing effects of certain gaze patterns. How these eye movements support memory performance, however, remains unclear.

Converging evidence from behavioral and neuroimaging studies suggests that older adults can achieve performance comparable to that of younger adults through compensation: the differential, extended, or overrecruitment of cognitive and/or neural resources by older adults relative to younger adults (for review, see Grady, 2012; Stern, 2009). At the behavioral level, several studies have reported age-equivalent performance when task demands tax cognitive processes that are spared with age (for review, see Salthouse, 2012; Umanath & Marsh, 2014). For example, when asked to recall the prices of realistically and unrealistically priced grocery store items, older adults performed similarly to younger adults by relying on prior knowledge to support recall for the realistically priced items (Castel, 2005). Likewise, in neuroimaging studies, overrecruitment of brain regions that are less likely to be compromised with age (particularly the prefrontal cortex) in older adults compared to younger adults has been thought to compensate for deficient activity in other (more posterior) regions that contribute to age-related cognitive declines (Cabeza, Anderson, Locantore, & McIntosh, 2002; Cabeza et al., 2004; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Du, Buchsbaum, Grady, & Alain, 2016; for review, see Park & Reuter-Lorenz, 2009).

Despite evidence of both preserved eye-movement-based performance benefits and cognitive and neural compensation in older adults, the eye movements of older adults have yet to be explored as a potential compensatory mechanism. Given its role in contextual reinstatement and memory maintenance and retrieval, we propose that fixation reinstatement might be used by older adults to support behavioral performance at or near the level of younger adults. In the present study, we investigate whether the eye movements of older adults play a compensatory role in memory maintenance by using a visuospatial memory task that has been previously shown to elicit predictive delay-period fixation reinstatement in younger adults (Olsen et al., 2014). If fixation reinstatement is indeed compensatory, older adults should show greater reinstatement relative to younger adults on the same task, and fixation reinstatement should correlate with behavioral performance.

Method

Participants

Participants were 20 younger adults ([YA] eight men, age: M =21.65 years, SD = 2.87), aged 18–27 and 20 older adults ([OA] six men, age: M = 69.75 years, SD = 4.82), aged 63-84 with corrected-to-normal vision. Power analyses (Champely, 2016) for bivariate measures of association indicated that a sample of n = 20was of sufficient size to detect a large correlation (r = .6) and difference between means (d = .95) with 80% power ($\alpha = .05$). Prior work showed effects of similarity and age at least this large (similarity, r = .71, Olsen et al., 2014; age, d = 1.02, Wynn et al., 2016). Participants were recruited through the Rotman Research Institute's adult participant pool. All participants provided informed consent before participating in the experiment in accordance with the ethical guidelines of the Rotman Research Institute and were compensated at a rate of \$10/hr for their participation. One younger adult and one older adult were excluded from analysis on the basis of having accuracy (overall percent correct) scores more than 2 standard deviations above and below their age group mean, respectively. Data from the remaining 19 participants in each group were analyzed. Prior to the start of the experiment, older adults completed the Montreal Cognitive Assessment (Nasreddine et al., 2005), a brief standardized neuropsychological test developed to screen for cognitive impairment, M = 26.8/30 (>25 = pass), SD =1.61.

Apparatus

Stimuli were presented on a $1,024 \times 768$ 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., Missisauga, Canada). Nine-point eye movement calibration was performed prior to the experiment and drift correction (>5°) was performed prior to each trial. *Saccades, blinks*, and *fixations* were defined by EyeLink as saccades greater than .5° visual angle, period in which saccade signal was missing for thee or more consecutive samples, and all remaining samples, respectively.

Stimuli

Stimuli were sets of three, four, or five abstract objects set against a gray background. The objects were created in Corel Draw (version 12; Ottawa, Ontario) and balanced in size and number of colors. All objects were uniquely shaped and colored so as to minimize perceptual interference and resemblance to real-life, nameable objects (which might have promoted a verbal rehearsal strategy). A subset of these objects was used previously in Olsen et al., 2014. Study arrays were created by dividing the screen into an 8×8 grid and assigning the abstract objects to three, four, or five of 48 possible grid locations. The 16 central grid spaces were always empty so as to reduce artificially high similarity scores driven by the tendency to fixate the center of the screen. All object locations were jittered by 20 pixels in a random direction to prevent detection of the grid pattern (which could be used to predict object locations). Every possible grid location was occupied by the target (i.e., the manipulated object) once in each of the 3-, 4-, and 5-load sets. On manipulated trials, the target object was shifted by 50 pixels in a random direction away from the studied location, such that the relative spatial relations between the objects were altered.

Visual masks were created using Adobe Photoshop (Adobe Systems Inc., San Jose, CA) by distorting the study image using a "wave function" such that the resulting mask resembled a highly distorted version of the study array with a predominantly gray back-ground and scattered pixels of color taken from the study objects. Visual masks were presented for 500 ms following the study phase to prevent an afterimage, which might be used to maintain/detect an object's spatial location.

Procedure

Participants completed a delayed-match-to-sample task (see Figure 1) in which they made change detection judgments regarding the spatial locations of abstract objects presented during temporally spaced study and test phases. Prior to the experiment, participants received verbal instructions to memorize the presented study arrays in preparation for a subsequent change detection task. Participants were told that the manipulations would involve a small shift of one of the studied objects in any direction. Participants completed six practice trials prior to the start of the experiment to become familiarized with the study paradigm. On each trial, participants were presented with a unique three-, four-, or five-object array for 2 s. After the 2-s study phase, a brief visual mask was flashed for 500 ms followed by a delay period ranging from 750-6,000 ms (750, 1,500, 2,250, 3,000, 3,750, 4,500, 5,250, 6,000). During the delay period, participants were free to move their eyes over the gray screen; no instructions were provided. After the delay phase, participants were again presented with an array of the same objects for 3 s. During this test phase, objects were either presented in their original studied positions (intact), or

one object was shifted slightly (manipulated). Participants were given 5 s after the offset of the test display to determine whether or not a change had been made and were asked to respond by button press.

Of the 144 unique trials presented, half of the test displays were intact and half were manipulated, with delays and loads distributed equally across the two target positions. Target position (intact, manipulated) and study and test object arrays were counterbalanced across participants to control for object-specific viewing effects.

Eye Movement Measures

To investigate whether eye movements during the delay phase were directed to locations that were visited during the study phase, we used a fixation similarity algorithm (implemented in Python) previously used by Olsen and colleagues (2014). The similarity algorithm converts the fixations from the study and delay phases into "heat maps," which are then compared to yield an overall similarity score reflecting the proximity of fixation locations between each of the phases. First, fixations from each trial of the study and delay phases were converted into $x \times y$ -dimensional coordinate vectors including all possible screen locations (i.e., an image grid). Coefficients of the vector values correspond to fixation durations, such that the value of each coordinate in the grid is proportional to the duration of the fixation in that location. Next, the coordinates were smoothed with a two-dimensional Gaussian kernel (full width at half maximum = 100 pixels), allowing nearby, nonoverlapping fixation locations to be granted partial weighting in the similarity index. The two fixation maps for the corresponding study and delay phases were then compared using a normalized Euclidean dot-product formulation, with the similarity metric defined as a measure of the angle theta, with values ranging from 0 (identical fixations) to 90 (no fixations in common). Finally, the similarity metric was rescaled from 0-100, with low similarity scores reflecting dissimilar fixation patterns and high similarity scores reflecting similar fixation patterns. For the purposes of the present study, temporal order of fixations was not considered in the



Figure 1. Display sequence for the change detection task. During the study phase, participants were instructed to view and memorize the locations of three, four, or five abstract objects, which were presented for 2 s followed by a 500-ms visual mask. A variable delay period (750-6,000 ms) preceded the test phase, during which participants were instructed to view the same array of objects and determine whether a change had been made in the position of one of the studied objects. Studied objects either appeared in the same locations (intact) or one object was shifted slightly in location (manipulated). Participants were given 5 s to make a response after the offset of the test display. See the online article for the color version of this figure.



Figure 2. Example trials yielding relatively high (64.86) and low (.052) similarity scores, taken from a younger adult participant and older adult participant, respectively. Heat maps reflect the spatial layout of fixations weighted by duration. Objects did not appear during the delay phase (the screen was blank) and are depicted here to illustrate the relationship between the fixation locations and the studied objects. See the online article for the color version of this figure.

similarity analysis. To ensure that the similarity analysis was not biased by differences in the number of study and delay phase fixations, only the first nine fixations (average number of study period fixations) were submitted for analysis. Examples of high and low similarity scores are provided in Figure 2 for the purpose of visualization.

Data Analysis

To compare accuracy and similarity across younger and older adults, we performed independent-samples t tests using data from all available trials. Accuracy was indexed by both overall percent

correct and corrected recognition (percent correct manipulated – percent incorrect intact). To examine whether fixation similarity for corresponding study and delay phases was greater than chance, a permutation analysis was conducted with data from each participant shuffled such that fixations from the study phase of one trial were compared (using the described similarity analysis) to fixations from the delay phase of another randomly selected trial. The resulting similarity scores were permuted 1,000 times to generate a null distribution of chance similarity, which was compared to the actual similarity scores derived from the comparison of trial-matched study and delay phase fixations. Given that object locations are trial unique, similarity of study and delay phase fixations across trials should be significantly lower than similarity of matched study and delay phase fixations.

To investigate factors contributing to performance on the change detection task, we fit a generalized linear mixed effects model with a binomial distribution and logistic link function (GLMM; glmer of package lme4, Bates, Maechler, & Bolker, 2012, in R, R Development Core Team) with accuracy (correct vs. incorrect) as the dependent variable and predictor variables including age (younger or older) as a participant-level factor, and load (three, four, or five objects), target position (intact or manipulated), delay (750 ms, 1,500 ms, 2,250 ms, 3,000 ms, 3,750 ms, 4,500 ms, 5,250 ms, or 6,000 ms), and similarity score (mean centered) as trial-level factors. To allow for simple effects analysis of significant interactions, we dummy coded each factor as follows: older adults were used as the reference category for age (i.e., coded as zero) and manipulated trials as the reference category for target position. Load was coded for a linear effect (number of objects minus 3), with the three-object load as the reference category.

To build the model, we used a backward selection approach, starting with a model that included fixed effects for all three-way interactions that included age and similarity score, as well as random intercepts for participant and item and random slopes for participantlevel load, delay, target position, and similarity score variables. Mod-



Figure 3. Overlaid histogram and kernel density plots of (a) accuracy (% correct) and (b) similarity scores, by age. White dashed lines denote age group means. Bin widths are 1.0 for accuracy and 0.8 for similarity score. See the online article for the color version of this figure.

els were compared using a likelihood ratio test. Variables with a pvalue less than 0.10 were retained in the model. Null hypothesis significance tests were performed at an α -level of 0.05.

To investigate participant-level effects in the relationship of similarity and accuracy, we fit a linear mixed effects model (LMEM; lmer of package lme4) with mean accuracy, indexed by overall percent correct, as the dependent variable. Both accuracy and similarity score were evaluated as the average across trials for each participant within each level of target position, delay, and load. Excluding item effects, all other specifications match those reported above. Effects that were significant at an alpha = .05 level were included in the final model.

Results

Performance on the change detection task was not significantly different between age groups—% correct: $M(SD)_{YA} = 70.52 (3.43)$,



Figure 4. Younger and older adult accuracy (% correct) for (a) delay, (b) load, and (c) target position. Error bars denote +/-1 SE. See the online article for the color version of this figure.

 $M(SD)_{OA} = 68.28 (5.40), t(36) = -1.53, p = .135, 95\%$ confidence interval (CI) [-5.23, .732], d = .495, see Figure 3a; corrected recognition: $M (SD)_{YA} = 0.41 (0.07), M (SD)_{OA} = 0.37 (0.11),$ t(36) = -1.52, p = .136, 95% CI [-.104, .105], d = .434. Interestingly however, older adults showed significantly greater fixation reinstatement (similarity score) during the delay period than younger adults—M (SD)_{OA} = 18.24 (4.51), range = 0–72.73, M (SD)_{YA} = 13.33 (3.95), range = 0-73.32, t(36) = 3.57, p = .001, 95% CI [2.11, 7.70], d = 1.158, see Figure 3b—with mean similarity for both groups—YA, 95% CI [12.89, 14.02]; OA, 95% CI [17.77, 18.85]-falling outside of the confidence intervals of the null distribution as determined by permutation analysis (YA, 95% CI [8.68, 9.48]; OA, 95% CI [11.70, 12.49]).

Before fitting the models, we visually examined accuracy by level of target position, load, delay, and age group to confirm whether our behavioral outcome was responsive to task manipulations and participant age. As demonstrated in Panels (b) and (c) of Figure 4, both younger and older adults responded similarly to manipulations of target position (intact > manipulated) and load (3 > 4 > 5). Notably however, accuracy for both groups declined considerably between the 2,250- and 3,000-ms delays, with younger adults' performance dropping approximately to the level of older adults' performance (Figure 4a). We subsequently recoded delay as a categorical variable, grouped into shorter delays (<2,500 ms) and longer delays (>2,500 ms). The shorter delay was used as the reference category and coded as 0.

GLMM

To examine trial-level effects of similarity on accuracy, we modeled trial-level binary accuracy as a function of load, delay, target position, and similarity score. Using the model building approach outlined above, we identified several key variables and interactions, which were included in a final GLMM. Results of this model are reported in Table 1.

Consistent with the findings reported by Olsen and colleagues (2014), results of the GLMM suggest that on a trial-by-trial basis, reinstating encoding-related eye movements increases the chance of successfully retrieving the accompanying memory trace and subsequently making a correct memory response. Trial-level accuracy was also significantly greater in younger adults relative to older adults and significantly decreased with increased delay and load.

Table 1 Results of the Full GLMM

Variable	β	t	р	95% CI
(Intercept)	1.018	11.41	<.000***	.843, 1.193
Age	.168	2.15	.032*	.015, .322
Similarity Score	.078	2.16	.031*	.007, .150
Load	114	-2.20	.028*	215,013
Delay	252	-3.24	.001**	404,099

Note. 95% CI = 95% confidence intervals. Results of the final generalized linear mixed effects model (GLMM) arrived at via model comparison. Reference groups for age, delay, and target position are older adults, short delays (<2,500 ms), and manipulated trials, respectively. Load was coded for a linear effect (number of objects minus 3), with the three-object load as the reference category. * p < .05. ** p < .01. *** p < .001.

Variable	β	t	р	95% CI
(Intercept)	.714	32.73	<.000****	.671, .756
Age	.061	1.94	.053	001, .122
Similarity score	.054	2.52	.012*	.012, .095
Load	017	-1.23	.222	044, .010
Delay	065	-3.18	.002**	105,025
Target position	.040	1.67	.101	007, .088
Age \times Similarity Score	094	-3.28	.001**	150,038
Age \times Load	010	56	.577	047, .026
Similarity Score \times Load	003	28	.781	027, .020
Age \times Delay	017	59	.557	075, .041
Similarity Score \times Delay	018	89	.373	058, .022
Similarity Score \times Target Position	027	-1.81	.070	056, .002
Age \times Similarity Score \times Load	.032	1.88	.061	001, .066
Age \times Similarity Score \times Delay	.066	2.27	.024*	.009, .123

Table 2 Results of the Full LMEM

95% CI = 95% confidence intervals. Results of the final linear mixed effects model (LMEM) arrived at Note. via model comparison. Reference groups for age, delay, and target position are older adults, short delays (<2,500 ms), and manipulated trials, respectively. Load was coded for a linear effect (number of objects minus 3), with the three-object load as the reference category. * p < .05. ** p < .01. *** p < .001.

LMEM

To investigate whether the relationship between similarity and accuracy varied between participants, we subsequently ran a LMEM using overall percent correct, averaged across participants and conditions, as the dependent variable, and load, delay, target position, and similarity score (averaged across participants and conditions) as predictor variables. Results of the final model arrived at via model comparison are reported in Table 2.

Results of the model¹ revealed a significant effect of delay on accuracy (shorter > longer), and nonsignificant effects of load, target position, and age. There were no significant interactions between age and load or age and delay. In line with our predictions, there was a significant effect of similarity score (for manipulated trials at shorter delays and low loads) on accuracy in older adults, with accuracy increasing with similarity (see Figure 5). This relationship was not found to change significantly across experimental manipulations (Similarity Score × Load, Similarity Score × Delay, Similarity Score \times Target Position). Interestingly, the effect of similarity was significantly attenuated, and even nominally reversed, in younger adults at shorter delays and low loads (Age \times Similarity Score). However, this effect was significantly attenuated at longer delays (Age \times Similarity Score \times Delay), indicating a positive increase in the relationship between similarity and accuracy with longer delays (see Figure 5).

Discussion

Reinstatement of encoding-related eye movements during memory maintenance and/or retrieval has been proposed to support behavioral performance by reestablishing the spatial layout of the encoded stimulus and its associated features (Ferreira et al., 2008). Access to these features, however, is reduced with age, resulting in relational memory deficits that have been well documented in both behavioral and eyetracking studies (Hannula et al., 2010; Old & Naveh-Benjamin, 2008). Despite these impairments, research using eye-movement-monitoring suggests that some gaze patterns are resistant to age-related decline (Madden, Whiting, Cabeza, & Huettel, 2004). Moreover, evidence from behavioral and neuroimaging studies suggests that older adults can, under some circumstances, achieve a level of performance similar to that of younger adults through compensation: the greater or differential engagement of cognitive processes and/or neural systems by older adults relative to younger adults (for review, see Grady, 2012; Stern, 2009). The present findings provide novel evidence of compensatory eye movements in older adults by demonstrating that greater delay-period fixation reinstatement by older adults relative to younger adults supports performance on a visuospatial-memory-based change detection task.

Normal aging has often been associated with declines in visual perception and memory (for review, see Old & Naveh-Benjamin, 2008; Park et al., 2002), and these changes are accompanied by age-related reductions in explicit oculomotor control (for review, see Kramer, Hahn, Irwin, & Theeuwes, 2000). While control of viewing by exogenous factors like visual saliency declines with

¹ To ensure that results were not biased by differences in the number of fixations made across groups, the model was run with fixation count (scaled) included as both a fixed and random effect (slope). The main effects of similarity score— $\beta = 0.032, t = 2.17, p = .032, 95\%$ CI [.003, .062]; delay, $\beta = -0.068$, t = -5.31, p = .000, 95% CI [-.093, -.043]; target position, $\beta = 0.023$, t = .78, p > .250, 95% CI [-.034, .079]; and age, $\beta = 0.062$, t = 1.68, p = .104, 95% CI [-.010, .134]—and the interactions of Similarity Score × Age, $\beta = -0.065$, t = -3.30, p = .001, 95% CI [-.103, -.026]; Similarity Score \times Delay, β = -0.019, t = -1.53, p = .114, 95% CI [-.042, .005]; Similarity Score × Target Position, $\beta = -0.017$, t = -1.90, p = .058, 95% CI [-.034, .001]; Age × Delay, $\beta = -0.005$, t = -.25, p > .250, 95% CI [-.042, .033]; and Similarity Score × Age × Delay, β = .056, t = 3.24, p = .001, 95% CI [.022, .091]-did not change significantly from the original model. However, although the interaction of Age \times Similarity Score \times Load was omitted from the model, there was a significant negative effect of load on accuracy, $\beta = -0.025$, t = -2.91, p = .006, 95% CI [-.041, -.008], and a significant positive interaction of Similarity Score \times Load, $\beta = 0.017$, t = 3.25, p = .001, 95% CI [.007, .027]. Fixation count and interactions including fixation count were omitted from the model (p > .1).



Figure 5. Visual characterization of the relationship between fixation reinstatement (scaled similarity score) and performance accuracy (percent correct) across high and low delays for younger and older adults. Thick lines are generated for each age group using the intercepts and slope coefficients from the linear mixed effects model (LMEM). Thin lines are generated using a participant-specific linear model. See the online article for the color version of this figure.

age (see Açık et al., 2010), older adults show preserved guidance of viewing by endogenous factors like task instructions (Shih et al., 2012), and memory (Wynn et al., 2016). For instance, when bottom-up information is controlled, older adults show a similar benefit for guided (by a predictive cue) over nonguided visual search as do younger adults (see Madden et al., 2004; Neider & Kramer, 2011). Our own work has additionally shown that older adults, like younger adults, can use memory for a previously viewed search display to speed target detection on repeated search events (i.e., contextual cueing; Wynn et al., 2016). In line with these findings, the present results show that older adults use fixation reinstatement, a gaze pattern that has been previously linked to memory maintenance (Olsen et al., 2014), and retrieval (Laeng et al., 2014; Wynn et al., 2016), to a greater extent than younger adults to support similar memory performance.

At the behavioral level, older adults' performance has been shown to benefit from certain task manipulations (e.g., cued recall > free recall, pictures > words; Craik & Rose, 2012) and instructions (e.g., enacted encoding > nonenacted encoding; Nyberg, Persson, & Nilsson, 2002). However, by manipulating encoding and/or retrieval, these studies have been unable to quantify and compare the spontaneous utilization of performance-enhancing strategies in younger and older adults. Neuroimaging studies, on the contrary, have demonstrated that across a range of tasks, greater activation of task-related regions and networks (e.g., prefrontal cortex) by older adults relative to younger adults, supports age-approximate or equivalent behavioral performance (Cabeza et al., 2002). In the present study, we extend evidence of spontaneous, quantifiable compensatory activity to eve movements, and specifically, fixation reinstatement during memory maintenance. Although we did not measure neural activity, we speculate that the use of this gaze pattern by older adults is reflected in part by the overrecruitment of neural regions related to both memory and eye movements. Compensatory overactivity in the dorsolateral prefrontal cortex (Spaniol & Grady, 2012), for example, is consistent its well-established role in memory function and voluntary saccade control, and its proposed role as a connectionist node linking key regions of the oculomotor and memory networks (see Shen et al., 2016). The center of these networks, the hippocampus, has also been implicated in compensation via connections with the dorsolateral prefrontal cortex (Dennis et al., 2008; Grady, McIntosh, & Craik, 2003), and with eye movement similarity for configurally similar scenes (Ryals et al., 2015). The link between these related forms of compensation, however, remains underexplored.

Finally, although the term *compensation* is typically used to characterize activity in older adults, the very nature of compensation suggests that even younger adults should recruit compensatory activity when task demands exceed cognitive resources (e.g., cognitive load, Cappell, Gmeindl, & Reuter-Lorenz, 2010; Reuter-Lorenz & Cappell, 2008; number of study presentations, Spaniol & Grady, 2012). Indeed, our findings, in line with the findings of Olsen and colleagues (2014), suggest that both younger and older adults can use fixation reinstatement to support memory maintenance on a trial-by-trial basis. Interestingly however, results of the LMEM suggest that at shorter delays, younger adults who show greater fixation reinstatement perform more poorly than younger adults who reinstate to a lesser extent. Given the literature on compensation in young adults, we might interpret these findings as supporting a link between compensation and the match between task demands and cognitive resources. In other words, when task demands are minimal (i.e., short delays), older adults, and some low performing younger adults, might recruit fixation reinstatement to support an otherwise insufficient memory, whereas average-to-high performing younger adults may rely on the same mechanism when task demands increase (i.e., long delays). Though the present study was relatively low difficulty (median delay time = 3,000 ms), we might speculate that with even longer delays, the relationship between similarity and accuracy in younger adults would increase further, whereas in older adults, accuracy, and the compensatory benefits of fixation reinstatement, would diminish. Indeed, an earlier version of this task using longer delays (770–20,000 ms, median delay time = 5,608 ms) showed that similarity and accuracy were positively correlated in younger adults (Olsen et al., 2014). Though we were only able to capture a small subset of the larger distribution of possible similarity and accuracy values, further work using a broader range of difficulty will be needed to fully address the relationship between age, compensatory fixation reinstatement and task demands.

In summary, the present findings contribute to a considerable collection of cross-modal evidence of compensation in older adults. Analogous to reports of neural compensation, our findings suggest that fixation reinstatement might support older adults' mnemonic performance by reinstating and maintaining the encoding context, and that the same mechanism might support memory in younger adults as cognitive loads increase. Still, many questions remain regarding fixation reinstatement, and the relationship between fixation reinstatement and other forms of compensation. For example, to what extent is fixation reinstatement compensatory, and what factors mediate this effect? And, are eye movements distinct from, or a consequence of compensatory neural activity, and how do these processes interact to support memory? Future studies should continue to explore the ways in which younger and older adults' spontaneous, or perhaps instructed use of fixation reinstatement, in conjunction with compensatory neural processes, can be leveraged to compensate for age-related cognitive deficits.

References

- Açık, A., Sarwary, A., Schultze-Kraft, R., Onat, S., & König, P. (2010). Developmental changes in natural viewing behavior: Bottom-up and top-down differences between children, young adults and older adults. *Frontiers in Psychology*, 1, 207.
- Bates, D., Maechler, M., & Bolker, B. (2012). *Ime4.0: Linear mixed-effects models using S4 classes* (R package version 0.999999–0). Retrieved from http://cran.R-project.org/package=lme4
- Bone, M., St-Laurent, M., Dang, C., McQuiggan, D., Ryan, J. D., & Buchsbaum, R. (2016). A gaze into the mid's eye: Gaze as an indicator of cortical reinstatement during mental imagery. bio- Rxiv Published online May, 23, 2017. http://dx.doi.org/10.1101/107953
- Brandstatt, K. L., & Voss, J. L. (2014). Age-related impairments in active learning and strategic visual exploration. *Frontiers in Aging Neuroscience*, 6, 19. http://dx.doi.org/10.3389/fnagi.2014.00019
- Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage*, 17, 1394–1402. http://dx.doi.org/10.1006/nimg.2002 .1280
- Cabeza, R., Daselaar, S. M., Dolcos, F., Prince, S. E., Budde, M., & Nyberg, L. (2004). Task-independent and task-specific age effects on brain activity during working memory, visual attention and episodic retrieval. *Cerebral Cortex*, 14, 364–375. http://dx.doi.org/10.1093/cercor/bhg133
- Cappell, K. A., Gmeindl, L., & Reuter-Lorenz, P. A. (2010). Age differences in prefontal recruitment during verbal working memory maintenance depend on memory load. *Cortex: A Journal Devoted to the Study* of the Nervous System and Behavior, 46, 462–473. http://dx.doi.org/10 .1016/j.cortex.2009.11.009
- Castel, A. D. (2005). Memory for grocery prices in younger and older adults: The role of schematic support. *Psychology and Aging*, 20, 718– 721. http://dx.doi.org/10.1037/0882-7974.20.4.718
- Champely, S. (2016). pwr: Basic functions for power analysis (R package version 1.2–0) Retrieved from https://cran.r-project.org/web/packages/ pwr/pwr.pdf

- Chan, J. P. K., Kamino, D., Binns, M. A., & Ryan, J. D. (2011). Can changes in eye movement scanning alter the age-related deficit in recognition memory? *Frontiers in Psychology*, 2, 92. http://dx.doi.org/ 10.3389/fpsyg.2011.00092
- Craik, F. I. M., & Rose, N. S. (2012). Memory encoding and aging: A neurocognitive perspective. *Neuroscience and Biobehavioral Reviews*, 36, 1729–1739. http://dx.doi.org/10.1016/j.neubiorev.2011.11.007
- Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Que PASA? The posterior-anterior shift in aging. *Cerebral Cortex*, 18, 1201–1209. http://dx.doi.org/10.1093/cercor/bhm155
- Dennis, N. A., Hayes, S. M., Prince, S. E., Madden, D. J., Huettel, S. A., & Cabeza, R. (2008). Effects of aging on the neural correlates of successful item and source memory encoding. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34*, 791–808. http://dx .doi.org/10.1037/0278-7393.34.4.791
- Dragan, M. C., Leonard, T. K., Lozano, A. M., McAndrews, M. P., Ng, K., Ryan, J. D., . . . Hoffman, K. L. (2017). Pupillary responses and memory-guided visual search reveal age-related and Alzheimer's-related memory decline. *Behavioural Brain Research*, 322, 351–361. http://dx .doi.org/10.1016/j.bbr.2016.09.014
- Du, Y., Buchsbaum, B. R., Grady, C. L., & Alain, C. (2016). Increased activity in frontal motor cortex compensates impaired speech perception in older adults. *Nature Communications*, 7, 12241. http://dx.doi .org/10.1038/ncomms12241
- Ferreira, F., Apel, J., & Henderson, J. M. (2008). Taking a new look at looking at nothing. *Trends in Cognitive Sciences*, 12, 405–410. http://dx.doi.org/10 .1016/j.tics.2008.07.007
- Foulsham, T., & Kingstone, A. (2013). Fixation-dependent memory for natural scenes: An experimental test of scanpath theory. *Journal of Experimental Psychology: General*, 142, 41–56. http://dx.doi.org/10.1037/a0028227
- Grady, C. (2012). The cognitive neuroscience of ageing. Nature Reviews Neuroscience, 13, 491–505. http://dx.doi.org/10.1038/nrn3256
- Grady, C. L., McIntosh, A. R., & Craik, F. I. M. (2003). Age-related differences in the functional connectivity of the hippocampus during memory encoding. *Hippocampus*, 13, 572–586. http://dx.doi.org/10.1002/hipo .10114
- Hannula, D. E., Althoff, R. R., Warren, D. E., Riggs, L., Cohen, N. J., & Ryan, J. D. (2010). Worth a glance: Using eye movements to investigate the cognitive neuroscience of memory. *Frontiers in Human Neuroscience*, 4, 166. http://dx.doi.org/10.3389/fnhum.2010.00166
- Johansson, R., Holsanova, J., Dewhurst, R., & Holmqvist, K. (2012). Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced during encoding. *Journal of Experimental Psychology: Human Perception and Performance*, 38, 1289– 1314. http://dx.doi.org/10.1037/a0026585
- Johansson, R., & Johansson, M. (2014). Look here, eye movements play a functional role in memory retrieval. *Psychological Science*, 25, 236– 242. http://dx.doi.org/10.1177/0956797613498260
- Kramer, A. F., Hahn, S., Irwin, D. E., & Theeuwes, J. (2000). Age differences in the control of looking behavior: Do you know where your eyes have been? *Psychological Science*, 11, 210–217. http://dx.doi.org/ 10.1111/1467-9280.00243
- Laeng, B., Bloem, I. M., D'Ascenzo, S., & Tommasi, L. (2014). Scrutinizing visual images: The role of gaze in mental imagery and memory. *Cognition*, 131, 263–283. http://dx.doi.org/10.1016/j.cognition.2014.01.003
- Laeng, B., & Teodorescu, D. S. (2002). Eye scanpaths during visual imagery reenact those of perception of the same visual scene. *Cognitive Science*, 26, 207–231. http://dx.doi.org/10.1207/s15516709cog2602_3
- Madden, D. J., Whiting, W. L., Cabeza, R., & Huettel, S. A. (2004). Age-related preservation of top-down attentional guidance during visual search. *Psychology and Aging*, *19*, 304–309. http://dx.doi.org/10.1037/ 0882-7974.19.2.304
- Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., . . . Chertkow, H. (2005). The Montreal Cognitive

Assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*, *53*, 695–699. http://dx.doi.org/10.1111/j.1532-5415.2005.53221.x

- Neider, M. B., & Kramer, A. F. (2011). Older adults capitalize on contextual information to guide search. *Experimental Aging Research*, 37, 539–571. http://dx.doi.org/10.1080/0361073X.2011.619864
- Noton, D., & Stark, L. (1971). Scanpaths in eye movements during pattern perception. *Science*, 171, 308–311. http://dx.doi.org/10.1126/science.171 .3968.308
- Nyberg, L., Persson, J., & Nilsson, L. G. (2002). Individual differences in memory enhancement by encoding enactment: Relationships to adult age and biological factors. *Neuroscience and Biobehavioral Reviews*, 26, 835–839. http://dx.doi.org/10.1016/S0149-7634(02)00074-X
- Old, S. R., & Naveh-Benjamin, M. (2008). Differential effects of age on item and associative measures of memory: A meta-analysis. *Psychology* and Aging, 23, 104–118. http://dx.doi.org/10.1037/0882-7974.23.1.104
- Olsen, R. K., Chiew, M., Buchsbaum, B., & Ryan, J. D. (2014). The relationship between delay period eye movements and visuospatial memory. *Journal of Vision*, *14*, 1–11.
- Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D., & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychology and Aging*, *17*, 299–320. http://dx.doi.org/10 .1037/0882-7974.17.2.299
- Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*, 60, 173–196. http://dx.doi.org/10.1146/annurev.psych.59.103006.093656
- Pearson, D. G., Ball, K., & Smith, D. T. (2014). Oculomotor preparation as a rehearsal mechanism in spatial working memory. *Cognition*, 132, 416–428. http://dx.doi.org/10.1016/j.cognition.2014.05.006
- Reuter-Lorenz, P. A., & Cappell, K. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, 17, 177–182. http://dx.doi.org/10.1111/j.1467-8721.2008.00570.x
- Ryals, A. J., Wang, J. X., Polnaszek, K. L., & Voss, J. L. (2015). Hippocampal contribution to implicit configuration memory expressed via eye movements during scene exploration. *Hippocampus*, 25, 1028– 1041. http://dx.doi.org/10.1002/hipo.22425

- Ryan, J. D., Althoff, R. R., Whitlow, S., & Cohen, N. J. (2000). Amnesia is a deficit in relational memory. *Psychological Science*, 11, 454–461. http://dx.doi.org/10.1111/1467-9280.00288
- Salthouse, T. (2012). Consequences of age-related cognitive declines. Annual Review of Psychology, 63, 201–226. http://dx.doi.org/10.1146/annurevpsych-120710-100328
- Shen, K., Bezgin, G., Selvam, R., McIntosh, A. R., & Ryan, J. D. (2016). An anatomical interface between memory and oculomotor systems. *Journal of Cognitive Neuroscience*, 28, 1772–1783. http://dx.doi.org/10 .1162/jocn_a_01007
- Shih, S. I., Meadmore, K. L., & Liversedge, S. P. (2012). Aging, eye movements, and object-location memory. *PLoS ONE*, 7(3), e33485. http://dx.doi .org/10.1371/journal.pone.0033485
- Spaniol, J., & Grady, C. (2012). Aging and the neural correlates of source memory: Over-recruitment and functional reorganization. *Neurobiology* of Aging, 33, 425e.3–425.e18.
- Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects. *Psychological Research*, 65, 235–241. http://dx.doi.org/10.1007/s004260100059
- Stern, Y. (2009). Cognitive reserve. *Neuropsychologia*, 47, 2015–2028. http://dx.doi.org/10.1016/j.neuropsychologia.2009.03.004
- Umanath, S., & Marsh, E. J. (2014). Understanding how prior knowledge influences memory in older adults. *Perspectives on Psychological Science*, 9, 408–426. http://dx.doi.org/10.1177/1745691614535933
- Whitehead, J. C., Li, L., McQuiggan, D. A., Gambino, S. A., Binns, M. A., & Ryan, J. D. (2016). Validation of a mobile eyetracking-based assessment of cognitive decline: The short-form Visual Paired Comparison (sVPC) task. Manuscript under review.
- Wynn, J. S., Bone, M. B., Dragan, M. C., Hoffman, K. L., Buchsbaum, B. R., & Ryan, J. D. (2016). Selective scanpath repetition during memory-guided visual search. *Visual Cognition*, 24, 15–37. http://dx.doi .org/10.1080/13506285.2016.1175531

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