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Research report

The relationship between eye movements and subsequent recognition: Evidence from individual differences and amnesia

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ABSTRACT

There is consistent agreement regarding the positive relationship between cumulative eye movement sampling and subsequent recognition, but the role of the hippocampus in this sampling behavior is currently unknown. It is also unclear whether the eye movement repetition effect, i.e., fewer fixations to repeated, compared to novel, stimuli, depends on explicit recognition and/or an intact hippocampal system. We investigated the relationship between cumulative sampling, the eye movement repetition effect, subsequent memory, and the hippocampal system. Eye movements were monitored in a developmental amnesic case (H.C.), whose hippocampal system is compromised, and in a group of typically developing participants while they studied single faces across multiple blocks. The faces were studied from the same viewpoint or different viewpoints and were subsequently tested with the same or different viewpoint. Our previous work suggested that hippocampal representations support explicit recognition for information that changes viewpoint across repetitions (Olsen et al., 2015). Here, examination of eye movements during encoding indicated that greater cumulative sampling was associated with better memory among controls. Increased sampling, however, was not associated with better explicit memory in H.C., suggesting that increased sampling only improves memory when the hippocampal system is intact. The magnitude of the repetition effect was not correlated with cumulative sampling, nor was it related reliably to subsequent recognition. These findings indicate that eye movements collect information that can be used to strengthen memory representations that are later available for conscious remembering, whereas eye movement repetition effects reflect a processing change due to experience that does not necessarily reflect a memory representation that is available for conscious appraisal. Lastly, H.C. demonstrated a repetition effect for fixed viewpoint faces but not for variable

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viewpoint faces, which suggests that repetition effects are differentially supported by neocortical and hippocampal systems, depending upon the representational nature of the underlying memory trace.

1. Introduction

Measures derived from eye movements have been used to characterize memory encoding, to reveal the nature of the representations that are stored in memory and to relate both to hippocampal function (reviewed by Hannula et al., 2010; Ryan & Cohen, 2003). The current investigation explored the contribution of eye movements to subsequent item memory as well as the role of the hippocampal system in eye movement sampling behavior and subsequent item memory.

Item recognition in healthy, neurologically intact individuals is likely supported by both the hippocampus as well as the neocortex, with the medial temporal lobe (MTL) cortices playing a central role (Brown & Aggleton, 2001; Cohen & Eichenbaum, 1993; Davachi, 2006; Mayes, Montaldi, & Migo, 2007). Our recent work has indicated that recognition memory for items is more heavily dependent on the hippocampus when items are presented and encoded from differing viewpoints (Olsen et al., 2015). We reported that compared to control participants, H.C., an individual with developmental amnesia due to hippocampal system compromise, demonstrated intact recognition for faces that were repeatedly studied from the same viewpoint, and impaired recognition for faces that were studied from multiple viewpoints. These results suggest that item recognition memory was differentially supported by the neocortex and hippocampus within the same experimental paradigm, depending on the presentation format (fixed or variable viewpoints) of study items. More generally, such findings suggest that the hippocampal system provides the ability to flexibly bind the features within an item, and performs a relational binding function, which supports memory for items that are physically modified across study repetitions.

Eye movement sampling behavior is functional for learning and memory such that subsequent recognition is higher when viewers are allowed to move their eyes during encoding compared to when they are required to maintain fixation (Henderson, Williams, & Falk, 2005). Other work has shown that increased cumulative sampling of visual stimuli is associated with better subsequent recognition for items (Loftus, 1972) in both healthy younger and older adults (Chan, Kamino, Binns, & Ryan, 2011; Firestone, Turk-Browne, & Ryan, 2007).

Despite research showing that eye movements are functional for the recognition of items, and that the hippocampus can contribute to item recognition, there is little research that examined the relationship between eye movement sampling behavior and later recognition for items that specifically depend on the hippocampus. In particular, it is unknown whether eye movement sampling would particularly benefit item representations that rely predominantly on hippocampal function. Moreover, it remains to be determined whether amnesic people would engage in more sampling behavior to compensate for impaired hippocampal function.

While considerable research suggests that eye movement sampling supports memory *acquisition*, another line of well-established research suggests that eye movement behavior can reflect the online *expression* of memory. Eye movement sampling is sensitive to prior experience, such that upon repeated exposures to an item, a *repetition effect* is observed: the previously viewed items are sampled with fewer eye fixations compared to novel items. This effect has been reported in numerous studies, and in various populations including younger adults, older adults, people with prosopagnosia, and memory-impaired individuals (Althoff & Cohen, 1999; Althoff et al., 1999; Bate, Haslam, Tree, & Hodgson, 2008; Heisz & Ryan, 2011; Ryan, Althoff, Whitlow, & Cohen, 2000; Smith & Squire, 2008).

In contrast to the consistent positive relationship between cumulative eye movement sampling and recognition memory, the relationship between the eye movement repetition effect and recognition is not straightforward, nor is the relationship between the repetition effect and its underlying neural substrates. Some studies have reported that the repetition effect can occur in the absence of explicit recognition, whereas others have found that the repetition effect is eliminated in individuals who have impaired recognition, such as hippocampal amnesics (Ryan et al., 2000; cf. Smith & Squire, 2008). Moreover, some research has shown that eye movement repetition effects are hippocampal-dependent (Smith & Squire, 2008; Smith, Hopkins, & Squire, 2006), whereas other work has reported intact repetition effects in hippocampal amnesia that are presumably driven by neocortical regions (Althoff & Cohen, 1999; Ryan et al., 2000). It may be the case that, depending on the particular paradigm, eye movement repetition effects can be supported by either hippocampal and/or neocortical memory representations. Paradigm differences may affect the relationship between eye movement repetition effects and subsequent recognition in healthy individuals, and influence the extent to which eye movement repetition effects are impaired in amnesia.

The current study investigated the relationship between cumulative eye movement sampling, the eye movement repetition effect, and subsequent recognition memory for faces, as well as the relation between the hippocampal system and these eye movement measures. We used the same paradigm as in our previous study (Olsen et al., 2015), which provided the novel opportunity to investigate both the acquisition and expression of memory, as indexed by eye movements, and their associations with recognition memory that can be

supported differentially by hippocampal or neocortical memory representations. We tested H.C. and a group of demographically matched, typically developing adults to allow for a thorough exploration of the relationship between eye movements, the hippocampal system, and recognition.

The differential reliance on distinct MTL structures for face recognition on this task provides different predictions regarding the relationship between cumulative sampling and subsequent recognition. Consistent with previous literature, we predicted that increased eye movement sampling would be associated with better recognition memory for faces presented from a fixed viewpoint, in both H.C. and controls, as memory for fixed viewpoint faces can be supported by neocortex. Increased sampling was also predicted to benefit recognition memory for faces presented across variable viewpoints, but only for control participants, as our previous work indicated memory for faces which are presented across viewpoints depends on an intact hippocampal system (Olsen et al., 2015). In contrast, we expected that the relationship between sampling behavior and subsequent recognition for variable viewpoint faces would be "broken" in H.C., as the primary neural structure supporting those memory representations is compromised. If this is the case, then equivalent sampling for subsequently remembered and subsequently forgotten faces should be observed in H.C. Additionally, it was expected that H.C. would demonstrate greater cumulative eye movement sampling relative to controls during encoding, potentially as a compensatory mechanism to support later recognition.

The relationship between eye movement repetition effects and subsequent memory may similarly be influenced by differential contributions from the MTL cortex and hippocampus on the fixed viewpoint and variable viewpoint conditions, respectively. If the MTL cortex enables repetition effects for faces studied from a fixed viewpoint (Althoff & Cohen, 1999; Althoff et al., 1999), a positive relationship would be expected in both controls and H.C. If repetition effects for faces studied from a variable viewpoint are dependent on the hippocampus, a positive relationship would also be expected for controls but not for H.C. If, however, repetition effects for both types of face presentations hinge on conscious recognition, we would expect positive correlations between repetition effects and recognition for both fixed and variable viewpoint faces for H.C. and the controls. A final possibility is that repetition effects are unrelated to conscious recognition, in which case no correlation would be expected for explicit recognition of either fixed or variable viewpoint faces in either H.C. or controls.

2. Methods

2.1. Participants

2.1.1. Controls

Participants were recruited from the Rotman Research Institute participant pool and from the University of Toronto. A group of 32 healthy young control participants (24 female; $M = 23.22$, $SD = 3.31$) were included in the control group. The level of education achieved by controls ($M = 16.78$, $SD = 2.34$) was not statistically different from that achieved by H.C. (14 years; $p_{\text{two-tailed}} = .25$). Portions of the data from the control group and from the developmental amnesia case, H.C., have been previously reported (Olsen et al., 2015) and are reproduced here for comparison purposes. All participants provided informed consent and were compensated for participation.

2.1.2. Developmental amnesia case

H.C. is a woman with developmental amnesia, aged 23 at the time of testing. H.C.'s bilateral hippocampal volume is significantly reduced (29.5% on the left and 31.2% on the right) compared to a group of age-, sex- and education-matched controls (Olsen et al., 2013). H.C.'s MTL cortices, on the other hand, are volumetrically normal; in fact, her left parahippocampal cortex was found to be marginally larger than that of the control group. While it was previously assumed that H.C. experienced a perinatal hypoxic episode associated with premature birth, a more recent examination of her neuroanatomical profile has indicated the possibility that abnormalities within the hippocampus and structures closely connected to it occurred prenatally, in early fetal development (Rosenbaum et al., 2014). In addition to the previously reported hippocampal volume loss, abnormal development of the extended hippocampal system is also evident, including: aplasia of the mammillary bodies, atrophy of the anterior thalamic nuclei bilaterally, hypogenesis of the fornices, and abnormal hippocampal shape and orientation (Rosenbaum et al., 2014). These developmental abnormalities likely restrict hippocampal output, which may lead to greater impairment than expected given her relatively modest hippocampal volume decrease.

H.C.'s neuropsychological profile is well-documented (Hurley, Maguire, & Vargha-Khadem, 2011; Olsen et al., 2015; Rosenbaum et al., 2011, 2014). Her IQ is in the average range, and she has relatively intact semantic memory, but impaired episodic and public event memory (Rosenbaum et al., 2011). She graduated from a mainstream high school and completed two years of post-secondary education.

2.2. Apparatus, classification of fixations, outlier trial rejection

Stimuli were presented on a 19″ Dell M991 monitor (resolution 1024 × 768) from a distance of 24″. Monocular eye movements were recorded with a head-mounted EyeLink II eyetracker (500 Hz; SR Research Ltd., Mississauga, ON, Canada). Eye movement calibration was performed at the beginning of the experiment, and drift correction (>2°), if needed, was performed immediately prior to the onset of each trial. Saccades were determined using the built-in EyeLink saccade-detector heuristic; acceleration and velocity thresholds were set to detect saccades greater than .5° of visual angle. Blinks are defined as periods in which the saccade-detector signal was missing for three or more samples in a sequence. Fixations are defined as the samples remaining after the categorization of saccades and blinks; no minimum duration for fixation definition was applied.

Outlier trials were defined using a Tukey boxplot method, by calculating the interquartile range (IQR) for both the

response time and number of fixations, for each block separately (Tukey, 1977). Probable outlier trials were those that exceeded the 75th percentile (Q3) by three times the IQR or fell below the 25th percentile (Q1) by three times the IQR. Prior to the subsequent memory analyses, estimates for the eye movement measures and d-prime scores were also examined for extreme values. The same outlier procedure (Tukey boxplot method) was used to eliminate extreme values.

2.3. Stimuli and pre-defined areas of interest

Realistic, three-dimensional face/head models (80 female, 80 male) were created using FaceGen Modeller's *Generate* function (Singular Inversions, Toronto, ON, Canada). Computer-generated faces were used as experimental stimuli to enable the precise manipulation of viewing angle and to make contact with previous literature on face memory and amnesia. All faces were posed with a neutral expression or with a slight smile. A range of skin tones, eye colors, facial shapes (e.g., cheekbones, jawline) and feature shapes/sizes were used across the set of faces. Special skin textures, available with the FaceGen Modeller software, were used to increase realism.

Each face model ($n = 160$) was captured in 6 different viewpoints: 0° (or front view), 5°, 10°, 15°, 20° or 25° turned to the viewer's right, for a total of 960 images. Face images were cropped above the eyebrows, below the chin, and on the sides so that the top of the head, most of the neck, and the ears were not shown. The crop box used for each face viewpoint was identical; all images measured 316 (width) × 405 (height) pixels. For all viewpoints, the top of the crop box was anchored to a horizontal position located approximately 15 pixels above the eyebrows.

To ascertain that the computer generated faces were distinguishable as male or female, even without the presence of hair, gender ratings on each face were collected by a separate group of participants ($n = 12$). These participants were able to accurately categorize both male ($M = .99$ $SD = .01$) and female ($M = .98$ $SD = .02$) faces.

2.4. Experimental design

The experimental testing session consisted of a study phase during which participants incidentally encoded faces while their eye movements were recorded, followed by a surprise recognition memory test phase. Eighty faces (half female) were repeated five times across the five study blocks (once per block). Each face was presented for four seconds and participants were asked to judge whether the face was male or female. Participants indicated their responses using a hand-held button box and response times (RTs) were recorded. Forty faces were presented in the identical viewpoint (***fixed*** condition) across the five study blocks and 40 faces were shown in a different viewpoint (***variable*** condition) for each study block. For example, if a face was shown in the variable condition, a participant might see it from the following viewpoints: block 1 = 5° rotated, block 2 = 20° rotated, block 3 = 25° rotated, block 4 = 10° rotated, block 5 = 0° rotated (front view); see Fig. 1). Faces were assigned to the fixed and variable conditions in a counterbalanced manner across participants. Front view (0°) and side view (5°–25°) faces were equally represented in the variable and fixed viewpoint conditions, such that face viewpoint was not diagnostic of study condition. The final study block was followed by a five-minute break, and then the recognition memory test.

During the recognition test, 160 faces were shown: 80 previously studied and 80 non-studied. Each face was presented for three seconds and participants judged whether the face had been previously presented in the study phase. Participants were instructed that some of the faces would be shown from different viewpoints than those that had been previously studied and to make their memory judgments based on face identity rather than viewpoint. Memory judgments were reported verbally to the experimenter using a five-point confidence scale (1 = sure new, 2 = probably new, 3 = guess, 4 = probably old, 5 = sure old). Of the 40 faces that were presented in the fixed condition during the study phase, half were tested in the previously studied viewpoint (***fixed-repeat viewpoint***) and half were shown in a novel viewpoint (***fixed-novel viewpoint***). Novel viewpoints were selected so that they were 15° away from the studied viewpoint (e.g., if the studied viewpoint was 20°, the tested viewpoint was 5°). Of the 40 faces presented in the variable condition during the study phase, 20 faces were tested in the same view that was presented in the 5th study block (***variable-repeat viewpoint***) and 20 faces were tested in a novel viewpoint (***variable-novel viewpoint***). As in the fixed-novel viewpoint condition, the viewpoint of the test faces in the variable-novel viewpoint condition were 15° away from the viewpoint shown in the final study block. Repeat viewpoint and novel viewpoint test probes were counterbalanced across participants as were studied versus non-studied faces. In addition, front viewpoint and side viewpoint faces were equally represented across the test conditions so that face viewpoint was not diagnostic of test condition.

2.5. Statistics

Repeated measures analysis of variance (ANOVA) in SPSS (IBM, v. 20) was used to assess differences in performance for within-subject conditions (e.g., variable *vs* fixed viewpoint conditions) among the controls. For between subject analyses examining the relationship between recognition memory (d-prime) and study phase viewing measurements, linear models were performed using the lm function in R Studio (version .99.893) using the R programming language (R Core Team, 2016). For within-subject analyses comparing study phase viewing and subsequent memory (confidence ratings), mixed effects linear regression was performed using the lmer function (version 1.1–11) in R Studio with subject and item specified as random factors (Bates, Maechler, Bolker, & Walker, 2015). *p*-Values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. This approach allowed for the appropriate statistical modeling of the data, even for unbalanced data cells resulting from the subsequent memory analysis (uneven number of trials per bin). To assess statistical significance between H.C. and age-matched controls, H.C.'s measures were compared to the 95% CI of the controls. To test for within-subject effects for H.C. (e.g., number of fixations made for faces she later remembered versus forgot) bootstrapping was performed using the adjusted bootstrap

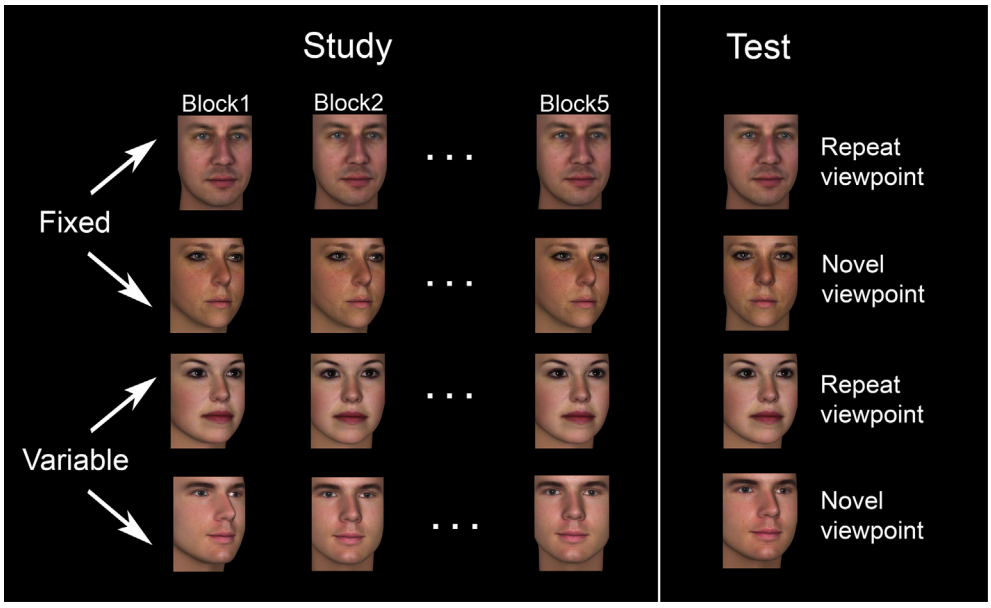

Fig. 1 – Task design (reproduced with permission from the Society for Neuroscience). Left panel: The study phase consisted of five study blocks in which 80 faces were presented. Each face was displayed for four seconds and participants made a gender judgment. Face viewpoint was either held constant across study blocks (fixed condition) or a different viewpoint was shown in each study block (variable condition). Right panel: Surprise memory test consisted of 80 previously studied faces and 80 non-studied faces. Among the previously studied faces, half were shown from a repeated viewpoint and half were shown from a novel viewpoint. For faces studied from variable viewpoints, the repeated viewpoint was the same as the viewpoint used in the fifth study block. Participants made a memory judgment using a 5-point recognition confidence scale (1 = sure new, 5 = sure old).

percentile (BCa) method in R (R Studio .98.1049) with the package boot. This function was used to produce 95% (Canty & Ripley, 2012, pp. 3–7; Davison & Hinkley, 1997; Efron, 1987). The alpha level was set to .05 to establish significance for all tests. Effect sizes are reported for ANOVA and linear regression results using partial eta squared (η_p^2) and odds ratio, respectively.

3. Results

3.1. Gender judgment accuracy and response times (RT)

Accuracy on the gender judgments, which were performed during the five study blocks during the incidental encoding of the faces, was assessed in the control group and compared to H.C. Among the controls, there was no main effect of viewpoint (fixed viewpoint: $M = .98$, $SD = .03$; variable viewpoint: $M = .98$, $SD = .03$; $F = 1.33$, $p = .26$) and no main effect of block (Blocks 1–5 $M = .98$; $F = .19$, $p = .94$) on gender judgment accuracy. A significant interaction between viewpoint and block ($F = 3.17$, $p = .02$, $\eta_p^2 = .09$) was observed. However, follow-up paired comparisons on the accuracy between the study conditions (fixed, variable viewpoint) did not reach statistical significance after correcting for multiple comparisons (all $ps > .01$).

H.C.'s accuracy on the gender judgment task fell slightly below the 95% CI of the controls for fixed viewpoint faces (controls: $M = .98$, 95% CI = [.97, .99]; H.C.: $M = .94$) and well below the 95% CI for controls for faces presented in variable viewpoints across study blocks (controls: $M = .98$, 95% CI = [.97, .99]; H.C.: $M = .88$).

To examine repetition-related reductions in RT (i.e., response priming), median RTs were computed for each participant, and RTs during the 1st block were compared to RTs during the 5th block. Among controls, RT on fixed viewpoint trials dropped from 850.13 msec to 752.28 across blocks (a decrease of 97.85 msec), and from 838.48 to 747.89 on variable viewpoint trials (a decrease of 90.59 msec). H.C.'s median RT dropped from 871.41 msec to 821.57 msec (a decrease of 49.83 msec) on fixed viewpoint trials, and from 857.85 msec to 797.32 msec (a decrease of 60.53 msec) on variable viewpoint trials. A proportional priming score was next calculated for each participant as a way to account for baseline differences in RT (Schnyer, Dobbins, Nicholls, Schacter, & Verfaellie, 2006). The mean RT proportional priming score among controls was .09, 95% CI [.04, .15], for faces presented in the fixed viewpoint condition and .09, 95% CI = [.02, .15], for faces presented in the variable viewpoint condition. A proportional priming score of .09 indicates that the controls were, on average, 9% faster during the 5th block compared to the 1st block. H.C. demonstrated a proportional RT priming score of .06 for fixed viewpoint faces and .07 for variable viewpoint faces, which indicates that the change in RT demonstrated by H.C. fell within the 95% CI of controls. RT Priming exhibited by H.C. did not significantly differ from that of the controls in either the fixed or variable viewpoint conditions.

3.2. Eye movements

The number of eye fixations made during the incidental encoding of faces was investigated for each block during the study phase (Fig. 2A and B). Among controls, there was a

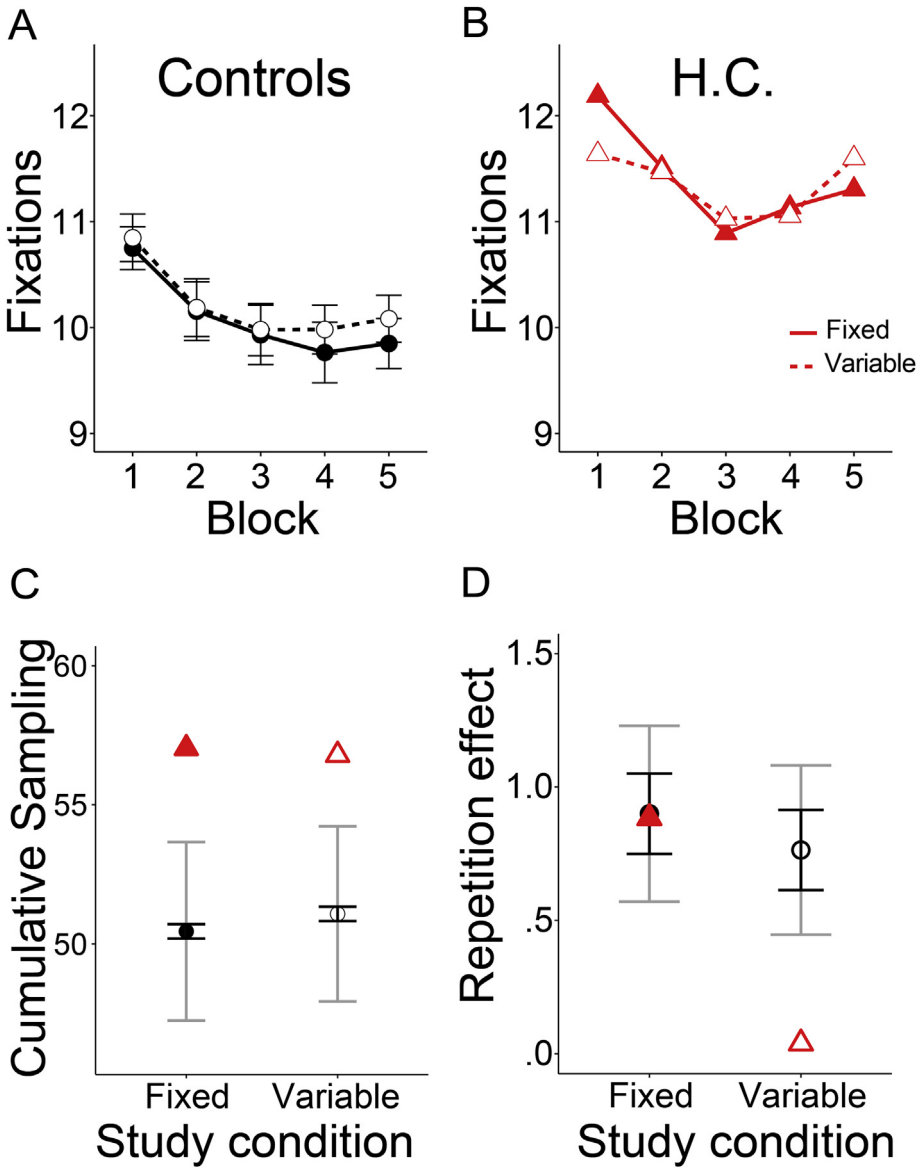

Fig. 2 – Eye movements during incidental encoding in controls and H.C.). A and B: The average number of fixations made by controls (A) and H.C. (B) toward a face during each study block, plotted separately for fixed viewpoint faces (sold line) and variable viewpoint faces (dashed lines). C: The total (cumulative) number of fixations made across the five study blocks plotted for fixed viewpoint faces (left) and variable viewpoint faces (right). H.C. is depicted by the red triangles. Black error bars denote the within subject 95% CIs for controls and gray error bars denote the between subject 95% CIs for controls. D: The magnitude of the repetition effect ([Block 1 fixations−Block 5 fixations]/Block 1 fixations) for fixed viewpoint faces (left) and variable viewpoint faces (right). Black error bars denote the within subject 95% CIs and gray error bars denote the between subject 95% CIs.

significant main effect of block ($F = 9.80$, $p < .001$, $\eta_p^2 = .24$) and a significant main effect of viewpoint on fixations [$F = 12.39$, $p < .001$, $\eta_p^2 = .29$ (variable viewpoint faces were viewed with more eye fixations than fixed viewpoint faces]. There was no significant interaction between viewpoint and block ($F = 1.13$, $p = .35$).

3.2.1. *Cumulative sampling*

Cumulative sampling was calculated for each participant by summing the mean number of fixations made during each block (Fig. 2C). Variable viewpoint faces were consistently viewed with higher cumulative fixations than fixed viewpoint faces (26/32 participants; Fixed: $M = 50.45$, 95% CI [47.24, 53.66]; Variable: $M = 51.08$, 95% CI [47.93, 54.23]; $F = 12.39$, $p < .001$, $\eta_p^2 = .29$). H.C. made a greater number of cumulative fixations than controls for both fixed and variable viewpoint faces (Fixed: $M = 57.03$; Variable: $M = 56.79$; Fig. 2C).

3.2.2. *Repetition effect*

The magnitude of the eye movement repetition effect was computed as a proportion of Block 1 fixations to account for any baseline differences in viewing ([Block 1 fixations−Block 5

fixations]/Block 1 fixations) for each participant (Fig. 2D). Among controls, the magnitude of the eye movement repetition effect was marginally, but consistently (27/32 participants), larger for fixed viewpoint faces compared to the variable viewpoint faces (Fixed: $M = .08$, $SD = .08$; Variable: $M = .07$, $SD = .07$; main effect of Viewpoint: $F = 3.04$, $p = .09$). While the repetition effect for variable viewpoint faces was slightly smaller than for fixed viewpoint faces, the 95% CI did not contain zero for either condition (95% CI for fixed viewpoint faces = [.06, .11]; 95% CI for variable viewpoint = [.04, .09]. H.C. demonstrated an intact eye movement repetition effect for fixed viewpoint faces compared to controls; however, H.C.'s repetition effect for variable viewpoint faces was close to zero, and this value fell well below the 95% CIs of the controls (Fixed: $M = .07$; Variable: $M = .003$).

3.3. Recognition memory

d-Prime was determined for each of the four test probe conditions: fixed-repeat viewpoint, fixed-novel viewpoint, variable-repeat viewpoint, and variable-novel viewpoint, for each participant (Fig. 3). There was a significant main effect of test viewpoint; accuracy was higher for the repeated versus novel viewpoint test probes ($F = 14.22$, $p = .001$, $\eta_p^2 = .31$). The effect of study viewpoint was not significant ($F = 1.41$, $p = .24$); however, a significant test viewpoint by study condition interaction was found ($F = 14.17$, $p = .001$, $\eta_p^2 = .31$). The test viewpoint by study condition interaction revealed a larger recognition advantage for repeated test viewpoints for faces studied in the fixed versus variable viewpoint condition. That is, recognition accuracy was higher for faces studied from the identical viewpoint across the 5 study blocks when it was subsequently tested in the same view than when it was tested in a novel viewpoint (d-prime for same test viewpoint: $M = 1.52$, 95% CI [1.31, 1.75] *vs* novel test viewpoint: $M = 1.07$, 95% CI [.88, 1.26]); however, this same viewpoint test-probe advantage was not as pronounced for faces studied in the variable viewpoint condition (d-prime for same test viewpoint: $M = 1.29$, 95% CI [1.06, 1.52] *vs* novel test viewpoint: $M = 1.21$, 95% CI [1.04, 1.38]).

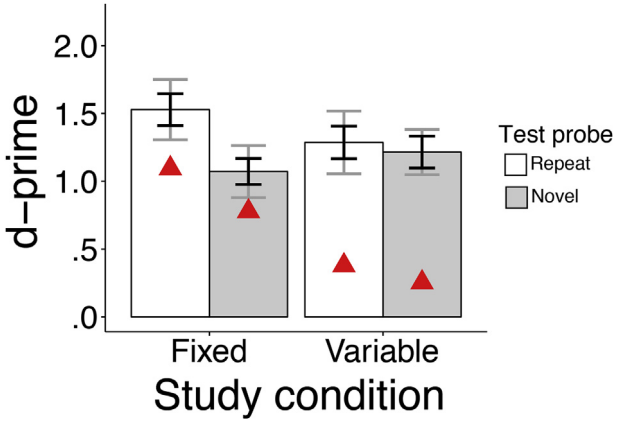

Fig. 3 – d-Prime scores plotted separately for fixed viewpoint faces and variable viewpoint faces for controls and H.C. (red triangles). Repeat viewpoint test probe faces are plotted in white and novel viewpoint test probe faces are plotted in gray. Black error bars denote the within subject 95% confidence intervals and gray error bars denote the between subject 95% error bars.

Comparisons between H.C. and controls for each of the four test probe conditions (fixed-repeat viewpoint, fixed-novel viewpoint, variable-repeat viewpoint, variable-novel viewpoint) were also tested. H.C.'s recognition was lower than controls for all four conditions (Fig. 3). Her recognition memory for fixed viewpoint faces was slightly below the 95% CI of the controls (fixed-repeat viewpoint: $M = 1.09$; fixed-novel viewpoint: $M = .78$) and as reported previously by Olsen et al. (2015),[1] H.C.'s recognition memory was greatly impaired for both variable-repeat and variable-novel viewpoint trials (variable-repeat viewpoint: $M = .38$; variable-novel viewpoint: $M = .25$; Fig. 3).

3.4. Cumulative sampling and subsequent memory

To examine the association between viewing behavior and recognition memory across control subjects (Fig. 4A), the relationship between cumulative sampling (total number of fixations made to faces across the five study blocks) and subsequent recognition was tested using a linear model with study condition (fixed viewpoint, variable viewpoint), test condition (repeat viewpoint, novel viewpoint) and cumulative sampling were modeled as predictors and d-prime as the outcome variable. This model was compared to a null model, which did not include cumulative sampling as a predictor, and model testing determined that including cumulative sampling as a predictor variable significantly increased the model fit ($F = 10.38$, $p = .002$). This means that variation in recognition memory performance across subjects is significantly better predicted when the cumulative sampling measure is taken into account. A second model was tested with interaction terms; however, model testing determined that the model with interaction terms was not a significantly better fit ($F = 1.04$, $p = .39$). Thus, only the model with main effects is presented. The main effect of cumulative fixations was significant ($t = 3.22$ $p = .002$), which indicated that greater cumulative sampling was associated with better recognition memory performance (see Fig. 4A for simply correlation, collapsed across conditions).

To examine the effect of viewing behavior within subjects, a mixed effects regression analysis examined the effect of cumulative sampling (total number of fixations made during the study phase) on subsequent memory (1–5 confidence ratings) on a trial-by-trial basis. In this model, study condition (fixed viewpoint, variable viewpoint), test condition (repeat viewpoint, novel viewpoint), and cumulative sampling were entered as fixed effects and subject and item were entered as random effects. This model was compared to a null model, which did not include cumulative sampling as a predictor variable. The model with cumulative sampling provided a significantly better model fit ($\chi^2 = 10.52$, $p = .001$) compared to the null model. A second model, which included interaction terms, was also

[1] The 2015 study compared H.C. and controls using Crawford's *t*-test. In this previous study, H.C.'s recognition memory fell significantly below controls for variable viewpoint trials but not for fixed viewpoint trials.

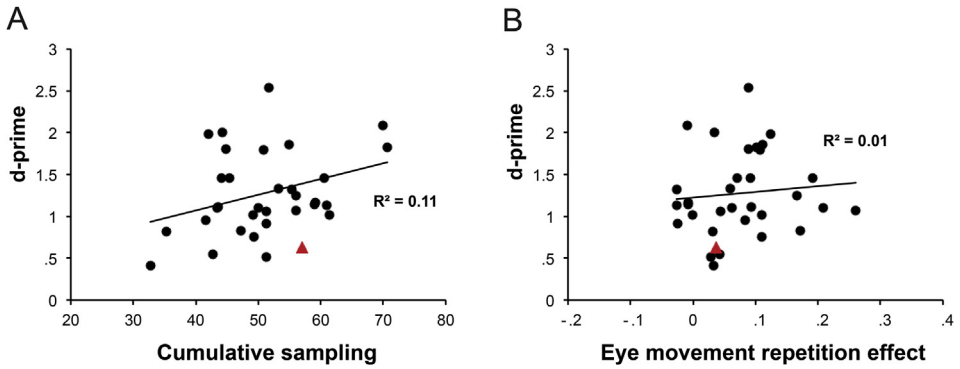

Fig. 4 – Individual differences analyses examining the relationship between eye movement measures and subsequent recognition performance among controls (black markers). H.C. is plotted (red triangles) but was not included in the between-subjects analyses. A: Correlation between cumulative viewing and d-prime. B: Correlation between the eye movement repetition effect and d-prime.

examined, but this model was not a significantly better fit than the reduced model ($\chi^2 = 8.44$, $p = .08$). Thus, results from the model that only tested the main effects are presented. A significant relationship between cumulative sampling and subsequent memory was found ($t = 3.25$ $p = .001$, Odds ratio = 1.15, 95% CI [1.06, 1.26]), which indicated that, among controls, a greater total number of fixations across study blocks was associated with higher subsequent confidence ratings (Fig. 5A).

To compare the number of fixations H.C. made for faces she later remembered versus forgot (Fig. 5A, red triangles), 95% CIs were computed using bootstrapping. Inspection of the 95% CIs revealed that the number of cumulative fixations was similar for subsequently remembered ("sure old": $M = 58.16$, 95% CI [56.09, 59.91]); and subsequently forgotten faces ("sure new": $M = 57.63$, 95% CI [54.13, 60.50]). Similar results were obtained when collapsing the high and low confidence old and new responses into hits (4 and 5 responses) and misses (1 and 2 responses).

The between-subjects and within-subjects analyses demonstrated that among the controls, there was a consistent positive relationship between cumulative sampling and the ability to subsequently remember a given face. Consistent with prior eye movement research, increased sampling of faces during encoding benefited later memory (Chan et al., 2011; Loftus, 1972; Henderson et al., 2005). While H.C.'s cumulative sampling exceeded the 95% CI of the control group, this increase in total sampling did not significantly benefit memory performance as it did in the control group.

3.5. *Eye movement repetition effects and subsequent memory*

The relationship between the eye movement repetition effect and subsequent memory was first assessed across the control participants, for each of the study/test viewpoint conditions. If eye movement repetition effects were driven by conscious awareness for prior study episodes of the faces, then individuals who demonstrate better subsequent memory should, on average, demonstrate a more robust eye

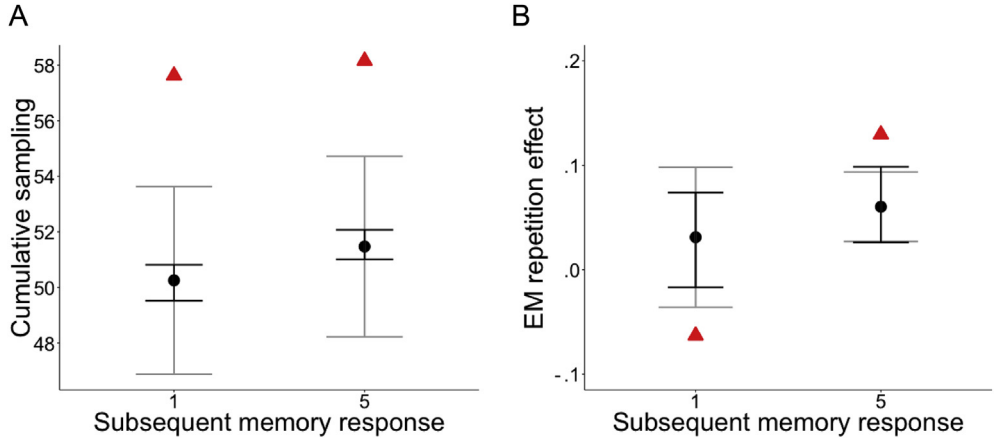

Fig. 5 – Eye movement measures plotted as a function of subsequent recognition memory within participants. A: Cumulative sampling (total fixations made across the five study blocks) as a function of subsequent memory response (1 = sure new and 5 = sure old). B: The magnitude of the eye movement repetition effect ([Block 1 fixations−Block 5 fixations]/Block 1 fixations), plotted as a function of subsequent memory response. Black error bars denote the within subject 95% CIs and gray error bars denote the between subject 95% CIs. Red triangles represent H.C.'s data; no significant differences were found for H.C. for cumulative sampling or for the repetition effect based on subsequent memory.

movement repetition effect. A linear model was used to examine linkages between the repetition effect and d-prime across subjects among the controls. Study condition (fixed viewpoint, variable viewpoint), test condition (repeat viewpoint, novel viewpoint) and repetition effect were modeled as predictor variables and d-prime was modeled as the outcome variable. Model testing determined that the models which included repetition effect as a fixed effect did not provide a significantly better fit than the null model ($F = 1.21$, $p = .27$); indicating that the magnitude of the repetition effect was not associated with better recognition memory performance across subjects (see Fig. 4B for simple correlation).

Mixed effects linear regression was used to examine whether eye movement repetition effects among controls were larger for subsequently remembered versus forgotten faces using a within subjects analysis (Fig. 5B). Study condition, test condition, and the eye movement repetition effect were entered as fixed effects and participant and item were entered as random effects. Compared to the null model, the model that included the repetition effect was not a significantly better fit ($\chi^2 = .85$, $p = .36$). These analyses indicate that there was no consistent relationship between the repetition effect magnitude and subsequent confidence ratings.

Next, the relationship between the eye movement repetition effect and subsequent memory was examined for H.C (Fig. 5B, red triangles). Examination of the 95% CI in H.C. indicated that the magnitude of the eye movement repetition effect did not differ for faces that were subsequently remembered versus forgotten [based on confidence ratings of "5" (sure old) *vs* "1" (sure new)]. The confidence intervals were overlapping for subsequently remembered ($M = .12$, 95% CI [.04, 022]) and subsequently forgotten faces ($M = -.06$, 95% CI [−.32, .06]). Similar results were obtained when collapsing across 1 and 2 responses for misses and 4 and 5 responses for hits. These analyses indicated that the magnitude of the eye movement repetition effect does not reliably relate to subsequent recognition memory in a consistent manner in controls or in H.C.

3.6. *The relationship between cumulative sampling and eye movement repetition effects*

The relationship between the cumulative sampling measure and the eye movement repetition effect measure was evaluated. Across control subjects, there was no significant relationship between the cumulative fixations and eye movement repetition effect measure ($t = -.81$, $p = .42$).

An analysis examined the effect of both cumulative sampling and the eye movement repetition effect on d-prime across control subjects within the same statistical model. This linear model indicated the model that included both the cumulative sampling and eye movement repetition effects as predictor variables was a significantly better fit than the linear model that only contained the eye movement repetition effect ($F = 11.04$, $p = .001$). The reverse was not true; the model which contained both eye movement measures did not provide a better fit than the model including only cumulative fixations as a predictor ($F = 1.89$, $p = .17$), again suggesting that the repetition effect does not explain additional variability in recognition performance across subjects above and beyond the effect of cumulative sampling.

A similar set of analyses examined the effect of both eye movement measures for a particular item using a mixed effects regression with cumulative sampling and the eye movement repetition effect included in the same model. This model, in which the confidence rating was the outcome variable, indicated that including both cumulative sampling and the eye movement repetition effect was a significantly better fit ($\chi^2 = 10.82$, $p = .001$) than the model that only included the eye movement repetition effect measure. In other words, subsequent memory (memory confidence) was better predicted when cumulative sampling was included as a predictor variable in addition to the magnitude of the repetition effect. By contrast, the model that contained both eye movement measures was not a significantly better fit than the model that included only cumulative fixations ($\chi^2 = 1.15$, $p = .28$) as a predictor. These results again indicate that the repetition effect does not account for additional variability in memory performance within subjects above and beyond the effect of cumulative sampling.

4. Discussion

We examined the relationship between eye movement measurements, the hippocampal system, and recognition memory. Cumulative sampling was significantly positively associated with subsequent recognition among controls, but not in H.C. Eye movement repetition effects expressed during encoding were not consistently related to subsequent recognition memory, suggesting that this type of memory expression can be driven by representations that are not necessarily available for conscious appraisal. While H.C. demonstrated a typical eye movement repetition effect for fixed viewpoint faces, her repetition effect was diminished for variable viewpoint faces (i.e., she made a similar number of fixations during the 1st and 5th blocks for variable viewpoint faces). Thus, repetition effects for information that changes across study repetitions may depend upon an intact hippocampal system, which is required to flexibly bind these changed items across repetitions (Olsen et al., 2015).

Our recent work provided evidence that item recognition is differentially supported by the hippocampal system and neocortex, depending upon the relational binding demands of the task (Olsen et al., 2015). When items are studied across different viewpoints, recognition memory for these items requires the hippocampal system, whereas the neocortex can support memory for items that are studied across identical viewpoints. Thus, the ability of the hippocampal system to form flexible associations across space and time seems essential for the successful formation of single item memory representations, just as it is critical for memory for relational representations across multiple items. The present study extends this work by outlining how eye movement patterns that reflect the development (cumulative sampling) and indirect expression of memory (repetition effect) were related to subsequent item recognition in developmental amnesic H.C. and a group of age- and education-matched controls. The current study further elucidates the role of the hippocampal system in both conscious and putatively non-conscious expressions of memory.

Greater sampling of the faces across the study repetitions was related to subsequent memory. Among controls,

cumulative sampling was positively correlated with better recognition, and items that received a greater number of fixations across encoding were more likely to be remembered than items that received fewer fixations. Increased sampling allows for more of the study image to be inspected at high visual acuity (Hollingworth & Henderson, 2002). Our results add to a body of literature showing that increased eye sampling is associated with successful learning and can help strengthen and/or maintain internal mnemonic representations (Hannula et al., 2010; Henderson et al., 2005; Johansson & Johansson, 2013; Olsen, Chiew, Buchsbaum, & Ryan, 2014).

Sampling of visual information, and the relationship between sampling and memory formation, is altered in individuals with hippocampal compromise. Healthy older adults (Firestone et al., 2007), and those who are at-risk for a clinically significant cognitive decline (Yeung, Ryan, Cowell, & Barense, 2013), have shown increased sampling behavior relative to younger adults, suggesting a possible compensatory mechanism by which older adults may try to boost later recognition memory for items. Interestingly, H.C. demonstrated greater cumulative sampling compared to controls, as observed previously in older adults. Increased sampling, however, was not associated with better memory in H.C., which indicates two possibilities. First, the type of sampling in which she is engaged is fundamentally different from that of controls, which is likely, given that we previously reported that H.C. fixates primarily on a single face feature whereas controls distribute their fixations among the different face features (Olsen et al., 2015). Secondly, increased sampling may not benefit H.C. because she is unable to flexibly bind information from different parts of the face due to her hippocampal system impairment. While there is some evidence from other amnesic patients that visual exploration is impaired due to hippocampal damage (Lee & Rudebeck, 2010; Voss et al., 2011; Yee et al., 2014), these studies are scarce and further research is needed.

The current study found no significant relationship between successful recognition and the magnitude of the eye movement repetition effect, as would have been expected if repetition effects were driven primarily by explicit recognition. Thus, while prior research has suggested that experience-dependent eye movement repetition effects reflect access to a conscious memory representation (Smith & Squire, 2008; Smith et al., 2006), our results offer evidence that the repetition effect is an expression of memory reflecting representations that may not necessarily be available to subsequent conscious appraisal. The relationship between eye movement repetition effects and subsequent recognition may depend on a variety of experimental factors employed by the particular study, such as the number of study presentations or the encoding task instructions (Althoff & Cohen, 1999; Heisz & Shore, 2008; Ryan et al., 2000; Smith & Squire, 2008; Smith et al., 2006). Comparing results across the studies that have examined the role of conscious recognition in eye movement repetition effects, it seems that the presentation structure/timing as well as the nature of the task instructions can significantly affect eye movement measurements of memory and this should be a topic of future study.

The current findings suggest that the repetition effect, similar to recognition memory, may depend differentially on the hippocampal system and neocortex, depending upon the relational binding processes occurring during encoding. The magnitude of H.C.'s eye movement repetition effect was decreased compared to controls for variable viewpoint faces—that is, she demonstrated a similar number of fixations upon the 5th study exposure as she did upon the 1st study exposure when the faces changed in viewpoint across repetitions. We would argue that this suggests that hippocampal system memory representations may contribute to eye movement repetition effects under conditions in which item information changes across repetitions, that is, under conditions that require relational binding (Olsen, Moses, Riggs, & Ryan, 2012; Olsen et al., 2015). According to this view, the hippocampus is either 1) forming viewpoint-invariant representation by linking multiple instances/traces of the same stimulus onto the same identity, or 2) supporting the multiple traces of the same stimulus, which are then linked to the same identity within the neocortex. Differences in viewpoint across repetitions may also cause disruptions in processes such as pattern separation and/or completion as a result of hippocampal damage; relational binding may make use of pattern completion processes in order to link multiple viewpoints onto the same identity. Interestingly, H.C. demonstrated intact behavioral (RT) priming for both fixed and variable viewpoint faces. This finding indicates that the formation of memory representations guiding the behavior associated with gender judgments does not rely on the hippocampus, even when the viewpoint of the faces changes across repetitions.

These findings have implications for the role of the hippocampal system in conscious/non-conscious expressions of memory. The repetition effect, when observed during incidental encoding, was not correlated with subsequent explicit recognition. Nonetheless, we observed that hippocampal system compromise resulted in a diminished repetition effect for variable viewpoint faces, consistent with prior research that has argued for a role of the hippocampus in the expression of the repetition effect for scene stimuli (Smith & Squire, 2008; Smith et al., 2006). This data suggests explicit recognition (or the absence thereof) is not driving the absence of the repetition effect in H.C. for variable viewpoint faces for two reasons. First, a subset of healthy controls who have poor recognition memory (i.e., d-prime scores near 0) still demonstrate a repetition effect (i.e., for the most part, there is no significant relationship between the repetition effect and subsequent memory; Fig. 4). Second, among healthy controls, repetition effects are observed for faces which are subsequently forgotten, even faces which were given a subsequent memory confidence rating of "1" or "SURE NEW" (Fig. 5B). Taken together, this pattern of results adds to the growing literature that the hippocampus is responsible for unconscious as well as conscious expressions of memory (Hannula & Ranganath, 2009; Henke, 2010; Moscovitch, Cabeza, Winocur, & Nadel, 2016; Ryan & Cohen, 2003).

It is important to note that these results are based on a single developmental amnesic case, who in addition to having reduced bilateral hippocampal volume, has damage/reduced volume to subcortical gray and white matter structures, such as the fornix and mammillary bodies, that receive projections from the hippocampus (Rosenbaum et al., 2014). Future studies should be conducted to ascertain whether these effects are

specifically due to hippocampal compromise in H.C. Furthermore, converging evidence from individuals with adult-onset amnesia is warranted to fully elucidate the role of the hippocampus proper in eye movement expressions of memory. Likewise, exploration of additional eye movement measures, such as viewing consistency across repetitions, in developmental and adult-onset amnesic cases may provide interesting avenues for future research that would increase our understanding of the role of the hippocampus in memory and the nature of the deficits observed in different variants of amnesia.

5. Conclusions

In summary, different eye movement measures relate to memory formation and expression in distinct ways (Hannula et al., 2010; Ryan & Cohen, 2003; Ryan et al., 2000). Cumulative sampling behavior is important for the formation of memories that can be consciously accessed, whereas the eye movement repetition effect signals access to stored information that influences the way visual information is sampled across repetitions, but may not necessarily be available to conscious appraisal. The present results further suggest that memory representations for repeated images are associated with indirect expressions of memory (i.e., repetition effects) that differentially rely on hippocampal and neocortical structures depending upon the presentation format of the items. Repetition effects for identical repetitions are most likely supported by extra-hippocampal neocortical systems, whereas the hippocampal system seems to support eye movement repetition effects for information that varies across repetitions. All together, this work provides key insights into the role of the hippocampal system in eye movement expressions of memory and contributes to our understanding of the underling nature of the memory representations differentially supported by the hippocampus and neocortex.

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