

Recognition Memory Impairments Caused by False Recognition of Novel Objects

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A fundamental assumption underlying most current theories of amnesia is that memory impairments arise because previously studied information either is lost rapidly or is made inaccessible (i.e., the old information appears to be new). Recent studies in rodents have challenged this view, suggesting instead that under conditions of high interference, recognition memory impairments following medial temporal lobe damage arise because novel information appears as though it has been previously seen. Here, we developed a new object recognition memory paradigm that distinguished whether object recognition memory impairments were driven by previously viewed objects being treated as if they were novel or by novel objects falsely recognized as though they were previously seen. In this indirect, eyetracking-based passive viewing task, older adults at risk for mild cognitive impairment showed false recognition to high-interference novel items (with a significant degree of feature overlap with previously studied items) but normal novelty responses to low-interference novel items (with a lower degree of feature overlap). The indirect nature of the task minimized the effects of response bias and other memory-based decision processes, suggesting that these factors cannot solely account for false recognition. These findings support the counterintuitive notion that recognition memory impairments in this memory-impaired population are not characterized by forgetting but rather are driven by the failure to differentiate perceptually similar objects, leading to the false recognition of novel objects as having been seen before.

Keywords: interference, perception, eye movements, mild cognitive impairment, medial temporal lobe

A fundamental assumption underlying most current theories of amnesia is that memory impairments arise because the information either is lost rapidly or is made inaccessible. Under this view,

previously encountered information appears as though it had never been seen before (i.e., *previously viewed information appears novel*). However, recent work has led to an alternative and counterintuitive account of memory impairments following medial temporal lobe (MTL) damage (McTighe, Cowell, Winters, Bussey, & Saksida, 2010). Under this view, damage to one MTL structure—the perirhinal cortex (PRC)—induces recognition memory impairments by causing *novel objects to appear as though they had been previously encountered* (Cowell, Bussey, & Saksida, 2006). Here, we developed a new version of the classic object recognition memory paradigm that is capable of distinguishing between these two possibilities: the more traditional view that recognition memory impairments arise because previously viewed items appear novel versus an alternative view that memory impairments arise because novel items appear as though they were previously viewed.

This article was published Online First August 12, 2013.

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Some of these data were previously presented in a master's thesis by Lok-Kin Yeung and in a poster presentation at the annual meeting of the Cognitive Neuroscience Society in Chicago (April 2012). This research was supported by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada to Morgan D. Barense. Jennifer D. Ryan is supported by the Canada Research Chairs program. We thank Hannah Bild-Enkin, Tina Emery, and Rita Vitorino for help with the neuropsychological battery; Alina Guna and Robin Nguyen for assistance with participant testing; David Huber and Nicholas Rule for advice on statistical analysis; and all the participants who took part in this study.

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In a traditional object recognition memory task, a participant views a study object (the study phase) and, after a delay, is shown the same previously viewed study object together with a perceptually distinct novel object (the test phase). Accurate object recognition is indicated by the selection of the previously viewed object over the novel object. When participants are unable to make an explicit response (e.g., when they are nonhuman animals or infants), recognition memory can be measured indirectly. In ro-

dents, object recognition memory is often assessed with the spontaneous object recognition (SOR) task, which exploits the fact that rodents have a strong, inherent preference for exploring novel items over previously viewed items. In infants, the preferential looking task is an analogous paradigm. In the SOR or preferential looking tasks, exploration or viewing time serves as a proxy for judgment of novelty: Greater exploration of an object indicates greater perceived novelty (Ennaceur & Delacour, 1988). Because the standard SOR procedure requires the novel and previously viewed objects to be simultaneously presented during the test phase, it is only possible to obtain a relative measure of novelty (i.e., whether one item is more novel than the other item). Thus, it cannot be determined whether object recognition impairments are due to the novel objects being perceived as though they were previously viewed or the previously viewed objects being perceived as though they are novel. To address this issue, a series of recent studies in rodents employed a modified version of the SOR task that decouples exploration of novel and previously viewed objects, thus allowing an absolute measure of novelty (Burke, Wallace, Nematollahi, Uprety, & Barnes, 2010; McTighe et al., 2010; Romberg et al., 2012). In this modified SOR paradigm, as in the original SOR paradigm, rodents first explored two identical copies of a study object during the study phase. During the subsequent test phase of the modified SOR task, the rodents explored two identical copies of an object (either two novel objects or two previously viewed objects), rather than exploring one novel and one previously viewed object simultaneously as in the original SOR task. Thus, the exploration of the novel and previously viewed objects was measured in isolation. Across all of these studies, healthy control rodents explored novel objects more than the previously viewed objects in the test phase (demonstrating a normal pattern of object recognition). By contrast, three distinct groups of memory-impaired rodents—rats with PRC lesions (McTighe et al., 2010), aged rats (Burke et al., 2010), and tgCND8 mice (a common mouse model of Alzheimer's disease [AD]; Romberg et al., 2012)—all explored the novel and previously viewed objects equally, demonstrating impaired object recognition. Paradoxically, this impairment was due to *reduced* exploration of the novel object (indicating false recognition of novel stimuli), rather than increased exploration of the previously viewed object (which would have indicated that the original information was lost or inaccessible). That is, the animals behaved as though they had seen the new objects before. Strikingly, performance in the memory-impaired rodents was recovered when visual interference during the delay period (between the study and test phases) was reduced by putting the animals in a dark environment. Thus, these studies revealed two very important findings: (a) object recognition memory impairments following PRC damage in rodents were due to false recognition of novel objects, and (b) this false recognition arose from an increased vulnerability to interference.

A new theoretical framework—the representational–hierarchical model—offers an account of these findings (Cowell et al., 2006; McTighe et al., 2010). Like many other models of visual object processing, this framework assumes that each successive region of the ventral visual stream supports increasingly complex stimulus representations, comprising conjunctions of simpler representations coded for in earlier (upstream) ventral visual stream areas (Desimone, Schein, Moran, & Ungerleider, 1985; Hubel & Wiesel, 1962;

Riesenhuber & Poggio, 1999). The representational–hierarchical account posits that the ventral visual stream continues into MTL, such that simple visual features of an object are represented individually in early posterior regions, whereas a fully specified, conjunctive representation of the whole object is found in MTL. In this regard, it differs from traditional models of MTL function, which emphasize the MTL's role as a dedicated declarative memory system, separate from a perceptual system located elsewhere in the brain (e.g., Squire & Wixted, 2011). In comparison, the representational–hierarchical account does not appeal to the notion of separate systems supporting memory and perception but instead focuses on the different levels of representations maintained by different brain regions. Under this view, there is no need to consider separate systems for memory and perception, because apparently distinct mnemonic and perceptual functions may arise from common computational mechanisms operating on different points within a shared representational hierarchy.

Computational simulations of the representational–hierarchical account provided an explanation for why conjunctive object-level representations are particularly critical for object recognition memory (Cowell et al., 2006). In the model, objects are composed of a limited set of visual features. Although many possible objects can be defined by unique conjunctions of those features, objects tend to share low-level features (e.g., a tennis ball and a lemon are both round and yellow). During the delay between the study and test phases of a memory task, participants are assumed to experience visual input in the form of exposure to a stream of unique objects. This visual input causes interference at the feature level, simply because individual visual features tend to repeat across different objects in the stream. Under normal circumstances, unique conjunctive representations of objects in the MTL can resolve this feature-level interference, because the exact conjunction defining the novel object presented in the test phase is extremely unlikely to have been seen during the delay (i.e., an object's conjunctive representation remains novel). However, when these conjunctive object representations are impoverished (e.g., due to damage to MTL), participants must rely on simple feature representations in the intact posterior regions to make perceptual/mnemonic judgments. When novel objects share many features with previously viewed objects, they can appear as though they have been studied previously, because, at the feature level, the objects are indeed familiar. However, if feature-level interference is reduced—for instance, by minimizing visual input during the delay (McTighe et al., 2010) or by minimizing the similarity of interfering stimulus material to the test objects (Bartko, Cowell, Winters, Bussey, & Saksida, 2010)—simple feature representations are sufficient to recognize the novel object, and impairments following MTL brain damage are not observed.

Recent experiments in humans provide further support for this theoretical position. In a visual discrimination task involving perceptually similar objects with overlapping features (Barense, Groen, et al., 2012), participants with MTL damage were initially able to perform the task, but their performance deteriorated as they repeatedly viewed items with similar, overlapping features (i.e., when feature-level interference grew). Crucially, their performance recovered when feature-level interference was reduced by replacing the perceptually similar objects with stimuli that did not share features with other tested items. Similar findings were re-

ported in participants with mild cognitive impairment (MCI; a putative transitional state between normal aging and AD; Petersen et al., 1999) and those at-risk for MCI (Newsome, Duarte, & Barense, 2012). These studies established that feature-level interference can impair visual discrimination performance. They did not, however, investigate whether the feature-level interference led to false recognition of novel stimuli (such that all stimuli are indistinguishable because they all appear previously viewed) or to forgetting of previously viewed stimuli (such that all stimuli are indistinguishable because they all appear novel).

In the present study, we investigated whether memory-impaired humans would, under conditions of high visual interference, also treat novel stimuli as though they had been previously viewed (as do PRC-lesioned rodents). Adapting the modified SOR paradigm for human participants, we presented young adults, healthy older adults, and older adults at risk for MCI with images of single real-world objects with varying levels of feature-level interference in an incidental viewing paradigm. We manipulated feature-level interference by varying the number of features novel objects shared with the studied objects. High-interference novel objects contained many features that had been previously viewed as part of a studied item. Analogous to the reduced-interference condition in the rodent studies, low-interference novel objects that shared fewer features with studied items were also included. We tracked participants' eye movements as they viewed these stimuli to provide a measure of novelty detection. Just as animals express a novelty preference by directing more exploration toward new objects, humans show an increase in visual sampling (i.e., more fixations) for individual novel stimuli than old stimuli (Althoff & Cohen, 1999; Heisz & Ryan, 2011; J. D. Ryan, Althoff, Whitlow, & Cohen, 2000; J. D. Ryan, Leung, Turk-Browne, & Hasher, 2007). Critically, the use of eyetracking obviated the need for participants to make explicit novelty judgments and provided a relatively pure index of memory uninfluenced by memory-related decision processes, response biases and strategies, and stereotype threat in older adults (Hannula, Baym, Warren, & Cohen, 2012). That is, explicit recognition responses reflect only the output of cognitive processing, whereas eyetracking reveals the nature of the cognitive processing itself. This design allowed us to disentangle whether abnormal novelty preferences arose because novel objects were treated as though they were previously viewed (consistent with the representational-hierarchical framework) or whether previously viewed objects were treated as though they were novel (because the memory trace had been lost rapidly or made inaccessible).

Method

Participants

Thirteen young adult participants (12 women, 1 man, $M_{\text{age}} = 20.9$ years, age range = 19–25 years, $M_{\text{education}} = 15$ years, education range = 13–19 years) and 33 older adult participants (27 women, 6 men, $M_{\text{age}} = 72.3$ years, age range = 65–80 years, $M_{\text{education}} = 15.2$ years, education range = 11–20 years) were recruited from the University of Toronto community. The Montreal Cognitive Assessment Test (MoCA; Nasreddine et al., 2005), a brief neuropsychological screening test shown to be highly sensitive in detecting MCI (Markwick, Zamboni, & De Jager, 2012; Nasreddine et al., 2005), was administered to the older adult

participants, who were categorized as either healthy (scored 26 or above, $M_{\text{score}} = 27.9$, score range = 26–30), or at-risk for MCI (scored 24 or below, $M_{\text{score}} = 22.6$, score range = 20–24). The healthy older adult group included 16 participants (13 women, 3 men, $M_{\text{age}} = 72.3$ years, age range = 66–79 years, $M_{\text{education}} = 14.7$ years, education range = 11–20 years), and the at-risk older adult group included 11 participants (8 women, 3 men, $M_{\text{age}} = 73.8$ years, age range = 65–80 years, $M_{\text{education}} = 15.7$ years, education range = 13–19 years). There was no significant difference between the two older adult groups in age, $t(25) = 1.45$, $p = .16$, $d = 0.35$, or years of education, $t(25) = 0.79$, $p = .44$, $d = 0.45$. Six participants who had a MoCA score of 25 were excluded from this analysis because this score cannot be unambiguously interpreted as evidence of possible MCI based on the MoCA norms (Nasreddine et al., 2005); a threshold of 24 or below was shown to have better predictive value for clinical purposes (Damian et al., 2011).

All participants were fluent English speakers (learned English before the age of 8); had normal or corrected-to-normal vision; and were screened for color blindness, neurological disorders, or brain damage (from stroke or trauma). All participants were informed about the nature of the experiment and its risks and gave written informed consent. This research received ethical approval from the Research Ethics Board of the University of Toronto. Young adults received \$10/hour for their participation, and older adults received \$16/hour, as per standard procedures at the University of Toronto.

Neuropsychological Battery

In a follow-up session (2–7 months after the initial session), both groups of older adult participants received a battery of neuropsychological tests to better characterize possible cognitive impairments in the two groups. Two participants (one healthy, one at-risk) were unable to participate in the neuropsychological testing. The battery consisted of the Logical Memory subtest from the Wechsler Memory Scale (4th ed.; Wechsler, 2009), Trails A and B (Reitan & Wolfson, 1985), the Digit Span subtest from the Wechsler Adult Intelligence Scale (4th ed.; Wechsler, 2008), the Rey–Osterrieth Complex Figure Test (Osterrieth, 1944), the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999), and the Visual Object and Space Perception battery (VOSP; Warrington & James, 1991).

Stimuli and Equipment

This study used 128 photographs of individual, common, real-world objects, belonging to 12 semantic categories (socks, coffee mugs, high-heeled shoes, desk lamps, sofas, electric guitars, handbags, diamond rings, teapots, umbrellas, throw pillows, and scarves). Within each category, half of the objects served as study objects. The other half were divided evenly between high-interference (HI) foils, which were perceptually similar to a specific study item in the same category, and low-interference (LI) foils, which were not perceptually similar to any specific study image in the same category (see Figure 1). Thus, HI foils had higher feature overlap with particular study objects than did LI foils. A group of 52 additional young participants who did not participate in the eyetracking study were asked to rate (on a scale of 1–7, with 7 being most similar) the perceptual similarity of each

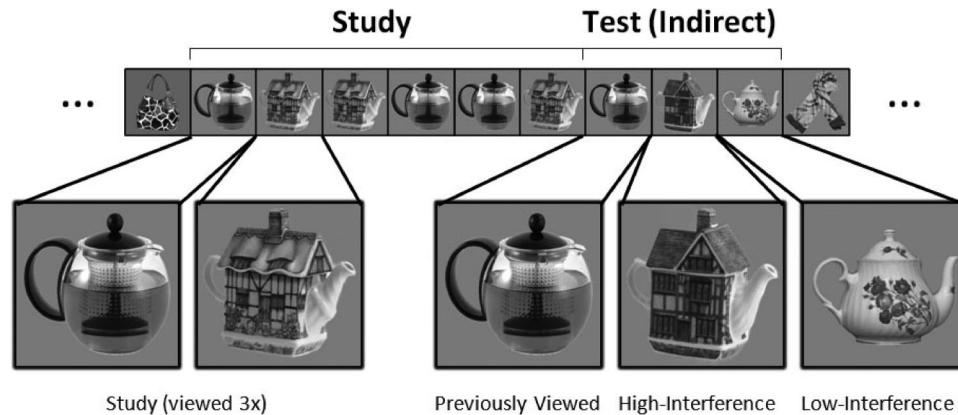


Figure 1. A sample block. Participants viewed each stimulus incidentally for 5 s while monitoring for an unrelated target stimulus (a black square). The stimuli were organized into blocks of objects that belonged to the same semantic category (e.g., teapots). Earlier items in the block served as “study” items. Each study item was repeated three times. The first viewing of each study item was used as a baseline to which the viewing of subsequent objects was compared. Later items in the block served as an indirect “test” phase, where participants were shown one of the following: (a) previously viewed items that had first been shown in the study phase; (b) high-interference (HI) novel items, which were perceptually similar to (and shared many features with) particular study items; or (c) low-interference (LI) novel items, which were not perceptually similar to (and did not share many features with) any particular study item. Because stimuli were presented one at a time, in a continual stream, participants were not aware of any distinction between the study and test phases. Note that in the actual study, all blocks had four, six, or eight unique study objects instead of the two displayed here. Participants completed six different blocks in this study.

study item paired with either its related HI foil or a LI foil in the same category. As expected, study items were rated as being more similar to their related HI foils ($M = 4.70$, $SD = 0.75$) than to the LI foils ($M = 2.43$, $SD = 1.03$), $t(51) = 16.16$, $p < .001$, $d = 2.55$. All images were collected from the Hemera Photo Clip Art collection (Hull, Quebec, Canada) or online from Google Image Search (Mountain View, CA), used under the fair dealings clause of the Copyright Act of Canada. The images varied in height (between 244 and 600 pixels tall, subtending 9.7° – 24.1°) and width (between 280 and 600 pixels wide, subtending 10.2° – 21.7°). All images were presented singly on a gray background.

The task was run on a Dell Latitude laptop and was presented on a connected 21.2-in. (36×30 cm) monitor at a resolution of 1024×768 pixels using Experiment Builder (SR Research, Mississauga, Ontario, Canada). Eyetracking measures were recorded with an Eye-link 1000 desktop-mounted eyetracker (SR Research, Mississauga, Ontario, Canada), sampling at a rate of 1000 Hz with a spatial resolution of 0.01° and accuracy of 0.25° . Participants were positioned 55 cm away from the monitor, with their heads placed on a chin rest to limit head motion. Nine-point calibration was performed prior to testing and was repeated until the average gaze error was less than 1° , with no point having a gaze error exceeding 1.5° .

Eyetracking Task

Participants passively viewed 144 images of individual real-world objects, presented for 5 s each, while their eye movements were recorded. As a means of encouraging participants to actively attend to the objects, their position was jittered around the screen with the center of the image being displaced up to 192 pixels

horizontally (in either direction) and 64 pixels vertically (in either direction) from the center of the screen. The entire image was always completely visible despite this displacement. Prior to each trial, drift correction was performed, with 9-point calibration being repeated if drift error exceeded 2° . In order to maintain a steady level of participant attentiveness across the entire study, we instructed participants to press a button in response to a distractor stimulus (a simple black square). These black square stimuli were presented alone and were interspersed throughout the experiment, appearing 30 times (approximately once for every five objects). Unlike the other stimuli, which appeared for a fixed length of time, the black square stimuli remained on the screen until participants made their response. Participants were instructed to look at but not respond to all other objects. They did not receive any explicit instructions to remember any objects. Prior to beginning the task, participants viewed 132 unrelated stimuli for a different study.

The objects were presented in six blocks, with each block contained objects from only one semantic category. Previous studies have shown that conceptual and perceptual false recognition may be mediated by different systems (Garoff-Eaton, Kensinger, & Schacter, 2007). Thus, by comparing only items within the same semantic category, this design limited the effects of conceptual false recognition and focused on perceptual false recognition. Each block contained a study phase, followed by a test phase, but participants were unaware of (and were not informed about) this distinction because all objects were presented continuously. During the study phase, 4, 6 or 8 unique items were presented three times each, with every item being presented once before any items were repeated (see Figure 1). Prior work—Althoff (1998) as cited by J. D. Ryan et al. (2000)—has shown reliable novelty differ-

ences in eye movement measures using the same number and duration of exposures as employed here.

During the test phase, three types of objects were presented: (a) previously viewed objects, which were identical to objects previously presented in the study phase of the same block; (b) HI novel objects, which were perceptually similar to (and shared many features with) specific study objects; and (c) LI novel objects, which were perceptually dissimilar to any specific study image (see Figure 1). All three types of test objects were interspersed during the test phase. The number of objects in each specific test condition was equal to half the number of unique study objects in that block. For example, in a block with four unique study objects, the test phase contained two previously viewed objects, two HI novel objects, and two LI novel objects. Similarly, blocks with six unique study objects contained three objects in each test condition, and blocks with eight unique study objects contained four objects in each test condition. Because there was no significant interaction (in terms of number of fixations made) between block length and test condition, $F(4, 144) = 1.50, p = .20, \eta_p^2 = .04$; nor between block length and participant group, $F(4, 72) = 1.84, p = .13, \eta_p^2 = .09$; our analysis collapsed across block length.

There were two counterbalanced versions of this task. In each version, six different categories of objects were shown in order to minimize the possibility that any effects observed were caused by the selection of particular categories of objects used. The order of the blocks was pseudo-randomized, as was the order of the individual objects. Among each age group (young adult and older adult), half of the participants received one version of the task and the other half received the other version. There were no significant differences in the number of fixations made to the two versions: A repeated-measures analysis of variance (ANOVA) showed no main effect of version, $F(1, 34) = 0.70, p = .41, \eta_p^2 = .02$; no interaction of version with participant group, $F(2, 34) = 1.18, p = .32, \eta_p^2 = .07$; and no interaction between version and test condition, $F(2, 68) = 2.77, p = .07, \eta_p^2 = .07$. Accordingly, all analyses collapsed across the two counterbalanced versions of the task.

Eyetracking Task Analysis

Participants' eye movements were tracked while they completed the task, and the number of fixations per object was computed with DataViewer (SR Research, Mississauga, Ontario, Canada). The number of fixations measure has consistently been used as a robust indicator of single item memory (see Hannula et al., 2010, for review). Other eye movement measures were not considered here, because they would be either redundant with the number of fixations measure (e.g., number of saccades, average fixation duration) or uninformative due to the presentation of single (rather than multiple) objects within a given trial paired with a fixed viewing time per trial (e.g., duration of viewing). Fixations were defined as the absence of any blinks or saccades (defined as an eye movement of at least 0.1° , with velocity $\geq 30^\circ/\text{s}$, and acceleration $\geq 8000^\circ/\text{s}^2$). A region of interest was drawn to include the entirety of each object, with an additional 15-pixel margin in all directions; all fixations outside this region of interest were ignored for the purposes of this analysis. The average number of fixations per object for each of the three test conditions (previously viewed, HI novel, LI novel) was computed for each participant. Additionally, the average number of fixations per object was computed for the first

viewing of each image in the study phase. Because all images were novel to participants when first viewed in the study phase, the average number of fixations directed to these images served as a baseline level of novelty (henceforth referred to as the baseline study condition).

Following the example of previous studies in rodents (Burke et al., 2010; McTighe et al., 2010; Romberg et al., 2012), a test:study ratio for each test condition was computed by normalizing the average number of fixations made to objects in that test condition to the average number of fixations made to the baseline study condition. Using test:study ratios for each participant instead of the raw number of fixations meant that each participant was equally weighted in the group average, instead of biasing results toward participants who made more fixations overall. A test:study ratio not significantly different from 1 meant that participants made a similar number of fixations to objects in a test condition as they did to objects in the baseline study condition, indicating that objects in that test condition were perceived to be novel. By contrast, a test:study ratio significantly less than 1 meant that participants made a reduced number of fixations to objects in a test condition compared to objects in the baseline study condition, indicating that the objects in that test condition were perceived to be less novel.

Our primary analyses were designed to answer three key questions:

1. Across participant groups, were there differences in perceived novelty in any particular test condition?
2. How did perceived novelty for each test condition differ from the other test conditions, in each participant group?
3. For each participant group, were objects in each of the three test conditions perceived to be as novel or less novel than objects in the baseline study condition?

Because all predictions were directional, all statistical tests were one-tailed.

Results

Neuropsychological Battery

Results of the Neuropsychological Battery are shown in Table 1. In brief, these indicated that, consistent with well-documented episodic memory impairments early in the course of AD and MCI (Hodges, 2000; Petersen et al., 1999), the at-risk older adult group performed in the borderline to low average range relative to established norms on the immediate recall condition of the Logical Memory test and the delayed recall of the Rey Complex Figure Test. Additionally, when we compared their performance to that of the healthy older adult group we found significant differences on all three subtests of the Logical Memory test and the memory component of the MoCA.

The at-risk group showed comparatively intact performance in other cognitive domains. Visual perception—as assessed by copy of the Rey figure and the VOSP—was unimpaired. Despite differences in performance between the healthy and at-risk older adult groups in the Rey copy, both groups scored within the normal range for their age. One important exception to these results was

Table 1
Average Raw Scores for Neuropsychological Battery Administered to Older Adult Groups

Test	Healthy older adults	At-risk older adults
MoCA (/30)**	28.0 (1.6)	22.8 (1.2)
	Normal range	Impaired
Visuospatial/Executive (/5)*	4.7 (0.5)	3.6 (1.4)
Naming (/3)*	2.9 (0.3)	2.5 (0.5)
Attention (/6)	5.6 (0.6)	5.4 (0.7)
Language (/3)	2.7 (0.6)	2.2 (0.8)
Abstraction (/2)	1.7 (0.6)	1.3 (0.6)
Memory (/5)**	4.2 (0.8)	2.2 (1.5)
Orientation (/6)	6 (0)	5.75 (0.5)
WMS-IV LM Immediate Recall (/50)*	27.3 (3.8)	20.9 (7.5)
	33%ile	9%ile
WMS-IV LM Delayed Recall (/50, 20-min delay)**	23.6 (5.6)	14.0 (9.0)
	75%ile	37%ile
WMS-IV LM Recognition (/30)**	26.3 (1.7)	21.7 (3.2)
	>75%ile	>75%ile
Rey Copy (/36)*	33.1 (2.2)	30.1 (3.8)
	63%ile	37%ile
Rey Immediate Recall (/36)	15.5 (5.7)	12.3 (4.1)
	50%ile	37%ile
Rey Delayed Recall (/36, 30-min delay)†	15.2 (5.6)	10.9 (6.0)
	50%ile	25%ile
WASI Verbal IQ*	120.9 (7.0)	111.7 (12.1)
	91–92%ile	77–79%ile
WASI Performance IQ	116.1 (11.8)	103.1 (23.7)
	86%ile	58%ile
WASI Full-Scale IQ*	120.7 (6.8)	108.5 (18.1)
	91–92%ile	70–73%ile
VOSP Shape Detection (/20)	19.1 (1.2)	18.9 (1.2)
(cutoff score < 15)	Pass	Pass
VOSP Incomplete Letters (/20)	19.6 (0.8)	18.7 (1.9)
(cutoff score < 16)	Pass	Pass
VOSP Silhouettes (/30)* ^{a,b}	20 (5.2)	14.8 (4.0)
(cutoff score < 15)	Pass	Fail
VOSP Object Decision (/20) ^{a,b}	16.8 (2.8)	15.7 (1.0)
(cutoff score < 14)	Pass	Pass
VOSP Progressive Silhouettes (/20)* ^b	11 (2.2)	13.5 (3.0)
(cutoff score > 15)	Pass	Pass
VOSP Dot Counting (/10) ^b	10 (0)	9.9 (0.3)
(cutoff score < 8)	Pass	Pass
VOSP Position Discrimination (/20) ^b	19.6 (0.6)	19.6 (0.7)
(cutoff score < 18)	Pass	Pass
VOSP Number Location (/10)	9.1 (1.0)	8.9 (1.4)
(cutoff score < 7)	Pass	Pass
VOSP Cube Analysis (/10)	9.4 (0.9)	8.9 (0.9)
(cutoff score < 6)	Pass	Pass
Trails A ^{†b}	34.7 s (15.9 s)	46.7 s (15.7 s)
	63%ile	25%ile
Trails B ^b	97.9 s (44.8 s)	113.5 s (48.9 s)
	50%ile	37%ile
Digit Span Forward (/9)	6.5 (1.2)	6.7 (0.8)
	Normal range	Normal range
Digit Span Backward (/8)	4.8 (1.4)	4.7 (1.3)
	Normal range	Normal range

Note. Maximum and cutoff scores on tests are listed in parentheses in the left column. Standard deviations are indicated in parentheses next to average raw scores. Percentile (%ile) scores for the group average relative to established norms, where available, are shown below the score for each group. All *t* tests were two-tailed. A dagger indicates a trend towards significant difference between healthy and at-risk older adults in terms of raw scores at $p < .10$. One asterisk indicates significant difference at $p < .05$. Two asterisks indicates significant difference at $p < .01$. MoCA = Montreal Cognitive Assessment; WMS-IV LM = Wechsler Memory Scale, 4th ed., Logical Memory subtest; Rey = Rey–Osterreith Complex Figure Test; WASI = Wechsler Abbreviated Scale of Intelligence; VOSP = Visual Object and Spatial Perception battery.

^a Missing one at-risk participant. ^b Missing one healthy participant.

found in the silhouettes subtest of the VOSP, in which the at-risk group was impaired. This result matches previously reported impairments on this subtest in patients with MCI (Nordlund et al., 2005) and AD (Binetti et al., 1996).

Although we observed significantly lower performance in the at-risk group relative to the healthy older adults on tests of semantic memory (Verbal IQ as assessed by the WASI), performance in the at-risk group fell within the normal range relative to established norms. On measures of executive function, there were no significant differences between the two older adult groups, and the performance of both groups were normal relative to established norms. In summary, the at-risk group showed particular difficulties with episodic memory but normal performance (relative to population-based norms) on other cognitive faculties.

Eyetracking Task Results

The test:study ratios for each test condition in each participant group are shown in Figure 2. The raw (unnormalized) average number of fixations in the stimulus conditions that were used to calculate these test:study ratios are shown in Figure 3A. Our specific hypothesis was that we would not observe differences across groups for previously viewed and LI novel objects, but that we should see a difference across groups for HI novel objects (in the form of reduced fixations to HI novel objects in the at-risk group). To compare differences across groups, we first examined the test:study ratios using a 3×3 repeated-measures ANOVA with a within-subject factor of test condition (previously viewed,

HI novel, LI novel) and a between-subject factor of participant group (young adults, healthy older adults, at-risk older adults). This revealed a main effect of test condition, $F(2, 74) = 30.68$, $p < .001$, $\eta_p^2 = .45$; no main effect of participant group, $F(2, 37) = 1.27$, $p = .16$, $\eta_p^2 = .09$; and a marginally significant test condition \times participant group interaction, $F(4, 74) = 1.75$, $p = .07$, $\eta_p^2 = .09$. However, the fact that this interaction was only marginally significant is not surprising, given that we expected only one of the three conditions (HI novel objects) to reveal a difference between groups. In addition, we had a strong a priori reasons for the prediction that the HI novel objects—which had the largest amount of feature overlap with study objects—would produce the largest group differences (driven by at-risk adults making fewer fixations relative to other groups), whereas the previously viewed objects would produce the smallest differences between groups. We therefore compared these two extreme conditions in a 2×3 repeated-measures ANOVA with a within-subject factor of condition (previously viewed, HI novel) and a between-subject factor of participant group (young adults, healthy older adults, at-risk adults). Again, we observed a main effect of test condition, $F(1, 37) = 33.10$, $p < .001$, $\eta_p^2 = .47$, and no main effect of participant group, $F(2, 37) = 0.77$, $p = .47$, $\eta_p^2 = .04$. As we predicted, however, there was a significant test condition \times participant group interaction, $F(2, 37) = 4.37$, $p = .01$, $\eta_p^2 = .19$. On the basis of the marginally significant 3×3 interaction and the highly significant 2×3 interaction, we investigated these effects further in the analyses reported below.

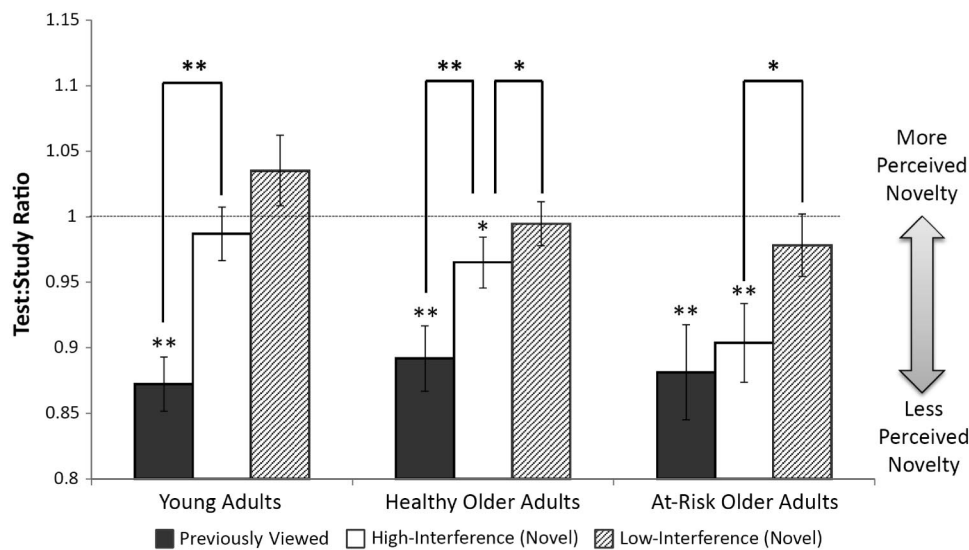


Figure 2. Test:study ratio of fixations in each of the three test conditions (previously viewed, high-interference novel, low-interference novel) for each of the three participant groups. Significant differences between the high-interference test condition and the other test conditions are shown with brackets; those between each test condition and the baseline study condition are shown by an asterisk above each bar. Because this graph is normalized to study, a ratio of 1 meant participants made the same proportion of fixations to that test condition as they did to baseline study objects (i.e., those test objects were perceived to be novel). A lower test:study ratio indicates a lower degree of perceived novelty for objects in a test condition. Error bars reflect standard error of the mean. * $p < .05$. ** $p < .01$.

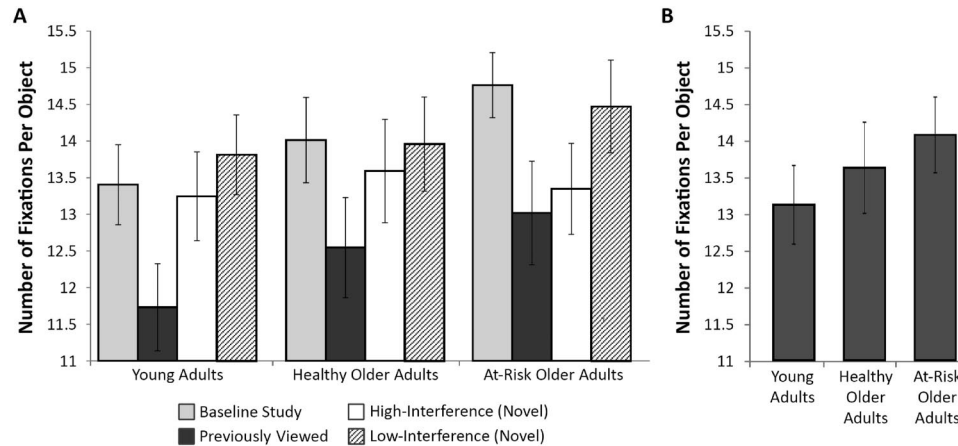


Figure 3. (A) Average raw number of fixations made to images during the baseline study condition and each of the three test conditions (previously viewed, high-interference novel, low-interference novel). These values were used to calculate the test:study ratios shown in Figure 2. (B) The overall average number of fixations for each participant group. Error bars reflect standard error of the mean.

1. Across Participant Groups, Were There Differences in Perceived Novelty in Any Particular Test Condition?

To investigate whether novelty responses differed between participant groups for each test condition, we conducted univariate ANOVAs on the study:test ratios for each test condition, using participant group (young adults, healthy older adults, at-risk older adults) as a between-subjects factor. These tests revealed no significant differences between the three participant groups for previously viewed objects, $F(2, 37) = 0.14, p = .44, \eta_p^2 = .008$, and no significant differences between the three participant groups for LI novel objects, $F(2, 37) = 1.63, p = .11, \eta_p^2 = .08$. However, there were significant differences among the participant groups for HI novel objects, $F(2, 37) = 3.17, p = .03, \eta_p^2 = .15$.

Independent-samples t tests on the HI novel object data showed that the at-risk older adults had a significantly lower test:study ratio than did both healthy older adults, $t(25) = 1.79, p = .04, d = 0.73$, and young adults, $t(22) = 2.35, p = .01, d = 1.01$. There was no such difference between healthy older adults and young adults, $t(27) = 0.77, p = .22, d = 0.30$. Together, these results suggest that the at-risk older adults viewed the HI novel objects as being less novel than the young adults and the healthy older adults, but that there were no significant differences in novelty detection between the latter two groups.

2. How Did Perceived Novelty for Each Test Condition Differ From the Other Test Conditions, in Each Participant Group?

To investigate whether novelty responses for each test condition differed within participant groups, we conducted univariate ANOVAs with a within-subject factor of test condition (previously viewed, HI novel, LI novel) on the study:test ratios for each participant group separately. These tests revealed significant differences between the three test conditions for each of

the three participant groups: younger adults, $F(2, 24) = 11.57, p < .001, \eta_p^2 = .49$; healthy older adults, $F(2, 30) = 16.69, p < .001, \eta_p^2 = .53$; at-risk older adults, $F(2, 20) = 7.30, p = .004, \eta_p^2 = .42$. To investigate these interactions further, we performed paired-samples t tests within each group across conditions.

For young adults and healthy older adults, paired-samples t tests showed that the test:study ratios for HI novel objects were significantly greater than the test:study ratio for previously viewed objects: young adults, $t(12) = 5.65, p < .001, d = 1.61$; healthy older adults, $t(15) = 3.54, p = .001, d = 0.84$. This result demonstrated the intact novelty preference of young adults and healthy older adults for HI novel objects when compared to previously viewed objects. For the at-risk older adults, however, there was no significant difference between the test:study ratios for HI novel objects and previously viewed objects, $t(10) = 1.07, p = .15, d = 0.21$. This result demonstrated the impaired novelty preference of at-risk adults for HI novel objects relative to previously viewed objects.

Comparisons between LI and HI novel objects indicated that young adults did not differ in their test:study ratios across these conditions, $t(12) = 1.18, p = .13, d = 0.58$. In contrast, for both the healthy and at-risk older adults, the test:study ratio for HI novel objects was significantly less than the test:study ratio for the LI novel objects: healthy older adults, $t(15) = 2.24, p = .02, d = 0.42$; at-risk older adults, $t(10) = 2.69, p = .01, d = 0.87$. This suggests that both healthy and at-risk older adults viewed the HI novel objects as less novel than the LI novel objects.

For all three participant groups, paired-samples t tests showed that the test:study ratios for LI novel objects were significantly greater than the test:study ratio for previously viewed objects: young adults, $t(12) = 4.14, p < .001, d = 1.96$; healthy older adults, $t(15) = 5.11, p < .001, d = 1.25$; at-risk older adults, $t(10) = 3.20, p = .004, d = 1.00$. This suggests that all three participant groups had intact novelty preference for LI novel objects relative to previously viewed objects.

3. For Each Participant Group, Were Objects in Each of the Three Test Conditions Perceived to Be as Novel or Less Novel Than Objects in the Baseline Study Condition?

We next asked how novelty preference in each of the three test conditions compared against the baseline study condition for each of the three participant groups. To this end, one-sample *t* tests were conducted to determine whether the test:study ratio for each test condition was significantly less than 1 (i.e., whether the number of fixations in each test condition was significantly less than in the baseline study condition) and thus indicated that objects in that condition were treated as being less novel than the objects in the baseline study condition.

One-sample *t* tests indicated that the test:study ratio for previously viewed objects was significantly less than 1 for all groups; that is, fewer fixations were directed toward the previously viewed objects than to the baseline study objects: young adults, $t(12) = 6.16, p < .001, d = 9.07$; healthy older adults, $t(15) = 4.34, p < .001, d = 1.58$; at-risk older adults, $t(10) = 3.26, p = .004, d = 1.46$. Thus, eye movements demonstrated that all three participant groups showed an intact reduction in novelty preference to previously viewed objects. These results are consistent with the findings of previous eyetracking studies (Althoff & Cohen, 1999; Heisz & Ryan, 2011; J. D. Ryan et al., 2007).

One-sample *t* tests also indicated that the test:study ratio for LI novel objects did not differ from 1 for all three groups: young adults, $t(12) = 1.31, p = .11, d = 1.93$; healthy older adults, $t(15) = 0.31, p = .38, d = 0.11$; at-risk older adults, $t(10) = 0.91, p = .19, d = 0.41$. This suggests that all three participant groups demonstrated normal novelty detection for the LI novel objects.

For HI novel objects, the test:study ratio in young adults was not significantly less than 1, $t(12) = 0.64, p = .27, d = 0.94$, thus showing a normal pattern of novelty detection. By contrast, the test:study ratio for HI novel objects in both healthy older and at-risk adults was significantly less than 1: healthy older adults, $t(15) = 1.79, p = .05, d = 0.65$; at-risk older adults, $t(10) = 3.20, p = .004, d = 1.43$. This result demonstrates impairments in novelty detection for HI novel objects in both older adult groups.

Summary of Results

Taken together, these findings indicate that the at-risk older adults, compared to healthy older adults and young adults, were impaired in their ability to perceive novelty accurately for HI but not LI novel objects. This impairment arose because they falsely recognized the HI novel objects as having been previously viewed. These findings show remarkable convergence with previous findings in rodents, in which PRC-lesioned, AD-model, and aged rodents also treated novel objects as though they were previously viewed under high-interference conditions (Burke et al., 2010; McTighe et al., 2010; Romberg et al., 2012).

It is important to note that these results cannot be explained by a global reduction in motivation, fatigue, or a general deficit in novelty processing. Both our at-risk participants and our healthy older adults accurately perceived the novelty of the LI novel objects (i.e., the test:study ratio did not differ from 1). Similarly, it was not the case that these groups merely made fewer fixations

overall. Although the differences in the total number of fixations were not significant (i.e., there was no significant main effect of group), $F(2, 37) = 0.47, p = .63, \eta_p^2 = .03$, at-risk older adults made numerically more fixations ($M = 13.899, SD = 2.083$) than did healthy older adults ($M = 13.526, SD = 2.623$) or young adults ($M = 13.048, SD = 2.157$; see Figure 3B).

Effects of MoCA Score vs. Age

To explore the relative contribution of MoCA score (as a proxy for overall cognitive decline) and age to the impaired novelty detection ability for HI novel stimuli, we collapsed across both our older adult groups and performed multiple regression analysis. Together, MoCA and age accounted for 22.5% of the variance, $R^2 = .225, F(2, 24) = 3.493, p = .047$. More important, MoCA score was a significant predictor of novelty detection for HI novel stimuli ($\beta = .474, p = .018, \text{semi-partial } r^2 = .21$), but age was not ($\beta = .254, p = .186, \text{semi-partial } r^2 = .06$). These results indicate that cognitive decline was associated with impaired novelty detection for HI novel objects, but age alone was not. In contrast, multiple regression showed that MoCA and age together did not account for variance in performance on the previously viewed stimuli, $R^2 = .043, F(2, 24) = 0.540, p = .590$, or the LI novel stimuli, $R^2 = .012, F(2, 24) = 0.144, p = .867$.

Discussion

Here, we report findings from a new object recognition memory paradigm that allowed us to distinguish whether object recognition memory impairments were driven by previously viewed objects being treated as if they were novel or by novel objects falsely recognized as having been previously viewed. We manipulated the degree of perceptual interference across images of real-world objects and investigated the effect on perceived novelty (as measured by the number of fixations directed to each object). We found that older adults at-risk for MCI directed fewer fixations to high-interference (HI) novel objects (which shared more features with studied items) than to novel objects in the baseline study condition, and that the number of fixations directed to HI novel objects was comparable to those directed to previously viewed objects. However, they directed a similar number of fixations to low-interference (LI) novel objects (which shared fewer features with studied items) as they did to the baseline study condition. Together, these results suggest that the at-risk older adults treated the HI novel objects as though they were previously viewed, but they were able to correctly identify the LI novel objects as being novel. These findings provide the paradoxical suggestion that the abnormal eye movements observed in the adults at risk for memory impairment were not characterized by forgetting but rather by the failure to differentiate between objects with a large number of overlapping features, leading to the false recognition of novel objects as having been previously viewed.

The false recognition for HI novel objects observed in the at-risk older adults was also present to a lesser extent in the healthy older adults. Healthy older adults also directed significantly fewer fixations to HI novel objects than to either LI novel objects or the baseline study objects, indicating a reduced novelty preference for the HI novel objects but preserved novelty preference for LI novel objects. However, the healthy older adults still directed a greater

number of fixations to the HI novel objects compared to the previously viewed objects, indicating that, to some extent, novelty preference for the HI novel objects was still intact. There have been a number of studies that reported age-related impairments in distinguishing between similar and/or overlapping stimuli (i.e., pattern separation); for instance, Burke and colleagues found that aged rats falsely recognized novel objects as having been previously viewed (Burke et al., 2010) and that aged monkeys took significantly more trials to learn a two-choice object discrimination task when the feature overlap between the two objects was very high but not when the feature overlap was lower (Burke et al., 2011). Similar results have been reported in human studies with healthy older adults. Older adults were impaired on an object discrimination task involving objects with many overlapping features (L. Ryan et al., 2012), and they were more likely to false alarm to perceptually similar lure objects on an explicit, continuous recognition memory paradigm (Toner, Pirogovsky, Kirwan, & Gilbert, 2009). In the current study, a multiple regression analysis was conducted to tease apart whether the observed pattern of false recognition was driven by overall cognitive decline (possibly related to AD pathology) or by age alone. MoCA scores were a significant predictor of novelty preference for the HI items, but age was not. This suggests that the false recognition of HI novel objects is associated with cognitive decline, above and beyond the effects of age alone. It is possible that previous reports of age-related pattern separation deficits could have been driven by some degree of undetected cognitive decline in the older participants.

The pattern of results observed in the two older adult groups—false recognition for HI novel objects but preserved novelty detection for LI novel objects—can be explained by the representational–hierarchical account described in the introduction (Cowell et al., 2006; McTighe et al., 2010; Saksida & Bussey, 2010). In brief, this model proposes that when an object is viewed, multiple representations of this object are activated throughout the entire ventral visual stream, with different representations occurring at different stages of the pathway. An object's low-level features are represented in early posterior regions, whereas conjunctions of features are represented in more anterior regions, with the most complex feature conjunctions—perhaps at the level of the whole object—being represented in the MTL. In the intact brain, these distinct object-level representations provide an unambiguous novelty signal that overrides familiarity signals from posterior feature-level representations (Barense, Ngo, Hung, & Peterson, 2012; Peterson, Cacciamani, Barense, & Scalf, 2012). However, when object-level representations are impoverished (as they are to differing extents in our older adult groups), novelty judgments are driven by familiarity signals at the feature level. Under high-interference conditions, these features repeat often across different objects. Although each object is novel and each trial is unique, the object's features overlap with those from other trials. Thus, in the absence of the object-level familiarity signal to override the feature-level familiarity signal, HI novel objects appear as though they have been seen before. However, under low-interference conditions, features do not often repeat across studied and test objects, and the feature-level representation is sufficient for accurate recognition.

The false recognition of novel objects as previously viewed under high-interference conditions has previously been reported in three memory-impaired rodent populations: rats with PRC lesions

(McTighe et al., 2010), aged rats (Burke et al., 2010), and tgCND8 mice (Romberg et al., 2012; although see Albasser et al., 2011). Here, in a novel adaptation of the SOR paradigm, we provide the first demonstration that these findings extend to humans with memory impairment. Further, the present study improves on the rodent paradigm in one significant way. Although prior studies merely contrasted the presence and absence of visual interference, the current study systematically varied the degree of visual interference (in terms of overlapping features) and demonstrated that object novelty detection was impaired in our at-risk group when feature-level interference was high but was normal when the degree of feature-level interference was lower. This systematic control over the degree of overlapping features provides strong support for the idea that false recognition occurs only when impoverished object-level representations are overwhelmed and does not occur when novelty judgments can be made using feature-level information.

We note that the two methods by which memory impairments may arise—treating novel objects as previously viewed versus treating previously viewed objects as novel—are not mutually exclusive. Indeed, previous studies have reported both effects simultaneously in the form of increased false alarms and decreased hits (e.g., Ally, Gold, & Budson, 2009; Beth, Budson, Waring, & Ally, 2009; Gallo, Chen, Wiseman, Schacter, & Budson, 2007; Gallo, Sullivan, Daffner, Schacter, & Budson, 2004; Pierce, Sullivan, Schacter, & Budson, 2005; Waring, Chong, Wolk, & Budson, 2008). However, if they were observed simultaneously in a memory task such as ours, any account would require two separate mechanisms operating side by side. An observation of the *previously viewed objects appear novel* phenomenon would require either a trace decay mechanism, in which familiarity information stored in neural circuits is lost or degraded, or a memory-loss interference mechanism (e.g., catastrophic interference), in which familiarity information for previously learned items is either overwritten (unlearned) or made inaccessible through competition. On the other hand, an explanation of the observation that novel objects appear previously viewed requires a mechanism very different from either trace decay or memory-loss interference. This mechanism must allow irrelevant feature-level familiarity information (e.g., the features of nontarget objects) to be acquired, rather than cause relevant object-level familiarity information to be eroded or overwritten. This sort of irrelevant memory-gain interference, as opposed to relevant memory-loss interference, is the kind proposed by the representational–hierarchical account. However, in our data, there is no evidence that previously viewed items appear novel for both groups of older adult participants (see Figures 2 and 3A); rather, we see only evidence that novel items appear previously viewed in this paradigm. In addition, the representational–hierarchical account can explain these findings parsimoniously using only an irrelevant memory-gain mechanism; the model does not invoke trace decay, and indeed such a mechanism is not required to account for the data.

There is a long and rich body of work demonstrating that patients with AD and MCI express false memories for items they never saw. Much of this work has focused on decision processes related to memory, suggesting that false memories may be the result of impaired retrieval-based monitoring (e.g., Abe et al., 2011; Gallo et al., 2004), an inappropriate liberal response bias (e.g., Beth et al., 2009; Budson, Daffner, Desikan, & Schacter,

2000; Budson et al., 2003; Deason, Hussey, Budson, & Ally, 2012), and impaired metamemory (e.g., Gallo, Cramer, Wong, & Bennett, 2012). For example, Budson et al. (2000) have shown that upon repeated presentations of a word list in the Deese–Roediger–McDermott paradigm, AD patients showed increased false recognition for lures related to the studied words as the number of trials increased. Unlike these studies, which used explicit responses to measure recognition, the present study employed an indirect object recognition task, allowing us to largely minimize the effects of memory-related decision processes and response bias. Our findings provide compelling evidence that the false recognition effect in memory-impaired populations cannot solely be attributed to either of these causes but rather also stem from more fundamental differences in perceptual processing. That is, by using an indirect eyetracking measure, we were able to demonstrate that there were underlying differences in how the individuals with memory impairment were *seeing* the stimuli.

Some studies examining perceptual gist-based memory (i.e., memory for general thematic content that lacks item-specific details; e.g., Brainerd & Reyna, 2002; Gutchess & Schacter, 2012; Koutstaal & Schacter, 1997) in AD appear to conflict with the present results. For example, Budson and colleagues systematically manipulated the visual similarity of distractor items to studied items and examined the effect on false alarm rate (i.e., erroneously indicating that a novel item had been seen before; Budson, Desikan, Daffner, & Schacter, 2001; Budson et al., 2003). When a baseline correction was applied to false alarm rates that involved subtracting out the false alarm rate to unrelated lures (items analogous to our LI objects), AD patients showed lower levels of false alarms to novel, perceptually related objects. These results were interpreted as reflecting impairments in gist memory: That is, the patients failed to encode and/or recall the gist, which led to lower levels of false alarms when lures and studied items were perceptually similar. However, it is possible to reconcile the results of the present study with these previous experiments by eschewing the baseline correction. In the present study, we did not perform the baseline correction, because it would have removed from the data some component of the predicted effect that the study was designed to test. In particular, the representational–hierarchical account predicts that, because all visual objects to some extent share low-level features, all items will tend to appear familiar to some degree to individuals with MTL damage. The extent to which each item appears familiar depends on how many features it shares with previously studied items (i.e., the degree of feature-level interference). Even the LI objects used in the current study share features with study objects (e.g., the LI teapots in Figure 1 have handles and spouts, like the study teapots), which induces a familiarity signal. The baseline correction would subtract this signal from reported levels of false recognition and thus could underestimate the magnitude of the effect. Of course, the greater number of shared features (i.e., the greater the degree of feature-level interference), the greater the perceived familiarity (as we observed here for HI vs. LI objects), but these differences are relative rather than absolute. Consistent with the notion that the baseline correction could alter the pattern of results, the uncorrected false alarm rates (i.e., without baseline correction) observed in previous studies were actually higher in AD patients under conditions of greater feature-level interference (Budson & Desikan, 2001; Budson et al.,

2003; Pierce et al., 2005), which is entirely consistent with the findings of the present study.

Although the representational–hierarchical account is not in accord with the idea that impaired gist memory is responsible for the present findings, it is largely in agreement with the account that there is increased reliance on gist memory when item-specific memory is impaired (Budson et al., 2000, 2003; Gallo et al., 2004). In both the representational–hierarchical account and the “increased reliance on gist memory” account, false recognition arises when there is feature-level interference, because memory judgments for specific items depend on non-item-specific representations (either a set of feature representations or a gist representation) built up over a number of trials. It is possible that feature representations and gist representations are coterminous, which would suggest that these two accounts are simply different ways of expressing the same idea, instead of being distinctly independent theoretical models. What is appealing about the representational–hierarchical interpretation, however, is that it makes more specific and precise predictions based on easily observable shared numbers of features, rather than appealing to a somewhat vaguer notion of general thematic content.

Although we prefer to explain our results in terms of impoverished object-level representations, one could argue that the present findings are the result of reduced precision during encoding of feature-level representations. Under this interpretation, false recognition would increase when feature-level interference is high, because feature representations have become less specific and more broadly tuned (see Zhang & Luck, 2008). That is, feature representations are activated not only by a specific feature (e.g., the specific black lid on the leftmost study teapot in Figure 1) but also by other similar features (e.g., any teapot lid, including the one on the LI ceramic teapot), which causes false recognition of novel features that are similar to previously studied features. Although the present study cannot distinguish between these two accounts, previous experiments suggest that impoverished object-level representations are responsible for the effects we have observed. These studies investigated perceptual impairments following PRC lesions and controlled for the exact level of familiarity at the feature level by generating novel objects that were recombinations of previously viewed features (Barense et al., 2005; Barense, Gaffan, & Graham, 2007; Barense, Rogers, Bussey, Saksida, & Graham, 2010; Bussey, Saksida, & Murray, 2002). Because at the feature level, objects in some conditions were identical, successful discrimination relied on intact object-level representations. Consistent with our argument here, PRC damage impaired those discriminations that required intact object-level representation but spared discriminations in other conditions that could be solved at the feature level. As such, these findings suggest that the impairments were not due to broad/imprecise tuning at the feature level (if so, some impairments would have been observed on the feature-level discriminations) but rather to an impairment in binding intact feature-level representations into a cohesive representation of the object as a whole. Nonetheless, these studies did not address false recognition, and future work using the current paradigm but with objects composed entirely of recombinations of previously viewed features would address this issue.

The present study involved only behavioral measures; thus, it was not possible to identify the neural structures responsible for the observed results. Nonetheless, theoretical considerations sug-

gest that damage to the PRC or to the hippocampus could be responsible. The role of the PRC in object recognition is well established (e.g., Baxter & Murray, 2001; Brown & Aggleton, 2001; Buffalo, Reber, & Squire, 1998; Devlin & Price, 2007; Henson, Cansino, Herron, Robb, & Rugg, 2003; Málková, Bachevalier, Mishkin, & Saunders, 2001; Meunier, Bachevalier, Mishkin, & Murray, 1993; Mumby & Pinel, 1994; O'Neil, Cate, & Köhler, 2009; Zola-Morgan, Squire, Amaral, & Suzuki, 1989), and the representational–hierarchical model suggests that it supports the conjunctive object representations necessary for the present task (Barense et al., 2005; Barense, Gaffan, & Graham, 2007; Bussey et al., 2002). In a study analogous to the present one, rats with PRC lesions showed a remarkably similar profile of false recognition under conditions of high interference (McTighe et al., 2010). Further, functional magnetic resonance imaging work in humans indicates that the PRC activation is involved in discriminations with a high, but not low, number of overlapping features (Barense, Groen, et al., 2012). Consistent with this idea, AD neurofibrillary pathology affects the medial portions of the PRC before it spreads to the hippocampus and entorhinal cortex (Braak & Braak, 1985; Taylor & Probst, 2008). The results of this study are also consistent with a hippocampus-based pattern separation model (e.g., Bakker, Kirwan, Miller, & Stark, 2008; Leutgeb, Leutgeb, Moser, & Moser, 2007; Marr, 1971; Norman & O'Reilly, 2003; Treves & Rolls, 1994). This model suggests that the dentate gyrus and the CA3 subfield of the hippocampus are critical for pattern separation. Volumetric studies have shown that the hippocampi of MCI and AD patients are significantly smaller than those of healthy controls (Du et al., 2001) and that the hippocampus shrinks even in the course of normal aging (Raz et al., 2005). This suggests that the results of the current study could be driven by impaired pattern separation ability due to changes in the hippocampus. Studies that afford anatomical precision are necessary before it is possible to identify the neural basis for the effects observed in the present study.

Finally, the findings reported here reveal important considerations for the design of future eye movement studies and the interpretation of their results. For instance, traditionally, a reduction in eye movement sampling for a given stimulus has been interpreted as an index of memory for that stimulus. In line with previous research, the present study found reduced sampling for previously viewed objects relative to novel objects (Althoff & Cohen, 1999; Heisz & Ryan, 2011; J. D. Ryan et al., 2007). However, the work here suggests that such an interpretation must include adequate comparisons with appropriate baseline/control conditions to avoid confounding the influence of interference with purported memory effects, particularly for participant groups that are at risk for, or are currently experiencing, significant cognitive decline. Likewise, any absence of a memory effect may be a secondary consequence of feature-level interference that causes novel objects to be treated as though they were previously viewed.

In conclusion, we found that participants at risk for MCI viewed novel objects as though they had been seen before. This abnormal novelty response was observed under conditions of high but not low visual feature-level interference. These findings challenge the commonly held assumption that pathological memory loss reflects a loss or diminished access to information (e.g., previously viewed objects appear to be novel). Here, we have shown that memory impairment in these individuals took the opposite form: Objects

that should have appeared novel instead appeared to have been previously viewed. These findings are not consistent with the characterization of memory loss as the dissolution of a memory trace but rather as the failure to differentiate between visually similar objects. This leads not to forgetting but to the false recognition of novel stimuli as though they had been previously encountered. These findings challenge fundamental assumptions regarding the genesis of memory deficits following brain damage, in particular the notion that trace decay or catastrophic interference are necessarily the central components of any explanation of pathological forgetting.

References

- Abe, N., Fujii, T., Nishio, Y., Iizuka, O., Kanno, S., Kikuchi, H., . . . Mori, E. (2011). False item recognition in patients with Alzheimer's disease. *Neuropsychologia*, *49*, 1897–1902. doi:10.1016/j.neuropsychologia.2011.03.015
- Albasser, M. M., Amin, E., Iordanova, M. D., Brown, M. W., Pearce, J. M., & Aggleton, J. P. (2011). Perirhinal cortex lesions uncover subsidiary systems in the rat for the detection of novel and familiar objects. *European Journal of Neuroscience*, *34*, 331–342. doi:10.1111/j.1460-9568.2011.07755.x
- Ally, B. A., Gold, C. A., & Bussey, T. J. (2009). The picture superiority effect in patients with Alzheimer's disease and mild cognitive impairment. *Neuropsychologia*, *47*, 595–598. doi:10.1016/j.neuropsychologia.2008.10.010
- Althoff, R. R., & Cohen, N. J. (1999). Eye-movement-based memory effect: A reprocessing effect in face perception. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*, 997–1010. doi:10.1037/0278-7393.25.4.997
- Bakker, A., Kirwan, C. B., Miller, M., & Stark, C. E. L. (2008, March 25). Pattern separation in the human hippocampal CA3 and dentate gyrus. *Science*, *319*, 1640–1642. doi:10.1126/science.1152882
- Barense, M. D., Bussey, T. J., Lee, A. C. H., Rogers, T. T., Davies, R. R., Saksida, L. M., . . . Graham, K. S. (2005). Functional specialization in the human medial temporal lobe. *Journal of Neuroscience*, *25*, 10239–10246. doi:10.1523/JNEUROSCI.2704-05.2005
- Barense, M. D., Gaffan, D., & Graham, K. S. (2007). The human medial temporal lobe processes online representations of complex objects. *Neuropsychologia*, *45*, 2963–2974. doi:10.1016/j.neuropsychologia.2007.05.023
- Barense, M. D., Groen, I. I. A., Lee, A. C. H., Yeung, L.-K., Brady, S. M., Gregori, M., . . . Henson, R. N. A. (2012). Intact memory for irrelevant information impairs perception in amnesia. *Neuron*, *75*, 157–167. doi:10.1016/j.neuron.2012.05.014
- Barense, M. D., Ngo, J. K. W., Hung, L. H. T., & Peterson, M. A. (2012). Interactions of memory and perception in amnesia: The figure–ground perspective. *Cerebral Cortex*, *22*, 2680–2691. doi:10.1093/cercor/bhr347
- Barense, M. D., Rogers, T. T., Bussey, T. J., Saksida, L. M., & Graham, K. S. (2010). Influence of conceptual knowledge on visual object discrimination: Insights from semantic dementia and MTL amnesia. *Cerebral Cortex*, *20*, 2568–2582. doi:10.1093/cercor/bhq004
- Bartko, S. J., Cowell, R. A., Winters, B. D., Bussey, T. J., & Saksida, L. M. (2010). Heightened susceptibility to interference in an animal model of amnesia: Impairment in encoding, storage, retrieval—or all three? *Neuropsychologia*, *48*, 2987–2997. doi:10.1016/j.neuropsychologia.2010.06.007
- Baxter, M. G., & Murray, E. A. (2001). Impairments in visual discrimination learning and recognition memory produced by neurotoxic lesions of rhinal cortex in rhesus monkeys. *European Journal of Neuroscience*, *13*, 1228–1238. doi:10.1046/j.0953-816x.2001.01491.x

- Beth, E. H., Budson, A. E., Waring, J. D., & Ally, B. A. (2009). Response bias for picture recognition in patients with Alzheimer disease. *Cognitive and Behavioral Neurology*, *22*, 229–235. doi:10.1097/WNN.0b013e3181b7f3b1
- Binetti, G., Cappa, S. F., Magni, E., Padovani, A., Bianchetti, A., & Trabucchi, M. (1996). Disorders of visual and spatial perception in the early stage of Alzheimer's disease. In R. J. Wurtman S. Corkin J. H. Growdon & R. Nitsch (Eds.), *Annals of the New York Academy of Sciences: Vol. 777. The neurobiology of Alzheimer's disease* (pp. 221–225). New York, NY: New York Academy of Sciences. doi:10.1111/j.1749-6632.1996.tb34422.x
- Braak, H., & Braak, E. (1985). On areas of transition between entorhinal allocortex and temporal isocortex in the human brain. Normal morphology and lamina-specific pathology in Alzheimer's disease. *Acta Neuropathologica*, *68*, 325–332. doi:10.1007/BF00690836
- Brainerd, C. J., & Reyna, V. F. (2002). Fuzzy-trace theory and false memory. *Current Directions in Psychological Science*, *11*, 164–169. doi:10.1111/1467-8721.00192
- Brown, M. W., & Aggleton, J. P. (2001). Recognition memory: What are the roles of the perirhinal cortex and hippocampus? *Nature Reviews Neuroscience*, *2*, 51–61. doi:10.1038/35049064
- Budson, A. E., Daffner, K. R., Desikan, R., & Schacter, D. L. (2000). When false recognition is unopposed by true recognition: Gist-based memory distortion in Alzheimer's disease. *Neuropsychology*, *14*, 277–287. doi:10.1037/0894-4105.14.2.277
- Budson, A. E., Desikan, R., Daffner, K. R., & Schacter, D. L. (2001). Perceptual false recognition in Alzheimer's disease. *Neuropsychology*, *15*, 230–243. doi:10.1037/08944105.15.2.230
- Budson, A. E., Michalska, K. J., Sullivan, A. L., Rentz, D. M., Daffner, K. R., & Schacter, D. L. (2003). False recognition in Alzheimer disease: Evidence from categorized pictures. *Cognitive and Behavioral Neurology*, *16*, 16–27. doi:10.1097/00146965-200303000-00003
- Buffalo, E. A., Reber, P. J., & Squire, L. R. (1998). The human perirhinal cortex and recognition memory. *Hippocampus*, *8*, 330–339. doi:10.1002/(SICI)1098-1063(1998)8:4<330::AID-HIPO3>3.0.CO;2-L
- Burke, S. N., Wallace, J. L., Hartzell, A. L., Nematollahi, S., Plange, K., & Barnes, C. A. (2011). Age-associated deficits in pattern separation functions of the perirhinal cortex: A cross-species consensus. *Behavioral Neuroscience*, *125*, 836–847. doi:10.1037/a0026238
- Burke, S. N., Wallace, J. L., Nematollahi, S., Uprety, A. R., & Barnes, C. A. (2010). Pattern separation deficits may contribute to age-associated recognition impairments. *Behavioral Neuroscience*, *124*, 559–573. doi:10.1037/a0020893
- Bussey, T. J., Saksida, L. M., & Murray, E. A. (2002). Perirhinal cortex resolves feature ambiguity in complex visual discriminations. *European Journal of Neuroscience*, *15*, 365–374. doi:10.1046/j.0953-816x.2001.01851.x
- Cowell, R. A., Bussey, T. J., & Saksida, L. M. (2006). Why does brain damage impair memory? A connectionist model of object recognition memory in perirhinal cortex. *Journal of Neuroscience*, *26*, 12186–12197. doi:10.1523/JNEUROSCI.2818-06.2006
- Damian, A. M., Jacobson, S. A., Hentz, J. G., Belden, C. M., Shill, H. A., Sabbagh, M. N., . . . Adler, C. H. (2011). The Montreal Cognitive Assessment and the Mini-Mental State Examination as screening instruments for cognitive impairment: Item analyses and threshold scores. *Dementia and Geriatric Cognitive Disorders*, *31*, 126–131. doi:10.1159/000323867
- Deason, R. G., Hussey, E. P., Budson, A. E., & Ally, B. A. (2012). Gist-based conceptual processing of pictures remains intact in patients with amnesic mild cognitive impairment. *Neuropsychology*, *26*, 202–208. doi:10.1037/a0026958
- Desimone, R., Schein, S. J., Moran, J., & Ungerleider, L. G. (1985). Contour, color and shape analysis beyond the striate cortex. *Vision Research*, *25*, 441–452. doi:10.1016/0042-6989(85)90069-0
- Devlin, J. T., & Price, C. J. (2007). Perirhinal contributions to human visual perception. *Current Biology*, *17*, 1484–1488. doi:10.1016/j.cub.2007.07.066
- Du, A. T., Schuv, N., Amend, D., Laakso, M. P., Hsu, Y. Y., Jagust, W. J., . . . Weiner, M. W. (2001). Magnetic resonance imaging of the entorhinal cortex and hippocampus in mild cognitive impairment and Alzheimer's disease. *Journal of Neurology, Neurosurgery & Psychiatry*, *71*, 441–447. doi:10.1136/jnnp.71.4.441
- Ennaceur, A., & Delacour, J. (1988). A new one-trial test for neurobiological studies of memory in rats. *Behavioural Brain Research*, *31*, 47–59. doi:10.1016/0166-4328(88)90157-X
- Gallo, D. A., Chen, J. M., Wiseman, A. L., Schacter, D. L., & Budson, A. E. (2007). Retrieval monitoring and anosognosia in Alzheimer's disease. *Neuropsychology*, *21*, 559–568. doi:10.1037/0894-4105.21.5.559
- Gallo, D. A., Cramer, S. J., Wong, J. T., & Bennett, D. A. (2012). Alzheimer's disease can spare local metacognition despite global anosognosia: Revisiting the confidence-accuracy relationship in episodic memory. *Neuropsychologia*, *50*, 2356–2364. doi:10.1016/j.neuropsychologia.2012.06.005
- Gallo, D. A., Sullivan, A. L., Daffner, K. R., Schacter, D. L., & Budson, A. E. (2004). Associative recognition in Alzheimer's disease: Evidence for impaired recall-to-reject. *Neuropsychology*, *18*, 556–563. doi:10.1037/0894-4105.18.3.556
- Garoff-Eaton, R. J., Kensinger, E. A., & Schacter, D. L. (2007). The neural correlates of conceptual and perceptual false recognition. *Learning & Memory*, *14*, 684–692. doi:10.1101/lm.695707
- Gutchess, A. H., & Schacter, D. L. (2012). The neural correlates of gist-based true and false recognition. *NeuroImage*, *59*, 3418–3426. doi:10.1016/j.neuroimage.2011.11.078
- 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*, Article 166. doi:10.3389/fnhum.2010.00166
- Hannula, D. E., Baym, C. L., Warren, D. E., & Cohen, N. J. (2012). The eyes know: Eye movements as a veridical index of memory. *Psychological Science*, *23*, 278–287. doi:10.1177/0956797611429799
- Heisz, J. J., & Ryan, J. D. (2011). The effects of prior exposure on face processing in younger and older adults. *Frontiers in Aging Neuroscience*, *3*, Article 15. doi:10.3389/fnagi.2011.00015
- Henson, R. N. A., Cansino, S., Herron, J. E., Robb, W. G. K., & Rugg, M. D. (2003). A familiarity signal in human anterior medial temporal cortex? *Hippocampus*, *13*, 301–304. doi:10.1002/hipo.10117
- Hodges, J. R. (2000). Memory in the dementias. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 441–459). Oxford, England: Oxford University Press.
- Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology*, *160*, 106–154.
- Hubel, D. H., & Wiesel, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *Journal of Neurophysiology*, *28*, 229–289.
- Koutstaal, W., & Schacter, D. L. (1997). Gist-based false recognition of pictures in older and younger adults. *Journal of Memory and Language*, *37*, 555–583. doi:10.1006/jmla.1997.2529
- Leutgeb, J. K., Leutgeb, S., Moser, M.-B., & Moser, E. I. (2007, February 16). Pattern separation in the dentate gyrus and CA3 of the hippocampus. *Science*, *315*, 961–966. doi:10.1126/science.1135801
- Málková, L., Bachevalier, J., Mishkin, M., & Saunders, R. C. (2001). Neurotoxic lesions of perirhinal cortex impair visual recognition memory in rhesus monkeys. *NeuroReport*, *12*, 1913–1917. doi:10.1097/00001756-200107030-00029
- Markwick, A., Zamboni, G., & De Jager, C. A. (2012). Profiles of cognitive subtest impairment in Montreal Cognitive Assessment (MoCA) in a

- research cohort with normal Mini-Mental State Examination (MMSE) scores. *Journal of Clinical and Experimental Neuropsychology*, 34, 750–757. doi:10.1080/13803395.2012.672966
- Marr, D. (1971). Simple memory: A theory for archicortex. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 262, 23–81. doi:10.1098/rstb.1971.0078
- McTighe, S. M., Cowell, R. A., Winters, B. D., Bussey, T. J., & Saksida, L. M. (2010, December 3). Paradoxical false memory for objects after brain damage. *Science*, 330, 1408–1410. doi:10.1126/science.1194780
- Meunier, M., Bachevalier, J., Mishkin, M., & Murray, E. A. (1993). Effects on visual recognition of combined and separate ablations of the entorhinal and perirhinal cortex in rhesus monkeys. *Journal of Neuroscience*, 13, 5418–5432.
- Mumby, D. G., & Pinel, J. P. J. (1994). Rhinal cortex lesions and object recognition in rats. *Behavioral Neuroscience*, 108, 11–18. doi:10.1037/0735-7044.108.1.11
- Nasreddine, Z. S., Phillips, N. A., Bedirian, 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. doi:10.1111/j.1532-5415.2005.53221.x
- Newsome, R. N., Duarte, A., & Barense, M. D. (2012). Reducing perceptual interference improves visual discrimination in mild cognitive impairment: Implications for a model of perirhinal cortex function. *Hippocampus*, 22, 1990–1999. doi:10.1002/hipo.22071
- Nordlund, A., Rolstad, S., Hellström, P., Sjögren, M., Hansen, S., & Wallin, A. (2005). The Goteborg MCI study: Mild cognitive impairment is a heterogeneous condition. *Journal of Neurology, Neurosurgery & Psychiatry*, 76, 1485–1490. doi:10.1136/jnnp.2004.050385
- Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review*, 110, 611–646. doi:10.1037/0033-295X.110.4.611
- O'Neil, E. B., Cate, A. D., & Köhler, S. (2009). Perirhinal cortex contributes to accuracy in recognition memory and perceptual discriminations. *Journal of Neuroscience*, 29, 8329–8334. doi:10.1523/JNEUROSCI.0374-09.2009
- Osterrieth, P. A. (1944). Le test de copie d'une figure complexe: Contribution à l'étude de la perception et de la mémoire [The test of copying a complex figure: A contribution to the study of perception and memory]. *Archives de Psychologie*, 30, 206–356.
- Petersen, R. C., Smith, G. E., Waring, S. C., Ivnik, R. J., Tangalos, E. G., & Kokmen, E. (1999). Mild cognitive impairment: Clinical characterization and outcome. *Archives of Neurology*, 56, 303–308. doi:10.1001/archneur.56.3.303
- Peterson, M. A., Cacciamani, L., Barense, M. D., & Scaif, P. E. (2012). The perirhinal cortex modulates V2 activity in response to the agreement between part familiarity and configuration familiarity. *Hippocampus*, 22, 1965–1977. doi:10.1002/hipo.22065
- Pierce, B. H., Sullivan, A. L., Schacter, D. L., & Budson, A. E. (2005). Comparing source-based and gist-based false recognition in aging and Alzheimer's disease. *Neuropsychology*, 19, 411–419. doi:10.1037/0894-4105.19.4.411
- Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., . . . Acker, J. D. (2005). Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex*, 15, 1676–1689. doi:10.1093/cercor/bhi044
- Reitan, R. M., & Wolfson, D. (1985). *The Halstead-Reitan Neuropsychological Test Battery: Therapy and clinical interpretation*. Tucson, AZ: Neuropsychological Press.
- Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, 2, 1019–1025. doi:10.1038/14819
- Romberg, C., McTighe, S. M., Heath, C. J., Whitcomb, D. J., Cho, K., Bussey, T. J., & Saksida, L. M. (2012). False recognition in a mouse model of Alzheimer's disease: Rescue with sensory restriction and memantine. *Brain*, 135, 2103–2114. doi:10.1093/brain/aw074
- Ryan, J. D., Althoff, R. R., Whitlow, S., & Cohen, N. J. (2000). Amnesia is a deficit in relational memory. *Psychological Science*, 11, 454–461. doi:10.1111/1467-9280.00288
- Ryan, J. D., Leung, G., Turk-Browne, N. B., & Hasher, L. (2007). Assessment of age-related changes in inhibition and binding using eye movement monitoring. *Psychology and Aging*, 22, 239–250. doi:10.1037/0882-7974.22.2.239
- Ryan, L., Cardoza, J. A., Barense, M. D., Kawa, K. H., Wallentin-Flores, J., Arnold, W. T., & Alexander, G. E. (2012). Age-related impairment in a complex object discrimination task that engages perirhinal cortex. *Hippocampus*, 22, 1978–1989. doi:10.1002/hipo.22069
- Saksida, L. M., & Bussey, T. J. (2010). The representational-hierarchical view of amnesia: Translation from animal to human. *Neuropsychologia*, 48, 2370–2384. doi:10.1016/j.neuropsychologia.2010.02.026
- Squire, L. R., & Zola-Morgan, M. (1991). The cognitive neuroscience of human memory since H. M. *Annual Review of Neuroscience*, 34, 259–288. doi:10.1146/annurev-neuro-061010-113720
- Taylor, K. I., & Probst, A. (2008). Anatomic localization of the transentorhinal region of the perirhinal cortex. *Neurobiology of Aging*, 29, 1591–1596. doi:10.1016/j.neurobiolaging.2007.03.024
- Toner, C. K., Pirogovsky, E., Kirwan, C. B., & Gilbert, P. E. (2009). Visual object pattern separation deficits in nondemented older adults. *Learning & Memory*, 16, 338–342. doi:10.1101/lm.1315109
- Treves, A., & Rolls, E. T. (1994). Computational analysis of the role of the hippocampus in memory. *Hippocampus*, 4, 374–391. doi:10.1002/hipo.450040319
- Waring, J. D., Chong, H., Wolk, D. A., & Budson, A. E. (2008). Preserved metamemory ability in patients with mild Alzheimer's disease: Shifting response bias. *Brain and Cognition*, 66, 32–39. doi:10.1016/j.bandc.2007.05.002
- Warrington, E. K., & James, M. (1991). *Visual Object and Space Perception Battery (VOSP)*. Oxford, England: Harcourt Assessment.
- Wechsler, D. (1999). *Wechsler Abbreviated Scale of Intelligence*. San Antonio, TX: Pearson.
- Wechsler, D. (2008). *Wechsler Adult Intelligence Scale (4th ed.)*. San Antonio, TX: Pearson.
- Wechsler, D. (2009). *Wechsler Memory Scale (4th ed.)*. San Antonio, TX: Pearson.
- Zhang, W., & Luck, S. J. (2008, May 8). Discrete fixed-resolution representations in visual working memory. *Nature*, 453, 233–235. doi:10.1038/nature06860
- Zola-Morgan, S., Squire, L. R., Amaral, D. G., & Suzuki, W. A. (1989). Lesions of perirhinal and parahippocampal cortex that spare the amygdala and hippocampal formation produce severe memory impairment. *Journal of Neuroscience*, 9, 4355–4370.

Received December 31, 2012

Revision received June 24, 2013

Accepted June 28, 2013 ■