

Neural effects of memory training to reduce false memories in older adults: Univariate and multivariate analyses

Indira C. Turney^a, Ashley C. Steinkrauss^b, Rebecca L. Wagner^b, Jordan D. Chamberlain^{b, d}, John T. West^b, Jonathan G. Hakun^c, Lesley A. Ross^d, Brenda A. Kirchhoff^e, Nancy A. Dennis^{b, *}

^a Laboratory of Epidemiology and Populations Sciences, National Institute on Aging, National Institutes of Health, Baltimore, MD, United States

^b Department of Psychology, The Pennsylvania State University, University Park, PA 16802, United States

^c Department of Neurology, The Pennsylvania State University, Hershey, PA 17033, United States

^d Department of Psychology, Clemson University, Clemson, SC 29634, United States

^e Department of Psychology, Saint Louis University, St. Louis, MO 63108, United States

ARTICLE INFO

Keywords:

False memories
Cognitive training
Monitoring
Univariate
Multivariate
Aging

ABSTRACT

The growing population of older adults emphasizes the need to develop interventions that prevent or delay some of the cognitive decline that accompanies aging. In particular, as memory impairment is the foremost cognitive deficit affecting older adults, it is vital to develop interventions that improve memory function. This study addressed the problem of false memories in aging by training older adults to use details of past events during memory retrieval to distinguish targets from related lures. We examined the neural basis of a retrieval-based monitoring strategy by assessing changes in univariate BOLD activity and discriminability of targets and lures pre and post training. Results showed training-related decreases in false memory rates with no alterations to hit rates. Both training and practice were associated with altered recruitment of a frontoparietal monitoring network as well as benefits to neural discriminability within network regions. Participants with lower baseline neural discriminability between target and lure items exhibited the largest changes in neural discriminability. Collectively, our results highlight the benefits of training for reductions of false memories in aging. They also provide an understanding of the neural mechanisms that support these reductions.

1. Introduction

Memory impairment is the foremost cognitive deficit affecting older adults (Jacoby and Rhodes, 2006), with research showing that age-related memory impairment arises equally from age-related increases in forgetting and increases in false memories (McCabe et al., 2009). A false memory is a memory for something that did not actually happen or that did not occur in the manner claimed. Examples include remembering that you left your keys on the kitchen counter when you left them on the dining table, or remembering that the doctor said to take your pills in the evening when in fact she said to take them in the morning. In most cases, a highly similar, but not identical, event to that which was falsely remembered actually did occur. This makes rejection of the false event (critical lure) at retrieval a demanding cognitive task. Given the prevalence of false memories in aging, it is important to identify means for mitigating them. The current study aims to examine the neural correlates underlying a retrieval-based monitoring strategy

(RBMS; training older adults to monitor details of past events during memory retrieval in order to differentiate between true events (targets) and related but new events (critical lures) to reduce false memories in aging.

Age-related increases in false memories are most pronounced when targets share common features (e.g., perceptual elements, semantic labels) with lures (Balota et al., 1999; Kensinger and Schacter, 1999; Koutstaal et al., 2003; Koutstaal and Schacter, 1997; Norman and Schacter, 1997; Schacter et al., 1997; Tun et al., 1998). Despite increased false memory rates in aging, hit rates to targets in the same studies have often been found to be similar across age groups. This resulting behavioral pattern suggests that older adults may use general features of category membership to make their memory decisions, while not relying on encoded details to differentiate targets from related lures. Such target-lure differentiation requires not only memory for encoding-related details of target events, but also the ability to monitor for such details at the time of retrieval (Johnson and Raye, 1981;

* Correspondence to: Department of Psychology, The Pennsylvania State University, 450 Moore Building, University Park, PA, United States.
E-mail address: nad12@psu.edu (N.A. Dennis).

<https://doi.org/10.1016/j.neurobiolaging.2024.12.007>

Received 8 November 2022; Received in revised form 12 November 2024; Accepted 19 December 2024

Available online 5 January 2025

0197-4580/© 2025 Elsevier Inc. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

Lindsay and Johnson, 2000; Lyle and Johnson, 2007; Mitchell et al., 2000). While studies have shown that impaired retrieval monitoring contributes to age-related increases in false memories (Dodson and Schacter, 2002; Schacter et al., 1998), it is also important to note that research finds that older adults do, in fact, typically encode the details that are needed to support a distinction between targets and lures, yet fail to use them effectively during retrieval (Bowman and Dennis, 2015; Bulevich and Thomas, 2012; Cohn et al., 2008; Koutstaal, 2003; Mitchell et al., 2013; Multhaup, 1995; Park et al., 1984; Pezdek, 1987; Rahhal et al., 2002). For example, whereas older adults have shown greater false recognition of related lures on a standard old/new recognition task, they have shown equal performance to that of younger adults when utilizing detail-based memory in repetition priming and meaning-based recognition. This suggests older adults do not utilize details that are successfully encoded as effectively as younger adults (Koutstaal, 2003). Further, when older adults are provided specific instructions at retrieval to search for relevant perceptual and contextual cues when making their memory decisions, they are able to reduce their false memories, thereby improving overall memory discrimination (Bulevich and Thomas, 2012; Henkel, 2008; Koutstaal et al., 1999; Thomas and Bulevich, 2006). The fact that the instructions in the foregoing studies came after encoding, but prior to retrieval, also supports the notion that older adults encode, but fail to use, encoded details effectively during retrieval.

Strategy-based cognitive training has shown to be successful in enhancing true memories in older adults (Ball et al., 2002; Belleville et al., 2006, 2011; da Silva and Sunderland, 2010; Jennings and Jacoby, 2003; Kirchhoff, et al., 2012a; Kirchhoff, et al., 2012b; Rebok et al., 2014; Willis, 1990). For example, following five days of adaptive training aimed at improving recollection, Jennings and Jacoby (Jennings and Jacoby, 2003) showed that older adults improved their ability to detect targets. Another study by Belleville et al. (2006) showed that following cognitive training via theoretical instruction and application to everyday life, both healthy older adults and older adults with mild cognitive impairment showed significant improvements on episodic memory tasks, including delayed list recall and face-name associations. Collectively, these findings suggest that specific strategy-based cognitive training can modify response criterion in older adults during memory retrieval.

In addition to the ability to modify behavior, neuroimaging studies have also shown that providing older adults with a memory strategy can improve performance through the modulation of neural processing during both encoding (Berry et al., 2010; Kirchhoff, et al., 2012a; Nyberg et al., 2003) and retrieval (Belleville et al., 2011; Hampstead et al., 2012; Kirchhoff, et al., 2012b). For example, Kirchhoff et al. (2012b) found that semantic strategy training not only led to increased recognition memory performance in older adults, but was associated with training-related neural increases in bilateral hippocampus, bilateral middle and inferior frontal gyri, and right superior temporal cortex during retrieval. Further, activity within the medial superior frontal gyrus and left middle and inferior frontal gyri was also associated with self-initiated semantic strategy use during encoding (Kirchhoff, et al., 2012b), suggesting that brain activity changes were due to older adults' increased use of semantic strategies that encourage the use of contextual information that enables recollection. Similarly, several studies report neural increases in dorsolateral prefrontal regions to support the demands of monitoring and evaluation during retrieval across the lifespan (De Chastelaine et al., 2016; Fletcher, 1998; Gallo et al., 2006a, 2010; Henson, et al., 1999a; McDonough et al., 2013; Rugg et al., 1999, 2003; Rugg, 2004). De Chastelaine et al. (2016) also identified retrieval monitoring effects in the anterior cingulate and right dorsolateral prefrontal cortex (DLPFC) among young, middle and older-aged adults. Further, Henson and colleagues (1999a) emphasized that activity in the right DLPFC reflects post-retrieval monitoring and evaluation operations, especially because correctly endorsing a non-target item requires more than identifying an item as 'old' but also the need to identify the source of that information. Rugg and colleagues (2003) also found

greater activity in DLPFC for source, compared with recognition judgements where greater demands on post-retrieval monitoring was necessary compared to mere detection of 'oldness'. (Belleville et al., 2011; Hampstead et al., 2012). Taken together, the results suggest that older adults are capable of utilizing training to engage effective memory strategies and that neural recruitment can be modulated to benefit memory performance in advanced aging. Yet, to date, such strategies have not been applied to the reduction of false memories.

Independent of memory, monitoring and cognitive control-based cognitive training has also been found to modulate prefrontal cortex functioning in aging (Basak et al., 2008; Braver et al., 2009; Braver and Barch, 2002). For example, Braver and colleagues (2009) enhanced proactive control in older adults by providing focused strategy-based cognitive training. While older adults showed inefficient increases in prefrontal cortex activity relative to younger adults prior to training, following training, they showed a similar pattern of neural recruitment to that of younger adults in lateral DLPFC and the inferior frontal junction. In another example, Olesen and colleagues (Olesen et al., 2004) found increased activation in the middle frontal gyrus and superior and inferior parietal cortices following working memory training. These results suggest that strategy-based cognitive training in older adults can directly influence cognitive control processes via changes in prefrontal function. Overall, prior strategy training results suggest that older adults are capable of utilizing cognitive training to enhance memory performance and that this is accompanied by modulated neural recruitment that benefits memory performance in advanced aging.

Multivariate analyses may provide more detailed information about unregulated neural recruitment, showing that brain regions may exhibit changes in the discriminability of memory-related neural patterns, reflecting changes in their ability to behaviorally differentiate between targets and related lures following memory training. For example, neural patterns associated with perceptual categories become less discriminable within the ventral visual stream in the context of increasing age (Carp et al., 2011; Trelle et al., 2020). This dedifferentiation of neural patterns is related to measures of fluid processing abilities and memory performance within older adults (Koen et al., 2019; Koen and Rugg, 2019; Park et al., 2010; Sommer et al., 2019). Multivariate neuroimaging approaches, specifically multivariate classification, have been useful in assessing such differences in neural patterns associated with memory performance and how these patterns are altered by age. In an early example, Quamme and colleagues (2010), used multivariate classification analyses to demonstrate that neural patterns associated with recollection and familiarity within middle temporal gyrus correlated with correct rejection rates. Additionally, work from our group (Bowman et al., 2019) found neural patterns associated with target and lure items of varying relatedness were discriminable in portions of the ventral visual stream during memory retrieval, and that older adults exhibited an age-related reduction in neural discriminability in select portions of the ventral visual cortex. Interestingly, while younger adults exhibited consistent positive relationships between neural discriminability and memory discriminability (d'), older adults depicted a negative relationship in fusiform gyrus. Classification searchlight results suggested that regions outside the ventral visual stream, such as medial temporal, parietal, and frontal regions, may also maintain discriminable neural patterns associated with mnemonic information that are impacted by age. Collectively, prior reports suggest that subtle differences in information processing related to previously seen and unseen items are behaviorally relevant, and susceptible to age-related dedifferentiation. While behavioral work suggests that behavior discrimination is improved with cognitive training, no study has examined the impact of cognitive training on neural discriminability within the context of memory processing in aging. It may be that targeted cognitive interventions could influence both the magnitude of brain activity as well as the discriminability of neural information in cortical regions.

The current study aims to examine the cognitive and neural effects of

RBMS training. Based on previous findings, we hypothesize that RBMS training will lead to reduced false memories to related lures as well as modulation of the frontoparietal monitoring network at retrieval. Specifically, we posit that RBMS training will be associated with enhanced activity within the frontoparietal monitoring network. We further hypothesize that RBMS training will result in increased neural discriminability within the frontoparietal retrieval network, and that such increases will be associated with decreases in false memories.

2. Methods

2.1. Participants

Fifty native English-speaking older adults were recruited from Centre County, Pennsylvania. Participants received fMRI screening over the phone, including screening for neurological disorders and psychiatric illness, alcoholism, drug abuse, and learning disabilities. Once fMRI eligibility was determined, participants visited the lab and completed a battery of cognitive assessments. Subsequently, participants were pseudo-randomly assigned to non-adaptive practice (i.e., active control) or training groups balanced for age and gender. Participants completed written informed consent, which was approved by the Pennsylvania State University IRB committee and were compensated for their participation.

Of the 50 older adults who participated in the study, three dropped out due to illness or other personal reasons. Data from four participants were excluded due to technical difficulties/errors. Two participants were unable to provide scanner eligibility documentation. One participant had an incidental MRI finding and could not continue. Data from two participants were removed due to noncompliance with task instructions. As a result, our final analyses included complete data from 38 participants (age range= 60–85 years old; mean age= 67.29; 15 males). Nineteen participants were in each group (see Table 1 for full cognitive assessment and demographic information for each group).

2.2. Stimuli

Stimuli consisted of 804 color pictures of common objects gathered from internet searches, including those used in previous lab studies (Bowman and Dennis, 2015; Dennis et al., 2012). All backgrounds were removed, and pictures were cropped and resized to an approximate size of 480 × 480 pixels. Images were presented focally and equated for resolution. Images were displayed by COGENT in MATLAB (Mathworks). Stimuli were then binned into categorical sets of 6 images. No categories were repeated during pre-training and post-training sessions.

Table 1
Demographic information of participants. M = Mean; SD = Standard Deviation; MMSE = Mini-Mental State Exam; RCFT = Rey Complex Figure Test; Immed. = Immediate; Rec. = Recognition. WRAML = Wide Range Assessment of Memory and Learning. All cognitive assessments were t-tested with Benjamini-Hochberg corrections, we observed no significant differences between groups.

	TRAIN M(SD)	PRACTICE M(SD)
Age	67.40 (6.67)	67.42 (7.21)
Education	17.74 (3.70)	16.00 (3.30)
Cognitive Assessments		
MMSE	29.50 (0.62)	29.39 (0.98)
RCFT Immed.	65.67 % (37.67)	56.50 % (25.77)
RCFT Delayed	64 % (33.02)	64 % (30.85)
RCFT Rec.	51.33 % (26.98)	58.56 % (26.31)
Digit Span	10.17 (2.48)	11.06 (2.94)
WRAML Design Immed.	8.56 (3.28)	8.56 (3.17)
WRAML Design Rec.	8.89 (2.99)	8.61 (3.27)
WRAML Picture Immed.	8.78 (2.58)	9.00 (2.22)
WRAML Picture Rec.	11.00 (2.54)	9.33 (2.54)
Symbol Search	13.28 (3.30)	11.89 (2.27)
Digit Symbol Coding	11.11 (3.34)	10.44 (2.28)

For each category, lure images were normed for their perceptual discriminability with respect to the target image on a scale of “easy,” “medium,” or “hard” (see Fig. 1 for example of lure difficulty). Specifically, a separate group of 20 individuals were shown images from each category and were asked to rate how difficult it was to discriminate between the two images on a three-point scale (1 = easy, 2 = medium, 3 = hard). For training purposes, easy pairings were those with an average rating below two, while medium and hard pairings were those with an average rating above two. Medium and hard training levels were then further distinguished in the task procedures by the inclusion of multiple exemplars and lures as well as retention interval (and not solely based on perceptual differences; see Section 2.3.2, Fig. 2 and Fig. 3 for a full understanding of easy, medium, and hard levels to training).

2.3. Procedures

2.3.1. Pre-training and post-training fMRI sessions

Procedures for “Pre-Training” and “Post-Training” days were identical (See Fig. 2 for an overview of the study design). Older adults first performed an intentional encoding task outside of the MRI scanner where participants viewed a total of 90 images (30 categories, three exemplars per category) across three presentation blocks, each lasting approximately two minutes and five seconds. Individual images were presented for three seconds on a black background followed by a 1000 ms interstimulus interval (ISI) where a fixation cross was presented. Participants were asked to make a size judgement (“Is the object smaller or bigger than a shoebox in real life?”) for each image and to record their responses with a keypress. The images were pseudorandomly ordered to ensure that the three images from any given category did not appear consecutively. The presentation order was then held constant across all participants. Following encoding, there was a 20-minute retention interval during which instructions for the retrieval task were provided, participants entered the scanner, and structural images were acquired (Fig. 3).

During the memory retrieval task inside the MRI scanner, participants viewed 195 images (90 targets, 90 related lures, and 15 unrelated lures) across five runs, each lasting approximately four minutes and 15 s. Images were presented for 3000 ms with a variable ISI (range: 1400 ms – 4900 ms) with a fixation cross. All images were presented in the center of the screen with a black background. Recognition response options with confidence ratings (“Old-High”, “Old-Low”, “New-Low”, “New-High”) were displayed below each image. Behavioral responses were recorded using a 4-button response box while each stimulus was presented on the screen. Participants were instructed that while some images would seem similar to those which were presented during the study phase, they should only respond ‘old’ if the exact image had been previously presented. The images were pseudorandomly presented to ensure that no more than three images from any one trial type (target, related lure, unrelated lure) appeared in a row. The presentation order of the images was held constant across all participants. Including set up, structural scans, and the retrieval task, the total duration of scanner time for each participant was approximately 45 min.

Immediately after completing the memory retrieval task in the scanner, participants completed a paper and pencil strategy-use questionnaire outside of the scanner. The questionnaire asked about the strategies, if any, the participant used to try to remember items during the retrieval memory test. Questions included two questions: 1) During the MEMORY TEST task, did you try to remember the objects that were presented to you? And 2) If so, what strategy or strategies did you use to try to remember the objects?

During the post-training scan session, no mention of the training task was provided. The experimenter present during this session was blind to the participant’s training group. Participants were debriefed at the end of the final scanning session (See Fig. 1 for examples of stimuli).

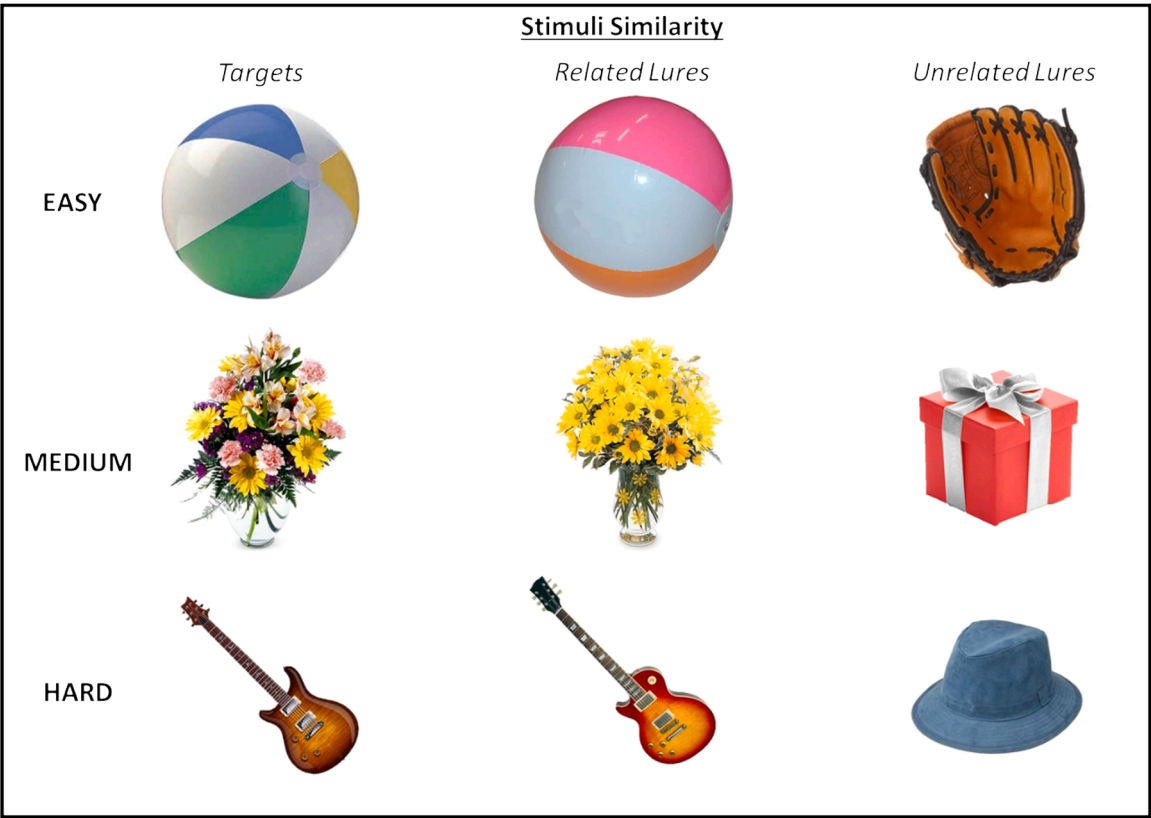


Fig. 1. Example task stimuli. Target items were shown in both encoding and retrieval phases. In addition to targets, related and unrelated lures were shown in the retrieval task. Examples of easy, medium, and hard related lures, as well as example unrelated lures are shown.

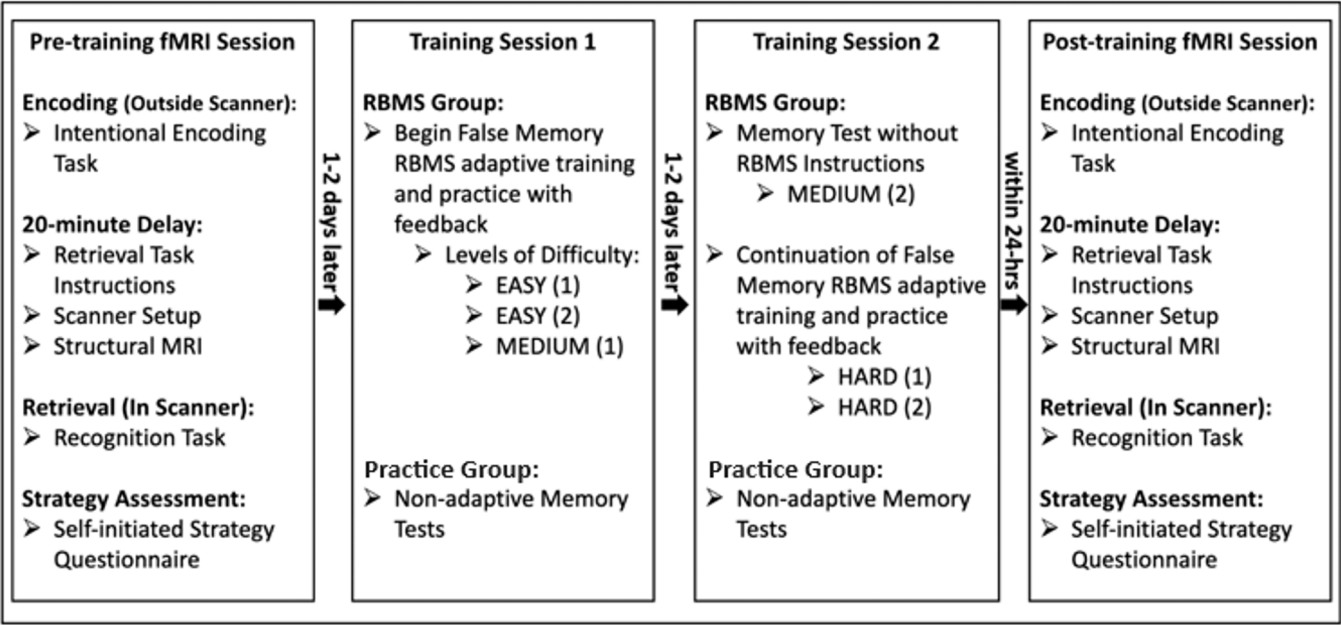


Fig. 2. Study overview. During the pre- and post-training fMRI sessions, participants performed an intentional encoding task outside of the scanner, followed by a 20-minute interval delay. Subsequently, participants completed a recognition task during fMRI scanning. During training session 1, Participants in the practice group completed non-adaptive memory tests, while participants in the training group received false memory warnings, along with adaptive Retrieval-Based Monitoring Strategy (RBMS) training. During training session 2, participants in the practice group continued to complete non-adaptive memory tests, while participants in the training group continued to receive adaptive RBMS training according to their accuracy level. Finally, all participants completed an intentional encoding task followed by an fMRI recognition task.

	EASY (1)	EASY (2)	MEDIUM (1)	MEDIUM (2)	HARD (1)	HARD (2)	TOTAL
RBMS Group							
Total # of Stimuli at Encoding/Retrieval (# categories)	5/12 (5)	5/12 (5)	16/36 (8)	30/68 (15)	15/33 (8)	30/70 (13)	101/231
Stimuli per Category for Target/Lure (# of Unrel. Lures)	1/1 (2)	1/1 (2)	2/2 (2)	2/2 (4)	2/2 (4)	2/2 (4)	XX (16)
Similarity Difficulty	E	M	M	E M H	E M H	E M H	-
Retention Interval	2 mins.	5 mins.	10 mins.	10 mins.	10 mins.	15 mins.	N/A
	TASK 1	TASK 2	TASK 3	TASK 4	TASK 5	TASK 6	TOTAL
Practice Group							
Total # of Stimuli at Encoding/Retrieval (# categories)	18/40 (18)	17/39 (16)	16/37 (16)	16/36 (16)	18/41 (18)	16/37 (16)	101/230
Stimuli per Category for Target/Lure (# of Unrel. Lures)	1-3 (4)	1-3 (4)	1-3 (5)	1-3 (4)	1-3 (5)	1-3 (5)	XX (27)
Similarity Difficulty	E M H	E M H	E M H	E M H	E M H	E M H	-
Retention Interval	8.4 mins.	8.4 mins.	8.4 mins.	8.4 mins.	8.4 mins.	8.4 mins.	N/A

Fig. 3. Retrieval-based Monitoring Strategy Training Design. Training was adaptive with feedback, gradually increasing in difficulty (i.e., EASY (1), EASY (2), MEDIUM (1), MEDIUM (2), HARD (1), HARD (2)), as participant's performance increases, by adding multiple exemplars within a category at encoding and retrieval, increasing the retention interval (time between encoding and retrieval), as well as varying item distinctiveness or similarity: E = Easy, M = Medium, H = Hard. Unlike the RBMS group, the practice group received 6 memory tasks, including all stimuli from the RBMS training phases. These tasks were not adaptable in nature, instead, in all 5 tasks, participants viewed 1–3 stimuli per category, stimuli included images from all 3 levels of the item distinctiveness, and retention interval were 8.4 s, which is the average retention interval to be completed by the RBMS training group. Unrel. = Unrelated.

2.3.2. Training sessions

Participants were randomized to either a non-adaptive practice or an RBMS training condition by an independent researcher. The participant groups underwent either non-adaptive practice or RBMS training on two separate days after the pre-training neuroimaging session. Training was provided individually to each participant by researchers blinded about how the participant performed at baseline, before training. Participants in the non-adaptive practice group were given no instruction or emphasis on monitoring or paying attention to perceptual details.

During the first training session (which occurred 1–2 days post T1 scanning, depending on the participant's schedule), participants in both groups first completed a DRM (Deese-Roediger-McDermott) task (Deese, 1959; Roediger et al., 2001; Roediger and McDermott, 1995) in which they studied lists of semantically related words (e.g., nurse, hospital, etc.). During encoding, participants were instructed to listen to a series of words. After encoding, they completed a recognition memory task of the words where they are asked whether they remember the previously presented words, among related, but not presented words (e.g., doctor). Two versions of the DRM task were administered, one during the pre-training session and another during the post-training session. One version of the list included critical words: anger, city, doctor, girl, king, lion, mountain, and music. The other version included critical words: bread, man, needle, pen, rough, smoke, spider, and sweet.

Participants in the RBMS training group were then given a brief overview of the theoretical basis of false memories. Participants were informed of the definition of a false memory and were provided with an explanation of how they may occur during a memory task. Participants were then given training aimed at helping them evaluate and monitor, during retrieval, the specific details of items from encoding so that they could distinguish whether an item was the same as one which was seen at encoding, or merely similar to it. For example, they were told that

focusing on details such as “a small, black, fluffy dog with brown spots” during encoding would help them make a correct memory decision during retrieval when presented with either the target dog or a similar small dog. Participants in the RBMS training group were instructed on how to search their memory and accomplish this strategy. It was explained that solely retrieving at a superficial, gist level (e.g., small dog) had the potential to lead to false memories and erroneous endorsement of a critical lure, such as a different, but similar dog. The use of these instructions and training were implemented first in simple perceptual discrimination tasks, and then for memory tasks. At the end of each task, participants received accuracy feedback (i.e., how well they performed) and were asked to explain to the experimenter how monitoring item-specific details helped their performance.

RBMS training was adaptive and gradually increased in difficulty as participants' performance improved. Specifically, participants in the RBMS group completed memory tests at three difficulty levels, starting with EASY (1) and EASY (2), followed by MEDIUM (1) and MEDIUM (2), and concluded with HARD (1) and HARD (2) tasks (different stimuli were used in each test). Participants repeated a level if their hit rate and/or false alarm rate was poor (hit rate below 60 % or false alarm rate above 60 %). Fig. 3 presents the number of stimuli during encoding and retrieval, the number of categories, the number of stimuli per category for targets and lures, the number of unrelated lures, the difficulty of stimulus discriminability, and the retention interval for each RBMS and non-adaptive training trial. The total duration of the first training session was approximately 1.5 h. The first training session always concluded with either a MEDIUM (1) or MEDIUM (2) level.

During the second training session (which occurred 1–2 days following the first training session, depending on participant's schedule), participants in the RBMS training group completed more memory training. A goal of the second training day was also to assess

how well each participant was able to spontaneously use the retrieval-based monitoring strategy. Therefore, for the first memory test given on training day 2, the participant was not instructed use the retrieval-based monitoring strategy. Instead, they completed a brief memory test trial and were given memory task instructions identical to those used during the pre-training fMRI scanning session. Following this first memory test, the participant was reminded of the importance of using the retrieval-based monitoring strategy and was re-instructed on how to execute it using examples from their own training session 1 training task performance. Training then resumed at the next MEDIUM difficulty level following where the participant left at the end of their first training session. Training subsequently continued through the HARD training tests. The second training session ended with another DRM task trial. The total duration of the second training session was approximately 1 h and 30 min.

Across both training days, the non-adaptive practice group completed multiple memory tests that used stimuli identical to those used for the RBMS training group (Fig. 3). The practice group spent an equal amount of time in the lab completing memory tests as the RBMS training group. However, no information about false memories or retrieval monitoring was provided to practice group participants. Instead, they were given memory task instructions identical to those used during the pre-training fMRI scanning session. Non-adaptive practice group participants were told that practice on memory tasks was known to lead to improved performance, so therefore they would be completing many practice trials/sessions. Participants returned to the lab for their second scanning session (T2) within 24 h of their second training session.

2.4. Image acquisition

Structural and functional brain images were acquired using a Siemens 3 T scanner equipped with a 12-channel head coil. A T1-weighted sagittal localizer was collected to locate the anterior (AC) and posterior (PC) commissures. A high-resolution anatomical image was then acquired with a 1650 ms TR, 2.03 ms TE, 256 mm field of view (FOV), and 2562 matrix with 160 1 mm thick axial slices resulting in 1 mm isotropic voxels. Echo-planar functional images were acquired using a descending acquisition scan with a 2500 ms TR, 25 ms TE, 240 mm FOV, and 802 matrix with 42 3 mm thick axial slices resulting in 3 mm isotropic voxels.

2.5. Behavioral analyses

We assessed potential demographic characteristics at baseline assessment via two-sample two-sided t-tests. Multiple linear regressions were used to test if training group (RBMS, Practice) and memory performance at time point one (T1; Pre-Training fMRI Scanning Session) significantly predicted group differences in memory performance at time point 2 for Hits and False Alarm Rates.

2.6. fMRI analysis

2.6.1. Imaging data preprocessing

Pre-processing of all functional images was carried out in SPM12 (Wellcome Institute of Cognitive Neurology, London, UK. www.fil.ion.ucl.ac.uk) using MATLAB (Mathworks Inc., Natick, MA, USA). The functional time series were first corrected for differences in slice timing acquisition. EPI images were then realigned to the first image of the functional run using a 6-parameter rigid body affine transformation and then spatially normalized to the standard MNI (Montreal Neurological Institute) EPI template implemented in SPM12. To do this, the raw T1 MPRAGE images were co-registered to the mean realigned functional image, and then this co-registered T1 MPRAGE image was segmented and registered to the MNI template. Lastly, the parameters from this registration process were applied to the slice time corrected and

realigned functional images to normalize them to the MNI template. As a final preprocessing step, all of the normalized functional images were smoothed using a 6 mm full-width-half-maximum Gaussian smoothing kernel. Normalized unsmoothed data were used for multivariate classification analyses.

2.6.2. Univariate analysis

At the first level, trial-related activity was modeled using the general linear model (GLM) with a stick function corresponding to trial onset convolved with a canonical hemodynamic response function. A second-level random effects GLM was created and one sample t-tests were conducted to investigate contrasts of interest. The data was sorted into the follow regressors: 1) All Hits, which were defined as both ‘Definitely Old’ and ‘Probably Old’ responses to related targets; 2) All Misses, which were defined as ‘Definitely New’ and ‘Probably New’ responses to related targets; 3) Related False Alarms (RFA), which were defined as both ‘Definitely Old’ and ‘Probably Old’ responses to related lures; and 4) Related Correct Rejections (RCR), which were defined as ‘Definitely New’ and ‘Probably New’ responses to related lures; 5) Unrelated Correct Rejections (UCR), which were defined as ‘Definitely New’ and ‘Probably New’ responses to unrelated lures; and 6) Unrelated False Alarms (UFA), which were defined as both ‘Definitely Old’ and ‘Probably Old’ responses to unrelated lures. All no response trials were coded with their own regressors and treated as regressors of no interest, as were movement parameters.

To examine brain regions that supported related monitoring, we contrasted related correct rejections with unrelated correct rejections. To examine successful monitoring, we contrasted related correct rejections with related false alarms. There was a minimum of 13 trials per participant in each regressor of interest: RCR ($M = 42.88$, $SD = 12.25$), UCR ($M = 14.73$, $SD = 0.53$), RFA ($M = 46.65$, $SD = 12.42$). Both whole-brain contrasts were conducted on pre-training fMRI data (T1), using an FDR correction of $p < .05$ whole brain, in order to identify regions of interest for conducting subsequent group analyses of training-related changes.

To examine neural changes associated with cognitive training and non-adaptive practice, we submitted subject-specific, first-level related monitoring and successful monitoring contrast maps at T1 and T2 to the Sandwich Estimator (SwE version 2.2.2) toolbox implemented in SPM (Guillaume et al., 2014); <http://www.nisox.org/Software/SwE/>). The SwE toolbox applied non-iterative marginal models to the dataset while also accounting for correlations due to repeated measurements and error variation across individual participants. The toolbox is well adapted to handle datasets that are small or potentially unbalanced. We first limited our analysis to regions that showed a significant differential BOLD amplitude at the second-level in the full sample ($N = 38$) during the pre-training fMRI session, i.e., survived the FDR correction at the group level at T1 (see Results; Table 2A for ROIs). This allowed us to examine changes in neural activity associated with related monitoring and successful monitoring in regions identified as relevant for either monitoring process in the present task. Specifically, we first examined any potential group differences in univariate activity at post-test while controlling for univariate activity at baseline. We then examined potential time-related changes in univariate activity. Since the T1 ROIs were selected using a conservative FDR correction, we employed an uncorrected threshold of $p < .05$ within these regions for investigating time related changes using the SwE analyses. We then repeated the analyses whole-brain to examine changes in regions not identified by the T1 contrasts, as cognitive training has been shown to lead to recruitment of new neural regions (Park and Reuter-Lorenz, 2009). Whole-brain investigations were conducted with a more conservative FDR clusterwise correction of $p < .05$.

We next conducted several exploratory regression analyses to look for effects outside of the aforementioned ROIs. Specifically, we used change in univariate contrast estimates between T2 and T1 as the outcome variable, and included group, contrast estimate at T1, and their

Table 2
A reports univariate activity for related monitoring (Related Correct Rejections > Unrelated Correct Rejections) and successful monitoring (Related Correct Rejections> Related False Alarms) in the full sample at baseline (T1), $p < .05$, FDR corrected. x, y, z represents peak MNI coordinates, k indicates cluster extent, H: hemisphere, L: left, R: right. Within these regions, Table 2B reports pre-post effects on univariate activity for each contrast at $p < .05$ within the corrected ROIs. SwE(Z): sandwich estimator z-statistic. ^indicates increased activity from pre-intervention (Time1) to post-intervention (Time2); * indicates decreased activity from Time1 to Time2.

A	Pre-Training (T1) Contrast Results						B					
	MNI Coordinates						ROI SwE Results					
	H	x	y	z	k	t	H	x	y	z	k	SwE (Z)
Related Correct Rejection > Unrelated Correct Rejection												
Superior Medial Frontal Gyrus*	L	−6	14	50	91	8.54	L	−3	14	47	16	2.14
Superior Parietal^	R	27	−61	53	40	6.67	R	15	−70	50	37	3.37
Related Correct Rejection > Related False Alarm												
Lingual	R	12	−76	−7	129	9.20	-	-	-	-	-	-
Superior Medial Frontal Gyrus*	R	9	20	44	208	7.94	L	−6	5	53	207	4.06
Precentral gyrus*	L	−39	−28	62	76	7.80	L	−36	−25	62	56	3.21
Precentral gyrus*	L	−36	−7	53	85	7.54	L	−30	−1	56	82	3.81
Precentral gyrus*	R	30	−19	62	43	6.79	R	21	−7	68	43	4.51
Postcentral gyrus*	L	−51	−19	20	45	6.10	L	−60	−28	35	40	3.18
Inferior Frontal Gyrus*	L	−51	28	20	56	7.79	L	−48	5	29	53	2.94
Inferior Frontal Gyrus*	L	−39	26	2	89	7.08	L	−57	11	17	45	3.45
Inferior Frontal Gyrus	L	−45	38	11	12	6.06	-	-	-	-	-	-
Inferior Frontal Gyrus	R	54	29	17	19	6.27	-	-	-	-	-	-
Putamen	L	−21	−1	11	10	6.72	-	-	-	-	-	-
Thalamus	L	−9	−16	8	12	5.93	-	-	-	-	-	-

interaction as predictor variables. We also examined if any changes in neural activity contributed to changes in correct rejection rates in older adults by conducting multiple linear regressions in which change in correct rejection rates (T2 minus T1) was the outcome variable and group, change in contrast estimate, and their interaction were predictor variables.

2.6.3. Multivariate classification analysis

In addition to examining univariate changes in neural activity following training, we were also interested in examining training-related changes in neural discriminability and how that may relate to behavioral improvements in older adults. To do so, we first estimated a second GLM in SPM12 defining one regressor per trial during memory retrieval (Zeithamova et al., 2017) with normalized unsmoothed data (Op de Beeck, 2010). We included six additional nuisance regressors for head motion. We estimated whole-brain beta parameter maps for each trial and for each participant. We then concatenated each beta parameter map across each retrieval run and submitted this data to classification analyses using the CoSMoMVPA toolbox (Oosterhof et al., 2016). Specifically, we conducted classification analyses distinguishing between patterns of neural activity underlying target and related lure items (Bowman et al., 2019). Regions of interest included regions identified as significant in the monitoring contrasts at T1, with any overlapping clusters collapsed to create a single ROI (see Supplemental Fig. 1). Critically, the ROIs were defined using contrasts examining lure-related memory responses, specifically correct rejections and false alarms, whereas the multivariate classification analysis utilized targets and lures, thereby negating potential circular analysis confounds. We utilized a support vector machine (SVM) classifier with a linear kernel and all voxels within each region of interest. We used a leave-one-out cross-validation approach in which the classifier was trained on three runs and tested on one run. We averaged across validation folds from all possible train/test permutations to estimate subject-level classification accuracy. We first conducted classification analyses in each region of interest, in each participant, at pre-test. To test if the SVM classifier was

able to discriminate neural patterns associated with targets and lures above chance (50 % accuracy), we used one-tailed one-sample t-tests in each region at T1 collapsing across the train and practice groups. We then repeated the above classification procedure for all participants and ROIs at T2, examining classifier performance in each group separately. To examine possible group differences in neural discriminability at T2 within regions that depicted significant above-chance classification accuracy while controlling for baseline discriminability, we conducted primary multiple linear regression analyses in which classification accuracy at T2 was the outcome variable, and group, classification accuracy at T1, and their interaction were predictor variables. We also conducted exploratory regression analyses in regions depicting above-chance classification. Specifically, change in accuracy between T2 and T1 was the outcome variable, and group, classification accuracy at T1, and their interaction were predictor variables. Finally, we wished to examine if any changes in neural discriminability contributed to changes in correct rejection rates in older adults. We therefore conducted multiple linear regressions in which change in correct rejection rates (T2 minus T1) was the outcome variable, and group, change in classification accuracy, and their interaction were predictor variables any significance was confirmed with using a linear permutation model (lmPerm 2.1.0 package) of 10,000 permutations.

3. Results

3.1. Demographics and cognitive assessment

The sample included 19 non-adaptive practice and 19 RBMS training participants. Demographic details of the 38 participants included in the analysis, separated by training group, are shown in Table 1. Participants were similar in age and years of education across training groups. Additionally, we observed no significant differences between training and practice groups in any of the cognitive assessment tasks (all p 's > .05).

3.2. Effects of RBMS training on hit and false alarm rates

To investigate the effectiveness of RBMS training, multiple linear regression was conducted to determine whether training group (RBMS, Practice) and/or memory performance at T1 predicted changes in memory performance (Hits and False Alarms) between T1 and T2. Group ($\beta = -0.076$, $p = 0.038$) and false memory rates at T1 ($\beta = -0.308$, $p = 0.021$) significantly predicted decreased rates of false memories from T1 to T2. False memory rates for the RBMS group at T1 ($M = 0.501$, $SD = 0.123$) were comparable to the practice group ($M = 0.573$, $SD = 0.150$), ($t(36) = -1.603$, $p = .118$). False memory rates for the RBMS group at T2 ($M = 0.385$, $SD = 0.098$) were significantly less than that of the practice group ($M = 0.511$, $SD = 0.173$), ($t(36) = -2.757$, $p = .009$). With respect to hit rates, Group did not significantly predict increases in hit rates at T2 ($\beta = -0.034$, $p = .242$). Hit Rates at T1 significantly predicted the difference between T1 and T2 hit rates ($\beta = -0.365$, $p = 0.006$). Hit Rates for the RBMS group at T1 ($M = 0.729$, $SD = 0.100$) were comparable to the practice group ($M = 0.777$, $SD = 0.126$), ($t(36) = -1.323$, $p = .194$). Hit Rates for the RBMS group at T2 ($M = 0.738$, $SD = 0.105$) were not significantly different compared to the practice group ($M = 0.802$, $SD = 0.115$), ($t(36) = -1.799$, $p = .080$).¹

3.3. Univariate activity

3.3.1. Related monitoring

Collapsing across participants at T1, related monitoring activity, as defined by the contrast of related correct rejections > unrelated correct rejections, was observed in the superior medial frontal gyrus and right superior parietal cortex (Table 2A).

Results of the SwE analysis conducted within these regions revealed a positive significant main effect of time, reflecting an increase in contrast estimates from T1 to T2 in both the superior medial frontal gyrus (MFG) and in the right superior parietal cortex (Table 2B; Fig. 4A). Whole-brain SwE results also showed a positive significant main effect of time, with increases in contrast estimates from T1 to T2 within several brain regions, including the left fusiform, right and left inferior temporal gyrus, right middle occipital, and left precuneus (Table 3, Fig. 4B). In both the ROI and whole-brain SwE analyses, there were no significant main effects or interactions associated with Group (See Supplemental Table 1 for results within each group separately). As an exploratory analysis, we examined if change in related monitoring contrast estimates could be predicted by group assignment or baseline performance with multiple linear regression. We observed no significant predictors of change in contrast estimates (all p 's > 0.05). We also examined if change in contrast estimates were predictive of change in correct rejection rates and observed no significant effects (all p 's > 0.05).

3.3.2. Successful monitoring

At T1, successful monitoring activity was observed in widespread regions across the cortex. Successful monitoring activity was observed in the right lingual, right superior medial frontal gyrus, right precentral

¹ As suggested by an anonymous reviewer, we conducted generalized linear mixed models (GLMMs) (Bates et al., 2015; Brauer and Curtin, 2018) to investigate whether the results of our multiple regression analyses concerning the effects of RBMS training on true and false memory remained consistent after accounting for between-participant and between-item variability. Both the analysis of true and false memory at the trial-level produced results consistent with the above analyses. While the Group by Time interaction effect was nonsignificant ($p = 0.106$) for the false memory GLMM, simple effects analyses show that the simple effect of Time is numerically stronger within the RBMS group ($z = 4.35$, $b = 0.70$, $SE = 0.16$, $p < 0.001$) compared to the Practice group ($z = 2.17$, $b = 0.34$, $SE = 0.16$, $p = 0.030$). Given that we had 19 participants per training group, we speculate that the lack of significance in the interaction term is likely due to reduced power to detect interaction effects within the GLMM analysis.

gyrus, left postcentral gyrus, right inferior frontal gyrus, left putamen, left thalamus, two peaks in the left precentral gyrus, and three peaks in the left inferior frontal gyrus (IFG) (Table 2A).

The results of the ROI-masked SwE analysis on the contrast of correct rejections > related false alarms revealed a decrease in neural activity from T1 to T2 in several brain regions identified at T1, including the superior MFG,² precentral gyrus, and IFG (Table 2B; Fig. 4A). Whole-brain SwE analyses also showed significant decreases in neural activity in the left superior medial frontal gyrus, left precentral gyrus, as well as additional decreases in activity within the right superior frontal and right and left inferior parietal (Table 3, Fig. 4B). In both ROI and whole-brain investigations there were no significant main effects or interactions associated with Group (See Supplemental Table 1 for results within each group separately). As an exploratory analysis, we examined if change in successful monitoring contrast estimates could be predicted by group assignment or baseline performance with multiple linear regression. We observed no significant predictors of change in contrast estimates (all p 's > 0.05). We also examined if change in contrast estimates were predictive of change in correct rejection rates and observed no significant effects (all p 's > 0.05).

3.4. Multivariate pattern classification

We next examined whether brain activity patterns associated with targets and lures were discriminable in regions defined by the pre-training (T1) full-sample univariate analysis, and if neural discriminability in the regions was altered by cognitive training. The left inferior frontal gyrus, right inferior frontal gyrus, left precentral gyrus, and medial superior medial frontal gyrus displayed classification accuracies greater than chance ($t(37) = 1.767$, $p = .043$; $t(37) = 1.792$, $p = .041$; $t(37) = 3.515$, $p = .001$; $t(37) = 2.617$, $p = .006$, respectively) in the full sample pre-training. We next examined classification accuracy during the post-training fMRI session in the full sample. Again, the left inferior frontal gyrus ($t(37) = 2.726$, $p = .005$) displayed classification accuracies greater than chance. Additionally, the post central gyrus ($t(37) = 2.657$, $p = .006$) and superior parietal gyrus ($t(37) = 2.419$, $p = .010$) displayed classification accuracies greater than chance (Fig. 5).

We also entered classification accuracy scores into multiple linear regressions to examine if there were any group changes in post-training classification accuracy when accounting for pre-training classification accuracy. Group assignment did not predict post-training classification accuracy within any ROI (all p 's > 0.05). We next ran multiple linear regression models with change-in-accuracy (post-training minus pre-training) as the outcome variable. We observed no significant group or group-by-pre-training interactions (all p 's > 0.05). However, we observed that pre-training (T1) classification accuracy significantly negatively predicted change in classification accuracy in all regions, including the right inferior frontal gyrus ($b(34) = -0.82$, $p = .000$), left inferior frontal gyrus ($b(34) = -1.02$, $p = .000$), ($b(34) = -0.92$, $p = .000$), ($b(34) = -1.18$, $p = .000$), right lingual ($b(34) = -1.05$, $p = .000$), left post central gyrus ($b(34) = -0.72$, $p = .000$), left precentral gyrus ($b(34) = -0.91$, $p = .000$), ($b(34) = -1.17$, $p = .000$), right precentral gyrus ($b(34) = -1.17$, $p = .000$), left putamen ($b(34) = -0.91$, $p = .000$), medial superior medial frontal gyrus ($b(34) = -1.10$, $p = .000$), right superior parietal ($b(34) = -1.05$, $p = .006$), and left

² Per the suggestion of an anonymous reviewer, we did explore the possibility of a “general monitoring” construct which would be defined by the overlap between the related and successful monitoring contrasts at T1. Our conjunction analysis of the two contrasts showed minimal overlap, with only one significant cluster ($k = 38$) within the superior medial frontal gyrus. However, additional SwE analyses did not support the involvement of this region in any generalized monitoring processes as activity in this cluster decreased from T1 to T2 in the successful monitoring contrast but showed no significant changes in the related monitoring contrast.

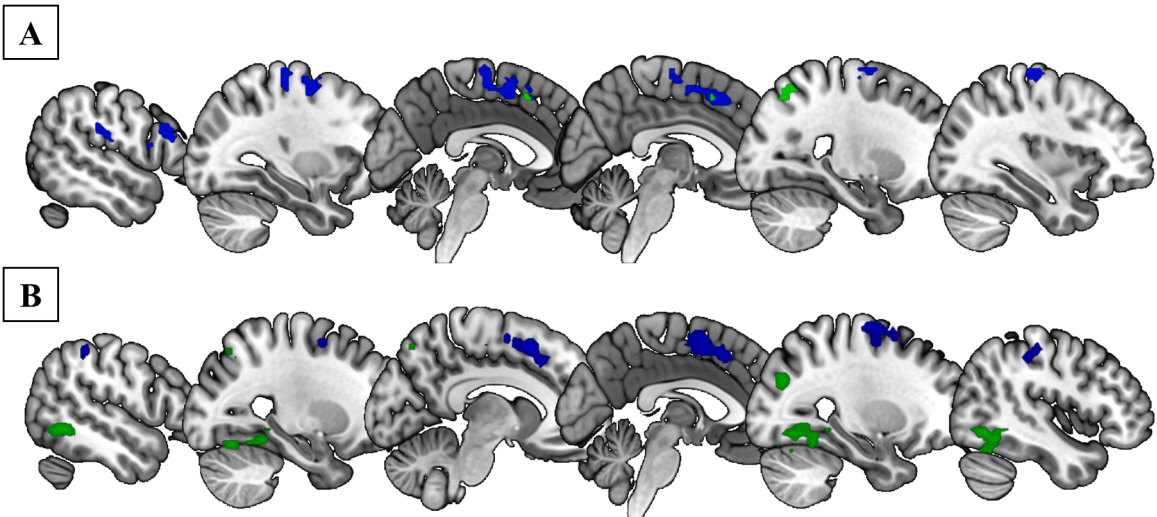


Fig. 4. A & B. **Fig. 4A** shows the results of the pre-post SwE analyses within regions that survived FDR cluster correction at the group level (N = 38) at Time 1 (T1). **Fig. 4B** shows the results of the whole-brain pre-post SwE analyses. Increases in related monitoring (Related CR vs Unrelated CR) shown in green and decreases in successful monitoring (Related CR vs Related FA) shown in blue. **Fig. 4A** MRIcroGL slice numbers: -52-30 -2 4 24 34. **Fig. 4B** MRIcroGL slice numbers: -50-25 -8-2 28 44.

Table 3
reports whole brain pre-post effects on univariate activity for related monitoring (Related Correct Rejections > Unrelated Correct Rejections) and successful monitoring (Related Correct Rejections > Related False Alarms) thresholded at $p < .05$, FDR corrected. x, y, z represents peak MNI coordinates, k: cluster extent, H: hemisphere, L: left, R: right, SwE(Z): sandwich estimator z-statistic.

		MNI Coordinates				
	H	x	y	z	k	SwE (Z)
Related Correct Rejection						
> Unrelated Correct Rejection						
Training Changes						
T2 > T1 (increased activity)						
Fusiform	L	-30	-64	-19	80	5.09
Inferior Temporal Gyrus	R	48	-58	-10	390	4.50
Inferior Temporal Gyrus	L	-51	-55	-7	61	4.40
Middle Occipital	R	30	-76	29	61	4.32
Precuneus	L	-12	-70	53	45	3.63
Related Correct Rejection						
> Related False Alarm						
Training Changes						
T1 > T2 (decreased activity)						
Superior frontal	R	21	-7	68	127	4.51
Superior medial frontal gyrus	L	-9	14	50	213	4.41
Inferior parietal	R	54	-34	47	51	3.90
Inferior parietal	L	-57	-28	44	78	3.79
Precentral gyrus	L	-30	-1	56	50	3.81

thalamus ($b(34) = -0.97, p = .000$). In these regions, individuals with the lowest pre-training classification accuracy showed the greatest increase in classification accuracy over time (Fig. 6). We next conducted exploratory multiple linear regression analyses that examined if changes in correct rejection rates over time were predicted by changes in classification accuracy. We observed no significant effects (all p 's > 0.05). We observed no changes in significance after conducting permutation testing.

4. Discussion

The goal of the current study was to investigate the cognitive and neural basis of a retrieval-based monitoring strategy training aimed at

reducing false memories. Specifically, older adults were trained to use details of past events during memory retrieval to distinguish targets from related lures, with the goal of reducing false memories. As predicted, participants in the RBMS training group showed a significant decrease in rates of false alarms following the intervention training, and a larger decrease than that seen in the non-adaptive practice (i.e., *active control*) group. Additionally, we examined both univariate and multivariate approaches to understand the underlying neural processing at T1 and T2. Neuroimaging results revealed modulation of the BOLD signal within multiple frontoparietal regions associated with monitoring, as well as evidence of benefits to neural discriminability, indexed by pattern classification, post-training within these regions. Together, these findings provide evidence supporting that training leads to older adults' improvements in behavioral discriminability between targets and lures during retrieval, with neural changes observed when considering both training and memory practice effects.

As mentioned earlier, older adults are prone to false recognition and misattribution errors. This is due, in part, to their reliance on general familiarity, as well as their decreased ability to retrieve specific recollections of the encoding event to either accept or reject a related lure presented during retrieval. Such failures in 'recall to reject' have been documented in both behavioral and neuroimaging work in aging (Cohn et al., 2008; Gallo et al., 2006b; Yassa et al., 2001). Nevertheless, previous studies also suggest that older adults do encode sufficient details to distinguish between targets and lures, but they are unable to self-initiate a strategy to bring these details back online (Koutstaal, 2003; Koutstaal et al., 1999). Focusing on these points, the RBMS training encouraged participants to specifically use encoded details during retrieval to determine whether the presented items were previously encountered (i.e., old) or new. As such, the training of previous work aimed at reducing false memories in older and younger adults by focusing on discriminating between details in autobiographical memory materials (McDonough and Gallo, 2013) as well as perceptual and contextual cues during memory retrieval (Bulevich and Thomas, 2012; Henkel, 2008; Koutstaal et al., 1999; Thomas and Bulevich, 2006). While the RBMS training significantly reduced rates of false alarms in our training group compared to those in the practice group, there was no change in rates of true memories between groups. This finding is consistent with work from Gallo's lab indicating the specific malleability in false alarms opposed to hits (Gallo, 2013). This finding demonstrates that the RBMS training lends specifically to the discrimination and identification of

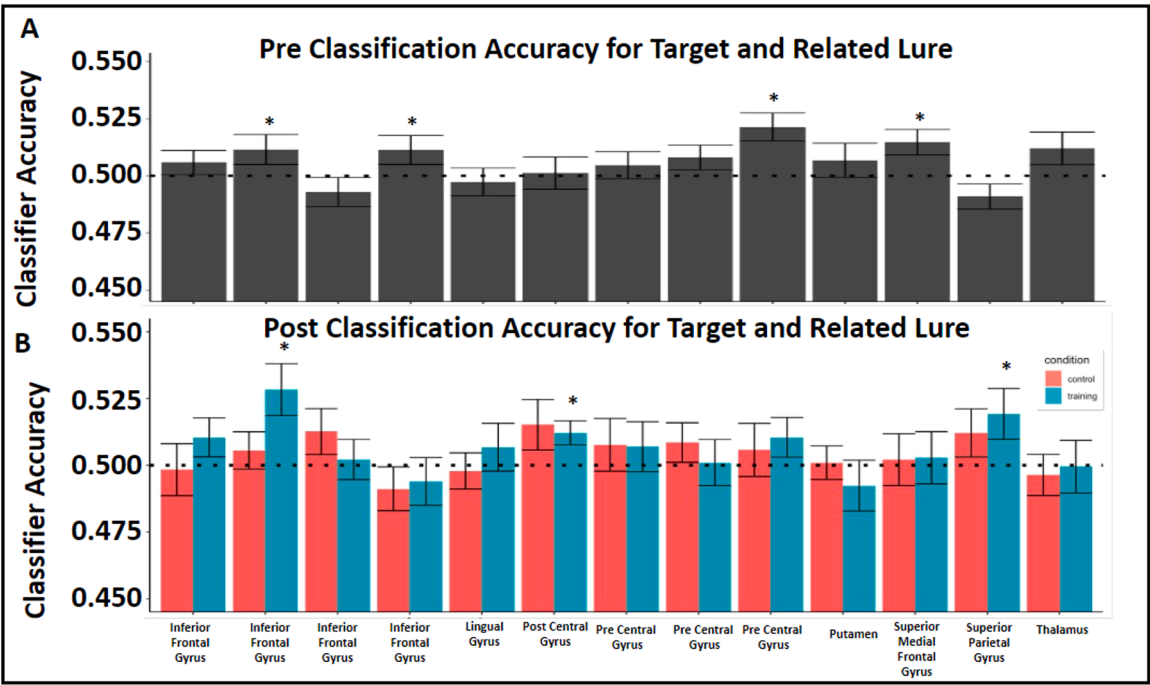


Fig. 5. Multivoxel classification accuracy. A) Pre-intervention (Time 1) classification accuracy for targets and related lures of each of the regions of interest. * indicates regions that were significantly above chance (50 %). B) Post-intervention (Time 2) classification accuracy for targets and related lures by group. * indicates the region and group that were significantly above chance (50 %).

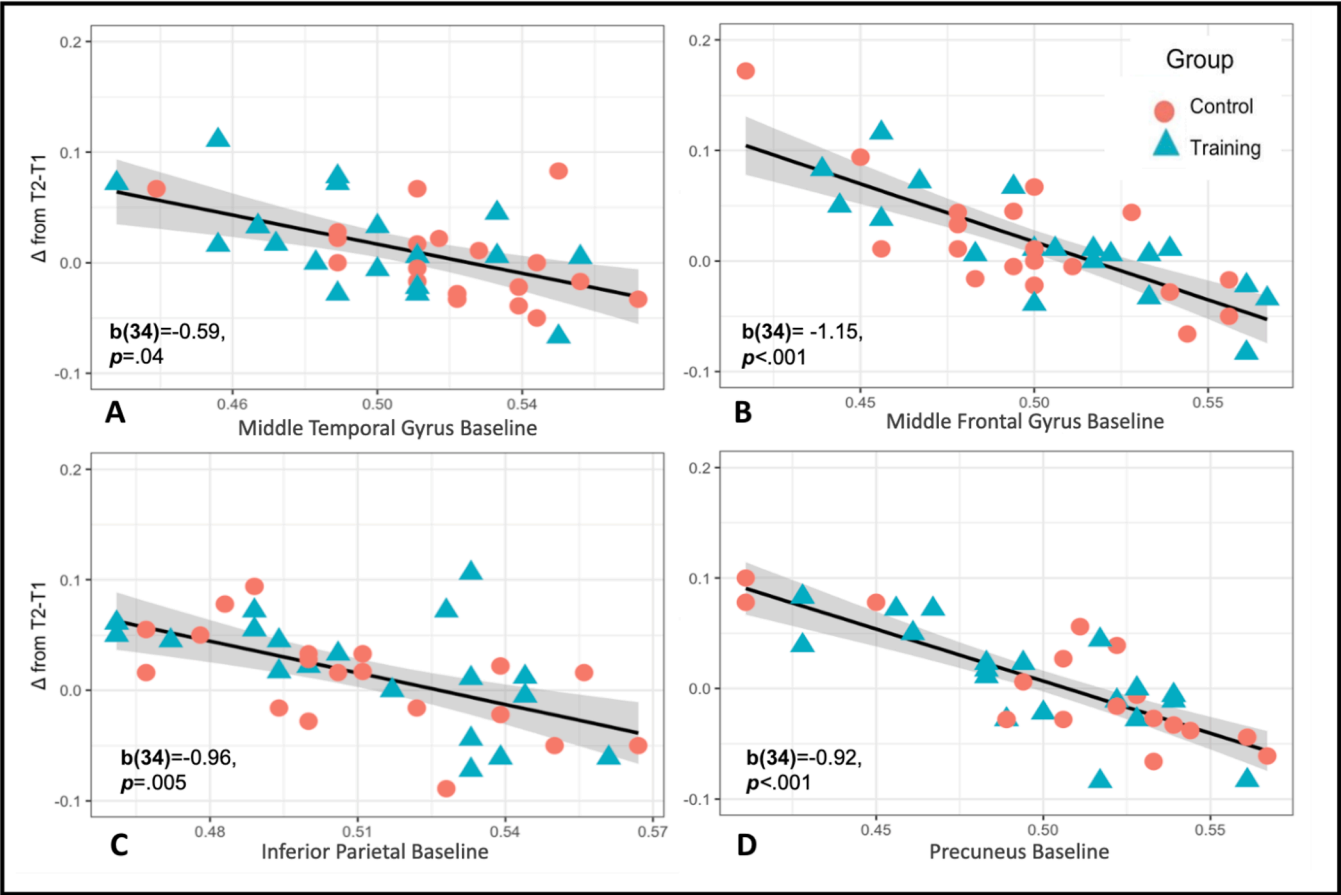


Fig. 6. Change in classification accuracy. Scatterplots depicting change in classification accuracy (Time 2 minus Time 1) versus baseline classification accuracy in the A) middle temporal gyrus, B) middle frontal gyrus, C) inferior parietal gyrus, and D) precuneus. B= beta value, p = p-value.

new items presented during retrieval. Prior memory training and strategy intervention studies have seen improvements in older adults' hit rates and behavioral discriminability (Ball et al., 2002; Belleville et al., 2006, 2011; da Silva and Sunderland, 2010; Jennings and Jacoby, 2003; Kirchhoff et al., 2012a, 2012b; Rebok et al., 2014). However, this study stands among the first training studies to focus specifically on reducing false memories and to show reductions in errors of commission. Expanding upon the work noted above, the training offers a unique contribution to methods aimed at improving age-related memory errors of commission.

In addition to the observed decrease in false alarms, the RBMS training group, along with the non-adaptive practice group, also exhibited changes in the neural processing within the frontoparietal monitoring network. Specifically, following both training and practice, older adults exhibited increased activity in regions underlying related monitoring and decreases in regions underlying successful monitoring (as defined by our analysis contrasts). While neural activity in parietal regions are theorized to guide attentional processes when presented with new information, frontal cortices are theorized to resolve conflict associated with incongruent information present in memory traces during retrieval (Devitt and Schacter, 2016; Koen and Rugg, 2019; Kurkela and Dennis, 2016; Spaniol and Bayen, 2005). As such, the two regions work together to evaluate and make decisions regarding the occurrence of a given stimulus during memory retrieval. With respect to false memory studies, activation within this frontoparietal network has been found during memory retrieval generally, with increased activation shown for related lures irrespective of the source of the false memory (i.e., semantic, perceptual, source error; Kim and Cabeza, 2007; Kubota et al., 2006; Kurkela and Dennis, 2016; Okado and Stark, 2003; Schacter et al., 1996; Schacter and Slotnick, 2004; Stephan-Otto et al., 2017; Turney and Dennis, 2017; Webb et al., 2016). Such increased activity has been taken as evidence for the difficulty associated with trying to resolve one's memory for a related lure with respect to what was presented during encoding.

Though both training and practice were met with both increases and decreases in neural activation within these regions, the pattern of these findings is consistent with past research on monitoring and false memories. With respect to related monitoring, we observed increases in neural activity from pre- to post- test in precuneus, superior parietal, inferior temporal gyrus and middle occipital gyrus. Previous false memory studies show that while unrelated lures can be rejected based upon category-level information, the correct rejection of related lures requires greater monitoring and evaluation of details because such lures differ from targets only in terms of specific details that are associated with individual exemplars drawn from the same categories (e.g., dogs, chair; Bowman and Dennis, 2015; Coane et al., 2007; Devitt and Schacter, 2016; Schacter and Slotnick, 2004). Thus, the correct rejection of related lures is posited to rely on the detection of highly specific perceptual and/or semantic differences between targets and lures during memory retrieval through memory monitoring processes. Within memory retrieval and monitoring, parietal cortices, and specifically the precuneus, have been shown to be associated with episodic source retrieval (e.g., Bonni et al., 2015; Cabeza and Nyberg, 2000; Lundstrom et al., 2003; Lundstrom et al., 2005) and directing attention to visual input (Cavanna and Trimble, 2006; Trimble and Cavanna, 2008). To this end, activity within these regions have also been associated with the ability to bring online internal representations that support accurate source retrieval (Ramanan et al., 2018; Rugg and King, 2018; Tibon et al., 2019). Related, inferior temporal cortex is a region that has been linked to object processing and object recognition (e.g., Haxby et al., 2001). As such, increased activity within these regions likely reflects the increased activation of internal representations of encoding memory traces that allow the individual to accurately identify the related lure in a "recall-to-reject" manner.

This finding is consistent with previous work by McDonough et al. (2015), who also observed alterations in the same regions in response to

cognitive training. Notably, they found increased activity in precuneus, superior parietal cortex and inferior temporal gyrus, despite expecting heightened engagement of cognitive control processes and activation in the DLPFC. Noted in the Introduction, several previous studies also identified modulation of DLPFC underlying monitoring processes during memory retrieval in adults (De Chastelaine et al., 2016; Fletcher, 1998; Gallo et al., 2006a, 2010; Henson et al., 1999a; McDonough et al., 2013; Rugg et al., 1999, 2003; Rugg, 2004). In our study, the absence of significant DLPFC changes may reflect a shift in neural resource allocation toward more posterior areas during high-demand retrieval tasks, suggesting a potential link between frontoparietal efficiency and task modulation, where enhanced monitoring capabilities facilitate optimized resource allocation. Furthermore, the training-related reductions observed in medial PFC activity may indicate a decrease in "hyperactivity," thereby enhancing task-specific efficiency and improving resource allocation across the frontoparietal network. We also propose that our related monitoring contrast can be framed as a "hard > easy" monitoring scenario, which supports the argument of improved efficiency through reduced BOLD activity in less challenging tasks, echoing the findings of McDonough et al. (2015) regarding enhanced neural engagement patterns.

While regions within the related monitoring contrasts showed increased modulation following both training and practice, the contrast of monitoring success was met with decreases in neural activity within superior and inferior frontal cortices, precentral gyri, superior medial frontal gyrus, and inferior parietal cortices. Critical to this finding, the superior medial frontal gyrus, inferior frontal gyrus, precentral gyrus, and inferior parietal cortex have been consistently linked to false memory errors across a wide variety of tasks (for a meta-analysis see Kurkela and Dennis, 2016), with increased activation observed for false alarms compared to correct rejections. Increased activation within medial PFC regions has also been associated with heightened monitoring in response to more difficult memory decisions when presented with related lures (Hofer et al., 2007; Von Zerssen et al., 2001). As such, prior work has found that when memory decisions to related lures become more certain, activity within medial PFC regions declines as monitoring demands decrease (Henson, et al., 1999a, 1999b; Volz et al., 2005; Zysset et al., 2006). The observed decreases in these regions following both training and practice support participants' ability to accurately monitor and detect the lure (and hence, not false alarm). Together with the aforementioned work, this finding also supports the idea that both training and practice led to greater ease in making required monitoring decisions to related lures. To that end, the current results extend this prior research, showing that when memory improves and correct rejections increase, there is a decrease in brain activation within regions that typically underlie false memory responses. Observed decreases in BOLD amplitude associated with successful monitoring align with prior studies observing decreased BOLD amplitude associated with improved, or increased, efficiency of cognitive processes (Lustig et al., 2009).

Modulation of the medial superior frontal gyrus and precentral gyrus was also found in prior work testing the effects of a strategy intervention aimed at improving accurate remembering in older adults (Kirchhoff et al., 2012a). While Kirchhoff et al. (2012a) did not implement a specific strategy training regimen as was conducted in the present study, they did encourage older adults to engage in any learned encoding strategy that suited their learning. Supporting this prior work, current results suggest that modulation of these specific regions in older adults can support increases in multiple metrics of memory accuracy (i.e., correct rejections as well as hit rates). Taken together with the above findings of increases elsewhere in frontoparietal regions, our findings suggest that older adults are able to benefit from the reorganization of the frontoparietal network, allowing for improved memory performance through this adaptive neural strategy. The fact that we were able to see modulation within regions following just a few days of training and practice speaks to the immediate plasticity of the frontoparietal network in aging (see also Kirchhoff et al., 2012a; Kirchhoff et al., 2012b) as

well as lays the groundwork for investigating larger and long-lasting changes following more intense strategic practice related to false memory training. The current results also continue to extend prior work to the domain of memory errors, showing that frontoparietal regions are critical for evaluating related lures throughout the adult lifespan (Bowman et al., 2019; Bowman and Dennis, 2015) and practice with memory tasks can have a significant impact on the recruitment of these neural resources.

Critically, the current results show not just the involvement of these regions in supporting memory success in aging, but also the ability of older adults to modulate and enhance neural processing within these regions following both memory practice and training. While frontoparietal activity has consistently been found in aging studies, age-related deficits within this network have frequently been observed in both general memory (Dulas and Duarte, 2011; Fandakova et al., 2014; Luo and Craik, 2009; McDonough et al., 2013; Mitchell et al., 2013; Velanova et al., 2007) and false memory studies (Bowman and Dennis, 2015; Dennis et al., 2014; Fandakova et al., 2014, 2018), with most studies attributing this finding to age-deficits in monitoring-related memory processes (e.g., Mitchell and Johnson, 2009). For example, Fandakova et al. (2018) found that young, but not older adults modulated activity across cingulo-opercular regions when making false alarms and low-quality correct rejections, consistent with the area's role in post-retrieval monitoring. Additionally, this same research group found that older adults who were able to bring online a more “youth-like” neural profile in regions including middle frontal gyrus, and portions of parietal cortex, were better able to accurately discriminate between targets and related lures (Fandakova et al., 2014). While this and previous work has identified individual differences with respect to the role of frontoparietal cortices in false memory errors (Dennis et al., 2014; Dennis and Turney, 2018; Fandakova et al., 2014; Webb and Dennis, 2019), the current results build upon this earlier work showing the flexibility of this network in older adults. As such, the current finding that recruitment of, and processing within frontoparietal regions, can be modified with both training and practice is an exciting step in identifying mechanisms by which age-related memory deficits can be ameliorated.

In addition to overall changes in frontoparietal activation as a result of training and practice, the multivariate classification results also replicate and extend recent work suggesting that neural patterns within portions of the frontoparietal network maintain discriminable information between targets and perceptual lures (Bowman et al., 2019; Ciaramelli et al., 2008; Gallo et al., 2006b). The current results show that prior to either intervention (at T1), patterns of neural activity in the inferior frontal and medial superior frontal gyri can reliably discriminate between targets and related lures. Following both training and practice (at T2), inferior frontal and superior parietal gyri showed target-lure discriminability greater than chance. By examining neural discriminability in these higher order processing regions, our results demonstrate that these regions can detect differences between old and new information, even when there is considerable overlap in the perceptual and semantic properties of the stimuli (see also Lee et al., 2019 for evidence that parietal cortex maintains signals that can reliably discriminate between false memories and correct rejections of related lures). These results provide additional supporting evidence that even as information related to item history becomes more semanticized in higher order processing regions, such as frontal and parietal cortices, neural patterns are still discriminable even into older adulthood. Moreover, shifts in the locality of regions showing target-lure discriminability post-intervention highlight the flexibility of frontoparietal neural systems in response to both training and practice. Together, these classification results further support the notion that older adults rely on not just visual information when discriminating between old versus new items, but that they also rely on semantic labels, contextual information, and attentional processes when presented with information of varying history (Ciaramelli et al., 2008; Dehon and Brédart, 2004; Kirchoff et al., 2012b; Park et al., 1984) and that these supportive processes are

malleable in older adults.

While the overall classification results showed both maintained and malleable neural discriminability between targets and lures in our older adult sample, we also found that time-related improvements in discriminability were negatively related to baseline levels of discriminability within parietal, temporal, and frontal cortices. Specifically, individuals who exhibited the lowest overall target-lure neural discriminability at baseline exhibited the greatest improvements following both practice and training within these regions. This finding is in line with a breadth of cognitive training work that observes a negative relationship between individuals' behavioral indices at baseline assessment and cognitive gains in attentional and episodic domains following training interventions (McDonough et al., 2015; Roheger et al., 2020; Roheger et al., 2020; Schiff et al., 2021; Shaw and Hosseini, 2021; Strobach and Karbach, 2021). Similar results have also been observed in attentional neural processes in participants recovering from traumatic brain injuries (Arneemann et al., 2015). Thus, it may be that older adults in our sample who were at a more optimal level of neural discriminability between targets and lures prior to training had less need for improvement while those with lower baseline behavioral and neural metrics had more “room for growth”, so to speak. This interpretation is further supported by the “supply-demand-mismatch” hypothesis put forward by Lövdén et al., 2010, which suggests that participants with lower cognitive and neural resources (“supply”) experience the greatest changes in neural and behavioral functioning when task demands are high. Applying this hypothesis to our sample, it is plausible that the older adults who were most at risk of cognitive declines stood to benefit the most from targeted cognitive interventions, including the randomized practice intervention completed by our non-adaptive practice group.

Taken together, the current study builds upon other cognitive training of memory experiments examining the neural mechanisms associated with memory improvements in healthy older adults. For example, a recent meta-analysis observed increased BOLD amplitude in parietal cortices in older participants following training (Duda and Sweet, 2020). In more targeted work, Kirchoff et al. (2012a), observed increased neural recruitment in medial and dorsolateral portions of frontal cortices associated with improvements in veridical recollection in aging. The authors interpreted this differential activity following training as evidence of the malleability of neural processes driven by behavioral modifications. In the current study, we demonstrate that frontoparietal regions are not only malleable to modifications aimed at increasing veridical memory performance, but also those targeting the reduction of erroneous memory commissions in healthy aging. Similar to this past work by Kirchoff et al. (2012a), older adults in the current sample showed neural changes following exposure to and practice with memory-related tasks. This offers evidence that while strategy instructions and training may lead to significant improvements in performance, practice continues to be an important factor in modulation of neural functioning throughout old age. Likewise, past large-scale cognitive training interventions have exhibited robust effects in improving true memory performance in older adults, in some cases with benefits lasting at least five years (Ross et al., 2016, 2018; Sprague et al., 2019). In the current study we demonstrate that not only are cognitive processes associated with true memory performance modifiable in healthy aging, but also cognitive processes related to false memory performance. These results suggest that both neural malleability and behavioral improvements are possible with cognitive training, providing promise for older adults who may be experiencing poor memory discriminability and increased false memories.

5. Limitations and future directions

The present study demonstrated that RBMS training can reduce older adults' false memories to a greater extent than non-adaptive memory practice. However, there are several limitations to this work that should

be considered. The observed improvements in neural discriminability across groups suggest that, given practice with a related-object memory task, older adults can exhibit shifts in their neural processing. However, the absence of time by group interactions within the neuroimaging analyses (see Supplemental Table 1) suggests that both practice as well as RBMS training led to the modulation of brain activity and neural discriminability. While the training focused on how to enhance monitoring of encoding details during memory retrieval, it is always possible that participants also adapted how they encoded information so to retain more details for later retrieval monitoring. Thus, we must acknowledge that participants may have altered both encoding and retrieval strategies and we are not able to separate the contributions of our intervention to a specific memory stage. Future work could also collect neural data during encoding to help address the possibility that the training impacted encoding processes as well as retrieval.

The lack of a group by time interaction may be a result of the smaller sample size in the current study. While we recruited 50 participants, only 38 saw the task through to the end (19 participants within each group). Future studies should aim to replicate the observed training-related reduction of false memories in larger and more diverse samples, and at longer intervals (years rather than days), to assess the large-scale efficacy of cognitive training on false memory performance in healthy aging. It is also a possibility that the null group differences were a result of the type of non-adaptive practice procedures used (versus more passive control groups). It was also the case that the memory tests performed by the non-adaptive practice group were similar to those performed by the RBMS training group. Specifically, the practice group viewed all of the same stimuli and performed the same memory tasks as the RBMS group, absent training instructions and adaptive task difficulty. Thus, participants had the opportunity to modulate their own strategic approaches to the task. To this end, responses from a strategy questionnaire suggest that a fraction (7 out of 19) of participants in the non-adaptive practice group reported a strategy that involved “searching for details during retrieval.” In comparison, a majority of the training group (14 out of 19) indicated that they used specific details when trying to remember the items during retrieval. Thus, while practice alone with the false memory paradigm did beget some self-initiated changes to memory strategies and subsequent improvements in reducing false memories, this was not as prolific as that observed in the RBMS training group. Future work comparing intervention manipulations should incorporate additional control groups (e.g., a no-contact control group) to explore the relative contributions of instructed training vs. practice to improvements in memory discriminability.

It is also a possibility that older adults would show neural changes due to time, absent of any training or practice with the memory task. Future work could address this possibility by testing a no-contact control group to further disentangle the effects of training, practice, and time on changes to neural activity in aging. Given the correlations between changes in neural discriminability and T1 discriminability there is the question of whether findings were influenced by regression to the mean across participants. While this cannot be ruled out, our rigorous permutation testing and overall behavioral improvements suggests against this possibility. It would also be of interest in future work to assess the relationship between individual differences in training with outcomes measures. Future work should examine whether similar strategy-based training during encoding could also reduce false memories.

Finally, the implications of these findings are significant for developing interventions aimed at mitigating false memories in older adults. By focusing on training strategies that enhance the monitoring processes within the frontoparietal network, we may be able to foster improved memory performance while reducing the cognitive burden often experienced by this population. It is important to note that our findings are based on a highly educated sample of older adults, which may limit the generalizability of our results to populations with varying educational backgrounds. Additionally, we utilized a limited number of tasks to evaluate retrieval, which may not include the full range of false memory

phenomena; thus, further studies should incorporate a broader array of tasks to better understand the underlying mechanisms of false memory in aging. Future research should also explore the longevity of these training effects and the potential for broader applications in clinical settings.

6. Conclusions

In conclusion, the current study aimed to reduce false memories in older adults via a retrieval-based monitoring strategy intervention and to investigate the neural correlates of training-associated behavioral changes. We observed a reduction in false memory rates in the RBMS training group but not in a non-adaptive practice group, thereby demonstrating the efficacy and specificity of the retrieval-based monitoring intervention that was designed to reduce memory errors of commission. Neurally, we observed both increases and decreases in BOLD amplitude associated with related and successful monitoring processes within our training and non-adaptive practice groups across regions within a frontoparietal network. Participants with lower baseline neural discriminability between target and lure items tended to receive the greatest benefits in neural discriminability due to both training and practice. Collectively, our results highlight the importance of examining the impact of cognitive training on false memory in older adults, and demonstrate that changes associated with retrieval training and practice are borne out neurally via both alterations in BOLD amplitude and neural discriminability. As such, the current study stands among the first to modulate false memory behavior and associated neural processing in healthy older adults and can provide a useful resource for investigators or clinicians aiming to develop effective methods for reducing older adults' memory errors.

Funding

This work was supported by grants from the National Science Foundation (BCS2000047, BCS1025709) awarded to NAD. It was also supported by three dissertation awards granted by the Penn State Social, Life, & Engineering Sciences Imaging Center (SLEIC), 3 T MRI Facility and the Research, Graduate Studies Office (RGSO) Dissertation Support Award, and an Alfred P. Sloan Minority Graduate Program Fellowship awarded to ICT.

Conflict of interest

The authors declare no competing financial interests.

Acknowledgements

We thank the Penn State Social, Life, & Engineering Sciences Imaging Center (SLEIC) 3 T MRI Facility. We also thank Chaleece Sandberg, Bradley Wyble, Charles Geier, Frank Hillary, Holly Richardson, Courtney Gerver, and Christina Webb for their assistance in planning and data collection for the current study.

Appendix a. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.neurobiolaging.2024.12.007](https://doi.org/10.1016/j.neurobiolaging.2024.12.007).

References

- Arneemann, K.L., Chen, A.J.-W., Novakovic-Agopian, T., Gratton, C., Nomura, E.M., D'Esposito, M., 2015. Functional brain network modularity predicts response to cognitive training after brain injury. *Neurology* 84 (15), 1568–1574. <https://doi.org/10.1212/WNL.0000000000001476>.
- Ball, K., Berch, D.B., Helmers, K.F., Jobe, J.B., Leveck, M.D., Marsiske, M., Morris, J.N., Rebok, G.W., Smith, D.M., Tennstedt, S.L., Unverzagt, F.W., Willis, S.L., for the ACTIVE Study Group, 2002. Effects of cognitive training interventions with older

- adults: a randomized controlled trial. *JAMA* 288 (18), 2271. <https://doi.org/10.1001/jama.288.18.2271>.
- Balota, D.A., Cortese, M.J., Duchek, J.M., Adams, D., Ili, L.R., McDermott, K.B., Yerys, B. E., 1999. Veridical and false memories in healthy older adults and in dementia of the Alzheimer's type. *Cogn. Neuropsychol.* 16 (3–5), 361–384.
- Basak, C., Boot, W.R., Voss, M.W., Kramer, A.F., 2008. Can training in a real-time strategy video game attenuate cognitive decline in older adults? *Psychol. Aging* 23 (4), 765–777. <https://doi.org/10.1037/a0013494>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1). <https://doi.org/10.18637/jss.v067.i01>.
- Belleville, S., Clément, F., Mella, S., Gilbert, B., Fontaine, F., Gauthier, S., 2011. Training-related brain plasticity in subjects at risk of developing Alzheimer's disease. *Brain* 134 (6), 1623–1634. <https://doi.org/10.1093/brain/awr037>.
- Belleville, S., Gilbert, B., Fontaine, F., Gagnon, L., Ménard, É., Gauthier, S., 2006. Improvement of episodic memory in persons with mild cognitive impairment and healthy older adults: evidence from a cognitive intervention program. *Dement. Geriatr. Cogn. Disord.* 22 (5–6), 486–499. <https://doi.org/10.1159/000096316>.
- Berry, A.S., Zanto, T.P., Clapp, W.C., Hardy, J.L., Delahunt, P.B., Mahncke, H.W., Gazzaley, A., 2010. The influence of perceptual training on working memory in older adults. *PLoS ONE* 5 (7), e11537. <https://doi.org/10.1371/journal.pone.0011537>.
- Bonni, S., Veniero, D., Mastropasqua, C., Ponzio, V., Caltagirone, C., Bozzali, M., Koch, G., 2015. TMS evidence for a selective role of the precuneus in source memory retrieval. *Behav. Brain Res.* 282, 70–75. <https://doi.org/10.1016/j.bbr.2014.12.032>.
- Bowman, C.R., Chamberlain, J.D., Dennis, N.A., 2019. Sensory representations supporting memory specificity: age effects on behavioral and neural discriminability. *J. Neurosci.* 39 (12), 2265–2275. <https://doi.org/10.1523/JNEUROSCI.2022-18.2019>.
- Bowman, C.R., Dennis, N.A., 2015. Age differences in the neural correlates of novelty processing: the effects of item-relatedness. *Brain Res.* 1612, 2–15. <https://doi.org/10.1016/j.brainres.2014.08.006>.
- Brauer, M., Curtin, J.J., 2018. Linear mixed-effects models and the analysis of nonindependent data: a unified framework to analyze categorical and continuous independent variables that vary within-subjects and/or within-items. *Psychol. Methods* 23 (3), 389–411. <https://doi.org/10.1037/met0000159>.
- Braver, T.S., Barch, D.M., 2002. A theory of cognitive control, aging cognition, and neuromodulation. *Neurosci. Biobehav. Rev.* 26 (7), 809–817. [https://doi.org/10.1016/S0149-7634\(02\)00067-2](https://doi.org/10.1016/S0149-7634(02)00067-2).
- Braver, T.S., Paxton, J.L., Locke, H.S., Barch, D.M., 2009. Flexible neural mechanisms of cognitive control within human prefrontal cortex. *Proc. Natl. Acad. Sci.* 106 (18), 7351–7356. <https://doi.org/10.1073/pnas.0808187106>.
- Bulevich, J.B., Thomas, A.K., 2012. Retrieval effort improves memory and metamemory in the face of misinformation. *J. Mem. Lang.* 67 (1), 45–58. <https://doi.org/10.1016/j.jml.2011.12.012>.
- Cabeza, R., Nyberg, L., 2000. Imaging cognition II: an empirical review of 275 PET and fMRI studies. *J. Cogn. Neurosci.* 12 (1), 1–47. <https://doi.org/10.1162/08989290051137585>.
- Carp, J., Park, J., Polk, T.A., Park, D.C., 2011. Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. *NeuroImage* 56 (2), 736–743. <https://doi.org/10.1016/j.neuroimage.2010.04.267>.
- Cavanna, A.E., Trimble, M.R., 2006. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain* 129 (3), 564–583. <https://doi.org/10.1093/brain/awl004>.
- Ciaramelli, E., Grady, C.L., Moscovitch, M., 2008. Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia* 46 (7), 1828–1851. <https://doi.org/10.1016/j.neuropsychologia.2008.03.022>.
- Coane, J.H., McBride, D.M., Raulerson III, B.A., Jordan, J.S., 2007. False memory in a short-term memory task. *Exp. Psychol.* 54 (1), 62–70. <https://doi.org/10.1027/1618-3169.54.1.62>.
- Cohn, M., Emrich, S.M., Moscovitch, M., 2008. Age-related deficits in associative memory: the influence of impaired strategic retrieval. *Psychol. Aging* 23 (1), 93–103. <https://doi.org/10.1037/0882-7974.23.1.93>.
- da Silva, L., Sunderland, A., 2010. Effects of immediate feedback and errorless learning on recognition memory processing in young and older adults. *Neuropsychol. Rehabil.* 20 (1), 42–58. <https://doi.org/10.1080/09602010903036731>.
- De Chastelaine, M., Mattson, J.T., Wang, T.H., Donley, B.E., Rugg, M.D., 2016. The neural correlates of recollection and retrieval monitoring: relationships with age and recollection performance. *NeuroImage* 138, 164–175. <https://doi.org/10.1016/j.neuroimage.2016.04.071>.
- Deese, J., 1959. On the prediction of occurrence of particular verbal intrusions in immediate recall. *J. Exp. Psychol.* 58 (1), 17.
- Dennis, N.A., Bowman, C.R., Peterson, K.M., 2014. Age-related differences in the neural correlates mediating false recollection. *Neurobiol. Aging* 35 (2), 395–407. <https://doi.org/10.1016/j.neurobiolaging.2013.08.019>.
- Dennis, N.A., Bowman, C.R., Vandekar, S.N., 2012. True and phantom recollection: an fMRI investigation of similar and distinct neural correlates and connectivity. *NeuroImage* 59 (3), 2982–2993. <https://doi.org/10.1016/j.neuroimage.2011.09.079>.
- Dennis, N.A., Turney, I.C., 2018. The influence of perceptual similarity and individual differences on false memories in aging. *Neurobiol. Aging* 62, 221–230. <https://doi.org/10.1016/j.neurobiolaging.2017.10.020>.
- Devitt, A.L., Schacter, D.L., 2016. False memories with age: Neural and cognitive underpinnings. *Neuropsychologia* 91, 346–359.
- Dodson, C.S., Schacter, D.L., 2002. Aging and strategic retrieval processes: reducing false memories with a distinctiveness heuristic. *Psychol. Aging* 17 (3), 405–415. <https://doi.org/10.1037/0882-7974.17.3.405>.
- Duda, B.M., Sweet, L.H., 2020. Functional brain changes associated with cognitive training in healthy older adults: A preliminary ALE meta-analysis. *Brain Imaging Behav.* 14, 1247–1262. <https://doi.org/10.1007/s11682-019-00080-0>.
- Dulas, M.R., Duarte, A., 2011. The effects of aging on material-independent and material-dependent neural correlates of contextual binding. *NeuroImage* 57 (3), 1192–1204.
- Fandakova, Y., Lindenberger, U., Shing, Y.L., 2014. Deficits in process-specific prefrontal and hippocampal activations contribute to adult age differences in episodic memory interference. *Cereb. Cortex* 24 (7), 1832–1844. <https://doi.org/10.1093/cercor/bht034>.
- Fandakova, Y., Sander, M.C., Grandy, T.H., Cabeza, R., Werkle-Bergner, M., Shing, Y.L., 2018. Age differences in false memory: the importance of retrieval monitoring processes and their modulation by memory quality. *Psychol. Aging* 33 (1), 119–133. <https://doi.org/10.1037/pag0000212>.
- Fletcher, P., 1998. The functional roles of prefrontal cortex in episodic memory. II. Retrieval. *Brain* 121 (7), 1249–1256. <https://doi.org/10.1093/brain/121.7.1249>.
- Gallo, D.A., 2013. Retrieval expectations affect false recollection: insights from a criterial recollection task. *Curr. Dir. Psychol. Sci.* 22 (4), 316–323. <https://doi.org/10.1177/0963721413481472>.
- Gallo, D.A., Kensinger, E.A., Schacter, D.L., 2006a. Prefrontal activity and diagnostic monitoring of memory retrieval: fMRI of the criterial recollection task. *J. Cogn. Neurosci.* 18 (1), 135–148. <https://doi.org/10.1162/089892906775250049>.
- Gallo, D.A., Kensinger, E.A., Schacter, D.L., 2006b. Prefrontal activity and diagnostic monitoring of memory retrieval: fMRI of the criterial recollection task. *J. Cogn. Neurosci.* 18 (1), 135–148. <https://doi.org/10.1162/089892906775250049>.
- Gallo, D.A., McDonough, I.M., Scimeca, J., 2010. Dissociating source memory decisions in the prefrontal cortex: fMRI of diagnostic and disqualifying monitoring. *J. Cogn. Neurosci.* 22 (5), 955–969. <https://doi.org/10.1162/jocn.2009.21263>.
- Guillaume, B., Hua, X., Thompson, P.M., Waldo, L., Nichols, T.E., 2014. Fast and accurate modelling of longitudinal and repeated measures neuroimaging data. *NeuroImage* 94, 287–302. <https://doi.org/10.1016/j.neuroimage.2014.03.029>.
- Hampstead, B.M., Sathian, K., Phillips, P.A., Amaraneni, A., Delaune, W.R., Stringer, A. Y., 2012. Mnemonic strategy training improves memory for object location associations in both healthy elderly and patients with amnesic mild cognitive impairment: a randomized, single-blind study. *Neuropsychology* 26 (3), 385–399.
- Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and Overlapping Representations of Faces and Objects in Ventral Temporal Cortex. *Science* 293, 2425–2430. <https://doi.org/10.1126/science.1063736>.
- Henkel, L.A., 2008. Maximizing the benefits and minimizing the costs of repeated memory tests for older adults. *Psychol. Aging* 23 (2), 250–262.
- Henson, R.N.A., Rugg, M.D., Shallice, T., Josephs, O., Dolan, R.J., 1999b. Recollection and familiarity in recognition memory: an event-related functional magnetic resonance imaging study. *J. Neurosci.* 19 (10), 3962–3972. <https://doi.org/10.1523/JNEUROSCI.19-10-03962.1999>.
- Henson, R.N.A., Shallice, T., Dolan, R.J., 1999a. Right prefrontal cortex and episodic memory retrieval: a functional MRI test of the monitoring hypothesis. *Brain* 122 (7), 1367–1381. <https://doi.org/10.1093/brain/122.7.1367>.
- Hofer, A., Siedentopf, C.M., Ischebeck, A., Rettenbacher, M.A., Verius, M., Golaszewski, S.M., Felber, S., Fleischhacker, W.W., 2007. Neural substrates for episodic encoding and recognition of unfamiliar faces. *Brain Cogn.* 63 (2), 174–181. <https://doi.org/10.1016/j.bandc.2006.11.005>.
- Jacoby, L.L., Rhodes, M.G., 2006. False remembering in the aged. *Curr. Dir. Psychol. Sci.* 15 (2), 49–53. <https://doi.org/10.1111/j.0963-7214.2006.00405.x>.
- Jennings, J.M., Jacoby, L.L., 2003. Improving memory in older adults: training recollection. *Neuropsychol. Rehabil.* 13 (4), 417–440. <https://doi.org/10.1080/09602010244000390>.
- Johnson, M.K., Raye, C.L., 1981. Reality monitoring. *Psychol. Rev.* 88 (1), 67–85.
- Kensinger, E.A., Schacter, D.L., 1999. When true memories suppress false memories: effects of ageing. *Cogn. Neuropsychol.* 16 (3–5), 399–415. <https://doi.org/10.1080/026432999380852>.
- Kim, H., Cabeza, R., 2007. Trusting our memories: dissociating the neural correlates of confidence in veridical versus illusory memories. *J. Neurosci.* 27 (45), 12190–12197. <https://doi.org/10.1523/JNEUROSCI.3408-07.2007>.
- Kirchhoff, B.A., Anderson, B.A., Barch, D.M., Jacoby, L.L., 2012a. Cognitive and neural effects of semantic encoding strategy training in older adults. *Cereb. Cortex* 22 (4), 788–799.
- Kirchhoff, B.A., Anderson, B.A., Smith, S.E., Barch, D.M., Jacoby, L.L., 2012b. Cognitive training-related changes in hippocampal activity associated with recollection in older adults. *NeuroImage* 62 (3), 1956–1964.
- Koen, J.D., Hauck, N., Rugg, M.D., 2019. The relationship between age, neural differentiation, and memory performance. *J. Neurosci.* 39 (1), 149–162. <https://doi.org/10.1523/JNEUROSCI.1498-18.2018>.
- Koen, J.D., Rugg, M.D., 2019. Neural differentiation in the aging brain. *Trends Cogn. Sci.* 23 (7), 547–559. <https://doi.org/10.1016/j.tics.2019.04.012>.
- Koustaal, W., Reddy, C., Jackson, E.M., Prince, S., Cendan, D.L., Schacter, D.L., 2003. False recognition of abstract versus common objects in older and younger adults: testing the semantic categorization account. *J. Exp. Psychol. Learn., Mem., Cogn.* 29 (4), 499–510. <https://doi.org/10.1037/0278-7393.29.4.499>.
- Koustaal, W., 2003. Older adults encode—but do not always use—perceptual details. *Psychol. Sci.* 14 (2), 189–193.
- Koustaal, W., Schacter, D.L., Galluccio, L., Stofer, K.A., 1999. Reducing gist-based false recognition in older adults: encoding and retrieval manipulations. *Psychol. Aging* 14 (2), 220–237.
- Koustaal, W., Schacter, D.L., 1997. Gist-based false recognition of pictures in older and younger adults. *J. Mem. Lang.* 37 (4), 555–583. <https://doi.org/10.1006/jmla.1997.2529>.

- Kubota, Y., Toichi, M., Shimizu, M., Mason, R.A., Findling, R.L., Yamamoto, K., Calabrese, J.R., 2006. Prefrontal hemodynamic activity predicts false memory—a near-infrared spectroscopy study. *NeuroImage* 31 (4), 1783–1789. <https://doi.org/10.1016/j.neuroimage.2006.02.003>.
- Kurkela, K.A., Dennis, N.A., 2016. Event-related fMRI studies of false memory: an activation likelihood estimation meta-analysis. *Neuropsychologia* 81, 149–167. <https://doi.org/10.1016/j.neuropsychologia.2015.12.006>.
- Lee, H., Samide, R., Richter, F.R., Kuhl, B.A., 2019. Decomposing Parietal Memory Reactivation to Predict Consequences of Remembering. *Cereb. Cortex* 29 (8), 3305–3318. <https://doi.org/10.1093/cercor/bhy200>.
- Lindsay, D.S., Johnson, M.K., 2000. False memories and the source monitoring framework reply to Reyna and Lloyd (1997). *Learn. Individ. Differ.* 12 (2), 145–161.
- Lundstrom, B.N., Ingvar, M., Petersson, K.M., 2005. The role of precuneus and left inferior frontal cortex during source memory episodic retrieval. *NeuroImage* 27 (4), 824–834. <https://doi.org/10.1016/j.neuroimage.2005.05.008>.
- Lundstrom, B., Petersson, K.M., Anderson, J., Johansson, M., Fransson, P., Ingvar, M., 2003. Isolating the retrieval of imagined pictures during episodic memory: activation of the left precuneus and left prefrontal cortex. *NeuroImage* 20 (4), 1934–1943. <https://doi.org/10.1016/j.neuroimage.2003.07.017>.
- Luo, L., Craik, F.I.M., 2009. Age differences in recollection: specificity effects at retrieval. *J. Mem. Lang.* 60 (4), 421–436. <https://doi.org/10.1016/j.jml.2009.01.005>.
- Lustig, C., Shah, P., Seidler, R., Reuter-Lorenz, P.A., 2009. Aging, training, and the brain: a review and future directions. *Neuropsychol. Rev.* 19 (4), 504–522. <https://doi.org/10.1007/s11065-009-9119-9>.
- Lyle, K.B., Johnson, M.K., 2007. Source misattributions may increase the accuracy of source judgments. *Mem. Cogn.* 35 (5), 1024–1033. <https://doi.org/10.3758/BF03193475>.
- McCabe, D.P., Roediger III, H.L., McDaniel, M.A., Balota, D.A., 2009. Aging reduces veridical remembering but increases false remembering: neuropsychological test correlates of remember-know judgments. *Neuropsychologia* 47 (11), 2164–2173. <https://doi.org/10.1016/j.neuropsychologia.2008.11.025>.
- McDonough, I.M., Gallo, D.A., 2013. Impaired retrieval monitoring for past and future autobiographical events in older adults. *Psychol. Aging* 28 (2), 457–466. <https://doi.org/10.1037/a0032732>.
- McDonough, I.M., Haber, S., Bischof, G.N., Park, D.C., 2015. The synapse project: engagement in mentally challenging activities enhances neural efficiency. *Restor. Neurol. Neurosci.* 33 (6), 865–882. <https://doi.org/10.3233/RNN-150533>.
- McDonough, I.M., Wong, J.T., Gallo, D.A., 2013. Age-related differences in prefrontal cortex activity during retrieval monitoring: testing the compensation and dysfunction accounts. *Cereb. Cortex* 23 (5), 1049–1060. <https://doi.org/10.1093/cercor/bhs064>.
- Mitchell, K.J., Ankudowich, E., Durbin, K.A., Greene, E.J., Johnson, M.K., 2013. Age-related differences in agenda-driven monitoring of format and task information. *Neuropsychologia* 51 (12), 2427–2441. <https://doi.org/10.1016/j.neuropsychologia.2013.01.012>.
- Mitchell, K.J., Johnson, M.K., Raye, C.L., Mather, M., D'Esposito, M., 2000. Aging and reflective processes of working memory: binding and test load deficits. *Psychol. Aging* 15 (3), 527–541.
- Mitchell, K.J., Johnson, M.K., 2009. Source monitoring 15 years later: what have we learned from fMRI about the neural mechanisms of source memory? *Psychol. Bull.* 135 (4), 638–677. <https://doi.org/10.1037/a0015849>.
- Multhaup, K.S., 1995. Aging, source, and decision criteria: when false fame errors do and do not occur. *10* (3), 492.
- Norman, K.A., Schacter, D.L., 1997. False recognition in younger and older adults: exploring the characteristics of illusory memories. *Mem. Cogn.* 25 (6), 838–848. <https://doi.org/10.3758/BF03211328>.
- Nyberg, L., Sandblom, J., Jones, S., Neely, A.S., Petersson, K.M., Ingvar, M., Bäckman, L., 2003. Neural correlates of training-related memory improvement in adulthood and aging. *Proc. Natl. Acad. Sci.* 100 (23), 13728–13733. <https://doi.org/10.1073/pnas.1735487100>.
- Okado, Y., Stark, C., 2003. Neural processing associated with true and false memory retrieval. *Cogn. Affect. Behav. Neurosci.* 3 (4), 323–334. <https://doi.org/10.3758/CABN.3.4.323>.
- Olesen, P.J., Westerberg, H., Klingberg, T., 2004. Increased prefrontal and parietal activity after training of working memory. *Nat. Neurosci.* 7 (1), 75–79.
- Oosterhof, N.N., Connolly, A.C., Haxby, J.V., 2016. CoSMoMVA: multi-modal multivariate pattern analysis of neuroimaging data in Matlab/GNU octave. *Front. Neuroinform.* 10, 27. <https://doi.org/10.3389/fninf.2016.00027>.
- Op de Beeck, H.P., 2010. Against hyperacuity in brain reading: spatial smoothing does not hurt multivariate fMRI analyses? *NeuroImage* 49 (3), 1943–1948. <https://doi.org/10.1016/j.neuroimage.2009.02.047>.
- Park, J., Carp, J., Hebrank, A., Park, D.C., Polk, T.A., 2010. Neural specificity predicts fluid processing ability in older adults. *J. Neurosci.* 30 (27), 9253–9259. <https://doi.org/10.1523/JNEUROSCI.0853-10.2010>.
- Park, D.C., Puglisi, J.T., Sovacool, M., 1984. Picture memory in older adults: effects of contextual detail at encoding and retrieval. *J. Gerontol.* 39 (2), 213–215. <https://doi.org/10.1093/geronj/39.2.213>.
- Park, D.C., Reuter-Lorenz, P., 2009. The adaptive brain: aging and neurocognitive scaffolding. *Annu. Rev. Psychol.* 60 (1), 173–196. <https://doi.org/10.1146/annurev.psych.59.103006.093656>.
- Pezdek, K., 1987. Memory for pictures: a life-span study of the role of visual detail. *Child Dev.* 58 (3), 807–815.
- Quamme, J.R., Weiss, D.J., Norman, K.A., 2010. Listening for recollection: a multi-voxel pattern analysis of recognition memory retrieval strategies. *Front. Hum. Neurosci.* 61. <https://doi.org/10.3389/fnhum.2010.00061>.
- Rahhal, T.A., May, C.P., Hasher, L., 2002. Truth and character: sources that older adults can remember. *Psychol. Sci.* 13 (2), 101–105. <https://doi.org/10.1111/1467-9280.00419>.
- Ramanan, S., Piguet, O., Irish, M., 2018. Rethinking the role of the angular gyrus in remembering the past and imagining the future: the contextual integration model. *Neuroscientist* 24 (4), 342–352. <https://doi.org/10.1177/1073858417735514>.
- Rebok, G.W., Ball, K., Guey, L.T., Jones, R.N., Kim, H.-Y., King, J.W., Marsiske, M., Morris, J.N., Tennstedt, S.L., Unverzagt, F.W., Willis, S.L., for the ACTIVE Study Group, 2014. Ten-year effects of the advanced cognitive training for independent and vital elderly cognitive training trial on cognition and everyday functioning in older adults. *J. Am. Geriatr. Soc.* 62 (1), 16–24. <https://doi.org/10.1111/jgs.12607>.
- Roediger, H.L., McDermott, K.B., 1995. Creating false memories: remembering words not presented in lists. *J. Exp. Psychol. Learn. Mem. Cogn.* 21 (4), 803–814. <https://doi.org/10.1037/0278-7393.21.4.803>.
- Roediger, H.L., Watson, J.M., McDermott, K.B., Gallo, D.A., 2001. Factors that determine false recall: a multiple regression analysis. *Psychon. Bull. Rev.* 8 (3), 385–407. <https://doi.org/10.3758/BF03196177>.
- Roheger, M., Kalbe, E., Corbett, A., Brooker, H., Ballard, C., 2020. Lower cognitive baseline scores predict cognitive training success after 6 months in healthy older adults: Results of an online RCT. *Int. J. Geriatr. Psychiatry* 35 (9), 1000–1008. <https://doi.org/10.1002/gps.5322>.
- Roheger, M., Meyer, J., Kessler, J., Kalbe, E., 2020. Predicting short- and long-term cognitive training success in healthy older adults: who benefits? *Aging. Neuropsychol. Cogn.* 27 (3), 351–369. <https://doi.org/10.1080/13825585.2019.1617396>.
- Ross, L.A., Freed, S.A., Edwards, J.D., Phillips, C.B., Ball, K., 2016. The Impact of Three Cognitive Training Programs on Driving Cessation Across 10 Years: A Randomized Controlled Trial. *Gerontologist* 57 (5), 838–846. <https://doi.org/10.1093/geront/gnw143>.
- Rugg, M.D., 2004. In: Gazzaniga, M.S. (Ed.), *Retrieval Processing in Human Memory: Electrophysiology and fMRI Evidence*, 3rd ed. MIT Press.
- Rugg, M.D., Fletcher, P.C., Chua, P.M.-L., Dolan, R.J., 1999. The role of the prefrontal cortex in recognition memory and memory for source: an fMRI study. *NeuroImage* 10 (5), 520–529. <https://doi.org/10.1006/nimg.1999.0488>.
- Rugg, M.D., Henson, R.N.A., Robb, W.G.K., 2003. Neural correlates of retrieval processing in the prefrontal cortex during recognition and exclusion tasks. *Neuropsychologia* 41 (1), 40–52. [https://doi.org/10.1016/S0028-3932\(02\)00129-X](https://doi.org/10.1016/S0028-3932(02)00129-X).
- Rugg, M.D., King, D.R., 2018. Ventral lateral parietal cortex and episodic memory retrieval. *Cortex* 107, 238–250. <https://doi.org/10.1016/j.cortex.2017.07.012>.
- Schacter, D.L., Buckner, R.L., Koutstaal, W., Dale, A.M., Rosen, B.R., 1997. Late onset of anterior prefrontal activity during true and false recognition: an event-related fMRI study. *NeuroImage* 6 (4), 259–269. <https://doi.org/10.1006/nimg.1997.0305>.
- Schacter, D.L., Curran, T., Galluccio, L., Milberg, W.P., Bates, J.F., 1996. False recognition and the right frontal lobe: a case study. *Neuropsychologia* 34 (8), 793–808. [https://doi.org/10.1016/0028-3932\(95\)00165-4](https://doi.org/10.1016/0028-3932(95)00165-4).
- Schacter, D.L., Norman, K.A., Koutstaal, W., 1998. The cognitive neuroscience of constructive memory. *Annu. Rev. Psychol.* 49 (1), 289–318.
- Schacter, D.L., Slotnick, S.D., 2004. The cognitive neuroscience of memory distortion. *Neuron* 44 (1), 149–160. <https://doi.org/10.1016/j.neuron.2004.08.017>.
- Schiff, S., Egglefield, D.A., Motter, J.N., Grinberg, A., Rushia, S.N., Rutherford, B.R., Sneed, J.R., 2021. Who benefits from computerized cognitive training? Lower processing speed predicts greater cognitive improvement. *J. Affect. Disord. Rep.* 5, 100149. <https://doi.org/10.1016/j.jadr.2021.100149>.
- Shaw, J.S., Hosseini, S.M.H., 2021. The Effect of Baseline Performance and Age on Cognitive Training Improvements in Older Adults: A Qualitative Review. *J. Prev. Alzheimers Dis* 8, 100–109. <https://doi.org/10.14283/jpad.2020.55>.
- Sommer, V.R., Fandakova, Y., Grandy, T.H., Shing, Y.L., Werkle-Bergner, M., Sander, M.C., 2019. Neural pattern similarity differentially relates to memory performance in younger and older adults. *J. Neurosci.* 39 (41), 8089–8099. <https://doi.org/10.1523/JNEUROSCI.0197-19.2019>.
- Spaniol, J., Bayen, U.J., 2005. Aging and conditional probability judgments: a global matching approach. *Psychol. Aging* 20 (1).
- Sprague, B.N., Freed, S.A., Webb, C.E., Phillips, C.B., Hyun, J., Ross, L.A., 2019. The impact of behavioral interventions on cognitive function in healthy older adults: A systematic review. *Ageing Res. Rev.* 52, 32–52. <https://doi.org/10.1016/j.arr.2019.04.002>.
- Stephan-Otto, C., Siddi, S., Senior, C., Muñoz-Samons, D., Ochoa, S., Sánchez-Laforga, A.M., Brébion, G., 2017. Visual imagery and false memory for pictures: a functional magnetic resonance imaging study in healthy participants. *PLOS ONE* 12 (1), e0169551. <https://doi.org/10.1371/journal.pone.0169551>.
- Strobach, T., Karbach, J. (Eds.), 2021. *Cognitive Training: An Overview of Features and Applications*. Springer International Publishing, p. 5. <https://doi.org/10.1007/978-3-030-39292-9>.
- Thomas, A.K., Bulevich, J.B., 2006. Effective cue utilization reduces memory errors in older adults. *Psychol. Aging* 21 (2), 379–389. <https://doi.org/10.1037/0882-7974.21.2.379>.
- Tibon, R., Fuhrmann, D., Levy, D.A., Simons, J.S., Henson, R.N., 2019. Multimodal integration and vividness in the angular gyrus during episodic encoding and retrieval. *J. Neurosci.* 39 (22), 4365–4374. <https://doi.org/10.1523/JNEUROSCI.2102-18.2018>.
- Trelle, A.N., Carr, V.A., Guerin, S.A., Thieu, M.K., Jayakumar, M., Guo, W., Nadiadwala, A., Corso, N.K., Hunt, M.P., Litovsky, C.P., Tanner, N.J., Deutsch, G.K., Bernstein, J.D., Harrison, M.B., Khazenon, A.M., Jiang, J., Sha, S.J., Fredericks, C.A., Rutt, B.K., Wagner, A.D., 2020. Hippocampal and cortical mechanisms at retrieval explain variability in episodic remembering in older adults. *eLife* 9, e55335. <https://doi.org/10.7554/eLife.55335>.

- Trimble, M.R., Cavanna, A.E., 2008. Chapter 3.7 The role of the precuneus in episodic memory (Elsevier). *Handb. Behav. Neurosci.* 18, 363–377. [https://doi.org/10.1016/S1569-7339\(08\)00220-8](https://doi.org/10.1016/S1569-7339(08)00220-8).
- Tun, P.A., Wingfield, A., Rosen, M.J., Blanchard, L., 1998. Response latencies for false memories: gist-based processes in normal aging. *Psychol. Aging* 13 (2), 230.
- Turney, I.C., Dennis, N.A., 2017. Elucidating the neural correlates of related false memories using a systematic measure of perceptual relatedness. *NeuroImage* 146, 940–950. <https://doi.org/10.1016/j.neuroimage.2016.09.005>.
- Velanova, K., Lustig, C., Jacoby, L.L., Buckner, R.L., 2007. Evidence for frontally mediated controlled processing differences in older adults. *Cereb. Cortex* 17 (5), 1033–1046. <https://doi.org/10.1093/cercor/bhl013>.
- Volz, K.G., Schubotz, R.I., Cramon, D.Y.V., 2005. Variants of uncertainty in decision-making and their neural correlates. *Brain Res. Bull.* 67 (5), 403–412. <https://doi.org/10.1016/j.brainresbull.2005.06.011>.
- Von Zerssen, G.C., Mecklinger, A., Opitz, B., Von Cramon, D.Y., 2001. Conscious recollection and illusory recognition: an event-related fMRI study. *Eur. J. Neurosci.* 13 (11), 2148–2156. <https://doi.org/10.1046/j.0953-816x.2001.01589.x>.
- Webb, C.E., Dennis, N.A., 2019. Differentiating true and false schematic memories in older adults. *J. Gerontol. Ser. B* 74 (7), 1111–1120. <https://doi.org/10.1093/geronb/gby011>.
- Webb, C.E., Turney, I.C., Dennis, N.A., 2016. What's the gist? The influence of schemas on the neural correlates underlying true and false memories. *Neuropsychologia* 93, 61–75. <https://doi.org/10.1016/j.neuropsychologia.2016.09.023>.
- Willis, S.L., 1990. Introduction to the special section on cognitive training in later adulthood. *Dev. Psychol.* 26 (6), 875–878.
- Yassa, M.A., Lacy, J.W., Stark, S.M., Albert, M.S., Gallagher, M., Stark, C.E.L., 2001. Pattern separation deficits associated with increased hippocampal CA3 and dentate gyrus activity in nondemented older adults. *Hippocampus* 21 (9), 968–979.
- Zeithamova, D., De Araujo Sanchez, M.-A., Adke, A., 2017. Trial timing and pattern-information analyses of fMRI data. *NeuroImage* 153, 221–231. <https://doi.org/10.1016/j.neuroimage.2017.04.025>.
- Zysset, S., Wendt, C.S., Volz, K.G., Neumann, J., Huber, O., Von Cramon, D.Y., 2006. The neural implementation of multi-attribute decision making: a parametric fMRI study with human subjects. *NeuroImage* 31 (3), 1380–1388. <https://doi.org/10.1016/j.neuroimage.2006.01.017>.