



Neural Reinstatement of Overlapping Memories in Young and Older Adults

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Abstract

■ When we update our episodic memories with new information, mnemonic competition between old and new memories may result because of the presence of shared features. Behavioral studies suggest that this competition can lead to proactive interference, resulting in unsuccessful memory updating, particularly for older adults. It is difficult with behavioral data alone to measure the reactivation of old, overlapping memories during retrieval and its impact on memory for new memories. Here, we applied encoding–retrieval representational similarity (ERS) analysis to EEG data to estimate event-specific encoding-related neural reinstatement of old associations during the retrieval of new ones and its impact on memory for new associations in young and older adults. Our results showed that

older adults' new associative memory performance was more negatively impacted by proactive interference from old memories than that of young adults. In both age groups, ERS for old associative memories was greater for trials for which new associative memories were forgotten than remembered. In contrast, ERS for new associative memories was greater when they were remembered than forgotten. In addition, older adults showed relatively attenuated target (i.e., new associates) and lure (i.e., old associates) ERS effects compared to younger adults. Collectively, these results suggest that the neural reinstatement of interfering memories during retrieval contributes to proactive interference across age, whereas overall attenuated ERS effect in older adults might reflect their reduced memory fidelity. ■

INTRODUCTION

Previous literature suggests that episodic memory capacity is typically reduced with age (Lindenberger & Ghisletta, 2009; Grady & Craik, 2000; Craik & Jennings, 1992; for reviews, see Mitchell & Johnson, 2009; Old & Naveh-Benjamin, 2008). Age-related deficits in episodic memory, including associative memory, may be at least partially explained by the inhibition deficit theory, which states that older adults are less efficient at inhibiting irrelevant information (Hasher & Zacks, 1988). In the case of proactive interference, for example, previous information that is no longer relevant, information interferes with the encoding and retrieval of new information. Struggling to remember a recently changed account password because of interference from the previous one is an example of how proactive interference manifests in the real world. Prior research has shown that older adults are more susceptible to proactive interference than are young adults across a range of memory tasks in both working memory (Lustig & Jantz, 2015; Emery, Hale, & Myerson, 2008; Bowles & Salthouse, 2003; Lustig, May, & Hasher, 2001) and episodic memory (Wahlheim, 2014; Healey, Hasher, & Campbell, 2013; McDonough & Gallo, 2013; Ikier, Yang, & Hasher, 2008) domains.

Episodic memory impairments have often been observed in tests of associative memory, in which the

ability to learn and remember the relationship between multiple items, such as words, objects, faces, and so forth, is assessed (reviewed in Old & Naveh-Benjamin, 2008). It is not clear, however, that older adults are more susceptible to proactive interference in associative memory than are young adults. That is, the results of previous studies are somewhat mixed in that some found no age differences in the susceptibility to proactive interference (Corbett & Duarte, 2020; Dulas & Duarte, 2016; Guez & Naveh-Benjamin, 2016), whereas others reported greater susceptibility in older adults than young adults (Burton, Lek, Dixon, & Caplan, 2019; Ebert & Anderson, 2009; Jacoby, Bishara, Hessels, & Toth, 2005). In associative memory, specifically, competition between similar or overlapping events can occur, and this mnemonic competition may be a primary reason why sought-after associations are forgotten (Kuhl, Rissman, Chun, & Wagner, 2011). Therefore, to understand how young and older adults' associative memory is impacted by previous, overlapping memories coming to mind, it is important to measure the degree of mnemonic competition between old and new associations. Typically, mnemonic competition is inferred from disruptions in behavioral performance such as lowered memory accuracy or longer RTs (Healey et al., 2013; Wahlheim, 2011; Anderson, 1983). However, fMRI studies have estimated neural representations of competition between overlapping memories more directly by applying multivoxel pattern analysis (Kuhl, Bainbridge, & Chun, 2012; Kuhl et al., 2011). For instance,

Kuhl et al. (2012) manipulated competition between memories with an A–B/A–C associative learning task. Specifically, participants first learned A–B, word–picture, pairs followed by A–C pairs, which shared the same word but with a new picture. During retrieval, participants were presented the studied words and asked to recall the picture most recently associated with them (A–C pairs). Using multivariate pattern analysis to covertly measure the degree of neural reactivation associated with old (A–B) and new (A–C) memories during retrieval, they found stronger reactivation of old, overlapping, memories for memory intrusions than for correct A–C decisions. This evidence indicates that mnemonic competition induced by the reactivation of older memories during attempts to retrieve new ones has a negative impact on memory performance.

However, no previous studies have examined the role of age on the neural competition between overlapping memories. Here, to address this gap, we examined how neural reactivation of old and new memories during retrieval impacts memory performance in young and older adults. A modified version of the A–B/A–C paired associative learning task was used in which participants studied objects paired with face or scene associates. The level of interference was manipulated by increasing the number of A–B pair repetitions. During retrieval, participants were asked to choose which associate category and specific associate within that category was most recently paired with the object. EEG was recorded to measure spontaneous neural reactivation of old associations during attempts to retrieve new associations.

To date, most memory reactivation studies have relied on fMRI data to identify reactivation in the hippocampus (e.g., van den Honert, McCarthy, & Johnson, 2016) and ventral occipitotemporal, visual association cortices and its impact on memory performance (e.g., Gordon, Rissman, Kiani, & Wagner, 2014; Kuhl et al., 2011, 2012). However, because of relatively low temporal resolution of fMRI, little is known about the temporal patterns of mnemonic reactivation. With EEG, we can examine the similarity between oscillatory or voltage activity that distinguishes subsequently correct from incorrect memories in different encoding periods and retrieval activity for the same as well as different periods, letting us understand temporal dynamics of the reinstatement of both old (lure) and new (target) memories. For instance, Zhang, Fell, and Axmacher (2018) identified stimulus-specific neural reinstatement from both early (100–500 msec) and late (~500 msec) poststimulus periods and found that only late period effects were related to memory performance. The authors suggested that the later part of the reinstatement is related to “deeper” semantic processing, which can support recognition of the stimuli. Jafarpour, Fuentemilla, Horner, Penny, and Duzel (2014), applying multivariate classification to magnetoencephalography (MEG) data, found that face and scene stimuli could be decoded early during encoding (~200 msec) and that this activity was

reinstated around 500 msec after retrieval cue. Sustained mnemonic reactivation (~500 msec) has been linked with postretrieval processes including maintenance or monitoring of retrieved information (Johnson, Price, & Leiker, 2015; Jafarpour et al., 2014). Collectively, these EEG/MEG studies suggest that perceptual reinstatement of encoded memories can begin early during retrieval whereas later reinstatement may reflect cognitive control processes such as semantic elaboration and postretrieval monitoring.

In the current study, we applied representational similarity analysis (Kriegeskorte, Mur, & Bandettini, 2008) to time–frequency EEG signals to measure the trial-specific similarity between both the oscillatory neural activity measured during encoding of A–B (old/lure) and A–C (new/target) pairings and the oscillatory activity measured during A–C pair retrieval. Using a spatio-temporal pattern similarity approach (Lu, Wang, Chen, & Xue, 2015), we could determine the specific periods of encoding activity that were reinstated and for which periods during retrieval as well as the spatial locations and frequency bands (i.e., alpha, beta, theta) in which these reinstatement effects were observed. A number of previous studies show that oscillatory power in different frequency bands is related to episodic memory performance (see Hanslmayr & Staudigl, 2014, for a review). For example, increased theta power (4–8 Hz) during encoding (Staudigl & Hanslmayr, 2013; Hanslmayr et al., 2011) and retrieval (Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013) predicts successful memory performance, consistent with the idea that theta reflects the activity of the hippocampo-cortical feedback loop (Klimesch, 1999). Similarly, alpha (8–12 Hz) and beta (14–30 Hz) desynchronization have been related to better episodic memory, especially when the task requires semantic elaboration (Fellner, Bauml, & Hanslmayr, 2013; Hanslmayr, Spitzer, & Bauml, 2009).

As Kuhl et al. (2012) showed in their previous study, if trial-specific reinstatement of older, interfering memories contributes to memory intrusions, then higher trial-specific encoding–retrieval similarity (ERS) between lure associate encoding and retrieval should predict worse memory for target associations. At the same time, studies not including mnemonic lures have shown that neural similarity between encoding and retrieval can support successful recognition or recollection of the event (Trelle et al., 2020; Yaffe, Shaikhouni, Arai, Inati, & Zaghoul, 2017; Wing, Ritchey, & Cabeza, 2015; Ritchey, Wing, LaBar, & Cabeza, 2013; Staresina, Henson, Kriegeskorte, & Alink, 2012). Therefore, we predict that greater trial-specific similarity between target associate encoding and retrieval supports better memory of targeted associates. However, whether older adults also show these ERS patterns remains as an open question. If older adults are more susceptible to proactive interference because they cannot properly inhibit the lure information (Hasher & Zacks, 1988), lure ERS might be greater in older than younger adults. On the other hand, as some previous studies have

shown reduced neural reinstatement in older adults (Trelle et al., 2020; Bowman, Chamberlain, & Dennis, 2019; McDonough, Cervantes, Gray, & Gallo, 2014; St-Laurent, Abdi, Bondad, & Buchsbaum, 2014) and that weaker reinstatement is related to lower memory performance (Trelle et al., 2020), we can predict overall lower ERS in older adults.

METHODS

Participants

On the basis of previous studies, we expected a small-to-medium effect size (Cohen's $f = 0.25-0.5$) for interaction between memory interference and age groups. With the expectation of minimum effect size (Cohen's $f = 0.25$) in this range, the a priori power analysis with G*Power 3.1.9.4 (Faul, Erdfelder, Buchner, & Lang, 2009) indicated that a total sample size of 36, 18 for each age group, is needed with a power of 0.90 at $\alpha = .05$ in a 3 (interference) \times 2 (age groups) repeated-measures ANOVA. Here, to account for data loss because of noise, performance, or participant attrition, we recruited 30 younger adults (18 women, ages 18–35 years) and 25 older adults (12 women, ages 65–77 years). All participants were right-handed and had normal or corrected-to-normal vision. Participants with neurological or psychological conditions were excluded. Data collected from three younger adults and two older adults were excluded because of technical failures, including loss of data (two younger adults) and unstable reference channel connection during recording (one younger adult, two older adults). Data from two younger adults whose EEG data were extremely noisy because of sweat-related drift resulting in more than 50% of trials being rejected were not included. In addition, data collected from one younger adult and one older adult whose memory performance was 2.5 SDs below the group mean were not used in the analysis.

Participants completed a standardized neurological battery (Montreal Cognitive Assessment) and were excluded if their score was lower than 23 of 30. Given this criterion, no participants were excluded. Although the traditional cutoff score for this assessment is 26 of 30, several studies have suggested that this cutoff does not fairly evaluate the

cognitive function of individuals with different educational, cultural, and racial backgrounds (Carson, Leach, & Murphy, 2018; Sink et al., 2015; Manly, 2005). Our samples were recruited to reflect the racial/ethnic diversity of the local community. A recently conducted meta-analysis reported that a cutoff score of 23 of 30 reveals the best diagnostic accuracy (Carson et al., 2018). Therefore, we utilized this cutoff score for our exclusionary criteria. In the analysis presented, 24 young adults and 22 older adults were included. The demographic information of the included participants is presented in Table 1. Participants were compensated with institutional course credits or \$15 per hour. All participants signed consent forms approved by the Georgia Institute of Technology Institutional Review Board.

Materials

The stimuli consisted of 216 pictures of nameable objects, eight pictures of face (four women and four men), and eight pictures of scenes (four indoor and four outdoor). The pictures of objects were taken from Hemera Technologies Photo-Objects DVDs or from Creative Commons. The pictures of faces were taken from the Max Planck Institute's FACES database (Ebner, Riediger, & Lindenberger, 2010), and the scene images were taken from the SUN database (Xiao, Hays, Ehinger, Oliva, & Torralba, 2010). Each object was paired with either a face or a scene, and all images were presented against a gray background.

Associative Memory Task

The associative memory task included three phases: encoding, retrieval, and postretrieval (see Figure 1A). In the encoding phase, objects were repeatedly paired with either faces or scenes under varying levels of interference. In the retrieval and postretrieval phases, participants were asked to memorize the most recent (target) associate each object was paired with. EEG data were collected during encoding and retrieval, but only results from the encoding period will be presented here.

The encoding phase consisted of four encoding blocks. In each encoding block, participants studied 216 objects

Table 1. Group Demographic Information of Participants

Measure	Young ($n = 24$)	Old ($n = 22$)
Age	23.6 (4.12)	69.04 (4.85)
Sex	13 female	11 female
Education	16.25 (1.81)	17.55 (2.50)
MoCA	28.48 (1.65)	26.68 (2.28)
Race/ethnicity	10 NHW, 3 BL/AA, 8 NHA, 3 UNK	13 NHW, 7 BL/AA, 2 UNK

Standard deviations are in parentheses. BL/AA = Black/African American; MoCA = Montreal Cognitive Assessment; NHW = not Hispanic White; NHA = not Hispanic Asian; UNK = unknown.



Figure 1. Experimental design. (A) Illustration of encoding, retrieval, and postretrieval tasks. (B) Three interference conditions. The no-interference condition has four target presentations. The low-interference condition has three targets and one lure presentation. For the high-interference condition, lure is presented in the first two encoding blocks and then target was presented in the last two blocks.

paired with either a face or a scene, under different levels of proactive interference. The lateral position of objects and the associate (i.e., face or scene) were counterbalanced across participants. As shown in Figure 1B, objects were evenly divided into three proactive interference conditions: the high-interference, low-interference, and no-interference conditions (72 objects per each condition). For the high-interference condition, the object was paired with one of the associates (i.e., a specific face) for the first two blocks and paired with another associate from the other category (i.e., a specific scene) for the last two blocks. As an example, in Figure 1, the headphone

was paired with the office scene for encoding Blocks 1 and 2 and then paired with the male face for Blocks 3 and 4. In this case, the male face, which is paired with the object in the latest block, is the target associate, whereas the office is the lure associate for the headphone. For the low-interference condition, the object was paired with the target associate for three blocks and paired with the lure associate from the other category for one other block. The presentation of lure associates can occur in one of the first three blocks. Because of a systematic error, 10 young adults and 20 older adults underwent 60 valid trials in the low-interference

condition. For the no-interference condition, the object was paired with only one associate from a single category for all four blocks, meaning there were no lure associates for the no interference trials (see Figure 1B). Before beginning the last encoding block, participants were informed that their memory would later be tested for the associations presented in that block only. With each pair presented in the encoding phase, participants indicated the difficulty or ease with which they imagined the object and the associate together on a 3-point scale. The response was recorded by a keypad where 1 = *easy*, 2 = *medium*, and 3 = *hard*. Each encoding block lasted for 15 min.

After the fourth encoding block was completed, the retrieval phase was initiated. In this phase, participants' memory for the 216 studied associations was tested. For each trial, an object was presented in the center of the screen and the participants were asked to select the most recent target associate category (face or scene) from the fourth block of encoding for the object. Half of the participants were asked to respond with "1" if the object was most recently paired with a face and "2" if the object was most recently paired with a scene. The other half of the participants were asked to respond with "1" if the object was most recently paired with a scene and "2" if the object was most recently paired with a face. Each trial was presented on the screen for 3000 msec, and the retrieval phase lasted 15 min.

Upon completing the retrieval phase and the Montreal Cognitive Assessment screening, participants began the postretrieval phase. In this phase, participants were again tested on all 216 studied objects. The postretrieval test was designed to evaluate more specific memories of the pairings. This task was split up into three blocks, with each block consisting of 72 trials, to lower the participants' fatigue level. For each trial, participants were presented with an object in the center of the screen. While the object was displayed, they were first asked to decide what associate category (i.e., face or scene) the object was most recently paired with (in the fourth block of encoding). Then, the participants were asked about specific details of the associate depending on which category was chosen. For example, if the participants answered "face" for the first question, they were then asked whether the face was "female" or "male." Likewise, if the participant answered "scene" for the first question, they were subsequently asked whether the scene was "indoor" or "outdoor." The third question involved asking the participants to identify exactly which face or scene (depending on which category was chosen) the presented object was most recently paired with from a selection of choices. For example, if the participants responded with "male" for the second question, they were then presented with the four male faces they were shown throughout the encoding phase and asked to choose a specific one. Each trial was presented on the screen for 3000 msec. However, if the participant entered a response earlier, they

were able to advance to the next question. Each of the three blocks lasted up to 12 min.

For memory performance, to assess interference and age-group differences for the general memory of the pairings, we calculated general memory accuracy for each interference condition as the percentage of responses in which the participant correctly identified the target category at retrieval. For specific memory performance, the percentage of correct specific memory responses (i.e., participants correctly select the exact associate [specific face or specific scene] the object was most recently paired with) was calculated for each interference condition. For all behavioral analyses, significant interactions at an alpha (α) level of .05 were followed up with subsidiary ANOVAs and *t* tests to determine the source of the effects. Where appropriate, reported *p* values were corrected using Huynh–Feldt corrections.

EEG Recording and Preprocessing

Continuous scalp-recorded EEG data were collected during encoding and retrieval from 128 Ag–AgCl electrodes using an ActiveTwo amplifier system (BioSemi). Left and right mastoid electrodes were used for offline rereferencing. Four additional facial electrodes were placed to record horizontal and vertical eye movements: Two electrodes placed superior and inferior to the right eye recorded vertical EOG, and two additional electrodes recorded horizontal EOG at the lateral canthi of the left and right eyes. The sampling rate of the EEG was 1024 Hz.

Offline preprocessing of the EEG data was done in MATLAB 2017b with the EEGLAB toolbox (Delorme & Makeig, 2004). First, the continuous data were downsampled to 256 Hz, referenced to the average of the left and right mastoid electrodes. The data were band-pass filtered between 0.5 and 100 Hz, and 60-Hz line noise was removed by using the PREP plugin (Bigdely-Shamlo, Mullen, Kothe, Su, & Robbins, 2015) in EEGLAB. Then, the data were epoched from –1000 msec before stimulus onset to 3500 msec. The time range of interest was from –500 to 2500 msec, but a longer epoch was required to compensate for the signal loss at both edges of the epoch during wavelet transform. First, extremely noisy epochs were visually inspected and rejected. On average, 5% of the epochs were rejected in this step. Then, independent component analysis was used to correct eye-movement artifacts. Components related to blinks and horizontal eye movements were detected based on visual inspection of topographic component maps and omitted from the data (Hoffmann & Falkenstein, 2008; Delorme, Sejnowski, & Makeig, 2007; Bell & Sejnowski, 1995). If noisy channels were identified with an automatic bad channel detection (i.e., above 5 *SDs* in spectral power) or visual inspection, they were removed and interpolated using the surrounding channels and 2.7 (*SD* = 3.7) channels were interpolated as an average. In addition, automated epoch rejection was conducted by rejecting epochs containing

voltage shifts (± 150 mV). After preprocessing, the average number of trials for each block in younger and older adults was as follows: younger: $M = 183.65$, $SD = 29.95$; older: $M = 195.18$, $SD = 21.99$.

Time-Frequency Analyses

After the preprocessing, each epoch was converted into the time-frequency domain using the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The frequency decomposition was performed using Morlet wavelets (Percival & Walden, 1993) with linearly spaced frequencies between 2 and 80 Hz, at 5 cycles. During the wavelet transformation, each epoch was reduced to the time range of interest (-500 to 2500 msec) and down-sampled to 50.25 Hz. The frequencies of interest were defined as theta ($4-8$ Hz), alpha ($8-12$ Hz), and beta ($12-30$ Hz). The gamma band was excluded from our analysis, because a number of previous studies have demonstrated that scalp-recorded gamma-band responses to visual stimuli can be contaminated by microsaccadic eye movement artifact (reviewed in Schwartzman & Kranczioch, 2011; Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008).

Representational Similarity Analyses

In this study, EEG data converted into spectral power were analyzed using representational similarity analysis

(Kriegeskorte et al., 2008). First, for every single trial from each participant, the spectral power of each frequency band was averaged across frequencies within the frequency band: theta ($4-8$ Hz), alpha ($8-12$ Hz), and beta ($12-30$ Hz). The electrodes were divided into six brain regions, which were left frontal, right frontal, left central, right central, left posterior, and right posterior (see Figure 2). The spectral power of each frequency band was then averaged across the electrodes within each of the aforementioned scalp regions to increase power and decrease the number of comparisons. Finally, spectral power for each frequency band was temporally segmented using a 210 -msec (12 -time-points) sliding window with a 75 -msec step size. Thus, each 2.5 -sec trial had 29 time bins. With this method, for each of the three frequency bands, every trial was associated with a spectral power vector for each of six scalp regions and 29 time bins. As each vector represents the spectral power within each spatial and temporal segment, we refer to them as spatio-temporal power vectors. To calculate the neural similarity between encoding and retrieval trials, spatio-temporal power vectors for every time bin of the encoding trial were correlated with those from every time bin of the retrieval trial for each frequency band and brain region, separately. This approach allowed us to examine the neural similarity between all combinations of time bins (Sommer et al., 2019). As a result, each pair of compared trials produced 3 (frequency bands) \times 6 (brain regions) \times 29 (time bins in

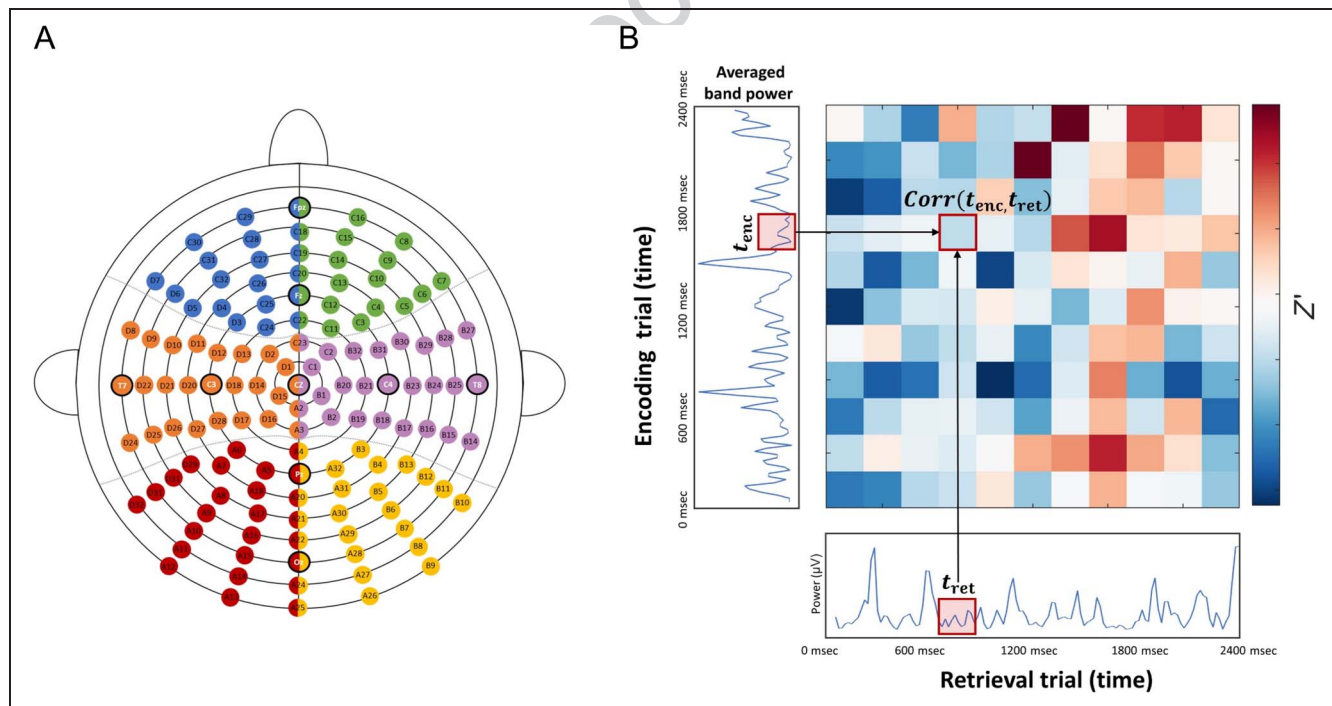


Figure 2. RSA methodology. (A) One hundred twenty-eight electrodes are divided into six brain regions: left frontal, right frontal, left central, right central, left posterior, and right posterior. (B) Similarity matrices between lure (or target) encoding and retrieval. Spectral power is averaged from each frequency band and each brain region separately. These averaged power vectors are temporally segmented into 29 time bins using a 210 -msec sliding window with a 75 -msec step size. Pearson correlations are calculated [indicated by $Corr(t_{enc}, t_{ret})$] between power vectors in a time bin from the retrieval trials (t_{ret}) and the lure or target encoding trials (t_{enc}). Power vectors from every time bin of the lure encoding trial are correlated with those from every time bin of the retrieval trial.

the encoding trial) \times 29 (time bins in the retrieval trial) similarity matrices. Finally, these similarity matrices were converted into Fisher's z scores for further analysis.

To estimate trial-specific similarity, we computed within-trial similarity and between-trial similarity first. Within-trial similarity was computed as similarity between spatio-temporal power vectors for a retrieval trial and spatio-temporal power vectors for its matched trial during encoding (i.e., both trials consisted of the "headphone" as an object). Between-trial similarity was computed as the average similarity between the spatio-temporal power vectors for a trial at retrieval and the spatio-temporal power vectors of all other trials during the encoding block. Between-trial similarity was separately calculated for the target-correct trials and target-incorrect trials, such that memory success did not influence between-trial similarity values. In addition, to ensure that our RSA result can capture the trial-specific reinstatement, rather than category-level reinstatement, the between-trial similarity was calculated separately for the face and scene trials (i.e., similarity between a correctly retrieved face-target trial and all other face-target correct trials). Finally, trial-specific similarity was computed as the difference between within-trial similarity and between-trial similarity. By using this contrast, we can assume that trial-specific similarity only reflects the neural reinstatement that occurred during that specific event, as global ERS that can be impacted by general cognitive mechanisms shared across trials as well as noncognitive factors such as individual differences in oscillatory power are removed.

To estimate the degree of lure reactivation during retrieval, we calculated the trial-specific similarity between the trials in the retrieval block and trials in the lure encoding block. Specifically, to address the relationship between trial-specific lure reactivation and subsequent memory performance (correct vs. incorrect) under proactive interference, we focused on the high-interference condition because it was the only condition that had a sufficient number of correct and incorrect trials for all participants. It is worth noting that most of the participants had a smaller number of incorrect trials compared to the correct trials. Some previous RSA studies with small and/or unbalanced numbers of trials have tried to deal with this issue by excluding participants with small numbers of trials (e.g., Zeithamova, de Araujo Sanchez, & Adke, 2017; Tomparry, Duncan, & Davachi, 2016; Kuhl & Chun, 2014) or artificially equating the number of trials across conditions by subsampling (e.g., Sommer et al., 2019; Dimsdale-Zucker, Ritchey, Ekstrom, Yonelinas, & Ranganath, 2018). Especially, Dimsdale-Zucker et al. (2018) proved that their RSA results were not greatly influenced by trial counts by showing consistent RSA results before and after implementing subsampling control. Thus, we also conducted two additional, control analyses to examine if our RSA results were influenced by low trial counts and/or imbalance between conditions. First, we excluded seven participants with the lowest number of incorrect trials (less than

six trials) and reconducted the RSA. Second, within a participant, we randomly subsampled correct trials to use equal numbers of trials across conditions and reestimated the similarity values. These additional controls did not change the pattern of our results, showing that our results were not biased by either low trial counts or trial imbalance between conditions. Here, we reported the original RSA results that used all of the usable trials and participants. We utilized the first lure encoding block, rather than the second lure encoding block, to reduce any potential influence of stimulus-related repetition suppression, in which neural activity is attenuated when stimuli are repeated (Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008; Grill-Spector, Henson, & Martin, 2006; Miller, Li, & Desimone, 1991). However, we utilized the last encoding block as the target encoding block, rather than the third encoding block, because participants were informed that their memory for the target associations presented in the last/fourth block would later be tested. Therefore, we assumed that target reinstatement during retrieval would be biased toward processing from the last encoding block.

In addition, to examine whether the reactivation of target associations supported subsequent target memory performance, trial-specific target similarity was calculated as well. We used high-interference trials in the fourth encoding (i.e., target-encoding) block and the trials in the retrieval block to calculate within- and between-trial similarities. Again, the trial-specific target similarity was computed as "within-trial similarity – between-trial similarity." Finally, the obtained trial-specific lure similarity and trial-specific target similarity matrices were averaged according to subsequent memory performance (i.e., target correct vs. target incorrect). As a result, each participant had two sets of trial-specific similarity matrices (trial-specific lure similarity and trial-specific target similarity), respectively, for target-correct and target-incorrect (lure intrusion) trials. To reduce the repeated wording, the term "target similarity" refers to the trial-specific target similarity and "lure similarity" means the trial-specific lure similarity, from this point onward in the article.

To determine whether target-incorrect (i.e., lure intrusion) trials showed greater lure reactivation than target-correct trials, we ran a paired t test comparing lure similarity for target-correct trials and target-incorrect trials. In the same way, we also tested the differences in the target similarity matrices between target-correct and target-incorrect trials. Because the paired t test was repeated on every 3 (frequency bands) \times 6 (scalp regions) \times 29 (time bins in encoding) \times 29 (time bins in retrieval) elements in the similarity matrices, multiple-comparison correction was done using nonparametric cluster-based permutation test. Nonparametric cluster-based permutation test (Maris & Oostenveld, 2007) in Fieldtrip toolbox was used. First, a statistical test (i.e., paired t test) was performed for every element in the similarity matrices, and the statistical values (t values) that

exceeded a threshold ($p = .05$) were selected and clustered based on the spatial and temporal adjacency. Then, the cluster-level test statistic was calculated by summing the t values within a cluster. To produce a referential distribution for the cluster-level test statistic, the Monte-Carlo method was utilized. The condition labels of similarity matrices (i.e., target correct or target incorrect) were shuffled 5000 times, and the maximum cluster statistic from each permutation was selected to make a null distribution of the cluster-level statistics. Finally, we ranked the observed cluster-level statistic in the distribution constructed by the permutation. In this study, the clusters whose p values fell below .025 for each tail were reported as statistically significant. If a significant cluster was identified after the multiple-comparison correction, further group-level comparisons were conducted with the mean similarity values averaged across the obtained cluster.

RESULTS

Behavioral Results

We were interested in the effect of age and level of proactive interference on general associative memory. This was calculated as the proportion of responses in which the participant correctly endorsed the target category (face or scene) during retrieval, where 50% is chance. Performance was significantly above chance for each interference level and age group ($t_s > 9.636, p_s < .001$). A 2 Age (young, old) \times 3 Interference Level (high, low, no) ANOVA conducted on general memory accuracy revealed a main effect of Age, $F(1, 44) = 15.373, p < .001, \eta_p^2 = .259$, a main effect of Interference, $F(2, 88) = 103.132, p < .001, \eta_p^2 = .701$, and an interaction of Age \times Interference, $F(2, 88) = 4.239, p = .026, \eta_p^2 = .088$. As can be seen in Figure 3, across interference levels, younger adults showed higher general memory accuracy compared to older adults.

Follow-up pairwise comparisons indicated that participants remembered associations better under no-interference conditions than under high-interference, $t(45) = 14.121, p < .001$, and low-interference, $t(45) = 8.357, p < .001$, conditions. General memory performance was also better for low-interference than high-interference trials, $t(45) = 6.228, p < .001$. As depicted in Figure 3, the Age \times Interference interaction reflects older adults' disproportionate memory impairment under high-interference conditions when compared to that of young adults. To assess the effect of age and level of proactive interference on memory for the specific details of the associations, we calculated the percentage of responses for which the participant correctly chose the specific target associate during postretrieval (i.e., if the object was paired with a forest and the participant chose "scene" at the first question, then "outdoor" in the second question and then chose "forest" among four different outdoor scenes in the third question). Chance is 6.25% for specific memory decisions because participants had to decide between two options for the general target category question, between two options for the subcategory question (indoor/outdoor, male/female), and, finally, between four options for the specific associate question during postretrieval. These percentages are displayed in Figure 3. Performance was significantly above chance for each interference level and age group ($t_s > 4.831, p_s < .001$). We additionally examined the specific memory performance when calculated for each of the postretrieval questions independently (i.e., first question: 50% chance with face vs. scene; second question: 50% chance with female vs. male; third question: 25% chance with Females 1–4). Both young and older adults performed above the chance for each level of interference ($t_s > 3.36, p_s < .01$). A 2 Age (young, old) \times 3 Interference (high interference, low interference, no interference) ANOVA was conducted. We observed main effects of Age, $F(1, 44) = 15.148, p < .001, \eta_p^2 = .256$,

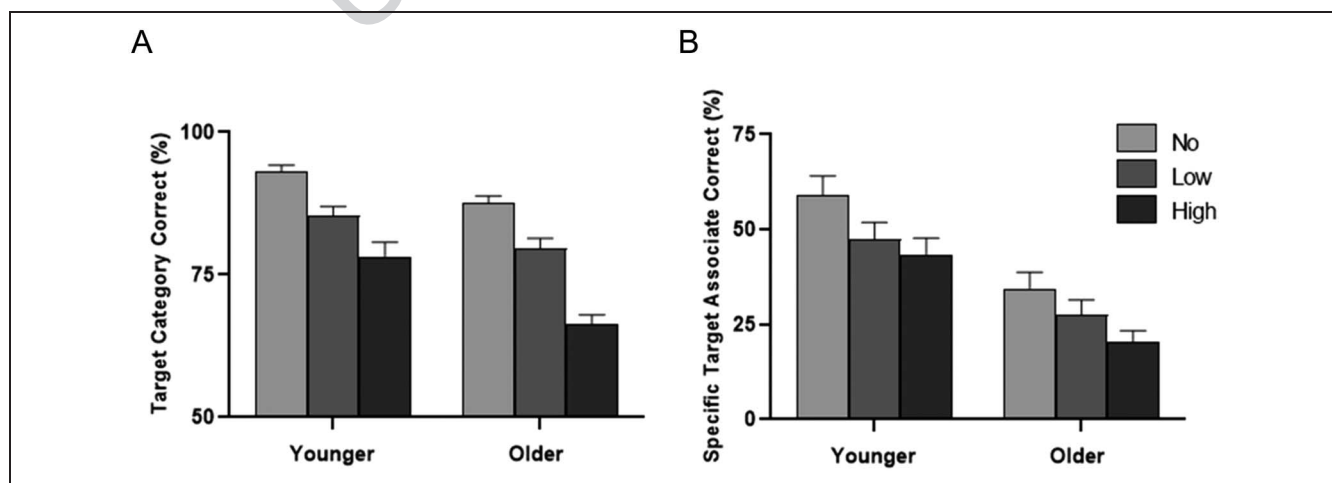


Figure 3. Associative memory accuracy. (A) The mean percentage of correct responses for target category separated by interference condition, for young and older adults. (B) The mean percentage of correct responses for the specific target associate separated by interference condition, for young and older adults. Error bars represent the SEM.

and Interference, $F(2, 88) = 71.725, p < .001, \eta_p^2 = .620$, but no Age \times Interference interaction, $F(2, 88) = 1.761, p = .18, \eta_p^2 = .038$. An estimated Bayes factor (alternative/null) for the Age \times Interference interaction effect suggested that data were 0.344 times more likely to occur under the alternative than the null. Younger adults demonstrated better specific memory performance than older adults, and participants remembered associations better for no interference than high-interference, $t(45) = 10.321, p < .001$, and low-interference, $t(45) = 7.377, p < .001$, conditions. Participants also showed better specific memory for low-interference than high-interference trials, $t(45) = 5.041, p < .001$.

Finally, we were interested in investigating whether proactive interference during target encoding impacted the specificity of the subsequent memory intrusions. More specifically, we wanted to determine whether participants would be more likely to choose the lure associate, presented during encoding, than the other incorrect scenes or faces, presented during postretrieval. The percentage of specific lure associate selection was calculated as the number of specific lure associates selected divided by the number of lure category intrusions made during postretrieval (i.e., “face” selected for a target scene trial). These percentages were only calculated for the high- and low-interference conditions as no-interference conditions did not include lures (Figure 4). The chance level was 12.5%, given that participants had to decide between two options for the subcategory question (indoor/outdoor, male/female) and between four options for the specific associate. Specific lure selection performance was significantly above chance for each interference level and age group ($ts > 4.556, ps < .001$). We additionally examined the specific lure memory performance when calculated for each of the postretrieval questions independently, as done for specific target memory above. Both

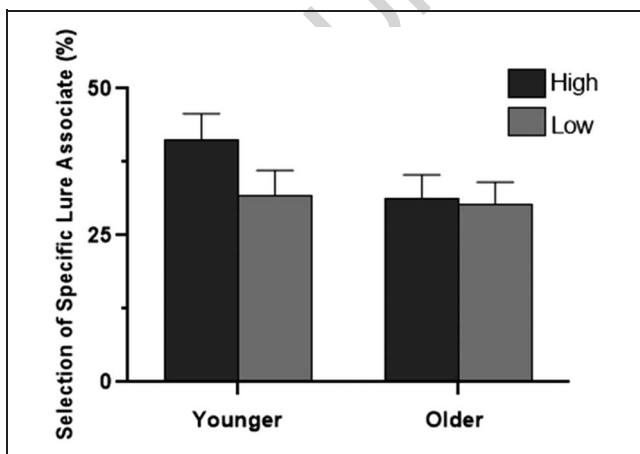


Figure 4. The mean percentage of specific lure associate selection in the postretrieval task. The percentage represents the number of specific lure associates selected divided by the number of target category incorrectly made during postretrieval. Error bars represent the SEM.

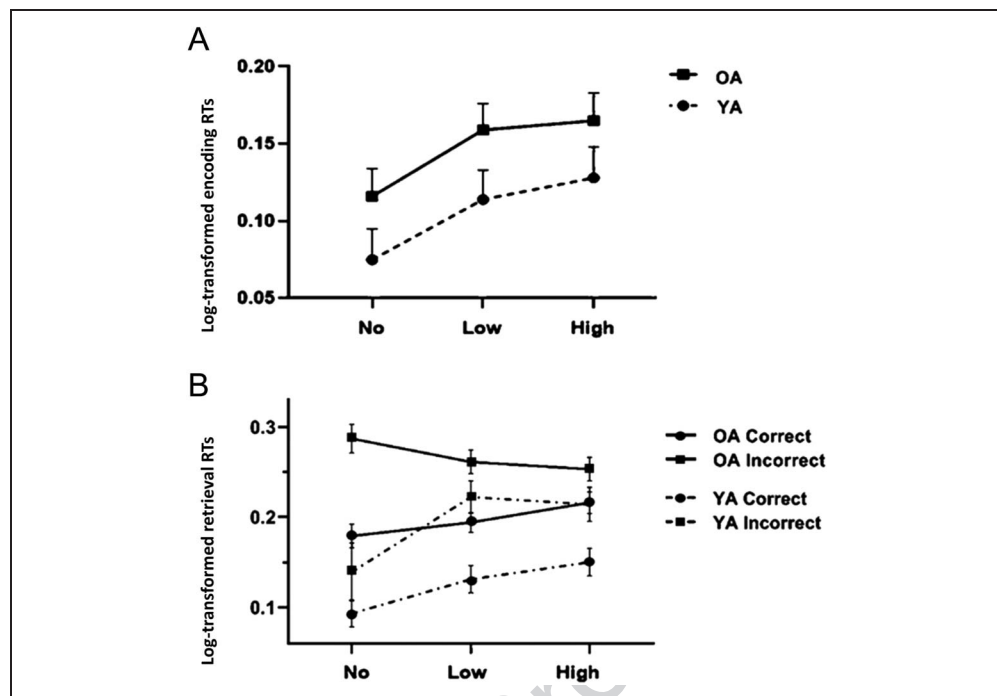
young and older adults selected the specific lure associates more often than chance when they were wrong in the first question ($ts > 3.86, ps < .01$). A 2 Interference (high, low) \times 2 Age (young, old) repeated-measures ANOVA revealed no significant effects (all $Fs < 3.427, ps > .07, \eta_p^2 < .072$). Given the estimated Bayes factor (alternative/null), there is weak evidence in favor of an absence of a main effect of Age (BF10 = 0.955), main effect of Interference (BF10 = 0.750), and an interaction between Age and Interference (BF10 = 0.808). These results confirm that, when young and older adults made memory intrusions, they were more likely to select the specific lure than other similar categorical lures.

RTs

To examine how RTs at encoding differed as a function of interference, memory performance, and age, we conducted a 3 Interference (high, low, no) \times 2 Memory Performance (target correct, target incorrect) \times 2 Age (young, old) repeated-measures ANOVA. Log-transformed RTs were used for the statistical testing to account for any multiplicative slowing effects of age (Faust, Balota, Spieler, & Ferraro, 1999). A main effect of Interference was observed, $F(2, 76) = 28.598, p < .001, \eta_p^2 = .429$, but no other effects were significant (all $Fs < 2.64, ps > .11, \eta_p^2 < .065$). Follow-up t tests showed that participants responded faster under the no-interference condition than the high-interference, $t(38) = 3.292, p = .002$, and low-interference, $t(38) = 2.111, p = .04$, conditions. No significant difference between RT for the high- and low-interference conditions was observed, $t(38) = 1.249, p = .218$. An estimated Bayes factor (alternative/null) for the main effect of age suggested that the data were 1.577 times more likely to occur under the alternative than the null, 0.150 times more likely for the Interference \times Age interaction, and 0.194 times more likely for the Memory \times Age interaction. These RTs, averaged across target-correct and target-incorrect responses, are shown in Figure 5A.

The same three-way ANOVA was conducted on log-transformed retrieval RTs. A main effect of Interference, $F(2, 78) = 13.320, p < .001, \eta_p^2 = .255$, a main effect of Memory Performance, $F(1, 39) = 83.018, p < .001, \eta_p^2 = .680$, and a main effect of Age, $F(1, 39) = 15.441, p < .001, \eta_p^2 = .284$, were significant. In addition, the interaction between Interference and Age, $F(2, 78) = 14.479, p < .001, \eta_p^2 = .271$, and a three-way interaction, $F(2, 78) = 6.710, p = .004, \eta_p^2 = .147$, were significant. For the effect of interference, follow-up t tests showed that RTs were faster for the no-interference condition than the high-interference, $t(40) = 3.341, p = .002$, and low-interference, $t(40) = 2.688, p = .01$, conditions. No significant difference between the high- and low-interference conditions was observed, $t(40) = 1.496, p = .142$. RTs were slower for incorrect trials than correct trials, and older adults' RT was slower than that of younger adults. The follow-up

Figure 5. (A) The mean log-transformed RT during target encoding separated by interference condition, for young and older adults. (B) The mean log-transformed RT during retrieval, separated by interference condition and memory performance for young and older adults. Error bars represent the SEM.



analysis for the three-way interaction reveals that the interaction between Interference \times Memory Performance was not significant in younger adults, $F(2, 36) = 1.728, p = .202, \eta_p^2 = .088$, whereas there was significant two-way interaction in older adults, $F(2, 42) = 11.939, p < .001, \eta_p^2 = .362$. As can be seen in Figure 5B, younger adults' RTs increased with higher interference, regardless of memory performance, whereas older adults showed longer RTs for higher interference correct trials only. These RTs are shown in Figure 5B.

RSA Results

One of our primary research interests was to examine whether trial-specific lure reactivation impacts the ability to successfully retrieve the updated target association category. Therefore, we compared lure similarity between target-correct and target-incorrect associative memory trials for general (i.e., categorical) retrieval. We conducted this analysis for the high-interference condition only, ensuring sufficient numbers of both target-correct and target-incorrect trials for each age group. Nonparametric cluster-based permutation test was applied to correct multiple comparisons.

We identified significant clusters (i.e., Monte Carlo p value $< .025$, for each tail) in the frontal regions from theta band ($p = .002$; 5000 permutations). In a time domain, the significant cluster was observed between 600 and 1200 msec at both encoding and retrieval trials. This cluster is shown in Figure 6A. Within this cluster, lure similarity was significantly greater for the incorrect than correct target trials. To compare the magnitude of this lure reactivation between age groups, we extracted the

Fisher's z -transformed Pearson correlation coefficients (i.e., trial-specific lure similarity value) for target-correct and target-incorrect trials from the identified cluster. The extracted trial-specific lure similarity values were averaged across the time bins within the cluster for each participant and for target-correct and target-incorrect trials separately. A Target Memory (target correct, target incorrect) \times Age (young, old) ANOVA revealed a main effect of Target Memory, $F(1, 44) = 39.885, p < .001, \eta_p^2 = .475$, a main effect of Age, $F(1, 44) = 8.261, p = .006, \eta_p^2 = .158$, and a significant interaction between Age and Target Memory, $F(1, 44) = 11.236, p = .002, \eta_p^2 = .203$. A follow-up independent t test revealed that the lure similarity difference between target-correct and target-incorrect trials was significantly greater in young adults than older adults, $t(44) = 3.352, p = .002$. These results suggest that lure reactivation was associated with a failure to correctly recover the target category across the age groups and that lure reinstatement was greater in younger compared to older adults.

We additionally compared target similarity between target-correct and target-incorrect trials using the same RSA procedure. After cluster-based permutation tests, significant clusters showing greater target similarity for target-correct than target-incorrect trials were identified from the alpha band over bilateral fronto-parietal scalp regions ($p = .023$, 5000 permutations). Temporally, the significant cluster was observed around 1100–1500 msec for both encoding and retrieval, which was later than the timing of the lure ERS cluster. This cluster is presented in Figure 6B. To compare these target RSA effects between age groups, we extracted the target similarity values (i.e., Fisher's z -transformed correlation coefficient) for target-correct and target-incorrect trials from the identified

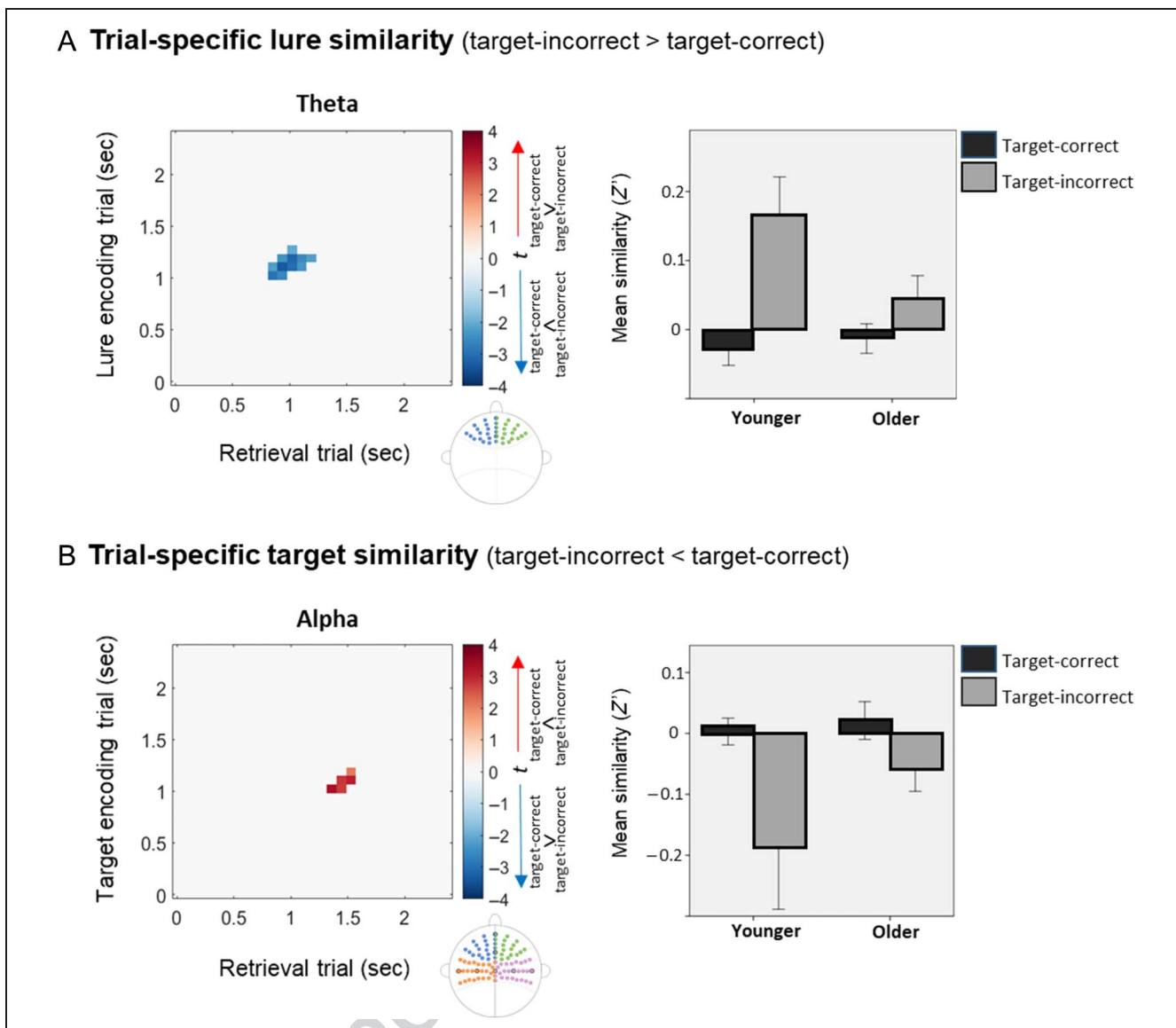


Figure 6. (A) ERS cluster in which lure similarity is significantly higher for target-incorrect trials than target-correct trials. The bar graph next to the cluster represents the mean lure similarity value for target-correct and target-incorrect trials in the identified clusters, separately for younger and older adults. (B) Significant cluster that shows greater target similarity for target-correct trials than that of target-incorrect trials. The bar graphs show the mean target similarity value for target-correct and target-incorrect trials in the identified clusters for each age group.

cluster and averaged these values across the time bins within the cluster for each participant. Target Memory (target correct, target incorrect) \times Age (young, old) ANOVA revealed a main effect of Target Memory, $F(1, 44) = 23.847, p < .001, \eta_p^2 = .351$, a main effect of Age, $F(1, 44) = 5.717, p = .021, \eta_p^2 = .115$, and an interaction between Target Memory and Age, $F(1, 44) = 4.058, p = .05, \eta_p^2 = .084$. A follow-up independent t test showed that the difference in target similarity between target-correct trials and target-incorrect trials was significantly greater in young adults than older adults, $t(44) = 2.071, p = .046$. These results suggest that target reactivation was associated with successful memory for the target category across the age groups and that the magnitude of this effect was greater in younger compared to older adults.

The above analyses showed that lure reactivation during attempts to retrieve target associations was greater for trials for which the lure category (i.e., face or scene) was incorrectly endorsed than for trials for which lures were rejected and targets were correctly remembered, whereas the opposite pattern was observed for target reactivation. However, it is not clear from these analyses if these reactivation patterns impact memory for the “specific” associate or only memory for the associate category (face vs. scene). To determine whether the level of trial-specific target and lure reactivation also contributed to specific associative memory performance measured during the postretrieval block, we divided high-interference trials into three levels based on participants’ specific memory performance: (1) specific-target correct, (2) general-target

correct, and (3) target incorrect. The specific-target correct trials are the trials for which participants correctly selected the specific target associate (e.g., specific male face) for a given object in the postretrieval task (see Figure 1). The general-target correct trials are the trials for which participants could successfully retrieve the target category (e.g., face) associated with the object but ended up failing to choose the specific target associate. Target incorrect trials are all trials for which participants selected the wrong target category. Four participants (two younger adults, two older adults) who had no specific-correct trials were excluded from this analysis. We extracted mean similarity values for specific-target-correct, general-target-correct, and target-incorrect trials from the ERS clusters identified in Figure 6. The mean similarity values for each specific-memory performance level are shown in Figure 7. A Specific Target Memory (specific-target correct, general-target correct, target incorrect) \times Age (young, old) ANOVA for trial-specific lure similarity values revealed a significant main effect of Specific Target Memory, $F(2, 80) = 4.832, p = .010, \eta_p^2 = .108$. None of the other effects were significant ($F_s < 0.502, p_s > .483, \eta_p^2_s < .012, BF10s < 0.268$). Follow-up pairwise comparisons indicated that lure similarity was greater for target-incorrect trials than both general-target-correct trials, $t(41) = 3.207, p = .003$, and specific-target-correct trials, $t(41) = 2.740, p = .009$. Lure similarity did not differ between general-target-correct trials and specific-target-correct trials, $t(41) = 0.867, p = .391$. On the other hand, Specific Target Memory (specific-target correct, general-target correct, target incorrect) \times Age (young, old)

ANOVA for the trial-specific target similarity showed no significant effect ($F_s < 0.755, p_s > .474, \eta_p^2_s < .019; BF10s < 0.302$).

DISCUSSION

This study aimed to investigate the effect of proactive interference on associative memory performance and to identify neural evidence of proactive interference during paired associate retrieval in young and older adults. Through the application of EEG-based RSA, we examined whether the neural reactivation of older, but not currently relevant, memories (i.e., lures) during the retrieval of new memories (i.e., targets) contributes to proactive interference effects on associative memory performance in young and older adults. We found that, although associative memory performance worsened as the level of proactive interference increased in both young and older adults, the negative impact was stronger in older adults. In addition, RSA results revealed that greater lure reactivation during new target associate retrieval was related to associative memory intrusions, whereas greater target reactivation supports associate memory for new memories across age groups. Moreover, we identified age group differences in the magnitude of trial-specific target and lure similarity pointing to an age difference in the fidelity of competing memories. The implications of these results are discussed below.

Behavioral Results

As predicted, associative memory accuracy for the general target category (i.e., face or scene) and the specific target associate (e.g., Male Face 2) worsened as the level of lure interference increased, in both young and older adults. This finding is consistent with previous results demonstrating the negative impact of proactive interference on associative memory performance (Corbett & Duarte, 2020; Dulas & Duarte, 2016; Yonelinas & Jacoby, 2012; Jacoby, Wahlheim, Rhodes, Daniels, & Rogers, 2010; Nee, Wager, & Jonides, 2007; Jacoby et al., 2005). These results suggest that higher interference from the lure associate can impair the subsequent retrieval of both categorical (face/scene) and trial-specific details of the target/new associate. Consistent with these accuracy results, RTs at encoding and retrieval increased as the level of interference increased. Such increases in RT have frequently been used as correlates of proactive interference in previous studies (see Jonides & Nee, 2006, for a review). This increase in RT likely reflects that the encoding and retrieval of the target/new association require more effortful processing under conditions, such as high interference, where lure associations are presented and strong. In addition to the age-related reduction in both general and specific associative memory across interference levels, there was a disproportionate impairment of general memory in high-interference trials. The lack of similar

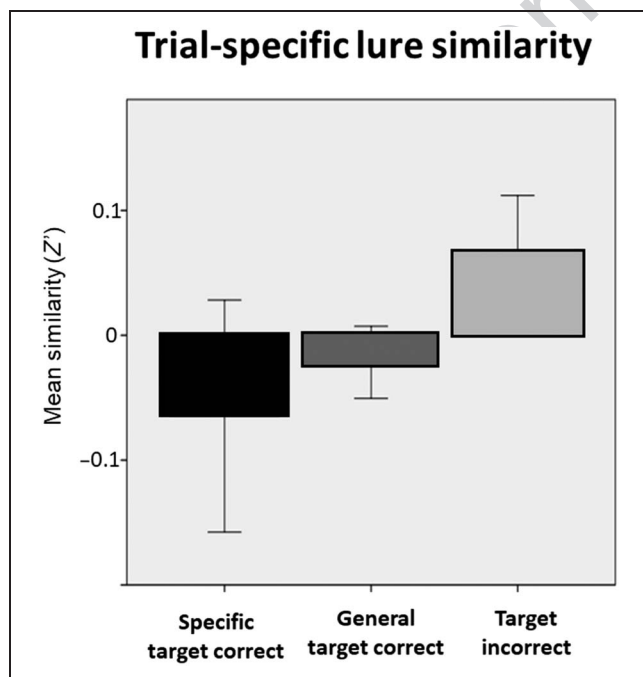


Figure 7. The mean lure similarity value within lure similarity cluster (see Figure 6A) for specific-target-correct, general-target-category-correct, and target-incorrect trials.

disproportionate susceptibility for specific associative memory could be related to the fact that specific memory performance was generally quite low and near chance for high-interference trials, obscuring any potential interactive effects of aging and interference.

Although age-related associative memory deficits have been found in numerous studies (Dulas & Duarte, 2011, 2012; Naveh-Benjamin, Brav, & Levy, 2007; Glisky, Rubin, & Davidson, 2001; Chalfonte & Johnson, 1996), evidence for disproportionate susceptibility to proactive interference in associative memory performance in aging has been mixed. More specifically, some previous associative memory studies reported that the impact of the proactive interference was similar for young and older adults (Corbett & Duarte, 2020; Dulas & Duarte, 2016; Guez & Naveh-Benjamin, 2016), whereas others found greater susceptibility in older adults (Burton et al., 2019; Ebert & Anderson, 2009; Jacoby et al., 2005). It is important to explore the potential explanations for this discrepancy. Increased susceptibility to proactive interference in older adults is more often found in studies employing cued recall designs than those employing associative recognition (see Rhodes, Greene, & Naveh-Benjamin, 2019, for a review). Furthermore, studies utilizing intentional encoding instruction tend to report age-related susceptibility to proactive interference more often, compared to the studies using elaborative encoding (e.g., “Is this a likely pairing?”; Glisky & Kong, 2008; Naveh-Benjamin et al., 2007; Glisky et al., 2001; Hay & Jacoby, 1999). Such task-related factors may serve to bolster older adults’ associative memory performance and reduce susceptibility to proactive interference. Nevertheless, neither of these factors can explain the greater negative impact of proactive interference on older adults in this study, as the task utilized both elaborative encoding instructions and paired associate recognition. Rather, we suspect that the sample of older participants is a potential contributing factor. More specifically, when recruiting older adults who are exceptionally healthy with little to no health problems that typically accompany increasing age, such as high blood pressure and diabetes, age differences in performance may be minimal. Although such participants are arguably not representative of the general older population (reviewed in Dotson & Duarte, 2020), they are recruited for many cognitive studies, particularly those involving neuroimaging. In fact, perhaps because of this sampling bias, two prior fMRI studies from our own laboratory with more particular exclusion criteria (e.g., no cardiovascular condition) failed to show increased susceptibility to proactive interference in associative memory for older adults (Corbett & Duarte, 2020; Dulas & Duarte, 2016), despite employing very similar task designs to that of this study. To avoid this sampling bias and increase the generalizability of the findings of this study, we did not exclude participants with cardiovascular and metabolic health conditions. Given the extensive research demonstrating the negative impact of such health problems on cognition

(see Stern & Carstensen, 2000, for a review), it is conceivable that older adults in fMRI and other cognitive studies with strict exclusionary criteria have fewer cognitive difficulties than older adults who better reflect the normal elderly population. The older participants in this study have generally good health without cognitive impairment and performed well above the chance level in the associative memory task even under the most challenging condition. However, compared to the younger adults, we believe these older adults were less able to engage the cognitive control processes necessary to resolve proactive interference to the same level as the younger adults. Collectively, these across-study discrepancies highlight the well-known interindividual differences in cognitive aging and the various factors that underlie them, including health (see Cabeza et al., 2018, for a review).

We have argued that different levels of mnemonic interference across conditions (i.e., high vs. low vs. no) reduced target encoding ability and subsequent categorical and specific target memory accuracy. It could also be argued that difficulty making recency decisions during retrieval contributes to reduced memory performance. We do not believe it is the sole contributor to memory performance, however. First, memory accuracy was lower for high-interference than low-interference conditions despite similar recency discrimination demands for these conditions. In addition, slower RTs for target associate encoding after lure associate encoding are more consistent with a mnemonic interference account than a recency discrimination one. Finally, across all age groups, when participants made intrusion errors, they were more likely to subsequently choose the specific lure associate than other face or scene lures during the postretrieval task. Collectively, these results support the idea that proactive interference hinders retrieval of new target across age and that the interfering memories retain specific details. Our EEG data, discussed below, further support the idea that the presence of old associates can interfere the retrieval of new associates.

RSA Results

By comparing ERS between oscillatory activity patterns associated with target and lure associations, we were able to determine if trial-specific lure ERS predicted worse target associative memory performance and the impact of age on this relationship. Indeed, lure ERS was greater for trials for which target associates were forgotten (and lures were incorrectly endorsed) than those for which the target category and the specific target associate were remembered across age. This result provides clear neural evidence of proactive interference as it shows the reinstatement of old associative memories can hinder the retrieval of new associations. These results are consistent with some previous neuroimaging studies showing that spontaneous memory reactivation elicited by overlapping events negatively influences associative memory

performance (Kuhl et al., 2011, 2012). For example, in one fMRI study examining mnemonic interference during paired associate retrieval of recent (target) associations, reactivation of old, face, scene, or object associations was greater for target-incorrect than target-correct trials (Kuhl et al., 2012). Similarly, a recent imaging study also reported that neural reinstatement of specific contextual information from an overlapping yet incorrect event during retrieval contributed to false memories (Carpenter, Thakral, Preston, & Schacter, 2021). This pattern was thought to signify currently irrelevant memories returning to the mind, thereby blocking access to recent target memories (Roediger & Neely, 1982). A similar argument could be made for the present data in that reactivation of old associations could have acted to block the ability to successfully retrieve newer ones. Collectively, these results seem to support the idea that keeping overlapping, potentially interfering, memories out of the mind allows for more effective encoding and retrieval of relevant memories (Anderson & Levy, 2002). To the best of our knowledge, this is the first study showing direct neural evidence of proactive interference in “both” young and older adults. Target ERS was greater for correct, both general (i.e., categorical) and specific target associate memory trials, than incorrect trials (i.e., lure intrusion). This result is consistent with neural models of episodic memory, which suggest that episodic retrieval engages the reinstatement of encoding-related neural activity (Norman & O’Reilly, 2003; McClelland, McNaughton, & O’Reilly, 1995; Alvarez & Squire, 1994; Kolers & Roediger, 1984). In addition, previous RSA studies have shown that event-specific reinstatement of encoding neural patterns is associated with successful episodic retrieval (Wing et al., 2015; Ritchey et al., 2013). For instance, Ritchey et al. (2013) applied RSA on fMRI data collected during encoding and retrieval of scenes and found greater ERS during successful compared to unsuccessful recognition.

Target and lure ERS effects were observed over the bilateral fronto-parietal scalp regions. Although most previous studies focused on item-specific neural reinstatement within visual cortex (Koen & Rugg, 2016; Wing et al., 2015; Ritchey et al., 2013; Staresina et al., 2012), likely reflecting recapitulation of perceptual features, reinstatement effects in fronto-parietal regions have also been observed (Xiao et al., 2017; Wing et al., 2015; St-Laurent et al., 2014; Ritchey et al., 2013). For instance, Wing et al. (2015) found that ERS in bilateral ventrolateral pFC (VLPFC) increased as a function of memory quality. This result was consistent with fMRI evidence of VLPFC contributions to episodic memory success at both encoding and retrieval phases (Kim, 2011; Prince, Dennis, & Cabeza, 2009; Spaniol et al., 2009). Wing et al. (2015) also suggested that ERS in the VLPFC might reflect reinstatement of cognitive control processes engaged during encoding. This seems a plausible explanation for the ERS effects in the current study, given that the associative memory task involved elaborative encoding and recency-based retrieval

under varying levels of mnemonic interference, which likely requires top-down control processes including selecting, maintaining, and updating relevant episodic features (Cabeza & St Jacques, 2007; Ranganath, Johnson, & D’Esposito, 2000; Rugg, Fletcher, Chua, & Dolan, 1999). pFC regions have also been implicated in detecting mnemonic competition (Kuhl et al., 2012; Kuhl, Dudukovic, Kahn, & Wagner, 2007; Norman, Newman, & Detre, 2007) and proactive interference (Dulas & Duarte, 2016; Nee, Jonides, & Berman, 2007; Badre & Wagner, 2005). Specifically, pFC activity sensitive to mnemonic competition has been suggested to support postretrieval selection and monitoring operations that evaluate the outcome of a retrieval attempt when multiple competing representations are active in memory (Dulas & Duarte, 2016; Badre & Wagner, 2007; Nee, Jonides, et al., 2007). Although it is difficult to pinpoint the underlying source of EEG activity, the fronto-parietal distribution of the ERS effects in this study is consistent with these cognitive control mechanisms.

Overall, the target and lure reinstatement effects were late onset and sustained (~500 msec), consistent with the time course of neural reinstatement in some previous studies (Staresina et al., 2019; Yaffe et al., 2014). A recent review (Staresina & Wimber, 2019) proposed that memory cue-related activity feeds into the hippocampus within 500 msec, followed by pattern completion (i.e., conversion of the partial cue to target). From ~500 msec, target memories are reinstated in the cortex via feedback loops from the hippocampus. Consistent with this neurobiological mechanisms, several EEG-based RSA (Zhang et al., 2018; Lu et al., 2015) and classification (Johnson et al., 2015; Jafarpour et al., 2014) studies showed stimulus-specific reinstatement effects sensitive to memory accuracy, particularly recollection, in late time points. The sustained time course of the reinstatement observed here, and in some previous studies (Johnson et al., 2015; Jafarpour et al., 2014), supports the idea that the products of neural reinstatement are subject to continued evaluation and postretrieval monitoring to make a recency or source judgment. Interestingly, target ERS effects were observed later than were lure ERS effects for high-interference trials. The temporal delay in ERS associated with target compared to lure memories is a likely reflection of the fact that target memories were weaker and likely harder to recover than were lures and their successful recover placed more demand on postretrieval operations.

The ERS effects observed here were evident in low-frequency bands including theta and alpha bands. Previous EEG, intracranial EEG, and MEG studies showed that activity in these frequency bands may contribute to episodic memory performance and reinstatement. For example, increased theta power (4–8 Hz) during encoding (Hanslmayr & Staudigl, 2014; Staudigl & Hanslmayr, 2013; Hanslmayr et al., 2011) and retrieval (Gruber et al., 2013) has been associated with successful recollection, and theta

oscillations are believed to reflect, in part, the interaction between hippocampus and neocortex during memory task (Gruber et al., 2018; Anderson, Rajagovindan, Ghacibeh, Meador, & Ding, 2010; Klimesch, 1999). In addition, some multivariate pattern analysis studies report higher similarity for remembered compared to forgotten words in the theta band (Schreiner, Doeller, Jensen, Rasch, & Staudigl, 2018) and content-specific temporal signatures of memory in theta range (Michelmann, Bowman, & Hanslmayr, 2016). More specifically, a recent study showed that the theta oscillation supports the formation of associative memory and stronger reinstatement is related to better recollection (Kota, Rugg, & Lega, 2020). Those findings proposed that the reinstatement in theta band might support greater fidelity of event-specific features. In addition, a number of empirical (Martín-Buro, Wimber, Henson, & Staresina, 2020; Fellner et al., 2013; Fell et al., 2011; Klimesch et al., 1996) and modeling (Parish, Hanslmayr, & Bowman, 2018) studies showed that alpha desynchronization during encoding and/or retrieval predicts episodic memory outcomes, suggesting desynchronization indicates amplified information processing. Recent studies also proposed that alpha frequencies are involved in neural reinstatement. For instance, Griffiths et al. (2021) found that alpha power decreases during encoding are reinstated during retrieval. In addition, Sutterer, Foster, Serences, Vogel, and Awh (2019) reported that alpha oscillations track the retrieval of spatial memories and the pattern of oscillatory activity during encoding is recapitulated during subsequent retrieval. On the basis of cumulative evidence showing the role of alpha frequency in selective attention and inhibition, the authors suggested that reinstatement in alpha might reflect the reinstatement of cognitive process (e.g., suppression of noise, sustained attention) supporting episodic memory (Griffiths, Martín-Buro, Staresina, Hanslmayr, & Staudigl, 2021; Sutterer et al., 2019). This interpretation is in line with the possibility that target reinstatement under high interference reflects greater cognitive control demands (e.g., postretrieval monitoring as discussed above). Collectively, these data, together with our results, demonstrate that oscillatory activity in low-frequency bands is related to the neural reinstatement supporting associative memory. Although those existing studies have been focused on young adults, we found that these trial-specific theta and alpha reinstatement effects are similar across both younger and older adults.

Although ERS effects were largely similar across age groups, there were some significant age-related differences as well. First, for trials for which younger adults endorsed the lure, they showed both greater lure ERS and less target ERS, compared to older adults. This result showed that, although younger adults experienced the mnemonic intrusion less frequently compared to older adults, lure memories can be richly reactivated while target memories were inhibited when intrusion occurred.

This ERS pattern is consistent with results of an fMRI study that found that mnemonic intrusions were characterized by a dominance of competitor reactivation and the absence of target reactivation in young adults (Kuhl et al., 2012). This pattern of results is in line with the idea that, when young adults experience mnemonic intrusions, strong, irrelevant memories may block access to target ones (Schacter, 1999; Anderson & Neely, 1996; Roediger & Neely, 1982).

In addition, both target and lure ERS differences between target-correct and target-incorrect trials were greater in younger than older adults (see Figure 6). Reduced event-specific ERS effects in older adults could be explained, in part, by neural dedifferentiation, in which neural distinctiveness between items or categories is reduced with age (Park et al., 2004, 2010, 2012; Carp, Park, Polk, & Park, 2011; Goh, Suzuki, & Park, 2010; Payer et al., 2006). Reduced neural distinctiveness between categories during encoding (Koen, Hauck, & Rugg, 2019; Koen & Rugg, 2019; Carp et al., 2011) and reduced reinstatement of encoded events in older adults (Trelle et al., 2020; Bowman et al., 2019; McDonough et al., 2014; St-Laurent et al., 2014) have been observed in prior imaging studies. For example, Hill, King, and Rugg (2021) reported that older adults showed reduced ERS for scenes compared to younger adults and suggested that age-related increases in neural dedifferentiation during encoding could account for this age-related reduction in ERS. Those findings support the idea that older adults have less fine-grained representations of events during encoding and, in turn, cannot effectively utilize perceptual details during retrieval (Daselaar, Fleck, & Cabeza, 2006; Koutstaal, 2003). It is worth noting that neural distinctiveness between scene and face categories (i.e., classification accuracy) was insensitive to age in our study (younger: 72.08%; older: 71.96%), $t(44) = 0.112, p = .91$. Thus, it seems unlikely that reduced neural distinctiveness between associate categories can fully account for age group differences in ERS.

The reduced ERS effects could potentially be explained by a reduced recollection but spared familiarity-based recognition account of age-related memory impairment (for reviews, see Koen & Yonelinas, 2014; Schoemaker, Gauthier, & Pruessner, 2014). It has been proposed that successful recollection is associated with reinstatement of neural patterns elicited when the recollected information was encoded (Xue, 2018; Rugg, Johnson, & Uncapher, 2015; Rissman & Wagner, 2012; Danker & Anderson, 2010; Johnson & Rugg, 2007; Nyberg, Habib, McIntosh, & Tulving, 2000; Wheeler, Petersen, & Buckner, 2000). Considering that trial-specific ERS magnitude differences between correct and incorrect trials were smaller in older than younger adults, we can infer that, even when older adults chose the correct target associate, their choice may have more often depended on familiarity rather than recollection of event-specifying contextual details compared to young adults. This explanation is also

supported by older adults' further compromised specific associative memory. Inconsistent with our prediction that older adults, who are more susceptible to interference, might show greater lure ERS than young adults, lure reinstatement was lower for older compared to young adults. This result points to the distinction between the "frequency" of mnemonic intrusions and the "magnitude" of reinstatement of intrusive memories. That is, although older adults made more memory intrusions, the fidelity of the interfering memory was lower than for young adults. In line with this finding, Carpenter and Schacter (2018b) reported that older adults showed fewer source memory errors than did young adults in an associative inference paradigm. That is, because of more successful associative inference (A–C memories) from overlapping events (AB, BC), young adults showed greater source misattribution than did older adults (Carpenter & Schacter, 2017, 2018a). The authors speculated that, even when older adults successfully infer the relationship between overlapping events, they reactivate less-rich/high-fidelity contextual details of the AB and BC events than do younger adults, reducing the overall number of source failures. Our target and lure ERS results provide direct support for the idea that older adults show reduced fidelity of both new/target and old/lure memories, which, in our study, likely contributes to their worse memory performance.

There are some limitations in this study. First, because of a coding error (see Methods), 12 of 72 trials in the low-interference condition presented an unintended associate in one of the encoding blocks. Therefore, those invalid trials were excluded from analysis. Although we found that there was no memory performance difference between participants who had 72 or 60 low-interference trials, it is difficult to fully rule out the potential impact of disproportionate number of trial counts on participants' behavior. Second, although we had different levels of proactive interference conditions (i.e., high, low, no), we were unable to compare the neural reinstatement of lures in mnemonic intrusion trials across interference conditions, because of lack of incorrect trials in the low- and no-interference conditions. Thus, we cannot examine how neural reinstatement of lures differed by level of proactive interference.

In summary, the current study revealed that older adults' associative memory is disproportionately susceptible to proactive interference. With RSA, we could estimate neural reinstatement of old (lure) associations during the retrieval of new ones and found that greater lure reinstatement is associated with memory intrusions and greater target reinstatement is associated with successful memory decisions, across age groups. Collectively, our findings suggest that neural reactivation of interfering memories contributes to subsequent mnemonic intrusions across age, but overall reinstatement effects, for old and new associative memories, are attenuated in older adults, which may reflect reduced memory fidelity.

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Kyoungun Lee: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing—Original draft. Soroush Mirjalili: Data curation; Methodology; Software. Ayesha Quadri: Data curation; Investigation; Visualization; Writing—Review & editing. Brittany Corbett: Conceptualization; Investigation; Software. Audrey Duarte: Conceptualization; Funding acquisition; Project administration; Resources; Supervision; Writing—Review & editing.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were $M(\text{an})/M = .407$, $W(\text{oman})/M = .32$, $M/W = .115$, and $W/W = .159$, the comparable proportions for the articles that these authorship teams cited were $M/M = .549$, $W/M = .257$, $M/W = .109$, and $W/W = .085$ (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: $M/M = .611$, $W/M = .124$, $M/W = .097$, and $W/W = .168$.

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