

Holding On to the Past: Older Adults Show Lingering Neural Activation of No-Longer-Relevant Items in Working Memory

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Abstract

■ Goal-relevant information can be maintained in working memory over a brief delay interval to guide an upcoming decision. There is also evidence suggesting the existence of a complementary process: namely, the ability to suppress information that is no longer relevant to ongoing task goals. Moreover, this ability to suppress or inhibit irrelevant information appears to decline with age. In this study, we compared younger and older adults undergoing fMRI on a working memory task designed to address whether the modulation of neural representations of relevant and no-longer-relevant items during a delay interval is related to age and overall task performance. Following from the theoretical predictions of the inhibitory deficit hypothesis of aging, we hypothesized that older adults would show higher activation of no-longer-relevant

items during a retention delay compared to young adults and that higher activation of these no-longer-relevant items would predict worse recognition memory accuracy for relevant items. Our results support this prediction and more generally demonstrate the importance of goal-driven modulation of neural activity in successful working memory maintenance. Furthermore, we showed that the largest age differences in the regulation of category-specific pattern activity during working memory maintenance were seen throughout the medial temporal lobe and prominently in the hippocampus, further establishing the importance of “long-term memory” retrieval mechanisms in the context of high-load working memory tasks that place large demands on attentional selection mechanisms. ■

INTRODUCTION

In our daily interactions with the world, we are faced with a continual stream of information, only a small part of which we can capture and retain. To effectively cope with this sensory onslaught, one may effectively regulate attention by boosting the processing of relevant information and suppressing the processing of irrelevant information. Such attentional regulation can be deployed to objects both in the external environment and also “inwardly”—that is, to the current contents of working memory (Baddeley & Hitch, 1974). Thus, representations of items stored in working memory should be enhanced when they are relevant to current goals and suppressed (or deleted) when they become irrelevant.

Behavioral research has shown that individuals differ widely on their ability to remember items after a retention delay, and some of this variability can be explained by individual differences in resistance to distraction (Gazzaley, 2011; Cowan & Morey, 2006; Lustig, May, & Hasher, 2001). Moreover, older people tend to show lower memory performance compared to younger adults, especially on memory tasks that involve distraction (Light & Singh, 1987; Hasher & Zacks, 1979). In fact, the ability to down-regulate neural activity corresponding to irrelevant

distractor stimuli, as measured by activation in specialized ROIs in the ventral visual cortex (Chadick, Zanto, & Gazzaley, 2014; Gazzaley et al., 2008; Gazzaley, Cooney, Rissman, & D’Esposito, 2005) and distributed patterns of neural activity throughout the whole brain, has been shown to correlate with the age-related deficit in memory (Zheng et al., 2018; St-Laurent, Abdi, Bondad, & Buchsbaum, 2014). However, it remains unknown whether the neural representations of irrelevant items tend to persist in working memory longer for older adults than for younger adults, thereby contributing to interference and a reduction of signal-to-noise ratio.

This study investigates the possibility that distractors, once encoded, remain active in older adults’ working memory because they are not adequately suppressed. This prediction follows directly from inhibitory deficit theory (Lustig, Hasher, & Zacks, 2007; Hasher, Zacks, & May, 1999; Hasher & Zacks, 1988), which dictates that interference from no-longer-relevant items in working memory is a major underlying cause of age-related reductions in explicit memory. Although there is a wealth of behavioral evidence suggesting older adults have difficulty “deleting” information from the contents of working memory (Cansino, Guzzon, Martinelli, Barollo, & Casco, 2011; Oberauer, 2001, 2005; Hedden & Park, 2001), there is currently little neural evidence for this idea.

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Here, we use a multivoxel pattern analysis (MVPA) and a working memory delayed match-to-sample task with a category retrocue (Souza & Oberauer, 2016; Buchsbaum et al., 2005) to examine how distributed neural representations for relevant and irrelevant information in memory are expressed and regulated in the brains of young and older adults. We first trained an MVPA classifier on a “localizer” task to distinguish between four image categories: faces, bodies, objects, and scenes. We then tested the classifier on young and older adults’ brain activity during a retrocue recognition task to track the time course of activation of relevant and irrelevant items throughout the task. On each trial of the recognition task, people studied four images—two from each of two categories—and were then cued to remember only one category of images for an upcoming recognition judgment. People were asked to maintain only images from the cued category throughout the retention delay. We then tested their memory for the cued items with a working memory match-to-sample task in which a probe image was always from the cued category. We hypothesized that no-longer-relevant (uncued) items would remain at a higher level of activation in older adults compared to young adults throughout the delay and that this persistence of irrelevant items in working memory would be detrimental to performance on the recognition task.

METHODS

Participants

Twenty older adult participants (ages 60–77 years; 10 women) and 20 young adult participants (ages 18–28 years; 10 women) were recruited from the Baycrest participant database and gave informed consent to be tested for the study. All participants were right-handed English speakers with normal or corrected-to-normal vision and no known neurological or neuropsychological conditions. They were in good health, with no participants reporting having untreated high blood pressure or diabetes and all older adults scoring 28 or higher out of 30 on the Mini-Mental State Examination (Folstein, Folstein, & McHugh, 1975). Older adults had an average of 16.4 ($SD = 2.4$) years of education, which was marginally more than younger adults who had an average of 15.0 ($SD = 1.9$) years, and all participants reported having completed high school. One older adult’s (72-year-old man) functional data were not included in the following analyses because of excessive (>5-mm framewise displacement) head motion.

Materials

One hundred twenty color photographs from four distinct visual categories—faces, objects, bodies, and scenes—were selected for use in the experiment. Face stimuli were collected from the Minear and Park (2004) face database and pictured people from the shoulders up

on white backgrounds. Faces were equally distributed across age (young adulthood to old age) and gender. Object stimuli were gathered from the BOSS database (boss.smugmug.com) and from the set used by Konkle, Brady, Alvarez, and Oliva (2008) and featured everyday objects on white backgrounds. Scene stimuli were from the set used by Konkle, Brady, Alvarez, and Oliva (2010) and contained ordinary scenes, both natural and man-made, containing no humans or animals. Body stimuli were modified from copyright-free images retrieved from an online search and based on those described by Downing, Jiang, Shuman, and Kanwisher (2001), featuring human bodies of different sizes and ages in various poses with heads and backgrounds digitally removed. Twelve images from each category were used as repeat trials in the 1-back task (classifier training phase) and did not reappear in the working memory task, but all other pictures appeared in both the 1-back and recognition tasks. To increase difficulty of the recognition task, pictures of the same category presented together at study as well as lure pictures on mismatch trials had the same verbal label (e.g., “sprinkled cookie” or “older white male”); that is, category lures were chosen to be semantically similar to the cued memory stimuli.

Accordingly, 48 pairs of similar pictures—across four categories—and 48 triplets of similar pictures were used in the 48 mismatch trials of the recognition task, and 96 pairs of similar pictures were selected for the 48 match trials.

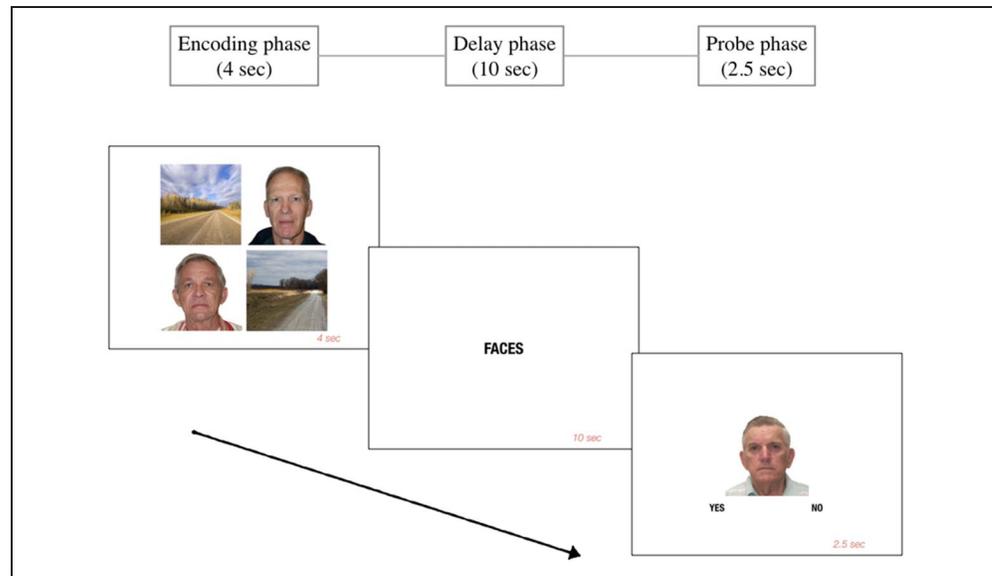
Procedure

Before MR scanning, participants filled out a consent form, a health information questionnaire, and an fMRI safety screening form to ensure it was safe for them to participate. The fMRI scan was done in a single 1.5-hr session that consisted of two phases: a classifier training phase followed by a recognition memory phase (Figure 1).

fMRI Task

The classifier training phase consisted of four 5-min runs of a 1-back task, each containing eight blocks of 16 images from the same category serially presented for 900 msec each with a 300-msec central fixation cross between images. Participants were instructed to view the images and press a button with their right index finger when they saw a picture repeat twice in a row, which occurred one to two times per block. To prevent potential carryover activation from one category block to the next, there was a 10-sec interval between blocks, and block order was balanced such that blocks of different categories followed each other equally often (e.g., face blocks were equally likely to come after scene blocks, object blocks, body blocks, and face blocks).

Figure 1. An example trial from the retrocue recognition task.



After a 10-min break in which participants rested and an anatomical scan was collected, the recognition phase began. The recognition task was performed in four 8-min runs, each containing 24 study-test trials. Each trial was divided into three phases: encoding, delay, and probe. During the encoding phase, participants studied four images—two each from two separate categories—arranged in a 2×2 array on the screen with images from the same category appearing diagonally opposite each other. People had 4 sec to study the images for a yes/no recognition task and were not informed which category would be tested until the study period ended. After study, the images were immediately replaced by a cue word indicating the to-be-tested category (e.g., “FACES”). The cue remained on the display for 10 sec, during which time participants were instructed to visualize the two images they had just seen that belonged to the cued category. After the 10-sec delay, a probe image from the cued category was presented for 2.5 sec, and people indicated whether the probe image had been present in the encoding phase (by pressing a button with their right index finger) or not (by pressing a button with their right middle finger). The probe image, whether a lure or a match, was always from the cued stimulus category. All possible category combinations were used equally often during encoding, and within these combinations, each category was cued and uncued equally often. Lure probes requiring a “no” response appeared on 50% of the trials. Trial order was randomized before test but constant across participants.

MRI Setup and Data Acquisition

Experimental stimuli were presented using E-Prime 2.0 (Psychology Software Tools) and projected onto a monitor that the participant viewed through a mirror attached to the head coil while they were lying down in the

scanner. Imaging data were collected from a 3-T Siemens MAGNETOM Trio MRI scanner and a 12-channel head coil. During the functional runs, T2*-weighted EPI scans measuring BOLD contrast were acquired with a two-shot gradient-echo EPI sequence (22.5×22.5 cm field of view with a 96×96 matrix, resulting in a 2.35×2.35 mm resolution for each of the thirty-five 3.5-mm slices with a 0.5-mm interslice gap, repetition time = 2.0 sec, echo time = 27 msec, flip angle = 62°). Whole-brain magnetization prepared rapid gradient echo T1-weighted anatomical scans were acquired between the first four and last four functional runs.

fMRI Data Analysis

Preprocessing

AFNI's *3dvolreg* program was used to convert functional images to NIFTI format, do motion correction, and spatially align them to the first run. Magnetization prepared rapid gradient echo anatomical scans were first normalized to the Montreal Neurological Institute (MNI) space using symmetric diffeomorphic registration implemented in the Advanced Normalization Tools software. Two average templates, one for the older group and one for the young group, were then created. A final template was then constructed by averaging the old and young templates together to create an age-neutral template. The Advanced Normalization Tools nonlinear registration was then rerun with the age-neutral template used as the reference. All nonlinear transformations were then saved and were used to warp the results of statistical analyses that were performed in native EPI space.

MVPA Overview

To examine age-related differences in neural pattern reactivation during the working memory task, we first used

a “whole-brain” classifier to examine hypothesized effects at the largest spatial scale and with the greatest statistical power. However, because of its distributed nature (because it involved “features” extracted from category-selective voxels throughout the brain), the whole-brain classifier was necessarily not spatially specific. Thus, we performed two additional analyses at a finer spatial scale: a searchlight analysis (Kriegeskorte, Goebel, & Bandettini, 2006) that examined multivariate patterns in small local regions throughout the brain, and an ROI analysis that was targeted at the medial temporal lobe (MTL), because of the area’s importance in memory and aging.

Whole-Brain MVPA Classifier

A multivariate pattern classifier (shrinkage discriminant analysis [SDA]; Ahdesmäki & Strimmer, 2010) was trained to discriminate between the four image categories for each participant individually. Before training, the scans from the four 1-back task runs were concatenated, and category labels were assigned to volumes recorded 9 sec after block onset through to 9 sec after the block ended to account for the lag in hemodynamic response. Features were selected for inclusion in the classifier if they significantly discriminated between categories, as determined by an ANOVA done on each voxel ($p < .005$).

To assess classifier performance on the training data set, cross-validation was performed using a leave-one-run-out technique in which three runs of the 1-back task served as training runs and the fourth served as a test run. Feature selection was always carried out on the training data to avoid a biased selection. Once each run had served as the test run in cross-validation, and all combinations of training and test runs were found to have high predictive accuracy, then overall classifier accuracy was calculated as the proportion of images that were assigned the correct category label by the classifier. This cross-validation procedure was used only to assess the accuracy of the classifier on the 1-back task and to evaluate any potential group differences that might influence the interpretation of the classifier’s ability to decode scans in the working memory task. To maximize the predictive accuracy of the 1-back classifier on the working memory task, however, we trained a final classifier using data from all four 1-back task runs. This final classifier was saved and subsequently used to decode category-specific pattern activity on the subsequent working memory task. Note that, for the purposes of the final predictive model, feature selection using the ANOVA procedure was carried out on the full training data set, because predictions were always made on the unseen working memory data, and thus double-dipping was avoided.

In the prediction phase, the SDA classifier produces a continuous output, a matrix of values that reflect the posterior probability that each scanned image corresponded

to one of the four trained categories. The probabilistic values could then be used to compute area-under-the-curve (AUC) metrics corresponding to the likelihood of correct prediction of category membership. AUC metrics were used both in the whole-brain analyses and in the follow-up searchlight and ROI analyses. The SDA classifier was tested on the four concatenated recognition task runs and tested at each sequential time point in the working memory trial spanning a period of 24 sec after trial onset. Each trial lasted 16.5 sec (4-sec encoding, 10-sec delay, 2.5-sec probe, and a mean ISI of 3.2 sec), and thus, we included time points that extended 10 sec after the onset of the probe, so that we could capture pattern activity associated with the probe response. Thus, the data could be analyzed and displayed as time courses so as to capture the dynamics of pattern activity over the course of the three trial phases: encoding, delay, and probe.

Searchlight Analysis

We performed a searchlight analysis (Kriegeskorte et al., 2006) over the entire brain to locate voxels that were most informative about category membership. An 8-mm spherical searchlight (Bießmann, Murayama, Logothetis, Müller, & Meinecke, 2012), centered on a single voxel, was moved over the entire brain, assigning posterior probabilities of category membership to each central voxel based on the multivariate activation pattern of its neighbors. Just as with the whole-brain classifier, the searchlight classifier was trained on four runs of the 1-back task and tested on four runs of the recognition task.

Encoding, delay, and probe phases were modeled within each trial of the recognition task using a Gaussian hemodynamic response function ($\mu = 6$, $\sigma = 2$) shifted in time and scaled to the length of the phase (i.e., 4 sec for encoding, 10 sec for delay, 2.5 sec for probe). The searchlight was run on every time point in the trial, and then weighted averages were computed on the output of the searchlight for each phase and compared between age groups for cued and uncued categories.

To test hypotheses related to main effects and group differences among searchlight-derived AUC scores computed at each voxel, we used t tests carried out at each voxel in MNI space. To evaluate statistical significance of t statistic maps formed at the group level, we used the permutation approach implemented in FSL *randomize* (Winkler, Ridgway, Webster, Smith, & Nichols, 2014) and null distributions based on 5000 permutations of the data. Voxels were considered significant if classifier evidence was in the top fifth-percentile of the permuted null distribution, yielding an alpha criterion of approximately .05. Planned contrasts that did not pass this significance level were evaluated at a more liberal uncorrected threshold of $p < .001$.

ROI Analysis

Similar to the whole-brain analysis above, SDA classifiers were used to examine the extent to which various regions of the MTL modulate the activation of neural representations of cued and uncued categories. Four regions of the MTL (hippocampus [HPC], entorhinal cortex [ERC], parahippocampal cortex [PHC], and perirhinal cortex [PRC]) were probabilistically defined using an averaged set of manual segmentations performed on high-resolution MRI scans from a separate sample of 20 young adults and 40 older adults (Olsen et al., 2013, 2017). The averaged probabilistic maps, which were already registered to MNI space, were back-transformed into each participant's native space, and then each region was combined across hemispheres. For each MTL region, an SDA classifier was trained on activity during the four runs of the 1-back task and tested on data from the recognition task, as described above. Encoding, delay, and probe phases were modeled in the same way as in the whole-brain searchlight analysis so that activation of the cued and uncued categories could be compared between age groups and phases in all eight regions. This yielded AUC time courses that were analyzed using linear mixed-effect models with the encoding, delay, and probe periods as fixed effects task regressors. The fixed effects regressors were created by convolving the hemodynamic response function "box-car" inputs that matched the relative onset and duration of each trial phase (encoding: 0–4 sec, delay: 5–14 sec, probe: 14–18 sec).

RESULTS

Behavioral Results: Classifier Training Task

Accuracy on the 1-back task was calculated as the proportion of hits minus the proportion of false alarms. Both

age groups detected repeating pictures with a high degree of accuracy (young adults: $M = 0.97$, $SD = 0.08$; older adults: $M = 0.95$, $SD = 0.05$), and accuracy did not differ as a function of age, $F < 1$, or picture category, $F < 1$, nor was there an interaction between age and category, $F < 1$. Both age groups performed at ceiling, suggesting attention to targets was high during classifier training.

Behavioral Results: Recognition Task

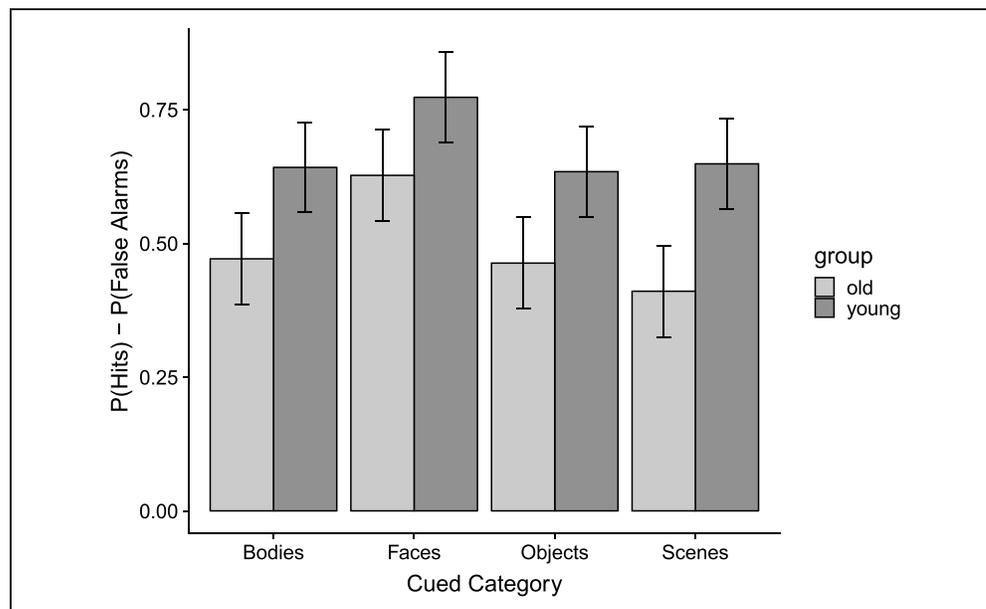
Accuracy scores on the recognition task, calculated as proportion of hits minus proportion of false alarms, were entered into a mixed ANOVA that showed a main effect of Age, $F(1, 37) = 20.16$, $p < .001$, such that young adults outperformed older adults by 18.1 points (Figure 2). There was also a main effect of Category, $F(3, 111) = 8.9$, $p < .001$, that did not interact with Age, $F < 1$, showing that corrected recognition scores for faces were better than the other three picture categories (Tukey-adjusted $ps < .0006$). There were no differences between other categories (Tukey-adjusted $ps > .88$).

fMRI Results

Whole-brain MVPA Classification Accuracy for Training Task

Accuracy of the classifier output was calculated as the proportion of 1-back trials on which the classifier predicted the correct category during hold-one-run-out cross-validation. Classification accuracy scores were entered into a 2 (Age) \times 4 (Category) mixed ANOVA that showed no effect of Age, $F < 1$, $p = .68$, suggesting that the classifier has similar accuracy for young and older adults. There was a significant main effect of Category, $F(3,$

Figure 2. Mean accuracy on the recognition task by picture category. Young adults performed better than older adults.



111) = 43.95, $p < .001$, $\eta_p^2 = .54$, indicating that the whole-brain classifier was better for some categories than others. Classification of faces and scenes was equally good, and both were better than classification of bodies and objects. Classification of bodies was better than that of objects (78% accurate for young adults, 77% accurate for older adults), which were the worst classified but still well above chance (25%; see Figure 3).

Whole-brain MVPA of Recognition Task

Because the primary goal of this study was to test for age differences in patterns of activation of cued and uncued items in working memory, we first analyzed classifier predictions derived using a classifier that was trained on all voxels that significantly discriminated between categories as assessed via a univariate one-way ANOVA. The median number of voxel features selected for the old and young groups was 4525 (interquartile range: 4100–5868) and 5706 (interquartile range: 4718–6903), respectively. Wilcoxon signed-rank test did not reveal a significant group difference in the number of features ($p = .06$).

Each participant's (feature-selected) whole-brain classifier produced probabilistic predictions for each category and time point for all participants. Classifier performance was assessed using the AUC relating the classifier prediction probabilities and the "target" category of each trial. Three AUC measures were computed, one in which the target category was the cued category (cued_auc), one in which the target category was the uncued category (uncued_auc), and one in which the target category was one of the two categories not present in the memory display (other_auc). For example, if a memory display contained faces and scenes and faces were cued, then cued_auc is the estimate of the strength of pattern activity for faces, uncued_auc is the estimate of the pattern activity for scenes, and other_auc is the average pattern activity for the other two categories in the experiment, namely, objects and body parts. We performed separate linear

mixed-effects models to test for age-related differences in cued and uncued reactivation measures, the results of which are described in the following paragraphs.

To examine age-related differences in pattern activity for the cued category, a linear mixed-effects model was computed where cued_auc was the dependent variable, age was a between-participant factor, and time-varying regressors for encoding, delay, and probe phases were entered as fixed effects covariates. A random intercept for participant and random slopes for each of the three fixed effect covariates (encoding, delay, and probe) were also added. The main effects of all the experimental phases were significant (encoding: $t = 12.44$, $p < .001$; delay: $t = 5.74$, $p < .001$; probe: $t = 18.41$, $p < .001$). As can be seen in Figure 4 (left panel), the cue-related classification performance roughly doubles from the encoding phase, in which the cued and uncued categories are presented together, to the probe phase, in which the cued category is presented alone. There were no differences over age groups for any of the trial phase covariates for the cued category, as assessed with likelihood ratio tests (LRTs) comparing the full and nested models (encoding: LRT = 0.95, $p = .32$; delay: LRT = 2.78, $p = .09$; probe: LRT = 1.91, $p < .14$). Note that the trend ($p = .09$) for a higher cued_auc value for young adults during the delay is evident as a small gap in the time courses displayed in Figure 4.

Next, we tested for age differences in uncued-category-related activity over all three trial phases with a new linear mixed-effects model including all of the same independent variables as above but now substituting uncued_auc as the dependent variable. The main effect of uncued activity was only significant for the encoding phase ($t = 14.8$, $p < .001$) and probe phase ($t = -11.7$, $p < .001$), where in the latter case, the negative t statistic indicates a below-zero effect, possibly related to a hemodynamic undershoot effect. A test of age effects across all trial phases revealed significant effects only during the delay period (LRT = 6.32, $p = .011$), where older

Figure 3. Mean classification accuracy by age group and picture category. The classifier was equally accurate for young and older adults.

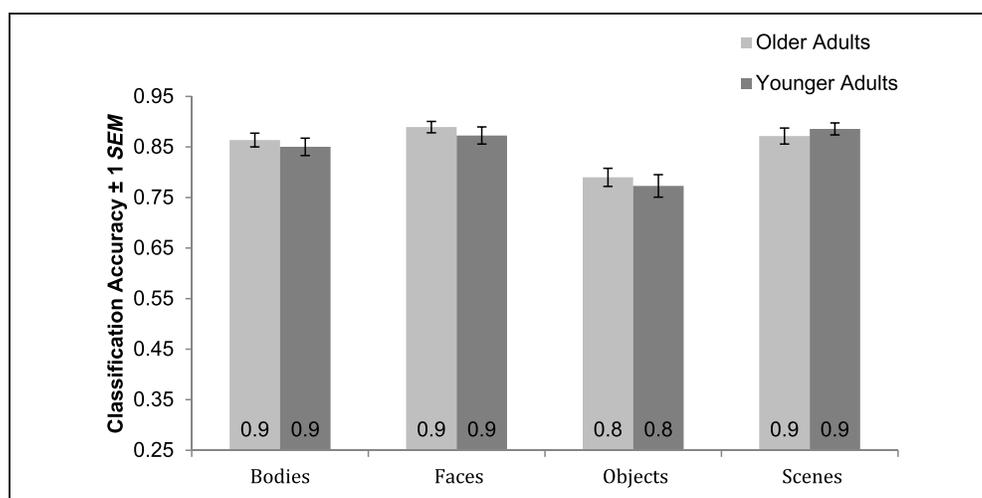
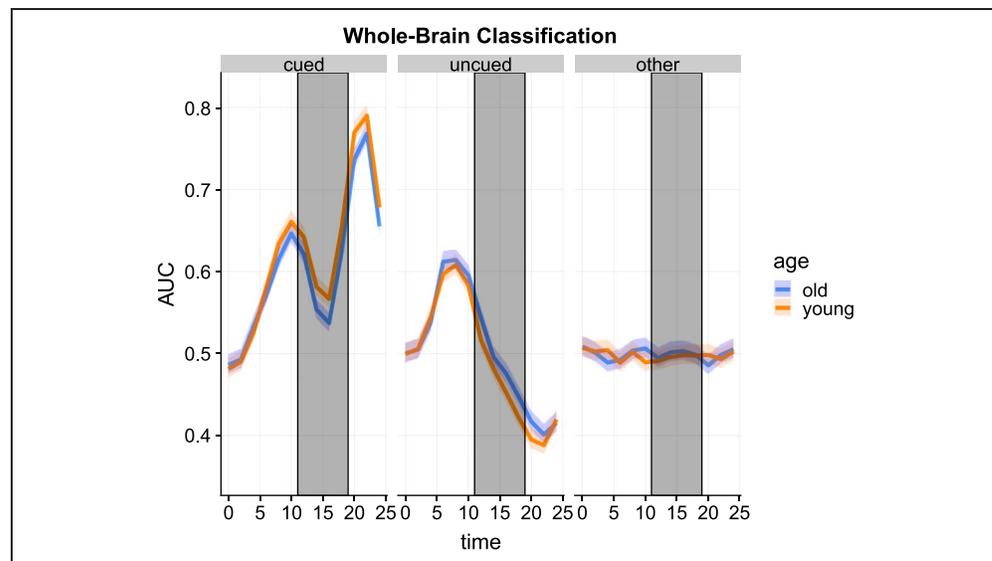


Figure 4. Whole-brain MVPA classification performance for cued and uncued items as a function of time and age group. Shaded area depicts the working memory retention period shifted 6 sec to account for lag in hemodynamic response.



adults, as predicted, had greater uncued activity than young adults (see Figure 4, middle panel).

Finally, we tested for age differences in pattern activity associated with the unrepresented categories where *other_auc* was the dependent variable and the independent variables were the same as above. There were no significant main effects for any of the trial phases, although there was a trend for a negative effect at the time of the probe ($t = 1.925, p = .057$) indicating that pattern activity for the “other” categories decreased somewhat when the probe from the cued category was presented. No age differences for any of the three trial phases were observed as tested by an LRT comparison of nested models that did or did not include Age group as an independent factor (all $ps > .12$). Because there was no evidence for age differences between pattern activity associated with the “other” categories and the AUC scores (see Figure 4, right panel) were close to 0.5 for all time points, all further analyses were focused on the *cued_auc* and *uncued_auc* variables.

The above linear mixed-effects analyses showed that pattern activity for the uncued category during the delay period is significantly greater in the older group than in the younger group. To examine whether the delay-period effect (young > old) for *cued_auc* and the opposite-going effect (old > young) during the delay period for the *uncued_auc* measure are statistically coupled, we computed a correlation between random slope estimates for these two effects over participants. The correlation was significantly negative ($r = -.78$), indicating that the amount of pattern reactivation for the cued category is inversely correlated with the amount of pattern activity for the uncued category.

To test whether delay-period pattern activity for the uncued item is significantly related to age even after accounting for cued pattern activity, we performed a logistic regression with age group as the dependent variable

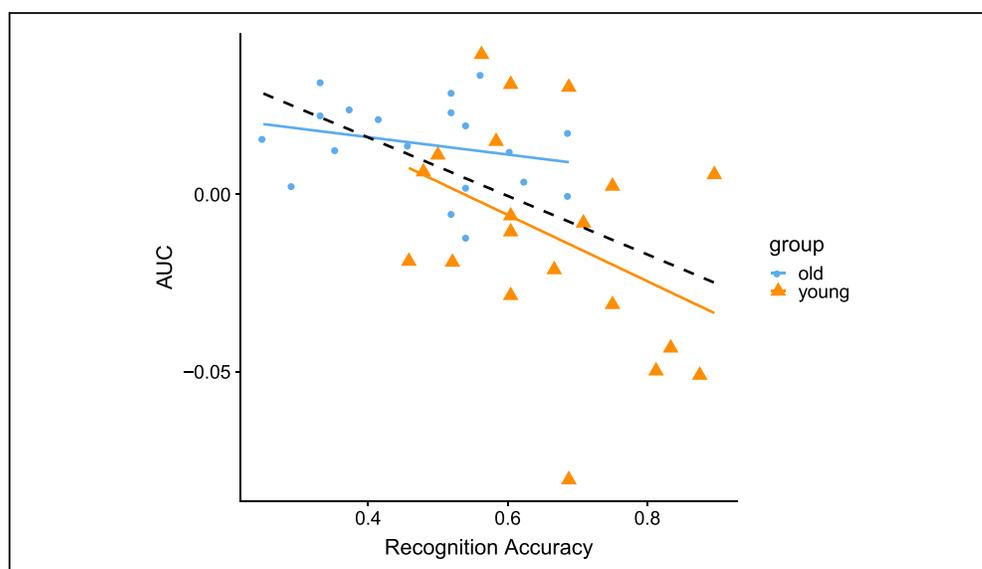
(coded as 0–1), and the estimated participant-specific random effects for the delay-period coefficients for cued and uncued models were the independent variables. The uncued delay slope estimates were a significant predictor of age group ($z = 2.250, p = .024$), whereas cued delay slope estimates were not ($z = .087, p = .93$). We then submitted the logistic fit to stepwise model selection using Akaike information criterion (AIC), which compared all variable subsets for the lowest AIC. The stepwise procedure indicated that the best model in terms of AIC was one including only the uncued delay-period predictor. Thus, it appears that delay-period pattern activity for the uncued category is associated with age even after correcting for the effect of cued item delay-period activity.

Whole-brain MVPA Classification and Individual Differences in Recognition Memory

We next tested whether cued and uncued delay-period activity was associated with individual differences in corrected recognition performance (hits – false alarms). These activity estimates were again taken from the random slope estimates for the delay-period regressor in the linear mixed models described above.

In separate linear regressions, uncued delay-period pattern classification performance was negatively associated with recognition memory for the cued items ($t = -2.12, p = .04$; see Figure 5), and cued activity trended toward a positive association ($t = 1.78, p = .08$). When both terms were entered in the same model with age group as a between-participant factor, neither variable was statistically significant, likely as a result of their substantial collinearity. Furthermore, there was no evidence in either model for an interaction with age. However, stepwise AIC model selection indicated that the best model was one with a main effect of age group (old/

Figure 5. Relationship between uncued delay-period pattern activity and individual differences in memory performance for cued items. Dashed line shows a simple regression line through the full data set without modeling age group.



young) and the uncued delay as independent variables and no interaction term. In other words, there was evidence for a relationship between uncued pattern activity and memory performance that did not significantly differ as a function of age (Figure 5).

Searchlight Analysis

The whole-brain classifier analysis described above identified age differences in delay-period pattern reactivation that is derived from ~5000 feature-selected voxels that are distributed over across the brain. Thus, this classifier has high sensitivity but low spatial resolution. In applying a searchlight analysis, we were therefore interested in identifying spatially specific regions of the brain that differentiate young and older groups on the basis of delay-period pattern activity for the cued and uncued stimulus categories, thereby offering some indication of the brain

regions that are primarily driving the age differences observed in the whole-brain analysis.

The whole-brain analysis of delay-period pattern activity confirmed that both older and younger adults maintained neural representations of the cued category in memory over the delay. The searchlight analysis further confirmed that the delay-period category information associated with the cued items was evident in a large set of regions throughout the brain—in both young and older adults—including but not limited to the ventral temporal areas that have been shown to code for visual categories. This is consistent with other studies showing that representations of visual memories are widespread and not limited to the posterior cortex (Bone et al., 2019; Lee, Kravitz, & Baker, 2019; Han, Berg, Oh, Samaras, & Leung, 2013; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012; Kuhl, Rissman, Chun, & Wagner, 2011).

Although the age difference in cued classifier evidence during the delay was not significant in the whole-brain

Figure 6. Searchlight analysis showing delay-period pattern reactivation for the cued stimulus category in young and older groups.

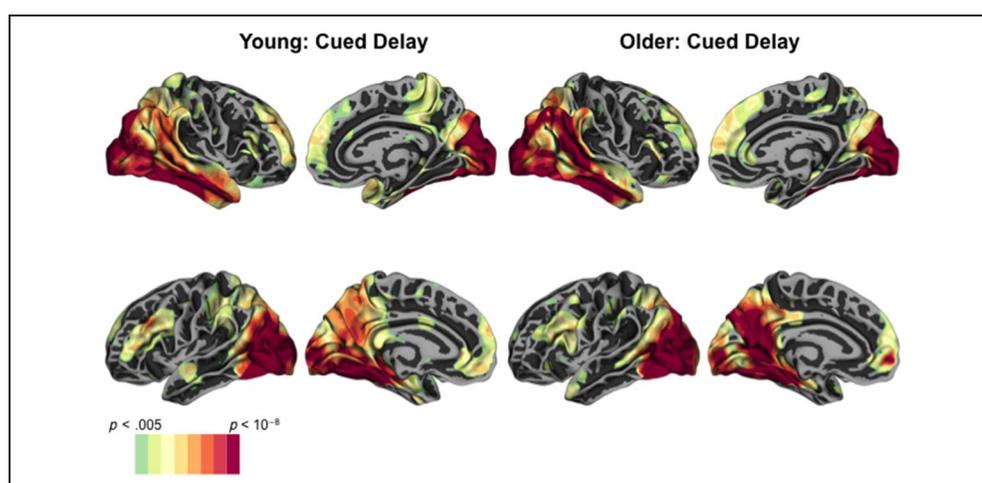


Table 1. Peak Activation Coordinates for Searchlight Analysis

| <i>x</i> | <i>y</i> | <i>z</i> | <i>Hemisphere</i> | <i>Label</i> | <i>t_{stat}</i> | <i>Voxels</i> |
|---|----------|----------|-------------------|---|-------------------------|---------------|
| <i>Searchlight maxima: cued category (older group; p < .05, corrected)</i> | | | | | | |
| 38.5 | -48 | -8.5 | Right | Temporal occipital fusiform cortex | 19.501879 | 23090 |
| -39.5 | -69 | 6.5 | Left | Lateral occipital cortex, inferior division | 14.604970 | 23090 |
| -18.5 | -63 | 12.5 | Left | Supracalcarine cortex | 14.196438 | 23090 |
| 38.5 | -81 | 6.5 | Right | Lateral occipital cortex, inferior division | 14.196416 | 23090 |
| -33.5 | -90 | 18.5 | Left | Lateral occipital cortex, superior division | 13.452430 | 23090 |
| -27.5 | -39 | -17.5 | Left | Temporal fusiform cortex, posterior division | 13.290330 | 23090 |
| 8.5 | -66 | 33.5 | Right | Precuneus cortex | 12.499668 | 23090 |
| -48.5 | -51 | -14.5 | Left | Inferior temporal gyrus, temporo-occipital part | 12.381753 | 23090 |
| 11.5 | -57 | 3.5 | Right | Lingual gyrus | 12.061674 | 23090 |
| 44.5 | -60 | 18.5 | Right | Lateral occipital cortex, superior division | 11.973586 | 23090 |
| 47.5 | -69 | -14.5 | Right | Lateral occipital cortex, inferior division | 11.795818 | 23090 |
| -0.5 | 57 | -2.5 | Left | Frontal pole | 10.412013 | 23090 |
| 11.5 | -78 | -20.5 | Right | Occipital fusiform gyrus | 8.285049 | 23090 |
| 2.5 | -90 | 18.5 | Right | Occipital pole | 7.550386 | 23090 |
| -3.5 | -45 | 45.5 | Left | Precuneous cortex | 7.128564 | 23090 |
| 65.5 | -18 | 24.5 | Right | Postcentral gyrus | 7.100398 | 23090 |
| -60.5 | -27 | 45.5 | Left | Supramarginal gyrus, anterior division | 6.267220 | 23090 |
| 47.5 | -39 | 48.5 | Right | Supramarginal gyrus, posterior division | 6.144204 | 23090 |
| 35.5 | 24 | 27.5 | Right | Middle frontal gyrus | 5.881325 | 23090 |
| 29.5 | -57 | 57.5 | Right | Lateral occipital cortex, superior division | 5.837641 | 23090 |
| -48.5 | 27 | 18.5 | Left | Inferior frontal gyrus, pars triangularis | 5.752784 | 1619 |
| -12.5 | 54 | 15.5 | Left | Paracingulate gyrus | 5.525141 | 23090 |
| -36.5 | 9 | 27.5 | Left | Precentral gyrus | 5.493749 | 1619 |
| 50.5 | -3 | 45.5 | Right | Precentral gyrus | 5.218664 | 23090 |
| 44.5 | 36 | 3.5 | Right | Frontal pole | 4.895035 | 23090 |
| -45.5 | 12 | -29.5 | Left | Temporal pole | 4.832359 | 33 |
| 29.5 | 36 | -11.5 | Right | Frontal pole | 4.719567 | 23090 |
| -27.5 | 27 | 48.5 | Left | Middle frontal gyrus | 4.624501 | 1619 |
| 62.5 | -9 | -5.5 | Right | Superior temporal gyrus, posterior division | 4.597537 | 23090 |
| -33.5 | 36 | -2.5 | Left | Frontal orbital cortex | 4.559279 | 1619 |
| 20.5 | 24 | 48.5 | Right | Superior frontal gyrus | 4.308446 | 23090 |
| -42.5 | -45 | 45.5 | Left | Supramarginal Gyrus, posterior division | 4.039254 | 23090 |
| 2.5 | 36 | 57.5 | Right | Superior frontal gyrus | 3.970701 | 23090 |
| <i>Searchlight maxima: cued category (young group; p < .05, corrected)</i> | | | | | | |
| -30.5 | -81 | 21.5 | Left | Lateral occipital cortex, superior division | 18.151562 | 33392 |
| 26.5 | -51 | -17.5 | Right | Temporal occipital fusiform cortex | 17.854553 | 33392 |
| -33.5 | -54 | -20.5 | Left | Temporal occipital fusiform cortex | 15.333787 | 33392 |

Table 1. (continued)

| <i>x</i> | <i>y</i> | <i>z</i> | <i>Hemisphere</i> | <i>Label</i> | <i>t_{stat}</i> | <i>Voxels</i> |
|----------|----------|----------|-------------------|---|-------------------------|---------------|
| 41.5 | -69 | 0.5 | Right | Lateral occipital cortex, inferior division | 14.904811 | 33392 |
| -18.5 | -60 | -8.5 | Left | Lingual gyrus | 13.309159 | 33392 |
| 35.5 | -18 | -23.5 | Right | Parahippocampal gyrus, anterior division | 12.950921 | 33392 |
| 26.5 | -81 | 27.5 | Right | Lateral occipital cortex, superior division | 12.352211 | 33392 |
| 47.5 | -72 | 27.5 | Right | Lateral occipital cortex, superior division | 10.214015 | 33392 |
| 17.5 | -51 | 48.5 | Right | Precuneus cortex | 9.659741 | 33392 |
| -0.5 | -66 | 15.5 | Left | Precuneus cortex | 8.612263 | 33392 |
| 17.5 | 39 | -11.5 | Right | Frontal pole | 7.951810 | 33392 |
| 47.5 | 27 | 21.5 | Right | Inferior frontal gyrus, pars triangularis | 7.791630 | 33392 |
| -15.5 | -9 | -17.5 | Left | Parahippocampal gyrus, anterior division | 7.741916 | 33392 |
| 5.5 | 57 | 24.5 | Right | Superior frontal gyrus | 7.623979 | 33392 |
| -45.5 | 27 | 30.5 | Left | Middle frontal gyrus | 7.153158 | 33392 |
| 47.5 | -48 | 15.5 | Right | Middle temporal gyrus, temporo-occipital part | 7.117825 | 33392 |
| -6.5 | -54 | 51.5 | Left | Precuneus cortex | 6.938123 | 33392 |
| 23.5 | 3 | -14.5 | Right | Parahippocampal gyrus, anterior division | 6.550254 | 33392 |
| 53.5 | -6 | -11.5 | Right | Superior temporal gyrus, anterior division | 6.530833 | 33392 |
| -33.5 | 36 | 9.5 | Left | Frontal pole | 6.410007 | 33392 |
| 44.5 | 24 | -17.5 | Right | Frontal orbital cortex | 6.408215 | 33392 |
| 2.5 | 54 | -11.5 | Right | Frontal medial cortex | 6.183889 | 33392 |
| -0.5 | 36 | 3.5 | Left | Cingulate gyrus, anterior division | 5.927786 | 33392 |
| -54.5 | -12 | -8.5 | Left | Superior temporal gyrus, posterior division | 5.895799 | 33392 |
| 38.5 | 9 | 54.5 | Right | Middle frontal gyrus | 5.407108 | 33392 |
| 41.5 | -45 | 57.5 | Right | Superior parietal lobule | 5.315515 | 33392 |
| -33.5 | -6 | -35.5 | Left | Temporal fusiform cortex, anterior division | 5.280563 | 33392 |
| -0.5 | -33 | 18.5 | Left | Cingulate gyrus, posterior division | 5.128522 | 33392 |
| 20.5 | 0 | 54.5 | Right | Superior frontal gyrus | 5.056464 | 33392 |
| -51.5 | -42 | 33.5 | Left | Supramarginal gyrus, posterior division | 5.011031 | 33392 |
| -30.5 | 60 | 15.5 | Left | Frontal pole | 4.515812 | 33392 |
| -42.5 | 15 | -14.5 | Left | Temporal pole | 4.456204 | 33392 |
| 32.5 | -12 | 15.5 | Right | IC | 4.341934 | 33392 |
| -0.5 | 3 | 30.5 | Left | Cingulate gyrus, anterior division | 4.275420 | 33392 |
| -51.5 | -6 | 48.5 | Left | Precentral gyrus | 3.731827 | 33392 |
| 14.5 | 42 | 51.5 | Right | Frontal pole | 3.707840 | 33392 |
| 29.5 | -21 | 57.5 | Right | Precentral gyrus | 3.487349 | 33392 |

Searchlight maxima: cued category (young > older; p < .05, corrected)

| | | | | | | |
|-------|-----|-------|------|---|----------|------|
| -33.5 | -51 | -20.5 | Left | Temporal occipital fusiform cortex | 4.993926 | 3325 |
| -36.5 | -39 | -2.5 | Left | Parahippocampal gyrus, posterior division | 4.776189 | 3325 |
| -15.5 | -42 | -17.5 | Left | Parahippocampal gyrus, posterior division | 4.761155 | 3325 |

Table 1. (continued)

| <i>x</i> | <i>y</i> | <i>z</i> | <i>Hemisphere</i> | <i>Label</i> | <i>t_{stat}</i> | <i>Voxels</i> |
|---|----------|----------|-------------------|---|-------------------------|---------------|
| 23.5 | 12 | -17.5 | Right | Frontal orbital cortex | 4.134859 | 3325 |
| 47.5 | -9 | -8.5 | Right | Planum polare | 3.866021 | 3325 |
| -57.5 | -63 | 12.5 | Left | Lateral occipital cortex, inferior division | 3.815808 | 113 |
| -15.5 | -3 | -20.5 | Left | Parahippocampal gyrus, anterior division | 3.701195 | 3325 |
| <i>Searchlight maxima: uncued category (older > young; p < .005, uncorrected)</i> | | | | | | |
| 47.5 | -48 | 12.5 | Right | Middle temporal gyrus, temporo-occipital part | 4.493668 | 23 |
| -51.5 | -69 | 12.5 | Left | Lateral occipital cortex, inferior division | 4.470580 | 28 |
| 11.5 | -9 | 18.5 | Right | Right thalamus | 4.118726 | 15 |

analysis, age differences were evident in the searchlight analysis (see Figure 6). Young adults showed higher classifier evidence than older adults for cued items in bilateral ventral visual areas and throughout the MTL (Table 1). No regions showed higher cued classifier evidence for older than younger adults. Increased classifier evidence in ventral visual regions suggests that young adults maintained more faithful representations of cued items throughout the retention delay (St-Laurent et al., 2014; Riggall & Postle, 2012; Kuhl et al., 2011; Kuhl, Rissman, Chun, & Wagner, 2010), which would be consistent with their better performance on the recognition task compared to older adults. The MTL—especially the HPC—has been shown to store representations of memories that can be detected using MVPA (Dandolo & Schwabe,

2018; Bonnici et al., 2012; Chadwick, Hassabis, & Maguire, 2011). Higher cued classifier evidence in the MTLs of young compared to older adults further supports the idea that young adults more effectively maintained cued items in the postencoding delay.

The same searchlight analysis was also conducted for the uncued items to identify regions where the representation of irrelevant information may linger in the neural pattern activity of older adults longer than it does in younger adults. Older adults showed relatively higher uncued delay-period pattern activity throughout the MTL—mirroring the age differences observed for the cued category—as well as the right middle temporal gyrus and left lateral temporo-parietal cortex, although these effects did not survive corrections for multiple comparisons. No regions showed

Figure 7. Searchlight analysis of age differences for cued and uncued delay-period pattern reactivation. Top shows regions where cued delay pattern activity was greater for the young group than the older group ($p < .005$, uncorrected for display). Bottom shows areas where uncued activity was greater in the older group than the younger group ($p < .005$, uncorrected for display). Note that, whereas the large MTL cluster in the top survived corrections for multiple comparison (see Table 1), the parietal clusters (old > young) in the bottom did not survive multiple comparison correction. Slice levels for top: axial, $z = -9$; coronal, $y = -29$; sagittal, $x = -24$. Slice levels for bottom: axial, $z = 13$; coronal, $y = -29$; sagittal, $x = -44$.

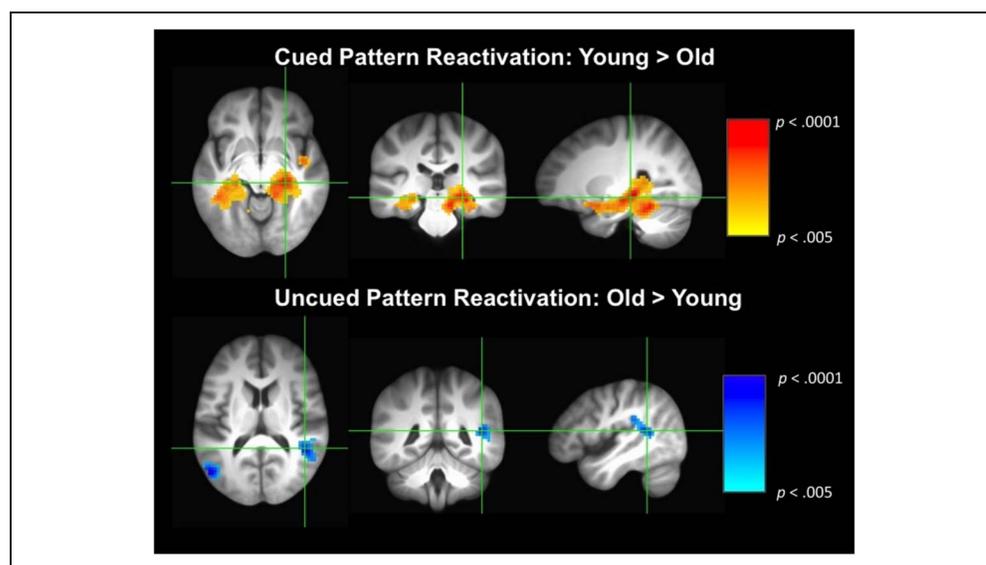
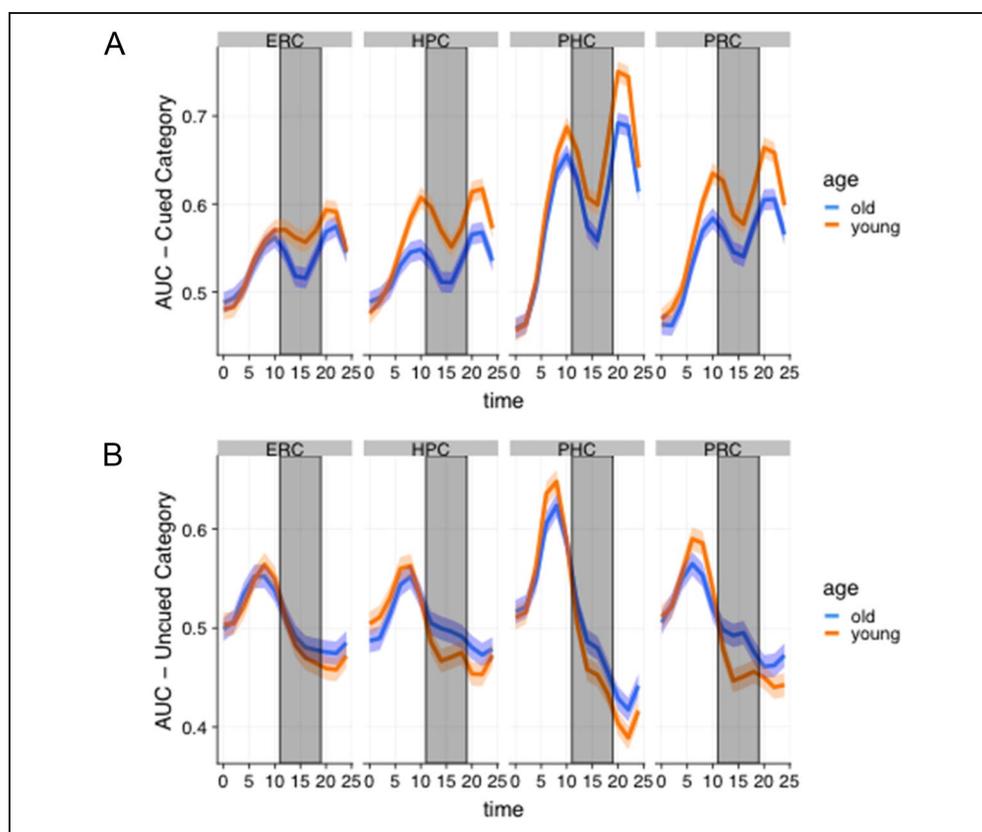


Figure 8. MVPA classification performance (AUC) in four MTL ROIs for (A) cued and (B) uncued categories as a function of time and age group. Shaded area depicts the 10-sec working memory retention period shifted 6 sec to account for lag in hemodynamic response.



higher uncued classifier evidence for young adults than older adults, supporting the idea that representations of irrelevant items remain active across a delay period in older adults (Figure 7).

ROI Analysis in MTL Structures

Because of the large and striking concentration of age-related differences in cued and uncued pattern activity in the MTL, we further examined these effects in a follow-up analysis in four probabilistically defined anatomical ROIs, namely, ERC, HPC, PHC, and PRC. The group-averaged AUC time courses for the cued category in each ROI are shown in Figure 8. In each region, there are large differences between age groups, with younger adults generally showing more cued category pattern reactivation across the trial. A linear mixed-effects model showed that younger adults showed more cued pattern activity (cued_auc) for all trial phases (young – old; encoding: $t = 2.46, p = .013$; delay: $t = 3.133, p = .003$; probe: $t = 3.2, p = .002$) and that the age differences did not vary significantly across ROIs ($p > .15$).

The same linear mixed-effects model was also estimated using the uncued pattern activity (uncued_auc) as a dependent variable. Here, there were age differences in the delay ($t = -2.586, p = .0126$) and probe ($t = -2.29, p = .0246$) phases, with older adults showing more uncued category pattern activity than younger adults. During encoding, younger adults showed marginally

more uncued pattern activity ($t = 1.883, p = .065$) than older adults. Here, we also found an interaction with ROI, such that the largest age difference was observed in the HPC ($t = -3.78, p = .0004$), marginal effects were observed in the PRC ($t = -2.136, p = .04$) and PHC ($t = -1.64, p = .11$), and no effect was observed in the ERC ($t = -1.35, p = .89$). Thus, overall age-related effects of cued-category-specific pattern activity were generally of a larger magnitude and more consistent across the subregions of the MTL than were the uncued effects, which showed an interaction effect over MTL ROIs and the largest age effect in the HPC.

DISCUSSION

Behavioral studies using measures such as RT and both explicit and implicit memory have suggested that older adults have prolonged access to no-longer-relevant items in memory (Hedden & Park, 2001; Oberauer, 2001; Hamm & Hasher, 1992). Using MVPA to track activation of relevant and irrelevant items throughout a retrocued recognition task, we provide direct neuroscientific support for the hypothesis that older adults are impaired in goal-directed modulation of neural activity during a working memory retention period. Using a whole-brain pattern classifier trained on an independent localizer task, we showed that older adults had more evidence of sustained activation of irrelevant items during the working memory delay period compared to young adults.

Furthermore, increased brain activity associated with the irrelevant category was associated with worse performance on the recognition task, irrespective of the age group.

Previous studies that have examined the effect of proactive interference on aging (Healey, Campbell, Hasher, & Osher, 2010; Lustig et al., 2001) have shown that older adults have impaired memory in the face of retrieval competition. Kuhl et al. (2011), as well as Wimber, Alink, Charest, Kriegeskorte, and Anderson (2015), have shown that the fidelity of neural representations active at retrieval predicts retrieval success. Thus, if no-longer-relevant items from the past are still activated for older adults, then their retrieval fidelity for relevant items will be lower and recall will suffer. The tendency for information to linger in memory, even when it is not evidently “relevant” to ongoing processes, has now been established in several studies of healthy younger adults. For example, episodic information spontaneously reactivates during post-memory-encoding rest periods (Staresina, Alink, Kriegeskorte, & Henson, 2013). Irrelevant information may be reactivated simply by virtue of temporal proximity to a set of cued items (Chan, Applegate, Morton, Polyn, & Norman, 2017) or during working memory maintenance tasks where incidental associations with items in active memory are automatically reactivated along with items in an explicit memory set (Hoskin, Bornstein, Norman, & Cohen, 2019). Our findings add to this literature in showing that older adults’ impairment at resolving interference between items that compete for access in working memory is associated with higher levels of category-specific activity for the irrelevant information in working memory. The presence of “lingering” neural representations for no-longer-relevant information may explain why older adults are slower to reject lures in directed forgetting tasks and generally show evidence of “holding on” to distracting information longer than younger adults.

Taken together, this work provides new support for the inhibitory deficit theory of aging (Hasher & Zacks, 1988). Suppression of encoded items in working memory is sometimes referred to as the deletion function of inhibition, and ERP work has suggested that older adults take longer than young adults to engage this function. In their study, Jost, Bryck, Vogel, and Mayr (2011) warned people before stimulus onset about which items were irrelevant, but relevant items appeared in unpredictable locations so people involuntarily encoded distractors and had to subsequently delete them. Using the magnitude of contralateral delay activity as a measure of the number of items maintained in working memory, they found that older adults maintained more items—both relevant and irrelevant—for a longer time compared to young adults, whose contralateral delay activity indicated that they deleted irrelevant items almost immediately. Deletion may be slowed rather than impaired among older adults, but our data demonstrate that, in older adults, irrelevant items show elevated activity in working memory

throughout a 10-sec delay. This work provides a more concrete way of thinking about deletion, specifically that it involves down-regulation of the same distributed neural representations of items that are active during perception.

Previous work has shown, at the time of encoding, greater low-level processing of distractors compared to young adults, and this lack of inhibition is associated with reduced deactivation of the medial pFC as well as disrupted connectivity between regions within the canonical default mode network (Chadick et al., 2014; Gazzaley et al., 2005, 2008). Complementary work has shown that, during encoding, older adults show reduced ability to ignore task-irrelevant visual information as indexed by neural adaption in the context of a face–scene perceptual decision-making task (Schmitz, Cheng, & De Rosa, 2010).

In the context of suppressing working memory, Clapp, Rubens, Sabharwal, and Gazzaley (2011) showed that older adults show greater disruptions in connectivity between the middle frontal gyrus and the visual cortex compared to young adults when they must suppress irrelevant information. During long-term memory retrieval, a region of the lateral pFC just anterior to the middle frontal gyrus has been shown to be involved in the suppression of irrelevant memories, and hippocampal–pFC connectivity has been linked to the ability to suppress “unwanted thoughts” (Schmitz, Correia, Ferreira, Prescott, & Anderson, 2017). Taken together, there is an increasing body of evidence indicating a role for inhibitory mechanisms, mediated primarily by pFC, in exerting top-down control over irrelevant perceptual and mnemonic sensations, memories, and unwanted thoughts (Lewis-Peacock, Kessler, & Oberauer, 2018).

Our whole-brain classification analysis was intended to capture distributed category-specific memory representations and to maximize our sensitivity to discovering the hypothesized effects. This analysis revealed an age effect consistent with the hypothesis that older adults would retain more irrelevant information in memory, but from this analysis, we could not pinpoint any regionally specific effects. In our searchlight and ROI analyses, we therefore sought to more precisely localize brain areas that were the primary drivers of the age differences we observed in the analysis of the whole-brain classifier. The searchlight analyses revealed that both young and older adults showed similar overall patterns of reactivation for the cued category during the working memory delay-period interval. Although the spatial distribution of effects was similar, we did observe large effects of age that were circumscribed to a few areas, namely, the MTL, the lateral occipital cortex, and the temporo-parietal area. The largest and most striking age difference was seen throughout the MTL, where younger adults showed a much larger expression of cued item pattern activity during the delay period of the working memory task. A follow-up analysis in four subregions of the MTL showed a large and consistent effect throughout this region, but with

particularly large age effects in the HPC (e.g., see Figure 8) for both cued and uncued analyses. There is a relatively recent body of work showing that, notwithstanding the traditional attribution of the MTL to “long-term memory” function, the HPC and other MTL regions appear to contribute to visual working memory performance in some cases (Kornblith, Quiñan Quiroga, Koch, Fried, & Mormann, 2017; Warren, Duff, Cohen, & Tranel, 2015; Olsen et al., 2009; Ranganath & D’Esposito, 2001; Stern, Sherman, Kirchoff, & Hasselmo, 2001). MTL involvement in working memory maintenance has been particularly implicated under high-load conditions with complex visual stimuli including faces and scenes (Schon, Quiroz, Hasselmo, & Stern, 2009; Axmacher, Schmitz, Wagner, Elger, & Fell, 2008; Rissman, Gazzaley, & D’Esposito, 2008). Here, we show further that in young adults the MTL maintains distributed category-specific representations over the working memory delay period and, moreover, that the magnitude of this effect is related both to aging and to individual differences in memory discrimination after a short delay. We suggest that enhanced delay-period pattern reactivation for cued items in young adults (and high-performing older adults) is related to a benefit conferred by greater high-resolution memory capacity provided by the HPC and surrounding structures. It has recently been proposed (Aly, Ranganath, & Yonelinas, 2013; Yonelinas, 2013; Olsen, Moses, Riggs, & Ryan, 2012) that the formation of high-resolution bindings between informationally rich elements during perception, working memory, and episodic memory is supported by computations performed in the HPC. A breakdown in the specificity or efficiency of such binding processes, as may occur with age, can have the effect of producing more links between irrelevant and relevant items, thereby increasing the likelihood of those items persisting in memory over both short and long delays, a phenomenon that has been termed “hyperbinding” (Powell, Strunk, James, Polyn, & Duarte, 2018; James, Strunk, Arndt, & Duarte, 2016; Campbell, Hasher, & Thomas, 2010). This indiscriminate binding of irrelevant items is because of age-related reduction in hippocampal efficiency (Fan, Wheatley, & Villeda, 2017; Leal & Yassa, 2015) that is further compounded by declining top-down modulation of hippocampal activity by pFC and related neocortical structures (Eichenbaum, 2017; Schmitz et al., 2017; Damoiseaux, Viviano, Yuan, & Raz, 2016).

Limitations

There are a number of limitations to this study that should be considered. First, the observation of an increase of pattern activity for the irrelevant category assumes in part that there are no systematic differences in nonneuronal (i.e., vascular) effects on the hemodynamic response profile. Previous studies have shown a variety of age-related changes in the amplitude and variability of the hemodynamic response (Huettel, Singerman, & McCarthy,

2001; D’Esposito, Zarahn, Aguirre, & Rypma, 1999), although findings have been somewhat inconsistent (Handwerker, Gonzalez-Castillo, D’Esposito, & Bandettini, 2012). For example, if older adults’ responses were abnormally delayed in category-selective visual area, then it is conceivable that this could affect measurements of pattern activity during the working memory delay period. However, if this were the case, it would most likely be a general effect that would be the same for relevant and irrelevant items. Thus, if older adults have a systematically delayed hemodynamic response, then this would be evident as wider pattern activity response profiles for both irrelevant and relevant items. However, that is not what is observed (refer to Figure 4); rather, we see an extended response for older adults for the irrelevant categories but not for the relevant items.

A second limitation of this study is that, because we used a retrocue task design in which the cue was always valid, we could not assess memory performance for the uncued/irrelevant memory items. Our findings of a link between delay-period pattern activity for the irrelevant category therefore come from across participant correlation between task performance and pattern accuracy scores. We are currently developing a retrocue paradigm using a similar task design but also incorporating both invalid and “non-informative cue” conditions to examine whether older adults perform better than younger adults on invalid cue trials.

Finally, the ability to distinguish behavioral or multivariate patterns associated with selecting or reactivating a target representation and suppressing or inhibiting an irrelevant distractor is notoriously difficult (see, e.g., MacLeod, 2007). Because MVPA cue probabilistic classification measures sum to one, an increase in the predicted probability of one class label will be associated with decreases in estimates for the other classes. We acknowledge this lack of independence between classifier estimates but have shown that, even after accounting for such dependencies, delay-period reactivation of uncued category activity is significantly predictive of individual differences in behavioral performance as assessed with logistic regression.

Conclusions

The ability to regulate and control the current contents of working memory as a way to enhance and select important information while suppressing and discarding irrelevant information is a critical cognitive function that appears to decline with age. Suppression may be a mechanism that permits thoughts and actions to remain coherent in the face of competition from nonrelevant information. Its reduced efficiency can be expected to have implications across a range of cognitive functions from comprehension to memory and reasoning as well as for goal satisfaction. We have shown that neural

patterns of activity associated with information that is no longer relevant to task goals are nevertheless maintained in active memory longer for older adults than for younger adults. Moreover, the magnitude of this effect is related to individual differences in performance across the lifespan. Regional analyses pinpoint the MTL as the locus of the larger magnitude differences in category-specific pattern activity during working memory, pointing to a key role for the area in the regulation and retrieval of information in working memory.

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