Neural evidence for age differences in representational quality and strategic retrieval processes

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Abstract

Mounting behavioural evidence suggests that declines in representational quality and impaired strategic retrieval processes contribute to age-related episodic memory decline. The present study sought to identify neural evidence for age-related change in these factors by measuring neural differentiation during encoding of paired associates, and changes in regional BOLD activity, functional connectivity, and cortical reinstatement during retrieval conditions that placed low (intact pairs) and high (recombined pairs) demands on strategic retrieval processes. The results revealed age-related declines in the differentiation of stimulus representations during encoding and cortical reinstatement during retrieval, though a relationship between these metrics was observed only during conditions of low strategic demand (hits). Both older and younger adults preferentially engaged hippocampus and angular gyrus during hits, but only younger adults exhibited increased recruitment of, and hippocampal connectivity with, lateral prefrontal regions during correct rejections, consistent with greater age-related impairments in engaging the retrieval control mechanisms necessary to support goal-directed retrieval. Collectively, these data provide further insights into the neural mechanisms underlying age-related decline in episodic memory.

Keywords: Aging, Episodic Memory, Dedifferentiation, Cortical Reinstatement, Cognitive Control

Introduction

Episodic memory decline is one of the most prominent cognitive changes experienced by older adults. These deficits tend to be more pronounced when discriminating between events that share overlapping content, relative to those that are more distinct (Koutstaal & Schacter, 1997; see Devitt & Schacter, 2016 for review). Similarly, older adults exhibit greater impairments when demands on cognitive control during retrieval are high, as compared to when memory can be supported by more automatic processes (Jennings & Jacoby, 1993; Koen & Yonelinas, 2016). Recent findings from our research group suggest that at least two separate factors contribute to this pattern of memory impairment: reductions in the specificity of event representations and impaired initiation and/or execution of cognitive control processes (Trelle et al., 2017). We found that reducing demands on either representational content or strategic retrieval alone did not eliminate memory deficits, but if both were reduced, age differences in memory performance were no longer observed, suggesting a contribution of both of these factors to age-related memory decline.

This evidence, together with findings from other groups (Cohn et al., 2008; Luo & Craik, 2009), provides important initial insights into the mechanisms underlying age-related decline in episodic memory, but is inherently limited by the need to use behavioural outcomes (i.e. memory retrieval accuracy) to make inferences about underlying event representations or the engagement of cognitive control processes. The inability to measure these factors directly makes it difficult to distinguish between deficits that originate during the initial encoding of an event (e.g., reductions in representational specificity), as compared to those that emerge during memory retrieval (e.g., declines in cognitive control processes that allow retrieval of stored representations). The present investigation aims to complement existing behavioural findings by using fMRI to identify more direct, neural evidence for each of these constructs. In particular, we use multivariate pattern similarity analysis to measure age-related changes in representational content during memory encoding and retrieval, and univariate activation and functional connectivity analyses to measure age differences in the engagement of cognitive control processes during memory retrieval.

Pattern similarity analysis uses the dissimilarity between voxelwise patterns of neural activity to make inferences about the ability to distinguish different event features during memory encoding or

retrieval (Kriegeskorte et al., 2008). Such effects tend to be localized in modality-specific areas of sensory cortex, with discrimination of visual stimulus features particularly evident in ventral temporal cortex (Carp et al., 2011; LaRocque et al., 2013). High levels of within-category similarity, coupled with low levels of between-category similarity, is reflective of greater neural selectively and *greater differentiation* or distinctiveness of visual category representations. Pattern similarity metrics can also be used to examine *cortical reinstatement*, or the overlap between neural activity patterns elicited during encoding and retrieval (Woodruff et al., 2005; Johnson et al., 2007). This reinstatement is thought to be driven primarily by hippocampal pattern completion, and to index recollection of stored details (Staresina et al., 2012; Gordon et al., 2014), with successful recall of event details in young adults associated with cortical reinstatement in the medial temporal lobe (Staresina et al., 2012; Tompary et al., 2016), ventral temporal cortex (Gordon et al., 2014; Kuhl & Chun, 2014), as well as inferior parietal cortex and prefrontal cortex (Kuhl & Chun, 2014).

Complementing these pattern analysis measures, univariate activation and functional connectivity analyses have been used to examine the recruitment of, and coupling between, brain areas implicated in different aspects of memory retrieval. Successful identification of previously experienced events, especially when accompanied by recollection of the original encoding event, is associated with increased recruitment of the hippocampus and inferior posterior parietal cortex, particularly within the angular gyrus (Wheeler & Buckner, 2003; Wagner et al., 2005; Rugg & Vilberg, 2013). Retrieval conditions that place increased demands on goal-directed, strategic retrieval processes are associated with preferential recruitment of ventral and dorsal areas within the inferior frontal gyrus (vIFG and dIFG) associated with cognitive control (Wheeler & Buckner, 2003; Lepage et al., 2003; Achim & Lepage, 2005), as well as increased frontal-hippocampal coupling (Barredo et al., 2015; Bowman & Dennis, 2016).

By combining these different measurement tools, we can examine age-related changes in representational content and controlled retrieval processes, and the impact that demands on strategic control processes have on older adults' ability to reinstate event content during memory retrieval. In particular, our previous work and that of others suggests that the ability to retrieve episodic details to support memory judgments may vary as a function of strategic retrieval demand. Older adults are

more successful in recalling event details when endorsing studied events as compared to rejecting experimentally familiar, but novel, events (Koutstaal, & Schacter, 1997; Trelle et al., 2018). Notably, rejecting these events is said to increase demands on a retrieval strategy called *recall-to-reject*, which involves the goal-directed retrieval and maintenance of task-relevant details, evaluation of retrieved content, and selection among competing representations (Gallo, 2004). However, these findings constitute only indirect evidence for this proposal, inferred by older adults' ability to discriminate between events in memory. The present study seeks to examine this question more directly by examining cortical reinstatement under conditions of high and low strategic retrieval demand.

We adapted an associative recognition memory paradigm here, in which participants were asked to discriminate between previously studied intact pairs and non-studied recombined pairs. Critically, evidence indicates that responding correctly to recombined pairs (correct rejections) necessitates strategic *recall-to-reject* processes, whereas endorsing intact pairs as studied is considered to minimize the need for such strategies, by virtue of providing greater environmental support in the form of a strong retrieval cue (Lepage et al., 2003; Cohn & Moscovitch, 2007). Consistent with this proposal, neuroimaging evidence involving younger adults has demonstrated the hippocampus and angular gyrus are preferentially recruited for associative hits, particularly when recognition is associated with recollection of the original encoding event (Wheeler & Buckner, 2003; Wagner et al, 2005; Rugg & Vilberg, 2013), but that vIFG and dIFG activity and hippocampal-vIFG connectivity increases are observed during rejection of non-studied lures during recognition memory (Barredo et al., 2015; Bowman & Dennis, 2016). Thus, although both hits and correct rejections in associative recognition can reflect accurate event memory, they are known to preferentially recruit different brain areas due to variable demands on cognitive control associated with making the correct judgment, making this a suitable paradigm with which to examine age differences in retrieval processes in the present study.

Moreover, this task design affords the opportunity to examine age-related changes in the presence and specificity of cortical reinstatement effects during retrieval, and how this may vary as a function of strategic demand at test. For example, it is possible that older adults are simply less likely than younger adults to actively retrieve stored details to support memory judgments, irrespective of

strategic demand at retrieval; instead relying on more automatic processes such as stimulus familiarity. However, it also possible that older adults are more likely to retrieve stored details to support successful memory judgments when external support is high and demands on strategic retrieval are low (e.g. intact pairs) but not when support is low and strategic retrieval demands are high (e.g. recombined pairs). Finally, it may be the case that older adults do retrieve stored details, but simply retrieve less specific information relative to that retrieved by younger adults, as suggested by disproportionate age-related deficits in memory for specific relative to more general event details (Koutstaal & Schacter, 1997; Luo & Craik, 2009). Such a tendency could be the result of increased demands on strategic control processes when retrieving and evaluating more fine-grained information, or the result of less differentiated representations available to older adults, which only support memory for more general event information.

To examine age differences in the presence and specificity of cortical reinstatement within each network during retrieval, as well as the nature of representations formed during encoding, the present study used word-picture paired associates comprised of trial-unique adjectives paired with one of 8 images (4 objects, 4 scenes). The word-picture pairs systematically varied in relatedness to one another. That is, some pairs shared a common stimulus category and overlapping content (e.g. MUDDY Umbrella and GOLDEN Umbrella), others shared a common category but non-overlapping content (e.g. MUDDY Umbrella and WOODEN Teapot), and others contained non-overlapping content from the opposite stimulus category (e.g. MUDDY Umbrella and STRIPED Office). This feature of the stimuli enabled us to explore the degree to which the specificity of stimulus representations during encoding are modulated across age groups, and to assess the specificity with which participants reinstate target information during retrieval. In particular, we were interested in assessing whether participants reinstate information about the specific associate paired with each word (e.g. the umbrella), as compared to more general information about the associate (e.g. an object rather than a scene). This was tested by contrasting encoding-retrieval similarity of corresponding events (e.g. encoding and retrieval of MUDDY Umbrella) to that of non-corresponding events that either a) contained overlapping content (e.g. GOLDEN umbrella) or b) contained dissimilar content (e.g. STRIPED Office). This contrast enabled us to assess the possibility that older adults retrieve

more general, conceptual or gist-like information about target associates to support memory performance, as opposed to specific target details (Luo & Craik, 2009; Devitt & Schacter, 2016), and to determine whether this tendency varies according to strategic retrieval demand at test.

In summary, the present study sought to characterise age differences in both representational quality and strategic retrieval, by directly measuring these constructs during memory encoding and retrieval using univariate and multivariate fMRI analysis. In particular, we examined the effects of age on: 1) the differentiation of event representations in ventral temporal cortex during encoding at different levels of stimulus relatedness, 2) the degree to which the recruitment of retrieval success regions (e.g., HIPP, ANG) and retrieval control regions (e.g. DIFG, VIFG) is modulated by strategic demand during retrieval, 3) the degree to which hippocampal connectivity with lateral cortical regions varies as a function of strategic demand at retrieval, and 4) the presence and specificity of cortical reinstatement during retrieval within each of these regions under conditions of high and low strategic demand, and whether this is related to neural differentiation during encoding.

Method

Participants

Twenty younger adults aged 21-30 (M = 24.9 years) and 22 older adults aged 63-79 (M = 71.4 years) participated in the study. Participants in both groups were recruited from the MRC Cognition and Brain Sciences Unit volunteer panel as well as the surrounding Cambridge community and received £30 for participating in the study. All participants were healthy, right-handed, had normal or corrected-to-normal vision and hearing, and had no psychiatric or neurological history. Data from two older adults are excluded from the analysis, one due to falling asleep in the scanner and failure to complete the session, and another due to performance below the normal range on the Montreal Cognitive Assessment (MoCA; cut off >= 26; Nasreddine et al., 2005). All remaining older adults performed within the normal range on the MoCA (M = 27.8). Older and younger adults did not differ with respect to years of formal education ($t(38) = 1.60$, $p = .118$), and older adults performed higher on the Shipley Institute of Living Scale ($t(38) = 3.55$, $p < .001$). Informed consent was obtained in accordance with the University of Cambridge Psychology Research Ethics Committee.

Materials

Experimental stimuli were 192 word-picture pairs comprised of trial-unique adjectives paired with one of eight colored pictures. Four of these pictures were of objects, two of which were living things and two were inanimate objects, and the remaining four pictures were of scenes, two depicting indoor settings and two outdoor settings (see Figure 1). Adjective-picture pairings were fixed across participants, and were designed to ensure that the picture could plausibly be imagined in accordance with the adjective. Word-picture pairs were randomly assigned to one of three 64-item study lists, with the constraint that each list contained eight pairs corresponding to each of the eight pictures. Half of the study items were subsequently presented as intact pairs during the test phase, and the other half were presented as recombined pairs. The assignment of pairs as intact or recombined was counterbalanced across participants.

Two characteristics of the test phase are important to note. First, recombined pairs comprised a studied word and a picture taken from the opposite stimulus category. This was done to ensure that neural activity patterns corresponding to the studied associate and the tested associate were maximally distinct. Critically, however, participants were not made aware of this manipulation, and were instructed to recall the original associate paired with each adjective. Second, during the test phase, each associate image was replaced with a common noun denoting the image (e.g., TEAPOT, BEDROOM). This feature of the design was intended to increase the ability to detect neural activity patterns that were driven by retrieval of stored details, rather than perceptual processing of the retrieval cue, as well as encourage participants to actively retrieve stored details from memory, rather than rely on stimulus fluency or familiarity to support performance.

The presentation of word-picture pairs during each study and test block was pseudo-randomized for each participant, with the constraint that no more than four images from the same category appeared in sequence, and that each image was not presented more than twice in a row. The test phase included the additional constraint that no more than four intact or recombined pairs occurred in sequence. Stimuli were presented using the Cogent software package implemented in MATLAB (Mathworks, Inc., USA).

Procedure

The experimental paradigm is depicted in Figure 1. Each study block comprised 64 trials in which participants were presented with a word-picture pair and were instructed to imagine the picture in accordance with the adjective (e.g., to imagine a golden umbrella), and to indicate whether they had been successful in doing so with a button press response (1 = successful, 2 = unsuccessful). Each study block was followed by a one-minute retention interval during which, to prevent rehearsal, participants were asked to covertly count backwards from a random number presented on the screen. The test phase commenced immediately afterwards. During each test trial, participants were presented with a studied adjective and a word corresponding to one of the eight pictures and asked to indicate with a single button press whether each pairing was previously studied together (old) or recombined (new). Both study and test trials lasted for a fixed duration of 5000 ms, with an inter-trial interval of 1000 ms. Responses not made within the allotted time were marked as no response and excluded from the subsequent analysis. Participants completed three alternating study-test blocks in this fashion, with a one-minute break between each cycle during which they were instructed to close their eyes and rest. The Shipley Vocabulary test and Montreal Cognitive Assessment were completed at the end of the session outside of the scanner.

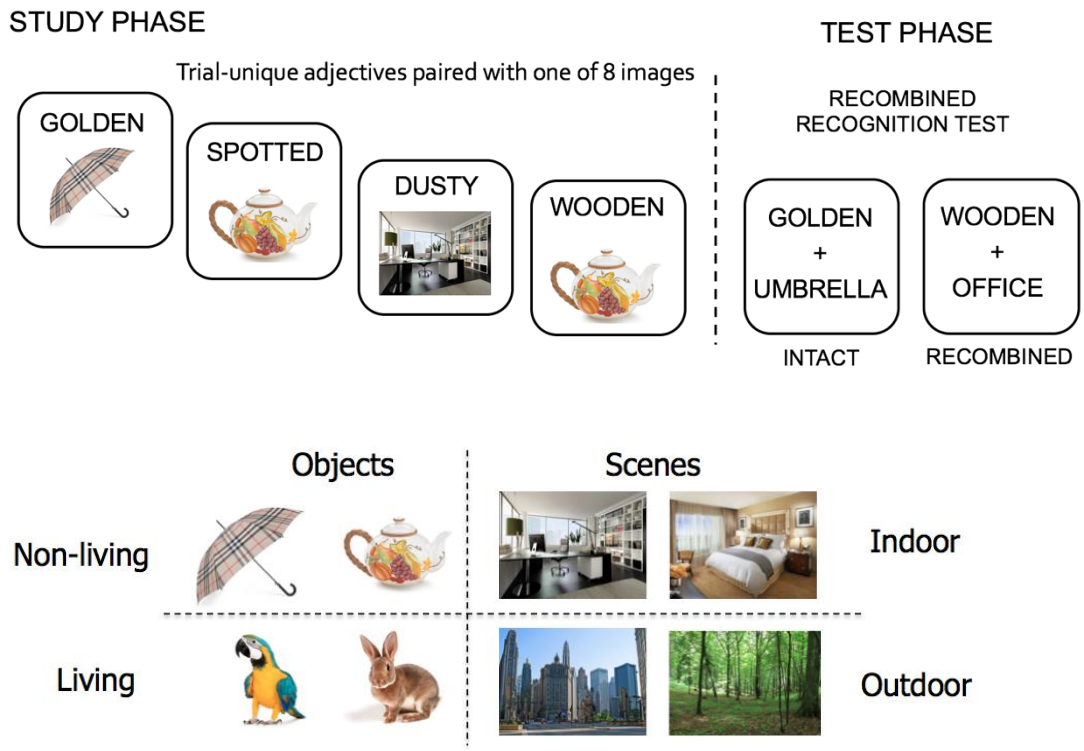

Figure 1. Schematic depicting experimental paradigm. Participants studied trial-unique adjectives paired with one of eight images pictured above. At test, participants were presented with studied (intact) and non-studied (recombined) pairs and made an old/new judgment for each. Pictures were replaced with word labels during the test phase to minimize perceptual overlap between study and test.

fMRI Data Acquisition and Pre-processing

Scanning was performed using a 3-T Siemens Prisma MRI system with a 32-channel head coil. Functional data was acquired using a descending Blood-Oxygenation-Level-Dependent (BOLD)-weighted echo-planar imaging (EPI) pulse sequence (repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle = 78). Each EPI volume consisted of 32 axial slices (3mm thick, 0.75 mm gap, 3 x 3 mm in-plane resolution) covering the whole brain. For each of the six sessions (3 study and 3 test blocks), 210 volumes were acquired. The first five volumes of each session were discarded to allow for magnetic field stabilization. A high-resolution (1 x 1 x 1 mm) T1-weighted anatomical image was also acquired at the beginning of the scanning session using a 3D magnetization-prepared rapid acquisition gradient echo (MP-RAGE) pulse sequence.

Data pre-processing and univariate analysis was conducted using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/) and batched using “automatic analysis” software (version 4; https://github.com/rhodricusack/automaticanalysis/). Preprocessing of image volumes included spatial realignment to correct for movement, followed by slice-timing correction, using the first acquired slice in each volume as a reference. The structural image of every participant was registered to a sample-specific template using the diffeomorphic flow-field method of DARTEL (Ashburner, 2007), and the template subsequently transformed to the Montreal Neurological Institute (MNI) stereotactic space using a 12-parameter affine transformation. The mean functional volume of each participant was coregistered to their structural image, and the DARTEL plus affine transformations applied to transform the functional images into MNI space.

Univariate Analysis

Univariate analyses assessed differences in BOLD activity between hits and correct rejections at test. EPI images were smoothed with an isotropic 8-mm full-width-at half-maximum (FWHM)

Gaussian kernel before modelling. Neural activity was modeled by delta functions at stimulus onset for each event of interest and convolved with a canonical hemodynamic response function (HRF). The resulting timecourses were downsampled at the reference slice for each scan to form regressors in the General Linear Model (GLM). The model contained two regressors of interest representing the two types of successful retrieval events: hits and correct rejections. All remaining trials (misses, false alarms, no response) formed a third regressor of no interest, and 6 additional regressors representing movement parameters estimated during spatial alignment (3 rigid-body translations, 3 rotations) were additionally included. Voxel-wise parameter estimates for each regressor were obtained by restricted maximum-likelihood estimation, using a temporal high pass filter (cut-off 128 s) to remove low-frequency drifts and an AR(1) model of temporal autocorrelation. First-level contrasts of the parameter estimates for each participant corresponding to the hits > CRs contrast were extracted from and averaged within each region of interest described above for statistical analyses. Note that we did not examine retrieval success effects (i.e. differences in regional BOLD activity during remembered vs forgotten trials) due to an insufficient number of forgotten trials in the younger group.

Functional Connectivity Analysis

Functional connectivity analyses examined differences in connectivity between the hippocampus and the remaining regions of interest during hits as compared to correct rejections. This analysis was conducted on the smoothed EPI images. Beta estimates for each test trial were obtained by modelling data from all three test sessions in a single GLM containing a separate regressor for each trial, as well as six movement parameters and the mean for each session as regressors of no interest. This procedure yielded separate beta images corresponding to each of the 192 test trials, which were submitted to functional connectivity analyses using the beta-series correlation method (Rissman et al., 2004). Using this method, functional connectivity is quantified as the Pearson correlation between the beta series. To assess how functional connectivity between the hippocampus and the rest of the brain varied during hits relative to correct rejections in each age group, we defined a hippocampal seed region on a subject-specific basis as a sphere of 5mm radius centered on each participant's peak BOLD activity within the hippocampus during retrieval (hits > CRs). The hippocampal beta series was calculated by averaging across the 19 voxels within the 5mm sphere. We

then conducted a whole brain seed-to-voxel connectivity analysis for each subject, and the results of the first-level contrast (H>CR) of the parameter estimates for each participant were extracted from and averaged within each region of interest for statistical analyses.

Regions of Interest: Univariate Analysis & Functional Connectivity Analysis

The univariate analyses focused on four a priori anatomical regions of interest (ROIs) within the left hemisphere: the hippocampus (HC), the angular gyrus (ANG), a ventral region of inferior frontal gyrus approximating BA45/47 (vIFG), and a more dorsal region of inferior frontal gyrus approximating BA44 (dIFG). The ANG, vIFG, and dIFG masks were defined as 10mm spheres centered on peak coordinates from a previous investigation examining the contributions of these regions to perceived oldness and cognitive control during retrieval, respectively (Wheeler & Buckner, 2003). The spatial localization of these coordinates within each anatomical region corresponds well with the coordinates reported in previous work examining the role of these regions in controlled retrieval processes (Badre & Wagner, 2007; Lepage et al., 2003; Wagner et al., 2005; Rugg & Vilberg, 2013). The hippocampus was defined anatomically based on the automated anatomical labelling (AAL) atlas. The functional connectivity analyses were conducted within the same set of a priori ROIs, focusing on connectivity between the hippocampus and the remaining regions, namely ANG, vIFG, and dIFG. The hippocampal seed region was defined in a subject-specific manner and restricted to a sphere centered on each individual's functional activity, to precisely identify the area of the hippocampus that was engaged during the task for each individual. For both the univariate and functional connectivity analyses, first-level contrasts (hits > CRs) of the parameter estimates for each participant were averaged within each ROI for each subject. Main effects of condition (hits vs CRs) within each ROI were assessed using one-sample *t* tests and age differences (age x condition interactions) were assessed using independent-samples *t* tests.

Representational Similarity Analysis

Representational similarity analysis (Kriegeskorte et al., 2008) used beta estimates produced by the same modelling approach described above for beta series correlation, with the exception that this analysis was conducted on unsmoothed data. Examination of the differentiation of stimulus representations during encoding focused specifically on the ventral temporal cortex (VTC). This ROI

was defined by functional masks created using independent data from the same subjects during a localizer task in which participants viewed all eight images from the remainder of the experiment while performing a simple colour detection task. We took the union of the results of the contrasts Objects > Scenes and Scenes > Objects (across all subjects) at a threshold of $p < .05$ FWE whole brain corrected, and masked the result to include only anatomical regions within bilateral ventral temporal cortex, defined as the parahippocampal cortex, fusiform gyrus, and inferior temporal cortex. This ROI was used to examine the differentiation of stimulus representations during encoding and cortical reinstatement effects during successful memory retrieval within ventral temporal cortex.

Cortical reinstatement analysis was additionally conducted within the same regions examined in the univariate and connectivity analyses, namely HC, ANG, vIFG, and dIFG. We selected the subset of voxels within each region that differentiated between our conditions of interest in the previous analyses, using a threshold of $p < .005$ uncorrected to increase the number of voxels (k) over which to perform pattern similarity analysis. Accordingly, ANG (k=281) and HIPP (k= 218) masks were defined by the peak clusters within each region from the H>CR contrast, whereas the dIFG (k=99) mask was defined by the peak cluster in this region identified in the univariate Condition X Age interaction, and the vIFG (k=257) mask was defined by the peak cluster in this region identified in the functional connectivity Condition X Age interaction.

Differentiation of Stimulus Representations During Encoding

To examine differentiation of event representations during encoding, we computed the Pearson correlation between all encoding trials, irrespective of subsequent memory accuracy, producing a 192 x 192 correlation matrix for each subject. We then computed the mean pairwise correlation across trials from independent runs for each of four event types, defined based on the image exemplar presented on each trial: Same Exemplar (e.g. MUDDY Umbrella and GOLDEN Umbrella), Same Subcategory (e.g. MUDDY Umbrella and WOODEN Teapot), Same Category (e.g. MUDDY Umbrella and PAINTED Rabbit) and Different Category (e.g. MUDDY Umbrella and STRIPED Office

Reinstatement of Encoding-Related Activity during Retrieval

To assess the reinstatement of encoding-related activity patterns during retrieval, pairwise correlations were computed between all study and test trials during which participants accurately endorsed intact pairs (hits) and rejected recombined pairs (correct rejections), producing a measure of encoding-retrieval similarity (ERS) for all possible pairwise comparisons. The events comprising each ERS measure were therefore matched with respect to cue type (intact, recombined), response type (old, new), and accuracy (correct only). The pairwise correlations from each matrix were then used to compute a measure of Within-Event ERS, which reflected the mean pairwise correlation between corresponding encoding and retrieval trials (i.e. values on the diagonal), and two measures of Between-Event ERS, which reflected mean pairwise correlation of non-corresponding encoding and retrieval events (i.e. off-diagonal values).

The two different measures of Between-Event ERS are depicted in Figure 2, and were chosen to determine the specificity of any observed reinstatement effects. The first was Same Exemplar ERS, which reflects the pattern similarity between non-corresponding encoding and retrieval events that share the same exemplar (e.g., encoding of MUDDY Umbrella and retrieval of GOLDEN Umbrella); the second was Different Category ERS, which reflects the pattern similarity between non-corresponding encoding and retrieval trials that belong to the opposite stimulus category (e.g., encoding of STRIPED Office and retrieval of WOODEN Teapot). Thus, the sole difference between Same Exemplar ERS and Different Category ERS was the level of conceptual and perceptual overlap between the target trial and the comparison trial: events that comprised Same Exemplar ERS shared a high degree of perceptual and conceptual overlap, whereas events that comprised Different Category ERS shared minimal perceptual and conceptual overlap.

Greater similarity between corresponding, relative to non-corresponding, events is thought to be indicative of reinstatement of encoding-related activity during retrieval (e.g., Staresina et al., 2012, Kuhl & Chun, 2014). Accordingly, we subtracted Same Exemplar ERS and Different Category ERS from Within-Event ERS to produce two difference scores reflecting Event-Level reinstatement and Category-level reinstatement, respectively. Both measures were computed separately for hits and

correct rejections, yielding four ERS measures. Positive values significantly greater than zero were considered evidence for Event-Level and Category-Level reinstatement.

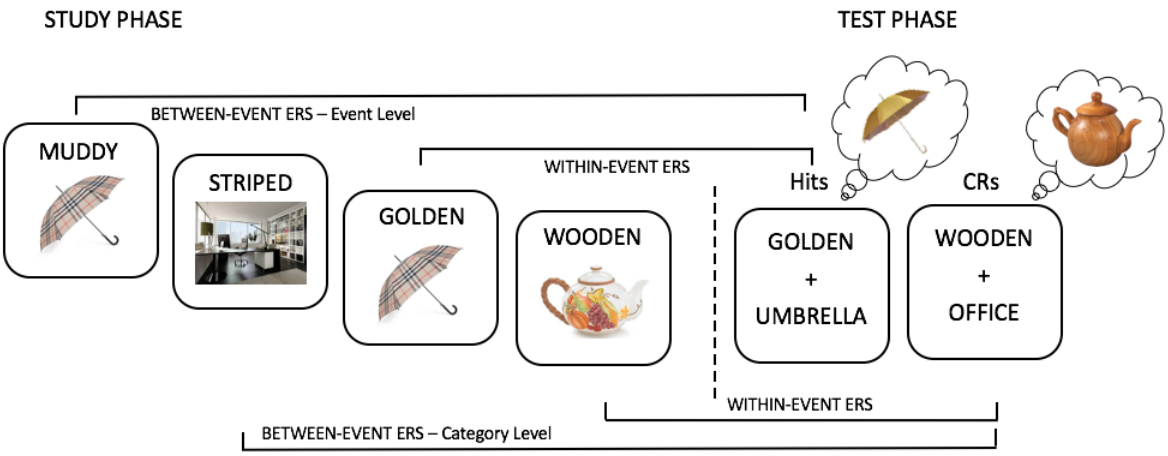

Figure 2: Depiction of Encoding-Retrieval Similarity (ERS) Measures. Within-Event ERS represents similarity between encoding and retrieval events that share the same trial-unique adjective ("corresponding events"), calculated separately for hits and correct rejections. 'Between-Event ERS – Event Level' describes the pattern similarity between encoding and retrieval events with different adjectives ("non-corresponding events") that share the same exemplar image, whereas 'Between-Event ERS – Category-Level' is the similarity between non-corresponding encoding and retrieval events containing images from the opposite stimulus category. Thought bubbles indicate retrieval of correct associate, as predicted by a recall-to-accept/reject strategy.

Results

Behavioural Results

Participants' responses were categorized as hits, correct rejections, false alarms, or misses. Trials in which participants did not respond within the allotted 5 seconds were marked as 'no response', and made up 1% and 2.5% of trials in younger and older adults, respectively. The number of trials comprising each trial type is presented in Table 1. Recognition memory performance was calculated as the proportion of hits to intact pairs corrected by the proportion of false alarms to recombined pairs. Independent samples *t*-tests revealed that memory performance was significantly impaired in older adults relative to younger adults, with older adults making fewer hits ($t(38) = 4.67$, $p < .001$, $d = 1.52$) and fewer correct rejections ($t(38) = 5.75$, $p < .001$, $d = 1.87$) relative to younger adults (see Figure 3). Due to the small number of incorrect trials in younger adults (misses: $M = 9.95$, $SD = 6.6$; false alarms: $M = 5.75$, $SD = 4.2$), we restrict our primary reinstatement analyses to hits and correct rejections.

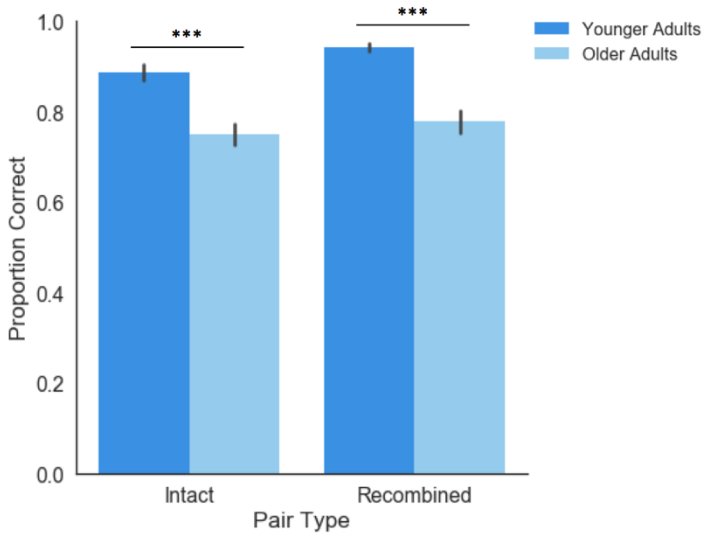

*Figure 3: Behavioural Performance. Mean proportion of hits to intact pairs and correct rejections of recombined pairs. Error bars represent standard error of the mean. Older adults made fewer hits and correct rejections relative to younger adults, *** $p < .001$.*

Table 1: Mean (SD) trial counts for each response type by age group

	Hits	CRs	FAs	Misses
Younger Adults	85.05 (7.3)	89.60 (4.8)	5.75 (4.2)	9.95 (6.6)
Older Adults	71.90 (10.3)	72.0 (11.8)	21.40 (11.5)	21.95 (9.2)

Stimulus Differentiation in VTC during Encoding

To assess age-related change in representational content, we tested whether pattern similarity between VTC stimulus representations at encoding varied as a function of event type (SE, SS, SC, and DC), and whether this differed with age (Figure 4). A 2x4 ANOVA revealed a main effect of event-type, $F(3,151)=25.27$, $p < .001$, with greatest pattern similarity between same exemplars (SE) and least between exemplars from the different category (DC). More importantly, though the main effect of age group was not significant ($F<1$), there was a significant interaction between event-type and age group, $F(3,151)=7.78$, $p < .001$, such that the young group showed higher similarity between same exemplars than the old group, but lower similarity between exemplars of the different category. Indeed, simple effects revealed that pattern similarity for events sharing the same exemplar was higher in younger adults than older adults ($t(38)=2.15$, $p =.038$), with a similar trend for events from

the same subcategory (t(38)=1.98, p =.055) and the same category (t(38)=1.75, p =.088). In contrast, pattern similarity for events containing associates from the opposite stimulus category was higher in older adults than younger adults (t(38)=4.12, p <.001). Thus, older adults exhibit both decreased pattern similarity for perceptually and conceptually similar events, as well as increased pattern similarity for events that are more distinct, yielding a net decline in discriminability.

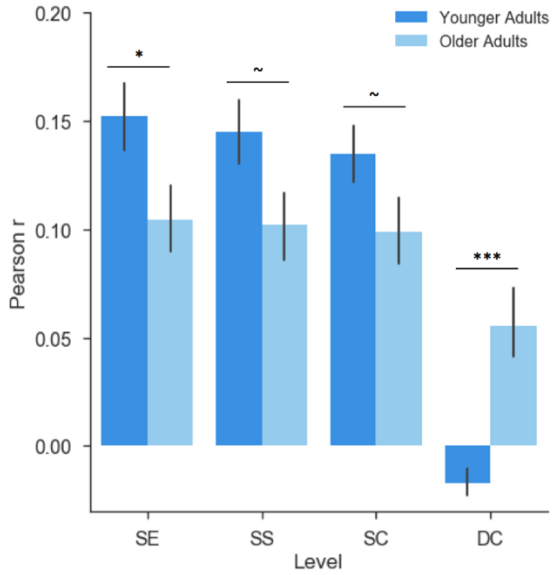

*Figure 4: Mean pairwise correlations between events of each type in older and younger adults during encoding; SE = Same Exemplar; SS = Same Subcategory; SC = Same Category; DC = Different Category. Error bars represent standard error of the mean versus zero. Significance of pairwise tests between age groups at each event-type are: *** p < .001; *p < .05; ~p < .10.*

Changes in Regional Univariate BOLD Activity during hits and correct rejections

We next sought to assess age differences in the engagement of strategic processes during retrieval by examining the recruitment of 'retrieval success' regions and 'retrieval control' regions during hits and correct rejections, respectively. To this end, we compared the magnitude of the contrast estimate (H-CR) across age groups for each of our ROIs to assess differences in regional BOLD activity during hits and correct rejections, and whether this differed as a function of age (Figure 5). Consistent with predictions, ANG exhibited greater activity during hits relative to CRs (t(39)=3.96, p <.001). Interestingly, the magnitude of this effect varied with age (t(39)=2.19, p = .038), reflecting a larger effect in older adults (t(19)=3.43, p = .0028) than younger adults (t(39)=2.56, p = .019). Similarly, HIPP exhibited greater activity during hits relative to CRs (t(39)=4.41, p <.001)

but the magnitude of this effect did not differ across age groups ($p > .49$). The difference between hits and CRs in vIFG varied with age ($t(39)=2.04$, $p = .049$), with older adults exhibiting significant activation ($t(19)=2.41$, $p = .026$), but not younger adults ($p > .914$). Recruitment of dIFG also varied significantly with age ($t(39)=3.02$, $p = .0047$), but now with the opposite pattern of significantly greater activation for correct rejections than hits in younger adults ($t(19)=3.13$, $p = .0055$) but not in older adults ($t(19)=1.37$, $p = .187$).

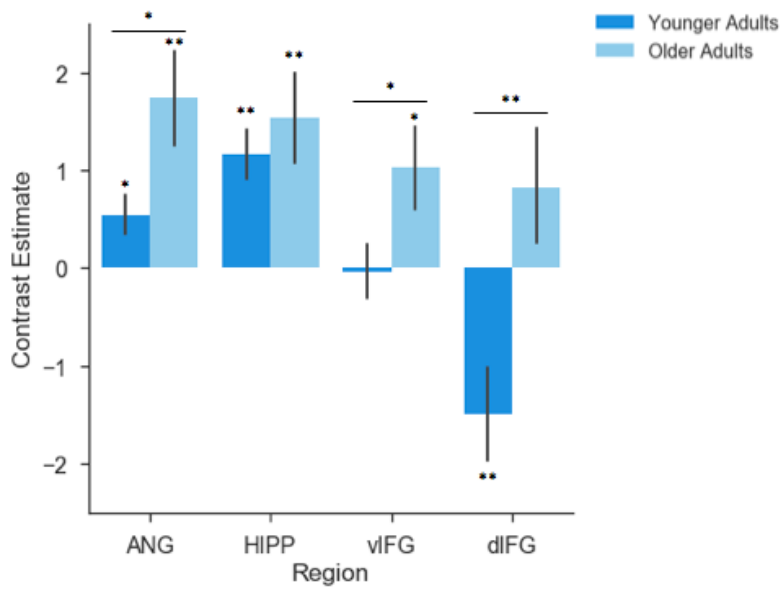

*Figure 5: Changes in regional BOLD activity during retrieval. Mean contrast estimate [hits-CRs] within each region of interest. Error bars represent standard error versus zero. ANG and HIPP exhibit greater activity during hits relative to correct rejections, whereas dIFG is recruited to a greater degree during CRs relative to hits, only within the younger group. Asterisks indicate significance: *** p < .001, ** p < .01, * p <.05.*

Changes in Functional Connectivity during hits and correct rejections

To further explore age differences in the ability to engage strategic retrieval processes, we next assessed whether hippocampal connectivity with lateral cortical regions varied as a function of demands on strategic retrieval, and whether this differed as a function of age (Figure 6). We again compared the magnitude of the contrast estimate (H-CR) across age groups for each of our ROIs, this time with this contrast estimate reflecting changes in hippocampal connectivity with each ROI rather than univariate activity within each ROI. The effect of strategic retrieval demand on hippocampal-vIFG connectivity varied across age groups ($t(39)=3.05$, $p = .0043$), with younger adults exhibiting

significantly greater connectivity during CRs relative to hits ($t(19)=4.03$, $p < .001$), whereas older adults exhibited similar connectivity across conditions ($p > .525$). The effect of strategic retrieval demand on dIFG-hippocampal connectivity showed a similar pattern that varied marginally with age ($t(39)=2.01$, $p = .052$), with a significant increase in connectivity during CRs in younger ($t(19)=2.74$, $p = .013$), but not older adults ($p > .61$). ANG-hippocampal connectivity did not vary significantly with strategic retrieval demand ($p > .216$), and this was true across age groups ($t(39)=1.43$, $p > .161$).

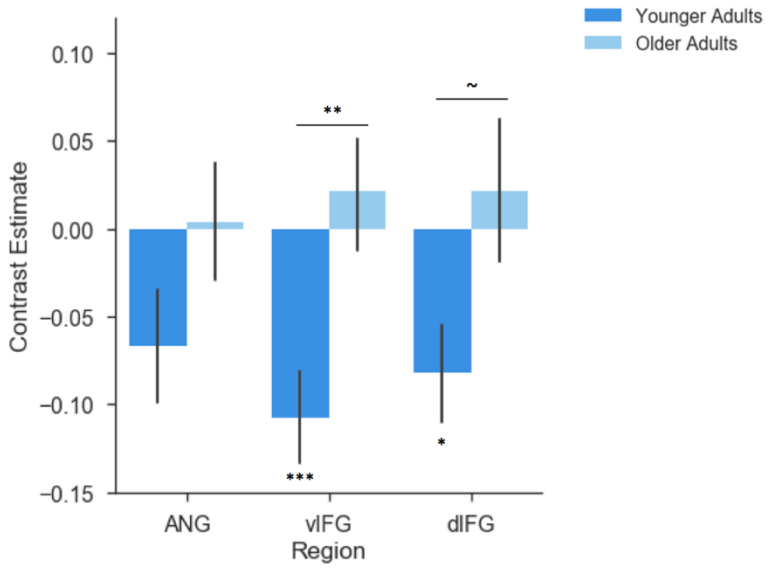

*Figure 6: Changes in hippocampal connectivity during hits-CRs. Mean contrast estimate [hits-CRs] within each region of interest. Error bars represent standard error. vIFG exhibits greater hippocampal connectivity during CRs relative to hits, but this is true only within the younger group. *p < .01, ~ p < .10.*

Cortical Reinstatement

To assess the degree to which older and younger adults engaged a recall-based retrieval strategy (i.e. recall-to-accept, recall-to-reject), we next examined whether evidence for cortical reinstatement was observed during hits or correct rejections, and whether the degree of reinstatement differed across age groups. Reinstatement was assessed using two metrics: event-level reinstatement (within-event ERS – within-category ERS), reflecting reinstatement of the specific word-picture association, and category-level reinstatement (within-event ERS – between-category ERS), enabling detection of reinstatement effects that include more general conceptual details. During hits (Figure 7), evidence for category-level reinstatement was identified in VTC ($t(19)= 4.80$, $p < .001$) within the

younger group, but not the older group ($t < 1$), although the difference between groups was only marginally significant ($t(38)=2.0$, $p = .053$). Evidence for category-level reinstatement during hits did not reach significance in the remaining regions in younger adults (ANG: $t(19) =1.48$, $p = .155$; dIFG: $t(19)=1.24$, $p =.23$; vIFG: $t(19)=1.70$, $p =.105$; HC: $t < 1$) or older adults (all $t < 1$). Evidence for event-level reinstatement (Figure 7) was not observed during hits in any of the ROIs among younger adults (dIFG and HC: $t<1$; ANG: ($t(19)=1.46$, $p =.161$); vIFG ($t(19)=1.13$, $p =.273$); VVC ($t(19)=1.17$, $p =.256$), or older adults (all $t < 1$).

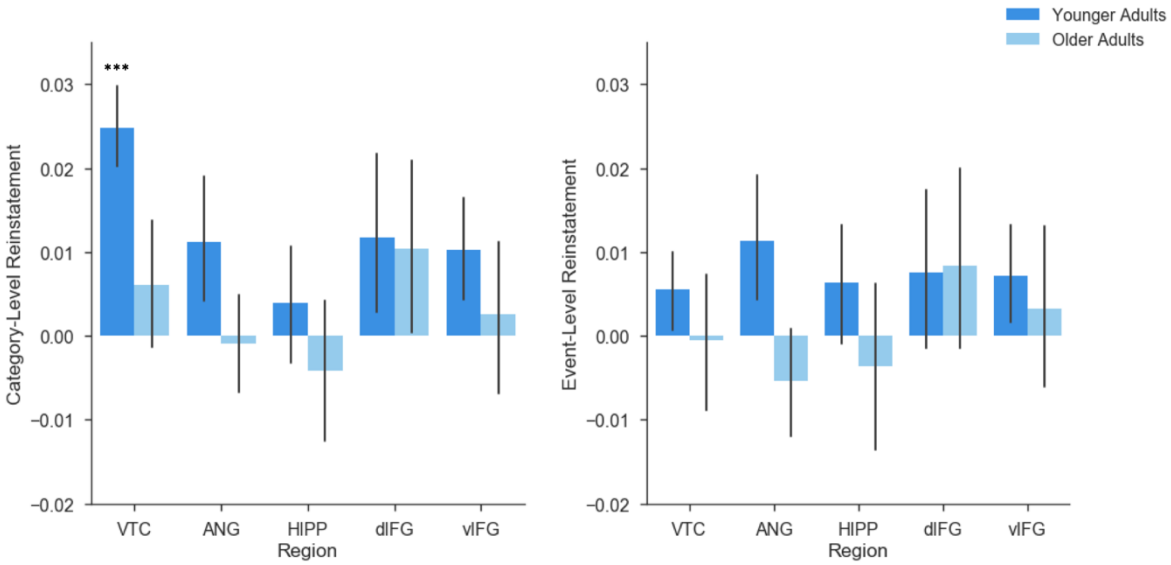

*Figure 7: Cortical Reinstatement during hits. Left: Category-level reinstatement (Within-event ERS – Between-category ERS). Right: Event-level reinstatement (Within-event ERS – Within-category ERS). Error bars represent standard error versus zero. Category-level reinstatement is evident in VTC, but this is true only within the younger group. Event-level reinstatement was not observed within any regions of interest across groups. *** $p < .001$.*

During correct rejections (Figure 8), evidence for category-level reinstatement was observed in vIFG in younger adults ($t(19)=3.30$, $p =.0038$), but not older adults ($t <1$), and this effect differed significantly across groups ($t(38)=2.98$, $p =.0058$). Category-level reinstatement during CRs was also observed in ANG among younger adults ($t(19)=2.15$, $p =.0447$), but not older adults ($t<1$), and the magnitude of reinstatement differed between groups ($t(38)=2.82$, $p =.0077$). Category reinstatement effects did not reach significance within the younger group in dIFG ($t(19)=1.50$, $p =.1511$), VTC ($t(19)=1.60$, $p =.127$), or HIPP ($t < 1$), nor did these effects emerge in older adults across regions (t

<1), although the level of reinstatement in VTC was greater in younger adults than older adults (t(38)=2.19, p =.0379).

Evidence for event-level reinstatement was identified in vIFG among younger adults (t(19)=3.67, p =.0016), but not older adults (t < 1), and this effect differed significantly between groups (t(38)=3.58, p =.0013). A similar trend for event-level reinstatement during CRs was also present in ANG (t(19)=1.80, p =.088) and dIFG (t(19)=1.86, p =.079) among younger adults, but not older adults (t <1), with the magnitude of reinstatement greater in the younger group than the older group within ANG (t(38)=2.59, p =.0135) but not dIFG (t(38)=1.53, p =.134). Although the magnitude of reinstatement was greater in younger adults than older adults in HC (t(38)=2.10, p =.043) and marginally in VTC (t(38)=1.85, p =.076), these effects did not reach significance in the younger group (all p > .22) or the older group (t < 1).

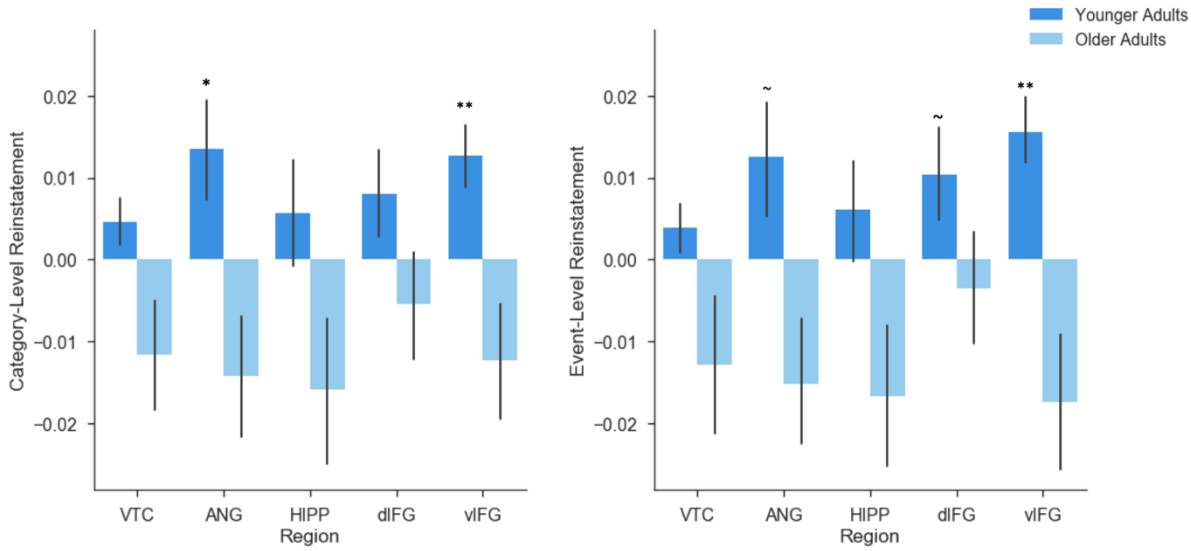

*Figure 8: Cortical-Level Reinstatement during CRs. Left: Category-level reinstatement (Within-event ERS – Between-category ERS). Right: Event-level reinstatement (Within-event ERS – Within-category ERS). Error bars represent standard error versus zero. Event-level reinstatement was evident in vIFG, with category-level reinstatement in both vIFG and ANG, but this is true only within the younger group. ** p < .01, *p < .05, ~p <.10*

Encoding-Retrieval Relationship

Given the observed decline in neural differentiation during encoding and the absence of significant reinstatement effects within the older group at retrieval, we next sought to determine whether the magnitude of cortical reinstatement during retrieval was related to the differentiation of

event representations during encoding. We assessed whether category discriminability in VTC at encoding [within category pattern similarity – between category pattern similarity] was related to category reinstatement in cortical regions during retrieval [within event ERS – between category ERS]. These analyses were conducted separately for hits and CRs. Among older adults, a significant positive relationship between these variables was evident during hits (r =.57, p < .009) but not during correct rejections (r = .028, p = 0.91) in dIFG (Figure 9). A similar pattern, that is, numerically larger correlation between differentiation in VTC at encoding and cortical reinstatement during retrieval during hits relative to correct rejections was observed in the remaining ROIs, but these relationships were not significant (vIFG: Hit: r =.31, p = .18, CR: r =-.035, p = .88; HIPP: Hit: r =.40, p = .089, CR: r = -.43, p = .06; ANG: Hit: r =.15, p = .53, CR: r =.044, p = .85; VTC: Hit: r =.26, p= .27, CR: r = -.11, p = .65). Among younger adults, category differentiation in VTC at encoding was not related to the magnitude of reinstatement during retrieval in any regions of interest during hits (all p > .31) or CRs (all p > .12).

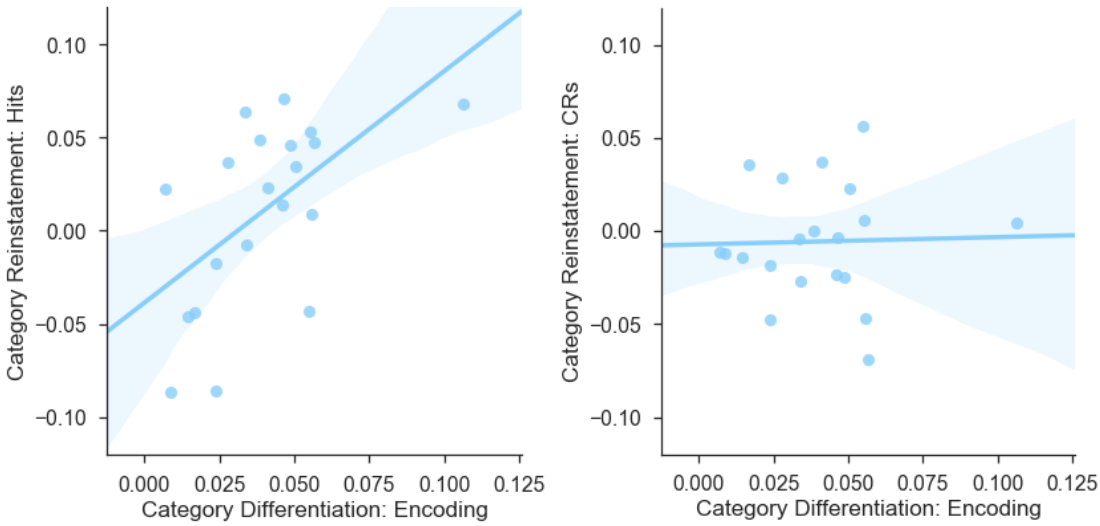

Figure 9: Category differentiation during encoding [within category-between category similarity] in VTC is related to the magnitude of cortical reinstatement in dIFG during hits (left) but not correct rejections (right) within the older group.

Discussion

The present study used univariate and multivariate analyses of fMRI data to establish whether age-related memory decline might be attributable to changes in representational content and/or strategic retrieval processes. We measured neural differentiation during encoding of paired associates

containing overlapping elements, and changes in regional BOLD activity, functional connectivity, and cortical reinstatement during retrieval conditions that placed low (intact pairs) and high (recombined pairs) demands on strategic retrieval processes. We obtained evidence for age-related reductions in the specificity of representational content during both encoding and retrieval, as well as selective deficits in the neural mechanisms necessary to reject recombined pairs, coupled with relatively intact mechanisms for endorsing intact pairs. These results demonstrate that age affects both representational quality and retrieval control processes, consistent with our claims from behavioural evidence (Trelle et al, 2017), but using fMRI to more directly measure representations and to separate effects at encoding from those at retrieval.

The observation that older adults exhibit a reduction in neural differentiation during encoding is consistent with disproportionate deficits in the ability to discriminate between events that share overlapping information, relative to those that are more distinct. In particular, whereas neural activity patterns in ventral temporal cortex could distinguish between events containing images from a different category (e.g., object vs scene) and subcategory (living vs nonliving object) in older adults, they could not reliably discriminate between different exemplars within a given subcategory (teapot vs umbrella). This is in contrast to younger adults, in which events could be discriminated based on neural activity patterns at each level, and in each case much more robustly than among older adults. This dedifferentiation within older adults manifested as both a reduction in pattern similarity for highly similar events (i.e. those sharing the same exemplar) coupled with increased pattern similarity for highly distinct events (i.e. those from the opposite stimulus category), relative to younger adults. This does not suggest a general increase in pattern similarity across events with age, nor a general decrease in pattern similarity with age, but rather a decline in both the *sensitivity* of neural responses to different stimuli and the *selectivity* of neural responses to different stimuli.

These results complement existing findings identifying both reduced within-category similarity and increased between-category similarity in older adults relative to younger adults during viewing of visual stimuli from different categories (e.g. faces, houses; Park et al., 2004; Carp et al., 2011). The present findings diverge however from some previous observations of age-invariant pattern discrimination between stimuli from different classes, such as words and pictures studied in

different semantic contexts (Wang et al., 2016) or between different audiovisual clips (St-Laurent et al., 2014). This difference across studies might reflect a reduction in the effect of age on discriminability of neural activity patterns when the information represented is more complex, e.g., multi-modal, automatically providing a more differentiated input. Importantly, the present data suggests that, at least within the visual domain, age-related dedifferentiation is present in ventral temporal cortex, and this represents one factor that likely contributes to deficits in episodic performance with age.

In addition to declines in representational quality during encoding, we predicted that the ability to engage frontally-mediated strategic retrieval processes would also be affected by age. In particular, older adults may be less likely than younger adults to engage strategic processes, such as recall-to-reject, to disqualify recombined pairs as having been studied. This proposal was supported by the present activation and connectivity results, as well as the results of the cortical reinstatement analyses. First, we identified age differences in the recruitment of *'retrieval control'* regions, as well as changes in hippocampal coupling with these regions, during memory retrieval. Specifically, whereas younger adults increased recruitment of vIFG and dIFG during correct rejections relative to hits, older adults recruited vIFG to a greater degree during hits relative to correct rejections, and did not vary recruitment of dIFG across trial types. Similarly, younger adults exhibited increased coupling between the hippocampus and vIFG during correct rejections relative to hits, whereas older adults did not modulate hippocampal coupling across conditions. Notably, the pattern of recruitment and connectivity exhibited by younger adults replicates that identified in previous work (Lepage et al., 2003, Achim & Lepage, 2005; Barredo et al., 2015; Bowman & Dennis, 2016), and is consistent with the goal-directed retrieval, selection, and monitoring of target details to disqualify recombined pairs as having been studied. The absence of this effect in older adults is consistent with existing findings of age-related reductions in the tendency to modulate recruitment of lateral prefrontal cortex in response to increasing demands on cognitive control processes during memory retrieval, and indeed to exhibit increased activity relative to younger adults in these regions under 'low' demand conditions (Giovanello & Schacter, 2011; McDonough et al., 2013). In the present study, the failure of older adults to increase recruitment of lateral prefrontal regions during correct rejections relative to hits may

indicate an impairment in the ability to recruit strategic retrieval processes, such as recall-to-reject, to successfully reject recombined pairs.

In further support of the proposal that younger adults are more likely than older adults to engage strategic recall-to-reject processes to support correct rejections, the present data revealed evidence for cortical reinstatement of encoding-related activity associated with the target associate's initial presentation during correct rejections only among younger adults. Specifically, younger adults exhibited evidence for cortical reinstatement in vIFG, dIFG, and angular gyrus, consistent with the goal-directed retrieval of target details by younger adults in order to disqualify recombined pairs as having been studied. Moreover, these data extend previous work identifying increased recruitment of these areas during recall-to-reject conditions by providing evidence that these regions, which are often implicated in controlled retrieval processes, play a role in representing the contents of goal-directed retrieval processes. This is also consistent with increased connectivity of the hippocampus with these regions, in particular the vIFG, during correct rejections relative to hits in younger adults. The absence of reinstatement effects during correct rejections among older adults is consistent with a reduced tendency to engage a retrieval strategy that involves the active retrieval of event details from memory, such as recall-to-reject. Instead, older adults may have relied primarily on the assessment of stimulus familiarity (Koen & Yonelinas, 2016), or the use of diagnostic monitoring heuristics to determine the likelihood that an event was previously experienced (e.g. "if I had seen this combination, I would have remembered it"; Gallo et al., 2006). Such a strategy would be unlikely to be associated with reinstatement of the same neural activity patterns that were elicited during encoding of the event, and could explain the absence of reinstatement effects among older adults during correct rejections.

Unlike rejecting recombined pairs, which places considerable demand on strategic retrieval processes (Rotello & Heit, 2000; Cohn & Moscovitch, 2007), endorsing intact pairs is thought to reduce these demands by increasing retrieval support through the presentation of a studied combination of items. Here we explored the possibility that this retrieval support may increase access to stored details among older adults, thus increasingly the likelihood that both groups might adopt a recall-to-accept strategy to endorse intact pairs. In partial support of this possibility, the results of the

univariate activity analyses revealed that both older and younger adults preferentially recruited the hippocampus and angular gyrus during hits relative to correct rejections. This finding is consistent with a growing literature identifying increased recruitment of these regions when endorsing previously experienced events, as compared to rejecting novel but experimentally familiar events (Bowman & Dennis, 2016). Notably, the engagement of these regions has frequently been associated specifically with successful recollection of previous events, as opposed to recognition based on a feeling of familiarity (Rugg & Vilberg, 2013; Wagner et al., 2005). This pattern raises the possibility that older and younger adults were engaging similar mechanisms to endorse intact pairs, and that this mechanism involved recollection of the target associate, which may have been facilitated by the correspondence between the stored representation and the retrieval cue (in this case, most likely based on semantic rather than perceptual information due to the absence of the pictorial stimuli at test). Such a possibility would be consistent with some existing behavioural observations of increased ability to access target details when endorsing intact pairs, as compared to rejecting recombined pairs (e.g. Cohn et al., 2008; Trelle et al., 2017).

The present cortical reinstatement results, however, offer only partial support for this possibility. In particular, evidence for reinstatement of target information was observed among younger adults during hits within ventral temporal cortex, but we did not observe evidence for cortical reinstatement among older adults. The absence of evidence for cortical reinstatement among the older group during hits is surprising given the pattern of univariate activation described above, as well as the present observation of category discriminability during encoding, which suggests that the events were at least perceived at this level of specificity within neural activity patterns in the older group. One possible explanation for our failure to detect cortical reinstatement in the older adult group is that the neural representations measured at test are less rich in information (e.g., perceptual or conceptual detail) than those measured at study. In particular, whereas the presence of pictorial input guided representational structure during encoding, this input was removed at retrieval (by replacement with word cues, in order to eliminate any recapitulation effects based solely on perception of the retrieval cue), and thus patterns related to a particular category had to be internally generated. Thus, it may be more difficult to detect the presence of category information in neural activity patterns during

retrieval, particularly among older adults, in which considerable declines in neural differentiation at the category level were observed during encoding.

Consistent with this possibility, the present data revealed a relationship between category differentiation during encoding in VTC and cortical reinstatement during hits in dIFG among older adults, such that those individuals with greater differentiation also exhibited greater reinstatement effects, at least within prefrontal cortex. This relationship suggests that individual differences in neural differentiation can constrain the ability to detect cortical reinstatement at retrieval, and that despite the absence of reinstatement evidence at the group level during hits, those older adults with greater neural differentiation also exhibited larger category-level reinstatement effects when endorsing intact pairs. As such, it may be the case that similar levels of reinstatement, at least at the category level, would be observed among older adults during hits if encoding quality were matched between older and younger adults. This possibility is consistent with existing work wherein age-related declines in cortical reinstatement in the context of a cued recall paradigm could be largely explained by neural dedifferentiation during encoding (Johnson et al., 2015), as well as work identifying comparable category-level classification accuracy during item recognition across age groups when group differences in category differentiation during encoding were absent (Wang et al., 2016). Thus, although we cannot draw definitive conclusions based on the current data, the relationship observed during hits is compatible with the possibility that older adults were able to retrieve general, categorical/semantic information about the target associate, and used this information to support a recall-to-accept strategy to endorse intact pairs.

Notably, the same relationship between differentiation at encoding and reinstatement during retrieval was not observed during correct rejections. This suggests that the relationship between encoding quality and reinstatement evidence may be modulated by demands on strategic processes during retrieval. That is, although representational quality is a critical prerequisite for reinstatement, a direct relationship may be observed only under conditions in which demands on strategic retrieval are relatively low, such as during hits to intact pairs in the present study, which may help to support the retrieval of event details. In contrast, under conditions that place considerably greater demands on cognitive control processes, such as rejecting recombined pairs, the ability to engage these processes

may become a more critical determinant of the degree to which episodic details are successfully retrieved, and reinstatement effects observed. This possibility may explain apparently contradictory findings in the literature, such as age-related reductions in reinstatement evidence despite comparable neural differentiation at encoding as younger adults when demands on strategic retrieval processes are high, such as in test of cued recall (St-Laurent et al., 2014) and source constrained retrieval (Abdulrahman et al., 2017), but comparable reinstatement effects when demands on these processes are low, such as during item recognition (Wang et al., 2016). The present results, together with previous work, highlight the importance of considering demands on cognitive control processes during memory retrieval, as well as demands on representational specificity (i.e. what type/level of representation is necessary to support successful task performance), when interpreting the presence/absence of cortical reinstatement effects among older adults.

Another factor that impacts the present study, as well as existing studies of cognitive aging, is the high level of heterogeneity observed within the older adult sample. That is, although we observe group differences between younger and older adults with respect to both neural differentiation and the ability to engage strategic control processes, there is variability in the degree to which these factors are impacted across older individuals. This variability is difficult to account for in small group experiments such as this, and instead require studies with larger samples of older adults, in which we can explore individual differences in these neural mechanisms, and the degree to which this can explain variability in episodic memory decline. Nevertheless, the present results point to two factors that are affected with age, namely representational quality and retrieval control processes, which are undoubtedly critical focal points for future research to explore further as we approach a more thorough understanding of the mechanisms underlying changes in episodic memory within the aging population.

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