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The Retrieval-related Anterior shift is Moderated by Age and Correlates with Memory Performance

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2 **The Retrieval-related Anterior shift is Moderated by Age and Correlates with Memory**
3 **Performance**

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13

14 **Abbreviated Title:**

15 Retrieval-related Anterior Shift, Age, and Memory

16

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19

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23

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25 None

26

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41 **Abstract**

42 Recent research suggests that episodic memory is associated with systematic differences in the
43 localization of neural activity observed during memory encoding and retrieval. The retrieval-related
44 anterior shift is a phenomenon whereby the retrieval of a stimulus event (e.g., a scene image) is associated
45 with a peak neural response which is localized more anteriorly than the response elicited when the
46 stimulus is experienced directly. Here, we examine whether the magnitude of the anterior shift, i.e., the
47 distance between encoding- and retrieval-related response peaks, is moderated by age, and also whether
48 the shift is associated with memory performance. Younger and older human subjects of both sexes
49 underwent fMRI as they completed encoding and retrieval tasks on word-face and word-scene pairs. We
50 localized peak scene- and face-selectivity for each individual participant within the face-selective
51 precuneus (PCU) and in three scene-selective (parahippocampal place area [PPA], medial place area
52 [MPA], occipital place area [OPA]) regions of interest (ROIs). In line with recent findings, we identified
53 an anterior shift in PPA and OPA in both age groups and, in older adults only, in MPA and PCU also. Of
54 importance, the magnitude of the anterior shift was larger in older than in younger adults. The shift within
55 the PPA exhibited an age-invariant across-participant negative correlation with source memory
56 performance, such that a smaller displacement between encoding- and retrieval-related neural activity was
57 associated with better performance. These findings provide novel insights into the functional significance
58 of the anterior shift, especially in relation to memory decline in older age.

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67 **Significance Statement**

68 Cognitive aging is associated with reduced ability to retrieve precise details of previously experienced
69 events. The retrieval-related anterior shift is a phenomenon in which category-selective cortical activity at
70 retrieval is localized anterior to the peak activity at encoding. The shift is thought to reflect a bias at
71 retrieval in favor of semantic and abstract information at the expense of low-level perceptual detail. Here,
72 we report that the anterior shift is exaggerated in older relative to younger adults, and we demonstrate that
73 a larger shift in the parahippocampal place area is associated with poorer memory performance. These
74 findings suggest that the shift is sensitive to increasing age and that it is moderated by the quality and
75 content of the retrieved episode.

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93 **1. Introduction**

94 Cognitive aging is associated with a disproportionate decline in memory for contextual details of
95 previously experienced episodes. Relative to younger adults, older adults tend to retrieve memories with
96 less specificity and fewer details (Levine et al., 2002; Addis et al., 2008), while memory for semantic
97 information and general knowledge remains relatively preserved (Nilsson, 2003; Nyberg et al., 2012).
98 Recent findings suggest that even when a memory of an event is successfully retrieved, the precision and
99 specificity of the retrieved content is reduced with increasing age (Nilakantan et al., 2018; Korkki et al.,
100 2020). These findings are consistent with the notion that older adults rely on relatively abstract or ‘gist-
101 like’ memories and experience a reduction in episodic detail (Koustaal & Schacter, 1997; Dennis et al.,
102 2007; 2008, Gallo et al., 2019).

103 Episodic memory retrieval is associated with the ‘reactivation’ of patterns of cortical activity
104 elicited when the episode was experienced, a phenomenon termed cortical reinstatement (for reviews see
105 Danker and Anderson, 2010; Rissman and Wagner, 2012; Rugg et al., 2015; Xue, 2018). The strength and
106 specificity of cortical reinstatement have been reported to be reduced in older age (Bowman et al., 2019;
107 St-Laurent & Buchsbaum, 2019; Folville et al., 2020; Hill et al., 2021, but see Wang et al., 2016; Thakral
108 et al., 2017). The strength of cortical reinstatement has also been reported to predict the likelihood of
109 successful retrieval, leading to the proposal that cortical reinstatement indexes the amount of retrieved
110 episodic content (e.g., Johnson et al., 2009; Trelle et al., 2020; Hill et al., 2021). Thus, age-related
111 reductions in the strength of cortical reinstatement may reflect older adults’ tendency to retrieve less
112 detailed episodic information than their younger counterparts.

113 Whereas cortical reinstatement is a well-established phenomenon, recent research demonstrates
114 that there are systematic differences in the localization of content-selective cortical activity observed at
115 encoding and retrieval, thus challenging the notion that the neural populations active at encoding are
116 merely reactivated at retrieval. Mental imagery and retrieval of perceptual stimuli (e.g., scene images)
117 have been reported to be associated with neural activation that peaks slightly anterior to the regions
118 maximally recruited during direct perception of the stimuli (for review, see Favilla et al., 2020). This

119 retrieval-related bias towards more anterior neural recruitment has been termed the ‘anterior shift’ (e.g.,
120 Rugg & Thompson-Schill, 2013; Bainbridge et al., 2021). The functional significance of the shift is
121 largely unknown, although it has been suggested that it reflects a ‘transformation’ of a mnemonic
122 representation such that different attributes of an event (such as perceptual details) are differentially
123 emphasized at encoding and retrieval (Favilla et al., 2020). Given that the posterior-anterior axis of
124 occipito-temporal cortex has been held to be hierarchically organized, forming a gradient of increasing
125 abstraction, the anterior shift may reflect a shift towards abstracted representations that emphasize
126 conceptual attributes of a stimulus event at the expense of ‘lower-level’ perceptual and sensory features
127 (e.g., Peelen & Caramazza, 2012; Martin et al., 2018).

128 Here, younger and older adults underwent fMRI as they viewed concrete words paired with
129 images of faces and scenes. Participants remained in the scanner to complete a retrieval task during which
130 they were presented with old or novel words under the requirement to retrieve the image associated with
131 each word judged to be old. We addressed two key questions. First, we examined whether the anterior
132 shift is moderated by age. In light of evidence suggesting that older adults tend to retrieve more gist-like
133 (abstracted) memories than younger individuals, the aforementioned ‘abstraction’ account of the anterior
134 shift leads to the prediction that it will be exaggerated in older relative to young adults. Second, we asked
135 whether the anterior shift is a moderator of individual differences in memory performance. According to
136 the abstraction account, to the extent that a memory test depends on the retrieval of detailed perceptual
137 information, a negative relationship between the magnitude of the shift and memory performance is
138 predicted.

139

140 **2. Materials and Methods**

141 Outcomes of analyses of data from the present experiment have been described in two prior
142 reports (Srokova et al., 2020; Hill et al., 2021). Descriptions of the experimental design, procedure, and
143 the outcomes of the behavioral analyses were reported previously and are summarized here for the

144 convenience of the reader. The analyses of the retrieval-related ‘anterior shift’ described below have not
145 been reported previously.

146 All experimental procedures were approved by the Institutional Review Boards of The University
147 of Texas at Dallas and The University of Texas Southwestern Medical Center. Each participant gave
148 informed consent prior to their participation in the study.

149

150 **2.1. Participants**

151 Twenty-seven younger and 33 older adult participants were recruited from the University of
152 Texas at Dallas and surrounding metropolitan Dallas communities. All participants were compensated
153 \$30/hour and were reimbursed up to \$20 for travel. Participants were right-handed, had normal or
154 corrected-to-normal vision, and were fluent English speakers before the age of five. None of the
155 participants had a history of neurological or cardiovascular disease, diabetes, substance abuse, or current
156 or recent use of prescription medication affecting the central nervous system. Potential MRI-eligible
157 participants were excluded if they did not meet pre-determined performance criteria on our
158 neuropsychological test battery (see below).

159 Three younger and nine older adults were excluded from subsequent analyses. Two participants
160 voluntarily withdrew from the study and one participant was excluded due to technical difficulties during
161 MRI scanning. Additionally, the behavioral performance of two participants resulted in critical memory
162 bins having too few trials, and six participants were excluded due to at- or near-chance source memory
163 performance (probability of source recollection, pSR , < 0.1). Lastly, one participant was excluded due to
164 an incidental MRI finding. The final sample consisted of 24 younger adults (15 females; age range = 18-
165 28 years, M (SD) = 22.4 (3.2) years) and 24 older adults (14 females; age range = 65-75 years, M (SD) =
166 70.1 (3.4) years).

167

168 **2.2. Neuropsychological Testing**

169 All participants completed a neuropsychological test battery which was administered on a
170 separate day prior to participation in the fMRI session. The battery consisted of the following tests: Mini-
171 Mental State Examination (MMSE), the California Verbal Learning Test II (CVLT: Delis et al., 2000),
172 Wechsler Logical Memory Tests 1 and 2 (Wechsler, 2009), the Symbol Digit Modalities test (SDMT;
173 Smith, 1982), the Trail Making Tests A and B (Reitan & Wolfson, 1985), the F-A-S subtest of the
174 Neurosensory Center Comprehensive Evaluation for Aphasia (Spreen & Benton, 1977), the Forward and
175 Backward digit span subtests of the revised Wechsler Adult Intelligence Scale (Wechsler, 1981),
176 Category fluency test (Benton, 1968). Raven's Progressive Matrices List I (Raven et al., 2000), and the
177 Wechsler Test of Adult Reading (WTAR; Wechsler, 2001). Potential participants were not accepted into
178 the study for any of the following reasons: if their MMSE score was below 27, if they scored more than
179 1.5 standard deviations below age- and education-adjusted norms on one or more long-term memory test
180 or on at least two non-memory tests, or if their estimated full-scale IQ was less than 100. These criteria
181 were employed to minimize the likelihood of including older participants with mild cognitive impairment
182 or early dementia.

183

184 **2.3. Experimental Materials**

185 Experimental stimuli were presented using Cogent 2000 (www.vislab.ucl.ac.uk/cogent_2000.php)
186 implemented in Matlab (www.mathworks.com). The study and test phases were completed inside the
187 scanner, and stimuli were projected onto a translucent screen placed at the rear end of the scanner bore
188 and viewed through a mirror fixed onto the head coil. The critical experimental stimuli comprised 288
189 concrete nouns, 96 colored images of faces (48 male, 48 female) and 96 colored images of scenes (48
190 urban, 48 rural). An additional 68 words and 40 images were used as practice stimuli or as filler trials
191 during the experiment proper. The critical stimuli were used to create 24 stimulus lists which were
192 assigned to yoked pairs of younger and older participants. Each study list consisted of 192 randomly
193 selected word-image pairs interspersed with 96 null trials (white fixation cross) and divided into 4 study
194 blocks. Consequently, a single study block comprised 48 critical word-image trials (divided equally

195 between male and female faces, and urban and rural scenes) and 24 null trials. The test list comprised 192
196 old (studied) trials, 96 new trials, and 96 null trials, evenly distributed into 4 test blocks. The orderings of
197 the items in the study and test lists were pseudorandomized while ensuring that participants experienced
198 no more than three consecutive critical trials of the same image category, no more than three new trials,
199 and no more than two null trials.

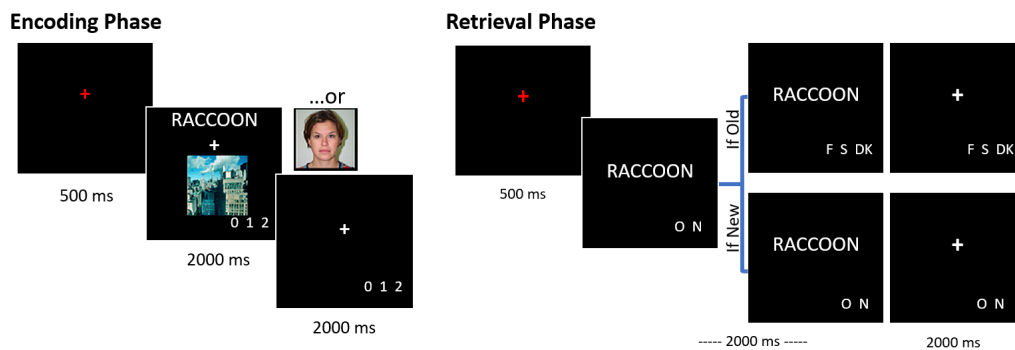
200

201 **2.4. Experimental Procedure**

202 Participants received instructions and completed practice study and test tasks prior to entering the
203 scanner. Participants then underwent fMRI as they completed two study-test cycles. Each cycle consisted
204 of two study runs (approx. 8 minutes each) followed by two test runs (approx. 10 minutes each). A
205 schematic of the study and test tasks is illustrated in Figure 1. Each study trial began with a red fixation
206 cross presented for 500 ms. The fixation cross was followed by the presentation of the word-image pair,
207 which remained on the screen for 2000ms. When presented with an image of a face, participants were to
208 imagine the person in the image interacting with the object. During scene trials, participants imagined the
209 object interacting or moving around within the scene. Participants rated the vividness of the imagined
210 scenario on a 3-point scale (“not vivid”, “somewhat vivid”, “very vivid”) using a scanner-compatible
211 button box and the index, middle, and ring fingers of the right hand, respectively. The presentation of the
212 word-image pair was followed by a white fixation cross that lasted for an additional 2000 ms. Participants
213 were allowed to make their vividness response from the onset of the word-image pair until the termination
214 of the white fixation cross, thus providing a 4000 ms response window.

215 Each test trial began with a red fixation cross for 500 ms, which was immediately replaced by the
216 test item for a duration of 2000 ms. Response prompts appeared underneath the item at its onset.
217 Participants were instructed first to indicate whether they remembered seeing the word at study by
218 making an “Old” or “New” response. For each word endorsed “Old”, participants went on to make a
219 source memory judgment, indicating whether the word had been studied with a face or a scene. A third
220 “Don’t Know” option was included to discourage participants from guessing. As with the study phase, the

221 test item was replaced with a white fixation cross for 2000 ms, and participants were allowed to make
 222 their memory judgments throughout the full 4000 ms response window. Responses were made using a
 223 scanner-compatible button box. Old / New responses were made with the index and middle fingers of the
 224 right hand with the ordering of the fingers counterbalanced across participants. The Face / Scene / Don't
 225 Know responses were made with the index, middle, and ring fingers of the right hand and were also
 226 counterbalanced across participants while ensuring that the Don't Know response was never assigned to
 227 the middle finger.



228
 229 **Figure 1:** Schematic of the encoding and retrieval tasks. At encoding, participants were presented with
 230 words paired with an image of a face or a scene. At retrieval, they were presented with a test word and
 231 required to indicate whether they remembered seeing the word during the encoding phase, and if so,
 232 whether it had been paired with an image of a face or a scene.
 233

234 **2.5. MRI Data Acquisition and Preprocessing**

235 Functional and structural MRI data were acquired using a Philips Achieva 3T MRI scanner
 236 (Philips Medical System, Andover, MA, US) equipped with a 32-channel head coil. Anatomical scans
 237 were acquired with a T1-weighted 3D magnetization-prepared rapid gradient echo (MPRAGE) pulse
 238 sequence (field of view [FOV] = 256 x 256 mm, voxel size = 1 x 1 x 1 mm, 160 slices, sagittal
 239 acquisition). Functional data was obtained with a T2*-weighted echo-planar-imaging (EPI) sequence
 240 (FOV = 240 x 240 mm, TR = 2 s, TE = 30 ms, flip angle = 70°). EPI volumes consisted of 34 axial slices
 241 acquired in an ascending order parallel to the anterior-posterior commissure, with an interslice gap of 1
 242 mm. The voxel size of the EPI volumes was 3 mm isotropic.

243 The MRI data were preprocessed using Statistical Parametric Mapping (SPM12, Wellcome
244 Department of Cognitive Neurology, London, UK) and custom Matlab code (MathWorks). The functional
245 data were realigned to the mean EPI image and slice-time corrected using *sinc* interpolation with
246 reference to the 17th slice. Following realignment, images were reoriented and normalized to MNI space
247 using a sample-specific EPI template according to previously published procedures (de Chastelaine et al.,
248 2011, 2016). This approach ensures an unbiased contribution of each age group to the normalization
249 template, minimizing age biases in the extent of the warping required to normalize each participant's
250 images (Buckner et al., 2004). Note that it is essential to characterize the anterior shift in a standardized
251 space (in the present case, defined by MNI coordinates) when contrasting group differences in the
252 magnitude of the shift and assessing its relationship with behavior. Lastly, the functional images were
253 smoothed with an 8 mm full-width at half-maximum Gaussian kernel. The time series of the study and
254 test runs were concatenated using the *spm_fmri_concatenate* function prior to the implementation of the
255 first-level general linear model (GLM; see below).

256

257 **2.6. Data Analysis**

258 **2.6.1. Whole-brain Univariate Analysis**

259 The functional data were analyzed with a two-stage univariate GLM approach. At the first stage,
260 separate GLMs were implemented for the study and test data of each participant. The study trials were
261 binned into two events of interest (face and scene trials) and the neural activity elicited by the trials was
262 modeled with a boxcar function extending over the 2s period during which the word-image pair remained
263 on the screen. The boxcar regressors were convolved with two canonical hemodynamic response
264 functions (HRFs): SPM's canonical HRF and an orthogonalized delayed HRF. The delayed HRF was
265 created by shifting the canonical HRF by one TR (2s) later and using the Gram-Schmidt procedure to
266 orthogonalize it with the canonical HRF (Andrade et al., 1999). The delayed HRF did not produce any
267 findings in addition to those described below and thus is not discussed further. In addition to the events of
268 interest described above, the GLM for the study phase also modeled the following trials as covariates of

269 no interest: filler trials, trials with missing or multiple responses, trials receiving a response before 500 ms
270 or after 4500 ms following stimulus onset, and the 30-second rest period. Additional covariates of no
271 interest comprised 6 motion regressors reflecting rigid-body translation and rotation, spike covariates
272 regressing out volumes with transient displacement > 1 mm or $> 1^\circ$ in any direction, and the mean signal
273 of each scanner run. The parameter estimates from the first level GLM were carried over to a 2 (age
274 group: younger, older) \times 2 (study trial: face, scene) mixed factorial ANOVA which was height-
275 thresholded at $p < 0.001$ uncorrected, retaining only those clusters which survived FWE correction at $p <$
276 0.05.

277 The test phase trials were binned into five events of interest: face trials associated with a correct
278 source memory judgement (face source correct), scene trials associated with a correct source memory
279 judgement (scene source correct), recognized old items which received an incorrect source memory
280 judgement or a Don't know response (source incorrect + DK), studied items attracting an incorrect 'new'
281 response (item miss), and new items attracting a correct 'new' response (correct rejection). Events of
282 interest were modeled with a delta function time-locked to stimulus onset (the choice of a delta function
283 was motivated by the presumed short-lived nature of the processing of the retrieval cue) and convolved
284 with the canonical and orthogonalized delayed HRFs. As with the encoding data, the delayed HRF did not
285 identify any additional clusters of interest. Covariates of no interest comprised filler trials, false alarms,
286 trials with missing or multiple responses, trials attracting a response before 500 ms and after 4500 ms
287 following stimulus onset, the 30 second rest periods, six motion regressors reflecting translational and
288 rotational displacement, motion spike covariates, and the mean signal for each run. The second level
289 GLM took the form of a 2 (age group: younger, older) \times 5 (test trial: face source correct, scene source
290 correct, source incorrect + DK, item miss, correct rejection) mixed factorial ANOVA. Analogous to the
291 GLM of the study data, the ANOVA was height-thresholded at $p < 0.001$ uncorrected and clusters were
292 retained if they exceeded the FWE corrected threshold of $p < 0.05$.

293

294 **2.6.2. Anterior shift in scene- and face-selectivity between study and test**

295 The primary aim of the analyses described below centered on examining age differences and the
296 functional significance of the retrieval-related anterior shift. Here, the term ‘anterior shift’ refers to a
297 statistically significant difference in the localization of neural activity observed at encoding and retrieval,
298 such that the retrieval of the memory of a perceptual stimulus (e.g., an image of a scene in the context of
299 the present study) is associated with a peak response in category-selective cortex that is anterior to the
300 peak response elicited when the image was experienced directly. The present analyses were restricted to
301 scene- and face-selective cortical regions where significant clusters could be identified across both age
302 groups (i.e. clusters surviving the FWE corrected threshold of $p < 0.05$) in both the encoding and retrieval
303 phases (see 3.2, Whole-Brain Results). The resulting scene-selective ROIs were localized to the
304 parahippocampal place area (PPA), medial place area (MPA; sometimes referred as retrosplenial cortex),
305 and occipital place area (OPA). Among face-selective clusters, only the precuneus (PCU) could be
306 identified at both encoding and retrieval. When examining the coordinates of peak scene- and face-
307 selective responses within these regions at the individual subject level, the analyses were restricted to
308 anatomical masks which corresponded to the cortical regions encompassing the clusters described above.
309 Each anatomical mask was defined by reference to SPM’s Neuromorphometrics atlas with the exception
310 of the MPA, which was not well captured by the labels provided by Neuromorphometrics and was instead
311 defined by reference to the Atlas of Intrinsic Connectivity of Homotopic Areas (AICHA; Joliot et al.,
312 2015). The PPA was delimited by the parahippocampal and fusiform gyrus labels. The OPA mask was
313 created using the atlas labels for the inferior and middle occipital gyri and the PCU mask comprised the
314 precuneus and posterior cingulate labels. The MPA was defined using the following AICHA labels:
315 precuneus (AICHA indices: 265, 267, 269 for the left hemisphere; 266, 268, 270 for the right
316 hemisphere), parieto-occipital (left hemisphere: 283, 285, 289, 291; right hemisphere: 284, 286, 290,
317 292), and posterior cingulate (left hemisphere: 253, 255; right hemisphere: 254, 256). The AICHA atlas
318 was resampled to 3mm isotropic voxels to match the resolution of the functional data prior to ROI
319 definition. More details about each mask are given in Table 1.

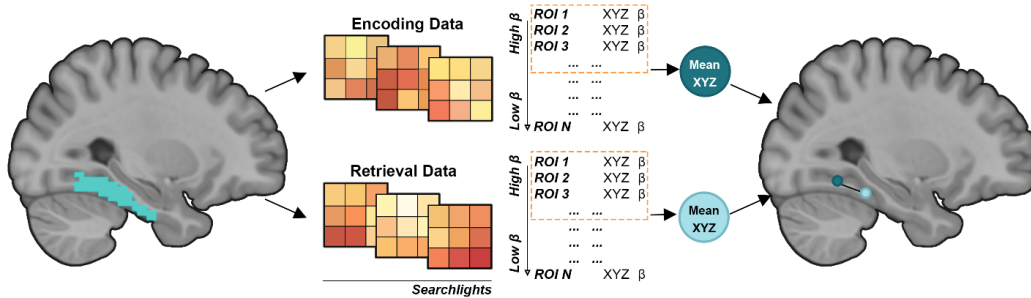
320 Using the outcome of each participant's 1st level GLMs, we computed *scenes > faces* and *faces >*
321 *scenes* contrasts from the encoding data, and *scene source correct > face source correct* and *face source*
322 *correct > scene source correct* contrasts from the retrieval data. The contrasts at retrieval were limited to
323 source correct trials to ensure that any age effects in the anterior shift were not confounded by differential
324 mixing of trials associated with successful and unsuccessful source recollection. Next, we performed
325 anatomically constrained univariate searchlight analyses on spherical ROIs (i.e. searchlights) of 5 mm
326 radius that were iteratively centered around each voxel falling within a given anatomical mask. The
327 voxels comprising each searchlight were restricted to those that fell within the relevant mask to ensure
328 that we did not intrude on adjacent cortical regions. This approach resulted in truncated spheres at the
329 mask edges, and any searchlights that contained fewer than 6 voxels were eliminated from the analysis.
330 The final numbers of searchlights included in these analyses and their sizes are given in Table 1. Note that
331 the anatomical masks comprised voxels common to all subjects and both task phases. As a result, any task
332 and age differences in the localization of category selectivity could not have arisen due to age or task
333 differences in the number of the searchlights employed within each ROI. We also conducted a secondary
334 analysis in which searchlights were allowed to extend over the mask edges into adjacent gray matter (as
335 defined by SPM's Tissue Probability Mask). This analysis yielded results that were essentially identical to
336 those described below.

337 For each participant, mean across-voxel parameter estimates corresponding to the scene- and
338 face-selective encoding and retrieval contrasts were extracted from each searchlight. We employed scene
339 *> faces* (encoding) and *scene source correct > face source correct* (retrieval) contrasts when examining
340 selectivity within the PPA, MPA and OPA. The face-selective *face > scene* and *face source correct >*
341 *scene source correct* contrasts were used in the case of the face-selective PCU. To localize peaks
342 manifesting maximal scene or face selectivity in each region, for each participant we ranked the
343 searchlights in terms of their mean category-selective responses and selected the top 5%. This was done
344 separately for the encoding and retrieval contrasts. The MNI coordinates of the centers of these spheres
345 were then averaged across each plane to compute the coordinates of their centroid, and this defined the

346 locus of peak selectivity. This approach resulted in two centroids for each participant and ROI, one
347 defining the location of peak category selectivity at encoding and the other at retrieval. Encoding-retrieval
348 shifts were defined as the distance (in mm) between the two centroids along the posterior – anterior plane
349 (i.e. the difference between the respective Y coordinates). Thus, negative values would indicate a
350 retrieval-related posterior shift (such that the peak category selectivity at retrieval is located posterior to
351 the encoding peak) and positive values indicate an anterior shift (such that the retrieval peak is localized
352 anterior to the encoding peak). A schematic describing the analysis approach is illustrated in Figure 2.
353 The searchlight approach to estimating peak selectivity was motivated by the aim of avoiding the pitfalls
354 associated with approaches such as identifying a single ‘peak voxel’. Notably, the size of the effect
355 estimated from a peak voxel overestimates the ‘true’ effect size by the virtue of the summation of signal
356 with positively biased noise (Kriegeskorte et al., 2010), inflating measurement error in the localization of
357 peak selectivity. The ‘multiple searchlight’ metric described above provides a spatially smoothed estimate
358 of the locus of a peak effect that minimizes the impact of measurement error caused by positive bias.

359 To ensure the results we report below were not dependent on the choice of searchlight parameters
360 (i.e., searchlight radius and proportion of top ranked searchlights), we conducted additional analyses
361 employing searchlights of 3 mm, 5 mm and 8 mm radius while selecting the top 1%, 5% or 10% of
362 searchlights to build the centroids. The effect of age group (see 3.3. *Retrieval-related Anterior Shift*
363 below) remained stable regardless of parameter choice. A reliable relationship across participants between
364 the size of the shift and memory performance in the PPA (see 3.4 *Relationship with Memory Performance*
365 below) was however evident only for the 5 mm and 8 mm searchlights. We note that since we eliminated
366 searchlights containing fewer than 6 voxels, and a full 3 mm searchlight contained only 7 voxels,
367 approximately 60% of the 3mm searchlights in the PPA were lost because they extended outside the
368 boundary of the anatomical mask (by contrast, only 5% were lost in the case of the 5 mm radius
369 searchlight). We attribute the failure to find a reliable relationship between the PPA anterior shift and
370 memory performance when employing the 3mm searchlights to this data loss and the attendant increase in
371 measurement noise.

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Figure 2: Schematic illustration of the encoding-retrieval displacement analysis pipeline. Searchlights were iteratively centered around every voxel inside a given anatomical mask. We selected the top 5% most category-selective spheres, separately for the encoding and retrieval data. The MNI coordinates of the searchlight centers were averaged to compute the center of mass (centroids) of category selectivity. The retrieval-related anterior shift was defined as the distance (in mm) between the encoding and retrieval centroids along the posterior-anterior plane. See main text for details.

381
382

Table 1: Size of the anatomical regions of interest, the number of searchlights from which parameter estimates were extracted, and the mean (SD) size of the searchlights.

	<i>Mask size (in voxels)</i>	<i>Number of searchlights</i>	<i>Mean (SD) searchlight size (in voxels)</i>
Scene ROIs			
<i>Left PPA</i>	410	388	11.56 (3.14)
<i>Right PPA</i>	404	381	11.73 (3.26)
<i>Left MPA</i>	633	625	14.28 (3.75)
<i>Right MPA</i>	688	669	14.51 (3.67)
<i>Left OPA</i>	645	636	13.37 (3.55)
<i>Right OPA</i>	561	550	13.12 (3.47)
Face ROIs			
<i>Left PCU</i>	913	902	13.79 (3.37)
<i>Right PCU</i>	816	806	13.33 (3.26)

383

384 **2.6.3. Statistical Analyses**

385 Statistical analyses were performed using R software (R Core Team, 2020). Statistical tests were
386 considered significant at $p < 0.05$ unless otherwise stated (e.g., see exploratory analyses in 3.4.
387 *Relationship with Memory Performance*, where we correct for family-wise error). ANOVAs were
388 performed using the afex package (Singmann et al., 2016) and degrees of freedom were corrected for
389 nonsphericity using the Greenhouse-Geisser procedure (Greenhouse and Geisser, 1959). All t-tests were

390 performed using the t.test function and regression analyses were performed using the lm function, both in
391 base R. Partial correlations were conducted using pcor.test in the ppcor package (Kim, 2015).

392

393 **3. Results**

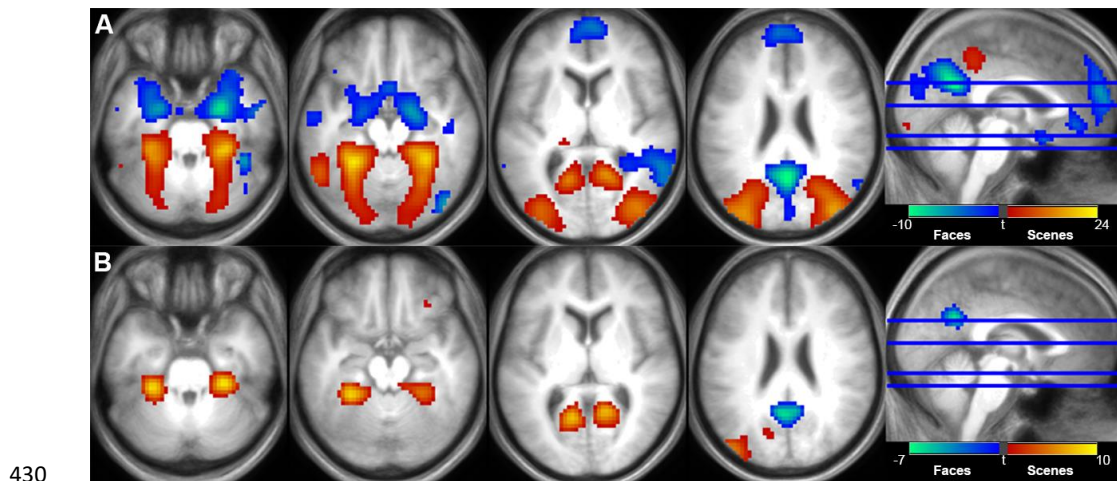
394 **3.1. Behavioral Results**

395 Behavioral performance and neuropsychological test performance have been reported previously
396 (Srokova et al., 2020; Hill et al., 2021) and are only briefly summarized below. With regards to
397 neuropsychological test performance, younger adults outperformed older adults on the CVLT Short Delay
398 – Free recall, CVLT recognition – False alarms, WMS Logical Memory I and II, SDMT, Trails A and B,
399 and Raven’s matrices. On the experimental task, item recognition (Pr) was operationalized as the
400 difference between hit rate (the proportion of items correctly endorsed ‘old’) and the false alarm rate (the
401 proportion of new items incorrectly endorsed ‘old’). ANOVA revealed a main effect of age ($F_{(1,46)} =$
402 10.112 , $p = 0.003$, $\text{partial-}\eta^2 = 0.180$), reflective of higher Pr in younger (M [SD] = 0.68 [0.17]) relative
403 to older adults (M [SD] = 0.54 [0.13]). The ANOVA also identified a main effect of image category
404 ($F_{(1,46)} = 5.443$, $p = 0.024$, $\text{partial-}\eta^2 = 0.106$), reflective of higher Pr for words studied with faces (M [SD]
405 = 0.63 [0.16]) relative to scenes (M [SD] = 0.60 [0.15]). The interaction between age group and image
406 category was not significant ($F_{(1,46)} = 0.766$, $p = 0.386$, $\text{partial-}\eta^2 = 0.016$). Source memory performance
407 (pSR) was operationalized by a single high-threshold model (Snodgrass and Corwin, 1988; see also
408 Gottlieb et al., 2010; Mattson et al., 2014) using the formula: $\text{pSR} = [\text{pSource correct} - 0.5 * (1 - \text{pDon't}$
409 $\text{Know})] / [1 - 0.5 * (1 - \text{pDon't Know})]$, where ‘pSource Correct’ and ‘pDon’t know’ refer to the
410 proportion of correctly recognized old trials receiving an accurate source memory judgement or a ‘Don’t
411 Know’ response, respectively. An independent samples t-test revealed that pSR was significantly lower in
412 older (M [SD] = 0.51 [0.16]) than in younger adults (M [SD] = 0.68 [0.18]; $t_{(45.51)} = -3.440$, $p = 0.001$).

413

414 **3.2. Whole-Brain Results**

415 Figure 3-A illustrates the *Scene > Face* and *Face > Scene* contrasts at encoding, and Figure 3-B
 416 depicts the *Scene source correct > Face source correct* and *Face source correct > Scene source correct*
 417 contrasts at retrieval. These results have been reported previously (Hill et al., 2021) and are re-reported
 418 here because of their relevance to the present analyses and ROI definition (we note however that Hill et
 419 al., 2021 focused on face and scene recollection contrasts [*face/scene source correct > source incorrect +*
 420 *DK*], the outcomes of which are highly similar to those reported here). At encoding, scene-selective
 421 clusters were identified along the parahippocampal and fusiform gyri, extending into the retrosplenial and
 422 medial occipital cortices. Face-selective clusters were identified in the precuneus/posterior cingulate
 423 cortex, medial prefrontal cortex, and along the medial temporal lobe bilaterally extending into the
 424 amygdala and anterior hippocampus. Face-selective clusters were also evident in middle temporal gyri
 425 and the right fusiform cortex. At retrieval, scene-selective clusters were evident in bilateral
 426 parahippocampal cortex, retrosplenial cortex, and the left middle occipital cortex along with a cluster in
 427 the right orbitofrontal cortex extending into the subgenual anterior cingulate cortex. The sole face-
 428 selective cluster at retrieval was observed in the precuneus, extending into the posterior cingulate cortex.
 429



430
 431 **Figure 3:** Univariate scene-selective (red) and face-selective (blue) effects at encoding (A) and retrieval
 432 (B), collapsed across age groups. Clusters are overlaid on the across-participant mean T1 image. In both
 433 cases, clusters are displayed at $p < 0.001$ after FWE cluster size correction ($p < 0.05$).

434

435

436

437 **3.3. Retrieval-related Anterior Shift**

438 First, we aimed to establish which ROIs, if any, exhibited a retrieval-related anterior shift. To this
 439 end, we examined whether the coordinates of retrieval centroids were systematically displaced relative to
 440 the encoding centroids. To achieve this, for each participant we measured the distance along the Y plane
 441 in MNI space between encoding and retrieval centroids. We then tested whether these distances were
 442 significantly different from zero, using a one sample t-test. As noted previously (see 2.6.2. *Anterior shift*
 443 *in scene- and face-selectivity between study and test*), distance measures greater than zero indicate that the
 444 retrieval centroid is shifted anteriorly to the encoding centroid, whereas negative values indicate a
 445 posterior shift. Figure 4 depicts the encoding and retrieval centroids and their corresponding distances for
 446 each individual participant. As is evident from Table 2, in younger adults there was a reliable anterior
 447 shift in bilateral PPA and OPA, while the shift was not significantly different from zero in either the MPA
 448 (for scenes) or the PCU (for faces). By contrast, older adults exhibited a reliable anterior shift in all ROIs
 449 except for the left MPA, where it approached significance. Given the consistent trend in all ROIs towards
 450 a retrieval-related anterior shift, in the interest of clarity we refer to this simply as the ‘anterior shift’ in
 451 the analyses described below.

452

453 **Table 2:** Mean (SD) of retrieval-related anterior shift (in mm) and the outcomes of one-sample t-tests
 454 against zero.

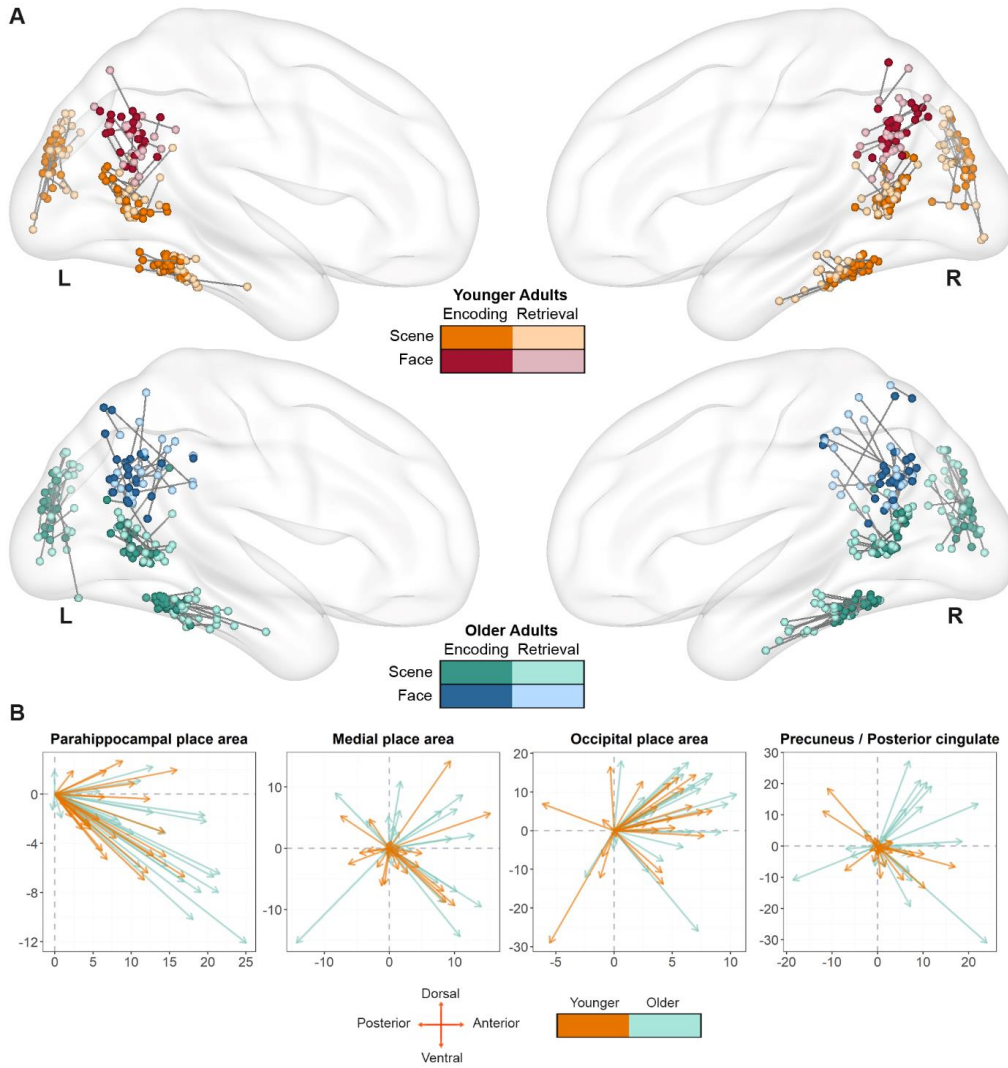
	<i>Younger Adults</i>	<i>Older Adults</i>
<i>Left PPA</i>	7.29 (5.79) t = 6.169, p < 0.001	11.09 (8.83) t = 6.159, p < 0.001
<i>Right PPA</i>	9.03 (6.40) t = 6.906, p < 0.001	13.82 (10.05) t = 6.741, p < 0.001
<i>Left MPA</i>	1.24 (6.69) t = 0.907, p = 0.374	3.45 (8.21) t = 2.059, p = 0.051
<i>Right MPA</i>	2.25 (5.51) t = 2.005, p = 0.057	3.70 (6.51) t = 2.784, p = 0.011
<i>Left OPA</i>	3.01 (4.21) t = 3.503, p = 0.002	4.34 (3.59) t = 5.927, p < 0.001
<i>Right OPA</i>	2.83 (5.55)	5.65 (4.90)

18

455
456

<i>Left PCU</i>	$t = 2.504, p = 0.020$	$t = 5.651, p < 0.001$
	0.99 (5.83)	5.83 (8.85)
<i>Right PCU</i>	$t = 0.833, p = 0.413$	$t = 3.229, p = 0.004$
	1.71 (7.31)	5.33 (11.88)
	$t = 1.146, p = 0.264$	$t = 2.197, p = 0.038$

For all *t*-tests: *df* = 23



457

458 **Figure 4.** (A): Encoding and Retrieval centroids for each subject plotted on a medial view of the brain
459 surface template provided by BrainNet (Xia et al., 2013). Each subject's centroid pair is linked with a

460 line. **(B)**: Retrieval-related shift (in mm) of the retrieval centroid (arrow) relative to the encoding centroid
461 (origin) for each subject, collapsing across the two hemispheres.
462

463

464

465 The shift metrics were entered into a 2 (Age group) x 4 (ROI) x 2 (Hemisphere) mixed effects
466 ANOVA. This revealed significant main effects of ROI ($F_{(2,25, 103.65)} = 14.672$, $p < 0.001$, $\text{partial-}\eta^2 =$
467 0.242), and age group ($F_{(1,46)} = 12.897$, $p = 0.001$, $\text{partial-}\eta^2 = 0.219$). The main effect of hemisphere was
468 not significant, ($F_{(1,46)} = 2.855$, $p = 0.098$, $\text{partial-}\eta^2 = 0.058$), and neither were any of the two- or three-
469 way interactions ($p > 0.456$). The main effect of age group is indicative of a greater anterior shift in the
470 older relative to younger adults and the absence of an ROI x age group interaction indicates that this age
471 difference did not differ according to ROI (see Figure. 5-A). The main effect of ROI reflected the fact the
472 anterior shift was greater in the PPA than in the remaining ROIs. However, when assessed across all
473 participants, the shift was robust in every ROI (PPA: $t_{(47)} = 10.826$, $p < 0.001$; OPA: $t_{(47)} = 7.221$, $p <$
474 0.001 ; MPA: $t_{(47)} = 2.943$, $p = 0.005$; PCU: $t_{(47)} = 2.914$, $p = 0.005$) Since no hemisphere effects in the
475 magnitude of the shift were identified (see Bainbridge et al., 2019 and Steel et al., 2020 for closely similar
476 findings), subsequent analyses were performed averaging across the hemispheres.

477

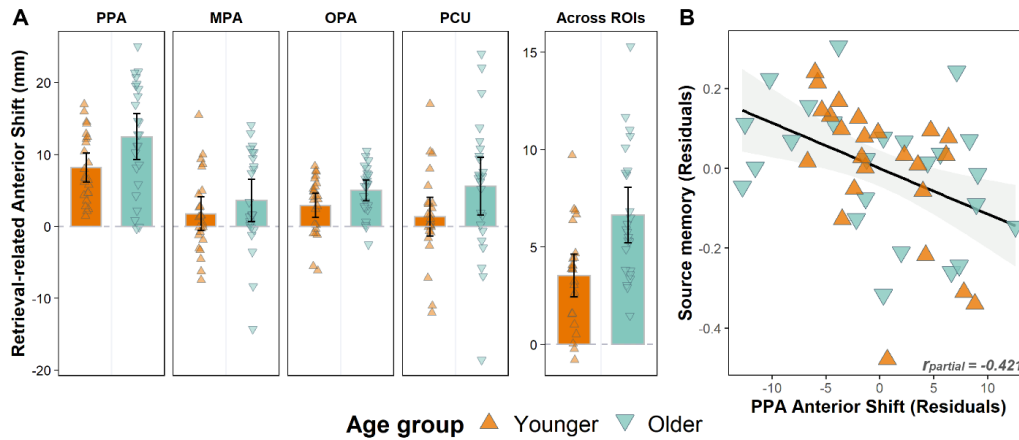
478 **3.4. Relationship between Anterior shift and Memory performance**

479 We performed a series of multiple regression analyses to examine whether the retrieval-related
480 anterior shift covaried across participants with their memory performance. Separate regression models
481 were constructed to predict Pr (collapsed across image category) and pSR, using age group, the anterior
482 shift in each ROI, and their interaction as predictors. The interaction term was included in the models to
483 examine whether any relationships between the anterior shift and memory performance were moderated
484 by age group. If the term was not significant, the regression analysis was followed-up by computing the
485 partial correlation between the anterior shift and memory, controlling for age group. Considering that
486 these analyses were exploratory in nature, we assessed the significance of any findings after Bonferroni

487 correction for family-wise error (8 tests; corrected significance level: $p < 0.00625$). For completeness,
488 effects that achieved significance before correction are also reported; these findings should however be
489 interpreted with caution and are not discussed further.

490 The interaction term in the regression model predicting Pr from the predictors of age group and
491 the anterior shift in the face-selective PCU was significant before ($p = 0.033$) but not following correction
492 ($p_{\text{(corrected)}} = 0.264$). The interaction terms in the remaining regression models were not significant ($p >$
493 0.052 before correction). Thus, there was little evidence to suggest that age group moderated any potential
494 relationships between the anterior shift and memory performance. Therefore, as noted previously, we
495 went on to examine partial correlations between anterior shift metrics and memory performance,
496 controlling for the influence of age group.

497 The only partial correlation to survive correction was that between the PPA anterior shift and pSR
498 ($r_{\text{partial}} = -0.421$, $p = 0.003$, $p_{\text{(corrected)}} = 0.024$). This result (see figure 5-B) reflected the fact that, regardless
499 of age group, a greater PPA anterior shift was associated with relatively lower source memory
500 performance. The correlation remained significant when either encoding- or retrieval-related selectivity
501 (see below) was included as an additional covariate ($r_{\text{partial}} = -0.409$, $p = 0.005$ and $r_{\text{partial}} = -0.476$, $p <$
502 0.001 respectively). Additionally, the MPA anterior shift exhibited a sizeable negative correlation with Pr
503 ($r_{\text{partial}} = -0.377$, $p = 0.009$), but this narrowly failed to survive correction ($p_{\text{(corrected)}} = 0.072$). A positive
504 correlation between pSR and the shift in the PCU ($r_{\text{partial}} = 0.316$, $p = 0.031$) also failed to survive
505 correction ($p_{\text{(corrected)}} = 0.248$). No other significant correlations were identified ($p > 0.120$, $p_{\text{(corrected)}} =$
506 0.960). In summary, after correcting for family-wise error, a single correlation met our criterion for
507 statistical significance: an age-invariant correlation between the PPA anterior shift and pSR.



508

509 **Figure 5. (A):** The anterior shift plotted separately for younger and older adults in each ROI. The
 510 distance values are plotted after collapsing across hemispheres, and an additional panel is provided
 511 illustrating the distances after collapsing across all ROIs to illustrate the main effect of age. Error bars
 512 signify 95% confidence intervals. **(B):** Age-invariant relationship between retrieval-related anterior shift
 513 in the PPA and source memory performance.
 514

515 3.5. Age differences in the localization of peak encoding and retrieval selectivity

516 Group differences in the anterior shift might have arisen due to differences in the localization of
 517 the peaks of either encoding or retrieval selectivity (or a combination of the two effects). To examine
 518 whether younger and older adults differed in respect of the localization of encoding or retrieval peaks, we
 519 entered the Y coordinates of the centroids that were employed to compute the anterior shift metrics into a
 520 2 (age) x 2 (phase; encoding vs. retrieval) x 4 (ROI) ANOVA. The ANOVA revealed a main effect of
 521 phase ($F_{(1,46)} = 138.763$, $p < 0.001$, $\text{partial-}\eta^2 = 0.751$) reflective of more anterior coordinates at retrieval
 522 relative to encoding, a main effect of age ($F_{(1,46)} = 7.973$, $p = 0.007$, $\text{partial-}\eta^2 = 0.148$) indicative of more
 523 anterior coordinates for older relative to younger adults and, of necessity, a main effect of ROI ($F_{(1,46)} =$
 524 994.765 , $p < 0.001$, $\text{partial-}\eta^2 = 0.956$). The ANOVA also identified a significant phase x age interaction
 525 ($F_{(1,46)} = 12.897$, $p < 0.001$, $\text{partial-}\eta^2 = 0.219$) and a significant phase x ROI interaction ($F_{(3,103.65)} =$
 526 14.672 , $p < 0.001$, $\text{partial-}\eta^2 = 0.242$). Neither the ROI x age nor the three-way interaction were
 527 significant ($F_{(3,103.65)} = 1.554$, $p = 0.211$, $\text{partial-}\eta^2 = 0.033$ and $F_{(3,103.65)} = 0.534$, $p = 0.6091$, $\text{partial-}\eta^2 =$
 528 0.011 , respectively).

529 The phase x ROI interaction reflected the fact that, as is already reported above, the anterior shift
530 was significantly greater in the PPA than the remaining ROIs. The phase x age interaction was followed-
531 up by examining the age differences in average Y coordinates for study and test. Age differences were
532 non-significant for the study phase coordinates (across ROIs: $t_{(45,38)} = 0.312$, $p = 0.756$; $\min p = 0.181$ for
533 individual ROIs). There was however a robust age effect at test, driven by relatively more anterior
534 coordinates in older than younger adults (across ROIs: $t_{(37,43)} = 3.702$, $p < 0.001$). Thus, the age effect in
535 the anterior shift was driven by age differences in the localization of peak selectivity at retrieval rather
536 than at encoding. These findings are illustrated in Figure 6-A.

537

538 **3.6. Age differences in neural selectivity and the relationship with anterior shift and memory**

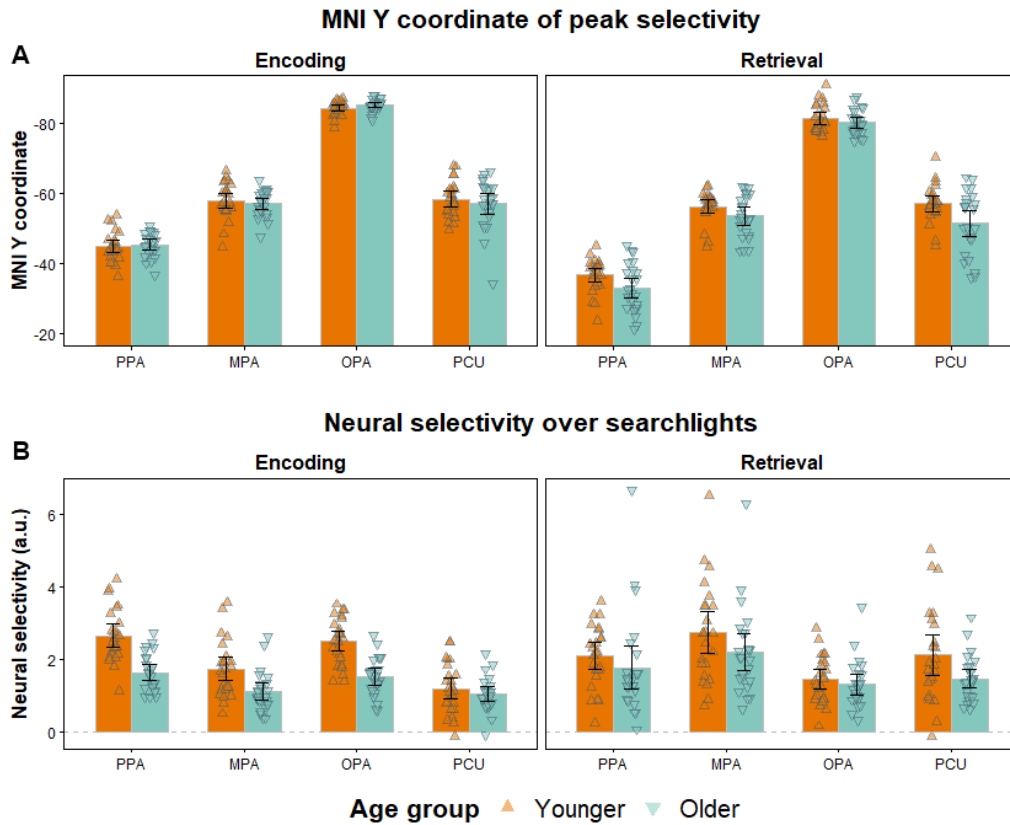
539 Next we examined whether there were age differences in peak neural selectivity identified in the
540 searchlights used to construct the centroids, and whether the degree of selectivity was associated with age
541 differences in the anterior shift and memory performance (Figure 6-B). This analysis was motivated by
542 prior findings that neural selectivity is reduced in older age (e.g., at encoding see Srokova et al., 2020;
543 and at retrieval see Hill et al., 2021), raising the possibility that age differences in anterior shift may arise
544 due to age differences in neural selectivity. We extracted the average parameter estimates for scene- and
545 face-selective contrasts within the searchlights used to construct the encoding and retrieval centroids. We
546 entered these into a 2 (age) x 2 (phase) x 4 (ROI) ANOVA. The ANOVA gave rise to a significant main
547 effect of phase, reflecting larger parameter estimates at retrieval ($F_{(1,46)} = 6.088$, $p = 0.017$, $\text{partial-}\eta^2 =$
548 0.117), a main effect of age, reflecting greater selectivity in younger adults ($F_{(1,46)} = 18.724$, $p < 0.001$,
549 $\text{partial-}\eta^2 = 0.289$), and a main effect of ROI ($F_{(3,87.55)} = 9.633$, $p < 0.001$, $\text{partial-}\eta^2 = 0.173$). The ROI x
550 age and the phase x age interactions were not significant ($F_{(1,46)} = 0.411$, $p = 0.654$, $\text{partial-}\eta^2 = 0.009$ and
551 ($F_{(3,87.55)} = 2.398$, $p = 0.128$, $\text{partial-}\eta^2 = 0.050$, respectively). The phase x ROI and the phase x ROI x age
552 interactions were both significant ($F_{(3,87.55)} = 25.132$, $p < 0.001$, $\text{partial-}\eta^2 = 0.353$ and ($F_{(3,87.55)} = 3.771$, p
553 $= 0.026$, $\text{partial-}\eta^2 = 0.076$, respectively).

554 In light of these findings, we went on to perform a series of independent samples t-tests to
555 examine age differences in selectivity at encoding and retrieval. At encoding, selectivity was lower in
556 older relative to younger adults in the scene-selective PPA ($t_{(41.16)} = 5.459$, $p < 0.001$), MPA ($t_{(41.70)} =$
557 3.230 , $p = 0.002$) and OPA ($t_{(44.31)} = 5.683$, $p < 0.001$), but not in the face-selective PCU ($t_{(40.49)} = 0.954$, p
558 $= 0.346$). At retrieval, there were no age differences in any of the scene-selective ROIs: (PPA ($t_{(38.10)} =$
559 0.967 , $p = 0.339$), MPA ($t_{(45.28)} = 1.423$, $p = 0.162$) and OPA ($t_{(46.00)} = 0.815$, $p = 0.162$). There was,
560 however, a significant age difference in the PCU, indicating greater selectivity in younger adults ($t_{(33.10)} =$
561 2.181 , $p = 0.036$).

562 To examine whether neural selectivity was related to the anterior shift, we correlated (controlling
563 for age group) the anterior shift metric for a given ROI with its selectivity metric at either encoding or
564 retrieval. In none of the ROIs did neural selectivity correlate with the magnitude of the shift ($ps > 0.170$).

565 Lastly, we also performed correlation analyses to examine whether either the encoding or retrieval
566 selectivity metrics covaried with memory performance. In neither case was the partial correlation
567 (controlling for age group) significant ($r_{\text{partial}} = 0.187$, $p = 0.207$, $r_{\text{partial}} = 0.258$, $p = 0.079$).

568



569

570 **Figure 6. (A):** Localization of peak selectivity at encoding and retrieval in younger and older adults. The
 571 figure depicts the Y coordinate in MNI space of the encoding and retrieval centroids. **(B):** Average neural
 572 selectivity over the searchlights which were used to define the encoding and retrieval centroids. In both
 573 panels, error bars signify 95% confidence intervals.
 574

575 **4. Discussion**

576 In the present study, we examined age effects on the retrieval-related anterior shift and its
 577 relationship with memory performance. In both young and older adults, we identified robust evidence for
 578 an anterior shift in two scene-selective cortical regions (PPA & OPA). In addition, in older adults only,
 579 the shift was reliable for scenes in the MPA and for faces in the PCU. Of importance, independently of
 580 ROI, the anterior shift was robustly larger in the older group. Moreover, the magnitude of the shift in the
 581 scene-selective PPA demonstrated an age-invariant, negative correlation with source memory

582 performance. In sum, consistent with the predictions outlined in the Introduction, the retrieval-related
583 anterior shift covaried positively with increasing age and negatively with memory performance.

584 The earliest findings suggestive of systematic differences in the loci of cortical activity associated
585 with perception versus memory were reported in studies contrasting color perception and color imagery
586 (e.g., Chao & Martin, 1999; Simmons et al., 2007). Extending these findings, more recent research has
587 reported that regions recruited during scene retrieval and scene imagery are localized anteriorly to the
588 regions recruited during scene perception (e.g., Chrastil 2018; Silson et al., 2019; Bainbridge et al., 2021;
589 Steel et al., 2021). These findings are consistent with the proposal that scene-selective cortical regions can
590 be sub-divided into two networks (Baldassano et al., 2016). The ‘posterior scene network’ is held to
591 include retinotopically organized regions responsible for processing visual input, while the ‘anterior
592 network’, which includes the hippocampus as one of its constituents, supports scene representations
593 retrieved from memory as well as spatial navigation and other memory-guided behaviors (e.g., visual
594 exploration). This subdivision is held to be honored within the PPA, which has been partitioned into
595 posterior (perceptual) and anterior (mnemonic) sub-divisions (Baldassano et al., 2016). However, our
596 findings, which demonstrate that the size of the anterior shift is sensitive to age and memory performance,
597 challenge the view that regions such as the PPA can be dichotomized into functionally distinct posterior
598 and anterior sub-regions. Furthermore, findings of analogous shifts in other scene-selective cortical
599 regions such as the OPA (see Figure 5-A), and for other perceptual categories (Lee et al. 2012), add
600 further weight to the proposal that the anterior shift reflects more than a segregation between two
601 functional networks (see also the discussion of the present findings for faces below).

602 In a recent review, Favila and colleagues (2020) proposed that mnemonic representations undergo
603 a ‘transformation’, with perceived and retrieved representations differing in terms of their quality, content
604 and amount of information. This transformation reflects a differential weighting of episodic attributes,
605 such that a retrieved representation is biased towards the representation of ‘high-level’ conceptual
606 information at the expense of lower-level perceptual detail. The differential emphasis on higher- versus
607 lower-level features is reflected in the localization of concurrent cortical activity. Notably, it has been

608 conjectured that cortical regions extending along the posterior-anterior axis are hierarchically organized,
609 such that more posterior regions support the processing of relatively low level stimulus properties, while
610 more anterior regions support higher-level semantic or conceptual processing (e.g. Simmons et al., 2007,
611 Peelen & Caramazza, 2012). This proposal implies the existence of a processing gradient along which
612 modality-specific perceptual properties are increasingly ‘abstracted away’ at the expense of higher-level
613 conceptual features (see Introduction). This ‘abstraction account’ leads to the prediction that the
614 magnitude of the anterior shift will vary depending on whether a retrieval test requires retrieval primarily
615 of conceptual information as opposed to high-fidelity, modality-specific detail (Simmons et al., 2007).

616 To date, reports of the anterior shift have been confined to young adults. The data from the
617 present study extend these findings by demonstrating that the shift is exaggerated in older adults. As
618 noted above, the abstraction account of the shift implies that it reflects a representational ‘transformation’
619 that de-emphasizes perceptual detail. This account allows for a simple explanation of the present effects
620 of age on the anterior shift, given the extensive evidence that retrieved episodic information contains less
621 detail, and is more ‘gist-based’ in older than younger adults (Koustaal & Schacter, 1997; Dennis et al.,
622 2007; 2008, Gallo et al., 2019). That is, whereas memory for the gist of an event is relatively spared in
623 older adults, the retention of more fine-grained, individuating features of an episode appears to be
624 especially susceptible to increasing age (Nilakantan et al., 2018; Korkki et al., 2020). We propose that the
625 neural expression of this age difference in retrieved episodic content accounts for the exaggerated anterior
626 shifts evident in our older sample in the present study.

627 Of importance, we identified a reliable anterior shift not only in scene selective cortical regions,
628 but in the face selective PCU also, albeit in older adults only. Our failure to identify an anterior shift for
629 faces in the PCU in younger adults is consistent with prior findings that face stimuli do not elicit a
630 retrieval-related anterior shift in this population (Steel et al., 2021). There are two possible explanations
631 for why we find an anterior shift in the PCU for faces in older but not younger adults. First, it could be
632 that this effect is specific to older adults; that is, for unknown reasons, younger adults did not retrieve face
633 representations that were abstracted away from the original stimulus event. Alternatively, the seeming

634 absence of a PCU effect in the younger adults might merely be a consequence of the fact that the shift in
635 this region is smaller than that in other regions (compare, for example, the magnitude of the shift in the
636 PPA vs. the PCU in the older participants illustrated in figure 5-A). By this argument, a shift might be
637 detectable in the PCU of young adults given sufficient spatial resolution and statistical power.

638 Whereas the notion of a cortical posterior-anterior gradient from perception to memory is well
639 supported, the question whether the magnitude of the retrieval-related anterior shift impacts memory
640 performance has been largely unexplored (but see Davis et al., 2021). Here, we sought for relationships
641 between the anterior shift and memory performance on the assumption that memory for the details of an
642 event is more likely to be accurate when there is strong overlap (indexed by a relatively small anterior
643 shift) between experienced and retrieved event representations (see Introduction). Consistent with this
644 prediction, we identified a negative, age-invariant correlation between the PPA anterior shift and source
645 memory performance. That is, regardless of age group, a greater anterior shift was associated with poorer
646 memory for the study pairs. This finding supports the proposal that the localization of retrieval-related
647 neural activity has implications for the content of retrieval, and it is also consistent with the notion that
648 more anterior regions of the PPA support mnemonic representations containing relatively sparse
649 perceptual detail (Bainbridge et al., 2021; Steel et al., 2021). Nonetheless, as alluded to earlier, the finding
650 that the shift (at least, in the PPA) both correlates with memory performance and is enhanced in older
651 adults suggests an intriguing mechanism that might partially account for age-related memory decline.

652 It is currently unclear why a relationship between the magnitude of the anterior shift and memory
653 performance was only evident in the PPA. One possibility is that the anatomy of the parahippocampal
654 and fusiform gyri (i.e., their length and orientation along the posterior-anterior axis) is well suited to
655 detecting functionally significant variance in the shift across participants. By this argument, similar
656 relationships might emerge for other ROIs in more highly-powered, higher resolution studies. Another
657 possibility is that the PPA supports one or more functions that are especially important for successful
658 episodic memory encoding and retrieval. One such function, for example, is the processing of
659 mnemonically-relevant contextual information in concert with the hippocampus (Aminoff et al., 2013).

660 By this account, the scene-related anterior shift in the PPA is a reflection of the role of this region in
661 supporting the encoding and retrieval of contextual information more generally. From this perspective, we
662 think that it is unlikely to be a coincidence that memory performance is also predicted by metrics of scene
663 selectivity derived from the PPA, with no evidence for such a relationship in other category-selective
664 cortical regions (see Koen et al., 2019; Srokova et al., 2020).

665 In conclusion, the present study revealed robust age differences in the retrieval-related anterior
666 shift in both scene-and face-selective cortical regions. We also demonstrate that the shift is (negatively)
667 associated with source memory performance, supporting the notion that low- and high-level stimulus
668 information is represented in different cortical regions at multiple levels of abstraction along the
669 posterior-anterior axis. Future research should examine whether the age effects observed here extend to
670 other stimulus categories (such as objects) or other sensory modalities (e.g. auditory stimuli). In sum, the
671 findings reported here shed light on the functional significance of the anterior shift in relation to memory
672 accuracy and potentially provide an increased understanding of the factors contributing to age-related
673 memory decline.

674

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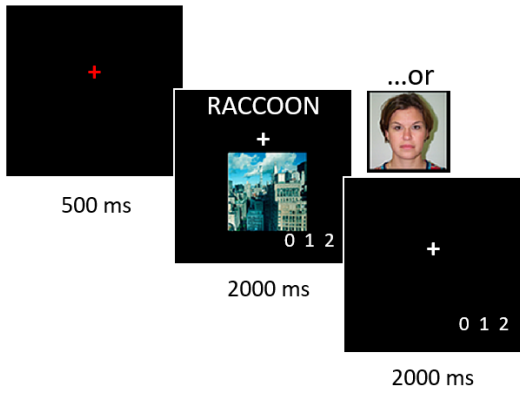
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Encoding Phase



Retrieval Phase

