
Research Articles: Behavioral/Cognitive

The relationship between age, neural differentiation, and memory performance

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1 Running Head: AGE, MEMORY, AND NEURAL DIFFERENTIATION

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3 **The relationship between age, neural differentiation, and memory performance**

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12 **Author Note**

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21

Abstract

22 Healthy aging is associated with decreased neural selectivity (dedifferentiation) in category-
23 selective cortical regions. This finding has prompted the suggestion that dedifferentiation
24 contributes to age-related cognitive decline. Consistent with this possibility, dedifferentiation has
25 been reported to negatively correlate with fluid intelligence in older adults. Here, we examined
26 whether dedifferentiation is associated with performance in another cognitive domain – episodic
27 memory – that is also highly vulnerable to aging. Given the proposed role of differentiation in
28 age-related cognitive decline, we predicted there would be a stronger link between
29 dedifferentiation and episodic memory performance in older than in younger adults. Young (18-
30 30 yrs) and older (64-75 yrs) male and female humans underwent fMRI scanning while viewing
31 images of objects and scenes prior to a subsequent recognition memory test. We computed a
32 differentiation index in two regions-of-interest (ROIs): parahippocampal place area (PPA) and
33 lateral occipital complex (LOC). This index quantified the selectivity of the BOLD response to
34 an ROI's preferred versus non-preferred category (scenes for PPA, objects for LOC). The
35 differentiation index in the PPA, but not the LOC, was lower in older than in younger adults.
36 Additionally, the PPA differentiation index predicted recognition memory performance for the
37 studied items. This relationship was independent of and not moderated by age. The PPA
38 differentiation index also predicted performance on a latent 'fluency' factor derived from a
39 neuropsychological test battery; this relationship was also age invariant. These findings suggest
40 that two independent factors, one associated with age, and the other with cognitive performance,
41 drive neural differentiation.

42

43

Significance Statement

44 Aging is associated with neural dedifferentiation – reduced neural selectivity in ‘category
45 selective’ cortical brain regions – which has been proposed to mediate cognitive aging. Here, we
46 examined whether neural differentiation is predictive of episodic memory performance, and
47 whether the relationship is moderated by age. A neural differentiation index was estimated for
48 scene- (PPA) and object- (LOC) selective cortical regions while participants studied images for a
49 subsequent memory test. Age related reductions were observed for the PPA, but not the LOC,
50 differentiation index. Importantly, the PPA differentiation index demonstrated age invariant
51 correlations with subsequent memory performance and a fluency factor derived from a
52 neuropsychological battery. Together, these findings suggest that neural differentiation is
53 associated with two independent factors: age and cognitive performance.

54

55

Introduction

56 Healthy aging is accompanied by numerous structural (Raz et al., 2005) and functional
57 (Spreng et al., 2010) brain changes believed to contribute to age-related cognitive decline (Raz
58 and Rodrigue, 2006). Of relevance here is research demonstrating that increasing age is
59 associated with reduced neural differentiation, or reduced selectivity of cortical regions sensitive
60 to a specific class of stimuli (Park et al., 2004). *Age-related neural dedifferentiation* has been
61 most commonly identified in the ventral visual cortex (Grady et al., 1994; Park et al., 2004,
62 2010, 2012; Chee et al., 2006; Payer et al., 2006; Voss et al., 2008; Carp et al., 2011b;
63 Kleemeyer et al., 2017; also see Berron et al., 2018), although the pattern has also been observed
64 in auditory (Du et al., 2016) and motor cortex (Carp et al., 2011a). Neural dedifferentiation is
65 believed to play an important role in cognitive aging (Li et al., 2001; Li and Sikström, 2002;
66 Goh, 2011). Consistent with this proposal, measures of neural dedifferentiation have been
67 reported to correlate negatively with cognitive performance in healthy older adults (Park et al.,
68 2010; Du et al., 2016).

69 Here, we examine the proposal that neural dedifferentiation contributes to age differences
70 in episodic memory (St-Laurent et al., 2014; Zheng et al., 2018). Healthy aging is associated
71 with disproportionate reductions in the ability to recollect details about past events (for review,
72 see Koen and Yonelinas, 2014; Schoemaker et al., 2014), and this deficit is largely attributed to
73 reduced efficacy of encoding processes (Craik, 1986; Craik and Rose, 2012; Friedman and
74 Johnson, 2014). Prior work investigating the relationship between neural dedifferentiation and
75 memory encoding has focused on the fidelity of neural patterns across repeated instances of a
76 given item *within* a stimulus category (St-Laurent et al., 2014; Zheng et al., 2018). The results
77 from these studies are mixed as to whether neural dedifferentiation during encoding might
78 contribute to age differences in memory performance. Here, we focus on indices of neural
79 dedifferentiation measured across different stimulus categories (i.e., objects and scenes; cf. Park
80 et al., 2004) during memory encoding, and whether these indices predict subsequent memory
81 performance.

82 Participants incidentally encoded images of objects and scenes for a subsequent memory
83 test while undergoing fMRI (see Figure 1). Objects and scenes were selected as stimuli because
84 they selectively engage distinct cortical regions in the ventral visual cortex. Specifically, relative
85 to scenes, viewing images of single objects engages the lateral occipital complex (LOC; Grill-
86 Spector et al., 2001). In contrast, viewing images of scenes activates posterior parahippocampal
87 and adjacent fusiform cortex – the ‘parahippocampal place area’ (PPA; Epstein and Kanwisher,
88 1998). We examined age differences in neural differentiation with a differentiation index
89 computed from individual trial BOLD responses to objects and scenes in the LOC and PPA
90 (Voss et al., 2008). This index reflects the scaled difference between a region-of-interest’s
91 (ROI’s) BOLD response to a preferred (e.g., scenes in the PPA) and not preferred (e.g., objects
92 in the PPA) stimulus category (see Materials and Methods). In a complementary analysis, neural
93 differentiation was also examined with multi-voxel pattern analysis (cf. Carp et al., 2011). We
94 examined the relationship between neural differentiation and two measures of memory
95 performance, namely item recognition and source recall. Our prediction was that higher values of
96 neural differentiation, which are indicative of increased levels of neural selectivity (Voss et al.,
97 2008), would predict higher performance on a subsequent memory test by virtue of the
98 mnemonic benefit associated from encoding relatively distinctive information (e.g., Murdock Jr.,
99 1960; Lockhart et al., 1976; Hunt, 1995). Like prior research (Park et al., 2010), we also

100 examined whether neural differentiation was associated with neuropsychological test
101 performance. If neural dedifferentiation contributes disproportionately to memory performance
102 (and, perhaps, performance in other cognitive domains) in older adults, differentiation should be
103 more strongly correlated with performance in an older relative to younger participants.

104

Materials and Methods

105 Ethics Statement

106 The Institutional Review Board of the University of Texas at Dallas approved the
107 experimental procedures described below. All participants provided written informed consent
108 prior to participation.

109 Experimental Design and Statistical Analysis

110 As will be elaborated in the remainder of the Materials and Methods, the main
111 independent variables in this experiment included age group (young versus older), image type
112 (scene versus object), and region of interest (PPA versus LOC). Results from all analyses were
113 considered significant at $p < .05$.

114 Statistical analyses were conducted with *R* software (R Core Team, 2017). ANOVAs
115 were conducted using the *afex* package (Singmann et al., 2016) and the Greenhouse-Geisser
116 procedure (Greenhouse and Geisser, 1959) was used to correct the degrees of freedom for non-
117 sphericity in the ANOVAs when necessary. Post-hoc tests on significant effects from the
118 ANOVAs were conducted using the *lsmeans* package (Lenth, 2016) with degrees of freedom
119 estimated using the Satterthwaite (1946) approximation. Effect size measures for results from the
120 ANOVAs are reported as partial- η^2 (Cohen, 1988). Linear regression models were implemented
121 using the *lm* function in the base *R* library. Principal components analysis (PCA; Hotelling,
122 1933; Abdi and Williams, 2008) was conducted using the *psych* package (Revelle, 2017).

123 Participants

124 A sample of 24 young and 24 older participants contributed to the data reported here.
125 Participants were recruited from the University of Texas at Dallas and the greater Dallas
126 metropolitan area and received monetary compensation (\$30/hour). Table 1 reports participant
127 demographics and neuropsychological test performance. All participants were right-handed and
128 reported having normal or corrected-to-normal vision and no contraindications to MRI scanning.
129 Exclusion criteria included a history of cardiovascular disease (other than treated hypertension),
130 diabetes, psychiatric disorder, illness or trauma affecting the central nervous system, substance
131 abuse, and self-reported current or recent use of psychotropic medication or sleeping aids. All
132 participants scored 27 or more on the Mini-Mental State Examination (MMSE; Folstein et al.,
133 1975) and scored within the normal range for their age group on a battery of neuropsychological
134 tests.

135

136

137 **Table 1.** Demographic and neuropsychological test data for young and older adults.

	Young Adults	Older Adults	<i>p</i> -value
N	24	24	-
Age	23.04 (3.46)	68.92 (3.23)	-
Sex	12/12	12/12	-
Education	15.92 (2.22)	17.12 (2.23)	.067
MMSE	29.54 (0.59)	29.42 (0.93)	.581
CVLT Short Delay – Free	13.08 (1.79)	10.83 (2.84)	.002
CVLT Short Delay – Cued	13.67 (1.81)	12.33 (2.32)	.032
CVLT Long Delay – Free	13.54 (2.06)	10.71 (2.91)	< .001
CVLT Long Delay – Cued	14.12 (1.62)	12.33 (2.46)	.005
CVLT Recognition – Hits	15.42 (0.83)	15.04 (1.00)	.164
CVLT Recognition – False Alarms	0.46 (0.66)	2.67 (2.08)	< .001
Logical Memory I	30.62 (4.95)	26.71 (5.09)	.010
Logical Memory II	28.12 (5.78)	23.25 (5.72)	.005
Digit Span Total ¹	21.04 (4.53)	17.58 (2.41)	.002
SDMT	65.38 (13.99)	47.21 (7.53)	< .001
Trails A (secs)	21.43 (7.97)	30.76 (10.77)	.001
Trails B (secs)	47.54 (19.53)	69.11 (24.64)	.002
F-A-S Total	48.29 (10.97)	45.96 (11.65)	.479
Category Fluency (Animals)	24.58 (5.67)	21.08 (4.82)	.026
WTAR (Raw)	41.42 (3.44)	43.62 (4.44)	.061
Raven’s (List 1)	11.08 (.97)	9.50 (2.23)	.003
Visual Acuity (logMar) ²	-.11 (.10)	.06 (.11)	< .001
Speed Factor (RC1) ³	-.64 (.67)	.33 (.75)	< .001
Memory Factor (RC2)	.55 (.73)	-.62 (1.00)	< .001
Crystallized Intelligence Factor (RC3)	.00 (.79)	.08 (.93)	.751
Fluency Factor (RC4)	.07 (.89)	-.21 (.72)	.257

138 *Note.* Standard deviations are reported in parentheses. The *p*-values were obtained from Welch *t*-tests comparing
 139 young and older adults. ¹Digit span total equals the sum of forward and backward span. ²Lower logMAR scores
 140 indicate better visual acuity. ³Negative factors on the speed factor (RC1) correspond to higher performance on
 141 measures of processing speed (e.g., shorter time to complete Trails A or B), whereas for other factors higher
 142 performance is indicated by higher scores. MMSE = Mini-mental State Exam; CVLT = California Verbal Learning
 143 Test II; SDMT = Symbol-Digit Modalities Test; WTAR = Wechsler Test of Adult Reading

144

145 Data from an additional 4 participants were excluded from the analyses reported here for
 146 the following reasons: 1 young adult male and 1 older adult male were excluded due to excessive
 147 in-scanner motion (> 8 mm frame displacement) and 2 older adult males were excluded for
 148 providing 2 or fewer source correct trials (see below).

149 Many participants in the present study participated in prior studies reported by our
 150 laboratory. Specifically, 18 young (10 females) and 16 older (4 females) participated in an ERP
 151 study reported by Koen and colleagues (2018). Additionally, 2 older adults (1 female)
 152 participated in a prior fMRI experiment reported by de Chastelaine and colleagues (2016).

153 **Neuropsychological Test Battery**

154 Participants completed a neuropsychological test battery on a separate day prior to the
 155 fMRI study. The battery included the MMSE, California Verbal Learning Test-II (CVLT; Delis
 156 et al., 2000), the symbol digit modalities test (Smith, 1982), forward and backward digit span
 157 subtests of the Wechsler Adult Intelligence Scale – Revised (Wechsler, 1981), trail making tests

158 A and B (Reitan and Wolfson, 1985), the F-A-S subtest of the Neurosensory Center
159 Comprehensive Evaluation for Aphasia (Spreen and Benton, 1977), the category fluency test for
160 animals (Benton, 1968), Wechsler test of adult reading (WTAR; Wechsler, 2001), the logical
161 memory subtest of the Wechsler Memory Scale (Wechsler, 2009), and List 1 of the Raven's
162 Progressive Matrices (Raven et al., 2000). Volunteers were excluded from participating in the
163 fMRI study if (1) one or more of the memory measures (i.e., CVLT or logical memory) were
164 more than 1.5 standard deviations below the age- and education-adjusted mean, (2) they had a
165 standard score below 100 on the WTAR, or (3) two or more scores on non-memory tests were
166 1.5 standard deviations below the mean (see below for the dependent measures that were used).

167 **Neuropsychological Data Analysis**

168 The scores on the neuropsychological test battery were reduced to factor scores based on
169 PCA applied to a prior dataset from our laboratory that included young, middle, and older adults
170 (de Chastelaine et al., 2016). Principal components with eigenvalues > 1 were kept and rotated
171 using Varimax rotation (Kaiser, 1958). The following variables were included in the PCA model:
172 CVLT composite recall measure (i.e., average number of words recalled on the short- and long-
173 delay free- and cued-recall tests), number of CVLT recognition hits, number of CVLT
174 recognition false alarms, a logical memory composite recall measure (i.e., average of immediate
175 and delayed recalls), completion time for both trails A and B, number of valid responses on the
176 SDMT, F-A-S, and Raven's, and estimated full-scale intelligence quotient derived from the
177 WTAR. The first four components were retained and explained 64.1% of the variance in the data
178 prior to rotation. The rotated components (RC) broadly correspond to factors representing
179 processing speed (RC1), memory (RC2), crystallized intelligence (RC3), and fluency (RC4). The
180 weights for the rotated factors from this prior data set are shown in Table 2. These weights were
181 applied to the identical variables in the present data set to extract factor scores for the analyses
182 reported here.

183

184

185 **Table 2.** Rotated factor loadings from the PCA (with Varimax rotation) of the neuropsychological test data reported
 186 by de Chastelaine et al. (2016).

	Speed (RC1)	Memory (RC2)	Crystallized Intelligence (RC3)	Fluency (RC4)
CVLT Composite	-.19	.84	.08	-.15
CVLT Hits	-.20	.42	.23	-.64
CVLT False Alarms	.21	-.69	.26	-.17
Logical Memory Composite	.10	.67	.18	.02
Trails A	.91	-.09	-.05	-.14
Trails B	.85	-.09	-.28	.08
SDMT	-.59	.40	.08	.30
Digit Span	-.16	.01	.80	-.08
Category Fluency (Animals)	-.34	.23	.14	.63
F-A-S	-.12	.06	.46	.57
WTAR (Full-Scale Intelligence)	-.12	.12	.79	.21
Raven's (List 1)	-.33	.48	.10	.05
Eigenvalue	3.65	1.70	1.28	1.06
% Variance (before rotation)	.20	.14	.11	.09
% Variance (after rotation)	.19	.19	.15	.11

187 *Note.* CVLT = California Verbal Learning Test II; SDMT = Symbol-Digit Modalities Test; WTAR = Wechsler Test
 188 of Adult Reading

189

190 **Visual Acuity Assessment**

191 Participants completed a visual acuity test using ETDRS charts (Precision Vision, La
 192 Salle, Illinois) during the neuropsychological test session. Visual acuity was measured separately
 193 for the left and right eyes, as well as with both eyes using the logMAR metric (Ferris et al., 1982;
 194 Bailey and Lovie-Kitchin, 2013). A different eye chart was used for each of the three tests.
 195 Participants prescribed corrective lenses wore them during the visual acuity test. Note that only
 196 the results from the visual acuity measured with both eyes is reported (see Table 1).

197 **Materials and Apparatus**

198 Stimuli were presented using Cogent 2000 software
 199 (www.vislab.ucl.ac.uk/cogent_2000.php) implemented in Matlab 2011b (www.mathworks.com).
 200 Stimuli in the scanned study phases were projected to a screen mounted at the rear of the magnet
 201 bore and viewed through a mirror mounted on the head coil. Responses during the study sessions
 202 were entered using two four-button MRI compatible response boxes (one for each hand). The
 203 test phase was completed on a laptop computer outside the scanner. The monitor resolution
 204 setting for both the study and test phases was set at 1024 x 768 pixels. All stimuli were presented
 205 on a grey background (RGB values of 102, 101 and,99).

206 The critical stimuli comprised 360 images obtained from a variety of internet sources.
 207 Half of the images were pictures of scenes and the remaining half were pictures of common
 208 objects. The 180 scenes comprised 90 rural (i.e., natural) scenes and 90 urban (i.e., manmade)
 209 scenes. The scenes contained objects (e.g., trees, cars, buildings, etc.), and we attempted to
 210 minimize overlap between the objects depicted in the scenes and the object images. The scenes
 211 were scaled and cropped to 256 x 256 pixels.

212 The 180 objects comprised 90 images of natural objects (e.g., food items, animals, plants)
213 and 90 images of manmade objects (e.g., tools, vehicles, furniture). The object images were
214 overlaid and centered on a light grey background (RGB values of 175, 180, and 184) with
215 dimensions of 256 x 256 pixels. Note that the background color for the object images differed
216 from the background of the monitor. The purpose of this was to roughly equate the area of the
217 monitor subtended by the object and scene images.

218 The above-described images were used to create 24 stimulus sets that were yoked across
219 young and older participants. Each stimulus set comprised a random selection of 120 objects and
220 120 scenes that served as study items. The 120 images of each type were divided into 5 groups of
221 24, and each group was randomly assigned to one of the five scanned study phases. Half of the
222 objects and scenes in each study session were assigned to each of the two different possible
223 judgments in the study phase (Pleasantness and Movie; see below). The test stimuli comprised
224 all the images from the study phase along with the remaining 60 objects and 60 scenes, which
225 served as new items. All stimulus lists were pseudorandomized such that there were no more
226 than three consecutive presentations of objects or scenes and no more than three consecutive
227 Pleasantness or Movie judgments.

228 An additional 16 objects and 16 scenes with similar characteristics to those described
229 above served as practice stimuli. The images in each practice list were the same for all
230 participants. There were 3 practice study lists (self-paced, speeded, real; see below), each
231 comprising 8 images (4 objects, 4 scenes). A practice test list was also created and comprised the
232 images from the speeded and real practice study phases (old items) and 8 images (4 objects, 4
233 scenes) as new items.

234 Procedure

235 **Overview.** The experiment was completed across two sessions on different days, with the
236 neuropsychological test battery completed in the first session, and the experimental fMRI session
237 completed in the second session. In the fMRI session, participants first completed a face-viewing
238 task in which they pressed a button when an inverted face appeared among a sequence of upright
239 faces. The face-viewing task is not discussed further here and will be the subject of a separate
240 report. Following the face-viewing task, participants completed the study phase of the
241 experiment described here, followed by a test phase administered outside of the scanner (see
242 Figure 1).

243

244 **Study Phase.** Participants completed the study phase during five consecutive fMRI
245 scanning sessions. The study phase was completed under intentional encoding conditions with
246 specific reference to the nature of the subsequent memory test.

247 The sequence and timing for each trial was as follows: get ready signal (green fixation
248 cross for 500 ms), task cue (red 'P?' or 'M?' for 500 ms), study image (object or scene for 2000
249 ms), and white fixation (1750 ms). The task cue informed participants which one of two
250 judgments they should make about the following image. Images preceded by a 'P?'
251 (Pleasantness) required participants to rate how pleasant they found the image using the
252 following scale: 'Very', 'Moderate', or 'Not at all'. Images preceded by a 'M?' (Movie) required
253 participants to determine which movie genre they believed was best associated with the object or

254 scene. There were three options for this judgment: ‘Action’, ‘Horror’, or ‘Comedy’. The
255 response options for the cued judgment always appeared below the image.

256 Participants were instructed to enter their responses quickly, and to attempt to do so while
257 the image was on the screen. Responses were entered with the index, middle and ring fingers
258 (respectively for the order of response options listed previously), and were accepted until the
259 beginning of the next trial. Responses for one judgment were entered with the right hand and
260 responses for the other judgment were entered with the left hand. The hand assigned to each
261 question was counterbalanced across participants. The instructions emphasized that responding
262 with the incorrect hand for a cued judgment counted as an incorrect response.

263 In addition to the critical trials, there were 24 null trials dispersed throughout each of the
264 5 scanned study sessions. The null trials displayed a white fixation cross for the duration of a
265 normal trial (4750 ms) and were distributed such that 12 objects and 12 scenes were each
266 followed by a single null trial. This was done to minimize any bias between the two image types
267 in estimating single trial BOLD responses. Null trials never occurred consecutively, resulting in
268 stimulus onset asynchronies of either 4750 or 9500 ms for both classes of image.

269 **Test Phase.** The test phase commenced outside of the scanner approximately 15 minutes
270 after the completion of the final study phase. Participants were shown images one at a time and
271 required to judge if the image was presented in the study phase while they were in the scanner
272 and, if so, which of the two encoding judgments they had made when they initially encountered
273 the image. These two mnemonic decisions were combined into a single judgment with four
274 possible options: ‘Old-Pleasant’, ‘Old-Movie’, ‘Old-Don’t Know’, ‘New’. A ‘New’ response
275 was required if the image was believed to be new or if participants had a low level of confidence
276 that the image was from the study list. An ‘Old-Pleasant’ or ‘Old-Movie’ response required
277 participants to have high confidence that they studied the image and high confidence in their
278 memory for the judgment made when the image was studied. Participants were instructed to
279 respond ‘Old-Don’t Know’ if they had high confidence they studied the image but had low
280 confidence in or were unable to remember the encoding judgment.

281 Responses were entered on the keyboard by pressing the ‘d’, ‘f’, ‘j’, and ‘k’ key, and
282 these keys were labeled ‘Old-Pleasant’, ‘Old-Movie’, ‘Old-Don’t Know’, and ‘New’,
283 respectively. Responses were self-paced, but participants were instructed to enter their responses
284 quickly without sacrificing accuracy. There was a brief 500 ms white fixation cross between test
285 trials. A short break was afforded to participants every 60 trials (totaling 5 breaks).

286 **Practice Phases.** Prior to MRI scanning, participants practiced both the study and test
287 phases outside of the scanner. Practice comprised 3 study phases and a single test phase. In the
288 self-paced practice phase, participants were presented with the trial sequence as described above,
289 with the exception that the image remained on the screen until a response was entered. Following
290 a response, participants received feedback as to whether they responded to the correct judgment
291 (i.e., whether they entered their judgment using the assigned hand for the Pleasantness or Movie
292 judgments). The trial was repeated in the event the incorrect hand was used, and this occurred
293 until the correct hand was used. The aim of this self-paced practice phase was to familiarize
294 participants with responding to each type of judgment using the correct hand.

295 Next, participants completed a speeded practice phase. This phase was identical to the
296 self-paced practice described above, with the exception that the image remained on the screen

297 only for 2000 ms. Participants were required to enter their response within this time window,
 298 otherwise they were given feedback that they did not enter a response in the allotted time. As
 299 with the self-paced practice study phase, a trial was repeated until the correct hand was used and
 300 a response was entered in the allotted time. The aim of this second practice study phase was to
 301 reinforce responding with the correct hand and to give participants experience with responding
 302 quickly. No null trials were included in the self-paced and speeded practice study phases. The
 303 final ‘real’ practice study phase mirrored the procedure for the study phase proper described
 304 above and included 4 null trials.

305 After the final practice study phase, participants completed the practice test phase. This
 306 mirrored the procedure for the test phase proper with the exception that no breaks were provided.

307 **Behavioral Data Analysis**

308 Trials that received no response or a response with the incorrect hand during the study
 309 phase were excluded from the analysis. Both study and test trials were binned according to the
 310 four possible test response outcomes: item hit with a correct source judgment, item hit with an
 311 incorrect source judgment, item hit accompanied by a don’t know response for the source
 312 judgment, and item misses. Note that new items do not have a source correct judgment, thus
 313 false alarms (i.e., incorrect ‘old’ responses to new images) were only classified as source
 314 incorrect or source don’t know trials. The three behavioral dependent measures analyzed
 315 included study reaction time (RT), item recognition accuracy, and source memory accuracy.
 316 Study RT was computed for each participant as the median RT for each image type and
 317 subsequent memory combination. There were three subsequent memory bins: source correct
 318 (SC), source incorrect/don’t know (SIDK), and item misses (Miss). Study RT was analyzed with
 319 a 2 (Age Group: Young, Older) X 2 (Image Type: Object, Scene) X 3 (Subsequent Memory: SC,
 320 SIDK, Miss) mixed-factorial ANOVA.

321 Item recognition accuracy was computed as the difference between the hit rate to studied
 322 images (regardless of source memory accuracy) and the false alarm rate to new images. Source
 323 memory was computed using a single-high threshold model (Snodgrass and Corwin, 1988) that
 324 accounts for the ‘guess rate’ (e.g., Mattson et al., 2014). Source accuracy was computed as
 325 follows:

326

$$source\ pR = \frac{Hit - .5 * [1 - DK]}{1 - .5 * [1 - DK]}$$

327

328 The *Hit* and *DK* variables in the above formula refer to the proportion of correct ‘old’ responses
 329 (i.e., hits) accompanied by an accurate or don’t know source memory judgments, respectively.
 330 The item and source memory scores were submitted to separate 2 (Age Group: Young, Older) X
 331 2 (Image Type: Object, Scene) mixed-factorial ANOVA.

332 **Identification of PPA and LOC Regions-of-Interest**

333 The analyses of the fMRI data focused on two regions-of-interest (ROIs) that show
 334 selective responses to scenes and objects, respectively: the parahippocampal place area (PPA);

335 Epstein and Kanwisher, 1998) and lateral occipital complex (LOC; Grill-Spector et al., 2001).
336 We identified these ROIs bilaterally using unpublished data from our laboratory obtained from a
337 sample of 22 participants (14 young and 8 older adults) who volunteered for a previous study
338 (see Figure 2A). Note that 1 young and 2 older participants from this unpublished study
339 overlapped with the participants reported here. The 22 participants viewed images of faces,
340 scenes, and articles of clothing (objects) in a mini-block design (e.g., Johnson et al., 2009;
341 McDuff et al., 2009; Wang et al., 2016) while providing a pleasantness rating for each image.
342 PPA and LOC ROIs were obtained from a second-level general linear model (GLM) contrasting
343 the BOLD response between scenes and objects. The two one-sided contrasts were thresholded at
344 a family-wise error (FWE) corrected threshold of $p < .05$, and were inclusively masked using
345 anatomical labels from the Neuroinformatics atlas included with SPM12. The bilateral PPA ROI
346 comprised 223 voxels (108 voxels in the left hemisphere) identified by the scene > object
347 contrast anatomically masked with the bilateral parahippocampal and fusiform gyri. The bilateral
348 LOC ROI comprised 225 voxels (98 voxels in the left hemisphere) identified by the object >
349 scene contrast anatomically masked inferior and middle occipital gyrus ROIs defined by the
350 Neuroinformatics atlas. The PPA and LOC ROIs used for the present study are depicted in
351 Figure 2A. Additionally, Figure 2B shows the statistical maps from the scene > object (warm
352 colors) and object > scene (cool colors) contrasts from a 2nd level GLM of our unpublished data
353 set without the anatomical inclusive mask. Figure 2C shows the same statistical contrast (at an
354 identical threshold to Figure 2B) for the 24 young and 24 older adults reported here. This is
355 included simply for comparison purposes. Note that differences in the magnitude and extent of
356 the contrasts in Figures 2B and 2C are likely attributable to the larger sample size in the present
357 study.

358

359 **MRI Data Acquisition**

360 MRI data were acquired with a 3T Philips Achieva MRI scanner (Philips Medical
361 Systems, Andover, MA, USA) equipped with a 32-channel receiver head coil. Functional images
362 were acquired with a blood oxygenation level dependent (BOLD), T2*-weighted echoplanar
363 imaging (EPI) sequence (SENSE factor = 1.5, flip angle = 70°, 80 × 80 matrix, FOV = 240 mm x
364 240 mm, TR = 2000 ms, TE = 30 ms, 34 ascending slices, slice thickness = 3 mm, slice gap = 1
365 mm), and were oriented parallel to AC-PC. Five “dummy” scans were acquired at the start of
366 each EPI session and discarded to allow for equilibration of tissue magnetization. A total of 180
367 functional volumes were acquired during each study session, for a total of 900 brain volumes.
368 T1-weighted images (MPRAGE sequence, 240 × 240 matrix, 1 mm isotropic voxels) were
369 acquired for anatomical reference following prior to the first study session.

370 **Formation of Study Specific MNI Templates**

371 A sample specific EPI template was created using the mean EPI image from all
372 participants included in the analysis following previously published procedures (de Chastelaine
373 et al., 2011, 2016). Each participant’s mean EPI image was first normalized to the standard EPI
374 template in SPM12, and the spatially normalized images were then averaged within age group to
375 create a young and older adult EPI template. The final template was created by averaging the two
376 age-specific templates.

377 **fMRI Preprocessing**

378 The functional data were preprocessed with Statistical Parametric Mapping (SPM12,
 379 Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab 2017b
 380 (The Mathworks, Inc., USA). The functional data were reoriented, subjected to a two-pass
 381 realignment procedure whereby images were first realigned to the first image of a session and
 382 then realigned to a mean EPI image, and corrected for slice acquisition time differences using
 383 sinc interpolation with reference to the middle slice. Finally, images were spatially normalized to
 384 a study specific EPI template (see Creation of Study Specific MNI Templates below), and
 385 smoothed with an 8mm full-width at half-maximum kernel.

386 The data from the five study sessions were concatenated and subjected to a least-squares-
 387 all (LSA) GLM to estimate the BOLD response to individual trials (Rissman et al., 2004;
 388 Mumford et al., 2014). Events were modeled as a 2 s-duration boxcar convolved with a canonical
 389 HRF. Covariates of no interest in this first level model included the 6 rigid body motion
 390 parameters estimated from the realignment procedure and 4 session specific means (for sessions
 391 2-5).

392 Differentiation Index Analysis

393 We computed a differentiation index for the PPA and LOC ROIs (see Identifying PPA
 394 and LOC Regions-of-Interest). For each trial, we extracted the average BOLD amplitude
 395 separately for each ROI (collapsed across hemisphere). These individual trial values were used to
 396 compute separate differentiation indices for each bilateral ROI using a similar formula to that
 397 employed by Voss and colleagues (2008). The index is essentially a discrimination metric similar
 398 to the d' signal detection measure (Macmillan and Creelman, 2005), and was computed using the
 399 following formula:

400

$$\text{Differentiation Index} = \frac{\mu_{Pref} - \mu_{Non-Pref}}{\sqrt{\frac{\sigma_{Pref}^2 + \sigma_{Non-Pref}^2}{2}}}$$

401

402 In the above equation, μ_{Pref} and σ_{Pref}^2 refer to the across-trial mean and variance, respectively,
 403 of the BOLD response to an ROI's preferred image type. The $\mu_{Non-Pref}$ and $\sigma_{Non-Pref}^2$ terms
 404 refer to the across-trial mean and variance, respectively, of the non-preferred image type. For the
 405 PPA, scenes were designated as the preferred image type and objects as the non-preferred image
 406 type, and this designation was reversed for the LOC.

407 Positive values of the differentiation index reflect higher 'selectivity' of responding to an
 408 ROI's preferred image type. We note two aspects of this index that bear mention. First, and
 409 importantly, the differentiation index is insensitive to across-participant variability in the
 410 hemodynamic response function and, therefore, is unbiased by putative systematic age-
 411 differences in such factors as cerebral vascular reactivity (see, for example, Liu et al., 2013).
 412 Second, the index is a metric of category selectivity, and does not measure selectivity at the 'item
 413 level' (for potential approaches to item level distinctiveness, see Goh et al., 2010; St-Laurent et

414 al., 2014; Xue et al., 2010). The differentiation index data were subjected to a 2 (Age Group) X 2
415 (ROI: PPA, LOC) mixed factorial ANOVA.

416 An additional ANOVA of the differentiation index data was conducted in which
417 subsequent memory bin (SC, SIDK, Miss) was included as a factor. This ANOVA produced
418 identical results to the 2 X 2 ANOVA described above, with no effects involving subsequent
419 memory. Thus, for simplicity's sake, we focus below on the differentiation index computed
420 across all trials regardless of subsequent memory judgment.

421 The differentiation index is ambiguous with respect to whether a group difference, if any,
422 is driven by reduced BOLD signal for the preferred image type (i.e., neural attenuation), an
423 increase in BOLD signal for the non-preferred image type (i.e., neural broadening), or by both
424 effects (cf. Park et al., 2012). To investigate this issue, we also examined the mean BOLD
425 responses elicited by each image type within the two ROIs using a 2 (Age Group) X 2 (ROI) X 2
426 (Image Type: Object, Scene) mixed factorial ANOVA.

427 A primary goal of the present study was to examine whether neural differentiation during
428 encoding is predictive of subsequent memory performance. We addressed this issue by
429 computing across-participant correlations between the PPA and LOC differentiation indices, and
430 performance on the experimental memory task (i.e., item recognition and source memory
431 scores). Additionally, we computed partial correlations between these indices after controlling
432 for several relevant variables, including age group, item or source memory performance (when
433 source and item memory were in the zero-order correlation, respectively), and visual acuity.

434 For clarity, we focus here on the partial correlations. Results from multiple regression
435 analyses led to conclusions identical to those derived from the partial correlation analyses
436 reported below. Of importance, the inclusion of an interaction term between age and the neural
437 differentiation indices in the regression models did not significantly increase the amount of
438 explained variance compared to models with only age group and differentiation indices as
439 predictors, F 's(1,44) < 2.83, $p \geq .100$, nor did the regression coefficients for the interaction terms
440 approach significance. Thus, we found no support that any of the reported correlations between
441 differentiation indices and memory performance were moderated by age group. Moreover, in the
442 analyses reported below, partial correlations were computed after averaging the memory
443 measures across image type, as there was no indication that the effects of interest were
444 moderated by this variable. Specifically, in a multilevel regression conducted with the *lmerTest*
445 package in *R* (Kuznetsova et al., 2015), no interaction term that involved that variable of image
446 type approached significance, all regression coefficients p 's $\geq .136$. The full results from these
447 multiple and multilevel regression analyses are available from the first author upon request.

448 In addition to the correlation analyses involving memory performance, we also examined
449 the relationship between the differentiation indices and the extracted factor scores for the
450 neuropsychological test battery (see Analysis of Neuropsychological Data), again with partial
451 correlations. Importantly, as with the two memory measures, multiple regression provided no
452 evidence that the relationship between any of the factor scores and the differentiation indices
453 were moderated by age group, F 's(1,44) < 1.66, $p \geq .204$. A multilevel regression model
454 including a factor for the four RC scores led to identical conclusions to those derived from the
455 partial correlations reported below. These regression analyses also are available from the first
456 author upon request.

457 **Pattern Similarity Analysis**

458 To complement the analyses of the univariate differentiation index described above, we
459 also conducted a pattern similarity analysis (PSA; Kriegeskorte et al., 2008). All similarity
460 computations were conducted on single-trial beta weights (see above) and were based on Fisher-
461 z transformed Pearson's correlation coefficients. A within-minus-between (henceforth within-
462 between) similarity metric was computed separately for each ROI with the preferred and non-
463 preferred image category serving as the within and between measure, respectively. For the PPA,
464 the within-category measure was the average across-voxel similarity between a given scene trial
465 with all other scene trials. The between-category similarity measure was the average correlation
466 between a given scene trial and all object trials. For each scene trial in the PPA, the within-
467 between measure was computed as the difference between the above described within and
468 between similarity metrics. A summary measure for a participant was computed by averaging all
469 of the trial-wise within-between measures. The same approach was used to compute the within-
470 between similarity metric for the LOC, except that object trials were used for the within-category
471 measures, and scene trials provided the between-category measures. We refer to the metric as the
472 'similarity index'. Analogous to the differentiation index described above, the similarity index is
473 a measure of similarity at the category and not the item level. The similarity indices were
474 subjected to a 2 (Age Group) X 2 (ROI: PPA, LOC) mixed factorial ANOVA.

475 As for the univariate differentiation index describe above, ANOVA of the similarity
476 metrics that included a subsequent memory factor (SC, SIDK, Miss) revealed no effects
477 involving subsequent memory. Therefore, we report the similarity findings collapsed across
478 subsequent memory judgment. Further echoing the analyses of the differentiation index, we
479 examined the associations between the pattern similarity index and memory and
480 neuropsychological test performance and report the findings in terms of partial correlations.
481 Analysis using multiple regression led to identical conclusions; crucially, there was no indication
482 that adding a term for the interaction between age group and the similarity index improved
483 model fit beyond that obtained with models without this term, $F's(1,44) < 1.35, p \geq .144$, and nor
484 did the regression coefficients for any of the interaction terms approach significance. Thus, we
485 found no evidence that the correlations reported between the pattern similarity index and
486 cognitive performance were moderated by age group.

487

488

Results

489 **Neuropsychological Test Performance**

490 The results from the different measures of the neuropsychological test battery are
491 reported in Table 1. The pattern of age differences is essentially identical to our prior report
492 (Koen et al., 2018), which is not surprising given the high degree of overlap between the samples
493 (see Participants section of the Methods). There were significant effects of age, with older adults
494 performing worse on tests assessing declarative memory, reasoning ability, category fluency, and
495 processing speed. However, older adults were equally proficient at word reading and verbal
496 fluency relative to young adults. Finally, as expected (e.g., Baltes and Lindenberger, 1997), older
497 participants had lower visual acuity than younger adults.

498 The bottom portion of Table 1 shows extracted factor scores derived from the test (see
 499 Table 2 for the rotated PCA loadings and the Neuropsychological Test Analysis section). Not
 500 surprisingly, and consistent with the analysis of the individual tests, there were age differences in
 501 the speed (RC1) and memory (RC2) factors. No age differences were observed for the factors
 502 corresponding to crystallized intelligence (RC3) and fluency (RC4).

503 **Study Reaction Time**

504 Table 2 shows the descriptive statistics of the median RTs for the study judgments. A 2
 505 (Age Group) X 2 (Image Type) X 3 (Subsequent Memory) mixed ANOVA revealed a main
 506 effect of subsequent memory, $F(1.96,90.31) = 24.43$, $MS_e = 8705$, $p < 10^{-8}$, $\text{partial-}\eta^2 = .35$, that
 507 was driven by faster RTs for subsequent source correct trials ($M = 1321$) relative to both source
 508 incorrect ($M = 1399$), $t(92) = 5.86$, $SE = 13.34$, $p < 10^{-4}$ and item miss trials ($M = 1404$), $t(92) =$
 509 6.23 , $SE = 13.34$, $p < 10^{-4}$. There was no significant difference between study RTs associated
 510 with subsequent incorrect source memory and item misses, $t(92) = .37$, $SE = 13.34$, $p = .712$. Nor
 511 were there any significant effects involving age group (all p 's involving Age Group $> .133$).

512
 513

Table 3. Mean (and standard errors) for the median RT (in ms) to judgments made during the study phase.

Subsequent Memory	Young Adults		Older Adults	
	Object	Scene	Object	Scene
Source Correct	1356 (63)	1314 (69)	1293 (31)	1320 (33)
Source Incorrect/Don't Know	1438 (63)	1424 (73)	1365 (45)	1368 (47)
Item Miss	1445 (58)	1444 (71)	1343 (50)	1383 (44)

514

515 **Memory Performance**

516 Table 4 shows the mean proportion of responses given to test items as a function of age
 517 group, image type, and study status (old or new), while Table 5 reports the item and source
 518 memory scores for objects and scenes in young and older adults. A 2 (Age Group) X 2 (Image
 519 Type) mixed factorial ANOVA on the item recognition measure revealed a significant main
 520 effect of image type, $F(1,46) = 187.97$, $MS_e = .01$, $p < 10^{-15}$, $\text{partial-}\eta^2 = .80$, reflecting better
 521 item recognition for objects than scenes. Although older adults ($M = .57$, $SE = .03$) demonstrated
 522 numerically lower item recognition scores than young adults ($M = .65$, $SE = .03$), the main effect
 523 of age group was not significant according to our *a priori* statistical threshold, $F(1,46) = 3.89$,
 524 $MS_e = .04$, $p = .055$, $\text{partial-}\eta^2 = .08$. The interaction between age and image type was not
 525 significant, $F(1,46) = 1.04$, $MS_e = .01$, $p = .312$, $\text{partial-}\eta^2 = .02$.

526

527 **Table 4.** Means (with standard errors) for the proportion of trials in each cell formed by age group, image type, and
 528 item type (old versus new) for the four possible memory response bins.

Test Response	Young Adults				Older Adults			
	Objects		Scenes		Objects		Scenes	
	Old	New	Old	New	Old	New	Old	New
Old+SC	.58 (.05)	–	.32 (.03)	–	.56 (.04)	–	.34 (.03)	–
Old+SI	.04 (.01)	.01 (.01)	.05 (.01)	.03 (.01)	.13 (.02)	.08 (.02)	.12 (.02)	.14 (.03)
Old+DK	.21 (.03)	.04 (.02)	.29 (.02)	.11 (.02)	.14 (.03)	.03 (.04)	.24 (.03)	.15 (.03)

529 New .17 (.03) .95 (.02) .33 (.04) .86 (.03) .17 (.02) .89 (.02) .30 (.03) .72 (.04)
 530 *Note.* It is impossible to have a source correct (SC) response for new trials. Thus, incorrect old responses to new
 531 items are classified as a source incorrect (SI) trial if participants selected one of the two encoding tasks or as a
 source don't know (DK) trial if participants selected the don't know response option.

532

533 An analogous 2 X 2 mixed factorial ANOVA on the source memory measure also
 534 produced a significant main effect of image type, $F(1,46) = 105.05$, $MS_e = .01$, $p < 10^{-12}$, partial-
 535 $\eta^2 = .70$ which was driven by better source memory for objects than for scenes (see Table 5).
 536 There was no significant difference in source memory accuracy between young and older adults,
 537 $F(1,46) = .81$, $MS_e = .06$, $p = .372$, partial- $\eta^2 = .02$, and nor was there a significant interaction
 538 between age and image type, $F(1,46) = .97$, $MS_e = .01$, $p = .329$, partial- $\eta^2 = .02$.

539

540 **Table 5.** Means (with standard errors) estimates of item and source memory discrimination.

Age Group	Item Recognition		Source Memory	
	Object	Scene	Object	Scene
Young Adults	.78 (.04)	.52 (.04)	.51 (.05)	.27 (.03)
Older Adults	.72 (.03)	.42 (.03)	.44 (.04)	.25 (.03)

541 *Note.* Item recognition reflects the difference between the hit and false alarm rate regardless of source memory
 542 accuracy. Source memory was computed with the pR formula (see Behavioral Data Analysis) only for studied
 543 images attracting an accurate 'old' response.

544

545 Differentiation Index

546 The results from the fMRI differentiation index are presented in Figure 3A. A 2 (Age
 547 Group) X 2 (ROI) mixed factorial ANOVA on these data produced a significant interaction,
 548 $F(1,46) = 20.31$, $MS_e = .06$, $p < 10^{-4}$, partial- $\eta^2 = .31$. The interaction was driven by significantly
 549 lower differentiation indices from the PPA in older relative to younger adults, $t(91.71) = 5.76$, p
 550 $< 10^{-4}$. No age differences were observed in the LOC differentiation index, $t(91.71) = .60$, $p =$
 551 $.551$.

552 To investigate if the age-related reduction in the PPA differentiation index resulted from
 553 reduced BOLD signal for the region's preferred stimulus type (i.e., neural attenuation), increased
 554 BOLD signal for an ROIs non-preferred stimulus type (i.e., neural broadening), or a mixture of
 555 the two, we conducted a 2 (Age Group) X 2 (ROI) X 2 (Image Type) mixed factorial ANOVA
 556 on the mean BOLD responses (see Figure 3B). The ANOVA produced a significant three-way
 557 interaction, $F(1,46) = 37.76$, $MS_e = .45$, $p < 10^{-6}$, partial- $\eta^2 = .31$. Post-hoc tests demonstrated
 558 that the mean BOLD response in the PPA was significantly lower for older relative to young
 559 adults when viewing scenes (i.e., the preferred stimulus type), $t(89.34) = 4.51$, $p < 10^{-4}$. No age
 560 differences were present in the PPA during object trials (i.e., the non-preferred stimulus type),
 561 $t(89.34) = .62$, $p = .535$, nor were age differences present in the LOC for either objects, $t(89.34)$
 562 $= 1.72$, $p = .088$, or scenes, $t(89.34) = 1.14$, $p = .257$.

563 **Relationship with Memory Performance.** The zero-order correlations between item and
 564 source memory (averaged across image type), the PPA and LOC differentiation indices, visual
 565 acuity, and age group are shown in Table 6. Our primary hypothesis concerned the relationship

566 between memory performance and the differentiation indices. As can be seen in Table 6, the
 567 differentiation index from the PPA, but not the LOC, was correlated with both item and source
 568 memory. Given the lack of significant correlations with the LOC, the results reported below
 569 focus solely on the PPA.

570

571

572

573

574

575 **Table 6.** Zero-order correlations between memory performance, differentiation index, similarity index, visual acuity,
 576 and age.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
(1) Item Recognition	-							
(2) Source memory	.71 ($< .001$)	-						
(3) PPA Differentiation Index	.53 ($< .001$)	.37 (.010)	-					
(4) LOC Differentiation Index	.09 (.559)	.03 (.837)	.00 (.988)	-				
(5) PPA Similarity Index	0.50 ($< .001$)	0.32 (.026)	.78 ($< .001$)	-.08 (.580)	-			
(6) LOC Similarity Index	.25 (.083)	.15 (.298)	.31 (.030)	.71 ($< .001$)	.19 (.188)	-		
(7) Visual Acuity	-.35 (.016)	-.16 (.268)	-.48 (.001)	.04 (.799)	-.45 (.001)	-.12 (.407)	-	
(8) Age Group	-.28 (.055)	-.13 (.372)	-.61 ($< .001$)	.07 (.632)	-.71 ($< .001$)	-.24 (.106)	.63 ($< .001$)	-

577 *Note.* Correlations were computed using Pearson's r . Item and source memory correlations are based on the
 578 measures after averaging across image type.

579

580 First, we focus on the correlation between item recognition and the PPA differentiation
 581 index. Importantly, this correlation remained significant after partialling out age group, $r_{\text{partial}}(45)$
 582 = .48, $p < .001$ (see Figure 4A). This result, in conjunction with the absence of a moderating
 583 effect of age (see Differentiation Index Analysis in the Methods), suggests that the correlation
 584 between item recognition and the PPA differentiation index is *age invariant*. It is possible that
 585 the correlation between item recognition and PPA differentiation index is due to shared variance
 586 with source memory. Critically, the partial correlation between item recognition and PPA
 587 differentiation index controlling for both age group and source memory remained significant,
 588 $r_{\text{partial}}(44) = .33$, $p = .023$ (see Figure 4B), suggesting that source memory does not account for
 589 the relationship between the differentiation index and item recognition. We also examined
 590 whether the correlation between item recognition and the PPA differentiation index was due to
 591 shared variance with visual acuity. Echoing the above analysis, the partial correlation between
 592 item recognition and the PPA differentiation index after controlling for both age group and visual
 593 acuity remained significant, $r_{\text{partial}}(44) = .46$, $p = .001$.

594 A similar set of partial correlations to that described above was computed for the
 595 relationship between source memory performance and the PPA differentiation index. As with
 596 item recognition, the partial correlation between source memory and the PPA differentiation
 597 index was significant after controlling for age group, $r_{\text{partial}}(45) = .36, p = .011$ (Figure 4C), and
 598 for both age group and visual acuity, $r_{\text{partial}}(44) = .35, p = .016$. However, the correlation was no
 599 longer significant and, indeed, near zero after controlling for age group and item recognition
 600 performance, $r_{\text{partial}}(44) = .04, p = .779$.

601

602 In summary, we observed a significant correlation between item recognition and PPA
 603 differentiation index that was *invariant* across age group, source memory performance, and
 604 visual acuity. Although the PPA differentiation index was significantly correlated with source
 605 memory, this association appeared to result from shared variance with item recognition.

606 **Relationship with Neuropsychological Test Performance.** Table 7 shows the zero-
 607 order correlation between the 4 neuropsychological factors (RCs), visual acuity, differentiation
 608 indices, and age group. The PPA, but not the LOC, differentiation index correlated significantly
 609 with the RCs corresponding to speed, memory, and fluency. To examine whether these
 610 correlations were independent of age, we computed partial correlations between the PPA
 611 differentiation index and the four RCs controlling for age. [It is important to reiterate that there
 612 was no indication of an interaction between age group and PPA differentiation index for any of
 613 the four RCs (see Analysis of Relationships Between Neural Differentiation and Cognition)].
 614 The partial correlation for the speed, $r_{\text{partial}}(45) = -.09, p = .561$, memory, $r_{\text{partial}}(45) = -.05, p =$
 615 $.759$, and crystallized intelligence, $r_{\text{partial}}(45) = .11, p = .468$, factors all failed to reach our
 616 significance threshold. Thus, the zero-order correlations between neural differentiation with the
 617 speed and memory factors reflect variance that is also shared with age group. In contrast, the
 618 partial correlation between the PPA differentiation index and the fluency factor remained
 619 significant, $r_{\text{partial}}(45) = .35, p = .017$ (see Figure 5), suggesting that neural differentiation and
 620 fluency have an age invariant relationship. This correlation remained significant after controlling
 621 for visual acuity in addition to age, $r_{\text{partial}}(44) = .36, p = .014$.

622

623 **Table 7.** Zero-order correlations between factor scores from the neuropsychological test performance,
 624 differentiation index, similarity index, visual acuity, and age.

	(1)	(2)	(3)	(4)
(1) Speed (RC1)	-			
(2) Memory (RC2)	-.46 (.001)	-		
(3) Crystallized IQ (RC3)	.16 (.279)	.10 (.498)	-	
(4) Fluency (RC4)	-.27 (.061)	-.27 (.061)	.16 (.287)	-
Correlations with:				
PPA Differentiation Index	-.40 (.004)	.31 (.030)	.06 (.700)	.37 (.009)
LOC Differentiation Index	-.02	.00	-.08	-.08

	(.908)	(.989)	(.612)	(.584)
PPA Similarity Index	-.48	.34	.09	.30
	(.001)	(.019)	(.560)	(.04)
LOC Similarity Index	-.23	.14	-.05	.20
	(.114)	(.345)	(.739)	(.182)
Visual Acuity	.40	-.41	.05	-.06
	(.005)	(.003)	(.738)	(.677)
Age Group	.57	-.56	.05	-.17
	(<.001)	(<.001)	(.751)	(.257)

625 *Note.* The correlations between Visual Acuity, PPA Differentiation/Similarity Index, LOC Differentiation/Similarity
626 Index, and Age Group are identical to those in reported in Table 6.

627

628 **Pattern Similarity Index**

629 A 2 (Age Group) X 2 (ROI) mixed ANOVA produced a significant interaction, $F(1,46) =$
630 25.11 , $MS_e = .003$, $p < 10^{-5}$, $\text{partial-}\eta^2 = .35$ (see Figure 6a). The interaction was driven by older
631 adults showing lower similarity indices relative to younger adults in the PPA, $t(91.97) = 8.55$, p
632 $< 10^{-12}$, but not in the LOC, $t(91.97) = 1.40$, $p = .164$. These findings mirror those observed for
633 the univariate differentiation index and offer strong convergent evidence for age-related neural
634 dedifferentiation in the PPA.

635 **Relationship with Memory Performance.** The zero-order correlations between item and
636 source memory (averaged across image type) and the pattern similarity indices are shown in
637 Table 6. As with the differentiation index, there were no significant correlations involving the
638 LOC similarity index. Thus, we focus the partial correlation analysis on the index from the PPA.
639 The correlation between item recognition and the PPA similarity index remained significant after
640 partialling out age group, $r_{\text{partial}}(45) = .45$, $p = .002$ (see Figure 6B). This result, in conjunction
641 with the absence of a moderating effect of age (see Pattern Similarity Analysis in the Methods),
642 suggests that the correlation between item recognition and the similarity index in the PPA is *age*
643 *invariant*. Moreover, the correlation remained significant after partialling out both age group and
644 source memory performance, $r_{\text{partial}}(44) = .33$, $p = .025$, and age group and visual acuity,
645 $r_{\text{partial}}(44) = .46$, $p = .002$. These latter two results suggest that the correlation between item
646 recognition and the PPA similarity index was not driven by variance shared with source memory
647 or visual acuity, respectively.

648 The correlation between source memory and the PPA similarity index was also age
649 invariant, $r_{\text{partial}}(45) = .32$, $p = .026$. Although this correlation remained significant when
650 partialling out age group and visual acuity, $r_{\text{partial}}(44) = .32$, $p = .028$, adding item recognition as
651 a covariate along with age group rendered the correlation non-significant, $r_{\text{partial}}(45) = .01$, $p =$
652 $.946$. Thus, the results using the pattern similarity index parallel those for the differentiation
653 index in that the metric of neural differentiation predicted item, but not source, memory in an age
654 invariant manner.

655

656 **Relationship with Neuropsychological Test Performance.** Table 7 shows the zero-
657 order correlation between the 4 neuropsychological factors (RCs) and the PPA and LOC
658 similarity indices. Again, we focus on the PPA as none of the zero-order correlations for the
659 LOC similarity index reached our significance threshold. The partial correlation for the speed,

660 $r_{\text{partial}}(45) = -.13, p = .367$, memory, $r_{\text{partial}}(45) = -.10, p = .512$, crystallized intelligence,
661 $r_{\text{partial}}(45) = .17, p = .258$, and fluency, $r_{\text{partial}}(45) = .26, p = .080$, factors all failed to reach our
662 significance threshold after controlling for age group. The lack of a significant partial correlation
663 between the PPA similarity index (controlling for age group) and the fluency factor stands in
664 contrast to findings for the differentiation index reported above. It is noteworthy, however, that
665 the correlation was sizeable and in the same direction as that for the differentiation index.

666

Discussion

667 We describe three main findings. First, we replicated prior findings (e.g., Park et al.,
668 2004, 2012; Voss et al., 2008) by showing age-related reductions in two measures of category-
669 level neural differentiation (henceforth, collectively termed neural differentiation indices). These
670 age differences were observed only in the PPA, and not in the LOC. Second, we found an age
671 invariant relationship between neural differentiation in the PPA and item recognition memory.
672 Lastly, a similarly age invariant relationship was evident between a ‘fluency’ factor derived from
673 neuropsychological test scores and neural differentiation (albeit, reaching significance only for
674 the differentiation index). Together, the findings suggest that neural differentiation in the PPA is
675 associated with two independent sources of variance: age and cognitive performance.

676 Absence of Age Differences in Item and Source Memory

677 No age differences were observed in study RT, item recognition, or source memory.
678 While age differences in RT might be expected, null age effects on study RT have been reported
679 previously in tasks very similar to the present one (e.g., de Chastelaine et al., 2011, 2016;
680 Mattson et al., 2014; Wang et al., 2016). The lack of an age difference in source memory is more
681 surprising given well-documented age-related deficits in recollection (Koen and Yonelinas,
682 2014; Schoemaker et al., 2014) and source memory (Spencer and Raz, 1995; Old and Naveh-
683 Benjamin, 2008). This null finding might reflect our employment of an atypical older sample.
684 This is a perennial concern in neuroimaging studies of aging (Rugg, 2017), but is mitigated here
685 by the ‘standard’ pattern of impaired and preserved neuropsychological test performance
686 demonstrated by our older participants (e.g., Drag and Bieliauskas, 2010; Park et al., 2002). A
687 second possibility is that age differences in source memory were masked by an especially
688 conservative response bias in young adults. This could have resulted from our instruction to
689 report source memory decisions only when confidence was high. In complying, young adults
690 might have withheld what would have been accurate decisions because their response criteria
691 were set above the threshold necessary for accurate responding, lowering their source accuracy
692 and attenuating potential age differences. Lastly, the encoding tasks might have
693 disproportionately benefited memory encoding in older adults, an effect that has sometimes been
694 reported to eliminate age differences in recollection (Luo et al., 2007). Although the last two
695 accounts are not mutually exclusive, the latter account also accommodates the null age effects on
696 item memory.

697 The Age Component of Neural Differentiation

698 Our findings replicate prior research demonstrating that age-related neural
699 dedifferentiation in the PPA is driven by diminished BOLD responses to scenes in older adults
700 (“neural attenuation”; Park et al., 2012). Counter to prior findings (Park et al., 2004; for related
701 findings, see Berron et al., 2018), we did not observe significant age differences in neural
702 differentiation in the LOC, a region selectively responsive to objects from a wide variety of

703 categories (Grill-Spector et al., 2001). This null finding for the LOC is not unprecedented: Chee
704 and colleagues (2006) also reported null age differences in the LOC for objects (relative to
705 scenes); relatedly, Voss and colleagues (2008) reported null effects of age on neural selectivity
706 for familiar words and colors.

707 Our results add to the evidence for age-related neural dedifferentiation, but do little to
708 elucidate its functional significance. Any account must, however, accommodate the present and
709 prior findings (see above) that age-related dedifferentiation is evident only for some stimulus
710 classes. One possibility (raised by a reviewer) is that the present findings have their origin not in
711 the way different neural regions represent visual categories as a function of age, but in age-
712 related differences in eye-movements. By this argument, the results for the PPA reflect the
713 adoption by older and younger adults of different scanning strategies when confronted with
714 scenes (e.g., Açıık et al., 2010). This account cannot be definitively ruled out in the absence of
715 eye-movement data (which, to our knowledge, have yet to be reported in any relevant study). We
716 note however that it cannot be a general explanation of age-related neural differentiation, which
717 has been reported not only for visual stimuli, but for auditory stimuli and motoric activity also
718 (Carp et al., 2011a; Grady et al., 2011a, 2011b).

719 A second account arises from the prosaic idea that perceptual experience and knowledge
720 accumulate over the lifespan because of an ever-increasing number of encounters with new
721 exemplars of different perceptual categories (for related findings showing that the neural
722 correlates of object processing are moderated by a variable related to life experience, namely
723 culture, see Goh et al., 2007; for review, see Goh and Park, 2009). Thus, when confronted with a
724 novel exemplar, older individuals are arguably better able to assimilate it into a pre-existing
725 representational structure (a perceptual “schema”; Gilboa and Marlatte, 2017) than are young
726 adults, who have had less opportunity to develop such schemas. Consequently, with increasing
727 age, perceptual processing of novel category exemplars will come to more closely resemble the
728 processing afforded previously experienced exemplars. By this hypothesis, therefore, age-related
729 neural dedifferentiation is not necessarily a detrimental consequence of increasing age.

730 This ‘familiarity hypothesis’ accounts for two important aspects of the present data. First,
731 it is consistent with the findings that age-related dedifferentiation in the PPA resulted from
732 neural attenuation. According to the above hypothesis, the processing of novel exemplars of a
733 visual category will more closely resemble the processing engaged by familiar exemplars in
734 older than in younger adults. Thus, when first encountered, such stimuli might be expected to
735 elicit smaller neural responses in older individuals, that is, to demonstrate ‘repetition
736 suppression’ – the much-studied neural correlate of perceptual priming (e.g., Henson and Rugg,
737 2003; Gotts et al., 2012; Barron et al., 2016).

738 Second, the hypothesis provides an explanation for the absence of age-related neural
739 dedifferentiation in the LOC reported here and previously (Chee et al., 2006), and its absence in
740 word- and color-selective cortical regions in Voss and colleagues (2008). The hypothesis
741 predicts that age differences in neural differentiation will be diminished for exemplars that are
742 similarly familiar to both young and older individuals. Arguably, even young adults have
743 experienced canonical objects of the kinds employed in the present study on numerous occasions
744 prior to the experimental session, resulting in a blunting of age-differences in neural
745 differentiation. Consistent with this proposal, Voss and colleagues (2008) failed to identify age-
746 related dedifferentiation for words, whereas Park and colleagues (2004) reported robust

747 dedifferentiation for pseudo-words, items that likely would not have been encountered by
748 members of either age group pre-experimentally.

749 **Relationship Between Neural Differentiation and Memory Performance**

750 We observed robust correlations between the PPA neural differentiation index and both
751 recognition memory performance for the experimental items, and a fluency factor derived from
752 neuropsychological test scores (for related findings, see Park et al., 2010; Du et al., 2016; Berron
753 et al., 2018). The finding that lower neural differentiation was predictive of poorer memory
754 performance is broadly consistent with our pre-experimental hypothesis that dedifferentiation
755 should impact memory encoding. Importantly, this relationship was age invariant, and suggests
756 that neural selectivity and item recognition are similarly coupled across much of the adult
757 lifespan (Rugg, 2017). As suggested by a reviewer, our failure to find age differences in memory
758 performance might have contributed to the failure to find a moderating effect of age on the
759 relationships between neural differentiation and cognitive performance. While we cannot
760 definitively rule out this possibility, we note that findings from prior studies indicate that null
761 effects of age on a behavioral measure are not a precondition for finding age-invariant brain-
762 behavior correlations (e.g., de Chastelaine et al., 2011, 2016; Wang et al., 2016; for related
763 findings, see Du et al., 2016).

764 Another important result is the seemingly selective relationship between neural
765 differentiation and item recognition. Whereas the correlation with recognition remained when
766 source memory performance was controlled for, the reverse was not the case. Thus, neural
767 differentiation was primarily a predictor of memory for the experimental items themselves, and
768 not for their study contexts, possibly suggesting that the relationship between neural
769 differentiation and memory performance is dependent on such factors as task demands. One
770 might predict that a unique relationship between source memory performance and neural
771 differentiation would have emerged had the studied scenes and objects been employed as source
772 features rather as test items.

773 As noted, we found an age invariant relationship between neural differentiation and one
774 of the latent factors – ‘fluency’ – derived from neuropsychological test performance. In line with
775 Park and colleagues (2010), who described an analogous relationship between neural
776 differentiation and fluid intelligence (in older adults only), the present finding suggests that
777 neural differentiation may index not just the precision with which perceptual information is
778 represented, but also broader aspects of neural efficiency. More generally, our findings that the
779 relationships between neural differentiation and item memory performance and fluency were age
780 invariant could be seen as a challenge to the view that neural dedifferentiation is a determinant of
781 cognitive aging (e.g., Li et al., 2001; Park et al., 2010). This conclusion should be treated as
782 provisional, however, until the present findings are replicated in larger and more diverse samples
783 of participants.

784

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984 **Figure 1.** Schematic overview of the memory task. Participants studied an intermixed list of object and scene
985 images under intentional encoding instructions while undergoing fMRI scanning. Each image was preceded by a
986 task cue that instructed participants to rate the image for pleasantness (P?) or to determine which movie genre the
987 image was best associated with (movie, M?). There were a total of 5 scanned study phases. After the final study
988 phase, an out-of-scanner recognition memory test was administered. The test phase comprised the studied objects
989 and scenes intermixed with new images. Participants were instructed to select one of four memory judgments for
990 each image. The four judgments comprised options for whether participants had high confidence both that they
991 studied the image and could recollect the study task (Old Pleasant and Old Movie responses), had high confidence
992 that they studied the image but were had low confidence in their memory for or could not remember the study task
993 (Old Don't Know response), or if they did not have high confidence that the image was studied (New response).
994 Two measures of memory performance were obtained from the test phase: item recognition and recall of the
995 encoding task (i.e., source recall).

996 **Figure 2.** (A) Voxels comprising the regions-of-interest (ROIs) in the parahippocampal place area (PPA; yellow
997 voxels) and lateral occipital cortex (LOC; red voxels) derived from an unpublished data set. Note that the ROIs were
998 anatomically masked using the Neuroinformatics atlas included in SPM12. The anatomical labels for this mask
999 included bilateral parahippocampal, fusiform, middle occipital, and inferior occipital gyri. (B) Statistical parametric
1000 maps (SPMs) from the unpublished experiment showing the one-tailed contrasts of Scene > Objects and Objects >
1001 Scenes. (C) SPMs for the Scene > Objects and Objects > Scene contrast in the 24 young and 24 older adults in the
1002 present data (collapsed across age group). The SPMs are thresholded at FWE of $p < .05$ (FWE).

1003 **Figure 3.** (A) Plot of the differentiation index computed from the LOC and PPA for young and older adults. (B) Plot
1004 of the across-trial mean beta-values for each image type and region of interest. Each green and orange circles
1005 represent an individual participant's data, and the black circle represents the group mean with error bars denoting ± 1
1006 standard error of the mean.

1007 **Figure 4.** Scatter plots showing the partial correlation between the PPA differentiation index and item recognition
1008 (A,B) and source memory (C,D). The partial plots control for age group (A,C), age group and source memory (C),
1009 and age group and item recognition (D).

1010 **Figure 5.** Scatter plots showing the partial correlation between the PPA differentiation index and the factor score for
1011 fluency (RC4) controlling for age.

1012 **Figure 6.** (A) Plot of the similarity index (within-between similarity for the preferred image type) computed from
1013 the LOC and PPA for young and older adults. (B) Scatter plot showing the partial correlation between the similarity
1014 index in the PPA and item recognition controlling for age group.

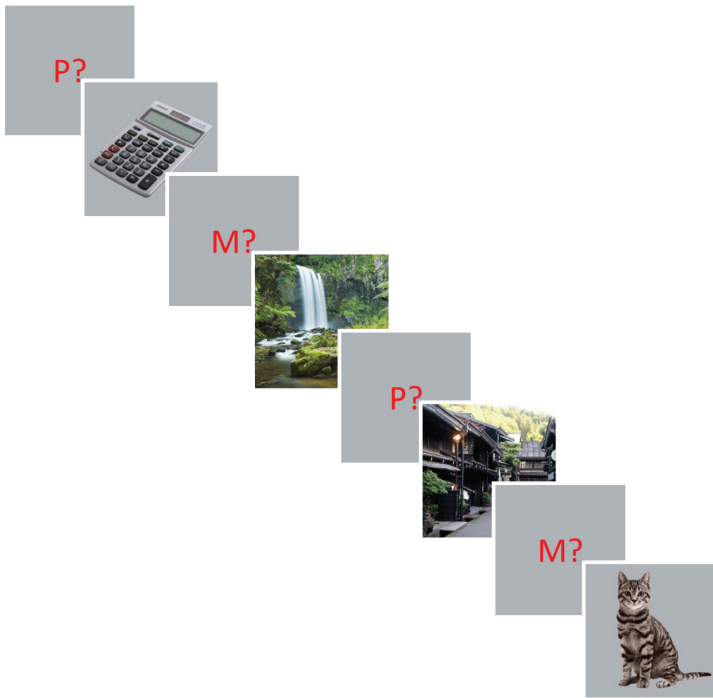
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Study



Test



Old Pleasant Old Movie Old Don't Know New

