

# 1 **Tracking age differences in neural distinctiveness across** 2 **representational levels**

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4 Abbreviated title: Age differences in neural distinctiveness

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31 The authors declare no competing financial interests.

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33

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45

46 **Abstract**

47 The distinctiveness of neural information representation is crucial for successful memory  
48 performance but declines with advancing age. Computational models implicate age-related  
49 neural dedifferentiation on the level of item representations, but previous studies mostly  
50 focused on age differences of categorical information representation in higher-order visual  
51 regions. In an age-comparative fMRI study, we combined univariate analyses and whole-brain  
52 searchlight pattern similarity analyses to elucidate age differences in neural distinctiveness at  
53 both category and item levels and their relation to memory. Thirty-five younger (18–27 years  
54 old) and 32 older (67–75 years old) women and men incidentally encoded images of faces and  
55 houses, followed by an old/new recognition memory task. During encoding, age-related neural  
56 dedifferentiation was shown as reduced category-selective processing in ventral visual cortex  
57 and impoverished item specificity in occipital regions. Importantly, successful subsequent  
58 memory performance built upon high item stability, that is, high representational similarity  
59 between initial and repeated presentation of an item, which was greater in younger than older  
60 adults. Overall, we found that differences in representational distinctiveness coexist across  
61 representational levels and contribute to interindividual and intraindividual variability in  
62 memory success, with item specificity being the strongest contributor. Our results close an  
63 important gap in the literature, showing that older adults' neural representation of item-specific  
64 information in addition to categorical information is reduced compared to younger adults.

65

66 Key words: episodic memory, aging, neural distinctiveness, neural dedifferentiation,  
67 representational similarity, fMRI

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69

## 70 **Significance Statement**

71 A long-standing hypothesis links age-related cognitive decline to a loss of neural specificity.  
72 While previous evidence supports the notion of age-related neural dedifferentiation of category-  
73 level information in ventral visual cortex, whether or not age differences exist at the item level  
74 was a matter of debate. Here, we observed age group differences at both levels as well as  
75 associations between both categorical distinctiveness and item specificity to memory  
76 performance, with item specificity being the strongest contributor. Importantly, age differences  
77 in occipital item specificity were largely due to reduced item stability across repetitions in older  
78 adults. Our results suggest that age differences in neural representations can be observed across  
79 the entire cortical hierarchy and are not limited to category-level information.

## 80 **Introduction**

81 A prominent theory of cognitive aging assumes that neural representations become less  
82 distinctive in old age and that this so-called neural dedifferentiation underlies age-related  
83 cognitive impairments (e.g., Koen and Rugg, 2019; Li et al., 2001; Park et al., 2010). In  
84 computational models, age differences have been ascribed to deficient neuromodulation that  
85 causes haphazard activation to identical informational input leading to lower stability (i.e.,  
86 consistency of neural activity across repetitions) of representations on the item level as well as  
87 increasing random activation variability within the network leading to a decrease in the  
88 distinctiveness of the network's representations (Li and Sikström, 2002; Li et al., 2000, 2001).  
89 Importantly, deficient neuromodulation thus results in age differences in neural information  
90 representation that coexist at various levels, i.e., at the level of item representations and the  
91 level of category representations, and jointly affect memory performance. However, previous  
92 age-comparative studies (mainly using functional magnetic resonance imaging; fMRI) have  
93 nearly exclusively focused on age-related dedifferentiation in categorical representations,  
94 neglecting age differences at the level of item representations that possibly occur already during  
95 earlier stages of visual processing. Hence, while long-standing observations from behavioral  
96 aging research suggest a close connection between age differences in sensory processing and  
97 decline in higher order cognition (e.g., Baltes and Lindenberger, 1997; Li and Lindenberger,  
98 2002; Lindenberger and Baltes, 1994; Schneider and Pichora-Fuller, 2000), the limited  
99 available evidence has not yet allowed to settle the debate whether or not age differences in  
100 neural distinctiveness already exist at the level of item representations (Koen and Rugg, 2019).  
101 We therefore set out to track age differences at different representational levels, ranging from  
102 item-level specificity to category selectivity, with the goal to delineate their unique and joint  
103 contribution to memory performance in younger and older adults.

104 The available evidence clearly supports the notion of age-related neural  
105 dedifferentiation of category information. Focusing on age differences in the representation of

106 broader categories such as faces, houses, or objects within the ventral visual cortex (VVC; Koen  
107 et al., 2019; Park et al., 2004, 2012; Payer et al., 2006; Srokova et al., 2020; Voss et al., 2008),  
108 previous studies made use of the preferential response of these regions to specific stimulus  
109 categories (Epstein and Kanwisher, 1998; Grill-Spector and Malach, 2004; Kanwisher et al.,  
110 1997). For example, using conventional univariate analyses, Park et al. (2004) demonstrated  
111 that, compared to young adults, older adults exhibited less category-selective blood oxygen  
112 level dependent (BOLD) responses to stimuli of faces, houses, chairs, and pseudowords,  
113 providing the first human evidence for age-related neural dedifferentiation in the VVC (see also  
114 Park et al., 2012; Payer et al., 2006, and, accounting for trial-wise BOLD variability: Koen et  
115 al., 2019; Voss et al., 2008). Directly probing the (dis-)similarity of distributed, multivariate  
116 activation patterns – with representational similarity (cf. Edelman, 1998; Kriegeskorte et al.,  
117 2008) or decoding techniques (cf. Haynes and Rees, 2006; Mur et al., 2009) – subsequent  
118 studies revealed that different stimulus categories were represented less distinctively in  
119 category-selective areas in the VVC in older compared with younger adults (Carp et al., 2011;  
120 Koen et al., 2019; Park et al., 2010; Trelle et al., 2019). A few age-comparative studies also  
121 investigated neural distinctiveness at the within-category (Goh et al., 2010) or even item level  
122 (Trelle et al., 2019). Unfortunately, with few exceptions (Sommer et al., 2019; St-Laurent et  
123 al., 2014), these studies focused on predefined category-specific regions. However, it is very  
124 likely that processing of item-specific representations is also supported by other brain regions  
125 than those showing category selectivity (see e.g., Kriegeskorte et al., 2007). We therefore  
126 speculated that age differences in item specificity may have gone unnoticed in most studies  
127 with region-of-interest (ROI) approaches that focused on category-specific brain regions.

128       Importantly, assuming that an altered signal-to-noise ratio in neural information  
129 processing leads to more variable neural responses in old age (Li et al., 2001), item-level  
130 specificity in older adults may depend critically on representational item stability, that is, the  
131 consistency with which individual items are represented across several instances of encoding.

132 However, while studies with young-adults-only samples have already revealed the importance  
133 of item stability (inside and outside of category-selective areas including, for instance, occipital  
134 cortex) for memory performance (Ward et al., 2013, Xue et al., 2010), so far only one study by  
135 Zheng et al. (2018) compared item stability across repeated encoding between younger and  
136 older adults. They found that, independent of their distinctiveness from other representations,  
137 item stability in the visual cortex was reduced in older adults and was associated with lower  
138 memory performance compared with young adults. Moreover, item stability was an important  
139 contributor to memory performance as indicated by subsequent memory effects (cf. Paller and  
140 Wagner, 2002). However, age differences were less clear regarding item specificity, a measure  
141 calculated similarly to item stability but corrected for similarity of items from the same  
142 category. This inconsistency provoked criticism regarding the validity of the results (see Koen  
143 and Rugg, 2019).

144 In sum, there is a clear tension between model-derived predictions for neural  
145 dedifferentiation and available empirical support. While many studies provided coherent  
146 evidence for neural dedifferentiation with age at the category level (for reviews, see Koen and  
147 Rugg, 2019; Koen et al., 2020), they did not directly test a central tenet of computational models  
148 of dedifferentiation (Li and Sikström, 2002; Li et al., 2000, 2001), namely reduced  
149 distinctiveness of single-item representations. Thus, whether age differences exist at the level  
150 of item representations is an ongoing debate in the field based on highly limited evidence (see  
151 e.g., Koen and Rugg, 2019). Hence, in the current age-comparative fMRI study, we combined  
152 conventional ROI-based univariate analysis and whole-brain searchlight pattern similarity  
153 analysis to elucidate age-related differences in neural specificity both at the level of categorical  
154 information as well as at the level of the individual items, and their relation to memory  
155 performance.

## 156 **Materials and Methods**

157 **Table 1.** Key resources

158

RESOURCE	SOURCE	IDENTIFIER
<b>Software and Algorithms</b>		
<b>Fieldtrip Toolbox</b>	<a href="http://www.fieldtriptoolbox.org">http://www.fieldtriptoolbox.org</a>	RRID:SCR_004849
<b>MATLAB 2020b</b>	<a href="http://www.mathworks.com">http://www.mathworks.com</a>	RRID:SCR_001622
<b>Psychtoolbox</b>	<a href="http://psychtoolbox.org">http://psychtoolbox.org</a>	RRID:SCR_002881
<b>SPM12</b>	<a href="https://www.fil.ion.ucl.ac.uk/spm">https://www.fil.ion.ucl.ac.uk/spm</a>	RRID:SCR_007037
<b>Fmriprep</b>	<a href="http://fmriprep.readthedocs.io">http://fmriprep.readthedocs.io</a>	RRID:SCR_016216

159

### 160 **Participants**

161 The face-house task described in the current report was embedded in a larger study with an  
162 overall sample consisting of 47 younger and 49 older healthy adults who participated in several  
163 structural MRI scans and additional behavioral tasks inside and outside the MR scanner. Thirty-  
164 nine young and 37 older adults completed the face-house task. We excluded 3 participants (2  
165 young adults and 1 older adult) due to memory performance below chance level and 6  
166 participants (2 young adults and 4 older adults) due to a failure to detect category-selective  
167 clusters (see below). Therefore, final analyses were based on a sample of 35 young adults (age:  
168  $M = 22.11$  years,  $SD = 2.70$ , 18–27 years; 17 female; 18 male) and 32 older adults (age:  $M =$   
169  $70.72$  years,  $SD = 2.26$ , 67–75 years; 19 female; 13 male) with normal or corrected-to-normal  
170 vision and no history of neurological or psychiatric diseases. No participant was taking any  
171 medications known to affect brain functions. A potential confounding factor of age differences  
172 in fMRI-based measures are age-related changes in the neurovascular system (cf. D’Esposito  
173 et al., 1999; Grinband et al., 2017; Lu and Liu, 2017; West et al., 2019). In the present study,  
174 participants were carefully screened for comorbidities and their medications that could affect  
175 blood flow, e.g., hypertension (cf. Gazzaley and D’Esposito, 2005). Furthermore, we screened

176 all older adults with the Mini-Mental State Examination (Folstein et al., 1975) and none scored  
177 below the threshold of 26 points ( $M = 29.19$ ;  $SD = 1.12$ ;  $range = 26-30$ ). All participants gave  
178 written informed consent to take part in the experiment. All procedures were approved by the  
179 ethics committee of the German Society for Psychological Research (DGPs).

180

## 181 **Stimuli and procedure**

182 *Stimulus material.* Overall, the stimulus set comprised 300 grey-scale pictures from three  
183 different categories: 120 neutral faces (adapted from the FACES database; Ebner et al., 2010),  
184 120 houses (in part adapted from Park et al. 2004 and in part obtained through web search) and  
185 60 phase-scrambled images (30 faces and 30 houses, constructed from randomly chosen  
186 pictures of the faces / houses sets) as control stimuli. Face stimuli furthermore consisted of four  
187 subcategories, split by age-group (i.e., young vs. old) and gender (i.e., female vs. male).  
188 Similarly, house stimuli comprised four subcategories, namely apartment buildings, family  
189 houses, sheds, and warehouses. In addition, three target stimuli were used for the encoding task,  
190 comprising a specific face image, a specific house image, and a phase-scrambled image with a  
191 white square in the center. All 240 non-target face and house stimuli were split into two sets of  
192 120 items (60 faces and 60 houses comprising 15 stimuli of each subcategory) to present one  
193 set during encoding and recognition (old items) and the other set only during recognition (new  
194 items). The same item sets were used as old or new items across subjects.

195 *Procedure.* Here, we focused on the face–house task consisting of an incidental  
196 encoding phase and a surprising recognition test, both conducted inside the MR scanner (see  
197 Figure 1A). After verbal and written instructions, giving consent, and performing several  
198 behavioral tasks including a short training of the encoding task, participants were positioned  
199 into the scanner. Here, they again practiced the task for a few trials. The encoding phase  
200 consisted of two identical runs including 9 stimulus blocks each (see Figure 1B). Stimuli were  
201 presented using Psychtoolbox (Psychophysics Toolbox) for MATLAB (The MathWorks Inc.,

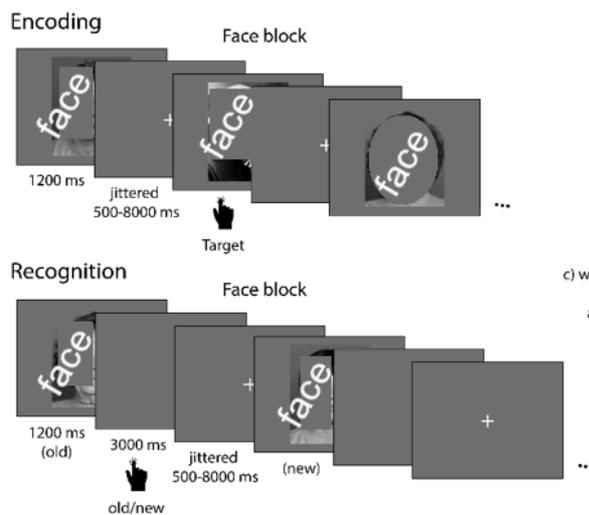
202 Natick, MA, USA). During each block, one target (for which participants had to respond) and  
203 20 non-target images of the same category (i.e., faces, houses, or phase-scrambled controls)  
204 were presented for 1200 ms with a fixation cross shown between trials (jittered; ranging from  
205 500 ms to 8000 ms). While face or house blocks included five images from each of the four  
206 subcategories, phase-scrambled blocks comprised ten scrambled face images and ten scrambled  
207 house images. Stimuli were randomly distributed into the blocks. Stimulus order was pseudo-  
208 randomized with the restriction that no subcategory appeared twice in a row and the target  
209 image was presented neither in the first four nor last four trials of a block. The order of the  
210 blocks was alternating and counterbalanced across participants with either starting with a face  
211 or house block. Due to a technical failure, the identical stimulus order solution was used for all  
212 participants starting with a face block and in 36 participants starting with a house block. To  
213 ensure attention to all stimuli during encoding, subjects were instructed to engage in a vigilance  
214 task asking them to press a button with their right index finger whenever one of the three target  
215 images was presented. Such target trials were excluded from further analyses. In the second  
216 run, blocks and trials were exactly repeated as in the first run, i.e., each image was presented  
217 twice during encoding. In total, the encoding task lasted 22 minutes.

218         After encoding, several structural scans were conducted (see below). Then, subjects had  
219 a break outside the scanner in which the surprise recognition test was explained to them before  
220 going back into the scanner to perform the recognition test. The duration between the encoding  
221 and recognition tasks was approximately 30 minutes. The recognition test consisted of three  
222 face and three house blocks presented in alternated and counterbalanced order. Each block  
223 contained 20 previously seen and 20 new images. Subjects were instructed to indicate whether  
224 a presented image was old or new via button press during stimulus presentation (1200 ms) or  
225 the following grey screen (3000 ms). The order of the trials was pseudo-randomized with the  
226 restriction that images of the same subcategory or four old or new images did not appear  
227 successively. Furthermore, trials were separated by a jittered fixation cross (500-8000 ms).

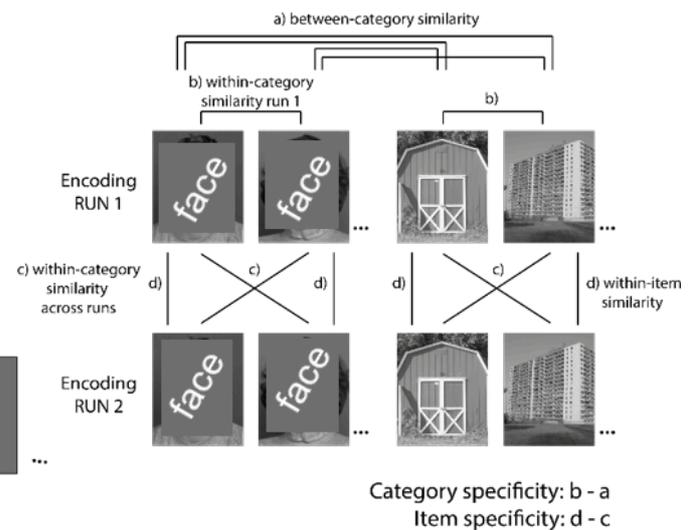
228 Again, due to a technical issue an identical stimulus order was used for 13 participants starting  
 229 with a face block and for 14 participants beginning with a house block. The recognition task  
 230 lasted about 26 minutes.

231

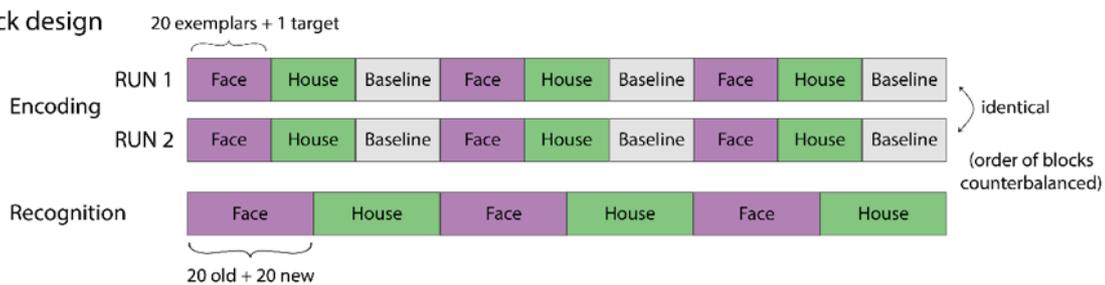
### A. Paradigm



### C. Representational similarity levels



### B. Block design



232

**Figure 1. Task design and schematic of representational similarity levels.**

**A.** The paradigm comprised an encoding (top) and recognition (bottom) task. During encoding, participants were asked to press a button whenever a previously trained target image appeared. During recognition, participants responded via button press whether each presented image was old or new. Here, only sample stimuli from a face block are shown for illustration but also houses and baseline control stimuli were presented. **B.** Illustration of the block design of encoding and recognition tasks. The encoding task consisted of two identical runs, each of which comprised 3 face, 3 house, and 3 baseline (phase-scrambled faces and houses) blocks in alternating and counterbalanced order (either starting with a face or house block). In each block, 20 exemplars of the respective category (face, house, baseline)

were presented plus one target stimulus. The recognition task consisted of 3 face and 3 house blocks in alternating and counterbalanced order. In each block, 20 old and 20 new faces/houses were presented.

**C. Simplified illustration of the computed representational similarity levels.** For each item presented in encoding run 1, neural pattern similarity was computed as the Pearson correlation of the BOLD pattern elicited by that item and the BOLD pattern(s) elicited by (a) all items of the respective other category in run 1 (between-category similarity), (b) all other items of the same category in run 1 (within-category similarity in run 1), (c) all other items of the same category in run 2 (within-category similarity across runs), (d) the same item in run 2 (within-item similarity; stability). For each subject, the respective similarity measure was averaged across items, resulting in one similarity value for each representational level. Category representation specificity was calculated as the difference of between-category and within-category similarity (b–a). Item representation specificity was calculated as the difference of within-category (across runs) and within-item similarity (d–c). These similarities were assessed based on regions of interests as well as a searchlight approach, see main text.

233

## 234 **Behavioral data analyses**

235 Behavioral data was analyzed using custom-written MATLAB scripts. Performance in the  
236 target detection task during encoding was measured as percentage of correct responses to  
237 targets. Memory performance in the recognition task was assessed by calculating the  
238 discrimination-index  $Pr$  (Snodgrass and Corwin, 1988), which is an unbiased parameter for  
239 recognition performance.  $Pr$  was calculated as the difference between the hit-rate (proportion  
240 of old responses to old images) and the false-alarm-rate (proportion of old responses to new  
241 images). We used  $t$ -tests to probe whether recognition performance was different from chance  
242 level, and whether memory performance differed for face and house images. Age differences  
243 in memory performance were assessed by computing an independent samples  $t$ -test between  
244 younger and older adults. For effect sizes, we report Cohen's  $d$ .

245

246

## 247 **FMRI data collection and preprocessing**

248 All MR images were acquired with a 3T Siemens Magnetom Tim Trio scanner. MRI data  
249 acquisition included a T1-weighted structural image (MP-RAGE sequence: TR = 2.5 ms, TE =  
250 4.77, flip angle = 7°, TI = 1.1 ms, voxel size = 1 × 1 × 1 mm<sup>3</sup>) and T2\*-weighted echoplanar  
251 images (TR = 2 s, TE = 30 ms, pixel size = 3 × 3 mm<sup>2</sup>) sensitive to blood oxygenation level-  
252 dependent (BOLD) contrast. EPIs were acquired in two separated encoding and retrieval  
253 sessions, which each comprised 270 volumes with 36 axial slices of 3 mm thickness, separated  
254 by 3.3 mm. As part of the larger study context, we additionally acquired turbo spin-echo proton  
255 density images (PD), diffusion tensor images (DTI) and fluid attenuation inversion recovery  
256 (FLAIR).

257 MRI data were first organized according to “Brain Imaging Data Structure”  
258 specifications (BIDS; Gorgolewski et al., 2016). Data processing was performed using the  
259 FMRIPrep toolbox (1.4.0) (Esteban et al., 2019) with the default processing steps incorporating  
260 the software packages: FSL, FreeSurfer, ANTs and AFNI. First, each T1-weighted volume was  
261 corrected for intensity non-uniformity and skull-stripped to reconstruct brain surfaces. Brain-  
262 extracted T1-weighted images were spatially normalized to the ICBM 152 Nonlinear  
263 Asymmetrical template version 2009c through nonlinear registration. Brain tissue segmentation  
264 of cerebrospinal fluid, white-matter and grey-matter was performed on the brain-extracted T1-  
265 weighted image. Functional data was slice time corrected, motion corrected and co-registered  
266 to the normalized T1-weighted template. For further details including software packages for  
267 each preprocessing step in FMRIPrep, please refer to the online documentation under  
268 <https://fmriprep.org/en/stable/>.

269 For univariate analyses, functional images were resampled to 4 mm isotropic voxels and  
270 spatially smoothed with a kernel of 4 mm full width at half maximum. We computed a  
271 voxelwise general linear model (GLM) including the first and second encoding run using  
272 SPM12. BOLD signal changes were modelled using separate regressors for face, house, and

273 phase-scrambled control image blocks and 6 nuisance motion regressors, which were all  
274 convolved with a canonical hemodynamic response function (HRF).

275 Pattern similarity analyses were conducted on functional images resampled to 2 mm  
276 isotropic voxels to enhance signal-to-noise ratio (Dimsdale-Zucker and Ranganath, 2018) and  
277 were based on single trial beta weights including one trial specific regressor, one regressor for  
278 all other trials, six motion regressors and one run specific mean (Mumford et al., 2012). Trial  
279 specific regressors were modelled as a 1.2 second duration boxcar function convolved with a  
280 canonical hemodynamic response function (HRF).

281

## 282 **Defining regions of interest**

283 We used a cluster-based approach to define individual functional ROIs most strongly engaged  
284 by processing faces or houses during both encoding runs. To restrict our analyses to category-  
285 selective processing areas, we defined an anatomical mask of the VVC using the automated  
286 anatomical labelling atlas (AAL) including bilateral fusiform gyrus, parahippocampal gyrus  
287 and the inferior temporal gyrus (Park et al., 2004). Within this mask, we then contrasted BOLD  
288 responses to face vs. phase-scrambled control image blocks and BOLD responses to house vs.  
289 phase-scrambled control image blocks for each subject. All adjacent voxels exceeding the  
290 uncorrected threshold of  $p < .005$  were defined as one cluster. As mentioned above, 2 young  
291 and 4 older participants were excluded because clusters included less than 10 voxels. The face-  
292 selective ROI was defined as the cluster with the highest averaged  $t$ -value for faces compared  
293 to phase-scrambled images and the house-selective ROI as the cluster with the highest averaged  
294  $t$ -value for houses compared to phase-scrambled images leading to the formation of two  
295 individual functional ROIs. We defined no cutoff of cluster size across subjects. The average  
296 number of voxels in the face and house selective clusters did not differ between young and  
297 older adults (face-selective ROIs:  $M_{young} = 78.8$ ;  $M_{old} = 82.3$ ;  $t(65) = -0.24$   $p = .810$ ; house-  
298 selective ROIs:  $M_{young} = 70.7$ ;  $M_{old} = 85.2$ ;  $t(65) = -1.11$   $p = .273$ ). Within participants, on

299 average only 4.15% (fusiform gyrus: 4.74%; parahippocampal gyrus: 1.64%; inferior temporal  
300 gyrus: 2.40%) of all voxels of the face- and house-selective ROIs overlapped, underlining  
301 separated category-selective clusters in the VVC.

302

### 303 **ROI analysis of category-selective processing**

304 To estimate the fMRI response magnitudes evoked by face and house images within each  
305 individual ROI, we first contrasted the BOLD signal elicited by face and house image blocks  
306 against the BOLD signal of phase-scrambled control image blocks within the first encoding  
307 run. Then, we averaged all  $t$ -values within each ROI to obtain a standardized response value to  
308 faces or houses, respectively. Category selectivity scores were computed by contrasting  
309 standardized BOLD responses to the preferred vs. non-preferred image category within each  
310 individual ROI, e.g., BOLD response to faces vs. BOLD response to houses in the face-selective  
311 ROI. To analyze selectivity scores on group-level, we used a 2 (Age Group)  $\times$  2 (ROI) mixed  
312 factorial ANOVA.

313 Category selectivity scores were collapsed across ROIs to calculate mean selectivity  
314 scores within each participant. This category selectivity score index was correlated with  $Pr$   
315 across all participants using Pearson correlation. Furthermore, we conducted partial correlations  
316 between category selectivity scores and  $Pr$  with age group as control variable to test whether  
317 this relationship is independent of age.

318

### 319 **ROI analysis of category representation specificity**

320 To estimate the specificity of neural category representations within category-selective clusters,  
321 we compared the within-category similarity to the between-category similarity within the first  
322 run using pattern similarity analysis (Kriegeskorte et al., 2008) (see Figure 1C). Similarity  
323 indices were based on Fisher  $z$ -transformed Pearson correlations between single trial beta  
324 weights calculated across voxels. Within and between-category similarity were calculated

325 separately in both ROIs. Within-category similarity was only calculated for items from the  
326 preferred category of the selected area (Koen et al., 2019) and was only computed for items  
327 from different blocks to control for potential confounds due to time dependent correlations in  
328 hemodynamic responses (Dimsdale-Zucker and Ranganath, 2018). For each item, the within-  
329 category similarity was computed as the average across-voxel Pearson correlation of the BOLD  
330 activity pattern of such item to all other items from the same preferred category in a category-  
331 selective area (e.g., similarity of a face trial to all other face trials in the face area). For each  
332 subject, we averaged within-category similarity across items resulting in one within-category  
333 similarity value for each region of interest. The between-category similarity of each item was  
334 calculated as the across-voxel Pearson correlation of the BOLD activity pattern of the item to  
335 the BOLD activity pattern of all items from the other category (e.g., similarity of a face trial to  
336 all house trials in the face area). We again averaged between-category similarity across items  
337 to estimate one between-category similarity value for each region of interest. To test for  
338 differences in pattern similarity values, we used a  $2$  (Age Group)  $\times$   $2$  (within/between-category  
339 similarity)  $\times$   $2$  (ROI) mixed factorial ANOVA. To link category specificity and memory  
340 performance, we collapsed category specificity across ROIs and calculated zero-order and  
341 partial Pearson correlations between category specificity and  $P_r$  controlled for age.

342

### 343 **Searchlight analyses of category representation specificity**

344 We conducted separated searchlight analyses for faces and houses. For each voxel in the brain,  
345 we compiled the difference of within- and between-category similarity (i.e., category  
346 specificity) within an 8 mm-radius sphere centered on that voxel using modified scripts of the  
347 Matlab Toolbox for RSA (Nili et al., 2014). Within and between-category similarity was  
348 calculated as described in the previous section. Thus, we derived a whole-brain map for each  
349 subject where each value indicated the category specificity of the according sphere.

350 We used nonparametric, cluster-based, random permutation statistics adapted from the  
351 fieldtrip toolbox (Oostenveld et al., 2011) to test for age differences in category specificity  
352 across the brain. First, independent *t*-tests were conducted comparing category specificity of  
353 young and older adults for each voxel. Adjacent voxels exceeding the defined threshold of  $p <$   
354  $.005$  were grouped into clusters. The sum of all *t*-values of these empirical clusters was  
355 determined as the respective test statistic. We used the Monte Carlo method to compute a  
356 reference distribution for the summed cluster *t*-values. Category specificity of both age groups  
357 was randomly assigned (1000 permutations) into two new category specificity sets. In every  
358 permutation an independent *t*-test was conducted between the newly generated random sets  
359 within each cluster. The sum of these *t*-values during each permutation was included in the  
360 estimation of the reference distribution of a cluster.

361

### 362 **Searchlight analyses of item representation specificity**

363 To investigate the specificity of item representations, we compared within-item similarity to  
364 between-item similarity (i.e., item specificity) using pattern similarity searchlight analysis (see  
365 Figure 1C). Matching the category specificity searchlight analysis, we compiled the within-  
366 minus-between item similarity for each voxel within an 8 mm-radius sphere. For each item,  
367 within-item similarity was calculated as the across-voxel Pearson correlation of the BOLD  
368 activity pattern of a given item from the first encoding run to the BOLD activity pattern of the  
369 same item from the second encoding run in each sphere. Between-item similarity was computed  
370 as the correlation of the BOLD activity pattern of an item of the first encoding run to the BOLD  
371 activity pattern of all other items from the same category of the second encoding run. For each  
372 participant, we then averaged within- and between-item similarity across items. We used the  
373 resulting within- and between-item similarity brain maps of each participant to calculate one  
374 item specificity brain map for each subject. To test for age differences in item specificity across  
375 the brain, we used nonparametric, cluster-based, random permutation statistics (see section

376 Searchlight analysis of category representation specificity). First level statistics compared item  
377 specificity of young and older adults for each voxel. Second level statistics compared the  
378 summed  $t$ -value of the empirical clusters to a reference distribution computed using the Monte  
379 Carlo procedure.

380 Furthermore, we averaged item specificity for faces and houses for each participant to  
381 estimate one item specificity score per participant. Respective item specificity scores were  
382 correlated with  $Pr$  across participants using Pearson correlations and partial correlations to  
383 control for age group differences.

384 All age comparisons of neural selectivity (see above) and specificity are based on  
385 within-person differences (e.g., the difference between responses to preferred and non-preferred  
386 image categories), which reduces the impact of potential confounding factors in the  
387 neurovascular system as opposed to comparing absolute measures such as absolute BOLD  
388 activation between age groups (cf. Rugg and Morcom, 2005). Crucially, the interaction with  
389 memory performance supports the interpretation that the identified age differences are indeed  
390 related to neurocognitive functions and not merely confounded by unspecific neurovascular  
391 differences.

392

### 393 **Analyzing the relationship between differentiation on multiple representational levels and** 394 **memory performance using LMM**

395 We used linear mixed models (LMM) to examine the contribution of our distinctiveness  
396 measures (category selectivity [Csel], category specificity [Cspec], and item specificity [Ispec])  
397 to memory success ( $Pr$ ). In order to remove main effect differences between the groups, we  
398 standardized (with a mean of zero and unit standard deviation) all variables within the  
399 respective age group. In order to test whether any association between the distinctiveness  
400 measures and memory success were dependent on age group membership, we also tested for  
401 the respective interactions. In addition, we allowed for a random intercept for each participant

402 (ID). In sum, using the fitglm function in MATLAB, we fit the following random intercept  
403 model (in Wilkinson notation, cf. (Wilkinson and Rogers, 1973):

404  $Pr \sim 1 + Csel + Cspec + Ispec + Csel:agegroup + Cspec:agegroup + Ispec:agegroup + (1|ID)$

405

#### 406 **Disentangling the effects of age and memory performance on item specificity**

407 We aimed to disentangle whether lower item representation specificity in older adults occurred  
408 due to lower item stability or higher between-item similarity in older adults compared to  
409 younger adults and which of these two factors was related to memory performance. Therefore,  
410 we averaged within and between-item similarity for later remembered and forgotten items  
411 separately in the significant face and house clusters of the conducted searchlight analyses. To  
412 test for differences in item similarity, we conducted a 2 (Age Group)  $\times$  2 (within-item/within-  
413 category similarity)  $\times$  2 (Memory: remembered/forgotten)  $\times$  2 (ROI) mixed factorial ANOVA.  
414 Furthermore, we examined item stability at the trial level by computing a generalized linear  
415 mixed model (GLM) with binary memory response outcome (hit or miss) as dependent variable,  
416 trial-wise item stability, i.e., within-item similarity (WI), between-item similarity (BI), age  
417 group, the respective interactions with age group, and the individual response bias (Br)  
418 calculated as false-alarm-rate/(1-Pr) (Corwin, 1994) as fixed effects, and subject ID as random  
419 effect (intercept). We used a binomial distribution with a logistic link function using restricted  
420 maximum likelihood estimation to fit the data.

421  $memory\ response \sim 1 + WI + BI + agegroup + Br + WI:agegroup + BI:agegroup + (1|ID)$

422

#### 423 **Resource availability**

424 Data and Code for all analysis of this manuscript will be made publicly available on osf upon  
425 publication.

426

## 427 **Results**

### 428 **Behavioral Results**

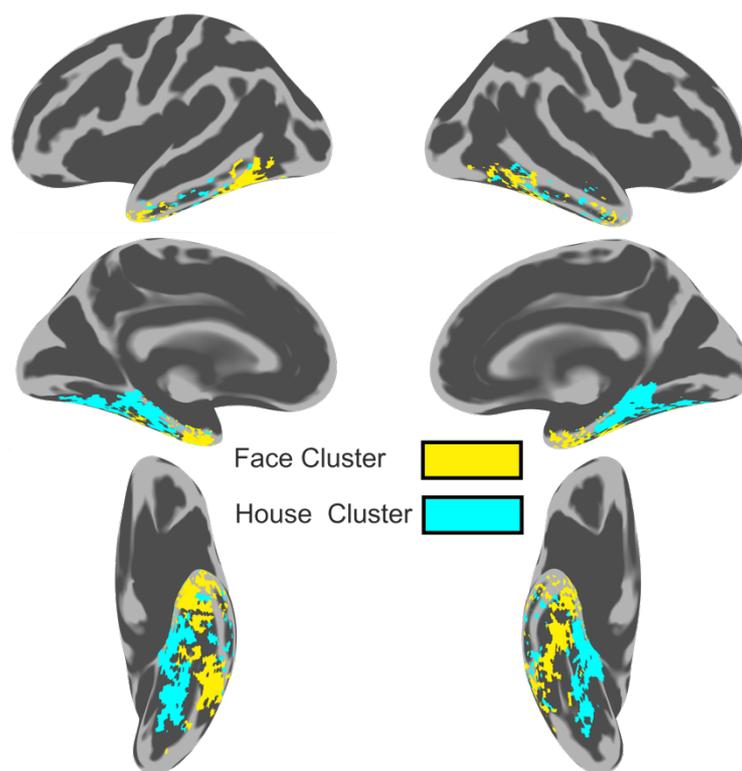
429 Healthy young adults ( $n = 35$ , age:  $M = 22.11$ ,  $SD = 2.70$ , 18–27 years) and older adults ( $n =$   
430  $32$ , age:  $M = 70.72$ ,  $SD = 2.26$ , 67–75 years) incidentally encoded images of faces and houses,  
431 followed by a surprise recognition test (see Figure 1A). To ensure adequate processing of the  
432 presented face and house images, participants performed a low-level vigilance task during  
433 encoding (i.e., pressing a button whenever an interspersed pre-defined target image appeared).  
434 Both younger and older participants performed near ceiling in the vigilance task (percentage of  
435 correct answers:  $M_{young} = 98.95\%$ ,  $SD_{young} = 4.69\%$   $M_{old} = 98.77\%$ ,  $SD_{old} = 3.54\%$ ), reflecting  
436 high engagement with the encoding task. Memory performance in the recognition task was  
437 assessed by the discrimination-index  $Pr$  calculated as the difference between the hit-rate and  
438 false-alarm-rate which can range from  $-1$  to  $1$  with  $0$  representing chance level. In both age  
439 groups, the mean memory performance exceeded chance level ( $Pr_{young} = 0.24$ ,  $t_{young}(34) =$   
440  $12.18$ ,  $p_{young} < .001$ ,  $d_{young} = 2.06$ ,  $Pr_{old} = 0.19$ ,  $t_{old}(31) = 9.16$ ,  $p_{old} < .001$ ,  $d_{old} = 1.62$ ) and did  
441 not differ between face and house images (faces:  $Pr_{young} = 0.23$ , houses:  $Pr_{young} = 0.25$ ,  
442  $t_{young}(35) = 0.93$ ,  $p_{young} = .358$ , faces:  $Pr_{old} = 0.17$ , houses:  $Pr_{old} = 0.21$ ,  $t_{old}(31) = 1.67$ ,  $p_{old} =$   
443  $.105$ ). Older adults gave more “old” responses for both previously learned (hit-rate<sub>young</sub> = 0.50,  
444 hit-rate<sub>old</sub> = 0.61,  $t(65) = -3.08$ ,  $p = .003$ ,  $d = 0.75$ ) and completely new images compared to  
445 younger adults (false-alarm-rate<sub>young</sub> = 0.26; false-alarm-rate<sub>old</sub> = 0.41;  $t(65) = -4.92$ ,  $p < .001$ ,  
446  $d = 1.34$ ). An independent samples  $t$ -test revealed no significant difference in memory  
447 performance ( $Pr$ ) between age groups ( $t(65) = 1.62$ ,  $p = .110$ ,  $d = 0.40$ ).

448

### 449 **Category-selective processing in the VVC differs between age groups and is related to** 450 **memory performance.**

451 Age-related neural dedifferentiation has previously been described as less distinct recruitment  
452 of category-selective areas located in the VVC (Park et al. 2004). Within category-selective

453 functional ROIs (see Figure 2), we calculated a *category selectivity score* as the difference in  
454 BOLD responses to images of the preferred versus the non-preferred category (e.g., the  
455 difference in BOLD responses to images of faces versus houses in the face-selective ROI). A 2  
456 (Age Group)  $\times$  2 (ROI) mixed factorial ANOVA revealed that older adults showed reduced  
457 category-selective processing compared to young adults ( $F(1,65) = 12.59, p < .001$ ; see Figure  
458 3A). Furthermore, the magnitude of the selectivity score did not differ between ROIs ( $F(1,65)$   
459  $= 0.22, p = .643$ ) and there was no interaction between ROI and age ( $F(1,65) = 0.06, p = .813$ ).  
460 Thus, replicating previous observations (Park et al., 2004; Koen et al., 2019), our findings  
461 emphasize that older adults engage category-selective areas in the VVC less distinctively  
462 compared to younger adults when encoding visual information.



463

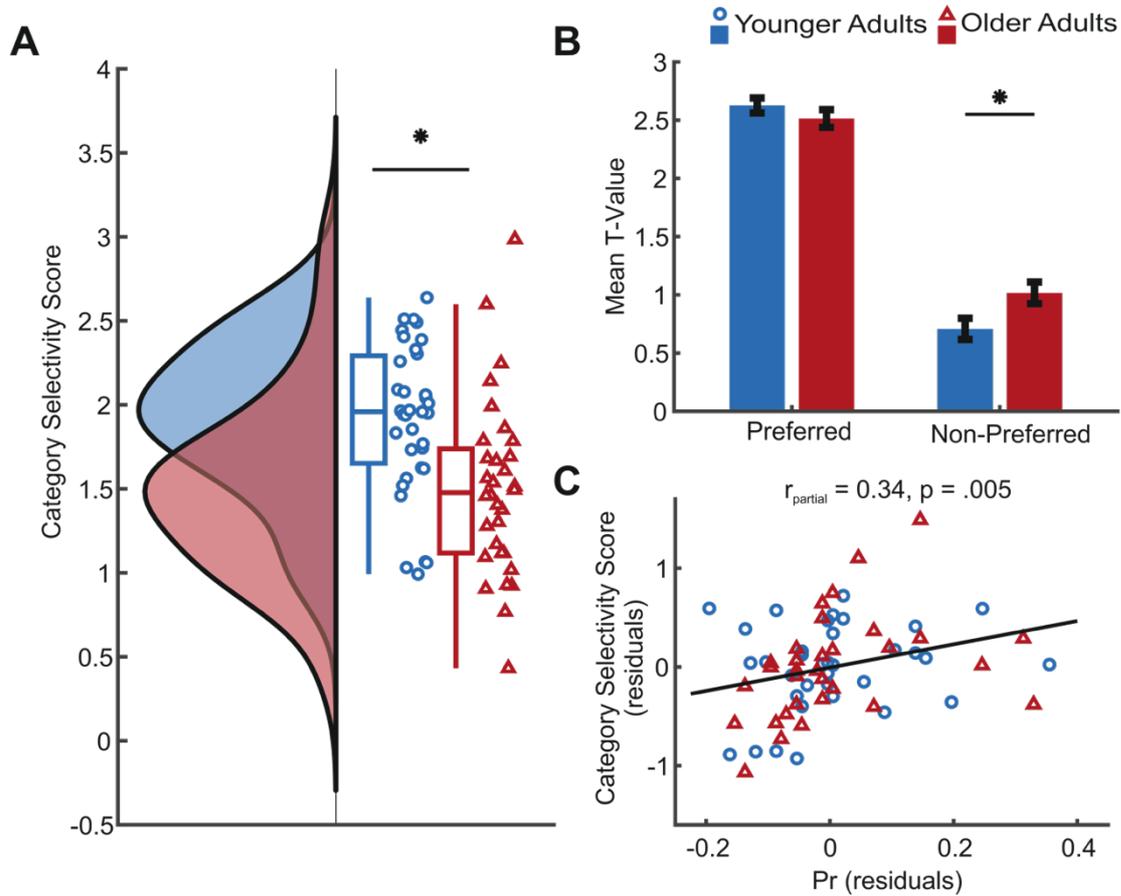
### Figure 2. Identification of category-selective clusters in VVC

Surface rendered illustration of non-overlapping category-selective ROIs across all participants. Yellow color indicates face-selective ROI. Cyan color depicts house-selective ROI. Notably, the face-selective ROI is predominantly located in the lateral VVC and the house-selective ROI in the medial VVC closely resembling the category-selective areas observed by Park et al. (2012).

464           If neural dedifferentiation occurred due to age-related increases of haphazard neural  
465 activation as claimed by Li and colleagues (2001), lower category selectivity should result from  
466 increased neural noise reflected in increased responses to images of the non-preferred category  
467 in older adults (i.e., neural broadening, Park et al., 2012). However, the current evidence is  
468 fairly mixed as there are studies supporting neural broadening and studies showing the opposite  
469 effect – reduced responses to images of the preferred category (i.e., neural attenuation; for  
470 review see Koen and Rugg, 2019). To unravel whether age-related reductions in category-  
471 selective processing occurred due to a) neural broadening, b) neural attenuation, or c) a mixture  
472 of both processes (see Park et al., 2012), we conducted post hoc *t*-tests and used Bonferroni  
473 correction to control for multiple comparisons (see Figure 3B). Across ROIs, older adults  
474 showed increased BOLD responses to images of the non-preferred category compared to  
475 younger adults ( $t(65) = 2.38, p = .040$ ), whereas BOLD responses to preferred images did not  
476 differ between age groups ( $t(65) = -1.13, p = .526$ ). Hence, the observed age-related neural  
477 dedifferentiation in category processing most likely resulted from an increased engagement of  
478 category-specific regions by non-preferred stimuli in line with the theoretical assumption that  
479 broadening effects of the neural tuning curve underlie the loss of neural distinctiveness in older  
480 adults (Li et al., 2001).

481           To test whether interindividual variability in category-selective processing was related  
482 to memory performance in the recognition task, zero-order and partial correlations were  
483 computed across participants using Pearson's *r*. Selectivity scores were averaged across face  
484 and house selective ROIs in the VVC. Across participants, selectivity scores were related to  
485 memory performance ( $r = 0.34, p = .005$ ; see Figure 3C). Importantly, this correlation remained  
486 significant when controlling for age group using partial correlations ( $r = 0.29, p = .019$ ). Thus,  
487 dedifferentiated visual processing in category-selective areas, as primarily observed in older  
488 adults, was related to poorer memory performance independent of age.

489



490

491 **Figure 3. Age differences in category-selective processing**

492 **A.** Selectivity score for younger adults (blue; circles) and older adults (red; triangles). Group  
493 distributions shown as unmirrored violin plot and boxplots with medians and 95% confidence interval  
494 with whiskers representing 2nd and 98th percentiles (Allen et al., 2019). **B.** BOLD response to preferred  
495 and non-preferred categories within functionally defined VVC ROIs. The BOLD response is expressed  
496 as the averaged *t*-values for preferred/non-preferred categories against phase-scrambled images within  
497 the respective ROIs. Error bars indicate standard error of the mean. **C.** Scatterplot illustrating partial  
498 correlation between selectivity scores and corrected recognition (*Pr*) controlling for age. Each  
499 circle/triangle represents an individual younger/older adult. For illustrative purposes, the best fitting  
500 least-squares line is plotted. Significant group differences ( $p < .05$ ) are indicated by asterisk.

501

502

503

504 **Age differences in category representation specificity are restricted to the VVC**

505 Since category selectivity as assessed with univariate methods relies on averaged BOLD signal  
506 changes and does not allow to quantify the distinctiveness of specific item representations, we  
507 next used pattern similarity analysis (Kriegeskorte et al., 2008) to investigate the categorical  
508 specificity of item representations. This analysis still focusses on differences on the categorical  
509 level but uses item-level information instead of averaged activation differences. Thus, we  
510 defined the specificity of neural category representations (*category specificity*) as the difference  
511 of within-category similarity and between-category similarity following an approach widely  
512 used in previous studies (Carp et al., 2011; Koen et al., 2019; Trelle et al., 2019).

513 A 2 (Age Group)  $\times$  2 (within vs. between-category similarity)  $\times$  2 (ROI) mixed factorial  
514 ANOVA revealed that within-category similarity was higher than between-category similarity  
515 across age groups ( $F(1,65) = 146.70, p < .001$ ; see Figure 4A). Moreover, the difference  
516 between within- and between-category similarity differed by Age Group ( $F(1,65) = 4.85, p =$   
517  $.031$ ) indicating lower category specificity in older than younger adults. Neither the main effects  
518 of age ( $F(1,65) = 2.07, p = .155$ ) or ROI ( $F(1,65) = 0.05, p = .820$ ) nor any further interactions  
519 reached significance ( $ps > .268$ ).

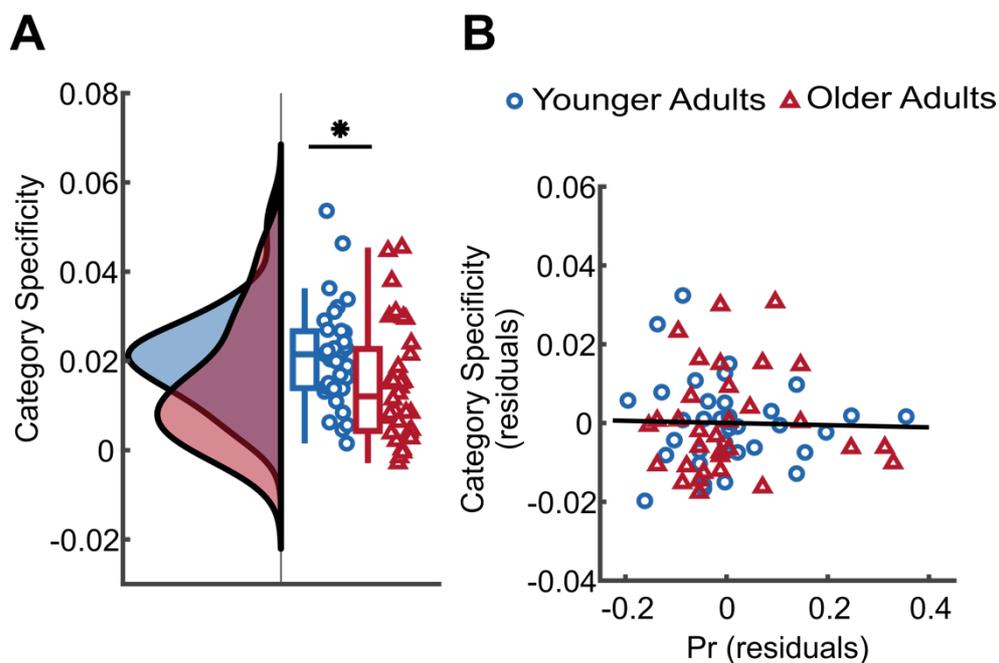
520 In contrast to most previous studies which restricted their analyses on category-selective  
521 areas in the VVC, we used a searchlight approach to explore age differences in category  
522 specificity across the whole brain (Nili et al., 2014). In contrast to the ROI analysis, whole-  
523 brain analyses revealed no group differences in category specificity for houses ( $p > .336$ ) and  
524 furthermore indicated that older adults showed higher category specificity for faces in the  
525 superior temporal gyrus ( $p = .006$ ). Thus, while the ROI-based multivariate approach provided  
526 evidence supporting age differences in category specificity as reported by several previous  
527 studies (Carp et al., 2011; Koen et al., 2019; Trelle et al., 2019), the whole brain approach did  
528 not. This result indicates that an age-related decline for category information may be restricted

529 to category-specific brain regions and less pronounced than thought, such that it does not  
530 survive exploratory whole brain analyses.

531 We also tested whether interindividual differences in the specificity of neural category  
532 representations in category-specific brain regions were related to memory performance across  
533 participants (see Figure 4B). Specificity of neural category representations was calculated as  
534 the difference of within- and between-category similarity averaged over face and house  
535 selective areas. Neural category representation specificity was not related to memory  
536 performance using zero-order ( $r = 0.03, p = .834$ ) or partial Pearson correlations controlling for  
537 age ( $r = -0.03, p = .829$ ). Thus, we found no evidence that the specificity of neural category  
538 representations was related to memory performance.

539 In addition to categories and individual items (see below), the presented stimuli can be  
540 subdivided into subcategories (e.g., young female faces, warehouses). We did not identify any  
541 significant associations between representational subcategory specificity and memory or age  
542 (but see Kuhl and Chun, 2014; Trelle et al., 2019).

543



544

545 **Figure 4. Category representation specificity in the VVC**

546 **A.** Category specificity calculated as the difference between within- and between-category similarity  
547 for younger adults (blue; circles) and older adults (red; triangles). Group distributions as unmirrored  
548 violin plot and boxplots with medians and 95% confidence interval with whiskers representing 2nd and  
549 98th percentiles. **B.** Partial Pearson correlation of category specificity and corrected recognition ( $Pr$ )  
550 controlling for age. For illustrative purposes, the best fitting least-squares line is plotted. Significant  
551 group differences ( $p < .05$ ) are indicated by asterisk.

552

553 **Item representation specificity in occipital regions is reduced in older adults and linked**  
554 **to memory performance**

555 In contrast to previous studies (Carp et al., 2011; Koen et al., 2019) our results only partially  
556 support lower *category specificity* in older adults (namely, when restricting the analyses to  
557 category-specific ROIs). However, theoretical accounts based on computational models  
558 emphasize that age-related dedifferentiation is particularly reflected in reduced specificity of  
559 neural representations of *individual items* (Li et al., 2001) which are not restricted to category-  
560 selective areas but are found in large-scale neural networks (Xue, 2018). Therefore, we applied  
561 pattern similarity analyses across the whole brain to investigate age-related changes in neural  
562 *item specificity*.

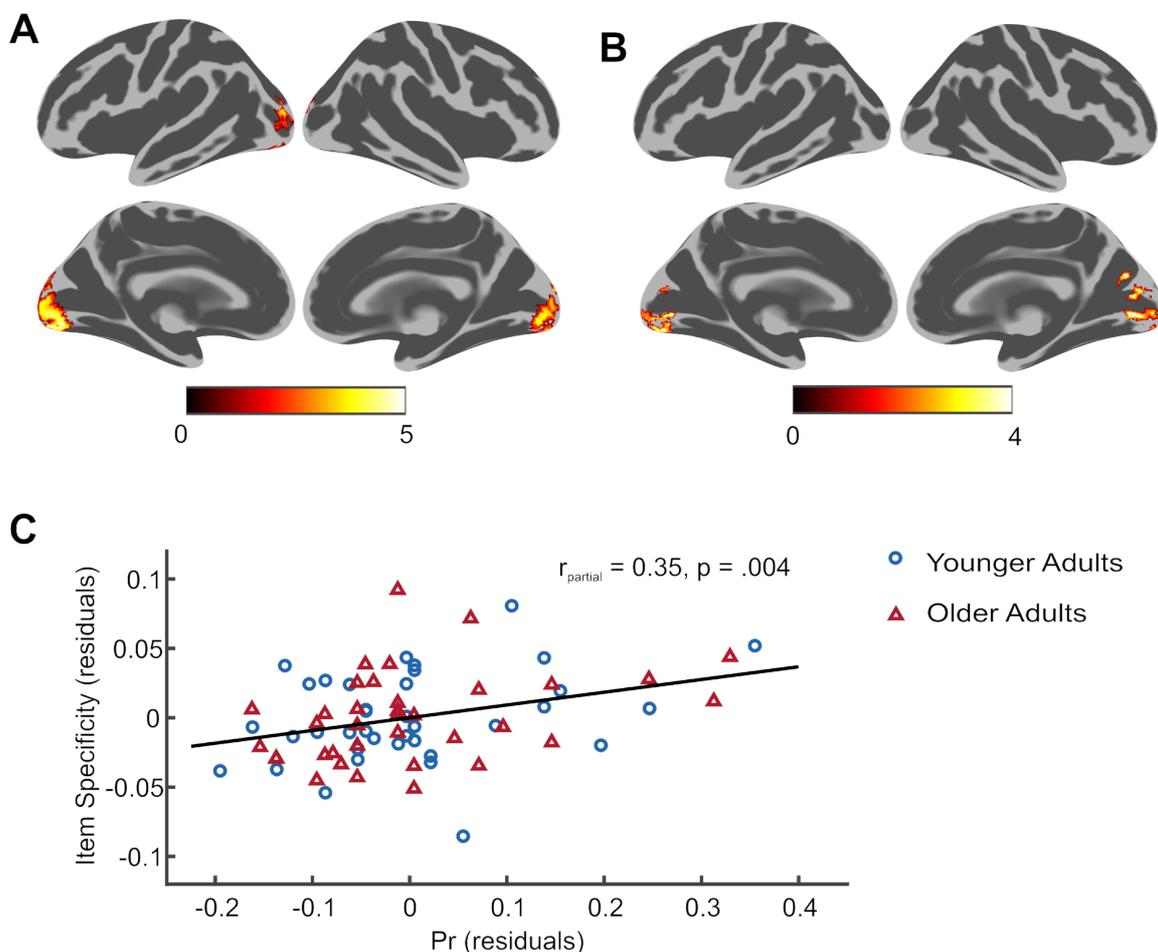
563 Within each sphere, within-item similarity was calculated as the similarity of BOLD  
564 activity patterns across the two repetitions of a given item (i.e., *item stability*; see Figure 1C).  
565 We compared this item stability to the respective within-category similarity to capture the  
566 specificity of neural item representations (i.e., *item specificity*). For faces, older adults showed  
567 smaller item specificity compared to younger adults in occipital regions ( $p < .001$ ) including  
568 bilateral intracalcarine cortex, lateral occipital cortex and occipital fusiform cortex (see Figure  
569 5A). For houses, older adults also showed smaller item specificity than younger adults in  
570 occipital areas ( $p = .006$ ) comprising bilateral lingual gyrus, intracalcarine cortex and left

571 occipital fusiform cortex (see Figure 5B). Thus, our findings underline that older adults form  
572 less specific item representations in occipital areas than younger adults.

573 We also tested whether interindividual differences in *item specificity* were related to  
574 overall memory performance (see Figure 5C). For this analysis, we averaged item specificity  
575 over both categories in their respective occipital clusters. Neural item representation specificity  
576 was related to memory performance using zero-order ( $r = 0.39, p = .001$ ) and partial Pearson  
577 correlations controlling for age ( $r = 0.35, p = .004$ ). Equivalently, *item stability* alone showed  
578 the same between-person association with performance (zero-order:  $r = 0.42, p < .001$ ; partial:  
579  $r = 0.38, p = .002$ ).

580 Thus, high item representation specificity/stability accounts for interindividual  
581 differences in memory performance of younger and older adults.

582



**Figure 5. Age differences in item representation specificity and relation to memory performance**

**A.** Significant age differences in item specificity, calculated as the difference between similarity of BOLD activity patterns across the two repetitions of a given item (i.e., *item stability*) and the respective within-category similarity, for faces indicated by t-values. Younger adults showed higher item specificity in occipital areas compared to older adults as depicted by the presented cluster. **B.** Significant age differences in item specificity for houses. Again, younger adults showed higher item specificity in occipital areas than older adults. **C.** Partial Pearson correlation of item specificity and corrected recognition (*Pr*) controlling for age (younger adults: blue circles; older adults: red triangles).

583

584 **Linking neural dedifferentiation across representational levels in relation to memory**  
585 **performance**

586 Given the coexistence of age differences in *category selectivity*, *category specificity*, and *item*  
587 *specificity* and their differential associations with recognition performance, we used linear  
588 mixed models (LMM) to examine their contribution to memory success and the interaction with  
589 age. We observed a significant association between memory success and item specificity (main  
590 effect:  $t(60) = 2.31$ ;  $p = .024$ ). Neither the main effect of category selectivity ( $t(60) = 1.45$ ;  $p =$   
591  $.15$ ) nor the main effect of category specificity ( $t(60) = -1$ ;  $p = .32$ ) reached significance.  
592 Crucially, none of the interaction effects reached significance (all  $|t| < 0.95$ ; all  $p > .34$ ),  
593 providing no evidence for differential associations between measures of distinctiveness and  
594 memory success across age groups.

595

596 To further investigate the association between distinctiveness at different  
597 representational levels, we correlated all measures with each other. All neural distinctiveness  
598 measures were related to each other across participants (see Table 2). However, the correlations  
599 between item and category measures appear to be mostly driven by overall age differences:  
600 When controlling for age using partial correlations, only the relationship between category

601 selectivity and category specificity remained significant ( $r = 0.37, p = .003$ ), whereas partial  
 602 correlations of item specificity to category selectivity ( $r = 0.14, p = .276$ ) and category  
 603 specificity ( $r = 0.17, p = .176$ ) were not significant. These results underline previous theoretical  
 604 distinctions between distinctiveness measures on category and item (Koen and Rugg, 2019;  
 605 Koen et al., 2020) and furthermore emphasize the close relationship between both  
 606 dedifferentiation measures on category level (Koen et al, 2019).

607

608 **Table 2.** Association between distinctiveness measures and memory performance (zero-order Pearson  
 609 correlations  $r$ , with  $p$  in parentheses)

	(1)	(2)	(3)	(4)	(5)
(1) Memory Performance					
(2) Category Selectivity	0.34 (.005)				
(3) Category Specificity	0.03 (.834)	0.43 (<.001)			
(4) Item Specificity	0.39 (.001)	0.35 (.003)	0.29 (.016)		
(5) Item Stability	0.42 (<.001)	0.36 (.002)	0.34 (.005)	0.99 (<.001)	
(6) Age Group	-0.20 (.110)	-0.40 (<.001)	-0.26 (.031)	-0.64 (<.001)	-0.63 (<.001)

610

611

612 **Age and performance differences in occipital item specificity are driven by item stability**

613 Our linear mixed model analysis revealed that differences in *item specificity* account for  
 614 interindividual differences in memory performance over and above the variance explained by  
 615 all variables combined. Importantly, if, as assumed by Li et al. (2001), more variable neural  
 616 responses are at the core of age-related reductions in neural specificity, *item specificity* in older  
 617 adults depends critically on the consistency with which individual items are represented across  
 618 several instances of encoding, that is, *item stability*. To test whether lower *item specificity* in  
 619 older adults was indeed due to lower *item stability* (within-item similarity) or higher between-  
 620 item (within-category) similarity compared to younger adults and whether specifically higher  
 621 *item stability* was related to a higher probability of successful memory retrieval, we compared

622 similarity indices in the observed occipital clusters with a 2 (Age Group)  $\times$  2 (within vs.  
623 between item similarity)  $\times$  2 (Memory: remembered/forgotten)  $\times$  2 (ROI) mixed factorial  
624 ANOVA.

625 Younger adults showed higher similarity scores compared to older adults ( $F(1,65) =$   
626  $22.25; p < .001$ ) and within-item similarity was generally higher than between-item similarity  
627 ( $F(1,65) = 435.87; p < .001$ ). In line with the searchlight analysis, the difference between  
628 within-item similarity and between-item similarity (i.e. *item specificity*) was smaller in older  
629 than in younger adults as indicated by a significant interaction of age and within/between-item  
630 similarity ( $F(1,65) = 25.05; p < .001$ ; see Figure 7A). Post-hoc tests revealed that within-item  
631 similarity (i.e. *item stability*) ( $t(65) = 4.94, p < .001$ ) was lower in older adults compared to  
632 younger adults, while between-item similarity ( $t(65) = 2.16, p = .069$ ) did not differ between  
633 age groups after multiple error correction. Within- and between-item similarity differences  
634 were not different across ROIs ( $F(1,65) = 3.53; p = .064$ ).

635 Most crucially, subsequently remembered items showed higher similarity scores  
636 compared to subsequently forgotten items ( $F(1,65) = 7.85, p = .007$ ) which interacted with  
637 within/between-item similarity ( $F(1,65) = 17.51; p < .001$ ; see Figure 7B). Post-hoc *t*-tests  
638 revealed that within-item similarity (i.e. *item stability*) was higher for subsequently remembered  
639 than forgotten items ( $t(66) = 3.90, p < .001$ ), while there was no difference in between-item  
640 similarity ( $t(66) = -1.17, p = .248$ ). We found no interaction between memory and age group  
641 ( $F(1,65) = 3.90; p = .052$ ) or other significant effects ( $ps > .316$ ).

642 In addition to the ANOVA computed above, which contrasts the average  
643 representational similarities of later remembered and forgotten stimuli and identifies a critical  
644 role of item stability, we also ran a generalized linear mixed model (GLM) to examine *trial-*  
645 *wise* variability in item stability and how it predicts memory outcome (see Figure 6C). We  
646 tested whether binary memory response outcome (hit or miss) could be predicted by trial-wise  
647 item stability, i.e., within-item similarity (WI), between-item similarity (BI), age group, the

648 respective interactions with age group, and the individual response bias (Br). In line with the  
649 previously applied mixed factorial ANOVA (see above), we found that trial-wise item stability  
650 predicted memory outcome (Log Odds = 0.12, 95% CI [0.06, 0.18]) in that trials showing larger  
651 item stability during encoding had a higher probability to be correctly recognized later on.  
652 Furthermore, there was a significant effect of response bias (Log Odds = 3.50, 95% CI [2.94,  
653 4.05]) showing that participants with a bias to respond “old” showed more hits compared to  
654 misses. In contrast, neither between-item pattern similarity, age group, nor any of the  
655 interactions reached significance (see Table 3).

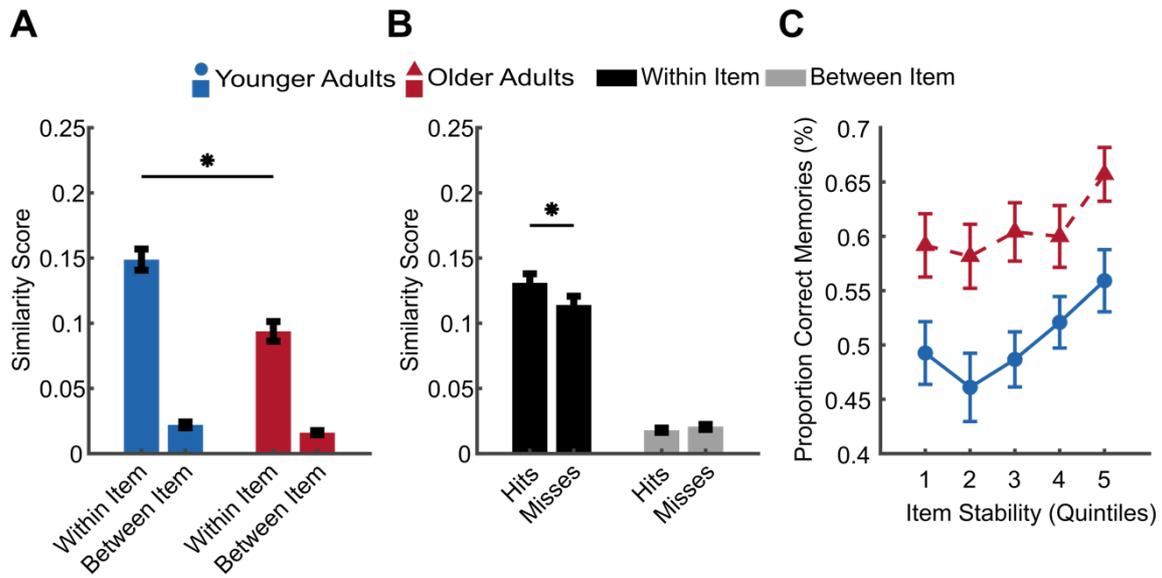
656

657 **Table 3.** Results for GLM: memory response ~ 1 + WI + BI + agegroup + Br + WI:agegroup  
658 + BI:agegroup + (1|ID)

Fixed effects predictors	Log Odds	<i>t</i>	<i>p</i>	95% CI lower	95% CI upper
Item stability (WI)	0.12	3.74	< 0.001	0.06	0.18
Between-item similarity (BI)	-0.02	-0.66	0.508	-0.08	0.04
Response bias (Br)	3.50	12.39	< 0.001	2.94	4.05
age group	-0.14	-1.49	0.136	-0.31	0.04
WI × age group	-0.001	-0.03	0.975	-0.09	0.09
BI × age group	-0.03	-0.71	0.474	-0.13	0.06

659

660 Thus, *item stability* was lower in older than in younger adults and supported subsequent  
661 recognition performance on a trial-wise level emphasizing the role of less stable item  
662 representations for age-related memory decline



663

### Figure 6. Item representation specificity and memory performance

**A.** Within-item and between-item similarity in both age groups indicates that lower item specificity in older adults is mostly driven by lower item stability. **B.** Comparing within- and between-item similarity for subsequently remembered items (hits) and not-remembered items (misses) across age groups shows that item stability was higher for later remembered than not-remembered items independent of age. **C.** Trial-wise item stability is linked to an increased probability of correct memories. For visualization, memory outcome was binned into quintiles according to trial-wise item stability in each subject. Within each age group proportion of correct memories was averaged across participants. Error bars represent standard error of the mean.

664

## 665 **Discussion**

666 The present fMRI study investigated age differences in the distinctiveness of neural information  
667 representations supporting episodic memory performance. We provided a comprehensive  
668 account of age differences at different representational levels ranging from *category selectivity*  
669 to *item specificity* and *item stability* and delineated their contribution to memory performance  
670 in younger and older adults. Combining conventional ROI-based univariate analysis and whole-  
671 brain multivariate pattern similarity analysis, we demonstrated that age differences in neural  
672 distinctiveness coexist at various representational levels, and take the form of reduced category-  
673 selective processing in VVC regions, and reduced specificity of item representations in occipital  
674 areas. The study revealed the contribution of both categorical distinctiveness and item  
675 specificity to memory performance, with item specificity being the strongest contributor to it.  
676 Age differences in occipital item specificity were largely due to reduced item stability across  
677 repetitions in older adults, and higher item stability was related to subsequent memory success.  
678 Whether or not age differences exist at the item level was a matter of debate that could so far  
679 not be settled due to limited evidence (Koen and Rugg, 2019). Our results close this gap in the  
680 literature by demonstrating that older adults' neural representation of item-specific information  
681 in addition to categorical information is indeed reduced compared to younger adults.

682

### 683 *Age-related neural dedifferentiation coexists at different representational levels*

684 Previous fMRI studies investigating neural dedifferentiation focused on broader concept  
685 representations by assessing univariate category-selective processing (e.g., Park et al., 2004)  
686 and/or multivariate category-specific representations (e.g., Carp et al., 2011), mainly in regions  
687 of the ventral visual cortex (VVC). In the current study, ROI-based analyses within category-  
688 specific regions of interest replicated previous findings: Univariate analyses revealed age-  
689 related neural dedifferentiation in terms of reduced category-selective processing (e.g., Park et  
690 al., 2004), and multivariate pattern similarity analyses revealed reduced categorical specificity

691 (e.g., Carp et al., 2011; Koen et al., 2019) in older compared with younger adults. As predicted  
692 by computational models (Li and Sikström, 2002; Li et al., 2000, 2001), age differences in  
693 neural category differentiation resulted from neural broadening, that is, increased activation to  
694 non-preferred stimuli in the older adults, with no age differences in activation differences for  
695 preferred stimuli. More importantly, applying a whole-brain searchlight approach in order to  
696 target specificity of neural representations on the item level, we found clear evidence for age  
697 differences in item-specific BOLD activation patterns in occipital regions.

698         Previous studies with young adults have established that reduced item specificity results  
699 in poor memory performance (Hasinski and Sederberg, 2016; Xue et al., 2010), but a pre-  
700 defined focus on category-specific regions in VVC (e.g., Koen et al., 2019) may have prevented  
701 previous age-comparative studies to reveal age differences in item-level specificity and  
702 delineate their role in cognitive decline. The current study demonstrates that age differences in  
703 item specificity are most prominent in occipital regions (including lateral occipital cortex and  
704 occipital face area for faces; see Figure 5), that are involved in early visual processing. Together  
705 with the fusiform gyrus, lateral occipital cortex has been shown to be critical for visual object  
706 (including face) perception (Grill-Spector and Malach, 2004; Grill-Spector et al., 1999; Nagy  
707 et al., 2012). Furthermore, the occipital face area, which is connected to the FFA and lateral  
708 occipital cortex, constitutes the lowest level in the face perception network and is suggested to  
709 represent and integrate facial components (Kadosh et al., 2011; Nagy et al., 2012; Pitcher et al.,  
710 2007, 2011). Thus, less precise item-specific activation patterns in older adults in these regions  
711 are likely to reflect differences in early processing of the incoming visual information which  
712 results in detrimental consequences for downstream (category level) processing. In sum, we  
713 argue that our results are in line with core assumptions of computational models (e.g., Li et al.,  
714 2001), namely that increased neural variability with age manifests as both degraded item  
715 representations in early visual regions and, as a downstream effect, reduced category selectivity

716 in VVC. Hence, we emphasize the important role of item specific and stable neural  
717 representations for memory functioning.

718 Here, we only investigated cortical representations, but these may depend on pattern  
719 separation in the hippocampus which is known to decline in aging (e.g., Reagh et al., 2018).  
720 Future research should study the interdependence of hippocampal and cortical representations  
721 and their joint association to memory performance during aging (cf. Danker et al., 2017).

722 In contrast to previous studies (e.g., Koen et al., 2019; Srokova et al., 2020), we did not  
723 observe differences in age-related neural dedifferentiation based on stimulus materials.  
724 However, the limited variety of different stimulus categories in our study does not allow to  
725 make strong claims for or against the proposition that neural dedifferentiation is ubiquitous in  
726 the aging brain. Differences between stimulus categories should thus be examined in a  
727 systematic investigation in the future including a broad range of different stimulus categories  
728 and other factors such as task demands.

729

730 *Inter- and intraindividual differences in neural distinctiveness are related to memory*  
731 *performance*

732 Next, using LMM, we explored the unique effects of interindividual differences in three  
733 measures capturing neural dedifferentiation at distinct representational levels (*category*  
734 *selectivity, category specificity, and item specificity*) on memory performance. Importantly, of  
735 the neural dedifferentiation measures, *item specificity* showed the strongest association with  
736 memory, over and above the shared effects of the distinctiveness measures across all  
737 representational levels combined. Since the recognition memory task used in the current study  
738 required participants to distinguish between highly similar face and house exemplars, rather  
739 than simply discriminating faces from houses, high item specificity was required to perform  
740 well. Category selectivity instead may rather be a general indicator of representational quality  
741 and a potential downstream effect of item-specific perceptual representations. However, when

742 tested by itself, category selectivity also showed to be related to memory performance across  
743 participants. The finding that category selectivity was associated with recognition performance  
744 while category specificity was not, was also observed by Srokova et al. (2020). However, in  
745 contrast to that, Koen et al., (2019) report a link between recognition memory and both category  
746 selectivity and specificity. These deviant results may result from methodological differences  
747 including stimulus materials (see also above) and task demands (incidental encoding versus  
748 intentional encoding). Overall, while our results nicely illustrate the coexistence of age  
749 differences at different representational levels, they clearly identify item specificity in early  
750 visual areas as the driving force for interindividual differences in memory performance.

751 Our results further revealed the importance of item specificity for the mnemonic fate of  
752 single items, that is, subsequent memory effects at the within-person level. In line with others,  
753 we defined item specificity as the comparison of activation patterns across stimulus repetitions  
754 in relation to their similarity to different stimuli of the same category (cf. Hasinski and  
755 Sederberg, 2016; Koen and Rugg, 2019; Zheng et al., 2018). In that way, item specificity is a  
756 joint effect of representational stability and representational distinctiveness. Thus, theoretically,  
757 reduced item specificity in old age may be due to decreased item stability (Zheng et al., 2018),  
758 increased within-category similarity (Goh et al. 2010), or both (cf. Koen and Rugg, 2019).  
759 However, the computational model by Li et al. (2001) suggests that item-level specificity in  
760 older adults is reduced due to increased neural response variability, thus reduced item stability.  
761 In line with this proposal, we observed that age difference in item specificity were due to a  
762 reduction in item stability in the older age group, whereas no age differences were observed for  
763 within-category similarity. Furthermore, item stability displayed an age-independent relation to  
764 memory, as indicated by a positive association with recognition probability, also on the trial  
765 level. Higher item stability in younger compared to older adults in visual regions being related  
766 to subsequent memory effects has also been reported by one previous age-comparative study  
767 (Zheng et al. 2018), however, the validity of that finding has been questioned (Koen and Rugg,

768 2019) because age differences in item specificity were not reliable. Our results clearly align  
769 with these prior results and highlight that item specificity and item stability are key contributors  
770 to age differences in memory performance.

771 The finding of impoverished item representations in older adults in early visual regions  
772 resonates with the long-standing suggestion in cognitive aging science that sensory and  
773 cognitive functions are increasingly linked to each other in the course of aging, which further  
774 reinforces the close connection of age-related deficits in perceptual processing and declining  
775 cognitive abilities (Baltes and Lindenberger, 1997; Li and Lindenberger, 2002; Lindenberger  
776 and Baltes, 1994; Schneider and Pichora-Fuller, 2000). The current study substantiates this  
777 claim by identifying reduced representational specificity coexisting at different representational  
778 levels but most prominently in early visual regions, which was furthermore linked to inter- and  
779 intraindividual differences in memory performance.

780 Although the current study clearly identifies a relationship between representational  
781 specificity and stability during encoding with later memory performance, the older adults  
782 group, who showed overall reduced specificity and stability, did not perform overall  
783 significantly worse than the young adult group (similar to findings by (Koen et al., 2019). Less  
784 pronounced or no age-related deficits in item recognition memory, compared to, for example,  
785 associative memory, are not uncommon, especially under incidental encoding conditions (cf.  
786 Old and Naveh-Benjamin, 2008; Sommer et al., 2020). Nevertheless, older adults often tend to  
787 respond “old” more frequently than younger adults, contributing to their higher rates of false  
788 memories (Koutstaal and Schacter, 1997; Schacter et al., 1997; Fandakova et al., 2013, 2020)  
789 which was also observed in the present study. Nevertheless, the present study clearly shows  
790 that differences in representational specificity and stability during encoding can account for  
791 differences in subsequent memory performance between as well as within participants.

792

793

794 *Neural dedifferentiation as a consequence of age-related neurotransmitter changes?*

795 In the current study, we proposed that age differences at various representational levels coexist  
796 based on a computational model (Li and Sikström, 2002; Li et al., 2000, 2001) that proposes  
797 deficient neuromodulation as the causal mechanism for reduced consistency of neural  
798 information processing with ensuing consequences for representational distinctiveness and age-  
799 related cognitive deficits. Of course, in the current study the precise mechanism underlying the  
800 observed representational differences at the various levels remains speculative. Nevertheless,  
801 evidence from other studies support the proposal of age differences in neuromodulation as a  
802 driving factor for neural dedifferentiation. While the original proposal emphasized age-related  
803 changes in dopamine (cf. Abdulrahman et al., 2017; Bäckman et al., 2006, 2010; Li et al., 2001;  
804 Rieckmann et al., 2018; Wong et al., 1984), more recently, several studies have revealed the  
805 contribution of age-related decline in gamma-aminobutyric acid (GABA) to cognition and  
806 neural information representation (cf. Leventhal et al., 2003). For example, using MR  
807 spectroscopy to quantify GABA concentrations in occipital voxels, Simmonite et al. (2019)  
808 found that lower occipital GABA levels in older adults were associated with declines in fluid  
809 processing abilities. Furthermore, Chamberlain et al. (2019; preprint) reported that individual  
810 differences in the category specificity of face versus house representations were linked to  
811 individual differences in VVC GABA concentrations in older adults, indicating a role of GABA  
812 in age-related neural dedifferentiation (see also Cassady et al., 2019; Gagnon et al., 2019;  
813 Lalwani et al., 2019). These findings substantiate the key role of proficient (particularly  
814 GABAergic) neuromodulation for high-fidelity (i.e., stable and distinct) neural representations  
815 and cognitive performance and lay the ground for future studies aiming to understand how age-  
816 related deficits in neuromodulation are related to neural dedifferentiation across  
817 representational levels.

818

819

820 *Conclusion*

821 The present fMRI study set out to investigate age differences in neural information  
822 representation and their relation to episodic memory performance. Previous studies have  
823 focused on neural dedifferentiation of categorical information but have neglected age  
824 differences at the item level. Our results show that differences in representational  
825 distinctiveness coexist at various levels and contribute to memory. Crucially, they emphasize  
826 the striking relevance of item specificity and item stability for the understanding of inter- and  
827 intraindividual differences in memory. Thus, the current study substantiates the claim of a close  
828 connection between age differences across processing levels (e.g., sensory and cognitive), as  
829 derived from long-standing observations in behavioral aging research. Longitudinal studies are  
830 needed to elucidate to what extent the different levels depend on or precede each other and  
831 whether a general mechanism (e.g., changes in neuromodulation) accounts for changes in  
832 representational properties.

833 **Author Contributions**

834 MK: Formal analysis, Writing - Original Draft, Writing - Review & Editing, Visualization,  
835 VRS: Conceptualization, Software, Investigation, Writing - Original Draft, Writing - Review  
836 & Editing, Visualization, AK: Investigation, Writing - Review & Editing, MWB:  
837 Conceptualization, Writing - Review & Editing, Supervision, Funding acquisition, Project  
838 administration, MCS: Conceptualization, Writing - Original Draft, Writing - Review & Editing,  
839 Supervision, Funding acquisition, Project administration

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