Tracking age differences in neural distinctiveness across representational levels

Abbreviated title: Age differences in neural distinctiveness

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Abstract

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

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

Significance Statement

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

Introduction

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

The available evidence clearly supports the notion of age-related neural 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.

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

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

156 ## Materials and Methods

157 **Table 1**. Key resources
158

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

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

Stimuli and procedure

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

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

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

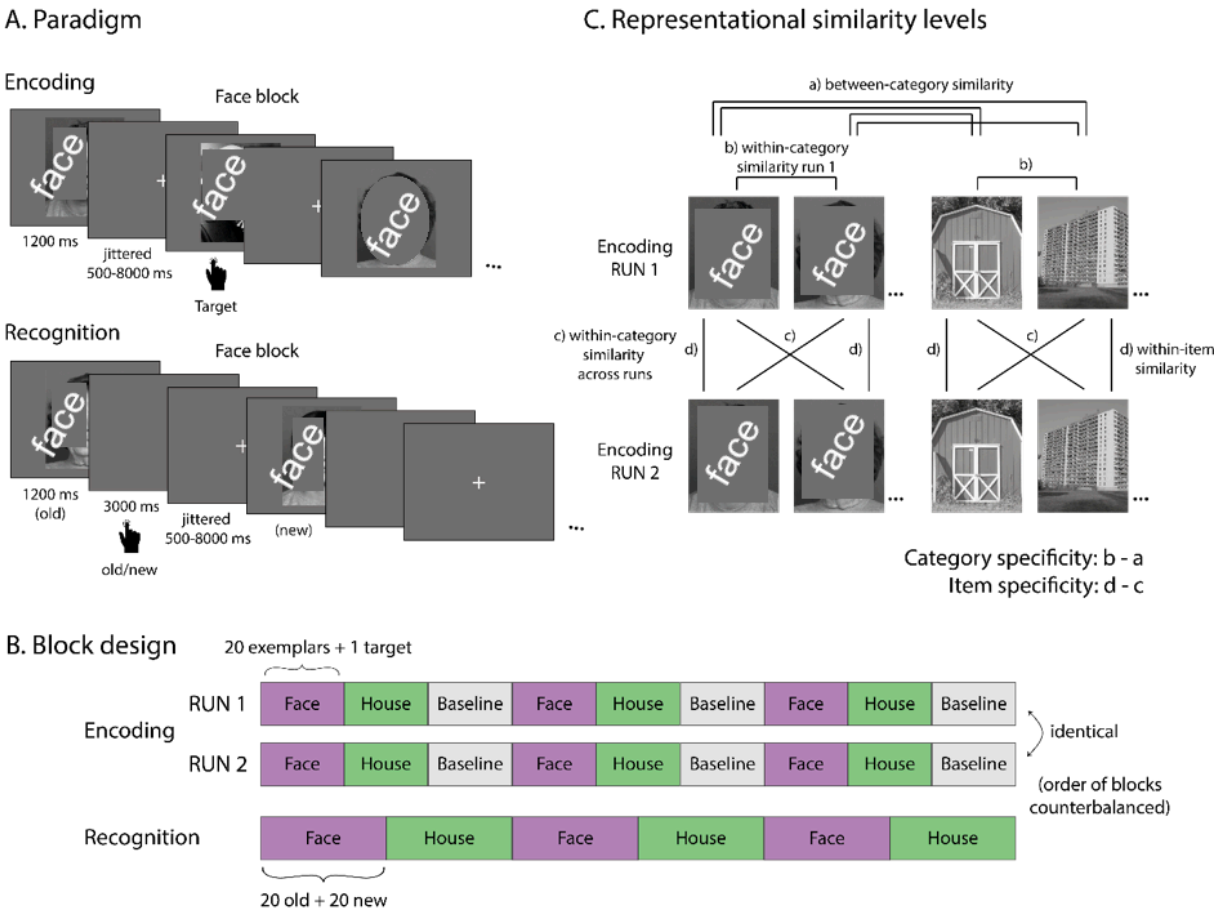


Figure 1. Task design and schematic of representational similarity levels.

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.

Behavioral data analyses

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

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^3) and T2*-weighted echoplanar
251 images (TR = 2 s, TE = 30 ms, pixel size = 3 × 3 mm^2) 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: $M_{young} = 78.8$; $M_{\text{old}} = 82.3$; $t(65) = -0.24$ $p = .810$; house-
298 selective ROIs: $M_{\text{young}} = 70.7$; $M_{\text{old}} = 85.2$; $t(65) = -1.11$ $p = .273$). 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) × 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

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

Searchlight analyses of category representation specificity

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

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

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

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

Analyzing the relationship between differentiation on multiple representational levels and memory performance using LMM

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

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

Pr ~ 1 + Csel + Cspec + Ispec + Csel:agegroup + Cspec:agegroup + Ispec:agegroup + (1|ID)

Disentangling the effects of age and memory performance on item specificity

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

memory response ~ 1 + WI + BI + agegroup + Br + WI:agegroup + BI:agegroup + (1|ID)

Resource availability

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

Results

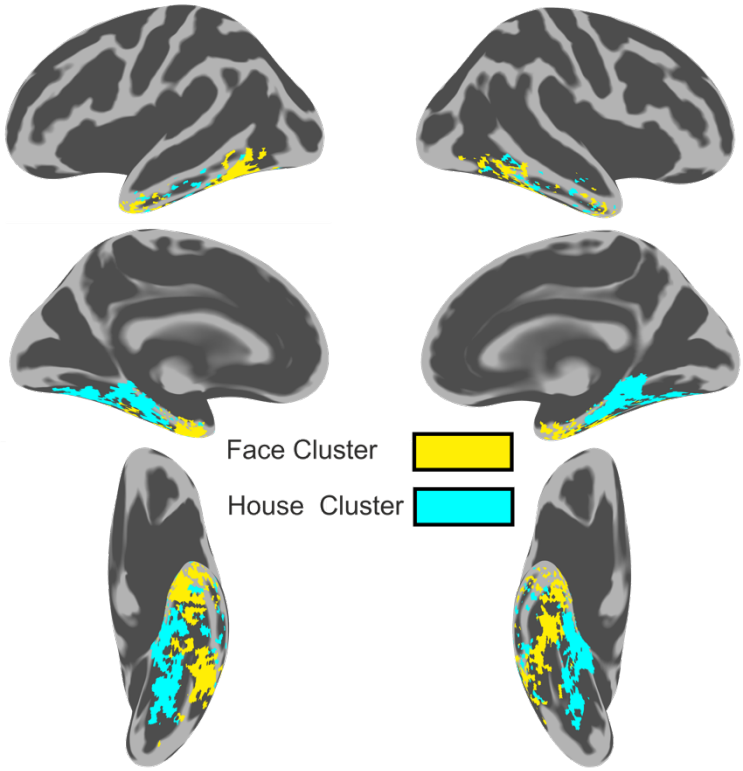
Behavioral Results

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

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

Age-related neural dedifferentiation has previously been described as less distinct recruitment 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) × 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).

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

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

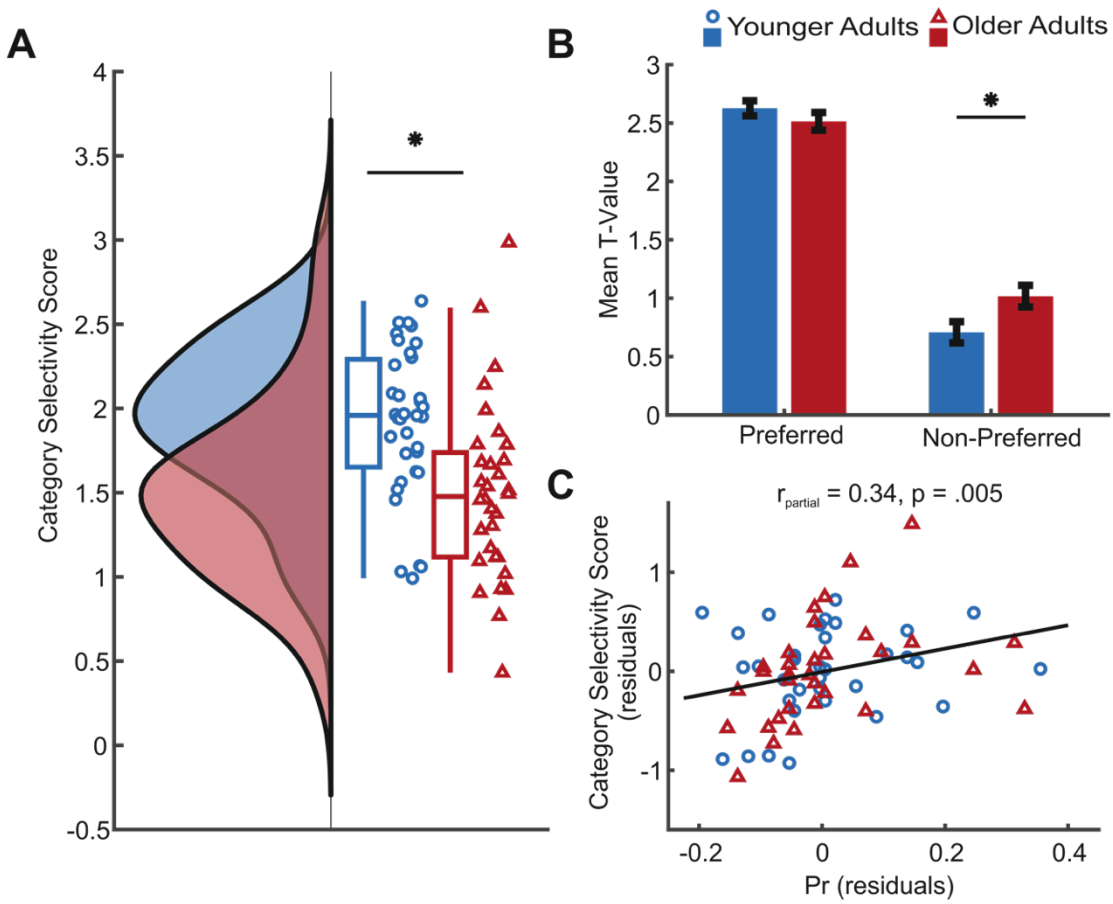


Figure 3. Age differences in category-selective processing

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

Age differences in category representation specificity are restricted to the VVC

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

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

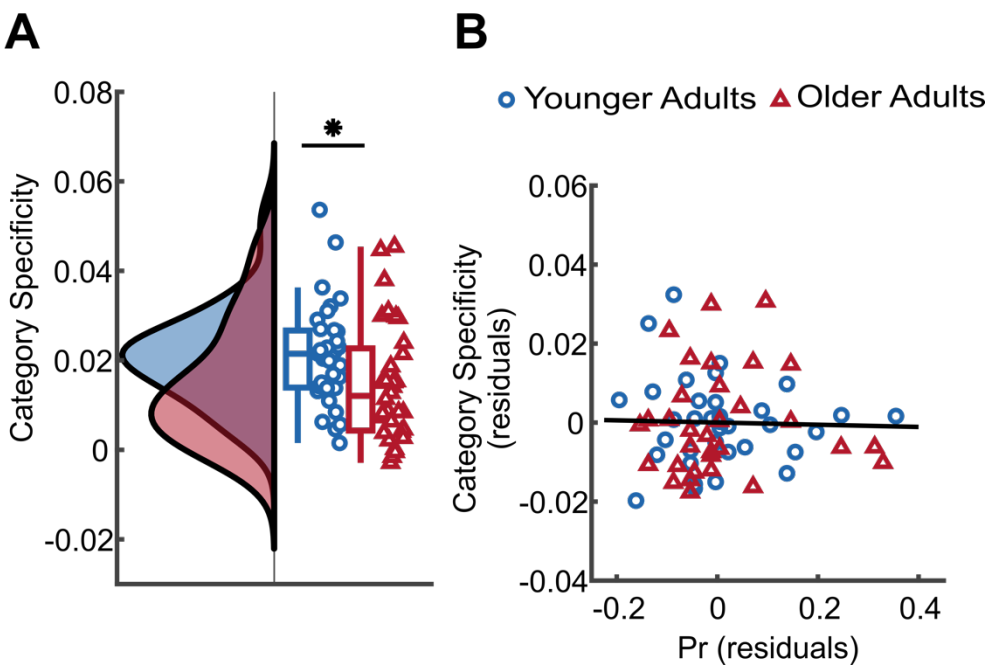
In contrast to most previous studies which restricted their analyses on category-selective areas in the VVC, we used a searchlight approach to explore age differences in category specificity across the whole brain (Nili et al., 2014). In contrast to the ROI analysis, whole-brain analyses revealed no group differences in category specificity for houses ($p > .336$) and furthermore indicated that older adults showed higher category specificity for faces in the superior temporal gyrus ($p = .006$). Thus, while the ROI-based multivariate approach provided evidence supporting age differences in category specificity as reported by several previous studies (Carp et al., 2011; Koen et al., 2019; Trelle et al., 2019), the whole brain approach did 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

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

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

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

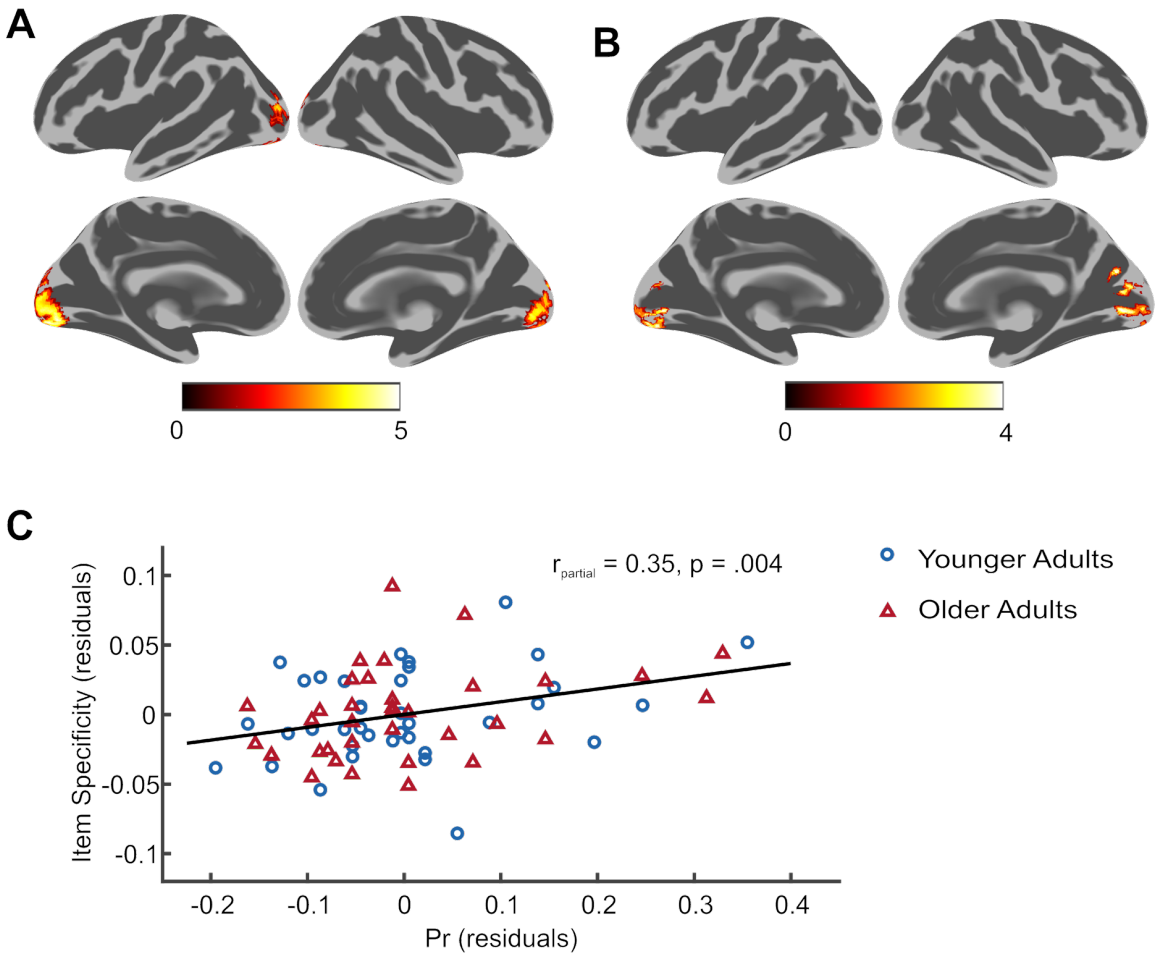


Figure 5. Age differences in item representation specificity and relation to memory performance **A.** Significant age differences in item specificity, calculated as the difference between similarity of BOLD activity patterns across the two repetitions of a given item (i.e., *item stability)* and the 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

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

Table 2. Association between distinctiveness measures and memory performance (zero-order Pearson 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)

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

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

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

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

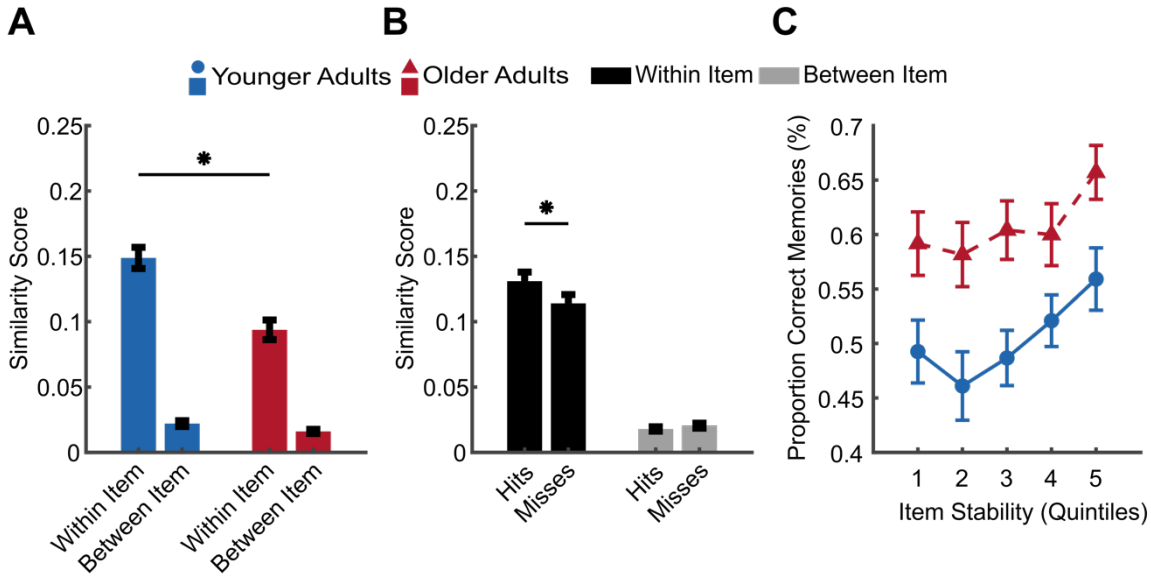
Most crucially, subsequently remembered items showed higher similarity scores compared to subsequently forgotten items ($F(1,65) = 7.85$, $p = .007$) which interacted with within/between-item similarity ($F(1,65) = 17.51$; $p < .001$; see Figure 7B). Post-hoc *t*-tests revealed that within-item similarity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

In addition to the ANOVA computed above, which contrasts the average representational similarities of later remembered and forgotten stimuli and identifies a critical role of item stability, we also ran a generalized linear mixed model (GLM) to examine *trial-wise* variability in item stability and how it predicts memory outcome (see Figure 6C). We tested whether binary memory response outcome (hit or miss) could be predicted by trial-wise 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	*t*	*p*	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

Discussion

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

Age-related neural dedifferentiation coexists at different representational levels

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

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

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

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

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

Conclusion

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

Author Contributions

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

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