

# Neural pattern similarity differentially affects memory performance of younger and older adults

Age differences in neural similarity and memory

Verena R. Sommer<sup>1</sup>, Yana Fandakova<sup>1</sup>, Thomas H. Grandy<sup>1</sup>, Yee Lee Shing<sup>1,2</sup>, Markus Werkle-Bergner<sup>1</sup>, and Myriam C. Sander<sup>1</sup>

<sup>1</sup>*Center for Lifespan Psychology, Max Planck Institute for Human Development, 14195 Berlin, Germany*

<sup>2</sup>*Institute of Psychology, Goethe University Frankfurt, 60629 Frankfurt am Main, Germany*

Corresponding authors: Verena R. Sommer ([vsommer@mpib-berlin.mpg.de](mailto:vsommer@mpib-berlin.mpg.de)) or Myriam C. Sander ([sander@mpib-berlin.mpg.de](mailto:sander@mpib-berlin.mpg.de)); Lentzeallee 94, 14195 Berlin, Germany

Number of pages: 33

Number of figures: 5

Number of words for Abstract: 221, Introduction: 628, Discussion: 1425

The authors declare no competing financial interests.

<sup>1</sup> Acknowledgements:

<sup>2</sup> This study was conducted within the "Cognitive and Neural Dynamics of Memory across the  
<sup>3</sup> Lifespan" (CONMEM) project at the Center for Lifespan Psychology, Max Planck Institute  
<sup>4</sup> for Human Development. The research was partially financed by the Max Planck Society.  
<sup>5</sup> MWB's work was supported by a grant from the German Research Foundation (DFG, WE

6 4269/3-1, YLS as Co-PI) as well as an Early Career Research Fellowship 2017–2019 awarded  
7 by the Jacobs Foundation. YLS and MCS were each supported via Minerva Research Groups  
8 awarded by the Max Planck Society. YLS is funded by the European Union (ERC-2018-StG-  
9 PIVOTAL-758898) and a Fellowship from the Jacobs Foundation (JRF 2018-2020). VRS is a  
10 fellow of the International Max Planck Research School on the Life Course. We thank Beate  
11 Mühlroth and Xenia Grande for organizing data collection, Kristina Günther for help in par-  
12 ticipant recruitment, Julia Delius for editorial assistance, Michael Krause for help with cluster  
13 computing, and all student assistants who helped with data collection. We are grateful to all  
14 members of the CONMEM project for helpful feedback on the analysis. Finally, we thank all  
15 study participants for their time.

16

17

## 18 **Abstract**

19 Age-related memory decline is associated with changes in neural functioning but little is known  
20 about how aging affects the quality of information representation in the brain. Whereas a  
21 long-standing hypothesis of the aging literature links cognitive impairments to less distinct  
22 neural representations in old age, memory studies have shown that high similarity between  
23 activity patterns benefits memory performance for the respective stimuli. Here, we addressed  
24 this apparent conflict by investigating between-item representational similarity in 50 younger  
25 (19–27 years old) and 63 older (63–75 years old) human adults (male and female) who studied  
26 scene-word associations using a mnemonic imagery strategy while electroencephalography was  
27 recorded. We compared the similarity of spatiotemporal frequency patterns elicited during  
28 encoding of items with different subsequent memory fate. Compared to younger adults, older  
29 adults' memory representations were more similar to each other but items that elicited the  
30 most similar activity patterns early in the encoding trial were those that were best remembered  
31 by older adults. In contrast, young adults' memory performance benefited from decreased  
32 similarity between earlier and later periods in the encoding trials, which might reflect their  
33 better success in forming unique memorable mental images of the joint picture–word pair.  
34 Our results advance the understanding of the representational properties that give rise to  
35 memory quality as well as how these properties change in the course of aging.

## 36 **Significance statement**

37 Declining memory abilities are one of the most evident limitations for humans when growing  
38 older. Despite recent advances of our understanding of how the brain represents and sto-  
39 res information in distributed activation patterns, little is known about how the quality of  
40 information representation changes during aging and thus affects memory performance. We  
41 investigated how the similarity between neural representations relates to subsequent memory  
42 quality in younger and older adults. We present novel evidence that the interaction of pattern  
43 similarity and memory performance differs between age groups: Older adults benefited from  
44 increased similarity during early encoding whereas young adults benefited from decreased si-  
45 milarity between early and later encoding. These results provide insights into the nature of  
46 memory and age-related memory deficits.

## 47 Introduction

48 A long-standing hypothesis in the cognitive neuroscience of aging holds that neural represen-  
49 tations become less specific with advancing age, with detrimental effects on cognitive perfor-  
50 mance. Reduced neural distinctiveness in older compared to young adults (Li et al., 2001)  
51 has been observed as increased similarity and/or reduced discriminability between neural  
52 activity patterns during different memory tasks (Carp et al., 2010; St-Laurent et al., 2011),  
53 between different stimulus categories (Carp et al., 2011; Park et al., 2004; Park et al., 2010;  
54 Park et al., 2012; Payer et al., 2006; Koen et al., 2019), and between different individual sti-  
55 muli (Goh et al., 2010; St-Laurent et al., 2014). However, these studies did not directly link  
56 this age-related reduction in neural specificity to differences in memory performance. A recent  
57 functional magnetic resonance imaging (fMRI) study by Koen et al. (2019) assessed neural  
58 distinctiveness during a memory encoding task and showed a general (age-invariant) associa-  
59 tion between neural category differentiation and recognition memory performance. However,  
60 they did not identify differences in distinctiveness between items that were later remembered  
61 or not remembered. A suitable approach to unravel the specific association between pattern  
62 distinctiveness and memory performance would be to examine whether items that are repre-  
63 sented less distinctly are also those that are less likely to be remembered. One fMRI study by  
64 Zheng et al. (2017) provided first evidence in this direction, showing that decreased memory  
65 performance in old age is associated with poorer item-specific representations in the visual  
66 cortex, even after controlling for differences in activation levels and variance.

67 Surprisingly, the hypothesis of the cognitive aging literature suggesting that reduced neural  
68 specificity underlies cognitive decline is in stark contrast to the prevalent evidence in gene-  
69 ral memory research that increased similarity is actually advantageous for performance: In  
70 young adult samples, various studies have shown that the representational similarity between  
71 different items is positively related to memory performance for these items (Davis et al., 2014;  
72 Lu et al., 2015; Wagner et al., 2016), which is in line with cognitive and computational models  
73 (Clark and Gronlund, 1996; Gillund and Shiffrin, 1984). Between-item pattern similarity may  
74 support memory by capturing regularities across experiences (LaRocque et al., 2013) and by  
75 giving rise to a sense of familiarity (Davis et al., 2014).

76 To date, most studies have used fMRI to estimate neural representations, prioritizing  
77 spatial resolution over temporal dynamics of representational patterns. In contrast, time-  
78 sensitive magneto-/electroencephalography (M/EEG) measurements are able to identify the  
79 precise time windows and processing stages at which representational similarity supports  
80 memory performance. Lu et al. (2015) showed that between approximately 420 ms and 580  
81 ms after stimulus onset, global spatiotemporal EEG pattern similarity was higher for later  
82 remembered than for forgotten symbols.

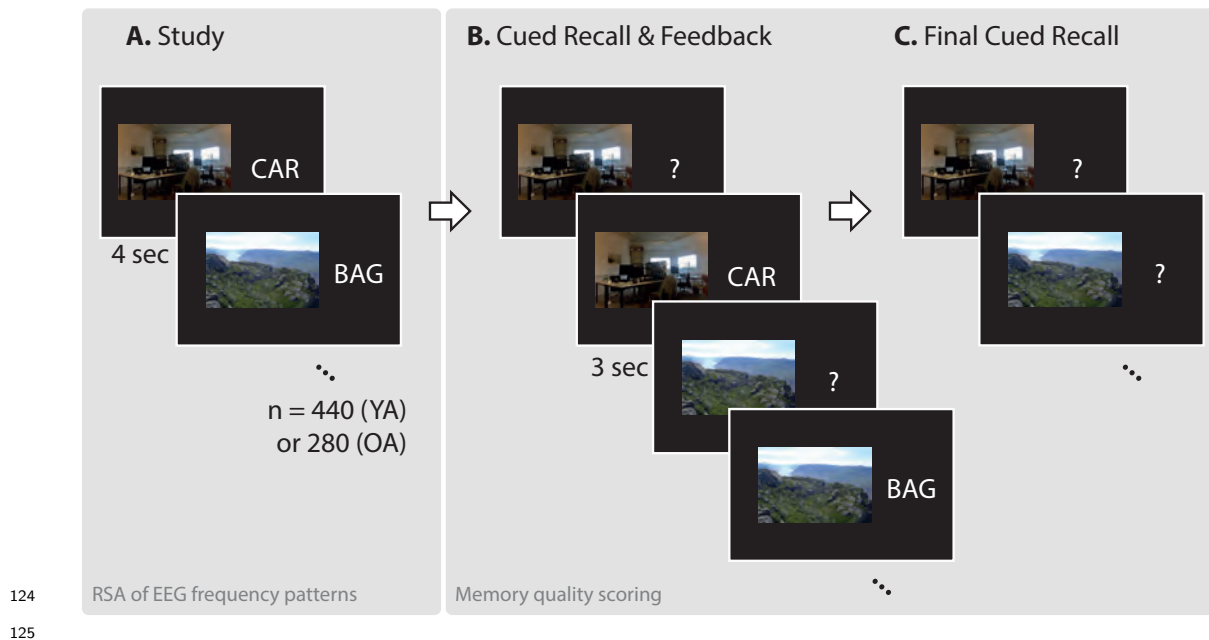
83 Recent scalp (Kerrén et al., 2018; Michelmann et al., 2016) and intracranial EEG studies  
84 (Staresina et al., 2016; Zhang et al., 2015) further demonstrated the particular potential of  
85 frequency-transformed activity patterns in identifying memory-relevant reactivation of item-  
86 specific signatures. For example, Michelmann et al. (2018) showed that desynchronized low-  
87 frequency brain oscillations carried stimulus-specific temporal activity patterns during an  
88 associative memory task. However, there are no previous reports on the relation of the  
89 similarity between these frequency-transformed activation patterns to later memory success  
90 for the studied items.

91 To our knowledge, the apparent conflict between the observed beneficial effect of global  
92 similarity in memory studies with young adults, and the potentially detrimental effect of  
93 decreasing distinctiveness in the aging literature has not been explicitly addressed. Here,  
94 we aim to resolve the question whether distinctiveness or similarity between different neural  
95 representations is beneficial for memory performance by a systematic investigation of the rela-  
96 tion between representational similarity and memory performance in young and older adults.  
97 For this, we examined the similarity of EEG frequency patterns elicited during encoding of  
98 scene-word pairs in relation to age and subsequent recall performance.

## 99 **Materials and Methods**

### 100 **Experimental design**

101 The research presented here comprises data from two associated studies that investigated age-  
102 related differences in associative memory encoding, consolidation, and retrieval (Fandakova et  
103 al., 2018; Muehlroth et al., in press; Sander et al., 2019). Despite subsequent procedural diffe-  
104 rences, an identical picture–word association task paradigm during which EEG was recorded  
105 was at the core of both studies. In this task, participants were asked to memorize scene–word  
106 pairs by applying a previously trained mnemonic imagery strategy. Specifically, they were  
107 instructed to imagine the scene and word content together in a unique and memorable mental  
108 image. Stimuli consisted of color photographs of indoor and outdoor scenes randomly pai-  
109 red with concrete German nouns (4–8 letters). During the initial study phase, scenes and  
110 words were presented next to each other on a black background for 4 s. After studying a  
111 pair, participants indicated on a four-point scale how well they were able to integrate the  
112 presented scene and word. Young and older adults studied 440 and 280 pairs, respectively.  
113 During the subsequent cued recall phase, scenes served as cues for participants to verbally  
114 recall the associated word. Recall time was not constrained. After each trial, the correct  
115 scene–word pair was presented again for 3 s and subjects were instructed to restudy the pair,  
116 independent of previous retrieval success. This recall and restudy phase was repeated one  
117 more time for the older adults. Finally, both young and older participants underwent a final  
118 cued recall round in which no feedback was presented. The number of to-be-studied pairs as  
119 well as recall repetitions differed between age groups in order to achieve comparable recall  
120 success of approximately half of the studied items. After each phase, we asked participants  
121 to indicate on a four-point scale how often they used the instructed imagery strategy or other  
122 specific memory strategies to memorize a pair. For a detailed description of the study design  
123 and stimulus selection, see Fandakova et al. (2018).



124  
125  
126 Figure 1: Memory task paradigm (cf. Fandakova et al., 2018). **A.** In the study phase, participants  
127 were asked to associate 440 (young adults; YA) or 280 (older adults; OA) scene–word pairs using an  
128 imagery strategy. Representational similarity analysis (RSA) was conducted on EEG data during this  
129 phase. **B.** During the cued recall and feedback phase, the scene was presented as a cue to verbally  
130 recall the associated word. Subsequently, the original pair was presented again for restudy. The cued  
131 recall and feedback phase was performed once for younger and twice for older adults. **C.** During final  
132 recall, no feedback was provided. Scene–word pairs were sorted into three memory quality categories  
133 based on recall performance in phases B and C (see Figure 2).



## 135 **Subjects**

136 The original sample of study 1 (Fandakova et al., 2018) consisted of 30 healthy young adults  
137 and 44 healthy older adults. Due to technical failures, one young adult and three older adults  
138 did not complete the study. Study 2 (Muehlroth et al., in press) involved 34 healthy young  
139 adults and 41 healthy older adults participated, with 4 younger and 4 older participants  
140 not completing the experiment for technical reasons. Due to missing or noisy EEG data,  
141 we additionally excluded 9 younger and 15 older adults, resulting in a total of 50 younger  
142 adults and 63 older adults across both studies, who are included in the analyses presented  
143 here (young adults:  $M(SD)\text{age} = 24.3(2.5)$  years, 19–27 years, 27 female, 23 male; old adults:  
144  $M(SD)\text{age} = 70.4(2.6)$  years, 63–75 years, 33 female, 30 male).

145 All participants were right-handed native German speakers, reported normal or corrected-  
146 to-normal vision, no history of psychiatric or neurological disease, and no use of psychiatric  
147 medication. We screened older adults with the Mini-Mental State Examination (MMSE;  
148 Folstein et al., 1975) and none had a value below the threshold of 26 points. Both studies  
149 were approved by the ethics committee of the Deutsche Gesellschaft für Psychologie and  
150 took place at the Max Planck Institute for Human Development in Berlin, Germany. All  
151 participants gave written consent to take part in the experiment.

## 152 **Behavioral analysis**

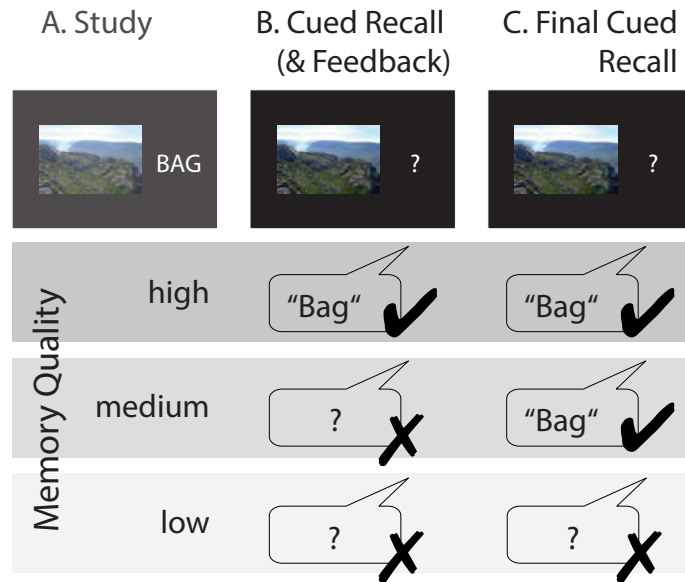
153 During the cued recall phases, participants had to verbally recall the word associated with  
154 the presented image. We report the proportion of correctly recalled words. False responses  
155 occurred rarely and were treated as no responses. Following the rationale of a subsequent  
156 memory analysis (Paller and Wagner, 2002), we sorted all trials according to whether the  
157 associated word was successfully recalled during the experiment or not. Items that were not  
158 remembered after repeated encoding were assumed to have only created a weak memory trace,  
159 not sufficient for successful recall (although maybe strong enough for successful recognition,  
160 see Fandakova et al., 2018). Importantly, given the repeated recall phases, we were able to  
161 further differentiate successfully recalled items and distinguish those that were immediately  
162 learned from those that were only acquired later in the experiment. We refer to those items as

163 high memory quality and medium memory quality items, respectively (see Figure 2). Older  
164 adults underwent one additional recall and restudy cycle due to close-to-floor performance  
165 in the first cycle. To keep the scoring of stimulus pairs as evincing high, medium, or low  
166 memory quality comparable across age groups, items that were recalled successfully in the  
167 last recall cycle were divided into those that were also already recalled in the previous cycle  
168 (high quality) and those that were only remembered in the final recall (medium quality)  
169 in contrast to never-recalled items (low quality). The few items that were remembered in  
170 an earlier but not later recall, were excluded from further analyses (see Results and Figure  
171 4). For both age groups, all EEG analyses were conducted on the EEG activity patterns  
172 elicited during the first learning phase such that all pairs were novel to the participants and  
173 no retrieval-related processes could influence the evoked activity patterns.

#### 184 **EEG recording and preprocessing**

185 EEG was recorded continuously with BrainVision amplifiers (BrainVision Products GmbH,  
186 Gilching, Germany) from 61 Ag/Ag-Cl electrodes embedded in an elastic cap. Three addi-  
187 tional electrodes were placed at the outer canthi (horizontal electrooculography (EOG)) and  
188 below the left eye (vertical EOG) to monitor eye movements. During recording, all electrodes  
189 were referenced to the right mastoid electrode, and the left mastoid electrode was recorded as  
190 an additional channel. The EEG was recorded with a pass-band of 0.1 to 250 Hz and digitized  
191 with a sampling rate of 1000 Hz. During preparation, electrode impedances were kept below  
192 5 k $\Omega$ .

193 EEG data preprocessing was performed with the Fieldtrip software package (develo-  
194 ped at the F. C. Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands;  
195 <http://fieldtrip.fcdonders.nl>; RRID: SCR\_004849) and custom MATLAB code (The MathWorks  
196 Inc., Natick, MA, USA; RRID: SCR\_001622). Data were downsampled to 250 Hz and an inde-  
197 pendent component analysis was used to correct for eye blink, (eye) movement, and heartbeat  
198 artifacts (Jung et al., 2000). Artifact components were automatically detected, visually chec-  
199 ked, and removed from the data. For analyses, the EEG was demeaned, re-referenced to  
200 mathematically linked mastoids, and band-pass filtered (0.2–100 Hz; fourth order Butter-  
201 worth). Following the FASTER procedure (Nolan et al., 2010), automatic artifact correction



174

175 Figure 2: Scoring of stimulus pairs into high, medium, or low memory quality based on  
176 learning history. For both younger and older adults, items that were correctly recalled in the last  
177 recall cycle (C) as well as the previous (B) were scored as high memory quality items. Pairs that  
178 were solely recalled in the final recall were scored as medium memory quality items. And items that  
179 were never correctly recalled were scored as low memory quality items. Not depicted: Items that  
180 were recalled in the earlier but not later recall were excluded. Older adults performed one more cued  
181 recall and restudy cycle (between A and B) that was not included in item scoring due to close-to-floor  
182 performance. Note that wrong and no responses were treated equally.

202 was performed for the remaining artifacts. Excluded channels were interpolated with spheri-  
203 cal splines (Perrin et al., 1989). Finally, data epochs of 4 seconds were extracted from -1 s to  
204 3 s with respect to the onset of the scene–word presentation during the study phase (Figure  
205 1A).

## 206 **EEG analysis**

207 Time-frequency representations (TFRs) of the data were derived using a multitaper approach.  
208 For the low frequencies (2–20 Hz), we used Hanning tapers with a fixed width of 500 ms,  
209 resulting in frequency steps of 2 Hz. For higher frequencies (25–100 Hz), we used DPSS  
210 (discrete prolate spheroidal sequences) tapers with a width of 400 ms in steps of 5 Hz with  
211 seven Slepian tapers resulting in  $\pm 10$  Hz smoothing. In this way, we obtained a TFR for  
212 each trial and electrode. Trial lengths were reduced to -0.752 s to 3 s relative to stimulus  
213 onset.

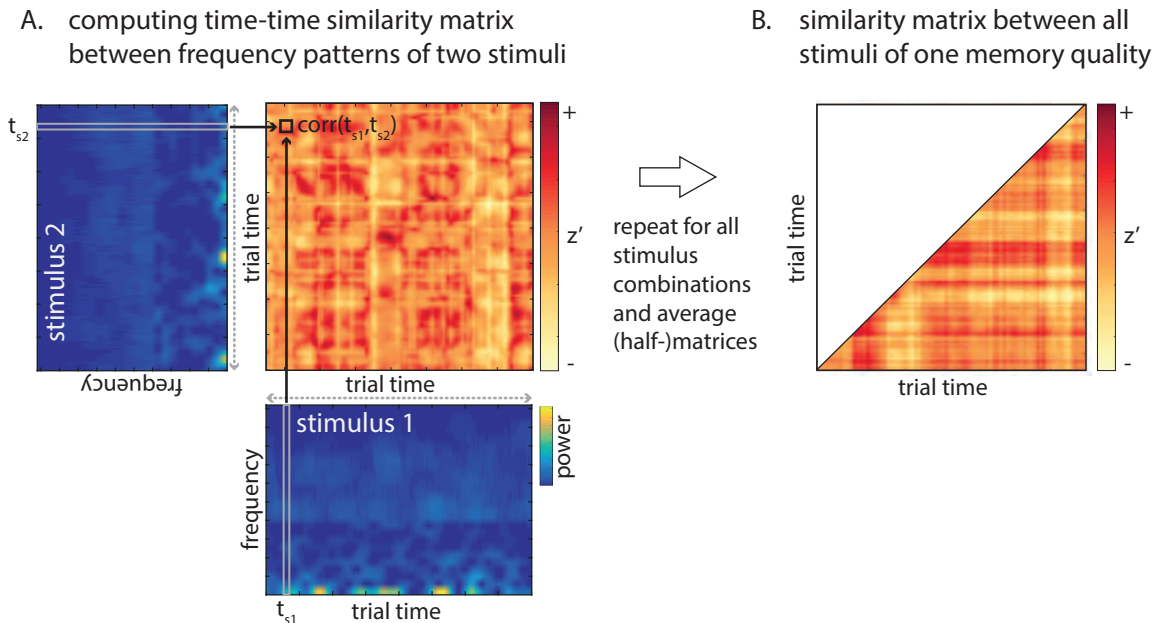
214 To counter the effect of intrinsically high correlations between frequency patterns due to  
215 the  $1/\text{frequency}$  power spectrum (Schönauer et al., 2017), we removed the mean background  
216 noise spectrum from the log-transformed TFRs following previously established procedures  
217 (i.e., as suggested by the “Better oscillation detection” (BOSC) method; Caplan et al., 2001;  
218 Kosciessa et al., 2018; Whitten et al., 2011). Because of structured noise, correlations between  
219 different activity patterns are very high and almost never at or below zero, meaning that the  
220 true null-distribution is higher than zero. For detailed discussions of these issues (in fMRI),  
221 see Allefeld et al. (2016); Cai et al. (2016).

## 222 **Multivariate EEG analysis**

223 EEG data were analyzed using representational similarity analysis (RSA; Kriegeskorte et al.,  
224 2008). RSA assesses the resemblance of patterns of neural activity, with similar patterns  
225 assumed to represent mutual information. In this study, we investigated between-item repre-  
226 sentational similarity during the first encoding phase in relation to memory quality. “Item”  
227 always refers to a scene–word pair. Figure 3 illustrates the procedure for analyzing the simila-  
228 rity between stimulus-specific spatiotemporal frequency representations. RSA was conducted  
229 for each participant and EEG channel independently. Stimuli were grouped according to high,

230 medium, and low memory quality (see Figure 2). In order to examine whether between-item  
231 representational similarities differed as a function of memory quality, we correlated the noise-  
232 corrected and log-transformed frequency patterns of every item with the frequency patterns  
233 of all other items of the same memory quality. That is, for each participant we ran three simi-  
234 larity analyses, namely for high, medium, and low memory quality items. In order to use the  
235 same number of items for each RSA of a given participant, we reduced them to the number of  
236 items available in the condition with the least items. For example, if there were 50 items with  
237 high, 180 items with medium, and 210 items with low memory quality for a given participant,  
238 the number of items used in the RSAs of medium and low quality items was reduced to 50 as  
239 well. Note that the category containing the fewest items was in most cases the group of high  
240 memory quality items (except for 6 younger and 6 older participants). We randomly sampled  
241 the respective number of items from all available trials of the respective memory quality. As  
242 the actual measure of similarity, we employed pairwise Pearson correlations between the cor-  
243 responding frequency patterns. In each of these correlations, every pair of frequency vectors  
244 (with 26 frequency bins) of all time points from the two respective trials were correlated with  
245 each other (470 time points, from 752 ms before stimulus onset to 3000 ms after stimulus  
246 onset). The resulting time-time similarity matrices were Fisher ( $z$ )-transformed. In order to  
247 prevent bias towards the randomly picked items, the item sampling was repeated 20 times.  
248 Finally, the matrices were averaged to obtain one between-item similarity matrix for each  
249 scene–word pair, which indicates the similarity of this pair to all other pairs of the same me-  
250 mory quality. The similarity matrices of all items within one memory quality were then again  
251 averaged to obtain the mean similarity matrices between all high, medium, and low memory  
252 quality items, respectively. This procedure was performed separately for each of the 60 scalp  
253 electrodes.

272 The resulting similarity matrices contain the time dimension on both the x- and the y-  
273 axis, revealing the frequency pattern resemblance not only at identical within-trial time points  
274 (diagonal) but also between all combinations of time points (in analogy to the temporal  
275 generalization method; Cichy et al., 2014; King and Dehaene, 2014). This enables us to  
276 identify whether certain parts of the memory representations were similar to each other at  
277 different times during encoding of the respective scene–word pairs.



256 Figure 3: Spectral representational similarity analysis methodology. **A.** The frequency vector from  
257 every time point (i.e., column) of the noise-corrected and log-transformed time-frequency pattern (from  
258 one electrode) corresponding to stimulus 1 (bottom) is Pearson-correlated with the vectors from every  
259 time point of stimulus 2 (left; tilted). For illustration, one example vector of stimulus 1 ( $t_{s1}$ ) and one  
260 example vector of stimulus 2 ( $t_{s2}$ ) are highlighted. Correlating these two vectors gives one correlation  
261 coefficient, i.e., one coordinate (highlighted with black box) on a matrix with time on both axes.  
262 Computing all pairwise time vector correlations results in a time-time similarity matrix representing the  
263 similarity of those two frequency patterns at all time point combinations. This procedure is repeated  
264 for all items of a certain memory quality (i.e., similarity of stimulus 1 with all others, stimulus 2 with  
265 all others, etc.). **B.** Averaging across all similarity matrices yields the mean similarity matrix showing  
266 the pattern similarity among all items of the same memory quality. Only one triangle and the diagonal  
267 of the matrix are relevant because the similarity of every two frequency patterns is computed twice,  
268 resulting in an identical correlation coefficient on both sides of the diagonal. Similarity is quantified as  
269 the Fisher  $z$ -transformed Pearson correlation coefficient ( $z'$ ). Not depicted: This procedure is repeated  
270 for all 60 electrodes, the three memory quality categories, and all subjects.

278 Because the similarity of any two items is computed twice and thus the identical correlation  
279 coefficients appear twice, namely on both sides of the diagonal, the similarity matrix was  
280 reduced to only one of the triangles plus the diagonal.

281 Representational similarity analyses were computed parallelized on a high-performance  
282 computing cluster. All computations and statistics were conducted with Matlab (The MathWorks,  
283 Inc., RRID: SCR\_001622) versions R2014b or R2016b. The Matlab-based Fieldtrip Toolbox  
284 (Maris and Oostenveld, 2007; Oostenveld et al., 2011) (Maris Oostenveld, 2007; Oostenveld et  
285 al., 2011; RRID: SCR\_004849) was used for performing time-frequency transformations and  
286 cluster-based permutation analyses.

## 287 **Statistical analysis**

### 288 *Memory performance and strategy use*

289 We computed two-sided independent samples *t*-tests in order to test for age differences in  
290 the proportion of items within each memory quality category (high, medium, low, forgot-  
291 ten/excluded) and the proportion of items remembered in the final recall task. To compare  
292 younger and older adults' strategy use in the first encoding phase, we used the Wilcoxon rank  
293 sum test to examine differences in their median responses of how often they used the imagery  
294 strategy.

### 295 *Differences in representational similarity*

296 Within both groups, we tested for differences in the representational similarity matrices  
297 between different memory quality categories by conducting non-parametric, cluster-based,  
298 random permutation tests (Fieldtrip Toolbox; Maris and Oostenveld, 2007; Oostenveld et al.,  
299 2011; RRID: SCR\_004849). Univariate two-sided, dependent samples regression coefficient *t*-  
300 statistics were calculated for the time-time similarity matrices at all channels. Clusters were  
301 formed by grouping neighboring channel  $\times$  time  $\times$  time samples with a *p*-value below 0.05  
302 (spatially and temporally). The respective test statistic was then determined as the sum of  
303 all *t*-values within a cluster. The Monte Carlo method was used to compute the reference  
304 distribution for the summed cluster-level *t*-values. Samples were repeatedly (100  $\times$ ) assigned

305 into three groups and the differences between these random groups were contrasted to the  
306 differences between the three actual conditions (high, medium, and low memory quality). For  
307 every repetition the  $t$ -statistic was computed and the  $t$ -values summed for each cluster. The  
308  $t$ -values were  $z$ -transformed for further analysis.

309 In addition to the linear regression of all three memory qualities mentioned above, we also  
310 compared each pair of memory quality categories using a two-sided, dependent samples  $t$ -test  
311 in the permutation analysis.

312 We regarded clusters whose test statistic exceeded the 97.5th percentile for its respective  
313 reference probability distribution as significant. If such clusters were obtained, we furthermore  
314 assessed the time-time intervals and the topographic distributions of the channels showing  
315 when and where, respectively, the differences were reliable. The clusters that were identified  
316 for each age group were further examined for age and memory quality effects (see below). In  
317 addition, we tested for main age group differences in a separate permutation analysis using  
318 independent samples  $t$ -tests.

### 319 *Age and memory quality effects in the identified clusters*

320 To explore potential age differences more closely, we further investigated the relationship  
321 between pattern similarity and memory quality by conducting independent samples regression  
322 coefficient  $t$ -statistics for each participant. We then extracted and averaged the individual ( $z$ -  
323 transformed regression coefficients within the time-time-electrode clusters that were identified  
324 in younger and older adults (see above). For both clusters and age groups we performed one-  
325 sample  $t$ -tests to test whether the correlation coefficients come from a distribution with a  
326 mean different from zero. Furthermore, we tested for differences between the age groups in  
327 both clusters using independent samples  $t$ -tests.

## 328 **Results**

### 329 **Memory performance and strategy use**

330 During the cued recall phases, participants had to respond verbally with the word they pre-  
331 viously learned to associate with the presented image. We sorted the trials according to



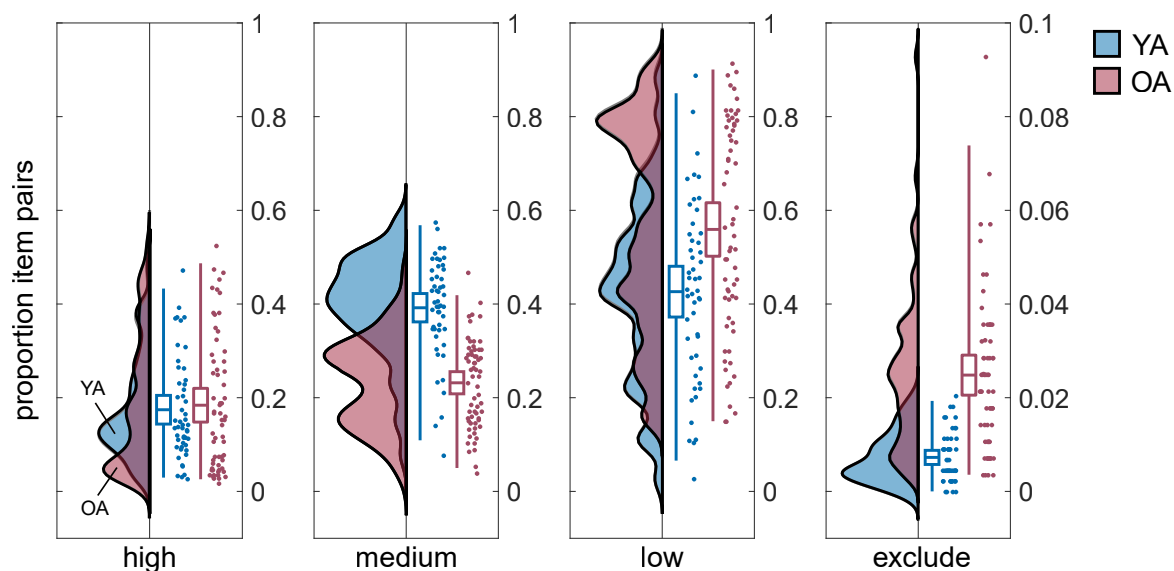
332 whether recall was successful, and when, into high, medium, and low memory quality items  
333 (see Methods). The proportion of high memory quality items did not differ between younger  
334 adults and older adults ( $M(\text{younger adults}) = 0.17$ ,  $SD(\text{younger adults}) = 0.11$ ,  $M(\text{older}$   
335  $\text{adults}) = 0.18$ ,  $SD(\text{older adults}) = 0.15$ ;  $t(111) = -0.4$ ,  $p = 0.69$ , two-sample  $t$ -test; see Fi-  
336 gure 4). In contrast, the proportion of items with medium memory quality was significantly  
337 larger for younger than older participants ( $M(\text{younger adults}) = 0.39$ ,  $SD(\text{younger adults}) =$   
338  $0.11$ ,  $M(\text{older adults}) = 0.23$ ,  $SD(\text{older adults}) = 0.09$ ;  $t(111) = 8.48$ ,  $p = 10^{-13}$ ), while older  
339 adults had a significantly higher proportion of low memory items ( $M(\text{younger adults}) = 0.43$ ,  
340  $SD(\text{younger adults}) = 0.19$ ,  $M(\text{older adults}) = 0.56$ ,  $SD(\text{older adults}) = 0.23$ ;  $t(111) = -3.31$ ,  
341  $p = 0.0012$ ). Note that in older adults we observed a higher proportion of items that were  
342 remembered in an early but not later recall phase, i.e., that were forgotten in the course of  
343 the experiment ( $M(\text{younger adults}) = 0.007$ ,  $SD(\text{younger adults}) = 0.005$ ,  $M(\text{older adults})$   
344  $= 0.025$ ,  $SD(\text{older adults}) = 0.02$ ;  $t(111) = -7.04$ ,  $p = 1.6 \times 10^{-10}$ ). Those item pairs were  
345 excluded from further analyses.

355 Our experimental procedure was successful in inducing variability in memory performance  
356 such that both groups could remember approximately half of the studied items: Young adults  
357 successfully recalled on average 56.64 % ( $SD = 10.7$ ) and older adults successfully recalled on  
358 average 41.6 % ( $SD = 12.06$ ) of the items (440 and 280, respectively). However, our procedure  
359 did not completely eliminate age differences since young adults still performed significantly  
360 better than older participants in the final recall task ( $t(111) = 3.82$ ,  $p = 0.0002$ , two-sample  
361  $t$ -test).

362 After the first study phase, we asked participants to indicate on a four-point scale how  
363 often they had used specific memory strategies for the task (1: almost always, 4: almost never).  
364 With regard to the imagery strategy, young adults indicated that they used it significantly  
365 more often than older adults (younger adults: median = 1.5, min = 1, max = 3; older adults:  
366 median = 2, min = 1, max = 4;  $z = -5.09$ ,  $p = 0.0000004$ , Wilcoxon rank sum test).

## 367 **Representational similarity**

368 Calculation of between-item representational similarity was based on the initial encoding phase  
369 (Figure 1A). To identify whether high pattern resemblance or high pattern distinctiveness



346

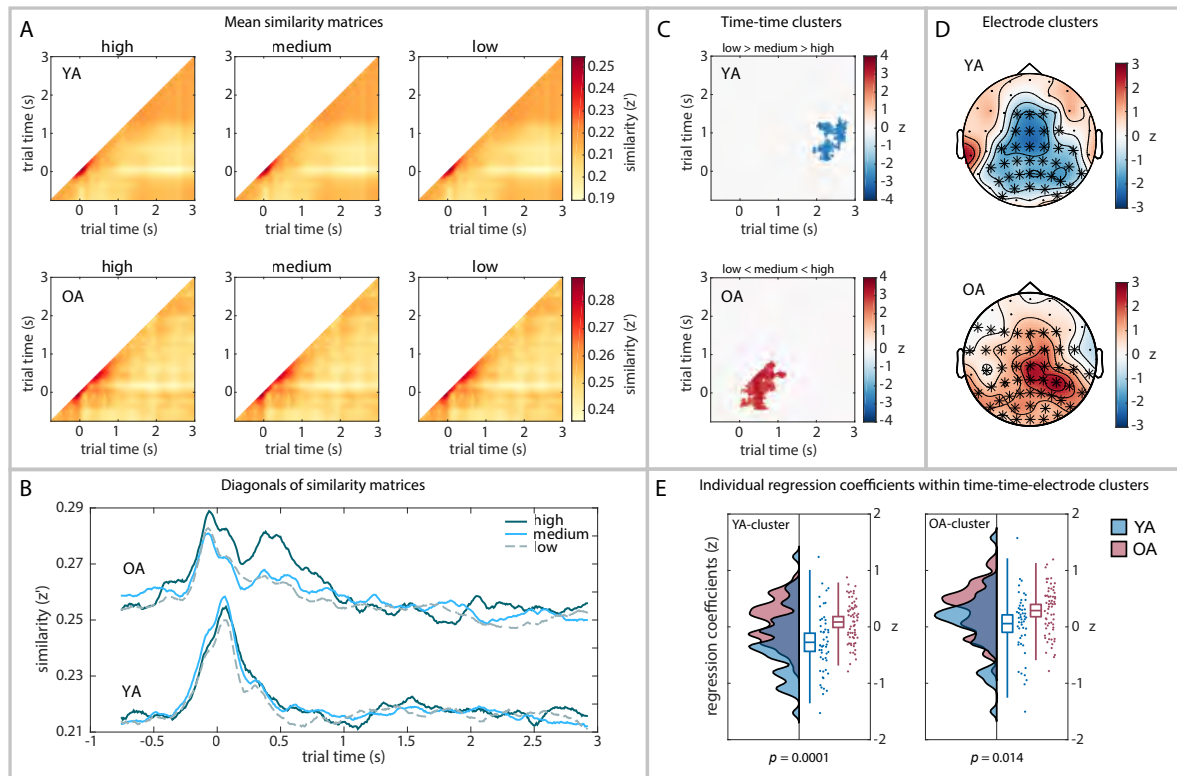
347

348 Figure 4: Proportion of item pairs with high, medium, and low memory quality as well as proportion  
349 of excluded items for 50 young adults (YA; blue) and 63 older adults (OA; red). Group distributions  
350 as un-mirrored violin plots (probability density functions), boxplots with means and 95% confidence  
351 intervals, whiskers with 2nd and 98th percentiles, and individual data points (horizontally jittered)  
352 (modified from Allen et al., 2018). Note that the y-axis for excluded items differs from that of the  
353 other categories. YA studied 440 pairs and OA studied 280 pairs.

370 during learning was beneficial for later memory success, we sorted all items according to  
371 subsequent memory performance and correlated the evoked spatiotemporal frequency pattern  
372 of each item with every other item in the same memory quality category. The resulting mean  
373 similarity matrices over all channels and scene–word pairs are shown in Figure 5A. These  
374 matrices display the similarity of the frequency representations at all possible within-trial  
375 time point combinations (-0.752 s to 3 s relative to stimulus onset at 0). In contrast, the  
376 diagonals of the similarity matrices (also plotted separately in Figure 5B) only show the  
377 similarity between items at identical time points and facilitate a visual comparison of the  
378 time courses of representational similarities for the different memory quality categories and  
379 age groups. Although this omits much of the similarity information, elevated similarities do  
380 occur largely along the diagonal. Note that the diagonals are only plotted for illustration  
381 purposes and all statistical tests were performed on the complete matrices as presented in  
382 Figure 5A.

383 *Older adults exhibit generally higher representational similarity than young adults*

384 Shortly before stimulus onset, similarity increased in both age groups and reached a peak  
385 around the time of onset (Figure 5A,B). Elevated similarity occurred mainly between iden-  
386 tical trial time points (diagonal) with slightly more persistent activity (elevated off-diagonal  
387 similarity) in older adults compared to young adults. Irrespective of later memory success,  
388 between-item pattern similarity was generally higher in older adults than in young adults  
389 (averaged across the whole time-time matrix and all 60 channels:  $M(\text{younger adults}) = 0.21$ ,  
390  $SD(\text{younger adults}) = 0.065$ ,  $M(\text{older adults}) = 0.25$ ,  $SD(\text{older adults}) = 0.068$ ; 500 cluster  
391 permutations,  $p = 0.002$ ).



392

393

394 Figure 5: Between-item pattern similarities and statistics. Similarity is quantified as Fisher  $z$ -transformed  
 395 Pearson correlation coefficient ( $z'$ ). On time axes, zero denotes stimulus onset. C and D show results  
 396 from cluster-based permutation analyses for each age group, E shows results from individual regression  
 397 analyses (see Methods). **A**. Mean time-time similarity matrices across all 60 channels and items within  
 398 each memory quality category (high, medium, low) for all 50 young adults (YA; top) and 63 older adults  
 399 (OA; bottom). Note that the scales differ between age groups. **B**. Diagonals from the time-time similarity  
 400 matrices (see A). **C**. Time-time clusters (masked  $z$ -scores) in which the three memory quality categories  
 401 differ significantly within each age group (averaged across reliable electrodes, see D). **D**. Topographic  
 402 representations of the electrode clusters that revealed reliable differences between memory quality cate-  
 403 gories within each age group (averaged across reliable time windows, see C). **E**.  $Z$ -transformed regression  
 404 coefficients extracted from time-time-electrode clusters identified in YA (left) and OA (right) (see C  
 405 and D). Group distributions (probability density functions), boxplots with means and 95% confidence  
 406 intervals, whiskers with 2nd and 98th percentiles, and individual data points (horizontally jittered) for  
 407 YA (blue) and OA (red) (modified from Allen et al., 2018). ( $P$ )-values are given for group differences  
 408 within each cluster (independent samples  $t$ -tests). Note the difference between  $z'$  (Fisher  $z$ -transformed  
 409 correlation coefficients) and  $z$  ( $z$ -transformed regression coefficients).

411 *Representational similarity differentially affects memory performance of younger and older*  
412 *adults*

413 Within both age groups, we tested for differences in the levels of representational similarity  
414 between scene–word pairs of different memory quality by conducting linear regressions. We  
415 controlled for multiple comparisons by using non-parametric cluster-based permutation tests.  
416 In both age groups we identified a cluster with a Monte Carlo  $p$ -value below 0.025, which  
417 indicates a reliable linear relationship between representational similarity and memory quality  
418 (young adults:  $p=0.0099$ ; older adults:  $p=0.0099$ ; see Figure 5C). Importantly, the direction  
419 of this relationship differed between groups: while the relation between similarity and memory  
420 quality was positive in older adults (low < medium < high), it was negative in young adults  
421 (low > medium > high) (Figure 5E).

422 The cluster obtained in older adults included most of the diagonal from 50 ms to 830 ms  
423 after stimulus onset and extended off-diagonally to 470 ms before and 1240 ms after stimulus  
424 onset (Figure 5C). Elevated similarity along the diagonal indicates similarity between neural  
425 representational patterns at identical trial time points, whereas off-diagonal time windows  
426 suggest similar activation patterns at different trial time points. The larger the distance of a  
427 coordinate from the diagonal, the more distant are the compared time points in the respective  
428 frequency patterns. Differences between memory quality categories were reliable in most (49  
429 out of 60) occipital, parietal, temporal, and central electrodes in older adults (Figure 5D).

430 In contrast to the cluster found in older adults, an off-diagonal cluster was identified  
431 for young adults, in which low memory quality items displayed significantly more similarity  
432 than medium and high memory quality items (Figure 5C). Compared to older adults, where  
433 differences between memory qualities were found to be most pronounced between early and  
434 neighboring trial time points, i.e., close to the diagonal, the off-diagonal cluster identified in  
435 young adults indicated that differences occurred at later and more distant trial time points.  
436 Specifically, differences were found between earlier (450 ms to 1400 ms after stimulus onset)  
437 and later time points (2640 ms to 2800 ms after onset) and at 34 mainly parietal-occipital  
438 and central electrodes (Figure 5D). Despite the relatively poor spatial resolution in EEG, the  
439 large electrode clusters in both young and older adults indicate that memory representations

440 are broadly distributed over the brain rather than specific to a particular region.

441 Additional analyses of pairwise comparison of the three memory quality categories instead  
442 of linear regression resulted in the same significant cluster only for high versus low quality  
443 items in older adults, and no significant differences among memory quality categories in young  
444 adults.

#### 445 *Age and memory quality effects in the identified clusters*

446 The cluster-based analyses reported above suggested differential memory-related represen-  
447 tational similarity in younger and older adults. To explore potential age differences more  
448 closely, we additionally tested for a linear relationship between representational similarity  
449 and memory quality in each participant by conducting individual linear regressions. We then  
450 extracted and averaged the individual  $z$ -transformed regression coefficients within each time-  
451 time-electrode cluster (see Figure 5E). In the young-adult cluster only the mean regression  
452 coefficients of the young adults differed from zero (young adults:  $t(49) = -3.42$ ,  $p = 0.0013$ ;  
453 older adults:  $t(62) = 1.79$ ,  $p = 0.08$ ; one-sample  $t$ -tests) and vice versa in the older-adult  
454 cluster (young adults:  $t(49) = 0.75$ ,  $p = 0.46$ ; older adults:  $t(62) = 5.27$ ,  $p = 0.000002$ ). In  
455 both clusters the regression coefficients differed significantly between younger and older adults  
456 (young-adult cluster:  $M(\text{young adults}) = -0.27$ ,  $SD(\text{young adults}) = 0.57$ ,  $M(\text{older adults})$   
457  $= 0.086$ ,  $SD(\text{older adults}) = 0.38$ ,  $t(111) = -4.03$ ,  $p = 0.0001$ ; older-adults cluster:  $M(\text{young}$   
458  $\text{adults}) = 0.058$ ,  $SD(\text{young adults}) = 0.55$ ,  $M(\text{older adults}) = 0.29$ ,  $SD(\text{older adults}) = 0.43$ ,  
459  $t(111) = -2.5$ ,  $p = 0.014$ ; independent samples  $t$ -tests) implying that age differences do exist  
460 in the relation between representational similarity and memory quality in these clusters.

## 461 Discussion

462 The present study aimed to reconcile an evident tension between theories relating neural pat-  
463 tern similarity and memory in the fields of cognitive neuroscience and cognitive aging research.  
464 We addressed the central question whether high pattern resemblance or high pattern distincti-  
465 veness benefits memory performance. To this end, we computed the similarity between the  
466 EEG frequency patterns elicited during encoding of different scene–word pairs at each elec-  
467 trode and related this measure of between-pair similarity to subsequent recall performance of  
468 younger and older adults.

469 For older adults, between-item representational similarity was generally higher compa-  
470 red to young adults, supporting the “dedifferentiation” hypothesis of declining neural dis-  
471 tinctiveness with age (Baltes and Lindenberger, 1997; Carp et al., 2011; Li et al., 2004;  
472 Park et al., 2004; Park et al., 2012; Payer et al., 2006; St-Laurent et al., 2014). Previous stu-  
473 dies suggested that the loss of neural specificity in old age may underlie age-related cognitive  
474 impairments. This was, for example, supported by the finding that the level of neural dis-  
475 tinctiveness and fluid intelligence were correlated (Park et al., 2010). However, most previous  
476 studies were not able to directly link neural item specificity with study participants’ perfor-  
477 mance since memory for the items themselves was not assessed. By measuring between-item  
478 representational similarity during the encoding phase of an associative memory task and sor-  
479 ting the trials according to subsequent memory performance, we were able to directly relate  
480 measures of neural distinctiveness during encoding to later recall success.

481 Specifically, based on learning history, we sorted the studied scene-word pairs into high,  
482 medium, and low memory quality items and, on the within-subject level, measured the linear  
483 relationship between the level of representational similarity and memory quality. Import-  
484 tantly, the direction of this relationship as well as the time window in which representational  
485 similarity mattered for subsequent memory performance differed between younger and older  
486 participants: For older adults, *high* similarity early during encoding (470 ms before stimulus  
487 onset to 1240 ms after stimulus onset) benefited memory performance. For young adults,  
488 *low* similarity between earlier (450 ms to 1400 ms after stimulus onset) and later time points  
489 during encoding (2640 ms to 2800 ms after onset) benefited memory performance.

490 That is, although older adults remembered significantly fewer items and revealed overall  
491 higher between-item similarity than younger adults, on the within-subject level, item represen-  
492 tations with high similarity to other items were actually those that older adults remembered  
493 best. Hence, while the age group differences replicated previous reports of increased neural  
494 similarity in older compared to younger adults, the within-person direction of the similarity-  
495 memory association among older adults corroborates cognitive models of memory (Clark and  
496 Gronlund, 1996; Gillund and Shiffrin, 1984; Hintzman, 1988) as well as previous memory  
497 studies with younger adults. These studies showed that higher similarity between different  
498 item representations (often called ‘global similarity’) is beneficial for subsequent recognition  
499 memory (LaRocque et al., 2013; Lu et al., 2015; Ye et al., 2016), memory confidence and  
500 categorization (Davis et al., 2014), fear memory (Visser et al., 2013), and associative memory  
501 formation (Wagner et al., 2016).

502 fMRI experiments located this beneficial effect of representational similarity in medial  
503 temporal lobe regions, whereas in the hippocampus, pattern distinctiveness supported me-  
504 mory (LaRocque et al., 2013). Indeed, impaired pattern separation computations in the  
505 hippocampus were reported for older adults (Shing et al., 2011; Wilson et al., 2006; Yassa  
506 et al., 2011) . While high pattern distinctiveness may be beneficial for memory performance  
507 to prevent false memories, high pattern similarity may support mnemonic decisions by cap-  
508 turing regularities across experiences (LaRocque et al., 2013) and by giving rise to a feeling  
509 of familiarity (Davis et al., 2014). Higher pattern similarity may also reflect more consistent  
510 processing that facilitates associative memory formation (Wagner et al., 2016). Strikingly, a  
511 tendency for more generalized memories (Koutstaal and Schacter, 1997; Koutstaal et al., 2001;  
512 Tun et al., 1998) and a stronger reliance on familiarity (Light et al., 2000; Prull et al., 2006;  
513 Yonelinas, 2002) is indeed often reported for older adults. Our findings suggest that these  
514 behavioral patterns result from an overall increased neural similarity.

515 Surprisingly, although for older adults items that were successfully learned also showed  
516 higher pattern similarity, we did not identify this beneficial effect of pattern similarity in  
517 young adults. Given that most of the studies that reported this effect in young adult samples  
518 tested recognition memory (Davis et al., 2014; LaRocque et al., 2013; Lu et al., 2015; Ye et  
519 al., 2016), the benefit may be less pronounced in (cued) recall tasks (but compare (Wagner



520 et al., 2016) who used a picture–location association task). Whereas a sense of familiarity as  
521 a consequence of high pattern similarity (Davis et al., 2014; Gillund and Shiffrin, 1984) can  
522 be sufficient for successful recognition, recall typically requires retrieval of specific details of  
523 the studied items ( Craik and Tulving, 1975). Therefore, the beneficial effects of high pattern  
524 similarity may be identified more easily in pure recognition memory tasks and/or participant  
525 groups who base their mnemonic decisions more strongly on familiarity signals, such as older  
526 adults.

527 The observed age group differences are in line with previous suggestions that external sti-  
528 muli exert a stronger drive on neural processing in older than in younger adults (Lindenberger  
529 and Mayr, 2014; Sander et al., 2012; Werkle-Bergner et al., 2012). In line with the “load-shift”  
530 model of executive functioning in aging (Velanova et al., 2007), the high, externally trigge-  
531 red similarity of scene–word pairs may have helped older adults to memorize pairs based on  
532 familiarity. At the same time it may have impaired their ability to form differentiated mne-  
533 monic representations early on. The resulting burden on late selection processes might have  
534 impaired older adults’ ability to engage elaboration mechanisms supporting the formation of  
535 distinctive memories. By contrast, the advantage of reduced similarity in younger adults may  
536 hint at their ability to engage elaborative mechanisms supporting future recall of detailed  
537 mnemonic information, as observed in the off-diagonal effect. In sum, we suggest that older  
538 adults’ advantage of high between-pair representational similarity early in the trial may stem  
539 from a reliance on familiarity-based remembering, while younger adults exploited more recall-  
540 based strategies, capitalizing on a higher capacity to form discrete representations later in  
541 the trial. We would like to speculate that the benefit of distinct neural activation patterns is  
542 especially prominent in the deployed task, in which participants were explicitly instructed to  
543 form very distinct mental images of the corresponding scene–word pair. Although older adults  
544 were extensively trained in using the imagery technique of forming salient mental images that  
545 integrate the associated picture and word, the post-encoding strategy questionnaire showed  
546 that they utilized this strategy less frequently than young adults. This may explain their  
547 lower recall performance despite having studied fewer pairs and having more opportunity to  
548 rehearse them. This conjecture is supported by previous research showing that older adults  
549 continue to use other mnemonic strategies even though they have learned about the benefits

550 of imagery (Hertzog et al., 2012).

551 So far, the prevailing available evidence on the relationship between representational simi-  
552 larity and memory performance has been based on fMRI studies and therefore lacks insights  
553 into the temporal dynamics of pattern similarity during the formation of memory represen-  
554 tations. Here, we demonstrate the advantage of dissociating different parts within the trial  
555 time course that reveal distinctions in the way representational similarity relates to memory  
556 performance of younger and older adults.

557 An open question is how between-item similarity links to item-specific representational  
558 stability (across item repetitions or between encoding and retrieval). Recent research suggests  
559 that representational stability benefits memory performance (Lu et al., 2015; Xue, 2018; Xue  
560 et al., 2010) and declines in old age (St-Laurent et al., 2014; Zheng et al., 2017). Understanding  
561 the mutual influences of between-item similarity and representational stability may be crucial  
562 to complete our comprehension of how memories are represented in the brain across the  
563 lifespan.

564 In summary, we provide critical new evidence that the often observed between-subject  
565 effect of generally higher similarity between neural representations in older adults does not  
566 predict their future memory success besides the fact that they perform worse than young  
567 adults who exhibit generally lower pattern similarity. Instead, on the within-subject level,  
568 older adults best remembered the items with the highest peak in pattern similarity early du-  
569 ring encoding. Moreover, we show that young adults benefited from eliciting distinct memory  
570 representations later during the encoding trial, which presumably reflects the implementation  
571 of the imagery strategy for scene-word binding. The work presented here extends our know-  
572 ledge about between-item pattern similarity as a memory-relevant representational property.  
573 In particular it shows how its relation to cognitive performance may change in the course of  
574 aging.

## 575 **References**

- 576 Allefeld C, Gørgen K, Haynes JD (2016) Valid population inference for information-based  
577 imaging: From the second-level t-test to prevalence inference. *NeuroImage* 141:378–392.
- 578 Allen M, Poggiali D, Whitaker K, Marshall TR, Kievit R (2018) Raincloud plots: a  
579 multi-platform tool for robust data visualization. *PeerJ Preprints* 6:e27137v1.
- 580 Baltes PB, Lindenberger U (1997) Emergence of a powerful connection between sensory  
581 and cognitive functions across the adult life span: a new window to the study of cognitive  
582 aging? *Psychology and Aging* 12:12–21.
- 583 Cai MB, Schuck NW, Pillow JW, Niv Y (2016) A Bayesian method for reducing bias in  
584 neural representational similarity analysis. In *Proceedings of the 30th International  
585 Conference on Neural Information Processing Systems*, pp. 4958–4966.
- 586 Caplan JB, Madsen JR, Raghavachari S, Kahana MJ (2001) Distinct patterns of brain  
587 oscillations underlie two basic parameters of human maze learning. *Journal of  
588 Neurophysiology* 86:368–380.
- 589 Carp J, Gmeindl L, Reuter-Lorenz PA (2010) Age differences in the neural representation  
590 of working memory revealed by multi-voxel pattern analysis. *Frontiers in Human  
591 Neuroscience* 4:217.
- 592 Carp J, Park J, Polk TA, Park DC (2011) Age differences in neural distinctiveness revealed  
593 by multi-voxel pattern analysis. *NeuroImage* 56:736–743.
- 594 Cichy RM, Pantazis D, Oliva A (2014) Resolving human object recognition in space and  
595 time. *Nature Neuroscience* 17:455–462.
- 596 Clark SE, Gronlund SD (1996) Global matching models of recognition memory: How the  
597 models match the data. *Psychonomic Bulletin & Review* 3:37–60.
- 598 Craik FIM, Tulving E (1975) Depth of processing and the retention of words in episodic  
599 memory. *Journal of Experimental Psychology: General* 104:268–294.

- 600 Davis T, Xue G, Love BC, Preston AR, Poldrack RA (2014) Global neural pattern  
601 similarity as a common basis for categorization and recognition memory. *Journal of*  
602 *Neuroscience* 34:7472–7484.
- 603 Fandakova Y, Sander MC, Grandy TH, Cabeza R, Werkle-Bergner M, Shing YL (2018)  
604 Age differences in false memory: The importance of retrieval monitoring processes and  
605 their modulation by memory quality. *Psychology and Aging* 33:119–133.
- 606 Folstein MF, Folstein SE, McHugh PR (1975) “Mini-mental state”: A practical method for  
607 grading the cognitive state of patients for the clinician. *Journal of Psychiatric*  
608 *Research* 12:189–198.
- 609 Gillund G, Shiffrin RM (1984) A retrieval model for both recognition and recall.  
610 *Psychological Review* 91:1–67.
- 611 Goh JO, Suzuki A, Park DC (2010) Reduced neural selectivity increases fMRI adaptation  
612 with age during face discrimination. *NeuroImage* 51:336–344.
- 613 Hertzog C, Price J, Dunlosky J (2012) Age differences in the effects of  
614 experimenter-instructed versus self-generated strategy use. *Experimental aging*  
615 *research* 38:42–62.
- 616 Hintzman DL (1988) Judgments of frequency and recognition memory in a multiple-trace  
617 memory model. *Psychological Review* 95:528–551.
- 618 Jung TP, Makeig S, Humphries C, Lee TW, McKeown MJ, Iragui V, Sejnowski TJ (2000)  
619 Removing electroencephalographic artifacts by blind source separation.  
620 *Psychophysiology* 37:163–178.
- 621 Kerrén C, Linde-Domingo J, Hanslmayr S, Wimber M (2018) An optimal oscillatory phase  
622 for pattern reactivation during memory retrieval. *Current Biology* 28:3383–3392.
- 623 King JR, Dehaene S (2014) Characterizing the dynamics of mental representations: The  
624 temporal generalization method. *Trends in Cognitive Sciences* 18:203–210.

- 625 Koen JD, Hauck N, Rugg MD (2019) The relationship between age, neural differentiation,  
626 and memory performance. *Journal of Neuroscience* 39:149–162.
- 627 Kosciessa JQ, Grandy TH, Garrett DD, Werkle-Bergner M (2018) Single-trial  
628 characterization of neural rhythms: potentials and challenges. *bioRxiv* doi:10.1101/356089.
- 629 Koutstaal W, Schacter DL (1997) Gist-based false recognition of pictures in older and  
630 younger adults. *Journal of Memory and Language* 37:555–583.
- 631 Koutstaal W, Schacter DL, Brenner C (2001) Dual task demands and gist-based false  
632 recognition of pictures in younger and older adults. *Journal of Memory and*  
633 *Language* 44:399–426.
- 634 Kriegeskorte N, Mur M, Bandettini P (2008) Representational similarity analysis -  
635 connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience* 2:4.
- 636 LaRocque KF, Smith ME, Carr VA, Witthoft N, Grill-Spector K, Wagner AD (2013)  
637 Global similarity and pattern separation in the human medial temporal lobe predict  
638 subsequent memory. *Journal of Neuroscience* 33:5466–5474.
- 639 Li SC, Lindenberger U, Hommel B, Aschersleben G, Prinz W, Baltes PB (2004)  
640 Transformations in the couplings among intellectual abilities and constituent cognitive  
641 processes across the life span. *Psychological Science* 15:155–163.
- 642 Li SC, Lindenberger U, Sikstrom S (2001) Aging cognition: From neuromodulation to  
643 representation. *Trends in Cognitive Sciences* 5:479–486.
- 644 Light LL, Prull MW, La Voie DJ, Healy MR (2000) Dual-process theories of memory in  
645 old age. In *Debates in psychology. Models of cognitive aging* (Perfect TJ, Maylor EA, ed),  
646 pp. 238–300. Oxford University Press, New York, NY, US.
- 647 Lindenberger U, Mayr U (2014) Cognitive aging: Is there a dark side to environmental  
648 support? *Trends in Cognitive Sciences* 18:7–15.
- 649 Lu Y, Wang C, Chen C, Xue G (2015) Spatiotemporal neural pattern similarity supports  
650 episodic memory. *Current Biology* 25:780–785.

- 651 Maris E, Oostenveld R (2007) Nonparametric statistical testing of EEG- and MEG-data.  
652 *Journal of Neuroscience Methods* 164:177–190.
- 653 Michelmann S, Bowman H, Hanslmayr S (2016) The temporal signature of memories:  
654 Identification of a general mechanism for dynamic memory replay in humans. *PLoS*  
655 *Biology* 14:e1002528.
- 656 Michelmann S, Bowman H, Hanslmayr S (2018) Replay of stimulus-specific temporal  
657 patterns during associative memory formation. *Journal of Cognitive*  
658 *Neuroscience* 30:1577–1589.
- 659 Muehlroth BE, Sander MC, Fandakova Y, Grandy TH, Rasch B, Shing YL,  
660 Werkle-Bergner M (in press) Precise slow oscillation-spindle coupling promotes memory  
661 consolidation in younger and older adults. *Scientific Reports* .
- 662 Nolan H, Whelan R, Reilly RB (2010) FASTER: Fully automated statistical thresholding  
663 for EEG artifact rejection. *Journal of Neuroscience Methods* 192:152–162.
- 664 Oostenveld R, Fries P, Maris E, Schoffelen JM (2011) FieldTrip: Open source software for  
665 advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational*  
666 *Intelligence and Neuroscience* 2011:156869.
- 667 Paller KA, Wagner AD (2002) Observing the transformation of experience into memory.  
668 *Trends in Cognitive Sciences* 6:93–102.
- 669 Park DC, Polk TA, Park R, Minear M, Savage A, Smith MR (2004) Aging reduces neural  
670 specialization in ventral visual cortex. *Proceedings of the National Academy of Sciences of*  
671 *the United States of America* 101:13091–13095.
- 672 Park J, Carp J, Hebrank A, Park DC, Polk TA (2010) Neural specificity predicts fluid  
673 processing ability in older adults. *Journal of Neuroscience* 30:9253–9259.
- 674 Park J, Carp J, Kennedy KM, Rodrigue KM, Bischof GN, Huang CM, Rieck JR, Polk TA,  
675 Park DC (2012) Neural broadening or neural attenuation? Investigating age-related  
676 dedifferentiation in the face network in a large lifespan sample. *Journal of*  
677 *Neuroscience* 32:2154–2158.

- 678 Payer D, Marshuetz C, Sutton B, Hebrank A, Welsh RC, Park DC (2006) Decreased  
679 neural specialization in old adults on a working memory task. *Neuroreport* 17:487–491.
- 680 Perrin F, Pernier J, Bertrand O, Echallier JF (1989) Spherical splines for scalp potential  
681 and current density mapping. *Electroencephalography and Clinical*  
682 *Neurophysiology* 72:184–187.
- 683 Prull MW, Dawes LLC, Martin III AM, Rosenberg HF, Light LL (2006) Recollection and  
684 familiarity in recognition memory: Adult age differences and neuropsychological test  
685 correlates. *Psychology and Aging* 21:107–118.
- 686 Sander MC, Fandakova Y, Grandy TH, Shing YL, Werkle-Bergner M (2019) Oscillatory  
687 mechanisms of successful memory formation in younger and older adults are related to  
688 structural integrity. *BioRxiv* .
- 689 Sander MC, Werkle-Bergner M, Lindenberger U (2012) Amplitude modulations and  
690 inter-trial phase stability of alpha-oscillations differentially reflect working memory  
691 constraints across the lifespan. *NeuroImage* 59:646–654.
- 692 Schönauer M, Alizadeh S, Jamalabadi H, Abraham A, Pawlizki A, Gais S (2017) Decoding  
693 material-specific memory reprocessing during sleep in humans. *Nature*  
694 *Communications* 8:15404.
- 695 Shing YL, Rodrigue KM, Kennedy KM, Fandakova Y, Bodammer N, Werkle-Bergner M,  
696 Lindenberger U, Raz N (2011) Hippocampal subfield volumes: Age, vascular risk, and  
697 correlation with associative memory. *Frontiers in Aging Neuroscience* 3:2.
- 698 St-Laurent M, Abdi H, Bondad A, Buchsbaum BR (2014) Memory reactivation in healthy  
699 aging: Evidence of stimulus-specific dedifferentiation. *Journal of*  
700 *Neuroscience* 34:4175–4186.
- 701 St-Laurent M, Abdi H, Burianová H, Grady CL (2011) Influence of aging on the neural  
702 correlates of autobiographical, episodic, and semantic memory retrieval. *Journal of*  
703 *Cognitive Neuroscience* 23:4150–4163.

- 704 Staresina BP, Michelmann S, Bonnefond M, Jensen O, Axmacher N, Fell J (2016)  
705 Hippocampal pattern completion is linked to gamma power increases and alpha power  
706 decreases during recollection. *eLife* 5:e17397.
- 707 Tun PA, Wingfield A, Rosen MJ, Blanchard L (1998) Response latencies for false  
708 memories: gist-based processes in normal aging. *Psychology and Aging* 13:230–241.
- 709 Velanova K, Lustig C, Jacoby LL, Buckner RL (2007) Evidence for frontally mediated  
710 controlled processing differences in older adults. *Cerebral Cortex* 17:1033–1046.
- 711 Visser RM, Scholte HS, Beemsterboer T, Kindt M (2013) Neural pattern similarity  
712 predicts long-term fear memory. *Nature Neuroscience* 16:388–390.
- 713 Wagner IC, van Buuren M, Bovy L, Fernandez G (2016) Parallel engagement of regions  
714 associated with encoding and later retrieval forms durable memories. *Journal of*  
715 *Neuroscience* 36:7985–7995.
- 716 Werkle-Bergner M, Freunberger R, Sander MC, Lindenberger U, Klimesch W (2012)  
717 Inter-individual performance differences in younger and older adults differentially relate to  
718 amplitude modulations and phase stability of oscillations controlling working memory  
719 contents. *NeuroImage* 60:71–82.
- 720 Whitten TA, Hughes AM, Dickson CT, Caplan JB (2011) A better oscillation detection  
721 method robustly extracts EEG rhythms across brain state changes: The human alpha  
722 rhythm as a test case. *NeuroImage* 54:860–874.
- 723 Wilson IA, Gallagher M, Eichenbaum H, Tanila H (2006) Neurocognitive aging: prior  
724 memories hinder new hippocampal encoding. *Trends in Neurosciences* 29:662–670.
- 725 Xue G (2018) The neural representations underlying human episodic memory. *Trends in*  
726 *Cognitive Sciences* 22:544–561.
- 727 Xue G, Dong Q, Chen C, Lu Z, Mumford JA, Poldrack RA (2010) Greater neural pattern  
728 similarity across repetitions is associated with better memory. *Science* 330:97–101.



- 729 Yassa MA, Mattfeld AT, Stark SM, Stark CEL (2011) Age-related memory deficits linked  
730 to circuit-specific disruptions in the hippocampus. *Proceedings of the National Academy of*  
731 *Sciences of the United States of America* 108:8873–8878.
- 732 Ye Z, Zhu B, Zhuang L, Lu Z, Chen C, Xue G (2016) Neural global pattern similarity  
733 underlies true and false memories. *Journal of Neuroscience* 36:6792–6802.
- 734 Yonelinas AP (2002) The nature of recollection and familiarity: A review of 30 years of  
735 research. *Journal of Memory and Language* 46:441–517.
- 736 Zhang H, Fell J, Staresina BP, Weber B, Elger CE, Axmacher N (2015) Gamma power  
737 reductions accompany stimulus-specific representations of dynamic events. *Current*  
738 *Biology* 25:635–640.
- 739 Zheng L, Gao Z, Xiao X, Ye Z, Chen C, Xue G (2017) Reduced fidelity of neural  
740 representation underlies episodic memory decline in normal aging. *Cerebral*  
741 *Cortex* 28:2283–2296.