

1 **The hippocampus shows an own-age bias during unfamiliar face viewing**

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24

Abstract

25 The present study investigated the neural correlates of the own-age bias for face recognition in a
26 repetition suppression paradigm. Healthy young and older adults viewed upright and inverted unfamiliar
27 faces. Some of the upright faces were repeated following one of two delays (lag 0 or lag 11). Repetition
28 suppression effects were observed in bilateral fusiform cortex. However, there were no significant
29 effects indicating an own-age bias in repetition suppression. The absence of these effects is arguably
30 inconsistent with perceptual expertise accounts of own-age biases in face processing. By contrast, the
31 right anterior hippocampus showed an own-age bias (greater activity for own- than other-age faces)
32 when viewing an unfamiliar face for the first time. Given the importance of the hippocampus for
33 episodic memory encoding, we conjecture that the increased hippocampal activity for own-age relative
34 to other-age faces reflects differential engagement of neural processes supporting the episodic
35 encoding of faces and might provide insight into the neural underpinnings of own-age biases in face
36 recognition memory.

37

Introduction

38 The ways in which we evaluate, attend to, and remember human faces are susceptible to own-
39 age biases (e.g., Bartlett and Fulton, 1991; Ebner, 2008; Wiese et al., 2008; Rhodes and Anastasi, 2012).
40 Notably, both young and older adults show better recognition memory for own-age faces (Rhodes and
41 Anastasi, 2012). These findings have motivated research that has demonstrated own-age biases in
42 neural correlates of face processing (e.g., Ebner et al., 2011a, 2011b, 2013; Neumann et al., 2015; Wiese
43 et al., 2008; Wolff et al., 2012; Ziaeи et al., 2019; for review, see Wiese et al., 2013). A growing body of
44 fMRI research aimed at identifying the neuroanatomical correlates of the own-age bias has reported
45 BOLD signal increases for own-age versus other-age faces in the amygdala, medial prefrontal cortex,
46 orbitofrontal cortex, and insula across a variety of conditions. (Ebner et al., 2013, 2011a; Wright et al.,
47 2008; Ziaeи et al., 2019; see also Golarai et al., 2017). Although the above studies did not report own-age
48 effects in the fusiform gyrus, a canonical face-processing region, Golarai et al. (2017) recently reported
49 such effects in the fusiform gyrus in both children (7-10 years) and young adults (18-40 years).

50 The present study had two goals. First, building on prior research, we investigated if own-age
51 biases are present in repetition suppression effects elicited by unfamiliar faces. Repeating a face elicits a
52 'repetition suppression' effect whereby the BOLD response is reduced for repeated compared to first
53 presentation faces (see Henson, 2016; Henson and Rugg, 2003). Repetition suppression in regions such
54 as the occipital and fusiform face areas are proposed to reflect modulation of processes contributing to
55 the identification of individual faces (Goh et al., 2010; Hermann et al., 2017). This proposal aligns with
56 perceptual expertise theories of the own-age bias arguing that own-age faces are processed more
57 efficiently and are better individuated than other-age faces due to more extensive experience with own-
58 age peers. Second, we aimed to conceptually replicate prior studies (Wright et al., 2008) by examining
59 own-age biases when viewing unfamiliar faces without employing a task that may induce strategy
60 differences between young and older adults.

61

Materials and Methods

Ethics Statement

63 This study was approved by Institutional Review Board of the University of Texas at Dallas and
64 University of Texas Southwestern Medical Center. All participants provided written informed consent
65 prior to participation.

Participants

67 A sample of 24 young and 26 older participants contributed to the analyses reported here.
68 Participants were recruited from the University of Texas at Dallas and the greater Dallas metropolitan
69 area and were financially compensated for their time (\$30/hour). The sample sizes were determined by
70 the requirements of a primary experiment in which the aim was to obtain usable data from 24 young

71 and 24 older adults for a memory encoding task (Koen et al., 2019). These were the largest samples that
72 could be accommodated given the resources available for the project. The higher number of participants
73 contributing to the analyses reported here results from the fact some participants were excluded from
74 the primary experiment but retained in the present study.

75 All participants were right-handed, reported having normal or corrected-to-normal vision and
76 had no contraindications to MRI scanning. Exclusion criteria included a history of cardiovascular disease
77 (other than treated hypertension), diabetes, psychiatric disorder, illness, or trauma affecting the central
78 nervous system, substance abuse, and self-reported current or recent use of psychotropic medication or
79 sleeping aids. All participants were considered cognitively normal as determined by performance on a
80 test battery (Table 1; for details of the battery see Koen et al., 2019). All participants scored 27 or more
81 on the Mini-Mental State Examination (MMSE; Folstein et al., 1975) and no more than 1.5 standard
82 deviations below age-normalized scores on any one memory measure or on two (or more) non-memory
83 measures. Data from an additional young adult male and one older adult male were excluded due to
84 excessive in-scanner motion (> 8 mm maximum frame-wise displacement) during the task.

85 **Materials and Procedure**

86 The critical stimuli comprised 208 faces from the CAL/PAL database (Ebner, 2008; Minear
87 and Park, 2004). All face stimuli were 640x480 pixels with a grey background. Half of the face
88 stimuli depicted younger adults (age range: 18-34 years) and half depicted older adults (age range: 60-
89 91 years). The 104 stimuli of each face age group were randomly assigned to the lag 0 repeat (24
90 faces), lag 11 repeat (24 faces), control (32 faces) and inverted (24 faces) conditions. The stimuli
91 were further split into two lists, with half of the stimuli from each of the face age by trial type
92 conditions. There were an equal number of male and females faces in each condition. An additional
93 8 images were used in a practice task completed outside of the scanner. Stimuli were presented to
94 participants via a mirror mounted to the head coil. Cogent software
95 (www.vislab.ucl.ac.uk/cogent_2000.php) as implemented in Matlab 2011b (www.mathworks.com)
96 was used for stimulus control and response logging.

97 The experimental procedure is depicted in Figure 1. Participants were shown a series of faces
98 (1 sec duration followed by a 1.25 sec white fixation cross) and were instructed to press a key with
99 their right index finger whenever an inverted face was presented. Speed was emphasized on the
100 button press to inverted faces. There were 48 null trials dispersed throughout the block to jitter the
101 stimuli, with no more than one null trial occurring consecutively. Responses were recorded until the
102 beginning of the next trial.

103 Each session of the task comprised 48 null trials and 152 face trials (80 first presentation
104 trials, 24 lag 0 repeats; 24 lag 11 repeats, 24 inverted faces; equally split across faces depicting young
105 and older adults). The decision to employ only two lags was driven by time constraints, the rather
106 limited number of stimuli, and our attempt to maximize the number of trials in 'short' and 'long'
107 repetition lags. Inverted faces were presented once only, and no more than two inverted trials
108 occurred in succession. Faces assigned to the repeat condition were presented twice with the
109 repetition occurring either on the immediately succeeding trial (lag 0) or after 11 intervening trials

110 (lag 11). Faces in the control condition were presented on only one occasion. Control faces and the
111 first presentations of repeated faces were collapsed into a single ‘first’ face condition.

112 **Behavioral Data Analysis**

113 The log-transformed reaction times to inverted face stimuli receiving a correct response were
114 submitted to a linear mixed model using the *mixed()* function from the *afex* package (Singmann et al.,
115 2021) in R (R Core Team, 2021). The model included fixed effect terms age group (young versus older),
116 face age congruency (own age versus other age), and their interaction. Same age faces were those faces
117 from the same age group as the participant (e.g., young faces were coded as same age faces for young
118 adults) whereas different age faces were those face stimuli depicting individuals not in the participants
119 age group (e.g., for young adults, older faces were coded as different age faces). The model included
120 random effects of participant, specifically a random intercept and random slope of face age congruency.
121 Degrees of freedom were estimated using the Satterthwaite (1946) approximation. Bayes factors for the
122 alterative (BF_{10}) hypothesis were computed using the *lmbf* function from the *BayesFactor*
123 package (Morey and Rouder, 2018) and *bayesfactor_inclusion* function from the *bayestestR* package
124 (Makowski et al., 2019).

125 **MRI Data Acquisition**

126 MRI data were acquired with a 3T Philips Achieva MRI scanner (Philips Medical Systems,
127 Andover, MA, USA) equipped with a 32-channel receiver head coil. Functional images were acquired
128 with a blood oxygenation level dependent (BOLD), T2*-weighted echoplanar imaging (EPI) sequence
129 (SENSE factor = 1.5, flip angle = 70°, 80 × 80 matrix, FOV = 240 mm × 240 mm, TR = 2000 ms, TE = 30 ms,
130 34 ascending slices, slice thickness = 3 mm, slice gap = 1 mm), and were oriented parallel to the AC-PC
131 line. Five “dummy” scans were acquired at the start of each fMRI session and discarded to allow for
132 equilibration of tissue magnetization. A total of 264 functional volumes were acquired during each of
133 the two task runs, for a total of 528 brain volumes. T1-weighted images (MPRAGE sequence, 240 × 240
134 matrix, 1 mm isotropic voxels) were acquired for anatomical reference. Note that this task was
135 completed prior to the encoding phase of a memory study that comprised object and scene images
136 (Koen et al., 2019).

137 **fMRI Data Preprocessing and Analysis**

138 The functional data were preprocessed with Statistical Parametric Mapping (SPM12, Wellcome
139 Department of Cognitive Neurology, London, UK) implemented in Matlab 2017b (The Mathworks, Inc.,
140 USA). The images were reoriented, subjected to a two-pass realignment procedure, whereby images
141 were initially realigned to the first image of a session and then realigned to the mean EPI image, and
142 then corrected for slice acquisition time differences using sinc interpolation with reference to the
143 middle slice. Finally, images were spatially normalized to a study specific EPI template (de Chastelaine et
144 al., 2011) and smoothed with an 8mm full-width at half-maximum kernel.

145 The fMRI data were analyzed with a two-stage random effects model. First level GLMs modeled
146 neural activity as a delta function convolved with a canonical HRF for the 8 event types formed by
147 crossing face age and the four item types (first, lag0 repeat, lag11 repeat, inverted face). The first level
148 GLM also included the 6 realignment parameters and session specific means as nuisance variables.

149 The second-level group analyses were performed by submitting the 8 first-level beta maps to a 2
150 (age group) by 8 (condition) mixed ANOVA using the factorial ANOVA module in SPM12. The 8 levels of
151 the condition factor were those described above for the first-level models, with one exception. Like the
152 analysis of the reaction time data, face age was coded as a face age congruency factor with own-age and
153 other-age faces. Planned contrasts were conducted to identify voxels showing significant effects of
154 repetition, face age congruency, and to examine whether these effects interacted with participant age
155 or lag. Additionally, effects of face inversion were examined. Effects were deemed significant if they
156 survived $p < .001$ with a cluster-wise correction ($p < .05$, FWE) based on Gaussian Random Field theory
157 or if the peak voxel of a cluster survived $p < .05$ FWE voxel-level correction. The rationale for using both
158 approaches was to avoid Type-II errors both for large clusters with (relatively) weak mean activation and
159 for more focal clusters with a strong peak response.

160 As noted in the Results, we further probed the whole-brain findings by extracting the mean beta
161 response from 5mm spheres centered on the peak effects. These values were subjected to mixed factor
162 ANOVAs using the JASP software (JASP Team, 2020). Bayes factors for effects favoring the alternative
163 (BF_{10}) hypothesis are reported for these follow-up analyses.

164 Results

165 Behavioral Data

166 Participants were accurate in identifying inverted faces ($\geq 98\%$) and very rarely false alarmed to
167 upright faces ($\leq .3\%$). The analysis of reaction times revealed null effects of age group, $F(1, 47.98) = 1.93$,
168 $p = .171$, partial- $\eta^2 = .04$, $BF_{10} = 0.693$, face age congruency, $F(1, 47.87) = 0.003$, $p = .958$, partial- $\eta^2 = .00$,
169 $BF_{10} = 0.069$, and the interaction between the two variables, $F(1, 47.87) = 1.36$, $p = .250$, partial- $\eta^2 = .03$,
170 $BF_{10} = 0.134$.

171 Face Inversion Effects

172 We first examined the effects of face inversion by contrasting the activity elicited by upright
173 (first presentation only) and inverted faces. There was an increase in the BOLD signal for inverted
174 relative to upright faces across a wide swath of the cortex with peaks primarily in the frontal and
175 temporal cortices, as well as the cerebellum. No voxels survived our statistical thresholds when looking
176 for voxels showing elevated BOLD signal for upright compared to inverted faces. An additional contrast
177 examining age differences in the face inversion effect identified clusters in the right pre- and post-
178 central gyri showing smaller face inversion effects for older relative to younger adults. No significant

179 clusters demonstrated an interaction between face inversion and face age congruency (own vs. other
180 age faces).

181 **Repetition Suppression**

182 The first planned contrast identified voxels showing effects of face repetition. No clusters
183 demonstrated significant repetition enhancement effects. However, clusters showing significant
184 repetition suppression effects were identified in bilateral fusiform gyrus (Table 2 and Figure 2A-B). The
185 suppression effects did not differ significantly between young and older adults, between repetition lags,
186 or between own-age and other-age faces according to follow-up analyses that exclusively masked the
187 repetition suppression contrast with interaction terms involving repetition and the other factors
188 (exclusive mask threshold set at $p < .10$, uncorrected). The absence of age group differences in
189 repetition suppression effects in the fusiform gyrus is consistent with some prior fMRI findings (Goh et
190 al., 2010). However, the lack of an effect of repetition lag is inconsistent with previous research on face
191 repetition (Henson et al., 2000; for related findings, see Nagy and Rugg, 1989); this inconsistency might
192 be due to the relatively short lag in our 'long-lag' condition (maximum of 11 intervening trials before a
193 face repeat) compared to prior studies.

194 We next conducted planned contrasts aimed at identifying voxels where face repetition effects
195 differed in magnitude between young and older adults (i.e., regions showing an Age Group by Repetition
196 Interaction, collapsed across lag). This contrast identified a cluster in the left interior temporal gyrus that
197 showed repetition suppression effects in older but not young adults (Figure 2C-D). Repetition
198 suppression indices (i.e., first minus repeat) extracted from a 5mm sphere centered on the peak voxel
199 manifesting the interaction revealed a significant repetition suppression effect for repeated faces in
200 older adults, $t(25) = 3.24$, $p = .003$, Cohen's $d = 0.635$, $BF_{10} = 11.93$, but repetition *enhancement* for
201 repeated faces in the younger adults, $t(23) = 2.85$, $p = .009$, Cohen's $d = 0.582$, $BF_{10} = 5.27$.

202 A further planned contrast found no evidence that face repetition effects interacted with
203 repetition lag or face-age congruency.

204 **Own-Age biases during novel face viewing**

205 We next conducted a planned contrast between the first presentation trials of upright, own-age
206 and other-age faces to identify voxels showing an own-age bias. Repeated faces were excluded to
207 mitigate the potentially confounding effects of familiarity or other repetition-related processes on own-
208 age bias effects, allowing us essentially to mirror the contrast employed to identify own-race effects
209 reported by Brown et al. (2017). The above-described contrast identified a cluster of voxels
210 demonstrating a face age congruency effect in the right anterior hippocampus (Table 2 and Figure 3).
211 The cluster demonstrated elevated BOLD activity for own-age relative to other-age faces. This effect did
212 not significantly differ in magnitude between young and older adults based on the outcome of an
213 exclusive mask (at $p < .10$) of the above contrast with the interaction contrast between age group and

214 face age congruency. Converging with this finding, a conjunction analysis performed by inclusively
215 masking the own-age versus other-age contrasts conducted separately for young and older adults (each
216 thresholded at $p < .01$) revealed a cluster that overlapped with that identified in the initial analyses.

217 Follow-up analyses investigated whether face repetition moderated the own-age bias effect
218 observed in the right anterior hippocampus. We conducted a 2 (age group) by 3 (face condition) by 2
219 (face age congruency) mixed ANOVA on beta estimates for the three upright face trial types (first, lag 0,
220 and lag 11) from a 5mm sphere centered on the peak of right anterior hippocampus cluster ($x = 22$, $y = -$
221 10, $z = -24$). Note that because the main effect of face age congruency is not independent of the
222 contrast used to define the original face age effect, the effect is circular and therefore not considered
223 here. The ANOVA revealed null effects for the two-way interaction between face age congruency and
224 age group, $F(1, 47) = 1.55$, $p = .219$, partial- $\eta^2 = .143$, $BF_{10} = 0.308$, for face condition, $F(1.85, 86.85) =$
225 1.21 , $p = .288$, partial- $\eta^2 = .025$, $BF_{10} = 0.147$, and for the three-way interaction, $F(1.98, 92.93) = 0.645$, p
226 $= .527$, partial- $\eta^2 = .143$, $BF_{10} = 0.176$. It is noteworthy that the Bayes factors provided moderate to
227 strong evidence favoring null effects ($BF_{10} < .333$) according to the definitions proposed by Jeffreys
228 (Jeffreys, 1939; Kass and Raftery, 1995). In short, these null findings suggest that none of factors
229 included in the ANOVA significantly moderated the own-age bias effect observed in the right anterior
230 hippocampus.

231 **Discussion**

232 The present study examined whether face age moderated repetition suppression effects elicited
233 by unfamiliar faces and whether there were any own-age biases in neural activity when viewing first
234 presentations of unfamiliar faces. There were three main findings. First, although we identified
235 significant age-invariant repetition suppression effects in bilateral fusiform gyrus, we did not identify any
236 clusters where suppression effects demonstrated an own-age bias. These null findings are arguably
237 inconsistent with perceptual expertise accounts of the own-age bias (Tanaka and Pierce, 2009;
238 Valentine, 1991; Wiese et al., 2013). Such accounts propose that own-age faces are more efficiently
239 processed than other-age faces due to more extensive experience with own-age peers. If face repetition
240 suppression effects reflect modulation of processes contributing to the identification of individual faces
241 (Hermann et al., 2017), then we might expect that own-age faces would elicit a greater suppression
242 effect than other-age faces, which we did not observe. However, one limitation of the present design is
243 that we only examined repetition effects for identical repeats and did not include a condition that could
244 examine 'release from suppression' (e.g., Goh et al., 2010; Reggev et al., 2020). Recently, Reggev et al.
245 (2020) argued in favor of a perceptual expertise account of own-race biases based on findings of greater
246 release from suppression for own-race relative to other-race faces. Future research employing designs
247 that allow measurement of release from suppression is needed to pursue this issue.

248 Second, we identified a cluster in left inferior temporal cortex that demonstrated repetition
249 suppression effects for older adults but repetition enhancement effects in young adults. This region has

250 been previously reported to demonstrate repetition suppression effects for familiar (e.g., yellow
251 banana) but not novel concepts (e.g., purple banana) (Reggev et al., 2016). Given that familiar concepts
252 are accrued through experience, it is possible that the present interaction reflects age group differences
253 in exposure to faces (Golarai et al., 2017; for a related discussion, see Koen and Rugg, 2019). By this
254 argument, the left inferior temporal gyrus is a region that is especially sensitive to cumulative lifetime
255 experience with a perceptual category such as faces. Future research will be needed to test the validity
256 of this proposal.

257 Lastly, we observed an own-age bias for the first presentation of unfamiliar faces in the right
258 anterior hippocampus. Both young and older adults showed elevated BOLD signal for own-age relative
259 to other-age faces. We stress that this finding of an own-age bias in the hippocampus requires
260 replication within an experimental task that allows for a behavioral assay of own-age bias, such as
261 recognition memory. Nonetheless, given the well-established role of the hippocampus in memory
262 encoding (Eichenbaum et al., 2007; Kim, 2011), we conjecture that the present finding is relevant to the
263 own-age bias that has been reported for recognition memory performance (Rhodes and Anastasi, 2012).
264 There are several possible accounts of this finding, which are not mutually exclusive. One possibility is
265 that it is easier to bind previously acquired personal or semantic knowledge about familiar individuals to
266 unfamiliar own-age than to other-age faces. Alternately, own-age faces may more readily attract
267 attention to discriminating facial features than other-age faces, in turn modulating encoding-related
268 hippocampal activity (Aly and Turk-Browne, 2015, 2017; Uncapher and Rugg, 2009). Another possibility
269 is that the present hippocampal effect reflects the formation of face representations with higher fidelity
270 than representations of other-age faces (for reviews, see Ekstrom and Yonelinas, 2020; Yonelinas, 2013).
271 Future studies that link the own-age bias in recognition memory to hippocampal effects promise to shed
272 light on these and other possibilities.

273 There are limitations to this study. First, we did not replicate prior findings of own-age biases in
274 regions such as the prefrontal cortex, insula, amygdala, and fusiform gyrus (Ebner et al., 2013, 2011a;
275 Golarai et al., 2017; Wright et al., 2008; Ziaeи et al., 2019). The reasons for this replication failure are
276 unclear. One possibility is that task demands (e.g., passive viewing versus emotion recognition)
277 contributed to the differences between the present and prior findings. Second, the own-age bias
278 observed in the hippocampus did not have a behavioral correlate. While this is a potential limitation, we
279 note that prior studies have reported own-age biases in neural data in the absence of analogous findings
280 in behavioral data (e.g., Ebner et al., 2013; Ziaeи et al., 2019).

281 In conclusion, we did not find evidence for own-age biases in face repetition suppression effects,
282 which is arguably inconsistent with perceptual expertise accounts of the own-age bias. Of importance, a
283 cluster in the right anterior hippocampus showed an own-age bias to the first presentation of unfamiliar
284 faces in both young and older adults, which we speculate to be related to own-age biases in memory.

285

References

286 Aly M, Turk-Browne NB. 2017. How Hippocampal Memory Shapes, and Is Shaped by, Attention In:
287 Hannula DE, Duff MC, editors. *The Hippocampus from Cells to Systems*. Cham: Springer
288 International Publishing. pp. 369–403. doi:10.1007/978-3-319-50406-3_12

289 Aly M, Turk-Browne NB. 2015. Attention Stabilizes Representations in the Human Hippocampus.
290 *Cerebral Cortex* bhv041. doi:10.1093/cercor/bhv041

291 Bartlett JC, Fulton A. 1991. Familiarity and recognition of faces in old age. *Memory & Cognition* **19**:229–
292 238. doi:10.3758/BF03211147

293 Brown TI, Uncapher MR, Chow TE, Eberhardt JL, Wagner AD. 2017. Cognitive control, attention, and the
294 other race effect in memory. *PLOS ONE* **12**:e0173579. doi:10.1371/journal.pone.0173579

295 de Chastelaine M, Wang TH, Minton B, Muftuler LT, Rugg MD. 2011. The Effects of Age, Memory
296 Performance, and Callosal Integrity on the Neural Correlates of Successful Associative Encoding.
297 *Cerebral Cortex* **21**:2166–2176. doi:10.1093/cercor/bhq294

298 Ebner NC. 2008. Age of face matters: Age-group differences in ratings of young and old faces. *Behav Res*
299 **40**:130–136. doi:10.3758/brm.40.1.130

300 Ebner NC, Gluth S, Johnson MR, Raye CL, Mitchell KJ, Johnson MK. 2011a. Medial prefrontal cortex
301 activity when thinking about others depends on their age. *Neurocase* **17**:260–269.
302 doi:10.1080/13554794.2010.536953

303 Ebner NC, He Y, Fichtentholtz HM, McCarthy G, Johnson MK. 2011b. Electrophysiological correlates of
304 processing faces of younger and older individuals. *Soc Cogn Affect Neurosci* **6**:526–535.
305 doi:10.1093/scan/nsq074

306 Ebner NC, Johnson MR, Rieckmann A, Durbin KA, Johnson MK, Fischer H. 2013. Processing own-age vs.
307 other-age faces: Neuro-behavioral correlates and effects of emotion. *NeuroImage* **78**:363–371.
308 doi:10.1016/j.neuroimage.2013.08.040

309 Eichenbaum H, Yonelinas AP, Ranganath C. 2007. The Medial Temporal Lobe and Recognition Memory.
310 *Annual Review of Neuroscience* **30**:123–152. doi:10.1146/annurev.neuro.30.051606.094328

311 Ekstrom AD, Yonelinas AP. 2020. Precision, binding, and the hippocampus: Precisely what are we talking
312 about? *Neuropsychologia* **138**:107341. doi:10.1016/j.neuropsychologia.2020.107341

313 Goh JO, Suzuki A, Park DC. 2010. Reduced neural selectivity increases fMRI adaptation with age during
314 face discrimination. *NeuroImage* **51**:336–344. doi:10.1016/j.neuroimage.2010.01.107

315 Golarai G, Liberman A, Grill-Spector K. 2017. Experience Shapes the Development of Neural Substrates
316 of Face Processing in Human Ventral Temporal Cortex. *Cerebral Cortex* **27**. doi:10/gmr7x9

317 Henson R, Shallice T, Dolan R. 2000. Neuroimaging Evidence for Dissociable Forms of Repetition Priming.
318 *Science* **287**:1269–1272. doi:10.1126/science.287.5456.1269

319 Henson RN. 2016. Repetition suppression to faces in the fusiform face area: A personal and dynamic
320 journey. *Cortex, Special Issue:Repetition suppression-an integrative view* **80**:174–184.
321 doi:10.1016/j.cortex.2015.09.012

322 Henson RNA, Rugg MD. 2003. Neural response suppression, haemodynamic repetition effects, and
323 behavioural priming. *Neuropsychologia* **41**:263–270. doi:10.1016/s0028-3932(02)00159-8

324 Hermann P, Grotheer M, Kovács G, Vidnyánszky Z. 2017. The relationship between repetition
325 suppression and face perception. *Brain Imaging and Behavior* **11**:1018–1028. doi:10.1007/s11682-
326 016-9575-9

327 JASP Team. 2020. JASP (Version 0.14.1) [Computer software].

328 Jeffreys J. 1939. Theory of probability, 1st ed. Oxford, UK: Oxford University Press.

329 Kass RE, Raftery AE. 1995. Bayes Factors. *Journal of the American Statistical Association* **90**:773–795.
330 doi:10/gdnbw3

331 Kim H. 2011. Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74
332 fMRI studies. *NeuroImage* **54**:2446–2461. doi:10.1016/j.neuroimage.2010.09.045

333 Koen JD, Hauck N, Rugg MD. 2019. The relationship between age, neural differentiation, and memory
334 performance. *Journal of Neuroscience* **39**:149–162. doi:<https://doi.org/10.1523/JNEUROSCI.1498-18.2018>

336 Koen JD, Rugg MD. 2019. Neural dedifferentiation in the aging brain. *Trends in Cognitive Sciences*
337 **23**:547–559. doi:10.1016/j.tics.2019.04.012

338 Makowski D, Ben-Shachar MS, Lüdecke D. 2019. bayestestR: Describing Effects and their Uncertainty,
339 Existence and Significance within the Bayesian Framework. *Journal of Open Source Software*
340 **4**:1541. doi:10.21105/joss.01541

341 Minear M, Park DC. 2004. A lifespan database of adult facial stimuli. *Behavior Research Methods,
342 Instruments, & Computers* **36**:630–633. doi:10.3758/bf03206543

343 Morey RD, Rouder JN. 2018. BayesFactor: Computation of bayes factors for common designs (manual).

344 Nagy ME, Rugg MD. 1989. Modulation of Event-Related Potentials by Word Repetition: The Effects of
345 Inter-Item Lag. *Psychophysiology* **26**:431–436. doi:<https://doi.org/10.1111/j.1469-8986.1989.tb01946.x>

347 Neumann MF, End A, Luttmann S, Schweinberger SR, Wiese H. 2015. The own-age bias in face memory
348 is unrelated to differences in attention—Evidence from event-related potentials. *Cognitive, Affective, & Behavioral Neuroscience* **15**:180–194. doi:[10.3758/s13415-014-0306-7](https://doi.org/10.3758/s13415-014-0306-7)

350 R Core Team. 2021. R: A language and environment for statistical computing (manual). Vienna, Austria.

351 Reggev N, Bein O, Maril A. 2016. Distinct Neural Suppression and Encoding Effects for Conceptual
352 Novelty and Familiarity. *Journal of Cognitive Neuroscience* **28**:1455–1470.
353 doi:[10.1162/jocn_a_00994](https://doi.org/10.1162/jocn_a_00994)

354 Reggev N, Brodie K, Cikara M, Mitchell JP. 2020. Human face-selective cortex does not distinguish
355 between members of a racial outgroup. *eNeuro*. doi:[10.1523/ENEURO.0431-19.2020](https://doi.org/10.1523/ENEURO.0431-19.2020)

356 Rhodes MG, Anastasi JS. 2012. The own-age bias in face recognition: A meta-analytic and theoretical
357 review. *Psychological Bulletin* **138**:146–174. doi:[10.1037/a0025750](https://doi.org/10.1037/a0025750)

358 Satterthwaite FE. 1946. An Approximate Distribution of Estimates of Variance Components. *Biometrics Bulletin* **2**:110. doi:[10.2307/3002019](https://doi.org/10.2307/3002019)

360 Singmann H, Bolker B, Westfall J, Aust F, Ben-Shachar MS. 2021. afex: Analysis of factorial experiments
361 (manual).

362 Tanaka JW, Pierce LJ. 2009. The neural plasticity of other-race face recognition. *Cognitive, Affective, & Behavioral Neuroscience* **9**:122–131. doi:[10/dwn4dz](https://doi.org/10/dwn4dz)

364 Uncapher MR, Rugg MD. 2009. Selecting for Memory? The Influence of Selective Attention on the
365 Mnemonic Binding of Contextual Information. *Journal of Neuroscience* **29**:8270–8279.
366 doi:[10.1523/jneurosci.1043-09.2009](https://doi.org/10.1523/jneurosci.1043-09.2009)

367 Valentine T. 1991. A Unified Account of the Effects of Distinctiveness, Inversion, and Race in Face
368 Recognition. *The Quarterly Journal of Experimental Psychology Section A* **43**:161–204.
369 doi:[10/c3mcjt](https://doi.org/10/c3mcjt)

370 Wiese H, Komes J, Schweinberger SR. 2013. Ageing faces in ageing minds: A review on the own-age bias
371 in face recognition. *Visual Cognition* **21**:1337–1363. doi:[10.1080/13506285.2013.823139](https://doi.org/10.1080/13506285.2013.823139)

372 Wiese H, Schweinberger SR, Hansen K. 2008. The age of the beholder: ERP evidence of an own-age bias
373 in face memory. *Neuropsychologia* **46**:2973–2985. doi:[10.1016/j.neuropsychologia.2008.06.007](https://doi.org/10.1016/j.neuropsychologia.2008.06.007)

374 Wolff N, Wiese H, Schweinberger SR. 2012. Face recognition memory across the adult life span: Event-
375 related potential evidence from the own-age bias. *Psychology and Aging* **27**:1066–1081.
376 doi:10.1037/a0029112

377 Wright CI, Negreira A, Gold AL, Britton JC, Williams D, Feldman Barrett L. 2008. Neural correlates of
378 novelty and face–age effects in young and elderly adults. *NeuroImage* **42**:956–968.
379 doi:10.1016/j.neuroimage.2008.05.015

380 Yonelinas AP. 2013. The hippocampus supports high-resolution binding in the service of perception,
381 working memory and long-term memory. *Behavioural Brain Research* **254**:34–44.
382 doi:10.1016/j.bbr.2013.05.030

383 Ziae M, Persson J, Bonyadi MR, Reutens DC, Ebner NC. 2019. Amygdala functional network during
384 recognition of own-age vs. other-age faces in younger and older adults. *Neuropsychologia* **129**:10–
385 20. doi:10.1016/j.neuropsychologia.2019.107500

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

	Young Adults	Older Adults	<i>p</i> -value
N	24	26	
Age	23.04 (3.46)	69.19 (3.27)	
Sex (M/F)	12/12	14/12	
Education	15.92 (2.22)	16.96 (2.24)	.104
MMSE	29.54 (0.59)	29.35 (0.94)	.378
CVLT Short Delay – Free	13.08 (1.79)	10.38 (3.16)	< .001
CVLT Short Delay – Cued	13.67 (1.81)	11.67 (3.57)	.016
CVLT Long Delay – Free	13.54 (2.06)	10.23 (3.27)	< .001
CVLT Long Delay – Cued	14.12 (1.62)	11.92 (2.78)	.001
CVLT Recognition – Hits	15.42 (0.83)	15.00 (0.98)	.110
CVLT Recognition – False Alarms	0.46 (0.66)	3.08 (2.53)	< .001
Logical Memory I	30.62 (4.95)	26.00 (5.50)	.003
Logical Memory II	28.12 (5.78)	22.62 (6.03)	.002
Digit Span Total ¹	21.04 (4.53)	17.77 (2.55)	.004
SDMT	65.38 (13.99)	46.42 (7.74)	< .001
Trails A (secs)	21.43 (7.97)	31.55 (10.76)	< .001
Trails B (secs)	47.54 (19.53)	70.52 (24.87)	.002
F-A-S Total	48.29 (10.97)	45.50 (11.42)	.382
Category Fluency (Animals)	24.58 (5.67)	21.00 (4.66)	.020
WTAR (Raw)	41.42 (3.44)	43.08 (4.78)	.163
Raven's (List 1)	11.08 (.97)	9.19 (2.50)	.001
Visual Acuity (logMar) ²	-.11 (.10)	.06 (.11)	< .001

387 *Note.* Standard deviations are reported in parentheses. The *p*-values were obtained from unequal-
388 variance independent *t*-tests comparing young and older adults. ¹Digit span total equals the sum of
389 forward and backward span. ²Lower logMAR scores indicate better visual acuity. MMSE = Mini-
390 mental State Exam; CVLT = California Verbal Learning Test II; SDMT = Symbol-Digit Modalities
391 Test; WTAR = Wechsler Test of Adult Reading

392 **Table 2.** Regions showing effects of face repetition and age congruency.

Region	MNI Coordinates				Cluster size	Peak z
	x	y	z			
<i>Inverted > Novel ($p < 1e^{-10}$, FWE-corrected height threshold)</i>						
Cerebellum	24	-55	-28		14458	18.75
	-24	-58	-28			16.49
	-33	-55	-34			15.78
R. Insula/Inferior Frontal Gyrus	42	14	-7		914	13.87
	36	20	-1			13.76
	57	11	8			12.61
L. Insula/Inferior Frontal Gyrus	-42	2	5		704	12.80
	-60	8	29			12.39
	-33	20	2			11.67
R. Superior Frontal Gyrus	33	47	17		228	11.16
L. Superior Frontal Gyrus	-33	47	20		151	10.58
R. Middle Temporal Gyrus	51	-25	-13		1	8.34
<i>Age Group by Face Inversion Interaction (Older > Young Adults)</i>						
R. Postcentral Gyrus ^{a,b}	60	-7	32		318	4.77
L. Precentral Gyrus ^{a,b}	-54	-7	41		136	4.24
<i>Face Repetition Suppression (First > Repeat)</i>						
R. Fusiform Gyrus ^{a,b}	39	-43	-28		493	5.82

L. Fusiform Gyrus ^a	-39	-46	-28	328	4.20
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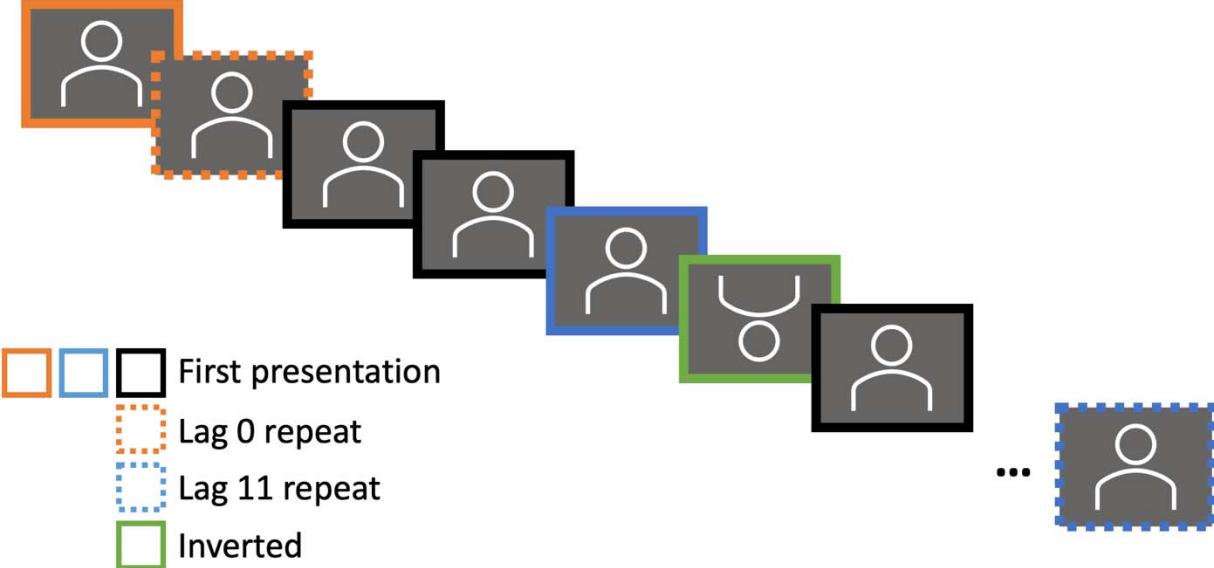
Age Group by Repetition Interaction (Older: Repetition Suppression, Young: Repetition Enhancement)

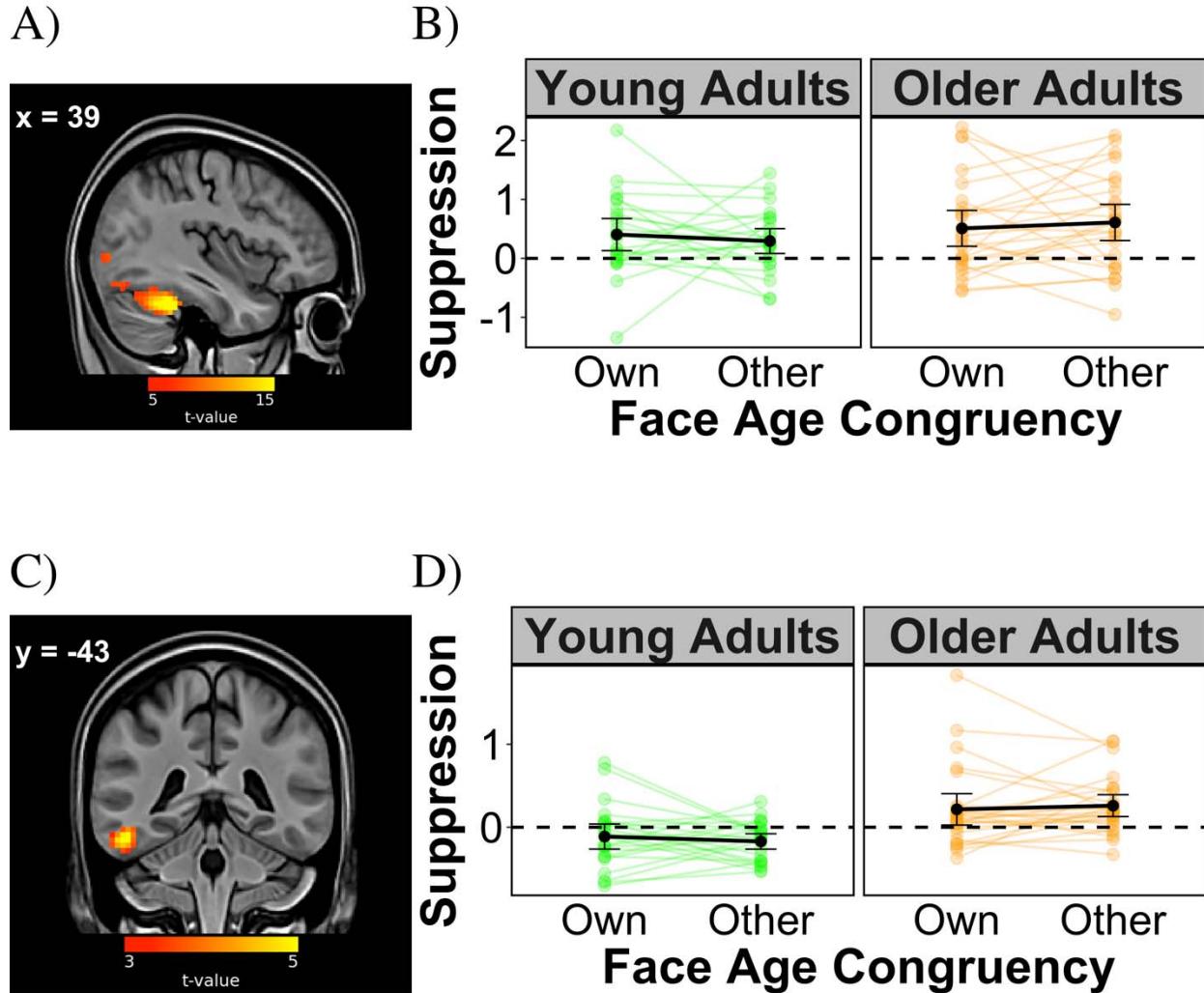
L. Inferior Temporal Cortex ^{a,b}	-51	-43	-19	128	5.22
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Face Age Congruency Effects (Own-Age > Other-Age Faces)

R. Hippocampus ^b	21	-10	-22	71	4.99
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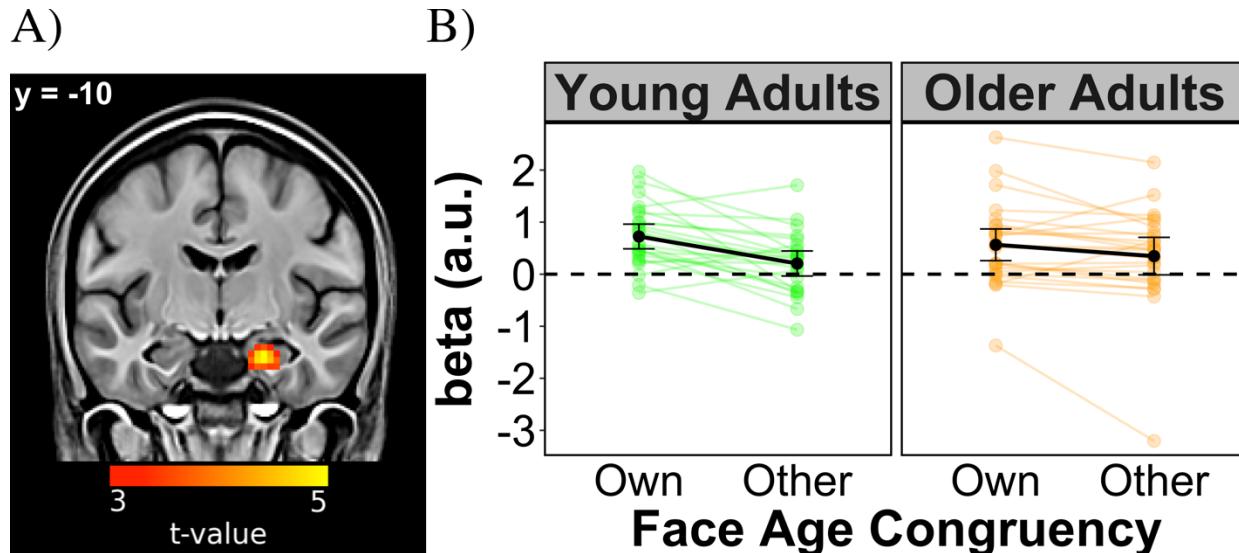
393 Note. The peaks for the Inverted > Upright contrast were obtained using a height threshold of $p < 1e^{-10}$
394 (FWE-corrected) to better delineate and characterize the peaks in the data. Regions showing repetition
395 suppression effects were identified from a planned contrast of first and repeated face trials (i.e., a main
396 effect of face repetition) without regard for other conditions (i.e., repetition lag, Age Group, and Face
397 Age Congruency). The left inferior temporal cortex was identified by a contrast modeling the Age Group
398 by Repetition (first vs. repeated) interaction regardless of Lag and Face Age Congruency. Face Age
399 Congruency effects were identified from an own-age versus other-age contrast for first presentation,
400 upright face trials. ^aSignificant at $p < .001$ height threshold with $p < .05$, FWE-corrected cluster
401 threshold). ^bSignificant at the voxel-level corrected threshold ($p < .05$, FWE-corrected height threshold).





409
410 **Figure 2.** Age-group invariant (top panels) and age-group dependent (bottom panels)
411 suppression effects. (A) A cluster in the right fusiform gyrus ($x = 39$, $y = -43$, $z = -28$) showing suppression
412 of the BOLD signal for repeated faces compared to the first presentation of faces in both young and
413 older adults. A similar pattern was observed in the left fusiform gyrus (not shown, see Table 1). (B)
414 Repetition suppression estimates (first minus repeated presentation) extracted from a 5mm sphere
415 centered on the right fusiform gyrus peak voxel. (C) A cluster in the left inferior temporal cortex ($x = 39$,
416 $y = -43$, $z = -28$) showing larger repetition suppression effects for older relative to younger adults. (D)
417 Repetition suppression estimates extracted from a 5mm sphere centered on the left inferior temporal
418 cortex peak voxel. The interaction in this region is driven by the combination of repetition suppression in
419 older adults and repetition enhancement in younger adults. (A) and (C) are shown at $p < .001$,
420 uncorrected, for visualization purposes, and depicted in neurological orientation (right is right). In (B)
421 and (D), the solid black circles represent condition means, and the green and orange points depict data

422 from individual participants. Error bars reflect the 95% confidence intervals computed from the
423 standard error of the observed data with custom code.



424

425 **Figure 3.** The BOLD signal in the right hippocampus was greater when young and older adults viewed
426 faces belonging to their own age group relative to other age faces. (A) Viewing the first repetition of
427 novel faces was associated with an own-age bias in the right anterior hippocampus ($x = 22, y = -10, z = -$
428 24). The image is shown at a threshold of $p < .001$ uncorrected, for visualization purposes. (B) The
429 beta values extracted from a 5mm sphere centered on the peak coordinate in the right hippocampus.
430 The solid black circles represent condition means, and the green and orange points depict data from
431 individual participants. Error bars reflect the 95% confidence intervals computed from the standard
432 error of the observed data with custom code.

433

Abbreviation List

434 AC-PC – Anterior/Posterior Commissure

435 ANOVA – Analysis of Variance

436 BF – Bayes Factor

437 BOLD – Blood Oxygenation-Level Dependent

438 CVLT – California Verbal Learning Test

439 EPI – Echo-planar Imaging

440 fMRI – Functional Magnetic Resonance Imaging

441 FWE – Family-Wise Error

442 GLM – General Linear Model

443 MMSE – Mini-Mental State Examination

444 MRI – Magnetic Resonance Imaging

445 MPRAGE - Magnetization Prepared Rapid Acquisition Gradient Echo

446 SDMT – Symbol-Digit Modalities Test

447 WTAR – Wechsler Test of Adult Reading