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

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Abstract

The present study investigated the neural correlates of the own-age bias for face recognition in a repetition suppression paradigm. Healthy young and older adults viewed upright and inverted unfamiliar faces. Some of the upright faces were repeated following one of two delays (lag 0 or lag 11). Repetition suppression effects were observed in bilateral fusiform cortex, with no evidence of an own-age bias. By contrast, the right anterior hippocampus showed an own-age bias (greater activity for own- than other-age faces) when viewing an unfamiliar face for the first time. Given the importance of the hippocampus to episodic memory encoding, we conjecture that the increased hippocampal activity for own-age relative to other-age faces reflects differential engagement of neural processes supporting the episodic encoding of faces and might provide insight into the processes giving rise to own-age biases in face recognition memory.

Introduction

The ways in which we evaluate, attend to, and remember human faces are susceptible to own-age biases (e.g., Bartlett and Fulton, 1991; Ebner, 2008; Wiese et al., 2008; for review, see Rhodes and Anastasi, 2012). Notably, both young and older adults show better recognition memory for own-age faces (Rhodes and Anastasi, 2012). These findings have motivated research that has demonstrated own-age biases in neural correlates of face processing (Ebner et al., 2011a, 2011b; Neumann et al., 2015; Wiese et al., 2008; Wolff et al., 2012; for review, see Wiese et al., 2013). Most studies have however used EEG to examine face-related neural activity, and thus little is known about the specific brain regions involved in own-age biases (Ebner et al., 2011a; Wright et al., 2008). Understanding the neuroanatomical correlates of the own-age bias will play an important role in understanding the processes contributing to this phenomenon.

In the present study, healthy young and older adults underwent a face repetition procedure (Figure 1). Repeating faces elicits a 'repetition suppression effect' which, in fMRI, is reflected by reduced BOLD responses for repeated compared to first presentation faces (for reviews, see Henson, 2016; Henson and Rugg, 2003). Repetition suppression effects in regions such as the occipital and fusiform face areas are proposed to reflect modulation of processes contributing to the identification of individual faces (Goh et al., 2010; Hermann et al., 2017). This proposal aligns with perceptual expertise theories of the own-age bias arguing that own-age faces are processed more efficiently and are better individuated than other-age faces due to more extensive experience with own-age peers. Here, we investigated whether own-age biases moderate repetition suppression effects elicited by unfamiliar faces and whether own-age biases are evident when viewing faces for the first time.

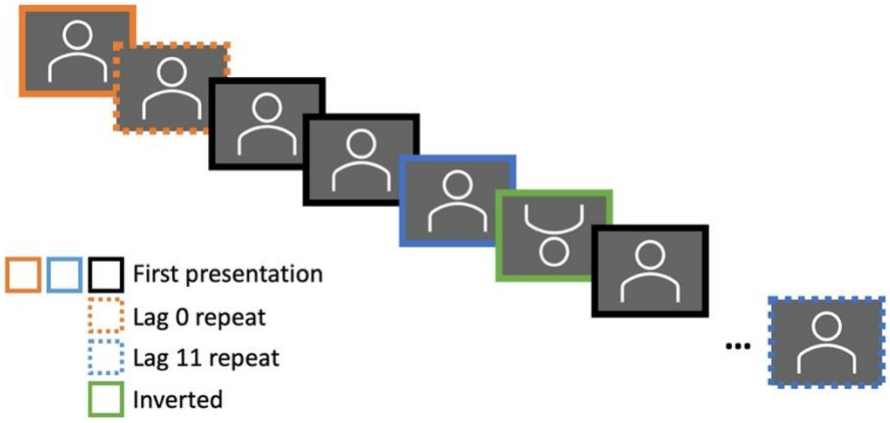

Figure 1. Schematic of the face repetition task. Participants saw a series of young and older adult faces in a face inversion task. Participants were instructed to make a button press if the face was inverted, and otherwise to simply view the faces. Each face was shown for 1 second and followed by an inter-trial interval (fixation cross) for 1.25 seconds. There was a total of 8 conditions formed by crossing Face Age (young, older) and Trial Type (first, lag 0 repeat, lag 11 repeat, inverted). Additional details are reported in the Materials and Methods section.

Results and Discussion

Data from 24 young (18-30 years of age) and 26 older (64-75 years of age) healthy, cognitively normal adults contributed data to the present report (see Supplemental Table S1 for sample demographics and neuropsychological test performance).

Face age was coded as a Face Age Congruency factor whereby own-age faces were those faces from the same age group as the participant (e.g., young faces were coded as same age faces for young adults) whereas other-age faces were those face stimuli depicting individuals not in the participants age group (e.g., for young adults, older faces were coded as different age faces).

Behavioral Results

There were no Age Group or Face Age Congruency differences in behavioral performance (median reaction time, accuracy, or false alarms; see Supplemental Material and Supplemental Table S2).

fMRI Results

Below, we describe the results from the second-level ANOVA model (see Materials and Methods) of the fMRI data. This model comprised an Age Group factor (young vs. older) and a Trial Type factor with eight levels formed by crossing the factors of face age (young, older) and trial type (novel, lag0 repeat, lag11 repeat, inverted). Below, we report planned contrasts derived from this model to examine effects of face repetition and own-age bias (see Table 1). Results relevant to face inversion effects are reported in Supplemental Materials.

Repetition Suppression

The first planned contrast aimed to identify voxels showing significant main effects of face repetition. No clusters showed repetition enhancement effects. However, clusters showing repetition suppression effects were identified in bilateral fusiform gyrus (Table 1 and Figure 2A-B). The suppression effects did not differ significantly between young and older adults, between repetition lags, or own-age and other-age faces according to follow-up analyses that exclusively masked the repetition suppression contrast with interaction terms involving repetition and the other factors (exclusive mask threshold set at $p < .10$). The absence of age group differences in repetition suppression effects in the fusiform gyrus is consistent with prior fMRI findings (Goh et al., 2010). The lack of an effect of repetition lag is however inconsistent with previous research reporting larger repetition suppression effects in fusiform cortex for immediate compared to long lag face repeats (Henson et al., 2000; for related findings, see Nagy and Rugg, 1989).

We next conducted planned contrasts aimed at identifying voxels where face repetition effects differed in magnitude between young and older adults (i.e., regions showing an Age Group by Repetition Interaction, collapsed across lag). This contrast identified a cluster in the left interior temporal gyrus (Figure 2C-D) that showed larger repetition suppression effects in older adults. Repetition suppression indices (i.e., first – repeat) extracted from a 5mm sphere around the peak voxel manifesting the interaction revealed a significant repetition suppression effect for repeated faces in older adults, $t(25) = 3.24$, $p = .003$, but repetition *enhancement* for repeated faces in the younger adults , $t(23) = 2.85$, $p = .009$. The location of this interaction is in the vicinity of a left inferior temporal cluster previously reported to show repetition suppression effects for familiar concepts (e.g., yellow banana), but not novel concepts (e.g., purple banana) (Reggev et al., 2016). Given that familiar concepts are accrued through experience, it is possible that the present interaction reflects age-group differences in exposure to faces (for a related discussion, see Koen and Rugg, 2019). By this argument, the left inferior temporal gyrus is a region that is especially sensitive to cumulative lifetime experience of a perceptual category such as faces. Future research will be needed to test the validity of this proposal.

A further planned contrast searched for voxels where face repetition effects differed in magnitude between repetition lag (i.e., voxels demonstrating a lag by repetition interaction). Consistent with the findings reported above, no suprathreshold clusters were identified by this contrast. Additionally, and of importance, no suprathreshold effects were identified by the planned contrast searching for evidence of an interaction between Face Age Congruency and Repetition.

Table 1. Regions showing effects of face repetition and age congruency.

Region	MNI Coordinates x	y	z	Cluster size	Peak *z*
Repetition Suppression					
R. Fusiform Gyrus[a,b]	39	-43	-28	493	5.82
L. Fusiform Gyrus[a]	-39	-46	-28	328	4.20
Age Group by Repetition Interaction (Older: Repetition Suppression, Young: Repetition Enhancement)					
L. Inferior Temporal Cortex[a,b]	-51	-43	-19	128	5.22
Face Age Congruency Effects (Own-Age > Other-Age Faces)					
R. Hippocampus[b]	21	-10	-22	71	4.99

Note. Regions showing repetition suppression effects were identified from a planned contrast of first and repeated face trials (i.e., a main effect of face repetition) without regard for other conditions (i.e., repetition lag, Age Group, and Face Age Congruency). The left interior temporal cortex was identified by a contrast modeling the Age Group by Repetition (first vs. repeated) interaction regardless of Lag and Face Age Congruency. Face Age Congruency effects were identified from an own-age versus other-age contrast for first presentation, upright face trials. [a]Significant at $p < .001$ height threshold with $p < .05$, FWE cluster threshold). [b]Significant at the voxel-level corrected threshold ($p < .05$, FWE, height threshold).

Own-Age Biases in First Presentation Face Trials

We next conducted a planned contrast between the first presentation trials of upright, own-age and other-age faces to identify voxels showing an own-age bias. Repeated faces were excluded from the analysis to mitigate potentially confounding effects of familiarity or other repetition-related processes (for the outcome of the contrast on repeated images, see Supplemental Materials and Supplemental Figure S1). The above-described contrast identified a cluster of voxels demonstrating a Face Age Congruency effect in the right anterior hippocampus (Table 1 and Figure 3). The cluster demonstrated elevated BOLD activity for own-age relative to other-age faces. This effect did not significantly differ in magnitude between young and older adults based on exclusively masking (at $p < .10$) the above contrast with the interaction contrast between Age Group and Face Age Congruency. Moreover, a conjunction analysis performed by inclusively masking the own-age versus other-age contrasts conducted separately for young and older adults (each at $p < .01$) revealed a cluster that overlapped with that identified in the initial analyses. Furthermore, a mixed effects ANOVA conducted on the means of the beta estimates extracted from a 5mm sphere centered on the hippocampus peak voxel revealed no evidence of an Age Group by Face Age Congruency interaction (see Supplemental Materials). There were no detectable repetition suppression effects in this hippocampal cluster (see Supplemental Materials and Supplemental Figure S3).

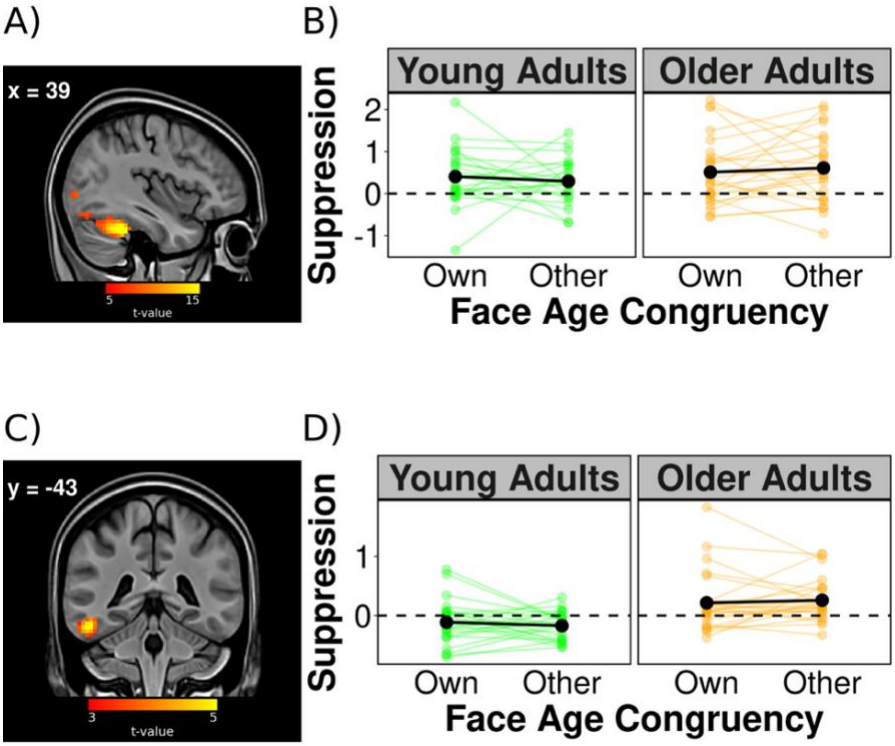

Figure 2. Age-group invariant (top panels) and age-group dependent (bottom panels) face repetition suppression effects. (A) A cluster in the right fusiform gyrus (x = 39, y = -43, z = -28) showing suppression of the BOLD signal for repeated faces compared to the first presentation of faces in both young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

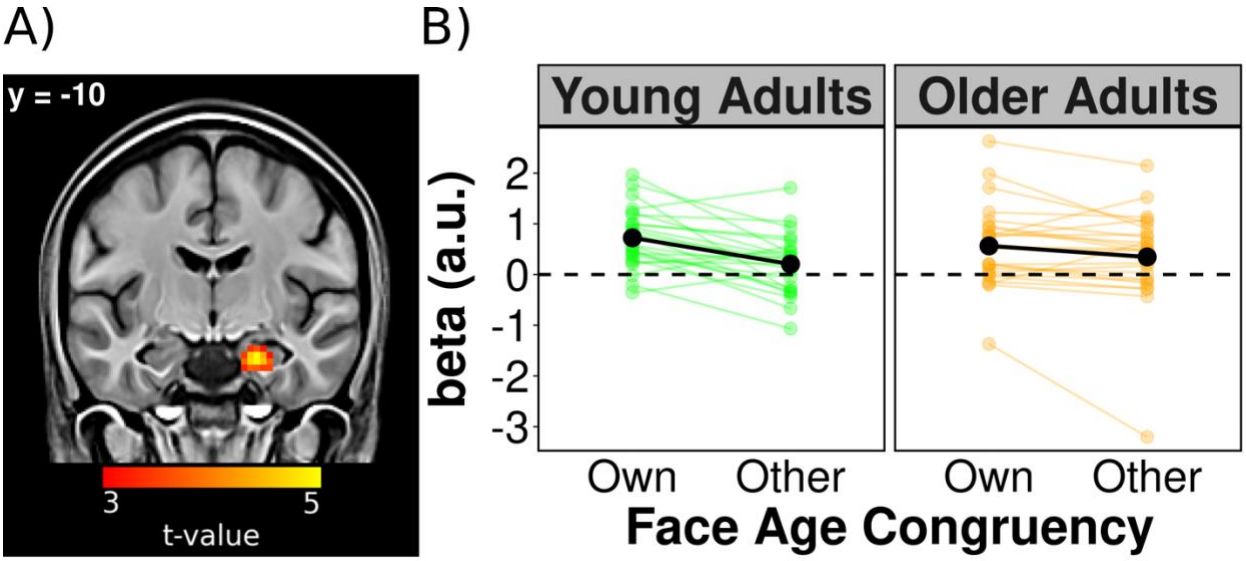

Figure 3. BOLD signals in the right hippocampus were greater when young and older adults viewed faces belonging to their own age group relative to other age faces. (A) Viewing the first repetition of novel faces was associated with an own-age bias in the right anterior hippocampus (x = 22, y = -10, z = -24). The cluster is thresholded at $p < .001$ for visualization purposes. (B) The beta values extracted from a 5mm sphere centered on the peak coordinate in the right hippocampus. The solid black circles represent condition means, and the green and orange points depict data from individual participants.

Conclusions

We did not identify any regions where repetition suppression effects demonstrated an own-age bias (for similar findings in the own-race bias literature, see Reggev et al., 2020). These null findings are arguably inconsistent with perceptual expertise accounts of the own-age bias. Such accounts propose that own-age faces are more efficiently processed with better individuation than other-age faces due to due to more extensive experience with own-age peers. If face repetition suppression effects reflect modulation of processes contributing to the identification of individual faces (Hermann et al., 2017), then we might expect that own-age faces would elicit a greater suppression effect than other-age faces. We did not observe this. Future research employing morphed faces (Goh et al., 2010) might shed additional light on this issue.

The only region that demonstrated an own-age bias was the right anterior hippocampus. We have no ready explanation for this finding, and stress that it needs replication. However, given the well-established role of the hippocampus in memory encoding (Eichenbaum et al., 2007; Kim, 2011), we conjecture that this own-age bias in face-elicited hippocampal activity might be related to the own-age bias evident in recognition memory (Rhodes and Anastasi, 2012). There are several possible accounts of this finding, which are not mutually exclusive. For example, it could be that it is easier to bind previously acquired personal or semantic knowledge about familiar individuals to unfamiliar own-age compared to other-age faces. Alternately, own-age faces may more readily attract attention to discriminating facial features compared to other-age faces, in turn modulating encoding-related hippocampal activity (Aly and Turk-Browne, 2015, 2017; Uncapher and Rugg, 2009). Another interesting hypothesis is that the own-age bias observed here in the hippocampus reflects the formation of face representations with higher fidelity than in the case of other-age faces (for reviews, see Ekstrom and Yonelinas, 2020; Yonelinas, 2013). Future studies that link the own-age

bias in recognition memory to these hippocampal effects promise to shed light on these and other possibilities.

Materials and Methods

Ethics Statement

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

Participants

A sample of 24 young and 26 older participants contributed to the analyses reported here. Participants were recruited from the University of Texas at Dallas and the greater Dallas metropolitan area and were financially compensation for their time ($30/hour). All participants were right-handed, reported having normal or corrected-to-normal vision and had no contraindications to MRI scanning. Exclusion criteria included a history of cardiovascular disease (other than treated hypertension), diabetes, psychiatric disorder, illness or trauma affecting the central nervous system, substance abuse, and self-reported current or recent use of psychotropic medication or sleeping aids. All participants scored 27 or more on the Mini-Mental State Examination (MMSE; Folstein et al., 1975) and scored within the normal range for their age group on a battery of neuropsychological tests (see Table 1). Details of the neuropsychological test battery are reported in Koen et al. (2019). Volunteers were excluded from participating in the fMRI study if any of the following criteria were met: (i) one or more of the memory measures (i.e., CVLT or logical memory) were more than 1.5 standard deviations below the age- and education-adjusted mean, (ii) two or more scores on non-memory tests were 1.5 standard deviations below the mean, or (iii) a standard score below 100 on the WTAR.

Data from an additional one young adult male and one older adult male were excluded due to excessive in-scanner motion (> 8 mm maximum frame-wise displacement) during the task. The participants contributing data to this report also contributed data to other experiments we have recently reported (Koen et al., 2018, 2019).

Materials and Procedure

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

The procedure for the task is depicted in Figure 1. In each session, participants were shown a series of faces and were instructed to press a key with their right index finger whenever an inverted face was presented. Speed was emphasized on the button press to inverted faces. Each face was presented centrally for 1 sec and followed by a 1.25 sec white fixation cross. A total of 48 null trials were dispersed throughout the block to jitter the stimuli, with no more than one null trial occurring consecutively. Responses were recorded until the beginning of the next trial.

Each session of the task comprised 152 face trials and 48 null trials. Each inverted face was presented once only, and no more than two inverted trials occurred in succession. Faces assigned to the repeat condition were presented twice with the repetition occurring either on the immediately succeeding trial (lag 0) or after 11 intervening trials (lag 11). Faces in the control condition were presented on only one occasion. Control faces and the first presentations of repeated faces were collapsed into a single 'novel' face condition for some of the analyses reported below.

MRI Data Acquisition

MRI data were acquired with a 3T Philips Achieva MRI scanner (Philips Medical Systems, Andover, MA, USA) equipped with a 32-channel receiver head coil. Functional images were acquired with a blood oxygenation level dependent (BOLD), T2*-weighted echoplanar imaging (EPI) sequence (SENSE factor = 1.5, flip angle = 70°, 80 × 80 matrix, FOV = 240 mm x 240 mm, TR = 2000 ms, TE = 30 ms, 34 ascending slices, slice thickness = 3 mm, slice gap = 1 mm), and were oriented parallel to the AC-PC line. Five "dummy" scans were acquired at the start of each fMRI session and discarded to allow for equilibration of tissue magnetization. A total of 180 functional volumes were acquired during each study session, for a total of 900 brain volumes. T1-weighted images (MPRAGE sequence, 240 × 240 matrix, 1 mm isotropic voxels) were acquired for anatomical reference. Note that this task was completed prior to the encoding phase of a memory study that comprised object and scene images, which is the focus of a different report (Koen et al., 2019).

fMRI Data Preprocessing and Analysis

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

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

The second-level group analyses were performed by submitting the 8 first-level beta maps to a 2 (age group) by 8 (condition) mixed ANOVA using the factorial ANOVA module in SPM. The 8 levels of the condition factor were those described above for the first-level models, with one exception. Face age was coded as a Face Age Congruency factor whereby same age faces were those faces from the same age group as the participant (e.g., young faces were coded as same age faces for young adults) whereas different age faces were those face stimuli depicting individuals not in the participants age group (e.g., for young adults, older faces were coded as different age faces). Planned contrasts were conducted to identify voxels showing significant effects of Repetition, Face Age Congruency, and and to examine whether these effects interacted with participant age or lag. Additionally, effects of Face Inversion are reported in the Supplemental Materials. Effects were deemed significant if they survived $p < .001$ with a cluster-wise correction ($p < .05$, FWE) based on Gaussian Random Field theory or if the peak voxel of cluster survived $p < .05$ FWE voxel-level correction. The rationale for using both of these approaches was to avoid Type-II errors both for

large clusters with (relatively) weak mean activation and for more focal clusters with a strong peak response.

Acknowledgements

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Competing Interests

The authors declare no competing interests.

References

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Koen JD, Horne ED, Hauck N, Rugg MD. 2018. Age-related Differences in Prestimulus Subsequent Memory Effects Assessed with Event-Related Potentials. *Journal of Cognitive Neuroscience* **30**:829–850. doi:10.1162/jocn_a_01249

Koen JD, Rugg MD. 2019. Neural Dedifferentiation in the Aging Brain. *Trends in Cognitive Sciences* **23**:547–559. doi:10.1016/j.tics.2019.04.012

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

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

Neumann MF, End A, Luttmann S, Schweinberger SR, Wiese H. 2015. The own-age bias in face memory 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

Reggev N, Bein O, Maril A. 2016. Distinct Neural Suppression and Encoding Effects for Conceptual Novelty and Familiarity. *Journal of Cognitive Neuroscience* **28**:1455–1470. doi:10.1162/jocn_a_00994

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

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

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

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

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

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

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

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

Supplemental Material for:

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

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Reaction Time Analysis

Median reaction times to inverted faces receiving a correct button press were submitted to a 2 (Age Group) by 2 (Face Age Congruency) mixed ANOVA. The mean reaction times are presented in Supplemental Table S2 Although older adults were numerically slower in their responses, we did not observe a significant effect of Age Group on median reaction times, $F(1,48) = 2.01$, $MSE = 10290$, $p = .162$, partial-$\eta^2 = .040$. Additionally, neither the main effect of Face Age Congruency, $F(1,48) = 1.89$, $MSE = 718$, $p = .176$, partial-$\eta^2 = .038$, nor the interaction term were significant, $F(1,48) = .522$, $MSE = 718$, $p = .474$, partial-$\eta^2 = .011$.

Own-Age Biases for Face Repeats

We conducted a whole-brain analysis contrasting Own- and Other-Age faces for repeated face trials (collapsed over lag) to mirror the analyses of own-age biases in first presentation face viewing reported in the main text. The voxel-wise analysis revealed no significant clusters (Supplemental Figure S1). This null finding was also observed in a similar contrast conducted separately for lag 0 and lag 11 items.

Repetition Suppression Effects in the Right Hippocampus

We investigated if there were repetition suppression effects in the right anterior hippocampus cluster where we identified an age group invariant own-age bias during the first presentation of the face stimuli. We conducted a 2 (Age Group) by 3 (Lag) by 2 (Face Age Congruency) mixed ANOVA on beta estimates for the three upright face trial types (first, lag 0, and lag 11) from a 5mm sphere centered on the peak of the hippocampus cluster reported in the main text (x = 22, y = -10, z = -24). The ANOVA revealed a main effect of Face Age Congruency, $F(1,48) = 8.01$, $MSE = .5.39$, $p = .007$, partial-$\eta^2 = .143$. This effect does not provide any additional information beyond that reported in the main text as it is derived from a circular analysis (i.e., not orthogonal to the contrast used to define the cluster). No other effects were significant, Fs < 2.44, ps $> .125$, partial-η^2s $< .048$. These null findings suggest that none of factors included in the ANOVA significantly modulated the own-age bias effect (i.e., effect of Face Age Congruency) observed in the region. A series of students t-tests on measures of repetition suppression (first minus repeat trials, collapsed across lag) failed to identify significant repetition suppression effects in any of the conditions, ts < 1.14, ps $> .266$ (Supplemental Figure S2).

Face Inversion Effects

We examined the effects of face inversion by contrasting the activity elicited by upright (first presentation only) and inverted faces. The results from this analysis demonstrated increases in BOLD signal for inverted relative to upright races across a wide swath of the cortex with peaks primarily in the frontal and temporal cortices, as well as the cerebellum (Supplemental Table S3 and Supplemental Figure S3). Note that the peaks in Supplemental Table S3 were derived after thresholding the whole-brain contrast at $p < 1e\text{-}10$ (FWE corrected) to better delineate and characterize the peaks in the data. Additionally, clusters in the right pre- and post-central gyri demonstrated smaller face inversion effects in older adults compared to younger adults (Supplemental Table S4 and Supplemental Figure S4). No clusters showing effects of Face Age Congruency (Own vs. Other faces) or interactions involving this factor survived our thresholding.

Supplemental Table S1. Demographic and neuropsychological test data for young and older adults.

	Young Adults	Older Adults	*p*-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

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

Supplemental Table S2. Proportion of accurate responses on inverted faces and the average of the median reaction times (in ms) of the accurate responses.

Age Group	Face Age Congruency	Accuracy	Reaction Time	False Alarms
Young Adults	Own Age	.98 (.002)	582 (3)	.001 (.0001)
	Other age	.99 (.002)	571 (3)	.003 (.0002)
Older Adults	Own Age	.98 (.001)	608 (3)	.001 (.0001)
	Other Age	.99 (.001)	604 (3)	.002 (.0002)

Note. Reaction times are rounded to the nearest millisecond. The standard error of the mean is provided in parentheses.

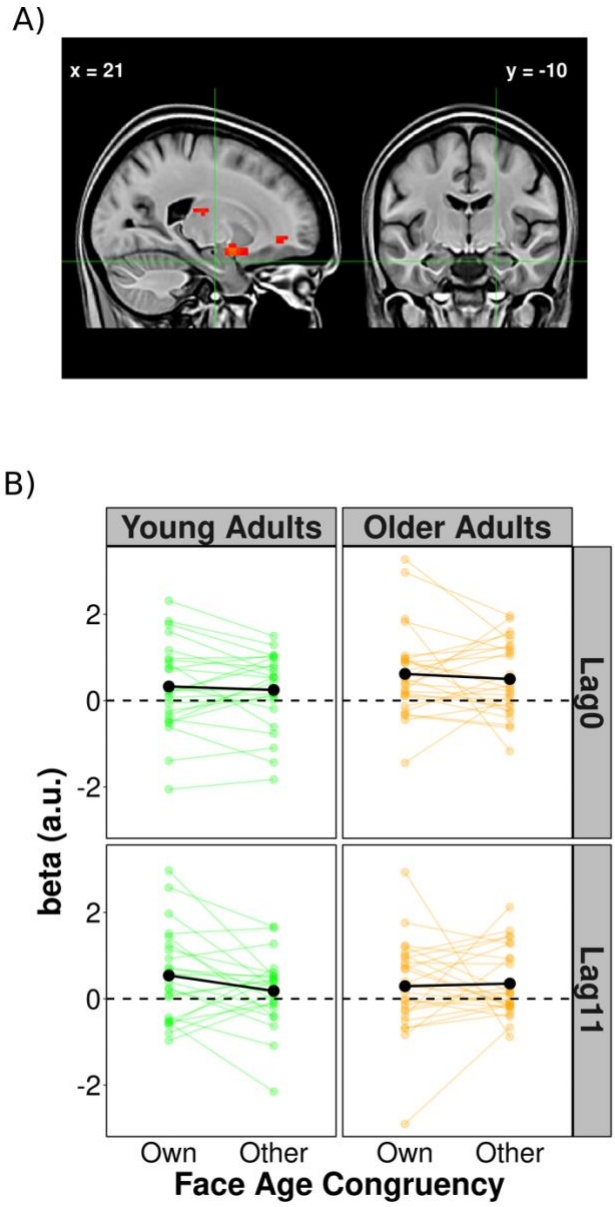
Supplemental Table S3. Peak Coordinates showing increased BOLD signal for Inverted compared to Upright (novel) faces.

	MNI Coordinates				
Region	x	y	z	Cluster size	Peak *T*
		Inverted > *Novel*			
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

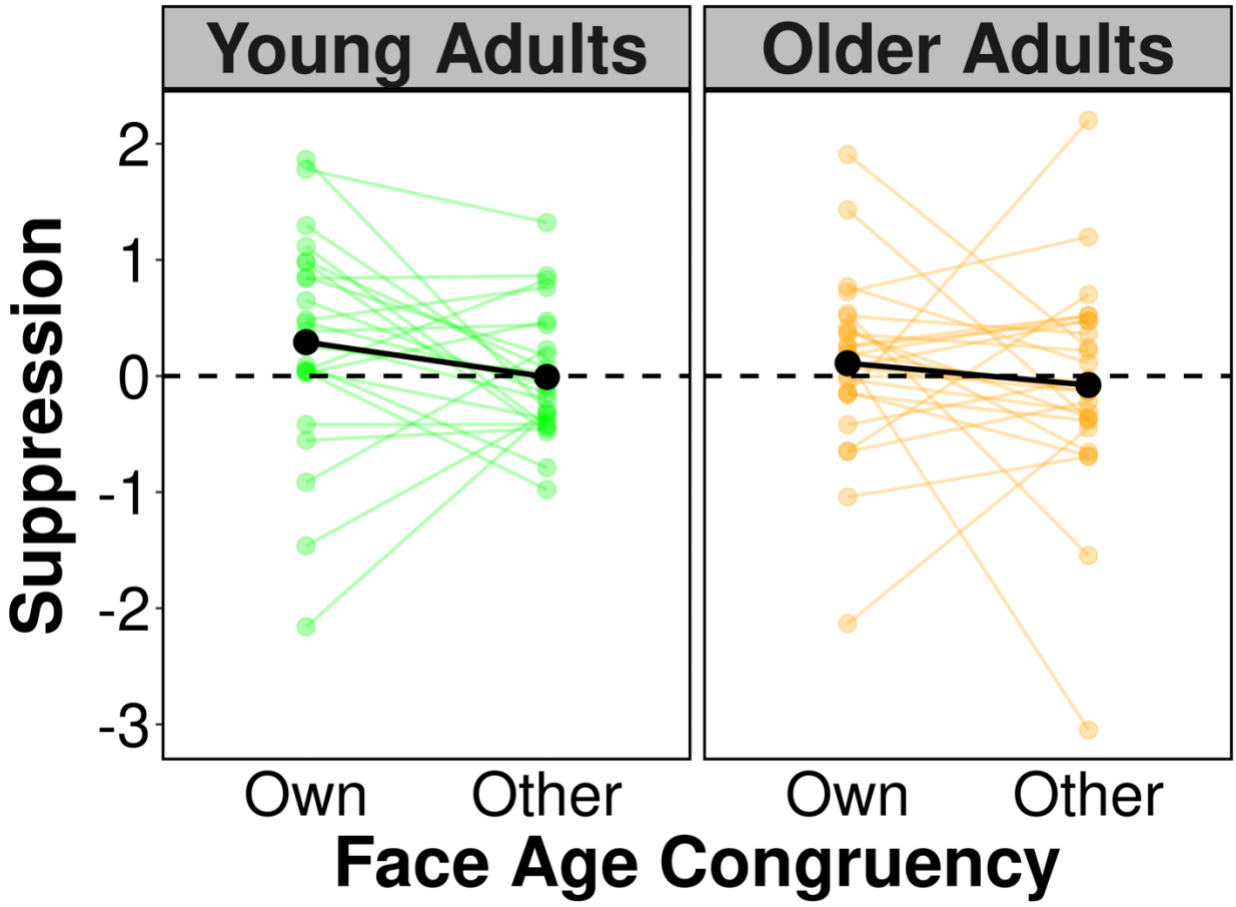
Note. Peaks reported with local maxima that are at least 8mm apart. Peak T reported as all peak Z values were infinite. Results shown at $p < 1e\text{-}10$ (FEW voxel-wise threshold) to better highlight the peaks in the data. The $p < .001$ contrast returned a single contiguous cluster (Cluster size = 44,224).

Supplemental Table S4. Peak Coordinates showing larger face inversion effects (Inverted > Upright) in older relative to younger adults.

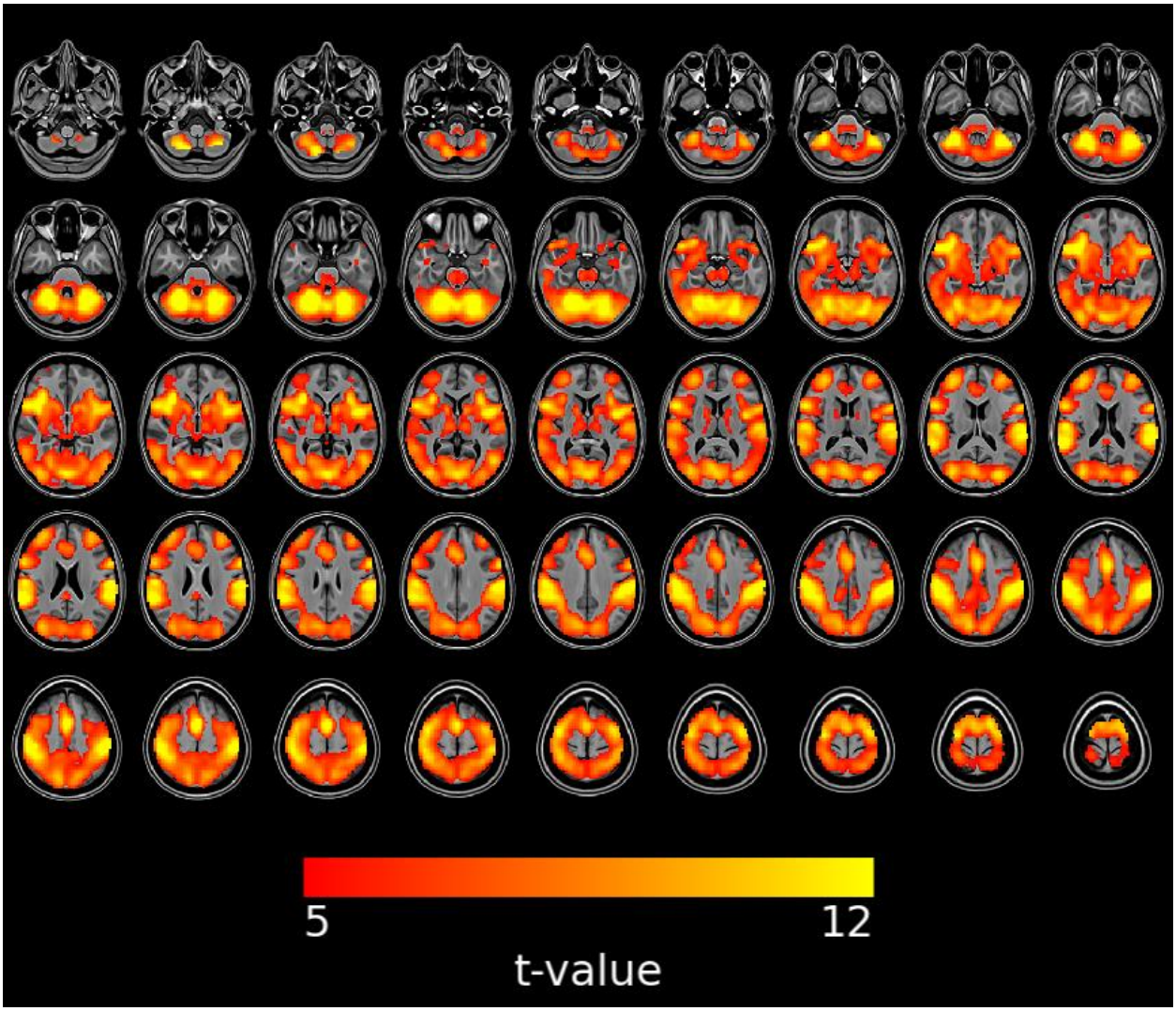
	MNI Coordinates				
Region	x	y	z	Cluster size	Peak *Z*
R. Postcentral Gyrus	60	-7	32	318	4.77
L. Precentral Gyrus	-54	-7	41	136	4.24



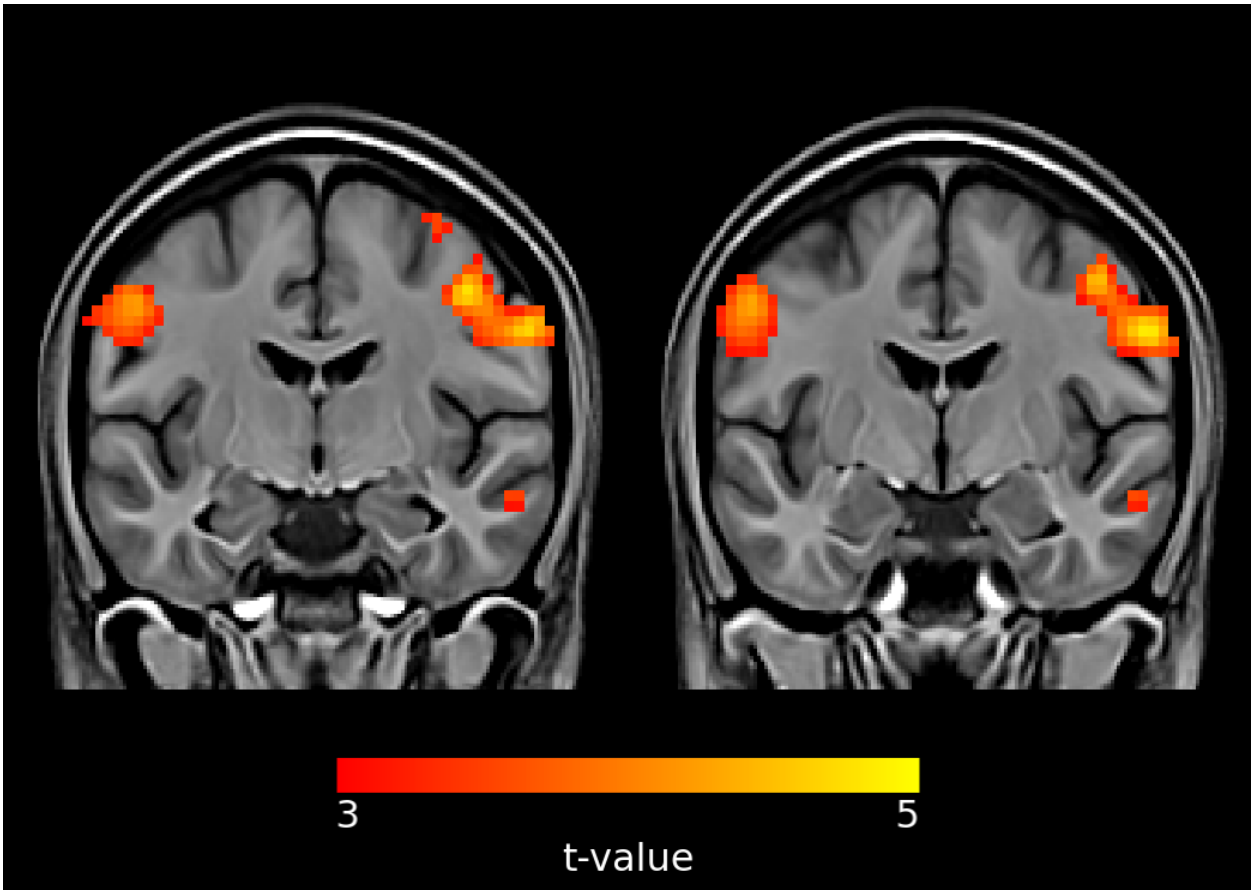
Supplemental Figure S1. (A) Same vs. Different age repeats (collapsed across lags). The green crosshair is centered on the peak from the novel face analysis (displayed at $p < .001$). The images are in neurological orientation (right is right). (B) Betas extracted from the peak hippocampus (x = 22, y = -10, z = -24) from the cluster reported in the main text. There was no Face Age Congruency by Trial Type (first, lag 0, lag 11) interaction, suggesting the hippocampal own-age bias was not statistically different between the three conditions.



Supplemental Figure S2. Repetition suppression estimates (first minus repeated) derived from a 5mm sphere centered on the peak voxel (x = 22, y = -10, z = -24) in the right anterior hippocampus cluster showing an own-age bias during first presentation of face trials. There was no evidence for repetition suppression to repeated faces in this cluster. Note that more positive values reflect increased repetition suppression (i.e., lower BOLD signal for repeated relative to novel face trials). The solid black circles represent condition means, and the green and orange points depict data from individual participants.



Supplemental Figure S3. Montage depicting voxels showing increased BOLD signal for Inverted relative to (first presentation) Upright faces. The data are displaying at $p < .001$ for visualization purposes only. The top left slice starts at z=-58, and the subsequent slices shown are spaced 3mm apart. The images are in neurological orientation (right is right).



Supplemental Figure S4. Montage depicting voxels showing increased BOLD signal for Inverted relative to (first presentation) Upright faces. The data are displaying at $p < .001$ with no cluster thresholding for visualization purposes. The slices are located at y = -7 and y = -10 for the left and right panels, respectively. The images are in neurological orientation (right is right).