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.

Rapic Communication

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. 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.

Repeating faces elicits a 'repetition suppression effect' whereby the BOLD response is reduced 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.

A total of 24 young (18-30 years of age) and 26 older (64-75 years of age) healthy, cognitively participated in this study (see Supplemental Table S1 for sample demographics and neuropsychological test performance). While undergoing fMRI, participants completed a face viewing task comprising a mixture of upright and inverted young and older adult faces (Figure 1). Participants made a button press to inverted faces. Upright faces were either presented on a single occasion or repeated after lags of 0 (immediately) or 11 trials. 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).

The behavioral results show no effects of Age Group, Face Age Congruency, or any interaction performance (median reaction time, accuracy, or false alarms; see Supplemental Material and Supplemental Table S2).

The fMRI data were modeled at the second level using an ANOVA model that included 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; see Supplemental Materials for more details). 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.

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.

In summary, 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.

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).

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.

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

	MNI Coordinates				
Region	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).

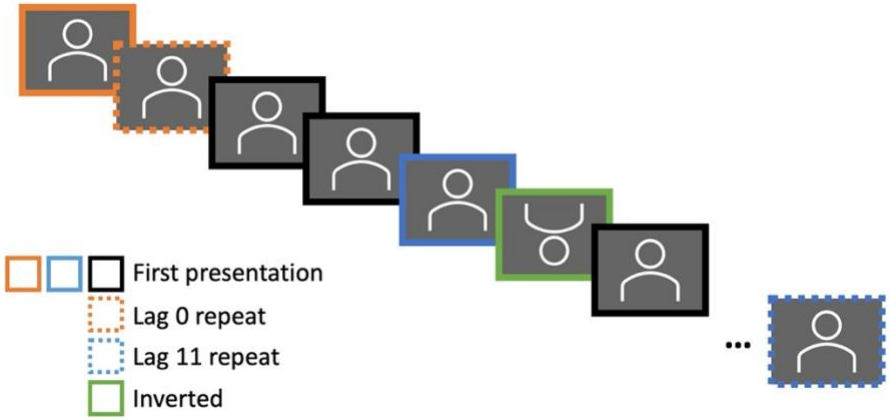

Figure 1. Schematic of the face repetition task. Participants saw a series of young and older adult faces in a face inversion task. Participants were instructed to make a button press if the face was inverted, and otherwise to simply view the faces. Each face was shown for 1 second and followed by an 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.

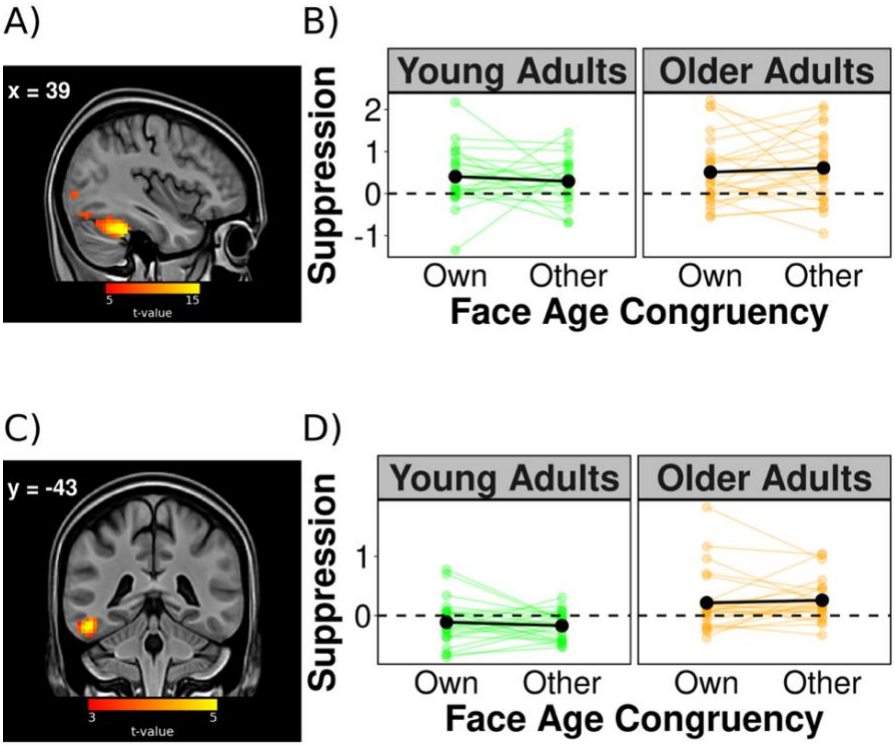

Figure 2. Age-group invariant (top panels) and age-group dependent (bottom panels) face repetition suppression effects. (A) A cluster in the right fusiform gyrus (x = 39, y = -43, z = -28) showing suppression of the BOLD signal for repeated faces compared to the first presentation of faces in both young 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.

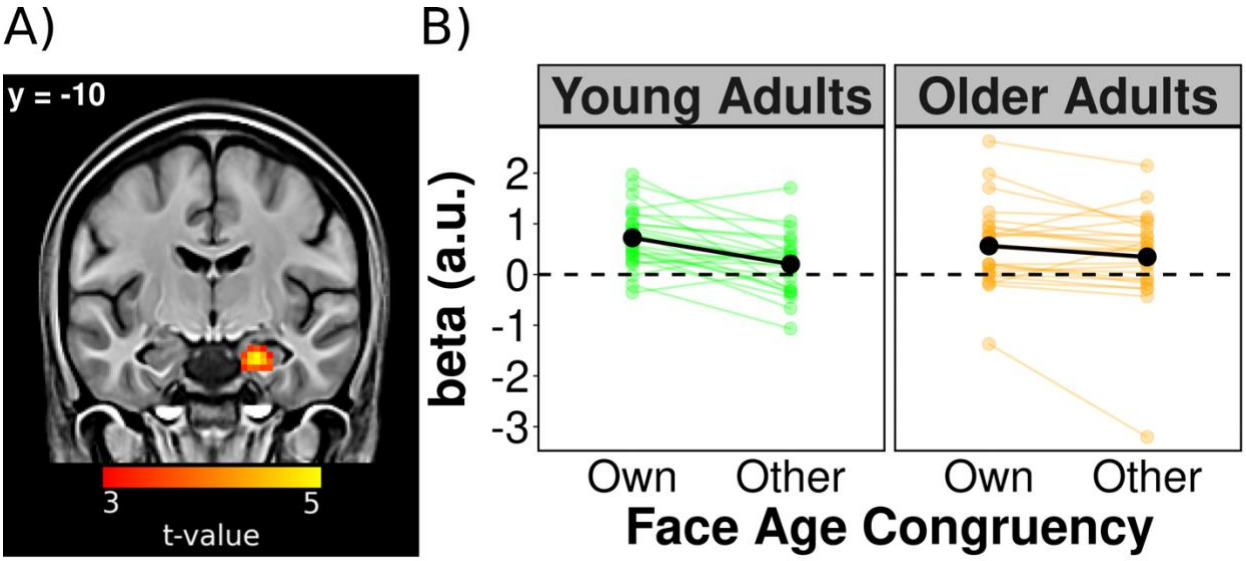

Figure 3. BOLD signals in the right hippocampus were greater when young and older adults viewed faces belonging to their own age group relative to other age faces. (A) Viewing the first repetition of novel faces was associated with an own-age bias in the right anterior hippocampus (x = 22, y = -10, z = -24). The image is shown at a threshold of at $p < .001$ uncorrected, 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.