PAPER

The development of race effects in face processing from childhood through adulthood: Neural and behavioral evidence

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Abstract

Most adults are better at recognizing recently encountered faces of their own race, relative to faces of other races. In adults, this race effect in face recognition is associated with differential neural representations of own- and other-race faces in the fusiform face area (FFA), a high-level visual region involved in face recognition. Previous research has linked these differential face representations in adults to viewers' implicit racial associations. However, despite the fact that the FFA undergoes a gradual development which continues well into adulthood, little is known about the developmental time-course of the race effect in FFA responses. Also unclear is how this race effect might relate to the development of face recognition or implicit associations with own- or other-races during childhood and adolescence. To examine the developmental trajectory of these race effects, in a cross-sectional study of European American (EA) children (ages 7–11), adolescents (ages 12–16) and adults (ages 18–35), we evaluated responses to adult African American (AA) and EA face stimuli, using functional magnetic resonance imaging and separate behavioral measures outside the scanner. We found that FFA responses to AA and EA faces differentiated during development from childhood into adulthood; meanwhile, the magnitudes of race effects increased in behavioral measures of face-recognition and implicit racial associations. These three race effects were positively correlated, even after controlling for age. These findings suggest that social and perceptual experiences shape a protracted development of the race effect in face processing that continues well into adulthood.

KEYWORDS
development, face processing, face recognition memory, fusiform face area (FFA), implicit association test, race effect

1 | INTRODUCTION

Most adults are better at recognizing recently encountered faces of their own race, relative to faces of other races (Malpass & Kravitz, 1969; Sauerland & Sporer, 2009; Sporer, 1991). Evidence of a race effect in face perception is found in infancy (Heron-Delaney et al., 2011; Markant et al., 2016; Sangrigoli & Schonen, 2004; Vogel et al., 2012; Wheeler et al., 2011; Xiao et al., 2013) and in adults, it is attributed to a combination of perceptual and motivational factors, such as greater levels of perceptual experience and social salience (see review (Young et al., 2012)). Also in adults, the neural substrates of face processing differently represent faces of own- vs.

other-races along the fusiform gyrus, a region collectively known as "the fusiform face area" (FFA) and specialized in face-identity recognition (Brosch et al., 2013; Golby et al., 2001; Grill-Spector et al., 2000; Kanwisher et al., 1997). Importantly, in adults differential representation of own- and other-race faces correlates with behavioral measures of race effect in face recognition (Golby et al., 2001), and of negative implicit associations with other-race faces (Brosch et al., 2013). In other words, the greater the FFA's responses are to own- relative to other-race faces, the better individuals are at recognizing own-race faces relative to other-race faces, and the more positive their associations with their own race relative to other-race associations. In adults, these FFA responses to own- and other-race faces are thought to reflect both the cumulative effect of perceptual expertise (Gauthier et al., 2000; Golby et al., 2001; McGugin et al., 2011), and also the transient effects of recent face-to-face interactions, social affiliation, and context (Bernstein et al., 2007; Blandon-Gitlin et al., 2014; Guassi Moreira et al., 2017; Marsh et al., 2016; Van Bavel & Cunningham, 2009; Van Bavel et al., 2008). However, little is known about the developmental time-course of differential representation of faces of own- and other-races in the FFA, or how it might relate to the developmental trajectories of the race effects in face recognition and implicit racial associations.

One possibility is that the race effect in face processing develops in early childhood and remains stable thereafter. Supporting this hypothesis, a few studies reported an adult-like magnitude of the race effect in face-recognition memory after age 7 (Anzures et al., 2014; Goodman et al., 2007; Pezdek et al., 2003). Indeed, some authors have suggested a lasting and disproportionate effect of experience during the first years of life (Cassia et al., 2009; Macchi Cassia, 2011), perhaps leading to an early and persistent own-race preference in face recognition. Also, implicit associations with own- and other-races are reportedly adult-like after age six (Baron & Banaji, 2006). Given the reported correlation between implicit racial attitudes and the FFA's differential responses to race of faces in adults (Brosch et al., 2013), these findings suggest a fixed magnitude of the race effect in face processing across age groups, implying little cumulative influence by perceptual and social experiences in shaping FFA representations of race of faces after age 7.

Alternatively, the race effect in FFA responses may develop progressively from childhood through adolescence and into adulthood. Indeed, several lines of evidence show substantial malleability in face processing and its neural substrates well into adolescence and adulthood. For example, behavioral studies based on large samples, wide age ranges (Chance et al., 1982), and sensitive measures of face discrimination (Chien et al., 2018), found a protracted development of the race effect in face processing that increased with age at least until age 12. In addition, other studies have found that face-recognition ability for *own-race* faces improves with the age of viewers well into adulthood (Germine et al., 2011). Moreover, the FFA undergoes a prolonged development in response to own-race faces (Cantlon et al., 2011; Gathers et al., 2004; Golarai et al., 2007, 2010, 2015; Peelen et al., 2009; Scherf et al., 2007, 2012), involving age-related increases in the spatial extent and magnitude of face

Research Highlights

- We found evidence of own-race preferences in neural and behavioral measures of face processing, manifesting as higher responses in FFA, better face-recognition memory, and more positive implicit associations for own- than for other-race faces among European American children (ages 7–11), adolescents (ages 12–16), and adults (ages 18–35).
- Our cross-sectional data revealed substantial age-related increases in the magnitude of all three race effects from childhood into adulthood.
- The three measures of race effect were positively correlated, after controlling for age.

selectivity that continues well into adolescence. The development of FFA correlates with the development of behavioral measures of recognition ability for own-race faces (Golarai et al., 2007, 2010). In fact, other evidence suggests that FFA development is associated with a progressive differentiation in how faces of various categories are represented. For example, the adult FFA responded differently to faces of different *ages*, in contrast with children's FFAs, which responded similarly to own- and other-age faces (Golarai et at, 2015). Generalizing from these findings, one might expect the race effect in FFA responses to continue to develop during childhood and adolescence before becoming adult like. Given FFA's key role in face recognition, the development of the race effect in FFA responses may mediate a concurrent increase in the magnitude of race effect in face-recognition memory.

Other lines of behavioral evidence also favor the idea that face-recognition ability remains malleable during childhood development and well into adulthood, due to various forms of social and perceptual experiences with faces of different groups. For example, the race effect in face recognition was reportedly reversed in adults who were adopted at ages 3–9 years old into other-race families (Sangrigoli et al., 2005), suggesting the malleability of the race effect after age 9. In other studies, elementary school teachers exhibited strong memory for child faces (Harrison & Hole, 2009) and maternity-ward nurses showed strong memory for infant faces (Cassia et al., 2009), contrasting with most adults' low recognition ability for other-age faces (Hills & Lewis, 2011). Furthermore, brief perceptual training among adults reduced the race effect in face recognition (Tanaka & Pierce, 2009). Even laboratory-created group affiliation rapidly induced an own-group preference in face processing (Bernstein et al., 2007; Blandon-Gitlin et al., 2014; Marsh et al., 2016; Van Bavel & Cunningham, 2009; Van Bavel et al., 2008). Importantly, the magnitude of this laboratory-induced preference increased with participants' age during childhood and adolescence (Guassi Moreira et al., 2017). Thus, during this period of development there may be an increase in own-group preference and a related enhancement in the neural representations of such group preferences, even in the context of recent group affiliation.

Together, these findings suggest a model of development of race effects whereby cumulative social and perceptual experiences along with current racial attitudes and social context, jointly shape the race effects in FFA responses and face-recognition performance to a degree that may increase with the age of viewers. However, the developmental trajectory of the race effect in FFA responses, and its links to measures of face recognition or racial attitudes during childhood or adolescence, remain untested.

In the present cross-sectional study, European American (EA) children, adolescents and adults, each participated in a three-part experiment. We used functional magnetic resonance imaging (fMRI) to measure FFA responses to EA and African-American (AA) faces. Outside the scanner, we examined recognition memory and implicit associations for own- (EA) and other-race (AA) faces. For each measure, we estimated a race effect, using own- and other-race faces. Then, we asked how the race effects changed with age, and examined their relationships across and within age groups.

2 | METHODS

2.1 | Participants

Healthy EA children (ages 7–11, $N = 20$, 13 females), adolescents (ages 12–16, $N = 10$, 4 females) and adults (ages 19–35, $N = 15$, 8 females) participated in fMRI and behavioral tests outside the scanner, and were included in the final data analysis reported in our study. Another three children and two adults were removed due to excessive motion during the fMRI scan (see below).

Participants were right-handed with normal or corrected vision, and reported no history of neurological or psychiatric conditions or structural brain abnormalities. Children and adolescents were recruited from Palo Alto schools. Adult participants were Stanford University students. Informed consent conformed to requirements of the Stanford Panel on Human Subjects in Medical Research.

2.2 | FMRI

2.2.1 | Methodological considerations

One of our goals in the design and analysis of fMRI experiments was to minimize systematic, between-group differences that could confound the race effects we measured. These methodological considerations are detailed in SuppInfo 1.

2.2.2 | Choice of stimuli

All faces were of adult males in a frontal view, displaying a neutral expression with no eye-glasses or jewellery and minimal facial hair. This choice was motivated by two considerations: Firstly, it enabled us to relate present results to previous developmental

findings on the FFA that used all adult male faces (Cantlon et al., 2011; Golarai et al., 2007, 2010, 2015; Peelen et al., 2009; Scherf et al., 2007). Secondly, this stimulus set minimized stimulus variation and any potential interactions between age of viewers with stimulus attributes that were not the focus of our study. Specifically, various behavioral studies suggest interactions between age of viewers and facial attributes such as age, expression and paraphernalia (Freire & Lee, 2001; Harrison & Hole, 2009; Hills & Lewis, 2011). Also, there are conflicting reports regarding 'gender effects' in face processing, as some studies report that adult females display better recognition memory for female compared to male faces (Lewin & Herlitz, 2002; Ino et al 2010), while others found no evidence of a gender effect (Scherf et al., 2017). In our study, evaluation of these factors and their potential interaction with the race of face or age of viewers would require substantially longer experimental sessions, rendering them unfeasibly taxing for the youngest children.

Face images were matched for distinctiveness and attractiveness by four adult observers. Then, we measured image similarity for faces of each race, based on the average of a pixel-wise intensity-discrepancy measure applied to all within-race pairs of images (Grill-Spector et al., 1999), and found no significant differences in the within-race, face similarity among AA versus EA faces (**AA faces:** 0.30 ± 0.01 (M ± SD); **EA faces:** 0.31 ± 0.01 (M ± SD)). We used pictures of abstract sculptures in order to equate stimulus novelty and level of verbal labeling across categories and age groups (Gauthier et al., 2000; McGugin et al., 2012).

2.2.3 | Stimulus presentation during fMRI

During fMRI, participants viewed 60 gray-scale photographic unique exemplars of each stimulus category (i.e., AA faces, EA faces and abstract sculptures, see Figure S1). Each image was presented only once (except for ~14% of images that repeated for a one-back task, see below). Each stimulus category was presented in five pseudo-randomly ordered blocks. Blocks were 14 s long, followed by 14 s of fixation. Images were presented every 1 s, for 970 ms, followed by a 30 ms fixation baseline. All images were projected via a mirror mounted on the MRI coil (visual angle ~15°). Images were presented and responses were recorded, using a Macintosh G3 computer with Matlab 5.0 (Mathworks) and Psychtoolbox extensions (http://www.psychtoolbox.org).

2.2.4 | Task during fMRI

Participants were instructed to fixate on each image and press a button whenever they detected identical images appearing successively (a one-back task). Data on the accuracy and response times during performance of the 1-back task is plotted in Figure S1. Responses during the one-back task in the scanner were highly accurate (>90%) and similar across age groups (Figure S1A). A

two-way rmANOVA on response accuracy including factors of age group and stimulus image category showed no significant main effects of age, image category, or age by image-category interaction whether we included responses to images of objects or only AA and EA faces ($F_{2,42} < 0.6$, $p > 0.5$). In contrast, response times (RT) were longer among children than for adolescents ($t_{28} = 4.6$, $p < 0.0001$) or adults ($t_{33} = 5.67$, $p < 0.0001$, Figure S1B), as expected (Kail & Salthouse 1994; Ratcliff et al., 2012; Cromer et al., 2015; Egami et al., 2015; Golarai et al., 2015). Importantly, however, there were no interactions between age of participants and race of faces in accuracy or response times ($F_{2,42} < 0.95$, $p > 0.8$, two-way rmANOVA, Figure S1B).

2.2.5 | Scanning

Brain imaging was performed on a 3-Tesla whole-body General Electric Signa MRI scanner (General Electric) at the Lucas Center for Imaging, Stanford University, equipped with a quadrature bird-cage head coil. Participants were instructed to relax and stay still. We placed ample padding around each participant's head and also made use of a bite bar (made of Impression Compound Type I, Kerr Corporation) to stabilize head position and reduce motion-related artifacts during the scans. First, a high-resolution three-dimensional Fast "SPGR" anatomical scan (124 sagittal slices, 0.938 mm ×0.938 mm, 1.5-mm slice thickness, 256 × 256 image matrix) of the whole brain was obtained. Next, a T2-weighted, fast-spin-echo, in-plane scan with a slice prescription identical to that of the functional scan was acquired. Functional images were obtained with a T2* sensitive, gradient echo, spiral-in/out, pulse sequence using BOLD contrast. Full brain volumes were imaged using 21 slices (4 mm thick plus 1 mm skip), oriented parallel to the line connecting the anterior and posterior commissures. Brain volume images were acquired continuously with the following parameters: 1,400 ms TR, 30 ms TE, 70° flip angle, 240 mm field of view, 3.75 mm × 3.75 mm in-plane resolution, and 64 × 64 image matrix.

2.2.6 | Pre-processing

The first ten functional volumes were discarded to allow for T1 equilibration. Functional scans were (1) 'median-filtered' with an in-house algorithm to remove any transient BOLD artifacts that deviated more than 2 SD from the global (i.e. whole-brain) mean of BOLD time-series in each participant (detailed in SuppInfo 2), and replace by the mean of neighboring images in the time series; (2) realigned to the first image of the run to correct for participant's motion during the scan (SPM, Wellcome Department of Cognitive Neurology, see SuppInfo 2); and (3) co-registered to the subject-specific high-resolution whole brain anatomical volume (SPGR) in the native space. Data were not spatially smoothed or normalized to a template. All analyses were conducted in participants' native brain space. Data from three children and two adults were excluded due to excessive

motion (>2 mm translation). For the remaining participants, the average motion or total number of excluded BOLD images during the time series, and the average motion during the scan were similar across age groups (Ps <0.5, see SuppInfo 2).

2.2.7 | General linear model

For each participant, statistical modeling was performed using a GLM on motion-corrected functional images (without smoothing or spatial normalization). The fit of the GLM (as measured by the average % residual error of GLM within the individually- and anatomically-defined regions of interest of mid fusiform gyrus, see below), was similar across age groups ($p < 0.3$, see SuppInfo 2).

2.2.8 | Individually defined regions of interest (ROIs)

We used single-subject analysis of fMRI data. In each participant's native brain space, we individually defined (1) anatomical ROIs (based on anatomical landmarks), (2) functional ROIs based a combination of anatomical landmarks and a functional contrast (see 'peak' and 'functional ROIs' in 2 and 4 below), and (3) concentric ROIs based on a combination of anatomical landmarks, a functional contrast, and volumetric constrains. We used these complementary analyses with individually defined ROIs in each participants' native brain space in order to minimize spatial distortions and volume averaging (especially given the smaller size of the FFA in younger participants), following best practices in developmental studies of category selective regions in the ventral stream (Cantlon et al., 2011; Centanni et al., 2018; Golarai et al., 2007, 2010, 2015; Lafer-Sousa et al., 2016; Peelen et al., 2009; Scherf et al., 2007), as detailed below.

1. Anatomical ROIs: We created anatomical ROIs of the mid fusiform gyrus (mFG) in order to increase the precision of our search space for face-selective voxels (see below). Previous studies with high resolution fMRI indicate that multiple face-selective patches may be found along the length of the mFG (reviewed in Grill-Spector et al., 2017). Thus, the anatomical ROIs of mFG allowed inclusion of all face-selective voxels in this region, regardless of the specific location within the mFG. The anatomical ROIs were hand drawn with MRIcro (http://www.mricro.com) on subject-specific high-resolution anatomical images by a well-trained person, who was blind to the identity and age of the brains. The boundaries of each individual's mFG ROIs included (1) the lateral bank of the collateral sulcus, (2) the lateral bank of the occipito-temporal sulcus (OTS), (3) the fundus of the posterior transverse collateral sulcus, and a coronal plane tangent to the posterior edge of the amygdala, similar to previous publications (Golarai et al., 2007, 2015).
2. Peak ROI: We individually defined the peak of face selectivity (i.e., the voxel with highest t-value for the contrast [(AA +EA faces) >

objects]) within the subject-specific anatomical ROI of mFG (described above).

3. Concentric ROIs: We individually defined three non-overlapping, concentric ROIs, all centred at the peak of face-selectivity (i.e., the voxel with highest t-value for the contrast [(AA +EA faces) > objects]) within the subject-specific anatomical ROI of mFG (described above). The three non-overlapping concentric ROIs were defined in each hemisphere as follows (see Figure 1): (1) an ROI consisting of three contiguous voxels, including the most face-selective ("peak") voxel in the individual's FFA ('P3'); (2) a "shell volume" lying between P3 and a sphere equal to the average volume of the FFA in children ('C'); (3) a shell volume lying between the outer bound of 'C' and a larger sphere equal to the average volume of the FFA in adults ('A').

These concentric ROIs minimized age-related confounds in estimating the race effect across age groups. Note that differential responses to own- versus other-race faces may be less pronounced at the edges of the FFA due to volume averaging in all participants. However, due to the smaller volume of the FFA in children, this boundary effect could disproportionately influence the overall magnitude of the race effect in children's FFA. The concentric ROIs minimized such age related confounds by enabling us to (1) select voxels independently of their response properties (except for a single voxel with highest face selectivity in each hemisphere) and (2) evaluate the spatial extent of the race effect at and around the FFA, by comparing responses near the peak of face selectivity and at increasing distances from the peak, providing an estimate of the spatial organization of the race effect across age groups.

4. Functional (cluster) ROIs: We functionally defined the FFA as clusters of supra-threshold voxels, using the contrast ([AA +EA faces >objects], at $p < 10^{-4}$, voxel level) within the anatomical ROI of mFG in each hemisphere (see Figure S2). These face-selective voxels (i.e. the FFA) tended to be found more reliably in the right than the left hemisphere and in adults and adolescents than in children. Namely, we found the right FFA (rFFA) in 17/20 children, 10/10 adolescents, 15/15 adults; and the left FFA (lFFA) in 14/20 children, 8/10 adolescents, and 14/15 adults. The volume of the FFA was smaller in children (rFFA: 853 ± 58 mm^3; lFFA: 798 ± 35 mm^3) compared to adolescents (rFFA: 1,984 ± 103 mm^3; lFFA: 1,326 ± 112 mm^3) and adults (rFFA: 3,132 ± 206 mm^3; lFFA:1,296 ± 136 mm^3). These data are consistent with previous reports of a substantial age-dependent increase in the magnitude and spatial extent of face selectivity in the fusiform gyrus from childhood into adulthood (Cantlon et al., 2011; Golarai et al., 2007, 2010, 2015; Peelen et al., 2009; Scherf et al., 2007).

Note that the functional ROIs were used for a *dependent* analysis, as the data extracted for analysis were the same as those used to define the ROIs. The criterion for voxel selection was agnostic to the relative response magnitudes to AA or EA faces, which was the main focus of our analyses. These functional ROIs provided a more conventional means of assessing FFA responses and completed our analysis of the concentric ROIs.

2.2.9 | Extraction of BOLD signals and a measure of race-effect in ROI responses

We extracted BOLD signals from the concentric and functionally defined ROIs to find the percent signal change in response to visual stimuli (AA, EA, objects; e.g. Figure S3) and a measure of race effect (e.g. Figure 1). The raw time-course data were extracted from each voxel, high-pass filtered (0.0052 Hz cut-off) and shifted in time by 3 seconds to account for hemodynamic lag. We measured the mean BOLD signal during the entire period of each block after accounting for hemodynamic lag. These data were averaged across voxels within the ROI. The percent BOLD signal change for each image category was calculated relative to the average BOLD signal during fixation blocks as: $100 \cdot \frac{(category - fixation)}{fixation}$ (Figure S3). We also calculated a measure of race effect in BOLD signals based in percent signal change as [(EA–AA)/(EA+AA)] in each participant and hemisphere and averaged data across participants for each hemisphere and age group (Figure 1).

2.3 | Face-recognition memory

2.3.1 | Experimental procedures

Outside the scanner, participants performed a recognition-memory task using images similar to but not overlapping with fMRI stimuli. This approach enabled us to use a sufficiently small number of face stimuli for recognition memory to avoid a "floor effect" in children (see McKone et al., 2012). Alternative approaches (e.g. performing the face recognition task during fMRI) would require at least 50–60 remembered exemplars for reliable BOLD signals, which would overwhelm children's memory capacity based on our pilot studies. We extrapolated from the reported positive correlations between FFA responses during fMRI and face-recognition memory ability for own-race faces during separate behavioral tests (Golarai et al., 2007, 2010), expecting to find analogous links between FFA responses and face recognition ability for own- and other-race faces in data obtained from each participant in separate sessions.

During encoding, participants performed a one-back task, while viewing 10 AA and 10 EA face images in blocks (similar to the block design during fMRI). Each image was presented for 2 seconds during the encoding phase. About 15 min after the conclusion of the encoding phase, participants were presented with a surprise recognition test, and viewed all the 20 images from the encoding session plus 20 new faces (half AA and half EA). These images were presented one at a time, in random order and at a self-paced rate. Participants were instructed to indicate if they had seen the image before ('old') or not ('new') by pressing one of two computer keyboard buttons.

2.3.2 | Data analysis and a measure of race effect in face recognition

Performance for the recognition task was calculated for each face type and participant as *Performance=[hits – false alarms]/[number of old images]*, (see Figure S4). We also calculated a measure of race effect in face-recognition performance as a difference in performance for own- versus other-race faces (*Performance [EA-AA]=(Performance [EA] – Performance [AA])*, see Figure 2B) for each participant, then averaged participants' data within each age group (Figure 2A).

Recognition-memory data (see Figure S4) showed that performance across all age groups was (1) matched on at least one set of face stimuli (AA faces) and (2) significantly above zero for both AA and EA faces, allowing meaningful between group comparisons for both races of faces.

2.4 | Implicit Association Test (IAT)

2.4.1 | Experimental procedures

Using a test of implicit racial associations and following published procedures (Baron & Banaji, 2006; Greenwald et al., 2003), we examined each participant's response times (RT) to images of own- or other-race faces (not seen during fMRI or face recognition experiments) in association with positive or negative written words. We verbally instructed participants to view faces or words on the screen. Their task was to classify faces according to race, and words according to their positive or negative meaning, by pressing one of two keys, quickly and accurately. Participants viewed 8 images of adult faces (half AA, half EA, and half female for each race of faces) and 8 written words (half positive (e.g., flower, love, joy, nice) and half negative [e.g., hate, vomit, bomb, hell]) that presented one-at-a-time on the screen. The order of presentation of all stimuli was randomized.

During an initial block of practice trials participants viewed only faces and categorized them according to the race of face. In another block of practice trials, participants viewed only words and categorized them according to positive or negative meaning of the word.

The order of face or word blocks was randomized and counter-balanced across participants. After these practice blocks, participants performed the critical trials for IAT where words and faces were presented in an intermixed sequence. Participants were again asked to classify the race of each face (AA or EA) or valence of each word (positive or negative). During one block participants used the same key to indicate EA faces and positive words and another key for AA faces and negative words (i.e., *consistent* with positive own-race associations). In another block participants used the reverse pairing of race and words (i.e., *inconsistent* with positive own-race associations). The order of consistent vs. inconsistent blocks were counter balanced across participants. We recorded accuracy and response times for each stimulus during a total of 144 trials (72 faces, half AA, half EA; 72 words, half positive, half negative).

2.4.2 | Data analysis and measure of race effect in IAT

Reaction times (RTs) from consistent and inconsistent trials were used to assess the strength of positive or negative implicit associations with own- or other-race faces. Shorter RTs suggest stronger associations. We excluded trials with incorrect classification or latencies outside the range of *mean (all consistent & inconsistent trials) ±2 (standard deviation of mean)* in each participant. Then we calculated D′ for RTs of consistent vs. inconsistent trials in each participant (Figure 2D), and averaged data by age group (Figure 2C). Inclusion of responses with incorrect categorizations did not change the group averaged IAT-D′ scores (see Figure S5, red triangles).

2.5 | Statistical analysis of measures of race effect

For each of the fMRI and behavioral measures of race effect, we examined between age-group differences after binning the data into three age groups and submitting to analysis of variance (ANOVA), repeated measures ANOVAs (rmANOVAs) and *t*-tests, analogous to previous


FIGURE 1 Race effect in BOLD responses from mid fusiform gyrus. The magnitude of race effect [(EA – AA)/(EA+AA)] in response to face stimuli from individually defined ROIs in each hemisphere. Positive values along the y-axis indicate higher responses to own- than to other-race faces; negative values indicate the reverse. (a) The magnitude of race effect in responses were extracted from three individually defined, concentric and non-overlapping ROIs that were centered at the peak of face selectivity in the mid fusiform gyrus (i.e. highest t-value for the contrast [EA+AA faces >object]) in each participant. The magnitude of the race effect in responses from each ROI was averaged for each age group. Dashed lines: children (ages 7–12, *n* = 20); solid gray lines: adolescents (ages 12–16, *n* = 10). Black lines: adults (19–35, *n* = 15). Error bars: group SEM. '**P3**': Three adjacent voxels including the peak of face-selectivity. '**C**': a shell volume lying between P3 and a sphere equal to the average volume of the FFA in children. '**A**': a shell volume lying between the outer bound of 'C' and a larger sphere equal to the average volume of the FFA in adults. rmANOVA revealed significant main effects of age (*p* = 0.0005), of ROI (*p* = 0.0005) and of hemisphere (*p* < 0.05). See Table 1. (b) The magnitude of race-effect in responses from the P3 ROI from Figure 1a (above) in each participant is plotted along the y-axis and age of participants along the x-axis for each hemisphere. Pearson correlation values (r) are listed for each hemisphere, which was significant in the left hemisphere (*p* = 0.0005). See Table 10. (c) The magnitude of the race effect from a dependent analysis of responses from the individually-defined FFA (i.e., all supra-threshold voxels in mid fusiform gyrus for contrast [EA +AA > objects], *p* < 10⁻⁴, voxel level) is averaged for each age group and separately plotted for each of the right and left FFAs (rFFA, lFFA). Note that no supra-threshold voxels were found in a subset of participants. Gray bars: children (ages 7–12, rFFA: *n* = 17/20; lFFA: *n* = 14/20). Dark gray bars: adolescents (ages 12–16, rFFA *n* = 10/10; lFFA: *n* = 8/10). Black bars: adults (19–35, rFFA *n* = 15/15; lFFA *n* = 14/15). Error bars: group SEM. 2-way ANOVA revealed a significant main effect of age (****p* = 0.02). See Table 3

studies on the development of the FFA (Cantlon et al., 2011; Golarai et al., 2007, 2010, 2015; Peelen et al., 2009; Scherf et al., 2007). We also examined the Pearson correlations between (1) the magnitude of the race effect versus age of participants as continuous measures and (2) among measures of race effect after controlling for age.

2.5.1 | Exploratory mediation analysis

We focused an exploratory mediation analysis on the hypothesis that the FFA mediates the influence of implicit associations on face recognition memory, given (1) FFA's key role in face perception and recognition (Golby et al., 2001; Grill-Spector et al., 2004; Kanwisher et al., 1997), (2) the association between the developments of the FFA and face-recognition ability (Golarai et al., 2007, 2010), (3) the potential role of the FFA in mediating top-down modulations on face processing (Wojciulik et al., 1998) and (4) the correlation between implicit racial association and FFA responses to race of faces (Brosch et al., 2013). We performed the mediation analysis on the entire data set from children, adolescents and adults by applying a standard multiple-regression and bootstrapping procedures (5,000 iterations; PROCESS method, model 6, Hayes, 2013) in SPSS (IBM).

Race effect in the mid fusiform gyrus
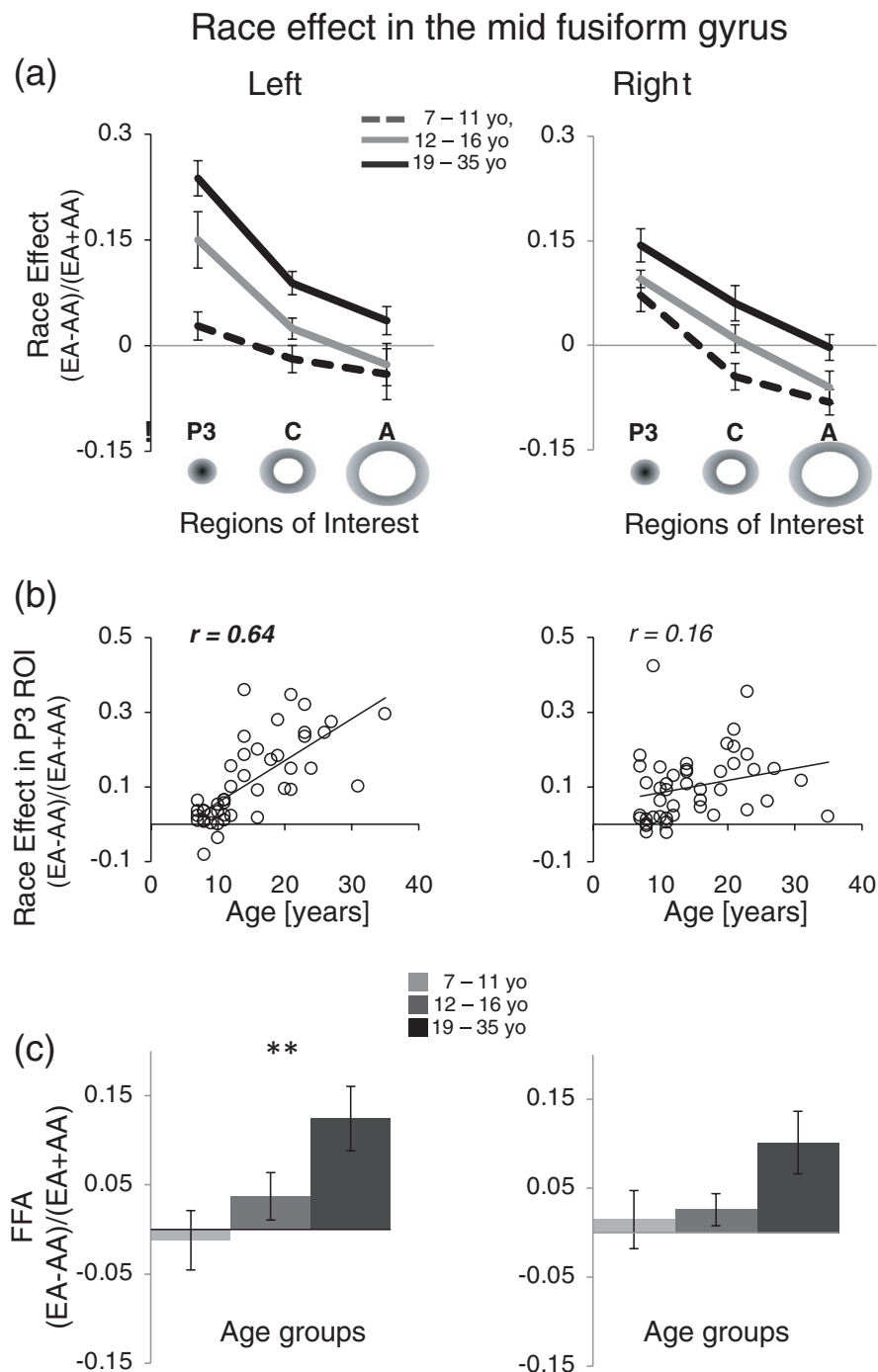
The results of this exploratory analysis supported correlations between the three measures of race effect, and a model where the FFA mediates the influence of implicit racial associations on racial bias in recognition memory, as summarized in SuppInfo 3. Given the cross-sectional nature of our data, our analyses do not establish causal relations. Also, given the limits of our statistical power we did not extend our analyses to compare all alternative models of how the three race effects may relate. Thus, we consider our analyses and their results exploratory. Yet, our findings confirm the statistical links among the three measures of race-effect that we report in Figure 3.

3 | RESULTS

In each EA participant we examined (1) brain responses to AA and EA faces in individually defined ROIs in the fusiform gyrus during fMRI; then outside the scanner we used new face stimuli and measured (2) face-recognition performance for AA and EA faces, and (3) implicit racial associations during the IAT. For each measure we determined the magnitude of the race effect by contrasting responses to own- versus other-race faces. We asked if the magnitude of race effects varied across age groups (Figures 1 and 2) and examined the relationship among these measures after controlling for age (Figure 3).

3.1 | The magnitude and spatial extent of the race effect in the fusiform gyrus increased with age

To test the hypothesis that FFA responses to own- versus other-race faces differentiate progressively with age, we examined the magnitude and spatial extent of the race effect in BOLD responses to AA and EA faces at and around the FFA among EA children, adolescents, and adults. First, we defined three concentric, non-overlapping ROIs of prespecified sizes, all centred on and at increasing distances from the most face-selective voxel in the mid fusiform gyrus (mFG) in each hemisphere and participant (see Methods). Then, we extracted signals from these ROIs and calculated a measure of race effect in their response amplitudes [(EA – AA)/(EA+AA)] (see Figure 1). These prespecified concentric ROIs enabled unbiased measurement and testing of age-related changes in the magnitude and spatial organization of responses to own- and other-race faces with uniform volumes and distances from peak of the FFA in every participant, circumventing potential confounds arising from the larger volume of the FFA in adults compared to children and adolescents (see Methods).

Figure 1a shows the magnitude of the race effect in each concentric ROI and age group.

To test the hypothesis that the magnitude of the race effect in responses within concentric ROIs at and around the FFA increased with age, we used a three-way repeated-measures analysis of variance (rmANOVA) on the magnitude of the race effect with factors of age group (children, adolescents, adults), ROI ('P3', 'C', 'A') and hemisphere (right, left). We found significant main effects of age group ($p < 0.0005$), ROI ($p < 0.0005$), and hemisphere ($p < 0.05$), but the 2- or 3-way interactions among these factors did not reach significance (see Table 1). Specifically, the magnitude of the race effect increased progressively from childhood into adulthood, as post hoc pair-wise comparisons among age groups showed significantly higher race effects in ROI responses among adults compared to children or adolescents, and among adolescents compared to children ($Ps<0.014$, see Table 2).

Regardless of age and hemisphere, the magnitude of the race effect was higher near the peak of face selectivity and declined in ROIs farther from this peak. Namely, pair-wise comparisons of ROIs showed significantly higher magnitudes of the race effect at 'P3' compared to 'C' and 'A' and at 'C' compared to 'A' ($t_{89}> 6.5$, $Ps<0.0001$). Finally, the overall magnitude of race effect was higher in the right than the left hemisphere ($p < 0.05$, Table 1). This hemispheric effect may be driven by differences in the magnitude of the race effect in the 'P3' ROI across the two hemispheres among children and adults (Figure 1A), consistent with a trend towards a three-way interaction between factors of age, ROI and hemisphere ($p = 0.09$, Table 1).

Next, we examined the correlation between participants age (as a continuous variable) and the magnitude of the race effect at each ROI. Consistent with the results of the ANOVA analysis, we found positive correlations between participants' age and the magnitude of the race effect among a subset of concentric ROIs bilaterally (see Figure 1B, Table 10). Furthermore, we found evidence of different spatial patterns in this age-related increase, depending on the hemisphere. Namely, in the left hemisphere this age effect was evident at ROIs that were close to the peak of face selectivity in mFG at 'P3' (Figure 1B) and 'C' ROIs (Table 10) and in the right hemisphere at the ROIs farther from the peak (i.e 'C' and 'A'; Table 10).

3.2 | The magnitude of the race effect in functionally defined FFA increased across age groups

Our analysis of the concentric ROIs supported the hypothesis that the magnitude of the race effect in responses of face-selective voxels of the FFA is greater in adults compared to the younger age groups. We further tested this hypothesis in functionally defined FFAs. We individually defined the FFA as the collection of all suprathreshold, face-selective voxels ([EA +AA > objects], $p < 10^{-4}$, voxel level) within the subject-specific, anatomical boundaries of the mFG in each hemisphere and then examined the magnitude of the race effect among these face-selective voxels (see data in Figure 1C). A two-way ANOVA, using the factors of age group (children, adolescents, adults) and hemisphere (right FFA, left FFA), showed a significant main effect of age group ($p = 0.02$, Table 3), but no effects of hemisphere or interactions between age group and hemisphere (see Table 3). Post hoc analyses showed a significantly higher race effect in adults compared to children ($p = 0.002$), and for adults compared to adolescents ($p < 0.05$–*1-tailed*, Table 4). Thus, the race effect in FFA responses increased from adolescence into adulthood.

Although our analysis did not show a significant main effect of hemisphere, separate post hoc analyses within each hemisphere

revealed an age-related increase in the magnitude of the race effect that was statistically significant in the left but not in the right FFA (left FFA: $F_{2,33}$ = 5.1, p = 0.002; right FFA: $F_{2, 39}$ = 2.66, p = 0.16, Bonferroni corrected for multiple comparisons, Figure 1C).

3.3 | Differentiation of responses to race of faces in functionally-defined FFA

We asked if the age-related increase in the magnitude of race effect in FFA responses was due to a race-of-face specific differentiation in these responses, or instead associated with a more general age-related change in the overall magnitude of FFA responses to both races of faces. Thus, we examined the percent signal change to each race of face (see Figure S3A). A 3-way rmANOVA on FFA response amplitudes to faces with factors of age group (children, adolescents, adults), race of faces (AA, EA), and hemisphere (right, left) showed a significant main effect of race of faces (p < 0.001) and a significant interaction between age group and race of faces (p < 0.002, Table 5, Figure S3A), consistent with an age-related differentiation in FFA responses to AA versus EA faces. Post-hoc comparisons revealed that this interaction was driven by significantly higher response amplitudes to EA versus AA faces among adult participants in the left hemisphere (t_{13} = 5.0, p < 0.003, 2-tailed paired t-test, Figure S3B). In contrast the difference in response amplitudes to AA versus EA faces was marginally significant among adolescents (t_7 = 1.7, p = 0.05, 1-tailed paired t-test) and not significant among children (t_{13} = 0.11, p = 0.91). Importantly, there were no significant effects of age group on the overall response amplitudes to faces (p = 0.45, Table 5), ruling out a generally lower responsiveness to faces in the FFA of younger age groups. Together, these findings suggest an age-related increase in the degree to which FFA responses to faces of own- versus other-races differ; likely due to age related increases in response amplitudes to own-race faces.

3.4 | The race effect in face-recognition performance increased across age groups

Face-recognition memory was overall better for own- than for other-race faces across the entire set of participants (t_{44} = 5.6, p = 0.0001 paired t-test, Figure 2A) and this race effect increased with the age of participants (p = 0.001, Table 6). Post hoc analysis showed a significantly higher race effect in adults compared to children (p = 0.001, Table 7). Likewise, there was a trend toward a positive correlation between age and the magnitude of race effect in face-recognition memory (Figure 2B, see Table 10). These data support an age-related increase in the magnitude of the race effect in face recognition during development from childhood into adulthood.

We asked if the age-related increase in this race effect was due to a differentiation in recognition memory for AA versus EA faces, or instead was associated with a general age-related change in the overall recognition performance for both race of faces. Thus, we examined a measure of recognition memory performance for each race of face in each individual and age group (Figure S4). A 2-way rmANOVA on recognition memory performance with factors of age group (children, adolescents, adults) and race of faces (AA, EA) showed a significant main effect of race of face stimuli (p < 0.0001, Table 8) and an interaction between age of participant and race of face stimuli (p < 0.003, Table 8). Importantly, however, the main effect of participants' age did not reach significance, as recognition memory improved with age only for EA faces (p < 0.0001, Table 9), but not for AA faces (p = 0.43, Table 9). Indeed, there were no age-related changes in recognition memory for AA faces in our data (see Figure S4). Thus, the age-related increase in the race effect in recognition memory was associated with an improvement in recognition performance for own-race faces contrasting with relatively stagnant recognition performance for other-race faces across age groups.

3.5 | Negative implicit racial associations increased across age groups

Scores from the implicit association test (IAT-D') revealed an own-race preference that was significantly higher than zero in each age group (ts>3.24, ps <0.013 2-tailed paired t-test, Figure 2C). This own-race preference in IAT-D' scores increased significantly with age, as shown by a one-way ANOVA ($F_{2, 42}$ = 6.67, p = 0.003). Post hoc analysis showed a significantly higher race effect in adults compared to children (p = 0.0001, 2-tailed t-test), and in adolescents compared to children (p = 0.05, 1-tailed t-test), but no difference between adults compared to adolescents (p = 0.23). Thus, the race effect in IAT scores became adult-like in adolescence.

We also found a corresponding trend toward a positive correlation between participants' age and the magnitude of the IAT-D' (Figure 2D, Table 10). These data are consistent with a progressive increase in the magnitude of the race effect in implicit racial associations during development from childhood into adolescence, likely reflecting social and cultural learning of group attitudes.

3.6 | Neural and behavioral measures of race effect were correlated

The three measures of race effect increased in magnitude across the age groups in our cross-sectional study (summarized in Figure S5). Moreover, the three measures of race effect were positively correlated across the entire group of participants after controlling for participants' age, (see Figure 3, Table 11). Namely, (after controlling for age) the magnitude of race effect in recognition memory was correlated with the magnitudes of race effect in the left FFA (Figure 3A) and the right FFA (data not shown), as well as the magnitude of race effect in IAT scores (Figure 3B). Meanwhile, (after controlling for age) IAT scores were positively correlated with the magnitude of race effect in the left FFA (Figure 3C) but not the right FFA (see Table 11).

To test if the strength of these correlations varied with age, we also examined and compared the correlations among these measures of race effect within each age group. However, we found no statistically significant differences among these correlations across age groups, despite of age group related numerical variations (Figure S6). These statistical links support the gradual development during childhood and adolescence of the three measures of race effect in our cross-sectional study. These findings are consistent with our working model of race-effect development, in which long-term and cumulative social and perceptual experiences along with current racial attitudes (e.g., implicit racial attitudes) together shape the race effects in FFA responses and face-recognition performance.

4 | DISCUSSION

We found that among EA participants who viewed faces of adult AAs and EAs, the magnitude of race effects increased with age during childhood and adolescence and into adulthood, manifesting as an advantage for own- over other-race faces in terms of (1) higher FFA response amplitudes, (2) better recognition memory performance, and (3) more positive implicit associations. Importantly, these three measures were correlated after controlling for age. Our results point to specific age-related increases in the magnitude of race effects that cannot be attributed to general maturational processes, such as improvements in task compliance, FFA responsiveness, or memory for all faces regardless of race.
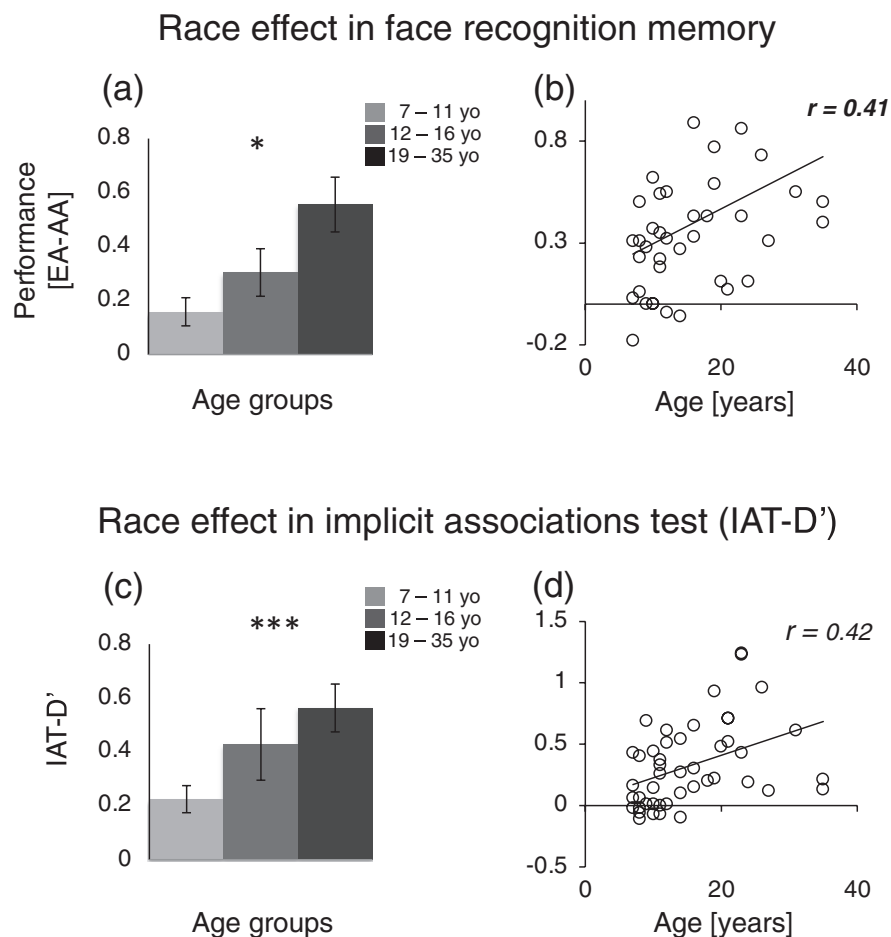

FIGURE 2 Race effect in behavioral measures. The magnitude of race effect in recognition-memory performance (top row) and implicit association test (IAT, bottom row) are each plotted as averages for each age group (left), and for each individual against participants' age (right). Gray bars: children (n = 20). Dark gray bars: adolescents (n = 10). Black bars: adults (n = 15). Error bars: group SEM. (a) Averaged recognition memory performance (defined in Methods) is plotted for each age group. Recognition memory was measured during a forced choice recognition test for AA and EA faces. A race effect was calculated as the difference scores in recognition memory performance for each race of face in each participant and averaged for each age group. One-way ANOVA revealed a significant main effect of age (*p = 0.001, Table 6). (b) Data from (A) are plotted for each individual as a function of participants' age. There was a trend toward a positive correlation between age and race effect in recognition memory (r = 0.41, p = 0.005), after Bonferroni correction for multiple comparisons, Table 10). (c) Average scores for the implicit association test (IAT) are plotted for each age group. IAT-D' was measured based on each participant's reaction times to AA and EA faces in association to positive or negative words. A race-effect was calculated as D' for each participant, and averaged for each age group. Pair-wise tests revealed significant differences between children and the other two age-groups, but no difference between adolescents and adults. One-way ANOVA revealed a significant main effect of age (***p = 0.003). (d) Data from (C) are plotted for each individual as a function of participants' age. The correlation between age and IAT-D' did not reach statistical significance (r = 0.42, p = 0.01) after Bonferroni correction for multiple comparisons (see Table 10)

Our findings reveal a gradual development of own-race preference in face processing and race-related implicit associations, suggesting that these differential responses to race of faces are shaped well into adolescence before becoming adult like among EA participants.

4.1 | Age-dependent differentiation in FFA representations of own-versus other-race faces

We found an age-related increase in differential responses of FFA to own- versus other-race faces in two complementary analyses. First,

in a series of expanding concentric ROIs centered at the peak of each participant's FFA (otherwise independent of response properties of the selected voxels), we found higher response amplitudes to own- than to other-race faces, and this race effect increased in magnitude and spatial extent from childhood into adulthood. Then, in a second (dependent) analysis based on functionally-defined FFA in each participant, we found a similar increase in the magnitude of the race effect in FFA responses in adults compared to children.

Together, these analyses revealed several features of the race effect in FFA responses and its development. First, response amplitudes tended to be higher to own- than to other-race faces among all age
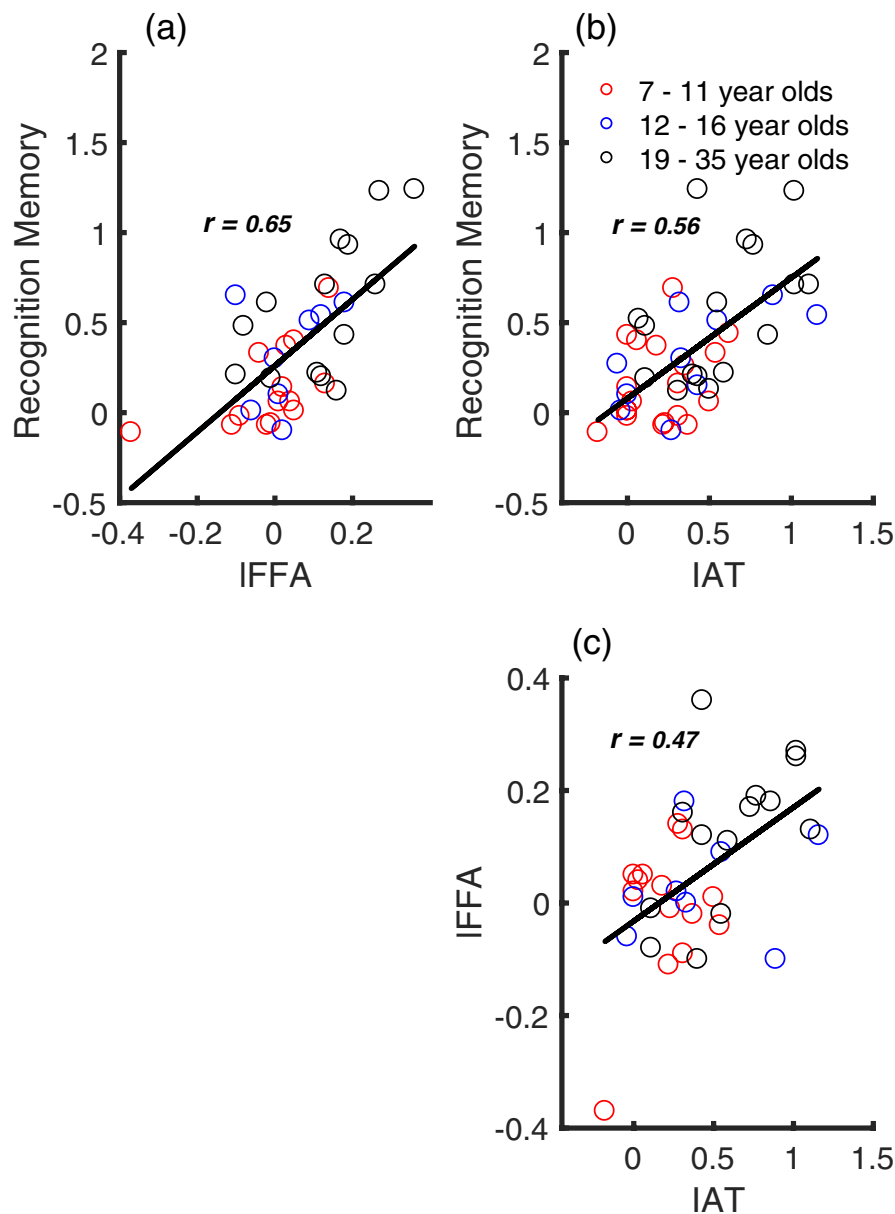

FIGURE 3 Correlations among measures of race effect. Plots show correlations among three measures of race effect. Each dot represents a single participant's score: red are children; blue are adolescents; black are adults. Each line represents the correlation among the measures of race-effect across all participants. The magnitude of race-effect in face recognition memory performance is plotted along the y-axis as a function of the race effect in (a) IFFA responses along the x-axis; and (b) IAT-D' scores along the x-axis. (c) The magnitude of race effect in IFFA responses is plotted along the y-axis as a function of race effect in IAT-D' scores along the x-axis. All Pearson correlations were controlled for age of participants and were statistically significant after Bonferroni correction for multiple comparisons ($p < 0.004$, Table 10).

TABLE 1 Results from a 3-way repeated measures ANOVA on magnitudes of race effect, including factors of age group, concentric ROI, and brain hemispheres

Source	F	p
Age group	25.53	**0.0005**
Concentric ROI	44.62	**0.0005**
Hemisphere	4.11	**0.046**
Age group × concentric ROI	0.37	0.83
Age group × hemisphere	2.04	0.14
Concentric ROI × Hemisphere	0.15	0.86
Age group × concentric ROI × Hemisphere	2.52	0.09

Significant effects are in bold. All p values are based on 2-tailed comparisons.

Concentric ROIs were centered at the voxel with the highest T value for the contrast *[(EA+AA)>object, at p < 0.0001]* within the mid fusiform gyrus, and included all voxels within the predefined volumes, regardless of functional properties. All concentric ROIs were defined in each hemisphere and in all participants: 20/20 children, 10/10 adolescents and 15/15 adults.

Age group: children, adolescents, adults.

Race of face: AA, EA.

Hemisphere: right, left.

groups in the most face-selective voxels of the FFA (i.e., in ROIs near the peak of face selectivity), consistent with an early onset of a race effect in higher order visual cortex before age 7. Second, the magnitude and spatial extent of this race effect in the mid fusiform gyrus increased with the age of participants during childhood and adolescence before reaching the adult level, consistent with the reported age related development of the FFA and its differential responses to face categories (Aylward et al., 2005; Cantlon et al., 2011; Gathers et al., 2004; Golarai et al., 2007, 2010, 2015; Peelen et al., 2009; Scherf et al., 2007, 2012). Third, this development was evident as an age-related increase in how differently the FFA responded to AA versus EA faces, and was not due to an overall lower responsiveness to faces in younger participants. Fourth, this development was associated with an age-related increase in the amplitude of responses to own-race faces. In contrast, the amplitude of responses to other-race faces was similar (and significantly above baseline) across all age groups. Thus, our findings could not be explained by a general inattention to face stimuli or lower BOLD signal quality in children during fMRI.

We found evidence of the development of a race effect in FFA responses in both hemispheres. However, we cannot rule out hemispheric differences in the magnitude and developmental trajectory of this race effect. Indeed, we found trends in our data suggesting a more protracted development of the race effect in the left than the right FFA, especially at the peak of face selectivity in the left mFG (e.g. Figure 1b). Previous studies found evidence of left lateralization of the race effect in FFA responses in adults (Golby et al., 2001), consistent with a role for the left hemisphere in categorization, in contrast with a role for the right hemisphere in fine-grain perceptual processes (Kosslyn et al., 1989). Future fMRI studies with higher spatial resolution and statistical power are needed to elucidate more

TABLE 2 Pair-wise, post hoc comparisons (Bonferroni corrected for multiple comparisons) for data in Table 1

Age groups	Mean difference	SE	p
Adults vs. Children	−0.11	0.01	**0.0005**
Adults vs. Adolescents	−0.06	0.02	**0.007**
Adolescents vs. Children	−0.05	0.02	**0.013**

TABLE 3 Results from 2-way ANOVA on magnitudes of race-effect in FFA (in percent signal change) responses to AA and EA face stimuli, including factors of age group and brain hemisphere

Source	F	p
Age group	**6.57**	**0.02**
Hemisphere	0.01	0.92
Age group × hemisphere	0.32	0.73

fully the anatomical details and hemispheric differences in the development of this race effect.

In adults, the FFA is involved in several stages of face processing, namely face perception, encoding, and recognition memory (Golby et al., 2001; Grill-Spector et al., 2004; Kanwisher et al., 1997). Behavioral studies report that the race effect in adults is evident during perceptual discrimination (Walker & Tanaka, 2003) and identity encoding and recognition (Ho & Pezdek, 2016). Given that participants in our study viewed unfamiliar faces and performed a one-back task during fMRI, the race effect in FFA responses that we found may reflect differences in perception of own- versus other-race faces. However, we cannot rule out the contribution of cognitive or mnemonic processes, such as automatic categorization of faces by race or incidental encoding, respectively.

The greater FFA responses to own- than to other-race faces could result from a combination of cumulative and short-term factors, such as viewers' greater perceptual expertise for faces of their own race (McGugin et al., 2011; Tanaka&, 2009; Yovel et al., 2012), and social motivation due to a culturally learned higher affinity for own-, as opposed to other-race, faces (Van Bavel et al., 2011; Young et al., 2012). Our findings suggest that cumulative perceptual and cultural experience may increasingly differentiate FFA responses to own- versus other-race faces during development that continues well into adulthood. This age-related increase in responsiveness to own-age faces is akin to experience-dependent enhancements associated with perceptual narrowing in visual or phoneme processing during infancy (Kelly et al., 2009; Nelson, 2001). Notably, we found that FFA's responses to other-race faces were stable across age groups, contrasting models of perceptual narrowing, involving *loss* of responsiveness to less frequently experienced categories (Maurer & Werker, 2014).

Other evidence suggests that development of the race effect in FFA responses is likely part of a broader process of perceptual specialization and socialization, involving a gradual differentiation in processing of own- versus other-group faces across a wide network of brain regions.

TABLE 4 Pair-wise post-hoc comparisons on data from Table 3

Age groups	Mean difference	SE	p
Adults vs Children	−0.11	0.03	**0.002**
Adults vs. Adolescents	−0.08	0.04	0.098
Adolescents vs. Children	−0.03	0.04	**1.0**

TABLE 5 Results from a 3-way repeated measures ANOVA on magnitudes of percent signal change to AA and EA face stimuli, extracted from the right and left FFA, including factors of age group, race of face, and brain hemisphere

Source	F	p
Age group	0.79	0.45
Race of face	11.35	**0.001**
Hemisphere	0.16	0.69
Age group × Race of face	6.59	**0.002**
Age group × hemisphere	0.12	0.89
Age group × Race of face × Hemisphere	0.34	0.71

Significant effects are in bold. All p values are based on 2-tailed comparisons.

The FFA was defined as all supra-threshold voxels within the anatomical boundaries of the mid fusiform gyrus for the contrast *[(EA+AA)>object, at p < 0.0001]*.

The right FFA was found in 17/20 children, 10/10 adolescents and 15/15 adults.

The left FFA was found in 14/20 children, 8/10 adolescents and 14/15 adults.

Age group: children, adolescents, adults.

Race of face: AA, EA.

Hemisphere: right, left.

For example, previous studies reported a similar development in the dependence of FFA responses on the *age* of faces, as adults responded more strongly to own- than other-age faces, but this own-age bias was weaker in children (Golarai et al., 2015). Likewise, a study that measured amygdala responses during a task involving matching facial emotions found a race effect that increased with the age of viewers, and correlated with their level of interracial contact (Telzer, Flannery, et al., 2013; Telzer, Humphreys, et al., 2013). In contrast, the present study was limited to analysis of FFA responses to adult male faces with neutral expression. Future studies with faces of different ages, expressions and genders, along with individual measures of perceptual expertise, social motivation and history of social contact, are needed to evaluate more fully the development of the race effect in relation to a wider range of neural substrates, affective contexts and social experience.

4.2 | The race effect in recognition of adult faces becomes more pronounced with age

A race effect in face-recognition memory was evident in all age groups and increased well into adolescence before reaching the adult level. The age-related increase in the race effect reflected improvement in recognition memory for EA faces with age, consistent with previous findings (Chance et al., 1982; Chien et al., 2018; Golarai et al., 2007, 2010; Goldstein & Chance, 1980; Weigelt et al., 2014). In contrast, we found that recognition memory for AA faces was relatively low and stable across age groups. Thus, recognition ability for own-race faces increased with age; recognition ability for other-race faces did not.

Although our findings suggest an age-related divergence in recognition ability for own- vs. other-race faces increasing into adulthood, published reports are inconsistent regarding the developmental trajectory of the race effect in face-recognition memory. Similar to our findings, some studies found an age-related increase in the magnitude of the race effect in face-recognition memory after age 7 (Chance et al., 1982; also see Chein et al., 2018) that was malleable to the changing racial composition of the social milieu during childhood and adolescence (Feinman & Entwisle, 1976; Sangrigoli et al., 2005). In contrast, others have reported stable levels of this race effect after age 7 (Anzures et al., 2014; Goodman et al., 2007; Pezdek et al., 2003), suggesting that early experience establishes a race effect that is relatively fixed and insensitive to subsequent experience (de Heering et al., 2010).

These contradictory findings may stem from variation in experimental design (e.g. in the number of faces presented during encoding or choice of encoding task). For example, some authors have questioned the reliability of reported measures of face-recognition memory in developmental studies due to between age-group differences in task difficulty, ability to maintain attention, memory or task compliance, and floor or ceiling effects (Crookes & McKone, 2009; McKone et al., 2012). In our study, the substantial and stable level of recognition-memory performance on AA faces across age groups suggests that none of these confounds could account for our developmental findings.

The development of face recognition memory for own-race faces reportedly lags the earlier development of face perception (Weigelt et al., 2014). Future studies are needed to elucidate the distinct contributions by perceptual and mnemonic processes in the development of the race effect in face recognition.

TABLE 6 Results from a 1-way ANOVA on magnitudes of race-effect in recognition memory

Source	F	p
Age group	**8.41**	**0.001**

TABLE 7 Pair-wise post-hoc comparisons on data from Table 6

Age groups	Mean difference	SE	p
Adults vs. Children	−0.41	0.1	**0.001**
Adults vs. Adolescents	−0.15	0.11	0.559
Adolescents vs. Children	−0.25	0.12	0.12

TABLE 8 Results from a 2-way repeated measures ANOVA on recognition memory performance for AA and EA face stimuli, including factors of age group and race of face

Source	F	p
Age group	1.89	0.16
Race of face	**36.5**	**0.0001**
Age group × Race of face	**6.80**	**0.003**

TABLE 9 Results from separate 1-way ANOVAs on recognition memory performance for AA or EA face stimuli for the factor of age group

Source	F	p
Age group: performance on AA faces	0.85	0.43
Age group: performance on EA face	**11.83**	**0.0001**

Significant effects are in bold. All *p* values are based on 2-tailed comparisons.

Age group: children, adolescents, adults.

Race of face: AA, EA.

4.3 | An own-race preference in implicit racial associations becomes more pronounced with age

We found that all age groups favored own- vs. other-race faces during an implicit association test. However, the magnitude of this race effect increased across age groups from childhood to adolescence before reaching the adult level.

The early onset of implicit racial bias in our data is consistent with previous findings in 6 year olds (Baron & Banaji, 2006; reviewed in Dunham et al., 2008), and may reflect differential contact, familiarity, and associations with own- versus other races, starting in early life. However, the increase in the magnitude of IAT-D' with age in our study contradicts earlier findings of adult-like IAT-D' among 6 and 10 year olds (Baron & Banaji, 2006). These divergent results may be due to cross-study variations in the age of face stimuli. Namely, we used adult faces for all participants during IAT, whereas Baron and Banaji (2006) used children's faces for all participants. One possibility is that negative racial attitudes are more evident in the context of own-age peers than other-age groups, involving an interaction between the age of viewer and age of face stimuli in the IAT scores. Future developmental studies with face stimuli from a range of ages are needed to determine the overall effect of age, and the potential interactions between the factors of age and race of participants and of target faces on IAT measures. Similarly, a variety of factors, such as social context (Lowery et al., 2001), perceptual experience (Lebrecht et al., 2009), familiarity with individuals of other races (Lebrecht et al., 2009; Roos et al., 2013), and beliefs about race (Hong et al., 2009), all reportedly influence measures of racial associations in adults. Future studies are needed to examine the influence of these factors in children.

The psychological processes underlying IAT performance, and the impact of implicit associations on social behavior, are currently debated (Carlsson & Agerstrom, 2016; Greenwald et al., 2009, 2015; Oswald et al., 2015). For example, implicit associations may reveal subjective feelings or attitudes towards a race, or instead reflect learning of cultural stereotypes - which may either align with or contradict personal beliefs and feelings. Our study was not designed to resolve this debate. However, our findings contribute to this literature by further establishing reported links between IAT scores and behavioral (Lebrecht et al., 2009) and neural (Brosch et al., 2013) measures of face processing in adults. Critically, our data revealed that race-related implicit associations with unfamiliar adult faces are not fixed in early childhood, but instead develop during childhood and into adolescence, consistent with the cumulative influence of social learning.

4.4 | Relations among FFA responses, recognition memory performance, and implicit associations

The three measures of race effect in our study were correlated with one another even after controlling for age. Accordingly, we hypothesized that implicit racial associations are statistically linked to differential neural representation of own- and other-race faces in the FFA. These representations are thought to contribute to the race effect in face recognition memory (Golby et al., 2001). Our exploratory mediation analysis supported this hypothesis. Future longitudinal studies are needed to determine the causal relations between implicit racial associations and the race effect in recognition memory, and the potential role of the FFA.

TABLE 10 Correlation of participants' age with measures of race-effect

	Right fusiform gyrus			Left fusiform Gyrus				
	3P	*C*	*A*	*3P*	*C*	*A*	*Memory*	*IAT*
age r	0.16	**0.20**	**0.44**	**0.64**	**0.48**	0.036	0.41	0.42
P	0.29	**0.003**	**0.002**	**0.0005**	**0.001**	0.016	0.005	0.01

Significant effects are in bold. All P values are based on two-way comparisons, and Bonferroni corrected significance for two-way tests at alpha =0.05 based on 14 correlation tests (*p* = 0.05/14 = 0.0036).

Data are from 20 children, 10 adolescents, 15 adults.

Concentric ROIs (*P3, C, A*) were defined in the right and left fusiform gyrus as described in methods.

Memory : race effect in face recognition memory performance.

IAT : race effect in implicit association test.

TABLE 11 Partial correlations after controlling for participants' age

	lFFA	rFFA	IAT
Memory			
R	0.65	0.54	0.56
P	0.0005	0.001	0.0005
IAT			
r	0.475	0.23	
P	0.003	0.18	
rFFA			
r	0.54		
P	0.001		

Bonferroni corrected significance at $p < 0.0036$, based on 14 comparisons in Tables 6&7, i.e. 0.05/14 = 0.0036.

The FFA was defined as all supra-threshold voxels within the anatomical boundaries of the mid fusiform gyrus for the contrast *[(EA+AA)>object*, *at $p < 0.0001$]*.

rFFA : The right FFA was found in 17/20 children, 10/10 adolescents and 15/15 adults.

lFFA : The left FFA was found in 14/20 children, 8/10 adolescents and 14/15 adults.

The influence of implicit racial attitudes on face processing may involve recursive interactions among a combination of short- and long-term mechanisms. In the short-term, racial attitudes may modulate viewers' attention and social motivation and shape the quality and quantity of face-to-face interactions, influencing face perception and memory. In other words, implicit racial attitudes may reflect aspects of cognitions and motivations that influence if and how people take advantage of possibilities for interaction with individuals of other races. Over time and with repetition, the short-term influences of implicit attitudes may cumulatively shape habitual patterns of face viewing, and long-term face representations (Valentine et al., 2016), leading to relatively persistent differences in processing of own- vs. other-race faces. Moreover, the interactions between implicit associations and face perception may be bidirectional (e.g., Lebrecht et al., 2009), consistent with a number of psychological models of recursive interactions between perception, affect and cognition (Cunningham & Zelazo, 2007; Gross, 2015; Walton & Wilson, 2018). Our experiments were not designed to resolve the developmental roles of the various short- vs. long-term influences on race effects in face processing. Nonetheless, our findings clearly show that racial attitudes and a difference in processing of own- and other-race faces develop during childhood and adolescence before becoming adult-like among our EA participants.

Future studies that include individuals from more racial groups (e.g. African-American, Asian-American) would be crucial to determine the developmental trajectories of these race effects across groups, and to test for any variations in these trajectories arising from differences in socio-cultural experiences across groups. Furthermore, studies with larger sample sizes are needed to determine more precisely the temporal trajectory of the various measures of race effect and any developmental changes in the strength of their correlations. Finally, longitudinal studies are needed to (1) determine the contribution of generational differences in our findings of age-related increases in the measures of race effect, (2) parse the contribution of short- vs. long-term processes of these race effects during development, and (3) elucidate their underlying causal mechanisms.

In conclusion, we found evidence among EA participants that race effects involving AA and EA face representations in FFA, performance in face-recognition memory, and implicit associations all developed during childhood and well into adolescence and adulthood, and were statistically linked. These findings suggest that social and perceptual experiences shape a protracted development of race effects in face processing well into adulthood.

REFERENCES

Anzures, G., Kelly, D. J., Pascalis, O., Quinn, P. C., Slater, A. M., de Vivies, X., & Lee, K. (2014). Own- and other-race face identity recognition in children: the effects of pose and feature composition. *Developmental Psychology*, 50, 469–481.

Aylward, E. H., Park, J. E., Field, K. M., Parsons, A. C., Richards, T. L., Cramer, S. C., & Meltzoff, A. N. (2005). Brain activation during face perception: Evidence of a developmental change. *Journal of Cognitive Neuroscience*, 17, 308–319.

Baron, A. S., & Banaji, M. R. (2006). The development of implicit attitudes. Evidence of race evaluations from ages 6 and 10 and adulthood. *Psychological Science*, 17, 53–58.

Bernstein, M. J., Young, S. G., & Hugenberg, K. (2007). The cross-category effect: mere social categorization is sufficient to elicit an own-group bias in face recognition. *Psychological Science*, 18, 706–712.

Blandon-Gitlin, I., Pezdek, K., Saldivar, S., & Steelman, E. (2014). Oxytocin eliminates the own-race bias in face recognition memory. *Brain Research*, 1580, 180–187.

Brosch, T., Bar-David, E., & Phelps, E. A. (2013). Implicit race bias decreases the similarity of neural represetations of Black and White. *Faces Psychology Science*, 24, 160–166.

Cantlon, J. F., Pinel, P., Dehaene, S., & Pelphrey, K. A. (2011). Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cerebral Cortex*, 21, 191–199.

Carlsson, R., & Agerstrom, J. (2016). A closer look at the discrimination outcomes in the IAT literature. *Scandinavian Journal of Psychology*, 57, 278–287.

Cassia, V. M., Kuefner, D., Picozzi, M., & Vescovo, E. (2009). Early experience predicts later plasticity for face processing: evidence for the reactivation of dormant effects. *Psychological Science*, 20, 853–859.

Cassia, V. M., Picozzi, M., Kuefner, D., & Casati, M. (2009). Why mix-ups don't happen in the nursery: evidence for an experience-based interpretation of the other-age effect. *Quarterly Journal of Experimental Psychology*, 62, 1099–1107.

Centanni, T. M., Norton, E. S., Park, A., Beach, S. D., Halverson, K., Ozernov-Palchik, O., Gaab, N., & Gabrieli, J. D. E. (2018). Early development of letter specialization in left fusiform is associated with better word reading and smaller fusiform face area. *Developmental Science*, 21, e12658. https://doi.org/10.1111/desc.12658

Chance, J. E., Turner, A. L., & Goldstein, A. G. (1982). Development of differential recognition for own- and other-race faces. *Journal of Psychology, 112*, 29–37.

Chien, S. H., Tai, C. L., & Yang, S. F. (2018). The development of the own-race advantage in school-age children: A morphing face paradigm. *PLoS One, 13*(4), e0195020. https://doi.org/10.1371/journal.pone.0195020

Cromer, J. A., Schembri, A. J., Harel, B. T., & Maruff, P. (2015). The nature and rate of cognitive maturation from late childhood to adulthood. *Frontiers in Psychology, 6*, 704.

Crookes, K., & McKone, E. (2009). Early maturity of face recognition: no childhood development of holistic processing, novel face encoding, or face-space. *Cognition, 111*, 219–247.

Cunningham, W. A., Preacher, K. J., & Banaji, M. R. (2001). Implicit attitude measures: Consistency, stability, and convergent validity. *Psychological Science, 12*, 163–170.

de Heering, A., de Liedekerke, C., Deboni, M., & Rossion, B. (2010). The role of experience during childhood in shaping the other-race effect. *Developmental Science, 13*, 181–187.

Dunham, Y., Baron, A. S., & Banaji, M. R. (2008). The development of implicit intergroup cognition. *Trends in Cognitive Sciences, 12*, 248–253.

Egami, C., Yamashita, Y., Tada, Y., Anai, C., Mukasa, A., Yuge, K., Nagamitsu, S., & Matsuishi, T. (2015). Developmental trajectories for attention and working memory in healthy Japanese school-aged children. *Brain and Development, 37*, 840–848.

Feinman, S., & Entwisle, D. R. (1976). Children's ability to recognize other children's faces. *Child Development, 47*, 506–510.

Freire, A., & Lee, K. (2001). Face recognition in 4- to 7-year-olds: processing of configural, featural, and paraphernalia information. *Journal of Experimental Child Psychology, 80*, 347–371.

Gathers, A. D., Bhatt, R., Corbly, C. R., Farley, A. B., & Joseph, J. E. (2004). Developmental shifts in cortical loci for face and object recognition. *NeuroReport, 15*, 1549–1553.

Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience, 3*, 191–197.

Germine, L. T., Duchaine, B., & Nakayama, K. (2011). Where cognitive development and aging meet: Face learning ability peaks after age 30. *Cognition, 118*, 201–210.

Golarai, G., Ghahremani, D. G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J. L., Gabrieli, J. D., & Grill-Spector, K. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neuroscience, 10*, 512–522.

Golarai, G., Liberman, A., & Grill-Spector, K. (2015). Experience Shapes the Development of Neural Substrates of Face Processing in Human Ventral Temporal Cortex. *Cerebral Cortex, 27*, 1229–1244.

Golarai, G., Liberman, A., Yoon, J. M., & Grill-Spector, K. (2010). Differential development of the ventral visual cortex extends through adolescence. *Frontiers in Human Neuroscience, 3*, 80.

Golby, A. J., Gabrieli, J. D., Chiao, J. Y., & Eberhardt, J. L. (2001). Differential responses in the fusiform region to same-race and other-race faces. *Nature Neuroscience, 4*, 845–850.

Goldstein, A. G., & Chance, J. E. (1980). Memory for faces and schema theory. *Journal of Psychology, 105*, 47–59.

Goodman, G. S., Sayfan, L., Lee, J. S., Sandhei, M., Walle-Olsen, A., Magnussen, S., Pezdek, K., & Arredondo, P. (2007). The development of memory for own- and other-race faces. *Journal of Experimental Child Psychology, 98*, 233–242.

Greenwald, A. G., Banaji, M. R., & Nosek, B. A. (2015). Statistically small effects of the implicit association test can have societally large effects. *Journal of Personality and Social Psychology, 108*, 553–561.

Greenwald, A. G., Nosek, B. A., & Banaji, M. R. (2003). Understanding and using the implicit association test: I. An improved scoring algorithm. *Journal of Personality and Social Psychology, 85*, 197–216.

Greenwald, A. G., Poehlman, T. A., Uhlmann, E. L., & Banaji, M. R. (2009). Understanding and using implicit association test: III. Meta-analysis of predictive validity. *Journal of Personality and Social Psychology, 97*, 17–41.

Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience, 7*, 555–562.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron, 24*, 187–203.

Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience, 3*, 837–843.

Grill-Spector, K., Weiner, K. S., Kay, K., & Gomez, J. (2017). The functional neuroanatomy of human face perception. *Annual Review of Vision Science, 3*, 167–196.

Gross, J. J. (2015). Emotion regulation: Current status and future prospects. *Psychological Inquiry, 26*, 1–26.

Guassi Moreira, J. F., Van Bavel, J. J., & Telzer, E. H. (2017). The neural development of 'Us and Them'. *Social Cognitive and Affective Neuroscience, 12*, 184–196.

Harrison, V., & Hole, G. J. (2009). Evidence for a contact-based explanation of the own-age bias in face recognition. *Psychonomic Bulletin & Review, 16*, 5.

Hayes, A. F. (2013). *Introduction to mediation, moderation, and conditional process analysis: A regression-based approach.* The Guilford Press.

Heron-Delaney, M., Anzures, G., Herbert, J. S., Quinn, P. C., Slater, A. M., Tanaka, J. W., Lee, K., & Pascalis, O. (2011). Perceptual training prevents the emergence of the other race effect during infancy. *PLoS One, 6*, e19858.

Hills, P. J., & Lewis, M. B. (2011). The own-age face recognition bias in children and adults. *Quarterly Journal of Experimental Psychology, 64*, 17–23.

Ho, M. R., & Pezdek, K. (2016). Postencoding cognitive processes in the cross-race effect: Categorization and individuation during face recognition. *Psychonomic Bulletin & Review, 23*, 771–780.

Hong, Y. Y., Chao, M. M., & No, S. (2009). Dynamic interracial/intercultural processes: The role of lay theories of race. *Journal of Personality, 77*, 1283–1309.

Kail, R., & Salthouse, T. A. (1994). Processing speed as a mental capacity. *Acta Psychologica, 86*, 199–225.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*, 4302–4311.

Kelly, D. J., Liu, S., Leec, L. K., Quinn, P. C., Pascalis, O., Slater, A. M., & Ge, L. (2009). Development of the other-race effect during infancy: Evidence toward universality? *Journal of Experimental Child Psychology, 104*(1), 105–114. https://doi.org/10.1016/j.jecp.2009.01.006

Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. (1989). Evidence for two types of spatial representations: hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 723–735.

Lafer-Sousa, R., Conway, B. R., & Kanwisher, N. G. (2016). Color-biased regions of the ventral visual pathway lie between face- and place-selective regions in humans, as in macaques. *Journal of Neuroscience, 36*, 1682–1697. https://doi.org/10.1523/JNEUROSCI.3164-15.2016

Lebrecht, S., Pierce, L. J., Tarr, M. J., & Tanaka, J. W. (2009). Perceptual other-race training reduces implicit racial bias. *PLoS One, 4*, e4215.

Lewin, C., & Herlitz, A. (2002). Sex differences in face recognition–women's faces make the difference. *Brain and Cognition, 50*, 121–128.

Lowery, B. S., Hardin, C. D., & Sinclair, S. (2001). Social influence effects on automatic racial prejudice. *Journal of Personality and Social Psychology, 81*, 842–855.

Macchi, C. V. (2011). Age biases in face processing: the effects of experience across development. *British Journal of Psychology*, *102*, 816–829.

Malpass, R. S., & Kravitz, J. (1969). Recognition for faces of own and other race. *Journal of Personality & Social Psychology*, *13*, 330–334.

Markant, J., Oakes, L. M., & Amso, D. (2016). Visual selective attention biases contribute to the other-race effect among 9-month-old infants. *Developmental Psychobiology*, *58*, 355–365.

Marsh, B. U., Pezdek, K., & Ozery, D. H. (2016). The cross-race effect in face recognition memory by bicultural individuals. *Acta Psychol (Amst)*, *169*, 38–44.

Maurer, D., & Werker, J. F. (2014). Perceptual narrowing during infancy: A comparison of language and faces. *Developmental Psychobiology*, *56*(2), 154–178. https://doi.org/10.1002/dev.21177

McGugin, R. W., Gatenby, J. C., Gore, J. C., & Gauthier, I. (2012). High-resolution imaging of expertise reveals reliable object selectivity in the fusiform face area related to perceptual performance. *Proceedings of the National Academy of Sciences*, *109*, 17063–17068.

McGugin, R. W., Tanaka, J. W., Lebrecht, S., Tarr, M. J., & Gauthier, I. (2011). Race-specific perceptual discrimination improvement following short individuation training with faces. *Cognitive Science*, *35*, 330–347.

McKone, E., Crookes, K., Jeffery, L., & Dilks, D. D. (2012). A critical review of the development of face recognition: experience is less important than previously believed. *Cogn Neuropsychol*, *29*, 174–212.

Nelson, C. A. (2001). The development and neural bases of face recognition. *Infant and Child Development*, *10*, 3–18.

Oswald, F. L., Mitchell, G., Blanton, H., Jaccard, J., & Tetlock, P. E. (2015). Predicting ethnic and racial discrimination: A meta-analysis of IAT criterion studies. *Journal of Personality and Social Psychology*, *105*, 171–192.

Peelen, M. V., Glaser, B., Vuilleumier, P., & Eliez, S. (2009). Differential development of selectivity for faces and bodies in the fusiform gyrus. *Developmental Science*, *12*, F16–25.

Pezdek, K., Blandon-Gitlin, I., & Moore, C. (2003). Children's face recognition memory: more evidence for the cross-race effect. *Journal of Applied Psychology*, *88*, 760–763.

Ratcliff, R., Love, J., Thompson, C. A., & Opfer, J. E. (2012). Children are not like older adults: A diffusion model analysis of developmental changes in speeded responses. *Child Development*, *83*, 367–381.

Roos, L. E., Lebrecht, S., Tanaka, J. W., & Tarr, M. J. (2013). Can singular examples change implicit attitudes in the real-world? *Frontiers in Psychology*, *4*, 594.

Sangrigoli, S., & De Schonen, S. (2004). Recognition of own-race and other-race faces by three-month-old infants. *Journal of Child Psychology and Psychiatry*, *45*, 1219–1227.

Sangrigoli, S., Pallier, C., Argenti, A. M., Ventureyra, V. A., & de Schonen, S. (2005). Reversibility of the other-race effect in face recognition during childhood. *Psychological Science*, *16*, 440–444.

Sauerland, M., & Sporer, S. L. (2009). Fast and confident: postdicting eyewitness identification accuracy in a field study. *Journal of Experimental Psychology: Applied*, *15*, 46–62.

Scherf, K. S., Behrmann, M., & Dahl, R. E. (2012). Facing changes and changing faces in adolescence: a new model for investigating adolescent-specific interactions between pubertal, brain and behavioral development. *Developmental Cognitive Neuroscience*, *2*, 199–219.

Scherf, K. S., Behrmann, M., Humphreys, K., & Luna, B. (2007). Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. *Developmental Science*, *10*, F15–30.

Scherf, K. S., Elbich, D. B., & Motta-Mena, N. V. (2017). Investigating the influence of biological sex on the behavioral and neural basis of face recognition. *eNeuro 4*, 104–117.

Sporer, S. L. (1991). Deep–deeper–deepest? Encoding strategies and the recognition of human faces. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *17*, 323–333.

Tanaka, J. W., & Pierce, L. J.(2009). The neural plasticity of other-race face recognition. *Cognitve Affective and Behavioral Neuroscience*, *9*, 9.

Telzer, E. H., Flannery, J., Shapiro, M., Humphreys, K. L., Goff, B., Gabard-Durman, L., Gee, D. D., & Tottenham, N. (2013). Early experience shapes amygdala sensitivity to race: an international adoption design. *Journal of Neuroscience*, *33*, 13484–13488.

Telzer, E. H., Humphreys, K. L., Shapiro, M., & Tottenham, N. (2013). Amygdala sensitivity to race is not present in childhood but emerges over adolescence. *Journal of Cognitive Neuroscience*, *25*, 234–244.

Valentine, T., Lewis, M. B., & Hills, P. J. (2016). Face-space: A unifying concept in face recognition research. *Quarterly Journal of Experimental Psychology*, *69*, 1996–2019.

Van Bavel, J. J., & Cunningham, W. A. (2009). Self-categorization with a novel mixed-race group moderates automatic social and racial biases. *Personality and Social Psychology Bulletin*, *35*, 321–335.

Van Bavel, J. J., Packer, D. J., & Cunningham, W. A. (2008). The neural substrates of in-group bias: a functional magnetic resonance imaging investigation. *Psychological Science*, *19*, 1131–1139.

Van Bavel, J. J., Packer, D. J., & Cunningham, W. A. (2011). Modulation of the fusiform face area following minimal exposure to motivationally relevant faces: Evidence of in-group enhancement (not out-group disregard). *Journal of Cognitive Neuroscience*, *23*, 3343–3354.

Vogel, M., Monesson, A., & Scott, L. S. (2012). Building biases in infancy: The influence of race on face and voice emotion matching. *Development Science*, *15*, 359–372.

Walker, P. M., & Tanaka, J. W. (2003). An encoding advantage for own-race versus other-race faces. *Perception*, *32*, 1117–1125.

Walton, G. M., & Wilson, T. D. (2018). Wise interventions: Psychological remedies for social and personal problems. *Psychological Review*, *125*, 617–655. https://doi.org/10.1037/rev0000115

Weigelt, S., Koldewyn, K., Dilks, D. D., Balas, B., McKone, E., & Kanwisher, N. (2014). Domain-specific development of face memory but not face perception. *Development Science*, *17*, 47–58.

Wheeler, A., Anzures, G., Quinn, P. C., Pascalis, O., Omrin, D. S., & Lee, K. (2011). Caucasian infants scan own- and other-race faces differently. *PLoS One*, *6*, e18621.

Wojciulik, E., Kanwisher, N., & Driver, J. J. (1998). Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *Neurophysiology*, *79*, 1574–1578. https://doi.org/10.1152/jn.1998.79.3.1574

Xiao, W. S., Xiao, N. G., Quinn, P. C., Anzures, G., & Lee, K. (2013). Development of face scanning for own- and other-race faces in infancy. *International Journal of Behavioral Development*, *37*, 100–105.

Young, S. G., Hugenberg, K., Bernstein, M. J., & Sacco, D. F. (2012). Perception and motivation in face recognition: a critical review of theories of the cross-race effect. *Personality & Social Psychology Review*, *16*, 26.

Yovel, G., Halsband, K., Pelleg, M., Farkash, N., Gal, B., & Goshen-Gottstein, Y. (2012). Can massive but passive exposure to faces contribute to face recognition abilities? *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 285–289.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.