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# Brain Network Activity During Face Perception: The Impact of Perceptual Familiarity and Individual Differences in Childhood Experience

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## Abstract

An extended distributed network of brain regions supports face perception. Face familiarity influences activity in brain regions involved in this network, but the impact of perceptual familiarity on this network has never been directly assessed with the use of partial least squares analysis. In the present work, we use this multivariate statistical analysis to examine how face-processing systems are differentially recruited by characteristics of the targets (i.e. perceptual familiarity and race) and of the perceivers (i.e. childhood interracial contact). Novel faces were found to preferentially recruit a large distributed face-processing network compared with perceptually familiar faces. Additionally, increased interracial contact during childhood led to decreased recruitment of distributed brain networks previously implicated in face perception, salience detection, and social cognition. Current results provide a novel perspective on the impact of cross-race exposure, suggesting that interracial contact early in life may dramatically shape the neural substrates of face perception generally.

**Key words:** brain networks, face perception, interracial contact

## Introduction

When making sense of our social environment, we take advantage of our extensive experience extracting meaningful information from faces. Even when encountering new individuals, perceptual facial cues rapidly and efficiently provide us with a wealth of information (e.g. sex, age, race, dominance, attractiveness, and intentions) to guide potential social interactions (Ito and Urland 2003; Cloutier et al. 2005; Willis and Todorov 2006). An extended distributed network of brain regions supports this ability to infer knowledge from faces (Haxby and Gobbini 2011) and components of this network have been shown to be modulated by perceptual familiarity (Kosaka et al. 2003; Gobbini and Haxby 2006; Kriegeskorte et al. 2007; Cloutier et al. 2011a). In the present work, we take advantage of advances in multivariate partial least squares (PLS) analysis to examine how the face-processing system, as a whole, is differentially recruited as a function of characteristics of the targets (i.e. familiarity and race) or those of the perceivers (i.e. face-processing expertize).

Among the brain regions believed to compose the network supporting face perception, the fusiform face area (FFA) located

in the ventral temporal cortex (VTC), the inferior occipital gyrus (IOG), and the posterior superior temporal sulcus (STS) have been suggested to respond preferentially to faces compared with other visual stimuli (Puce et al. 1996; Kanwisher 2010; Haxby and Gobbini 2011). These regions, ostensibly comprising the core system for the visual analysis of faces, operate in concert with an extended system to extract social meaning from faces. A number of regions including the amygdala, the insula, the nucleus accumbens (NAcc), and the orbitofrontal gyrus (OFC) support emotion processing and face evaluations (Cloutier et al. 2008). Many of these regions are also believed to be involved in novelty and saliency detection (Whalen and Phelps 2009; Menon and Uddin 2010). An additional brain network supporting social cognition and mentalizing, including the medial prefrontal cortex (mPFC), the temporoparietal junction (TPJ), and the precuneus/posterior cingulate cortex (PC/PCC) (Mar 2011; Frith and Frith 2006; Adolphs 2009; Cloutier et al. 2011b; Haxby and Gobbini 2011), is preferentially recruited when processing familiar others (Leibenluft et al. 2004; Gobbini and Haxby 2007; Cloutier et al. 2011a). In light of the complex networks of brain regions involved in the ubiquitous act of processing and inferring meaning from the faces of others, investigating human face perception would benefit from further consideration of the factors shaping these distributed neural systems.

Functional specialization of brain networks supporting face perception is believed to occur during development (Johnson 2011; for a review of age-related changes, see Burnett et al. 2011). In addition to age-related increases in size and selectivity of the FFA (Golarai et al. 2007; Peelen et al. 2009), adults display increased activation in a number of core face-processing regions (Joseph et al. 2011). Developmental changes in face-processing efficiency may also be tied to the greater connectivity between primary visual areas and limbic regions in adults (18–43 years) when compared with children (5–12 years) (Joseph et al. 2012). This developmental trajectory in face-processing specialization is believed to result from continuous privileged experience with facial stimuli (Johnson 2011; Haist et al. 2013; He et al. 2015).

Extensive research concerning the impact of early experience on face processing has taken place within the race perception literature, often with an emphasis on explaining the well-documented recognition advantage for own-race faces (Tanaka et al. 2004; Hugenberg et al. 2010). Although motivational factors contribute to the asymmetry in performance (Ostrom et al. 1993; Hehman et al. 2010), the ability to better discriminate between faces of one's own race has been attributed to extensive contact with in-group members (e.g. see Tanaka et al. 2004; Sangrigoli et al. 2005; Bar-Haim et al. 2006). Although increased visual experience with faces from a given racial group is suggested to increase face-processing ability (i.e. face recognition) due to exposure to larger numbers of exemplars from that social group, the impact of extensive experience with diverse racial exemplars in childhood on the extended brain network supporting face processing has not been investigated.

The current study aimed to explore the impact of perceptual familiarity, race, and perceivers' childhood experience with racial out-group individuals on the brain networks supporting face perception. Despite well-documented evidence of the existence of a distributed human neural system supporting face perception (Ishai et al. 2005; Haxby and Gobbini 2011), the current study is, to our knowledge, the first to implement a data-driven multivariate approach to characterize the simultaneous recruitment of multiple neural systems based on both basic experimental conditions (i.e. familiarity and race) and individual difference measures (i.e. childhood interracial contact). This investigation and analysis methodology will reveal if interracial exposure early in life significantly impacts the neural substrates of person perception by shaping brain networks involved in face perception, salience detection, and social cognition.

Given that that novel faces are more salient than familiar faces and that perceptual familiarity attenuates activity in a number of brain regions implicated in face processing (e.g. the fusiform gyrus and the amygdala, see Gobbini and Haxby 2006; Cloutier et al. 2011a; Cloutier et al. 2014), we predicted greater activity to experimentally manipulated novel versus familiar faces in an extended network of brain regions supporting face processing. In addition, given that race is shown to shape early attention (Ito and Urland 2003; Correll et al. 2006) and that preferential amygdala activity is often found in response to Black faces (Phelps et al. 2000; Cunningham et al. 2004; Wheeler and Fiske 2005; Kubota et al. 2012), we also predicted greater activity in a network including the amygdala and other brain regions supporting saliency detection [i.e. the anterior insula and the anterior cingulate cortex (ACC)] in response to Black versus White faces. Finally, based on research suggesting that interracial exposure may lead to greater face-processing efficiency (Lebrecht et al. 2009; Tanaka and Pierce 2009; Telzer et al. 2013; Cloutier et al. 2014; Davis et al. 2015), we predicted attenuation of brain activity in an extended face-processing network as a result of higher cross-race exposure during childhood.

## Materials and Methods

### Participants

Forty-seven participants self-identified as White American participated in the study. Data from 2 participants were excluded due to either incomplete questionnaires or movement (larger than 2.5 mms) during the scanning session, and data from the remaining 45 participants were analyzed ($M_{age}$ = 24.2 years, SD = 4.28 years; 24 female) (Two participants provided invalid or nonretrievable ZIP codes for the places they lived and they did not provide sufficiently specific city or town information that allowed for obtaining corresponding demographic information. Because population density was calculated based on ZIP codes, data from these two participants were excluded in the PLS analyses using ZIP codes as the behavioral measure, as well as in the PLS analyses where population density was controlled for.).

### Stimuli

Forty male faces (20 Black and 20 White) from the Chicago Face Database were used as the stimuli for the fMRI component of the study (Ma et al. 2015). Of the 40 faces, 20 faces (10 from each race) were introduced in a pre-scan familiarity training task and served as the perceptual familiar faces during the scanning session. The remaining 20 faces were presented as the novel faces. Stimulus presentation and data collection were programmed using E-Prime 2.0. A back-projection system was used for stimulus presentation in the scanner.

### Procedure

#### *Perceptual Familiarization Training Session*

Prior to the scanning session, face familiarity was introduced by asking participants to associate 10 Black and 10 White faces with 20 different letters (adapted from Lebrecht et al. 2009). The familiarity training procedure consisted of 4 sessions of self-paced training and testing blocks, followed by a speeded testing block to further consolidate memory of the faces and letters.

During the training blocks, each of the 20 faces was paired with a unique letter displayed below the face and pseudo-randomly presented 3 times in each block. Participants were instructed to press the key corresponding to the letter on the keyboard while learning the association between the identity of the face and the letter. Each trial started with a 250-ms fixation cross, followed by the presentation of the face-and-letter pairs.

During the testing blocks, participants were presented with each face once and asked report the letters with which they were paired during the training block. Participants were informed that they would need to achieve 100% accuracy during the testing block in order to proceed. At the end of the testing block, participants were provided feedback based on their performance: "You did not achieve 100% accuracy in this round. Please press okay to review the faces and letters." or "You have successfully completed the task. Please proceed." In the former case, participants were directed to the beginning of the learning block to review the faces and completed the testing block again. In the latter case, participants proceeded to the next training session.

The training procedure concluded with a speeded testing block during which participants were asked to provide their responses within 2 s. Again, 100% accuracy was required in the speeded testing block.

### *fMRI Session Task*

During the event-related scanning session, participants were asked to form impressions of novel and familiar Black and White faces based on their gut reactions, while performing a one-back task. Participants were asked to press two buttons simultaneously with both hands when two faces of the same identity were presented in a consecutive manner. Each trial consisted of a face presented for 1100 ms and a fixation cross presented for 1100 ms, comprising a TR lasting 2200 ms. Jitters were introduced pseudo-randomly to create intertrial intervals of 1100, 3300, 5500, or 7700 ms.

### *Individual Difference Measure*

Participants completed a battery of questionnaires designed to measure contact with members from racial out-group members during childhood. Questionnaires included an interracial contact measure assessing exposure to members of different racial groups through self-report and ZIP codes of previously lived places (although we validated the ZIP codes based on the names of the cities or towns provided along with the ZIP codes, when ZIP-code information was invalid or nonretrievable, we obtained demographic information using the names of the cities or towns, resulting in reduced specificity and increased margin of errors in the racial and ethnic makeup of participants' immediate social environment). Participants reported the racial and ethnic makeup of their social networks at three distinct periods during childhood (i.e. before age 6, age from 6 to 12, and age from 13 to 18 years) for adults and peers separately (e.g. "Not including family, what percentage of the adults/children you knew during this time belonged to each of the following categories?" Participants are asked to consider individuals in their immediate social networks such as friends, caretakers, neighbors, classmates, etc.). Because the impact of diversity in racial makeup might be confounded by population density, we additionally controlled for population density. In addition, based on the ZIP codes of cities or towns where the participants had lived, we were able to obtain population and land area based on the ZIP codes, and calculated population density as the ratio of population to land area (miles$^2$). Two participants provided invalid or nonretrievable ZIP codes for the places they lived and they did not provide sufficiently specific city or town information that allowed for obtaining corresponding demographic information. Therefore, data from the remaining 43 participants were analyzed when investigating the impact of contact coded using ZIP codes and population density. We used the 2010 census to retrieve demographic information and land area data (verified from the 2013 US Gazetteer file) associated with ZIP codes.

### *fMRI Data Acquisition*

The fMRI session lasted approximately 16 min (each of the three runs lasted 316.8 s). Anatomical and functional imaging was performed on a 3T Philips Achieva Quasar scanner at the University of Chicago Brain Research Imaging Center. High-resolution structural images were acquired in the sagittal plane using a T1-weighted 3D Turbo Field Echo (TFE/MP-RAGE) anatomical scan (TR = 8.5 ms, echo time = 4.0 ms, FOV = 240 × 228 mm, 1.0 mm slice thickness, no gap, 240 × 228 mm matrix, 1.0 × 1.0 × 1.0 mm$^3$ voxel size). Functional images were collected in three functional runs of 144 TRs each, using pulse sequence parameters (TR/echo time = 2200/28 ms, flip angle = 79°, contiguous slices with 3.28 mm thickness, gap = 0.72 mm, FOV = 210 × 210 mm, approximately 64 × 64 mm matrix, 3.28 × 3.28 mm$^2$ voxel size). Functional imaging data were preprocessed to remove sources of noise and artifacts using the SPM8 (Wellcome Department of Cognitive Neurology), and realigned within and across runs to correct for head movement and transformed into a standard anatomical space (3 mm isotropic voxels) based on the ICBM 152 brain template (MNI, Montreal Neurological Institute) which approximates the Talairach and Tournoux atlas space (Talairach and Tournoux 1988). Normalized data were then spatially smoothed (8 mm FWHM) using a Gaussian Kernel to increase the signal to noise ratio and reduce the impact of anatomical variability not corrected for by stereotaxic normalization.

### *PLS Analysis*

We applied the PLS analysis to obtain data-driven identification of significant relationships between brain networks and experimental variables. We used task PLS analysis to explore patterns of neural activity related to perceptual familiarity and race across the whole brain. In addition, we used behavioral PLS analysis to characterize the relationship between brain activity and childhood interracial contact, and to identify how the relationship varies as a function of perceptual familiarity or race of the face stimuli.

To assess the effect of perceptual familiarity and experience on distributed activity patterns, we applied multivariate PLS (McIntosh and Lobaugh 2004; Krishnan et al. 2011) analysis. The PLS implementation software was downloaded from Randy McIntosh's lab at: https://www.rotman-baycrest.on.ca/index.php?section=84. The version of PLS that we implemented was created on 05-JAN-2005 by Jimmy Shen and updated as part of Pls.zip: 16-MAY-2012.

PLS is a multivariate statistical technique that relates two sets or "blocks" of data to one another. In functional neuroimaging, one data set typically represents Blood Oxygenation Level-Dependent (BOLD) activity in multiple voxels, while the other set may represent the study design (task PLS) or one or more demographic or behavioral measures (behavioral PLS). The goal of the analysis is to find weighted patterns of the original variables (termed "latent variables" or "LVs") that maximally co-vary with one another. In task PLS, these LVs represent a differentiation between experimental tasks (interpreted as a contrast), as well as a spatial pattern of voxel

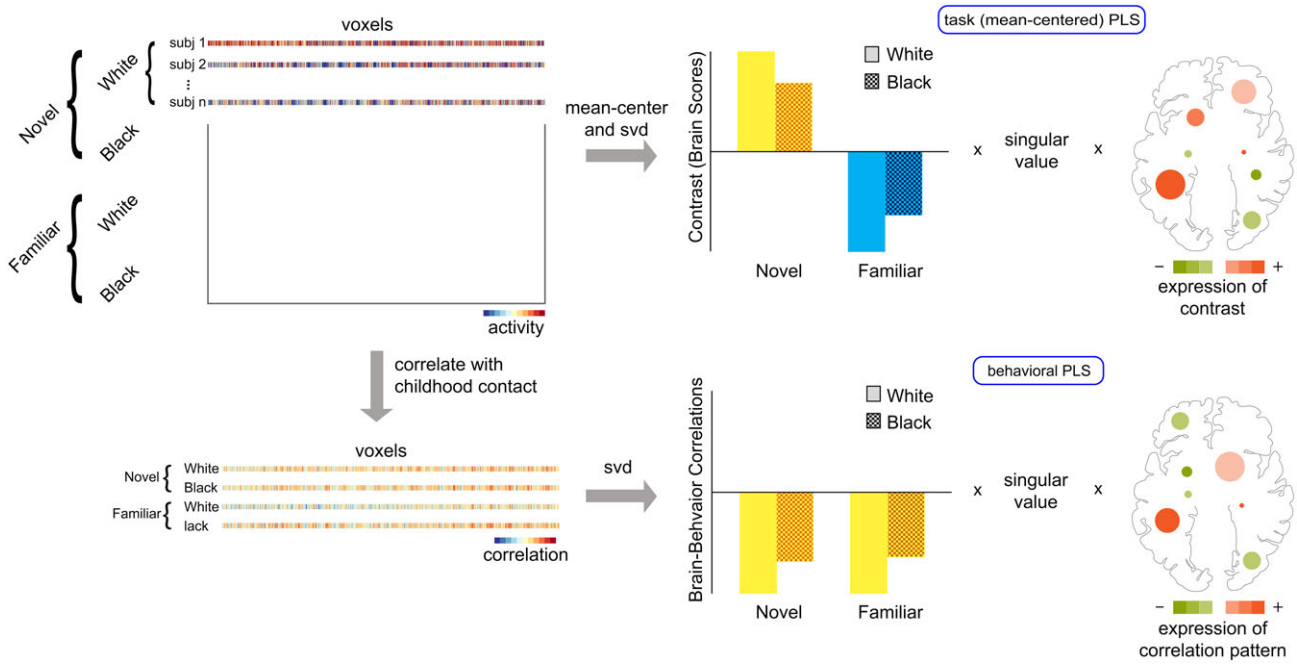


**Figure 1.** Schematic diagram of PLS. The upper panel describes task PLS analysis. Whole brain activation maps are flattened to 1-dimensional vectors. Each row represents a single participant's activation map for a particular condition. Each column represents the activity of a single voxel. The experimental conditions are stacked on top of each other, that is all participants' novel white face condition activation maps, then all of the participants' novel black face condition activation maps, etc. This matrix then undergoes mean-centering and SVD to obtain a weighted combination of experimental conditions and voxel activities that maximizes the relationship (i.e. covariance) between the two sets of data (i.e. experimental conditions and brain activity). The lower panel describes behavioral PLS analysis. Behavioral PLS is used to examine the relationship between brain and behavior as a function of experimental condition. In behavioral PLS, the "crossblock" covariance is between the design variables (i.e. the experimental conditions) and the correlation between brain and behavior. Rather than each voxel representing activity, each voxel now represents the correlation of activity with the behavioral variable of interest (e.g. interracial contact) across participants. The LVs then reflect how different experimental conditions modulate brain and behavior relationships. The correlated activity matrix then undergoes SVD to obtain a weighted combination of experimental conditions and voxels that maximizes the relationship between the two sets of data. Importantly, the y-axis of the experimental condition side represents the correlation of voxel activity and the behavioral variable of interest (e.g. interracial contact).

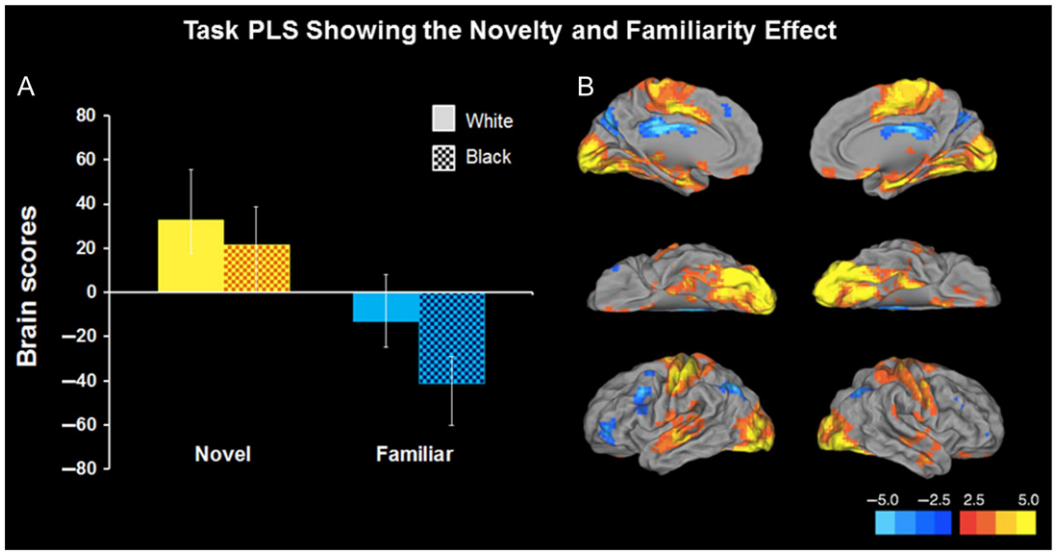


**Figure 2.** (*A*) The main effect of novelty emerged as the 1st significant LV in the task PLS. Brain score represents the strength of the relationship between the network of brain regions and the task conditions. The error bars represent confidence interval. (*B*) Patterns of whole-brain activities during the presentation of novel versus familiar faces. Top and bottom panel represent sagittal slices, middle panel represents ventral slices. Left panel represents left hemisphere, right panel represents right hemisphere. Top and bottom panels represent sagittal slices and middle panel represents ventral slices. Voxels were thresholded at BSR $\geq$ 2.5 or BSR $\leq$ −2.5. Note that the directionality of brain activities needs to be interpreted in conjunction with the bar graph, as warm colors indicate higher whole-brain activations in response to novel faces, and cool colors indicate higher whole-brain activations in response to familiar faces.

activity that supports that contrast. In behavioral PLS, the LVs represent a particular cognitive-behavioral profile, as well as a spatial pattern of voxel activations that supports that profile. PLS is computed via singular value decomposition (SVD; Eckart and Young 1936). The covariance between the two data sets **X** (e.g. brain activity) and **Y** (e.g. behavior) is computed (**X′Y**) and is subjected to the SVD:

$$\mathrm{SVD}(\mathbf{X}'\mathbf{Y}) = \mathbf{USV}',$$

yielding a set of orthonormal matrices **U** and **V** (termed left and singular vectors), as well as a diagonal matrix **S** of singular values. The number of LVs from the analysis is equal to the rank of the covariance matrix **X′Y**, which is the smallest dimension of its constituent matrices. In most neuroimaging experiments, where the number of voxels is typically larger than the number of conditions, this will be equal to the degrees of freedom in the experimental design. The ith LV is comprised of a triplet of ith left singular vector, the ith right singular vector, and the ith singular value. The left and right singular vectors provide weights (often referred to as "saliences") for voxels and tasks, respectively. The scalar singular value is proportional to the "crossblock covariance" between **X** and **Y** captured by the LV, and is naturally interpreted as the effect size of this statistical association.

The LVs capture networks, or more precisely, linear combinations of voxel activities across the whole brain whose combinations are differentially instantiated for different experimental conditions. These networks are based on SVD as described above, unlike other network analysis techniques that are based on graph-theoretic measures (Bullmore and Sporns 2009). Unlike univariate contrasts, which do not have the potential to capture

**Table 1** Results of task PLS analysis

| | BA | Region | Cluster size | Coordinates | | | BSR |
|---|---|---|---|---|---|---|---|
| | | | | *x* | *y* | *z* | |
| *Novel > familiar* | | | | | | | |
| R | BA19 | Posterior Fusiform Gyrus | 19 250 | 27 | −81 | −9 | 8.75 |
| R | BA37 | Middle Fusiform Gyrus | | 33 | −51 | −18 | 6.8 |
| L | BA19 | Posterior Fusiform Gyrus | | −30 | −75 | −12 | 6.72 |
| L | BA1 | Postcentral Gyrus | | −45 | −18 | 60 | 6.01 |
| R | BA19 | Parahippocampal Gyrus | | 18 | −48 | −9 | 5.94 |
| R | BA34 | Amygdala | | 21 | −6 | −21 | 5.76 |
| L | BA19 | IOG | | −33 | −84 | −12 | 5.7 |
| L | BA19 | Lingual Gyrus | | −21 | −54 | −3 | 5.67 |
| L | BA37 | Middle Fusiform Gyrus | | −39 | −45 | −21 | 5.47 |
| R | BA19 | Lingual Gyrus | | 15 | −54 | −6 | 5.45 |
| L | BA36 | Anterior Fusiform Gyrus | | −30 | −33 | −24 | 5.26 |
| L | BA4 | Precentral Gyrus | | −33 | −24 | 69 | 5.2 |
| R | BA24 | Middle Cingulate Gyrus | | 3 | −6 | 45 | 5.11 |
| R | BA19 | IOG | | 39 | −84 | −9 | 5.11 |
| L | BA22 | Middle Temporal Gyrus | | −54 | −15 | 0 | 4.64 |
| R | BA4 | Precentral Gyrus | | 36 | −27 | 63 | 4.62 |
| R | BA6 | Supplementary Motor Area | | 3 | −9 | 60 | 4.5 |
| L | BA34 | Amygdala | | −18 | −6 | −24 | 4.44 |
| R | BA37 | Lateral Fusiform Gyrus | | 45 | −54 | −18 | 4.23 |
| R | BA36 | Anterior Fusiform Gyrus | | 30 | −36 | −21 | 4.19 |
| R | | Insula | | 36 | −6 | −6 | 4.13 |
| R | BA22 | Superior Temporal Gyrus | | 45 | −15 | −3 | 3.88 |
| L | | Insula | | −51 | −6 | −6 | 3.68 |
| R | BA1 | Postcentral Gyrus | | 42 | −24 | 54 | 3.59 |
| R | BA28 | Temporal Pole | | 21 | 12 | −39 | 3.57 |
| R | | Cerebellum | | 39 | −39 | −51 | 3.4 |
| L | BA28/36 | Parahippocampal Gyrus | | −24 | −15 | −30 | 2.73 |
| L | | Cerebellum | 31 | −21 | −45 | −51 | 3.08 |
| L | BA38 | Temporal Pole | 39 | −39 | 15 | −42 | 2.82 |
| | BA11 | mPFC/OFC | 181 | 0 | 48 | −12 | 3.76 |
| R | BA8 | Superior Frontal Gyrus | 43 | 15 | 42 | 48 | 2.56 |
| *Familiar > novel* | | | | | | | |
| L | BA46 | Middle Frontal Gyrus | 99 | −39 | 45 | 0 | 3.99 |
| L | BA7 | PC | 405 | −9 | −72 | 30 | 5.41 |
| R | BA7 | PC | | 12 | −66 | 36 | 4.06 |
| L | BA23 | PCC | 474 | −9 | −24 | 27 | 7.49 |
| L | BA8 | Middle Frontal Gyrus | 203 | −42 | 15 | 36 | 4.81 |
| R | BA9 | Middle Frontal Gyrus | 25 | 45 | 21 | 33 | 2.92 |
| L | BA7 | Inferior Parietal Lobule/TPJ | 861 | −33 | −63 | 39 | 5.65 |
| R | BA7/40 | Inferior Parietal Lobule/TPJ | 206 | 39 | −60 | 39 | 4.16 |
| L | BA8 | Dorsal mPFC | 23 | −3 | 36 | 42 | 3.31 |

BA, Brodmann areas; L, left; R, right. BSR indexes reliability of each cluster. Voxels were thresholded at BSR ≥ 2.5 and cluster size ≥ 20.

activities in networks or patterns of brain regions, multivariate methods applied to fMRI data offer a novel opportunity to discover meaningful associations between distributed patterns of brain activities and experimental conditions.

To test the significance of each LV, a set of 1000 permuted samples were created by randomly re-ordering subjects and condition labels without replacement for the brain set (note: groups and conditions are permuted because PLS is uncovering the weighted pattern of groups and conditions that explains the most covariance between the experimental conditions and brain activity) while the labels for the design set are maintained resulting in 1000 new covariance matrices. These covariance matrices embody the null hypothesis that there is no relationship between brain activity and task. They are subjected to SVD as before resulting in a null distribution of singular values. The significance of the original LV is assessed with respect to this null distribution. The *P* value is calculated as the proportion of the permuted singular values that exceed the original singular value.

The reliability with which each voxel contributes to the overall multivariate pattern is determined with bootstrapping. A set of 1000 bootstrap samples are created by re-sampling subjects with replacement within each condition (i.e. preserving condition labels). Each new covariance matrix is subjected to SVD as before, and the singular vector weights from the resampled data are used to build a sampling distribution of the saliences from the original data set. The purpose of a constructed bootstrapped sampling distribution is to determine the reliability of each salience (i.e. saliences that are highly dependent on which participants are included in the analysis will have wide distributions). A single index of reliability (termed "bootstrap" ratio, or "BSR") is calculated by taking the ratio of the salience to its bootstrap estimated standard error. A BSR for a given voxel is large when the voxel has a large salience (i.e. makes a strong contribution to the LV) and when the bootstrap estimated standard error is small (i.e. the salience is stable across many resamplings). Figure 1 (upper panel) demonstrates graphically how the task PLS analysis is implemented.

In the present study, BSR maps were thresholded at the 95% confidence interval, corresponding to voxels whose BSRs were above 2.5 and those whose BSRs were below −2.5. We used a custom-written matlab script, utilizing the MATLAB function, "bwconncomp," which is a connected components function, to report the clusters of voxels that showed significant BSRs at these thresholds. Using this function we identified contiguous clusters of voxels with BSRs all above 2.5 or all below −2.5. This was not implemented for the purpose of statistical analysis, but rather was implemented for reporting tables displaying significant clusters of voxels across brain regions within the obtained brain networks as well as their corresponding peak BSR values.

In the present report, we used task PLS analysis to explore patterns of neural activity related to familiarity and race across the whole brain. This analysis would find the linear combination of voxels that optimally varied by race and familiarity of the faces. In our design we had 4 viewing conditions: familiar Back faces, novel Black faces, familiar White faces, and novel White faces. In addition, one can also perform another variant of task PLS, called contrast PLS, where one can prescribe an a priori orthogonal contrast to test the significance of this contrast with a multivariate analysis. This differs from task PLS, where task PLS attempts to find the "optimal" contrast in a data-driven way. Following up on the results obtained from task PLS, we implemented contrast PLS to test if there was a significant interaction between race and novelty on brain activity and also if there was a main effect of race on brain activity.

Another implementation of PLS, behavioral PLS, which is a variant of task PLS, was used to examine the relationship between brain and behavior as a function of experimental condition. In behavioral PLS, the "crossblock" covariance is between the design variables (i.e. the experimental conditions) and the correlation between brain and behavior. The LVs then reflect how different experimental conditions modulate brain and behavior relationships. We used behavioral PLS analysis to characterize the relationship between brain activity and childhood interracial

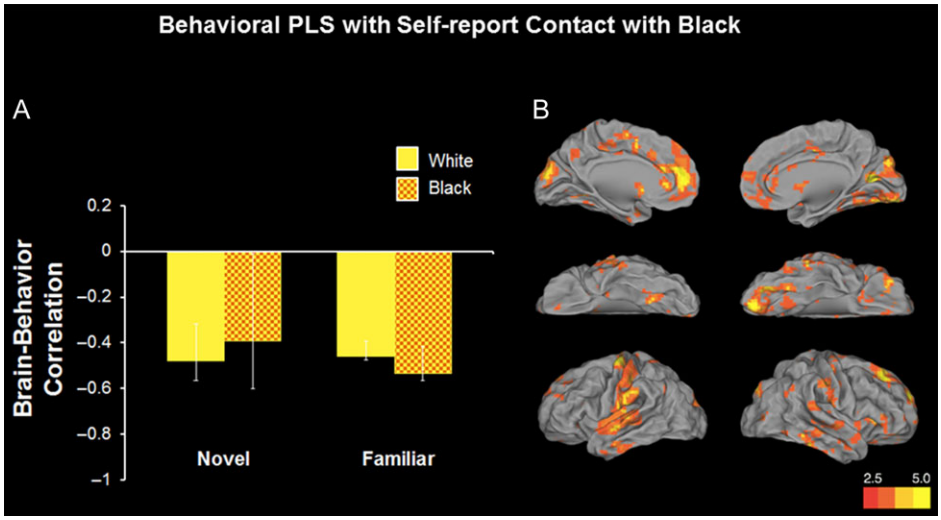


**Figure 3.** (*A*) Self-report childhood interracial contact with Black individuals emerged as the 1st significant LV in the behavioral PLS. Negative brain-contact correlation indicates negative correlation between the amount of interracial contact and brain activities (i.e. less childhood contact, more activity). The error bars represent confidence interval. The mean brain-contact correlation for each condition reliably contributes to the LV if the confidence interval does not include zero. (*B*) Patterns of whole-brain activities co-varying with self-report childhood interracial contact with Black individuals. Top and bottom panels represent sagittal slices and middle panel represents ventral slices. Left panel represents left hemisphere and right panel represents right hemisphere. Voxels were thresholded at BSR ≥ 2.5 or BSR ≤ −2.5. Note that the directionality of brain activities needs to be interpreted in conjunction with the bar graph, as greater activities indicates higher negative correlations as represented by the directionality of the bars in Panel *A*.

contact, to identify how the relationship between brain activity and childhood interracial contact varies as a function of perceptual familiarity or race of the face stimuli. Figure 1 (lower panel) shows graphically how behavioral PLS is implemented.

In the current study, we implemented PLS to identify how perceptual familiarity shapes neural responses during person perception. Importantly, we also explored how activities across networks of brain regions co-vary with childhood interracial contact, and how the relationship differs by experimental conditions. Therefore, the present research used task PLS and behavioral PLS to take advantage of the data-driven property of the PLS technique and to identify the relationship between brain activities and experimental designs (Krishnan et al. 2011). Specifically, a task PLS analysis was used to identify the distributed patterns of brain regions responsive to race and familiarity. The behavioral PLS analysis was used to examine activities in brain networks that correlated with individual differences in childhood interracial contact within the race and familiarity conditions. Lastly, contrast PLS was used to test contrasts of interest in a nondata-driven way (i.e. these contrasts did not emerge as maximizing the covariance between experimental conditions and brain, but were implemented to directly explore potential contrasts of interest).

## Results

### Behavioral Data

We refer to the interracial contact obtained from participants' self-report as "self-report" interracial contact, and the interracial contact obtained from ZIP codes and census data as "ZIP-code" interracial contact in reporting the results. The mean self-report childhood contact with Black individuals was 9.30% (SD = 10.49%, minimum = 0.33%, maximum = 47.50%), suggesting that Black individuals (e.g. friends, caretakers, neighbors, classmates, etc.) made up approximately 9% of the average participants' social network during childhood (see "Materials and Methods" section for the description of this assessment). The mean ZIP-code interracial contact was 10.40% (SD = 15.60%, minimum = 0.40%, maximum = 74.60%). The mean population density (defined by population per miles$^2$) of the previously lived places was 4237.49 (SD = 5445.62, minimum = 58.60, maximum = 28 170.21). A marginally significant correlation suggested that self-report exposure to Black individuals is related to population density, $r(41) = 0.294$, $P = 0.055$, as well as for ZIP-code contact and population density, $r(41) = 0.357$, $P = 0.019$. Therefore, following up on our first behavioral PLS analysis using childhood contact with Black individuals, we controlled for population

**Table 2** Results of behavioral PLS analysis using self-report childhood contact with Black

| | BA | Region | Cluster size | Coordinates | | | BSR |
|---|---|---|---|---|---|---|---|
| | | | | x | y | z | |
| *Decreased activity with contact* | | | | | | | |
| R | BA31 | Cuneus | 10 844 | 18 | −63 | 15 | 6.29 |
| R | BA8 | Superior Frontal Gyrus | | 21 | 33 | 45 | 6.28 |
| R | BA20 | Inferior Temporal Gyrus | | 57 | −33 | −30 | 5.73 |
| L | BA4 | Precentral Gyrus | | −36 | −12 | 60 | 5.52 |
| R | BA18 | Lingual Gyrus | | 15 | −84 | −6 | 5.46 |
| L | BA10 | Superior Frontal Gyrus | | −12 | 51 | 9 | 5.43 |
| L | | Medial Prefrontal Gyrus | | −3 | 48 | 15 | 5.37 |
| L | BA32 | ACC | | −9 | 27 | 18 | 5.18 |
| L | BA22 | Middle STS | | −60 | −18 | 9 | 5.06 |
| R | BA19 | Posterior Fusiform Gyrus | | 27 | −72 | −9 | 4.72 |
| R | BA7/19 | Superior Parietal Lobule | | 21 | −81 | 39 | 4.68 |
| R | BA22 | STS | | 63 | −45 | 15 | 4.68 |
| L | | Insula | | −36 | 3 | −9 | 4.36 |
| L | | Caudate Nucleus | | −9 | 9 | 0 | 4.25 |
| L | BA18 | Cuneus | | −12 | −87 | 30 | 4.06 |
| R | | Putamen/Caudate Nucleus/NAcc | | 15 | 21 | −3 | 4.23 |
| R | BA37 | Middle Fusiform Gyrus | | 30 | −51 | −12 | 4.13 |
| R | BA37 | Middle Temporal Gyrus | | 60 | −57 | −9 | 3.57 |
| R | | Insula | | 39 | 0 | −12 | 3.49 |
| L | BA6 | Middle frontal gyrus | | −30 | 15 | 39 | 3.46 |
| R | BA37 | Anterior Fusiform Gyrus | | 27 | −48 | −15 | 3.4 |
| L | BA7 | PC | | −6 | −60 | 36 | 3.12 |
| L | BA28/38 | Temporal Pole | 21 | −18 | 18 | −36 | 3.11 |
| L | | Cerebellum | 27 | −24 | −51 | −36 | 3.42 |
| R | BA36 | Parahippocampal Gyrus | 20 | 33 | −36 | −12 | 3.14 |
| R | BA39 | Middle Temporal Gyrus | 511 | 51 | −72 | 24 | 4.43 |
| R | BA40 | TPJ | | 54 | −63 | 30 | 3.73 |
| L | BA39 | Angular Gyrus | 173 | −51 | −69 | 24 | 4.01 |
| L | BA39 | TPJ | | −48 | −60 | 30 | 3.42 |
| L | BA22/39 | STS | | −57 | −51 | 12 | 3.27 |
| R | BA6 | Precentral Gyrus | 425 | 30 | −12 | 75 | 5.22 |
| R | BA7 | Superior Parietal Lobule | 44 | 33 | −48 | 63 | 3.53 |
| *Increased activity with contact* | | | | | | | |
| | | NA | | | | | |

BA, Brodmann areas; L, left; R, right. BSR indexes reliability of each cluster. Voxels were thresholded at BSR ≥ 2.5 and cluster size ≥ 20.

density in our second behavioral PLS analysis, by regressing out population density from the childhood interracial contact scores (and using the residuals) to account for the possibility that individuals with increased childhood contact may also have been exposed to a greater number of face exemplars.

## Functional Neuroimaging Data

### *Task PLS*

The task PLS analysis revealed one significant LV ($P = 0.002$), which explained 63.14% of the crossblock covariance (Fig. 2A) and dissociated novel from perceptually familiar faces. This LV represented increased BOLD responses for novel compared with perceptually familiar faces in many brain regions overlapping with the distributed network supporting face perception, including the IOG, VTC (extending from the anterior, medial, to the posterior fusiform), amygdala, and OFC. Perceptually familiar faces evoked preferential activity in contrast to novel faces in brain regions believed to support processing facial familiarity, including the PC/PCC (Table 1). This LV demonstrated a main effect of novelty, where increased BOLD activity in the IOG, VTC, OFC, and amygdala was associated with novel faces independent on whether they were Black or White faces (Fig. 2B). In addition, we explicitly tested for the interaction between familiarity and race using contrast PLS (using the following contrast of experimental conditions: [1 −1 −1 1] with the order: novel White faces, familiar White faces, novel Black faces, familiar Black faces), and we did not obtain a significant LV, $P = 0.499$. To follow-up on this we ran another contrast PLS to test for a main effect of race, and again, we did not obtain a significant LV, $P = 0.064$. Lastly, to examine the difference even further, as Figure 2 suggested that there may be some differences between familiar Black and White faces, we isolated the contrast between familiar Black and White faces and again, did not obtain a significant LV, $P = 0.075$. In summary, we found the LV differentiating brain regions implicated in the distributed network supporting face perception in response to novel versus perceptually familiar faces, but we did not find significant effects as a function of race (i.e. race did not emerge to be a significant factor for any LV).

### *Behavioral PLS*

The behavioral PLS analysis revealed a significant effect of self-reported childhood exposure to Black individuals as the 1st LV ($P < 0.001$), which explained 85.75% of the crossblock covariance (Fig. 3A). Childhood interracial exposure was associated with decreased activity in multiple brain regions overlapping with networks implicated in salience detection and social cognition (Fig. 3B). Specifically, greater childhood interracial exposure to Black faces was found to be associated with reduced activity in regions implicated in salience detection and social cognition (Table 2). These regions included the insula and the ACC, which are implicated in salience detection, as well as the mPFC, TPJ, STS, which are part of the social cognition network. This relationship was not impacted either by the perceptual familiarity or race of the faces.

A similar pattern was identified when using childhood contact with Black individuals, controlling for population density, where the 1st significant LV emerged to explain 85.10% of the crossblock covariance ($P < 0.001$) (Fig. 4A). In other words, the association between childhood interracial exposure to Black individuals and the reduced co-activation in regions including the mPFC, PC/PCC, ACC, temporal pole, and insula held above and beyond population density (Fig. 4B), emphasizing the importance of cross-race contact rather than exposure to greater number of face exemplars (Table 3). Again, this relationship was not impacted either by the perceptual familiarity or race of the faces.

Given that participants retrospectively reported their interracial contact during childhood, we ran additional behavioral PLS analysis using contact acquired from ZIP codes of cities or

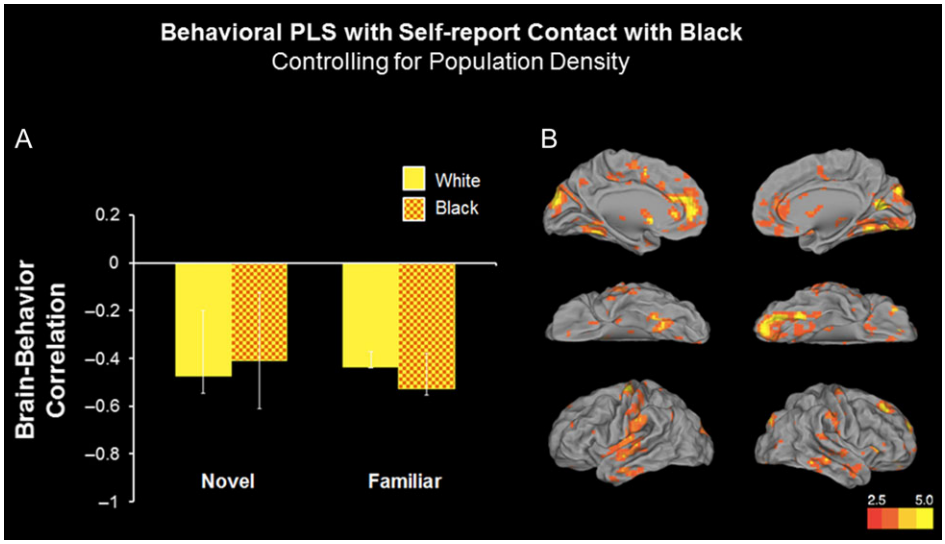


**Figure 4.** (*A*) Self-report childhood interracial contact with Black individuals emerged as the 1st significant LV in the behavioral PLS when population density was controlled for. The similarity between the bar graph in Figures 2A and 3A suggests that the correlation between contact and brain activities holds above and beyond population density. Negative brain scores indicate negative correlation between the amount of interracial contact and brain activities (i.e. less childhood contact, more activity). The error bars represent confidence interval. (*B*) Patterns of whole-brain activities co-varying with self-report childhood interracial contact with Black individuals. Top and bottom panels represent sagittal slices and middle panel represents ventral slices. Left panel represents left hemisphere and right panel represents right hemisphere. Voxels were thresholded at BSR ≥ 2.5 or BSR ≤ −2.5.

**Table 3** Results of behavioral PLS analysis using self-report childhood contact with Black, controlling for population density

| | BA | Region | Cluster size | Coordinates | | | BSR |
|---|---|---|---|---|---|---|---|
| | | | | x | y | z | |
| *Decreased activity with contact* | | | | | | | |
| L | BA4/6 | Precentral Gyrus | 6140 | −30 | −12 | 51 | 6.65 |
| L | BA24 | ACC | | −9 | 27 | 18 | 5 |
| L | BA32 | Middle Cingulate Cortex | | −6 | 3 | 45 | 4.73 |
| R | BA4 | Precentral Gyrus | | 27 | −12 | 54 | 4.68 |
| R | BA24 | Middle Cingulate Cortex | | 12 | −6 | 39 | 4.41 |
| L | BA2 | Postcentral Gyrus | | −60 | −21 | 30 | 4.2 |
| L | BA6 | Medial Frontal Gyrus | | −12 | −15 | 54 | 4.06 |
| R | BA22 | STS | | 66 | −42 | 12 | 4.05 |
| L | BA21 | Middle Temporal Gyrus | | −63 | −9 | −18 | 3.94 |
| L | | Insula | | −39 | −15 | 3 | 3.89 |
| L | BA40 | Inferior Parietal Lobule | | −48 | −33 | 54 | 3.58 |
| L | BA24 | PCC | | −3 | −15 | 39 | 3.49 |
| L | BA38 | Temporal Pole | | −33 | 0 | −48 | 2.9 |
| L | BA1 | Postcentral Gyrus | | −36 | −33 | 63 | 3.12 |
| R | BA38 | Temporal Pole | 139 | 24 | 15 | −33 | 3.08 |
| L | BA19 | Lingual Gyrus | 335 | −15 | −48 | −9 | 4.43 |
| L | BA37 | Middle Fusiform Gyrus | | −24 | −48 | −12 | 3.9 |
| L | BA36 | Anterior Fusiform Gyrus | | −24 | −36 | −18 | 3.5 |
| L | BA35 | Parahippocampal Gyrus | | −24 | −36 | −15 | 3.19 |
| L | BA19 | Posterior Fusiform Gyrus | | −27 | −60 | −6 | 3.17 |
| R | BA31 | PC | 2189 | 18 | −60 | 15 | 7.08 |
| R | BA19 | Posterior Fusiform Gyrus | | 27 | −75 | −9 | 5.66 |
| R | BA37 | Middle Fusiform Gyrus | | 30 | −51 | −12 | 5.37 |
| R | BA17 | Lingual Gyrus | | 15 | −84 | −6 | 5.42 |
| L | BA18 | Cuneus | | −12 | −87 | 33 | 4.61 |
| R | | Insula | | 42 | −18 | 6 | 4.45 |
| R | BA20 | Inferior Temporal Gyrus | | 42 | −3 | −42 | 4.39 |
| R | BA19 | Superior Occipital Gyrus | | 21 | −81 | 36 | 4.36 |
| R | BA39/40 | Supramarginal Gyrus | | 54 | −60 | 33 | 3.8 |
| R | BA19 | Middle Occipital Gyrus | | 42 | −78 | 36 | 3.62 |
| L | BA18 | Middle Occipital Gyrus | | −21 | −87 | 0 | 3.61 |
| R | BA39 | Middle Temporal Gyrus | | 48 | −69 | 15 | 3.46 |
| R | BA40 | Inferior Parietal Lobule | | 51 | −57 | 48 | 3.2 |
| R | BA19 | Parahippocampal Gyrus | | 15 | −48 | −6 | 3.09 |
| R | BA36 | Anterior Fusiform Gyrus | | 27 | −39 | −18 | 3 |
| L | | Dorsal mPFC | 1130 | −6 | 45 | 18 | 4.82 |
| L | BA11 | OFC | | −9 | 36 | −9 | 3.62 |
| R | BA11 | OFC | | 6 | 39 | −21 | 3.24 |
| R | BA47 | Inferior Frontal Gyrus/OFC | 65 | 33 | 36 | −15 | 4.11 |
| L | BA22 | STS | 31 | −54 | −51 | 15 | 3.01 |
| L | BA39 | Angular Gyrus/TPJ | 66 | −51 | −69 | 24 | 3.45 |
| L | BA39 | Superior Temporal Gyrus/Angular Gyrus | | −48 | −60 | 30 | 3.16 |
| L | BA8 | Superior Frontal Gyrus | 167 | 21 | 33 | 45 | 5.35 |
| R | BA7 | Superior Parietal Lobule | 27 | 30 | −48 | 63 | 3.19 |
| *Increased activity with contact* | | | | | | | |
| | | NA | | | | | |

BA, Brodmann areas; L, left; R, right. BSR indexes reliability of each cluster. Voxels were thresholded at BSR ≥ 2.5 and cluster size ≥ 20.

towns in which participants lived. Similarly, albeit weaker, we identified a similar pattern using ZIP-code contact with Black individuals. The 1st significant LV emerged to explain 78.82% of the crossblock covariance ($P < 0.001$). ZIP-code contact was associated with reduction in co-activation in regions including the mPFC, insula, and PC (Table 4). When controlling for population density, the 1st significant LV emerged to explain 79.77% of the crossblock covariance ($P < 0.001$), and again identified mPFC and PC. Again, this relationship was not impacted either by the perceptual familiarity or race of the faces (Table 5).

## Discussion

The present study utilized a data-driven multivariate approach to identify whether distributed brain networks implicated in face processing are differentially recruited by perceptual familiarity and race of faces. As hypothesized, and based on established neural models of face perception (Gobbini and Haxby 2006; Haxby and Gobbini 2011), viewing novel faces were found to preferentially recruit a large distributed face-processing network when compared with perceptually familiar faces. Indeed, expanding on previous studies (Kosaka et al. 2003; Gobbini and

**Table 4** Results of behavioral PLS analysis using ZIP-code childhood contact with Black

| | BA | Region | Cluster size | Coordinates | | | BSR |
|---|---|---|---|---|---|---|---|
| | | | | x | y | z | |
| *Decreased activity with contact* | | | | | | | |
| R | BA20 | Inferior Temporal Gyrus | 267 | 57 | −42 | −27 | 3.4 |
| L | BA37 | Inferior Temporal Gyrus | 160 | −57 | −51 | −21 | 3.19 |
| L | BA21 | Middle Temporal Gyrus | 82 | −63 | −21 | −18 | 3.58 |
| R | BA21 | Middle Temporal Gyrus | 40 | 60 | 6 | −24 | 2.57 |
| R | BA19 | Posterior Fusiform Gyrus | 1767 | 39 | −72 | −15 | 6.74 |
| R | BA19 | IOG | | 39 | −72 | −15 | 6.74 |
| R | BA19 | Middle Occipital Gyrus | | 42 | −75 | 18 | 6.56 |
| R | BA17 | Lingual Gyrus | | 12 | −84 | −3 | 6.26 |
| R | BA19 | Middle Fusiform Gyrus | | 21 | −66 | −12 | 5.66 |
| R | BA19 | Superior Occipital Gyrus | | 24 | −78 | 39 | 3.89 |
| R | BA40 | Inferior Parietal Lobule | | 39 | −57 | 45 | 3.49 |
| R | BA7 | PC | | 3 | −57 | 54 | 3.26 |
| R | BA37 | Anterior Fusiform Gyrus | | 36 | −42 | −15 | 2.8 |
| L | BA34 | Amygdala | 115 | −30 | 0 | −21 | 3.8 |
| L | | Insula | | −36 | −3 | −9 | 3.12 |
| L | | Putamen | | −30 | −3 | −6 | 3.12 |
| L | BA37 | Middle Fusiform Gyrus | 140 | −27 | −48 | −15 | 4.19 |
| L | BA37 | Anterior Fusiform Gyrus | | −24 | −42 | −18 | 3.75 |
| L | BA19 | Parahippocampal Gyrus | | −18 | −48 | −3 | 3.64 |
| L | BA18 | Lingual Gyrus | | −21 | −63 | 0 | 2.94 |
| L | BA19 | Posterior Fusiform Gyrus | | −27 | −60 | −6 | 2.96 |
| L | BA22 | STS | 20 | −48 | −9 | −9 | 3 |
| L | BA18 | Superior Occipital Gyrus | 328 | −21 | −81 | 15 | 4.17 |
| L | BA17 | Lingual Gyrus | | −15 | −87 | 0 | 3.45 |
| L | BA19 | Superior Occipital Gyrus | | −18 | −87 | 33 | 3.17 |
| L | BA18 | Cuneus | | −15 | −90 | 21 | 2.71 |
| L | BA40 | Inferior Parietal Lobule | 1596 | −48 | −30 | 57 | 5.77 |
| L | BA4 | Precentral Gyrus | | −42 | −12 | 57 | 5.19 |
| L | BA6 | Superior Frontal Gyrus | | −21 | −12 | 72 | 3.71 |
| R | BA22 | Superior Temporal Gyrus | 52 | 60 | −39 | 18 | 4 |
| R | BA4/6 | Precentral Gyrus | 26 | 57 | 3 | 15 | 3.11 |
| R | BA9 | Dorsal mPFC | 66 | 15 | 51 | 24 | 4.34 |
| L | BA6 | Precentral Gyrus | 35 | −45 | 0 | 30 | 3.93 |
| R | BA2 | Postcentral Gyrus | 59 | 57 | −24 | 33 | 3.29 |
| L | BA31 | Posterior Cingulate Gyrus | 120 | −15 | −24 | 36 | 4.49 |
| R | BA24 | Middle Cingulate Gyrus | | 3 | −15 | 45 | 2.74 |
| L | BA8 | Middle Frontal Gyrus | 41 | −36 | 21 | 39 | 3.89 |
| R | BA8 | Middle Frontal Gyrus | 48 | 24 | 24 | 57 | 3.32 |
| R | BA6 | Medial Frontal Gyrus | 68 | 3 | 9 | 72 | 4.37 |
| R | BA4 | Precentral Gyrus | 149 | 24 | −30 | 72 | 5.41 |
| R | BA7 | Superior Parietal Lobule | 21 | 18 | −57 | 66 | 4.07 |
| *Increased activity with contact* | | | | | | | |
| L | BA6 | Superior Frontal Gyrus | 30 | −33 | 6 | 72 | 3.73 |

BA, Brodmann areas; L, left; R, right. BSR indexes reliability of each cluster. Voxels were thresholded at BSR ≥ 2.5 and cluster size ≥ 20.

Haxby 2006; Summerfield et al. 2008), a network including the core system for visual analysis of faces (e.g. IOG and fusiform gyrus) and components of the extended system for emotion and face evaluation (e.g. amygdala and OFC) was preferentially recruited by novel faces. Furthermore, reinforcing the proposition that face processing is supported by an extended brain network that includes regions tied to attentional processes (Haxby et al. 2000), the results also revealed the preferential activity for novel faces in occipital regions and in areas comprising both the ventral and dorsal attention pathways (Petersen and Posner 2012). These findings converge with the results of previous fMRI research. Indeed, novel visual stimuli have previously been shown to preferentially activate a large network of brain regions, including primary and secondary visual areas (Marois et al. 2000; Gur et al. 2007) and the ventral and dorsal attention pathways (Marois et al. 2000).

In contrast, and again converging with previous investigations (Kosaka et al. 2003; Cloutier et al. 2011a), a network including the PC and bilateral areas of the parietal cortex was preferentially involved when processing perceptually familiar faces. However, contrary to our hypothesis and to research identifying race-based differences in brain activity during face processing (Kubota et al. 2012), race did not impact the brain networks involved during the processing of novel or perceptually familiar faces.

**Table 5** Results of behavioral PLS analysis using ZIP-code childhood contact with Black, controlling for population density

| | BA | Region | Cluster size | Coordinates | | | BSR |
|---|---|---|---|---|---|---|---|
| | | | | x | y | z | |
| *Decreased activity with contact* | | | | | | | |
| R | BA19 | Posterior Fusiform Gyrus | 3362 | 33 | −69 | −9 | 7.14 |
| R | BA18 | Lingual Gyrus | | 9 | −84 | −9 | 7.1 |
| R | BA19 | Middle Fusiform Gyrus | | 21 | −60 | −12 | 5.08 |
| L | BA37 | Middle Fusiform Gyrus | | −27 | −51 | −15 | 4.46 |
| L | | Hippocampus | | −30 | −27 | −15 | 4.39 |
| L | BA19 | Posterior Fusiform Gyrus | | −27 | −63 | −6 | 4.19 |
| R | | Hippocampus | | 33 | −27 | −15 | 3.98 |
| R | BA37 | Anterior Fusiform Gyrus | | 33 | −45 | −15 | 3.83 |
| L | BA37 | Anterior Fusiform Gyrus | | −24 | −42 | −18 | 3.56 |
| L | BA19 | Lingual Gyrus | | −21 | −54 | −9 | 3.36 |
| R | BA20 | Inferior Temporal Gyrus | 60 | 57 | 3 | −39 | 4 |
| L | BA20 | Inferior Temporal Gyrus | 51 | −51 | 3 | −42 | 4.4 |
| L | BA37 | Inferior Temporal Gyrus | 243 | −57 | −51 | −21 | 3.11 |
| L | BA22 | Superior Temporal Gyrus | 195 | −51 | 6 | −3 | 3.75 |
| R | BA21 | Middle Temporal Gyrus | 47 | 63 | 3 | −24 | 3.39 |
| R | BA47 | OFC | 49 | 57 | 36 | −6 | 3.35 |
| L | BA19 | Middle Occipital Gyrus | 38 | −48 | −75 | 3 | 3.08 |
| L | BA4 | Precentral Gyrus | 2953 | −45 | −9 | 63 | 6.43 |
| L | BA2 | Postcentral Gyrus | | −45 | −30 | 54 | 5.51 |
| L | BA7 | PC | | −18 | −51 | 57 | 4.18 |
| L | BA23 | PCC | | −15 | −27 | 33 | 3.76 |
| R | BA24 | Middle Cingulate Cortex | | 3 | −15 | 45 | 2.97 |
| R | BA9 | Superior Frontal Gyrus | 25 | 15 | 51 | 24 | 3.73 |
| R | BA43 | Postcentral Gyrus | 77 | 57 | −12 | 21 | 3.99 |
| L | BA39 | Angular Gyrus | 22 | −45 | −75 | 30 | 3.59 |
| R | BA4 | Postcentral Gyrus | 55 | 57 | −15 | 42 | 3.06 |
| R | BA7 | Superior Parietal Lobule | 123 | 36 | −51 | 63 | 4.51 |
| L | BA8 | Dorsal mPFC | 31 | −9 | 45 | 45 | 4.37 |
| L | BA6 | Supplementary Motor Area | 101 | −3 | 6 | 72 | 3.86 |
| R | BA6 | Supplementary Motor Area | | 15 | 0 | 60 | 2.94 |
| *Increased activity with contact* | | | | | | | |
| R | | Cerebellum | 78 | 15 | −87 | −36 | 3.06 |
| R | BA10 | OFC | 31 | 21 | 63 | −9 | 3.19 |

BA, Brodmann areas; L, left; R, right. BSR indexes reliability of each cluster. Voxels were thresholded at BSR ≥ 2.5 and cluster size ≥ 20.

Importantly, increased interracial contact during childhood had an overwhelming influence on a large distributed brain network, including regions previously implicated in face perception, salience detection (i.e. amygdala, anterior insula, and ACC) (Menon and Uddin 2010; Uddin 2014), and social cognition (i.e. the mPFC, TPJ, PC/PCC, and STS) (Frith and Frith 2006; Adolphs 2009; Mar 2011). Whereas previous localized univariate analysis demonstrated that interracial contact during childhood reduces amygdala response to perceptually familiar Black faces (Cloutier et al. 2014), the relationship between childhood interracial contact and brain network activity, reported here, suggests that contact considerably impacts distributed whole-brain activity during face perception irrespective of the targets' race or perceptual familiarity. Although the occipital and VTC clusters obtained in this behavioral PLS analysis were more restricted than the ones obtained in the task PLS analysis, regions outside of the face-processing network, including the parahippocampal and lingual gyrus, were again identified. Building on our interpretation of the task PLS results suggesting that these regions may be preferentially involved when processing novel targets (Marois et al. 2000; Gur et al. 2007), it is possible that increased face-processing efficiency following exposure to diverse face exemplars may manifest itself through modulation of this broad functional network.

This apparent discrepancy in findings suggests the complementary nature of the data-driven PLS multivariate analysis approach, which characterizes patterns of co-activation across large brain networks rather than simple increases or decreases in particular regions. These findings reveal that increased experience in processing individuals from another race can shape extended functional networks supporting person perception, presumably by increasing the efficiency with which all faces are processed. Increased interracial exposure during childhood exposes perceivers to more diverse face exemplars. This diversity may modulate the otherwise preferential attention to in-group faces, and attenuate the perceptual boundary between in-group and out-group faces. Cross-race contact may ultimately equip perceivers with broader perceptual face-processing expertize, allowing perceivers to process faces varying in race or familiarity with greater ease. The results obtained suggest that such face-processing efficiency may lead not only to reductions in brain activity among areas supporting visual analysis, but also attenuate the recruitment of brain networks involved in saliency detection and social cognition.

The identification of such large functional network sensitive to face novelty (i.e. task PLS analysis) and the perceivers' childhood experience (i.e. behavioral PLS analysis) underscore the need for additional research implementing designs and analyses better suited to distinguish the potential unique contributions of

finer scale patterns within the components of these functional brain networks. For example, activations in nonface-specific regions, such as the cerebellum, were found to be sensitive to both face novelty and to perceivers' individual differences in childhood exposure. Recent research has identified functional connectivity between the cerebellum and cerebral networks supporting a variety of cognitive functions beyond motor planning and execution, including attention (Buckner 2013) and social cognitive (Van Overwalle et al. 2015; Van Overwalle and Mariën 2016) functions, suggesting much broader functional roles for the cerebellum. Unfortunately, the current data cannot distinguish between these interpretations. In the future, approaches taking advantage of functional connectivity analyses (Buckner 2013; Van Overwalle and Mariën 2016), advances in graph-theoretic analysis (Power et al. 2011; Chan et al. 2014), or the implementation of searchlight hyperalignment in combination with representational similarity analysis (Kriegeskorte et al. 2008; Haxby et al. 2011; Guntupalli et al. 2016), for example, could complement a PLS approach to further characterize the functions of brain regions within these broad neural networks. Such research should lead to the continuous refinement in our understanding of functional brain networks, as well as how these networks coordinate with each other during psychological engagements.

Despite decades of efforts devoted to understanding how interracial contact contributes to improvement in the processing of out-group faces, empirical support for this relationship is often mixed (e.g. see Meissner and Brigham 2001). Using a data-driven multivariate approach, we demonstrated how the functional brain networks supporting face perception are differentially impacted both by the perceptual familiarity of faces and the childhood interracial contact of perceivers. These results provide a novel perspective on the impact of cross-race exposure, suggesting that interracial contact early in life may dramatically shape brain networks involved in face perception, salience detection, and social cognition. Future research should explore how the quality of interracial contact (e.g. self-initiated positive interracial contact in contrast to negative interactions or passive contact) may differentially modulate the recruitment of this network and explore how these differences may be related to social cognitive abilities.

## Notes

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