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Neural correlates of own- and other-race face perception: Spatial and temporal response differences

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ABSTRACT

Humans show an “other-race effect” for face recognition, with more accurate recognition of own- versus other-race faces. We compared the neural representations of own- and other-race faces using functional magnetic resonance imaging (fMRI) data in combination with a multi-voxel pattern classifier. Neural activity was recorded while Asians and Caucasians viewed Asian and Caucasian faces. A pattern classifier, applied to voxels across a broad range of ventral temporal areas, discriminated the brain activity maps elicited in response to Asian versus Caucasian faces in the brains of both Asians and Caucasians. Classification was most accurate in the first few time points of the block and required the use of own-race faces in the localizer scan to select voxels for classifier input. Next, we examined differences in the time-course of neural responses to own- and other-race faces and found evidence for a temporal “other-race effect.” Own-race faces elicited a larger neural response initially that attenuated rapidly. The response to other-race faces was weaker at first, but increased over time, ultimately surpassing the magnitude of the own-race response in the fusiform “face” area (FFA). A similar temporal response pattern held across a broad range of ventral temporal areas. The pattern-classification results indicate the early availability of categorical information about own- versus other-race face status in the spatial pattern of neural activity. The slower, more sustained, brain response to other-race faces may indicate the need to recruit additional neural resources to process other-race faces for identification.

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Introduction

It is well known from human memory studies that people recognize faces of their own race more accurately than faces of other-races (e.g., Feingold, 1914; Malpass and Kravitz, 1969; cf., meta-analysis in Bothwell et al., 1989; Meissner and Brigham, 2001). The perceptual correlate of this *other-race effect* can be summed up with the old adage, “They all look alike to me.” More formally, the difficulty we have in differentiating among other-race faces limits our ability to perceive and encode the uniqueness of individual other-race faces (e.g., Walker and Tanaka, 2003; Walker and Hewstone, 2006). Levin (2000) has argued that the recognition processes applied to other-race faces are driven by perceptual mechanisms that place emphasis on racial categorization at the cost of individuating faces. This view is supported by findings indicating that other-race faces can be categorized “by race” more quickly and efficiently than own-race faces (Levin, 2000). Combined, studies of human perception and memory suggest both a categorization and recognition component of the other-race effect, with more efficient

categorization of other-race faces “by race” and less accurate ability to differentiate among individuals of other-races.

The neural underpinnings of the other-race effect have been explored previously in several studies. The focus of these investigations has been *either* on neural basis of the socio-affective differences in processing own- versus other-race faces (Hart et al., 2000; Phelps et al., 2000; Lieberman et al., 2005; Cunningham et al., 2004) or on visual processing differences (Golby et al., 2001; Kim et al., 2006). The socio-affective studies indicate differential activation of the amygdala to own-versus other-race faces (Hart et al., 2000; Phelps et al., 2000; Lieberman et al., 2005; Cunningham et al., 2004), although the direction of these differences has not been entirely consistent (Hart et al., 2000 and Cunningham et al., 2004 show greater amygdala response to other-race faces; Phelps et al., 2000 and Lieberman et al., 2005 suggest that amygdala response depends on culturally acquired knowledge about a social group).

To date, only two studies have examined visual processing differences in the neural responses to own- versus other-race faces in the ventral temporal (VT) cortex. Golby et al. (2001) measured neural responses to African-American and Caucasian faces in the brains of African-Americans and Caucasians. They reported a larger neural response for own- versus other-race faces in the functionally defined right FFA (Kanwisher et al., 1997), but failed to find a correlation

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between a behavioral measure of the other-race effect and the neural response differences in FFA to own- versus other-race faces.

In contrast to the lack of relationship between behavioral and neural measures in the FFA, Golby et al. (2001) found the neural and behavioral measures to be correlated in the broader regions of the anatomically localized, left fusiform gyrus—an area that did not respond differentially to own- versus other-race faces. Based on these findings, Golby et al. (2001) proposed two distinct processes mediating the other-race effect. They suggested that the right FFA may be involved in individuating faces and the left fusiform may be more important for categorizing faces by race.

Kim et al. (2006) have also examined the neural correlates of own- and other-race face perception in face-selective areas, focusing on differences between familiar (famous) and unfamiliar faces. They found greater response to own-race faces in the FFA, but only when the faces were unfamiliar. No response difference was found to own- versus other-race famous faces. Kim et al. (2006) suggested that familiarity with individual faces may mediate neural processing differences for own- and other-race faces.

At a more general level of analysis, Ng et al. (2006) examined the neural codes underlying the facial category representations of ethnicity and gender using an fMR-adaptation (fMR-A) method (e.g., Grill-Spector et al., 1999), which they combined with a psychophysics-based face adaptation paradigm (e.g., Webster et al., 2004). fMR-A methods make use of the finding that neural responses tend to adapt with repeated presentations of the “same” stimulus (e.g., the fMR-A method, Grill-Spector et al., 1999; response suppression, Henson et al., 2000). The primary finding of Ng et al. (2006) was that the cortical regions showing strong adaptation-based selectivity for the visual face configurations underlying ethnicity, gender, and identity did not align well with traditional face-selective regions. They interpreted this result in terms of the differences between the types of magnitude-based measures of face selectivity used in functional localizer methods and the selectivity of adaptation responses to the individual dimensions of faces. They note that the presentation of a “random” assortment of faces in the localizer may minimize *selective* adaptation effects and may miss brain regions that are tuned to respond to particular configurations that specify face categories. Thus, Ng et al. (2006) suggest a distributed code for the configural information in faces across the fusiform gyrus, inferior occipital cortex, and cingulate gyrus.

The method used by Golby et al. (2001) relies primarily on magnitude-based measures of neural responses in targeted brain areas. In the present study, we focused on differences in the pattern of neural activity elicited by own- and other-race faces. Human memory data suggest that the complexity and completeness of face representations for own- and other-race faces may differ across several levels of visual analysis, from the basic feature selection and processing to the expertise-based coding of facial identity. A pre-requisite to understanding these differences is to be able to characterize the patterns of neural response to own- and other-race faces. One way to examine these differences is to use a pattern-based classifier to separate the neural activity maps elicited in response to own- versus other-race faces in high-level visual areas. Pattern classifiers are well suited to this task and have been applied successfully to the problem of discriminating high-level visual codes for faces and objects (e.g., Haxby et al., 2001; O'Toole et al., 2005). They have also been used to separate the neural responses to individual faces (Kriegeskorte et al., 2007; Natu et al., 2010) and within-category differences between objects (Eger et al., 2008).

The first goal of the present study was to examine differences in the spatial mapping of own- versus other-race faces across high-level visual areas in the ventral temporal (VT) cortex. We applied a pattern-based classification algorithm to separate the neural activity patterns elicited in response to own- and other-race faces. Based on the findings of Golby et al. (2001), Ng et al. (2006), and our own recent study (see Natu et al., 2010) we examined a relatively broad area of the VT cortex (including the FFA). In Natu et al. (2010), the neural responses to individual face

identities were discriminable only when voxels beyond the classic face-selective areas were included. Combined with results from previous studies (Ishai et al., 2005; Ishai et al., 1999), it is evident that high-level visual areas that are not strictly face-selective may play a role in the neural coding of faces.

Our second goal was to examine differences in the time course of neural activity in response to own- and other-race faces. Specifically, we looked at the magnitude of the blood oxygen level dependent (BOLD) signal to own- versus other-race faces over *time*, as individual face identities from own- or other-race were repeated using different images of a person. The ubiquitous nature of adaptation effects for faces, in combination with Ng et al.'s (2006) demonstration of a dissociation between adaptation to *faces* and *face-types*, suggests the importance of understanding the temporal components of the neural response to both individual faces and to faces that remain constant with respect to a categorical identity.

Methods

Participants

Ten participants (5 Asian and 5 Caucasian, age-range 20–45, 5 males) with normal or corrected-to-normal vision volunteered to participate in the fMRI experiment. At the time of the study, the Asian participants all lived in Texas, U.S., with an average of 9 years of continuous residency in the U.S. Each participant gave written informed consent to participate in the study. The Institutional Review Board committees at the University of Texas at Dallas and the University of Texas Southwestern Medical Center at Dallas approved the experimental protocol.

Stimuli

The stimulus set used for the fMRI experiment consisted of a set of digital photographs of four Caucasian and four Asian young adult male faces selected from a database developed at Notre Dame University (Phillips et al., 2010). These faces were chosen based on a behavioral identity matching experiment for own- versus other-race faces, because they elicited maximally different identity matching ratings from Asian and Caucasian participants (Phillips et al., *in press*). We used four different frontal-view images for each facial identity. All images were high-resolution and were taken under controlled illumination conditions, with a plain grey backdrop.

fMRI Experimental Protocol and Task

The experimental protocol consisted of a localizer session followed by an experimental session.

Localizer Session

An independent localizer session was used to select voxels in the ventral temporal cortex that showed significant variation in neural response to faces, objects, and scrambled images. Each participant viewed “own-race” faces in the localizer. Asian participants viewed grey scale images of Asian faces, objects (chairs and bottles), and scrambled images (Haxby et al., 2001) and Caucasian participants viewed grey scale images of Caucasian faces, objects, and scrambled images. None of these images appeared in the experimental sessions. For the purpose of comparison, we also collected localizer data for five Asian participants, using the Caucasian face localizer. This was used for a comparison test of the ability of the pattern classifier to separate the responses to Asian and Caucasian faces.

The localizer procedure was similar to that used by Natu et al. (2010) and included the Haxby et al. (2001) localizer images, plus an additional 24 Asian faces. Participants viewed six replications of three consecutive 12 s blocks, with each block containing 12 images of a single category, presented in a random order. Each image appeared for 200 ms, followed

by an 800 ms blank inter-stimulus interval. The blocks were preceded by 10 s of fixation. Participants performed a one-back task during the scan, responding “same” or “different” to the consecutively presented images.

Experimental session

The experimental data were collected during four replications (i.e., scanning runs) of eight blocked conditions. The eight conditions consisted of four identity-constant Asian face blocks and four identity-constant Caucasian face blocks. Within each face block, four different frontal-images of a single Asian or Caucasian identity were presented four times each in a random order. A block lasted for 32 s and was preceded by a 10-s fixation point. An image within a block appeared for 500 ms, followed by a 1500-ms blank inter-stimulus interval. The image location on the screen was set randomly to one of eight locations to avoid effects of apparent motion. Participants performed a one-back task in both the Asian and Caucasian face blocks, responding “same” when the exact same image followed the previous image. To minimize confounds of repetition, we presented alternate Asian and Caucasian face blocks. The stimulus sequences were presented using E-Prime 1.1 (Psychological Software Tools, Pittsburgh, PA) using a Windows PC.

Data Acquisition and Image Processing

Functional images were acquired on a 3-T MR system (Achieva; Philips Medical Systems, Best, The Netherlands) with an eight-channel SENSE head coil. A high-resolution (voxel size = $1 \times 1 \times 1$ mm) MP-RAGE structural scan was acquired prior to the functional scans. The BOLD signal was obtained with echo-planar imaging (EPI) transverse images (TR = 2000 ms, TE = 30 ms, flip-angle = 80° , FOV = 220 mm, 38 slices, voxel size = $3.44 \times 3.44 \times 4.00$ mm) that covered the entire cortex.

The localizer and experimental imaging data obtained for each participant were preprocessed using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm5/>). Functional data were motion-corrected using a 6-parameter rigid body realignment procedure, slice time corrected to the middle slice using sinc interpolation, co-registered to the in-plane anatomical image using mutual information optimization in SPM5.

Voxel selection for input to classifier

Datasets from the localizer and experiments were analyzed with MATLAB (version 7.2 2006). Feature selection was performed on the independent localizer session conducted prior to the experimental session. The corresponding experimental data of the voxels chosen from localizer session, was then used for classification purposes. For reasons detailed in the introduction, we employed a more liberal voxel selection process than used in most previous studies. Using the localizer data, voxels within the ventral temporal region were selected based on BOLD response that varied significantly across the three stimulus categories (faces, objects, and scrambled images). An analysis of variance was performed on individual voxel values to generate a functional mask of voxels for input to the classifier. The p -cutoff we chose for voxel selection was aimed at equating the separability of the neural response patterns for Asian and Caucasian faces in the brains of the Asian and Caucasian participants, at its optimal across-race level. Thus, we set a p cutoff value for Asian and Caucasian participants separately. We report data using $p = 0.00001$ for the Asian participants and $p = 0.0000001$ for the Caucasian participants. It is worth noting that more accurate classification could have been achieved by allowing the p cutoff to vary individually for participants.

For all participants, the *VT mask* included, but was not limited to, regions in and around the fusiform gyrus and lateral occipital face areas. An example *VT mask* appears in Fig. 1. We found a significant difference in the number of voxels in the *VT masks* of Caucasian participants ($M = 313.8$; $SD = 66.2$) versus Asian participants ($M = 762.8$, $SD = 334.4$) ($t(8) = 2.94$, $p < 0.05$). Using these parameters, the neural

responses elicited by Asian and Caucasian faces were roughly equally discriminable in the brains of the Asian and Caucasian participants. We will discuss this voxel number difference in more detail in the Discussion section.

In addition to the broad *VT cortex* analysis, Golby et al.'s (2001) finding that the FFA activates more strongly to own-race faces than other-race faces suggested the need to look for separability of neural response patterns to Asian and Caucasian faces in the FFA. To do this, we functionally isolated the FFA using data from the localizer. Specifically, a contrast analysis was used to select voxels that were significantly more active in response to faces than objects (faces > objects; $p < 0.00001$). To focus on the FFA rather than other face-selective areas, we eliminated face-selective voxels clusters outside the fusiform gyrus. In contrast to the voxel number difference we found for the *VT mask*, there was no difference in the number of FFA voxels for the Asian ($M = 12$; $SD = 2.44$) and Caucasian ($M = 21.4$; $SD = 9.6$) participants ($t(8) = 0.84$, *ns*). Across all participants, we obtained an average of 15.5 voxels in the right hemisphere and 12.3 voxels in the left hemisphere. Given the relatively small number of FFA voxels in these masks, we also experimented with a less conservative p cutoff value ($p = 0.001$), which yielded a larger number of voxels across both Asian ($M = 73.6$, $S.D = 52.1$) and Caucasian ($M = 83$, $S.D = 55.5$) participants. Again there was no difference in the number of voxels for Asian and Caucasian participants' masks ($t(8) = 0.24$, *ns*).

Neural response patterns to Caucasian and Asian faces: *VT mask*

A pattern-based classifier was implemented to measure the neural discriminability of the Asian and Caucasian faces in the brains of both Caucasian and Asian participants. The pattern classifiers were implemented separately for each participant. Two counter-balance conditions were made from different halves of the data, using the odd and even runs of the experimental session (cf., Haxby et al., 2001). Specifically, even runs served as training data and odd runs served as test data in one counterbalance condition, with these data sets reversed for the second counterbalance. The use of odd and even runs required the classifier to generalize predictions to brain scans taken at a very different times in the scan session. Given the high correlation of scans close in time, this procedure provided a better test of generalization than would be possible with training and test sets closer in time.

In what follows, we report the pattern classification results computed in the first four TRs of each block, which yielded the most accurate discrimination. Note that the entire data set was shifted by two TRs to account for hemodynamic lag and so the first 4 TRs refer to the scans following this shift. For completeness, we also report classification accuracy over the entire time-course of the block, using a sliding window approach. In this sliding window test, we implemented the classifier on 4 TRs at a time, sliding a 4-TR time span across the entire block advancing two TRs at a time. In each counterbalance condition, the training and test data sets contained brain scans with N voxels per scan, where N is equal to the number of pre-selected voxels. Specifically, for each counterbalance condition, there were 32 brain scans in each training set and 32 scans in each test set. As we will discuss in the section on the time course of neural response, from a theoretical perspective, the importance of time was anticipated due to the repetition of a facial identity in a given face block, which in previous studies has been shown to produce adaptation (e.g., Pourtois et al., 2005a,b; Eger et al., 2005). From a more practical perspective, a preliminary look at the data indicated that the time-course of neural response to Asian and Caucasian faces for Asian and Caucasian participants differed.

The classification algorithm followed a procedure used in previous work (Natu et al., 2010). Before classification, all scans were normalized to unit vector length (1.0), thus equalizing the amplitude of the scans across all time points. Principal component analysis (PCA) was applied to the scans from the training set. Each scan was then represented as a vector of coordinates, based on its projection into the PCA space. These

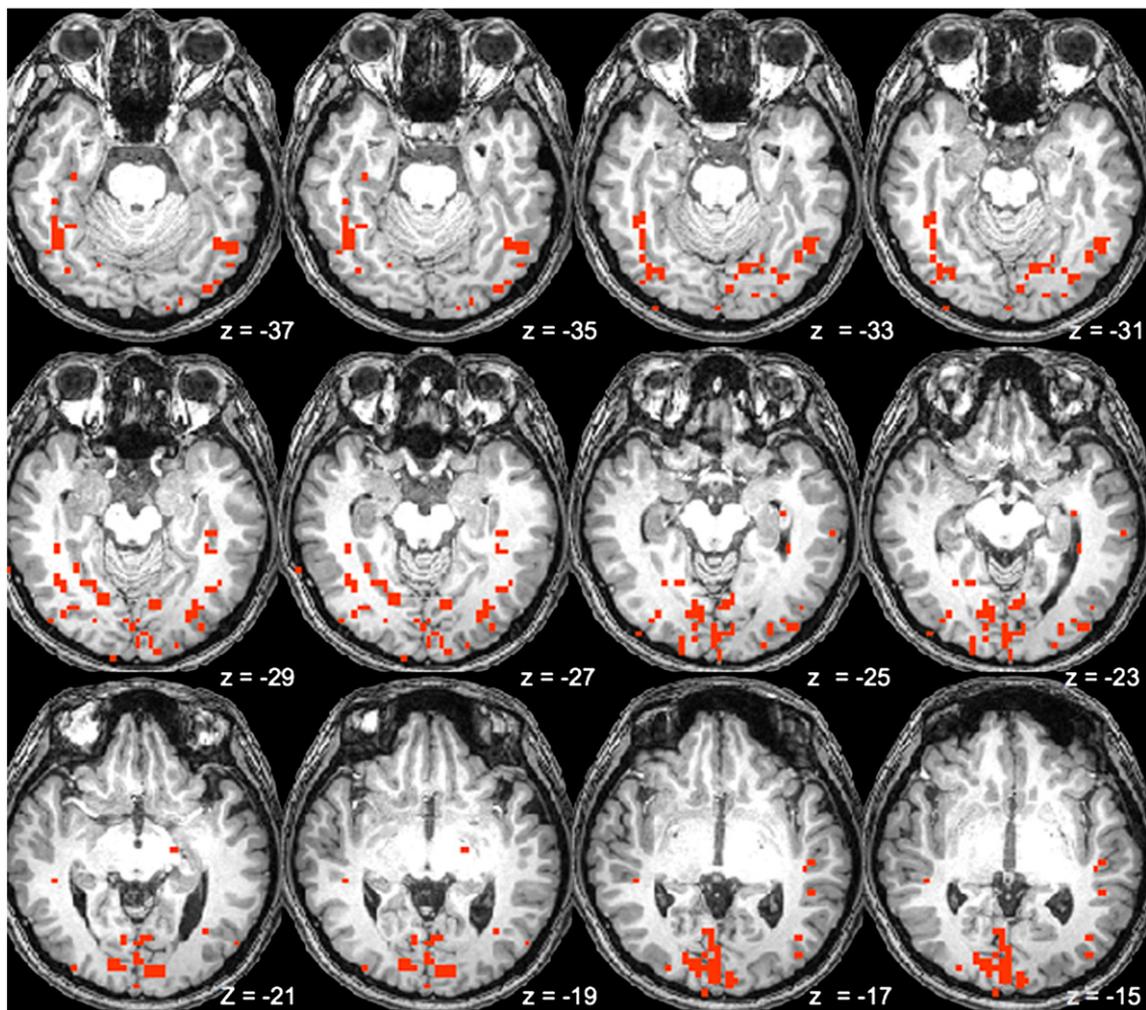


Fig. 1. Multiple axial slices showing the neural regions included in the VT voxel mask for a single participant. The VT mask included the fusiform gyrus and the lateral occipital cortex for all participants (the *right hemisphere* appears on the *right* for the brain images). All highlighted voxels were included in the VT mask.

vectors of coordinates served as input to the classifier. Next, we selected individual PCs for inclusion in an *optimal* classifier, based on their ability to discriminate the neural response patterns for Asian and Caucasian faces using the training scans (cf., O'Toole et al., 2007, for a discussion of the utility of individual PCs for neural pattern discrimination). By *optimal*, we mean only that the dimensions used for the classification were pre-screened for utility using the training set. Selection of the individual dimensions was implemented by training a series of single-dimension linear discriminant classifiers using the coordinates of the scans on the individual principal components. Performance of the individual PCs in these classifiers was measured using the signal detection measure d' , computed as z -score (hit rate) – z -score (false alarm rate). Specifically, in discriminating the neural response patterns for Asian versus Caucasian faces, the hit rate was defined as the proportion of Asian face patterns classified correctly and the false alarm rate was the proportion of Caucasian faces patterns classified incorrectly. The use of d' corrects for classifier bias to categorize scans into a particular category. A threshold d' was set on the training data to select PCs to be combined into a multi-dimensional optimal classifier for categorizing scans from the test data. In selecting the individual PCs, we tested a range of thresholds to verify the stability of the discrimination and to find values that optimized accuracy. Again, we set one cutoff threshold within participant race. The d' threshold for inclusion in the Asian subject classifiers was 0.30. The d' threshold for inclusion in the Caucasian subject classifiers was 0.41. The average number of dimensions in the combined optimal classifier was 15.1.

In the final step of the procedure, the selected PC dimensions were combined to create the optimal linear discriminant classifier to separate the neural responses to Asian and Caucasian faces. This classifier was evaluated on its ability to classify the left-out test scans. The classification procedure was applied to each counterbalance condition for each participant. The d' values we report are averaged across the two counterbalance conditions and averaged separately across the Asian and Caucasian participants.

Results

Neural discrimination of Asian and Caucasian face responses

The neural activity elicited in response to own- and other-race faces was discriminable using the pattern classifier applied to voxels in the VT mask. Specifically, the d' discrimination index for the response maps generated by viewing Asian and Caucasian faces appears in Fig. 2a and shows above chance discrimination in the brains of both Caucasian ($t(4) = 3.87, p = 0.01$) and Asian ($t(4) = 4.69, p < 0.001$) participants. The discriminability of the neural responses to Asian and Caucasian faces did not differ significantly for Asian and Caucasian participants ($t(8) = 0.54, ns$). Given that we had the complete classifier response distributions, we also include the full ROC curves (see Fig. 2b) plotted with the derived theoretical ROC for the average classification d' across all participants ($d' = 0.4$). The ROCs presentation is more complete, because each within-subject classifier operated at a particular criterion

(i.e. sampled the hit rate and false-alarm rate at a different place in the distribution). The ROC curves confirm that the underlying distributions would produce similar d' 's across the range of possible criteria.

In the **Methods** section, we noted that classification accuracy was best in the first four TRs of the block. More formally, to examine how discrimination varied over the block, we tested classification accuracies as a function of time window, using a sliding window of 4 TRs. Specifically, we assessed classification accuracy using sub-blocks of 4 TRs that moved from the beginning to the end of the block in 2-TR steps (e.g., 1–4, 3–6, 5–8, etc). All other aspects of the method, including the d' threshold for Asian and Caucasian participant were the same as those used for the previous analysis of the first 4 TRs.

Fig. 2c shows the classification performance for same- versus other-race faces as a function of time. The first four TRs of each block yielded the most accurate discrimination scores, with performance falling to chance levels by the middle of the block. Notably, we see a small classification accuracy rebound in the final time-points of the block. For completeness, we also tested discrimination in the first two TRs (those omitted in the hemodynamic shift). As expected, performance was at chance at this time point.

Next, we repeated the classification procedure using the voxels selected in the FFA mask. We were unable to obtain above chance discriminability scores using the FFA mask for either the Caucasian or Asian participants. Given the relatively small number of voxels we obtained in the FFA, we also tried classification with the expanded FFA mask we created with a less stringent p cutoff value. This mask had numbers of voxels typical of those reported for the FFA in the literature (Berman et al., 2010). Again, we failed to obtain above chance discrimination between the neural response patterns to Asian and Caucasian faces. This null finding in FFA does not suggest categorically that FFA does not contain information for discriminating these neural responses, (i.e., it might be possible with higher resolution, etc.). What it

does indicate clearly is that regions outside of traditional face selective areas can provide useful information for determining the race of a face.

Own- vs. other-race localizer

It is important to note that the reliable discrimination scores we report in Fig. 2a for Asian and Caucasian participants were obtained using *own-race* localizers (i.e., localizer with Asian faces for Asian participants and localizer with Caucasian faces for Caucasian participants). Over the course of the experiment, we obtained two sets of localizer data for five Asian participants—one set using the localizer with Caucasian faces and a second set using the localizer with Asian faces. The VT masks obtained with the own- and other-race localizers were created identically (cf., section on voxel selection for input to classifier). Of note, the number of voxels using the own- ($M = 762.8$, $SD = 334.4$) versus other-race ($M = 1030.8$; $SD = 611.6$) localizers were comparable ($t(8) = 0.85$, ns.). Fig. 2d (lower panel, right) shows the comparison of the discriminability scores for these participants using the Asian (own-race) (data repeated from Fig. 2a) versus Caucasian (other-race) localizer. The separability of the neural responses to Asian and Caucasian faces was near chance with the other-race face localizer, indicating that the use of own-race faces was instrumental in adequately localizing the VT cortex areas that contribute to the discrimination of own- and other-race faces.

Spatial activation maps

To visualize the patterns of neural activity that effectively discriminated the brain signals for Asian and Caucasian faces we created *importance or contrast maps* for each participant, as follows. An importance map was calculated for each participant as a weighted sum of the dimensions (PCs) useful for discriminating neural responses to Asian and Caucasian faces. The weights comprised the post-training classifier input strengths on the individual dimensions of the optimal

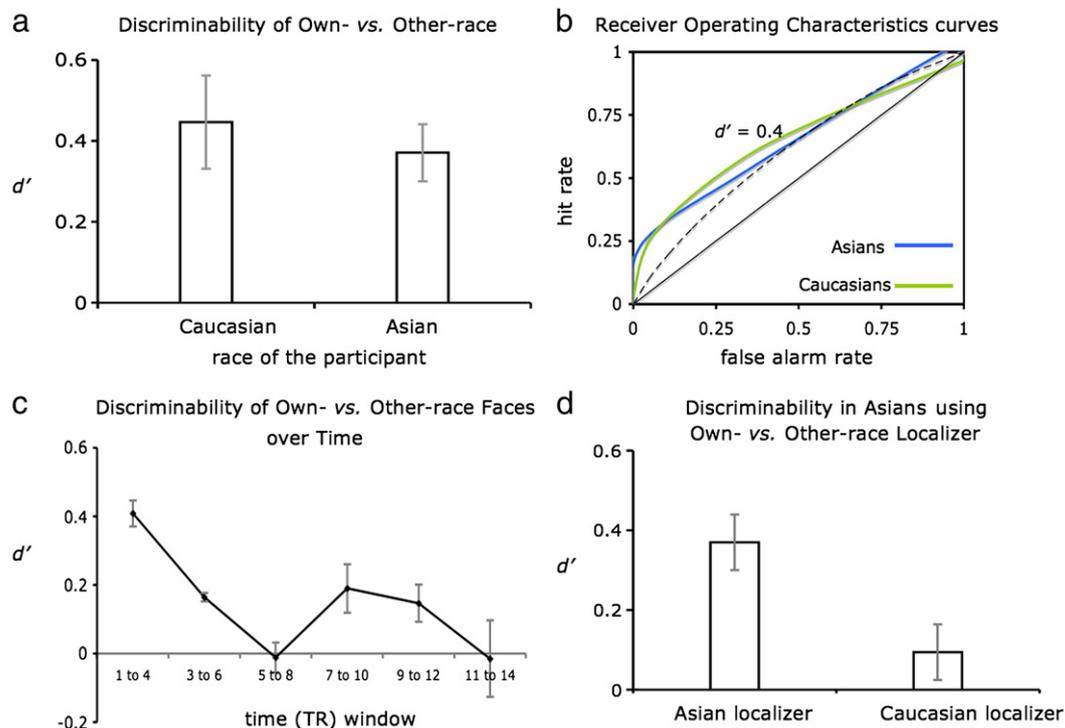


Fig. 2. (a) The neural discriminability of the brain activity patterns elicited in response to Asian and Caucasian faces for Asian and Caucasian participants. Error bars indicate standard error of the mean across the participants within each race. (b) The Receiver Operating Characteristics (ROC) curves representing the complete classifier response distributions for the Caucasian (in green) and Asian (in blue) participants. The dotted black line shows the derived theoretical ROC curve for the average ($d' = 0.4$) reported across all participants. (c) The neural discriminability for own- vs. other-race faces as a function of time in the block shows that discrimination is most accurate at early time points in the block. Error bars indicate standard error of the mean across all the participants. (d) A comparison of neural discriminability in Asian participants, with the use of Asian- vs. Caucasian faces in the localizer shows the importance of the own-race localizer for classification success.

classifier for the participant. To evaluate the different brain maps across multiple participants, the importance maps for the individual participants were normalized to the Montreal Neurological Institute (MNI) template. Once all the brain maps were transformed into a single template, we averaged these MNI normalized importance maps separately for the Caucasian and Asian participants, separately. These averages were projected onto the average MNI normalized anatomical brain. Next, we performed a *t*-test to determine voxels that differed significantly ($p < 0.01$) for Asian and Caucasian faces, within the brains of Asian and Caucasian participants. This provides an approximation of the brain areas that contributed to the discrimination. Note averaging of these non-contiguous masks across participants potentially underestimates the extent of the useful brain regions in individuals. We nonetheless provide the figure as a guide to the neural regions used to discriminate own- and other-race faces.

The importance maps for the Asian and Caucasian participants appear in Fig. 3. Consistent with the findings of Ng et al. (2006), the spatial map useful for dissociating the Caucasian and Asian faces spanned a relatively broad region in the VT cortex, including the fusiform gyrus (right 39 ± 7 , -50 ± 4 , -20 ± 6 ; left -43 ± 5 , -52 ± 4 , -19 ± 4) and the ventral lateral occipital areas (right 43 ± 3 , -70 ± 6 , -7 ± 4 ; left -46 ± 4 , -71 ± 5 , -10 ± 4) across all participants. Consistent with the larger number of voxels obtained in the VT masks for Asians than Caucasians, the spread of the fusiform and lateral occipital areas appears to be larger in the brains of Asian participants than Caucasian participants.

Time-course of own- vs. other-race face response

We examined differences in the temporal structure of neural activation in response to own- and other-race faces for Asian and Caucasian participants over the time-course of a block of faces. A strong motivation for looking at this time course came from the finding that the classifier could separate the spatial maps for own- and other-race faces best at early time points in the block. The temporal analysis was conducted separately using the voxels selected in the VT and FFA masks. As with the classifier analysis, the scans were shifted by two TRs in order

to account for the hemodynamic lag. For each participant, the neural response magnitudes were z-scored and averaged at each TR across all voxels in the mask. The Asian and Caucasian face blocks were then averaged separately at each of the 15 TRs in a block. This yielded a base neural response profile for Asian and Caucasian faces over time within blocks. This profile shows a standard hemodynamic response function, with repetition-based face adaptation for both own- and other-race faces (cf. Fig. 4c, for the FFA function). The final step was to calculate the z-scored *response amplitude difference* (i.e., Caucasian face response minus Asian face response) at each time point and to average these separately for the Asian and Caucasian participants. Fig. 4a and b show the temporal structure of the response amplitude difference functions for own- versus other-race faces using the VT and FFA mask, respectively.

There was a clear difference in the temporal pattern of neural response for own- versus other-race faces in both the FFA and broader VT cortex. This indicates a temporal “other-race” effect. For the FFA, the brain responds more strongly to own-race faces than to other-race faces over the first few time points of the block. This pattern reverses at later time-points in the block. For other-race faces, the response is weaker at first, but increases monotonically over time, ultimately overtaking the magnitude of the neural response to own-race faces. This temporal structure was consistent for both Caucasian and Asian participants, and in the FFA this structure appeared linear. To examine this structure more formally, we computed a correlation between response amplitude difference (Caucasian face response minus Asian face response) and time for the Caucasian and Asian participants. We found a strong negative correlation for Caucasians, ($r = -0.75$), (significance of *r* test, $r(13) = -0.75$, $p < 0.001$) and a strong positive correlation for Asian participants, ($r = 0.80$), (significance of *r* test, $r(13) = 0.80$, $p < 0.001$). The response advantage for own-race faces in the FFA early on in the time-course is consistent with the Golby et al. (2001) finding of a larger FFA response to own-race faces.

As noted previously, the neural response profile over time was similar for both own- and other-race faces, following a standard hemodynamic activation function with repetition-based face adaptation

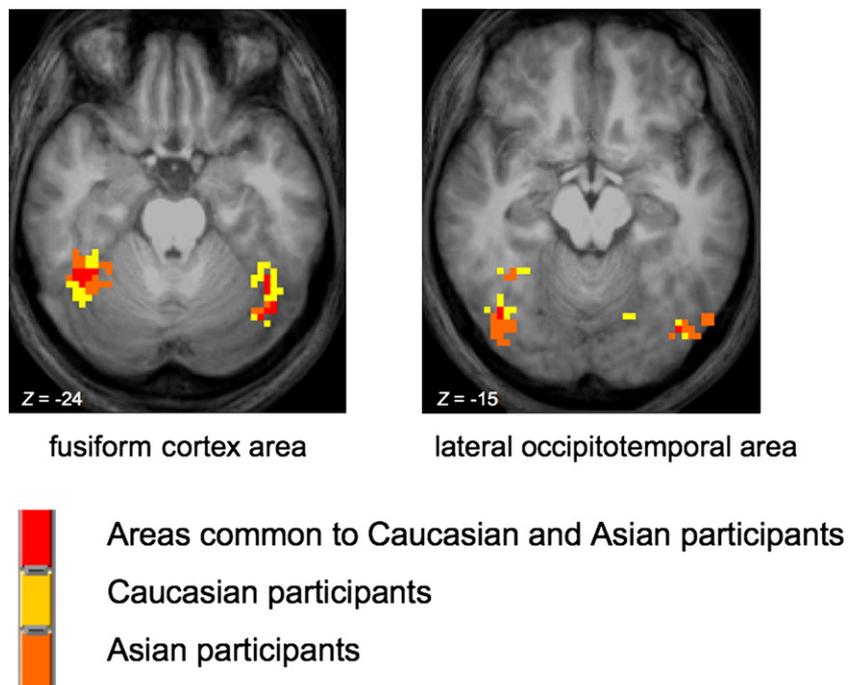


Fig. 3. Axial slices showing the regions that maximally contrast neural response patterns for Asian and Caucasian faces in the brains of the Asians (orange) and Caucasians (yellow). Areas common to all participants appear in red. The displayed orange voxels were observed in the spatially-normalized classification importance maps of the 5 Asian participants, the yellow voxels were observed in importance maps of the 5 Caucasian participants, and the red voxels were observed for all 10 participants (these include the across-race overlap areas).

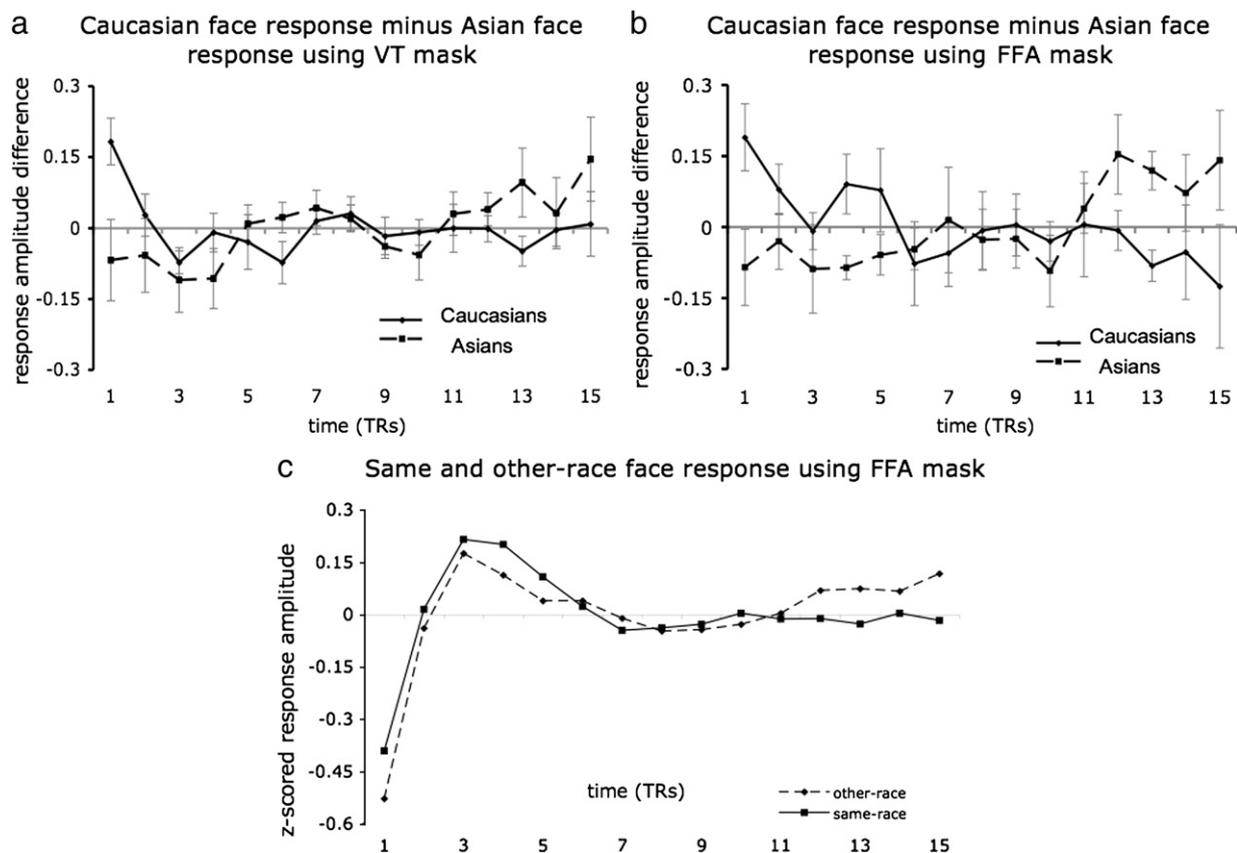


Fig. 4. The temporal response to own- vs. other-race faces in the VT mask (a, top left) and in the FFA (b, top right), shown as the z-scored response to Caucasian faces minus the z-scored response to Asian faces. The magnitude of own-race faces dominates at early time points and the pattern reverses later in the block. This indicates a temporal other-race effect. Temporal structure of the z-scored neural response to own- (solid line) and other-race (dotted line) faces in the fusiform face area (c, lower panel).

(Fig. 4c). The difference functions in Figs. 4a and b, therefore, capture an initial response advantage for own-race faces followed by a more efficient adaptation of the own-race face response. The comparable base profiles suggest a generally similar course of processing for own and other-race faces, with response amplitude differences spread over time.

For the VT mask, the temporal response pattern is analogous, but more complicated. The brain response function in this case was well-fitted by a line for the Asian participants (significance of r test, $r(13) = 0.81, p < 0.01$). However, the Caucasian brain response was better fit using an exponential decay function, of following form, $y = -0.84 + 10.6e^{-1.9x}$, which achieved a fit that explained 0.76 of the variance. As for the FFA, the balance of neural activation for own- versus other-race faces shifts over the time course of the block, with the strongest response to own-race faces at the outset and with increasing response to other-race faces over time. This pattern is superimposed, however, on a response magnitude advantage for Asian faces. Thus, it seems that in the broader areas of VT cortex, beyond the FFA, the Asian faces elicited a larger response. We discuss possible interpretations of this difference in the Discussion.

Discussion

The two major findings of this study are as follows. First, using pattern classification techniques, the neural activity patterns elicited in response to own- versus other-race faces were dissociable in the brains of both Asian and Caucasian participants. In other words, from the pattern of brain response across VT cortex, it was possible to determine whether a person was looking at a face of their own-race or a face of another race. This dissociation was possible with the broader VT cortex, but not with the FFA alone. Moreover, discrimination was most accurate using data from the first few time points of the face block and was only above chance when *own-race* faces were used in the localizer procedure

to select voxels for the classifier. The time sensitivity of neural discrimination suggests that the *pattern* of brain regions activated in response to own- and other-race faces differs most in early processing. Because the neural activity vectors were normalized prior to classification, this discrimination could not have been based on magnitude differences in response to own- and other race faces. The inability of the classifier to separate own- and other-race face processing across all time points in the block, suggests either a greater convergence of neural response patterns during these time epochs, or less systematic or predictable differences in the pattern of brain patterns to own- and other-race faces at these time points.

The second novel finding of our study was the difference in the *magnitude* of neural response to own- and other-race faces over time. The time course was characterized by an initially stronger activation to own-race faces that attenuated quickly, and an inversion of this relative response pattern for other-race faces. The inverted magnitude differences to own- and other-race faces were symmetric in FFA, with other-race face responses dominating own-race face responses by the end of the block. In the broader VT cortex, there was an analogous inverted response pattern, superimposed on a moderate activation advantage for Asian faces throughout.

A decrease in response magnitude to faces over the time course of the block was anticipated in our experiment based on previous studies, which have reported neural adaptation (fMR-A) in the FFA and broader fusiform gyrus with repeated presentations of face identities (cf., Andrews and Ewbank, 2004; Ewbank and Andrews, 2008; Eger et al., 2005; Pourtois et al., 2005a,b; Rotshtein et al., 2005). We found a base response pattern consistent with this expectation for all faces, but with relative activation differences for own- and other-race faces. In combination with the initially weaker FFA and VT cortex response to other-race faces, the relative increase in response

magnitude to other-race faces suggests slower, less efficient, processing of other-race faces.

This temporal pattern for own- and other-race faces may be related to a finding reported by Henson et al. (2000). They measured repetition effects elicited in response to familiar and unfamiliar face and symbol stimuli. Repetition of the familiar stimuli gave rise to response suppression, whereas the unfamiliar stimulus repetition elicited response enhancement. Henson et al. (2000) suggest that the suppression reflects the high efficiency associated with processing familiar stimuli. The enhancement, by contrast, may indicate the recruitment of additional psychological processing resources. If we consider other-race faces to be less familiar than own-race faces, the Henson et al. (2000) findings may provide a theoretical context for understanding the present results. These results may also provide a link to those of Kim et al. (2006) who found differences in neural response to own- versus other-race faces, only when the faces were unfamiliar. It is possible, therefore, that familiarity with individual faces can bridge some of the processing differences we found here for own- versus other-race faces.

In linking the neural data to the psychological processes, from behavioral studies, we know that face categorization by race is fast, and that other-race faces are categorized by race *more quickly* than own-race faces (cf., Levin, 2000). Although there is limited data on identification speed for own- and other-race faces, a recent study Marcon et al. (2010) suggests that other-race faces are identified *more slowly* than own-race faces. Support for this claim comes from Marcon et al.'s finding of a magnified other-race effect, when they limited encoding/processing times to be brief. Thus, it seems likely that the relative increase in the magnitude of neural responses for other-race faces over time may indicate temporally extended identity processing of other-race faces. The fact that this response magnitude remained elevated over time, not only in the FFA, but in the broader VT cortex, suggests the involvement of more than purely face-selective areas in this temporally extended identity processing. This finding fits well with Golby et al.'s (2001) report of a correlation between the behaviorally measured other-race effect and the neural response recorded in areas outside of the functionally defined FFA. It also fits with Ng et al.'s (2006) finding that the cortical regions showing strong adaptation-based selectivity for the visual face configurations underlying ethnicity and identity did not align well with traditional face-selective regions. In sum, the neural data suggest a role for *both* the FFA and a broader range of VT cortical areas in other-race face identification.

For categorizing faces by race, the role of FFA is less evident. Although the FFA response magnitude differences early in the block might enable fast categorization of own- versus other-race faces, it is unclear whether this magnitude difference would be quantitatively precise enough to distinguish own-race faces from, for example, other objects, which also elicit weaker responses in the FFA than (own-race) faces.

One question that arises is whether the increase in response magnitude over time reflects greater activation of a common set of voxels and/or whether it represents a spreading or shift in equipotent activation across a larger number of voxels. Strictly speaking, this question cannot be answered unambiguously with the present data. A comparison of the temporal results between the FFA and VT cortex, however, offers some speculative insights into the question. The symmetry of the response difference inversion for own- and other-race faces in FFA is at least consistent with the idea that identification processing in the FFA for own- and other-race faces shares common voxels, but unfolds over a different time course.

The results for the broader VT cortex are difficult to interpret due to the imbalance in the number of voxels in the VT mask for the Asian and Caucasian participants. Recall that the average number of the voxels in VT mask was greater for Asian participants. As noted previously, because our goal was to classify own- versus other-race faces, we allowed voxel number, rather than discrimination accuracy, to vary across participant race, on the assumption that behaviorally, race categorization is trivial and is unlikely to differ as a function of the race of the participant. We digress briefly to discuss this voxel number imbalance.

One possible reason for the greater number of voxels in the Asian participants' brains is that the Asians in this study were all born outside the United States, but had been living in a community with a strong Caucasian majority for an average of approximately 9 years. There is evidence that both developmental contact (Kelly et al., 2007) and intense shorter-term experience (cf., Webster et al., 2004) may contribute to the other-race effect. Differences in these short- and long-term experience profiles of the Asian participants as compared to the Caucasian participants may have contributed to variation in the extent of the localized VT regions.

The present study strongly highlights the need to consider both the spatial and temporal components of a neural response. Other recent studies have likewise highlighted this point, using different kinds of methods. An EEG study by Caldara and Vizioli (2010) found differences N170 time signatures for own- versus other-race face processing. At a more general level, Carlson et al. (2006) used a method of slowly revealing face stimuli to participants and measuring processes related to visual information, task, and response. They found differences in the spatio-temporal neural response patterns for the FFA and LO, with limited influence from the stimulus itself. Finally, at the level of connectivity among brain regions in the face processing neural network, Fairhall and Ishai (2007) found evidence for temporally expanded processing, and changes in the spatial patterns overtime, using dynamic causal modeling techniques.

In summary, the spatio-temporal response characteristics of the face system as a whole may require methods that get beyond averaging neural activity over time. One advantage of using a pattern-based classification analysis is that it allows for a functional assessment of whether neural response patterns at any given time can be used to achieve a targeted task. Pattern classification methods can be used to assess the discriminability over time, but are not generally applied in this way. In the present study, the task was to classify neural patterns elicited in response to own- and other-race faces. Differences we found in spatial discriminability over time pointed to a temporal other-race effect. This suggests that there may be limited gain from studying differences the neural codes for own- and other-race face processing, and perhaps for other important components of facial codes, without explicit attention to the time-course of processing.

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