doi:10.1093/scan/nsq060 SCAN (2010) 5, 227–235

Culture differences in neural processing of faces and houses in the ventral visual cortex

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Behavioral and eye-tracking studies on cultural differences have found that while Westerners have a bias for analytic processing and attend more to face features, East Asians are more holistic and attend more to contextual scenes. In this neuroimaging study, we hypothesized that these culturally different visual processing styles would be associated with cultural differences in the selective activity of the fusiform regions for faces, and the parahippocampal and lingual regions for contextual stimuli. East Asians and Westerners passively viewed face and house stimuli during an functional magnetic resonance imaging experiment. As expected, we observed more selectivity for faces in Westerners in the left fusiform face area (FFA) reflecting a more analytic processing style. Additionally, Westerners showed bilateral activity to faces in the FFA whereas East Asians showed more right lateralization. In contrast, no cultural differences were detected in the parahippocampal place area (PPA), although there was a trend for East Asians to show greater house selectivity than Westerners in the lingual landmark area, consistent with more holistic processing in East Asians. These findings demonstrate group biases in Westerners and East Asians that operate on perceptual processing in the brain and are consistent with previous eye-tracking data that show cultural biases to faces.

Keywords: ventral-visual; selectivity; culture; faces; houses

INTRODUCTION

There is growing interest in how differences in cultural experiences impact the way we process the visual world. Several behavioral studies have shown that Westerners, who come from a cultural background that values independence and individualism (Schwartz, 1990; Markus and Kitayama, 1991; Hong *et al.*, 2001; Chiao *et al.*, 2008), tend to process visual stimuli more analytically, with greater attention to objects and their features (Nisbett *et al.*, 2001; Nisbett, 2003; Nisbett and Miyamoto, 2005). In contrast, East Asians are enmeshed in a culture that emphasizes interdependence and collectivism, and thus East Asians process visual stimuli more holistically with greater attention to contextual information. In this present study, we focused on how these culturally different visual processing styles might affect the selectivity of responses in specialized areas of the ventral visual cortex for processing faces and houses (Kanwisher *et al.*, 1997; Aguirre *et al.*, 1998a and b; Epstein and Kanwisher, 1998). In keeping with the cultural biases reported in previous studies, we hypothesized that Westerners would process faces more analytically whereas East Asians would process faces more holistically, and that these differences should lead to greater face selectivity in the ventral visual areas in Westerners. In contrast, East Asians should attend more to houses as contextual information, which should be associated with greater house selectivity.

There is clear evidence that human faces are processed selectively in a region of the fusiform gyrus known as the fusiform face area (FFA; Kanwisher *et al.*, 1997). The FFA shows selectively higher blood oxygen level dependent (BOLD) responses to faces but is not as responsive to stimuli containing objects, scenes and houses. Importantly, FFA selectivity for face stimuli is not necessarily an automatic response in every situation. Indeed, Yi *et al.* (2006) showed that when viewing stimuli consisting of both faces and houses at the same time, attention to faces increased FFA processing, whereas attention to houses reduced FFA processing, suggesting that attentional processes can modulate FFA responses. Current evidence suggests that there may be perceptual and attentional differences related to cultural biases that might influence FFA processing when Westerners and East Asians view face stimuli (Goh and Park, 2009). A recent eye-tracking study by Blais *et al.* (2008) showed that while Westerners tend to move their eyes to focus on the eyes and lips of faces, East Asians tended to maintain fixation on the nose or central area. This finding was consistent with a tendency towards analytic visual processing in Westerners with greater attention paid to the features of the face that carry more distinguishing information. In contrast, East Asians focus on one central

Received 10 December 2009; Accepted 25 May 2010
Advance Access publication 16 June 2010

The authors would like to thank Marion Reeds, Peggy Charney, Blair Flicker, Lucas Jenkins, Karren Chen, Karen Chan and Sunny Kort for assisting in data collection. National Institutes of Health grant numbers (R-01-AG015047-09 and R-37-AG006265-26 to D.C.P.). This work was supported by the National Institute on Aging NIA R01 AG015047 awarded to Denise Park.

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point of the face, consistent with a holistic processing bias. We hypothesized that due to a tendency to process faces differently, along with the effects of attentional modulation on ventral visual activity (Yi *et al.*, 2006), Westerners would show greater selectivity than East Asians when processing face stimuli relative to other visual stimuli in the FFA.

In addition, cultural differences in face processing styles may affect responses in the two hemispheres of the brain differently. Previous studies have found that the right hemisphere is more sensitive to holistic face information while the left hemisphere is involved in processing face features (Sergent, 1982; Rhodes, 1985). Rossion *et al.* (2000) showed that the right fusiform region responded more when participants attended to whole-faces rather than face parts whereas the left fusiform was more responsive during attention to face parts rather than whole-faces. Rotshtein *et al.* (2007) also showed that individual differences in responses in the right FFA were correlated with behavioral performance when processing changes in the spatial configuration of face components rather than changes in specific face features. In keeping with greater attention to facial features in Westerners, we postulated that Westerners should specifically show greater left FFA face selectivity than East Asians. In contrast, East Asians may engage equivalent (or greater) holistic processing in the right FFA relative to Westerners. Thus, due to these cultural differences in left and right FFA selectivity, East Asians should show greater right lateralized FFA selectivity compared to Westerners, consistent with less processing of featural face details and a bias for holistic processing of faces in East Asians compared to Westerners.

In contrast to faces, stimuli consisting of houses and scenes tend to engage selectively higher BOLD responses in more medial ventral visual regions, primarily in the anterior parahippocampal gyrus (parahippocampal place area—PPA; Epstein and Kanwisher, 1998). Other studies have also reported selectivity for landmarks in the lingual gyrus (lingual landmark area—LLA; Aguirre *et al.*, 1998a and b), more posterior to the PPA. These regions show an enhanced BOLD response to houses, buildings, and scenes, but little or no response to face stimuli, and may be involved in perceptual processing of spatial configurations and landmarks within the immediate visual environment (Epstein *et al.*, 2003; Epstein and Ward, 2010; although these may subserve higher-level contextual memory processing as well; see Aminoff *et al.*, 2007; Bar *et al.*, 2008).

In relation to cultural differences, findings from several behavioral and eye-tracking studies suggest that East Asians attend more to contextual information than Westerners (Boduroglu *et al.*, 2009; Chua *et al.*, 2005; Goh *et al.*, 2009; Kitayama *et al.*, 2003; Masuda and Nisbett, 2006). In particular, East Asians have been shown to be better at judging line-lengths relative to size changes of a contextual square frame while Westerners were better at maintaining the absolute line-length regardless of frame size changes (frame line test; Kitayama *et al.*, 2003). Also, during a change-blindness study, East Asians were faster than Westerners at detecting changes that occurred in contextual background scenes, while Westerners detected more changes that occurred in focal objects within the scenes (Masuda and Nisbett, 2006). Note that prior imaging studies have not shown cultural effects on neural activity in the PPA when participants processed scene stimuli despite cultural differences in object-processing regions (Gutchess *et al.*, 2006; Goh *et al.*, 2007). Based on the behavioral and eye-tracking work, however, we hypothesized that the neural correlates of cultural differences in attention to contextual information, if any, should be associated with greater selective activity in the PPA and LLA in East Asians compared to Westerners, when processing houses relative to other categories of visual stimuli.

In this study, we presented Western and East Asian participants with visual stimuli consisting of faces, houses and phase-scrambled control images (Figure 1) in a simple blocked design functional magnetic resonance imaging (fMRI) experiment and measured how selective the neural responses in the FFA, PPA and LLA were in these two groups. We postulated that cultural differences in visual processing styles for face and contextual stimuli should be associated with cultural differences in selective responses to faces in the FFA and houses in the PPA and LLA relative to the non-preferred stimuli for these regions respectively. Specifically, we expected that Westerners should represent faces as more distinctive in the FFA, and thus show more selectivity of responses in this region for faces relative to houses. In addition, we expected East Asians to show a more right lateralized response to faces in the FFA relative to Westerners reflecting more holistic face processing. We also hypothesized that East Asians would show more selectivity in the PPA or LLA.

Fig. 1 Sample stimuli used in the blocked-design fMRI passive viewing experiment.

METHODS

Participants

Ninety-seven healthy right-handed participants were recruited in this blocked-design fMRI study with informed consent approved by the Institutional Review Boards (IRBs) at the University of Illinois at Urbana-Champaign as well as the National University of Singapore. There were 50 Young Westerners (25 males, 25 females; mean age: 22.1, range: 20–29) and 47 young East Asians (25 males, 22 females; mean age: 24.2, range: 20–30). Westerners were American students from the University of Illinois at Urbana-Champaign, USA, and community residents around the university. The ethnic breakdown of this Western sample consisted of 7 African Americans, 1 Hispanic and 42 Caucasians. East Asians were all Chinese Singaporeans recruited from the local universities and communities in Singapore. Singapore is a multiracial nation, consisting of Chinese, Malay and Indian cultural groups that predominantly subscribes to East Asian values (http://www.geert-hofstede.com). In order to keep our sample representative of East Asians as in previous studies, all participants were ethnic Chinese born in Singapore. Participants who had health-related counter-indications for MRI scanning were excluded from this study. Visual acuity in the scanner was corrected to 20/40 on the Snellen scale. Participants were remunerated for both MRI scanning and neuropsychological behavioral testing. The neuropsychological test battery included (i) the Schwartz Value Survey (SVS), which measures how much emphasis each individual places on values that have been associated with individualism and collectivism (Schwartz, 1992), (ii) a test of processing speed—pattern matching (Salthouse, 1996) and (iii) tests of working and long-term memory—letter-number sequencing, mental control and word list recall (Wechsler, 1997).

Stimuli and procedure

One hundred and eighty photographs of faces and houses were used to compose the picture stimuli. Sixty face stimuli were drawn from the Minear and Park (2004) database (https://pal.utdallas.edu/facedb/) along with additional photographs of 60 faces obtained with permission from Singaporean volunteers, approved by the IRBs. Singaporean participants were shown an Asian face set, and American participants were shown a Western face set that reflected community distributions of faces. There were an equal number of males and females in each face stimuli group. For house stimuli, we used 60 pictures of residential structures (30 houses, 30 apartments) from Singapore and USA. In the control condition, stimuli consisted of phase-scrambled pictures from the original stimuli so that the visual intensity levels were equated across the face, house and scrambled picture conditions. All stimuli were presented in grayscale and equated for luminance by adjusting the range of intensity values using auto-level in Adobe Photoshop (sample stimuli shown in Figure 1).

Stimuli were back-projected onto a screen in the scanner room, with participants viewing the stimuli using an angled mirror mounted on the head-coil. All stimuli occupied the same visual viewing angle, which was $\sim 4.6^{\circ} \times 6.3^{\circ}$. Participants were instructed to pay attention and simply view the stimuli. There was one experimental run (370 s long), with four blocks each of the face, house and scrambled conditions. Fifteen pictures were presented per block with stimulus duration of 2000 ms, with the order of conditions randomized across participants.

Imaging protocol

Functional images of the brain were acquired using identical 3.0 T Siemens Allegra scanner (Siemens, Erlangen, Germany) systems with a single-channel head coil at two locations. One scanner was located at the Cognitive Neuroscience Lab, Singapore, and another at the University of Illinois at Urbana-Champaign, USA. Extensive tests were done to ensure signal comparability between the two magnets (Sutton *et al.*, 2008). There were 32 axial slices oriented along with the anterior and posterior commissural axis, with slice thickness of 4 mm (0.4 mm gap), and 3×3 mm in-plane voxel sizes, 64×64 matrix, giving an in-plane FOV of 192×192 mm. One hundred and eighty-five functional scans were obtained, using TR 2 s and echo-time 32 ms. Co-planar structural T2 images were acquired to register and overlay the functional images to a 3D-MPRAGE T1 structural image also acquired for each participant.

Imaging analysis

The functional time-series data were analyzed using SPM5. Pre-processing was applied to correct for motion and slice-time differences only. Functional images were not smoothed and were not normalized to a common anatomical template so that all time-series data were analyzed in each participant's native brain space. The use of each participant's native space avoided biases that could be introduced during the normalization step due to possible differences in brain sizes and anatomical structure between Westerners and East Asians (Chee M.W.L. *et al.*, 2010), as well as individual differences in the location of the face and house processing areas. For each participant's data, a general linear model was applied to each voxel, consisting of a design matrix with face, house and scrambled condition onset predictors convolved with the canonical hemodynamic response function.

To isolate regions-of-interest (ROIs) for the FFA, PPA and LLA, we used techniques for comparing between-group differences in FFA and PPA similar to that reported by Park *et al.* (2004) when contrasting young with old adults. Our first step was to identify, within each participant, a peak voxel that responded maximally to a category on the left and right side for the fusiform (for faces) and on the left and right parahippocampal and lingual gyri (for houses). Within the fusiform regions (FFA), we contrasted face > house responses, and identified the peak voxel on left and right hemisphere from this contrast. Within the parahippocampal and lingual regions (PPA and LLA), we contrasted house > face responses, and identified the peak voxels in each of these two regions. For all contrasts, the identified voxels had a minimum threshold of $P < 0.05$. This lenient threshold was used so that nearly all participants contributed six peak voxels to the analyses (one from the left and right hemisphere for each of the three regions; Figure 2). Participants with no identifiable peak for an ROI even at this low threshold were excluded from the analysis for that ROI (Table 2). Approximate locations of the identified peaks from each participant are depicted in Figure 2 projected on an Montreal Neurological Institute (MNI) template brain (see Table 2 for mean coordinates).

Next, for each of the participants' peaks, we defined an ROI as a sphere of 15 mm radius around the peak (the sphere contained 269 voxels total). From the 15 mm sphere ROIs, we selected the top 10 most significant voxels and extracted their responses to the face and house relative to the same voxels' responses to scrambled stimuli (Supplementary Figure 1). We then took these top category voxels and contrasted the same voxels' activation to the alternate category (e.g. in the right FFA 15 mm sphere, we contrasted the activation of the top 10 face voxels with the activation level of these same voxels to houses). The mean of this activation difference across the top 10 voxels constituted the selectivity index for the right FFA. We performed the same operation for the PPA and LLA, except that we contrasted activation for houses with their activation level to the face stimuli. Larger values of these selectivity indices indicate greater selectivity of that ROI for the preferred category, for that participant. All subsequent group comparisons of selectivity indices were performed with one-tailed independent samples *t*-tests. We also repeated the ROI analysis using the top 15 and 20 most significant voxels within the 15 mm spheres to examine whether the effects we observed were replicated when considering more voxels. This method of identifying ROIs involves the least assumptions about the locations of the most selective voxels in each participant. This method also avoids the issue of selecting ROIs with different number of active voxels across individual participants, which is an issue when using functional threshold procedures. Moreover, this method is most fair to each participant since it examines differences in selectivity in voxels that are already the most selective in each individual (see Spiridon and Kanwisher, 2002; Park *et al.*, 2004).

Evaluation of the hemispheric symmetry of selectivity between the left *vs* right ROIs was performed using a laterality index (LI; Yovel *et al.*, 2008) for the selectivity measures computed for each participant:

$$\mathrm{LI} = \frac{\mathrm{rROI_{selectivity}} - \mathrm{lROI_{selectivity}}}{\mathrm{rROI_{selectivity}} + \mathrm{lROI_{selectivity}}}.$$

RESULTS

Neuropsychological test performance

Results of neuropsychological testing for the Western and East Asian participant are shown in Table 1. There was evidence that the two cultures subscribed more to

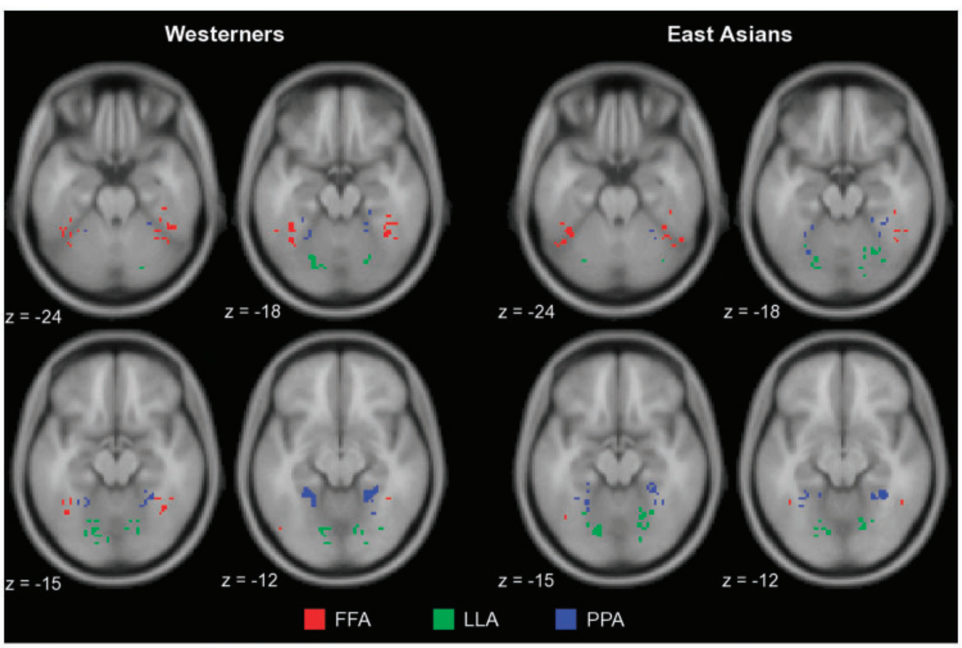

Fig. 2 Axial slices showing the peak FFA, LLA and PPA voxels of each individual participant identified in their own anatomical brain space and projected onto an MNI template brain. Note that the projections onto this group-based brain map are approximate so that individuals' peaks may not correspond exactly to the anatomical structures.

Table 1 Mean scores of Westerners and East Asians in the neuropsychological test battery with s.e. in parentheses

Test	Sub-test	Means scores (s.e.)		t-test
		Westerners	East Asians	t-value
Schwartz value scale	Power	9.1 (0.7)	12.6 (0.6)	4.00**
	Achievement	18 (0.4)	17.9 (0.5)	0.17
	Hedonism	9 (0.3)	8.1 (0.4)	1.89*
	Stimulation	11.6 (0.5)	12.3 (0.5)	1.03
	Self-direction	24.3 (0.8)	23.4 (0.5)	0.98
	Universalism	34.9 (1.1)	34.8 (0.8)	0.04
	Benevolence	23.6 (0.5)	25.4 (0.5)	2.66**
	Tradition	12.8 (0.7)	18.3 (0.5)	6.32**
	Conformity	15.1 (0.5)	17.9 (0.5)	3.72**
	Security	18.3 (0.5)	22.5 (0.6)	5.46**
Pattern matching		41.9 (0.8)	43.5 (0.9)	1.31
WMS-III letter number sequencing		14.4 (0.4)	13.3 (0.5)	1.65
WMS-III mental control		28.7 (0.8)	28.5 (0.5)	0.24
WMS-III word list recall	Trial 1 (immediate)	8.7 (0.3)	8.6 (0.3)	0.27
	Trial 2 (immediate)	12.4 (0.3)	12.2 (0.3)	0.36
	Trial 3 (delayed)	10.2 (0.4)	11 (0.4)	1.41

T-tests conducted were independent samples tests with equal variances assumed. *$P < 0.05$, **$P < 0.01$.

Table 2 Number of participants with identifiable peaks for each ROI (N_{ident}), and the approximate center coordinates of the peaks across participants projected in MNI space

	Westerners ($N = 50$)				East Asians ($N = 47$)			
		Centroid coordinates				Centroid coordinates		
ROI	N_{ident}	x	y	z	N_{ident}	x	y	z
L FFA	46	−39	−50	−21	38	−42	−50	−24
R FFA	49	41	−48	−22	41	43	−49	−22
L LLA	48	−14	−76	−12	45	−19	−73	−13
R LLA	50	16	−73	−10	45	20	−69	−14
L PPA	50	−26	−49	−11	47	−28	−49	−12
R PPA	50	26	−46	−13	47	30	−46	−13

Peaks were identified using a lenient threshold of $P < 0.05$ to allow participants with weak selective voxels to also contribute to the between-groups analyses ('Methods' section).

culture-specific values. Westerners rated the individualistic value—hedonism—more highly than East Asians. East Asian participants rated the collectivistic values (benevolence, tradition, conformity and security) significantly higher than Westerners. East Asians also rated the individualistic value of power more highly, possibly because of the East Asian emphasis on success and prosperity. There were no cultural differences on neuropsychological measures of processing speed (pattern-matching) or working and long-term memory (letter number sequencing, mental control and word list recall), indicating comparable cognitive functioning in both groups.

Greater face selectivity in FFA in Westerners than East Asians

The left and right FFA were identified in the fusiform regions of the Western and East Asian participants ('Methods' section; Figure 2; Table 2). Face selectivity was then measured in the top 10, 15 and 20 most selective voxels in these ROI for each participant ('Methods' section; Figure 3). Figure 3 shows that Westerners had greater face selectivity than East Asians in the left FFA across all levels of the number of voxels considered within the ROIs [top 10 voxels: $t(82) = 1.91$, $P < 0.05$; top 15 voxels: $t(82) = 1.94$, $P < 0.05$; top 20 voxels: $t(82) = 1.93$, $P < 0.05$]. There were no significant group differences in face selectivity in the right FFA.

To compare the hemispheric lateralization of FFA responses in Westerners and East Asians, we computed LI from the Face selectivity measures for each participant (Table 3, 'Methods' section). We found some evidence that supported more right lateralized Face selectivity (larger positive LI values) in the FFA of East Asians compared to Westerners, with a significant difference for the top 10 voxels, and a trend for the top 15 and top 20 [top 10 voxels: $t(81) = 1.79$, $P < 0.05$; top 15 voxels: $t(81) = 1.57$, $P < 0.07$; top 20 voxels: $t(81) = 1.39$, $P < 0.09$].

Taken together, these findings of greater left FFA face selectivity in Westerners, with East Asians showing somewhat more right lateralized FFA selectivity, is consistent with an analytic style of face processing in Westerners and a holistic processing style in East Asians.

Minimal group differences in house selectivity in LLA and PPA

The analysis of house selectivity in the PPA, identified in the parahippocampal gyrus, and LLA, in the lingual gyrus ('Methods' section; Supplementary Figure 2; Table 2), showed no evidence for group differences in the PPA and limited evidence for a group difference in the LLA. There were some non-significant but consistent indications of greater attention to houses in East Asians in the LLA. Supplementary Figure 2 shows that in both left and right LLA, there were trends toward greater House selectivity in East Asians than Westerners [left LLA; top 10 voxels: $t(92) = 1.37$, $P < 0.09$; top 15 voxels: $t(92) = 1.65$, $P < 0.06$; top 20 voxels: $t(92) = 1.48$; $P < 0.08$; right LLA; top 10 voxels: $t(93) = 1.28$; $P = 0.10$; top 15 voxels: $t(93) = 1.34$; $P < 0.10$; top 20 voxels: $t(93) = 1.33$; $P < 0.10$]. There were no differences in lateralization of house selectivity between both groups for both PPA and LLA (Table 3).

Correlating culture values and ventral visual selectivity

In a follow-up analysis, we sought to relate differences in cultural values to the group differences in ventral visual selectivity for faces and houses. We correlated participants' ratings on each of the SVS sub-scales with their selectivity indices in the left and right FFA, LLA and PPA ROIs identified earlier (as in Chiao *et al.*, 2009). When considering

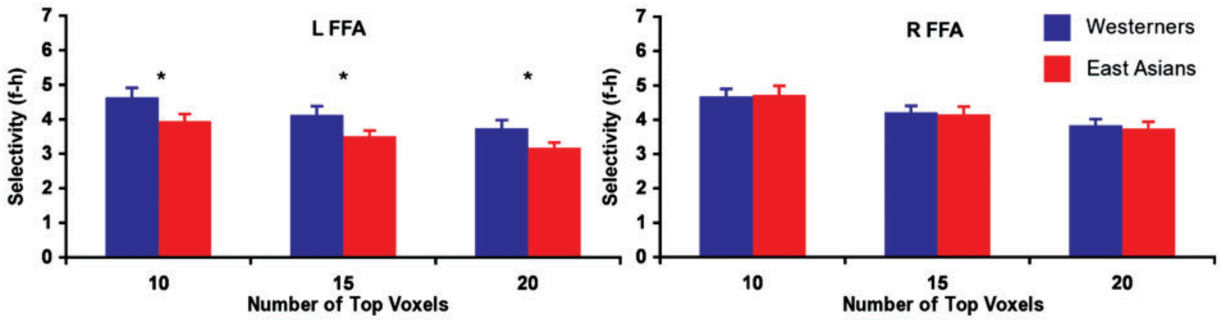

Fig. 3 Differences in face selectivity between Westerners and East Asians in the most significant 10, 15 and 20 voxels of the right and left FFA for the face > house (f–h) contrast. $^*P < 0.05$.

Table 3 Mean laterality indices (expressed as log exponentials of 10^{-2}) for Westerners and East Asians based on the most significant 10, 15 and 20 voxels of each ROI (s.e. in parentheses)

	Westerners			East Asians		
ROI	10	15	20	10	15	20
FFA	2.9 (2.3)	3.6 (2.2)	4.0 (2.2)	8.8 (2.4)	8.8 (2.4)	8.5 (2.4)
LLA	3.0 (1.5)	3.5 (1.4)	3.6 (1.3)	1.4 (1.9)	1.1 (1.8)	1.7 (1.7)
PPA	4.7 (1.8)	4.6 (1.7)	4.7 (1.6)	3.1 (2.0)	2.9 (1.8)	2.9 (1.7)

Larger positive values indicate more right lateralization and values closer to zero indicate more bilaterality.

Westerners and East Asians as one group, we found only one significant negative correlation between the SVS value of security and face selectivity in the left FFA ($r = -0.24$, $P < 0.05$), suggesting that higher ratings on this collectivistic value was associated with reduced Face selectivity in this ROI. When performing this correlation separately for each of the two groups, however, the relationship became non-significant. We also performed a whole-brain analysis (with individual participants' brain images normalized to MNI space), regressing each of the SVS sub-scale ratings on the face and house selectivity index in each voxel. There were no meaningful patterns of voxel correlations at a statistical threshold of $P < 0.001$, uncorrected for multiple comparisons. Overall, while our functional differences above were consistent with expected differences in visual processing styles, we did not find a strong direct relationship between cultural values and ventral visual selectivity for faces and houses.

DISCUSSION

Cultural differences in visual processing between Westerners and East Asians have been reliably demonstrated in previous behavioral, eye-tracking and neuroimaging studies (Nisbett and Miyamoto, 2005; Han and Northoff, 2008; Goh and Park, 2009). Across all these studies, the evidence consistently point to a more analytic style of visual processing in Westerners involving greater attention to objects and features, and a more holistic visual processing style in East Asians that involves greater attention to contextual information. The findings in the current study show that cultural differences are observable during a simple fMRI experiment involving passive viewing of faces and houses in the highly specialized ventral visual areas. Westerners showed more analytic processing of faces with greater left FFA selectivity than East Asians for faces relative to houses. This cultural difference in left but not right FFA selectivity was further characterized by a more right lateralized Face selectivity in the FFA in East Asians compared to the more bilaterally selective response to faces in Westerners. There was also a trend for somewhat greater selectivity in the LLA for East Asians than Westerners for houses relative to faces, suggestive of greater context processing bias. Finally, although the functional differences were consistent with expectations based on cultural differences in visual processing style, we also note that we did not find reliable direct associations between participants' values (as measured by the SVS) and ventral visual selectivity in this study.

Our finding of greater selectivity for faces in the left FFA in Westerners than East Asians, characterized by a more right lateralized response in East Asians, constitutes a novel finding that is consistent with analytic face processing in Westerners and a holistic bias in East Asians,[1] as evinced by eye-tracking data (Blais *et al.*, 2008; Caldara *et al.*, 2010; Kelly *et al.*, 2010). Greater selectivity of left FFA responses in Westerners may stem from the cultural value for individualism that tends to emphasize differences between individual identities. In contrast, East Asians value collectivism, which tends to de-emphasize differences between individuals and may result in reduced left FFA selectivity observed in our study. In addition, the asymmetry of left and right FFA function across cultures is consistent with studies that suggest different roles that each cerebral hemisphere has in face

[1]Note that we also analyzed face selectivity in the superior temporal sulcus and occipital face area, regions that are sometimes additionally implicated in face processing. We obtained ROIs for these regions according to the manner described in our methods. Examining the functional responses in these ROIs, however, did not reveal any significant cultural differences in face selectivity.

processing. Specifically, the right hemisphere, which shows similar magnitudes of face selectivity in both Westerners and East Asians, has been implicated in holistic processing of faces, where the components of the face and their spatial configuration are processed as a composite whole. The left hemisphere, however, shows greater selectivity in Westerners than in East Asians, and may be more involved in analytic processing of face features, such as the color and shape of the eyes and lips. This culturally dissociated pattern of FFA hemispheric lateralization is again consistent with the eye-movements to faces reported in Blais *et al.* (2008) with Westerners focusing on eyes and lips, and East Asians focusing on the nose, across different types of face processing tasks. Interestingly, recent neuroimaging evidence also showed that these differences in lateralized FFA activity are reliable within the individual across sessions, supportive of a stable individual bias for the way a person processes faces across different tasks (Rotshtein *et al.*, 2007; Yovel *et al.*, 2008). Further work is necessary to parse out more specific cognitive and behavioral consequences of these culturally different processing styles in the FFA on face identification and recognition.

The finding of minimal cultural differences in the PPA and LLA is consistent with previous studies that did not find cultural differences in PPA activity when processing scenes (Gutchess *et al.*, 2006; Goh *et al.*, 2007). Such consistency of PPA responses across groups seen here and in previous studies deserves some comment. The PPA has been shown to be sensitive to the spatial-structural relationships in the immediate visual environment (Epstein *et al.*, 2003; Epstein and Ward, 2010). As such, visual processing of the external environment in the PPA may involve more veridical representations that closely reflect the stimuli, independent of how a participant perceives the stimuli. As for the LLA, although we found some evidence for greater selectivity in this region in East Asians, suggestive of greater attention to contextual landmarks information when processing contexts, we note that this was only a marginally significant trend. Overall, group differences related to scene processing regions of the ventral visual cortex are not as reliable as those observed in the left FFA and in object-processing regions seen in other studies (Gutchess *et al.*, 2006; Goh *et al.*, 2007). This suggests that certain brain regions such as the PPA and LLA may be more involved in representing objective stimulus properties and are not as susceptible to cultural differences in visual perception and attention.

It is important to note that cultural differences in ventral visual selectivity operates in conjunction with the primary role of the ventral visual cortex in parsing visual information into categories. Both Westerners and East Asians in our sample showed highly reliable face selectivity in the FFA; and house selectivity in the PPA and LLA (Supplementary Figure 1). Thus, selectivity for categorical information is a robust primary function of the ventral visual cortex that is largely similar even across individuals who grew up in culturally different environments. At the same time, however, external experiences also have an influence on ventral visual activity, with individual differences in activity in these regions associated with differences in cognitive processing abilities, experiences and strategies (Gauthier *et al.*, 2000; Epstein *et al.*, 2005; Rotshtein *et al.*, 2007). In this present as well as previous culture neuroimaging studies, differences in ventral visual activity of East Asians and Westerners were consistent with the postulated cultural differences in processing styles. While the effects of culture may not be as strong as the effects of stimulus selectivity in these ventral visual ROIs, corroborative evidence give credence to the role that culture plays in modulating ventral visual activity.

In our final follow-up analysis, we sought to relate differences in cultural values to the observed group differences in ventral visual selectivity (as in Chiao *et al.*, 2009). In general, however, the analysis did not reveal reliable relationships between participants' values and functional selectivity in the ventral visual cortex. This may be because the SVS was not sufficiently sensitive to detect neural differences, or the effect of cultural values on ventral visual function operates through some other cognitive process such as attention. In addition, our index of ventral visual selectivity necessarily incorporates difference data, which adds variability to this neural measure that may obscure its relationship to behavioral variables. Thus, while our functional findings align with the expected results based on cultural differences in visual processing styles, it remains difficult to conclude that the functional differences in these regions are directly due to cultural values alone. It is also possible that other factors apart from cultural values may also bear on the functional differences. For example, differences in health and lifestyles (Colcombe *et al.*, 2004; Raz and Rodrigue, 2006), education (Manly, 2008), as well as cohort-specific societal experiences (Schaie, 2008; Whitfield and Morgan 2008), may impact brain structure and function (Park, 2008; Park *et al.*, 1999). In addition, task dependent effects may also play a role on cultural differences in brain function (Hedden *et al.*, 2008). Future studies that directly evaluate the role of these different factors will help elucidate the specific cognitive mechanism and relative contribution of cultural effects on brain function.

In conclusion, the cumulative evidence from this and previous imaging studies suggest that processing of visual stimuli, especially objects and faces, is sculpted by experiences to some extent (Park *et al.*, 1999; Park and Gutchess, 2002; Han and Northoff, 2008; Goh and Park, 2009). The neural correlates of cultural differences in ventral visual processing are reliable and operate in conjunction with the selectivity of ventral visual cortex for specific visual categories. The assumptions of the universality of perceptual representations in the brain must therefore be tempered with an awareness of the cultural backgrounds and experiences of the individual.

SUPPLEMENTARY DATA

Supplementary data are available at *SCAN* online.

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