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ORIGINAL RESEARCH ARTICLE

Cultural influences on the neural correlates of intergroup perception

Lynda C. Lin[1] · Yang Qu[2] · Eva H. Telzer[3]

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Abstract

Intergroup biases influence how people engage with members of their ingroup and outgroup. However, less is known about how culture plays a role in the neural mechanisms involved in intergroup perception. In this study, European American and Chinese participants engaged in an emotion perspective-taking task where they viewed images of ingroup and outgroup members while undergoing an fMRI scan. Results revealed culture-specific patterns of neural activation in the fusiform gyrus when perceiving ingroup and outgroup members in emotional contexts: American participants showed greater fusiform activation to the outgroup than ingroup, whereas Chinese participants showed greater fusiform activation to the ingroup than outgroup. Functional connectivity analyses also revealed distinct patterns of neural connectivity between the fusiform and amygdala between cultures. Taken together, these findings contribute to our understanding of the neural correlates involved in intergroup perception and highlight how culture can modulate activation and functional connectivity in the fusiform gyrus.

Keywords Culture · Cultural neuroscience · Intergroup perception

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✉ Lynda C. Lin
llin90@illinois.edu

[1] Department of Psychology, University of Illinois at Urbana-Champaign, 603 E Daniel St., Champaign, IL 61820, USA

[2] School of Education and Social Policy, Institute for Policy Research, Northwestern University, Evanston, IL, USA

[3] Department of Psychology and Neuroscience, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA

Introduction

Intergroup biases and intergroup perception

Social categorization allows people to navigate their complex environments by helping them make sense of the world. One of the most basic categorizations individuals make is the ingroup–outgroup distinction, or categorizing people into those who are similar and those who are different. Group membership provides people with multiple benefits, such as a sense of belonging and access to resources, but can also lead to detrimental consequences such as discrimination, prejudice, and social exclusion (Van Bavel and Cunningham 2009; Hewstone et al. 2002). Socially ingrained processes, such as cultural upbringing, can shape automatic social categorizations. For example, cultural values and practices emphasize different motivations to engage with ingroup and outgroup members and thus can influence how people perceive members from their own group and other groups. In this study, we used a neuroimaging approach to investigate how culture shapes the neural processes involved in intergroup perception as participants engaged in an emotion perspective-taking task.

Cultural influences on intergroup biases

One common finding across domains in the area of intergroup behavior is that people tend to favor their ingroup over their outgroup—a term referred to as ingroup favoritism. For example, individuals tend to be more cooperative with and display more empathy towards ingroup (vs. outgroup) members (Hammond and Axelrod 2006; Chiao and Mathur 2010). While ingroup favoritism seems to be universal, cultural values also influence the extent to which people engage in ingroup favoritism (Chen et al. 1998). More specifically, in Chinese culture, where there is an emphasis on the interconnectedness of the self with close others (Markus and Kitayama 1991), people tend to be more ingroup-oriented than those in individualistic cultures, where people perceive less differences between ingroup and outgroup members (Triandis and Trafimow 2003).

In emotional contexts, these differences in the motivation to engage with ingroup and outgroup members can also shape intergroup behavior. Given the importance of maintaining intergroup harmony in East Asian cultures, Chinese individuals tend to be more attuned to the emotional states of those in their ingroup over those in their outgroup (Chen et al. 2002; Cheon et al. 2013). Indeed, previous research has found that East Asians tend to have higher accuracy in perceiving other people's emotional states compared to Westerners, which can be supported by cultural values that emphasize the importance of maintaining group harmony (Atkins et al. 2016). Higher empathic accuracy in interdependent cultures is also seen to a higher degree for close others than for strangers (Ma-Kellams and Blascovich 2012; Meyer et al. 2015).

In contrast, in Western cultures, people tend to be less differentially attuned to the emotions of ingroup and outgroup members. On the one hand, in situations of low-threat, those with individualistic orientations might show interpersonal behavior, or focus on individual attributes of members of the outgroup. On the other hand, in situations of high threat, strong individualistic values might heighten the uniqueness of individuals in the ingroup, leading to intergroup (e.g., not focusing on individual attributes of those in their outgroup) rather than interpersonal behavior. This can then result in the outgroup being perceived as homogeneous (Triandis and Trafimow 2003). Thus, in non-threatening environments, those with individualistic tendencies might show more interpersonal rather than intergroup behavior, attempting to perceive the internal attributes of those with whom they are less familiar. Consistent with this idea, Westerners show higher empathic accuracy than East Asians for strangers than close others (Ma-Kellams and Blascovich 2012).

Together, these findings suggest that members of East Asian and Western cultures might be differentially motivated to attend to the emotional states of ingroup and outgroup members, with the former showing a strong ingroup bias and the latter displaying flexible intergroup boundaries, and in non-threatening contexts, even exhibiting higher motivation to engage with outgroup than ingroup members. These different motivational goals can influence person perception and guide visual processing (Balcetis and Dunning 2006; Hughes and Zaki 2015).

Neural regions associated with intergroup perception

Given that intergroup perceptual processes are often implicit and automatic, one way to examine cultural influences on motivated intergroup perception is through the use of neuroimaging methods. In recent years, social neuroscience techniques have increased our understanding of intergroup categorization by allowing researchers to investigate the relatively automatic and early phases of perceptual processing that are harder to examine through self-report measures and behavioral techniques alone. Previous studies investigating the neural substrates of ingroup and outgroup categorization have focused on regions such as the fusiform gyrus, the amygdala, and the temporoparietal junction (TPJ).

Fusiform gyrus

The fusiform is a common area involved in face perception and attention that is important for intergroup processing (Kanwisher et al. 1997; Shkurko 2012; Golby et al. 2001; Van Bavel et al. 2011). According to a recent meta-analysis, the fusiform plays a key role in social categorization through top–down modulation of social perception, processing socially meaningful stimuli, and is sensitive to the social context of tasks (Shkurko 2012). Motivational goals can exert top–down influences on the fusiform (Van Bavel et al. 2011) and fusiform activation could indicate increased individuation or attention biases attributed to motivationally relevant targets, exemplifying how motivation can guide perception and bias information processing (Balcetis and Dunning 2006; Hughes and Zaki 2015).

Given that top–down motivational goals and attentional biases can influence how the fusiform responds differently to stimuli, activation in this region might differ based on the task and depth of the processing goals (Van Bavel and Cunningham

2009; Wojciulik et al. 1998). As previously discussed, motivational goals can be shaped by cultural values, with East Asian and Western cultures showing differences in their motivations to engage with ingroup and outgroup members. Thus, it stands to reason that these differences in motivation to engage with others might be reflected in the fusiform. More specifically, in an intergroup perspective-taking context, early motivated perceptual processes might result in increased fusiform activation in Chinese participants when perceiving the emotions of ingroup relative to outgroup members, whereas American participants might show increased fusiform activation to outgroup than ingroup members.

Amygdala

The amygdala is another brain region that has been commonly implicated in intergroup processes and is activated for both ingroup and outgroup targets (Shkurko 2012). It is involved in emotion processing (Phelps and Ledoux 2005) and is thought to orient responses to salient and biologically relevant stimuli (Adolphs 2009; Pessoa and Adolphs 2010). Amygdala activation can vary as a function of an individual's goals and values (Cunningham and Brosch 2012). Top–down motivations and attention can shape amygdala responses to motivationally relevant stimuli (Cunningham et al. 2008; Pessoa et al. 2002; Wheeler and Fiske 2005) and amygdala activation can bias attention towards what is motivationally relevant through feedback projections to visual-processing regions (Amaral 2002; Todorov 2012). It is plausible that this feedback loop can be fine-tuned through interactions in a certain environment, such as cultural context, that can gradually tune the amygdala's biased response to motivationally relevant stimuli (Cunningham and Brosch 2012).

In the primate brain, the amygdala is also functionally and structurally connected to other brain regions involved in sensory processing, such as those in the visual system (including the fusiform gyrus) (Amaral 2002; Catani et al. 2003; Vuilleumier et al. 2004), as well as regions involved in higher order processing, such as the prefrontal cortex (Cunningham and Brosch 2012), making it strategically located to modulate attention towards what is motivationally relevant (Adolphs 2010; Todorov 2012). In face perception, amygdala–fusiform connectivity has been implicated in studies of perception of emotional facial expressions (Bajaj et al. 2013; Vuilleumier and Pourtois 2007). For example, there is differential coupling between the amygdala and the fusiform gyrus when paying attention (vs. not paying attention) to faces (Pessoa et al. 2002). Other research providing more directional information found that there is bidirectional communication between the fusiform and amygdala in the context of face perception and that fusiform tuning by the amygdala can be dependent on experience and stimulus salience, further providing support for the idea that the amygdala helps guide attention to motivationally relevant stimuli (Herrington et al. 2011).

TPJ

The TPJ is a neural region that is involved in inferring the mental state of others (Saxe and Kanwisher 2003; Van Overwalle 2009). It is recruited differentially for ingroup and outgroup targets in different contexts, such as those involving empathy and prosociality (Cheon et al. 2011; Fourie et al. 2017; Park et al. 2017; Telzer et al. 2015). In addition, cultural membership can influence TPJ activation in intergroup contexts. For example, in an intergroup empathy task, Korean participants exhibited more TPJ activation to racial ingroup (vs. outgroup) members compared to Caucasian–American participants (Cheon et al. 2011), illustrating how ingroup biases can be reflected in the TPJ and how this activation can also be modulated by cultural context.

Current study

Taken together, previous research suggests that top–down modulation and joint action between the fusiform and amygdala can direct visual processing by guiding attention to socially-relevant cues, such as ingroup and outgroup members' emotional states. However, less is known about how culture can shape these processes. In this study, we investigated whether individuals of two different cultures (European American and Chinese) show differences in neural activation when perceiving members of their ingroup and outgroup in an emotion perspective-taking context. In line with previous evidence suggesting that culture influences motivations to engage with ingroup and outgroup members and that motivated cognition can shape the neural systems involved in perception, attention, and mentalizing, we hypothesized that there would be cultural differences in neural activation and connectivity when perceiving ingroup and outgroup members in areas that have been previously associated with intergroup perception, such as the fusiform, the amygdala, and the TPJ. More specifically, given cultural differences in motivations to engage with ingroup and outgroup members, we hypothesized that whereas Chinese participants would show increased fusiform, amygdala and TPJ activation when perceiving ingroup (vs. outgroup) members, American participants would show the reverse: more activation to outgroup (vs. ingroup) members. In addition, we hypothesized that there would be cultural differences in the way that the fusiform and amygdala would be functionally connected across the task. More specifically, we hypothesized that Chinese individuals would show increased functional connectivity between the fusiform and the amygdala for ingroups (vs. outgroups), and that American individuals would show the reverse: increased connectivity between the fusiform and the amygdala for outgroup (vs. ingroup) members.

Methods

Twenty-nine first-year undergraduate students, 14 American (seven female, M = 19.02 years) and 15 Chinese (seven female, M = 19.38 years), completed the study. All of the American participants were born in the United States and self-identified as White and/or European American. All of the Chinese participants were international students born and raised in China who had spent less than 1 year living in the United States at the time of the scan. All subjects provided written consent prior to participating in the study in accordance with the University of Illinois's Institutional Review Board.

Procedure

All instructions and materials were translated and back translated to Chinese by bilingual speakers (Brislin 1980). American participants were administered the English version of the tasks and Chinese participants were administered the Chinese version. A native Mandarin speaker and a native English speaker conducted the study for Chinese and American participants, respectively.

fMRI task

The fMRI task (see Fig. 1) consisted of 96 trials. For each trial, participants saw a picture of a person in various positive (e.g., graduation) and negative (e.g., funeral) emotional contexts for an average of 2.5 s. For each picture, participants were instructed to look at the image, imagine they, their parent, or their peer was the person in the picture (as indicated by a label on top of the picture), and feel their emotional response to those situations. They were then asked to regulate (increase or decrease) their emotional reaction to the images (6 s) and finally provide a rating for how they were feeling on a scale from 1 (extremely negative) to 10 (extremely positive) (2.5 s). Participants completed the task in three blocks (self, parent, and peer) of 32 trials each. Tasks such as these involve higher order processes that first must undergo lower-level perceptual processing—here we were interested in examining cultural differences in these early perceptual processes. Therefore, for

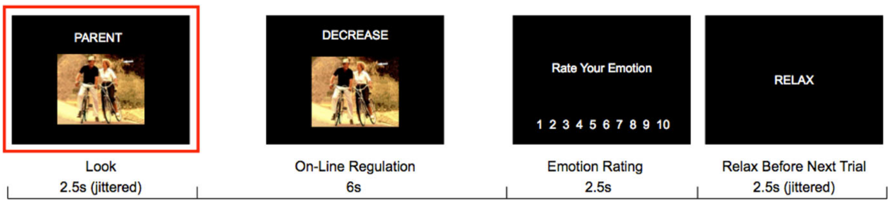

Fig. 1 Illustration of fMRI task. Timeline for events on each trial. Participants are first instructed to imagine the target person in a scene is themselves, their best friend, or their mother, and feel their emotional response to those situations. This is followed by a regulation period during which participants follow the instruction to increase or decrease their emotion. Participants then provide a rating of their current affect, and relax before the onset of the next trial. In this study, we only focused on the first part of the trial when participants first perceive the images (highlighted in red). (Color figure online)

the purposes of this study, we only analyzed the initial 2.5 s of each trial where participants first perceive the images and not the emotion regulation part of the task, which is published elsewhere (Qu and Telzer 2017).

All stimuli used in the fMRI task were naturalistic visual scenes (350 × 280 pixels) portraying either White or Asian individuals in emotional contexts (96 total stimuli). All photos were standardized for size, luminosity and background color. All pictures were rated by a separate group of 21 raters (9 American and 12 East Asian) who were asked to indicate using a 7-point Likert scale the valence of their emotional response to the photo (from "very negative" to "very positive") and the arousal (from "not at all" to "very much") to ensure there were no differences in perceptions of valence or arousal of the emotional scenes based on the culture of the target in the picture (Supplementary Table 1). There were no significant differences in ratings between American and East Asian raters, and the images showing White and Asian individuals were matched on valence and arousal (see Supplementary Table 1 for details on the means and standard deviations).

fMRI data acquisition and analysis

All imaging data were acquired using a 3 Tesla Siemens Trio MRI scanner. T2*-weighted echoplanar images (EPI) [slice thickness = 3 mm; 38 slices; TR = 2 s; TE = 25 ms; matrix = 92 × 92; FOV = 230 mm; voxel size 2.5 × 2.5 × 3 mm^3] were acquired during completion of the fMRI task. Structural scans consisted of a T2*weighted, matched-bandwidth (MBW), high-resolution, anatomical scan (TR = 4 s; TE = 64 ms; matrix = 192 × 192; FOV = 230 mm; slice thickness = 3 mm; 38 slices) and a T1* magnetization-prepared rapid-acquisition gradient echo (MPRAGE; TR = 1.9 s; TE = 2.3 ms; matrix = 256 × 256; FOV = 230 mm; sagittal plane; slice thickness = 1 mm; 192 slices). The orientation for the MBW and EPI scans was oblique axial to maximize brain coverage.

fMRI data preprocessing and analysis

Neuroimaging data were preprocessed and analyzed using Statistical Parametric Mapping (SPM8; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). Preprocessing for each participant's images consisted of spatial realignment to correct for head motion (no participant exceeded 2.5 mm of maximum image-to-image motion in any direction on more than 10% of slices, and slices with movement were censored). The realigned functional data were then coregistered to the high resolution MPRAGE and segmented into cerebrospinal fluid, grey matter, and white matter. The normalization transformation matrix resulting from the segmentation step was then applied to the functional and T2 structural images, thus transforming them into standard stereotactic space as defined by the Montreal Neurological Institute and the International Consortium for Brain Mapping. In order to increase the signal-to-noise ratio, the normalized functional data were also smoothed using an 8 mm Gaussian kernel, full-width-at-half maximum.

Statistical analyses were conducted using the general linear model (GLM) in SPM8. Each trial was convolved with the canonical hemodynamic response function. High-pass temporal filtering with a cutoff of 128 s was performed to remove low-frequency drift in the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model order of 1.

In each participant's fixed-effects analysis, a GLM was created with the regressors of interest, which included perception (i.e., participants looked at the photos) of ingroup and outgroup targets (as defined by the cultural membership of the participant and the target stimuli). The regulation periods (i.e., participants upregulated or downregulated their emotions) and ratings of emotion were modeled as separate regressors. The task was modeled as an event-related design, such that we included the onset and duration of each of the trials rather than the onset and duration of each whole block in order to specifically model the initial perception period separately from the regulation period. The duration of each perception trial lasted about 2.5 s. Jittered inter-trial intervals were not explicitly modeled and therefore constituted an implicit baseline.

Linear contrast images comparing our main condition of interest (ingroup > outgroup) were created based on the parameter estimates resulting from the GLM. Random effect analyses were conducted on all individual subject contrasts using GlmFlex (http://mrtools.mgh.harvard.edu/index.php/GLM_Flex). At the group level we ran whole brain, two-sample *t*-tests (Chinese-American) to examine cultural differences in the neural correlates underlying intergroup perception of ingroup–outgroup scenes.

In addition, given that the fusiform is modulated by other neural regions such as the amygdala, we conducted functional connectivity analyses to examine functional coupling between the fusiform and other regions. We conducted psychophysiological interaction (PPI) analyses (Friston et al. 1997) using the fusiform (identified from the two-sample *t* test above) as the seed region (see Results for how the ROI was defined). PPI analyses were performed using a generalized form of context-dependent PPI. More specifically, the automated gPPI toolbox in SPM (gPPI; McLaren et al. 2008) was used to (i) extract the deconvolved time series from the fusiform ROI for each participant to create the physiological variables; (ii) convolve each trial type with the canonical HRF, creating the psychological regressor; and (iii) multiply the time series from the psychological regressors with the physiological variable to create the PPI interaction terms. The interaction term indicated regions that covaried in a task-dependent manner with the fusiform. At the first level, one regressor representing the deconvolved BOLD signal was included alongside each psychological and PPI interaction term for each condition type to create a gPPI model. At the group level, we ran a whole-brain two sample-test to analyze cultural differences in functional coupling between the fusiform and other brain regions during ingroup perception compared to outgroup perception.

Monte Carlo simulations were implemented using 3dClustSim in the software package AFNI (Ward 2000; updated version April 2016) to correct for multiple comparisons, estimating the smoothness of the data with the acf command in 3dFWHMx. Results of the simulation indicated a voxel-wise threshold of $p < 0.005$

combined with a minimum cluster size of 79 voxels for the two-sample *t*-tests, and 68 voxels for the two-sample *t*-test PPI corresponding to $p < 0.05$, family wise error (FWE) corrected. All results are available on Neurovault (Gorgolewski et al. 2015; see https://neurovault.org/collections/LREHHYEB/).

Results

Cultural differences in neural activation when perceiving ingroup and outgroup members

We first examined whether American and Chinese participants showed different patterns of neural activation when perceiving ingroups and outgroups. To this end, we conducted a whole brain two-sample *t*-test comparing American and Chinese participants [Chinese-American] to [Ingroup–Outgroup]. Results indicated that Chinese participants showed greater activation in the fusiform gyrus than American participants when perceiving the emotions of their ingroup compared to their outgroup (Fig. 2a; see Table 1 for a full list of all of the clusters of activation). For descriptive purposes, we extracted parameter estimates of signal intensity from the fusiform cluster for ingroup and outgroup (relative to baseline) separately, and plotted the mean activation for Chinese and American participants. As shown in Fig. 2b, Chinese participants showed heightened activation in the fusiform to the ingroup, whereas American participants showed heightened activation to the outgroup. In order to further unpack this interaction, we conducted post hoc one-sample *t*-tests within each culture separately, focusing solely on the fusiform with a threshold of $p < 0.05$. We found Chinese participants showed greater activation in the fusiform gyrus when perceiving the emotions of their ingroup relative to their outgroup (left fusiform: xyz = − 27 − 46 − 8, $t(13) = 6.06$; right fusiform: xyz = 33 − 43 − 8, $t(14) = 5.09$) and American participants showed greater fusiform activation when perceiving the emotions of their outgroup relative to their

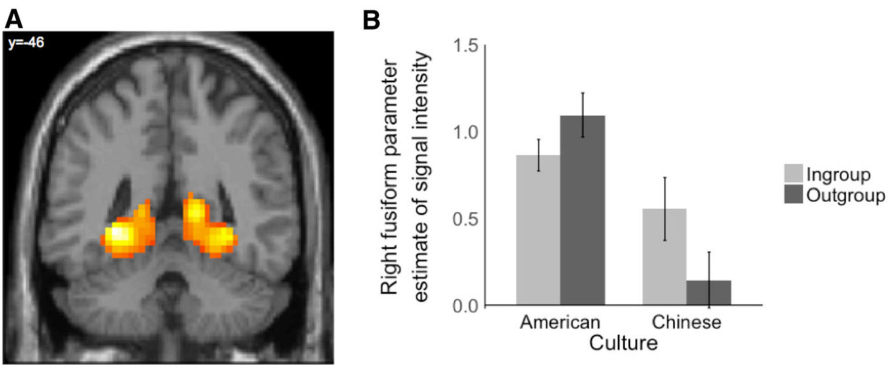

Fig. 2 Cultural differences in neural activation when perceiving ingroup and outgroup members. **a** Chinese participants showed increased fusiform activation compared to American participants when perceiving ingroup over outgroup members. **b** Extracted parameter estimates from **a** for descriptive purposes

Table 1 Cultural differences in brain regions that showed increased activation to ingroup over outgroup members

Anatomical region	x	y	z	*t*	*k*
Two sample *t*-tests (Chinese vs. American; ingroup–outgroup)					
Chinese > American					
L fusiform	− 27	− 46	− 8	7.87	532[a]
L parahippocampal gyrus	− 30	− 46	− 5	8.61	[a]
L calcarine gyrus	− 18	− 58	10	5.46	[a]
R fusiform	33	− 43	− 8	6.07	545[b]
R lingual gyrus	15	− 46	4	6.62	[b]
R parahippocampal gyrus	21	− 34	− 11	5.43	[b]
L middle occipital gyrus	− 36	− 79	10	4.83	205
R middle temporal gyrus	45	− 67	13	4.45	79
R inferior frontal gyrus	45	29	10	3.57	269[c]
R putamen	30	11	10	3.17	[c]
American > Chinese					
L middle frontal gyrus	− 33	26	52	− 4.70	129[d]
L superior medial gyrus	− 9	38	55	− 3.91	[d]
R cerebelum	48	− 70	− 35	− 4.47	115

L and *R* refer to the left or right hemisphere, *x*, *y*, and *z* refer to MNI coordinates, *t* refers to the *t*-score at those coordinates (local maxima), *k* refers to the number of voxels in each significant cluster. Regions with the same superscript signify they belong to the same cluster of activation

ingroup (left fusiform: xyz = − 27 − 46 − 8, $t(13) = -5.09$; right fusiform: xyz = 33 − 43 − 8, $t(13) = -3.56$). Contrary to our hypothesis, we did not find cultural differences in neural activation in the amygdala or TPJ when perceiving ingroup (vs. outgroup) members.

Cultural differences in fusiform–amygdala functional connectivity when perceiving ingroup and outgroup members

Next, we examined cultural differences in functional connectivity between the fusiform and other brain regions when perceiving ingroup relative to outgroup members. To this end, we used the significant fusiform cluster obtained from the two-sample *t*-test identified above as the seed region to examine whether there were cultural differences in how the fusiform was coupled with other brain regions. Given that the cluster was relatively large, we thresholded it at $p = 0.0001$ to create a smaller cluster, which included 360 voxels combined across the left and right fusiform.

Whole-brain PPI analyses revealed American participants showed more functional coupling between the fusiform and the amygdala than Chinese participants when perceiving the emotions of their ingroup compared to their outgroup (Fig. 3a; see Table 2 for a full list of all of the clusters of activation). For

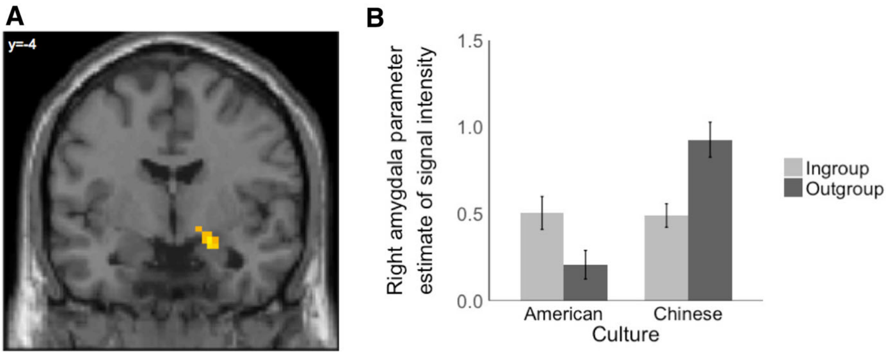

Fig. 3 Cultural differences in functional connectivity between the fusiform and the amygdala when perceiving ingroup and outgroup members. **a** American participants showed increased functional connectivity between the fusiform and the amygdala compared to Chinese participants when perceiving ingroup over outgroup members. **b** Extracted parameter estimates from **a** for descriptive purposes

Table 2 Cultural differences in brain regions that showed increased functional connectivity with the fusiform for ingroup over outgroup members

Anatomical region	x	y	z	*t*	*k*
Two sample *t*-tests (Chinese vs. American; ingroup–outgroup)					
American > Chinese					
R amygdala	21	− 4	− 14	− 3.43	85[a]
R temporal pole	36	8	− 20	− 3.65	[a]
R thalamus	21	− 31	1	− 5.39	69

L and *R* refer to the left or right hemisphere, *x*, *y*, and *z* refer to MNI coordinates, *t* refers to the *t*-score at those coordinates (local maxima), *k* refers to the number of voxels in each significant cluster. No regions showed increased functional connectivity with the fusiform for Chinese more than American when perceiving ingroup over outgroup members. Regions with the same superscript signify they belong to the same cluster of activation

descriptive purposes, we extracted parameter estimates from the significant fusiform–amygdala connectivity cluster for ingroup and outgroup targets separately for American and Chinese participants. As shown in Fig. 3b, American participants showed increased coupling between the fusiform and amygdala when perceiving ingroup relative to outgroup members, whereas Chinese participants showed the opposite pattern: increased coupling between the fusiform and amygdala when viewing outgroup relative to ingroup members. In order to further unpack this interaction, we conducted post hoc one-sample *t*-tests within each culture separately, focusing solely on the amygdala with a threshold of $p < 0.05$. We found American participants showed greater fusiform–amygdala connectivity when perceiving the emotions of their ingroup relative to their outgroup (xyz = 21 − 4 − 14, $t(13) = 1.99$), and Chinese participants showed greater fusiform–amygdala connectivity when perceiving the emotions of their outgroup relative to their ingroup (xyz = 21 − 4 − 14, $t(14) = -2.69$).

Discussion

In this study, we examined cultural influences on the neural regions involved in intergroup perception in the context of an emotion perspective-taking task. We found supporting evidence that culture influences the neural processes involved in ingroup versus outgroup perception. Whereas Chinese individuals showed more fusiform activation to the ingroup (vs. outgroup), American participants showed increased fusiform activation to the outgroup (vs. ingroup). Contrary to our hypothesis, we did not find cultural differences in neural activation in the amygdala or TPJ when perceiving ingroup and outgroup members. We also found cultural differences in functional connectivity between the fusiform and the amygdala though not in our expected direction: Chinese individuals showed greater coordinated activity between the fusiform and the amygdala for outgroups (vs. ingroups), whereas American participants showed increased connectivity between the fusiform and the amygdala for ingroups (vs. outgroups).

Previous findings have linked the fusiform to human face processing (Kanwisher and Yovel 2006), attention, and emotion processing (Vuilleumier 2005) and have shown that activation in this region is modulated by motivational goals and attentional biases (Van Bavel and Cunningham 2009; Wojciulik et al. 1998). Consistent with previous behavioral research that observed higher empathic accuracy in East Asian cultures for close others than for strangers (Ma-Kellams and Blascovich 2012), results from our study suggest that ingroup biases that make Chinese individuals more motivated to attend to the emotional states of those in their ingroup more so than those in their outgroup might be reflected in the fusiform gyrus. Similarly, higher emphatic accuracy for strangers than close others in Westerners (Ma-Kellams and Blascovich 2012) might be reflected in American individuals' greater recruitment of the fusiform when perceiving the outgroup compared to the ingroup. Results from our study suggest that the fusiform's role in the perception of ingroup and outgroup members is sensitive to the motivational goals that are shaped by cultural context. Our findings converge with previous behavioral studies using eye-tracking that have documented how cultural environment and experience shape the strategies used for facial and emotion perception (Caldara 2017).

At first our findings with the fusiform may seem inconsistent with previous studies on face perception that show that Black and White individuals tend to show more activation in the fusiform to ingroup than outgroup members (Golby et al. 2001; Van Bavel et al. 2011). However, we describe some differences between our study and previous ones that could have resulted in these divergent results. Our task is different from these previous studies in that although we focused on analyzing differences in intergroup perception, participants in the other studies predominantly had categorization goals while our study involved the higher goal of engaging in perspective taking in an emotional context. Given that the fusiform has interconnections with other regions, such as the amygdala (Amaral 2002; Catani et al. 2003), it is possible that when engaging in higher order cognitive and affective tasks, the fusiform might respond differently than when engaging in face-categorization tasks.

These findings qualify previous studies that found that ingroup members are processed in more depth than outgroup members (Van Bavel and Cunningham 2009). Results from our study suggest that (1) ingroup members might be processed in more depth only if there is no higher order motivation to engage with the targets in the pictures (for example, in perspective-taking), and (2) biases in intergroup perception might be modulated by cultural background.

It is interesting to note that cultural differences were found in areas related to perception (fusiform) but not in those related to mentalizing, such as TPJ (Saxe and Kanwisher 2003; Van Overwalle 2009). Previous research has found a similar pattern of results as the current study in the TPJ: when engaging in an intergroup empathy task, Korean participants showed more activation to the ingroup than outgroup whereas Caucasian Americans showed more activation to the outgroup than ingroup in the TPJ (Cheon et al. 2011). There are several reasons why we may have failed to see cultural differences in TPJ activation in this study when compared to the results from Cheon et al. (2011). Some of these differences could stem from the nature of the stimuli: whereas Cheon et al. (2011) displayed images depicting people in pain and in neutral situations, our images were negative and positive. There could also be differences due to sample characteristics (Chinese vs. Korean). In addition, our more conservative cluster threshold may have impacted our ability to detect cultural differences in neural activation in this region. But overall, the similar pattern of results but in a different brain region might suggest that participants in our study were not engaging in mentalizing processes, but rather, it was their perception and attention that differed. When performing a task that requires them to emotionally engage with others, participants from different cultures might recruit neural regions involved in face perception and attention in different ways.

Of note, we found a different pattern of results for our fusiform univariate analyses and fusiform–amygdala functional connectivity results: American participants showed more functional coupling between fusiform and amygdala for the ingroup versus outgroup, while Chinese participants showed the opposite—increased functional coupling for the outgroup versus ingroup. While our univariate and functional connectivity results may seem discordant, Herrington et al. (2011) propose an intriguing hypothesis regarding the fusiform's dependence on and independence from the amygdala: "years of experience with faces may result in a highly responsive FG [fusiform gyurs] that continues to be influenced by amygdala, but also maintains substantial functional independence from it" (p. 2354). Thus, it is possible that the fusiform independence from the amygdala and likely modulation from other neural regions might have resulted in the low amygdala-fusiform coordinated activity seen for outgroup members in American participants and for ingroup members in Chinese participants. In contrast, functional dependence between the amygdala and the fusiform may have resulted in their high functional connectivity for ingroup members for Americans and outgroup members for Chinese.

Our findings provide new insights into how connectivity between fusiform and amygdala varies by context (whether perceiving ingroup or outgroup members) and culture (American vs. Chinese). On the one hand, for American individuals, fusiform and amygdala co-activation suggests that person perception and emotion processing work in concert but only when perceiving ingroup members. When perceiving outgroup members, amygdala and fusiform function more independently from one another and therefore suggest that perception and emotional reactivity might not be as tightly coupled when perceiving outgroup members compared with ingroup members. On the other hand, for Chinese individuals, the opposite might be true: low amygdala-fusiform connectivity for ingroup members could suggest that Chinese individuals might perceive and attend to the faces of their ingroup independently of their emotional reactivity to the faces. When perceiving outgroup members, amygdala might be recruited to both process and attend to the faces as well as process emotional responses to the faces. However, these hypotheses are speculative and more research is needed to test whether and under what circumstances the fusiform can act both dependently and independently from the amygdala. We also stress that functional connectivity analyses do not say anything about the causal direction of connectivity (i.e., whether amygdala causes changes in fusiform, or vice versa). Other analytical approaches, such as dynamic causal modeling, could help in clarifying the patterns of results observed in this study.

There were some limitations that could be addressed in future studies. For example, we had a relatively small sample size and future studies with larger samples would be needed to support our findings. In addition, Chinese participants were international students and it is possible that the neural differences in the fusiform may have been driven by their minority status rather than by cultural influences. Some studies have found that in situations where there is a majority and minority group, more attention is allocated to minority group members, resulting in increased ingroup biases in minority members and decreased ingroup biases in majority members (Mullen et al. 1992). Thus, one possible explanation for American participants' lack of ingroup orientation in our study that may have resulted in enhanced fusiform activation to outgroup relative to ingroup targets may have been due to focusing on the minority group. However, the results on intergroup biases based on group size are context dependent and can be influenced by confounding factors such as status and power (Hewstone et al. 2002). One way to reject the alternative majority-minority explanation for our observed results could be to run the study in China and see if the same cultural differences in fusiform activation and fusiform–amygdala connectivity are found between Chinese and European Americans living in China.

Based on previous findings that greater fusiform activity to ingroup relative to outgroup members was associated with greater memory for the ingroup (Golby et al. 2001), future studies could also see if the observed cultural differences in neural activation for ingroup and outgroup members might be associated with behavioral indices, such as participants' subjective rating of the extent to which they engaged in perspective taking. Associations with behavioral findings might improve our understanding of whether group membership effects on perceptual encoding can influence affective, cognitive and social behaviors or whether similar behavioral results might be present but with distinct underlying neural mechanisms. Moreover, inclusion of self-report measures assessing different cultural values or beliefs can lend insights into understanding the specific cultural constructs that might be influencing the different neural effects observed in this study (Han et al. 2013).

In sum, we investigated how cultural membership influences people's perceptions of ingroup and outgroup members in the context of an emotion perspective-taking task. We demonstrate that culture shapes the neural processes involved in intergroup perception, particularly in the fusiform gyrus and its functional connectivity with the amygdala.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicting interests.

References

Adolphs, R. (2009). The social brain: Neural basis of social knowledge. *Annual Review of Psychology, 60,* 693–716.

Adolphs, R. (2010). What does the amygdala contribute to social cognition? *Annals of the New York Academy of Sciences, 1191*(1), 42–61.

Amaral, D. G. (2002). The primate amygdala and the neurobiology of social behavior: Implications for understanding social anxiety. *Biological Psychiatry, 51*(1), 11–17.

Atkins, D., Uskul, A. K., & Cooper, N. R. (2016). Culture shapes empathic responses to physical and social pain. *Emotion, 16*(5), 587.

Bajaj, S., Lamichhane, B., Adhikari, B. M., & Dhamala, M. (2013). Amygdala mediated connectivity in perceptual decision-making of emotional facial expressions. *Brain Connectivity, 3*(4), 386–397.

Balcetis, E., & Dunning, D. (2006). See what you want to see: Motivational influences on visual perception. *Journal of Personality and Social Psychology, 91*(4), 612.

Brislin, R. W. (1980). Translation and content analysis of oral and written materials. In H. C. Triandis & J. W. Berry (Eds.), *Handbook of cross-cultural psychology* (Vol. 2, pp. 389–444)., *Methodology* Boston, MA: Allyn & Bacon.

Caldara, R. (2017). Culture reveals a flexible system for face processing. *Current Directions in Psychological Science, 26*(3), 249–255.

Catani, M., Jones, D. K., Donato, R., & Ffytche, D. H. (2003). Occipito-temporal connections in the human brain. *Brain, 126*(9), 2093–2107.

Chen, Y., Brockner, J., & Chen, X. (2002). Individual-collective primacy and ingroup favoritism: Enhancement and protection effects. *Journal of Experimental Social Psychology, 38*(5), 482–491.

Chen, Y., Brockner, J., & Katz, T. (1998). Toward an explanation of cultural differences in in-group favoritism: The role of individual versus collective primacy. *Journal of Personality and Social Psychology, 75*(6), 1490.

Cheon, B. K., Im, D. M., Harada, T., Kim, J. S., Mathur, V. A., Scimeca, J. M., et al. (2011). Cultural influences on neural basis of intergroup empathy. *Neuroimage, 57*(2), 642–650.

Cheon, B. K., Im, D. M., Harada, T., Kim, J., Mathur, V. A., Scimeca, J. M., et al. (2013). Cultural modulation of the neural correlates of emotional pain perception: The role of other-focusedness. *Neuropsychologia, 51*(7), 1177–1186.

Chiao, J. Y., & Mathur, V. A. (2010). Intergroup empathy: How does race affect empathic neural responses? *Current Biology, 20*(11), R478–R480.

Cunningham, W. A., & Brosch, T. (2012). Motivational salience: Amygdala tuning from traits, needs, values, and goals. *Current Directions in Psychological Science, 21*(1), 54–59.

Cunningham, W. A., Van Bavel, J. J., & Johnsen, I. R. (2008). Affective flexibility: Evaluative processing goals shape amygdala activity. *Psychological Science, 19*(2), 152–160.

Fourie, M. M., Stein, D. J., Solms, M., Gobodo-Madikizela, P., & Decety, J. (2017). Empathy and moral emotions in post-apartheid South Africa: An fMRI investigation. *Social Cognitive and Affective Neuroscience, 12*(6), 881–892.

Friston, K. J., Buechel, C., Fink, G. R., Morris, J., Rolls, E., & Dolan, R. J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage, 6*(3), 218–229.

Golby, A. J., Gabrieli, J. D., Chiao, J. Y., & Eberhardt, J. L. (2001). Differential responses in the fusiform region to same-race and other-race faces. *Nature Neuroscience, 4*(8), 845.

Gorgolewski, K. J., Varoquaux, G., Rivera, G., Schwarz, Y., Ghosh, S. S., Maumet, C., et al. (2015). A web-based repository for collecting and sharing unthresholded statistical maps of the human brain. *Frontiers in Neuroinformatics, 9,* 8.

Hammond, R. A., & Axelrod, R. (2006). The evolution of ethnocentrism. *Journal of Conflict Resolution, 50*(6), 926–936.

Han, S., Northoff, G., Vogeley, K., Wexler, B. E., Kitayama, S., & Varnum, M. E. (2013). A cultural neuroscience approach to the biosocial nature of the human brain. *Annual Review of Psychology, 64,* 335–359.

Herrington, J. D., Taylor, J. M., Grupe, D. W., Curby, K. M., & Schultz, R. T. (2011). Bidirectional communication between amygdala and fusiform gyrus during facial recognition. *Neuroimage, 56*(4), 2348–2355.

Hewstone, M., Rubin, M., & Willis, H. (2002). Intergroup bias. *Annual Review of Psychology, 53*(1), 575–604.

Hughes, B. L., & Zaki, J. (2015). The neuroscience of motivated cognition. *Trends in Cognitive Sciences, 19*(2), 62–64.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*(11), 4302–4311.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 361*(1476), 2109–2128.

Ma-Kellams, C., & Blascovich, J. (2012). Inferring the emotions of friends versus strangers: The role of culture and self-construal. *Personality and Social Psychology Bulletin, 38*(7), 933–945.

Markus, H. R., & Kitayama, S. (1991). Culture and the self: Implications for cognition, emotion, and motivation. *Psychological Review, 98*(2), 224.

McLaren, D., Ries, M., Xu, G., Fitzgerald, M., Kastman, E., Gliori, G.,… & Johnson, S. (2008). *A method for improved sensitivity and flexibility of psychophysiological interactions in event-related fMRI experiments*. Annual Meeting of the Organization for Human Brain Mapping.

Meyer, M. L., Masten, C. L., Ma, Y., Wang, C., Shi, Z., Eisenberger, N. I., et al. (2015). Differential neural activation to friends and strangers links interdependence to empathy. *Culture and Brain, 3*(1), 21–38.

Mullen, B., Brown, R., & Smith, C. (1992). Ingroup bias as a function of salience, relevance, and status: An integration. *European Journal of Social Psychology, 22*(2), 103–122.

Park, B., Blevins, E., Knutson, B., & Tsai, J. L. (2017). Neurocultural evidence that ideal affect match promotes giving. *Social Cognitive and Affective Neuroscience, 12*(7), 1083–1096.

Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience, 11*(11), 773–783.

Pessoa, L., McKenna, M., Gutierrez, E., & Ungerleider, L. G. (2002). Neural processing of emotional faces requires attention. *Proceedings of the National Academy of Sciences, United States of America, 99*(17), 11458–11463.

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: From animal models to human behavior. *Neuron, 48*(2), 175–187.

Qu, Y., & Telzer, E. H. (2017). Cultural differences in beliefs, practices, and neural mechanisms of emotion regulation. *Cultural Diversity and Ethnic Minority Psychology, 23,* 36–44.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: The role of the temporo-parietal junction in "theory of mind". *Neuroimage, 19*(4), 1835–1842.

Shkurko, A. V. (2012). Is social categorization based on relational ingroup/outgroup opposition? A meta-analysis. *Social cognitive and affective neuroscience, 8*(8), 870–877.

Telzer, E. H., Ichien, N., & Qu, Y. (2015). The ties that bind: Group membership shapes the neural correlates of in-group favoritism. *Neuroimage, 115,* 42–51.

Todorov, A. (2012). The role of the amygdala in face perception and evaluation. *Motivation and Emotion, 36*(1), 16–26.

Triandis, H. C., & Trafimow, D. (2003). Culture and its implications for intergroup behavior. In R. Brown & S. L. Gaertner (Eds.), *Blackwell handbook of social psychology: Intergroup processes* (pp. 367–385). Oxford: Blackwell Publishers Ltd.

Van Bavel, J. J., & Cunningham, W. A. (2009). A social neuroscience approach to intergroup perception and evaluation. In W. P. Banks (Ed.), *Encyclopedia of consciousness* (pp. 379–388). New York: Academic Press.

Van Bavel, J. J., Packer, D. J., & Cunningham, W. A. (2011). Modulation of the fusiform face area following minimal exposure to motivationally relevant faces: Evidence of in-group enhancement (not out-group disregard). *Journal of Cognitive Neuroscience, 23*(11), 3343–3354.

Van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. *Human Brain Mapping, 30*(3), 829–858.

Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences, 9*(12), 585–594.

Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: Evidence from functional neuroimaging. *Neuropsychologia, 45*(1), 174–194.

Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience, 7*(11), 1271–1278.

Ward, B. D. (2000). Simultaneous inference for fMRI data. http://afni.nimh.nih.gov/pub/dist/doc/manuals/AlphaSim.pdf.

Wheeler, M. E., & Fiske, S. T. (2005). Controlling racial prejudice: Social-cognitive goals affect amygdala and stereotype activation. *Psychological Science, 16*(1), 56–63.

Wojciulik, E., Kanwisher, N., & Driver, J. (1998). Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *Journal of Neurophysiology, 79*(3), 1574–1578.