Cultural Specificity in Amygdala Response to Fear Faces

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Abstract

■ The human amygdala robustly activates to fear faces. Heightened response to fear faces is thought to reflect the amygdala's adaptive function as an early warning mechanism. Although culture shapes several facets of emotional and social experience, including how fear is perceived and expressed to others, very little is known about how culture influences neural responses to fear stimuli. Here we show that the bilateral amygdala response to fear faces is modulated by culture. We used functional magnetic resonance imaging to measure amygdala response to fear and nonfear faces in two distinct cultures. Native Japanese in Japan and Caucasians in the United States showed greater amygdala activation to fear expressed by members of their own cultural group. This finding provides novel and surprising evidence of cultural tuning in an automatic neural response. ■

INTRODUCTION

The facial expression of fear serves as an adaptive social signal, simultaneously warning others of nearby threat and soliciting their help (Ekman & Friesen, 1971; Darwin, 1872). The human amygdala is a subcortical brain region highly specialized for evaluating and responding to cues signaling impending threat, including facial expressions of fear (Phelps & Ledoux, 2005; Adolphs, 2002; Davis & Whalen, 2001; LeDoux, 1996). Both subliminal and supraliminal facial fear stimuli robustly elicit amygdala activation across a majority of neuroimaging studies (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Glascher & Adolphs, 2003; Wager, Phan, Liberzon, & Taylor, 2003; Whalen et al., 1998). However, because prior neuroimaging studies have only examined amygdala response to emotional facial stimuli in participants living within the same cultural environment, mostly within the United States or Europe, it remains unknown whether culture affects the neural response to fear faces.

Anthropologists and cultural psychologists have argued that culture[1] influences emotional processes, including the evaluation of and response to facial expressions of fear (Mesquita & Frijda, 1992; Lutz & White, 1986). A meta-analytic review examining the judgments of emotional faces across cultural and ethnic groups found two ways in which the recognition of the fear expression is moderated by culture (Elfenbein & Ambady, 2002). First, prior research has demonstrated a "cultural specificity" effect in emotion recognition whereby people are better at recognizing own-culture emotional expressions relative to other-culture emotional expressions (Elfenbein & Ambady, 2002). Second, past behavioral studies have also revealed a "cultural variation" effect in emotion recognition, such that culture shapes how and when fear is expressed in the face (Elfenbein & Ambady, 2002). For example, people infer nationality[2] (e.g., Japanese–American versus Japanese) significantly better from facial expressions of emotion, such as fear, than from their neutral facial expression, suggesting that subtle, but significant, cultural variation in the way that fear is expressed in the face can serve as an additional cue to cultural group membership (Marsh, Elfenbein, & Ambady, 2003). Additionally, cultural variation may exist in displays rules that govern when it is culturally appropriate to express a particular emotion, such as fear (Ekman, Sorenson, & Friesen, 1969).

However, whether culture affects neural mechanisms underlying fear recognition in a similar manner as observed in behavioral studies remains unknown. One hypothesis is that given the automatic, prepotent nature of amygdala response to fear faces and the adaptive importance of responding to any signal of imminent danger in the environment, cultural affiliation will not affect the amygdala response to fear faces. An alternative hypothesis is that amygdala response may be enhanced for own-culture fear faces, given the greater similarity between self and other members of the same cultural group. A threat to another member of the same cultural group, as inferred by that member's fear facial expression,

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may be a more salient signal of impending threat to oneself. The purpose of the present work was to investigate these two competing hypotheses regarding culture and neural activation in response to fear faces.

Here we used event-related functional magnetic resonance imaging in two distinct cultures to investigate cultural specificity in the amygdala's response to fear faces. During scanning, native Japanese in Japan and Caucasians in the United States recognized Japanese and Caucasian fearful and nonfearful (e.g., angry, happy, neutral) faces. Because of the robustness of the responses to fear faces in the human amygdala and prior behavioral evidence of cultural specificity in the perception and expression of fear faces, we hypothesized that the human amygdala would respond preferentially to fear expressed by members of one's own versus other cultural group, but not to other types of emotions such as happiness or anger.

METHODS

Participants

Twenty-two right-handed healthy participants, 12 native Japanese living in Japan (6 men, 6 women), and 10 Caucasians living in the United States (5 men, 5 women), between the ages of 18 and 25 years, with corrected-to-normal vision, participated in this study. Two Japanese participants were dropped from analysis due to excessive head movement, as both of their movement parameter graphs indicated greater than 6 mm of movement in the *x* and *y* translation over the course of the study, exceeding our a priori cutoff of 5 mm.

Stimuli

Digitized grayscale pictures of 80 faces, each with either a fearful, a neutral, a happy, or an angry expression taken from Japanese and Caucasian posers (20 men and 20 women from each cultural group) were used (see Figure 1). In order to ensure that facial expressions of emotion were from people of different cultural, rather than racial or ethnic groups, all posers were self-identified as either native Japanese or Caucasian–American and all photographs of posers were taken in their native country (i.e., Japan or USA). All photographs were standardized for size and background using Adobe Photoshop and were pretested to control for average emotional intensity across conditions (Ekman & Friesen, 1976). Stimuli were projected onto a transparent screen hanging on the bore of the magnet approximately 65 cm from the participants' eyes.

Experimental Procedure

All participants were tested within their own culture by an experimenter who conducted the study in their native language. The study consisted of four event-related functional runs, with 80 trials each. Each trial began with the presentation of a facial photograph (1500 msec)

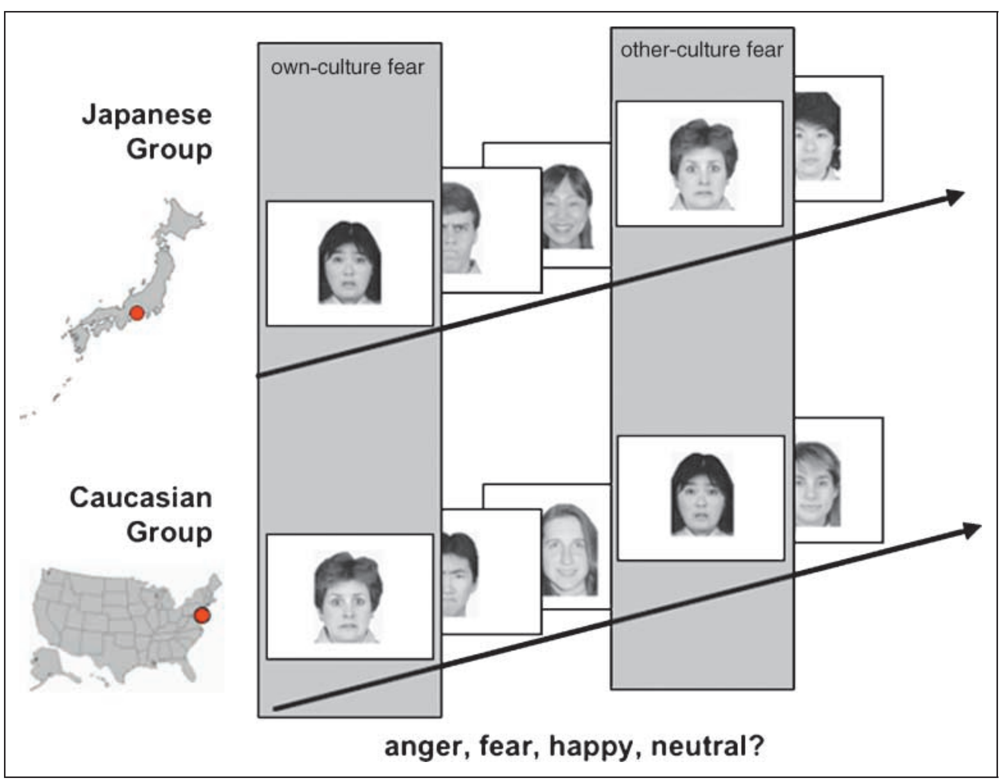

Figure 1. Schema of experimental design.

followed by a blank screen (500 msec) and then fixation (3000 msec). Trials were separated by a centered fixation, which was presented in a jittered manner ranging from 2000 to 6000 msec (average duration of intertrial interval = 4000 msec). For each trial, participants made an emotion categorization judgment (e.g., fear, angry, happy, or neutral) using one of four button presses. The order of stimuli was randomized within and between functional runs.

fMRI Data Acquisition

Functional brain images were acquired at two neuroimaging facilities. Japanese participants were scanned at the National Institute for Physiological Sciences in Okazaki, Japan. Caucasian participants were scanned at the Athinoula A. Martinos Center for Biomedical Imaging in Charlestown, MA.[3]

Scanning at both facilities occurred on a 3.0-Tesla Siemens Allegra MRI scanner equipped with single-shot, whole-body, echo-planar image [repetition time (TR) = 2300 msec; echo time (TE) = 30 msec; flip angle = 80°; FOV = 192 mm, 64 × 64 matrix; 26 slices; voxel size = 3 × 3 × 4 mm], sensitive to BOLD contrast. After discarding the first 6 images, the remaining 266 successive images in each run were subjected to analysis. In addition, a coplanar image was acquired [repetition time (TR) = 300 msec; echo time (TE) = 4.6 msec; flip angle = 90°; FOV = 192 mm, 256 × 256 matrix; 26 slices; voxel size = 0.75 × 0.75 × 4 mm]. A high-resolution anatomical T1-weighted image was also acquired [TR = 1970 msec; TE = 4.3 msec; flip angle = 8°; FOV = 210 mm; 256 × 256 matrix; 26 slices; voxel size = 0.82 × 0.82 × 1.2 mm] for each subject. The fMRI experiment was controlled using Presentation software (Neurobehavioral Systems, Albany, CA).

fMRI Data Analysis

Data were analyzed using SPM99 software (Wellcome Department of Imaging Neuroscience, London, UK). First, all volumes were realigned spatially to the first volume and the signal in each slice was realigned temporally to that obtained in the middle slice using sinc interpolation. The resliced volumes were normalized to the Montreal Neurological Institute (MNI) space using a transformation matrix obtained from the normalization process of the high-resolution image of each individual subject to the MNI template. The normalized images were spatially smoothed with an 8-mm Gaussian kernel. After preprocessing, statistical analysis for each individual subject was conducted using the general linear model (Friston et al., 1995). At the first level, each single event was modeled as a hemodynamic response function and its temporal derivative. Given that accuracy across all emotion conditions was near ceiling (mean accuracy >86%), all trials were included in the SPM model to ensure equal number of trials per condition. For each subject, a linear and quadratic regressor was applied to filter noise. In the subtraction analysis, 16 conditions [2 (culture of face: Japanese or Caucasian) × 4 (emotion: angry, fear, happy and neutral) × 2 (sex: female or male)] were modeled separately. A statistical image for the contrast of own-culture versus other-culture stimuli was obtained for each face type and participant.

RESULTS

Comparable fMRI Signal Quality across Scanner Sites

A number of previous cross-site neuroimaging studies have demonstrated the viability of analyzing fMRI data collected from multicenter sites (Friedman & Glover, 2006; Casey et al., 1998). In particular, interscanner variability has been shown in prior studies as negligible when two or more scanner sites used identical vendor's instrumentation and parameters (Friedman & Glover, 2006). To confirm that fMRI signal quality was comparable across the two scanner sites in the current study, we compared susceptibility related signal drop out due to B0 inhomogeneity within the anatomically defined bilateral amygdala region across the Caucasian–American and native Japanese participant groups (Ojemann et al., 1997). Results of this analysis revealed no significant difference between Caucasian–American and native Japanese participants in percentage of voxels in bilateral amygdala for the own-culture fear > other-culture fear contrast that survived at $p < .01$, uncorrected threshold, extant threshold > 0 voxels [L amygdala: US, $M = 4.78\%$, $SD = 17.6\%$, Japan, $M = 7.24\%$, $SD = 9.2\%$, $t(19) = 0.39$, $p > .05$; R amygdala: US, $M = 1.5\%$, $SD = 3.6\%$, Japan, $M = 14.6\%$, $SD = 21.9\%$, $t(19) = 1.76$, $p > .05$]. Given the similarity in vendor's instrumentation and fMRI parameters as well as no significant difference in signal dropout within the bilateral amygdala region, we conclude that there was comparable fMRI signal quality across the two scanner sites.

Behavioral Results

As previously shown in behavioral studies, both participant groups demonstrated highly accurate emotion recognition performance (Table 1). Caucasian participants, however, were significantly more accurate at recognizing fear in own-culture relative to other-culture faces [$t(9) = 2.49$, $p < .05$, two-tailed]. Japanese participants were significantly faster in recognizing fear relative to Caucasian participants [$F(1, 18) = 6.53$, $p < .02$].

fMRI Results

To test our specific hypothesis of cultural specificity in the amygdala response to fear faces, we focused on the

Table 1. Behavioral Recognition Accuracy (Shown as Percent Correct and Standard Error) and Reaction Time (Shown in Milliseconds and Standard Error) Averaged across the Four Experimental Runs

	Japanese Group		*Caucasian Group*	
Faces	*Japanese*	*Caucasian*	*Japanese*	*Caucasian*
Accuracy				
Fear	86.0 (4.4)	91.5 (2.4)	86.7 (2.9)	94.0 (3.1)
Anger	89.8 (3.8)	90.0 (2.8)	93.5 (1.5)	92.7 (2.2)
Happy	93.3 (2.2)	93.5 (3.1)	95.8 (1.8)	93.5 (2.3)
Neutral	93.0 (3.6)	91.3 (2.9)	91.2 (3.0)	95.0 (2.6)
Reaction Time				
Fear	1142 (89)	1071 (82)	1366 (67)	1337 (62)
Anger	1058 (70)	1068 (67)	1339 (75)	1396 (73)
Happy	932 (59)	939 (58)	1216 (61)	1228 (53)
Neutral	978 (75)	1007 (70)	1357 (45)	1255 (47)

interaction of culture of face and culture of participant in the amygdala response to fear faces in both voxelwise whole brain and anatomical region-of-interest (ROI) functional imaging analyses. First, a 2 (culture of face: Japanese or Caucasian) × 2 (culture of participant: Japanese or Caucasian) × 4 (emotion: anger, fear, happy or neutral) voxelwise whole-brain random effects analysis was conducted to identify regions of activation for the contrast of own-culture versus other-culture fear and nonfear faces at a statistical threshold of $p < .001$, extant threshold = 10 voxels. Second, to determine whether cultural effects within the bilateral amygdala response to fear were observable after statistically correcting for multiple comparisons, anatomically defined amygdala ROI analyses were conducted for all own-culture > other-culture face contrast images. Coordinates for the left ($x = -23.5$, $y = -1.95$, $z = -18.5$) and right ($x = 27.1$, $y = -0.573$, $z = -18.8$) amygdala ROIs used in these analyses were previously defined in the Marsbar AAL ROI library (Brett, Anton, Valabregue, & Poline, 2002; Tzourio-Mazoyer et al., 2002). All anatomical ROI analyses (random effects analyses and percent signal change extraction) were conducted using Marsbar software tools for use with SPM99. MNI coordinates were extracted from SPM99 and converted to Talairach space using the mni2tal algorithm developed by Matthew Brett. Consistent with our hypotheses, voxelwise whole-brain analyses revealed greater activation within regions of the left and right amygdala for own-culture compared to other-culture fear faces (left amygdala: $x, y, z = -30, -8, -20$, $t = 3.78$, p uncorrected < .001; right amygdala: $x, y, z = 18, -6, -12$, $t = 4.85$, $p < .001$) (Table 2). Greater response to own-culture fear faces was also found in medial-temporal regions critical to the successful encoding and retrieval of faces (Golby, Gabrieli, Chiao, & Eberhardt, 2001), such as the left hippocampus and the right parahippocampal gyrus, as well as brain regions previously implicated in socioemotional perception (Adolphs, 2002), including the right superior temporal gyrus, right caudate, right middle gyrus, and left superior frontal gyrus.

To examine whether a culture of participant and culture of face interaction in amygdala response to fear faces was present at more stringent statistical thresholds, anatomical ROI analyses were also conducted. Random effects analyses performed within the entire anatomically defined regions of the left and right amygdala for the own-culture compared to other-culture fear contrast confirmed that amygdala response was significantly greater for expressed by members of one's own compared to other cultural groups after correcting for multiple comparisons (left amygdala: $x, y, z = -23.5, -1.95, -18.5$, $t = 2.25$, p corrected < .05; right amygdala: $x, y, z = 27.1, -0.57, -18.8$, $t = 3.55$, p corrected < .003) (Figure 2). Consistent with our prediction, eight Japanese participants and seven Caucasian–American participants demonstrated greater amygdala response in both the left and right amygdala, two Japanese participants in the right amygdala only, and two Caucasian participants in the left amygdala only, to own-culture versus other-culture fear faces.

Random effects analyses conducted on own-culture compared to other-culture nonfear contrast images revealed no other significant interactions between culture of participant and culture of face within the left or right amygdala anatomical ROIs for angry (all ps corrected > .70), happy (all ps corrected > .70) or neutral (all ps corrected > .17) face conditions. Additionally, there were no significant interactions between culture of participant

Table 2. Results from Whole-brain Analyses Showing Regions with Greater Activation for Own-culture Fear Face > Other-culture Fear Face (in MNI Coordinates), $p < .001$, Extant Threshold = 10 Voxels

Cortical Region	*Cluster Size*	*x*	*y*	*z*	*t*
Own-culture Fear > Other-culture Fear					
Left hippocampus	65	−24	−12	−16	6.34
Right superior temporal gyrus	11	50	18	−18	5.28
Right caudate	81	24	6	22	5.28
Left superior frontal gyrus	13	−4	10	64	4.96
Right parahippocampal gyrus	48	12	−36	−8	4.96
Right amygdala	62	18	−6	−12	4.85
Right middle frontal gyrus	12	38	36	−16	4.57
Left amygdala	33	−30	−8	−20	3.78

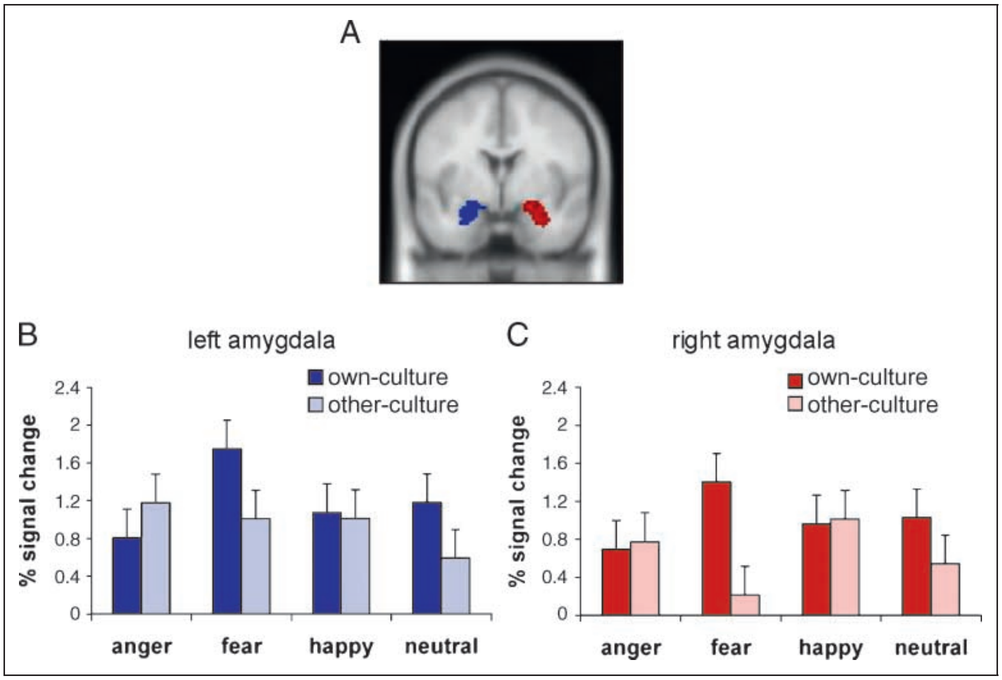

Figure 2. Cultural specificity in amygdala response to fear faces. (A) Anatomical definition of the entire left amygdala ($x, y, z = -23.5, -1.95, -18.5$) and right amygdala ($x, y, z = 27.1, -0.57, -18.8$) ROIs used in the ROI analyses. Significantly greater activity in (B) left amygdala ($t = 2.25$, p corrected $< .05$) and (C) right amygdala ($t = 3.55$, p corrected $< .003$) for own- relative to other-culture fear, but not for angry, happy, or neutral faces.

and culture of face for reverse contrasts of other-culture compared to own-culture fear (all ps corrected $> .90$), anger (all ps corrected $> .60$), happy (all ps corrected $> .40$), or neutral (all ps corrected $> .90$) faces within left and right amygdala anatomical ROIs. There was also no significant main effect of culture of face within the right or left amygdala ROIs (all ps corrected $> .50$). Regression analyses between accuracy, reaction time, and mean percent signal change within the amygdala anatomical ROIs across all participants revealed no significant relationships (all ps $> .05$).

DISCUSSION

Amygdala responsivity increases when fear is detected in members of one's own relative to other cultural groups. The present evidence shows how cultural group membership of both the expressor and perceiver of the fear signal modulates the magnitude of the response within this limbic region. Heightened bilateral amygdala response may indicate heightened arousal to or vigilance for fear expressed by members of one's own cultural group because this expression serves as an indicator of impending threat (Glascher & Adolphs, 2003; Davis & Whalen, 2001). More specifically, fear perceived in a member of one's own cultural group may be interpreted as more likely to indicate danger for one's self compared to fear perceived in a member from another cultural group (Elfenbein & Ambady, 2002).

The term "culture" rather than "race" or "nationality" best characterizes the observed preferential amygdala response to fear in the present study for two reasons. First, native Japanese and Caucasian–Americans participants in the current experiment self-reported living their entire lives only in Japan and in the United States, respectively; thus, there is some basis to infer that these participants also have a certain degree of unique cultural experience, values, practices, and beliefs. Second, prior research has shown that facial expressions of emotion vary across cultures even when controlling for race (e.g., Japanese–American fear is distinguishable from Japanese fear) (Marsh et al., 2003). Hence, the term "culture" rather than "race" or "nationality" most accurately reflects the group characteristics of the experimental stimuli and participants included in the current experiment.

Previous neuroimaging research has demonstrated that Caucasian–Americans show greater amygdala response for African–American neutral faces when presented both unconsciously (Cunningham et al., 2004) and consciously (Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005). Amygdala response to neutral faces has also been shown to correlate with implicit negative associations toward African–Americans (Cunningham et al., 2004; Phelps et al., 2000). Our results show, in contrast, an increase in amygdala response to fearful faces of one's own cultural group rather than to faces of other cultural groups.

Interestingly, neither Japanese nor Caucasian participants in the present study showed a greater amygdala response to neutral faces of other cultural group members. The current result suggests that previous findings of greater amygdala activity for outgroup neutral faces may reflect cultural knowledge of negative stereotypes specifically about African–Americans, rather than general negative stereotypes about other outgroup members. In support of this view, Lieberman et al. (2005) found that

African–American participants also show greater amygdala response to African–American neutral faces, suggesting that amygdala response is due to cultural knowledge of negative stereotypes about African–Americans, rather than automatic negative arousal to outgroup members per se. Moreover, Caucasian–Americans often have positive, rather than negative, stereotypes about Asians and Asian–Americans (Shih, Ambady, Richeson, Fujita, & Gray, 2002). Future research examining intergroup dynamics between other ethnic and cultural groups is necessary to determine the extent to which neutral faces may elicit a heightened amygdala response for neutral faces.

The observed amygdala bias for own-culture fear faces may result from neural tuning to subtle variations in fear expressions over the course of development. Previous neuroimaging research has demonstrated that children do not display as robust an amygdala response to fear relative to neutral faces as adults (Thomas et al., 1999), suggesting a significant developmental change in what kinds of perceptual information the amygdala detects and interprets as cues of potential threat, a view corroborated by studies of emotion processing in monkeys with amygdala lesions from early childhood (Skuse, Morris, & Lawrence, 2003). Given the prior behavioral evidence indicating cultural variation in how fear is expressed, we suggest that greater experience with and exposure to a particular set of facial expressions of fear (e.g., Japanese or Caucasian) may sensitize the amygdala to optimally respond to facial configurations of fear specific to one's own cultural group by adulthood (Marsh et al., 2003; Skuse et al., 2003). The importance of early experience in sculpting adult competence toward a set of perceptual cues has previously been shown in face recognition (Pascalis, De Haan, & Nelson, 2002) and phonetic perception (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992). Future research is needed to determine whether the amygdala bias to own-culture fear faces observed in adults in the current study arises from a similar experience-dependent process.

Our finding may also provide initial evidence of a neurobiological mechanism for group selection previously observed in altruistic behavior (Wilson & Sober, 1994). The fear expression not only signals danger but also solicits others for help in either fighting or fleeing the source of danger (Marsh, Kozak, & Ambady, 2007). Given the role of central nucleus of the amygdala in producing a fear response, we speculate that the cultural specificity in amygdala activity to fear faces demonstrated in the current study could also reflect an enhanced arousal for (Anderson & Phelps, 2001) or physiological preparedness (Phelps & LeDoux, 2005; LeDoux, 1996) to respond to fear expressed by a member of one's own cultural group. This enhanced neurobiological response for own-culture fear faces may further result in directing prosocial behaviors (e.g., cooperation and altruism) toward members of one's own cultural group to a greater extent. Future research is needed to determine the relationship between cultural specificity in amygdala response to fear faces and group selectivity in prosocial behavior.

Research in affective neuroscience has not yet considered the role of culture in mediating emotional processes at a neurobiological level, despite a growing corpus of demonstrations of the psychological significance of cultural membership and exposure across a broad range of emotional phenomena, such as appraisal (Mesquita & Frijda, 1992), experience (Marsh, Ambady, & Kleck, 2005; Tsai, Chentsova-Dutton, Friere-Bebeau, & Przymus, 2002), and subjective well-being (Lam, Buehler, McFarland, Ross, & Cheung, 2005). The present research provides a starting point into examining how culture may affect neural circuitry underlying a broader range of emotional and social cognitive processes involving the amygdala (e.g., empathy, emotion regulation; Chiao & Ambady, 2007; Carr, Iaocoboni, Dubeau, Mazziotta, & Lenzi, 2003).

In sum, the current study demonstrates that cultural group membership modulates the brain's primary response to fear. This finding is particularly surprising, given the previous demonstration of the automatic, prepotent nature of the amygdala response to fear faces (Anderson et al., 2003; Glascher & Adolphs, 2003; Adolphs, 2002; Whalen et al., 1998), and underscores the significance of further cross-cultural investigations at the neural level.

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Notes

1. The term ''culture'' is used here to refer to a social group whose members share one or more of the following: a common meaning system, social practices, geographical space, social and religious values, language, ways of relating, diet, and ecology (Markus & Kitayama, 1991).
2. The term ''nationality'' is used to refer to a social group whose members share a state of origin, loyalty, and/or cultural identity. Unlike culture, nationality is a type of social group membership that can be acquired (e.g., citizenship by marriage) without necessarily sharing cultural experience, values, practices, or beliefs.
3. The term ''race'' is used here to refer to a social group whose members share a common ethnic heritage and a subset of physical attributes (e.g., skin tone, facial, and body shape) (Bonham, Warshauer-Baker, & Collins, 2005). Similar to

nationality, race is a type of social group membership that also does not necessarily involve shared cultural experience, values, practices, or beliefs (e.g., Japanese–Americans and native Japanese belong to the same racial group, but do not necessarily have similar cultural experiences).

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