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Cultural differences in human brain activity: A quantitative meta-analysis

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ABSTRACT

Psychologists have been trying to understand differences in cognition and behavior between East Asian and Western cultures within a single cognitive framework such as holistic versus analytic or interdependent versus independent processes. However, it remains unclear whether cultural differences in multiple psychological processes correspond to the same or different neural networks. We conducted a quantitative meta-analysis of 35 functional MRI studies to examine cultural differences in brain activity engaged in social and non-social processes. We showed that social cognitive processes are characterized by stronger activity in the dorsal medial prefrontal cortex, lateral frontal cortex and temporoparietal junction in East Asians but stronger activity in the anterior cingulate, ventral medial prefrontal cortex and bilateral insula in Westerners. Social affective processes are associated with stronger activity in the right dorsal lateral frontal cortex in East Asians but greater activity in the left insula and right temporal pole in Westerners. Non-social processes induce stronger activity in the left inferior parietal cortex, left middle occipital and left superior parietal cortex in East Asians but greater activations in the right lingual gyrus, right inferior parietal cortex and precuneus in Westerners. The results suggest that cultural differences in social and non-social processes are mediated by distinct neural networks. Moreover, East Asian cultures are associated with increased neural activity in the brain regions related to inference of others' mind and emotion regulation whereas Western cultures are associated with enhanced neural activity in the brain areas related to self-relevance encoding and emotional responses during social cognitive/affective processes.

Introduction

Cultural psychologists have shown ample evidence for differences in cognition and behavior between East Asian and Western cultures (Markus and Kitayama, 1991; Nisbett and Masuda, 2003; Oyserman et al., 2002). For instance, Westerners tend to focus on a salient object independently of its context whereas East Asians tend to attend to the relationship between an object and its context during perception (Nisbett and Miyamoto, 2005). Memory contents tend to focus on events oriented to an individual in Westerners but on events with a group or social interactions in East Asians (Conway et al., 2005). Westerners are inclined to attribute human behaviors predominantly to their internal dispositions while East Asians tend to explain the same behavior in terms of social contexts (Choi et al., 1999). Cultural differences in multiple psychological processes have been explained within a single cognitive framework. For example, Nisbett and colleagues propose that East Asians prefer holistic thoughts that facilitate attending to the entire field and assigning causality to it, whereas Westerners favor analytic thoughts that enhance attention primarily to the object and the categories to which it belongs (Nisbett et al., 2001). Markus and Kitayama (1991) have suggested that East Asians emphasize the fundamental relatedness of individuals to each other whereas Westerners seek to maintain their independence from others and that distinct self-construals can account for cultural differences in cognition, emotion, and motivation.

While cultural differences in multiple psychological processes have been understood within a single cognitive framework, it remains unclear whether cultural differences in distinct psychological processes are mediated by the same or different neural networks in the brain. Functional magnetic resonance imaging (fMRI) studies have revealed several neural circuits that are engaged in different psychological processes (Kennedy and Adolphs, 2012; Lieberman, 2010; Stanley and Adolphs, 2013). Social perceptual tasks, such as face/biological motion perception and action observation, engage the fusiform gyrus, posterior superior temporal sulcus (STS), amygdala, inferior parietal lobule (IPL), and lateral prefrontal cortex (LPFC). Social cognitive tasks, such as inference of others' mental states, self-reflection or self-control, activate the medial prefrontal cortex (MPFC), precuneus/posterior cingulate (PCC),

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temporoparietal junction (TPJ), temporal pole, IPL LPFC, dorsal anterior cingulate cortex (dACC). Social affective tasks, such as empathy for others' emotional states or social rejection, recruit the dACC, supplementary motor area (SMA), amygdala, anterior insula (AI) and LPFC (see Lieberman, 2010 for review).

These fMRI findings indicate that the neural circuits involved in different task domains (e.g., perceptual, cognitive, or affective) consist of common and distinct brain regions. Thus it is possible that there are specific brain regions that exert cultural modulations of neural activities involved in different task domains. This hypothesis predicts a common neural network or a brain region that differentiates between East Asian and Western cultures across task domains. Alternatively, culture may show task-domain-specific influences on neural correlates of human cognition. This hypothesis predicts distinct neural networks that differentiate between East Asian and Western cultures depending on task domains. Apparently, these hypotheses cannot be clarified by only examining individuals' behavioral performances or by a single neuroimaging study.

Recent cultural neuroscience studies have shown increasing evidence for cultural differences in neural correlates of cognition and behavior by comparing fMRI results from East Asians and Westerners or by priming participants with East Asian or Western cultural values (see; Ames and Fiske, 2010; Chiao et al., 2013; Han and Northoff, 2008; Han et al., 2013). However, each of the previous cultural neuroscience studies recruited a specific task and was unable to provide a global view of the relationship between culture and neural correlates of different tasks in a specific domain. A meta-analysis of cultural neuroscience studies allows us to explore cultural differences in neural activity engaged in various tasks in a specific domain and to test whether the same or distinct neural networks underlie cultural variations in human brain activity across different task domains. We summarized 35 fMRI studies of cultural effects on human cognition (published before December 2013) and conducted a whole-brain quantitative meta-analysis that allows for identification of cultural differences in brain activity that are activated in a specific task domain. We included fMRI studies that compared participants from East Asian (Chinese, Japanese, and Korean) and Western (American and European) societies and classified these studies into three domains that employed social cognitive, social affective, and non-social cognitive tasks, respectively. Our meta-analyses focused on brain activity that differentiates between East Asian and Western cultures in these task domains.

Methods

Literature search and selection

A step-wise procedure was used to identify relevant research articles that compared brain activity between individuals from East Asian and Western societies published prior to December 2013. As recent studies have shown that cultural values mediate cultural group differences in neural activity involved in social cognition (e.g., Ma et al., 2014), our meta-analyses also included the studies that examined brain activity coupling with cultural values (i.e., independence vs. interdependence or individualism vs. collectivism) in individuals from the same society. We first selected studies through a standard search in PubMed (http://www.pubmed.gov) and ISI Web of Science (http://apps.isiknowledge.com) using keywords ['cultural' OR 'cultural difference' OR 'cultural influence' OR 'East Asian AND Western' OR 'interdependence, independence' OR 'individualism, collectivism'] AND ['fMRI' OR 'functional MRI' OR 'functional magnetic resonance imaging']. Next, we collected additional studies by reviewing the reference list of the relevant papers found in the first step, or through the 'related article' function of the PubMed database.

A study was considered culture-relevant if it involves a group comparison between East Asians and Westerners, or if it examines cultural effects (e. g., interdependent/independent self-construal, individualism/collectivism) on brain activity using a cultural priming procedure or a whole-brain regression with cultural values. Thus cultural effects were identified in the contrasts between East Asian and Western individuals, between individuals temporally primed with East Asian or Western cultural values, or in the analyses of whole-brain regression with cultural values. The neural activity being positively correlated with individualistic cultural values or negatively correlated with collectivistic cultural values was integrated with those being stronger in Western than East Asian individuals, whereas the neural activity being positively correlated with collectivistic cultural values or negatively correlated with individualistic cultural values was integrated with those being stronger in East Asian than Western individuals. Based on the task employed by each study, we classified studies into 3 categories, i.e., social cognitive studies that used tasks such as self-reflection, theory of mind, face perception, moral judgment, persuasion, and self-recognition; social affective studies that used tasks such as empathy, emotion recognition, emotion, and reward; and non-social studies that used tasks such as visual attention, visual spatial or object processing, arithmetic, and physical causal attribution. We calculated the contrasts of "East Asian versus Western" and "Western versus East Asian" separately to identify stronger neural responses in East Asian and in Western cultures, respectively.

We excluded studies that did not use functional imaging techniques, and did not report coordinates in either Montreal Neurological Institute (MNI; Collins et al., 1998) or Talairach (Talairach and Tournoux, 1988) space. This meta-analysis was limited to regional activation changes, thus studies that focused on functional connectivity, structural data, or resting-state were not included. Consequently, we identified 35 relevant fMRI studies to reveal cultural influence on brain activity (see Table 1 for detailed information about the studies included in our meta-analyses). We included 28 fMRI studies that investigated cultural differences in neural correlates of either cognitive or affective dimension of social cognition, and 7 studies that examined cultural differences in neural substrates underlying non-social processes.

Activation likelihood estimation analysis

Our meta-analysis was based on the Activation Likelihood Estimation (ALE) method (Laird et al., 2005; Turkeltaub et al., 2002), using the revised ALE algorithm (Turkeltaub, 2012) in GingerALE 2.3 (Eickhoff, 2009; Laird et al., 2005; Turkeltaub, 2012). The ALE is a method for performing coordinate-based meta-analysis in order to determine whether there is anatomical convergence among results from different studies. GingerALE switched ALE methods from fixed effects to random effects, incorporated variable uncertainty based on the number of subjects in each study included in the meta-analysis (Eickhoff, 2009), and added the thresholding methods (Eickhoff, 2009; Laird et al., 2005). GingerALE has been applied to reveal between-group brain activity differences in previous meta-analytic studies (Ma, in press; Menzies et al., 2008; Minzenberg et al., 2009).

The procedure involved the modeling of all reported coordinates of the selected contrasts as the peaks of 3D Gaussian probability distribution. We individually screened all the articles for the presence of Talairach or MNI coordinates. Coordinates in Talairach space were converted to MNI coordinates and were reported in the MNI space in the current study. The 3D Gaussian distributions were summed to produce a statistical map that estimated the likelihood of activation for each voxel as determined by all the studies included in the analyses. The ALE value was computed using permutation testing (5000 permutations) against the null-distribution of random spatial associations of foci across contrasts (Eickhoff, 2009). We used a p-threshold corrected for multiple comparisons using the False Discovery Rate (FDR) fixed to 0.05 (Laird et al., 2005). Additionally, all clusters were set to a minimum of 300 mm^3. The thresholded ALE result images were visualized using Mango (rii.uthscsa.edu/mango), and overlaid onto an anatomical template (Colin27_T1_seg_MNI.nii, www.brainmap.org/ale).

Table 1
A list of the selected studies for the current meta-analyses.

First author	Year	Comparison type	Category	Paradigm/task	Stimuli	No. of contrast E > W	No. of contrast W > E
Grön et al., 2003	2003	E vs. W	Non-social	Visual memory task	Geometric patterns	5	5
Moriguchi et al., 2005	2005	E vs. W	Social	Passive viewing	Happy/fear/neural faces	1	1
Tang et al., 2006	2006	E vs. W	Non-social	Number comparison	Symbol/Numbers	1	1
Kobayashi et al., 2006	2006	E vs. W	Social	Theory of mind	False belief stories	2	2
Gutchess et al., 2006	2006	E vs. W	Non-social	Pleasant rating	Objects/Scene pictures	2	2
Kobayashi et al., 2007	2007	E vs. W	Social	Theory of mind	False belief stories/Cartoon	3	3
Zhu et al., 2007	2007	E vs. W	Social	Self-referential	Words	0	1
Sui et al., 2007	2007	Priming	Social	Self recognition	Self/friend/scramble faces		1
Hedden et al., 2008	2008	E vs. W	Non-social	Visuospatial task	Line/box	1	1
Kobayashi et al., 2008	2008	E vs. W	Social	Theory of mind	False belief stories	0	2
Derntl et al., 2009	2009	E vs. W	Social	Explicit emotion recognition	Anger/disgust/fear/happy/sad/neutral faces	0	1
Freeman et al., 2009	2009	E vs. W	Social	Passive viewing	Subordinate/dominate gesture	0	0
Zamboni et al., 2009	2009	Regression	Social	Agreement judgment	Political statements	1	1
Chiao et al., 2009	2009	E vs. W	Social	Self-referential	Words	2	1
Adams et al., 2010a	2010	E vs. W	Social	Reading mind in eye	Pictures of eyes	1	0
Goh JO	2010	E vs. W	Social	Passive viewing	Face, House, Scramble	0	1
Adams et al., 2010b	2010	E vs. W	Social	Passive viewing	Emotional faces	1	0
Chiao et al., 2010	2010	Priming	Social	Self-referential	Words	0	0
Ray et al., 2010	2010	Regression	Social	Self-referential	Words	1	0
Gutchess et al., 2010	2010	E vs. W	Social	Relationship judgment	Words	3	2
Falk et al., 2010	2010	E vs. W	Social	Passive viewing	Persuasive text	1	1
Rule et al., 2010	2010	E vs. W	Social	Voting decision	Japanese/American election winner/loser	1	1
Cheon et al., 2011	2011	E vs. W	Social	Empathic rating	Korean/American painful/neutral picture	1	1
Sul et al., 2012	2012	Regression	Social	Self-referential	Words	1	1
Han et al., 2011	2011	E vs. W	Non-social	Physical causal attribution	Moving-ball videos	2	0
Koelkebeck et al., 2011	2011	E vs. W	Social	Theory of mind	Moving-shapes videos	0	1
de Greck et al., 2012	2012	E vs. W	Social	Implicit/explicit empathy for angry	Fearful/neutral faces	2	2
Han et al., 2014	2014	E vs. W	Social	Moral dilemma decision making	Personal/impersonal moral dilemma stories	6	5
Cheon et al., 2013	2013	E vs. W	Social	Empathic rating	Korean/American painful/neutral picture	1	1
Goh et al., 2013	2013	E vs. W	Non-social	Visuospatial task	Line/box	1	1
Kang et al., 2013	2013	E vs. W	Social	A card game	Card	1	1
Ma et al., 2014	2014	E vs. W	Social	Self-referential	Words	2	3
Prado et al., 2013	2013	E vs. W	Non-social	Multiplication	Digits	1	1
Varnum et al., 2014	2014	Priming	Social	Card-guessing game	Cards	0	1
Ma Y in press	In press	Regression	Social	Self-referential	Words	5	5

E vs. W: Group comparison between individuals from East Asian and Western cultures.
Priming: East Asian and Western cultural priming.
Regression: Whole-brain regression with cultural values as regressor.

Results

Thirty-five studies (listed in Table 1) were included in our ALE meta-analysis to reveal cultural differences in brain activity, including 28 studies that examined cultural effects on neural correlates of social cognition and 7 studies that examined cultural differences in non-social neural processes. Fifty-six contrasts (28 contrasts of East Asian > Western and 28 contrasts of Western > East Asian) examined cultural difference in social cognitive processes. The ALE meta-analysis on the 28 contrasts, which compared East Asian culture with Western culture, uncovered greater activity in the right insula/inferior frontal cortex (IF), dorsal MPFC (dMPFC), left IF, right inferior parietal cortex and right TPJ. In contrast, stronger activity in the ACC, ventral MPFC (vMPFC), bilateral insula, right superior frontal cortex, left precentral gyrus, and right claustrum was observed when performing ALE meta-analysis on the contrasts that compared Western versus East Asian cultures (see Fig. 1 and Table 2). The meta-analysis of the studies that focused on affective processes of social cognition revealed stronger activity in the right dorsal LPFC (dLPFC) when comparing East Asian versus Western cultures (based on 8 contrasts) but greater activity in the left insula and right temporal pole when comparing Western versus East Asian cultural effects (based on 11 contrasts, Fig. 1, Table 3). These results suggest that different neural networks underlay the cultural differences in social cognitive and affective processes.

To assess cultural differences in neural correlates of non-social processes, we conducted a meta-analysis of fMRI studies that focused on cultural differences in object processing, visual–spatial learning, visual attention, physical causal attribution, arithmetic, etc. Seven studies (see Table 1) were included, which presented 13 contrasts to compare East Asians versus Westerners and 11 contrasts to compare Westerners versus East Asians. This meta-analysis revealed stronger activity in the left inferior parietal cortex, left middle occipital and left superior

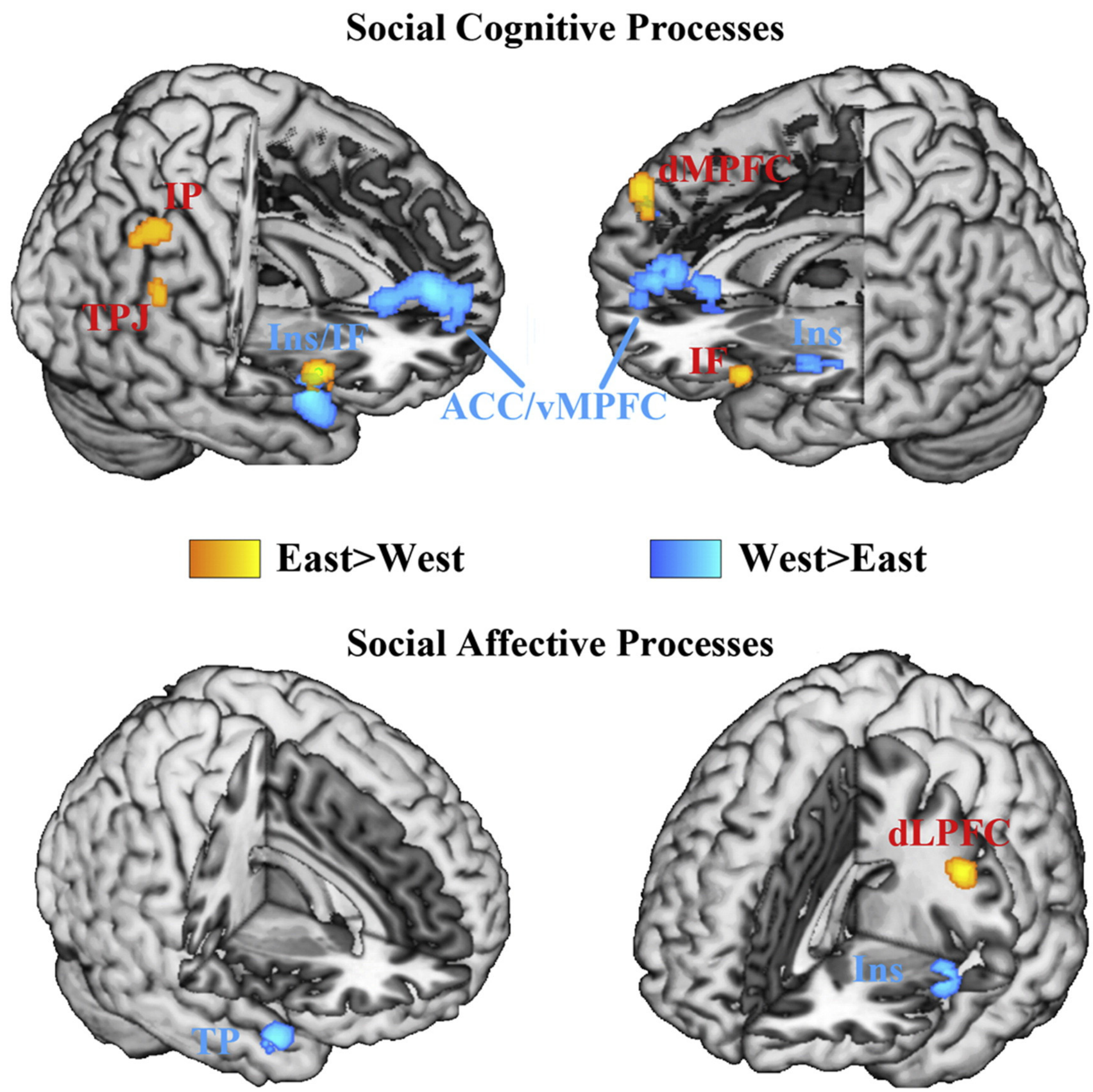

Fig. 1. Illustration of the meta-analysis results of cultural effects on brain activity engaged in social cognitive and affective processes. Activations in orange indicated stronger activity in East Asian compared to Western cultures, and activations in blue indicated stronger activity in the reverse comparison. Activations were identified using a threshold of $p < 0.05$ (FDR corrected). IP = inferior parietal cortex; TPJ = temporoparietal junction; Ins/IF = insula/inferior frontal cortex; ACC = anterior cingulate cortex; dMPFC = dorsal medial prefrontal cortex; vMPFC = ventral medial prefrontal cortex; TP = temporal pole; dLPFC = dorsal lateral prefrontal cortex.

Table 2
Cultural differences in brain activity involved in social cognitive tasks.

Brain regions	Hemi.	BA	Weighted center			MNI coordinates			Volume (mm^3)
East Asian > Western (28 contrasts)									
Insula/IF	R	13	45.76	14.29	−4.22	46	14	−4	760
dMPFC	R	8	11.01	54.57	34.13	12	54	36	560
IF	L		−50.14	18.92	−3.61	−50	18	−4	520
TPJ	R	13	47.45	−43.24	27.57	48	−44	28	376
Inferior parietal	R	40	42.41	−46.89	46.25	42	−46	46	368
Western > East Asian (28 contrasts)									
ACC	L	32	−1.31	45.25	3.38	−2	48	6	3136
ACC	L	24				−2	32	0	
vMPFC	L	10				−4	56	2	
vMPFC	R	10				8	54	0	
Insula	R	13	51.11	12.99	−12.68	50	12	−12	1424
Claustrum	R		38.24	−3.22	7.2	38	−4	6	520
Superior frontal	R	9	17.42	50.76	28.1	18	50	26	424
Insula	L	13	−40.85	−7.3	−7.67	−42	−16	−6	328
Precentral	L	44	−62.21	7.03	1.39	−62	8	2	328

dMPFC = dorsal medial prefrontal cortex; IF = inferior frontal cortex; vMPFC = ventral medial prefrontal cortex; TPJ = temporal parietal junction; ACC = anterior cingulate cortex.

Table 3
Cultural differences in brain activity involved in social affective tasks.

Brain regions	Hemi.	BA	Weighted center			MNI coordinates			Volume (mm^3)
			x	y	z	x	y	z	
East Asian > Western (8 contrasts)									
dLPFC	L	6	−44.6	−8.6	32.6	−44	−8	32	576
Western > East Asian (11 contrasts)									
Insula	L	13	−40.07	−1.93	−7.54	−40	−2	−8	512
Temporal pole	R	38	55.27	17.05	−18	54	16	−18	448

dlPFC: dorsolateral prefrontal cortex.

parietal cortex in East Asians compared to Westerners. Westerners, however, showed greater activations in the right lingual gyrus, right inferior parietal cortex and precuneus relative to East Asians (Fig. 2 and Table 4).

Discussion

Several conclusions arise from the results of our meta-analyses. First, East Asian/Western cultural differences exist in several key nodes of the social brain network such as the MPFC, TPJ, ACC, AI, etc. Second, the social brain network in East Asian cultures is characterized by enhanced activity in brain regions that have been shown to be involved in inference of others' minds (e.g., dMPFC, TPJ, Gallagher et al., 2000; Saxe and Kanwisher, 2003; Han et al., 2005; Ge and Han, 2008), social perception (e.g., STS, Vaina et al., 2001), and self-control/emotional regulation (e.g., LPFC, Figner et al., 2010; Ochsner et al., 2012). Third, the social brain network in Western cultures is characterized by enhanced activity in brain regions that have been shown to be engaged in self-reflection (e.g., vMPFC, Kelley et al., 2002; Northoff et al., 2006; Ma and Han, 2011; Ma et al., 2014), socioemotional processing (e.g., temporal pole, Olson et al., 2007), one's own emotional responses and empathy for others' emotional states (e.g., ACC and insula, Singer et al., 2004; Jackson et al., 2005; Saarela et al., 2007; Gu and Han, 2007; Han et al., 2009; Gu et al., 2010; Fan et al., 2011; Lamm et al., 2011).

The results of our meta-analyses provide possible neural accounts of cultural differences in cognition and behavior observed in the previous behavioral studies. For example, East Asians believe dispositions to be malleable and that social contexts are more important when explaining human behavior, whereas Westerners prefer explanations of human behavior in terms of their traits, dispositions, or other internal attributes (Choi et al., 1999). East Asians emphasize fundamental social connections and are sensitive to information related to significant others, attending to intimate others as much as to the self. In contrast, Westerners are inclined to attend to self-focused information and to the self more than to others (Markus and Kitayama, 1991). Regarding the affective states that people strive for, or ideal affects, East Asians value low-arousal emotional states more whereas Americans value high-arousal emotional states more and such cultural differences in ideal affect influence interpersonal communications, religious texts, and cultural products (Tsai, 2007). These findings can be understood consistently from a neuroscience perspective. Our meta-analysis indicates that East Asian cultures are characterized by enhanced activity in the social brain network underlying perception and inference of others' mind in the dMPFC, TPJ and STS and this provides a neural basis for increased sensitivity to contextual social information including others' mental states. East Asian cultures are also linked with increased lateral frontal activity that satisfies the need of self-control and emotional regulation for low-arousal emotional states. In contrast, Western cultures exhibit enhanced activity in the social brain network that underlies coding of self-relevance in the vMPFC and increased activity in the social brain network that supports emotional responses in the dACC and insula. Taken together, it may be proposed that the Western/East Asian cultures influence the social cognitive and affective processes by modulating the weight of different nodes of the social brain network. Such cultural modulations of the social brain network produce culturally specific cognitive/neural strategies (e.g., holistic versus analytic stance, paying attention to self versus others, or keeping high versus low arousal states), which allow individuals to fit into their sociocultural environments and behave in culturally appropriate ways during social interactions.

Enhanced brain activity in one compared to another cultural group may not always manifest adoption of a culturally preferred cognitive strategy. An alternative possibility is that increased brain activity is a reflection of greater cognitive or emotional demand or effort during tasks that are incompatible with ordinary cultural practices. For example, East Asians showed stronger activity in the prefrontal and parietal cortices

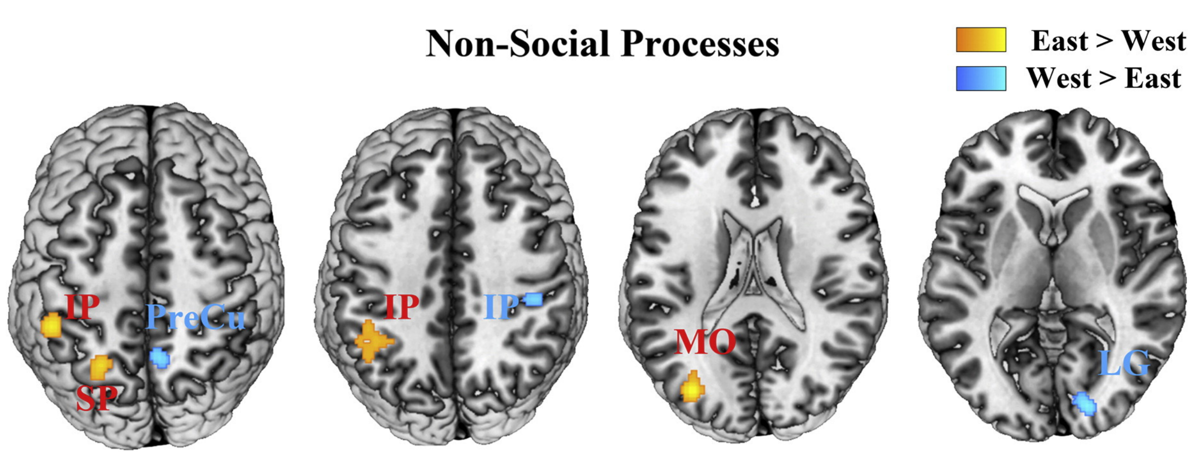

Fig. 2. Illustration of the meta-analysis results of cultural effects on brain activity engaged in non-social processes. Activations in orange indicated stronger activity in East Asian versus Western cultures and activations in blue indicated stronger activity in the reverse comparison. Activations were identified using a threshold of $p < 0.05$ (FDR corrected). IP = inferior parietal cortex; SP = superior parietal cortex; MO = middle occipital cortex; LG = lingual gyrus; PrecCu = precuneus.

Table 4
Cultural differences in brain activity involved in non-social tasks.

Brain regions	Hemi.	BA	Weighted center			MNI coordinates			Volume (mm^3)
			x	y	z	x	y	z	
East Asian > Western (13 contrasts)									
Inferior parietal	L	40	−46.57	−44.79	47.56	−50	−42	52	1664
Supramarginal	L					−44	−44	42	
Middle occipital	L	19	−33.21	−76.71	17.78	−34	−78	18	920
Superior parietal	L	7	−24.68	−62.66	52.19	−24	−62	52	672
Western > East Asian (11 contrasts)									
Lingual gyrus	R	17	17.58	−85.58	3.77	18	−86	4	720
Precuneus	R	7	6.21	−58.07	55.21	6	−58	56	416
Inferior parietal	R	40	43	−28	42	42	−28	42	304

during a context-independent task, whereas Americans exhibited greater prefrontal and parietal activity during a context-dependent task (Hedden et al., 2008). In this case, the enhanced prefrontal and parietal activity may be a consequence of infrequent practice of context-independent tasks in East Asians and of context-dependent tasks in Americans because East Asians and Westerners prefer context-dependent and context-independent tasks, respectively (Nisbett and Masuda, 2003).

It should be noted that the observed cultural group differences in the brain activity do not *demonstrate* causal relationships between culture and the functional organization of the human brain. Fortunately, current cultural neuroscience research has been trying to develop methods that can be used to further examine the causal relationship between culture and brain function (Han et al., 2013). For example, researchers in the field examined whether the brain activity underlying cognitive/affective processes is associated with a specific cultural value (e.g., interdependence, Chiao et al., 2009; Ma et al., 2014) across individuals. In addition, the mediation analysis has been used in cultural neuroscience studies to examine whether the observed East Asian/Western cultural group differences in brain activity are mediated by a specific cultural value (e.g., Lewis et al., 2008; Ma et al., 2014). Another elegant paradigm, i.e., cultural priming, has been used to examine the causal relationship between cultural value and brain activity (Han et al., 2013; Oyserman et al., in press). It has been shown that priming interdependent (versus independent) self-construals resulted in changes of brain activity related to self-face recognition (Sui and Han, 2007), empathy (Jiang et al., 2014) and reward (Varnum et al., 2014). Exposure of Chinese or Western pictorial cultural icons to bicultural individuals also led to changes of the brain activity associated with reflection of personality traits of oneself and one's mother (Ng et al., 2010). These findings demonstrate variations of brain activity as a function of recent use of a cultural system (Hong et al., 2000) and thus suggest a causal link between culture value and brain activity. Finally, brain imaging studies of immigrants have revealed dissimilar brain activity in people who have the same ethnic origin but develop in different sociocultural contexts (e.g., Chen et al., 2013; Zuo and Han, 2013) and thus contribute to the understanding of how cultural experiences influence the functional organization of the human brain.

Another important issue related to the cultural neuroscience findings is that the observed East Asian/Western cultural group differences in the brain activity do not necessarily only reflect the effect of cultural contexts and cultural experiences. Biological factors such as gene may also contribute to the observed group differences in brain activity. Cultural neuroscience studies have shown evidence for individual differences in brain activities involved in multiple cognitive/affective processes within the same cultural group (e.g., Chiao et al., 2009; Ma et al., 2014), which may reflect the effect of individuals' genetic makeup. In addition, recent research has uncover associations between cultural value and allelic frequency of a specific genetic polymorphism. For example, Chiao and Blizinsky (2010) showed that countries dominated by collectivistic cultures are significantly more likely to comprise individuals carrying the short allele of the serotonin transporter functional polymorphism. Luo and Han (in press) also found that the A allelic frequency of the oxytocin receptor gene polymorphism (rs53576) in populations is positively correlated with collectivistic cultural values. These findings suggest that genetic backgrounds may be interwoven with cultural values to influence the functional organization of the human brain (Kim and Sasaki, 2014). It is, however, a challenge for cultural neuroscience research to explore how individuals' genetic makeup interacts with culture to modulate the brain activity. Recent research has shown that long/long compared to short/short allele carriers of the serotonin transporter gene exhibit a stronger association between a cultural orientation (e.g., interdependence) and neural activities during reflection of personality traits of oneself and close other (Ma et al., in press) and suggests a possible way of gene–culture interaction on neural correlates of social cognition. A challenge for future research is to discover new methods for examining gene–culture interactions on the social brain.

The cultural differences in brain activity involved in non-social tasks are manifested mainly over the posterior part of the brain, which are different from cultural differences in brain activity associated with social cognitive/affective processes that are most salient over the anterior part of the brain. Such anterior–posterior differences cannot be attributed to discrepant stimulus modalities employed in these studies because all the studies included in our meta-analysis used visual stimuli except that the stimuli used in Falk et al. (2010) were presented both visually and aurally. However, most of the non-social tasks used geometric shapes or object/scene pictures that required perceptual processes whereas most of the social tasks demanded the processing of mental attributes or emotional states. Thus the anterior–posterior differences between social and non-social tasks may mainly reflect the effect of processing domain in each category. In other words, cultural differences in brain activity are domain-dependent, being more salient over the parietal/occipital areas during the processing of perceptual features but over the anterior frontal/temporal areas during the processing of social attributes.

There are two possible accounts regarding the relationship between cultural influences on social cognitive/affective and non-social processes in the human brain. One account is that cultural practices and experiences shape the neural correlates of social processes through its effects on non-social processes. Given that the maturation of cortical regions involved in perception (e.g., occipital and inferior temporal cortices) occurs earlier than the maturation of cortical regions engaged in social cognition (e.g., prefrontal cortex, Gogtay et al., 2004), sociocultural environments may shape the neural substrates of non-social perceptual/attentional processes earlier compared to social cognitive/affective processes. This requires that cultural influences on the neural correlates of non-social processes match cultural influences on the neural correlates of social processes so that social and non-social systems can work in a coherent way to guide culturally appropriate behaviors. For instance, East Asian cultures foster sensitivity to social information such as others' intentions/beliefs and emotional states. East Asian cultures also encourage enhanced attention to contextual or background information during perceptual/attentional processing of non-social information. These cultural effects give rise to a congruent style of social and non-social information processing that facilitate social behaviors appropriate to East Asian cultural contexts. Alternatively, the social cognitive/affective system and non-social perceptual/attentional systems may interact mutually during development, and culture may affect the social cognitive/affective system via its effects on the non-social perceptual/attentional systems or vice versa. Such mutual interactions between the social and non-social systems eventually produce a culturally specific cognitive style that allows the two systems to fit with each other so as to guide efficient social behaviors in a specific sociocultural context.

To our knowledge, there is much less evidence for cultural influences on the motor system activity. However, a recent work found that perceiving interdependent versus independent self-construal prime words increased motor-evoked potentials elicited with transcranial magnetic stimulation during an action observation task (Obhi et al., 2011). This finding suggests that motor cortical output is modulated by priming of cultural orientations. Thus there seems to be broad cultural influences on the social cognitive/affective system, non-social cognitive system and motor system. What is the relationship between cultural influences on social, non-social and motor processes? One possibility is that culture may shape the motor system through cultural influences on social/non-social processes. In other words, cultural influences on social/non-social processes may mediate the observed cultural effects on the motor process. Alternatively, cultural norms or behavioral scripts regulate human behaviors and actions during development, which in turn pass cultural norm/values to the social cognitive/affective system and resulting in culture specific functional organization of the social brain.

In sum, the findings of cultural neuroscience studies indicate that sociocultural environments influence neural activity in the social cognitive/affective, non-social perceptual/attentional and motor systems through cultural practices and experiences. These influences result in both culturally universal and culturally specific neural mechanisms in these systems, depending on similarities and discrepancies in cultural values and norms, and behavioral scripts across different societies. The social brain also produces feedback to sociocultural environments by guiding human actions toward the environment. These processes constitute a sociocultural–environment–brain interaction loop in which both sociocultural environments and the brain continuously change at both ontogenetic and phylogenetic time scales.

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