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Culture modulates brain activity during empathy with anger

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ABSTRACT

Interdependent cultures (such as the Chinese) and independent cultures (such as the German) differ in their attitude towards harmony that is more valued in interdependent cultures. Interdependent and independent cultures also differ in their appreciation of anger — an emotion that implies the disruption of harmony.

The present study investigated if interdependent and independent cultures foster distinct brain activity associated with empathic processing of familiar angry, familiar neutral, and unfamiliar neutral faces.

Using functional MRI, we scanned Chinese and German healthy subjects during an intentional empathy task, a control task (the evaluation of skin color), and a baseline condition. The subject groups were matched with regard to age, gender, and education.

Behaviorally, Chinese subjects described themselves as significantly more interdependent compared to German subjects. The contrast 'intentional empathy for familiar angry'>'baseline' revealed several regions, including the left inferior frontal cortex, the left supplementary motor area, and the left insula, that showed comparable hemodynamic responses in both groups.

However, the left dorsolateral prefrontal cortex had stronger hemodynamic responses in Chinese subjects in the contrast 'intentional empathy for familiar angry'>'baseline'. Germans, in contrast, showed stronger hemodynamic responses in the right temporo-parietal junction, right inferior and superior temporal gyrus, and left middle insula for the same contrast. Hemodynamic responses in the latter three brain regions correlated with interdependences scores over all subjects.

Our results suggest that enhanced emotion regulation during empathy with anger in the interdependent lifestyle is mediated by the left dorsolateral prefrontal cortex. Increased tolerance towards the expression of anger in the independent lifestyle, in contrast, is associated with increased activity of the right inferior and superior temporal gyrus and the left middle insula.

Introduction

Interdependence describes a lifestyle, in which an individual is attuned to the social environment, adjusts his behavior to others, and takes the perspective of others. Independence, in contrast, refers to a lifestyle, in which an individual primarily refers to his own thoughts and feelings (Chiao et al., 2009; Markus and Kitayama, 2010). Typically, most Asian cultures engage an interdependent lifestyle, whereas in most Western cultures an independent lifestyle is prevalent (Chiao et al., 2009; Markus and Kitayama, 1991). Interestingly, both lifestyles do not completely exclude each other. Rather, they can coexist to some degree in one and the same individual (Singelis, 1994). Interdependent and independent lifestyles are considered to be responsible for a large amount of cultural differences in emotional experience, cognition and behavior (Markus and Kitayama, 1991).

A key concept, which is appreciated very differently in interdependent and independent cultures, is harmony. Harmony, which describes the balance, positive mood and social peace within a group, is important in interdependent cultures and often rooted in their cultural traditions (Markus and Kitayama, 1991; Uno, 1991 as described in Kim and Markus, 1999). Independent cultures, in contrast, rather stress the importance of uniqueness (Kim and Markus, 1999).

For instance, as shown by Kwan et al. (1997), relationship harmony is more important for life satisfaction in interdependent cultures (in this study Hong Kong students) compared to independent cultures (namely US students). In independent cultures (such as the United States or Germany), in contrast, life satisfaction is closer related to the affective well-being of the individuals (Suh et al., 1998). Interestingly, in the study conducted by Suh et al. Germans showed the strongest correlation of affective well-being and life satisfaction.

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In addition, two studies showed that, relative to individuals from independent cultures, individuals in interdependent cultures can tolerate disharmony less and are more prone to react with depressive reactions to negative social events (Chen et al., 2006; Tafarodi and Smith, 2001). Individuals from interdependent cultures also seek less social support in the case of stressing events in order to maintain social harmony (Taylor et al., 2004).

Given the differential significance of harmony for interdependent and independent cultures, one might also expect cultural differences in the appreciation of anger (Kövecses, 2000) because a crucial characteristic of anger is the disruption of harmony (Markus and Kitayama, 1991). Indeed, it is argued that the expression of anger is less prevalent in interdependent than in independent cultures (Markus and Kitayama, 1991). In a study investigating the reaction of 11 month old infants towards vocal expressions of emotions in the voice of their mothers, infants from interdependent cultures reacted stronger to the vocal expression of anger (but not joy or fear) compared to independent cultures (Miyake et al., 1986). The authors concluded, that the expression of anger happens less often in interdependent cultures (and is related to extreme situations). Moreover, in interdependent cultures (in this case China), the control of anger is related to high social functioning of school children (Zhou et al., 2004). In addition, individuals from interdependent cultures tolerate less anger. When anger was expressed in simulated negotiations (as part of recent study conducted by Adam and colleagues), Asians and Asian Americans made smaller concessions. In contrast, European Americans made larger concessions (Adam et al., 2010).

Moreover, there are differences between interdependent and independent cultures concerning the suppression of anger. The suppression of anger can lead to depression in individuals from interdependent and independent cultures; however, the link between suppressed anger and depression is significantly stronger in interdependent cultures (Cheung and Park, 2010; Park et al., 2010).

Interestingly, there is a special psychiatric disorder “hwa-byung” (English: “fire disease” or “anger disease”), which is explicitly associated with the suppression of anger and strictly bound to the Korean (i.e. interdependent) culture (Min, 2008; Min et al., 2009).

A suitable approach to investigate cultural differences in emotional processing is to implement an empathy task. Regarding this, empathy implies the capability to understand and share the emotional states of other creatures without losing the ability to differentiate between one's own feelings and the feelings of others (Decety and Jackson, 2004; Preston and de Waal, 2002).

To our knowledge, no study examined cultural differences in emotional empathy so far. One study however, explored differences in brain activity during “Theory of Mind” (TOM) – a paradigm, which is related to empathy – between interdependent and independent individuals. Investigating American and Japanese children using a cartoon TOM task, Kobayashi et al. (2007) found stronger hemodynamic responses in the right temporo-parietal junction (TPJ) in American children. The authors suggested that diminished TPJ activity during TOM might reflect a “demoted sense of self-other distinction in the Japanese culture”.

The current study investigated differences in brain activity during empathy with anger between individuals stemming from interdependent and independent cultures. For this, we used fMRI and an empathy paradigm, which was recently introduced by our group (de Greck et al., 2011). The paradigm allowed us to investigate automatic as well as intentional empathic responses, and to control for the effects of emotion and familiarity. (As recently shown by Xu et al. (2009), in particular familiarity can significantly modulate empathic processes.) We recruited two groups of healthy subjects from an interdependent culture (namely China) and from an independent culture (namely Germany).

With regard to the avoiding attitude towards anger prevalent in interdependent cultures, we hypothesized less activity in Chinese subjects (compared to German subjects) during empathy with anger in regions typically involved in emotional empathy and emotional processing such as insula, anterior cingulate cortex, inferior frontal cortex and superior temporal sulcus (Blair et al., 1999; Carr et al., 2003; de Greck et al., 2011; Hooker et al., 2008, 2010; Jabbi and Keysers, 2008; Jabbi et al., 2007; Ochsner et al., 2004a; Phillips et al., 1997; Sprengelmeyer et al., 1998; Wicker et al., 2003).

In addition, we expected more activity in Chinese in brain regions connected to emotion regulation, such as the prefrontal cortex (MacDonald et al., 2000; Ochsner and Gross, 2005; Ochsner et al., 2004b; Vanderhasselt et al., 2006).

Finally, considering the familiarity of empathy and TOM, we expected stronger activity in the right TPJ in German subjects (Kobayashi et al., 2007).

Methods

Participants

A group of Chinese students ($n = 16$) and a group of German students ($n = 16$) were recruited in this study. Both groups were scanned in Beijing, China, using the same fMRI scanner. Table 1 illustrates subjects' information about the two cultural groups. The study was approved by a local ethics committee. After a detailed explanation of the study design and any potential risks, all subjects gave their written informed consent. All subjects were reimbursed for their participation.

Paradigm

Experimental design

The fMRI experiment was divided into 7 blocks of 312 s duration each. Prior to entering the scanner each subject read detailed information of the paradigm in their native language and completed a couple of trial runs in order to familiarize fully with the task. While lying in the scanner, the stimuli were displayed using the software package ‘Presentation’ (Neurobehavioral Systems, Albany, CA, USA) and were projected onto a matte screen via an LCD projector, visible through a mirror mounted on the head coil. Each block started with a 10 s pause to control for epi-saturation effects. A total number of 24 trials (12 intentional empathy trials and 12 trials skin color evaluation trials) were presented in a randomized order in each block. Fig. 1 illustrates the intentional empathy task, the control task and the baseline condition.

Stimuli

Two sets of stimuli were used for Chinese and German subjects. Each stimulus set consisted of 12 different face stimuli — four stimuli (two female, two male) of each condition (namely ‘familiar angry’,

Table 1
Characteristics of the two subject groups.

	Chinese	Germans
Number	16	16
Age	Mean 22.9 years	Mean 23.3 years[b]
	95% CI[a]: 22.3–23.5 years	95% CI: 22.2–24.3 years
Gender	10 f/6 m[c]	10 f/6 m
Culture	16 Han Chinese raised in China by Chinese parents	16 Germans raised in Germany by German parents
Occupation	16 students	16 students

[a] The 95% confidence interval.
[b] There was no significant difference regarding the age of both groups ($t(30) = 0.681$, $p_{[two\text{-}tailed]} = 0.501$).
[c] In addition, there was no significant difference with regard to the gender distribution in both groups ($\chi^2(1) = 1$, $p = 0.317$).

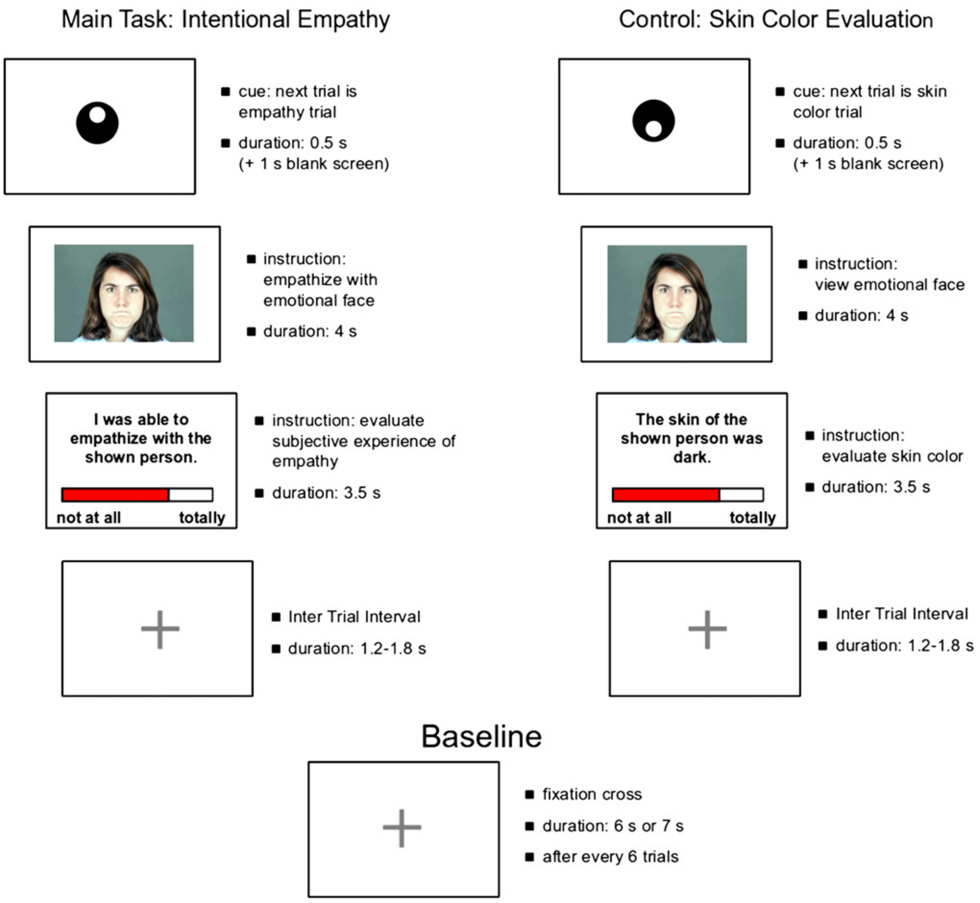

Fig. 1. Paradigm. A cue indexed the task at the start of each trial. The cue had the shape of a black circle with a small white circle in the 'North'- or 'South'-position. The white circle in the 'North'-position indexed an intentional empathy trial; the white circle in the 'South'-position cued a skin color evaluation trial. In intentional empathy trials, subjects were instructed to empathize with perceived emotional or neutral faces. After a 4 s lasting viewing period, subjects were supposed to rate their subjective impression of empathy capability in the evaluation period, which lasted for 3.5 s. By virtually moving a red bar, they were instructed to make a statement on a visual analog scale. In control trials subjects were instructed to concentrate on the skin color of the presented faces. Analog to the intentional empathy task, a 4 s lasting viewing period was followed by a 3.5 s lasting evaluation period. After every trial a short inter trial interval of 1.2 s to 1.8 s duration was presented. The face stimuli consisted of familiar angry, familiar neutral, and unfamiliar neutral faces. Both groups of subjects had different sets of stimuli: For Chinese subjects familiar faces consisted of Chinese faces and unfamiliar faces consisted of Caucasian faces. For German subjects familiar faces consisted of Caucasian faces and unfamiliar faces consisted of Chinese faces. Because of time constraints, we did not include unfamiliar angry stimuli. After every 6 trials, a baseline trial was presented; during baseline trials, the fixation cross was displayed for 6 s or 7 s.

'familiar neutral', and 'unfamiliar neutral'). Stimuli for German subjects for the conditions 'familiar angry' and 'familiar neutral' were taken from the "Japanese and Caucasian Facial Expressions of Emotion (JACFEE) and Neutral Faces (JACNeuF)" — battery provided by Matsumoto and Ekman (1988). Stimuli for German subjects for the condition 'unfamiliar neutral' were photographed and preprocessed for presentation by our own group (de Greck et al., 2011). These pictures were taken in front of a comparable background and under comparable conditions to match them as close as possible to the pictures taken from the JACNeuF battery.

Stimuli for Chinese subjects for the condition 'familiar neutral' were exactly those stimuli, as presented to German subjects in the condition 'unfamiliar neutral'. Analogously, stimuli for Chinese subjects for the condition 'unfamiliar neutral' were exactly the same stimuli as presented to German subjects in the condition 'familiar neutral' (i.e. these stimuli were taken from the JACNeuF-picture battery). Stimuli for Chinese subjects for the condition 'familiar angry' were also photographed and preprocessed for presentation by our own group, as described above. Each stimulus was presented twice during each block: once during intentional empathy, once during skin color evaluation.

The term "familiar" as used in our study refers to the concept of "race-based familiarity" and not "personal familiarity" (Liew et al., 2011).

Psychological scales

Interpersonal Reactivity Index (IRI)

The "Interpersonal Reactivity Index" (IRI, Davis, 1983) is a commonly used self evaluation questionnaire to measure the subjective impression of different empathic skills. The IRI uses four sub-scales related to 'empathic fantasy', 'empathic concern', 'personal distress', and 'perspective taking'.

Self-Construal Scale (SCS)

The "Self-Construal Scale" (SCS, Singelis, 1994) bases on the concept of interdependent and independent self-construals, which was introduced by Markus and Kitayama (1991, 2010). The SCS implements two scales related to 'interdependence' and 'independence'.

Behavioral data analysis

Behavioral data where analyzed using the software packages "PERL" (http://www.perl.org) and "R" (http://www.r-project.org/, R Development Core Team, 2009). Repeated measurements Analyses of Variance (ANOVAs) and post-hoc independent samples t-tests were used to test for significant differences; Spearman correlations were implemented to analyze associations between different behavioral scores.

fMRI data acquisition

The study was conducted using a General Electrics 3 Tesla Magnetic Resonance Imaging Scanner. Functional data (24 slices parallel to the AC–PC plane, slice thickness 5 mm, TR 2000 ms, TE 30 ms, flip angle $\alpha = 90°$, 64×64 voxels per slice with $3.75\ \text{mm} \times 3.75\ \text{mm} \times 5\ \text{mm}$) were acquired in seven scanning sessions containing 156 volumes per session for each subject. In addition, T1-weighted images of each subject were recorded.

fMRI data analysis

The statistical analysis of the fMRI data was performed using the software packages "Analysis of Functional NeuroImages" (AFNI, http://afni.nimh.nih.gov/afni/, Cox, 1996), "Python" (http://www.python.org), "PERL" (http://www.perl.org) and "R" (http://www.r-project.org/, R Development Core Team, 2009).

The first three volumes were discarded to compensate for saturation effects. All functional images were slice-time corrected with reference to the acquisition time of the first slice and corrected for motion artifacts by realignment to the first volume. The images were spatially normalized to a standard EPI-template provided by AFNI ('TT_EPI') and re-sampled to $3\ \text{mm} \times 3\ \text{mm} \times 3\ \text{mm}$. Finally, all functional images were smoothed with an isotropic 6 mm full-width half maximum Gaussian kernel. T1-weighted images of each subject were normalized to a standard T1-template provided by AFNI ('TT_avg152T1').

For each subject, regressors of interest were created by the convolution of a canonical, fixed shape hemodynamic response function with the according stimulus time functions (Josephs et al., 1997). Regarding this, all relevant periods (namely viewing periods with correct later responses for both tasks and all three conditions, evaluation periods with correct responses for both tasks and all three conditions, viewing and evaluation periods for tasks with incorrect responses, and the baseline event) were included in the model. In addition, six movement parameters resulting from motion correction, as well as nine regressors for the 3rd degree polynomial model of the baseline of each block were included as regressors to account for any residual effects of head motion and baseline fluctuations respectively. Contrast images were calculated by employing linear contrasts to the parameter estimates for the regressors of each event. The resulting contrast images were then submitted to a second level random-effects analysis. Here, one-sample t-tests (including the 16 Chinese and the 16 German subjects in one group) and independent two sample t-tests (comparing the 16 Chinese and the 16 German subjects) were applied (Friston et al., 1994). To control for the multiple testing problem, we performed a false discovery rate correction (Nichols and Hayasaka, 2003) and calculated family-wise error probabilities. The anatomical localization and labeling of significant activations were assessed with reference to the standard stereo-tactic atlas of Talairach and Tournoux, (1988) and by superimposition of the group contrast images on a mean brain generated by an average of each subject's normalized T1-weighted image. In a second step, we performed a statistical analysis of the raw fMRI signals. Using the significant clusters from the different contrasts as regions of interest, we extracted fMRI signal timecourses from activations found in the second level analysis using sphere shaped regions of interest with a radius of 5 mm. The timecourses were linearly interpolated and normalized with respect to a time window ranging from 0 s to 30 s after the onset of each event. fMRI signal changes of every event were calculated with regard to the fMRI signal value of the onset of the according event. Mean normalized fMRI signal values from two following time steps (6 s to 8 s after onset of the according event) were included in the statistical analysis. We used paired t-tests, to analyze the effects of the factors 'task' (['intentional empathy for familiar angry' + 'intentional empathy for familiar neutral' + 'intentional empathy unfamiliar neutral'] − ['control for familiar angry' + 'control for familiar neutral' + 'control for unfamiliar neutral']), 'emotion' ('intentional empathy for familiar angry' − 'intentional empathy for familiar neutral'), and 'familiarity' ('intentional empathy for familiar neutral' − 'intentional empathy unfamiliar neutral'). In addition, Spearman correlations were applied to analyze the association of different behavioral scores (namely the intra-scanner empathy ratings for angry faces, the IRI 'personal distress' score and the SCS 'interdependence' score) with hemodynamic responses of our regions of interest.

Results

Behavioral results

Intra-scanner empathy ratings

We used a 2×3 factorial repeated measure analysis of variance (ANOVA) with Group (Chinese vs. Germans) as a between-subjects factor and Condition ('familiar angry', 'familiar neutral', and 'unfamiliar neutral') as a within-subjects factor to analyze mean intra-scanner empathy ratings. We detected a significant main effect of Condition ($F(2,60) = 50.793$, $p < 0.001^{**}$) and a significant interaction of Group × Condition ($F(2,60) = 4.017$, $p = 0.023^{*}$); the main effect for Group was not significant ($F(1,30) = 1.209$, $p = 0.280$). Post-hoc t-tests revealed a significant group difference only for the condition 'unfamiliar neutral'. German subjects rated higher subjective impression of empathy for unfamiliar neutral faces compared to Chinese subjects ($t(30) = 2.782$, $p_{[\text{two-tailed}]} = 0.009^{**}$), while there were no differences between both groups for the conditions 'familiar angry' ($t(30) = 0.339$, $p_{[\text{two-tailed}]} = 0.737$) and 'familiar neutral' ($t(30) = 0.317$, $p_{[\text{two-tailed}]} = 0.764$; Fig. 2a).

Interpersonal Reactivity Index (IRI)

The 2×4 factorial ANOVA with Group (Chinese vs. Germans) as a between-subjects factor and Sub-scale ('empathic fantasy', 'empathic concern', 'personal distress', and 'perspective taking') as a within-subjects factor revealed a significant effect of Sub-scale ($F(3,90) = 46.634$, $p < 0.001^{**}$) and a significant interaction of Group × Sub-scale ($F(3,90) = 3.418$, $p = 0.021^{*}$). The main effect of Group was not significant ($F(1,30) = 0.039$, $p = 0.844$). Post-hoc t-tests showed significant higher ratings of Chinese for 'personal distress' ($t(30) = 2.496$, $p_{[\text{two-tailed}]} = 0.018^{*}$) but lower ratings of 'empathic concern' ($t(30) = 1.935$, $p_{[\text{two-tailed}]} = 0.062^{(*)}$) compared to Germans. We did not find significant differences with regard to the IRI scales 'empathic fantasy' ($t(30) = 0.689$, $p_{[\text{two-tailed}]} = 0.496$) and 'perspective taking' ($t(30) = 0.261$, $p_{[\text{two-tailed}]} = 0.796$) though (Fig. 2b).

Subjects, who score high on 'personal distress' typically agree to the statements of the following kind: "I sometimes feel helpless when I am in the middle of a very emotional situation", "Being in a tense emotional situation scares me", and "I tend to lose control during emergencies".

Subjects, who score high on 'empathic concern', in contrast, typically agree to these statements: "I often have tender, concerned feelings for people less fortunate than me", "When I see someone being taken advantage of, I feel kind of protective towards him", and "I would describe myself as a pretty soft-hearted person" (Davis, 1983).

Self-Construal Scale (SCS)

Independent samples t-tests confirmed higher ratings of Chinese compared to Germans in the 'interdependence'-scale ($t(30) = 3.469$, $p_{[\text{two-tailed}]} = 0.002^{**}$), while both groups did not differ with regard to the 'independence'-scale ($t(30) = 0.710$, $p_{[\text{two-tailed}]} = 0.483$; Fig. 2c). Subjects, who score high on the 'interdependence'-scale, typically agree to the statements which include the following: "It is important for me to maintain harmony within my group", "I will sacrifice my self-interest for the benefit of the group I am in", and

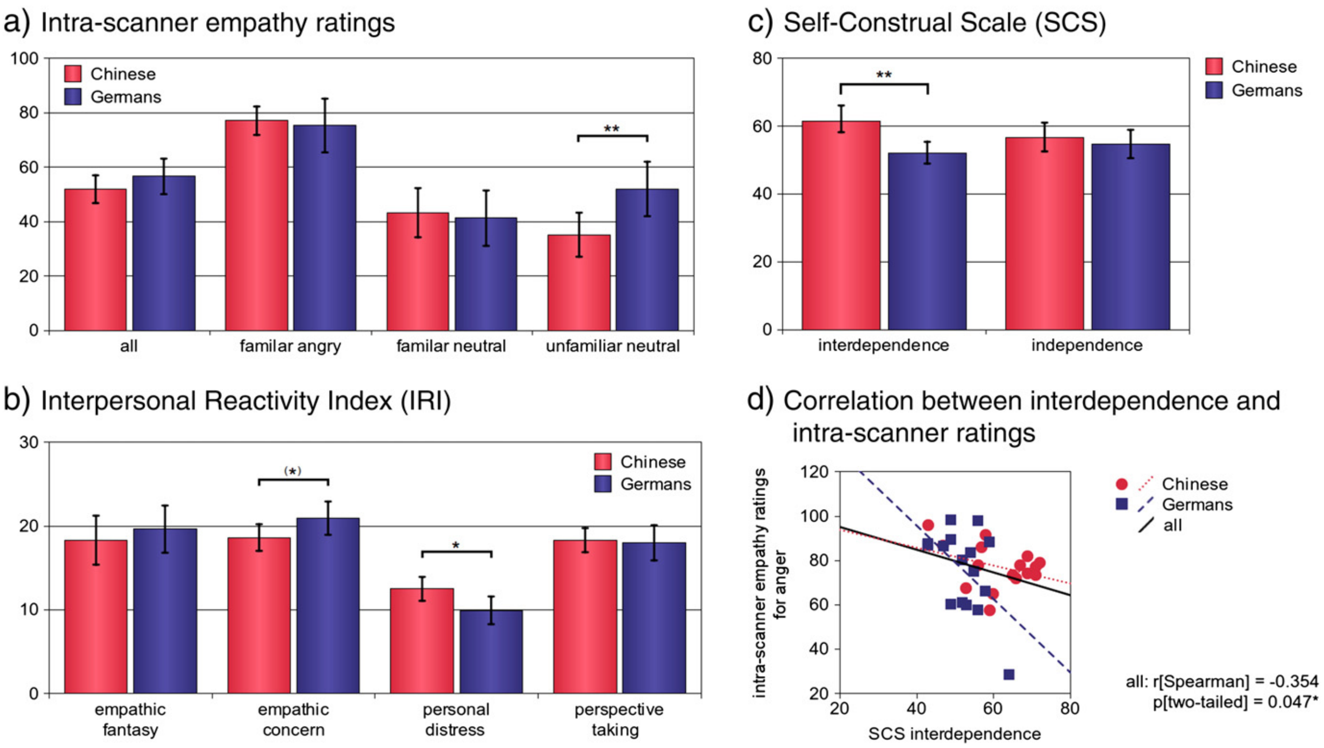

Fig. 2. Behavioral results. a. Intra-scanner empathy ratings. German subjects compared to Chinese subjects reported significantly more subjective empathy during the condition 'unfamiliar neutral', while there were no differences between both groups for the conditions 'familiar angry' and 'familiar neutral'. b. Interpersonal Reactivity Index (IRI). German subjects described significantly less 'personal distress' and more 'empathic concern' compared to Chinese subjects. However, we did not find significant differences with regard to the IRI scales 'empathic fantasy' and 'perspective taking'. c. Self-Construal Scale (SCS). Chinese subjects scored significantly higher with regard to the 'interdependence' scale of the SCS. There was, however, no difference with regard to the 'independence' scale. d. Correlation between interdependence and intra-scanner empathy ratings. Subjects' interdependence scores predicted their intra-scanner empathy ratings for the condition 'familiar angry'. Subjects, who described themselves as interdependent, reported less subjective empathic understanding for angry faces during the experiment.

"Even when I strongly disagree with group members, I avoid an argument" (Singelis, 1994).

Correlation analyses of behavioral scores

We tested for correlations between the different behavioral scores (namely the intra-scanner empathy ratings for 'familiar angry', 'personal distress', and 'interdependence') using Spearman correlations. We found a significant negative correlation between intra-scanner empathy ratings during 'familiar angry' and 'interdependence' scores ($r_{[Spearman]} = -0.354$, $p_{[two\text{-}tailed]} = 0.047^*$; Fig. 2d). We did, however, neither find a significant correlation of 'personal distress' scores with 'interdependence' scores ($r_{[Spearman]} = -0.070$, $p_{[two\text{-}tailed]} = 0.704$) nor a correlation of 'personal distress' scores with intra-scanner empathy ratings ($r_{[Spearman]} = 0.245$, $p_{[two\text{-}tailed]} = 0.176$).

fMRI results

'Intentional empathy for familiar angry'>'baseline' — transcultural constants

We implemented a whole brain analysis of all 32 subjects to investigate the transcultural constants of the contrast 'intentional empathy for familiar angry'>'baseline'. Regarding this, we calculated voxel-wise one-sample t-tests for both groups and implemented an inclusive masking analysis that included only those clusters which showed significant activity in both groups. Brain regions with transcultural constant brain activity included the bilateral inferior frontal gyrus, the bilateral supplementary motor area, bilateral anterior insula, bilateral parahippocampal gyrus, and other areas (see Table 2).

'Intentional empathy for familiar angry'>'baseline' — cultural differences

To investigate cultural differences in empathy with anger, we implemented voxel-wise independent-samples t-tests using the contrast 'intentional empathy for familiar angry'>'baseline'. Here, we found one region with stronger hemodynamic responses in Chinese subjects: the left dorsolateral prefrontal cortex (DLPFC). In addition, four regions showed stronger hemodynamic responses in German subjects: the right temporo-parietal junction (TPJ), the right inferior temporal gyrus (ITG), the right superior temporal gyrus (STG), and the left middle insula (MI). See Table 3 and Fig. 3 for details.

Correlation of hemodynamic responses with behavioral scores

We used Spearman correlation analyses to investigate the association of hemodynamic responses during 'intentional empathy for familiar angry' (more exact: the difference between 'intentional empathy for familiar angry' and 'baseline') and behavioral scores (namely the 'personal distress' score of the IRI and the 'interdependence' score of the SCS). We found a significant positive correlation of 'personal distress' scores with hemodynamic responses in the left DLPFC (see Fig. 3a). In addition, we detected significant negative correlations of 'interdependence' scores with hemodynamic responses in the right ITG (see Fig. 3c), the right STG (see Fig. 3d), and the left MI (see Fig. 3e).

Moreover, we tested for correlations of intra-scanner empathy ratings during anger and hemodynamic responses of the five regions. We detected a marginal correlation of empathy ratings and hemodynamic responses from the left DLPFC ($r_{[Spearman]} = 0.304$, $p = 0.091^{(*)}$) but not for the right TPJ ($r_{[Spearman]} = -0.031$, $p = 0.867$), the right ITG ($r_{[Spearman]} = 0.148$, $p = 0.418$), the right STG ($r_{[Spearman]} = 0.025$, $p = 0.892$), or the left MI ($r_{[Spearman]} = 0.276$, $p = 0.126$).

Modulation of hemodynamic responses by task

We used paired t-tests (['intentional empathy for familiar angry' + 'intentional empathy for familiar neutral' + 'intentional

Table 2
'Intentional empathy for familiar angry'>'baseline' — transcultural constants.

No.	Region		BA	x, y, z [mm]			n	$p_{[FWE]}$(C)	$p_{[FWE]}$(G)	Modulation by		
										Task	Emo.	Fam.
2.01	Left	Inferior frontal gyrus	6	−42	−3	24	2342	<0.001	<0.001			
2.02	Left	Inferior frontal gyrus	45	−39	−24	18						
2.03	Right	Middle frontal gyrus	6	27	9	54				$e<c^{**}$		
2.04	Left	Supplementary motor area	6	−6	−3	52				$e>c^{**}$		
2.05	Right	Supplementary motor area	6	9	−6	45				$e>c^{*}$	$a>n^{(*)}$	$f<u^{*}$
2.06	Left	Anterior insula	13	−28	−26	−1				$e>c^{**}$		
2.07	Left	Putamen		−18	−12	−6				$e>c^{**}$	$a>n^{(*)}$	
2.08	Right	Occipital cortex	17, 18	33	84	−18	1241	0.003	<0.001		$a>n^{*}$	$f<u^{(*)}$
2.09	Right	Cerebellum		36	−57	−30						
2.10	Left	Occipital cortex	17, 18	−15	90	−18	780	0.088	0.001			
2.11	Left	Cerebellum		−39	51	−33					$a>n^{(*)}$	
2.12	Left	Supramarginal gyrus	40	−30	51	30	627	0.232	0.008	$e<c^{*}$		
2.13	Left	Precuneus	7	−24	72	24				$e<c^{**}$	a>n(*)	
2.14	Left	Cuneus	7	−6	75	33					a>n(*)	
2.15	Right	Inferior frontal gyrus	9	39	−6	24	470	0.585	0.049			
2.16	Right	Anterior insula	13	30	−24	0				$e>c^{*}$	$a>n^{(*)}$	$f<u^{(*)}$
2.17	Right	Putamen		21	−12	0				$e>c^{*}$		
2.18	Right	Cuneus	18	24	60	18	128	0.999	0.998			
2.19	Right	Precuneus	19	30	66	42						
2.20	Left	Posterior midbrain		−3	33	−18	58	0.999	1	$e>c^{*}$		$f<u^{(*)}$
2.21	Right	Posterior midbrain		7	33	−17				$e>c^{**}$		$f<u^{*}$
2.22	Right	Parahippocampal gyrus	36	24	33	−12	25	0.999	1			$f<u^{*}$
2.23	Left	Middle temporal gyrus	37	−48	45	−6	15	0.999	1	$e>c^{**}$	$a>n^{*}$	
2.24	Left	Parahippocampal gyrus	36	−21	33	−15	14	0.999	1			
2.25	Left	Thalamus		−6	30	15	11	0.999	1		$a>n^{*}$	

The table lists the peak voxels of all clusters which showed significant activation ($p_{[FDR]} \leq 0.05$) in the contrast 'intentional empathy for familiar angry'>'baseline' for both groups (inclusive masking). Clusters smaller than 10 voxels were not considered. ('x, y, z' are coordinates referring to the Talairach and Tournoux stereo-tactic space; 'n' reflects the number of significant voxels inside the cluster; '$p_{[FWE]}$(C)' and '$p_{[FWE]}$(G)' show the probability that a cluster of the given size might appear as a false positive in the group of Chinese (C) and Germans (G); the last three columns list the significances of the paired t-tests (two-sided) investigating the effects of the factors 'task', 'emotion', and 'familiarity'; e>c: 'intentional empathy'>'control'; a>n: 'intentional empathy for familiar angry'>'intentional empathy for familiar neutral'; f>u: 'intentional empathy for familiar neutral'>'intentional empathy for unfamiliar neutral'; $^{(*)}$: $p<0.1$; *: $p<0.05$; **: $p<0.01$).

empathy for unfamiliar neutral'] − ['control for familiar angry' + 'control for familiar neutral' + 'control for unfamiliar neutral']) to investigate whether hemodynamic responses of the regions listed in Tables 2 and 3 were modulated by the task. Several regions with transcultural constant activity showed stronger hemodynamic responses during 'intentional empathy' compared to 'control': the bilateral supplementary motor area (SMA, 2.04, 2.05), the bilateral anterior insula (AI, 2.06, 2.16), the bilateral putamen (2.07, 2.17), the bilateral posterior midbrain (2.20, 2.21), the left middle temporal gyrus (MTG, 2.23), and others (see Table 2). The right STG (3.04) and left MI (3.05), which showed stronger activity in German subjects, also showed stronger activity during 'intentional empathy' (Table 3). In addition, several regions with transcultural constant activity showed the opposite effect (i.e. decreased hemodynamic responses during 'intentional empathy' compared to 'control'): the right middle frontal gyrus (2.03), the left supramarginal gyrus (2.12), and the bilateral precuneus (2.13, 2.19) (Table 2). The right TPJ (3.02), which was stronger activated in Germans, also showed less activity during 'intentional empathy' (statistical trend — Table 3). In addition, there were a number of regions without modulation by task (see Tables 2 and 3).

Modulation of hemodynamic responses by emotion

We used paired t-tests ('intentional empathy for familiar angry' − 'intentional empathy for familiar neutral') to investigate whether hemodynamic responses of regions listed in Tables 2 and 3

Table 3
'Intentional empathy for familiar angry'>'baseline' — cultural differences.

No.	Region		BA	x, y, z [mm]			t	n	$p_{[FWE]}$	Modulation by		
										Task	Emo.	Fam.
Chinese > Germans												
3.01	Left	Dorsolateral prefrontal cortex	9	−44	−8	32	5.000	26	0.258			
Germans > Chinese												
3.02	Right	Temporo-parietal junction	40	55	45	31	6.796	113	<0.001	$e<c^{(*)}$	$a>n^{*}$	
3.03	Right	Inferior temporal gyrus	20	57	16	−18	5.499	44	0.033			
3.04	Right	Superior temporal gyrus	22	53	−12	−7	4.603	30	0.167	$e>c^{**}$	$a>n^{**}$	$f<u^{*}$
3.05	Left	Middle insula	13	−41	−1	−9	4.991	13	0.819	$e>c^{***}$	$a>n^{*}$	$f<u^{*}$

The table presents the centers of mass of all clusters which showed significant differences between Chinese and Germans in the contrast 'intentional empathy for familiar angry'>'baseline'. Voxels with $p_{[FDR]}>0.05$ were masked. In addition, voxels were masked, which were not included in a cluster of minimum 10 voxels. ('x, y, z' are coordinates referring to the Talairach and Tournoux stereo-tactic space; 'n' reflects the number of significant voxels inside the cluster; '$p_{[FWE]}$' shows the probability that a cluster of the given size might appear as a false positive; the last three columns list the significances of the paired t-tests (two-sided) investigating the effects of the factors 'task', 'emotion', and 'familiarity'; e>c: 'intentional empathy'>'control'; a>n: 'intentional empathy for familiar angry'>'intentional empathy for familiar neutral'; f>u: 'intentional empathy for familiar neutral'>'intentional empathy for unfamiliar neutral'; $^{(*)}$: $p<0.1$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$.).

were modulated by emotion. A number of regions, including the right SMA (2.05), the left MTG (2.23), the left putamen (2.07), the left precuneus (2.13), the left cuneus (2.14), the right AI (2.16), and others, showed stronger hemodynamic responses during intentional empathy with angry faces compared to neutral faces (see Table 2).

In addition, several regions of the contrast 'intentional empathy for familiar angry'>'baseline' did not show any modulation emotion (Table 2). Many of these regions are hence also listed for the contrast 'intentional empathy for familiar neutral'>'baseline' (Table 4) with similar or identical coordinates (for instance the left and right inferior frontal cortex (2.01/4.01, 2.15/4.03), the left and right occipital cortex (2.10/4.12, 2.08/4.10), the left and right cerebellum (2.11/4.13, 2.09/4.11), or the left and right parahippocampal gyrus (2.24/4.23, 2.22/4.22)).

The same was the case for some of those regions, which showed different activity in both groups. The left DLPFC (3.01/5.01), the right inferior temporal gyrus (3.03/5.03), and the left MI (3.05/5.02) showed activity in both contrasts ('intentional empathy for familiar angry'>'baseline' (Table 3) and 'intentional empathy for familiar neutral'>'baseline' (Table 5)).

Modulation of hemodynamic responses by familiarity

Paired t-tests ('intentional empathy for familiar neutral'>'intentional empathy for unfamiliar neutral') were applied to investigate whether hemodynamic responses of regions listed in Tables 2 and 3 were modulated by 'familiarity'. This was the case for a number of regions, which showed stronger hemodynamic responses for the unfamiliar neutral compared to the familiar neutral condition: the right SMA (2.05), the right occipital cortex (2.08), the right AI (2.16), the bilateral midbrain (2.20, 2.21), and the right parahippocampal gyrus (2.22).

In addition, two regions with culture-related differences in hemodynamic responses – the right STG (3.04) and the right MI (3.05) – showed stronger responses during the 'unfamiliar' condition when compared to the 'familiar condition'.

Discussion

Summary of findings

Questionnaire measurements indicate differences in empathy and self-construals between the subject groups. Chinese subjects reported more 'personal distress' and more 'interdependence' relative to German subjects.

Comparing brain activity during empathy with anger of the two subject groups showed both transcultural constants and cultural differences. Cultural constants included increased activity associated with intentional empathy for anger in the bilateral inferior frontal gyrus (IFG), left supplementary motor area (SMA), left anterior insula (AI), and other brain regions. Cultural differences in empathy with anger were observed in the left dorsolateral prefrontal cortex (DLPFC) where Chinese subjects showed stronger hemodynamic responses compared to German subjects. Subjects' hemodynamic responses in this region correlated with their 'personal distress' scores and their intra-scanner empathy ratings for the 'familiar angry' faces (statistical trend). German subjects showed stronger hemodynamic responses associated with empathy for anger in the right temporo-parietal junction (TPJ), the right inferior temporal gyrus (ITG), the right superior temporal gyrus (STG), and the left middle insula (MI). There was a significant correlation of hemodynamic responses of the right ITG, right STG, and left MI with 'interdependence' scores.

The right STG and left MI revealed stronger hemodynamic responses during intentional empathy compared to control; whereas the right TPJ showed the opposite effect. The left DLPFC and the right ITG were not modulated by the task at all. None of the five regions with culturally different activity showed a significant modulation by emotion.

Brain regions with transcultural constant activity

Brain regions that were active in empathy for anger in both cultural groups and revealed stronger activity for the 'intentional empathy' task compared to the control task included the bilateral SMA, bilateral AI, and bilateral putamen — brain areas, which are well known for their involvement in empathy (Carr et al., 2003; Fan et al., 2011; Hooker et al., 2008, 2010; Jabbi and Keysers, 2008; Jabbi et al., 2007; Lamm et al., 2007; Mathur et al., 2010; Singer et al., 2004). In addition, we found areas with transcultural constant activity for the contrast 'intentional empathy for familiar angry'>'baseline' in both groups, but less activity during 'intentional empathy' when compared to the control task. The left inferior frontal gyrus, left supramarginal gyrus and bilateral precuneus were among these regions.

Interestingly, we did not find increased activity of the amygdala for this contrast; in addition, the amygdala was not among those regions which revealed culturally different activity. In several previous studies the amygdala showed reliable activity during the processing of emotional (including angry) faces (Derntl et al., 2009; Gur et al., 2002; Hariri et al., 2002; Loughead et al., 2008; Whalen et al., 2001; Yang et al., 2002). However, a recent meta-analysis suggests, that the amygdala is not consistently involved in the processing of angry faces (Fusar-Poli et al., 2009). The lack of amygdala activity in our study might be explained by our task, which focused on empathic emotional sharing of the presented stimuli. It is likely that the instruction to intentionally share the emotional state of the presented angry models led to reduced hemodynamic responses in the amygdala, while we found significant activity in the bilateral IFG, bilateral SMA and bilateral AI.

Brain regions with culture-based differences in brain activity

As initially hypothesized, the left DLPFC showed stronger activity in Chinese subjects. In addition, its hemodynamic responses correlated with individual scores of 'personal distress' and intra-scanner empathy ratings (statistical trend). Since previous studies reported the involvement of the DLPFC in emotion regulation and inhibition (MacDonald et al., 2000; Ochsner and Gross, 2005; Ochsner et al., 2004b; Shackman et al., 2009; Vanderhasselt et al., 2006), one explanation of our finding is that the left DLPFC was activated by subjects with high 'personal distress' scores and high subjective impression of empathy to protect themselves against emotional over-arousal.

The right TPJ showed stronger hemodynamic responses in Germans, a finding which is also in accordance with our initial hypotheses; however, hemodynamic responses did neither correlate with 'personal distress' nor 'interdependence' scores. The TPJ is known to be involved in the attribution of mental states towards others ("theory of mind", TOM) in Western cultures (Castelli et al., 2000; Gallagher et al., 2000; Mitchell, 2008; Saxe and Kanwisher, 2003; Saxe and Powell, 2006; Saxe and Wexler, 2005).

Moreover, the (right) TPJ is also known for its role in attention shifting (Astafiev et al., 2006; Corbetta and Shulman, 2002; Corbetta et al., 2000; Kincade et al., 2005; Mitchell, 2008; Serences et al., 2005; Shulman et al., 2003) (see the paper of Mitchell (2008) for an overview about the overlap of brain activity related to TOM and attention shifting). Interestingly, in a study comparing children (at the age of 8 to 11 years) from interdependent and independent cultures (Japanese and Americans) during a non-verbal TOM task, Kobayashi et al. (2007) found the right TPJ with stronger hemodynamic responses in American children. The authors argued that diminished self-other differentiation, which is connected to interdependent cultures (Markus and Kitayama, 1991, 2010) might be the explanation for this finding. Indeed, the TPJ is also known for its involvement in self-agency and self-awareness (Decety and Grèzes, 2006; Farrer and Frith, 2002; Vogeley et al., 2001). Unfortunately, in this study we did not test for self-other differentiation.

The role of the right TPJ is more complex, however: In a recent study investigating culture-based differences in brain activity during

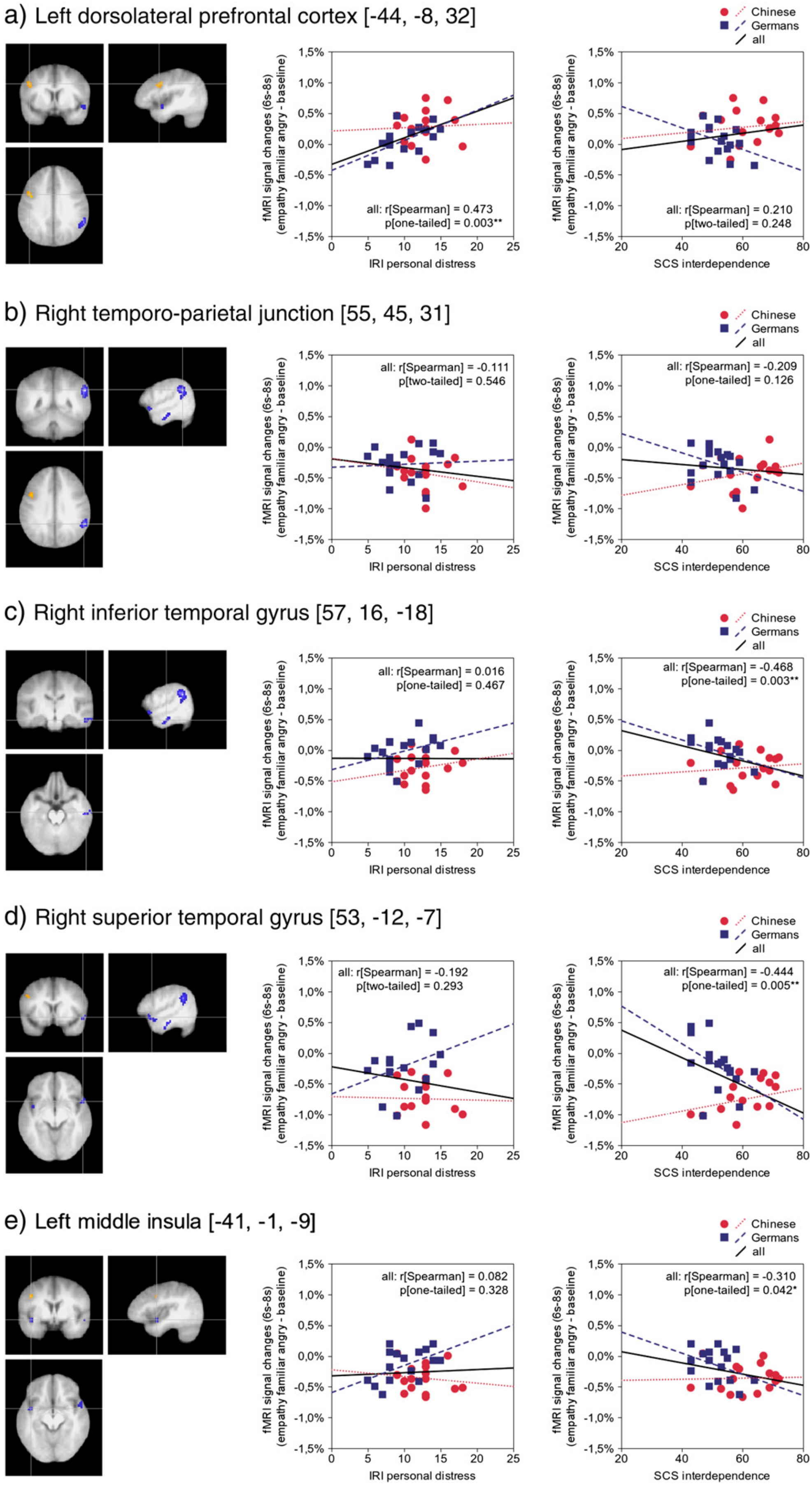
a) Left dorsolateral prefrontal cortex [-44, -8, 32]
Chinese
Germans
all
fMRI signal changes (6s-8s) (empathy familiar angry - baseline)
all: r[Spearman] = 0.473
p[one-tailed] = 0.003**
IRI personal distress
all: r[Spearman] = 0.210
p[two-tailed] = 0.248
SCS interdependence
b) Right temporo-parietal junction [55, 45, 31]
all: r[Spearman] = -0.111
p[two-tailed] = 0.546
all: r[Spearman] = -0.209
p[one-tailed] = 0.126
c) Right inferior temporal gyrus [57, 16, -18]
all: r[Spearman] = 0.016
p[one-tailed] = 0.467
all: r[Spearman] = -0.468
p[one-tailed] = 0.003**
d) Right superior temporal gyrus [53, -12, -7]
all: r[Spearman] = -0.192
p[two-tailed] = 0.293
all: r[Spearman] = -0.444
p[one-tailed] = 0.005**
e) Left middle insula [-41, -1, -9]
all: r[Spearman] = 0.082
p[one-tailed] = 0.328
all: r[Spearman] = -0.310
p[one-tailed] = 0.042*
1,5%
1,0%
0,5%
0,0%
-0,5%
-1,0%
-1,5%
0 5 10 15 20 25
20 40 60 80

Table 4
'Intentional empathy for familiar neutral'>'baseline' — transcultural constants.

No.	Region		BA	x, y, z [mm]			n	$p_{[FWE]}$(C)	$p_{[FWE]}$(G)	Modulation by		
										Task	Emo.	Fam.
4.01	Left	Inferior frontal gyrus	44	−42	−3	24	2591	<0.001	<0.001			
4.02	Left	Inferior frontal gyrus	45	−39	−24	18						
4.03	Right	Inferior frontal gyrus	44	45	−9	24						
4.04	Right	Middle orbital gyrus	11	24	−42	0					$a<n^{(*)}$	
4.05	Left	Supplementary motor area	6	−6	−3	54				$e>c^{**}$		
4.06	Right	Supplementary motor area	6	9	−6	46				$e>c^{*}$	$a>n^{(*)}$	$f<u^{*}$
4.07	Left	Anterior insula	13	−27	−27	0				$e>c^{**}$		
4.08	Right	Anterior insula	13	30	−24	−3				$e>c^{*}$	$a>n^{(*)}$	
4.09	Left	Putamen		−21	−9	−3				$e>c^{**}$	$a>n^{(*)}$	
4.10	Right	Occipital cortex	17, 18	33	84	−18	1078	0.006	<0.001		$a>n^{*}$	$f<u^{(*)}$
4.11	right	Cerebellum		36	57	−30						
4.12	Left	Occipital cortex	17,18	−18	90	−15	722	0.103	0.001			
4.13	Left	Cerebellum		−39	54	−30					$a>n^{*}$	
4.14	Left	Cerebellum		−36	78	−30						
4.15	Left	Angular gyrus	39	−30	54	30	470	0.509	0.023	$e<c^{**}$		
4.16	Left	Precuneus	7	−9	72	39						
4.17	right	Precuneus	31	24	66	18	96	0.999	1			
4.18	right	Precuneus	7	15	69	39				$e<c^{*}$		
4.19	Left	Posterior midbrain		−3	33	−15	54	0.999	1	$e>c^{(*)}$		$f<u^{*}$
4.20	Right	Posterior midbrain		7	35	−20				$e>c^{**}$		$f<u^{(*)}$
4.21	Left	Caudate tail		−24	33	21	52	0.999	1			
4.22	Right	Parahippocampal gyrus	36	24	30	−12	30	0.999	1			$f<u^{*}$
4.23	Left	Parahippocampal gyrus	36	−21	33	−15	18	0.999	1			

The table lists the peak voxels of all clusters which showed significant activation ($p_{[FDR]} \leq 0.05$) in the contrast 'intentional empathy for familiar neutral'>'baseline' for both groups (inclusive masking). Voxels, which were not included in a cluster of minimum 10 voxels, are not counted in. ('x, y, z' are coordinates referring to the Talairach and Tournoux stereotactic space; 'n' reflects the number of significant voxels inside the cluster; '$p_{[FWE]}$(C)' and '$p_{[FWE]}$(G)' show the probability that a cluster of the given size might appear as a false positive in the group of Chinese (C) and Germans (G); the last three columns list the significances of the paired t-tests (two-sided) investigating the effects of the factors 'task', 'emotion', and 'familiarity'; e>c: 'intentional empathy'>'control'; a>n: 'intentional empathy for familiar angry'>'intentional empathy for familiar neutral'; f>u: 'intentional empathy for familiar neutral'>'intentional empathy for unfamiliar neutral'; $^{(*)}$: $p<0.1$; *: $p<0.05$; **: $p<0.01$).

a "Reading the mind in the eyes"-task, Adams et al. (2010) found *stronger* activity in the right TPJ in interdependent (i.e. Japanese) subjects when compared to subjects stemming from an independent culture (i.e. USA). In addition, the right TPJ was activated more strongly in interdependent (i.e. Chinese) subjects when compared to independent (i.e. Danish) subjects during a task which included the self-reflection of social attributes (Ma et al., in preparation). At this time, a definite explanation of these complex cultural differences in TPJ activity is certainly too early and further research has to be done. However, with regard to our finding that cultural differences in TPJ activity are neither associated to 'interdependence' nor to 'personal distress', one is tempted to assume that other factors could play an important role here — for instance additional differences related to language.

In addition, the right inferior temporal gyrus and the right superior temporal gyrus (temporal pole region) showed stronger hemodynamic responses in German subjects; moreover, hemodynamic responses of both regions negatively correlated with 'interdependence' scores. Both regions are known to play an important role in social communication, the attribution of mental states and the understanding of intentions (Britton et al., 2006; Castelli et al., 2000; Enrici et al., 2010; Freeman et al., 2010; Frith and Frith, 1999, 2003; Gallagher and Frith, 2003).

Finally, the left MI showed stronger hemodynamic responses in German subjects; and again, hemodynamic responses of this region negatively correlated with 'interdependence' scores.

While the AI (which was amongst those regions which displayed transcultural constant activity) is known for its involvement in affective sharing (Fan et al., 2011; Jabbi et al., 2007; Keysers and Gazzola, 2007; Singer et al., 2004) the MI is involved in perspective taking (Lamm et al., 2007).

Taken together, Chinese subjects showed enhanced neuronal activity in regions associated to emotion regulation (right DLPFC), whereas German subjects showed stronger neuronal activity in regions connected to emotional understanding and perspective taking (TPJ, ITG, STG, MI).

How culture affects brain activity during intentional empathy with anger

As behavioral studies show, individuals from interdependent and independent cultures differ in their attitude towards anger, which is less often expressed and relatively more controlled in interdependent cultures (Markus and Kitayama, 1991; Miyake et al., 1986; Zhou et al., 2004). The DLPFC is the key brain region in the neuronal mechanisms of this emotional control. Why do individuals from interdependent cultures engage their DLPFC in order to control their anger responses? The answer to this is twofold: (i) because they are relatively more afraid to be overwhelmed by negative emotions (as shown by a significant difference in 'personal distress' and the correlation of 'personal distress' scores with DLPFC activity) and (ii) because they value harmony more than individuals from independent cultures (Markus and Kitayama, 1991) and have therefore a higher motivation to maintain harmony by the suppression of anger.

Individuals from independent cultures in contrast do not only express anger more often, they also can tolerate anger better in social interactions (Adam et al., 2010). Our data suggest that the increased

Fig. 3. 'Intentional empathy for familiar angry'>'baseline' — cultural differences. The figure presents all five regions which showed significant group differences in the comparison of Chinese and Germans with regard to the contrast 'intentional empathy for familiar angry'>'baseline' ($p_{[FDR]}<0.05$, minimum cluster size 10 voxels, see also Table 3). The picture on the left of each row explains the location of the active region. The diagram in the center of each row presents the correlation of hemodynamic responses (the difference of hemodynamic responses during 'intentional empathy for familiar angry' and 'baseline') with 'personal distress' scores, as obtained in the 'Interpersonal Reactivity Index' (IRI). The diagram on the right of each row shows the correlation of hemodynamic responses (again the difference of hemodynamic responses during 'intentional empathy for familiar angry' and 'baseline') with the 'interdependence' score, as obtained in the 'Self-Construal Scale' (SCS). In both diagrams, each Chinese subject is symbolized by a red circle and each German subject by a blue square. The black continuous line reflects the fitted response of all 32 subjects together, the red dotted line reflects the fitted response of the 16 Chinese subjects, and the blue discontinuous line reflects the fitted response of the 16 German subjects.

Table 5
'Intentional empathy for familiar neutral'>'baseline' — cultural differences.

No.	Region		BA	x, y, z [mm]			t	n	$p_{[FWE]}$	Modulation by		
										Task	Emo.	Fam.
Chinese>Germans												
5.01	Left	Dorsolateral prefrontal cortex	9	−45	−9	33	5.555	23	0.068			
Germans>Chinese												
5.02	Left	Middle insula	13	−39	−3	−6	6.122	19	0.145	e>c***	a>n**	f<u*
5.03	Right	Inferior temporal gyrus	20	54	18	−18	5.383	10	0.562			

The table presents the centers of mass of all clusters which showed significant differences between Chinese and Germans in the contrast 'intentional empathy for familiar angry'>'baseline'. Voxels with $p_{[FDR]}>0.05$ were masked. In addition, voxels were masked, which were not included in a cluster of minimum 10 voxels. ('x, y, z' are coordinates referring to the Talairach and Tournoux stereo-tactic space; 'n' reflects the number of significant voxels inside the cluster; '$p_{[FWE]}$' shows the probability that a cluster of the given size might appear as a false positive; the last three columns list the significances of the paired t-tests (two-sided) investigating the effects of the factors 'task', 'emotion', and 'familiarity'; e>c: 'intentional empathy'>'control'; a>n: 'intentional empathy for familiar angry'>'intentional empathy for familiar neutral'; f>u: 'intentional empathy for familiar neutral'>'intentional empathy for unfamiliar neutral'; (*): $p<0.1$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$.).

tolerance of anger in less interdependent individuals is related to increased neuronal activity in brain regions responsible for the understanding of social intentions (TPJ, ITG, STG, and MI).

In contrast to our initial hypotheses we did not find culture based differences in neuronal activity of key empathy regions such as the AI, ACC, or IFG. These regions are reliably involved in basic empathic processes. The AI is responsible for interoceptive processing and is crucially involved in the conscious processing of emotions (Craig, 2002, 2004, 2009) and affective sharing (Fan et al., 2011; Jabbi et al., 2007; Keysers and Gazzola, 2007; Singer et al., 2004). The ACC was in a recent review article by Shackman et al. (2011) described as being responsible for the integration of negative affect, cognitive control, and pain as well as the generation of "aversely motivated behavior". In addition, the ACC has been found to be active during emotional empathy (including empathy with positive and neutral emotions) in several studies (Blair et al., 1999; Carr et al., 2003; de Greck et al., 2011; Hooker et al., 2008; Ochsner et al., 2004a). The IFG is a crucial part of the human mirror neuron system (MNS), a system which was first detected in monkeys (Ferrari et al., 2003; Gallese et al., 1996; Rizzolatti and Craighero, 2004). The MNS consists of brain areas which are activated during the generation of actions and also during the perception of (the same) actions performed by others (Carr et al., 2003; Grèzes et al., 2003; Iacoboni, 2005; Iacoboni et al., 1999; Kaplan and Iacoboni, 2006) In addition, the human MNS including the IFG is reliably activated during empathy (Carr et al., 2003; de Greck et al., 2011; Kaplan and Iacoboni, 2006). One possible explanation for this negative finding, i.e. a lack differences in neuronal activity of AI, ACC, and IFG between both groups, might be that these regions provide empathic processes which are too basic to be influenced by cultural differences with regard to interdependence.

Limitations

Concerning some limitations of our study, we would like to mention that the design of our study did not include an 'unfamiliar angry' condition. To investigate the effect of familiarity, we hence relied on the comparison of 'familiar neutral' and 'unfamiliar neutral' In future studies, it might be interesting to investigate the effect of familiarity in the presence of emotions.

Another limitation concerns the possible bias of genetic differences between the groups of Chinese and Germans, since all Chinese were members of the East Asian race, whereas the Germans were members of the Caucasian race. Hence, we cannot exclude for certain, that genetic (and not cultural) differences between both groups are responsible for the differences in brain activity. If one wanted to investigate cultural differences and at the same time control for genetic differences, the ideal (but rare) subjects would have been Chinese (raised in China) and Germans who are of Chinese origin but born in Germany (and ideally raised by a German family) — and vice versa.

This matter is even more complicated though: as has been shown by Chiao and Blizinsky (2010), genetic differences are inextricably intertwined with cultural differences. However, in this study we concentrated on the effect of culture on brain activity, whereas it was not our aim to highlight the causes of cultural differences.

Conclusion

In summary, our brain imaging findings indicate that the interdependent lifestyle, which implies a relative high appreciation of harmony and lower anger acceptance, leads to less neuronal activity in regions responsible for the understanding of social intentions (inferior and superior temporal gyrus, middle insula) during intentional empathy with angry faces.

High ratings of 'personal distress' explained high activity in the dorsolateral prefrontal cortex during intentional empathy with angry faces — probably as a means to prevent emotional over-arousal.

Our findings are in concordance with previous behavioral studies and provide a neurobiological basis for the observed cultural differences between interdependent and independent cultures in their handling with anger.

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