Neural Signatures of Fairness-Related Normative Decision Making in the Ultimatum Game: A Coordinate-Based Meta-Analysis

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Abstract: The willingness to incur personal costs to enforce prosocial norms represents a hallmark of human civilization. Although recent neuroscience studies have used the ultimatum game to understand the neuropsychological mechanisms that underlie the enforcement of fairness norms; however, a precise characterization of the neural systems underlying fairness-related norm enforcement remains elusive. In this study, we used a coordinate-based meta-analysis on functional magnetic resonance imaging (fMRI) studies using the ultimatum game with the goal to provide an additional level of evidence for the refinement of the underlying neural architecture of this human puzzling behavior. Our results demonstrated a convergence of reported activation foci in brain networks associated with psychological components of fairness-related normative decision making, presumably reflecting a reflexive and intuitive system (System 1) and a reflective and deliberate system (System 2). System 1 (anterior insula, ventromedial prefrontal cortex [PFC]) may be associated with the reflexive and intuitive responses to norm violations, representing a motivation to punish norm violators. Those intuitive responses conflict with economic self-interest, encoded in the dorsal anterior cingulate cortex (ACC), which may engage cognitive control from a reflective and deliberate System 2 to resolve the conflict by either suppressing (ventrolateral PFC, dorsomedial PFC, left dorsolateral PFC, and rostral ACC) the intuitive responses or over-riding self-interest (right dorsolateral PFC). Taken together, we suggest that fairness-related norm enforcement recruits an intuitive system for rapid evaluation of norm violations and a deliberate system for integrating both social norms and self-interest to regulate the intuitive system in favor of more flexible decision making. *Hum Brain Mapp 36:591–602, 2015.* © 2014 Wiley Periodicals, Inc.

INTRODUCTION

Humans comply with social norms (e.g., equity and fairness pertaining to resource distribution) and they are willing to punish norm violators at the expense of personal costs [Fehr and Fischbacher, 2004; Fehr and Gächter, 2002]. This costly norm enforcement termed altruistic punishment is a hallmark of human culture and plays a key role in promoting widespread cooperation among genetically unrelated strangers in human societies [Fehr et al., 2002; Henrich et al., 2006]. Humans develop preferences for social norms as early as 7–8 year old [Fehr et al., 2008; Güroğlu et al., 2011; Steinmann et al., 2014] and maintain those prosocial preferences across lifespan [Harlé and Sanfey, 2012; Roalf, 2010].

A common, widely used research approach to probe human social norm enforcement is the employment of well-structured interactive economic games [Camerer, 2003; Fehr and Camerer, 2007; Sanfey, 2007]. For example, during the one-shot interaction in the ultimatum game (UG) [Güth et al., 1982], two players must assent to split of a sum of money or both get nothing. The first player (proposer) offers a way to divide the sum between the two players and the second player (responder) can either accept (both get paid accordingly) or reject (neither gets paid) the offer. Responders perceive fair offers (i.e., norm compliance) as rewards and simply accept those offers [Tabibnia and Lieberman, 2007; Tabibnia et al., 2008]. When responders are treated fairly, brain regions engaged in reward processing such as ventromedial prefrontal cortex (vmPFC) or striatum are involved [Baumgartner et al., 2011; Fliessbach et al., 2007; Guo et al., 2014; Tabibnia et al., 2008; Wu et al., in press].

In contrast, unfair offers (i.e., norm violation) induce motivational conflict between economic self-interest and norm enforcement: responders are tempted to accept those offers for monetary reward, whereas they are also motivated by prosocial preferences to reject those offers [Fehr and Camerer, 2007]. Researchers from various research disciplines are interested in studying the neuropsychological mechanisms underlying the reconciling of different motivations in response to norm violations. For example, previous studies have indicated that responders reject unfair offers at about 50% chance and punish proposers who violate fairness norms by offering less than 20%–30% of the sum [Camerer, 2003; Güth et al., 1982], demonstrating human willingness to incur personal cost to enforce social norms.

Early models addressing human social preferences in fairness-related norm enforcement have postulated the significant roles of inequality aversion [Fehr and Schmidt, 1999] and intention inference [Blount, 1995; Rabin, 1993].

In recent decades, those initial theoretical models have been extensively elaborated due to interdisciplinary studies in the fields of psychology, economics, and neuroscience [Rilling and Sanfey, 2011; Sanfey et al., 2006]. Recent evidence revealed that fairness-related norm enforcement in response to norm violations (as measured in UG) consists of multiple psychological components that are implemented by separable neural systems [Buckholtz and Marois, 2012; Sanfey and Chang, 2008], including a reflexive and intuitive system (System 1) and a reflective and deliberate system (System 2) [Lieberman, 2007; Sanfey et al., 2006].

In terms of UG, System 1 is thought to represent psychological components involved in the initial evaluations of norm violations, including brain areas such as the anterior insula (AI) signaling norm violations [Civai, 2013] or emotional processing via representations of (especially aversive) internal states [Chang and Sanfey, 2013; Corradi-Dell'Acqua et al., 2013; Guo et al., 2013; Sanfey et al., 2003], the amygdala signaling transient negative emotional response to norm violations [Gospic et al., 2011; Haruno and Frith, 2010; Haruno et al., 2014; Yu et al., 2014] and the vmPFC encoding subjective values of perceived offers [Baumgartner et al., 2011; Dawes et al., 2012; Xiang et al., 2013]. Those intuitive responses to norm violations contribute to altruistic punishments of transgressions [Gospic et al., 2011; Sanfey et al., 2003], supporting the notion that reflexive and emotional responses implemented by System 1 lie at the core of human prosocial preferences [Haidt, 2001; Roch et al., 2000; Sanfey and Chang, 2008; Scheele et al., 2012; Zaki and Mitchell, 2011, 2013].

System 2 presumably represents more deliberate psychological components responsible for reappraising and regulating System 1 in favor of either economic self-interest [Brüne et al., 2012; Sanfey and Chang, 2008] or enforcement of social norms (e.g., fairness) [Fehr and Camerer, 2007]. The unfairness-evoked aversive responses (norm enforcement) and self-interest (due to the possibility to gain the monetary reward) contradict each other and result into a motivational conflict that is monitored by the dorsal anterior cingulate cortex (dACC) [Fehr and Camerer, 2007; Sanfey et al., 2003]. This conflict can be resolved in two ways: on the one hand, the reflexive reactions of System 1 can be suppressed, probably implemented by brain regions associated with emotion regulation such as ventrolateral prefrontal cortex (vlPFC) and dorsomedial PFC (dmPFC), leading to an increased acceptance of unfair offers [Civai et al., 2012; Grecucci et al., 2013; Tabibnia et al., 2008]. On the other hand, the conflict can be also reconciled by over-riding economic self-interest, likely manifested as executive control in the right dorsolateral PFC (dlPFC) [Baumgartner et al., 2011;

TABLE I. Summary of studies included for the meta-analysis focusing on the responder in UG

Study	N	Task and contrast	No. of foci
Fair Offer			
Baumgartner et al. [2011]	32	Responders in UG, fair>unfair	4
Civai et al. [2012]	19	Responders in a modified UG/DG, equal>unequal	3
Harlé and Sanfey.[2012]	38	Responders in UG, fair>unfair	3
Roalf [2010]	27	Responders in UG, fair>unfair	2
Tabibnia et al. [2008]	12	Responders in UG, fair>unfair	1
Tomasino et al. [2013]	17	Responders in UG, fair>unfair	3
White et al. [2013]	20	Responders in UG, parametric analysis, negative correlation with unfairness level	1
White et al. [2014]	21	Responders in UG, parametric analysis, negative correlation with unfairness level	3
Wright et al. [2011]	30	Responders in UG, parametric analysis, negative correlation with inequity	10
Wu et al. [in press]	18	Responders in UG, parametric analysis, positive correlation with subjective utility	4
Zhou et al. [2014]	28	Responders in UG, fair>unfair	1
Unfair Offer			
Baumgartner et al. [2011]	32	Responders in UG, unfair>fair	17
Civai et al. [2012]	19	Responders in a modified UG/DG, unequal>equal	12
Haruno et al. [2014]	62	Responders in UG, parametric analysis, positive correlation with inequity.	4
Gospic et al. [2011]	17	Responders in UG, unfair>fair	4
Guo et al. [2014]	18	Responders in UG, unfair>fair	10
Guo et al. [2013]	21	Responders in UG, unfair>fair	13
Güroğlu et al. [2011]	68	Responders in UG, unfair>fair	9
Halko et al. [2009]	23	Responders in UG, unfair>fair	22
Harlé and Sanfey. [2012]	38	Responders in UG, unfair>fair	12
Kirk et al. [2011]	40	Responders in UG, unfair>fair	11
Roalf [2010]	27	Responders in UG, unfair>fair	8
Sanfey et al. [2003]	19	Responders in UG, unfair>fair	17
White et al. [2013]	20	Responders in UG, parametric analysis, positive correlation with unfairness level	8
White et al. [2014]	21	Responders in UG, parametric analysis, positive correlation with unfairness level	7
Wu et al. [in press]	18	Responders in UG, parametric analysis, negative correlation with subjective utility	7
Zheng et al. [in press]	25	Responders in UG, unfair>fair	15
Zhou et al. [2014]	28	Responders in UG, unfair>fair	4

N, number of subjects

Knoch et al., 2006, 2008]. Overall, System 2 may contribute to detect and reconcile the motivational conflict between norm enforcement and self-interest in favor of flexible decision making.

Recent neuroscientific studies have begun examining the neural signatures of isolated components of the fairness-related norm enforcement and a couple of descriptive reviews have explored the biological basis of human normative decision making from a larger perspective [Buckholtz and Marois, 2012; Rilling and Sanfey, 2011; Ruff and Fehr, 2014]. However, a precise characterization of the neural systems underlying fairness-related norm enforcement remains elusive. In this study, we used a coordinate-based meta-analysis on fMRI studies using the UG with the goal to provide an additional level of evidence for the refinement of the underlying neural architecture of fairness-related norm enforcement. We expect that enforcement of social norms in the UG recruits multiple brain regions, which have been previously separated into two interacting neural systems [Buckholtz and Marois, 2012; Sanfey and Chang, 2008]: (i) a reflexive and intuitive system (System 1: AI, amygdala, and vmPFC) for recognizing and evaluating norm violations and (ii) a deliberate system (System 2: dACC, dlPFC, vlPFC, and dmPFC) for reappraising and regulating System 1 in favor of either economic self-interest or norm enforcement.

TABLE II. ALE meta-analysis results for fair offers (fair > unfair contrast)

| Brain regions | BA | MNI coordinates (mm) | | | ALE ($\times 10^{-2}$) | Cluster size (mm^3) |
		x	y	z		
vmPFC/vACC	32/10	6	46	−12	0.97	2736
R vACC	32	6	46	−12	0.97	
L vmPFC	10	−2	54	−12	0.97	
R vmPFC	10	6	52	−16	0.89	
L posterior insula/STG	13/22	−54	−12	6	0.92	1688
L STG	22	−54	−12	6	0.92	
L posterior insula	13	−40.5	−15	1.5	0.89	
L PCC	23	−8	−58	16	1.08	1192
L PCC	23	−8	−58	16	1.08	
R posterior insula	13	42	−24	24	0.92	952
R posterior insula	13	42	−24	24	0.92	
L precuneus	7	−8	−59	56	0.80	912
L precuneus	7	−8	−59	56	0.80	
R ITG	20	60	−48	−12	0.93	648
R ITG	20	60	−48	−12	0.93	

BA, Brodmann area; L, left; R, right; ALE, activation likelihood estimation; vmPFC, ventromedial prefrontal cortex; vACC, ventral anterior cingulate cortex; STG, superior temporal gyrus; PCC, posterior cingulate cortex: ITG, inferior temporal gyrus

MATERIAL AND METHODS

Literature Search and Selection

We performed a systematic online database search in July of 2014 on PubMed and ISI Web of Science by entering various combinations of relevant search items (e.g., ["normative decision making" OR "fair" OR "altruistic punishment" OR "ultimatum game"] AND ["fMRI" OR "magnetic resonance imaging" OR "neuroimaging"]) and conducted a follow-up search by examining the bibliography and citation indices of the preselected articles. The search resulted into 53 potential studies that were further assessed according to the following criteria: (i) subjects were recruited as responders in UG: (ii) fMRI was used as the imaging modality; (iii) whole-brain general-linear-model-based analyses (rather than region of
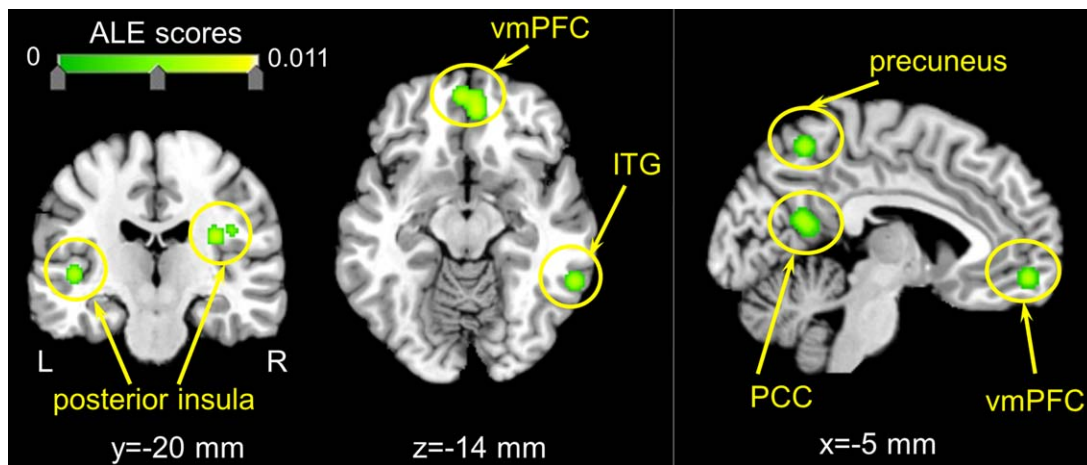
Figure 1.

Significant clusters from the coordinate-based activation likelihood estimation (ALE) meta-analysis (5,000 permutations, q(FDR) < 0.05, min. volume of 600 mm³) for fair offers (fair->unfair contrast). Consistent maxima comparing fair with unfair offers in UG were found in posterior insula, ventromedial pre- frontal cortex (vmPFC), inferior temporal gyrus (ITG), precun- ceus, and posterior cingulate cortex (PCC). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE III. ALE meta-analysis results of unfair offers (unfair > fair contrast)

Brain regions	BA	MNI coordinates (mm)			ALE ($\times 10^{-2}$)	Cluster size (mm^3)
		x	y	z		
dACC/pre-SMA	32/6	−4	16	48	2.59	14168
L dACC	32	−4	16	48	2.59	
R dACC	32	8	22	40	2.35	
L pre-SMA	6	−6	2	64	0.97	
R pre-SMA	6	10	24	58	1.46	
R AI/putamen/vlPFC	13/47	38	20	0	3.10	9456
R AI	13	38	20	0	3.10	
R putamen	/	22	12	2	0.96	
R vlPFC	47	34	21	−18	0.62	
L AI/vlPFC	13/47	−30	24	2	2.79	7376
L AI	13	−30	24	2	2.79	
L vlPFC	47	−44	24	−8	1.00	
R dlPFC: R middle frontal gyrus/SFG	9/8	40	36	26	1.95	3768
R middle frontal gyrus	9	40	36	26	1.95	
R SFG	8	38	22	48	0.82	
R dlPFC: R middle frontal gyrus/SFG	10	30	66	2	1.55	1272
R SFG	10	30	66	2	1.55	
R middle frontal gyrus	10	30	64	12	1.22	
R dlPFC: SFG/middle frontal gyrus	9/10	26	48	22	1.05	664
R SFG	9	26	48	22	1.05	
R middle frontal gyrus	10	34	48	18	0.87	
L dlPFC: L middle frontal gyrus	9/8	−30	38	30	1.03	1016
L middle frontal gyrus	9	−30	38	30	1.03	
L middle frontal gyrus	8	−36	40	38	0.88	
L dlFPC: SFG	9	−20	54	30	0.94	648
L SFG	9	−20	54	30	0.94	
R dmPFC	9	8	60	16	1.06	1024
R dmPFC	9	8	60	16	1.06	
R dmPFC	9	4	54	26	0.97	680
R dmPFC	9	4	54	26	0.97	
L rACC/medial PFC	10/32	−12	46	4	0.92	616
L medial PFC	10	−12	46	4	0.92	
L rACC	32	−7	47	4	0.31	
L IPL	40	−32	−46	42	0.93	1136
L IPL	40	−32	−46	42	0.93	
L IPL	40	−44	−46	52	1.24	816
L IPL	40	−44	−46	52	1.24	
L pSTG	22	−48	−40	4	0.91	632
L pSTG	22	−48	−40	4	0.91	
L STG/ATL	22	−52	−16	−8	1.03	664
L STG/ATL	22	−52	−16	−8	1.03	
R precuneus	7	14	−68	40	0.96	664
R precuneus	7	14	−68	40	0.96	
L fusiform gyrus	19	−44	−72	−8	1.07	672
L fusiform gyrus	19	−44	−72	−8	1.07	
R lingual gyrus	18	10	−80	0	0.98	672
R lingual gyrus	18	10	−80	0	0.98	

BA, Brodmann area; L, left; R, right; ALE, activation likelihood estimation; dACC, dorsal anterior cingulate cortex; pre-SMA, pre-supplementary motor area; AI, anterior insula; vlPFC, ventrolateral prefrontal cortex; SFG, superior frontal gyrus; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; rACC, rostral anterior cingulate cortex; IPL, inferior parietal lobule; pSTG, posterior superior temporal gyrus; ATL, anterior temporal lobe.
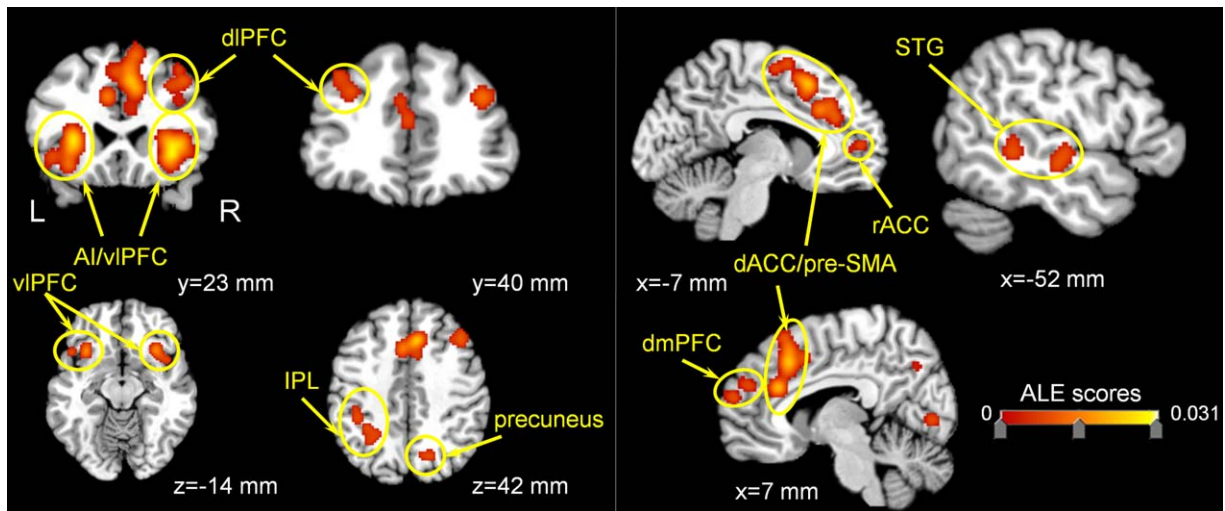
Figure 2.

Significant clusters from the coordinate-based activation likelihood estimation (ALE) meta-analysis (5,000 permutations, q(FDR) < 0.05, min. volume of 600 mm³) for unfair offers (unfair > fair contrast). Consistent maxima comparing unfair with fair offers in UG were found in dorsolateral prefrontal cortex (dlPFC), anterior insula (AI), ventrolateral PFC (vlPFC), infe-rior parietal lobule (IPL), precuneus, dorsal anterior cingulate cortex/presupplementary motor area (dACC/pre-SMA), rostral ACC (rACC), dorsomedial PFC (dmPFC), and superior temporal gyrus (STG). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

interest [ROI] analyses) were applied; (iv) statistical models for fairness-related contrasts (i.e., fair > unfair or unfair > fair) or relevant parametric analyses were reported; and (v) activations were presented in a standardized stereotaxic space (Talairach or MNI). Note that for studies reporting Talairach coordinates a conversion to the MNI coordinates was implemented [Brett, 1999]. Filtering search results according to the inclusion/exclusion criteria yielded a total of 20 published fMRI articles with 17 "unfair > fair" contrasts (180 foci) and 11 "fair > unfair" contrasts (35 foci) reported in a standardized stereotaxic space (Table I).

Activation Likelihood Estimation *Approach*

A coordinate-based meta-analysis of reported fMRI experiments was conducted using the revised activation likelihood estimation (ALE) algorithm [Eickhoff et al., 2009] implemented in the GingerALE software (version 2.3, http://www.brainmap.org/ale/). Applying the ALE algorithm, the reported coordinates of brain areas associated with fairness-related norm enforcement were converged across different experiments. A random-effects analysis was performed to determine statistical significance using a permutation test of randomly generated foci with 5,000 permutations (full-width at half-maximum of 10 mm) [Eickhoff et al., 2012; Turkeltaub et al., 2012]. The resulting ALE maps were thresholded using the false discovery rate (FDR, q(FDR) < 0.05) correction for multiple comparisons [Genovese et al., 2002; Laird et al., 2005] and

all clusters were set to a minimum volume of 600 mm³ [Lamm et al., 2011]. The meta-analysis results were overlaid onto an anatomical template (Colin27_T1_seg_MNI.nii, www.brainmap.org/ale) and displayed using the Mango software (http://rii.uthscsa.edu/mango/).

RESULTS

Consistent maxima were found in the following brain regions comparing fair with unfair offers in UG: bilateral vmPFC and posterior insula, left posterior cingulate cortex (PCC) and precuneus, and right inferior temporal gyrus (ITG; Table II and Fig. 1). Comparing unfair with fair offers in UG, consistent maxima were found in the following brain regions: bilateral dACC/pre-supplementary motor area (pre-SMA), AI/vlPFC and dlPFC, left rostral ACC (rACC), posterior superior temporal gyrus (pSTG), STG/anterior temporal lobe (ATL), inferior parietal lobule (IPL) and fusiform gyrus, right dmPFC, precuneus, and lingual gyrus (Table III and Fig. 2). The AI clusters revealed in this contrast were primarily located in subregion of the dorso-AI, according to Kelly et al.'s (2012) templates of insular subregions (Fig. 3).

DISCUSSION

The willingness to incur personal costs to enforce prosocial norms represents a hallmark of human civilization. Recent neuroscience studies have used UG to understand
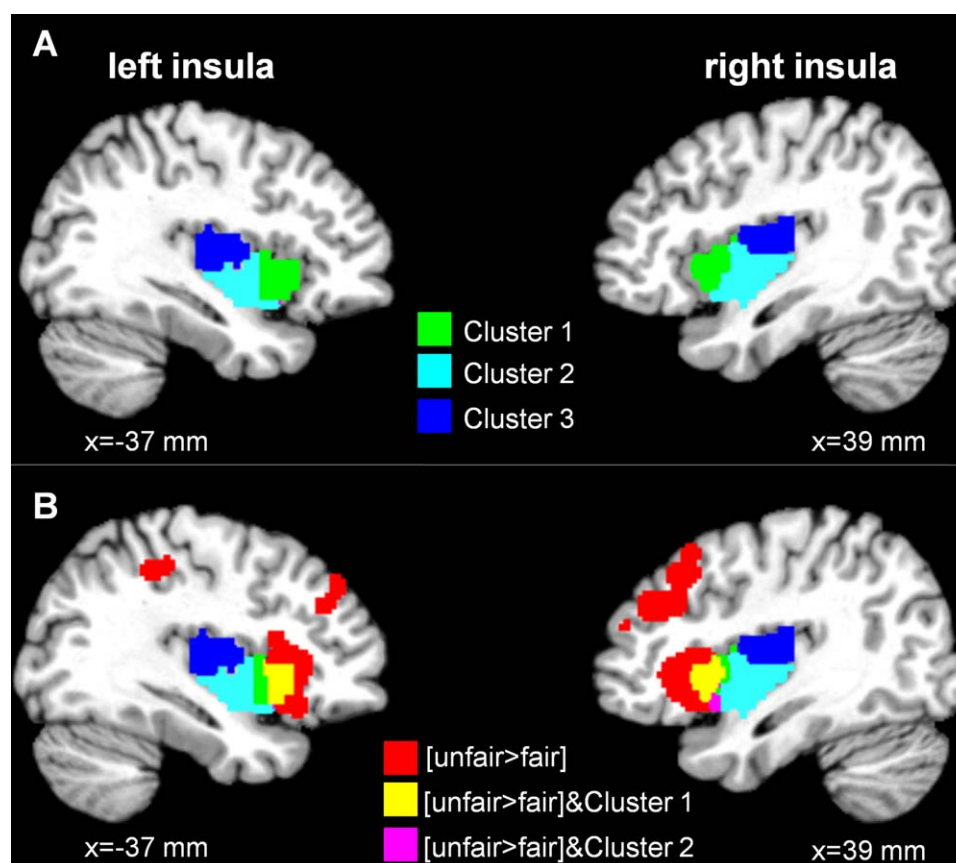
Figure 3.

Subregions of insular cortex. (**A**) Insular subregions (Cluster 1 [green]: dorsoanterior insula, Cluster 2 [cyan]: ventroanterior insula, Cluster 3 [blue]: posterior insula) according to Kelly et al.'s template ($K = 3$ solutions). (**B**) Significant clusters from the coordinate-based ALE (activation likelihood estimation) for unfair offers (red: unfair > fair contrast) and overlaps between those clusters and different insular subregions intersected by Kelly et al.'s template (yellow: intersection of clusters from ALE analysis for unfair offers and dorsoanterior insula; reddish yellow: intersection of clusters from ALE analysis for unfair offers and ventroanterior insula). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the neuropsychological mechanisms that underlie enforcement of fairness-related norms [Fehr and Camerer, 2007; Sanfey, 2007]. The purpose of this coordinate-based meta-analysis study was to quantitatively synthesize the results of recent fMRI studies regarding fairness-related norm enforcement with the aim of identifying consistent activation patterns of the neural signatures underlying this human puzzling behavior. Our results demonstrated a convergence of reported activation foci in brain networks associated with normative decision making [Buckholtz and Marois, 2012; Krueger et al., 2008; Rilling and Sanfey, 2011; Sanfey and Chang, 2008], and these brain regions have been thought to represent two interacting neural systems [Buckholtz and Marois, 2012; Sanfey and Chang, 2008]: a reflexive and intuitive system (System 1) for recognizing and evaluating norm violations and a deliberate system (System 2) for integrating both social norms and

economic self-interest to regulate System 1 in favor of flexible decision makings.

In UG, the responder has to decide whether to accept or to reject fair or unfair offers from proposers. Regarding fair offers, previous findings have indicated that those offers are considered as rewards [Harlé et al., 2012; Tabibnia and Lieberman, 2007; Tabibnia et al., 2008]. Accordingly, the vmPFC, a core region associated with reward processing showed consistent activation across fMRI studies in response to fair offers compared to unfair offers. Presumably, the vmPFC is associated with computing positive values of fairness, owning to its role in representing values of normatively valued goods [Aoki et al., 2014; Moretti et al., 2009; Tricomi et al., 2010]. In accord with this view, the activation of vmPFC to fair offers remains after controlling for momentary payoff [Tabibnia et al., 2008].

The meta-analysis also revealed the consistent involvement of the posterior insula in response to fair offers, which is consistent with its role in coding fairness or equality [Hsu et al., 2008; Wright et al., 2011]. Moreover, involvement of the PCC was identified, which role in reward processing has also been demonstrated in previous studies [Ballard and Knutson, 2009; Levy and Glimcher, 2011; McClure et al., 2007], but it remains unknown whether this region encodes the positive value of fairness or just the monetary payoff in UG. By contrast, the meta-analysis did not reveal consistent activation of the ventral striatum in response to fairness, since most of the previous studies reporting a ventral striatum response to fairness applied an ROI analysis approach [Tabibnia et al., 2008; Tricomi et al., 2010; Wu et al., in press].

Responders in UG react to unfair offers with negative emotional feelings, which are thought to play a pivotal role in costly punishment/norm enforcement [Koenigs and Tranel, 2007; Pillutla and Murnighan, 1996; Van't Wout et al., 2006; White et al., 2014; Xiao and Houser, 2005; Yamagishi et al., 2009]. Our meta-analysis revealed that brain regions of System 1 such as bilateral AI were consistently involved in those intuitive and reflexive responses [Sanfey and Chang, 2008; Sanfey et al., 2003]. The AI may be associated with the visceral experience of negative feelings by signaling aversive interoceptive states due to fairness-related norm violations [Critchley et al., 2004; Singer et al., 2009]. Previous studies using the UG have shown that emotion infusion [Harlé et al., 2012; Harlé and Sanfey, 2007] and emotion regulation [Grecucci et al., 2013] modulate the unfairness-evoked AI responses, which predict normative decision making at the behavioral level [Harlé et al., 2012; Kirk et al., 2011; Sanfey et al., 2003; Tabibnia et al., 2008]. However, recent studies have indicated that unfairness-evoked negative feelings cannot completely account for the activation of AI [Civai, 2013], because neural response to norm violations in the AI is also evident when participants play a role of indifferent third-party [Civai et al., 2012; Strobel et al., 2011] and when unfair offers are better than expectations [Xiang et al., 2013; Yu et al., 2014]. Furthermore, recent evidence has demonstrated a functional heterogeneity of different AI subregions related to norm violations in UG [Zhou et al., 2014]. In particular, a tripartite subdivision of the insula has been proposed with dorsoanterior, ventroanterior, and posterior portions contributing to cognitive, affective, and sensorimotor processing, respectively [Chang et al., 2013; Kelly et al., 2012]. Recent evidence suggests that the dorsal AI associated with cognition is consistently activated by norm violation in most of previous neuroimaging studies using UG [Zhou et al., 2014]. In lights of these recent findings, it is more likely that the consistent activation of primarily dorsal AI represents a cognitive heuristic to detect norm violations rather than emotional resentment [Civai, 2013; Civai et al., 2010, 2012, 2013].

The emotion processing in response to norm violations may be implemented by other brain regions, including vmPFC and amygdala, both of which are frequently associated with social decision making and affective processing [Buckholtz and Marois, 2012; Buckholtz et al., 2008; Gospic et al., in press]. As discussed above, numerous studies have revealed the role of vmPFC in tracking the positive and negative values/feelings of goods [Grabenhorst and Rolls, 2011; O'Doherty, 2004], including normatively valued goods such as equality [Baumgartner et al., 2011; Tricomi et al., 2010]. Therefore, the lower activation (and often deactivation) of vmPFC in response to unfair offers may reflect negative feelings to norm violations, a viewpoint supported by the correlation between subjective feelings of offers and vmPFC activation [Xiang et al., 2013].

The amygdala is thought to reflect the early and transient emotional response to norm violations, and the failure to detect a consistent activation of this region in the meta-analysis may be attributed to the coarse onset timing used in most studies [Gospic et al., 2011]. Nevertheless, recent studies have revealed the crucial role of this area in social preferences. For example, amygdala activation to unfair offers predicts individual differences in social preferences for equitable outcomes [Haruno and Frith, 2010; Haruno et al., 2014] and willingness to enforce social norms [Gospic et al., 2011; Yu et al., 2014]. Moreover, Gospic et al. [2011] demonstrated a causal role of amygdala in the norm enforcement by showing that pharmacological attenuation of amygdala response led to decreased costly punishment in UG.

Economic self-interest constitutes another essential motivation in UG and conflicts with the intuitive response mediated by System 1 [Sanfey and Chang, 2008; Sanfey et al., 2006]. The meta-analysis identified the dACC—a key region of System 2—in response to norm violations. Based on the role of the dACC in conflict monitoring [Botvinick et al., 2001, 2004], this region presumably monitors the conflict between economic self-interest and intuitive response to norm violations and signals the need to resolve it [Fehr and Camerer, 2007; Sanfey et al., 2003]. Previous evidence revealed that the neural response to norm violations in dACC is evident only when self-interest is involved in norm enforcement [Civai et al., 2012] and the response is stronger for those responders who are more prone to self-interest, and therefore, experience larger conflicts [Güroğlu et al., 2010, 2011; Xiang et al., 2013; Zhou et al., 2014]. However, other potential suggested functions of dACC in the context of UG, such as detection of norm violations [Chang and Sanfey, 2013; Güroğlu et al., 2010; White et al., 2013], emotion appraisal [Etkin et al., 2011; Harlé et al., 2012], and cognitive control [Grecucci et al., 2013; Kerns et al., 2004] have not been well dissociated and are worth elaborating in future studies.

On the one hand, the motivational conflict encoded in the dACC may be resolved by regulating/suppressing the reflexive response of System 1 [Rilling and Sanfey, 2011; Sanfey and Chang, 2008]. Our meta-analysis identified potential brain regions recruited in favor of the acceptance of unfair offers, including vlPFC [Halko et al., 2009;

Tabibnia et al., 2008], rACC [Yu et al., 2014], left dlPFC [Güroğlu et al., 2011; Harlé and Sanfey, 2012], and dmPFC [Grecucci et al., 2013], all of which are generally involved in emotion regulation or cognitive reappraisal [Buhle et al., in press; Etkin et al., 2006; Ochsner et al., 2012; Silvers et al., 2013]. Specifically, the vlPFC may exert top-down control in regulating AI activity [Tabibnia et al., 2008] by accessing conceptual knowledge represented in the lateral temporal areas as an intermediary to reinterpret the meaning of a situation, which then feeds forward the reinterpreted representation to dorsal AI as a target region of System 1 [Silvers et al., 2013]. The rACC is associated with resolving emotional conflict through top-down inhibition of amygdala activation [Etkin et al., 2006, 2011]. For example, Yu et al. [2014] observed that rACC suppresses amygdala-mediated negative emotional response to norm violations, and this coupling between rACC and amygdala predicts attenuated costly punishment. Furthermore, the modulations of left dlPFC on amygdala and vmPFC have been reported in the literature of reappraisal-relevant emotion regulation [Ochsner et al., 2012], and the left dlPFC may be recruited together with inferior parietal regions to direct attention to reappraisal-relevant events and maintain reappraisal goals [Ochsner et al., 2012; Silvers et al., 2013]. Finally, given the role of dmPFC in overtly thinking about the internal mental states of others (i.e., mentalizing) [Frith and Frith, 2003; Lieberman, 2007], this region probably supports selective attention to and elaboration of intentions of proposers in UG [Frith and Singer, 2008; Rilling et al., 2004].

On the other hand, the motivational conflict between self-interest and fairness norm enforcement could also be resolved by over-riding temptations of self-interest in favor of the rejection of unfair offers. The right dlPFC as identified in the meta-analysis has been previously associated with this cognitive mechanism of System 2 [Knoch and Fehr, 2007]. Previous evidence showed that activation of right dlPFC in UG is positively correlated with altruistic punishment behavior [Guo et al., 2014; Roalf, 2010; Zheng et al., in press]. Importantly, disruption of the right dlPFC due to transcranial magnetic stimulation or cathodal transcranial direct current stimulation diminishes the enforcement of fairness norms in UG, providing evidence for a causal role of the right dlPFC in enforcing social norms [Knoch et al., 2006, 2008; Van't Wout et al., 2005].

Besides the role of cognitive control implemented by the prefrontal and cingulate cortex (System 2), an alternative account proposes that these brain areas may contribute to integrating different sources of information (e.g., expectations) and optimizing response selection in specific social contexts [Buckholtz and Marois, 2012; Sanfey et al., 2014]. The "integration-and-selection" hypothesis is consistent with recent findings showing that functions served by System 2 are context-dependent [Grecucci et al., 2013; Ruff et al., 2013]. For instance, brain stimulation of right dlPFC caused opposite effects on norm compliance under different social contexts: it enhances the compliance of social norms in the context of potential sanctions but attenuates voluntary norm compliance [Ruff et al., 2013].

Taken together, normative decision making in the UG may engage two separable but interacting neural systems. System 1 (AI and vmPFC) may be associated with the reflexive and intuitive responses to norm violations, representing a motivation to punish the violators. Those intuitive responses conflict with economic self-interest, resulting into a conflict signal encoded by the dACC, which may activate cognitive control from a reflective and deliberate System 2 to resolve the conflict by either suppressing (vlPFC, rostral ACC, dmPFC, and left dlPFC) the intuitive responses of System 1 or over-riding self-interest (right dlPFC).

Several limitations should be noted as they relate to this meta-analysis. First, like most neuroimaging meta-analysis methods, the procedures of the ALE meta-analysis consider only the reported coordinates and number of subjects from each study, but not other potential mediator variables (e.g., fMRI-scanning and data-analysis parameters) that are different between studies and may influence final results. Second, the number of papers used in this meta-analysis was relatively small (especially for the [fair > unfair] contrast), but statistical power for interpretation of results will increase for future meta-analyses due to an accumulating number of neuroimaging studies on human normative decision making. In addition, because of the limited number of studies in this domain, it allowed us only to perform a basic contrast between unfair and fair but not moderator analyses (e.g., contextual factors and individual differences), which might have been helpful in differentiating the reflexive and reflective systems. Third, the potential functions of brain regions involved in fairness-related norm enforcement were evaluated in the context of evidence from neuroscientific studies in the past decades, but the specific functions of many brain areas remain to be clarified. For example, the potential functions of dACC in UG have been rarely dissociated in previous studies, although this brain region constitutes the most consistent reported cluster in this meta-analysis. Furthermore, to the best of our knowledge, no study has yet provided evidence for a causal role of AI in costly punishment, although many researchers have considered that psychological components mediated by this region play a pivotal role in norm enforcement. Finally, this study identified Systems 1 and 2 involved in the normative decision making; however, the interactions between these neural systems remain to be elucidated. Future functional and effective connectivity fMRI studies applying the UG are necessary to investigate the temporal and causal relationships among regions, which would provide a more comprehensive picture of human norm enforcement.

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