



Review article

Neural signatures of social conformity: A coordinate-based activation likelihood estimation meta-analysis of functional brain imaging studies



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ABSTRACT

People often align their behaviors with group opinions, known as social conformity. Many neuroscience studies have explored the neuropsychological mechanisms underlying social conformity. Here we employed a coordinate-based meta-analysis on neuroimaging studies of social conformity with the purpose to reveal the convergence of the underlying neural architecture. We identified a convergence of reported activation foci in regions associated with normative decision-making, including ventral striatum (VS), dorsal posterior medial frontal cortex (dorsal pMFC), and anterior insula (AI). Specifically, consistent deactivation of VS and activation of dorsal pMFC and AI are identified when people's responses deviate from group opinions. In addition, the deviation-related responses in dorsal pMFC predict people's conforming behavioral adjustments. These are consistent with current models that disagreement with others might evoke "error" signals, cognitive imbalance, and/or aversive feelings, which are plausibly detected in these brain regions as control signals to facilitate subsequent conforming behaviors. Finally, group opinions result in altered neural correlates of valuation, manifested as stronger responses of VS to stimuli endorsed than disliked by others.

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1. Introduction

Human preferences, judgments, and attitudes are highly sensitive to social influence, such that people often adjust their behaviors to match the responses of others (Cialdini and Goldstein, 2004; Wood, 2000). One of the most basic and best-known forms of social influence is the human conformity behavior initially reported in the seminal work of Solomon Asch (Asch, 1951, 1956), wherein participants were asked to judge relative lengths of lines alone or in the presence of confederates posing as other subjects. Participants invariably gave the correct answer when they performed the task alone. Importantly, however, about 37% of participants conformed to the erroneous judgments of confederates in this simple task (Asch, 1951, 1956). Since these initial findings, social conformity has been identified in various tasks (e.g., Alquist et al., 2013; Gabbert et al., 2003; Koban and Wager, 2016). For instance, when there is a discrepancy between one's own and group's preferences or memories, people often subsequently change their responses to the same items to decrease the discrepancy (Campbell-Meiklejohn et al., 2010; Edelson et al., 2011; Izuma and Adolphs, 2013; Klucharev et al., 2009b). Those behavioral adjustments induced by normative opinions have been thought to be driven by two separate and interacting motivations (Allen, 1965; Kelman, 1961; Peterson et al., 1985): (i) mere public compliance, i.e., agreeing with others on the surface while maintaining one's intrinsic attitudes (e.g., Berns et al., 2010); or (ii) private acceptance, i.e., internalizing the preferences, judgments, and attitudes of others (e.g., Huang et al., 2014; Nook and Zaki, 2015).

Building on the extensive behavioral research in the social psychology literature, the past decade has witnessed a surge of interest in unveiling the neural mechanisms of social influence (e.g., Berns et al., 2005; Campbell-Meiklejohn et al., 2012a; Chen et al., 2012; Chua et al., 2011; Edelson et al., 2011; Izuma and Adolphs, 2013; Klucharev et al., 2009b; Klucharev et al., 2008; Shestakova et al., 2013). The neuroscientific approach provides additional level of evidence in validating psychological theories of social influence. For instance, as the first study to examine the neural mechanisms underlying social conformity, Berns et al. (2005) demonstrated that human conforming behaviors were paralleled by altered perceptual representations of visual stimuli in an occipital–parietal network. Likewise, social influence leads to long-lasting alterations in people's memory via modifying neural mnemonic representations in the hippocampus and amygdala (Edelson et al., 2011; Edelson et al., 2014). Last but not least, many studies have indicated that the opinions of others change people's preferences and alter neural representations of value assigned to stimuli, manifested as the modulated engagement of ventral striatum (VS) and orbital frontal cortex (OFC) (Campbell-Meiklejohn et al., 2010; Charpentier et al., 2014; Zaki et al., 2011). These findings together suggest a possibility that people internalize judgments and preferences of other people; and therefore, are thought to support the account of private acceptance (but see Berns et al., 2010).

Furthermore, a plethora of neuroscientific studies on social conformity has examined the neural responses to the discrepancy between one's own and group opinions. In particular, the consensus between oneself and others in judgments recruits brain activations of VS that plays an important role in reward-driven behaviors (Campbell-Meiklejohn et al., 2010; Klucharev et al., 2009b). In contrast, the disagreement between oneself and others induces neural activations in the dorsal posterior medial frontal cortex (dorsal pMFC, comprising dorsal anterior cingulate cortex, posterior medial frontal cortex, and supplementary motor area) and anterior insula (AI) (Izuma and Adolphs, 2013; Klucharev et al., 2009b) that are implicated in encoding negative emotions (Corradi-Dell'Acqua et al., 2016; Lamm et al., 2011; Phan et al., 2002) and monitoring conflicts/errors (Garrison et al., 2013; Ridderinkhof et al.,

2004). Notably, disagreement-dependent neural responses of these regions are predictive of people's subsequent decisions to conform group opinions (Berns et al., 2010; Burke et al., 2010; Campbell-Meiklejohn et al., 2010; Huber et al., 2015; Klucharev et al., 2009b; Nook and Zaki, 2015; Prehn et al., 2014).

The involvement of dorsal pMFC and AI in detecting first-person experience of deviating from group norms in social conformity tasks complements previous observations that these regions are engaged by norm violations conducted by another person (Buckholtz and Marois, 2012; Rilling et al., 2008; Sanfey et al., 2003; Strobel et al., 2011). For instance, in the Ultimatum Game (UG), the first player (the Proposer) proposes how to divide the money; and the second player (the Responder) decides to accept (both get paid accordingly) or reject (neither gets paid) this proposal (Güth et al., 1982). In UG, the Responder usually compares the Proposer's decisions with a fairness norm (e.g., equality) and "corrects" deviations from social norms by rejecting the unfair proposals (Xiang et al., 2013). As such, the engagement of dorsal pMFC and AI has also been consistently identified when another person's behaviors deviate from social norms (Gabay et al., 2014; Sanfey et al., 2003). The common engagement of these regions in detecting norm violations independent of agents suggests a "generic" neural system consisting of dorsal pMFC and AI for detecting deviations from group norms to facilitate behavioral adjustments in line with normative opinions (see also Montague and Lohrenz, 2007; Tomlin et al., 2013; Xiang et al., 2013).

There are many explanations regarding specific functions of brain regions involved in the social conformity. For instance, the reinforcement learning (RL) account holds that the involvement of VS, dorsal pMFC, and AI reflects the detecting of general prediction errors (i.e., the differences between outcomes and expectations) that play a crucial role in guiding people's adaptive behaviors (Campbell-Meiklejohn et al., 2010; Klucharev et al., 2009b; Klucharev et al., 2011; Shestakova et al., 2013). In this regard, the consensus between oneself and others might be experienced as a rewarding outcome (Campbell-Meiklejohn et al., 2010; Nook and Zaki, 2015). In contrast, the conflicts between one's own responses and group norms might be detected as a negative prediction error which calls for the need to correct deviance from norms, i.e., aligning one's responses with normative opinions (see also Klucharev et al., 2009b; Montague and Lohrenz, 2007). Further, a "cognitive balance" account posits that the discrepancy between one's own and group opinions might be represented separately from general prediction errors (Izuma, 2013; Izuma and Adolphs, 2013). According to this account, deviations from normative opinions might specifically engage a subset of neurons in the dorsal pMFC, rather than share identical neuronal populations with general error signals in RL (Izuma and Adolphs, 2013). Lastly, some researchers have interpreted the engagement of dorsal pMFC and AI as physiological arousal and negative affective states in response to disagreement with group opinions (Berns et al., 2010). These interpretations are not necessary to be mutually exclusive, and while a meta-analysis will not allow for directly testing these accounts; we will discuss our findings in light of these models.

In this study, we employed a coordinate-based meta-analysis on fMRI studies utilizing conformity-related paradigms with the goal to identify regions most robustly involved in the following aspects of social conformity, which are often interested in the current literature: (i) the influence of group opinion on neural representation of subjective values assigned to stimuli in value-based tasks; (ii) the neural basis of agreement and disagreement between one's own and group opinions; and (iii) the associations between disagreement-dependent neural responses and conformity behaviors. Finally, by assessing correspondence across disagreement-related contrasts in social conformity tasks and unfairness-related contrasts in UG, the current meta-analysis

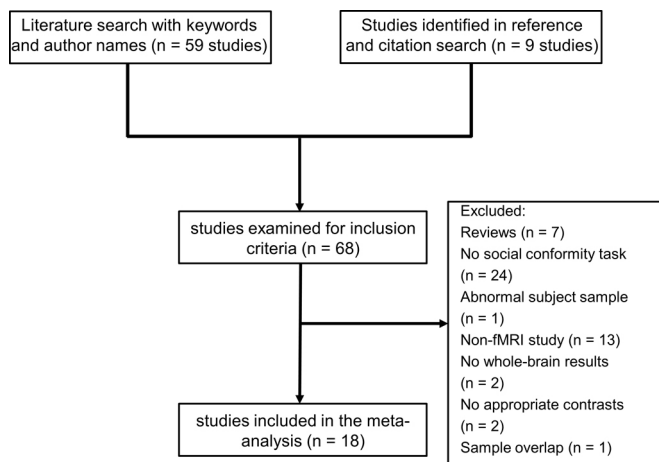


Fig. 1. Flow chart of the study selection process for the meta-analysis.

aimed to explore the common neural network involved in detecting deviations from group norms independent of agents.

2. Material and Methods

2.1. Literature search and selection

We performed a systematic online database search in June of 2016 on PubMed, ISI Web of Science, and Google Scholar by entering various combinations of relevant search items, including 'social conformity', 'confirming', 'herding', 'social influence', 'attitude', 'fMRI', 'magnetic resonance imaging', 'neuroimaging'. In addition, we explored several other sources, including (1) the bibliography and citation indices of the pre-selected articles and review papers, and (2) direct searches on the names of frequently occurring authors.

The search resulted in 68 potential publications that were further assessed according to the following inclusion criteria (Fig. 1). First, the publication reported at least one experimental study, i.e., not a review paper (e.g., Izuma, 2013). Second, the study employed a social conformity task, i.e., investigating the influence of group opinion on people's behaviors (Cialdini and Goldstein, 2004). Accordingly, studies focusing on the influence of a single individual were excluded (e.g., Meshi et al., 2012; Prehn et al., 2014; Stallen et al., 2013). Third, participants were free from psychiatric or neurological diagnoses and neuropharmacological influence. Please note that a group of marijuana users was recruited in Gilman et al.'s study (2016). This study was included in the current meta-analysis for following reasons: (i) the authors only selected recreational uses (i.e., light to moderate users) rather than substance-dependent individuals; (ii) the marijuana group was asked to refrain from using all substances on the day of the study; and (iii) there was no differences between controls and marijuana users in activation to agreeing or disagreeing with others (Gilman et al., 2016). Notably, excluding this study from the current meta-analysis did not produce any qualitative changes in the results (Table S5). Fourth, fMRI was used as the imaging modality. Fifth, whole-brain general-linear-model-based analyses (rather than only region of interest [ROI] analyses) were applied. Sixth, statistical models for appropriate contrasts were reported. For instance, Welborn et al.'s study (2015) was excluded due to the reason that this study only reported contrasts between the presence and absence of group opinion. Seventh, the study did not include subject sample overlap with an already-included study. Finally, the study reported activations in a standardized stereotaxic space (Talairach or MNI). Note that for studies reporting Talairach coordi-

nates a conversion to the MNI coordinates was implemented (Brett, 1999). Filtering search results according to the inclusion/exclusion criteria yielded a total of 18 published fMRI articles (Table 1). The detailed reasons for including or excluding each selected publication were provided in Table S1 & S2. Furthermore, similar strategy of literature search and selection was employed for UG task (Table S3), which was detailed in Feng et al. (2015).

2.2. Activation likelihood estimation (ALE) approach

A coordinate-based meta-analysis of reported fMRI experiments was conducted by employing the revised ALE algorithm (Eickhoff et al., 2009) implemented in the GingerALE software (version 2.3.6, <http://www.brainmap.org/ale/>). ALE determines the convergence of foci reported from different functional (e.g., blood-oxygen-level dependent [BOLD] contrast imaging) or structural (e.g., voxel-based morphometry) neuroimaging studies with published foci in Talairach or MNI space (Laird et al., 2005; Turkeltaub et al., 2002). ALE interprets reported foci as spatial probability distributions, whose widths are based on empirical estimates of the spatial uncertainty due to the between-subject and between-template variability of the neuroimaging data (Eickhoff et al., 2009). Within each included study, a modulated activation (MA) map is firstly created by taking the maximum probability associated with any one focus (always the closest one) for each voxel (Turkeltaub et al., 2012). An advantage of the modified ALE algorithm is that multiple foci from a single study would not jointly influence the individual MA value of a single voxel. Furthermore, to prevent studies with multiple contrasts based on the same subject sample influencing ALE values more than others, different contrasts from the same subject sample were combined into a single contrast rather than treated as independent contrasts (see also Turkeltaub et al., 2012).

The union of individual MA maps corresponding to each selected study is then calculated to obtain an ALE map across studies. This ALE map is assessed against a null-distribution of random spatial association between studies using a non-linear histogram integration algorithm (Eickhoff et al., 2012; Turkeltaub et al., 2012). The resulting *P* value maps were thresholded using the cluster-level family-wise error (FWE) correction at $P < 0.05$ with a cluster defining threshold of $P < 0.005$ and 5000 permutations (Eickhoff et al., 2012). 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/>).

Applying the ALE algorithm, the reported coordinates of brain areas associated with conformity-related contrasts converged across different experiments. Specifically, the neural correlates of social conformity were converged in the following meta-analyses: (i) 5 studies (including a total of 19 peak foci) were identified for inclusion in the meta-analysis of social influence on neural correlates of valuation (e.g., stimuli endorsed by others vs. stimuli disliked by others); (ii) 10 studies (52 peak foci in total) were included in the meta-analysis of neural responses to agreement with group opinions; (iii) 15 studies (129 peak foci in total) were included in the meta-analysis of neural responses to disagreement with group opinions; and (iv) 5 studies (32 peak foci in total) were included in the meta-analysis of neural predictors of conforming behavioral adjustment. Please note that for the last contrast, only within-subjects contrasts or correlations (i.e., parametric analysis) were included. In contrast, the interindividual correlations between neural responses and conforming behaviors (e.g., Campbell-Meiklejohn et al., 2010; Korn et al., 2014) were excluded from the analysis due to the reason that intraindividual and interindividual correlations are often independent of each other (Molenaar and Campbell, 2009). Details (i.e., the number of included studies and peak foci) for studies included in each of above

Table 1
Summary of studies included for the meta-analysis.

Study	N	Contrast	No. of foci
Social influence on neural correlates of valuation			
Campbell-Meiklejohn et al. (2010)	28	songs chosen by others > songs not chosen by others	2
Mason et al. (2009)	12	popular symbols > unpopular symbols	2
Nook and Zaki (2015)	21	foods with higher ratings of others > foods with lower ratings of others	3
Chung et al. (2015)	56	choices, positively tracking other-conferred utility (parametric analysis)	1
Zaki et al. (2011)	14	faces with higher ratings of others > faces with lower ratings of others	11
Agreement with group opinions			
Berns et al. (2005)	32	agreeing with others > disagreeing with others	4
Berns et al. (2010)	27	parametric analysis, negative correlation with absolute differences in self-rating and popularity	6
Burke et al. (2010)	17	agreeing with others > disagreeing with others	1
Campbell-Meiklejohn et al. (2010)	28	congruent social feedback > incongruent social feedback	6
Gilman et al. (2016)	35	agreeing with others > disagreeing with others	5
Izuma and Adolphs (2013)	18	congruent social feedback > incongruent social feedback	3
Klucharev et al. (2009a)	21	congruent group feedback > incongruent group feedback	6
Korn et al. (2014)	104	parametric analysis, negative correlation with discrepancies with group opinions	6
Nook and Zaki (2015)	21	congruent group feedback > incongruent group feedback; agreeing with others > disagreeing with others	12
Wei et al. (2013)	29	consistent with group's choices > no group's choices	3
Disagreement with group opinions			
Berns et al. (2005)	32	disagreeing with others > agreeing with others	2
Berns et al. (2010)	27	parametric analysis, positive correlation with absolute differences in self-rating and popularity	3
Burke et al. (2010)	17	disagreeing with others > agreeing with others	1
Cascio et al. (2015a)	65	incongruent group feedback > no group feedback; incongruent group feedback > congruent group feedback	34
Charpentier et al. (2014)	20	inconsistent group feedback > consistent group feedback	1
Chung et al. (2015)	59	incongruent social information > congruent social information	5
Edelson et al. (2011)	20	incongruent social information > congruent social information	5
Edelson et al. (2014)	20	incongruent social information > congruent social information	9
Gilman et al. (2016)	35	disagreeing with others > agreeing with others	4
Izuma and Adolphs (2013)	18	parametric analysis, positive correlation with incongruence levels of social information	4
Klucharev et al. (2009b)	21	incongruent group feedback > congruent group feedback	22
Korn et al. (2014)	104	parametric analysis, positive correlation with discrepancies with group opinions	9
Nook and Zaki (2015)	21	incongruent group feedback > congruent group feedback	4
Tomlin et al. (2013)	86	parametric analysis, positive correlation with incongruence levels of social information	16
Wei et al. (2013)	29	inconsistent with group's choices > no group's choices; inconsistent with group's choices > consistent with group's choices.	10
Neural predictors of conforming behavioral adjustments			
Berns et al. (2010)	27	parametric analysis, correlation with behavioral conformity in a subjective rating task; group opinions that results in behavior changes vs. no changes	11
Cascio et al. (2015a)	65	group opinions that results in behavior changes vs. no changes	3
Edelson et al. (2011)	20	persistent vs. transient conforming to social influence in a memory task	6
Klucharev et al. (2009a)	21	group opinions that results in behavioral changes vs. no changes	4
Wei et al. (2013)	29	group opinions that results in behavioral changes vs. no changes	8

N, number of subjects.

meta-analyses were summarized in Table 1. Lastly, a subsequent conjunction analysis was employed to examine correspondence between (i) contrasts of disagreement with group opinions and conforming behavioral changes; (ii) disagreement- and unfairness-related contrasts; and (iii) conforming behavioral adjustment and unfairness-related contrasts. To implement the latter two conjunction analyses, the reported coordinates of brain areas linked to unfairness-related contrasts were converged across previous neuroimaging studies on UG. Details for studies included in the meta-analysis of UG were summarized in Table S3.

3. Results

3.1. Social influence on neural correlates of valuation

Compared with stimuli disliked by others, stimuli that are endorsed by others consistently evoked the activation of left VS (Fig. 2 & Table 2).

3.2. Agreement and disagreement with group opinions

Regarding contrasts associated with agreement with group opinions, consistent maxima were found in bilateral VS (Fig. 3a &

Table 3). Regarding contrasts associated with disagreement with group opinions, consistent maxima were identified in dorsal pMFC, right AI, and left superior parietal lobule (Fig. 3b & Table 3).

3.3. Neural predictors of conforming behavioral adjustment

Converging reported activation peaks that were associated with conforming behavioral changes identified the consistent maxima in dorsal pMFC (Fig. 4 & Table 4).

3.4. Common activation associated with norm violations in conformity tasks and UG

ALE meta-analysis results for norm violations (i.e., comparing unfairness with fairness) in UG were shown in the Supplementary material (Fig. S1 & Table S4).

First, the conjunction analysis revealed convergence in dorsal pMFC for the contrasts of disagreement with group opinions and conforming behavioral changes. That is, disagreement-related activity in dorsal pMFC predicts conforming behavioral adjustment (Fig. 5a & Table 5).

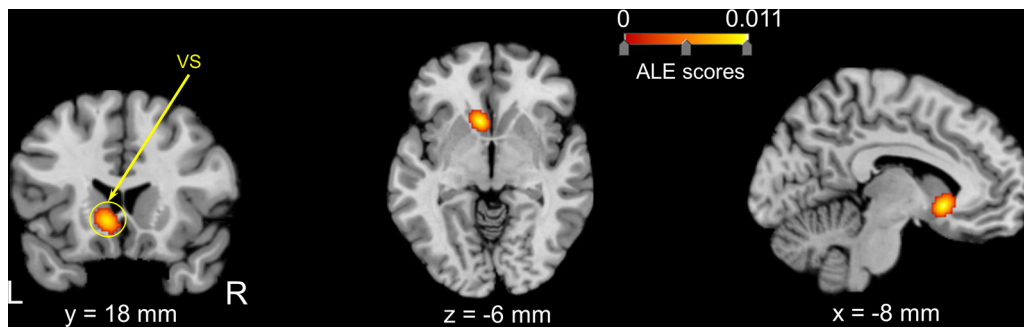


Fig. 2. ALE meta-analysis results for social influence on neural correlates of valuation (5000 permutations, $P < 0.05$ corrected for multiple comparisons at the cluster level). L, left; R, right; VS, ventral striatum; ALE, activation likelihood estimation.

Table 2

ALE meta-analysis results for social influence on neural correlates of valuation.

Brain Regions	BA	MNI Coordinates (mm)			ALE ($\times 10^{-2}$)	Cluster Size (mm^3)
		x	y	z		
L caudate	-	-8	16	-6	1.14	1824
L caudate head	-	-8	16	-6	1.14	
L caudate body	-	-6	12	4	0.84	

BA, Brodmann area; L, left; R, right; ALE, activation likelihood estimation. $P < 0.05$ corrected for multiple comparisons at the cluster level.

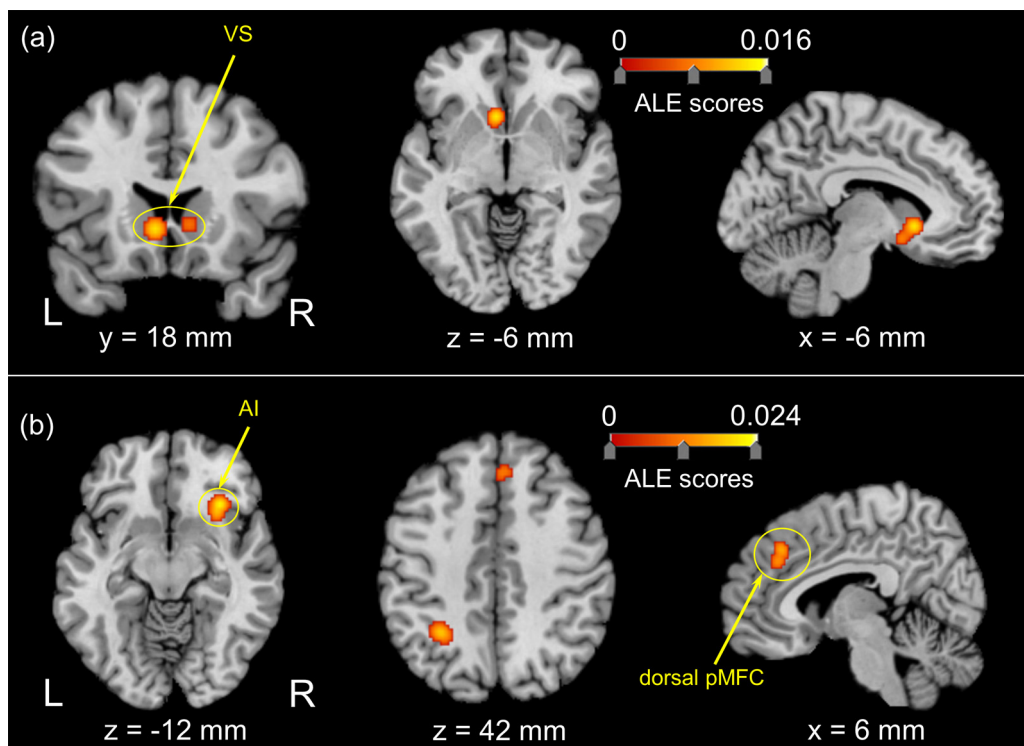


Fig. 3. ALE meta-analysis results for the agreement (a) and disagreement (b) with group opinions (5000 permutations, $P < 0.05$ corrected for multiple comparisons at the cluster level). L, left; R, right; AI, anterior insula; dorsal pMFC, dorsal posterior medial frontal cortex; ALE, activation likelihood estimation.

Second, disagreement-related contrasts and unfairness-related contrasts demonstrated correspondence in right AI and dorsal pMFC (Fig. 5b & Table 5).

Third, conforming behavioral adjustment and unfairness-related contrasts converged in dorsal pMFC (Fig. 5c & Table 5).

4. Discussion

Recent neuroscience studies on social conformity often utilize a paradigm that creates a discrepancy between one's own and group's judgments and test whether people change their responses to decrease the discrepancy (Campbell-Meiklejohn et al., 2010; Edelson et al., 2011; Izuma and Adolphs, 2013; Klucharev et al.,

Table 3
ALE meta-analysis results for the agreement and disagreement with group opinions.

Brain Regions	BA	MNI Coordinates (mm)			ALE ($\times 10^{-2}$)	Cluster Size (mm ³)
		x	y	z		
Agreement with group opinions						
caudate	–	–6	16	–4	1.61	1800
L caudate head	–	–6	16	–4	1.61	
R caudate head	–	10	16	–2	0.84	
Disagreement with group opinions						
R anterior insula	13	32	20	–16	3.29	2408
R anterior insula	13	32	20	–16	3.29	
medial frontal gyrus	8	4	32	38	1.68	1536
medial frontal gyrus	8	4	32	38	1.68	

BA, Brodmann area; L, left; R, right; ALE, activation likelihood estimation.
 $P < 0.05$ corrected for multiple comparisons at the cluster level.

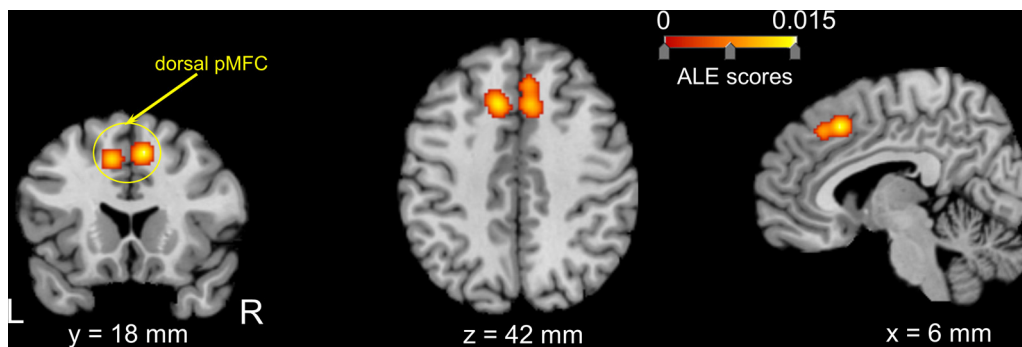


Fig. 4. ALE meta-analysis results for neural predictors of conforming behavioral adjustments (5000 permutations, $P < 0.05$ corrected for multiple comparisons at the cluster level). L, left; R, right; dorsal pMFC, dorsal posterior medial frontal cortex; ALE, activation likelihood estimation.

Table 4
ALE meta-analysis results for neural predictors of conforming behavioral adjustments.

Brain Regions	BA	MNI Coordinates (mm)			ALE ($\times 10^{-2}$)	Cluster Size (mm ³)
		x	y	z		
R medial frontal gyrus	6	8	18	46	1.51	2016
R medial frontal gyrus	6	8	18	46	1.51	
R medial frontal gyrus	8	6	30	42	0.94	
R cingulate gray matter	24	4	16	34	0.93	

BA, Brodmann area; L, left; R, right; ALE, activation likelihood estimation.
 $P < 0.05$ corrected for multiple comparisons at the cluster level.

Table 5
ALE meta-analysis results for common regions associated with norm violations in conformity tasks and Ultimatum Game.

Brain Regions	BA	MNI Coordinates (mm)			ALE ($\times 10^{-2}$)	Cluster Size (mm ³)
		x	y	z		
Disagreement \cap conforming behavioral adjustments						
R medial frontal gyrus	8	4	30	42	0.82	104
R medial frontal gyrus	8	4	30	42	0.82	
Disagreement \cap unfairness						
R anterior insula	47	32	22	–12	2.15	896
R anterior insula	47	32	22	–12	2.26	
L cingulate gyrus	32	–4	32	32	1.01	72
L cingulate gyrus	32	–4	32	32	1.01	
R cingulate gyrus	32	8	30	36	0.92	24
R cingulate gyrus	32	8	30	36	0.92	
R cingulate gyrus	32	4	28	38	0.8	8
R cingulate gyrus	32	4	28	38	0.8	
Conforming behavioral adjustments \cap unfairness						
R medial frontal gyrus	6	8	18	46	1.51	1368
R medial frontal gyrus	6	8	18	46	1.51	
R medial frontal gyrus	8	6	28	42	0.9	184
L medial frontal gyrus	32	–8	20	44	1.05	
L medial frontal gyrus	32	–8	20	44	1.05	

BA, Brodmann area; L, left; R, right; ALE, activation likelihood estimation.

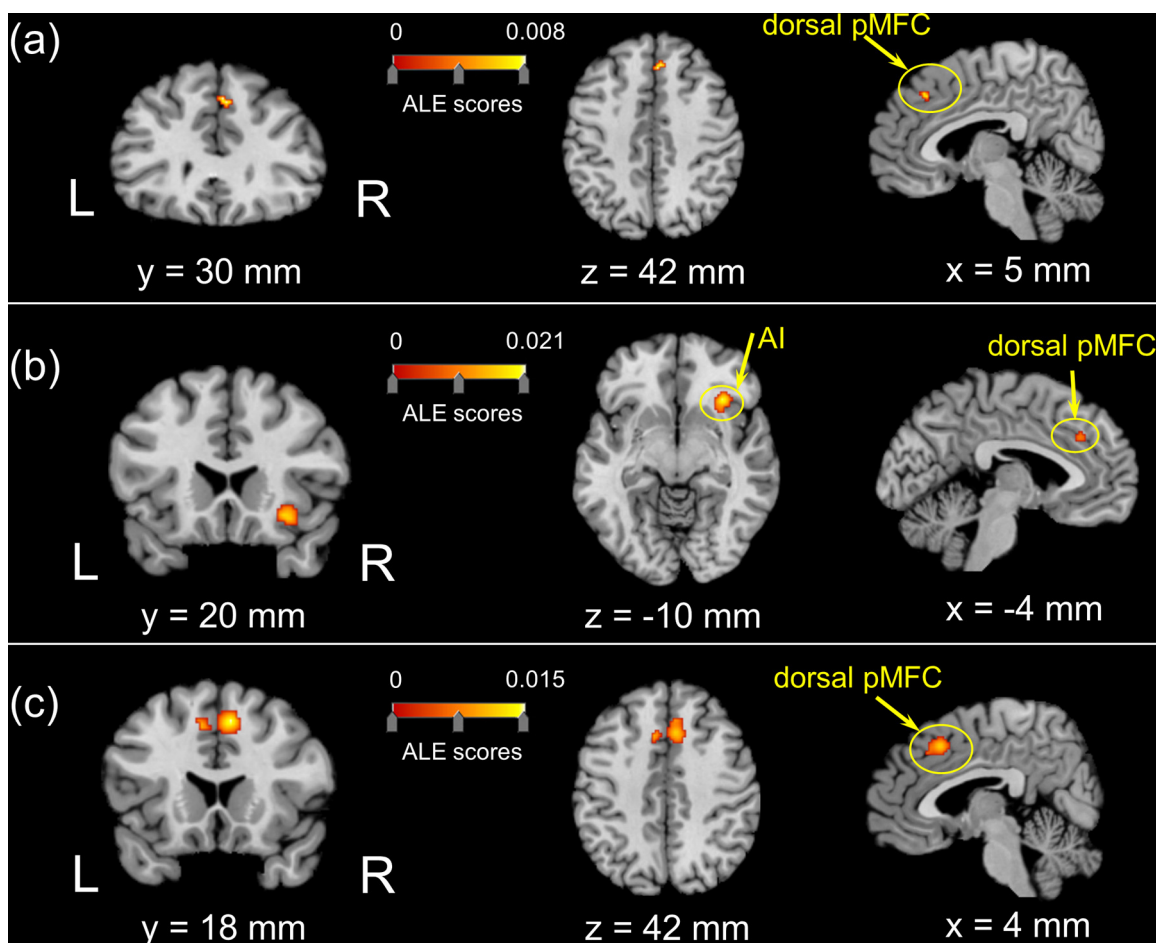


Fig. 5. ALE meta-analysis results for common regions associated with norm violations in conformity tasks and Ultimatum Game, including overlap of activation between being disagreement with group opinions and conforming behavior adjustment (a), between being disagreement with group opinions and seeing unfair behaviors of another person (b), and between conforming behavioral adjustment and seeing unfair behaviors of another person (c). L, left; R, right; dorsal pMFC, dorsal posterior medial frontal cortex; AI, anterior insula; ALE, activation likelihood estimation.

2009b; Tobler et al., 2016). In addition, a couple of narrative reviews have explored the biological basis of social influence from a larger perspective (Cascio et al., 2015b; Falk et al., 2012; Izuma, 2013; Morgan and Laland, 2012; Raafat et al., 2009; Schnuerch and Gibbons, 2014; Stallen and Sanfey, 2015; Toelch and Dolan, 2015). However, a precise characterization of the neural systems underlying social conformity remains elusive. The objective of this coordinate-based meta-analysis was to quantitatively synthesize the results of previous fMRI studies regarding social conformity with the aim of identifying consistent activation patterns of the neural signatures underpinning this psychological phenomenon. Our results identified a convergence of reported activation foci in neural circuits associated with normative decision making (Buckholtz and Marois, 2012; Izuma, 2013; Rilling and Sanfey, 2011; Schnuerch and Gibbons, 2014), including VS, dorsal pMFC, and AI. These regions have been thought to convey general prediction errors (Klucharev et al., 2009b), cognitive inconsistency (Izuma and Adolphs, 2013), and/or aversive physical arousal (Berns et al., 2010), which might serve as control signals to guide subsequent conforming behaviors.

The current meta-analysis first demonstrated that VS is consistently activated by stimuli that are endorsed than disliked by others. Considering the role of VS in encoding and learning value assigned to a stimulus (Cromwell and Schultz, 2003; Lebreton et al., 2009), these findings have been thought to reflect neural modifications that track the changes in valuation of a stimulus caused by

group opinions (Campbell-Meiklejohn et al., 2010; Mason et al., 2009; Nook and Zaki, 2015; Zaki et al., 2011). However, it is premature to conclude that those socially mediated changes in value-related activity of VS reflect adjustments in intrinsic preference for a stimulus or choice, since socially endorsed choices are more likely to induce agreement with others (e.g., Chung et al., 2015). In this case, it is difficult to separate the added value from a choice due to agreement with others from changes in intrinsic valuation. Notably, several studies addressing this issue have identified the influence of group opinions on neural correlates of valuation after excluding the confounding of agreement of others (Mason et al., 2009; Nook and Zaki, 2015; Zaki et al., 2011). Further, other neuroimaging studies have indicated that opinions of others result in altered neural correlates of perceptual or mnemonic representations in a perception or memory task, respectively (Berns et al., 2005; Edelson et al., 2011; Edelson et al., 2014). Taken together, recent neuroimaging findings dovetail with the claim that social conformity is driven by intrinsic modifications of representation of reality shaped by opinions of other people (private acceptance) more than mere compliance to normative opinions on the surface (public compliance) (but see Berns et al., 2010) (public compliance, but see Berns et al., 2010).

Our meta-analysis further unveiled that social conformity is consistently engaged the involvement of a neuronal network consisting of VS, dorsal pMFC, and AI. On the one hand, the consistency between oneself and normative opinions induces stronger neu-

ral responses of VS, indicating that the agreement with others are assigned to a higher subjective value as compared with the disagreement with others (Nook and Zaki, 2015). These findings complement previous observations on the increased VS responses to norm compliance engaged by other normative decision-makings (Tabibnia and Lieberman, 2007). For instance, fair or cooperative outcomes that are in line with social norms usually evoke stronger activity in this region (Rilling et al., 2002; Tabibnia et al., 2008; Tricomi et al., 2010; Wu et al., 2014). On the other hand, disagreement with others evokes consistent activity in dorsal pMFC and AI that occupy a central role in encoding aversive feelings (Harlé et al., 2012; Lamm et al., 2011) and monitoring errors/conflicts in both social and non-social contexts (Botvinick et al., 2004; Chang and Sanfey, 2011; Lieberman and Eisenberger, 2015; Ullsperger et al., 2010; Xiang et al., 2013). In line with current findings, events that are worse than expectations or deviate from social norms often evoke the activity of dorsal pMFC (Chang and Sanfey, 2011; Holroyd et al., 2004; Xiang et al., 2013). Moreover, AI is important in signaling norm violations or emotion processing via representations of (especially aversive) internal states (Corradi-Dell'Acqua et al., 2016; Feng et al., 2015).

There are several models to account for the neural correlates of social conformity. First, the RL account holds that social conformity shares a similar neural mechanisms with RL, such that conformity could be regarded as a behavioral adjustment to correct deviations from group norms (Campbell-Meiklejohn et al., 2010; Klucharev et al., 2009b; Nook and Zaki, 2015). According to this account, the VS might play a role in reinforcing conforming behaviors by representing consensus with group opinions as positive prediction errors. In contrast, disagreement with others is presumably computed by dorsal pMFC and AI as aversive prediction errors that facilitate conforming behavioral adjustments (Klucharev et al., 2009b). Although the RL model has been often employed to explain the brain functions of social conformity, it is noteworthy that few studies have directly tested the general RL mechanism in human social conformity. Preliminary evidence in favor of the RL account indicates that dorsal pMFC is commonly engaged by the disagreement with others and negative outcomes in a reward task (Izuma and Adolphs, 2013). Moreover, a pharmacological study indicated that conforming behaviors were modulated by methylphenidate (Campbell-Meiklejohn et al., 2012b), an indirect catecholamine agonist that increases dopaminergic responses to appetitive events (Volkow et al., 2001) and facilitates reinforcement-associated synaptic plasticity and behavior (Tye et al., 2010). Second, the “cognitive balance” account proposed that a population of neurons in the dorsal pMFC might specifically encode social disagreement and is insensitive to general error signals in RL (Izuma and Adolphs, 2013). This account could be tested in future studies by directly comparing social disagreement and general error signals, with advanced imaging techniques (e.g., multi-voxel pattern analysis and fMRI adaptation paradigms) or intracranial electrophysiological recordings in human patients. Third, the activity of dorsal pMFC and AI might reflect aversive physiological arousal of anxiety induced by disagreement with others (Berns et al., 2010). However, this emotion account does not necessarily contradict the other two accounts, since both aversive prediction errors and cognitive imbalance could serve as progenitors of negative feelings (Izuma and Adolphs, 2013; Xiang et al., 2013).

We next demonstrated that the activity of dorsal pMFC is consistently predictive of conforming behaviors, and the conformity-related activity of dorsal pMFC overlaps with disagreement-dependent activity in this region. The association between the activity of dorsal pMFC and social conformity complements observations from other lines of research. First, disruption of dorsal pMFC due to transcranial magnetic stimulation reduces conform-

ing behavioral adjustments (Klucharev et al., 2011). Second, recent event-related potential (ERP) studies have demonstrated that the discrepancy between oneself and group opinions induces stronger responses of feedback-related negativity (FRN) (Chen et al., 2012; Kim et al., 2012; Schnuerch and Gibbons, 2015; Schnuerch et al., 2014; Shestakova et al., 2013), a negative deflection that reflects activity of dorsal pMFC and plays a crucial role in triggering general behavioral adjustments (Cohen and Ranganath, 2007; Frank et al., 2005; Gehring et al., 1993; Hayden et al., 2011; Holroyd and Coles, 2002; Nieuwenhuis et al., 2004; Walsh and Anderson, 2012). Similar to the link between dorsal pMFC activation and social conformity, deviation-related FRN responses predict people's conformity behaviors (Schnuerch and Gibbons, 2015). Lastly, it is noteworthy that our meta-analysis did not reveal consistent link between conforming behavioral adjustments and derivation-related responses in the VS and AI, although several studies have reported that activity in these regions is predictive of conforming changes in people's responses (Campbell-Meiklejohn et al., 2010; Izuma and Adolphs, 2013; Klucharev et al., 2008).

The present meta-analysis finally identified the correspondence across social conformity and fairness decision-making within dorsal pMFC and AI. That is, the activation of dorsal pMFC and AI triggered by first-person experience of deviating from group norms overlaps with activation when seeing norm violations conducted by another person in the UG task (Feng et al., 2015; Gabay et al., 2014). The common activations of dorsal pMFC and AI in these norm-based tasks implicate a possibility that these regions are involved in a “generic” form of detection of norm violations independent of agents (Montague and Lohrenz, 2007). In line with this conjecture, the involvement of dorsal pMFC and AI has been identified in other norm-based paradigms including cognitive dissonance, wherein people's overt behaviors deviate from one's own intrinsic norms (i.e., prior attitudes) (Izuma et al., 2010; Kitayama et al., 2013; Van Veen et al., 2009). As expected, deviation-related responses in these areas predict people's tendency to align their attitudes with overt behaviors (Izuma et al., 2010; Jarcho et al., 2011; Van Veen et al., 2009).

The correspondence within dorsal pMFC and AI observed in social conformity and other norm-based paradigms implicates a shared neural mechanism underlying various kinds of normative decision making. That is, people compare their own and other people's behaviors with expected group norms during social interactions, and deviation are detected when one's own or other people's experience differs too much from the norm. The deviation then serve as error signals, cognitive imbalance, or aversive feelings that drive people to adjust behaviors in the direction of group norms. Depending on specific task demands or choices at hand, people's behavioral adjustments could manifest as either changing one's behavior to match with group opinions or punishing other people who violate group norms (Buckholz and Marois, 2012; Montague and Lohrenz, 2007). In short, a generic neural system consisting of dorsal pMFC and AI for the detection of norm violations offers a potential mechanism to bridge two separate but relevant literatures: one from social conformity, examining neural and behavioral responses when one's own behaviors deviate from normative opinions; and a second from costly punishment, assessing neural and behavioral responses when another person violates group norms. However, it is worthy to note that this account is tentative and needs to be considered with caution due to following reasons: (i) the overlap in activation does not necessarily mean the same mechanism as discussed above; and (ii) there is a personal loss in both cases of social conformity and UG. The latter confounding has been addressed in previous studies wherein neural responses of dorsal pMFC and AI to norm violations remained evident when participants acted as an indifferent third party (Civai

et al., 2012; Strobel et al., 2011) or when unfair offers are better than expectations (Xiang et al., 2013; Yu et al., 2014).

Several limitations related to this meta-analysis should be acknowledged. First, as many other neuroimaging meta-analysis algorithms, the coordinate-based ALE meta-analysis provides only the measurements of the convergence of reported peak coordinates but not the effect size of activation at the peak. Second, compared to other coordinate-based approaches, the ALE approach provided the most similar results with image-based meta-analysis (Salimi-Khorshidi et al., 2009). However, future meta-analyses would still benefit from the image-based approach employing unthresholded statistical maps which would have provided insight beyond existing reports that may have been biased to report matches to existing publications. Third, the number of papers included in this meta-analysis was relatively small, but statistical power for interpretation of results will increase for future meta-analyses due to a rapidly growing literature on neural signatures of social conformity. Relevantly, the limited number of studies did not allow us cover every aspect of social conformity as a heterogeneous phenomenon. For instance, previous studies have examined the general effects of group feedback independent of agreement (e.g., Welborn et al., 2015) and neural predictors of conforming behaviors from the level of interindividual variation (e.g., Campbell-Meiklejohn et al., 2010; Korn et al., 2014). The absence of these contrasts in the meta-analysis by no means indicates that they are trivial. A better understanding of social conformity requires further investigation on this phenomenon from a variety of viewpoints. Lastly, this meta-analysis focused on only one type of social influence, and future meta-analytic studies are needed to test whether different kinds of social influence (e.g., social conformity vs. persuasion) are underpinned by similar or distinct neural architecture (Cascio et al., 2015b; Izuma, 2013).

In conclusion, social conformity may be driven by a neural system comprising VS, dorsal pMFC, and AI among other regions that are responsible for detecting generic error signals, cognitive imbalance, and/or negative feelings to guide behavioral adjustments. Importantly, group opinions do not only influence people's overt behaviors but also result in altered neural correlates of valuation, which could be attributed to either agreement-dependent values added to a stimulus or modified intrinsic preferences associated with a stimulus.

Conflict of interest

None of the authors has conflicts of interests to declare.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neubiorev.2016.08.038>.

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