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Brain responses to social norms: Meta-analyses of fMRI studies

Oksana Zinchenko[1] | **Marie Arsalidou**[2,3]

[1]Centre for Cognition and Decision Making, National Research University Higher School of Economics, Moscow, Russian Federation
[2]Department of Psychology, National Research University Higher School of Economics, Moscow, Russian Federation
[3]Department of Psychology, Faculty of Health, York University, Toronto, Canada

Correspondence
Oksana Zinchenko, Centre for Cognition and Decision Making, National Research University Higher School of Economics, 101000, Moscow, 3 Krivokolenny Pereulok, Russian Federation.
Email: ozinchenko@hse.ru

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Abstract
Social norms have a critical role in everyday decision-making, as frequent interaction with others regulates our behavior. Neuroimaging studies show that social-based and fairness-related decision-making activates an inconsistent set of areas, which sometimes includes the anterior insula, anterior cingulate cortex, and others lateral prefrontal cortices. Social-based decision-making is complex and variability in findings may be driven by socio-cognitive activities related to social norms. To distinguish among social-cognitive activities related to social norms, we identified 36 eligible articles in the functional magnetic resonance imaging (fMRI) literature, which we separate into two categories (a) social norm representation and (b) norm violations. The majority of original articles (>60%) used tasks associated with fairness norms and decision-making, such as ultimatum game, dictator game, or prisoner's dilemma; the rest used tasks associated to violation of moral norms, such as scenarios and sentences of moral depravity ratings. Using quantitative meta-analyses, we report common and distinct brain areas that show concordance as a function of category. Specifically, concordance in ventromedial prefrontal regions is distinct to social norm representation processing, whereas concordance in right insula, dorsolateral prefrontal, and dorsal cingulate cortices is distinct to norm violation processing. We propose a neurocognitive model of social norms for healthy adults, which could help guide future research in social norm compliance and mechanisms of its enforcement.

KEYWORDS
brain mapping, functional magnetic resonance imaging, social norms, prefrontal cortex, humans, cognition, norm violation

1 | INTRODUCTION

Most of us benefit by following social norms to some degree. Social norms are spoken or unspoken rules of behavior that are formed within group situations and are considered appropriate within a society. For instance, common courtesy and culturally appropriate manners for cooperative actions and bilateral exchange can be referred to as social norms (Sherif & Sherif, 1953). Because we live, act, and interact among others in a society we often have to equipoise our personal wants and social norms (Cialdini, Reno, & Kallgren, 1990; Bicchieri 2016). Deviation from social norms is often met with increasing pressure to conform. From early studies we know that if social expectations remain unmet, deviation from social norms often results with exclusion of the norm violator from the group or higher likelihood of reduced payoffs to the norm violator (Schachter, 1951; Sherif & Sherif, 1953). Thus, going against social norms has critical consequences. In other words, threatening norm violators with some form of social punishment enforces norm compliance. Punishment is usually given by individuals who are directly affected by norm violations of others (i.e., second parties), yet individuals who are not directly affected by norm violations of others (i.e., third parties) are also willing to give punishment (Fehr & Fischbacher, 2004).

A common approach to investigate norm violation and norm enforcement is by using interactive economic games (Camerer, 2003; Fehr & Camerer, 2007; Sanfey, 2007), such as the Ultimatum Game introduced by (Güth et al. 1982; see Gabay, Radua, Kempton, & Mehta, 2014 for a meta-analysis), the Prisoner's Dilemma (Dickinson, Masclet, & Villeval, 2015), and the Dictator Game (Tammi, 2013). Behavioral findings suggest that unfair treatment leads to negative emotions, such as anger (Batson et al., 2007; Pedersen, 2012), guilt (Wagner, N'diaye, Ethofer, & Vuilleumier, 2011), and embarrassment (Melchers et al., 2015) that drive individuals to punish their opponent at the expense of monetary reward or consider the opponent guilty. Performance on tasks with monetary outcomes highly depends on the participant's understanding of relative and absolute fairness/unfairness of the situation at hand. In case of unfair situations, participants presented with economic paradigms, such as the Ultimatum Game are asked to accept or reject financial offers depending on subjective equality of the offered distribution. Some researchers identify this rejection rate to reflect social punishment (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Tabibnia, Satpute, & Lieberman, 2008). For instance, rejection rate in an Ultimatum Game gradually increases as the proposer's offer becomes lower, such that a lower proposal is perceived as more unfair (Corradi-Dell'Acqua et al., 2013; Rilling & Sanfey, 2011). In other words, decision-making in this situation is influenced by social norms and differs according to the responder's understanding of norms and their violation, consistent with the claim that social norms are self-enforcing (Young, 2015). Overall, behavioral studies show that consequences of social norms are related to both social violations and social punishment; however, it is difficult to parse out the underlying mechanisms of such complex processes with behavioral paradigms alone.

Many functional magnetic resonance imaging (fMRI) and lesion studies examined the brain correlates of social norms (e.g., Dimitrov, Phipps, Zahn, & Grafman, 1999; Koenigs et al., 2007; Buckholtz & Marois, 2012; Sanfey & Chang, 2008; Harlé, Chang, Wout, & Sanfey, 2012; Wright, Symmonds, Fleming, & Dolan, 2011; Hu et al., 2016). An advantage of functional neuroimaging is that it allows for tracking of continuous processes as healthy participants are working on tasks. A recent fMRI meta-analysis on the Ultimatum Game distinguishes two brain systems responsible for norm enforcement behavior; an intuitive-emotional system, also called System 1, involving the anterior insula and ventromedial prefrontal cortex and a cognitive-rational system, or System 2, involving ventrolateral, dorsomedial, left dorsolateral prefrontal cortices, and rostral anterior cingulate cortices (Feng, Luo, & Krueger, 2015). Regions involved in System 1 represent a drive to punish norm violators, whereas System 2 is responsible for cognitive control and suppression of economic self-interest (i.e., to save money; Feng et al., 2015). It has been suggested that both these systems would underline quick detection of norm violations, evaluation of benefits, and costs of punishment to decide its necessity, supporting the dual process theory (Kahneman, 2003; Kahneman, 2011). The meta-analysis by Feng et al. (2015) provides knowledge on the brain correlates related to the Ultimatum Game (Feng et al., 2015); however, does not distinguish between different aspects of social norms and focuses only on a single task. Critically, some of Feng et al. (2015) methodological choices may be problematic or outdated. First, the analyses include data from children and adults (i.e., Güroğlu et al., 2011; White et al., 2013) when behavioral evidence show differences in performance between children, adolescents and adults (Hamlin, Wynn, Bloom, & Mahajan, 2011; Steinbeis, Bernhardt, & Singer, 2012). Second, the analyses used a low number of studies (i.e., < 17) with a threshold for multiple comparison control (i.e., false discovery rate, FDR) that is currently not recommended practice (Eickhoff, Laird, Fox, Lancaster, & Fox, 2017). Moreover, according to GingerALE developers, older versions of the software (i.e., older than 2.3.6) had a computational error, which did not appropriately control thresholding procedures (Eickhoff et al., 2017). Thus, an understanding of how healthy adults process social norms is still lacking. In this article, we focus on social norms and possible distinctions among (a) social norm representation and (b) norm violations.

1.1 | Theoretical approach

To frame our hypotheses, we adopted a recent neurofunctional model of social norms (Montague & Lohrenz, 2007). Montague's model is a product of a classic review of research studies that explored brain activity related to adherence to shared social norms (Montague & Lohrenz, 2007; Xiang, Lohrenz, & Montague, 2013). They proposed that the brain could flexibly adjust behavior according to social norms in order to develop a program of further behavior. To interact with others in any social group, the following circumstances are required: (a) a representation of a well-known norm as a behavioral rule about something that is expected to be true (e.g., Montague & Lohrenz, 2007), (b) the possibility to detect any violations of this norm, and (c) a chance to look at an ongoing situation from a third-party perspective so to act and make congruent decisions to maintain norm compliance (e.g., Montague & Lohrenz, 2007; Xiang et al., 2013). Because norm compliance is not always voluntary and mostly requires sanction inducement, social punishment is used for social norm enforcement. In line with this model that predicts differential brain regions for mental processes associated with social norms, for our meta-analyses we differentiate among social norms into two subcategories: (a) social norm representation and (b) norm violation, and expected different brain regions to underlie these processes.

1.2 | Social norm representation

We define social norm representation as commonly expected appropriate behavior in a certain situation (i.e., shared norms; Cialdini & Goldstein, 2004). Our category for social norm representation includes both moral and social norms as a kind of normative attitudes as both moral and social norms are accepted rules or normative principles. Here we categorize experiments (i.e. contrasts) as belonging to social norm representation if the action in the task possesses the social preferences ("good" versus "bad," or neutral etc.) or if a comparison between social and non-social domain has been made ("moral" versus "semantic," etc.). Unlike social norm representation studies, which reflect voluntary actions individuals do because they think they are appropriate (Bicchieri, 2016), social conformity studies have participants confronted with direct peer pressure (Wei, Zhao, & Zheng, 2013; Zaki, Schirmer, & Mitchell, 2011). Studies of social conformity were not included as a separate category because of insufficient studies (i.e., < 17 experiments; Eickhoff et al., 2017). We are interested in global normative judgments that regard others, such as fairness-related norms modeled in the Ultimatum Game (Brennan, González, Güth, & Levati, 2008), norms of equality (Elster, 1989), and others used to maintain social order. Recent studies report that the ventromedial prefrontal cortex, critical for social cognition, strongly correlates with distinguishing "good" and "bad" in the moral domain (Bechara, Damasio, & Damasio, 2000; Dimitrov et al., 1999; Heekeren et al., 2005; Koenigs et al., 2007). Such moral evaluations reflect internal representations of social norms (Prehn et al., 2008). Although most social norm studies report activity in the prefrontal cortex, the location is inconsistent: orbitofrontal (e.g., Koenigs and Tranel, 2007) and dorsolateral (e.g., Lieberman, 2007 for review; Prehn et al., 2008; Yoder and Decety, 2014) cortices. Based on past literature, we expect that concordant brain locations responding to "social norm representation" will be revealed in dorsolateral prefrontal cortex.

1.3 | Norm violation

We define norm violation as behavioral deviations from shared social norms (i.e., inappropriate behavior). Norm violations of another person could affect the observer's self-concept by threatening his or her social identity (Melchers et al., 2015). Many functional neuroimaging studies focus on brain responses to norm violation situations and how norm violations influence decision-making. Specifically, they examine perceived unfairness/fairness (Buckholtz & Marois, 2012; Sanfey & Chang, 2008), negative moral emotions—guilt (Wagner et al., 2011) or embarrassment as a consequence of norm violation (Takahashi et al., 2004, 2008). Some fMRI studies examining norm violations show key areas being active in the insula (Denke, Rotte, Heinze, & Schaefer, 2014; Güroğlu, Bos, Dijk, Rombouts, & Crone, 2011; Sanfey et al., 2003) and others in the orbitofrontal and dorsomedial cortex (Wagner et al., 2011), yet others highlight activity in the cingulate cortex (Denke et al., 2014; Güroğlu et al., 2011). Considering this broad representation of activation following norm violation processing, a meta-analysis is needed to quantitatively verify which areas are concordantly active. Based on previous findings, we expect that tasks in the "norm violation" category will show concordant brain locations in insular and cingulate cortices.

2 | MATERIALS AND METHODS

2.1 | Literature search and article selection

The literature was searched using the standard engines of Web of Science (http://apps.webofknowledge.com/), Scopus (https://www.scopus.com/home.uri), and PubMed (https://www.ncbi.nlm.nih.gov/pubmed/). We looked for keywords (fMRI and norm violation), and (fMRI and social norms) on April 3, 2017. This search yielded a total of 181 articles. After removing duplicates, articles were subjected to a series of selection criteria (Figure 1). First, articles needed to report experiments with human participants that used fMRI or PET to study tasks related to social norms (social norm representation, norm violation) and be written in English. These resulted in 116 articles that underwent full-text review. Articles that reported no fMRI data, only region of interest (ROI) results, only patient data, data on children, reviews, and articles with irrelevant tasks were excluded. Articles, which survived these criteria, underwent a full text review and were screened for healthy adults, reporting stereotaxic coordinates (Talairach or Montreal Neurological Institute, MNI) of whole-brain, within-group results using random effects analysis. To keep methodology constant, we included only experiments that used subtraction contrasts (i.e., A > B) and excluded experiments that addressed relations with specific task ratings (i.e., "negative correlation with unfairness level"). We also searched the references of all articles that passed the selection criteria and identified 14 additional articles that were eligible. Thus, data from a total of 36 articles were eligible for these meta-analyses.

To control within-group effects, a single experiment (i.e., contrast) from each article reporting coordinates relating to overall social norms was selected (Table 1). Experiments were further grouped into the two categories based on careful evaluation of the task description and responses required by the participant, as explained below. Social norm representations were defined as behavioral rules implicitly given, rather than explicitly given (i.e., laws and policies), related to maintenance of social order, such as criteria of fairness, moral beauty, and willingness to help. Eighteen articles reported experiments related to social norm representation by examining social integration and "good" actions such as maintenance of social integration and understanding morality (Table 1). The majority of articles used tasks that investigated social norms through the evaluation of social welfare and exchange of financial resources: these included the Public Goods Game (Cooper, Kreps, Wiebe, Pirkl, & Knutson, 2010), Ultimatum Game (Civai, Crescentini, Rustichini, & Rumiati, 2012; Corradi-Dell'Acqua et al., 2013; Harlé & Sanfey, 2012; Servaas et al., 2015; Tabibnia et al., 2008; Tomasino et al., 2013; Wu, Zang, Yuan, & Tian, 2015; Zhou, Wang, Rao, Yang, & Li, 2014), Trust Game (Delgado, Frank, & Phelps, 2005), and a Dictator Game (Feng et al., 2016; Strobel et al., 2011; Hu, Strang, & Weber, 2015). Players interacting in the Ultimatum and Dictator Games have different roles. In the Dictator Game, a dictator is given the opportunity to distribute points between himself and a recipient, whereas in the Ultimatum Game a recipient could accept or reject a dictator's offer. In the Dictator Game the dictator's offer remains unchanged. A dictator's 50–50 offer is considered as normatively fair, whereas any deviation (e.g., 60–40) is considered unfair. It has been shown that people not only prefer fair distributions (Güth, Schmittberger, & Schwarze, 1982) but also tend to spend their own resources to prevent norm violation at their own cost (Fehr & Fischbacher, 2004). Four articles used linguistic material ratings (moral versus semantic; Heekeren et al., 2005; Moll, Oliveira-Souza, Bramati, & Grafman, 2002; Prehn et al., 2008). One article used a social interaction task (Yoder and Decety, 2014). For sufficient power to detect sized effects in ALE meta-analyses, a minimum of 17 studies are needed (Eickhoff et al., 2017), thus, due to lack of experiments we did not examine moral ($n = 4$) and social ($n = 14$) norm representations separately.

Norm violation was defined as behavioral actions of not following behavioral rules related to the maintenance of social order. For this category, we selected contrasts related to activity elicited by negative emotions associated to situations with violation of norms, such as perception of embarrassing stories related to themselves or others, and unfair behavior related to the participant's self or the whole social group. Twenty nine articles used such tasks. These paradigms involved unfair behaviors (Baumgartner, Knoch, Hotz, Eisenegger, & Fehr, 2011; Cooper et al., 2010; Civai et al., 2012; Delgado et al., 2005; Feng et al., 2016; Gospic et al., 2011; Guo et al., 2013; Guo et al., 2014; Halko,

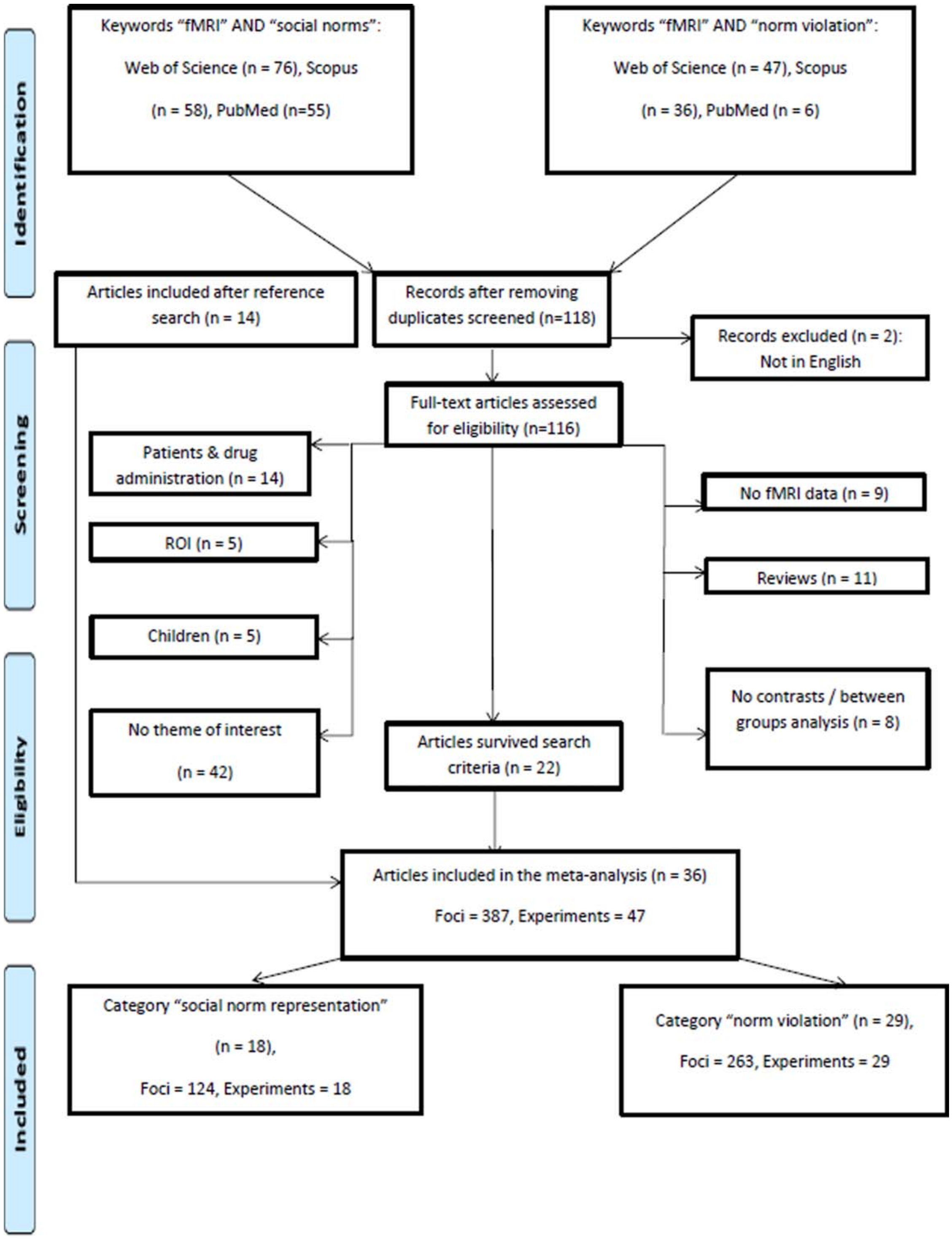

FIGURE 1 PRISMA flowchart for identification and eligibility of articles (template by Moher et al., 2009) [Color figure can be viewed at wileyonlinelibrary.com]

Hlushchuk, Hari, & Schürmann, 2009; Harlé et al., 2012; Hu et al., 2016; Kirk, Downar, & Montague, 2011; Sanfey et al., 2003; Servaas et al., 2015; Wu et al., 2015; Zheng et al., 2015) with more focus at disadvantageous inequity, which directly violate social norms (Fliessbach et al., 2012) and unfair behavior in terms of cooperation, like Prisoner's Dilemma (Rilling et al., 2008). In the case of the Prisoner's Dilemma task, two players decide to cooperate or betray each other, decisions that directly influence the player's budgets. Specifically, the fairest decision is to cooperate as both players increase their budgets slightly. If one player betrays the other the betrayer has higher gains than the other player. The worse circumstance is when both players betray each other, which results in loss of resources for both players. Others presented participants with personal embarrassing-norm violation stories (Berthoz et al., 2002), sentences about moral depravity (Takahashi

TABLE 1 Descriptive information of studies and contrasts used in the meta-analyses

First author, year	*N*	*F*	Education	Handedness	Age	Task	Contrast	Foci	Category
Baumgartner, 2011	32	0	n/r	Right	21.6 ± 2.2	Ultimatum game	Unfair > fair	17	NV
	32	0	n/r	Right	21.6 ± 2.2	Ultimatum game	Fair > unfair	4	NR
Berthoz, 2002	12	0	n/r	Right	19–37	Personal-impersonal, embarrassing-violation stories	Intentional violation > normal stories	18	NV
Civai, 2012	19	12	n/r	Right	n/r	Second-party and third-party splitting task	Unequal > equal	5	NV
	19	12	n/r	Right	n/r	Second-party and third-party splitting task	Equal > unequal	3	NR
Cooper, 2010	38	18	University	Right	18–46	Public goods game	Low > high (donation condition)	2	NV
	38	18	university	Right	18–46	Public goods game	High > low (donation condition)	1	NR
Corradi-Dell'Acqua, 2013	23	9	n/r	n/r	18–35	Ultimatum game	Ultimatum game > free win	17	NR
Delgado, 2005	12	n/r	n/r	Right	26.64 ± 4.11	Trust game	Share > keep	8	NR
	12	n/r	n/r	Right	26.64 ± 4.11	Trust game	Keep > share	2	NV
Denke, 2014	17	8	n/r	n/r	25 ± 3.54	Observation of norm-violation behavior's scenarios and norm-confirming behavior	Immoral > moral	3	NV
Feng, 2016	22	11	n/r	n/r	22.9 ± 1.6	Third-party punishment paradigm in monetary task	Unfair > Fair	19	NV
	22	11	n/r	n/r	22.9 ± 1.6	Third-party punishment paradigm in monetary task	Fair > unfair	16	NR
Fliessbach, 2012	64	32	n/r	n/r	22–33	Advantageous/disadvantageous payoffs	DI > E	1	NV
Gospic, 2011	17	12	n/r	Right	23.7 ± 4.2	Ultimatum game	(*u* > *f*) placebo	4	NV
Guo, 2013	21	n/r	n/r	n/r	22.44 ± 3.49	Ultimatum game	Unfair > fair	13	NV
Guo, 2014	18	5	n/r	Right	21.0 ± 2.10	Ultimatum game	Unfair > fair	10	NV
Halko, 2009	23	8	12 years of schooling/ university	Right	22–46	Ultimatum game	Unfair > fair (no competition)	12	NV
Harenski, 2006	10	10	n/r	Right	18–29	Watch-decrease picture evaluation task	Watch moral > odd– even baseline	7	NV
Harlé, 2012	38	23	n/r	n/r	18–70	Ultimatum game	Unfair > fair	12	NV
	38	23	n/r	n/r	18–70	Ultimatum game	Fair > unfair	3	NR

(Continues)

TABLE 1 (Continued)

First author, year	*N*	*F*	Education	Handedness	Age	Task	Contrast	Foci	Category
Heekeren, 2005	12	2	n/r	Right	25.75 ± 1.54	Linguistic material rating (moral\immoral, semantically correct\incorrect)	Moral decision > semantic decision	8	NR
Hu, 2015	36	24	n/r	n/r	22.72 ± 2.85	Dictator game	"Help" > "help_control"	10	NR
Hu, 2016	23	n/r	University	Right	19–25	Ultimatum game	Unfair > fair	3	NV
Luo, 2006	20	11	n/r	n/r	20–36	Illegal and legal behavioral scenarios' observation	Illegal > legal	9	NV
Kirk, 2011	40	21	n/r	n/r	n/r	Ultimatum game	Unfair > fair (controls)	11	NV
Melchers, 2015	60	39	University	n/r	22.95 ±5.38	Perception of embarrassments' films and normal films	Vicarious embarrassment films > control films	6	NV
Moll, 2002	7	4	n/r	Right	30.3 ± 4.7	Moral and non-moral sentences judgement	Moral > neutral	3	NR
Prehn, 2008	23	23	University	Right	25.17 ± 6.56	Socionormative and grammatical judgements rating	Socio-normative judgments > grammatical judgments	6	NR
Rilling, 2008	20	15	n/r	Right	21.2 ± 2.9	Prisoner's Dilemma	Unreciprocated > reciprocated cooperation	6	NV
Sanfey, 2003	19	0	n/r	n/r	n/r	ultimatum game	Unfair > fair	17	NV
Schreiber, 2012	19	n/r	University	n/r	20–23	Perception of norm-violating versus norm-consistent images	Norm-violating versus norm-consistent Images	5	NV
Servaas, 2015	120	120	University	Right	18–25	Ultimatum game	Unfair > fair	32	NV
	120	120	University	Right	18–25	Ultimatum game	Fair > unfair	4	NR
Tabibnia, 2008	**12**	**9**	Undergraduate	Right	**21.8**	Ultimatum game modification	High fairness > low fairness	8	NR
Takahashi, 2008	15	n/r	n/r	Right	20.1 ± 0.8	Sentences (neutral, moral beauty, and moral depravity)	Moral depravity-neutral	2	NV
	15	n/r	n/r	Right	20.1 ± 0.8	Sentences (neutral, moral beauty, and moral depravity)	Moral beauty > neutral	5	NR
Tomasino, 2013	17	0	n/r	Right	27.35 ± 3.88	Ultimatum game	Fair > unfair	3	NR
Treadway, 2014	41	n/r	n/r	n/r	n/r	Scenarios rating (neutral, emotionally harmful)	Intentional > unintentional (all subjects)	18	NV
Wagner, 2011	18	18	n/r	n/r	25–30	Emotion conditions task	Guilt > shame + sadness	2	NV

(Continues)

TABLE 1 (Continued)

First author, year	*N*	*F*	Education	Handedness	Age	Task	Contrast	Foci	Category
Wu, 2015	32	24	University	Right	22.31 ± 2.35	Ultimatum game, dictator game	Unfair > fair Ultimatum Game	1	NV
	32	24	University	Right	22.31 ± 2.35	Ultimatum game, dictator game	Fair Ultimatum Game > unfair Ultimatum Game	3	NR
Yoder, 2014	40	21	n/r	n/r	21 ± 2	Social interactions' modulation task	Bad > good actions	9	NV
	40	21	n/r	n/r	21 ± 2	Social interactions' modulation task	Good > bad actions	15	NR
Zheng, 2015	25	18	n/r	Right	21.44 ± 3.38	Ultimatum game	Unequal > equal	15	NV
Zhou, 2014	28	15	University	Right	25.07 ± 3.35	Ultimatum game	Unfair > fair	4	NV
	28	15	University	Right	25.07 ± 3.35	Ultimatum game	Fair > unfair	1	NR

et al., 2008), scenarios with norm-violations (Denke et al., 2014), picture evaluation task with scenes with moral norm violations (Harenski and Hamann, 2006), norm violated behavior's scenarios (Luo et al., 2006), embarrassing content (Melchers et al., 2015), norm-violating images (Schreiber and Iacoboni, 2012), a task that modulated social interaction (Yoder and Decety, 2014), different scenarios based on intentional and unintentional norm violation (Treadway et al., 2014), and a task that modulated of emotions related to social content (Wagner et al., 2011). Overall, 29 experiments included in this category reflect social emotions associated with norm violation.

2.2 | Meta-analysis

Activation likelihood estimation (ALE) is a meta-analysis method, which can be used for whole-brain, random-effects voxel-wise imaging analysis (Eickhoff et al., 2009, 2017; Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012). For our study, we used GingerAle version 2.3.6 (freely available at brainmap.org/ale). It uses foci combined from different studies to create a probabilistic map of activation that is thresholded and compared against a null distribution at a voxel-by-voxel level.

This map provides the clusters (peak and volume) that have a significant likelihood of being detected across studies within a stereotaxic coordinate space. Specifically, activation likelihood estimates are calculated for each voxel by modeling each coordinate with an equal weighting using a 3-D Gaussian probability density function. ALE values can be thresholded using a cluster-forming (i.e., in terms of magnitude) and a cluster-level (i.e., in terms of the size of the cluster) criterion. Thus, ALE values provide information about statistical maps of estimated activation regarding tasks included in the analyses. To create ALE maps we used contrast coordinates (i.e., experiments) reported in eligible, previously published fMRI studies that include experiments on social norms "overall" and subcategories for (a) social norm representation and (b) norm violation. The overall analysis (i.e., social norms overall) allows for identifying concordance at the single study level with higher power as more studies are included in this analysis; however, contrast analysis allows for examining the conjunction and differences between the subcategories. Montreal Neurological Institute (MNI) coordinates were transformed into Talairach coordinates. Significance is assessed using a cluster-level correction for multiple comparisons at $p = .05$ and a cluster-forming threshold $p < .001$ (Eickhoff et al., 2012, 2017). A contrast analysis was performed on the thresholded ALE maps of social norm representation and norm violation categories to identify concordance that was common (i.e., conjunction) and different for these categories. Because ALE maps are already thresholded for multiple comparisons a threshold of uncorrected 0.01, with 5000 permutations, minimum volume 50 mm^2 was used (e.g., Arsalidou, Pawliw-Levac, Sadeghi, & Pascual-Leone, 2017; Sokolowski, Fias, Mousa, & Ansari, 2017).

3 | RESULTS

Articles included in the meta-analyses report data on 993 participants (Table 1). Eight articles did not report gender; of the remaining articles, 52% were female participants. About a half of articles that reported

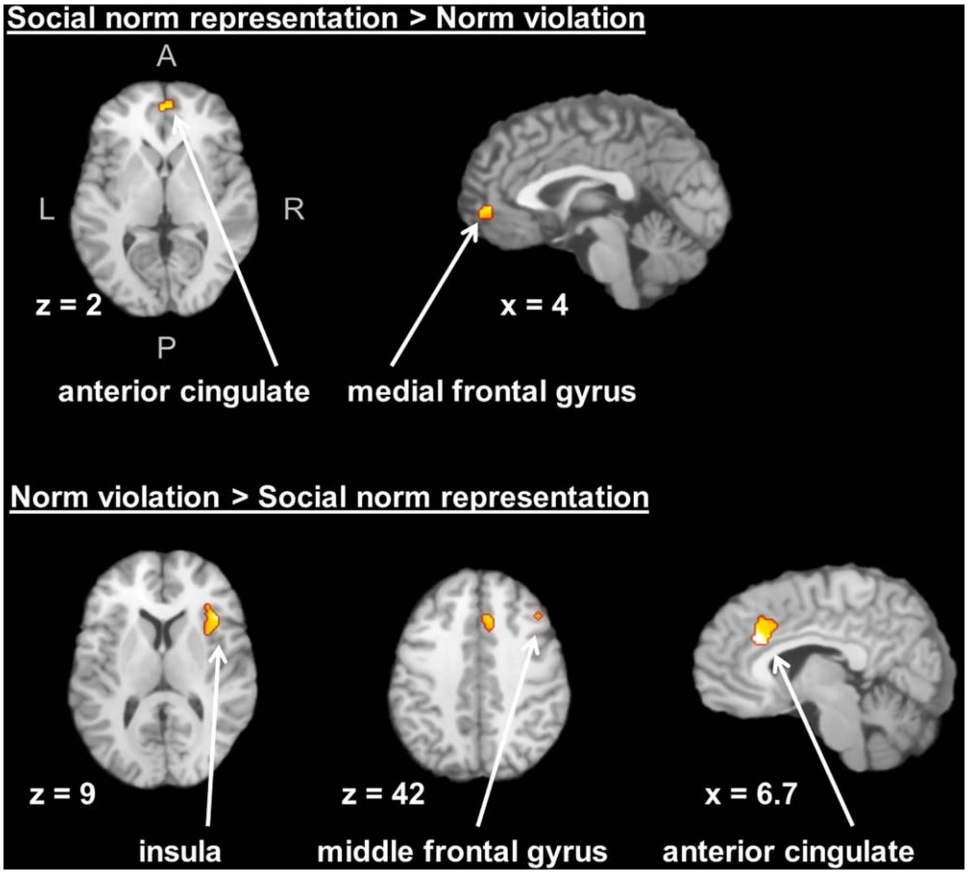

FIGURE 2 Brain maps demonstrating significant ALE values for each category. Left = left. Note: coordinates are in Talairach space. Cluster-level correction $p = .05$ for multiple comparisons with cluster forming threshold $p < .001$ [Color figure can be viewed at wileyonlinelibrary.com]

handedness (42%) tested participants who were right-handed (100%). Four articles did not report the age of the participants. When an age range was given, the median of the age range was used in calculating the average of the sample, which was a 23.89 ± 6.28 year. Twenty-five percent of the articles reported the education level of participants, and 100% of the participants were reported to have some university education (undergraduate or graduate). Bottom of Figure 1 shows the number of articles, number of experiments, and number of foci included in each meta-analysis.

3.1 | ALE maps

3.1.1 | Social norms (overall)

All tasks related to social norms show concordance in five clusters (Table 2). The largest cluster with the highest ALE value is found in the right insula (BA 13). The second largest cluster is found in the left medial frontal gyrus (BA 32) that extended to the cingulate gyrus (BA 32). Prefrontal activity is also observed in the right superior and middle frontal gyri (BA 9 and BA 10). Other regions include the left insula and claustrum.

3.1.2 | Social norm representation

Social norm representations show concordance in a cluster that includes the left anterior cingulate and right medial frontal gyrus (BA 10; Figure 2 and Table 2).

3.1.3 | Norm violation

Five suprathreshold clusters were detected for norm violation (Figure 2 and Table 2). The one with the highest likelihood of being detected is in the right insula (BA 13). Other regions include right cingulate gyrus (BA 32), left insula (BA 13) and claustrum, and right middle and superior frontal gyri (BA 9 and 10).

3.1.4 | Social norm representation versus norm violation

No common clusters survive the conjunction between social norm representation and norm violation. Compared to norm violation, social norm representation shows greater concordance in the anterior cingulate gyri (BA 32) and right medial frontal gyrus (BA 10), whereas compared to social norm representation, norm violation shows greater concordance in the right insula and claustrum and more dorsal parts of the cingulate gyrus (BA 24, 32; Table 2).

4 | DISCUSSION

We examined neural correlates of social norms using quantitative ALE meta-analyses. Processing tasks that assess social norms show concordance mainly in frontal regions with clear significant distinctions between instances of social norm representation and norm violation. Specifically, our results reveal two key findings. First, norm violation tasks show that the area with the highest likelihood of being active is

TABLE 2 Concordant areas for each category

Category	Volume mm^3	ALE value	Talairach coordinates x	y	z	Brain area	BA
Social norms (overall)	4016	0.0480	34	18	4	Right insula	13
	3392	0.0429	−4	10	46	Left medial frontal gyrus	32
		0.0342	4	20	38	Right cingulate gyrus	32
		0.0306	4	22	28	Right cingulate gyrus	32
	1808	0.0270	−30	20	8	Left insula	13
		0.0253	−30	14	−2	Left claustrum	
		0.0251	−34	14	0	Left insula	13
	1736	0.0276	36	40	20	Right middle frontal gyrus	10
		0.0236	34	26	32	Right middle frontal gyrus	9
	936	0.0297	8	52	24	Right superior frontal gyrus	9
Social norm representation	1184	0.0163	−4	50	−2	Left anterior cingulate	10
		0.0116	10	48	6	Right medial frontal gyrus	10
Norm violation	4368	0.0472	34	18	4	Right insula	13
	4192	0.0339	6	18	38	Right cingulate gyrus	32
		0.0329	−4	10	48	Left superior frontal gyrus	6
		0.0306	4	22	28	Right Cingulate gyrus	32
		0.0203	−6	28	30	Left cingulate gyrus	9
	1912	0.0258	−30	20	8	Left insula	13
		0.0239	−30	14	−2	Left claustrum	
	1464	0.0236	34	26	32	Right middle frontal gyrus	9
		0.0175	34	42	22	Right middle frontal gyrus	10
		0.0150	42	22	40	Right middle frontal gyrus	8
	856	0.0255	6	52	24	Right superior frontal gyrus	9
Social norm representation > norm violation	1080	3.7190	2	45	−.7	Right anterior cingulate gyrus	32
		3.5400	4	48	2	Right anterior cingulate gyrus	
		3.3528	−1	52	−2	Left anterior cingulate gyrus	
		3.2389	4	52	0	Right medial frontal gyrus	10
		3.0902	5	51	−4	Right medial frontal gyrus	10
Norm violation > social norm representation	2848	3.7190	40.3	19.2	3.9	Right insula	13
		3.5401	37	21	2	Right insula	13
		3.2389	37	13	9	Right insula	13
		3.1560	34.8	10.8	3.7	Right insula	13
	1976	3.7190	6.7	24.3	27.3	Right anterior cingulate gyrus	24
		3.5400	0	26	26	Left cingulate gyrus	32
		3.3528	−2	30	30	Left cingulate gyrus	32
		3.2389	6.5	20.6	35.2	Right cingulate gyrus	32
		3.0902	9.3	16	36.7	Right cingulate gyrus	32
		2.9478	−6	24	26	Left anterior cingulate gyrus	24
	616	3.0902	35.3	24.7	36.7	Right middle frontal gyrus	9
		2.9112	34.9	23.1	32.2	Right middle frontal gyrus	9
		2.7703	41	22	42	Right middle frontal gyrus	8
Conjunction between norm violation and social norm representation						No clusters found	

the insula, along with dorsolateral prefrontal regions and dorsal parts of the cingulate gyrus. Secondly, social norm representations rely on activity mainly in ventromedial prefrontal regions; medial frontal and anterior cingulate gyri. Findings are in agreement with Montague and Lohrenz (2007) hypothesis, which suggests that different systems underlie different social norm processes. We did not replicate any of the concordance of posterior brain regions observed by Feng et al. (2015), likely because these were smaller clusters that did not survive our cluster-level correction for multiple comparisons. Alternatively, lack of concordance in posterior regions may be due to visual-spatial heterogeneity in task paradigms assessing "social norms." Importantly, we show that according to contrast analyses, the anterior cingulate and medial frontal gyri are significantly more concordant for social norm representation processing, whereas the right insula, dorsolateral prefrontal, and the dorsal cingulate cortices are significantly more concordant to norm violation processing.

4.1 | Social norm representation

Social norm representation tasks show concordant activity in the left anterior cingulate (BA 32) extended to right medial frontal gyrus (BA 10). BA 10 is mainly implicated in inferences of another person's intentions, mostly social intentions (Ciaramidaro et al., 2007; Frith & Frith, 2003). The "gateway hypothesis" states that BA 10 activity supports mechanisms that allow individuals to react to environmental stimuli based not on immediate perceptual information but on self-generated and maintained representations (Burgess, Dumontheil, & Gilbert, 2007). Thus, this region seems to be mainly involved in processes of relational integration by manipulation of self-generated information and highly abstract information (Christoff et al., 2001; Christoff, Keramatian, Gordon, Smith, & Mädler, 2009). Previous fMRI and transcranial direct current stimulation (tDCS) findings propose the right lateral prefrontal cortex to play a key role in the behavioral control and judgment between fair and selfish responses (Ruff, Ugazio, & Fehr, 2013). The findings suggest that activity in the dorsal anterior cingulate cortex has been implicated in processing the detection and appraisal of social processes, such as exclusion and "social pain" phenomenon (Corradi-Dell'Acqua, Tusche, Vuilleumier, & Singer, 2016; Dedovic, Slavich, Muscatell, Irwin, & Eisenberger, 2016; Kawamoto, Ura, & Nittono, 2015). We suggest that prefrontal BA 10 serves to support abstract representation of existing norms. It would be interesting to examine the involvement of these regions in newly formed social norm representations.

4.2 | Norm violation

Processing norm violations elicits activity in the insular cortex. The anterior insula is generally considered as a relay station that sends interoceptive information to the cortex (Menon & Uddin, 2010; Seeley et al., 2007; Taylor, Seminowicz, & Davis, 2009). However, its activity is also associated in all sorts of cognitive and affective activities (Duerden et al., 2013; Uddin, 2015). Social-emotional tasks reveal activity in the anterior-ventral insula, while cognitive tasks elicited activation in the anterior-dorsal part (Kurth, Zilles, Fox, Laird, & Eickhoff, 2010). It was suggested that the insula also plays a role in fairness-related behavior (Moll, Oliveira-Souza, & Zahn, 2008; Corradi-Dell'Acqua, 2013). In particular, the right insula (BA 13) and anterior cingulate have been also shown to activate to first-hand and vicarious experiences of unfairness (Cheng et al., 2015; Cheng et al., 2017), lie evaluation (Lelieveld, Shalvi, & Crone, 2016), and detection of distributional inequity in economic tasks (Zhong, Chark, Hsu, & Chew, 2016), which could be explained as a violation of social norms. Patients with damaged insula have abnormal expressions of trust in economics tasks such as the Trust Game, which leads to an inability to detect norm violation effectively (Belfi, Koscik, & Tranel, 2015). Moreover, insular activation has an indirect influence on social preferences as aversive emotional states increase the frequency of receiving unfair monetary offers, which correspond to worse detection of norm violation (Harlé et al., 2012).

We also find concordance in the anterior cingulate cortex. Previous findings also suggest that anterior cingulate cortex is implicated in social behavior and possibly processing costs and benefits (Apps, Rushworth, & Chang, 2016). Specifically, the anterior cingulate cortex activates when processing rewards that other people receive (Lockwood, Apps, Roiser, & Viding, 2015) and when others make decisions related to prediction error (Apps, Green, & Ramnani, 2013). It was shown that anterior cingulate cortex to anterior insula connectivity may also reflect basic prosocial motivation (Hein, Morishima, Leiberg, Sul, & Fehr, 2016). Furthermore, people with higher egoistical motivation, who more frequently violate social norms, have weaker connectivity between these regions (Hein et al., 2016). This is consistent with the hypothesis that the cingulate gyrus and insula are involved in conversion of affective goals into cognitive goals (Arsalidou & Pascual-Leone, 2016) as a feeling of effort in cognitively demanding situations (Arsalidou et al., 2017). A generic role of the insula as part of a salience network has been suggested (Menon & Uddin, 2010; Uddin, 2015). We propose that the role of the insula in norm violation may be related to a generic sense of cognitive demand related to the "inequity encoding" (Hsu, Anen, & Quartz, 2008) and fairness-related behavior.

Other areas related to norm violation include the right cingulate gyrus and left claustrum. A meta-analysis suggests that cingulate cortex is implicated in six domains according to the activation's map: attention, pain, language, action execution, emotions, and memory (Torta & Cauda, 2011). The cingulate cortex has received extensive attention in its role in social norms and was studied under paradigms of altruistic punishment in social dilemmas (Fehr & Camerer, 2007; Feng et al., 2016; Sanfey, Loewenstein, McClure, & Cohen, 2006). Moreover, the dorsal anterior cingulate cortex through its strong connectivity with the insula could be related to the detection of social norm violations during conflict monitoring and moral context evaluation (Güroğlu et al., 2011; Denke et al., 2014). Therefore, in processing norm violations, we suggest that the role of the dorsal cingulate to be a hub for information where signals are sent to the insula to help evaluate possible norm violation; such process would not be pertinent during social norm representation.

Norm violation studies also show concordant activity in the right middle frontal gyrus (BA 10). The middle frontal gyrus BA 10 has been associated with general abstract representations that require processing of internally generated information (Christoff & Gabrielli, 2000; Chrisoff et al., 2009). Specific to social cognition, the right lateral prefrontal cortex has been shown to be linked to processing of context-dependent social interaction regulated by norms of fairness in case of financial exchange (Ruff et al., 2013), understanding of social standards related to fairness norms and good reputation (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; Knoch, Schneider, Schunk, Hohmann, & Fehr, 2009), and inferences of another person's intentions, mostly social intentions (Ciaramidaro et al., 2007; Frith & Frith, 2003). Evidence from lesions studies and meta-analysis show that BA10 is also involved in performance theory of mind tasks, and social cognition in general (Gilbert et al., 2006; Roca et al., 2011). We suggest that BA 10 contribution to processing social norms could be related to the detection of norm violation and the possibility to process knowledge about the existing norm. According to the "gateway hypothesis" (Burgess et al., 2007), BA 10 contributes to forming self-generated representations that are not necessarily environmentally based. This hypothesis is consistent with claims that suggest BA 10 to process highly abstract information (Christoff et al., 2001; Christoff et al., 2009). Based on this literature, we suggest that BA 10 contribution to processing social norms could be related to the detection of norm violation and the possibility to process knowledge about the existing norm. This interpretation is also consistent with Montague and Lohrenz (2007) model that suggests the existence of specific brain representations to keep information about existing social norms.

Another significantly concordant region for norm violation is the claustrum, a region adjacent to the insula. The claustrum due to the numerous input–output connections with limbic, prefrontal, sensory, motor, and associative cortices was assumed to act as a cross-modal integrator (Goll, Atlan, & Citri, 2015). It has also to been identified as a key region of a network that supports consciousness (Koubeissi, Bartolomei, Beltagy, & Picard, 2014). Claustrum activation is also reported in studies of fairness-related inequity during decision-making (Nihonsugi, Ihara, & Haruno, 2015); however, its role was not semantically defined. A meta-analysis reports that claustrum is involved in general empathy and pain-related empathy processing (Gu, Hof, Friston, & Fan, 2013). Concordant activity in this region supports its nonrandom appearance in social cognition studies. Although further work is needed to clearly define the functions of the claustrum, some evidence point to its special impact on social behavior. Studies show that claustrum activity is related to processes such as fear recognition (Stein, Simmons, Feinstein, & Paulus, 2007) and associative learning in animals (Chachich & Powell, 2004), and multimodal information processing and emotional responses (Bennett & Baird, 2006) in healthy humans. Anatomically the volume of the claustrum is deficient in clinical populations that suffer from socio-cognitive deficits. For instance, claustrum volume in autism patients is 22% reduced compared to healthy children from 4 to 8 years (Wiegel et al., 2014). Examination of altered connectivity in individuals with autism and comparison with behavioral performance suggest that claustrum and its network interactions could significantly contribute in social and communication development (Wiegel et al., 2014). Owing to this multimodal integration, we propose that the claustrum could integrate aversive emotional signals and signals from associative cortices in norm violation processing.

Our analysis also found concordant activity in left superior frontal gyrus (BA 6). The superior frontal gyrus (BA 6) has been linked to higher cortical functions such as internal guidance of the behavior and its control (Luria, 1966), hand motor representations (Vara et al., 2014), and working memory (Wager & Smith, 2003 for review; du Boisgueheneuc et al., 2006). Specifically, it is suggested that this region is involved in fronto-parietal cortical network associated with attention, working memory, episodic retrieval, and conscious perception (Naghavi & Nyberg, 2005 for review). In addition, an activation of cingulate cortex/superior frontal cortex has been found during processing psychological self (Hu et al., 2016). It has been suggested that cingulate cortex is involved in conflict monitoring (Botvinick, Cohen, & Carter, 2004), which could be applicable for socially driven interactions (Lavin et al., 2013). Thus, cingulate cortex activation during norm violation processing could be related to direct conflict monitoring and evaluation with self-reference (i.e., what does norm violation mean for me). We suggest that activation of the left superior frontal gyrus in the same cluster as the right cingulate gyrus corresponds with the need to continuously monitor and adjust information about others behavior in working memory relevant to norm violation processing. Overall, concordant fMRI findings suggest that activation of the lateral prefrontal cortex during affective information processing, of the anterior cingulate cortex during monitoring any conflict, and of the insula during emotional processing of aversive signals and responses to unfairness may be involved into driving a motivation to act against norm violations.

5 | LIMITATIONS

Data presented here represent concordance across fMRI studies that investigated social norms overall and as two different subcategories in healthy adults. Optimally, further cortical differentiation would be possible with additional social norm subcategories such as social norm representation in social and moral domains and social conformity. However, an insufficient number of experiments did not allow for examining concordance in these subcategories (i.e., $n < 17$; Eickhoff et al., 2017). Second, we examine the activity to various tasks that may elicit a differentiated brain response, such as moral paradigms (scenario ratings) and classic economic tasks (e.g., Ultimatum Game, Trust Game). In the future, as more experiments become available, it could be possible to distinguish between these domains within social norms. Task characteristics (e.g., visual-spatial features and task demands such as economic games versus reading and rating tasks) could also influence heterogeneity across studies. Importantly, our goal was to identify common patterns in brain locations related to social norms regardless of task specificities, and our results show that this concordance is observed in anterior brain areas. Last, a shortcoming of the ALE method is that it does not use effect sizes (as seed-based mapping (SDM; Radua & Mataix-Cols, 2012; Radua et al., 2012)). Although there are no available methods for performing robustness analyses with GingerALE, simulations of ALE analyses have been performed to test sensitivity, ensuing cluster sizes, number of incidental clusters, and statistical power (Eickhoff et al., 2016). They did so by systematically varying the overall number of experiments and experiments activating the simulated "true" location (Eickhoff et al., 2016 for details) and a recommended minimum number of experiments to reach sufficient power ($n = 17–20$; Eickhoff et al., 2017). Despite these shortcomings, the current meta-analyses present new knowledge on the topic of social norms with a meta-analytic methodology that provides coordinates in stereotaxic space, which is advantageous to standard reviews.

6 | CONCLUSION

Social norms are fundamental for our daily social interactions and our meta-analyses show that different aspects associated with social norms elicit activity in distinct brain regions. The right anterior cingulate and medial frontal gyri (BA 10) are critical for social norm representation (social and moral), whereas the insula, dorsolateral, and dorsal cingulate cortices are key for processing norm violation. Stereotaxic coordinates reported here can serve as a normative adult framework for targeted future studies and may be beneficial for studies investigating social norm compliance and enforcement in patients with disorders such as autism spectrum disorder.

CONFLICT OF INTEREST

The authors declared that they have no conflict of interest.

ORCID

Oksana Zinchenko http://orcid.org/0000-0002-7976-3224
Marie Arsalidou http://orcid.org/0000-0001-9879-3894

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