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Review article

## Neural basis of in-group bias and prejudices: A systematic meta-analysis

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## ABSTRACT

In-group favoritism and prejudices relate to discriminatory behaviors but, despite decades of research, understanding of their neural correlates has been limited. A systematic coordinate-based meta-analysis of functional magnetic resonance imaging (fMRI) studies (altogether 87 original datasets,  $n = 2328$ ) was conducted to investigate neural inter-group biases, i.e., responses toward in-group vs. out-group in different contexts. We found inter-group biases in some previously identified brain regions (e.g., the medial prefrontal cortex, insula) but also in many previously non-identified brain regions (e.g., the cerebellum, precentral gyrus). Sub-group analyses indicated that neural correlates of inter-group biases may be mostly context-specific. Regarding different types of group memberships, inter-group bias toward trivial groups was evident only in the cingulate cortex, while inter-group biases toward “real” groups (ethnic, national, or political groups) involved broader sets of brain regions. Additionally, there were heightened neural threat responses toward out-groups’ faces and stronger neural empathic responses toward in-groups’ suffering. We did not obtain significant publication bias. Overall, the findings provide novel implications for theory and prejudice-reduction interventions.

## 1. Introduction

The United Nations Commission on Human Rights (1998) has postulated that international community should “protect effectively the human rights of all persons belonging to national or ethnic, religious and linguistic minorities without any discrimination and in full equality before the law”. Also, the EU Charter of Fundamental rights states that “any discrimination based on any ground such as sex, race, colour, ethnic or social origin, genetic features, language, religion or belief, political or any other opinion, membership of a national minority, property, birth, disability, age or sexual orientation shall be prohibited”.

As is widely known, prejudices and discrimination toward minorities reached extreme levels during the World Wars, including e.g. imprisonments and executions of minority members. Although prejudices and discrimination toward minorities, in general, have apparently reduced from those times, it seems that the decrease has ceased within the past decades. Specifically, it has been reported that prejudices toward ethnic minorities have increased within the past decade in many countries such

as Ireland (Gilligan and Lloyd, 2006) and the Netherlands (Thijs et al., 2018). Further, as much as approximately 20 % of European citizens would not like to have Muslims as their neighbors (Strabac and Listhaug, 2008) and ethnic discrimination in hiring decisions has remained widespread in the OECD countries between 1990–2015 (Zschirnt and Ruedin, 2016). Discrimination and prejudices constitute a societal challenge not only in the Western countries but globally: for example, in Latin America (Patrinos, 2000), Middle East and Africa (Vogt et al., 2016), and Russia (Bessudnov and Shcherbak, 2020). Lastly, recent reports have clearly indicated that concern about the COVID-19 pandemic has resulted in a slight increase in general xenophobia and negative attitudes toward some populations (Dhanani and Franz, 2021; Reny and Barreto, 2020).

Over decades, a number of interventions have been developed to alleviate prejudices: for example, educational interventions, collaborative projects with out-group members, and mass-media interventions (Lemmer and Wagner, 2015; Rutland and Killen, 2015). Many of the previously developed interventions, however, are found to be ineffective

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**Table 1**  
Previous neural models of in-group bias, prejudices, and prejudice regulation.

Model	Mental function(s)	Involved brain region (s)
In-group bias network (Molenberghs and Louis, 2018)	Facial and action perception	Amygdala, fusiform face area
	Empathy	Dorsal anterior cingulate cortex, anterior insula
	Mentalizing	Medial prefrontal cortex, temporoparietal junction
	Moral sensitivity	Lateral orbitofrontal cortex
	Reward system	Medial orbitofrontal cortex, striatum
Prejudice network (Amodio, 2014)	Early affective responses	Amygdala
	Impressions, empathy, mentalizing	Ventral medial prefrontal cortex
	Visceral subjective emotions	Insula
	Reward processing, anticipation of outcomes	Striatum
Prejudice regulation network (Amodio, 2014)	Affective judgment, monitoring of social cues, adjustment of behavior, contingency-based learning	Orbitofrontal cortex
	Conflict processing	Dorsal anterior cingulate cortex
	Representation of interpersonal cues	Medial prefrontal cortex
	Monitoring of external cues	Rostral anterior cingulate cortex
	Response selection	Dorsolateral prefrontal cortex
	Response inhibition	Inferior frontal gyrus

among at least some groups of individuals (Lemmer and Wagner, 2015; Rutland and Killen, 2015). Some interventions may even increase prejudices in individuals with prejudice-prone styles of thinking (Asbrock et al., 2012) or high baseline level of prejudices (Vorauer and Sasaki, 2010). In addition, it appears that intervention-induced reductions in prejudices are typically less evident among minorities (Lemmer and Wagner, 2015). Overall, current evidence has implied that most effective interventions for reducing prejudices may include direct or indirect contacts with out-group members (Lemmer and Wagner, 2015; Pettigrew and Tropp, 2006). However, also contact-based interventions can have adverse outcomes for intergroup relations. Indeed, negatively experienced contacts may increase racism and avoidance more strongly than positively experienced contacts may reduce them (Barlow et al., 2012). To date, a major open question has been *why* contact-based interventions may be more effective than other interventions, and in which situations could contacts most effectively reduce prejudices (Lemmer and Wagner, 2015). It has been emphasized that increasing knowledge about neural correlates of inter-group biases could enhance understanding about the effectiveness of prejudice-related interventions (Molenberghs, 2013).

A central source of discrimination is suggested to be in-group bias (Greenwald and Pettigrew, 2014). In-group bias (often called also as “in-group favoritism”) refers to differences in mental processing of in-group vs. out-group members (or cues closely related to identities of in-group or out-group such as national flags). In-group bias can be both implicit and explicit (Amodio and Mendoza, 2010) and occur between any types of social groups such as political, ethnic, national, regional, or even trivial groups (i.e., groups that can be artificially created and differentiated by trivial criteria such as the color of clothing) (Otten, 2016; Tajfel et al., 1971). Typical examples of in-group bias include making moral decisions that are favorable for one’s in-group (Cadsby et al., 2016) and higher prosocial behavior toward in-group compared to

out-group members (Fiedler et al., 2018). Accordingly, in-group bias is a close concept to prejudices that refer to negative evaluations or affective responses toward members of a social group on the basis of pre-conceptions (Amodio, 2014). In this paper, we use the concept of “inter-group bias” referring to either positively or negatively biased processing of in-group vs. out-group.

Recent reviews have postulated brain networks for in-group bias, prejudices, and prejudice regulation. The models are presented in Table 1. Taken together, the models propose that, first, in-group bias and prejudices can be observed in a variety of brain regions, including both subcortical and cortical regions. Second, the models postulate that in-group bias and prejudices are evident throughout stages of processing: from primary responses (e.g., the amygdala) to higher-level cognitive processing (e.g., the inferior frontal cortex). Third, the models make an important proposal that neural correlates of in-group bias and prejudices involve largely overlapping brain regions and, thus, cannot be separated from each other at a neural level.

Two important issues, however, have remained unclear in the neural models related to inter-group bias. First, previous neural models of in-group bias or prejudices have not differentiated between different types of group membership; that is, whether similar neural correlates of inter-group biases are present between ethnic, national, regional, political, and trivial groups. Thus, the models implicitly suppose that any type of group membership would possibly correlate with an approximately similar brain network. Nevertheless, there are reasons to suppose that there might be differences in neural inter-group biases in contexts of different group memberships. Specifically, current social psychological models propose that inter-group bias involve relatively stable belief systems about out-groups and immediate negative responses toward out-groups (Hodson, 2014). It can be speculated that such stabilized belief systems may be more likely present toward ethnic out-groups (as ethnicity is stable over one’s life course) than toward trivial out-groups (that can be experimentally acquired and extinguished within very short periods of time). Moreover, immediate affective responses might be more easily evoked toward ethnic out-groups (who can be identified by merely visual inspection from bodily appearance) than toward political out-groups (accessible only via higher-level cognitive processing of individual’s political opinions). In addition, inter-group bias is stronger in presence of a realistic possibility for an inter-group conflict (Zarate et al., 2004) that, in turn, may more likely occur between “real” groups such as different political or national groups than trivial groups. Finally, single fMRI studies have supported the idea about different neural correlates in context of different types of group memberships. For example, neural inter-group bias during empathic processing may be stronger toward ethnic than toward trivial groups (Contreras-Huerta et al., 2013). To date, a meta-analysis examined neural correlates of racial categorization during visual perception (Bagnis et al., 2020) but no meta-analysis has investigated other types of group memberships and compared their neural correlates.

Another aspect that remains unclear in the previous neural models of inter-group bias and prejudices is whether neural inter-group bias would be more evident during some mental processes than others: for example, during face perception, empathy-related processing, or higher-level cognitive processing. This issue has remained unclear not only in the neural models (Amodio, 2014; Molenberghs and Louis, 2018) but also in behavioral models of inter-group bias: some researchers have emphasized that inter-group bias results primarily from spontaneous negative emotional responses toward out-group members (Wilder and Simon, 2001), while others have postulated that inter-group bias and prejudices develop as an interplay between biases at many stages of mental processing, starting from immediate affective responses and ranging to higher-level cognitive belief systems and memory functions (Hodson, 2014). Additionally, also empirical evidence from fMRI studies on this topic have been inconclusive. For instance, some studies have found evidence for a clear inter-group bias during social judgment (Falk et al., 2012; Lin et al., 2018), face processing (Chiao et al., 2008; Kaplan et al.,

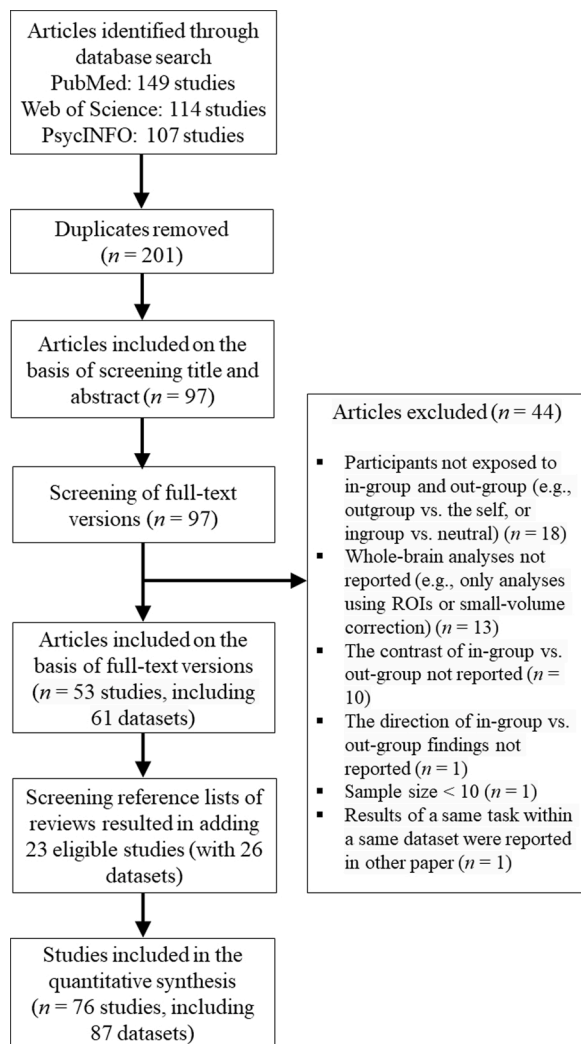


Fig. 1. Literature search process.

2007), or higher-level cognitive processing (Brown et al., 2017), while other studies have obtained no neural inter-group bias (Kang et al., 2021; Katsumi and Dolcos, 2017; Littlefield et al., 2015; Steines et al., 2020). During empathic processing, studies have consistently reported some kind of neural inter-group bias but no consensus has been reached on involved brain regions (Cao et al., 2015; Mathur et al., 2010). Overall, it can be supposed that the brain may recruit different neural networks in a flexible way according to skills that are needed in each context: different perceptual, emotional, and cognitive brain networks may be recruited when one should help an in-group member, when one should recognize an out-group member's facial expressions, and when one needs to memorize an out-group member's actions. Accordingly, a review emphasized that "[d]epending on the bias (e.g., perceptual vs. empathic bias) and the modalities (e.g., faces vs. words) implicated, different neural networks might be involved" but more knowledge on this topic is needed (Molenberghs and Louis, 2018).

The aim of the current study was to conduct a systematic literature search and meta-analysis of functional magnetic resonance imaging (fMRI) studies to investigate the neural basis of inter-group bias in healthy adults. Our primary research question was whether there are differences in responses of the blood-oxygenation-level dependent (BOLD) signal toward in-group vs. out-group. As secondary research questions, we aimed to examine (1) whether different types of group memberships (i.e., ethnic, national or regional, political, or trivial groups) elicit different neural inter-group biases, and (2) whether neural

inter-group bias is more evident during specific mental processes than others (i.e., during face processing or empathy-related processing, social judgment, moral evaluation, or higher-level cognitive processing).

On the basis of previous neural models of in-group bias and prejudices, our primary hypothesis was that inter-group bias is evident in the neural activity. As secondary hypothesis, in accordance with previous neural models, we supposed that neural correlates of inter-group bias are approximately similar in context of different types of group memberships (i.e., between ethnic, political, national, or trivial groups). Finally, based on the previous models, we hypothesized that there would be a neural inter-group bias at all phases of mental processing but in different brain regions: (i) inter-group bias during face processing would be evident in the amygdala and fusiform face area, (ii) inter-group bias during empathy-related processing in the insula and anterior cingulate cortex; (iii) inter-group bias during moral processing in the orbitofrontal cortex and striatum; (iv) inter-group bias during social judgment in the medial prefrontal cortex, temporoparietal junction, and orbitofrontal cortex; and (v) inter-group bias during higher-level cognitive processing (e.g., memory and learning) in the dorsolateral prefrontal cortex and inferior frontal cortex.

## 2. Methods

### 2.1. Literature search

The article selection process is illustrated in Fig. 1. The MOOSE (Meta-analysis of Observational Studies in Epidemiology) Checklist was followed throughout the meta-analysis (see Supplementary Material). Additionally, the most recent recommendations for conducting a neuroimaging meta-analysis were followed through the process (when applicable) (Müller et al., 2018). The literature search was conducted using PsycINFO, PubMed, and Web of Science. There were no restrictions regarding language, publication date (published before the 9th March 2021), number of citations, or publication status, and the search was directed to the fields of title and abstract. Search terms were: ("fmri" OR "functional MRI" OR "BOLD") AND ("prejudice" OR "ingroup" OR "outgroup" OR "group membership" OR "group bias" OR "ingroup favoritism" OR "racial bias" OR "ethnic bias") (for more details, please see Supplementary Methods).

After removing duplicates, all identified studies were screened based on the title and abstract and defined as eligible/ineligible for the meta-analysis. After reviewing the titles and abstracts, the identified full-text articles were screened more precisely on the basis of the exclusion and inclusion criteria (described in the next section). In addition to original research papers, the reference lists of all meta-analyses and reviews (identified by the search terms) were manually checked for any additional eligible studies. The primary reasons for excluding articles are presented in Supplementary Table 1 (on the basis of screening titles and abstracts) and in Supplementary Table 2 (on the basis of reading full-text versions). In case some necessary information was missing, the authors of the original articles were contacted in May–June 2021 (Supplementary Table 5 describes the studies that we received additional information about from the authors). The references of the included studies are listed in Supplementary Material. The literature search was conducted by A.S. (PhD in psychology; PhD in medicine; and PhD in educational sciences), and in order to increase the transparency of the literature search, we have provided descriptive information of the included studies in Supplementary Tables 3–5. Finally, the full statistical data (with all the coordinates and statistical estimates) can be requested from the corresponding author, in order to increase transparency.

### 2.2. Inclusion and exclusion criteria

#### 2.2.1. Inclusion criteria

We had the following inclusion criteria: an original peer-reviewed research article;  $n \geq 10$ ; an fMRI study; the study design included

exposure to in-group and out-group members (or other material very closely related to in-group and out-group such as national flags); adult sample (mean age > 18 years); non-clinical sample (the participants did not have any reported diseases or medications); *T* or *Z* statistics or *p* values of the observed BOLD response toward in-group vs. out-group members were available; the coordinates were reported using the Talairach Atlas (Tal) or the Montreal Neurological Institute (MNI) space; the study reported results of whole-brain analyses or analyses with very limited masking. More specifically, regarding masking, we included original datasets if masking was limited to regions such as the brain stem and occipital lobe that are clearly not theoretically interesting in the context of inter-group bias (e.g., Lau and Cikara, 2017), if the authors had proved that masking did not limit regions where significant in-group vs. out-group differences could be obtained (e.g., Rauchbauer et al., 2015), or if masking was limited to such brain regions that, in preliminary analyses, were found to correlate with the mental process under investigation (e.g., in-group vs. out-group contrast during empathic processing was investigated in regions that were significant in pain vs. no-pain contrast) (e.g., Contreras-Huerta et al., 2013).

### 2.2.2. Exclusion criteria

The exclusion criteria for the identified studies were: not an original study (e.g., a review or commentary); sample size < 10; findings of a same fMRI task within a same dataset were reported in another included study; a clinical sample (e.g., participants had been exposed to traumatic events or medications); not exposure to a clearly defined out-group and in-group (e.g., in-group vs. neutral group, or out-group vs. the self); group membership was only defined via sociodemographic factors (age or gender); whole-brain analyses were not reported (e.g., only ROI-based, small-volume corrected, or strongly masked analyses); only connectivity-based analyses were conducted; or some necessary statistical information was not available.

### 2.3. Data extraction

The following information was collected from the studies (if available): type of group membership under investigation (i.e., ethnic or political groups), participants' in-group, participants' ethnic group, country where the study was conducted, type of fMRI task (e.g. empathy-related or facial processing), publication year, sample size, age and gender distribution, smoothing kernel (mm), used analyzing software package for fMRI (1 = SPM, 2 = FSL, 3 = mixed or other), magnetic field strength (Tesla), threshold value for statistical significance (in case the study had used cluster-based analyses, the cluster-forming threshold was selected), use of correction for multiple comparisons (correction based on either voxel height or voxel extent), and possible covariates. Additionally, when applicable, we collected the *x*-, *y*- and *z*-coordinates (reported using Tal or MNI) of statistically significant findings and the direction of the observed findings (in-group > out-group or vice versa).

If *T* statistics were not available, a web-based tool provided by the SDM software (<https://www.sdmproject.com/utilities/?show=Statistic>) was used to convert *Z* statistics or *p* values into *T* statistics. All *T* values of the pairwise comparisons were reversed so that positive *T* values referred to greater BOLD responses to in-group than out-group, and negative *T* values referred to greater BOLD responses to out-group than in-group. If a study did not report an exact *T* or *Z* or *p* value for the in-group vs. out-group contrast, the SDM software imputed an estimated *T* value on the basis of direction of the contrast (e.g., in-group > out-group) and the statistical threshold used in the study.

If a study reported findings using two or more different thresholds or corrections, we had the following criteria for selection of statistical estimates. First, if a study reported both corrected and uncorrected results of whole-brain analyses, uncorrected results were selected because the SDM software makes more accurate estimations if it has information from more peaks (Radua and Albajes-Eizaguirre, 2019). Second, if a threshold value was not reported (but all other necessary information

was available), the threshold value  $p < .001$  was used as has been recommended previously (Radua and Albajes-Eizaguirre, 2019). Third, if a study reported pairwise comparisons of in-group vs. close/competitive out-group and in-group vs. distant out-group, the comparison between in-group vs. close/competitive out-group was selected. Fourth, if authors had divided their sample into several subsamples (e.g., an analysis in the full sample and a separate analysis among participants with greatest behavioral empathy-related bias; or an analysis in the full sample and separate analyses among Caucasian and Chinese participants), the analyses with most precise reporting were selected. If the findings were reported with a same degree of accuracy, the analyses with largest sample size were selected. Finally, if a study reported several comparable pairwise comparisons (comparisons with similar sample size and similar statistical accuracy), the findings of all comparisons were included. Supplementary Table 5 describes the contrasts that were selected from each study.

### 2.4. Meta-analytical models

All the analyses were conducted with the Seed-based *d* Mapping (SDM) software (version 6.21). The meta-analytical details of the SDM have been described elsewhere (Albajes-Eizaguirre et al., 2019; Radua et al., 2012, 2014).

In all the analyses, during pre-processing of the data, the lower and upper bounds of the possible effect-size values of the studies were estimated (full anisotropy = 1.0, full width at half maximum of Gaussian kernel = 20 mm, voxel size = 2 mm). Then, a mean analysis was conducted, representing the weighted mean difference in the fMRI activity (i.e., BOLD responses) toward in-group vs. out-group. It has been demonstrated that high statistical stability can be acquired with 20 imputations (Radua et al., 2012). For safety, our analyses were conducted using 50 imputations. The statistical threshold consisted of uncorrected voxel *p* value < 0.005, cluster extent  $\geq 10$  voxels, and *SDM-Z* < 1, in accordance with previous recommendations (Radua et al., 2012). Regarding other analytical details, we used the default settings of the SDM software (Albajes-Eizaguirre et al., 2019; Radua et al., 2012, 2014).

#### 2.4.1. Main analysis

First, a main analysis was conducted where all the original datasets were included (regardless of the type of fMRI task or type of group membership under investigation). In this analysis, such statistical contrasts were used that were as general (non-task-specific or non-condition-specific) as possible. For example, if a study had reported (a) the main effect of group membership (over all tasks or conditions, e.g. over conditions with neutral and angry faces) and (b) the contrast of in-group vs. out-group during angry faces, the main effect over all conditions was selected (see Supplementary Table 5 for the contrasts that were selected from each study). Age and gender were included as covariates in the main analysis.

**2.4.1.1. Heterogeneity and publication bias of the findings.** In order to investigate robustness of the results, heterogeneity was assessed using  $I^2$  statistics (i.e., the percentage of total variance between studies resulting more likely from heterogeneity than chance). Moreover, publication bias was evaluated with visual inspection funnel plots and metabias tests (Radua and Albajes-Eizaguirre, 2019).

#### 2.4.2. Sub-group analyses

In order to conduct sub-group analyses, each eligible original study was classified on the basis of (1) type of fMRI task used in the study and (2) type of group membership under investigation. Ten original studies was used as the minimum number for conducting sub-group analyses. In all the sub-group analyses, age and gender were included as covariates.

**2.4.2.1. Sub-group analyses on the basis of type of group membership under investigation.** The original studies were classified into the following categories: (1) *ethnic group membership*: in-group and out-group members belonged to different ethnic groups, such as (i) Caucasian/White/European-American, (ii) African/African-American/Black, (iii) Asian/Chinese/Korean, or (iv) Arab/Middle Eastern; (2) *national or regional group membership*: in-group and out-group members had an approximately similar ethnic background (i.e., belonged to a same ethnic group as listed before) but represented different national or regional groups (e.g., Chinese vs. South Korean, or Dutch vs. German); (3) *political group membership*: in-group and out-group members had different political orientations (e.g., Obama vs. McCain supporters, or Democratic vs. Republican, or liberal vs. conservative); or (4) *trivial or “minimal” group membership*: in-group and out-group members were (randomly or pseudo-randomly) assigned to different groups at the beginning of an experiment (e.g., “Team Red” vs. “Team Blue”, or “Eagles” vs. “Rattlers”). There were also a few additional studies with other types of group memberships that could not be categorized in any these sub-categories (i.e., were included only in the main analysis).

These five categories were determined, first, on the basis of previous research literature emphasizing that it would be necessary to examine inter-group bias in the contexts of different types of group memberships (Molenberghs and Louis, 2018). Second, the study classification was conducted so that, within the restrictions of original publications, each category would be as internally consistent as possible and include a sufficient number of studies for sub-group analyses (i.e., very narrow categories with only few studies were not possible).

In this group membership-related sub-group analysis, such statistical contrasts were used that were as general (non-task-specific or non-condition-specific) as possible. This was done in order to be able to obtain potential group membership-related brain responses as independently as possible from an fMRI task under investigation. For example, if a study had reported (a) the main effect of group membership (over all tasks or conditions, e.g. over painful and non-painful conditions) and (b) the contrast of in-group vs. out-group during painful condition, the main effect over all conditions was selected (see Supplementary Table 5 for the contrasts that were selected from each study).

**2.4.2.2. Sub-group analyses on the basis of type of fMRI task under investigation.** The original studies were classified into five categories. The first category included studies with *face processing* (i.e., processing faces of in-group and out-group members with either neutral or affective facial expressions) since face processing is found to involve a comparatively distinct brain network including subcortical and cortical regions (Duchaine and Yovel, 2015; Johnson, 2005). The second category included studies with *empathy-related processing* (i.e., observing in-group or out-group members in non-painful vs. physically or emotionally painful situations) because there is accumulating evidence for an empathic brain circuit (Engen and Singer, 2013; Fan et al., 2011). The third category consisted of studies with fMRI tasks on *social judgment*: tasks with social encounters (e.g., exposure to approach or avoidant behavior of in-group or out-group members), mentalizing or perspective-taking (e.g., ascribing beliefs to in-group and out-group members), or imitation of in-group and out-group members. The internal consistency of this category was supported by current research evidence demonstrating that those three aspects (i.e., social encounters, mentalizing, imitation) activate largely overlapping brain regions in a multi-directional interplay with each other (Frith and Wolpert, 2003; Sperduti et al., 2014). Empathy-related studies were not included in this category because empathizing and mentalizing involve mostly distinct neural networks and developmental trajectories (Kanske et al., 2016; Singer, 2006). Also, fMRI tasks with simple action perception were not included in this third category because a meta-analysis showed differential brain activity patterns between action perception and imitation

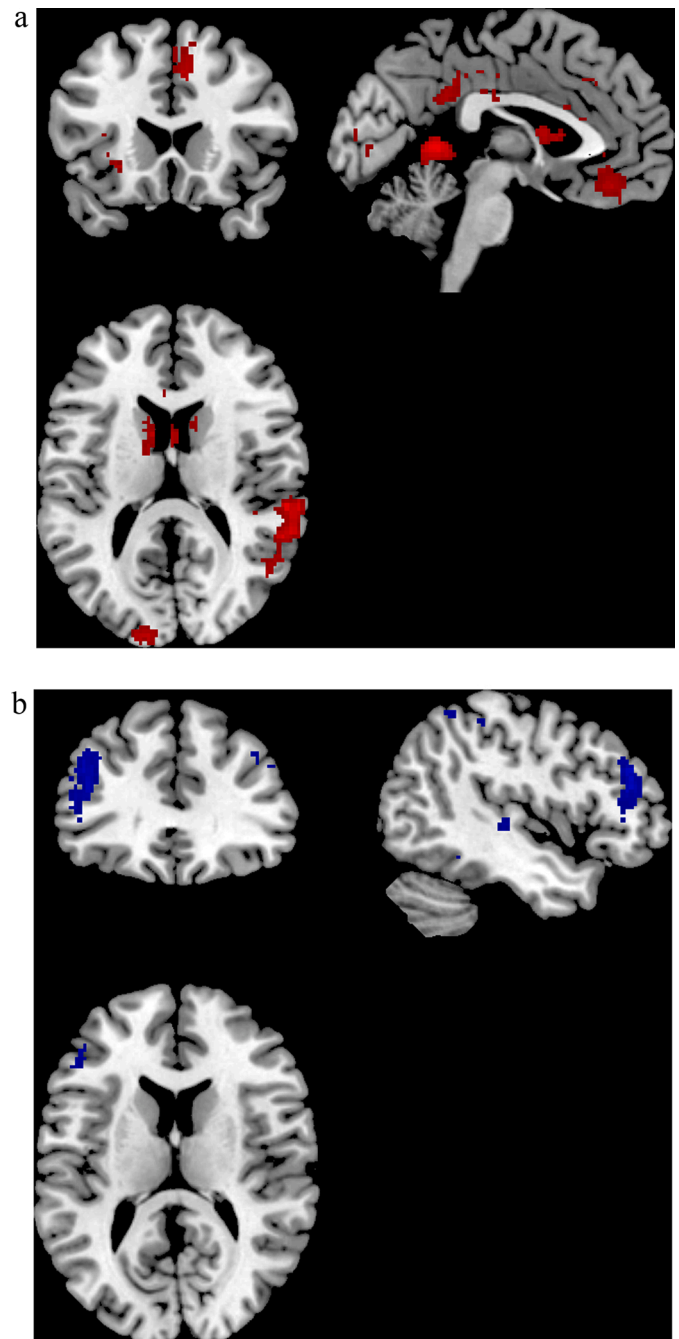
<b>a</b>	<b>Face processing</b>	21 datasets $n = 605$ $M_{\text{age}} = 31.2$ years 44.8 % female
	<b>Empathy-related processing</b>	25 datasets $n = 539$ $M_{\text{age}} = 24.7$ years 46.0 % female
	<b>Social judgment</b>	12 datasets $n = 351$ $M_{\text{age}} = 22.3$ years 56.1 % female
	<b>Moral processing</b>	11 datasets $n = 324$ $M_{\text{age}} = 22.4$ years 61.1 % female
	<b>Higher-level cognitive processing</b>	15 datasets $n = 366$ $M_{\text{age}} = 23.3$ years 44.6 % female
<b>b</b>	<b>Ethnic group membership</b>	47 datasets $n = 1213$ $M_{\text{age}} = 25.3$ years 49.4 % female
	<b>Political group membership</b>	10 datasets $n = 293$ $M_{\text{age}} = 23.9$ years 53.8% female
	<b>Trivial group membership</b>	17 datasets $n = 432$ $M_{\text{age}} = 23.5$ years 58.6% female
	<b>National or regional group membership</b>	16 datasets $n = 489$ $M_{\text{age}} = 21.6$ years 45.7% female

**Fig. 2.** A short summary of the categories of included studies (a) on the basis of type of fMRI task and (b) on the basis of type of group membership under investigation.

**Table 2**  
The results of meta-analysis of inter-group bias including all eligible studies.

MNI coordinates of peak voxels	<i>SDM-Z</i>	<i>p</i>	Number of voxels	Description
(a) In-group > Out-group				
58,-30,14	4.177	0.000014782	757	Right superior temporal gyrus, BA 42
-2,-50,4	4.405	0.000005305	358	Cerebellum, vermic lobule IV / V
-8,38,-18	3.688	0.000112891	354	Corpus callosum
-12,-96,16	3.504	0.000229418	179	Left superior occipital gyrus, BA 17
0,-40,36	3.231	0.000616908	158	Left median cingulate / paracingulate gyri, BA 23
-28,16,-8	3.769	0.000081778	143	Left insula, BA 48
-10,64,-8	4.195	0.000013649	127	Left superior frontal gyrus, medial orbital, BA 11
6,22,42	3.388	0.000351548	130	Right superior frontal gyrus, medial, BA 32 (undefined)
0,6,12	3.879	0.000052512	96	Left caudate nucleus
-10,8,14	3.519	0.000216961	96	Right precentral gyrus, BA 4
36,-26,60	3.166	0.000771761	59	Right caudate nucleus
12,12,14	3.169	0.000765383	58	Right cerebellum, hemispheric lobule IV / V, BA 30
20,-30,-20	2.930	0.001694202	44	Right middle occipital gyrus, BA 19
32,-82,32	3.371	0.000374794	39	Left insula, BA 48
-36,12,8	3.016	0.001281857	39	Left median cingulate / paracingulate gyri, BA 23
0,-18,40	3.068	0.001077771	26	Right inferior temporal gyrus, BA 19 (undefined), BA 48
44,-68,-10	3.173	0.000754654	21	Right rolandic operculum, BA 48
28,16,-12	3.109	0.000939548	21	Right superior frontal gyrus, medial orbital, BA 10
38,-32,20	2.880	0.001987994	14	
6,50,-4	2.874	0.002028048	12	
(b) Out-group > In-group				
-44,38,28	-4.001	0.000031531	288	Left middle frontal gyrus, BA 45
28,-56,46	-3.959	0.000037670	128	Corpus callosum
-50,-30,48	-3.081	0.001029909	55	Left inferior parietal (excluding supramarginal and angular) gyri, BA 2
-48,-22,2	-3.200	0.000687003	53	Corpus callosum
38,34,36	-2.883	0.001971543	20	Right middle frontal gyrus, BA 46
-46,-50,56	-2.877	0.002004325	11	Left inferior parietal (excluding supramarginal and angular) gyri, BA 40
-50,-46,-16	-2.987	0.001410484	11	Left inferior temporal gyrus, BA 20

(Caspers et al., 2010). The fourth category included studies with fMRI tasks requiring *moral processing*. Moral processing is defined to include moral response decisions (i.e., one's own decisions to reward or punish in-group or out-group members) and moral evaluation (i.e., rating appropriateness of others' moral choices) that are found to share a common activity pattern in several brain regions (Eres et al., 2018; Garrigan et al., 2016; Han, 2017). Morality-related and empathy-related studies were classified into separate categories because moral processing seems to involve more strongly self-referential processing (e.g., increased activity in the default mode network) (Han, 2017). Finally, the fifth category included fMRI tasks with *higher-level cognitive processing*. This category consisted of fMRI tasks including decision-making,



**Fig. 3.** Brain regions with higher activity (a) toward in-group compared to out-group (marked with red color) and (b) toward out-group compared to in-group (marked with blue color) in all studies.

memory encoding, associative learning, and verbal processing that are shown to activate brain regions via complex neural interactions with each other that cannot be clearly distinguished from each other (Pennartz et al., 2009).

In these task-related sub-group analyses, it was used as task-specific statistical contrasts as possible in order to be able to obtain task-related neural responses. For example, within the empathy-related sub-analysis, if a study had reported (a) the main effect of group membership (over all tasks or conditions, e.g. over painful and non-painful conditions) and (b) the contrast of empathic responses to in-group vs. out-group in pain, the latter contrast was selected (see Supplementary Table 5 for the contrasts that were selected from each study).

**Table 3**  
The results of meta-analyses of different types of inter-group bias.

MNI coordinates of peak voxels	<i>SDM-Z</i>	<i>p</i>	Number of voxels	Description	Direction of the difference
<b>(a) Ethnic inter-group bias</b>					
56,-48,18	3.245	0.000587046	106	Right superior temporal gyrus, BA 22	In-group > Out-group
62,-32,6	3.278	0.000523210	105	Right superior temporal gyrus, BA 21	In-group > Out-group
18,-30,-20	2.926	0.001717865	60	Right cerebellum, hemispheric lobule III	In-group > Out-group
10,24,46	3.178	0.000740886	42	Corpus callosum	In-group > Out-group
-20,-74,46	3.281	0.000517547	24	Left superior parietal gyrus, BA 7	In-group > Out-group
34,14,2	-3.421	0.000311911	86	Right insula, BA 48	Out-group > In-group
<b>(b) National or regional inter-group bias</b>					
0,32,16	4.012	0.000030100	758	Left anterior cingulate / paracingulate gyri, BA 24	In-group > Out-group
34,6,-18	2.892	0.001914501	42	(undefined), BA 38	In-group > Out-group
54,-20,22	2.753	0.002950609	27	Right Rolandic operculum, BA 48	In-group > Out-group
60,-26,24	2.699	0.003481507	18	Right supramarginal gyrus, BA 48	In-group > Out-group
-30,10,-20	2.956	0.001557112	17	Left insula, BA 38	In-group > Out-group
46,-62,-8	2.827	0.002347410	16	Right inferior temporal gyrus, BA 37	In-group > Out-group
<b>(c) Political inter-group bias</b>					
22,-64,-2	2.918	0.001762569	22	Right inferior network, inferior longitudinal fasciculus	In-group > Out-group
0,-30,38	2.810	0.002473772	19	Left median cingulate / paracingulate gyri, BA 23	In-group > Out-group
8,-86,8	2.894	0.001900852	18	Right calcarine fissure / surrounding cortex, BA 17	In-group > Out-group
<b>(d) Trivial inter-group bias</b>					
-4,34,30	2.903	0.001850307	26	Left anterior cingulate / paracingulate gyri, BA 32	In-group > Out-group

### 3. Results

#### 3.1. Descriptive information of the included studies

The literature search resulted in altogether 76 eligible original studies with 87 datasets (some studies consisted of several datasets) including altogether 2328 subjects ( $M_{\text{age}} = 25.2$  years, 49.0 % female). Short summaries of the categories of the included studies can be found in Fig. 2a and b. More detailed descriptive information of the included studies is summarized in Supplementary Table 3 (studies categorized on the basis of type of group membership under investigation) and Supplementary Table 4 (studies categorized on the basis of type of fMRI task). Supplementary Table 5 presents additional descriptive information of the included studies (e.g., statistical software, field strength, and study country).

#### 3.2. Results of the main analysis including all the studies

The results of a meta-analysis including all eligible studies are shown in Table 2 and Fig. 3. There was higher activity in response to in-group than out-group in a variety of brain regions: in the right superior temporal gyrus, right inferior temporal gyrus, cerebellum, corpus callosum, left superior occipital gyrus, right middle occipital gyrus, left median cingulate / paracingulate gyri, left insula, left and right superior frontal gyrus, left and right caudate nucleus, right precentral gyrus, and right Rolandic operculum (Table 2a, Fig. 3). In addition, there was higher activity to out-group than in-group in many regions: in the left and right middle frontal gyrus, corpus callosum, left inferior parietal gyri, and left inferior temporal gyrus (Table 2b, Fig. 3). The NIfTI images of the thresholded results can be downloaded from Supplementary Material.

##### 3.2.1. Publication bias and heterogeneity

In the results of the main analyses, there was not significant publication bias, as indicated by visual inspection of the funnel plots (see Supplementary Fig. 1) and the results of metabias tests ( $p = 0.98$ – $1.00$  for each peak voxel). Heterogeneity of the findings was mostly very low in the peak voxels ( $I^2 < 0.00$ – $6.05$ ). Slightly higher heterogeneity was obtained in the left insula ( $I^2 = 12.16$ ), right Rolandic operculum ( $I^2 = 10.23$ ), left middle frontal gyrus ( $I^2 = 15.47$ ), and left inferior parietal gyrus ( $I^2 = 18.44$ ); and clearly higher heterogeneity was found in right superior frontal gyrus ( $I^2 = 54.08$ ).

#### 3.3. Results of sub-group analyses: type of group membership

Next, we examined whether there would be differences in neural correlates of inter-group bias in the context of different types of group memberships.

##### 3.3.1. Meta-analysis of ethnic inter-group bias

The results of the meta-analysis of ethnic inter-group bias are shown in Table 3a and Fig. 4a. There was higher activity to in-group than out-group in the right superior temporal gyrus, right cerebellum, corpus callosum, and left superior parietal gyrus. Moreover, the results showed higher activity to out-group than in-group in the right insula.

##### 3.3.2. Meta-analysis of national or regional inter-group bias

The results of meta-analysis of national or regional inter-group bias are shown in Table 3b and Fig. 4b. There was higher activity to in-group than out-group in the left anterior cingulate / paracingulate gyri, right Rolandic operculum, right supramarginal gyrus, left insula, and right inferior temporal gyrus. No region exhibited higher activity in response to out-group than in-group.

##### 3.3.3. Meta-analysis of political inter-group bias

There was higher activity to in-group than out-group in the right inferior network (inferior longitudinal fasciculus), left median cingulate or paracingulate gyri, and right calcarine fissure (Table 3c, Fig. 4c). No region showed higher activity to out-group than in-group (Table 3c, Fig. 4c).

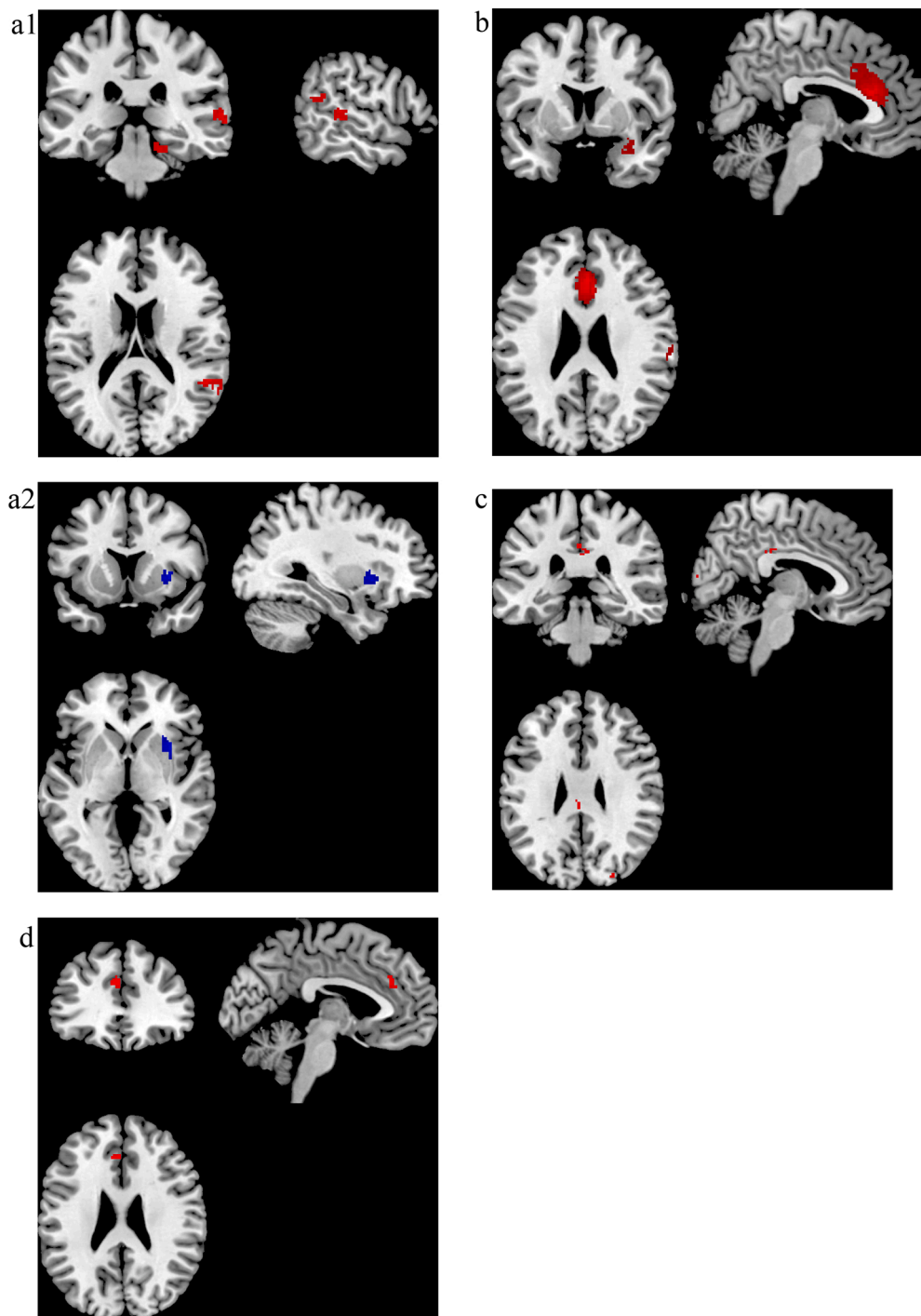
##### 3.3.4. Meta-analysis of trivial inter-group bias

There was higher activity in the left anterior cingulate / paracingulate gyri in response to in-group than out-group (Table 3d, Fig. 4d). No region showed higher activity to out-group than in-group (Table 3d, Fig. 4d).

The NIfTI images of the thresholded results can be downloaded from Supplementary Material.

#### 3.4. Results of sub-group analyses: type of fMRI task

Finally, we examined whether there would be differences in neural correlates of inter-group bias in the context of different types of mental processes (i.e., during different types of fMRI tasks).



**Fig. 4.** (a) Brain regions with higher activity toward ethnic in-group than ethnic out-group (marked with red color), and brain regions with higher activity toward ethnic out-group than in-group (marked with blue color). (b) Brain regions with higher activity toward national/regional in-group than national/regional out-group (marked with red color). (c) Brain regions with higher activity toward political in-group than political out-group (marked with red color). (d) Brain regions with higher activity toward trivial in-group than trivial out-group (marked with red color).

#### 3.4.1. Meta-analysis of inter-group bias during face processing

During face processing, there was higher activity to out-group than in-group in the right insula and left and right amygdala (Table 4a, Fig. 5a). No region showed higher activity to in-group than out-group during face processing (Table 4a).

#### 3.4.2. Meta-analysis of inter-group bias during empathy-related processing

During empathy-related processing, there was higher activity in response to in-group than out-group in the left median cingulate / paracingulate gyri, right supramarginal gyrus, left lingual gyrus, and left insula (Table 4b, Fig. 5b). The results showed no regions with higher activity to out-group than in-group.

#### 3.4.3. Meta-analysis of inter-group bias during moral processing, social judgment, or cognitive processing

No differences were found in any brain region in response to in-group than out-group or vice versa when using the previously recommended thresholding (uncorrected voxel  $p$  value < 0.005, cluster extent  $\geq 10$  voxels, and  $SDM-Z < 1$ ) (Radua et al., 2012). The NIfTI images of the thresholded results can be downloaded from Supplementary Material.

Finally, additional sensitivity analyses were conducted on the subgroup analyses with null findings (i.e., subgroup analyses of moral processing, social judgment, and cognitive processing). First, we examined whether there might be some modest trend-level inter-group biases. Hence, we thresholded the findings with a less stringent threshold (uncorrected voxel  $p$  value < .01, cluster extent 10 voxels,



**Table 4**  
The results of meta-analysis of inter-group bias during different types of fMRI tasks.

MNI coordinates of peak voxels	SDM-Z	p	Number of voxels	Description	Direction of the difference
(a) Inter-group bias during face processing					
36,22,0	-3.473	0.000257552	122	Right insula, BA 47	Out-group > In-group
-20,-4,-16	-3.495	0.000237286	86	Left amygdala, BA 34	Out-group > In-group
26,0,-20	-3.332	0.000431776	75	Right amygdala, BA 34	Out-group > In-group
-8,-44,-52	-2.896	0.001890540	29	(undefined)	Out-group > In-group
(b) Inter-group bias during empathy-related processing					
-2,14,36	5.646	~0	1332	Left median cingulate / paracingulate gyri, BA 24	In-group > Out-group
54,-42,28	3.518	0.000217676	275	Right supramarginal gyrus, BA 48	In-group > Out-group
2,-82,0	3.351	0.000402331	181	Left lingual gyrus, BA 17	In-group > Out-group
-30,20,6	3.151	0.000814617	47	Left insula, BA 48	In-group > Out-group
12,-2,10	3.182	0.000731587	41	(undefined)	In-group > Out-group
(c) Inter-group bias during moral processing					
No significant findings					
(d) Inter-group bias during social judgment					
No significant findings					
(e) Inter-group bias during cognitive processing					
No significant findings					

$SDM-Z > 1$ ), including a higher sensitivity but also a higher likelihood for false positive findings. During moral processing or social judgment, no significant brain regions emerged. During higher-level cognitive processing, we obtained higher activity toward in-group compared to out-group in the left anterior cingulate / paracingulate gyri (MNI peak coordinates = 0, 30, 20,  $SDM-Z = 2.696$ ,  $p = 0.0035$ , cluster size = 59 voxels), right rolandic operculum (MNI peak coordinates = 42, -24, 20,  $SDM-Z = 2.700$ ,  $p = 0.0035$ , cluster size = 38 voxels), and in an undefined region (MNI coordinates = -28, -4, -24,  $SDM-Z = 2.774$ ,  $p = 0.0028$ , cluster size = 22 voxels).

Next, as further sensitivity analyses, we examined whether neural inter-group biases could be evident if using more homogeneous but smaller (fewer original studies) sub-group categories. In these analyses, we did not include covariates. Regarding moral processing, we reran the sub-group analysis so that only punishment-related (but not reward-related) contrasts were included (7 studies, marked with “\*” in Supplementary Table 4). This analysis was done because social reward and punishment may involve partly different brain networks (Martins et al., 2021). Regarding social judgment, we reran the sub-group analysis so that we included only tasks that required participants to make mentalizing judgments (i.e., the largest sub-category of tasks related to social judgment, including 6 studies, marked with “#” in Supplementary Table 4). Regarding higher-level cognitive processing, we reran the sub-group analysis so that only tasks that required retaining of semantic memories on in-group and out-group were included (i.e., the largest sub-category of tasks related to higher-level cognitive processing, including 6 datasets, marked with “§” in Supplementary Table 4). In these sensitivity analyses, no significant clusters emerged.

## 4. Discussion

### 4.1. A summary of the main findings

Overall, the results showed that an inter-group bias was evident in some previously identified brain regions (e.g., the medial prefrontal cortex, insula) but also in many brain regions not previously identified as neural correlates of inter-group bias (e.g., the cerebellum, supramarginal gyrus). There was no significant publication bias. The sub-group analyses indicated that neural correlates of inter-group biases were largely context-specific. Regarding type of group membership, inter-group bias toward trivial groups was evident only in the cingulate cortex, while inter-group biases toward “real” groups (ethnic, national, or political groups) involved broader sets of brain regions. Regarding

phase of mental processing, there was not any neural inter-group bias during moral processing, social judgment, or higher-level cognitive processing (e.g., during memory and learning), but there was a clear neural inter-group bias during face processing and empathy-related processing. Taken together, the results increase understanding of neural basis of inter-group bias in different contexts.

### 4.2. Inter-group bias over all studies

The meta-analysis of all original studies provided six implications. First, the neural basis of inter-group bias may include a wide set of brain regions (see Fig. 3): some regions exhibiting higher activity toward in-group compared to out-group, and other regions vice versa. Second, the midline structures seemed to be more active toward in-group and lateral prefrontal regions toward out-group. Hence, processing of in-group may more strongly involve self-referential thinking, while processing of out-group may reflect more generally social information processing. Third, the results partly supported previous models (Amodio, 2014; Molenberghs and Louis, 2018): inter-group bias correlated with, for example, activity in the caudate nucleus (involved in anticipation of outcomes and reward-related processing) (Amodio, 2014; Molenberghs, 2013), the medial prefrontal cortex (involved in affective mentalizing, stereotyping, and many other socioemotional processes) (Hehman et al., 2014; Takahashi et al., 2015), and inferior parietal cortex (e.g., action perception) (Molenberghs, 2013). Fourth, the findings did not confirm some of the previously hypothesized neural loci of inter-group biases, such as the fusiform face area. Fifth, the findings identified many novel regions involved in inter-group bias: for example, the cerebellum, precentral gyrus, and rolandic operculum that are involved in e.g. somato-motoric mirroring and affective processing (Clausi et al., 2017; Kilner and Lemon, 2013). Finally, most identified brain regions were involved in inter-group bias only or mainly in specific contexts: either in context of specific group memberships or in context of specific phases of mental processing. Hence, the results are discussed next in a more context-specific way.

### 4.3. Inter-group bias in contexts of different group memberships

#### 4.3.1. Inter-group bias between trivial groups

The left cingulate cortex was the only brain region that responded differently to trivial in-group vs. out-group (see Fig. 4d), indicating that trivial group membership produces a more restricted neural inter-group bias than “real” group memberships. This is contrary to previous social-

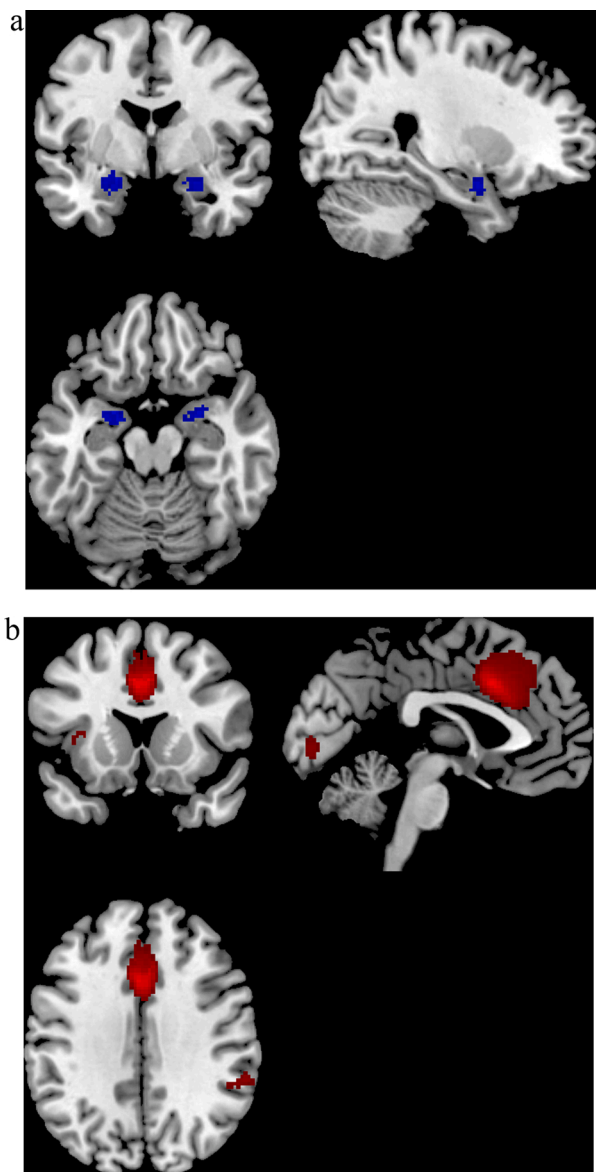


Fig. 5. (a) Brain regions that showed higher activity toward out-group compared to in-group (marked with blue color) during face processing. (b) Brain regions that showed higher activity toward in-group compared to out-group (marked with red color) during empathy-related processing.

psychological postulations that identification with *any* group (e.g. trivial or “real” group) would produce an approximately similar in-group bias (Moghaddam and Stringer, 1986). Additionally, as the left cingulate cortex correlated also with political and national inter-group bias, this region seems to compose some kind of a common core of neural inter-group bias. This appears feasible as the cingulate cortex is a central region for a variety of socioemotional processes such as affective empathy and perspective taking, approach–avoidance decisions, processing of social conflicts, emotional appraisal, and conditioned learning, among others (Amodio, 2014; Banissy et al., 2012; Stevens et al., 2011). The central role of the cingulate cortex for inter-group bias has been identified also previously (Amodio, 2014; Molenberghs and Louis, 2018). Finally, the limited findings toward trivial groups may be explained by that individuals, in general, show less activation toward trivial than “real” groups. However, we could not find any direct statistical comparison of “overall” BOLD responses toward trivial groups vs. “real” groups when reviewing the original studies. Hence, more studies are needed to confirm this alternative interpretation empirically.

#### 4.3.2. Inter-group bias between ethnic groups

First, ethnic inter-group bias (see Fig. 4a) correlated with activity in the right superior temporal gyrus that plays a role in stimulus-centered spatial processing (Shah-Basak et al., 2018). Another brain region, also involved in spatial attentive processes, was the left superior parietal gyrus that showed higher activity toward ethnic in-group (vs. out-group) members. It is a part of the dorsal frontoparietal network that is thought to maintain a “salience map” and direct attention to such external stimuli that are salient on the basis of semantic knowledge (Corbetta and Shulman, 2002). Thus, information may be more actively retained from semantic memory and knowledge when processing cues related to ethnic in-group than out-group. This is line with social-psychological theories suggesting that inter-group bias relates to “stable belief systems” (Hodson, 2014).

Additionally, ethnic inter-group bias correlated with the right cerebellum. Originally, the cerebellum has been regarded as a center of motor adjustments, but later studies have confirmed its crucial role in connecting information from multiple sources and emotional and cognitive associative learning (Clausi et al., 2017; Timmann et al., 2010). Interestingly, ethnic inter-group bias also related to the corpus callosum that is involved in understanding of paradoxical sarcasm, integration of textual and visual social cues, and comprehension of emotional-prosodic cues (Paul et al., 2003; Symington et al., 2010). Traditionally, white matter findings in fMRI studies have been regarded as artefacts but, more recently, it has been confirmed that fMRI captures also white matter activations, for example, in the corpus callosum (Gawryluk et al., 2014; Mazerolle et al., 2010). Thus, if not regarded as an artefact, our findings indicate that ethnic inter-group bias correlates especially with regions that modulate processing of complex social information coming from multiple sources.

#### 4.3.3. Inter-group bias between national or regional groups

Besides of the left cingulate cortex (i.e., a common region of many types of inter-group biases), national inter-group bias (see Fig. 4b) correlated with activity (1) in the right inferior temporal gyrus that contributes to visual object recognition (Gerlach et al., 1999) and metaphorical and abstract meanings (Stringaris et al., 2007) and (2) in the right supramarginal gyrus that seems to produce a social context to sensory perceptions such as others’ postures and gestures (Hamilton and Grafton, 2009), rhythms (Schaal et al., 2017), and visual words (Stoekel et al., 2009). Thus, the neural basis of political inter-group bias may involve brain regions that process abstract, social, or metaphorical meanings of visual perceptions (e.g., national flags), different types of speech (i.e., regional accents), or gestures (e.g., culturally-specific gestures). Additionally, our findings indicated that political inter-group bias may relate to brain regions processing egocentricity bias and exteroceptive-interoceptive processes. This is because the supramarginal gyrus is also involved in reducing emotional egocentricity in social situations (Silani et al., 2013), and political inter-group bias was related also to the right rolandic operculum that contributes to interoceptive awareness and bodily self-consciousness (Blefari et al., 2017).

#### 4.3.4. Inter-group bias between political groups

Besides of the left cingulate cortex, political inter-group bias correlated with activity in the right inferior network, in the inferior longitudinal fasciculus (see Fig. 4c). It is a white matter tract connecting temporo-occipital regions and a part of the ventral visual pathway, and its role is to process and modulate visual cues (Herbet et al., 2018) and possibly also semantic autobiographical memories (Hodgetts et al., 2017). Hence, in case not regarding this finding as an artefact in light of previous evidence (Gawryluk et al., 2014; Mazerolle et al., 2010), this white matter tract might be involved in political inter-group bias via integrating visual cues of political group memberships (such as visual symbols or objects related to political parties) to previous semantic knowledge about political leaders. Accordingly, political inter-group bias also correlated with activity in the right calcarine fissure that also

is involved in visual processing of objects' spatial features, colors, and movements (Lysne, 2010), further indicating that political inter-group bias occurs mainly in the brain regions responsible for encoding visual information.

#### 4.4. Inter-group bias during different mental processes

##### 4.4.1. Inter-group bias during face processing

Contrary to hypotheses and a neural model of in-group bias (Molenberghs and Louis, 2018), inter-group bias did not correlate with activity in the fusiform face area. In accordance with hypotheses, there was higher activity toward out-group compared to in-group in the amygdala bilaterally (see Fig. 5a). This may likely reflect an elevated primary threat response and a heightened alarm system in response to out-groups, possibly developed via fear conditioning (Amodio, 2014). Interestingly, heightened amygdala reactivity toward out-groups may also reflect social fears: fears that the self could seem as having prejudices toward out-group members in others' presence (Amodio, 2014). Additionally, there was higher activity toward out-group compared to in-group in the right insula that, together with the amygdala, is a part of the salience network and involved in allocating attentional resources to emotionally relevant targets (Menon and Uddin, 2010). Stronger insula reactivity toward out-groups may also reflect a stronger disgust reaction toward out-group members (Amodio, 2014).

##### 4.4.2. Inter-group bias during empathy-related processing

First, in line with previous models (Amodio, 2014; Molenberghs and Louis, 2018), the results identified higher activity in response to in-group than out-group in the left median cingulate cortex and left insula (see Fig. 5b). These findings are likely to reflect a stronger activation of the mirror neuron system and stronger prosocial emotions such as empathic concern when perceiving in-group (vs. out-group) members' suffering (Amodio, 2014; Molenberghs and Louis, 2018). Importantly, during empathy-related processing, there was an inter-group bias in two novel regions not proposed by previous models: higher activity toward in-group vs. out-group in the right supramarginal gyrus and left lingual gyrus. As the supramarginal gyrus is found to include mirror neurons (Welberg, 2008) and is crucial to "overcome egocentricity bias in social judgment" (Silani et al., 2013), this finding further supports the idea of higher empathic concern toward in-group compared to out-group members' suffering. The left lingual gyrus, in turn, is involved in working memory for schematic faces (Kozlovskiy et al., 2014) and was likely activated because stimulus material of the original datasets commonly included faces with painful or non-painful expressions. This finding tentatively implies that, during empathic processing, in-group (vs. out-group) members' painful facial expressions may be more carefully encoded.

##### 4.4.3. Inter-group bias during cognitive processing

This meta-analysis did not obtain neural inter-group bias in the contexts of moral processing, social judgment, or memory- or learning-related cognitive processing. Interestingly, there are studies clearly demonstrating discriminatory behaviors or differential moral processing toward out-group and in-group members: for example, courts are more likely to give harsh sentences to Black than White individuals in the US (Demuth and Steffensmeier, 2004). Hence, it appears that there may not be any inter-group bias when being alone (such as within an fMRI scanner) but there may be an inter-group bias in real-world social group situations. This, in turn, implies that inter-group bias in moral processing and social judgment may not result from necessarily arousing biological brain responses (possibly developed over evolution) but possibly from certain group dynamics or learned social norms. Additionally, it is possible that inter-group bias during higher-level cognitive processing is very situation-dependent that, in turn, prevented from obtaining any general inter-group bias. For example, it has been suggested that *more* mentalizing about out-group members' may be useful if out-group

members are planning to hurt in-group members, while *less* mentalizing may be useful if in-group members are conducting transgressions toward out-group members (Molenberghs and Louis, 2018).

Moreover, it is necessary to consider that there were comparatively heterogeneous sets of tasks in the sub-group analyses of higher-level cognitive processing memory, learning, verbal processing etc.) and social judgment (imitation, social encounters, mentalizing etc.) that may have prevented from obtaining any significant findings in these analyses. Finally, it has been recommended that there should be at least 20 studies for a neuroimaging meta-analysis (Eickhoff et al., 2016). The sub-group analyses of moral processing, social judgment, and higher-level cognitive processing, however, included 11–15 datasets. Hence, more original studies are needed to conduct more reliable sub-group analyses and to make any firm conclusions.

#### 4.5. Methodological considerations

Alongside with the inclusion criteria, this meta-analysis was limited to datasets of non-clinical adult samples. The original datasets were approximately balanced by sex (44.6–61.1 % were female in different meta-analyses). There was, however, a sampling bias with regard to age: a majority of the original samples consisted of young adults, most typically university students (mean age ranged between 21.6–31.2 years). Therefore, our results cannot be directly generalized to children, older adults, or clinical populations.

In accordance with previous recommendations (Radua et al., 2012), such original datasets were excluded that reported only small-volume corrected analyses or ROI-based analyses. This resulted in exclusion of 13 original datasets (listed in Supplementary Table 2). Only studies with whole-brain analyses and studies with very limited masking were included (more details about masking can be in the methods section). Overall, it has been emphasized that exclusion of studies with ROI-based analyses, small-volume corrected analyses, or strongly masked analyses is recommendable as it increases reliability of findings (Radua et al., 2012).

It is necessary to consider that each sub-group analysis of different group memberships (i.e., ethnic, political, national or regional, and trivial) included a different combination of fMRI tasks. That is, some fMRI tasks (e.g., face processing tasks) had been more commonly used in the context of ethnic than trivial groups. Similarly, each category of mental processing (face processing, empathy-related processing, social judgment, moral processing, and cognitive processing) included a different proportion of each group membership. Hence, this meta-analysis did not investigate, for example, whether empathy-related inter-group bias may be more evident in context of some group memberships than others, as has been suggested previously (Molenberghs and Louis, 2018). Nevertheless, due to the number of original datasets available, it was not possible to examine inter-group bias at each phase of mental processing separately in the contexts of ethnic, national or regional, political, and trivial group memberships. This remains as an intriguing research question for future studies.

Participants' task during fMRI acquisition differed in original studies: whether participants' attention was explicitly directed to group categorization (via pressing a button) or whether group categorization was rather implicitly processed. For example, in different original studies, participants were asked to press a button on the basis of how much empathy did he/she felt toward a target person (Cheon et al., 2011), or on the basis of group categorization (Van Bavel et al., 2008), or on the basis of facial emotion of a target person (Chiao et al., 2008). This variation in participants' tasks may have influenced BOLD responses to in-group vs. out-group, for example, in the amygdala (Amodio, 2014). Overall, more research is needed about how BOLD responses toward in-group vs. out-group are modulated by pressing a button on the basis of different criteria.

As a limitation, it is necessary to consider that article screening was conducted by one author (A.S.). In general, it is recommended that

Implications for theory	Implications for research	Implications for interventions
<ul style="list-style-type: none"> <li>▪ Inter-group bias may be evident in many non-suggested brain regions.</li> <li>▪ Neural correlates of inter-group bias may be mostly context-specific.</li> <li>▪ The cingulate cortex may compose a core of inter-group biases.</li> <li>▪ Neural inter-group bias may be more restricted toward trivial groups than “real” groups.</li> <li>▪ There may be a neural inter-group bias during face processing (i.e., higher threat responses to out-groups) and during empathy-related processing (i.e., stronger empathic responses to in-groups).</li> <li>▪ Inter-group biases in social interaction or moral behaviors (e.g., discriminative acts) may derive rather from group dynamics or norms than naturally arousing brain responses.</li> </ul>	<ul style="list-style-type: none"> <li>▪ Studies could use more naturalistic stimulus material, such as animations or 360° videos or utilize virtual reality.</li> <li>▪ More studies are needed in other populations than college students.</li> <li>▪ More research is needed on inter-group bias toward mutually contradictory or compatible group memberships (e.g., ethnic in-group but political out-group).</li> <li>▪ Future studies could examine differences in the neural basis of inter-group bias among minorities vs. majorities.</li> <li>▪ fMRI studies on inter-group bias could avoid selecting too restricted regions-of-interest (ROIs).</li> <li>▪ More research is needed on possible white matter correlates of inter-group bias.</li> </ul>	<ul style="list-style-type: none"> <li>▪ Amygdala responses (i.e., threat responses) toward out-groups might be deactivated via safely experienced repetitive contacts with out-group members.</li> <li>▪ Because there may be a neural inter-group bias during empathic processing, empathy-related interventions could be effective.</li> <li>▪ As there may not be a neural inter-group bias in higher-level cognitive processing, this may explain why interventions promoting an individual’s higher-level processing (e.g., knowledge-focused diversity training) may not be effective.</li> <li>▪ Prejudice-reduction interventions could focus on preventing adverse social group dynamics (e.g., the “bystander effect”) and adverse norms.</li> </ul>

Fig. 6. A summary of the study implications.

article screening would be conducted by at least two authors. In order to increase transparency of this study, an array of material is available in the supplementary files: full search terms (Supplementary Methods), primary reasons for excluding original articles in the first phase (on the basis of screening titles and abstracts) and in the second phase (on the basis of reading full-text versions) (Supplementary Tables 1–2), a large variety of descriptive information of the included studies (Supplementary Tables 3–5); and the NIfTI files of the thresholded results to be explored (see the supplementary files).

Some social psychological theories have indicated that “in-group love” and “out-group hate”, although being interrelated or even overlapping concepts, may also be partly dissociated concepts (Brewer, 1999; Hamley et al., 2020). Hence, it would have been interesting to investigate whether neural inter-group bias would be stronger during in-group favoritism or out-group derogation. Nevertheless, this was not possible in this meta-analysis because, first, most brain regions (e.g., the amygdala, insula, frontal regions) process both positive and negative emotions and typically also other information (e.g., complex social and cognitive cues) in a complex way. Thus, BOLD responses cannot be directly categorized as reflecting “positive” or “negative” responses. Second, BOLD responses cannot be directly interpreted as reflecting *changes* in activity level (i.e., increased vs. decreased activity) but *difference* in activity level (i.e., higher vs. lower activity). Consequently, when obtaining a significant difference (e.g., higher activity toward out-group), it cannot be directly interpreted whether it reflects increased activity toward out-group or decreased activity toward in-group (when compared to the baseline condition). Finally, there were very few original studies using fMRI tasks that clearly measured in-group favoritism or out-group derogation (e.g., BOLD responses during punishment of in- vs. out-group; and BOLD responses during rewarding in- vs. out-group). Due to a low number of these studies, we could not conduct separate sub-group analyses during in-group favoritism and out-group derogation. Finally, previous neural models of in-group favoritism vs. prejudices toward out-group have indicated that those concepts cannot be clearly separated at a neural level (Amodio, 2014; Molenberghs and Louis, 2018).

#### 4.6. Implications

The implications of this meta-analysis are summarized in Fig. 6.

#### Declaration of Competing Interest

None.

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neubiorev.2021.10.027>.

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