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Intergroup empathy: Enhanced neural resonance for ingroup facial emotion in a shared neural production-perception network

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ABSTRACT

Introduction: Empathic behavior and related neural processing are strongly modified by group membership. Shared neural circuits for the production and perception of facial emotional expressions represent mirror neuron mechanisms which play a pivotal role for empathy. In this study, we investigate the influence of group membership on mirror neuron mechanisms for emotional facial expressions.
Methods: In a functional magnetic resonance imaging task, 178 healthy subjects perceived emotional and neutral facial expressions of artificial ingroup and outgroup members, displayed as 5 s video clips, and produced these facial expressions themselves. Before scanning, artificial group membership was manipulated ad-hoc through a minimal group paradigm.
Results: Shared neural activity for emotional facial expression production and perception was revealed in a large network with right-hemispheric preponderance encompassing motor mirror neuron regions, i.e., inferior frontal gyrus, supplementary motor area and middle temporal gyrus, in addition to limbic regions, i.e., amygdala, hippocampus, para-hippocampus, and insula. Within this network there was greater neural activation for ingroup compared to outgroup members in temporal poles, amygdalae, the left insula, the left inferior frontal gyrus, and the inferior and middle temporal gyrus, the right hippocampus and parahippocampus.
Discussion: We validate and extend knowledge on brain regions with mirror neuron properties. Most crucially, we provide evidence for the influence of group membership on regions within the mirror neuron system, indicating more neural resonance (mirroring) for ingroup facial emotional expressions.

The production and perception of an action lead to an activation of shared neural circuits which is commonly defined as mirror neuron activity (Iacoboni and Dapretto, 2006). The mirror neuron system (MNS) is activated by body movements including emotional facial expressions (Kircher et al., 2013; Rizzolatti, 2005; van der Gaag et al., 2007). Activation of the MNS for emotional facial expressions includes emotion-processing brain areas, e.g., the amygdala and insula (Molenberghs et al., 2012; Pohl et al., 2013). The MNS has been related to empathy following the idea that the emotions of others are “mirrored” in neural circuits which also process one's own emotions (Rizzolatti and Sinigaglia, 2016). The ability to empathize is influenced by personality traits and by contextual factors such as group membership (Cikara, 2015; Cikara et al., 2014, 2011). Little is known about how group membership influences MNS activation (Eres and Molenberghs, 2013).

For the investigation of mirror neuron mechanisms both, a production and perception condition are crucial in order to detect neural production-perception activity. Therefore, in this study we use the terms MNS and ‘shared neural production-perception network’ synonymously. There are only a few studies on MNS activation for facial emotions which include an active production condition (Molenberghs et al., 2012). Common neural activity for the production and perception of emotional facial expressions has been shown in the amygdalae, the inferior frontal gyri, superolateral prefrontal cortices, the middle cingulate cortex as well as the insulae and inferior parietal lobuli (Carr et al., 2003; Hennenlotter et al., 2005; Kircher et al., 2013; Leslie et al., 2004; van der Gaag et al., 2007). However, this set of brain regions, revealed by the latter

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important studies, has not yet been shown comprehensively to be activated. Hence, a validation and possibly extension of the resulting shared neural production-perception network for facial emotional expressions in a larger study is still lacking. Furthermore, until now no study has directly investigated the influence of group membership on these shared neural circuits for facial emotion production and perception (Eres and Molenberghs, 2013).

Previous neuroscientific studies have investigated the relation of group membership on pain empathy. An ingroup bias in neural activation for the perception of members of the own race, the favorite sport team and of fair (vs. unfair) players receiving painful stimuli has been shown (Cikara and Fiske, 2011; Hein et al., 2010; Singer et al., 2006, 2004; Xu et al., 2009). Strikingly, there is also evidence, that group membership affects the motor system regarding empathy for pain: in a TMS-study motor-evoked potentials were measured on one hand while watching needle penetration (or Q-tip touch) of the same hand of a racial ingroup and a racial outgroup. Evoked potentials were reduced while watching ingroup but not outgroup pain administration (Avenanti et al., 2010). Hence, group membership leads to a neural modulation of sensorimotor empathic brain responses.

Regarding neural activation for neutral facial expression perception a racial outgroup repeatedly led to a stronger amygdala activation (Cunningham et al., 2004; Hart et al., 2000; Phelps et al., 2000). Neural responses, induced by racial group membership, is, however, strongly modified by contextual factors such as the conscious perception of the presented stimuli (Cunningham et al., 2004), by the familiarity of the presented faces (Hart et al., 2000), and, strikingly, by the amount of prejudice towards the racial outgroup (Gutsell and Inzlicht, 2010). The latter interaction makes the investigation of group membership effects challenging: when using race, gender, political party, favorite sport team etc. in order to establish an experimental group it remains unclear whether effects are due to pure group membership or relate to other aspects, e.g., prejudices.

An elegant possibility to circumvent such a potential bias is the minimal group paradigm, where participants are ad hoc and randomly assigned to arbitrary groups (e.g. red vs. blue, Tiger vs Lyon etc.). In the original experiment membership to a minimal group led to an ingroup bias in a money distribution game: having more money than the outgroup was more important to the participants than the maximum joint profit (Tajfel et al., 1971). Since then, adapted versions of the minimal group paradigm have been used in numerous behavioral and neuroscientific studies investigating the effects of group membership in humans (Cikara and Van Bavel, 2014; Krautheim et al., 2018; Molenberghs, 2013).

Molenberghs and colleagues chose an interesting approach: after a minimal group manipulation there was an ingroup bias for the assessment of observed hand speed, which was associated with enhanced neural activity in the left inferior parietal lobule (Molenberghs et al., 2013). Since the inferior parietal lobule is part of the MNS the authors argued that their finding might represent a modulation of brain activation including mirror activity by minimal group membership. Following this idea, minimal group membership would have a direct and unconscious influence on a perceptual level (Xiao et al., 2016). Indeed, in an ERP study, participants performed a face categorization task where they had to correctly identify (minimal) group members. For ingroup members, larger N170 amplitudes were reported (Ratner and Amodio, 2013). N170 amplitudes relate to face processing (Bentin et al., 1996), and they are modulated by the degree of familiarity of the processed faces (Caharel et al., 2005). This implies that minimal ingroup faces are more readily processed at an initial stage of face perception, e.g. via a priming process (Ratner and Amodio, 2013). An fMRI study investigated neural activity for neutral face perception of minimal ingroup vs. minimal outgroup members while each group equally consisted of both, black and white colored faces: using an uncorrected threshold, the authors revealed enhanced neural activity for minimal ingroup compared to minimal outgroup neutral face perception in the amygdala, fusiform gyri, orbitofrontal cortex, and dorsal striatum– which was not moderated by the implicit racial group factor (Bavel et al., 2008). In a subsequent study the same authors could reveal enhanced neural activity by minimal group membership in a fusiform face area region of interest (ROI) (Van Bavel et al., 2011). The results of these studies suggest, that minimal group membership amplifies the activation of the MNS for facial emotions. But yet, there is no proof of this assumption since no study directly investigated this relation by testing the influence of minimal group membership on shared neural activation for the production and perception of emotional facial expressions.

In order to fill this gap, we scanned 178 healthy subjects with fMRI while they either perceived emotional and neutral facial expressions, each displayed as 5 s video clip, of artificial ingroup and outgroup members or produced these facial expressions themselves. Before scanning, group membership was manipulated through a minimal group paradigm.

First, we wanted to validate and extend the current knowledge on mirror neuron mechanisms for the processing of facial emotions. We predicted MNS activity in limbic (amygdala) and frontal areas (inferior frontal gyrus) as well as in the insula and the inferior parietal lobule. Second, and more importantly, we hypothesized a stronger MNS activation for emotional facial expressions of ingroup as compared to outgroup members.

1. Methods

1.1. Subjects

198 healthy, right-handed, Caucasian German native speakers aged 19–39 years participated in the study (M: 24.04 years; SD: 3.25 years, 50% males). Vision of the participants was normal or corrected to normal during the experiment. Participants had to have at least an upper-secondary (high school) education. Psychology or sociology students and staff members from our laboratory were excluded, due to their possible knowledge of experimental manipulation strategies. Participants received €50 after completing the experiment. We excluded 18 subjects due to head movement exceeding one voxel size (3.6 mm) during fMRI scanning and two subjects due to insufficient engagement in post-scanning behavioral tasks and the incidental finding of a brain pathology, leaving 178 participants for the final analysis. Our study was approved by the local ethics committee, according ritten informed consent prior to the commencement of the study.

1.2. fMRI task and procedure

1.2.1. Minimal group paradigm manipulation

Before the fMRI session, subjects completed a 15-item false psychological test where they answered questions regarding personality and problem-solving strategies. They were told that the purpose of this test was to identify strategies for solving a problem. After completing the test, which took about five to 10 min, participants were told that they were either a “conclusive” problem solver with a “holistic approach” or a “sequential” problem solver with an “analytical approach”. The participants then received written information about the problem-solving strategies of the own and the other problem-solver type. In fact, these problem-solver types do not exist, and subjects had been randomly assigned to one of these groups before the experiment. Before and after the fMRI session, identification with those of the same (=ingroup) and the other (=outgroup) problem-solver type was assessed on a seven-point Likert scale. In addition, after scanning, the participants rated the likeability of ingroup and outgroup members they had been shown in the scanner on a seven-point Likert scale. Our manipulation strategy has been published previously (Krautheim et al., 2018; Ruckmann et al., 2015).

1.2.2. Stimuli

We used five-second video clips presenting dynamic facial expressions that had been described and validated in another group of subjects (Kircher et al., 2013). Briefly, in these video clips professional actors depicted happy, angry, neutral emotional facial expressions (the latter consisting of no facial movement), and lip-protrusion. The video clips were framed with a colored strip (either blue or green) according to the actor's (false) identity as either a sequential or conclusive problem solver, enabling participants to make ingroup/outgroup associations. In addition, scrambled (pixelated) faces were used in a production condition where the participants produced happy, angry, neutral facial expressions, and lip-protrusion. In sum, there were twelve conditions (3 × 4 matrix). All video clips began with a neutral facial expression (about 1 s) and progressed to the particular facial expression (3 s) before ending with a neutral facial expression (1 s).

1.2.3. fMRI stimulus setup

We used a block design with three perception conditions: “facial expression” (happy vs. angry vs. neutral vs. lip-protrusion) and “group” (participants perceiving ingroup vs. outgroup, with groups coded by colored video frames, see Fig. 1). Half of the actors were ingroup members, while the other half were outgroup members. In both groups gender was equally distributed. The paradigm was structured in twelve subunits, each consisting of two blocks of the production condition and four blocks of the perception condition. All four facial expressions (happy, anger, neutral, and lip-protrusion) were observed in each subunit. Within a subunit all perceptual conditions were presented only by members of the ingroup or the outgroup. Both, the order of perception blocks versus production blocks and the order of the perception conditions (happy, anger, lip-protrusion, and neutral) were pseudo-randomized. The facial expression of a particular production block was always different than the facial expression which had been observed in the preceding block in order to prevent imitation bias. Low-level baseline (fixation cross) was presented always after two subunits. Altogether there were twelve subunits consisting of 72 blocks. The whole scanning session lasted about 36 min. Each condition was presented in six blocks consisting of four video clips. Each block lasted 27 s and was introduced with an instruction slide (2 s, e.g. “happy perceive” or “angry produce”) followed by four video clips (5 s each) presenting the same facial expression and a white fixation cross (5 s). We used a variable jitter at the beginning of each block. The three production conditions were composed in the same manner but instead of the four video clips presenting the same facial expression, the participants produced the same facial expression (happy vs. angry vs. neutral vs. lip-protrusion) while observing pixelated faces as a visual input. In addition, there were six blocks where only a white fixation cross was presented as a low-level baseline (25 s); these were also introduced by instruction slides (2 s). During scanning the instructor watched the faces of the participants via a recording video camera to ensure engagement in the task. There were 2 × 2 × 2 × 2 versions of the paradigm due to permutation of the following parameters: (1) the first condition of the paradigm was either an ingroup or an outgroup trial, (2) the ingroup was constituted either by the “sequential” or the “conclusive” problem solver type, (3) the associated colors of the group (blue or green) were interchanged, and (4) there were two groups of actors (consisting each of half male and half female actors) which represented either the ingroup or the outgroup. Each version was completed by 12 participants. Before scanning, the participants received instructions for the fMRI-task. They were informed that they would see sequential and conclusive problem solvers expressing different facial emotions (happy, angry, and neutral facial expressions) and that, in separate blocks, they would produce each of the same facial expressions themselves. On a computer screen, they watched examples of stimuli (depicting other actors than they would see in the scanner). Training occurred for both the perception and production of the different facial expressions. Correct understanding of the task was assured. Participants were instructed to watch the facial expressions closely.

1.2.4. fMRI data acquisition

Imaging was conducted on a 3T MRI scanner (MAGNETOM Trio, Siemens, Erlangen, Germany) equipped with a 12-channel head coil. Echo-planar T2*-weighted images were acquired (TR = 2250 ms, TE = 30 ms, flip angle 90°, FOV = 230 mm, distance factor = 20%) using 36 slices in an oblique axial orientation (slice order = ascending, voxel size = 3.6 mm^3, interslice gap = 0.72 mm).

1.2.5. fMRI data analysis

Data were analyzed using SPM8 standard routines and templates (Wellcome Department of Imaging Neuroscience, London, UK). Five initial brain volumes of each run were excluded. The remaining images were realigned to the mean image and then normalized to the standard Montreal Neurological Institute (MNI) template with volume units of 2 mm × 2 mm x 2 mm and finally smoothed with an 8 mm Gaussian filter at full width at half maximum (FWHM). The following analyses were based on an ordinary least-squares estimation method using a general

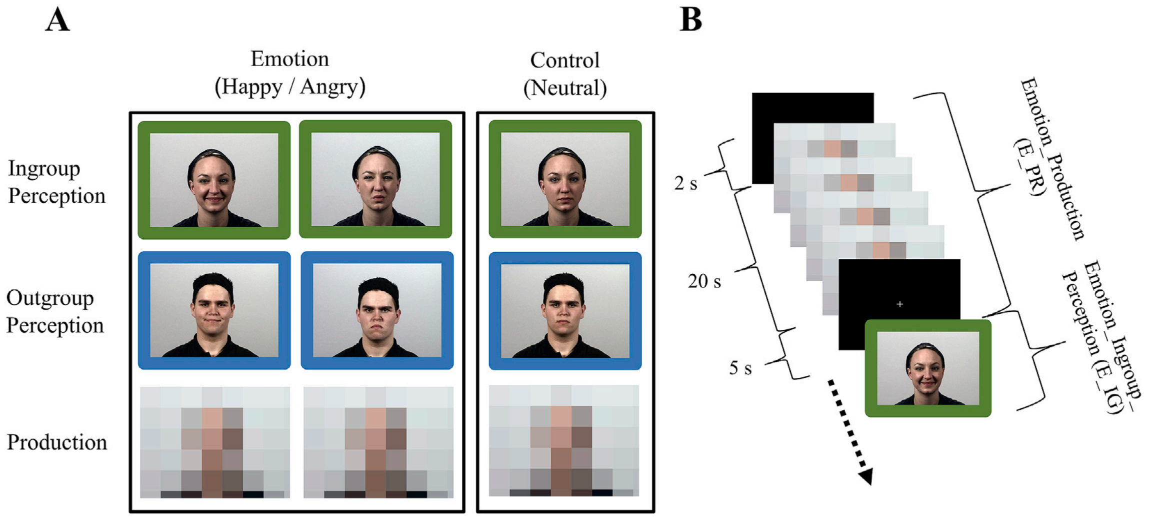

Fig. 1. **(A)** During perception conditions, participants watched dynamic video clips depicting emotional (happy/angry) or neutral (no movement) facial expressions of ingroup or outgroup members. Group membership was indicated by the color of the frame (blue or green). During production conditions, participants produced the facial expressions themselves while watching dynamic pixelated videos. **(B)** Each block lasted 27 s and consisted of an information slide (2 s), four videos depicting actors or pixelated faces (each 5 s), and a fixation cross (5 s).

linear model (GLM). At the single-subject level, regressors were created from the time course of each condition (modeled as blocks with 20 s duration) and convoluted with a canonical hemodynamic response function. The opposite emotions happy and anger were treated as a joint factor in the fMRI analysis aiming to cover a wide range of aspects of emotion for the investigation of the shared neural production-perception network for facial emotion. Movement parameters from realignment were integrated in the model as regressors of no interest. The low-level baseline condition was not included in the model. High-pass filtering (cut off period of 128 s) was applied.

Contrast images for each of the following conditions (compared to the implicit baseline) were calculated and fed into a flexible factorial ANOVA model with subjects treated as random effects:

(i) Emotion_Ingroup_Perception (E_IG);
(ii) Emotion_Outgroup_Perception (E_OG);
(iii) Emotion_Production (E_PR);
(iv) Neutral_Ingroup_Perception (N_IG);
(v) Neutral_Outgroup_Perception (N_OG);
(vi) Neutral_Production (N_PR)

The condition lip-protrusion was modeled on the subject-level but not included in the group analysis. The overall shared neural production-perception network for facial emotion was calculated with the following conjunction: emotion perception (E_IG, E_OG > N_IG, N_OG) $\bigcap$ emotion production (E_PR > N_PR), minimum t-statistic, corrected at $p < .05$ family-wise error (FWE) on a voxel level and a minimum cluster size of 10 voxels. To investigate the motor and emotional aspects of the production-perception coupling we chose the neutral condition (without any facial motion) as a control condition. In a second step, we identified the potential ingroup bias within the shared neural production-perception network for facial emotion. Therefore, we used the resulting activation of the latter contrast as a region of interest (ROI) in which we tested (E_IG > E_OG), correcting for the size of the ROI at $p < .05$ family-wise error (FWE) on a voxel level and a minimum cluster size of 10 voxels. Hereafter, time series were extracted for each participant from each activation cluster using first eigenvariates. In order to test the emotion specificity of the modulation by ingroup and outgroup, general estimation equations (GEE) with a multi-factorial design were used to test the 2 × 2 interaction of emotion/neutral by ingroup/outgroup. Time series of all clusters were exploratorily correlated with the difference of identification with ingroup and outgroup before and after scanning and as well with the difference of likeability ratings of ingroup and outgroup members. Several post-hoc analyses were conducted: Firstly, we tested (E_OG > E_IG) in the ROI. Secondly, although the factors facial emotional expressions and biological movement cannot be fully detangled, we repeated the fMRI analysis using lip-protrusion as a non-emotional movement control condition in order to test the emotion specificity of the ingroup bias. Finally, we repeated all analyses splitting the factor emotional facial expression into happy and angry facial expressions in order to detect potential ingroup bias being specific for the two different emotional valences.

2. Results

2.1. Minimal group paradigm manipulation

In a post-fMRI debriefing, all participants correctly remembered their own problem-solver type, its associated color and the faces of group members presented to them during scanning. Identification with the ingroup (id_IG) was significantly higher than with the outgroup (id_OG) both before and after fMRI scanning (before fMRI scanning: id_IG = 4.93; id_ OG = 3.42; $p < .001$; after fMRI scanning: id_ IG = 5.21; id_ OG = 2.98; $p < .001$). Remarkably, the difference of identification with the ingroup and with the outgroup (id_IG – id_OG) significantly increased after completing the paradigm in the scanner (before fMRI scanning: id_IG – id_OG = 1.52; after fMRI scanning id_IG – id_OG = 2.24; $p < .001$). After scanning, participants rated pictures of ingroup members they had seen in the scanner as significantly more likeable than pictures of outgroup members (mean likeability of ingroup members = 4.00; mean likeability of outgroup members = 3.77; $p < .001$). In addition, the difference of identification with the ingroup and with the outgroup after scanning correlated positively with the difference of likeability of ingroup and outgroup members (Pearson correlation coefficient $r = .148$; $p < .05$). Furthermore, there was a significant positive correlation of the increase of ingroup vs outgroup identification pre and post scanning with the indicated likeability of ingroup and outgroup members (Pearson correlation coefficient $r = .16$; $p < .05$). There was no significant correlation of these measures with neural activation.

2.2. fMRI results

2.2.1. Shared neural production-perception network

The conjunction analysis of emotion production and perception (E_IG, E_OG > N_IG, N_OG) $\bigcap$ (E_PR > N_PR) revealed a bilateral activation network with right-sided preponderance in frontal, parietal, temporal, and limbic areas as well as the cerebellum (whole brain analysis, $p < .05$ FWE corrected., minimum cluster size: 10 voxels, see Fig. 2, Table 1).

2.2.2. Ingroup bias in the shared neural production-perception network

Within this shared neural production-perception network for facial emotion (E_IG, E_OG > N_IG, N_OG) $\bigcap$ (E_PR > N_PR), used as a ROI, stronger activation for perceiving emotional facial expressions of ingroup compared to outgroup members (E_IG > E_OG) was revealed in the temporal poles, amygdalae, the right hippocampus and parahippocampus, the left insula, the left inferior frontal gyrus (pars orbitalis), and the inferior and middle temporal gyrus ($p < .05$, FWE corrected, minimum cluster size: 10 voxels, see Fig. 3 and Table 2). Using the extracted eigenvariates of the strongest activation cluster, we found a significant interaction of the factors emotion/neutral and ingroup/outgroup (Wald chi-square = 8.89, $p < .05$; see Fig. 3). There was no main effect of emotion/neutral (Wald chi-square = 3.39, $p > .05$) and ingroup/outgroup (Wald chi-square = 0.72, $p > .05$). There was no significant activation for outgroup compared to ingroup facial emotion (E_OG > E_IG) within the shared neural production-perception network for facial emotion. In a new model where we split the factor emotion into happy and anger, we tested for ingroup compared to outgroup facial expressions in a shared neural production-perception network for happy and anger independently and found no significant activation. In the additional fMRI-analysis using lip-protrusion as a control condition, significant activation for ingroup compared to outgroup emotional facial expressions in the adapted shared neural production-perception network was found in the right amygdala extending to the right parahippocampus ($x = 32$, $y = 2$, $z = -26$; $T = 4.44$, $K = 31$; $p < .05$, FWE corrected, minimum cluster size: 10 voxels) reflecting an activation cluster of the original analysis (see Table 1).

3. Discussion

To our best knowledge, this is the first fMRI-study, which combined the two following approaches: (i) we identified shared neural production-perception coupling (mirror neuron mechanisms) for facial emotion and (ii) investigated the effect of minimal group membership on this shared neural circuit. With our study we could (i) validate and extend varying results of past research on MNS activation for facial emotions: in a total of 178 participants, common neural activity for the perception and production of facial emotions was found in a bilateral network with right-sided preponderance, encompassing limbic areas, e.g. amygdalae and hippocampi and frontal regions, e.g., inferior frontal gyri and the right middle frontal gyrus, as well as regions of motor MNS in the parietal and temporal lobe and the cerebellum (see Fig. 2, Table 1). More importantly, we could (ii) reveal that there is enhanced neural resonance for the

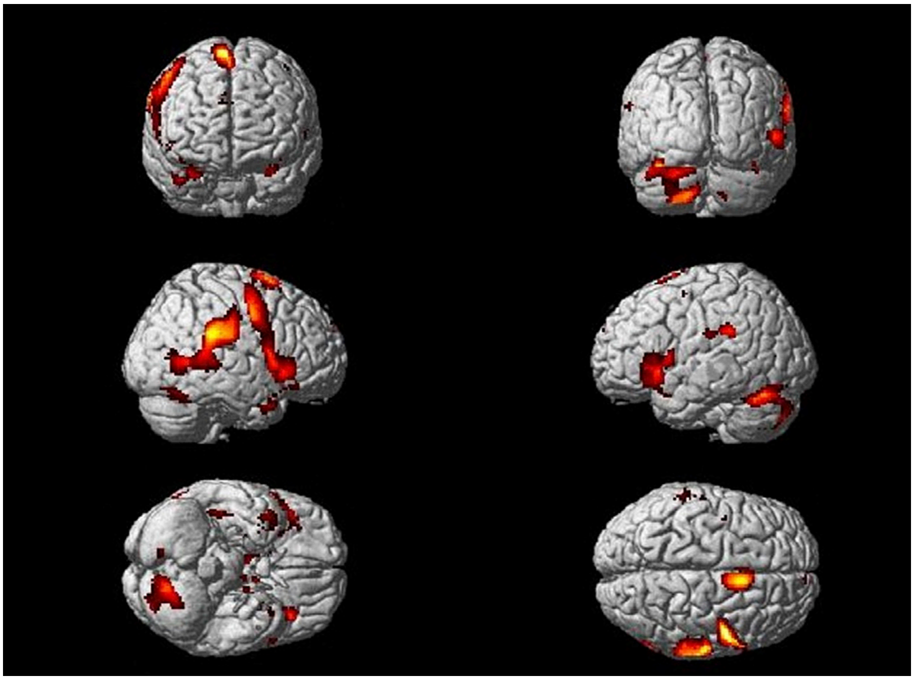

Fig. 2. The shared neural production-perception network for facial emotional expressions, activated by the contrast (E_IG, E_OG > N_IG, N_OG) ⋂ (E_PR > N_PR), whole-brain analysis, $p < .05$ FWEcorr., minimum cluster size: 10 voxels.

perception of ingroup compared to outgroup facial emotional expressions within shared neural production-perception network for facial emotion. Such ingroup bias was present for the temporal poles, amygdalae, the right hippocampus and parahippocampus, the left insula, the left inferior frontal gyrus (pars orbitalis), and the inferior and middle temporal gyrus (Fig. 3, Table 2). So far, previous studies could only speculate that a brain region related to an ingroup bias is part of the MNS. Our results provide proof that there is an enhanced neural response for the processing of ingroup emotional facial expressions in the MNS.

Emotional mirror neuron properties have been investigated in previous studies (Molenberghs et al., 2012). However, regarding emotional facial expressions, there are only few studies on emotional mirror neuron properties that integrated both, a production or imitation and a perception condition. Shared neural activity was found in the inferior frontal gyrus, pre-supplementary motor area, the superior temporal sulcus, the inferior parietal lobule, the amygdala, and the insula (Carr et al., 2003; Hennenlotter et al., 2005; Kircher et al., 2013; Leslie et al., 2004; van der Gaag et al., 2007). Our results validate these findings and show shared neural production-perception activity for emotional facial expressions in (amongst others) the right middle frontal gyrus, right middle and inferior temporal gyrus, right superior frontal gyrus, right supramarginal gyrus, left fusiform gyrus, right putamen, right thalamus, right globus pallidus, left hippocampus, and left olfactory sulcus (see Fig. 2, Table 1).

We found enhanced neural activation for perceiving minimal ingroup compared to outgroup emotional facial expressions inside the MNS in the temporal poles. Greater temporal pole activity has, so far, only been shown for racial ingroup compared to outgroup facial observation (Lieberman et al., 2005). We could generalize this finding and relate it clearly to group membership by using a minimal group design which does not invoke a racial bias. Furthermore, we demonstrated that this ingroup bias relates to the activation of the MNS. The temporal pole is highly interconnected with the amygdala and is thought to play a crucial role in emotional processing and behavior (Olson et al., 2007). Symptoms which can be induced by an amygdala lesion can partially be induced as well by an isolated lesion of the temporal pole; those symptoms include, inter alia, diminished fear, hyperorality, social disinterest, and also rejection from social groups (Olson et al., 2007). Speculatively, the enhanced neural activity in this region for ingroup facial emotions could relate to the emotional and social relevance of the ingroup. Indeed, while watching a friend being socially rejected temporal pole activation correlated with the emotional closeness to this friend (Beeney et al., 2011).

Our results, further, revealed enhanced MNS activation for ingroup compared to outgroup facial expressions in the amygdalae. The amygdala is highly interconnected, besides the temporal pole, with the sensory cortices, the hippocampus, and the prefrontal cortex, among others. It is crucially involved in a large variety of emotional processing including emotional learning, processing of social stimuli, and emotion's influence on memory, attention and perception (Phelps, 2006). It also responds to arousing stimuli our attention is focused on (Phelps, 2006). This might explain why earlier studies reported greater amygdala activation for face perception of a racial outgroup (Cunningham et al., 2004; Hart et al., 2000; Phelps et al., 2000). Such a relation would also make plausible that this effect did not survive when the presented faces of the racial outgroup were familiar to the participants (Phelps et al., 2000). Furthermore, enhanced amygdala activation for the perception of minimal ingroup faces was independent of an additional (implicit) racial group factor (Bavel et al., 2008). This emphasizes the importance of contextual factors, such as the social relevance of a group, for effects of group membership (Bavel et al., 2008). Social factors i.e., the 'need to belong' or previous social exclusion led to an amplified ingroup bias in memory to minimal ingroup compared to outgroup faces (Van Bavel et al., 2012). Remarkably, both social factors ('need to belong' and 'social exclusion'), which led to a superior memory for ingroup members, enhance the emotional relevance of ingroup members. Emotional relevance, and specifically the associated arousal induced by a stimulus, has a strong impact on hippocampal-dependent episodic memory consolidation. The amygdala and its connectivity to the hippocampal complex plays a crucial role for this phenomenon (Phelps, 2006). This relationship might explain the hippocampal and parahippocampal involvement in enhanced MNS activity for ingroup emotional facial expressions, as for the first time revealed by our study.

We also found greater MNS activation for emotional facial expressions in the insula. In the past it has been shown that the anterior insula is involved in the production and perception of facial emotions (Kircher et al., 2013; Pohl et al., 2013). At the same time, the anterior insula has

Table 1

Regions of the shared neural production-perception network for emotional facial expressions, activated by the contrast (E_IG, E_OG > N_IG_N_OG) ⋂ (E_PR > N_PR), whole-brain analysis, $p < .05$ FWEcorr., minimum cluster size: 10 voxels.

Brain region	Hemisphere	x	y	z	T	K
Precentral gyrus, extending to:	R	54	0	50	12.94	2363
Inferior frontal gyrus, pars opercularis						
Inferior frontal gyrus, pars orbicularis						
Putamen						
Amygdala						
Thalamus						
Middle frontal gyrus						
Hippocampus						
Globus pallidus						
Inferior frontal gyrus, pars triangularis						
Insula						
Temporal pole						
Parahippocampus						
Caudate nucleus						
Rolandic operculum						
Superior frontal gyrus						
Postcentral gyrus						
Inferior temporal gyrus						
Cerebellum, crus I, extending to:	L	−14	−72	−48	12.14	1312
Cerebellum, lobule VI						
Cerebellum, lobule VIII						
Cerebellum, crus II						
Cerebellum, lobule VIIb						
Fusiform gyrus						
Supplementary motor area, extending to:	R	8	10	66	11.82	635
Supplementary motor area	L					
Superior frontal gyrus	R					
Right supramarginal gyrus, extending to:	R	58	−32	28	11.30	2482
Superior temporal gyrus						
Middle temporal gyrus						
Postcentral gyrus						
Rolandic operculum						
Inferior temporal gyrus						
Middle occipital gyrus						
Fusiform gyrus						
Inferior frontal gyrus, pars orbicularis, extending to:	L	−36	28	0	8.49	1045
Insula						
Inferior frontal gyrus, pars triangularis						
Amygdala						
Inferior frontal gyrus, pars opercularis						
Temporal pole						
Hippocampus						
Rolandic operculum						
Olfactory sulcus						
Precentral gyrus						
Supramarginal gyrus, extending to:	L	−54	−38	30	7.60	208
Postcentral gyrus						
Middle occipital gyrus (nearest labeled area)	L	−34	−64	8	7.46	44
Fusiform gyrus, extending to:	R	44	−58	−24	6.88	106
Cerebellum, lobule 6						
Cerebellum, crus I						
Globus pallidus, extending to:	L	−14	6	2	6.14	118
Putamen						
Superior medial frontal gyrus (nearest labeled area), extending to	R	4	62	30	6.11	20
Superior medial frontal gyrus	L					
Cerebellum, lobule VIIb	R	14	−76	−46	5.86	20
Cerebellum, lobule VIII						
Cerebellum, crus II						
Thalamus (nearest labeled area)	R	8	−28	−2	5.70	32

also been related to numerous intergroup processes: enhanced neural activity in the anterior insula has been, for example, revealed for the observation of ingroup pain compared to outgroup pain (Hein et al., 2010; Xu et al., 2009). Highlighting the emotional relevance of this region in intergroup contexts, one study reported enhanced insula activation for positive events happening to ingroup members, which was associated with decreased willingness to harm ingroup members (Cikara and Fiske, 2011). Regarding minimal group membership, increased anterior insula activation for the observation of neutral facial expressions during both a pain condition (needle penetration) and a control condition (Q-tip) has been reported (Shen et al., 2018). Yet, another study could show that a racial ingroup bias in insula activation was enhanced by a prior priming of an interdependent self-construal vs. an independent self-construal (Wang et al., 2014). This underlines the relevance of social factors for mirror mechanisms (Cikara and Van Bavel, 2014). Our results, further, reveal that an ad hoc created social factor such as minimal group membership influences shared neural production-perception network activation in the anterior insula being a major hub in the processing of group membership and empathy related neural activation.

We found enhanced MNS activation for ingroup emotional facial expressions also in the inferior frontal gyrus. Higher inferior frontal gyrus activity has previously been reported for racial ingroup compared to outgroup pain in a face observation task (Wang et al., 2014). Lesions in the inferior frontal gyrus have also been demonstrated to be related to deficits in emotional empathy (Shamay-Tsoory et al., 2009). The inferior frontal gyrus has not only emotional mirror neuron properties (Molenberghs et al., 2012), it also activates during self-face perception processing (Devue and Brédart, 2011). On a behavioral level, it could repeatedly be shown that group membership strongly relates to the self-concept (Brewer and Gardner, 1996). And indeed, a study reported greater adjacent inferior frontal gyrus activity for ingroup compared to outgroup face processing as well as for self-face compared to similar face processing (Scheepers et al., 2013). Hence, the increased neural response for ingroup compared to outgroup emotional facial expressions in shared neural production-perception activity in this region, as our results reveal, supports the idea that enhanced empathy-related neural activity for ingroup members is also tied to the self-construct.

From previous research investigating non-emotional motor actions it is known that the middle and inferior temporal gyri have mirror neuron properties (Molenberghs et al., 2012). With our study we could confirm, that the middle and inferior temporal gyri are also part of the shared neural circuit for the production and perception of emotional facial expressions (van der Gaag et al., 2007). We could furthermore reveal an ingroup bias in these two regions while functioning as a part of this circuit. This is in particular surprising against the background that until now these two regions have not been identified as sensitive to ingroup favoritism (Molenberghs, 2013). Interestingly, reduced grey matter volume in the middle and inferior temporal gyri could be related to developmental prosopagnosia (Garrido et al., 2009). Suggesting a relevance for interpersonal relation, grey matter volume in the middle temporal gyrus was positively associated with the level of use of the social networking site ‘Facebook’ (Turel et al., 2018). The implications of the

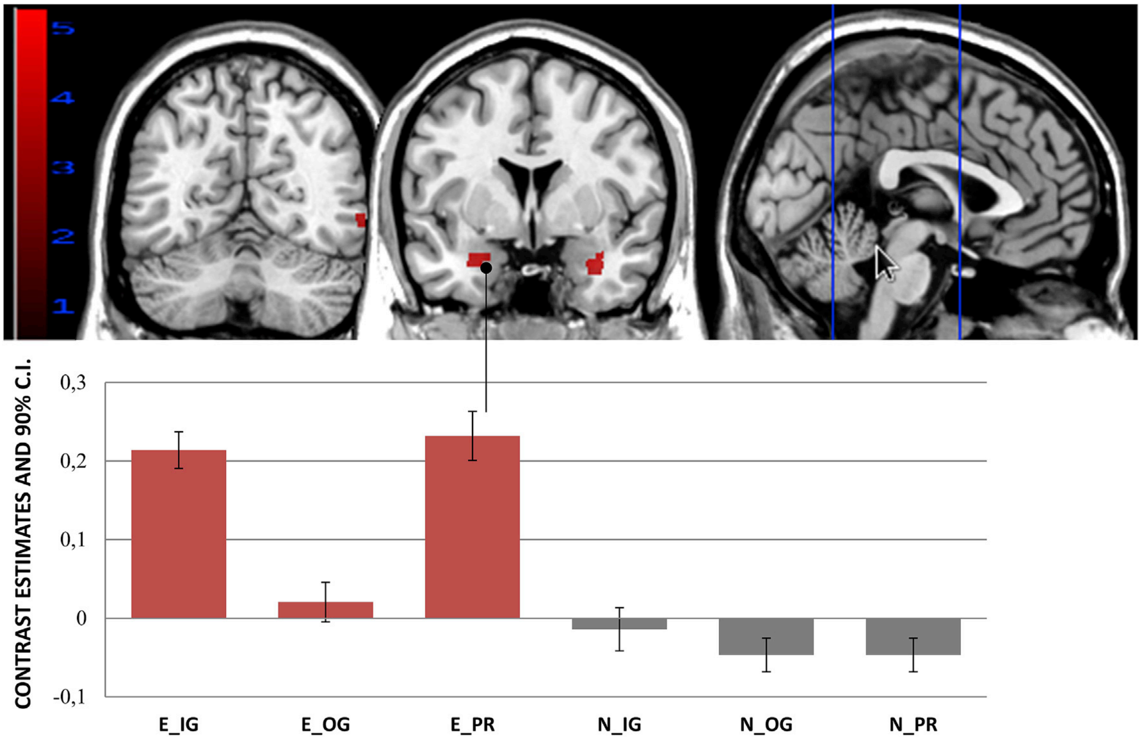

Fig. 3. Ingroup bias in mirror neuron mechanisms reflected in comparison of neural activation for minimal ingroup and outgroup emotional facial expressions within the shared neural production-perception network for facial emotion. We tested (E_IG > E_OG) using the result of our first analysis (see Table 1, Fig. 1) as a region of interest (ROI), p < .05 FWEcorr., minimum cluster size: 10 voxels. The plot illustrates the activation pattern of the strongest activation cluster encompassing temporal pole, amygdala, insula, and inferior frontal gyrus.

Table 2
Ingroup bias in mirror neuron mechanisms reflected in comparison of neural activation for minimal ingroup and outgroup emotional facial expressions within the shared production-perception network for facial emotion: we tested (E_IG > E_OG) using the result of our first analysis (see Table 1, Fig. 1) as a region of interest (ROI), p < .05 FWEcorr., minimum cluster size: 10 voxels. The table shows the activated brain regions.

Brain region	Hemisphere	x	y	z	T	K
Temporal pole, extending to Amygdala Insula Inferior frontal gyrus, pars orbitalis	L	−26	6	−24	5.66	87
Amygdala, extending to Parahippocampus Temporal pole Hippocampus	R	36	−4	−20	4.67	65
Inferior temporal gyrus, extending to Middle temporal gyrus	R	58	−60	−4	4.33	15

results of these studies support our finding that the inferior and middle temporal gyri are recruited during facial emotion production-perception processing.

Together, our findings validate and extend the current knowledge on shared neural activity for the production and perception of facial emotion as well as on ingroup bias in facial emotion perception. But most importantly, our study combines both approaches and could reveal enhanced neural resonance for ingroup facial emotions in the shared neural production-perception network.

3.1. Limitations

Some limitations have to be noted. A strength of our study is that we had a perception and a pure production condition, so that we could identify shared neural production-perception activation via a conjunction of both contrasts. At the same time, this approach hinders a differentiation between ingroup and outgroup in the production condition, which could have been done applying an imitation condition. Future studies should investigate brain activation during the production of different emotional facial expressions while interacting with ingroup or outgroup members. Furthermore, we investigated neural modulation of ingroup membership in the shared neural production-perception network for emotional facial expressions by combining two different valences: happy (positive) and angry (negative). This network therefore incorporates mirror mechanisms of facial expressions of different emotional valences – an approach which also has been used in the past (Carr et al., 2003; Dapretto et al., 2006). Indeed, the temporal pole, amygdala, insula, inferior frontal gyrus, hippocampus, and middle temporal gyrus, which showed ingroup bias in mirror mechanisms in our study, have been activated for both, positive and negative facial emotions (Chen et al., 2009; Likowski et al., 2012; Perrett et al., 2002; Tsukiura and Cabeza, 2008; Vuilleumier et al., 2002; Wild et al., 2003; Williams et al., 2005). The ingroup bias in shared neural production-perception activation for facial expressions, as revealed by our study, is emotion specific but not valence specific. Additional post-hoc analyses revealed no valence specific effects. This might be due to the fact that splitting the factor emotion into happy and angry reduced the number of trials per condition, and consequently reduced the power of our analysis. However, considering the large number of participants of our study, not only the statistical power might be the reason for finding no such effect. Speculatively, differences in depicted emotional valence did not have enough relevance in our paradigm. Future studies could possibly increase the effect size of valence specific ingroup bias by embedding the facial expression in a social context within the fMRI task (i.e., differing the emotional valence of a depicted facial expression depending on prior task reactions of the participant). Another approach would be to make use of the possibilities of pattern classification analyses, where for example a classifier could be trained on production conditions and is then tested on perception conditions. This machine learning approach can potentially generate profound and new insights about mirror neuron functioning. This might also lead to new insights about valence specific effects of group membership.

3.1. Conclusions

Our study provided, for the first time, evidence of an ingroup bias (using artificial, at hoc groups) in the MNS for facial emotion. The strong modulation of limbic activity by group membership in our study was all based on ad hoc, minimal groups, created only minutes earlier. This suggests that at least parts of intergroup conflict and misunderstanding between different groups could be explained by reduced emotional mirroring. This process can be strongly modulated by contextual factors. Therefore, knowledge from neuroscience studies could be relevant for societies with increasingly complex intergroup relations. We took a step forward in this direction by providing evidence for an ingroup bias of brain regions with emotional mirror neuron properties.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.03.048.

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