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The human mirror neuron system—A common neural basis for social cognition?

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Abstract

According to the theory of embodied simulation, mirror neurons (MN) in our brain's motor system are the neuronal basis of all social-cognitive processes. The assumption of such a mirroring process in humans could be supported by results showing that within one person the same region is involved in different social cognition tasks. We conducted an fMRI-study with 75 healthy participants who completed three tasks: imitation, empathy, and theory of mind. We analyzed the data using group conjunction analyses and individual shared voxel counts. Across tasks, across and within participants, we find common activation in inferior frontal gyrus, inferior parietal cortex, fusiform gyrus, posterior superior temporal sulcus, and amygdala. Our results provide evidence for a shared neural basis for different social-cognitive processes, indicating that interpersonal understanding might occur by embodied simulation.

KEYWORDS

affective empathy, affective ToM, distress, fMRI, IFG, mentalizing, shared voxels, STS

1 | INTRODUCTION

Mirror neurons (MN) which might enable us to understand other people's emotions and even to infer their intentions (e.g., Gallese, 2007) fascinate scientists and non-scientists alike. The theory of embodied simulation (Gallese, 2007) proposes that we have an immediate understanding of another person's emotional and mental state by automatic simulation of their motor state in MN of our own brain. If this theory holds true, MN should not only be involved in selected social-cognitive processes but should provide a common neural basis for all social-cognitive processes. We add to this theory by providing evidence for a shared neural basis for the three fundamental social-cognitive processes imitation, empathy, and theory of mind (ToM) both *within* and *across* participants.

An MN mechanism was first presented in 1992 (di Pellegrino et al., 1992) when the authors identified neurons in the monkey brain area F5 that fired not only when the monkey performed a hand movement, but also when it observed the same movement performed by the human experimenter. Since then, many studies applying single-cell recordings have revealed such neurons in the monkey brain (e.g., Gallese et al., 1996; Rizzolatti & Luppino, 2001). Importantly, it was shown that MN code not only for an action, but also for the goal of an action, as also demonstrated in experiments where part of the action was hidden, or only heard (Kohler et al., 2002; Umilta et al., 2001), and therefore, allow prediction (Rizzolatti et al., 2014). The idea how this MN mechanism helps us to understand others is called embodied simulation (Gallese, 2007); that is, by motor resonance, we feel how others feel, and thus, recognize their current state and even their intention. fMRI studies have shown activity in the inferior prefrontal cortex, premotor cortex, inferior parietal lobe (IPL), and posterior superior temporal sulcus (pSTS) in humans observing and imitating actions (e.g., Buccino et al., 2004; de la Rosa et al., 2016; Iacoboni, 2009). A meta-analysis of 125 fMRI studies identified several regions frequently associated with activity for execution and observation of actions (Molenberghs et al., 2012). Among the most frequent regions were inferior (Brodmann Area (BA) 44 and BA9) and middle frontal gyrus (BA6), inferior (BA40), and superior parietal lobe (BA7), as well as the insula (BA13). In particular the inferior prefrontal cortex with adjacent middle frontal gyrus, comprising BA44 and BA6, is considered a key region of the human MNS (e.g., Enticott et al., 2012; Rizzolatti & Craighero, 2004), not only because it was found to be a structural homolog of the monkey mirror neuron area F5, but also because it is assumed to represent actions, and even the intentions and goals of actions (e.g., Iacoboni et al., 2005; Iacoboni & Dapretto, 2006; Umilta et al., 2001). Interestingly, Buccino and colleagues showed that the human cortex topographically represents actions according to the body region, with foot movements represented in BA6 and mouth movements rather in BA44 (Buccino et al., 2004), suggesting a homunculus of action mapping.

Beyond the mere representation of emotionally neutral actions, such as grasping, or finger tapping, the MNS seems to be involved in the recognition of emotions, in empathy, and in ToM (e.g., Mier, Sauer, et al., 2010; Molenberghs et al., 2012; Schulte-Ruther et al., 2007). Recognizing emotional facial expressions results in activation in the regions of the MNS (e.g., Mier, Sauer, et al., 2010) as well as in the face processing network, including fusiform gyrus, STS, and amygdala (Haxby et al., 2000). Importantly, a separation of brain regions as belonging to either the face processing network or the MNS is not clear cut and uniformly agreed upon. For example, one alternative model proposes "shared circuits," comprising the ventral premotor cortex as well as temporal and parietal regions, as being responsible for shared actions, sensations, and emotions (Keysers & Gazzola, 2006). Whereas classically, only the motor regions BA44 and IPL would be considered part of the MNS, newer studies show that also other, nonmotor regions may have mirror properties (see, for example, the meta-analysis by Molenberghs et al., 2012); on the contrary, classical MNS regions, such as BA44, are involved in processes beyond mere mirroring and motor processing (e.g., Koelsch et al., 2006). Notwithstanding these aspects, but to allow a verbal differentiation between these networks, we use the terms MNS and face processing network in reference to their predominant description related to motor versus emotional processing.

Studies on imitation of emotional facial expressions (e.g., Leslie et al., 2004), as well as studies for investigating additional social-cognitive processes, such as ToM and empathy, reveal activation in regions of the face processing network and the MNS (e.g., Carr et al., 2003; Mier, Sauer, et al., 2010; Schulte-Ruther et al., 2007). Mier and colleagues (Mier, Sauer, et al., 2010) demonstrated that emotion recognition and ToM activate comparable brain regions. Importantly, activation in the MNS regions was stronger for ToM than for emotion recognition, suggesting enhanced activation in the MNS with increasing demands for social cognition. Thus, an interesting question is not only whether there is common activation for different social-cognitive processes, but also whether the brain differentiates between these different social-cognitive processes.

Despite the long line of research, studies on the human MNS still suffer from some severe methodological problems. Electrophysiological single-cell recordings, which are required for a clear-cut demonstration of MN properties, are not feasible in healthy humans (for a study in patients with epilepsy, see Mukamel et al., 2010). Therefore, the majority of studies approaching MN in humans rely on methods with lower spatial or temporal resolution such as fMRI, which is one of the best choices when aiming for good spatial resolution, but still an indirect method relying on blood oxygenation (BOLD signal) and not directly measuring neuronal activity. Also, the validity of results of fMRI-based MN research may be compromised by two common steps of data processing: (a) Smoothing of brain activation smudges brain activity so that activation in neighboring voxels overlaps, and thus, becomes less discriminable. (b) Averaging over participants allows no insight into whether individuals show activation in the same region for two or more tasks, or whether the result is due to the averaging. To speak of mirror neuron activity however, it is essential for activation to take place in the same neurons within participants. Furthermore, it is currently unclear whether different tasks of social cognition are being performed by a common network of brain regions, that is, whether the MNS provides a unified substrate for all facets of social cognition. fMRI studies showed activity in a number of recurring areas during several tasks involving observing and imitating actions (e.g., Buccino et al., 2004; de la Rosa et al., 2016; Iacoboni, 2009; Molenberghs et al., 2012), but this provides only indirect evidence, as the activity is not only compared between different participants but even between different studies with different designs.

In this study, we extend previous research on the human MNS by attempting to identify a common network of social cognition in humans using fMRI recordings. The impracticability of single-cell recordings of neuronal activity in healthy humans cannot be circumvented but the additional problems outlined above may be solved. We developed a new set of social-cognitive tasks that use the same stimulus materials (i.e., facial expressions) to test three fundamental processes of social cognition: imitation, empathy, and ToM within and across participants. Imitation can be defined as a process that reproduces the form and intention of an action (Sevlever & Gillis, 2010), which in our study means moving one's face according to a perceived facial configuration. Empathy has many definitions but is commonly divided into cognitive and affective empathy (Cuff et al., 2016). For our study, we adopted the definitions by Walter (2012): Affective empathy is an affective state, elicited by the assumed affective state of another person, similar to that state, and oriented toward them. Importantly, the observer is able to distinguish between self and other, and is aware of the causal relation of own and the other's affective state. Cognitive empathy requires a cognitive understanding of the perceived affective state of another person but needs not involve an affective state in the observer (Walter, 2012). If the negative affective state of another person invokes negative feelings in the observer, the observer is considered to be in personal distress (Walter, 2012). Finally, ToM is defined as the cognitive understanding of not only affective but also all mental states, including the intentions of another individual (Walter, 2012). Because in our study, the focus of the ToM task lies on the affective mental state of the observed individual, our paradigm can be considered as measuring the “affective ToM” component.

Based on previous literature (Carr et al., 2003; Gallese, 2007; Mier, Sauer, et al., 2010; Schulte-Ruther et al., 2007), we hypothesize that all three tasks activate regions associated with the emotional face processing network and the MNS, specifically the amygdala, fusiform gyrus, pSTS, BA44, and IPL. We first analyze activation within the individual tasks *across* participants with smoothed data. To avoid (a) smudging of activity due to smoothing, and (b) the possibility that common activation is based on averaging activation of participants, we extend this approach by investigating shared activation across these tasks by group analyses on smoothed data *across* participants, as well as by analyzing the smoothed and unsmoothed data *within* participants. This last step, which is crucial to identify regions with MN properties in humans, is made possible by using the approach of shared voxels (sVx), published in a seminal paper by Gazzola and Keysers (2009), based on the work of Morrison and Downing (2007). The approach allows for comparison of activation from different tasks using the very same unaltered spatial position and puts the focus on shared activation *within* participants, thus, overcoming the problems introduced by smoothing and group analyses.

Because we assess different social-cognitive functions, we expect not only activation that is common to all of these functions, but also distinct activation patterns specific to the individual tasks and conditions within tasks, for example, increased activation in the MNS in ToM compared to emotion recognition (Mier, Sauer, et al., 2010). Thus, we additionally exploratorily focus on differences between the different subprocesses of social cognition by comparing activation patterns within tasks.

2 | METHOD

2.1 | Participants

We recruited 80 persons, 5 of which had to be excluded from the final analyses due to more than 3 mm translation or 3° rotation ($N = 1$), anatomical aberrations ($N = 1$), or technical issues ($N = 3$). The number of participants was determined before data acquisition, based on earlier analyses of sample sizes for imaging genetics analyses, which were also part of the project, plus possible drop-out (Mier et al., 2010). Inclusion/exclusion criteria were established prior to data analysis. The final sample for analyses consisted of 42 females and 33 males between ages 18 and 36 years (mean: 23.45 years, ± 3.83) with higher education entrance certification. All participants reported no history of psychiatric or neurologic disease and fulfilled the inclusion criteria for MRI measurements.

2.2 | Study procedure

Participants were informed about study procedure and aims, signed written informed consent, and practiced all tasks on a laptop. The study was approved by the ethics committee of the Medical Faculty Mannheim, University of Heidelberg, and is part of a larger project on the human mirror neuron system. Participants joined two appointments, the first appointment with a simultaneous EEG-fMRI set-up and the second appointment with transcranial magnetic stimulation prior to fMRI scanning. Data reported in this manuscript refer to the fMRI-results of the first appointment.

2.3 | Experimental design

We used three experimental paradigms covering different processes of social cognition: An imitation task, an empathy task, and a ToM task. For all three tasks, we used pictures from the Karolinska Directed Emotional Faces stimulus set (Lundqvist et al., 1998) of five females and five males.

The individuals in these pictures were selected to be of young adult Caucasian appearance, to ensure the highest familiarity with the study participants. In addition, the actors had no piercings, glasses, beard, or visible makeup in the pictures. Of each stimulus person, one angry and one fearful facial expression were presented in the Imitation and Empathy task. For the ToM task, the neutral facial expression of these stimulus persons was additionally used. As our main focus is on the MNS, we chose fear and anger, because they are both related to negative valence and high arousal (Russell, 1980), and with this allow low variance in brain activation due to possible effects of differences in valence and arousal.

For all tasks, we created control stimuli without social information, which are described in greater detail in the following sections. Tasks were implemented with Presentation Software (Version 18.1; Neurobehavioral Systems, www.neurobs.com) and presented via video goggles. Responses in the empathy task and ToM task were given with the thumb of the right hand on a diamond-shaped 4-button device (Current Designs, Inc., Philadelphia, PA, USA). Task order 1. Imitation, 2. Empathy, 3. ToM was identical for all participants, because at the second appointment half of the participants received TMS, the other half sham; introducing randomization of the task order would have increased variance in the TMS-effects. Please note that for the Imitation task and the ToM task, there is a condition with the same name, that is, an Imitation condition and a ToM condition, respectively. Whenever we refer to the task, we will use the word task (i.e., imitation task), whenever we refer to a condition, we will use the name of the condition and capitalization (i.e., Imitation), or when we refer to the design the additional word "block" (i.e., Imitation block).

2.3.1 | Imitation

The imitation task (Figure 1-d1) had three experimental conditions: Imitation, Execution, and Observation, as well as a

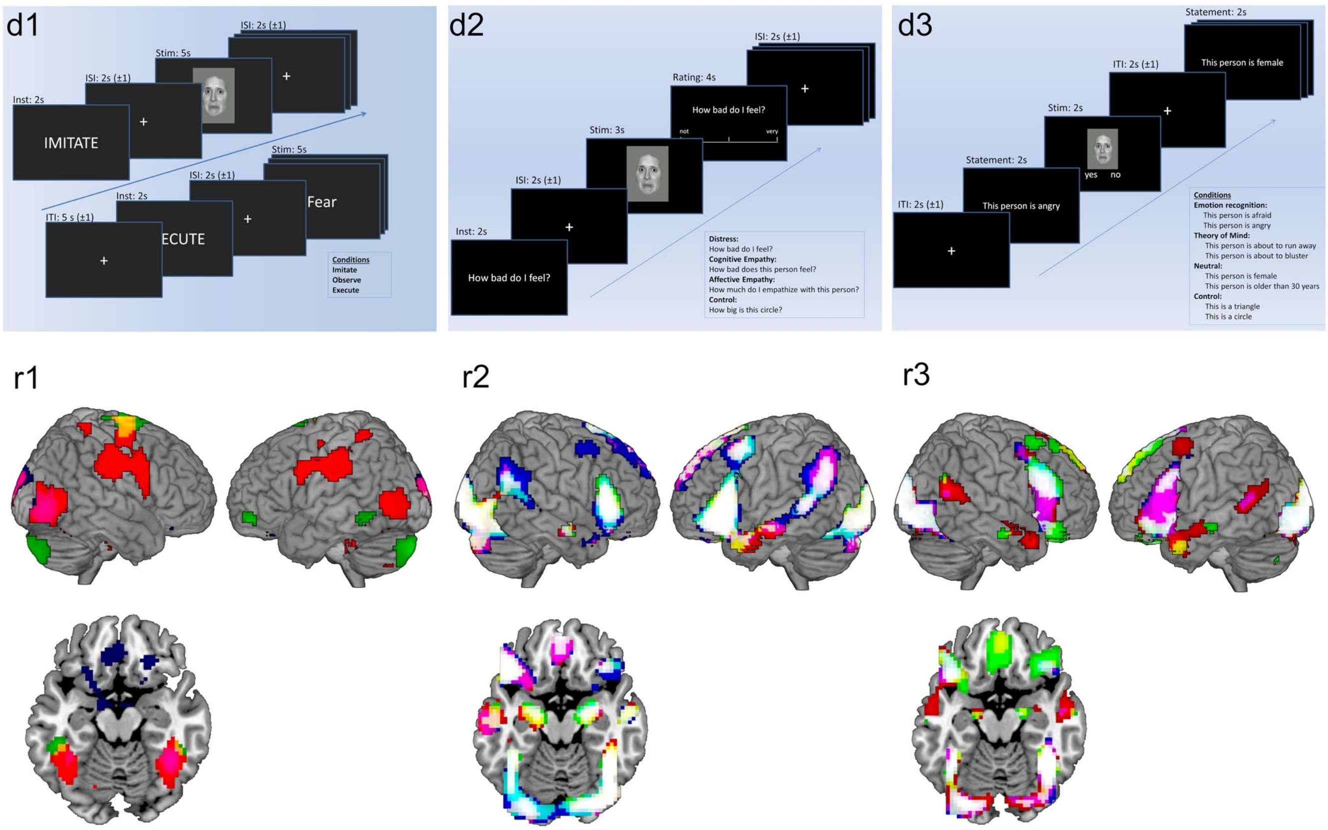

FIGURE 1 Task designs and fMRI activation for each of the three paradigms: d1: Imitation task: Imitation task flow showing order and lengths of all events, exemplarily for two conditions. r1: fMRI activation in the Imitation task: fMRI activation of all conditions of the Imitation task compared to the nonsocial Control condition, slice coordinate $Z = 56$. Red: Imitation > Control. Blue: Action > Control. Green: Observation > Control. Pink: overlap of red and blue. Yellow: overlap of red and green. Significance threshold $p < .05$, FWE-corrected, minimal cluster size $k = 10$. d2: Empathy task: Empathy task flow showing order and lengths of all events, exemplarily for one condition. All questions of the instruction and the rating of the four conditions are shown in the lower right corner. r2: fMRI activation in the Empathy task: fMRI activation of all conditions of the Empathy task compared to the nonsocial Control condition, slice coordinate $Z = 56$. Red: Affective Empathy > Control. Blue: Distress > Control. Green: Cognitive Empathy > Control. Pink: overlap of red and blue. Yellow: overlap of red and green. Cyan: overlap of blue and green. White: overlap of all three contrasts. Significance threshold $p < .05$, FWE-corrected, minimal cluster size $k = 10$. d3: ToM task: ToM task flow showing order and lengths of all events. All statements of the four conditions are shown in the lower right corner. r3: fMRI activation in the ToM task: fMRI activation of all conditions of the ToM task compared to the nonsocial Control condition, slice coordinate $Z = 56$. Red: ToM > Control. Blue: Emotion Recognition > Control. Green: Neutral > Control. Pink: overlap of red and blue. Yellow: overlap of red and green. Cyan: overlap of blue and green. White: overlap of all three contrasts. Significance threshold $p < .05$, FWE-corrected, minimal cluster size $k = 10$

Control condition. At the beginning of each block the instruction cue "Observe," "Imitate," or "Execute" was presented. The stimuli for the Observation and Imitation block were angry and fearful faces of five men and five women. Each emotional face of each individual was displayed once in the Imitation condition and once in the Observation condition. In the Imitation block, participants had to imitate the facial expression as accurately as possible, in the Observation block to passively view the facial expression. In the Execution block, participants read the word "anger" ["Ärger"] or "fear" ["Angst"] and had to produce the corresponding facial expression. In the Control condition participants had to pronounce the German letter "Ä" or "A" aloud. Ä and A were chosen by the authors to roughly resemble the facial movements during anger and fear, respectively. Participants were instructed to imitate, execute, or say the letter for the whole duration of the cue presentation. The conditions were designed to shed further light on imitation and its subprocesses: The Observation condition covers the process of looking at an emotional face, the Execution condition combines face movement with emotional content in the absence of a face stimulus, and the Control condition is pure facial movement without facial stimulus or emotional content. Imitation is the combination of Observation and Execution. Figure 2 gives a graphical illustration of the relationship between subprocesses and shows the basis for the contrasts of interest.

Blocks were presented in a fixed order for a total of five times. Each block of the three experimental conditions contained four stimuli, making a total of 20 stimuli. To avoid carry-over effects between experimental conditions, control stimuli were divided into blocks of two stimuli and were presented in alternation with the experimental blocks. As there were three experimental conditions, there were also three blocks of the Control condition for each run, and 15 blocks over the whole experiment, resulting in a total of 30 stimuli for the Control condition.

The instruction cues prior to each block were presented for 2 s, the face stimuli for 5 s, control stimuli for 3 s. Stimuli within the blocks were presented in pseudo-randomized order and were separated by an inter-stimulus-interval of 1–3 s. The instruction cues initiating a new block were preceded by an inter-block-interval of 4–6 s. Task duration was 13 min.

2.3.2 | Empathy

The empathy task (Figure 1-d2) again consisted of three experimental conditions: Affective Empathy, Cognitive Empathy and Distress, and one Control condition.

Each condition was associated with one specific question. At the beginning of each block, the instruction cue "How bad do I feel? [Wie schlecht fühle ich mich?]" (Distress), or "How bad does the presented person feel [Wie schlecht fühlt sich die Person?]?" (Cognitive Empathy), or "How much do I empathize with the presented person [Wie sehr fühle ich mit der Person mit?]?" (Affective Empathy), or "How big is the circle?" [Wie groß ist der Kreis?] (Control condition) was shown. Task conditions were selected to capture major facets of empathy.

Participants were instructed to think about the cued question while watching fearful or angry faces. After each stimulus, the question was displayed again, together with a

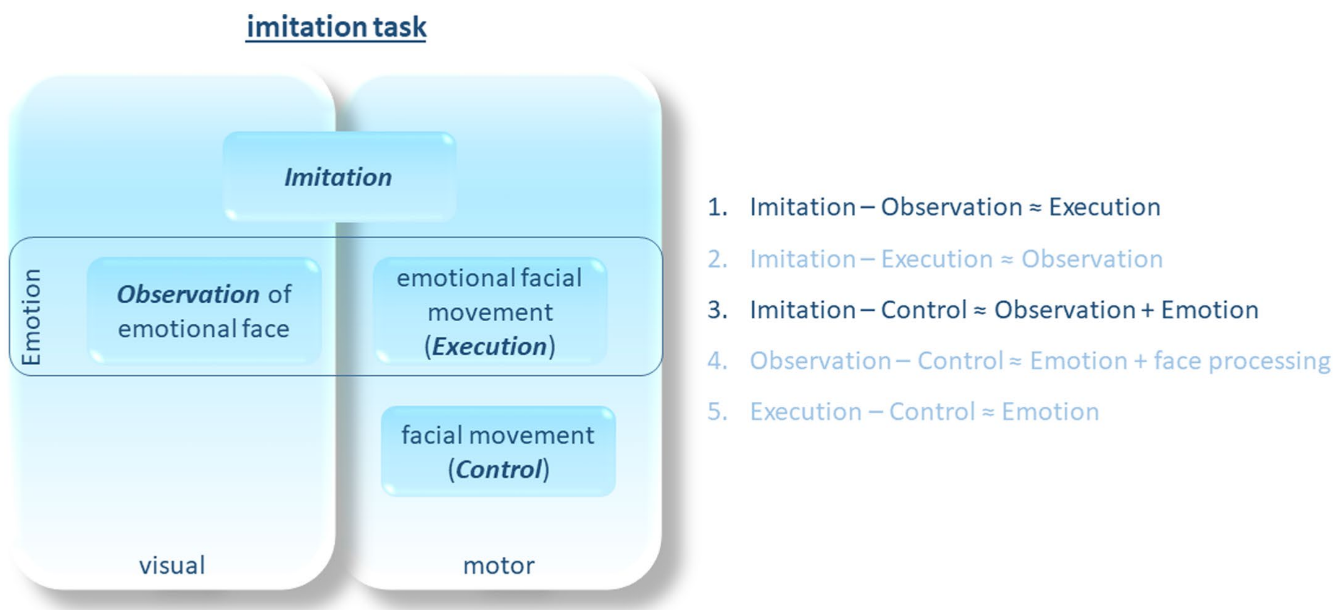

FIGURE 2 Illustration of the conditions of the imitation task and investigated subprocesses. Task conditions are in italics, all contrasts of interest created in the first-level models are written to the right. Contrasts of interest in dark font are used in the conjunction and sVx analyses

continuous visual analog scale from "not at all" on the left to "very much" on the right (Control condition: "small" to "large"), on which participants had to indicate their answer. Participants were instructed that when someone else is feeling very bad, oneself might also feel bad and also might feel strong empathy for the other person, but that this needs not necessarily always be the case. In addition, the question how much one empathizes with someone is not the same as feeling bad because of the suffering of the stimulus person. The face stimuli were taken from five women and five men and presented once for each experimental condition. The control stimulus was a black line figure, specifically a circle, designed to have a similar background color and texture as the experimental stimuli, and the same size. The circle on each of the seven control stimuli differed in size. The Control condition was designed as a low-level control, to assess visual processing and response selection on a rating scale. Please refer to Figure 3 for an illustration of the conditions of the empathy task and the basis for the contrasts of interest.

Analogous to the imitation task, we chose a design with experimental blocks of four stimuli alternating with a control block of two stimuli, all in a fixed order. The instruction cues prior to each block were presented for 2 s, the face and control stimuli for 3 s, and the visual analog scale for 4 s. Stimuli within the blocks were presented in pseudo-randomized order and were separated by a jittered inter-stimulus-interval of 1–3 s. The instruction cues initiating a new block were preceded by a jittered inter-block-interval of 4–6 s. Each experimental block was presented five times and each control block 15 times, making 20 trials for each experimental block and 30 total control trials. Presentation of the control block was alternated with the experimental blocks to prevent the effects of one block only influencing the control effects. Number and duration of control trials was adjusted to yield a total presentation time similar to that of the experimental conditions. Total duration of the task was 17 min.

2.3.3 | Theory of mind

The ToM task (Figure 1-d3) was adopted from a previous study (Mier, Sauer, et al., 2010) and also had three experimental conditions: Affective ToM, Emotion Recognition, Neutral Face Processing, and a Control condition. The different conditions were implemented by different statements preceding the facial or control stimuli, with one statement per emotion for each condition, which corresponds to a total of 8 statements, and 16 trials per condition (one correct statement-picture pair and one incorrect statement-picture pair). The conditions reflect major aspects of social cognition, such as face processing, emotion recognition, and affective Theory of Mind. The Control condition was added as low-level control, to assess visual processing and response selection. Figure 4 gives a graphical illustration of the conditions, and the contrasts of interest.

The participants' task was to indicate by button press whether the picture matched the previous statement (left: yes; right: no). Statements were the German versions of: "This person is about to bluster [Diese Person schimpft gleich]" and "This person is about to run away [Diese Person läuft gleich weg]" for the Affective ToM condition, "This person is angry [Diese Person ärgert sich]," and "This person is afraid [Diese Person fürchtet sich]" for the Emotion Recognition condition, "This person is female [Diese Person ist weiblich]" and "This

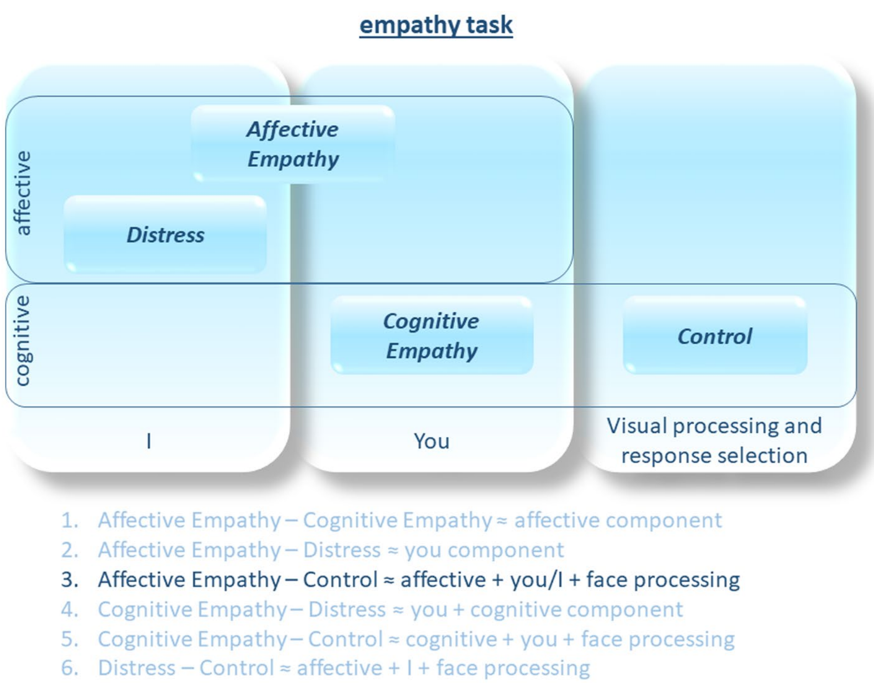

FIGURE 3 Illustration of the conditions of the empathy task and investigated subprocesses. Task conditions are in italics, all contrasts of interest created in the first level models are written at the bottom. Contrasts of interest in dark font are used in the conjunction and sVx analyses

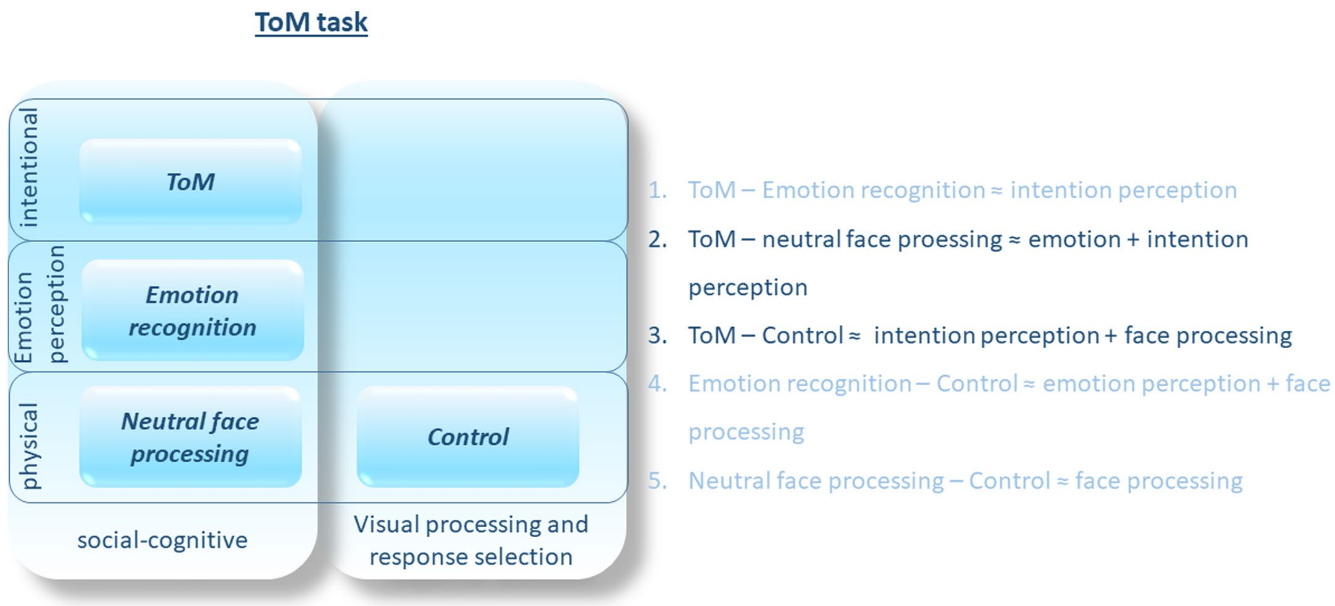

FIGURE 4 Illustration of the conditions of the ToM task and investigated subprocesses. Task conditions are in italics, all contrasts of interest created in the first-level models are written to the right. Contrasts of interest in dark font are used in the conjunction and sVx analyses

person is older than 29 years old [Diese Person ist älter als 29 Jahre]" for the Neutral Face Processing condition, and "This is a circle [Dies ist ein Kreis]" and "This is a triangle [Dies ist ein Dreieck]" for the Control condition.

The experimental stimuli were the angry, fearful, and neutral facial expressions of each of the five male and female identities described above. For each identity, each facial expression was presented once per respective condition and statement. The control stimuli, again, were black line figures of circles and triangles of five different sizes, each presented twice over the whole task.

The ToM task was presented in an event-related design. Each statement was presented for 2 s and the subsequent stimulus for an additional 2 s. A jittered inter-trial interval of 1–3 s was applied. All trials were presented in a pseudo-randomized order, with 20 trials per condition, making a total of 80 trials. The order was the same for all participants. All in all, this task took about 8 min.

2.4 | fMRI data acquisition and analysis

fMRI data were acquired using a 12 channel head coil in a 3T Siemens Magnetom Trio at the Central Institute of Mental Health in Mannheim, Germany. During the tasks, we used echo-planar imaging with 32 descending 3 × 3 × 3 mm slices with 1 mm gap, TR = 2,000 ms, TE = 30 ms; flip angle = 80°, field of view = 192 mm; matrix = 64 × 64. Prior to functional imaging, an MPRage was acquired of each participant (TR = 1,570 ms, TE = 2.75 ms; flip angle = 15°, field of view = 256 mm; matrix = 256 × 256; voxel size 1 × 1 × 1 mm).

Data were analyzed with Statistical Parametric Mapping 8 (SPM8, http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). Preprocessing included slice time correction, realignment to the mean image, normalization with coregistration to the MPRage, and resampling with 3 × 3 × 3 mm voxel size. First-level analyses were run twice, once with unsmoothed data and once with smoothed data, using an 8 mm Gaussian kernel. For all first-level analyses, the face stimuli were modeled as events (folding the HRF with a stick function) as regressors in the general linear model (GLM), and the according six movement parameters derived from realignment were used as regressors of no interest. For each task, a separate GLM was built, so there were three GLM in total.

In detail, for the Imitation task, we modeled the face or figure events for each condition, resulting in four regressors (Imitation, Observation, Execution, Control). The same was true for the ToM task with four regressors (affective ToM, Emotion Recognition, Neutral Face Processing, Control). For the empathy task, we also modeled the face or figure events for each condition (Affective Empathy, Cognitive Empathy, Distress, Control), and additionally one regressor for all responses, making five regressors in total. No separate regressors for anger and fear were built.

Contrast of interest for second level analyses for the imitation task were: Imitation > Control, Observation > Control, Execution > Control, Imitation > Observation, Imitation > Execution; for the empathy task: Affective Empathy > Control, Cognitive Empathy > Control, Distress > Control, Affective Empathy > Cognitive Empathy, Affective Empathy > Distress, Cognitive Empathy > Distress; and for the ToM task: ToM > Control, Emotion Recognition > Control, Neutral Face Processing > Control, ToM > Neutral Face Processing, ToM > Emotion Recognition. To identify a stepwise increase or decrease from ToM over Emotion Recognition to Neutral Face Processing, we additionally included a multiple regression based on the respective first level contrasts: [ToM > Control] − [Emotion Recognition > Control] − [Neutral Face Processing > Control].

The significance threshold was set to $p < .05$ FWE corrected, k = 10 for the whole brain analyses within tasks. For the conjunction analyses, a full factorial model was defined. The significance threshold for the conjunction analyses was set to $p < .001$ without a cluster size threshold. The threshold was chosen analogous to the threshold for the sVx analyses that is described below. Region of interest analyses were conducted for the IPL (left: 870 voxels, right: 868 voxels), BA44 (left: 252 voxels, right: 255 voxels), pSTS (left: 324 voxels, right: 161 voxels), fusiform gyrus (left: 617 voxels, right: 627 voxels), and the amygdala (left: 47 voxels, right: 47 voxels). Masks for IPL, BA44 fusiform gyrus and amygdala were taken from the WFU PickAtlas tool (Maldjian et al., 2003, 2004). As to our knowledge, there is no posterior STS mask in the WFU PickAtlas, we used one based on activity in a former study with the ToM task (Mier, Sauer, et al., 2010), which has been successfully applied in further studies with the ToM task (Mier et al., 2014). ROI analyses were performed using small-volume correction at a significance threshold of $p < .05$ ($p_{FWE} < .05$ peak voxel), and minimal cluster size $k = 10$ for the single tasks, but without cluster size threshold for the conjunction analyses. For the figures in this manuscript, thresholded SPM maps were exported and overlaid on the “ch2bet.nii” template in MRIcron (https://www.nitrc.org/projects/mricron).

Behavioral data were analyzed with IBM SPSS Statistics V20 (https://www.ibm.com/us-en/marketplace/spss-statistics), applying repeated measures ANOVAs, as well as post hoc *t*-tests.

2.5 | sVx analysis

We based the sVx analyses on the first level models described above, for two sets of contrasts: (a) (Imitation > Control) & (Affective Empathy > Control) & (ToM > Control), and (b) (Imitation > neutral) & (ToM > neutral). The second set of contrasts was selected to account for face processing (the empathy task is not included in the second set, because no social control condition is available). Based on Gazzola and Keysers (2009), the significance threshold for the sVx analyses (with smoothed and with unsmoothed data) was set so that the probability to incorrectly define a voxel as sVx in a single participant was less than .001 (i.e., for each of the three contrasts in set 1, we set $p < .05$, corresponding to a total probability for the set of $.05^3 = .000125$, and for each of the two contrasts in set 2, we set $p < .01$, corresponding to a total set probability of $.01^2 = .001$ to incorrectly define a voxel as sVx). Based on Boolean maps of the single contrasts, we calculated the logical “&” to obtain the sVx maps containing the intersections of voxels over the contrasts. These sVx maps served to count the number of sVx in the ROIs as well as the whole brain. For each participant, the individual brain/ROI volume was taken as a reference for the required number of sVx to surpass chance level. The required number of sVx was based on a cumulative binomial distribution function with a voxel-wise level of .001 and a threshold of $p < .05$ for finding the returned number of voxels by chance. The number of participants with sVx and the number of participants with sVx above chance level is reported.

3 | RESULTS

3.1 | Imitation is linked to activation in the mirror neuron system

Whole-brain analyses for the comparison of Imitation with the Control condition mainly revealed activity in the inferior parietal, frontal, and temporal regions, premotor cortex and visual cortex, as well as in the basal ganglia. The comparison of Imitation with Observation and with Execution revealed similar patterns in both cases. Figures S2 and S3 show the activation of Control versus baseline and Execution versus baseline, respectively, to illustrate that these conditions were associated with the expected motor activation. Figures S5 and S6 show the activation patterns of the different conditions in greater detail. In agreement with our hypotheses, small-volume correction for our ROIs confirmed significantly higher activation in all ROIs for Imitation than for the other conditions. Comparison of Execution with Control mostly resulted in activation in cerebellum and inferior temporal lobe. ROI analyses showed higher activation for Execution than Control in fusiform gyrus and pSTS bilaterally, as well as in left IPL and left BA44. Observation > Control revealed mainly activation in the visual and cortex, in the orbitofrontal cortex and in the parahippocampal gyrus, reaching into the amygdala. ROI analyses showed significant activation in bilateral fusiform gyrus, bilateral amygdala, and right pSTS, but in disagreement with our hypotheses no significant activation in BA44 and IPL was revealed. The comparison of the experimental conditions with the Control conditions, including the overlap between conditions, is displayed in Figure 1-r1. Further results of the imitation task can be found in Figure S4 as well as Tables S1 and S2, for whole-brain and ROI analyses, respectively.

3.2 | Empathy is linked to activation in the mirror neuron system

Whole-brain analyses revealed increased activation in several cortical regions for Affective Empathy compared to Control, including posterior superior temporal sulcus, inferior parietal cortex, inferior frontal gyrus and visual cortices, medial frontal gyrus and precuneus, as well as the amygdala. A comparable picture occurred when comparing Cognitive Empathy with Control and Distress with Control. In agreement with our hypotheses, all Empathy conditions in comparison to the Control condition resulted in enhanced activation in all ROIs. Figure 1-r2 displays activity in the experimental conditions in comparison to the Control condition, including the overlap between conditions. Figures S7 and S8 show the activation patterns of the different conditions of the empathy task in greater detail. Behavioral results of the empathy task are displayed in Figure S1a).

Comparison of the Empathy conditions showed significantly higher activity for Distress than for Affective and Cognitive Empathy in the temporoparietal junction (TPJ) bilaterally, as well as in the precuneus. ROI-analyses additionally showed that Distress resulted in enhanced activation in right BA44, bilateral IPL, and bilateral pSTS compared to Cognitive Empathy. ROI-analyses comparing Distress and Affective Empathy revealed significantly higher activation during Distress in bilateral fusiform gyrus, as well as in bilateral IPL and pSTS. Affective Empathy was linked to higher activation in left TPJ than Cognitive Empathy. Accordingly, ROI-analyses showed significantly higher activation in the left IPL for Affective Empathy compared to Cognitive Empathy. Cognitive Empathy led to stronger activation than Affective Empathy in the executive control network, including regions of parietal and frontal cortex. ROI-analyses for Cognitive compared to Affective Empathy showed significant activity in right BA44, left pSTS, and bilateral IPL, but in a more dorsal part of the IPL than for Affective compared to Cognitive Empathy. Further results of the empathy task can be found in Figure S4 as well as Tables S3 and S4, for whole-brain and ROI analyses, respectively.

3.3 | ToM is linked to activation in the mirror neuron system

Whole-brain regression analysis showed that activation in the pSTS and inferior frontal gyrus was highest for ToM, medium for Emotion Recognition, and lowest for neutral faces. Whole-brain analyses of ToM in comparison to Control, as well as in comparison to neutral faces mainly showed activation in pSTS, inferior frontal gyrus reaching into the insula, visual regions, and premotor cortex. As expected, ROI analyses for both ToM compared to Control and ToM compared to neutral revealed significantly increased activation for ToM in all ROIs. Whole brain comparison of ToM to Emotion Recognition mainly revealed enhanced activation in the TPJ region. In line with our hypotheses, the corresponding ROI-analyses comparing ToM with Emotion Recognition showed higher activation for ToM in all ROIs, except for BA44. Whole-brain analyses for Emotion Recognition compared to Control and to neutral both revealed a similar pattern as the comparison of ToM with these conditions (i.e., inferior frontal gyrus, pSTS, and premotor cortex). The corresponding ROI-analyses for Emotion Recognition compared to Control and to neutral showed activation in all ROIs, except for the IPL in the comparison with Control, and the amygdala in the comparison with neutral. The comparisons of the experimental with the Control condition, including overlaps between conditions, are depicted in Figure 1-r3. Further results of the ToM task can be found in Figures S4, S9, and S10, as well as Tables S5 and S6, for whole-brain and ROI analyses, respectively. Results of the ToM-task are also presented in a recent publication regarding endophenotypes of schizophrenia (Yan et al., 2020). Behavioral results of the ToM task are displayed in Figure S1b).

3.4 | Common activation in the mirror neuron system exists across tasks

A whole-brain conjunction analysis to investigate activation *across* participants and tasks including ToM, Affective Empathy and Imitation, each compared to Control, mainly revealed bilateral activation in amygdala, fusiform gyrus and pSTS, as well as activation in inferior frontal gyrus and premotor cortex (Figure 5a). In agreement with our hypotheses, ROI-analyses confirmed significant activation in all of these regions, except for right BA44. To assure that these effects are not merely representing the processing of the faces that were used in all conditions, we also conducted a conjunction analysis on ToM compared to Neutral and Imitation compared to Observation. This conjunction analysis (comparing both task conditions with their social Control condition) revealed common activation in pSTS and IPL bilaterally, as well as in bilateral inferior frontal gyrus, and in premotor cortex (Figure 5b). The corresponding ROI-analyses revealed activation in bilateral pSTS and IPL, as well as in left BA44. Detailed results of the conjunction analyses can be found in Tables S7 and S8, for whole-brain and ROI analyses, respectively.

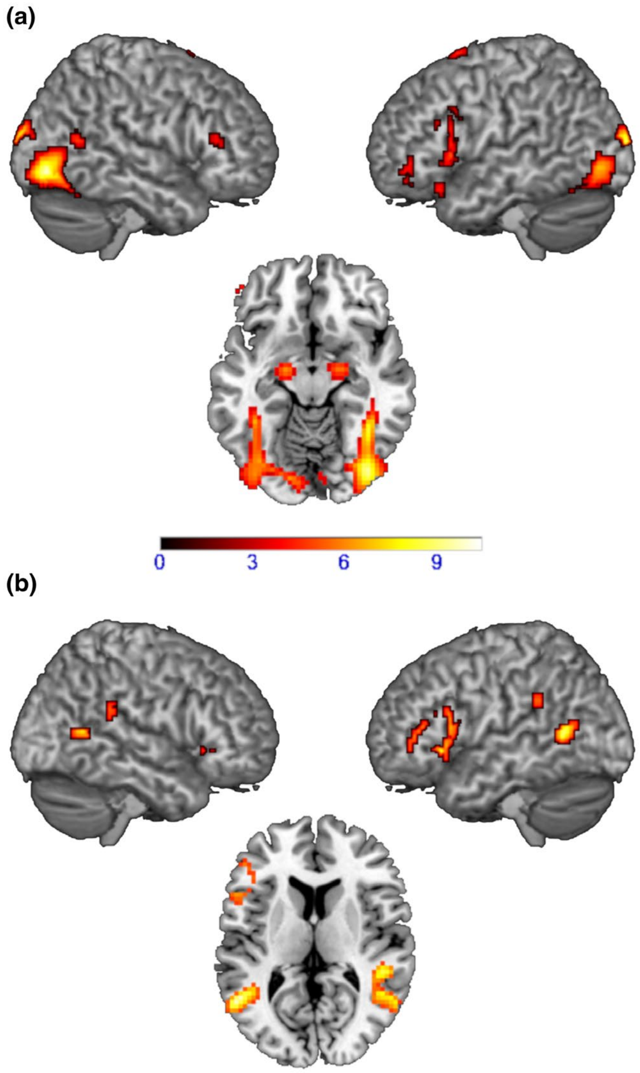

FIGURE 5 fMRI activation of the conjunction analyses: fMRI activation of the conjunction analyses. (a) Of all three tasks ((Imitation > Control) & (Affective Empathy > Control) & (ToM > Control), smoothed data), slice coordinate $Z = 60$, (b) of the Imitation and the ToM task ((Imitation > Observation) & (ToM > Neutral), smoothed data), slice coordinate $Z = 82$. Color bar indicating t values. Significance threshold $p < .001$, uncorrected, minimal cluster size $k = 10$

3.5 | Shared voxel counts show activation in the mirror neuron system within participants

To investigate activation *within* participants across tasks, sVx were counted. As shown in Table 1, more than 80% of participants had a significant number of sVx across tasks (i.e., (Imitation > Control) & (Affective Empathy > Control) & (ToM > Control)) on a whole-brain level. For the sVx count of Imitation compared to Observation and ToM compared to neutral, again sVx were revealed in all of our ROIs (Table 2). However, in this case, the number of sVx was reduced for amygdala and fusiform gyrus. For both contrasts, performing the analyses on unsmoothed data, compared to smoothed data, resulted in more participants with sVx. In Figure 6, brain renders and slices with the sVx counts from unsmoothed data over all three tasks compared to Control are shown.

4 | DISCUSSION

Using a combination of three social-cognitive tasks (Imitation, Empathy, and ToM) based on emotional facial expressions and three different methods of analysis (analysis of individual tasks, conjunction analysis, and sVx counts), we found converging evidence for a common network of brain regions underlying the different social-cognitive processes. Importantly, the combination of different analyses allowed us to confirm that common activation was present both *across* and *within* participants (Gazzola & Keysers, 2009), a result which has not been presented so far for processes of social cognition. The present study does not prove the existence of mirror neurons in the human brain, but it strongly emphasizes a neural mirroring process during social cognition (Molenberghs et al., 2012; Mukamel et al., 2010). Furthermore, we were able to show that activation in the network differentiates between different social-cognitive processes, in particular in the TPJ region.

4.1 | Common activation across tasks

Analyses of the single tasks revealed activation in BA44 and IPL, as well as in fusiform gyrus, pSTS, and amygdala. These results are in agreement with earlier studies showing an involvement of the emotional face processing network, as well as the MNS in different aspects of social cognition (Carr et al., 2003; Mier, Lis, et al., 2010).

This pattern of common activation from the single task analyses was statistically confirmed by the conjunction analyses that revealed shared activation across tasks in all regions of interest, except right BA44, strongly suggesting a common neural basis for different social cognitive-processes. Importantly, when restricting the analyses to ToM and Imitation (that each allowed contrasting with a social Control condition), only classical motor MNS regions were revealed as regions with common activation, further emphasizing the importance of these regions for social cognition. This analysis also suggests that in contrast to the common activation in regions classically associated with emotional face processing, namely fusiform gyrus and amygdala, the motor MNS effects were not merely linked to the processing of the facial stimuli, but are specific for social-cognitive processing. Both BA44 and IPL are homologs to monkey brain areas containing motor neurons (Rizzolatti et al., 1998) and

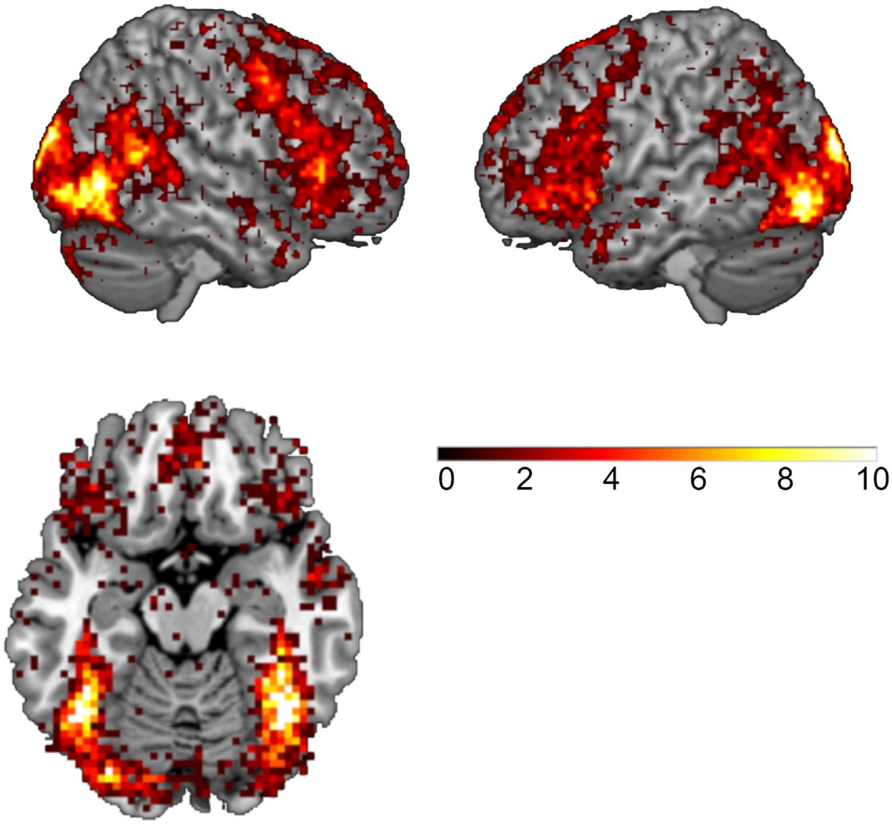

FIGURE 6 sVx counts for all three tasks (Imitation > Control) & (Affective Empathy > Control) & (ToM > Control): Number of participants with sVx for each voxel, unsmoothed data, slice coordinate $Z = 56$. Color bar indicating the number of participants

TABLE 1 Number of participants with shared voxels (sVx) in the regions of interest. Numbers in brackets indicate number of participants with number of sVx greater than chance level. Contrasts: (Imitation > Control) & (Affective Empathy > Control) & (ToM > Control)

		Amygdala[2]	BA44[3]	IPL[5]	pSTS[3]	FG[4]	Brain[1]
Smoothed	Left	12 (12)	29 (24)	15 (8)	34 (31)	62 (52)	75 (62)
	Right	12 (12)	19 (14)	16 (8)	43 (40)	66 (61)	
Unsmoothed	Left	6 (6)	36 (20)	53 (20)	57 (45)	66 (58)	75 (69)
	Right	9 (9)	22 (16)	44 (19)	58 (49)	73 (55)	

Note: Number of sVx at chance level: [1]:80–85 depending on brain size. [2]:0. [3]:1. [4]:2, [5]:3.

Abbreviations: BA44, Brodmann area 44; FG, fusiform gyrus; IPL, inferior parietal lobe; pSTS, posterior superior temporal sulcus.

TABLE 2 Number of participants with shared voxels (sVx) in the regions of interest. Numbers in brackets indicate number of participants with number of sVx greater than chance level. Contrasts: (Imitation > Observation) & (ToM > Neutral)

		Amygdala[2]	BA44[3]	IPL[5]	pSTS[3]	FG[4]	Brain[1]
Smoothed	Left	2 (2)	25 (24)	22 (17)	33 (29)	17 (9)	71 (58)
	Right	2 (2)	19 (13)	30 (16)	18 (15)	16 (6)	
Unsmoothed	Left	3 (3)	28 (17)	44 (11)	40 (27)	31 (6)	75 (58)
	Right	1 (1)	33 (17)	43 (19)	27 (8)	31 (5)	

Note: Number of sVx at chance level: [1]:80–85 depending on brain size. [2]:0. [3]:1. [4]:2, [5]:3.

Abbreviations: BA44, Brodmann area 44; FG, fusiform gyrus; IPL, inferior parietal lobe; pSTS, posterior superior temporal sulcus.

have been reported to show a pattern of activation in humans (Kilner et al., 2009; Molenberghs et al., 2012; Rizzolatti & Craighero, 2004; Rizzolatti et al., 1998; Thomas et al., 2018) that has been described from monkey research on MN. In contrast, the STS is not thought to have motor neurons (Rizzolatti & Craighero, 2004). It is, however, a key region for processing variable aspects of the face and biological motion, and has been shown to be substantial for intention recognition (Carr et al., 2003; Liu et al., 2010). A meta-analysis by van Overwalle (Van Overwalle, 2009) pointed out involvement of the STS in forwarding visual input to the MNS. Thus, the STS not only plays a role as part of the extended face processing system (Haxby et al., 2000), but also provides visual input to the MNS, and seems to be important for social cognition beyond mere face processing.

In line with the study of Gazzola and Keysers (2009), the conjunction analyses were supported by the sVx analyses that revealed sVx *within* participants in each of our regions of interest. This was true when analyzing sVx across all three tasks with nonsocial stimuli as a Control condition. When analyzing activation across those two tasks with a facial expression as a Control condition (Imitation compared to Observation and ToM compared to neutral face processing) sVx also occurred in all ROIs, but the number of sVx in amygdala and fusiform gyrus was reduced, again supporting a special role of the MNS for social cognition. Those analyses with unsmoothed data resulted in a higher number of sVx, reflecting the obvious fact that a better spatial resolution of the signal is beneficial for detecting sVx. Interestingly, in the conjunction analysis with smoothed data, no common activation was found in right BA44—one of the core regions of the MNS. Thus, the sVx analysis seems to be a valuable and maybe even necessary additional step to account for interindividual variance in the MNS.

4.2 | Differences between the task conditions

All tasks were associated with activation in the face processing network and in the MNS, but there were also differences between different conditions of the tasks. For the imitation task, the Execution condition presented activation in regions with motor neurons, while the Observation condition resulted in activation in the amygdala and fusiform gyrus. The activation in the Execution task can be explained by the motor performance of the participants. The lack of activation in motor MNS regions for the Observation condition, however, is in contrast to previous studies on the observation and imitation of emotional facial expressions (van der Gaag et al., 2007) and contradicts the major assumption of the simulation theory: the notion that motor simulation occurs automatically without cognitive influence (Gallese, 2003; Gallese & Goldman, 1998). This lack of significant activation in BA44 and IPL during Observation is discussed in the limitations and perspectives section.

In the Empathy task, the different conditions showed distinct involvement of the ROIs. Possibly most importantly, Distress in comparison to Cognitive and Affective Empathy resulted in higher activity in the precuneus and the TPJ bilaterally, which links posterior superior temporal with inferior parietal regions. Affective Empathy was also linked to higher left TPJ activation than Cognitive Empathy. TPJ and precuneus are key regions of the default mode network (Greicius et al., 2003) that has been linked to self-referential processing. Whereas distress ("how bad do I feel") is focused on the self, Affective Empathy ("how much do I feel for the person") demands focus on both the self and the other person, and cognitive Empathy ("how bad does the person feel") puts the focus completely on the other person. Albeit not expected a priori to this study, considering that the default mode network highly overlaps with our regions of interest that are involved in social cognition (Mars et al., 2012) it is plausible that the Affective Empathy and the Distress conditions elicit strong TPJ activation. In particular, the left TPJ seems to play an important role in self-reference during social cognition.

In agreement with earlier studies using the same ToM task, activation in the motor MNS regions is highest during ToM, followed by Emotion Recognition (Mier et al., 2014, 2016; Mier, Sauer, et al., 2010), suggesting that social-cognitive demands are reflected in the height of activation. The result of higher activation for distress than Cognitive Empathy in the Empathy task in the TPJ region suggests that further regions can be integrated into the social-cognitive process, depending on the social-cognitive demands. Thus, the "social brain" seems to differentiate between different social-cognitive processes by the strength of activation within certain regions, as well as by integrating further regions.

To summarize, whereas all tasks have common activation in MNS and face processing networks, single task conditions can be characterized by distinct features. Whereas the Distress condition of the Empathy task involves DMN activation, reflective of self-referential processing, the Emotion Recognition and ToM conditions of the ToM task mainly differ in their strength of motor MNS activation.

4.3 | Limitations and perspectives

Using the same stimuli for all tasks has the advantage of preventing differences between tasks due to stimulus material, but this approach also increases familiarity and the risk of habituation processes. We assume that these possible effects have no major impact on our results because within tasks each condition would be affected to the same amount by familiarity effects. In addition, habituation to the stimuli could lead to reduced attention, and therefore, less task-specific brain activation, therefore, weakening the study results, not resulting in false-positive effects. Because habituation should also evolve across tasks, in particular the conjunction analyses would have suffered from habituation effects. Future studies might consider using different stimuli out of the same stimulus set, to allow for comparability while keeping the stimuli novel, and therefore, avoiding the risk of habituation effects during the course of the experiments.

Because the different conditions and tasks were designed to address different social-cognitive processes, task difficulty across tasks or conditions could not be equalized. For example, observing a face should always require less cognitive effort than interpreting the emotion, which automatically also entails observing the face. Future studies might focus on disentangling the influences of task difficulty on social-cognitive processes. In addition, we used a fixed order of conditions in the imitation task and empathy task, so order effects cannot be completely ruled out.

Our analyses were performed on a data set of simultaneous EEG-fMRI measurements. The gradient artifact of the MRI which is present in the EEG signal is a well-known problem and several correction methods have been established (e.g., Moosmann et al., 2009). Vice versa, previous studies also indicated an influence of EEG caps on MRI data quality (Klein et al., 2015; Luo & Glover, 2012). These studies report quality impairments in the structural data, but functional data seem to be reliable. Furthermore, data quality should have been affected equally over all conditions and each result reported in the manuscript is based on comparisons between conditions.

One possible limitation is anticipatory motor preparation in the ToM task and empathy task. Because responses in the empathy task were given after face presentation, an additional regressor could be used to control for button presses. As the Control conditions required responses comparable to the experimental condition, possible confounding effects should be low.

By combining different tasks and different methods of analysis within the same study, we were able to overcome some of the methodological problems that are inherent in fMRI research. However, it has to be clearly acknowledged that we still rely on a measure that assesses mass signals of neurons converted to changes in blood flow and oxygen saturation. Thus, all our results are still indirect and rather coarse-grained. Facing these limitations, it becomes an urgent matter to enhance the theoretical understanding of the neuronal response underlying the BOLD signal. In particular, local, spiking network models of individual brain regions (Hass et al., 2016) could allow for such a deepened understanding, when constrained by data from human fMRI. The development of such models is an integral aspect of our ongoing project to understand the human MNS.

The methodological limitations outlined above may also provide explanations for some of the unexpected results. In particular, we did not find significantly increased MNS activity during the Observation of emotional faces, which challenges the idea of embodied simulation. Such a null result in fMRI does not necessarily imply the lack of such activation—it could also mean that activity of MN was too short or too weak to elicit the compensatory blood flow that generates a detectable BOLD signal. Another interesting interpretation is opened by a study by the group around Keysers and Gazzola testing the influence of the participants' levels of responsibility on their empathy for pain (Cui et al., 2015). Interestingly, the empathic brain response was reduced when participants were not responsible for the observed pain. These results suggest that MNS activation can be reduced depending on the context. In our tasks, the Observation condition was the only condition, in which the participant had no further task than to observe a facial expression. Similar to the pain study summarized above, neural activation might be reduced if no active involvement is required. Or framed differently, it has been shown that activation in the MNS is stronger when intentionality comes into play. This is especially evident in studies showing that MNS activation is higher for meaningful actions than for meaningless actions (Iacoboni et al., 2005; Koski et al., 2002; Rizzolatti et al., 2014) and in studies showing that MNS activation can be modified by motivation (Cheng et al., 2006).

The sVx analysis, although in best support of a common ground of social cognition, also suffers from methodological problems that need discussion. In particular, it needs to be emphasized that a voxel of 3 mm^3 contains, depending on the specific region and calculation, several hundreds of thousands up to more than a million neurons. Consequently, to be counted as a sVx of the MNS, a voxel needs to contain many thousands of MN. The method is thus too coarse to prove the influence of a subset of neurons within a region. This limitation may be the reason why, albeit significant, only part of the participants and only few voxels within the MNS regions had sVx properties. Furthermore, the tasks are not the strongest to elicit activation in motor neurons, because movement is neither observed, nor expressed (except in the imitation task). However, we aimed to probe social-cognitive skills, and commonly, facial expressions are very subtle in comparison to large body movements. Thus, tasks that rely on rather large-scale motions (e.g., finger tapping, or hand movements) might more easily find more sVx. In addition, there is evidence that the MNS differentiates between different actions, meaning that different actions are represented in different parts of the MNS (Buccino et al., 2004). Thus, another option is that we found fewer shared voxels due to a more fine-grained response in the MNS that also differs between different emotions and social-cognitive processes. Future studies might use experimental designs that target MNS processing of different emotions, or that use repetition suppression designs to investigate the human MNS (Fuelscher et al., 2019).

4.4 | Conclusions

This is the first study investigating a variety of social-cognitive processes within the same participants, allowing the assessment of a shared neural response to social stimuli. Conjunction, as well as sVx analyses revealed common neural activation in amygdala, pSTS, fusiform gyrus, IPL, and BA44 across tasks, suggesting an involvement of the emotional face processing network and the MNS for social cognition. Our findings support the assumption that the MNS is at the heart of our interpersonal understanding.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Stephanie Nicole Lyn Schmidt: Data curation; Formal analysis; Investigation; Methodology; Software; Visualization; Writing-original draft; Writing-review & editing. **Joachim Hass:** Conceptualization; Funding acquisition; Writing-review & editing. **Peter Kirsch:** Resources; Supervision; Writing-review & editing. **Daniela Mier:** Conceptualization; Funding acquisition; Investigation; Project administration; Resources; Supervision; Writing-original draft; Writing-review & editing.

DATA AVAILABILITY STATEMENT

Research data are not shared.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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