NeuroImage 81 (2013) 294–305

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Differential role of the Mentalizing and the Mirror Neuron system in the imitation of communicative gestures

A.G. Mainieri [a,b,*], S. Heim [a,b,c,d], B. Straube [e], F. Binkofski [d], T. Kircher [e]

[a] Department of Psychiatry, Psychotherapy and Psychosomatics, Medical School, RWTH Aachen University, Pauwelsstr. 30, 52074 Aachen, Germany
[b] JARA—Translational Brain Medicine, Germany
[c] Institute of Neuroscience and Medicine (INM-1), Research Centre Jülich, Leo-Brandt-Straße 5, 52428 Jülich, Germany
[d] Section Clinical and Cognitive Neurosciences, Department of Neurology, Medical School, RWTH Aachen University, Pauwelsstr. 30, 52074 Aachen, Germany
[e] Department of Psychiatry und Psychotherapy, Philipps-University Marburg, Rudolf- Bultmann-Straße 8, 35039 Marburg, Germany

ARTICLE INFO

Article history:
Accepted 4 May 2013
Available online 17 May 2013

Keywords:
Imitation
Communicative intentions
Mentalizing system
Mirror neuron system

ABSTRACT

Successful social interaction requires recognising the intention of another person's communicative gestures. At a neural level, this process may involve neural activity in different systems, such as the mentalizing system (MS) and the mirror neuron system (MNS). The aim of the present study was to explore the neural correlates of communicative gestures during observation and execution of these gestures. Twenty participants watched video clips of an actor executing social gestures (S), non-social gestures (NS) and meaningless gestures (ML). During fMRI data acquisition, participants were asked to observe (O) and subsequently to execute (E) one of two tasks: imitate the gesture presented (IMI) or perform a motor control task (CT). For the contrast IMI > CT we found activations in the core areas of the MNS [inferior parietal lobule (IPL) and inferior frontal cortex, the posterior part of pars opercularis], as well as in areas related to the MS [superior temporal sulcus (STS) and middle cingulate cortex]. For S > NS, we found activations in the left medial orbitofrontal cortex (mOFC), right superior frontal cortex and middle cingulate cortex. The interaction of stimulus condition (S vs NS) and task (IMI vs CT) revealed activation in the right IPL. For the interaction between observation vs execution (O vs E), task (IMI vs CT) and stimulus condition (S vs NS) we found activation in the right mOFC. Our data suggest that imitation is differentially processed in the MNS as well as in the MS. The activation in IPL is enhanced during the processing of social gestures most likely due to their communicative intention. The activation of IPL together with medial frontal areas may contribute to mentalizing processes. The interaction in the mOFC suggests an involvement of self-referential processes in the processing of social gesture.

Introduction

Humans use communication as a social tool to affect and modify others' mental states. Through verbal and gestural modalities humans construct the meaning of their communication directed to another person. There is a vast amount of literature on the communicative processes of speech. However the gestural communicative modality without accompanied speech, such as facial expressions, eye gaze, gestures, and body position has received much less attention. Thus the aim of the present study is to investigate the neural correlates of communicative gestures during observation and actual imitation.

According to the pragmatic view of communication (Bara, 2011; Searle, 1981), human communicative competence is based on the ability to recognise and to process a specific kind of mental state, namely, communicative intention. Communicative intention is defined as two intentions that occur simultaneously: (1) the communicator's intention to convey meaning to someone else, and (2) the communicator's intention that the receiver recognises that he/she has a communicative intention (Enrici et al., 2011; Frith, 2007; Walter et al., 2004). Recognition of communicative intent is a complex process in which the receiver has to recognise the communicator's intentions: (1) the communicator's conveyed meaning presented in actions (words and gestures), and (2) the communicator's state of mind about the effects of his/her actions over the receiver's mental state. Thus the recognition of communicative intent involves a second order representation of mental states in which the receiver has to infer (represent): (1) the meaning of communicator's actions (words and gestures); and (2) the communicator's representation of his/her own (receiver's) mental state.

We infer mental states via mentalizing, the psychological ability to understand and predict other people's behaviours by attributing mental states to them (Astington et al., 1988; Baron-Cohen, 1995; Premack and Woodruff, 1978). In the field of developmental psychology, mentalizing is defined as the ability to psychologically simulate

* Corresponding author at: Department of Psychiatry, Psychotherapy and Psychosomatics, Medical School, RWTH Aachen University, Pauwelsstr. 30, 52074 Aachen, Germany. Fax: +49 241 8082422.
E-mail addresses: amainieri@ukaachen.de (A.G. Mainieri), sheim@ukaachen.de (S. Heim), straubeb@med.uni-marburg.de (B. Straube), fbinkofski@ukaachen.de (F. Binkofski), psychiat@med.uni.marburg.de (T. Kircher).

1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.05.021

another person's psychological state or being able to "put oneself into others' shoes" (Carruthers and Smith, 1996; Happe, 2003). Thus, psychological simulation would involve two processes, probably acting in concert: (1) imagining (simulating) an intention, desire or belief in particular; and (2) imagining (simulating) actions resulting from this mental state. The product of these two processes can be attributed to oneself and others in order to predict or explain one's own or someone else's actions (Harris, 1991). Whether the computation of these two simulation processes occur *in sequence* or *in parallel* is not clear in the literature. However, mentalizing abilities are theoretically assumed necessary to encode the abstract intentions of others, that is, mental states like beliefs, feelings and desires (Frith, 2007; Wimmer and Perner, 1983).

Based on functional imaging studies, a neural system for mentalizing abilities, the Mentalizing system (MS), has been proposed to comprise the temporoparietal junction (TPJ, including the posterior part of the superior temporal sulcus [pSTS]) and medial frontal cortex (Abu-Akel, 2003; Bradshaw and Sheppard, 2000; Calder et al., 2002; Ciaramidaro et al., 2007; David et al., 2006b; den Ouden et al., 2005; Fletcher et al., 1995; Krach et al., 2008; Newen and Vogeley, 2003; Tavares et al., 2008). However, only a few fMRI studies explored the neural correlates of the MS in relation to communicative gestures with content related to abstract mental states (hand action with symbolic connotation, for example, waving goodbye) (Gallagher and Frith, 2004; Liew et al., 2011; Marsh and Hamilton, 2011; Straube et al., 2010).

Behaviourally, gestures are nothing more than intended actions that could be learned by observation and imitation. The ability to understand another person's action and imitate that action is a core component of human social behaviour and learning (Meltzoff and Decety, 2003). A distinct set of neural regions underlie the imitative process—the Mirror Neuron system (MNS) (Buccino et al., 2001; Gallese et al., 1996; Pineda, 2008; Rizzolatti et al., 1996), which is activated when an individual performs an intentional action (goal-directed action) and when s/he observes another person's intentional action (Binkofski and Buccino, 2004; Buccino et al., 2007; Decety and Grezes, 1999; Iacoboni, 2009; Meltzoff and Decety, 2003; Rizzolatti and Craighero, 2004). The MNS comprises the inferior parietal lobule (IPL) and the posterior part of inferior frontal gyrus (IFG, the posterior part of par opercularis). In the context of gesture observation and imitation, the MNS possibly has the function of extracting the motor intentions from the gesture, or action concatenation of motor meaning (Rizzolatti and Sinigaglia, 2007). However, further processes would be necessary to extract communicative intentions, or the abstract mental states underlying the observed gestures. Therefore MS might be also activated during observation and imitation of communicative gestures that also have embedded abstract mental states, like beliefs and feelings (Carrington and Bailey, 2009; Liew et al., 2011; Schippers et al., 2010).

In summary the MS and MNS would work in concert in order to take an observed communicative gesture as communicative intended. In an imaging study this hypothesis has been explored further, Schippers et al. (2009) investigated the neural basis of gestural communication during a social game (charade) where pairs of participants had to either produce meaningful gestures or interpret meaningful gestures of the other. They found that during passive observation or interpretation the MNS and TPJ (bilateral) were activated, while during the gesture production the MNS was activated and the mPFC was deactivated. These results suggest that the MS and MNS work separately but in parallel in extracting the communicative intention (MS) and the motoric meaning (MNS) of gestures. All gestures performed by the participants in Schippers et al. (2009) study were considered communicative due to the nature of the task (charades). However, the content of the gestures (meaning) were not related to abstract mental states but to a description of procedural actions (i.e. ride a bike or peel a fruit). It might be that the deactivation of the mPFC during gesturing was because the conveyed meaning of the gestures performed were not related to abstract mental states.

Self-referential processes might also take part in the imitation process of communicative gesture, as the content of the gesture imitated mirror or resonate with self experiences and memories of the observer and not just goals in the external world (Schippers et al., 2010). In a meta-analyses study comprising 107 neuroimaging studies of self- and other-related judgments the mPFC activation was associated with both self- and other judgments (Denny et al., 2012). Specifically the ventral aspect of mPFC (BA24, BA32 and BA10) responds preferentially for both self-referential processing and mental state inferences about others (Schippers et al., 2010; Tamir and Mitchell, 2010). Thus during imitative processes it would be possible to simulate similar abstract inner states by adopting the perspective of the other during acting (imaginatively or actual acting).

In sum what it is not known to date is the neural correlates of observation and imitation of communicative gestures with content related to abstract mental states: what are the different contributions of the MS and MNS for the understanding of communicative gestures with content that mirror self and other abstract mental states? We hypothesise that the MS (mFC and pSTS) and MNS (IFG and IPL) act in parallel (but complementarily) during observation and execution of communicative gestures in a social context (imitative behaviour) and with socially relevant content (content related to abstract mental states). Thus we designed an experiment manipulating: (a) task (imitation [IMI] vs motor control task [CT]); (b) stimulus content (social [S], non-social [NS], meaningless [ML]) and (c) experimental phase (observation [O] vs execution [E]).

The novelty of the present study in the context of MS and MNS lays in the imitation of communicative gestures that mirror the self and other abstract mental states. During face-to-face interaction they elicit similar abstract mental states in the sender and receiver 'as if' the receiver mirrors the inner state of the sender simultaneously. The focus of this paper is not in investigating the specificities of MNS or MS. Rather we want to investigate the possible contexts in which parts of both systems are activated. In particular, we predicted: (1) activation in neural areas related to the MNS (such as the posterior inferior frontal gyrus [pars opercularis] and IPL [area PFt]) for the imitation task contrasted to the control task during both observation and execution phases; (2) activation in areas related to the MS (such as cingulate, paracingulate cortex and STS/TPJ) for social vs non-social gestures (Amodio and Frith, 2006; Mitchell, 2009), (3) activation in areas related to the MNS and MS specifically for social gestures modulated by imitation task (IPL, IFG and pSTS); (4) activation in the medial frontal cortex for social gestures modulated by the imitation task due to self-referential processing (David et al., 2006a; de Greck et al., 2008; Northoff et al., 2006; Spengler et al., 2009).

Material and methods

Participants

Twenty-seven right-handed, healthy male participants, with an average age of 24.6 years (SD = 3.23) were recruited from the staff of the RWTH University Hospital and were paid for their participation. Participants reported no past or present medical, psychiatric or neurological disorders and were not taking any psycho-pharmacological medication at the time of the study or within the past year. All participants had normal or corrected-to-normal visual acuity, were native German speakers and provided informed consent. The study was approved by the local ethics committee. Only data from 20 participants are reported; seven participants were excluded due to excessive head movement (see data analyses) during the fMRI session.

Stimuli

The video clips were chosen from a pool of clips developed by our group (Green et al., 2009; Kircher et al., 2009b; Straube et al., 2009, 2010, 2011a, 2011b). In each video, the same male actor performed

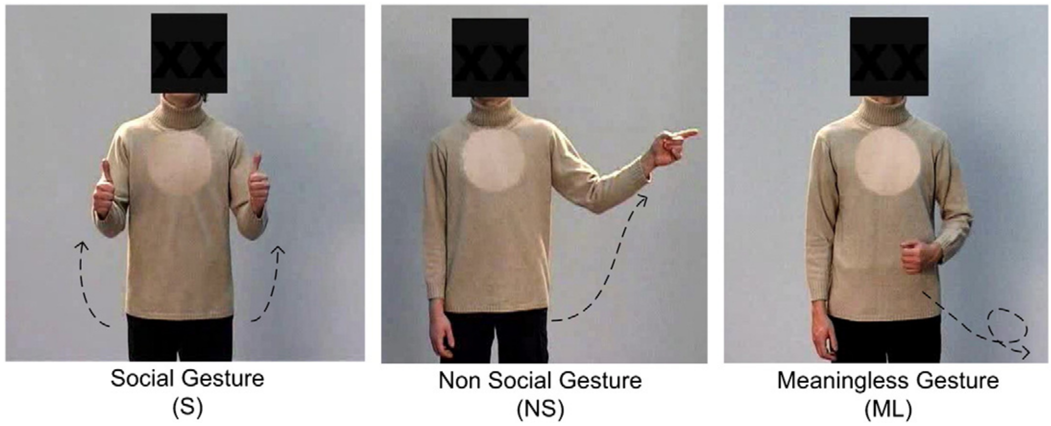

Fig. 1. Examples of each gesture category.

social, non-social or meaningless gestures in a natural and spontaneous way, and with no speech. That is, the actor scripted his own gestures as to obtain maximal naturalness. Each stimulus video clip was originally 5 s in duration, including 500 ms before and after the scene during which the actor did not move and with his hands at his sides. For the purpose of this study, the videos were all edited to 4 s with at least 100 ms before and after each scene to account for the variable lengths of the gestures and to standardise the videos. Importantly, the execution of the gestures was actor-driven so as to obtain maximal naturalness (for a more detailed description of the stimulus material production and evaluation see Kircher et al., 2009; Straube et al., 2009; Green et al., 2009).

The speechless video clips depicted the same male actor with his face covered; wearing a pullover with a dark or light circle, executing a gesture with one or both hands and arms (Fig. 1). The colour of the circle was included after recording the videos, so the two versions are identical except the circle colour. For a more detailed description of the stimulus material production and evaluation, see Kircher et al. (2009), Straube et al. (2009), and Green et al. (2009).

For stimulus selection, 196 video clips were presented to 20 participants in a pilot study. These 20 subjects were different from those who participated in the fMRI study. The participants had to observe the gestures and immediately afterward rate it, on a scale of 1 to 7, according to comprehensibility (of the action content), communicative intention (action with communicative intention related to self and actor's mental states) and emotionality. We define communicative intention as actions that promote in the sender and receiver a recognition of two conditions at the same time: (a) the signals are sent (by the sender) with the intention of altering the receiver's mental state; and (b) the receiver attributes mental states to the sender (Frith, 2007; Walter et al., 2004). The participants had to indicate if the gesture observed mirrors their own inner state during observation, since not all communicative gestures elicit similar inner states in receiver and sender, for example, pointing to indicate a route (Table 1, Non-Social Gesture). Participants also had to describe in short sentences what they understood as the meaning of each gesture.

The stimulus material was selected with regards to the stimulus characteristics of interest (social [S]: meaningful and high communicative intention; non-social [NS]: meaningful and low communicative intention; Meaningless [ML]: meaningless and low communicative intention).

For the imaging study we selected 20 items per each condition (S, NS and ML).[1] Mean and standard deviation (SD) values were used in order to select the video clips and create the conditions for the fMRI study (Table 1). The general criteria for the best rated videos used in the fMRI study were gestures with the clearest meanings as indicated by very similar interpretations among the participants' written descriptions and with low variability across participants for all ratings based on mean and standard deviation (SD) of ratings (SD $\leq$ 1.5 for comprehensibility, communicative intention and emotionality; Table 1). As the imaging study included an imitation task, only video clips of gestures without head and/or shoulder movements were included in order to prevent movement artefacts during the scanner sessions. In all three conditions the same number of gestures was performed with one or both arms and hands. There was no difference in the average distance of all gestures from the circle on the actor's pullover.

For the social condition (S), gestures which elicited in the participant a state of communicative intention and mirror in his/herself similar mental state addressed to the actor (‘wave a greeting’, ‘well done’, ‘look up’), were included. For this category, videos with high ratings (Mean $\geq$ 4.5) for comprehensibility, communicative intention and emotionality were chosen. The non-social condition (NS) included gestures/mimes which depicted common actions in the physical world (‘take a note’, ‘cut something with scissors’, ‘turn around’). For this category, videos with high ratings for comprehensibility (Mean $\geq$ 4.5) and low ratings for communicative intention (Mean $\leq$ 3.6) and emotionality (Mean $\leq$ 3.1) were chosen. For the meaningless condition (ML), random gestures with low ratings for comprehensibility, communicative intention and emotionality (Mean $\leq$ 3.1) were chosen.

The final set of videos used for the fMRI study comprised 20 videos for each of the 3 conditions were selected (social [S]: meaningful and high communicative intention; non-social [NS]: meaningful and low communicative intention; Meaningless [ML]: meaningless and low communicative intention). In this final set, communicative intention was rated significantly higher for social than for non-social videos ($t(19) = 13.83$; $P < .0005$) as well as higher for social than for meaningless stimuli ($t(19) = 14.78$; $P < .0005$). Similarly, comprehensibility was rated significantly higher for social than for meaningless stimuli ($t(19) = 29.15$; $P < .0005$) and for non-social compared to meaningless stimuli ($t(19) = 24.09$; $P < .0005$). Finally, emotionality was rated significantly higher for social than for non-social ($t(19) = 10.59$; $P < .0005$) and for social than for meaningless stimuli ($t(19) = 10.59$; $P < .0005$). The average duration of the gestures (measured from arm movement onset to arm movement offset) did not differ in the stimulus conditions [S vs NS ($t(19) = -1.12$; $P < .275$); S vs ML ($t(14) = -1.74$; $P < .097$); NS vs ML ($t(16) = -.37$; $P < .714$)].

Task

The fMRI experiment was divided into four sessions. All sessions had the same structure and length, and basically reflected a 3 (S, NS,

[1] In the present study, meaningless gestures were used as catch trails in which the participants observed and executed meaningless human manual actions without meaning. This procedure was used to control for transition probability with respect to meaningful vs meaningless actions.

Table 1
Ratings for gesture categories used in the fMRI study.

	Comprehensibility		Communicative intention		Emotionality	
	Mean	SD	Mean	SD	Mean	SD
Social	6.63	.59	5.31	1.24	5.71	1.13
Non-social	5.70	.63	2.74	.48	2.94	.33
Meaningless	2.88	.48	2.34	.64	2.58	.49

ML) × 2 (IMI, CT) × 2 (O, E; see Fig. 2) repeated measures within subjects. The design used was event-related, the events were modelled as stick functions (duration = 0 s) using the canonical HRF function.

During the imitation sessions (IMI) participants were instructed to watch the video clip and afterwards imitate the gesture performed by the actor. We instructed participants to perform specular imitation (execution of the movement as if looking at a mirror), as it is considered more natural than anatomical imitation according to developmental studies, and it has been shown to lead to stronger engagement of the MNS than anatomic imitation (Koski et al., 2003).

During the control task (CT) the participants were instructed to watch the video clip and discriminate the colour of the circle depicted on the actor's pullover (dark or light brown). Participants were asked to indicate their decision, at the end of the video, by moving their arm over their chest and tapping their contralateral shoulder. This movement was counterbalanced across the CT session according to the colour of the circle: right arm for dark brown and left arm for light brown circle. This procedure was used in order to control for the movements during the imitation session and to equate for motor preparation during both tasks.

The instruction for each task was presented once for 10 s at the beginning of the session, and the sequence of sessions (IMI-CT-IMI-CT or CT-IMI-CT-IMI) was counterbalanced across participants. Each of the four experimental sessions lasted 14 min. One session consisted of 45 trials with the following sequence: observation phase (O), attention cue (green square), execution phase (E). The green square was used to cue participants to prepare for performing the task (IMI or CT). A temporal jitter (1–4 s) was inserted between video clip presentation and cue. A jitter of 6–8 s was also inserted after the execution phase (see Fig. 2). Order of video clip conditions in each session and order of videos within each condition were pseudorandomised and counterbalanced. Each video clip was presented three times and always in the same condition (IMI or CT) in order to keep the conditions independent.

The participants were instructed to perform the movements as comfortably as possible. To minimise the amount of head movement, each participant's head was stabilised with foam padding and upper arms (shoulders) were partially strapped with Velcro bands in such a way to still allow free movement of lower arms, hands, and fingers.

Presentation of all stimuli was controlled by a computer using the Presentation 11 software package (Neurobehavioural Systems, http://www.neurobs.com). The stimuli were presented with MR-compatible LCD goggles and a headset (VisuaStim XGA, Resonance Technology Inc., Los Angeles, USA).

All participants had two different training sessions immediately before the scanning session. The first training took place outside of the scanner to clarify the task to the participant. In the second training, participants practiced movements while lying in the MR scanner to help them habituate themselves to executing movements in the scanner. Both training sessions used video clips different to those used in the actual experiment.

fMRI data acquisition

Images were collected with a 3T whole body scanner (Philips) with echoplanar imaging (EPI) capability using a radio-frequency head coil or sense coil. Multislice T2*-weighted echo-planar images were obtained from a gradient-echo sequence with the following parameters: TE = 30 ms, TR = 2000 ms, NS = 31, FA = 80°, FOV = 224, ST = 3.5 mm, IG = 1 mm, in-plane resolution 3.5 × 3.5 mm, 31 axial slices in a matrix of 64 × 64. In order to control for possible anatomical malformations T1-weighted images 3D FFE sequence (TR = 25 ms; TE = 4.59 ms; NS = 170 (sagittal); ST = 2 mm; IG = 1 mm; FOV 256 × 256; voxel size = 1 × 1 × 2 mm) were acquired for each subject.

Image processing and data analysis

The entire data analysis was performed with SPM5 (Statistical Parametric Mapping Software; The Welcome Trust Center for Neuroimaging, University College London, London, UK) run on MATLAB (The Mathworks, Inc., Natick, MA). The first four images of each run were discarded to allow for T1 equilibration. For each participant, all volumes were spatially realigned to the first volume of the first session and unwarped to correct for between-scan motion. A mean image from the realignment volume was created. This image was spatially normalised to the Montreal Neurological Institute (MNI) EPI brain template available in SPM5. The derived spatial transformation was then applied to the realignment T2—2 × 2 × 2 mm^3 voxels using sinc interpolation in space. All functional volumes were then spatially smoothed (FWHM 8).

Data were analysed using a random-effect model. Single subject fMRI responses were modelled in a general linear model (GLM) by a design matrix compromising the onsets of the observation phase (O; video clip), the attention cue (green square) and the execution phase (E) according to the experimental task and gesture category. In order to control for movement artefacts, participants with more than 3 mm translation and 4° rotation movements were excluded

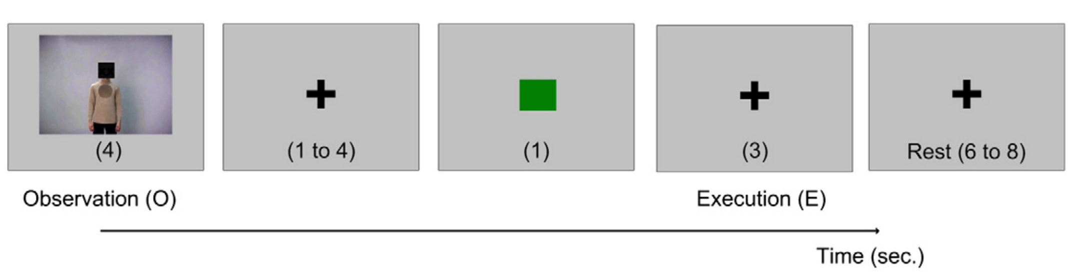

Fig. 2. The sequence and duration of each event in one trial. Four sessions were performed: two for each task (IMI and CT). Task instruction was displayed at the beginning of every session, and 45 trials were performed in each session.

Table 2
Effects of interest—summary of contrasts.

	Hypothesis	Contrast
Task	Mirror properties (MNS) for imitation task during both experimental phases for all gesture categories (posterior inferior frontal gyrus [pars opercularis] and IPL [area PFt])	Conjunction (t-test) $[IMI_O (S + NS + ML) > CT_O (S + NS + ML)] \cap [(IMI_E (S + NS + ML) > CT_E (S + NS + ML))]$
Gesture content	Mentalizing properties (MS) for social vs non-social gestures during both experimental phases (O + E) and tasks (IMI + CT) (cingulate, paracingulate cortex and STS/TPJ)	Main Effects (t-test) $[(S (IMI_O + CT_O + IMI_E + CT_E) > NS (IMI_O + CT_O + IMI_E + CT_E)]$
Interaction of task and gesture content (observation)	Mentalizing properties (MS) during observation phase (O) for imitation of social vs non-social gestures (cingulate, paracingulate cortex and STS/TPJ)	Interaction effect (t-test) $(S\text{-}IMI_O > NS\text{-}IMI_O) > (S\text{-}CT_O > NS\text{-}CT_O)$
Interaction of task and gesture content (observation and execution)	Mentalizing (MS) and mirror (MNS) properties in both experimental phases (O + E) for imitation of social vs non-social gestures - Interaction effect of task and gesture content (IPL, IFG and pSTS)	Interaction effect (F-test) $[(S\text{-}IMI_O > S\text{-}CT_O) + (S\text{-}IMI_E > S\text{-}CT_E)] > [(NS\text{-}IMI_O > NS\text{-}CT_O) + (NS\text{-}IMI_E > NS\text{-}CT_E)]$
Interaction of task, gesture content and phase	Self referential processes during imitation of social vs non-social gestures—interaction effect of experimental phase (O > E), task (IMI > CT) and gesture content (S > NS) (mPF)	Interaction effect (F-test) $[(S\text{-}IMI_O > NS\text{-}IMI_O) > (S\text{-}CT_O > NS\text{-}CT_O)] > [(S\text{-}IMI_E > NS\text{-}IMI_E) > (S\text{-}CT_E > NS\text{-}CT_E)]$

from analysis. We also included the six head movement parameters as covariates of no interest for each participant. Twelve different simple contrasts concerning task (IMI, CT) and gesture category (S, NS, ML) of observation (O) and execution phase (E) were performed. For the second level or group analysis, these corresponding contrast images for task and gesture category of observation phase (O) and execution phase (E) of the first stage for each participant ($S\text{-}IMI_O$, $NS\text{-}IMI_O$, $ML\text{-}IMI_O$, $S\text{-}IMI_E$, $NS\text{-}IMI_E$, $ML\text{-}IMI_E$, $S\text{-}CT_O$, $NS\text{-}CT_O$, $ML\text{-}CT_O$, $S\text{-}CT_E$, $NS\text{-}CT_E$, $ML\text{-}CT_E$) were entered into a flexible factorial ANOVA, in which subjects were treated as random variables.

As we expected small effects for the mentalizing system, we decided to employ the Monte-Carlo simulation of the whole brain volume to establish an appropriate voxel contiguity threshold (Slotnick et al., 2003). This correction has the advantage of higher sensitivity to smaller effect sizes, while still correcting for multiple comparisons across the whole brain volume. Assuming an individual voxel type I error of $P < .01$, a cluster extent of 90 contiguous resample voxels was necessary to correct for multiple voxel comparisons at $P < .05$. Additionally, we decided to consider only local maxima also significant at $P < .0001$.

The voxel coordinates of activation peaks are reported in MNI atlas space using the SPM Anatomy toolbox (Eickhoff et al., 2005).

Effects of interest

To test the influence of task (IMI or CT) and gesture content (social [S], non-social [NS] and meaningless [ML]) on activation in brain regions implicated in the MNS and MS during observation (O) and execution of gestures (E), we analysed the following effects (see Table 2 for the summary of contrasts):

1. Task effect. For the MNS the additional constraint was that "mirror properties" of corresponding regions (IPL and the posterior part of IFG) are present and reflected in common activations during observation and execution. To test this hypothesis we calculate a conjunction between the main contrasts of imitation vs control task during both experimental phases: $[(IMI_O (S + NS + ML) > CT_O (S + NS + ML)) \cap (IMI_E (S + NS + ML) > CT_E (S + NS + ML))]$. We hypothesised that the process of understanding the communicative intentions implied in others' actions (mentalizing process) takes place preferentially during observation phase and might be driven by the content (social [S] > non social [NS]) and task (observation in order to imitate (imitation [IMI] > pure observation [CT])). To test this hypothesis we performed an interaction analysis of task and gesture during observation phase $[(S\text{-}IMI_O > NS\text{-}IMI_O) > (NS\text{-}CT_O)]$.
2. Gesture content effect. We hypothesised that the MS is specifically involved in processing and production of social gesture. To test this hypothesis we calculated the main effect of gesture content across all conditions $[S (IMI_O + CT_O + IMI_E + CT_E) > NS (IMI_O + CT_O + IMI_E + CT_E)]$.
3. Interaction effect of task and gesture content. We tested the interaction of task (IMI > CT) and gesture content (S > NS) to see if areas of the MNS (IPL and posterior IFG) and MS (TPJ, pSTS and medial frontal cortex) would be activated especially when gestures with communicative intention (S > NS) are imitated (IMI > CT) during both experimental phases: $[(S\text{-}IMI_O > S\text{-}CT_O) + (S\text{-}IMI_E > S\text{-}CT_E)] > [(NS\text{-}IMI_O > NS\text{-}CT_O) + (NS\text{-}IMI_E > NS\text{-}CT_E)]$.
4. Interaction effect of task, gesture content and experimental phase. We hypothesised that activation in the medial frontal cortex for social gestures is modulated by imitation due to self-referential processing. In order to test this hypothesis, we tested interaction effects with phase (O > E), task (IMI > CT) and gesture content (S > NS) as factors in order to test the influence of imitation and social gestures during observation and execution: $[(S\text{-}IMI_O > NS\text{-}IMI_O) > (S\text{-}CT_O > NS\text{-}CT_O)] > [(S\text{-}IMI_E > NS\text{-}IMI_E) > (S\text{-}CT_E > NS\text{-}CT_E)]$.

Results

Task effect: imitation vs control task during observation and execution phase $[(IMI_O > CT_O) \cap (IMI_E > CT_E)]$

During both tasks the participants were observing ($_O$) and executing ($_E$) gestures. For the IMI > CT (imitation neural network) in both phases $[(IMI_O (S + NS + ML) > CT_O (S + NS + ML)) \cap (IMI_E (S + NS + ML) > CT_E (S + NS + ML))]$ we found bilateral activation of the superior and inferior parietal lobule, including the supplementary motor area (SMA) and sensorimotor cortex (SPL), as well as the posterior aspect of the inferior frontal cortex (pars opercularis) and superior temporal gyrus (extending to right STS) (Table 3; Fig. 3). We found no significant activations for the reverse contrast (CT > IMI).

Gesture content effect: social vs non social (S > NS)

We compared the gesture conditions (main effect) in order to investigate if the mentalizing system is specifically involved in the processing of social vs non-social gestures $[S (IMI_O + CT_O + IMI_E + CT_E) > NS (IMI_O + CT_O + IMI_E + CT_E)]$. We found significant activation in the right middle cingulate (BA 24/32; 12, 32, 32; t = 3.54; 355 voxels), the left medial orbitofrontal (BA 24/32/10; −10, 32, −10; t = 3.55; 319 voxels), and the right superior frontal cortices (BA 9/10; 24, 52,

Table 3
Imitation vs control task.

Local maxima	Cluster size	Left				Right				Percent overlap of clusters with cytoarchitectonic areas	
$(IMI_O > CT_O) \cap (IMI_E > CT_E)$		x	y	z	T	x	y	z	T		%
Supplementary motor	595	−4	8	50	3.27	26	−2	54	5.05	Right area 6	29.6
area (SMA)	449									Left area 6	43.7
Middle temporal gyrus	282	−48	−58	−2	3.6	50	−72	18	3.12	Right IPC	61.3
	108										
Superior parietal lobule	207	−24	−58	58	3.22					Left SPL (7 A)	70.0
										Right SPL (5 M)	10.8
										Left SPL (5 M)	7.1
										Left area 4 a	4.1
										Left SPL (7P)	2.9
Inferior parietal lobule	169	−34	−38	40	3.01					Left IPC	22.3
	92	−54	−24	38	3.63					Left area 2	17.7
										Left hIP2	15.6
										Left hIP1	8.1
										Left hIP 3	7.2
										Left SPL (7PC)	1.9
										Left IPC (PFt)	58.0
										Left area 2	36.8
										Left IPC (PF)	5.2
Superior temporal gyrus	140	−64	−50	19	3.53	48	−42	12	3.73	Left IPC	2.3
	129										
Precentral gyrus	126					54	6	28	3.6	Right area 44	43.8
Postcentral gyrus	123					36	−36	54	3.12	Right area 2	74.8
										Right area 3 b	22.7
Middle cingulate cortex	111	−14	−28	40	3.50					Left SPL (5 Ci)	33.6
										Left area 31	18.0
Middle temporal gyrus	111					38	−66	−4	2.97	Right hOC5	2.7
Pallidum	395	−18	2	0	3.77						
Thalamus	303					8	−22	−2	3.14		
Putamen	161					24	12	−4	3.01		

Significant cluster activations at $P < .05$ (Monte Carlo corrected). Coordinates are listed in MNI atlas space; SPM Anatomy tool box (Eickhoff et al., 2005). Abbreviations: SMA (Supplementary Motor Area); V5/MT + (visual motor area 5); SPL (superior parietal lobule); IPL (inferior parietal lobule).

12; t = 2.62; 230 voxels) for social in contrast to non-social gestures. Contrast estimates (Fig. 4) indicate that activation in the right middle cingulate cortex (BA 24/32) is predominantly a response to social gestures during observation phase (O) in both tasks (Fig. 4B). By contrast activation of the left medial orbitofrontal cortex (BA 24/32/10) seems to be related to social gestures only during imitation ($S\text{-}IMI_O > NS\text{-}IMI_O$; Fig. 4C). Finally, significant activation of the right superior frontal cortex (BA 9/10) seems to be predominantly related to activations for social gestures during the imitation task in both phases of the experiment (Fig. 4A). We found no significant clusters of activation for the reverse contrast (all-NS > all-S).

Interaction effect of task (IMI vs CT) and gesture content (S vs NS)

For the interaction of task ($IMI_O > CT_O$) and gesture content ($S_O > NS_O$) during observation phase ($S\text{-}IMI_O > NS\text{-}IMI_O$) > ($S\text{-}CT_O > NS\text{-}CT_O$), we found activation in the postcentral gyrus and middle cingulate cortex (Table 4). For the reverse contrast, we did not find any significant activations.

To test for specific activation for social gestures during imitation in contrast to the control task, we performed an interaction analysis including task and gesture content as factors: [($S\text{-}IMI_O > S\text{-}CT_O$) + ($S\text{-}IMI_E > S\text{-}CT_E$)] > [($NS\text{-}IMI_O > NS\text{-}CT_O$) + ($NS\text{-}IMI_E > NS\text{-}CT_E$)]. This analysis revealed activation in the right inferior parietal lobule (area PFt) [local maxima: 50, −34, 46; F = 12.67; 266 voxels]. Contrast estimates of the activation in each condition (Fig. 5a and b) indicate that activation of this region is specifically related to social gestures during imitation. In order to assess whether this observation holds statistically, we subsequently performed post-hoc analyses. Contrasts with peak values at the same peak of the interaction are indicated on the bar graph of contrast estimates, along with t-values (Fig. 5a: $S\text{-}IMI_O > NS\text{-}IMI_O$ (t = 2.96), $S\text{-}IMI_E > NS\text{-}IMI_E$ (t = 2.71); Fig. 5b: S-IMI > S-CT (t = 5.20), NS-IMI > NS-CT (t = 3.48)).

Interaction effect of task (IMI vs CT), gesture content (S vs NS) and phase (O vs E)

Finally, to investigate the differences in self-referential processes between action observation (O) in contrast to execution (E) of social gestures, we performed an interaction analysis of gesture content (S > NS), task (IMI > CT) and experimental phase (O > E): [($S\text{-}IMI_O > NS\text{-}IMI_O$) > ($S\text{-}CT_O > NS\text{-}CT_O$)] > [($S\text{-}IMI_E > NS\text{-}IMI_E$) > ($S\text{-}CT_E > NS\text{-}CT_E$)]. This analysis revealed activation in the medial orbital gyrus. Contrast estimates indicate a context dependent activation of the medial orbitofrontal cortex (12, 40, −4; F = 12.81; 205 voxels) during observation and execution of social gesture (see Fig. 6). In order to assess whether this impression also holds statistically, we subsequently performed a post-hoc analyses. Contrasts with peak values on the same peak of the interaction are indicated on the bar graph of contrast estimates, along with t-values [Fig. 6 bar graph: $S\text{-}IMI_O > NS\text{-}IMI_O$ (T = 2.63), $S\text{-}IMI_O > S\text{-}IMI_E$ (t = 2.41), $S\text{-}CT_E > NS\text{-}CT_E$ (t = 3.56)].

Discussion

The aim of the present study was to investigate the neural correlates of communicative gestures related to abstract mental states during observation and execution. The novel aspect of the study is its investigation of communicative gestures that represent the abstract mental states of both sender and receiver (communicative intention) via imitation (social behaviour). We investigated if parts of the MS and MNS are both relevant for the observation and production of communicative gestures. We demonstrated that activation of the MNS can be modulated by task (imitation vs control), gesture content (social vs non social) and by an interaction between task (imitation vs control) and gesture content (social vs non social) with activation in the right IPL, suggesting that activity in this area is enhanced by social gestures due to the presence of communicative intention inbuilt in

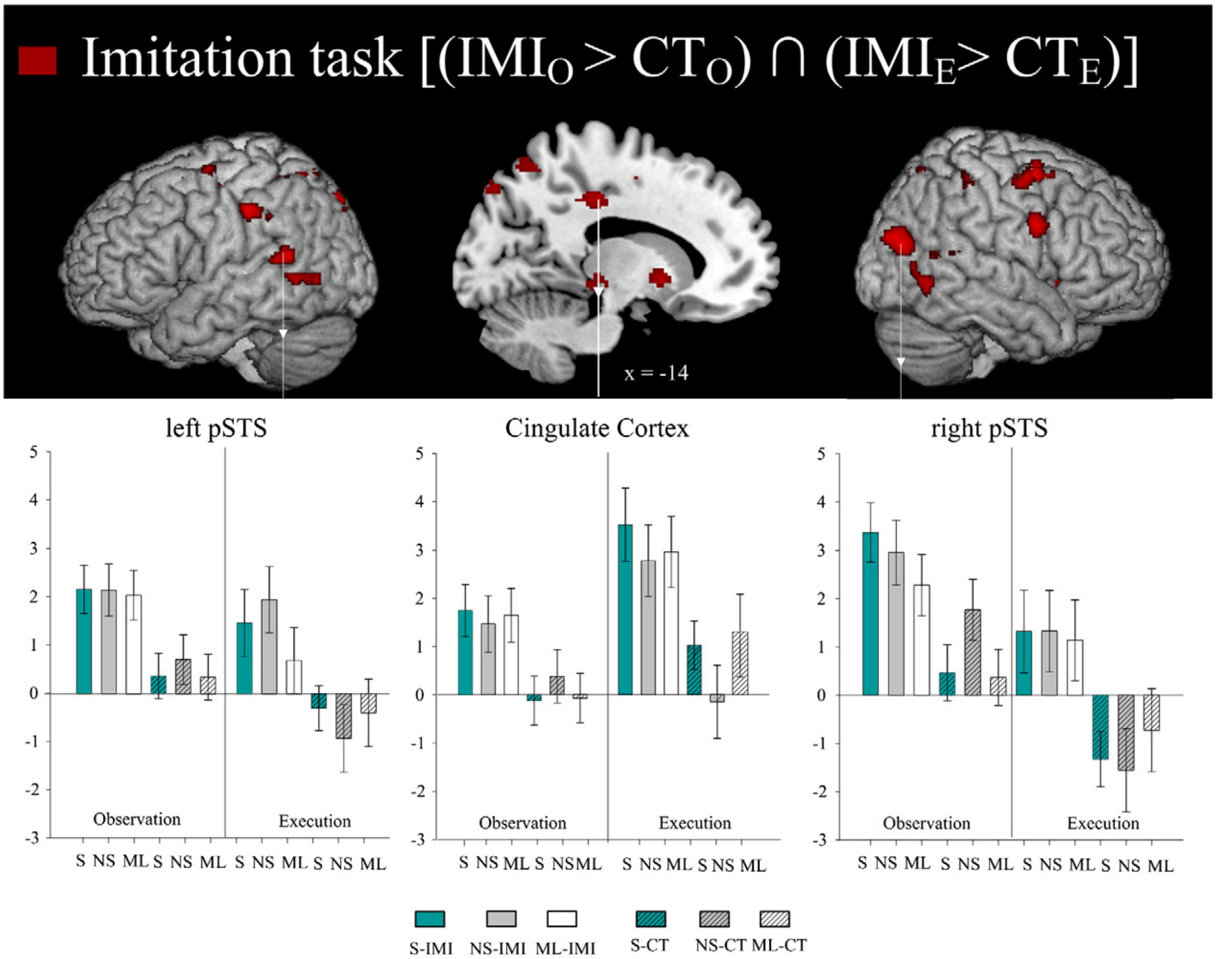

Fig. 3. The significant activations for imitation task [$(\mathrm{IMI_O} > \mathrm{CT_O}) \cap (\mathrm{IMI_E} > \mathrm{CT_E})$]. For illustration, bar graphs display the contrast estimates of gesture content (S: social gesture, NS: non-social gestures, ML: meaningless gestures) and task (IMI: imitation task, CT: control task) during observation (O) and execution phases (E). These regions were selected due to our hypothesis but the same effects are present in all other clusters. Significant cluster activations at $P < .05$ (Monte Carlo correction). Voxel coordinates are in MNI atlas space; SPM Anatomy tool box (Eickhoff et al., 2005).

the gestures. We also demonstrated that the medial frontal gyrus is more engaged during observation of social than non social gestures suggesting that this area, as part of the MS, contributes to the processing of communicative intentions in social gestures (Amodio and Frith, 2006; Ciaramidaro et al., 2007; Gallagher et al., 2000; Hooker et al., 2008).

However, our findings go beyond this in showing an interaction effect between task (imitation vs control), stimulus content (social vs non social) and experimental phase (observation vs execution) with activation in the mOFC. In accordance with our hypotheses and given the evidence that different cortical midline structures are implicated in self-referential processes (Northoff et al., 2006), activity in mOFC may thus indicate that self-referential processes are also relevant for the representation of communicative gestures, which mirror self and other abstract mental states.

Imitation: do the MNS and MS contribute to the computation of communicative gestures during imitation?

In general, the pattern of activation for imitation in contrast to the control task [$(\mathrm{IMI_O} > \mathrm{CT_O}) \cap (\mathrm{IMI_E} > \mathrm{CT_E})$] in our study is consistent with findings on enacted or mental imitation, including the inferior frontal gyrus (BA 6/44), premotor cortex (BA 6), superior (BA 7) and inferior parietal lobule (PFt area) (Baumgaertner et al., 2007; Caspers et al., 2010; Clark et al., 2004; Hermsdorfer et al., 2001; Iacoboni et al., 1999; Lewis, 2006; Muhlau et al., 2005; Tanaka et al., 2001).

In addition to the neural network related to imitation we also found activation in the middle posterior cingulate cortex and pSTS during both observation and execution. The posterior cingulate cortex has been found to be implicated in thinking about one's intentions and consequent actions (sustaining intention to perform an action in the near future) (den Ouden et al., 2005) and in self-referential representation (Lombardo et al., 2010). Likewise, the right pSTS has been found to be activated during false belief (TOM) and attention tasks (Mitchell, 2008). Taken together, our data indicate that in addition to imitation neural network, areas previously found in relation to processing of intentions, self-reference and attention are also activated during imitation when both observing and when executing.

Mentalizing might occur preferentially in the first stages of imitation, that is, during action observation. Thus, we explored the neural correlates of task (IMI > CT) and gesture content (S > NS) during the observation phase. Our results suggest that regions of the MNS (IPL) and cortical midline structures might be modulated by how salient the intentionality (communicative intention) is embedded in the social gestures during observation with the intention to imitate. We found an interaction effect in the postcentral gyrus (area PFt) and middle posterior cingulate cortex for imitation of social gestures during observation phase (Table 4). The PFt area is the main area involved in imitation (Caspers et al., 2010) and the posterior middle cingulate cortex has been found to be involved in the process of self-awareness and self-related processing (den Ouden et al., 2005; Lombardo et al., 2010; Marsh and Hamilton, 2011; Ruby and Decety,

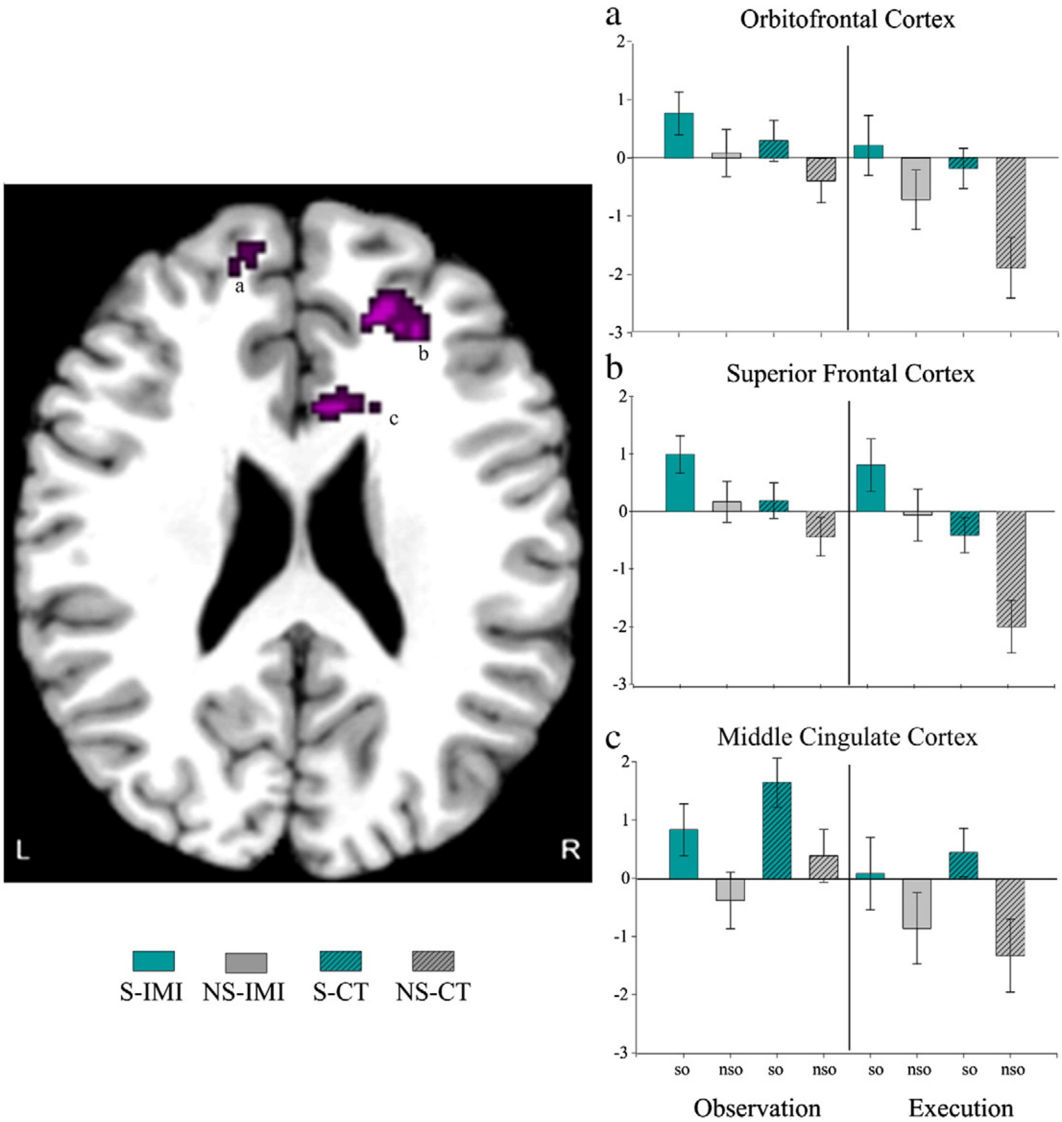

Fig. 4. Significant activations for social gestures [S ($IMI_O + CT_O + IMI_E + CT_E$) > NS ($IMI_O + CT_O + IMI_E + CT_E$)]. Significant cluster activations at $P < .05$ (Monte Carlo correction). For illustration, bar graphs display the contrast estimates of gesture content and task during observation and execution phases. Voxel coordinates are in MNI atlas space; SPM Anatomy tool box (Eickhoff et al., 2005). Local maxima: (a) superior frontal gyrus: 24, 52, 12 (t = 2.62; 230 voxels); (b) middle cingulate gyrus: 12, 32, 32 (t = 3.54; 355 voxels); (c) orbitofrontal: −10, 32, −10 (t = 3.55; 319 voxels).

2004). We also found an interaction effect of social compared to non-social gestures for the imitation task in the right inferior parietal cortex (PFt area) during both observation and execution phases (see Fig. 5, bar graph B). The analysis indicates that the activation in the PFt area is statistically significant only between social compared to non-social gestures during imitation task contrasts (see Fig. 5, bar graph A), suggesting that the communicative intention embedded in the social gestures was more salient during both phases (O and E) of the imitation in contrast to the control task. This effect indicates that this region might be driven by the communicative intentions during the imitative process. It seems that the neural correlates underlying imitation of social gestures might be modulated by the communicative intention implied in the action observed. Liew et al. (2011) showed similar results investigating familiar versus unfamiliar gestures during

Table 4
Interaction of gesture ($S_O > NS_O$) and task ($IMI_O > CT_O$)—observation phase.

Local maxima	cluster size	Left				Right				Percent overlap of clusters with cytoarchitectonic areas	
($S\text{-}IMI_O > NS\text{-}IMI_O$) > ($S\text{-}CT_O > NS\text{-}CT_O$)		x	y	z	T	x	y	z	T		%
Postcentral gyrus	205					50	−32	50	3.22	Right area 2	10.6
										Right IPC (PFt)	12.0
Posterior middle cingulate cortex	128	−8	−36	46	3.73					SPL (5 M)	13.8
										SPL (5CI)	10.6

Significant cluster activations at $P < .05$ (Monte Carlo correction). Coordinates are listed in MNI atlas space; SPM Anatomy tool box (Eickhoff et al., 2005). Abbreviations: IPL (inferior parietal lobule), hIP (human anterior intraparietal sulcus) and SPL (superior parietal lobule).

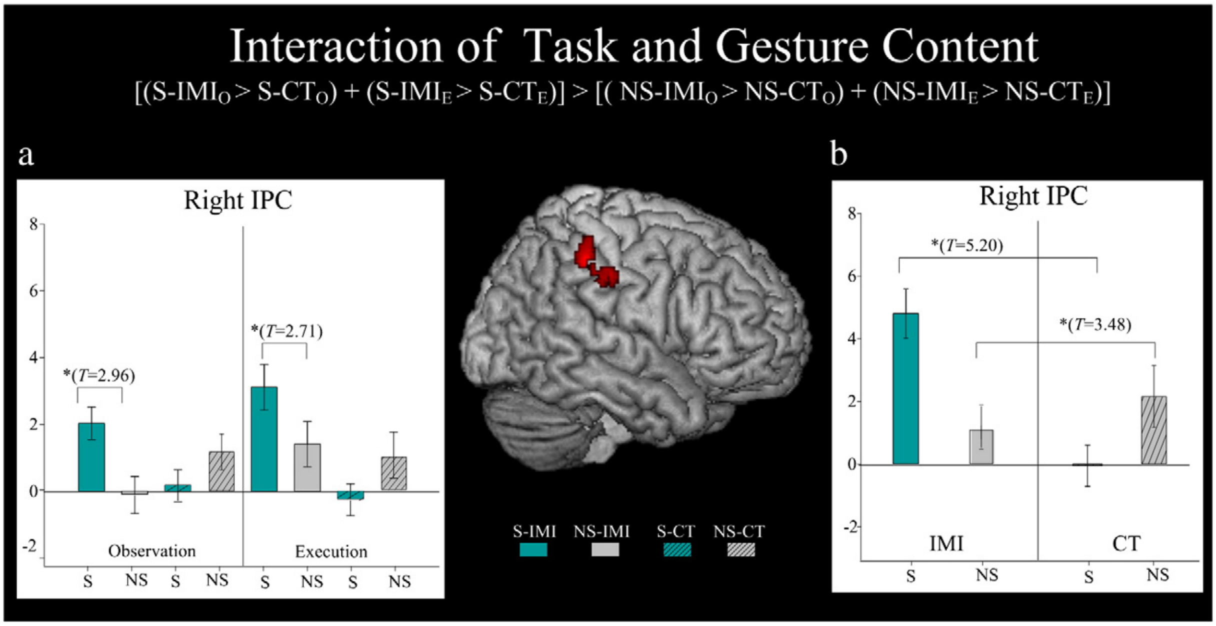

Fig. 5. Interaction of task [imitation (IMI) vs control task (CT)] and gesture content [social (S) and non-social (NS)]. Inferior Parietal Cortex (IPC); local maxima: 50, −34, 46 (F = 12.67; 266 voxels). (a) For illustration, bar graphs display the contrast estimates of gesture content (S: social gesture, NS: non-social gestures) and task (IMI: imitation task, CT: control) during observation (O) and execution phases (E). (b) For illustration, bar graphs display the contrast estimates of gesture content (S: social gesture, NS: non-social gestures) according to task (IMI: imitation task, CT: control) during both observation and execution phase (O + E). All post-hoc tests of the interaction are whole brain t-tests at every voxel; the required post-hoc- and the t-statistics presented have been adjusted for multiple comparisons on top of cluster thresholding for the number of voxels used for the whole-brain analyses. The regions shown in the figure are the overlap between the whole brain post-hoc- and the interaction results. * indicates $P < .05$, corrected for multiple comparisons.

passive observation. Here the participants were requested to make active inferences about the actor's intention while watching short video clips. Both familiar and unfamiliar gestures activated neural areas related to MS and MNS. The authors suggested that the unique social demands of inferring intentions modulate neural activity in MNS (IPL) and MS (posterior cingulate cortex) regions differently during passive

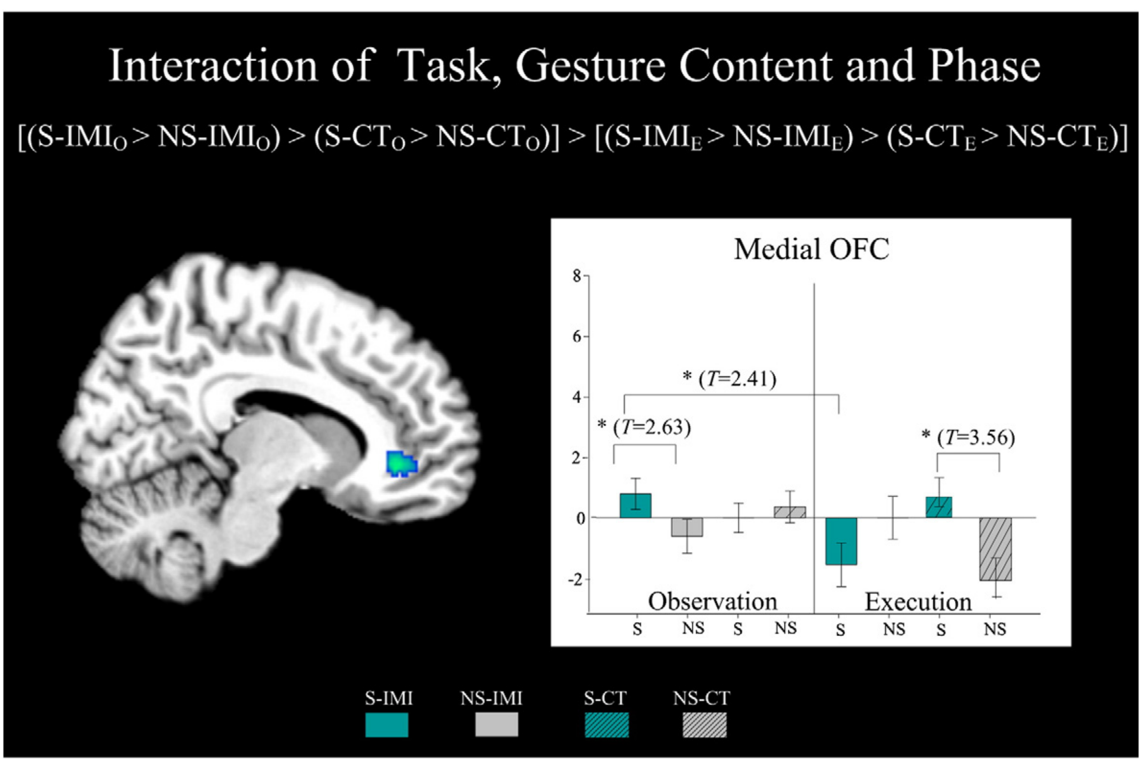

Fig. 6. Interaction of observation and execution of intended actions in imitation vs control task [(S-IMI$_O$ > NS-IMI$_O$) > (S-CT$_O$ > NS-CT$_O$)] > [(S-IMI$_E$ > NS-IMI$_E$) > (S-CT$_E$ > NS-CT$_E$)]. For illustration, bar graphs display the contrast estimates of gesture content and task during observation and execution. Local maxima: medial orbitofrontal gyrus (OFC) 12, 40, −4 (F = 12.81; 205 voxels). Significant cluster activation at $P < .05$ (Monte Carlo correction). Voxel coordinates are in MNI atlas space; SPM Anatomy toolbox (Eickhoff et al., 2005). All post-hoc tests of the interaction were whole brain t-tests at every voxel; the required post-hoc- and the t-statistics presented have been adjusted for multiple comparisons on top of cluster thresholding for the number of voxels used for the whole-brain analyses. The region shown in the figure is the overlap between the whole brain post-hoc and the interaction results. * indicates $P < .05$ corrected for multiple comparisons.

observation. Both results, ours and those from Liew et al. (2011), reveal a complex interplay between one's perceptual and motor experiences and the other's action observed. Moreover, these results indicate that task instruction might play a central role in modulating MNS and MS during action observation.

Overall, our data suggest that the right IPL and IFG contribute in different ways to processing communicative intentions of gestures during imitation, depending on the phase: observation or execution. Moreover, activation in the middle posterior cingulate cortex during observation of social gestures with intention to imitate seems to be driven by the abstract mental states underlying social gestures (self/other processing). However, the IPL is a multi-modal region commonly associated with grasp affordances, motor attention, body awareness and action planning (Fogassi and Luppino, 2005; Oztop and Arbib, 2002). Likewise, posterior cingulate cortex and IFG are also involved in autobiographical memory, emotion recognition and emotion regulation (Pfeifer and Peake, 2012; Viard et al., 2011). Therefore, additional research might help us to elucidate whether these results are due to strategies employed to understand the observed actor's gesture in order to imitate [e.g. trying to simulate the gesture vs trying to objectively reasoning about the gesture itself] or the affective component (emotionality) present in our social gestures.

Mentalizing: is the MS active during observation and execution of social gestures?

In line with our hypotheses the results indicate that the medial frontal cortex, as part of the MS, is involved in the processing/production of social communicative gestures. We investigated the effects for social in contrast with non-social gestures in all conditions, and we found activations in the cingulate gyrus (BA 32/24), orbitofrontal cortex (BA 24/32/10) and superior frontal cortex (BA 9/10). Taking into account the contrast estimates (see Fig. 4 bar graphs), the areas of the medial frontal cortex were predominantly activated while the participants were observing social gestures in order to imitate (IMI_O). As we expected, areas related to mentalizing processes (mPFC) were preferentially activated during observation of social gestures (communicative intention). Our data is also consistent with findings from studies about self and other (Vogeley et al., 2001), perspective taking (Schilbach et al., 2007), inferring deceit in the actions of others (Grezes et al., 2004), social game tasks (Kircher et al., 2009a), body orientation on the neural processing of speech accompanied by gestures (Straube et al., 2010), and face and word processing (Kircher et al., 2000). The mPFC is also more activated during observation than execution of social gestures, indicating that MS is more involved in observation of social gestures than in their execution, as we hypothesised and also in line with Schippers et al. (2009).

In the present study social gestures are actions that represent mental states with the following characteristics: (a) the signals are sent (by the sender) with the intention of altering the receiver's mental state and (b) the receiver (observer) attributes mental states to the sender (Frith, 2007; Walter et al., 2004). Thus, we assumed that recognising the communicative intention of another person (sender) toward oneself (receiver) would trigger the mentalizing mechanism, because the other's intention is built into the action (sender's intention to alter the mental state of the receiver) and, at the same time, one's own mental states (receiver's altered mental state according to sender's intentions). Thus, the activations in the mFC and right IPL (Fig. 5) for social gestures during imitation might indicate that parts of the MNS and MS are more engaged during imitation of gestures with communicative intention in a socially relevant context (imitation). In this sense the MNS and MS both seem to contribute to the understanding of communicative gestures with communicative intentions.

Does imitation of social gestures require self referential processes?

For imitation of social gestures we found activation only in the medial orbitofrontal cortex (extending to the cingulate and paracingulate areas) (Fig. 6), suggesting that this area has different roles during observation and execution of intended actions according to phase, task and intention-content of the gesture. The mOFC was significantly more active for social gestures during observing than executing (see Fig. 6, bar graph). The mOFC was also significantly more active for social than non-social gestures during execution phase (see Fig. 6, bar graph). These results suggest that the communicative intention embedded in the social gestures was more salient during the imitation condition (social task/imitative behaviour) than during the control condition (non-social task/colour discrimination).

One possible interpretation might be that social gestures include content and contexts that can be experienced as strongly related to one's self, especially if imitation is required, suggesting that the activation of the mOFC might be due to self-referential processing (Kircher et al., 2000; Northoff et al., 2006). According to the simulation theory of mind reading, the observer tries to mimic or to convert one's mental state into the other person's, leading to shared mental states between observer and the observed. This requires self-referential processing once the other's person mental state resonates with the observer's mental state (Schippers et al., 2010). Therefore, to imitate social gestures, it is necessary to distinguish between self and other mental states during the observation phase, while during the execution phase it is just the execution of a motor plan. Previous investigators have suggested that the ventromedial or orbitofrontal cortex lesions are associated with mind reading deficits (Stuss et al., 2001) and, patients with bilateral orbitofrontal cortex lesions were impaired in tasks that required more subtle social reasoning (i.e., detecting a social faux pas) but not in typical false-belief theory of mind tasks (Stone et al., 1998). Moreover, in three different studies on the mentalizing system, similar local activation in the medial frontal cortex was found [observing of animated shapes (Martin and Weisberg, 2003); choosing an ending of a cartoon story (Walter et al., 2004); false communicative intention (irony) with cartoons (Wakusawa et al., 2007)], suggesting that the mOFC takes part in the process of mentalizing, even if it is rarely found in traditional mentalizing tasks.

An alternative explanation for the activation of mOFC in our study could be related to the affective component (emotionality) present in our social gestures. Further studies are necessary to disentangle the emotional aspect. The role of the mOFC is manifold. Anatomically both the mOFC and vmPFC receive connections from all regions associated with primary and/or secondary exteroceptive sensory modalities (olfactory, gustatory, somatosensory, auditory, visual) (Kringelbach and Rolls, 2004), suggesting that these areas might have implications in a number of mental processes.

Limitations and future directions

Altogether, there is a possibility that the process of social in comparison to meaningless gestures might be driven by semantic aspects (Supplementary material: Tables S5, S6, S7 and S8). Due to methodological constraints (length of the sessions) we did not include a control task for semantic processes. Future studies applying a similar paradigm and controlling for semantic processes could provide additional insights into the differences between meaningful and meaningless gestures in the context of gesture communication.

Conclusion

In a nutshell, our study suggests that processing of social intentions mediated by communicative gestures require both MS and MNS. Our data support the assumption that the MNS and MS both contribute to the process of gestures with communicative intention. At a neural level, both the MNS and MS act in concert during imitation of social gestures. More specifically, we found increased activation in the IPL and mPF for gestures with communicative intentions and related to abstract mental states. Performing an action during a social interaction not only requires the presence of intentions or states of mind in the action *per se* (content or goal), but also that the communicative intention would be recognised by the receiver (Frith, 2007; Walter et al., 2004). In this way gestures are social tools. The interaction analysis of gesture content and imitation task indicates that the right inferior parietal lobule might be recruited to distinguish gestures with communicative social intentions from general actions during social context. Moreover, the medial frontal brain regions are important for the differentiation of observation and execution processes in the context of social and non-social gesture processing. The representation of communicative intentions might require a capacity mediated by the mFC related to the MS, although other networks, such as the MNS, might have an additional role in extracting the motoric meaning. However, our findings go beyond this in showing an interaction effect between task, stimuli and experimental phase (observation and execution), in the mOFC, suggesting possible self-referential processes for the representation of communicative social intention with the discrimination of self and other mental states.

Acknowledgments

We would like to thank Ph.D. Gina Joue for improving the English language used in this paper. AM is supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/Brazil); B.S. is funded by the German Federal Ministry of Education and Research (BMBF; project no. 01GV0615).

Conflict of interest statement

The authors declare no conflict of interest with respect to this article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.05.021.

References

Abu-Akel, A., 2003. A neurobiological mapping of theory of mind. Brain Res. Rev. 43, 29–40.
Amodio, D.M., Frith, C.D., 2006. Meeting of minds: The medial frontal cortex and social cognition. Nat. Rev. 7, 268–277.
Astington, J.W., Harris, P.L., Olson, D.R., 1988. Developing theories of mind. Cambridge University.
Bara, B.G., 2011. Cognitive pragmatics: The mental processes of communication. Intercult. Pragmat. 8, 443–485.
Baron-Cohen, S., 1995. Mindblindness: An essay on autism and theory of mind. MIT Press, Cambridge, MA.
Baumgaertner, A., Buccino, G., Lange, R., McNamara, A., Binkofski, F., 2007. Polymodal conceptual processing of human biological actions in the left inferior frontal lobe. Eur. J. Neurosci. 25, 881–889.
Binkofski, F., Buccino, G., 2004. Motor functions of the Broca's region. Brain Lang. 89, 362–369.
Bradshaw, J.L., Sheppard, D.M., 2000. The neurodevelopmental frontostriatal disorders: Evolutionary adaptiveness and anomalous lateralization. Brain Lang. 73, 297–320.
Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G., Freund, H.J., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. Eur. J. Neurosci. 13, 400–404.
Buccino, G., Baumgaertner, A., Colle, L., Buechel, C., Rizzolatti, G., Binkofski, F., 2007. The neural basis for understanding non-intended actions. NeuroImage 36 (Suppl. 2), T119–T127.
Calder, A.J., Lawrence, A.D., Keane, J., Scott, S.K., Owen, A.M., Christoffels, I., Young, A.W., 2002. Reading the mind from eye gaze. Neuropsychologia 40, 1129–1138.
Carrington, S.J., Bailey, A.J., 2009. Are there theory of mind regions in the brain? A review of the neuroimaging literature. Hum. Brain Mapp. 30, 2313–2335.
Carruthers, P., Smith, P.K., 1996. Theories of mind. Cambridge Univ. Press, Cambridge.
Caspers, S., Zilles, K., Laird, A.R., Eickhoff, S.B., 2010. ALE meta-analysis of action observation and imitation in the human brain. NeuroImage 50, 1148–1167.
Ciaramidaro, A., Adenzato, M., Enrici, I., Erk, S., Pia, L., Bara, B.G., Walter, H., 2007. The intentional network: How the brain reads varieties of intentions. Neuropsychologia 45, 3105–3113.
Clark, S., Tremblay, F., Ste-Marie, D., 2004. Differential modulation of corticospinal excitability during observation, mental imagery and imitation of hand actions. Neuropsychologia 42, 105–112.
David, N., Bewernick, B.H., Cohen, M.X., Newen, A., Lux, S., Fink, G.R., Shah, N.J., Vogeley, K., 2006. Neural representations of self versus other: Visual–spatial perspective taking and agency in a virtual ball-tossing game. J. Cogn. Neurosci. 18, 898–910.
David, N., Bewernick, B.H., Cohen, M.X., Newen, A., Lux, S., Fink, G.R., Shah, N.J., Vogeley, K., 2006. Neural representations of self versus other: Visual–spatial perspective taking and agency in a virtual ball-tossing game. J. Cogn. Neurosci. 18, 898–910.
de Greck, M., Rotte, M., Paus, R., Moritz, D., Thiemann, R., Proesch, U., Bruer, U., Moerth, S., Tempelmann, C., Bogerts, B., Northoff, G., 2008. Is our self based on reward? Self-relatedness recruits neural activity in the reward system. NeuroImage 39, 2066–2075.
Decety, J., Grezes, J., 1999. Neural mechanisms subserving the perception of human actions. Trends Cogn. Sci. 3, 172–178.
den Ouden, H.E., Frith, U., Frith, C., Blakemore, S.J., 2005. Thinking about intentions. NeuroImage 28, 787–796.
Denny, B.T., Kober, H., Wager, T.D., Ochsner, K.N., 2012. A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. J. Cogn. Neurosci. 24, 1742–1752.
Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. NeuroImage 25, 1325–1335.
Enrici, I., Adenzato, M., Cappa, S., Bara, B.G., Tettamanti, M., 2011. Intention processing in communication: A common brain network for language and gestures. J. Cogn. Neurosci. 23, 2415–2431.
Fletcher, P.C., Happe, F., Frith, U., Baker, S.C., Dolan, R.J., Frackowiak, R.S., Frith, C.D., 1995. Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. Cognition 57, 109–128.
Fogassi, L., Luppino, G., 2005. Motor functions of the parietal lobe. Curr. Opin. Neurobiol. 15, 626–631.
Frith, C.D., 2007. The social brain? Philosophical transactions of the Royal Society of London Series B. Biol. Sci. 362, 671–678.
Gallagher, H.L., Frith, C.D., 2004. Dissociable neural pathways for the perception and recognition of expressive and instrumental gestures. Neuropsychologia 42, 1725–1736.
Gallagher, H.L., Happe, F., Brunswick, N., Fletcher, P.C., Frith, U., Frith, C.D., 2000. Reading the mind in cartoons and stories: An fMRI study of 'theory of mind' in verbal and nonverbal tasks. Neuropsychologia 38, 11–21.
Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. Brain 119 (Pt 2), 593–609.
Green, A., Straube, B., Weis, S., Jansen, A., Willmes, K., Konrad, K., Kircher, T., 2009. Neural integration of iconic and unrelated coverbal gestures: A functional MRI study. Hum. Brain Mapp. 30, 3309–3324.
Grezes, J., Frith, C., Passingham, R.E., 2004. Brain mechanisms for inferring deceit in the actions of others. J. Neurosci. 24, 5500–5505.
Happe, F., 2003. Theory of mind and the self. Ann. N. Y. Acad. Sci. 1001, 134–144.
Harris, P.L., 1991. The work of the imagination. In: Whiten, A. (Ed.), Natural theories of mind. Oxford Blackwell.
Hermsdorfer, J., Goldenberg, G., Wachsmuth, C., Conrad, B., Ceballos-Baumann, A.O., Bartenstein, P., Schwaiger, M., Boecker, H., 2001. Cortical correlates of gesture processing: Clues to the cerebral mechanisms underlying apraxia during the imitation of meaningless gestures. NeuroImage 14, 149–161.
Hooker, C.I., Verosky, S.C., Germine, L.T., Knight, R.T., D'Esposito, M., 2008. Mentalizing about emotion and its relationship to empathy. Soc. Cogn. Affect. Neurosci. 3, 204–217.
Iacoboni, M., 2009. Imitation, empathy, and mirror neurons. Annu. Rev. Psychol. 60, 653–670.
Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286, 2526–2528.
Kircher, T.T., Senior, C., Phillips, M.L., Benson, P.J., Bullmore, E.T., Brammer, M., Simmons, A., Williams, S.C., Bartels, M., David, A.S., 2000. Towards a functional neuroanatomy of self processing: Effects of faces and words. Brain Res. 10, 133–144.
Kircher, T., Blumel, I., Marjoram, D., Lataster, T., Krabbendam, L., Weber, J., van Os, J., Krach, S., 2009. Online mentalising investigated with functional MRI. Neurosci. Lett. 454, 176–181.
Kircher, T., Straube, B., Leube, D., Weis, S., Sachs, O., Willmes, K., Konrad, K., Green, A., 2009. Neural interaction of speech and gesture: Differential activations of metaphoric co-verbal gestures. Neuropsychologia 47, 169–179.
Koski, L., Iacoboni, M., Dubeau, M.C., Woods, R.P., Mazziotta, J.C., 2003. Modulation of cortical activity during different imitative behaviors. J. Neurophysiol. 89, 460–471.
Krach, S., Hegel, F., Wrede, B., Sagerer, G., Binkofski, F., Kircher, T., 2008. Can machines think? Interaction and perspective taking with robots investigated via fMRI. PLoS One 3, e2597.
Kringelbach, M.L., Rolls, E.T., 2004. The functional neuroanatomy of the human orbitofrontal cortex: Evidence from neuroimaging and neuropsychology. Prog. Neurobiol. 72, 341–372.
Lewis, J.W., 2006. Cortical networks related to human use of tools. Neuroscientist 12, 211–231.
Liew, S.L., Han, S., Aziz-Zadeh, L., 2011. Familiarity modulates mirror neuron and mentalizing regions during intention understanding. Hum. Brain Mapp. 32, 1986–1997.
Lombardo, M.V., Chakrabarti, B., Bullmore, E.T., Sadek, S.A., Pasco, G., Wheelwright, S.J., Suckling, J., Baron-Cohen, S., 2010. Atypical neural self-representation in autism. Brain 133, 611–624.
Marsh, L.E., Hamilton, A.F., 2011. Dissociation of mirroring and mentalising systems in autism. NeuroImage 56, 1511–1519.
Martin, A., Weisberg, J., 2003. Neural foundations for understanding social and mechanical concepts. Cogn. Neuropsychol. 20, 575–587.
Meltzoff, A.N., Decety, J., 2003. What imitation tells us about social cognition: A rapprochement between developmental psychology and cognitive neuroscience. Philosophical transactions of the Royal Society of London Series B. Biol. Sci. 358, 491–500.

Mitchell, J.P., 2008. Activity in right temporo-parietal junction is not selective for theory-of-mind. Cereb. Cortex 18, 262–271.

Mitchell, J.P., 2009. Social psychology as a natural kind. Trends Cogn. Sci. 13, 246–251.

Muhlau, M., Hermsdorfer, J., Goldenberg, G., Wohlschlager, A.M., Castrop, F., Stahl, R., Rottinger, M., Erhard, P., Haslinger, B., Ceballos-Baumann, A.O., Conrad, B., Boecker, H., 2005. Left inferior parietal dominance in gesture imitation: An fMRI study. Neuropsychologia 43, 1086–1098.

Newen, A., Vogeley, K., 2003. Self-representation: Searching for a neural signature of self-consciousness. Conscious. Cogn. 12, 529–543.

Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., Panksepp, J., 2006. Self-referential processing in our brain—A meta-analysis of imaging studies on the self. NeuroImage 31, 440–457.

Oztop, E., Arbib, M.A., 2002. Schema design and implementation of the grasp-related mirror neuron system. Biol. Cybern. 87, 116–140.

Pfeifer, J.H., Peake, S.J., 2012. Self-development: Integrating cognitive, socioemotional, and neuroimaging perspectives. Dev. Cogn. Neurosci. 2, 55–69.

Pineda, J.A., 2008. Sensorimotor cortex as a critical component of an 'extended' mirror neuron system: Does it solve the development, correspondence, and control problems in mirroring? Behav. Brain Funct. 4, 47.

Premack, D., Woodruff, G., 1978. Does the chimpanzee have a theory of mind? Behav. Brain Sci. 1, 515–526.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Rizzolatti, G., Sinigaglia, C., 2007. Mirror neurons and motor intentionality. Funct. Neurol. 22, 205–210.

Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and the recognition of motor actions. Brain Res. 3, 131–141.

Ruby, P., Decety, J., 2004. How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. J. Cogn. Neurosci. 16, 988–999.

Schilbach, L., Koubeissi, M.Z., David, N., Vogeley, K., Ritzl, E.K., 2007. Being with virtual others: Studying social cognition in temporal lobe epilepsy. Epilepsy Behav. 11, 316–323.

Schippers, M.B., Gazzola, V., Goebel, R., Keysers, C., 2009. Playing charades in the fMRI: Are mirror and/or mentalizing areas involved in gestural communication? PLoS One 4, e6801.

Schippers, M.B., Roebroeck, A., Renken, R., Nanetti, L., Keysers, C., 2010. Mapping the information flow from one brain to another during gestural communication. Proc. Natl. Acad. Sci. U. S. A. 107, 9388–9393.

Searle, J., 1981. Speech acts. Cambridge University, Cambridge.

Slotnick, S.D., Moo, L.R., Segal, J.B., Hart Jr., J., 2003. Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. Brain Res. 17, 75–82.

Spengler, S., von Cramon, D.Y., Brass, M., 2009. Control of shared representations relies on key processes involved in mental state attribution. Hum. Brain Mapp. 30, 3704–3718.

Stone, V.E., Baron-Cohen, S., Knight, R.T., 1998. Frontal lobe contributions to theory of mind. J. Cogn. Neurosci. 10, 640–656.

Straube, B., Green, A., Weis, S., Chatterjee, A., Kircher, T., 2009. Memory effects of speech and gesture binding: Cortical and hippocampal activation in relation to subsequent memory performance. J. Cogn. Neurosci. 21, 821–836.

Straube, B., Green, A., Jansen, A., Chatterjee, A., Kircher, T., 2010. Social cues, mentalizing and the neural processing of speech accompanied by gestures. Neuropsychologia 48, 382–393.

Straube, B., Green, A., Bromberger, B., Kircher, T., 2011. The differentiation of iconic and metaphoric gestures: Common and unique integration processes. Hum. Brain Mapp. 32, 520–533.

Straube, B., Green, A., Chatterjee, A., Kircher, T., 2011. Encoding social interactions: The neural correlates of true and false memories. J. Cogn. Neurosci. 23, 306–324.

Stuss, D.T., Gallup Jr., G.G., Alexander, M.P., 2001. The frontal lobes are necessary for 'theory of mind'. Brain 124, 279–286.

Tamir, D.I., Mitchell, J.P., 2010. Neural correlates of anchoring-and-adjustment during mentalizing. Proc. Natl. Acad. Sci. U. S. A. 107, 10827–10832.

Tanaka, S., Inui, T., Iwaki, S., Konishi, J., Nakai, T., 2001. Neural substrates involved in imitating finger configurations: An fMRI study. Neuroreport 12, 1171–1174.

Tavares, P., Lawrence, A.D., Barnard, P.J., 2008. Paying attention to social meaning: An FMRI study. Cereb. Cortex 18, 1876–1885.

Viard, A., Chetelat, G., Lebreton, K., Desgranges, B., Landeau, B., de La Sayette, V., Eustache, F., Piolino, P., 2011. Mental time travel into the past and the future in healthy aged adults: An fMRI study. Brain Cogn. 75, 1–9.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., Maier, W., Shah, N.J., Fink, G.R., Zilles, K., 2001. Mind reading: Neural mechanisms of theory of mind and self-perspective. NeuroImage 14, 170–181.

Wakusawa, K., Sugiura, M., Sassa, Y., Jeong, H., Horie, K., Sato, S., Yokoyama, H., Tsuchiya, S., Inuma, K., Kawashima, R., 2007. Comprehension of implicit meanings in social situations involving irony: A functional MRI study. NeuroImage 37, 1417–1426.

Walter, H., Adenzato, M., Ciaramidaro, A., Enrici, I., Pia, L., Bara, B.G., 2004. Understanding intentions in social interaction: The role of the anterior paracingulate cortex. J. Cogn. Neurosci. 16, 1854–1863.

Wimmer, H., Perner, J., 1983. Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. Cognition 13, 103–128.