How do we infer others' goals from non-stereotypic actions? The outcome of context-sensitive inferential processing in right inferior parietal and posterior temporal cortex

Roman Liepelt a,⁎, D. Yves Von Cramon a, Marcel Brass a,b

a Max Planck Institute for Human Cognitive and Brain Sciences, Department of Cognitive Neurology, Stephanstr. 1A, 04103 Leipzig, Germany
b Ghent University, Department of Experimental Psychology and Ghent Institute for Functional and Metabolic Imaging, Ghent, Belgium

Article history:
Received 28 January 2008
Revised 11 July 2008
Accepted 4 August 2008
Available online 16 August 2008

Abstract

Humans permanently monitor others’ behaviour and reason about their goals and intentions. Recent studies provided evidence suggesting that a very simple mechanism might underlie these functions. When observing stereotypic actions of others, goal inference seems to work through internal simulation of these actions in the self. However, less is known about the functional mechanisms and brain areas that are involved in inferring goals from others’ actions when these actions are not stereotypic. Here we investigated the neural processes that are involved in goal inference processing of simple, non-stereotypic actions using functional brain imaging. We developed a paradigm in which we compared four simple finger lifting movements that differed in plausibility and intentionality as varied by action context. We found three regions that seem to be involved in goal inference processing of non-stereotypic implausible actions: (1) The superior temporal sulcus, (2) the right inferior parietal cortex, at the junction with the posterior temporal cortex (TPJ), and (3) the angular gyrus of the inferior parietal lobule. In line with teleological reasoning accounts of action understanding, inferring others’ goals from non-stereotypic actions seems to be the outcome of context-sensitive inferential processing. In agreement with previous findings, we found the mirror system to be more strongly activated for intentionally produced actions [Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G., 2005. Grasping the intentions of others with one’s own mirror neuron system. PLoS Biol. 3, e79], indicating an involvement of the IFG in representing intentional actions. Our findings support the idea that goal inference processing for non-stereotypic actions is primarily mediated by reasoning about action and context rather than by a direct mapping process via the mirror system.

© 2008 Elsevier Inc. All rights reserved.

Introduction

Inferring other people’s goals is a crucial ability that underlies most social interactions. Understanding the goals of others is specifically relevant in situations where the observed action is novel or non-stereotypic. In such situations, contextual information is an important cue that can help interpreting the action.

One potential functional mechanism to infer others’ goals is related to motor simulation. It has been argued that we directly map observed actions onto our own motor repertoire (Brass et al., 2000; Iacoboni et al., 1999; Decety and Grezes, 1999). This mechanism might be well suited to facilitate the understanding of other people's behaviour (Gallese and Goldman, 1998) by ascribing goals that are normally connected with the same action in the self (internal simulation). This view recently gained indirect evidence by the discovery of mirror neurons in the premotor cortex of monkeys. Mirror neurons fire when the monkey performs object-directed (transitive) actions such as grasping a piece of food, as well as when the monkey observes the same action performed by others (Gallese et al., 1996; Rizzolatti et al., 1996, 2001; di Pellegrino et al., 1992). Evidence from functional Magnetic Resonance Imaging (fMRI) studies suggests that mirror activity of this kind is also found in the inferior frontal gyrus (IFG) and in the anterior part of the parietal cortices in humans (Buccino et al., 1999, 2001; Decety and Grezes, 1999; Gazzola et al., 2007; Iacoboni et al., 1999, 2001). Molnar-Szakacs and colleagues used fMRI to show that activity in the fronto-parietal mirror network varied according to the motoric complexity of observed transitive actions. This suggests that the human mirror system does not only represent basic action kinematics but also provides a fairly accurate simulation of the motoric complexity of an action (Molnar-Szakacs et al., 2006). Other studies on the human mirror system go even further, claiming that the mirror system is also involved in goal and intention understanding. Iacoboni and colleagues, for example, found a higher activation in the right IFG for actions embedded in a stereotypic drinking context than for those presented in a less stereotypic cleaning context (Iacoboni et al., 2005). They concluded from these data that the mirror system is involved in understanding the ‘intentions’ behind actions. Using
repetition suppression, Hamilton and Grafton (2006) found the anterior intraparietal sulcus (IPS) to be sensitive to object-directed grasping actions but not to action trajectories, also suggesting that the mirror system codes the goals of actions rather than the kinematic properties. These findings indicate that activity in the mirror system is modulated by an action context that indicates the likely goal of an action and/or the intention behind it.

Csibra and Gergely (2007) pointed out the limitations of internal simulation for action understanding. They argued that internal simulation is well suited for recognition of others’ goals as long as the action is plausible or embedded in a plausible context. To understand a goal via motor simulation, a connection between a goal and the action in the observer’s action repertoire must already be established. However, if the input consists of a novel or implausible action, requiring goal prediction as the output, then internal simulation would not provide a satisfactory solution. This view is supported by recent brain imaging work. Stevens and colleagues investigated changes in brain activity during perception of biologically impossible and biologically possible movement paths as varied by the interstimulus interval of static pictures. They found an involvement of motor and parietal cortex only for possible motion paths but not for impossible motion paths. Such a response pattern indicates that activity in mirror regions is selectively found for actions that are present in the action repertoire of the observer (Stevens et al., 2000). A mechanism well suited for inferring goals from novel or implausible actions is teleological reasoning, an inferential process that assigns a goal to an action following the principle of rationality (Csibra and Gergely, 1998; Gergely and Csibra, 2003). Goal assignment requires the recruitment of relevant background knowledge that the observer accumulated about the physical constraints of the situation and of the actor (Csibra and Gergely, 2007).

Brain imaging studies that involve context-sensitive inferential processing have been found to be related to regions along the superior temporal sulcus (STS), the temporo-parietal junction (TPJ) area, the anterior fronto-median cortex, and the posterior cingulate cortex (Brass et al., 2007; Frith and Frith, 2006; Grezes et al., 2004; Pelphrey et al., 2004b; Saxe et al., 2004).

Most studies investigating goal inference processing used highly stereotypic actions or provided context information that directly indicated the action goal, as for example a tea cup and a grasping movement (Hamilton and Grafton, 2006; Iacoboni et al., 2005). In contrast, brain areas involved in novel or non-stereotypic actions have rarely been investigated (for an exception, see a study by Brass et al. (2007) on action understanding of complex, transitive actions). The aim of the present study was to identify the neural processes involved in goal inference of simple, non-stereotypic actions. This was done by showing subjects a range of simple intransitive finger lifting actions, which differed in plausibility.

The actions we used to investigate the present research question have previously been shown to effectively manipulate effects of goal inference processing in a behavioural motor priming paradigm (Liepelt et al., 2008). In one condition participants saw a model trying to lift the index or middle finger against a metal clamp (‘restrained movement condition’, RMC). Even though only a tiny movement was visible in this condition, the observed movement gives the impression that the model tries to fully lift the index or middle finger. In our behavioural study this movement yielded a substantial motor priming effect, suggesting that participants automatically attributed a goal to the action. In order to investigate areas involved in goal inference processing, we added a second condition in which the same movement was presented without the clamp. Unlike the restrained movement, the movement in the ‘micro movement condition’ (MMC) does not give the impression that the model tries to completely lift his/her index or middle finger. Accordingly, this movement did not produce a motor priming effect in our previous experiment, suggesting that no automatic goal attribution process takes place. Therefore, we predicted that this condition requires a more effortful goal-attribute process. In addition to these two conditions we also showed a movement where the model lifted the index or the middle fingers completely (‘standard movement condition’, SMC). Finally, we showed a kinematically identical movement in which the fingers were passively lifted by a mechanical device, the ‘passive movement condition’ (PMC). The latter condition reflects a movement that is produced without the actor’s intention. In our behavioural study, this movement yielded a reduced motor priming effect compared to the standard movement condition (for a list of abbreviations of all movement conditions, see Table 1). The standard and passive movement as well as the restrained and micro movement are identical with respect to action kinematics.

We predicted that areas involved in goal inference processing of non-stereotypic actions situations should be more strongly activated for micro movements (MMC) than for restrained movements (RMC). Analogous findings are predicted when comparing the micro movements (MMC) with the standard movements (SMC). Inference-related activity was expected to be similar for restrained (RMC) and standard movements (SMC). In line with the simulation account (Iacoboni et al., 2005), we predicted a stronger activation for intentionally produced standard movements (SMC) than for passive movements (PMC).

### Methods

#### Subjects

We tested twenty healthy subjects (10 males, mean age: 25.8) who were all right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971). We obtained written consent from all 20 participants prior to the scanning session. All subjects had normal or corrected-to-normal vision. No subject had a history of neurological, major medical, or psychiatric disorders.

#### Stimuli and apparatus

Each trial consisted of two frames. The first frame was an image of a right hand in a resting position presented in the center of the screen. The second frame, which was the imperative stimulus, consisted of an image showing the model’s right hand lifting either the index or the middle finger (see Fig. 1). To control for perceptual similarity between conditions, we added the clamp that restrains the movements in the RMC to the thumb and ring fingers of the other conditions. With a viewing distance of approximately 80 cm, the hand on the screen subtended a visual angle of $9.57^\circ \times 10.27^\circ$. The hand was filmed from a first-person viewing perspective (see Fig. 1).

Displaying the two frames sequentially gives the impression of a realistic finger movement. In order to encourage attention during stimulus observation, a number of catch trials were introduced in which the lifted finger was brought back to the resting position after a short interval. Catch trials were generated from the images of each of the four conditions.

#### Procedure and design

All conditions were presented in one session using an event-related design. In catch trials the observed moving finger returned to

### Table 1

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Name of condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMC</td>
<td>Standard movement condition</td>
</tr>
<tr>
<td>PMC</td>
<td>Passive movement condition</td>
</tr>
<tr>
<td>RMC</td>
<td>Restrained movement condition</td>
</tr>
<tr>
<td>MMC</td>
<td>Micro movement condition</td>
</tr>
</tbody>
</table>
the resting position 400 ms after it was lifted, and was shown in this position for another 1515 ms. Catch trials were presented randomly.

Subjects observed a total of 176 finger-lifting movements (32 per condition), interspersed by 16 catch trials and 32 null events (blank screen). The movement consisted of two frames. A static hand was presented for 800 ms and was then replaced by the second frame showing a hand with a lifted finger for 1915 ms (imperative stimulus). Each trial was preceded by a blank screen of variable duration (0, 500, 1000 or 1500 ms). In the remaining time a blank screen was shown so that each trial lasted 6 s.

Participants were instructed to watch all stimuli carefully and attentively. In order to encourage attention to the stimuli, participants were instructed to indicate catch trials by pressing a button with their left thumb. Prior to scanning we presented all four movement conditions to the participants. All participants had to perform each of the four movement conditions twice for each finger with their own right hand under the same conditions as presented on the display during the experiment. For the SMC participants had to perform a full blown finger-lifting movement. For the PMC participant’s fingers were passively lifted up to the same extend as in the SMC, but the movement was triggered by an electronical device so that participant’s fingers were unintentionally lifted up. For the RMC participants were asked to try to lift their fingers but the full movement was hindered by a metal clamp so that they could only perform a tiny finger-lifting movement. For the MMC participants were instructed to perform only a tiny finger lifting movement. Before going into the scanner we told participants that they would see these four movement conditions performed by another person during the scanning.

**Plausibility ratings**

To test for differences in plausibility across conditions we performed a behavioural experiment in which we presented all four movement conditions twice to a new group of 19 participants (8 males, mean age: 25.5). Presentation order was counterbalanced.
across participants. After having observed all four movement condi-
tions, participants had to complete a questionnaire in which they were
asked to give possible reasons why the model could have performed
the observed movements. We determined the number of possible
reasons given for each of the observed actions across participants by
sorting them into categories. While this rating does not provide a
measure of automatic attribution of goals, it gives an indication of the
plausibility of the different conditions.

**fMRI scanning**

All participants were placed on the scanner bed, with the thumb of
the left hand on a response button. The participants’ hands were
carefully stabilized, and form-fitting cushions were used to prevent
arm, hand, and head motion. To attenuate scanner noise, participants
were provided with earplugs. Imaging was conducted on a Bruker 3 T
system (Medspec 30/100, Bruker, Ettlingen). The fMRI data were
acquired with a T2* echoplanar sequence using BOLD (blood oxygenation level dependent) contrast. Each functional brain volume
comprised 24 slices (4 mm thickness, 1 mm spacing, 19.2 cm FOV,
or oxygenation level dependent) contrast. Each functional brain volume
were provided with earplugs. Imaging was carried out on a Bruker 3 T
arm, hand, and head motion. To attenuate scanner noise, participants
fMRI scanning

were asked to give possible reasons why the model could have performed
the observed movements. We determined the number of possible
reasons given for each of the observed actions across participants by
sorting them into categories. While this rating does not provide a
measure of automatic attribution of goals, it gives an indication of the
plausibility of the different conditions.

**Data analysis**

Analysis of the fMRI data was performed using the LIPIA software
package (Lohmann et al., 2001). First, functional data were corrected
for movement artefacts. The temporal offset between the slices
acquired in one scan was then corrected using a sinc interpolation
algorithm which is based on the Nyquist–Shannon-Theorem. Data
were filtered using a spatial Gaussian filter with \( \sigma = 0.8 \) (FWHM =
5.65 mm). A temporal high-pass filter with a cutoff frequency of 1/
80 Hz was used for baseline correction of the signal. All functional
data sets were individually registered into 3D space using the
subjects’ individual high-resolution anatomical images. To align the
functional data slices with a 3D stereotactic coordinate reference
system, a rigid linear registration with six degrees of freedom (3
rotational, 3 translational) was performed. The rotational and
translational parameters were acquired on the basis of the MDEFT
(Ugurbil et al., 1993; Norris, 2000) and EPI-T1 slices to achieve an
optimal match between these slices and the individual 3D reference
data set.

This 3D reference data set was acquired for each subject during a
previous scanning session. The MDEFT volume data set with 160 slices
and 1 mm slice thickness was standardized to the Talairach
stereotactic space (Talairach and Tournoux, 1988). The rotational and
translational parameters were subsequently transformed by linear
scaling to a standard size. The resulting parameters were then used to
transform the functional slices using trilinear interpolation, so that the
resulting functional slices were aligned with the stereotactic coordi-
rate system.

The statistical evaluation was based on a least-squares estimation
using the general linear model for serially autocorrelated observations
(Friston et al., 1995; Worsley and Friston, 1995). The design matrix was
generated with a synthetic hemodynamic response function (Friston
et al., 1998; Josephs et al., 1997) and its first derivative. The onset of the
hemodynamic response was placed on the onset of the first frame. The
length epoch had a duration of 2800 ms (we also tested a model where
the onset of the hemodynamic response was modelled from the onset
of the finger movement, and the results revealed the same activation
pattern). The model equation, the design matrix and the error term,
was convolved with a Gaussian kernel of dispersion of 4 s FWHM to
deal with the temporal autocorrelation (Worsley and Friston, 1995). In
the following, contrast-images, i.e. estimates of the raw-score
differences between specified conditions, were generated for each
participant. The single-participant contrast-images were then entered
into a second-level random-effects analysis for each of the contrasts.
The group analysis consisted of a one-sample t-test across the contrast
images of all subjects that indicated whether observed differences
between conditions were significantly distinct from zero (Holmes and
Friston, 1998). The t-values were subsequently transformed to
z-scores.

To protect against false positive activations, only regions with z-
score greater than 3.09 (\( p < 0.001 \); uncorrected) and with a volume
greater than 225 mm^3 (corresponding to 5 adjacent voxels) were
considered.

The signal strength analysis was carried out by extracting the mean
beta value from the most activated voxel and the 32 adjacent voxels
determined from the mean contrast across participants (superior
temporal sulcus: \( x = 61, y = -36, z = 3 \); temporoparietal junction area:
\( x = 40, y = -51, z = 33 \); inferior parietal lobule: \( x = 34, y = -63, z = 42 \). The
same signal strength analysis was also performed for two regions of
interest (ROI). ROIs were defined as spheres. For the ROI analyses, we
selected the specific coordinates of the right IFG (\( x = 52, y = 8, z = 20 \)
from Molnar-Szakacs et al.‘s (2005) study and of the anterior IPS (\( x =
-51, y = -29, z = 42 \)) in Hamilton and Grafton’s (2006) study which
defined the centers of the spheres. We centered the ROI analysis these
coordinates. The same ROIs were used for all subjects and conditions.

**Results**

**Behavioural results**

Error analysis showed that in only 4% of all catch trials participants
performed an error indicating that attention to observation trials was
high during the entire experiment.

**Plausibility ratings**

A chi-square test indicated that participant’s response patterns
across all four conditions were not equally distributed (\( \Delta \chi^2 (3) = 7.14,\n\( p < 0.05 \)). The number of different possible reasons for why the model
could have performed the observed movement ranged from four
(RMC), five (SMC), or six (PMC) to 13 (MMC). Importantly, participants
gave significantly more reasons for the MMC where a small movement
was presented without the clamp over the moving fingers as
compared to the RMC (\( \Delta \chi^2 (1) = 4.77, p < 0.05 \)) as well as when
compared to the SMC (\( \Delta \chi^2 (1) = 3.56, p < 0.05 \)). All other conditions
did not differ statistically. This indirectly indicates that the MMC
condition was seen as less prototypical.

**fMRI analysis**

The basic contrast with which we isolated brain areas involved in
goal inference compared the MMC with the RMC. This contrast yielded
three significant activations (\( p < 0.001 \)) along the STS and the inferior
parietal lobule (see Fig. 2A). One local maximum was found in the
posterior STS at the border to the middle temporal gyrus (MTG)
[Talairach coordinates: \( x = 61, y = -36, z = 3 \), another in the TPJ
[Talairach coordinates: \( x = 40, y = 51, z = 33 \)] and a third in the IPL
[Talairach coordinates: \( x = 34, y = -63, z = 42 \)]. As can be seen in Fig. 2A,
all three maxima were only present in the right hemisphere (see also
Table 2). The STS/MTG activation was a small activation focus in the
posterior part of the STS/MTG. Anatomically this activation was
located close to areas that have previously been shown to be involved
in the detection of human body movement (Allison et al., 2000; Bonda
et al., 1996; Frith and Frith, 1999; Grezes et al., 2001). The TPJ
activation was located in the ascendant limb of the STS and can be
described as the superior part of the TPJ. The IPL activation is located in
the angular gyrus of the right inferior parietal lobule (IPL) corresponding to BA 40. It is located at the border of the angular gyrus to the intraparietal sulcus (IPS). This area is clearly located posterior \((y = -63)\) to the anterior IPS region \((y = -32)\) that is assumed to be part of the human mirror system. We found no region to be activated more strongly in the RMC than in the MMC. To better understand activation patterns across the other conditions, we carried out signal strength analyses in the STS/MTG, the TPJ, and the IPL (Fig. 2B).

The beta value diagram for the STS/MTG indicates relatively higher activations for the micro movement and the passive movement as compared to the SMC and the RMC \((t = 2.7, p < .05)\). In line with the findings of the whole brain contrast, we found the MMC activation to be significantly stronger than the RMC activation \((t = 3.7, p < .05)\).

The TPJ was most strongly activated for the MMC, and showed a very similar pattern of activation across all other conditions. The activation in the MMC differed significantly from the activation in the RMC \((r = 2.0, p < .06)\). The activation in the RMC, however, did not differ from the SMC \((r = 1.3, p > .21)\). Further, this region did not differ between the SMC and the PMC \((r = .7, p > .52)\). The beta value pattern in the IPL equalled that found for the TPJ.

Furthermore, we contrasted the MMC with the SMC condition (Fig. 3A and Table 3). We found a significant activation with one local maximum in the TPJ [Talairach coordinates: \(x = 40, y = -60, z = 36\)] very similar to the previous TPJ activation. This is also supported by the beta value analysis (Fig. 3B), which indicates a similar activation pattern in the present region and the TPJ region found when contrasting the MMC and the RMC condition \((F = .94, p > .42)\). The beta value diagram shows the highest activation for the MMC and a very similar activation level for the three other conditions. In line with the whole brain analysis, we found a significant difference between the MMC and the RMC \((r = 3.7, p < .05)\) and also between the MMC and the SMC \((r = 3.5, p < .05)\). However, as predicted, the activation in the RMC did not differ from the SMC \((r = .7, p > .52)\).

Fig. 2. (A) Shows the resulting zmap overlaid onto an anatomical reference image for the contrast Micro movement-Restrained movement. The zmap was thresholded at \(z = 3.09\), which corresponds to an alpha-level of 0.001. The coordinates represent the values where the slices are presented. L—left hemisphere, R—right hemisphere. (B) Shows corresponding mean beta values for TPJ \([x = 40, y = -51, z = 33]\), IPL \([x = 34, y = -63, z = 42]\) and STS \([x = 61, y = -36, z = 3]\).
Since we did not find any significant activation in the mirror system (inferior frontal cortex or anterior inferior parietal cortex), we carried out two additional ROI analyses to investigate the activation pattern in the mirror system. We selected coordinates from a study of Molnar-Szakacs et al. (2005) in which data from several fMRI studies were pooled showing IFG activation during action observation and imitation of simple finger movements. These coordinates are located in the right inferior frontal gyrus [IFG, \(x=52, y=8, z=20\)], an area assumed to be part of the mirror system (see Fig. 4). The activation pattern in the IFG showed general higher activations for intentionally produced actions with the highest activation in the SMC (Fig. 4). The most important finding was that the activation in the IFG was significantly stronger in the SMC as compared to the kinematically identical but unintentionally produced movement in the PMC (\(t=2.4, p_{\text{Bonferroni}}<0.05\)). Planned \(t\)-tests did not reveal a statistically reliable difference between the RMC and the MMC (\(t=0.8, p>0.42\)) and only a statistical trend of a difference between the SMC and the MMC (\(t=1.8, p<0.09\)).

We carried out a second ROI analysis on the anterior IPS using the coordinates Hamilton and Grafton (2006) found to be related to goal understanding [\(x=-51, y=-29, z=42\)]. Planned \(t\)-tests did not reveal statistically reliable differences in activation of this region between conditions in the present experiment.

**Discussion**

The aim of the present study was to identify the neural processes involved in goal-inference processing of simple, non-stereotypic actions. In two conditions of the experiment participants observed the hand of a human model performing simple, tiny intransitive finger lifting movements differing in plausibility as varied by action context. Differences in plausibility between conditions were assessed in an additional rating study. These data showed that, compared to the condition where a small movement was plausible because the movement range was restricted by a metal clamp (RMC), participants came up with a significantly larger number of potential reasons for the model's tiny movement when it was presented without the context of the clamp (MMC).

In line with the behavioural data we found a differential activation pattern when comparing this relatively implausible action with one where the same action was given in a plausible context (a clamp). Even though both conditions were identical with respect to their

<table>
<thead>
<tr>
<th>Anatomical location</th>
<th>Volume size</th>
<th>Mean</th>
<th>(z_{\text{max}})</th>
<th>Talairach coordinates</th>
</tr>
</thead>
<tbody>
<tr>
<td>IPL (BA 40)</td>
<td>1782</td>
<td>3.38</td>
<td>4.09</td>
<td>R(34−63 42)</td>
</tr>
<tr>
<td>TPJ (BA 40)</td>
<td>LO 3.87</td>
<td>3.27</td>
<td>3.41</td>
<td>R(40−51 33)</td>
</tr>
<tr>
<td>STS/MTG (BA 21/22)</td>
<td>297</td>
<td>3.33</td>
<td>3.72</td>
<td>R(61−36 3)</td>
</tr>
</tbody>
</table>

LO: Local maxima within a larger activation area.
The detection of intentional agents (Saxe et al., 2004). However, with an area in the posterior STS previously found to be involved in this conclusion is also in line with an overlap of the present activity depicting goals or intentions of the implausible action rather than a motor-simulation based account of goal inference when observing non-stereotypic actions. This conclusion is further supported by a second contrast in which we compared the implausible action with a highly plausible standard finger-lifting movement, revealing again an activation in the TPJ close to that found in the previous contrast between implausible and plausible actions. In contrast, we found no TPJ activation when comparing two movement conditions (RMC and SMC) that were more similar with respect to their plausibility.

Interestingly, a region of interest analysis in the right IFG revealed a stronger activation in mirror areas for intentionally produced actions (SMC) than for a situation where the identical action was unintentionally produced (PMC). This supports an involvement of internal simulation in situations where we automatically attribute intentions to an observed movement.

The role of the pSTS in inferring intentions of non-stereotypic actions

The STS/MTG region that we found to be activated when contrasting micro movements with restrained movements is slightly more posterior as compared to an area that was previously shown to be involved in the detection of human body movement (Allison et al., 2000; Bonda et al., 1996; Grezes et al., 2001). We found STS activity only in the right hemisphere, which is consistent with the findings of a range of studies using non-verbal material such as movements of the hand and other body parts (Gallagher et al., 2000; Pelphrey et al. 2003, 2004a, 2005; Puce et al., 1998). This might suggest a special role of the right STS in the analysis of action goals (Frith and Frith, 2003) and the signalling of intentional activity (Gallagher et al., 2000) that is not restricted to verbal material. We assume that attentional functions also play a crucial role in goal inference processing. This is consistent with the proposed right lateralization of the corresponding fronto-parietal attentional network (Decety and Lammm, 2007). The right pSTS has a unique position to integrate motion, spatial, and object information (Boussauaud et al., 1990), which may be needed to analyze interactions of movement and context in order to signal movements produced by intentional agents.

TPJ and IPL functions for goal inference of non-stereotypic actions

The TPJ was the only area we found in both contrasts that differed regarding goal inference processing. The superior part of the right TPJ was previously found to be functionally connected to the activation of low-level processes of attention re-orientation (Astaffiev et al., 2006; Corbetta et al., 2000; Shulman et al., 2007). A more inferior part of the TPJ was found to be involved in the attribution of higher-order mental states (Den Ouden et al., 2005; Gallagher et al., 2000). Anatomically our TPJ activation peak seems to be located in a transition area between these two regions. In disagreement with the idea of such discrete patches within the TPJ, Mitchell (2008) recently showed an involvement of a single TPJ region in social ‘TOM’ tasks as well as in non-social attentional tasks. This might suggest that a part of the TPJ is involved in very basic and stimulus-independent functions required by both task types (Mitchell, 2008). Since our experiment can be considered to involve ‘social’ components as well as strong attentional components, such an interpretation of the present activation would be highly plausible.

In line with the findings of Mitchell (2008), our activation peak in the right TPJ might reflect a functional overlap between attentional tasks, tasks involving goal inference processing, and social tasks. One important function needed in all these tasks could be to signal incongruent stimulus relations that violate the observer’s expectations. The TPJ as a heteromodal association cortex (Decety and Sommerville, 2003) seems to be well suited for this function due to its reciprocal connections to various external (visual, auditory) and internal sources of information. However, whether such a function can be fulfilled by the TPJ remains an open question. Inferring goals from non-stereotypic actions seems to be the result of rather domain-general processing taking place in the TPJ and IPL (see also Decety and Lammm, 2007).

The role of the IFG in intention attribution

The findings presented here seem to complement recent studies showing an involvement of the mirror system for goal inference processing (Hamilton and Grafton, 2006; Iacoboni et al., 2005). These studies found an involvement of the mirror system during observation of actions presented in a stereotypic drinking context. This is between an external and an internal event (the observed and the expected action). An open question concerns the lateralisation of functional specialisation of STS functions. Different interpretations could be given to pSTS in the left or right hemisphere. Some studies reported bilateral STS activation elicited by the attribution of mental states (Castelli et al., 2000). Studies using the verbal domain for ‘theory of mind’ (TOM) tasks mostly find bilateral STS/TPJ activations, whereas a right lateralization is found when TOM tasks from the visual domain were used (Gallagher et al., 2000). Left sided activations of this region have been attributed to semantic knowledge of single words (Damasio et al., 1996; Gallagher et al., 2000). This is also in line with the extension of speech-related areas in the left temporal lobe (Buchsbaum et al., 2001). We found STS activity only in the right hemisphere, which is consistent with the findings of a range of studies using non-verbal material such as movements of the hand and other body parts (Gallagher et al., 2000; Pelphrey et al. 2003, 2004a, 2005; Puce et al., 1998). This might suggest a special role of the right STS in the analysis of action goals (Frith and Frith, 2003) and the signalling of intentional activity (Gallagher et al., 2000) that is not restricted to verbal material. We assume that attentional functions also play a crucial role in goal inference processing. This is consistent with the proposed right lateralization of the corresponding fronto-parietal attentional network (Decety and Lammm, 2007). The right pSTS has a unique position to integrate motion, spatial, and object information (Boussauaud et al., 1990), which may be needed to analyze interactions of movement and context in order to signal movements produced by intentional agents.
completely consistent with our finding of a higher activation of mirror areas, for intentionally produced actions as compared to non-intentionally produced actions with matched kinematic features. Therefore, our data support previous findings suggesting that the interpretation of the movement modulates activity in mirror areas (Iacoboni et al., 2005). We assume that goal inference of intentionally produced action can be automatically achieved by mapping it onto the corresponding motor representations of the observer’s action schemes. The IFG could be involved in the representation of the corresponding goal or intention.

This interpretation would be in line with previous findings showing a modulation of motor priming by intention attribution (Liepelt et al., 2008) as well as with studies showing a stronger mirror system response to actions for which the observer has greater motor experience (Calvo-Merino et al., 2005).

Mechanisms involved in goal inference processing

A recent study of Brass et al. (2007) showed an involvement of mentalizing areas when observing implausible compared to plausible complex transitive actions. The present results are in line with, and extend, Brass et al.’s (2007) findings by revealing that a very similar set of mentalizing areas, such as the TPJ and the STS, are also involved in understanding very simple and intransitive finger-lifting movements when these movements are not stereotypic. Another novel finding regarding the functional dissociation of ‘mirror areas’ and ‘ToM areas’ within the present experiment is that our data suggest that the mirror network is involved in action understanding on a very basic level representing intentional actions. On the other hand, inferring intentions from non-stereotypical situations seems to involve ‘ToM’ areas (Brass et al., 2007). These findings indicate that teleological reasoning and internal simulation may be understood as complementary mechanisms that can account for goal inference processing in qualitatively different task situations (Csibra and Gergely, 1998, 2007). Therefore, both mechanisms do not contradict but may complement each other. This interpretation is also consistent with a recent finding by de Lange and colleagues who could show a dissociation of ‘ToM areas’ and ‘mirror areas’ in intention attribution (de Lange et al., 2008).

Conclusions

The present study suggests that goal-inference processing in non-stereotypic action situations is the product of a set of lower-level computational processes taking place in the right inferior parietal cortex, at the junction with the posterior temporal cortex (TPJ) and the posterior STS. Intention attribution seems to involve mirror system areas such as the IFG. Finally, our data suggest that these lower-level domain-general computational mechanisms are crucial for higher-level social cognitive processing important for social interactions.

Acknowledgments

This research was supported by a European Union funded project aimed at understanding the evolutionary, developmental, and intentional control of imitation (EDICI-12929). We express our appreciation to Helge Gillmeister for proofreading and three anonymous reviewers for helpful comments on earlier versions of this article.

References
