



Minds, persons, and space: An fMRI investigation into the relational complexity of higher-order intentionality

Anna Abraham^{a,*}, Markus Werning^b, Hannes Rakoczy^c, D. Yves von Cramon^{a,e},
Ricarda I. Schubotz^{a,d,e}

^a Department of Cognitive Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstr. 1a, D-04103 Leipzig, Germany

^b Department of Philosophy, Heinrich-Heine University Duesseldorf, Universitaetsstr. 1, D-40225 Duesseldorf, Germany

^c Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany

^d Institute of Psychology II, Otto von Guericke University Magdeburg, Universitaetsplatz 6, D-39106 Magdeburg, Germany

^e Max Planck Institute for Neurological Research, P.O. Box 410629, D-50866 Cologne, Germany

ARTICLE INFO

Article history:

Received 28 February 2008

Available online 10 April 2008

Keywords:

Intentionality

Mental state reasoning

Mentalizing

Theory-of-mind

Personhood

Relational complexity

ABSTRACT

Mental state reasoning or theory-of-mind has been the subject of a rich body of imaging research. Although such investigations routinely tap a common set of regions, the precise function of each area remains a contentious matter. With the help of functional magnetic resonance imaging (fMRI), we sought to determine which areas are involved when processing mental state or intentional metarepresentations by focusing on the relational aspect of such representations. Using non-intentional relational representations such as spatial relations between persons and between objects as a contrast, the results ascertained the involvement of the precuneus, the temporal poles, and the medial prefrontal cortex in the processing of intentional representations. In contrast, the anterior superior temporal sulcus and the left temporo-parietal junction were implicated when processing representations that refer to the presence of persons in relational contexts in general. The right temporo-parietal junction, however, was specifically activated for persons entering spatial relations. The level of representational complexity, a previously unexplored factor, was also found to modulate the neural response in some brain regions, such as the medial prefrontal cortex and the right temporo-parietal junction. These findings highlight the need to take into account the critical roles played by an extensive network of neural regions during mental state reasoning.

© 2008 Elsevier Inc. All rights reserved.

1. Introduction

Research on the ascription of mental states, often referred to as theory of mind (Premack & Woodruff, 1978), has for long been a prominent topic in the domains of cognitive developmental and comparative psychology. For more than a decade now, functional imaging studies have followed suit in attempting to uncover the neural basis of mentalizing (Frith, Morton, & Leslie, 1991) or theory-of-mind (Frith & Frith, 2003, 2006; Gallagher & Frith, 2003; Saxe, Carey, & Kanwisher, 2004) using a wide variety of stimuli, including stories (Fletcher et al., 1995; Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006; Saxe & Kanwisher, 2003; Saxe & Powell, 2006), static cartoons (Brunet, Sarfati, Hardy-Bayle, & Decety, 2000; Gallagher et al., 2000), interactive games (Gallagher, Jack, Roepstorff, & Frith, 2002), animations of interacting shapes (Castelli, Happe, Frith, & Frith, 2000; Schultz, Friston, O'Doherty, Wolpert, & Frith, 2005), movies of entities carrying out an intentional action

* Corresponding author. Fax: +49 341 35521750.

E-mail address: abraham@cbs.mpg.de (A. Abraham).

(German, Niehaus, Roarty, Giesbrecht, & Miller, 2004; Grezes, Frith, & Passingham, 2004; Pelphrey, Morris, & McCarthy, 2004), and virtual reality simulations (Spiers & Maguire, 2006). Significant activations have been consistently reported in one or more of the followings areas in the brain during mental state reasoning: the medial prefrontal cortex (mPFC), the temporo-parietal junction (TPJ), the temporal poles and the posterior superior temporal sulcus (pSTS).

The involvement of the temporal poles in mentalizing has been postulated to be indicative of access to social script knowledge (Frith & Frith, 2003, 2006), but there is little agreement concerning the precise roles of the other structures. Some have argued for a common function for the TPJ and the pSTS for detecting agency based on the involvement of these areas in spatial perspective-taking and responsiveness to biologically relevant movement (Frith & Frith, 2003, 2006; Gallagher & Frith, 2003). Others claim that this is only true of the pSTS and that the TPJ is instead involved in the representation of mental states (Saxe, 2006; Saxe et al., 2004). The specific role of the mPFC is also an open question. While it was initially viewed as the key area involved in the representation and manipulation of mental state content (Gallagher & Frith, 2003), contemporary proposals argue for mPFC involvement in processing communicative intent (Frith & Frith, 2006) and triadic social relations (Saxe, 2006). However, activity in the mPFC is also found in tasks that do not involve either of these components, such as in investigations on mental state knowledge (Mitchell, Banaji, & Macrae, 2005) and self-referential thought (Mitchell, Macrae, & Banaji, 2006; Ochsner et al., 2005; Zysset, Huber, Ferstl, & von Cramon, 2002). This picture is further complicated by neuropsychological findings which argue against domain specificity in theory-of-mind (Apperly, Samson, & Humphreys, 2005). The objective of our study was therefore to tease apart the roles of the various structures by focusing on the relational facet of intentional or mental state knowledge.

Mental states such as beliefs and desires characteristically exhibit “intentionality,” which refers to the capacity of the mind to be about or to represent things, properties and states of affairs (Dennett & Haugeland, 1987; Perry, 1994). The concept of intentionality was introduced as the “mark of the mental” in that all mental phenomena involve directedness to an object (Brentano, 1973). Intentional states can differ not only with respect to content, but also with respect to the kind of attitude expressed by them (Clapin, 2002). For example, to believe that the local bakery sells cream puffs is to have an attitude of belief towards this particular proposition. A different attitude could be made to the same proposition by substituting the intentional verb—hoping that the local bakery sells cream puffs, doubting that the local bakery sells cream puffs, and so on. In all of these situations, there is a binding relation between a person’s propositional attitude and the intentional object it is directed to, and this relational facet is one of the central features of intentionality.

In the present study, we draw on this determinant feature of intentionality in distinguishing between the representations of mental states relative to non-mental states. We employ a novel approach to determine which areas of the brain are recruited depending on whether a scenario involves intentional (mental state) relations or non-intentional (spatial) relations between persons. By additionally employing non-intentional spatial relations between objects as a control condition, we sought to determine which neural areas are implicated when processing intentional representations as opposed to representations involving the mere presence of persons. To this end, we developed an fMRI experimental paradigm (Figs. 1 and 2) where the statements for the intentional condition (M) involved mental state relations between people, whereas that of structurally comparable non-intentional conditions entailed spatial relations between persons sitting in a theatre (P) or objects in a room (O).¹

The degree of relational complexity of the conditions was also varied (Figs. 1 and 2). Relational complexity is defined by the number of relations between the entities in a task that have to be concurrently maintained in order to be able to comprehend and reason about the content (Halford, Wilson, & Phillips, 1998). Most studies on mental state reasoning investigate reasoning about 1st order intentionality. The present study focuses instead on reasoning about 2nd order (M2) and 3rd order (M3) intentionality, which vary in the level of relational complexity. To provide a fitting contrast for the intentional conditions, the relational complexity for the non-intentional conditions were also correspondingly varied for persons (P2, P3) and objects (O2, O3).² The inclusion of this variable was to determine whether processing intentional and non-intentional representations would be quantitatively or qualitatively different with respect to relational complexity. This is an issue which has not received any attention thus far within this research domain.

2. Materials and methods

2.1. Subjects

After excluding one participant due to severe imaging movement artifacts, the sample included 17 right-handed healthy volunteers (9 females; mean age: 25.65; age range: 22–30) with normal or corrected-to-normal visual acuity.

¹ A seemingly related paradigm was adopted in a study by (Kumaran & Maguire, 2005), on the role played by the hippocampus in cognitive maps and relational memory processing. Subjects were required to either spatially or socially navigate through their network of friends in service of a goal. Comparing social navigation (from one friend to another based on whether they knew each other) to spatial navigation (from one friend to another based on how close to one another they lived) led to activations in mentalizing relevant areas although there were no explicit mental state relations to be processed. The hippocampus along with the parahippocampal, retrosplenial, and posterior parietal cortices were activated in the opposite contrast.

² It is to be noted that the type of relational complexity of the intentional and non-intentional representations are not identical. It is in fact impossible to make these variables equivalent on all counts because only intentional representations can have propositions as an argument. The intentional conditions (M) thus consist of embedded relations [*ThinksAbout(A, ThinksAbout(B, p))*], whereas the non-intentional conditions (P, O) are comprised of intertwined relations [*Behind(A, B) and LeftOf(B, C)*]. This does not affect the relative level of complexity as the 3rd order conditions (M3, P3, O3) are inherently more relationally complex than the 2nd order conditions (M2, P2, O2).

	2nd order representations	3rd order representations
M	Scenario Peter believes that Nina thinks that she is a good dancer.	Thomas supposes that Peter believes that Nina thinks that she is a good dancer.
Question	Nina believes that she is a bad dancer. Is that what Peter thought?	Peter thinks that Nina believes that she is a good dancer. Would that surprise Thomas?
P	Scenario Peter sits in front of Nina who is a good dancer.	Thomas sits left of Peter who sits in front of Nina who is a good dancer.
Question	Nina is a good dancer. Is that true?	Nina sits in front of Peter who sits right of Thomas. Is that true?
O	Scenario The armchair stands left of the table that has a glass surface.	The cabinet stands opposite the armchair which stands left of the table that has a glass surface.
Question	The table stands opposite the armchair. Is that true?	The table has a metal surface. Is that true?

Fig. 1. The top panel of the figure presents examples of scenarios and questions for all experimental conditions. The similarity of the sentences across conditions in the figure is only to serve as an aid in understanding the differences between the conditions. All trials in the experiment were unique in their propositional content. The bottom panel of the figure shows a schematic representation of the sequence of events in a trial (trial length: 20 s). To enhance the temporal resolution of the BOLD signal, variable jitter times were inserted before and after the scenario. For the baseline rest condition, a blank screen was presented through the entire trial.

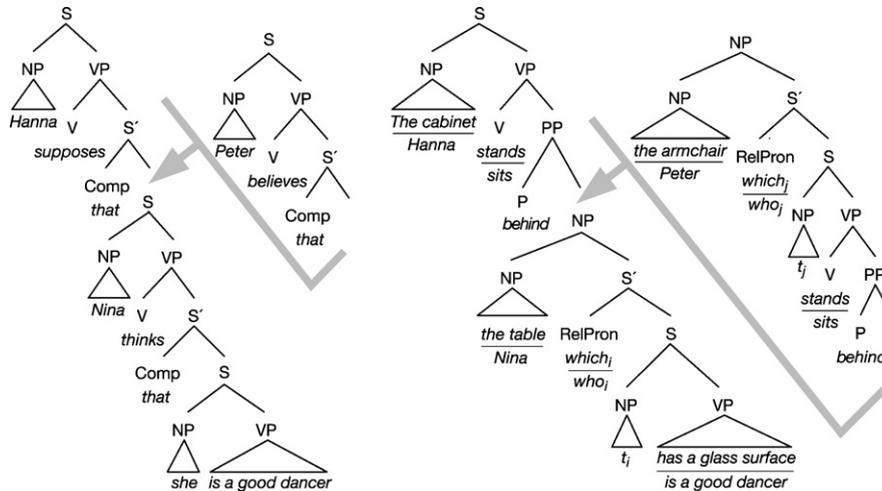


Fig. 2. Linguistic structural trees of the conditions. The M2 tree along is shown on the left side of the left panel. The add-on to the sentence that would convert the M2 tree to a M3 tree is represented on the right side of the left panel next to the arrow which indicates where the section would be inserted within the tree. As the P and O trees are structurally identical, one tree (right panel) is used to present representations of both. A horizontal line is used to distinguish between words that belong to either of the two representations, with the word above the line representing the O condition and the word below the line representing the P condition. The add-on to the sentence that would convert the P2/O2 tree to a P3/O3 tree is represented on the right panel next to the arrow which indicates where the section would be inserted within the tree.

All were native German speakers with no history of neurological or psychiatric illness and none were taking medication at the time of measurement. The participants gave informed consent before participation. The experimental standards were approved by the local ethics committee of the University of Leipzig in Germany. The participants were instructed prior to the MRI experiment and underwent a 5-min practice session in order to be familiar with all trial types.

2.2. Experimental design

A 2×2 factorial design was employed with 24 trials per condition. One factor varied the type of relation: mental state or intentional relations (M) vs. non-intentional relations (PO). The non-intentional variable was further subdivided into person-spatial (P) and object-spatial (O) relations. In the second factor, the degree of relational complexity of the representation was varied: second-order (M2, P2, O2) vs. third-order (M3, P3, O3) complexity. Examples of each trial type are given in Fig. 1. Number of trials per trial subtype were 6 for the M2 condition trials and 3 for the M3 condition trials. The experimental conditions and a resting control baseline condition (10 trials) were presented in a random trial design. With a trial length of 20 s and total of 106 trials, the experimental session spanned 35.33 min.

2.3. Stimuli

The stimulus parameters as well as the timing of trial events were determined on the basis of two behavioral pilot studies. The experimental material consisted of written sentences in German (font size: 26), which were presented in the centerfield of a screen (resolution: 800×600) spanning three or four lines depending on the length of the sentence (Fig. 1). The proper names used in the conditions involving persons were taken from a pool of 20 males and 20 females common German one- and two-syllable names. In the M2 and M3 conditions, six mental state verbs were employed in third person singular form that reflected belief propositional attitudes—believes (*glaubt*), supposes (*meint*), thinks (*denkt*)—and desire propositional attitudes—wants (*will*), would like (*möchte*), wishes (*wünscht*).³ In the P2 and P3 conditions, the non-intentional verb “sits” was used to refer to a relational scenario between two or three individuals sitting in a theatre where their spatial relations were expressed by one or more of these prepositions: left of, right of, in front of, behind. In the O2 and O3 conditions, the non-intentional verbs “is located” or “stands” were employed to convey spatial relations between two or three objects in an office. The spatial relations were expressed by one or more of these prepositions: left of, right of, in front of, under, above, behind, opposite. Examples of each trial type are given in Fig. 1. The “that” clause expressing the propositional content in the M conditions was made analogous to the non-intentional conditions by employing a relative clause in the P conditions (“who”) and O conditions (“that”). The content of the clauses differed for each trial. Moreover, the frequency of the names (number of occurrences and combinations with other names) was randomized, the combinations of intentional verbs and person-spatial relations were balanced, and in the O conditions, both object-type and object-relations were varied for each trial. The structural complexity of the P and O conditions, as shown in the syntax trees (Fig. 2), are identical for each complexity level. The structural complexity of the M conditions (Fig. 2), although not identical to that of the P and O conditions, was made as complementary as possible to that of the latter conditions.⁴

The questions posed after the scenario were designed so as to minimize the possibility of early response selection. In the M conditions, the questions relating to beliefs (Would that surprise *the protagonist*? Is that what *the protagonist* thought?) or desires (Would that please *the protagonist*? Would that disappoint *the protagonist*?) resulted in a yes-or-no response depending on the question type after the altered or unaltered question scenario. In the P and O conditions, the question (Is that true?) was related to the spatial relation between the persons or objects on half of the trials and to the content of the relative clause in the rest of the trials. This was to ensure that participants attended to all aspects of the sentence when reading the scenario.

2.4. Experimental task

Across all experimental conditions, each trial (Fig. 1) began with a fixation cross (duration: 500 ms) which was followed by the presentation of single sentence for 6000 ms that introduced a certain scenario. Following a variable delay, another sentence in which information related to the scenario was changed or unchanged, and a question regarding the nature of this change were presented, to which the participant was required to respond. This remained on the computer screen for a maximum of 4000 ms or till the subject responded (yes-or-no) by pressing the appropriate button (index finger or middle

³ No neuroimaging study thus far has reported differences between the processing of dissimilar intentional attitudes. Belief and desire ascriptions were systematically varied within the intentional condition such that a preliminary parametric contrast could be carried out (results not reported here) to allow us to build hypotheses for later investigations.

⁴ One potential concern is that, theoretically, subjects could break down the sentences in the P3 and O3 conditions in a manner that is impossible in the M3 condition, i.e., by processing each spatial relation within the scenario in isolation from the other, and answering the subsequent question by determining whether each separate spatial relation is maintained or not. However, the behavioral data (lower percentage of correct responses in P3) and participants' feedback (imagining L-shaped constructions) clearly speak against such a simplification strategy.

finger) on a response box placed under the right-hand. Two variable jitter times were inserted before the scenario (Jitter 1: 500, 1000, 1500, or 2000 ms) and before the question (Jitter 2: 2500, 3000, 3500, or 4000 ms) to enhance the temporal resolution of the blood oxygenation level-dependent (BOLD). To investigate which areas of the brain are involved when processing intentional and non-intentional representations, activations that resulted during the reading of the scenario were analyzed.

2.5. MRI scanning procedure

Imaging was carried out on a 3 T Bruker (Ettlingen, Germany) Medspec 30/100 system equipped with the standard bird-cage head coil. Participants were placed on the scanner bed in a supine position with their right index and middle fingers positioned on the appropriate response buttons of a response box. The participants' hands were carefully stabilised and form-fitting cushions were utilized to prevent head, arm, and hand movements. They were also provided ear plugs so that scanner noise would be attenuated. The sentences were presented using the VisuaStim Digital MRI Video System (Resonance Technology, Northridge, USA), which is a high-resolution visor (800 × 600) comprising two small TFT-screens placed close to the subjects' eyes.

Twenty-four axial slices (19.2 cm field of view; 64 × 64 pixel matrix; 4 mm thickness; 1 mm spacing; in-plane resolution of 3 × 3 mm) parallel to the bicommissural line (AC-PC) covering the whole brain were acquired using a single-shot gradient echo-planar imaging (EPI) sequence (TR = 2000 ms; TE = 30 ms; flip angle = 90°; acquisition bandwidth = 100 kHz) sensitive to blood oxygenation level-dependent contrast. Prior to the functional imaging, 24 anatomical T1-weighted MDEFT images (Norris, 2000; Ugurbil et al., 1993) (data matrix = 256 × 256; TR = 1300 ms; TI = 650 ms TE = 10 ms) and 24 T1-weighted EPI images with the same spatial orientation as the functional data were acquired.

2.6. fMRI data analysis

The fMRI data were processed using the software package LIPSIA (Lohmann et al., 2001), which contains tools for preprocessing, registration, statistical evaluation and presentation of fMRI data. Functional data were first motion-corrected using a matching metric based on linear correlation. To correct for the temporal offset between the slices acquired in one image, a cubic-spline interpolation was employed. Low-frequency signal changes and baseline drifts were removed using a temporal highpass filter with a cut-off frequency of 1/200 Hz. Spatial smoothing was performed with a Gaussian filter of 5.65 mm FWHM.

To align the functional data slices onto a three-dimensional stereotactic coordinate reference system, a rigid linear registration was performed with 6 degrees of freedom (3 rotational, 3 translational). The rotational and translational parameters were acquired on the basis of the MDEFT and EPI-T1 slices to achieve an optimal match between these slices and the individual three-dimensional reference data set. This high-resolution three-dimensional 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 & Tournoux, 1988). These rotational and translational parameters were subsequently normalized, i.e., transformed by linear scaling to a standard size. The normalized parameters were then used to transform the functional slices using trilinear interpolation so that the resulting functional slices were aligned with the stereotactic coordinate system, thus generating output data with a spatial resolution of 3 × 3 × 3 mm (27 mm³). This linear normalization process was enhanced by a subsequent processing step involving an additional nonlinear normalization (Thirion, 1998).

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston et al., 1995; Worsley & Friston, 1995). The design matrix was generated with a box-car function, convolved with the hemodynamic response function. Brain activations were analyzed in an epoch-related design, time-locked to the presentation of the first sentence (the scenario) of all presented trials. The analyzed epoch comprised the full duration of the presented scenario (6000 ms). The model equation, including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to account for the temporal autocorrelation (Worsley & Friston, 1995). In the following, contrast images, i.e., beta value estimates of the raw-score differences between specified conditions were generated for each participant. As all individual functional data sets were aligned to the same stereotactic reference space, the single-subject contrast images were entered into a second-level random-effects analysis for each of the contrasts. One-sample *t* tests were employed for the group analyses across the contrast images of all subjects which indicated whether observed differences between conditions were significantly distinct from zero. *t* values were subsequently transformed into *Z* scores. To minimize the probability of false positives (type I error) only regions with *Z* score > 3.09 (*P* < .001; uncorrected) and with a minimum volume of 243 mm³ (9 contiguous voxels) were considered to be significant (Forman et al., 1995). All reported activations hence survived a threshold corresponding to *P* < .001 at the cluster level.

In order to allow for the comparison of the varying complexity levels, percentage signal change (PSC) analyses of the BOLD response were carried out where the mean PSC over the 6 s epoch was extracted from selected voxels within significantly activated brain areas for the experimental and resting baseline conditions. The mean PSC of a voxel for each condition was calculated in relation to the mean signal intensity of that voxel across all time steps.

Table 1

Descriptive data (mean and standard deviation) of the behavioral measures (reaction time and percentage of correct responses) for all variables: M2 (intentional 2nd order), P2 (person-spatial 2nd order), O2 (object-spatial 2nd order), M3 (intentional 3rd order), P3 (person-spatial 3rd order), and O3 (object-spatial 3rd order)

	Reaction time (in ms)		Percentage correct	
	Mean	SD	Mean	SD
M2	3179.29	397.04	85.29	13.1
P2	2402.24	276.28	85.78	12.42
O2	2344.82	350.45	87.74	9.37
M3	3698.18	332.8	73.28	16.34
P3	2946.47	352.78	65.69	14.09
O3	2897.12	184.85	75.98	12.46

3. Results

3.1. Behavioral results

The descriptive data (mean and standard deviation) for reaction time (RT) and percentage correct responses (PCR) across all experimental conditions are presented in Table 1. Using a repeated measures ANOVA for RT, main effects were found for representation type, $F_{2,15} = 83.53$, $P < .001$, and level of complexity, $F_{2,15} = 206.96$, $P < .001$ on correct trials. The repeated measures ANOVA for PCR revealed one significant main effect for complexity, $F_{1,16} = 81$, $P < .001$. No significant interaction effects were found for either RT or PCR. Within-complexity t -test contrasts for RT showed that reaction time for M2 was longer than for P2 ($t_{16} = 9.06$, $P < .001$) and for O2 ($t_{16} = 9.08$, $P < .001$), and that of M3 was longer than for P3 ($t_{16} = 10.84$, $P < .001$) and O3 ($t_{16} = 10.93$, $P < .001$). The PCR was also significantly lower for P3 relative to O3 ($t_{16} = -2.38$, $P = .03$).

The behavioral findings hence indicate that the more complex conditions were accompanied by longer reaction times and lower percentage of correct responses. The intentional conditions were associated with longer response times than the non-intentional conditions, and the percentage of correct responses was significantly lower for the P3 condition relative to the O3 condition.⁵ Given that the analyzed epoch involved the period when the scenario was read as opposed to when the behavioral response was made, the behavioral findings are not directly relevant to the task at hand. These findings will therefore not be discussed in greater detail.

3.2. fMRI results (mental vs. non-mental)

To verify which regions of the brain are involved when processing intentional or mental state representations, two contrasts were carried out: a general contrast (M > PO) and a contrast that specifically controlled for the presence of persons in a scenario (M > P). Both produced highly similar activation maps for the M conditions (Table 2). Regions of activation included the mPFC, left and right temporal poles, precuneus/posterior cingulate (PCC), pSTS, fusiform gyrus, occipital cortex and the postcentral gyrus. Statistical analyses were carried out across conditions on the activation profiles of areas that were most pertinent to the study. The graphs depict the mean percent signal change (PSC) value of a selected voxel and its 26 adjacent neighboring voxels during the reading of the scenario across all trials for each condition.⁶ Using representation type as one factor (mental, person-spatial, object-spatial) and complexity level as a second factor (2nd order, 3rd order), 3×2 repeated measures ANOVAs were carried out on the mean PSCs of each region.

Fig. 3 shows the activation maps and the mean PSCs for two clusters in the mPFC. In the more anterior of the two areas (mPFCa; Fig. 3), the results show higher activations during the M conditions (M2 and M3) and the P2 condition relative to the P3 and O conditions (O2 and O3). The 3×2 findings show a main effect for representation type ($F_{2,15} = 7.014$, $P = .003$) and a main effect for complexity type ($F_{1,16} = 4.691$, $P = .046$). Simple contrasts revealed that activations in the M condition were significantly higher than in the P condition ($F_{1,16} = 12.613$, $P = .003$) and the O condition ($F_{1,16} = 8.159$, $P = .011$). There was also a significant interaction effect of Representation Type \times Complexity ($F_{2,15} = 3.658$, $P = .037$). The simple contrasts revealed that this effect was driven by the dissociation between the P and O conditions with respect to complexity ($F_{1,16} = 4.474$, $P = .05$), and also by the M and P condition as a function of different levels of complexity ($F_{1,16} = 5.079$, $P = .039$).

This region thus appears to be responsive when processing intentional content as well as non-intentional content, but in the latter case only in the less complex scenario involving two persons. The dissociation of the findings for these two

⁵ The disparity between RT and response accuracy in the P3 condition could reflect a speed-accuracy trade-off in this condition. As the participants found it difficult to correctly solve the P3 statements within the allotted time, perhaps they attempted to respond as rapidly as possible in their responses in an effort to improve at least one aspect of their behavioral performance.

⁶ To rule out the possibility that some of the more complex conditions, particularly P3, were too complex for subjects to parse—as might be suggested by the behavioral data (low percentage correct responses)—and thus produced artifacts, we also carried out these analyses using only the correctly responded to trials. The resulting pattern of findings was very similar to the reported findings with all trials. We therefore present the above findings because (a) having more trials increases the power of the design, and (b) we only analyze the neural response during the reading of the scenario and not when the behavioral response was made.

Table 2

Mental state processing: anatomical specification, Talairach co-ordinates, maximum Z value and volume (mm^3) of the significantly activated areas in the M > PO and M > P contrasts

Area	M > PO					M > P				
	x	y	z	mm^3	Z	x	y	z	mm^3	Z
Medial PFC (mPFCa)	-11	47	33	2403	4.171	-11	47	33	999	3.644
Medial PFC (mPFCb)	1	53	18		4.722	1	53	21		3.880
Left temporal pole	-41	2	-33	3618	4.078	-41	2	-33	1512	3.993
Left temporal pole	-41	10	-27		3.805	-47	11	-21		3.396
Left temporal pole	-53	-1	-21		3.773					
Right temporal pole	52	20	-12	3267	4.247	37	-1	-27	459	3.556
Right temporal pole	40	5	-24		4.090					
Superior temporal gyrus	58	-28	9	270	3.882	58	-28	9	405	3.678
Superior temporal gyrus	-56	-16	0	405	3.834					
Medial occipital gyrus	34	-79	18	13419	4.572	34	-82	18	11583	4.890
Medial occipital gyrus	25	-88	15		4.544					
Medial occipital gyrus	43	-73	3		4.132					
Fusiform gyrus	25	-70	-9		4.511	28	-67	-6		4.189
Fusiform gyrus	22	-55	-9		4.436					
Fusiform gyrus	34	-55	-12		4.868					
Lingual gyrus	-38	-67	-3	243	3.503	1	-91	-6	837	3.720
Postcentral gyrus (right)	55	-16	24	2970	4.732	61	-7	21	1809	3.937
Postcentral gyrus (left)	-53	-10	18		3.615	-47	-16	33	1755	3.861
Postcentral gyrus (left)	-44	-7	27	1296	3.616	-47	-7	24	432	3.040
Postcentral gyrus (left)						-38	-34	24	297	4.008
Supplementary motor area	-2	-16	54	1188	3.732	-11	-10	45	1134	4.106
Precentral gyrus						43	-7	12	1053	3.901
Superior occipital gyrus						-14	-82	39	324	3.633
Precuneus/posterior cingulate	1	-52	33	2673	4.339					
Anterior cingulate	-14	41	3	324	3.958					

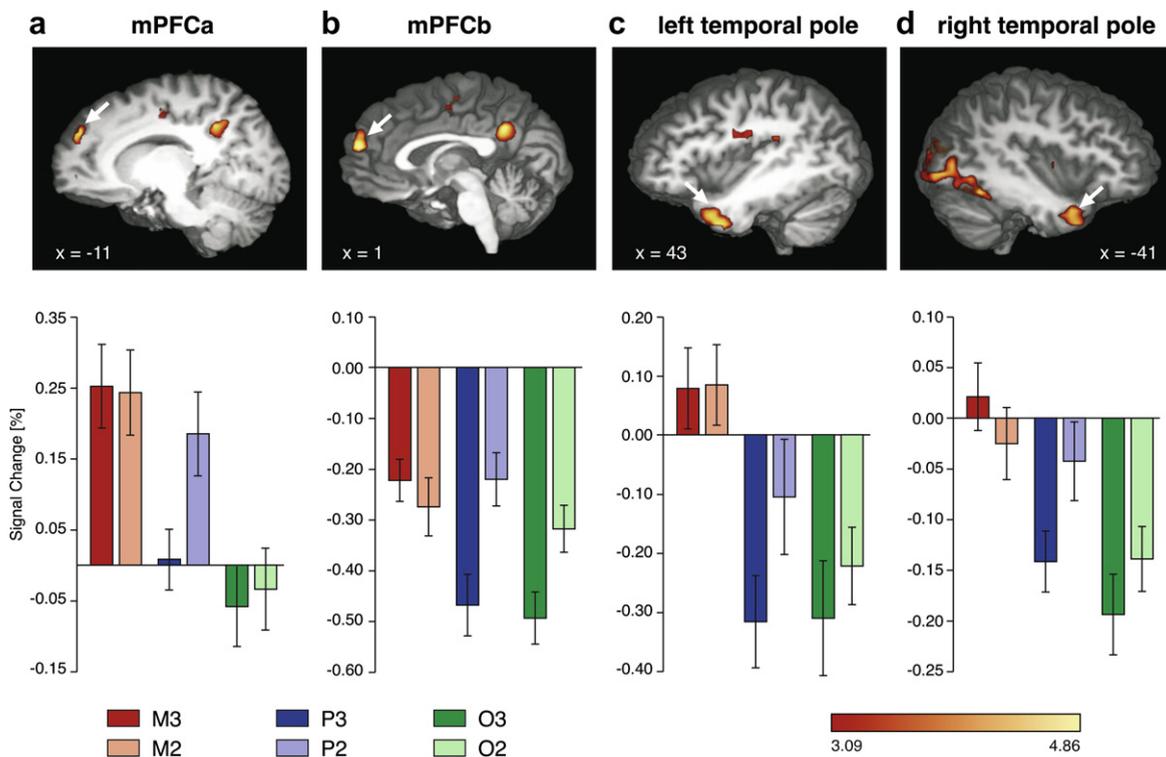


Fig. 3. Processing of intentional representations (M > PO): contrast maps and mean PSC plots for (a) an anterior region in the medial prefrontal cortex (mPFCa: -11, 47, 33), (b) a more medial region in the medial prefrontal cortex (mPFCb: 1, 53, 18), (c) the left temporal pole (43, 2, -30), and (d) the right temporal pole (-41, 2, -33) which showed significantly greater activation during the processing of intentional relative to non-intentional information. The zero point on the plots reflects the resting baseline.

conditions suggests that even when a scenario involves no explicit mental state processing the sheer presence of two persons may inadvertently trigger it. There were significant main effects for representation type for the left temporal pole ($F_{2,15} = 10.61, P < .001$) and the right temporal pole ($F_{2,15} = 8.137, P = .001$). Simple contrasts revealed that, in both cases, activations in the M condition were significantly higher than in the O condition (left temporal pole: $F_{1,16} = 20.253, P < .001$; right temporal pole: $F_{1,16} = 13.576, P = .002$) and the P condition (left temporal pole: $F_{1,16} = 9.629, P = .007$; right temporal pole: $F_{1,16} = 7.766, P = .013$). A significant main effect for complexity was also seen in the left temporal pole ($F_{2,15} = 12.534, P = .003$). No significant interaction effects were, however, found in either area. So although the pattern of activations seen in the temporal poles, especially in the right hemisphere, appear to be similar to that of the mPFC (Fig. 3), the effect is not strong enough to be significant.⁷

A different picture emerges from the more medial and posterior mPFC cluster (mPFCb; Fig. 3), where the mean PSC plot shows a similar profile for all the 2nd order conditions (M2, P2, and O2) and the M3 condition as distinct from the P3 and the O3 conditions. This is confirmed in the 3×2 analyses, which revealed a main effect for representation type ($F_{2,15} = 5.913, P = .007$) and a main effect for complexity type ($F_{1,16} = 11.64, P = .004$). Simple contrasts revealed that activations in the M condition were significantly higher than in the O condition ($F_{1,16} = 12.614, P = .003$) and the P condition ($F_{1,16} = 6.306, P = .023$). The significant interaction effect of Representation Type \times Complexity ($F_{2,15} = 4.49, P = .019$) was driven by the dissociation between the M and O conditions ($F_{1,16} = 4.449, P = .051$) as well as the M and P conditions as a function of different levels of complexity ($F_{1,16} = 6.476, P = .022$).

The significant findings in this contrast resulted from differences between strong task-induced decreases in BOLD activity in the 3rd order non-intentional conditions. This is a common finding in this cortical region as it is involved in self-generated and self-referential mental activity, and it is among the areas in the brain with the highest baseline metabolic activity at rest, which is postulated to reflect a default mode of brain function (Gusnard, Akbudak, Shulman, & Raichle, 2001). This is also confirmed in the present data by the high levels of activity during the baseline rest condition. So the greater the task demands, the less the activation in this area. As the 2nd order scenarios are easier to understand and take less time to read than the 3rd order scenarios, lower task demands could explain why the signals of the 2nd order conditions are so similar in their pattern. However, this rationale cannot account for the higher signal in the M3 condition which, like the P3 and O3 conditions, was greater in complexity. This is supported by the 3×2 interaction results. We therefore propose that the activation in this region reflects a combination of the default mode of brain function (self-referential thinking) and the processing of higher-order intentional representations, both of which involve processing mental state content.

3.3. fMRI Results (person- vs. object-spatial)

The $P > O$ contrast determined which areas in the brain are activated as a function of the mere presence of persons in the scenario when controlling for the processing of information concerning spatial relations. Significant activations were found in the left and right TPJ, the precuneus and the anterior superior temporal sulcus (aSTS) (Fig. 4 and Table 3). The 3×2 analyses revealed a significant main effect for representation type in the left TPJ ($F_{2,15} = 18.093, P < .0001$), such that activations in the O condition were significantly lower than in the M ($F_{1,16} = 16.327, P = .001$) and the P conditions ($F_{1,16} = 34.228, P < .0001$). This was also true for the aSTS where there was a main effect for representation type ($F_{1,16} = 10.459, P < .0001$) and activations in the O condition were significantly lower than in the M ($F_{1,16} = 6.959, P = .018$) and the P conditions ($F_{1,16} = 25.149, P < .0001$). The precuneus/PCC showed a similar pattern with a main effect for representation type ($F_{2,15} = 32.606, P < .0001$), where activations in the M condition were larger than in the P ($F_{1,16} = 39.189, P < .0001$) and O conditions ($F_{1,16} = 36.446, P < .0001$). But the precuneus/PCC additionally showed a strong trend for larger activations in the M condition relative to the P condition ($F_{1,16} = 4.333, P = .054$). A significant main effect for representation type ($F_{2,15} = 13.2, P < .0001$) and complexity ($F_{1,16} = 13.306, P < .0001$) were found in the right TPJ. The simple contrasts revealed that activations in the P condition were significantly larger than that of the M condition ($F_{1,16} = 11.177, P = .004$) as well as the O condition ($F_{1,16} = 38.173, P < .0001$).

The PSC analyses thus revealed that the left TPJ and the aSTS responded to personhood in general. The right TPJ was specifically involved in scenarios that involved persons in space, whereas the precuneus/PCC not only responded to the presence of persons, but also tended to be recruited even more strongly during mental state reasoning.

4. Discussion

The current findings suggest that, when we read texts about other people, the underlying cerebral substrates for the processing of mental representations differ depending on whether the content is intentional or non-intentional, what kind of person information is present, and the level of relational complexity of the representations. Information processing of scenarios containing any kind of person information activated the aSTS and the left TPJ, whereas representations of persons-in-space selectively activated the right TPJ. The mPFC, the left and right temporal poles and the precuneus/PCC were more

⁷ The higher inter-individual variability associated with activation in the temporal poles may be due to magnetic susceptibility artifacts (from the nearby auditory canal, for instance) that are commonly associated with this area. Such artifacts often lead to MR imaging signal intensity loss or variability (Ojeman et al., 1997). Differences in brain size can especially lead to variability in the BOLD signal in regions near brain cavities.

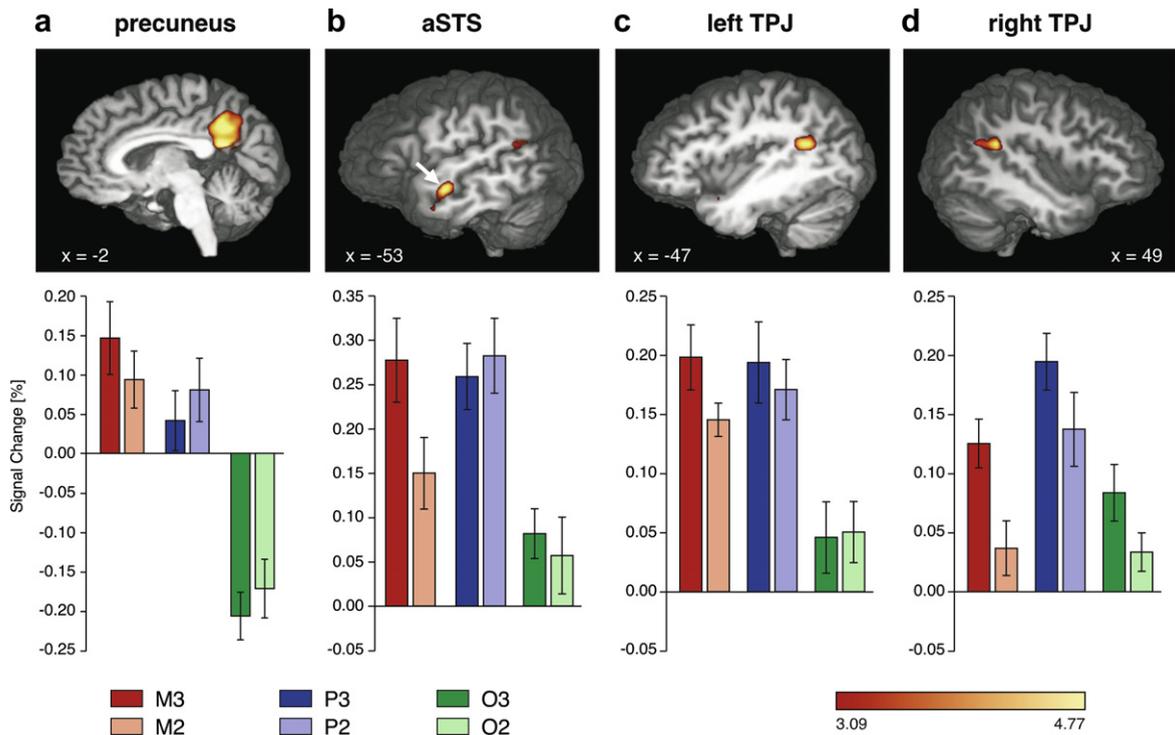


Fig. 4. Processing of person representation ($P > O$): contrast maps and mean PSC plots for regions in the (a) precuneus ($-2, -55, 33$), (b) anterior superior temporal sulcus (aSTS: $-53, -7, -9$), (c) left temporo-parietal junction (left TPJ: $-47 -52 21$), and (d) right temporo-parietal junction (right TPJ: $49 -55 21$). All regions were significantly activated during the selective processing of person information relative to object information. The zero point on the plots reflects the resting baseline.

Table 3

Person processing ($P > O$): anatomical specification, Talairach co-ordinates, maximum Z value and volume (mm^3) of the significantly activated areas

Area	x	y	z	mm^3	Z-max
Temporo-parietal junction (r)	40	-46	21	1566	4.366
Temporo-parietal junction (l)	-41	-52	21	2052	4.267
Precuneus/posterior cingulate	-5	-52	21	9126	4.77
Precuneus/posterior cingulate	-2	-55	33		4.43
Superior temporal sulcus	-53	-7	-9	945	4.237

R, right; l, left.

strongly implicated in mental state reasoning. Significant interactions with respect to relational complexity surfaced for the mPFC and the right TPJ. All of these areas have been regularly implicated in different aspects of social cognition. What is clear from the present study is that these areas are activated even when simply reading information about intentional and non-intentional states, although the subject is not required to make inferences about another person's mental states.

4.1. Mental state reasoning

With regard to the areas implicated when processing the intentional conditions, activation of the temporal poles is generally considered to be reflecting access to social script knowledge in the brain (Frith & Frith, 2003, 2006). The precuneus has been shown to be involved in processes related to episodic memory retrieval, self-processing and visuo-spatial imagery (Cavanna & Trimble, 2006). The role of the dorsal mPFC is, in contrast, a matter of contention. A recent proposal for the function of this area is that it is activated when a task taps components of triadic social relations, which is relevant for mentalizing (Saxe, 2006). Triadic relations refer to the seemingly unique ability of human beings to engage collaboratively in joint attention towards an object or a shared goal (Tomasello, Carpenter, Call, Behne, & Moll, 2005)—You, Me, and an Object (Saxe, 2006). Developing this idea further, it has been suggested that the mPFC activations reflects communicative intent (Frith & Frith, 2006). This is based on findings where the mPFC was found to be selectively involved in processing intentional action within a social interactive context relative to intentional actions of a single person or two persons in a non-socially interactive context (Walter et al., 2004).

The extent to which such ideas can account for the wide range of findings associated with this area is, however, still debatable. The observation that the dorsal mPFC has been reported to be involved in not only processing triadic (Walter et al., 2004; Williams, Waiter, Perra, Perrett, & Whiten, 2005) but also dyadic relations (Kampe, Frith, & Frith, 2003; Schilbach et al., 2006) is in fact an argument against a specific role for this area in triadic interactions (Saxe, 2006), and is instead suggestive of a basic underlying function that is common to both dyadic and triadic relations. Similarly, the communicative intent hypothesis does not account for dorsal mPFC involvement in investigations on mental state knowledge (Mitchell et al., 2005) and self-referential tasks (Mitchell et al., 2006; Ochsner et al., 2005; Zysset et al., 2002), where no explicit communicative intention is implicated. The findings of the present study indicate that the reason the mPFC is involved during such tasks is because these paradigms typically involve taking into consideration information that generally refers to intentional states.

4.2. Processing of person information

The possibility that the mPFC, the temporal poles and the precuneus are merely responsive to the presence of persons in a scenario is ruled out with the present findings. The mPFC and the temporal poles were not activated for the higher-order person-spatial condition (P3) and the precuneus was not only more highly activated in the person-spatial (P) than in the object spatial (O) conditions, but also in the intentional (M) relative to both the person-spatial (P) and object-spatial conditions (O). In contrast, the aSTS, left TPJ and right TPJ were the regions that were significantly activated when representations involved the presence of persons.

The aSTS has been shown to be involved in different facets related to the perception of socially relevant stimuli (Allison, Puce, & McCarthy, 2000). The TPJ is involved in visuo-spatial perspective-taking (Vogeley et al., 2004) and is considered critical for the multisensory coding of the human body and bodily self-processing (Blanke & Arzy, 2005; Blanke, Landis, Spinelli, & Seeck, 2004). In the theory-of-mind literature, there are conflicting views about whether the activity in the TPJ reflects its role in detecting agency (Gallagher & Frith, 2003) or in representing mental states (Saxe, 2006). The present findings suggest that the aSTS and left TPJ are selectively responsive to person-based information, regardless of whether this information is intentional or non-intentional in nature (responsive to both M and P conditions), whereas the right TPJ is selective in being responsive to persons in space (responsive in P conditions only).

The finding in the case of the right TPJ activation for persons in space is especially noteworthy because the right TPJ and the extrastriate body area (EBA) have been found to be crucial for the sense of embodiment, or the feeling of being located within one's physical body (Arzy, Seeck, Ortigue, Spinelli, & Blanke, 2006a; Arzy, Thut, Mohr, Michel, & Blanke, 2006b; Blanke & Arzy, 2005). The right TPJ in particular coded for disembodied (extracorporeal) mental self location, i.e., when imagining oneself occupying a different space from the body's actual location (Arzy et al., 2006b). These findings on the sense of self-embodiment together with those of the present study on the representation of spatial relations between persons, are indicative of the role of the right TPJ for more abstract representations that could stem from the foundational capacity in representing spatial transformations of the body away from the embodied space.

4.3. Relational complexity

The findings also pointed to an intriguing interplay between the factors of relational complexity and representation type in different brain regions. The right TPJ, in addition to being activated in the P conditions, was more responsive to highly relationally complex stimuli regardless of the representation type. The more caudal mPFC area (mPFCb), on the other hand, showed the opposite effect and was more generally responsive to less complex stimuli of all representation types in addition to being selectively activated in the M3 condition. The more anterior mPFC area (mPFCa), was also more responsive to less complex stimuli, but only in the case of the person-spatial (P2) stimuli. The mean percent signal change here for the lower complexity spatial condition (P2) was akin to that of the intentional conditions, whereas that of the higher complexity spatial condition (P3) was similar to that of the object-spatial conditions.

We propose that this latter pattern of findings in the mPFC could reflect the possibility that even when a scenario does not involve the representation of mental states, the sheer presence of persons may involuntarily elicit internally generated mental state content processing provided the situational elements allow for it.⁸ The higher complexity spatial condition (P3) had extremely high spatial processing demands (example in Fig. 1). The behavioral results (low response accuracy) as well as feedback from the participants indicated that this was a very difficult condition. This is not very surprising because, unlike the case of imagining configurations of objects in space, we are not as accustomed to envisioning and having to grasp such configurations of persons in space. So, within the context of the current task, the potentially socially relevant person connotations may have been disregarded as the entire focus is absorbed by the tough spatial task demands and the entities in question are perhaps conceived of in a similar manner as objects in space.

⁸ Accessing social script knowledge, which is held to be subserved by the temporal poles, is also likely to be necessary in processing potentially social situations even when no explicit intentional understanding is required, such as in the P2 condition. Indeed, the pattern of activation across conditions in the temporal poles seen in Fig. 3, although non-significant, indicate a tendency in the predicted direction. Please refer to footnote 6 for more information on the temporal pole findings.

The scenario in the P2 condition is, however, easier to process and integrate and indeed, very often this spatial relation is an indicator of more complex underlying socially relevant information. The person one sits next to in a theatre or in a classroom is very likely to be someone one knows and interacts with. Dyadic relations, or interactions between two persons, in fact, allow for the most concrete level of social interaction, and experience with dyadic interactions begin very early on in life starting with the parent–child dyad. Alternatively, it may be the case that the use of proper names (e.g., Nina sits next to Paul) are inherent cues of social relevance because first names are usually only known when one is familiar with a person.

These latter proposals are admittedly speculative, but they offer an initial framework from which to understand these dissociations between the P2 and P3 conditions. The possibility that the mention of person information inadvertently evokes mental state processing, depending on the situation at hand, may not be that far-fetched, as we are complex social beings that are inherently geared towards the rapid detection of cues, be it subtle or unmistakable, that reflect the dynamics of potentially relevant intentional information. This could explain why some studies have shown mPFC activity as a response to mental state representations as well as to representations that do not involve explicitly represented mental states, but contain information that hint at the implicit intentions of the protagonists or are rife with other socially relevant information (Perner et al., 2006; Saxe & Kanwisher, 2003; Saxe & Powell, 2006).

4.4. Conflicting findings in the literature

Saxe and Powell (2006) have reported findings that could be interpreted as having the reverse pattern as ours. They found that the mPFC showed an undifferentiated response to stories about appearances, bodily sensations and thoughts of people, whereas the left and right TPJ had a very strong response only for the thoughts-condition. We put forward two proposals to account for the discrepancy between the two studies. It should be noted, however, that both studies employ very different experimental designs and stimuli.

Two of the three conditions in the Saxe and Powell (2006) paper explicitly refer to mental states: Bodily sensations (phenomenal mental states) and Thoughts (intentional mental states), and the third condition included highly socially relevant evaluative information (Appearances). In fact, the authors even state in their paper that they contrast attribution of representational mental states (thoughts) with that of early developing reasoning about socially relevant information more broadly (including physical appearance). The undifferentiated response of the mPFC in all three conditions in the Saxe and Powell study is thus not unexpected in light of the mPFC findings in the present study.

Saxe and Powell (2006) also report a strong response in the TPJ for the thoughts-condition relative to the other conditions. A closer look at the stimuli they use reveals that the degree of relational complexity within the stimuli used in the thoughts-condition is considerably higher than in the other conditions.⁹ So a higher response of the TPJ in the thoughts-condition could be aligned with our own findings, which indicated a stronger response in the right TPJ for representations with a higher degree of relational complexity, regardless of the type of representation.

On a related note, our findings on the effect of complexity and representation type in the right TPJ and the mPFC may also go some way in accounting for why different paradigms and types of methods with varying levels of stimulus complexity lead to conflicting conclusions about the function of these different brain structures in mentalizing tasks, especially when compared to person-based control tasks. Many studies have used non-verbal stimuli, such as static cartoons and animations of interacting shapes, to study mental state reasoning. One shortcoming of using such stimuli is that it is difficult to put any tabs on the range of thoughts that is going through a person's mind when making sense of such stimuli. Other studies have used stories, which provide a more circumscribed scenario based on which the subjects have to make inferences.

We took this a step further by stripping down the stimuli employed to a single sentence level. While this kind of stimuli is admittedly quite unnatural, what it allows as a substantial benefit is better technical control over the stimuli. Instead of only controlling for variables, such as reading time or the numbers of words per story, which only deal with the superficial comparability of the conditions, we are able to better control for facets that seem to have a significant effect of the stimuli, such as the number of protagonists and the approximate comparability of the structural complexity of the representations across conditions. The use of such stimuli could help unravel finer details regarding the more specific roles of the network of areas commonly implicated in studies on mental state reasoning. This study provides a first step in this direction.

5. Conclusions

In all, the findings suggest that the wide range of neural areas implicated in mental state reasoning have distinct and selective roles, which are differentially modulated by the factors relating to intentionality, personhood and relational complexity of the representations. Clear patterns emerged in the case of the aSTS, the left TPJ, and the right TPJ. The former two were responsive to personhood in general, while the right TPJ was selectively activated for representations of persons in

⁹ The stimuli used in the thoughts-condition were more relationally complex than that of the appearances- and bodily sensations-conditions as they crucially involved a triangle of intertwined relations: An intentional relation T between a person A and the intentional object C is established only after C has been identified, relative to A , via another object B by a chain of intertwined relations R_1 and R_2 of, e.g. kinship or possession. To process the task properly, the subject has to represent the relational triangle $R_1(A, B)$ & $R_2(B, C)$ & $T(A, C)$. This pattern of intertwined relations is, to some extent, similar to the pattern of relations within some of the stimuli in our study. In the appearances- and bodily sensations-conditions, in contrast, the stimuli contained either no relations at all or, at least, no intertwined relations.

space. The temporal poles were primarily responsive to intentional representations. The precuneus/PCC was activated most strongly in relation to intentional representations and less strongly for representations of persons in space, and was activated more strongly for both of these relative to representations of objects in space. One region in the mPFC was responsive to intentional representations, but also to less complex person-spatial representations. This led to the discussion of whether this area, even in the absence of explicit mental state representations to process, is geared towards dealing with mental state content attributions that, under certain conditions, are internally generated when faced with socially relevant information. Finally, the right TPJ and a second region in the mPFC were significantly related to complexity with more complex stimuli generally activating the former area, and less complex stimuli activating the latter area.

Acknowledgments

We thank Andrea Gast-Sandmann for her assistance with the figures, Stefan Zysset for his advice concerning the fMRI data preprocessing, and Albert Ortmann for his help with determining the syntactic complexity of the stimuli.

References

- Allison, T., Puce, A., & McCarthy, G. (2000). The precuneus: Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267–278.
- Apperly, I. A., Samson, D., & Humphreys, G. W. (2005). Domain-specificity and theory of mind: Evaluating neuropsychological evidence. *Trends in Cognitive Sciences*, 9(12), 572–577.
- Arzy, S., Seeck, M., Ortigue, S., Spinelli, L., & Blanke, O. (2006a). Induction of an illusory shadow person. *Nature*, 443(7109), 287.
- Arzy, S., Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006b). Neural basis of embodiment: Distinct contributions of temporoparietal junction and extrastriate body area. *Journal of Neuroscience*, 26(31), 8074–8081.
- Blanke, O., & Arzy, S. (2005). The out-of-body experience: Disturbed self-processing at the temporo-parietal junction. *Neuroscientist*, 11(1), 16–24.
- Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscopia of neurological origin. *Brain*, 127(Pt 2), 243–258.
- Brentano, F. (1973). *Psychology from an empirical standpoint*. London: Routledge and Kegan Paul.
- Brunet, E., Sarfati, Y., Hardy-Bayle, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage*, 11(2), 157–166.
- Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage*, 12(3), 314–325.
- Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, 129(Pt 3), 564–583.
- Clapin, H. (2002). *Philosophy of mental representation*. Oxford: Clarendon Press.
- Dennett, D., & Haugeland, J. (1987). Intentionality. In R. L. Gregory (Ed.), *The Oxford companion to the mind* (pp. 161–164). New York: Oxford University Press.
- Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S., et al (1995). Other minds in the brain: A functional imaging study of “theory of mind” in story comprehension. *Cognition*, 57(2), 109–128.
- Forman, S., Cohen, J., Fitzgerald, M., Eddy, W., Mintun, M., & Noll, D. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance in Medicine*, 33(5), 636–647.
- Friston, K., Holmes, A., Worsley, K., Poline, J., Frith, C., & Frackowiak, R. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189–210.
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society London. Series B: Biological Sciences*, 358(1431), 459–473.
- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, 50(4), 531–534.
- Frith, U., Morton, J., & Leslie, A. M. (1991). The cognitive basis of a biological disorder: Autism. *Trends in Neuroscience*, 14(10), 433–438.
- Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of ‘theory of mind’. *Trends in Cognitive Sciences*, 7(2), 77–83.
- 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(1), 11–21.
- Gallagher, H. L., Jack, A. I., Roepstorff, A., & Frith, C. D. (2002). Imaging the intentional stance in a competitive game. *Neuroimage*, 16(3 Pt 1), 814–821.
- German, T. P., Niehaus, J. L., Roarty, M. P., Giesbrecht, B., & Miller, M. B. (2004). Neural correlates of detecting pretense: Automatic engagement of the intentional stance under covert conditions. *Journal of Cognitive Neuroscience*, 16(10), 1805–1817.
- Grezes, J., Frith, C. D., & Passingham, R. E. (2004). Inferring false beliefs from the actions of oneself and others: An fMRI study. *Neuroimage*, 21(2), 744–750.
- Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98(7), 4259–4264.
- Halford, G. S., Wilson, W. H., & Phillips, S. (1998). Processing capacity defined by relational complexity: Implications for comparative, developmental, and cognitive psychology. *Behavioral and Brain Sciences*, 21(6), 803–831 [discussion 831–864].
- Kampe, K. K., Frith, C. D., & Frith, U. (2003). “Hey John: Signals conveying communicative intention toward the self activate brain regions associated with “mentalizing,” regardless of modality. *Journal of Neuroscience*, 23(12), 5258–5263.
- Kumaran, D., & Maguire, E. A. (2005). The human hippocampus: Cognitive maps or relational memory? *Journal of Neuroscience*, 25(31), 7254–7259.
- Lohmann, G., Muller, K., Bosch, V., Mentzel, H., Hessler, S., Chen, L., et al (2001). LIPSI: A new software system for the evaluation of functional magnetic resonance images of the human brain. *Computerized Medical Imaging and Graphics*, 25(6), 449–457.
- Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005). General and specific contributions of the medial prefrontal cortex to knowledge about mental states. *Neuroimage*, 28(4), 757–762.
- Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron*, 50(4), 655–663.
- Norris, D. G. (2000). Reduced power multislice MDEFT imaging. *Journal of Magnetic Resonance Imaging*, 11(4), 445–451.
- Ochsner, K. N., Beer, J. S., Robertson, E. R., Cooper, J. C., Gabrieli, J. D., Kihlstrom, J. F., et al (2005). The neural correlates of direct and reflected self-knowledge. *Neuroimage*, 28(4), 797–814.
- Ojeman, J. G., Akbudak, E., Snyder, A. Z., McKinstry, R. C., Raichle, M. E., & Conturo, T. E. (1997). Anatomic localization and quantitative analysis of gradient refocused echo-planar fMRI susceptibility artifacts. *Neuroimage*, 6(3), 156–167.
- Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience*, 16(10), 1706–1716.
- Perner, J., Aichhorn, M., Kronbichler, M., Staffen, W., & Ladurner, G. (2006). Thinking of mental and other representations: The roles of left and right temporo-parietal junction. *Social Neuroscience*, 1(3 & 4), 245–258.
- Perry, J. (1994). Intentionality. In S. Guttenplan (Ed.), *A companion volume to the philosophy of mind* (pp. 386–395). Oxford: Blackwell.
- Premack, D., & Woodruff, G. (1978). Chimpanzee problem-solving: A test for comprehension. *Science*, 202(4367), 532–535.
- Saxe, R. (2006). Uniquely human social cognition. *Current Opinion in Neurobiology*, 16(2), 235–239.

- Saxe, R., Carey, S., & Kanwisher, N. (2004). Understanding other minds: Linking developmental psychology and functional neuroimaging. *Annual Review of Psychology*, 55, 87–124.
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in “theory of mind. *Neuroimage*, 19(4), 1835–1842.
- Saxe, R., & Powell, L. J. (2006). It’s the thought that counts: Specific brain regions for one component of theory of mind. *Psychological Science*, 17(8), 692–699.
- Schilbach, L., Wohlschlaeger, A. M., Kraemer, N. C., Newen, A., Shah, N. J., Fink, G. R., et al (2006). Being with virtual others: Neural correlates of social interaction. *Neuropsychologia*, 44(5), 718–730.
- Schultz, J., Friston, K. J., O’Doherty, J., Wolpert, D. M., & Frith, C. D. (2005). Activation in posterior superior temporal sulcus parallels parameter inducing the percept of animacy. *Neuron*, 45(4), 625–635.
- Spiers, H. J., & Maguire, E. A. (2006). Spontaneous mentalizing during an interactive real world task: An fMRI study. *Neuropsychologia*, 44(10), 1674–1682.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Thirion, J. P. (1998). Image matching as a diffusion process: An analogy with Maxwell’s demons. *Medical Image Analysis*, 2(3), 243–260.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, 28(5), 675–691 [discussion 691–735].
- Ugurbil, K., Garwood, M., Ellermann, J., Hendrich, K., Hinke, R., Hu, X., et al (1993). Imaging at high magnetic fields: Initial experiences at 4 T. *Magnetic Resonance Quarterly*, 9(4), 259–277.
- Vogeley, K., May, M., Ritzl, A., Falkai, P., Zilles, K., & Fink, G. R. (2004). Neural correlates of first-person perspective as one constituent of human self-consciousness. *Journal of Cognitive Neuroscience*, 16(5), 817–827.
- 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. *Journal of Cognitive Neuroscience*, 16(10), 1854–1863.
- Williams, J. H., Waiter, G. D., Perra, O., Perrett, D. I., & Whiten, A. (2005). An fMRI study of joint attention experience. *Neuroimage*, 25(1), 133–140.
- Worsley, K. J., & Friston, K. J. (1995). Analysis of fMRI time-series revisited-again. *Neuroimage*, 2(3), 173–181.
- Zysset, S., Huber, O., Ferstl, E., & von Cramon, D. Y. (2002). The anterior frontomedian cortex and evaluative judgment: An fMRI study. *Neuroimage*, 15(4), 983–991.