

The Role of the Right Temporoparietal Junction in Social Interaction: How Low-Level Computational Processes Contribute to Meta-Cognition

JEAN DECETY and CLAUS LAMM

Departments of Psychology and Psychiatry, and Center for Cognitive and Social Neuroscience,
The University of Chicago, Chicago, IL

Accumulating evidence from cognitive neuroscience indicates that the right inferior parietal cortex, at the junction with the posterior temporal cortex, plays a critical role in various aspects of social cognition such as theory of mind and empathy. With a quantitative meta-analysis of 70 functional neuroimaging studies, the authors demonstrate that this area is also engaged in lower-level (bottom-up) computational processes associated with the sense of agency and reorienting attention to salient stimuli. It is argued that this domain-general computational mechanism is crucial for higher level social cognitive processing. *NEUROSCIENTIST* 13(6): 580–593, 2007. DOI: 10.1177/1073858407304654

KEY WORDS *Temporoparietal junction, Self/other distinction, Agency, Social cognition, Theory of mind, Empathy, Attention*

Accumulating evidence from neuroimaging studies, as well as lesion studies in neurological patients, indicates that the right inferior parietal cortex at the junction with the posterior temporal cortex plays a critical role in comparing signals arising from self-produced actions with signals from the environment (Blakemore and Frith 2003; Jackson and Decety 2004). Interestingly, it appears that this computational mechanism is also crucial for the higher-level cognitive processing involved in social cognitions such as empathy and theory of mind. Both empathy and theory of mind involve an ability to simultaneously distinguish between different possible perspectives on the same situation (Decety and Jackson 2004; Decety and Lamm 2006). A large body of evidence, mainly from functional neuroimaging studies, indicates that the neurobiological underpinnings of these abilities depend upon the coordinated interaction between the brain regions involved in the processing of social cues, particularly the medial prefrontal cortex and the posterior temporal gyrus at the junction with the parietal cortex. Because of its anatomical location, that latter region was termed the temporoparietal junction (TPJ).

An important question is whether the function of the TPJ can be associated with computation useful to mental function. This issue is also relevant to the theoretical debate of whether social cognition is domain specific or domain general (Stone and Gerrans 2006). The former viewpoint posits that social cognition (e.g., mental state attribution) is instantiated in specific dedicated modules underpinned by distinct neural regions or networks. The alternative view assumes that social cognition has gradually arisen from general pervasive perception-action coupling mechanisms (a view dubbed *motor cognition*; Jackson and Decety 2004; Sommerville and Decety 2006).

The TPJ is a region encompassing the supramarginal gyrus, caudal parts of the superior temporal gyrus, and dorsal-rostral parts of the occipital gyri. The TPJ is a heteromodal association cortex, which integrates input from the lateral and posterior thalamus, as well as visual, auditory, somesthetic, and limbic areas. It has reciprocal connections to the prefrontal cortex and to the temporal lobes. Because of these anatomical characteristics, this region is a pivotal neural locus for self-processing that is involved in multisensory body-related information processing, as well as in the processing of phenomenological and cognitive aspects of the self (Blanke and Arzy 2005). Damage of this cortical area can produce a variety of disorders associated with body knowledge and self-awareness, such as anosognosia (i.e., denial of illness), asomatognosia (i.e., lack of awareness of the condition of all or parts of one's own body), or somatoparaphrenia (i.e., delusional beliefs about the body; Berlucchi and Aglioti 1997). For instance, Blanke and colleagues (2002) demonstrated that out-of-body experiences (i.e., the experience that oneself is located outside of

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Address correspondence to: Jean Decety, Social Cognitive Neuroscience, Departments of Psychology and Psychiatry, The University of Chicago, 5848 S University Avenue, Chicago, IL 60637 (e-mail: decety@uchicago.edu).

one's own body) can be induced by electrical stimulation of the TPJ in neurological patients.

Furthermore, evidence from functional neuroimaging studies indicates that the TPJ is systematically associated with a variety of social cognitive tasks such as perspective-taking (e.g., Ruby and Decety 2003), empathy (e.g., Jackson and others 2006; Lamm and others 2007), and theory of mind (e.g., Lawrence and others 2006; Saxe and Wexler 2005). This led to the speculation that the right TPJ is specialized for the possibly uniquely human ability to reason about others' affective and cognitive mental states (Saxe 2006).

However, it is important to note that the right TPJ is activated not only during higher-level social-cognitive processes but also when individuals must distinguish themselves from others (Decety and Sommerville 2003). Indeed, a handful of studies on the sense of agency, that is, the feeling of being the cause of one's own actions, desires, or thoughts, which relies on the comparison between self-generated and externally produced sensory signals, have consistently resulted in activation of the right TPJ (e.g., Ruby and Decety 2001; Farrer and Frith 2002; Farrer and others 2003). In support of this function and of particular interest, a recent study demonstrated selective impairment of self-other distinction when repetitive transcranial magnetic stimulation was applied over the right inferior parietal lobule as participants performed a perceptual task involving discrimination between self-faces and other familiar faces (Uddin and others 2006). These results provide direct evidence for a causal role for this region in self-other discrimination.

In addition, the TPJ region is also activated by the violations in expectation about external physical events—such as the presentation of visual stimuli in a noncued screen location (Corbetta and Shulman 2002). Similarly, the multimodal detection of sensory changes in the environment leads to stronger TPJ involvement (e.g., Downar and others 2000). However, the same region has also been shown to contribute to directing attention to salient events and enabling a variety of responses to those events (Astafiev and others 2006). Thus, the requirement to compare internal predictions with actual external events might be an alternative interpretation for right TPJ involvement during social cognition.

The goal of this article is to propose a more parsimonious account of the role of TPJ in social cognition that can elucidate how this region may implement a single computational mechanism subserving multiple aspects of cognition. We argue that high-level meta-cognitive processing such as theory of mind or empathy depends at least in part on low-level computational processes involved in the prediction of external events. This view is radically different from the notion that the TPJ plays a specific role in social cognition in general and in theory of mind in particular. It is, however, consistent with the view that social cognition relies on both domain-specific abilities and domain-general abilities (Decety and Grèzes 2006).

To this end, we computed function/location meta-analyses (Fox and others 1998) of the available neuroimaging

studies on agency, empathy, and theory of mind, on one hand, and the reorienting of attention, on the other hand.

Our results demonstrate a substantial overlap in brain activation between low-level processing such as reorienting of attention or the sense of agency and higher-level social-cognitive abilities such as empathy or theory of mind. These results provide strong empirical support for a domain-general mechanism implemented in the TPJ.

Materials and Methods

Literature Search and Coordinates Selection

We used a step-wise procedure to identify the relevant experimental papers to compute four independent function/location meta-analyses of agency, empathy, reorienting of attention, and theory of mind. As a first step, we performed four searches (on December 19, 2006) of the PubMed database (<http://www.pubmed.gov>) using the search terms ["magnetic resonance imaging"[MeSH Terms] OR Fmri[Text Word] OR PET[All Fields] OR "positron emission tomography"[All Fields]], combined with [(Theory AND Mind) OR mentalizing], [agency], [empathy], or [attention].

Second, we used the "related articles" function of the PubMed database to identify additional papers. Third, we manually searched tables of contents and advance publication papers (Epub ahead of print) of two recently appeared new journals that are not listed in PubMed yet (*Social Neuroscience*, Psychology Press; *Social, Cognitive and Affective Neuroscience*, Oxford University Press), as well as the advance publication lists of journals publishing functional neuroimaging studies. Out of the resulting list of papers, we identified the relevant hits and searched for activations in and around rTPJ (see appendix for a complete list of selected publications and coordinates).

A paper was classified to study empathy if participants were engaged in a task involving some sort of affective sharing with another person. This definition does not include empathy for sensations, such as touch. Theory of mind or mentalizing studies were defined as reasoning about beliefs, intentions, or thoughts. If the experimental manipulations made participants either explicitly or implicitly think about the ownership of their own or another's actions, a study was considered to be on agency. As for attention reorienting and change detection, we included paradigms requiring participants to reorient their attention to a cue in a noncued location or to detect and reorient to unexpected changes in the external sensory environment.

As unequivocal structural markers or boundaries cannot define the TPJ, we included activations that were localized in the posterior parts of the superior temporal sulcus (STS) and in the inferior parietal lobe/angular gyrus. If activation was reported to be located in or around the right TPJ, we included it also, after verifying whether this labeling was in line with our own definition of rTPJ. This led to the exclusion of one activation cluster that we considered as too ventral (Downar and others 2002; Talairach and Tournoux coordinates $x/y/z = 55/-53/4$).

Table 1. Coordinates (Talairach and Tournoux 1988) of Weighted Centers and Peaks of Clusters Derived from the Four ALE Analyses

	Weighted Center			Peak			Peak Value
	x	y	z	x	y	z	
Attention	54	-46	23	52	-50	28	0.05
Empathy	51	-55	20	50	-56	20	0.018
Theory of mind	50	-53	21	54	-52	18	0.037
Difference map							
Theory of mind > Attention	48	-57	22	52	-52	18	0.022
Attention > Theory of mind	55	-43	26	52	-48	28	0.036

We then extracted the reported stereotactic coordinates (x/y/z) and, if necessary, converted them from the Montreal Neurological Institute space to the Talairach and Tournoux (TAL) space using the transformation proposed by Brett (1999). If the analysis space could not be clearly determined, we contacted the authors of the paper for clarification. We also contacted the authors if activation in rTPJ was reported or suspected but no coordinates were provided.

Meta-analysis

Analysis of activation peaks was performed using activation likelihood estimation (ALE; Laird, Fox, and others 2005; Laird, Lancaster, and others 2005). Analyses were implemented in version 3.2.1 of the Search&View program developed by the Research Imaging Center at the University of Texas, San Antonio (<http://brainmap.org>). ALE performs quantitative function/location meta-analyses by using activation peaks in a stereotactic space as the input data. These peaks are modeled using a 3-D Gaussian distribution with a user-specified kernel width (full-width-at-half-maximum, FWHM) and pooled across studies to generate an estimate of the likelihood of activation at each individual voxel. To assess the statistical significance of the resulting map, nonparametric permutation testing is used to test the null hypothesis that the activation foci are spread randomly (uniformly) throughout the acquired brain volume. The resulting *P* value map is corrected for multiple comparisons by controlling the false discovery rate (FDR; Benjamini and Hochberg 1995; Genovese and others 2002).

For the current analysis, separate meta-analyses were computed for the four target conditions, with an FWHM of 10 mm, 5000 permutation tests, and an FDR threshold of $q = 0.05$. In addition to those analyses that localized activation for each condition separately, differences in activation between theory of mind and attention reorienting were computed using difference maps (Laird, Fox, and others 2005). The resulting thresholded ALE maps were visualized on a flat-map representation of a standardized brain atlas (PALS-B12 human atlas) using Caret, version 5.5 (<http://brainmap.wustl.edu/caret.html>; Van Essen and others 2001; Van Essen 2002).

Results

The appendix lists the studies and coordinates that were included in the meta-analyses. The literature searches yielded 18 studies with 29 coordinates on attention reorienting, 15 studies with 18 coordinates on agency, 13 studies with 13 coordinates on empathy, and 24 studies with 28 coordinates on theory of mind.

Figure 1 illustrates that the four different conditions led to highly similar and overlapping ALE clusters in the right TPJ. Table 1 displays the coordinates of the weighted center and the peak of the activation cluster with the highest activation—showing that the centers of activation of the four conditions are located in closely together. Figure 2 provides a color-coded map of activation overlaps related to attention reorienting, empathy, and theory of mind. The white area centered over the TPJ delineates the area where all three conditions show significant activation, demonstrating a considerable overlap for the three different conditions. Note, however, that there are also activation differences between the four conditions. In particular, attention reorienting and agency seem to show activation centers that are slightly more dorsal than the ones of theory of mind and empathy. Table 1 contains the results of the quantitative comparison between theory of mind and attention. Figure 3 illustrates that these two conditions show slightly differing activations along a dorso-ventral axis, with the activation maxima being located on opposing sides of the angular gyrus. Reorienting attention extends into posterior STS, whereas theory of mind expands more into the posterior direction. Note that we chose to compare only these two conditions directly because a comparable number of foci were available for them. Computing difference maps between all social-cognitive conditions and reorienting might have resulted in biased results due to the large difference in the number of available activation foci.

Discussion

The goal of this study was motivated by the intriguing observation of similar activation sites in the TPJ area across several seemingly distinct domains including theory of mind, empathy, the sense of agency, and attention orientation.

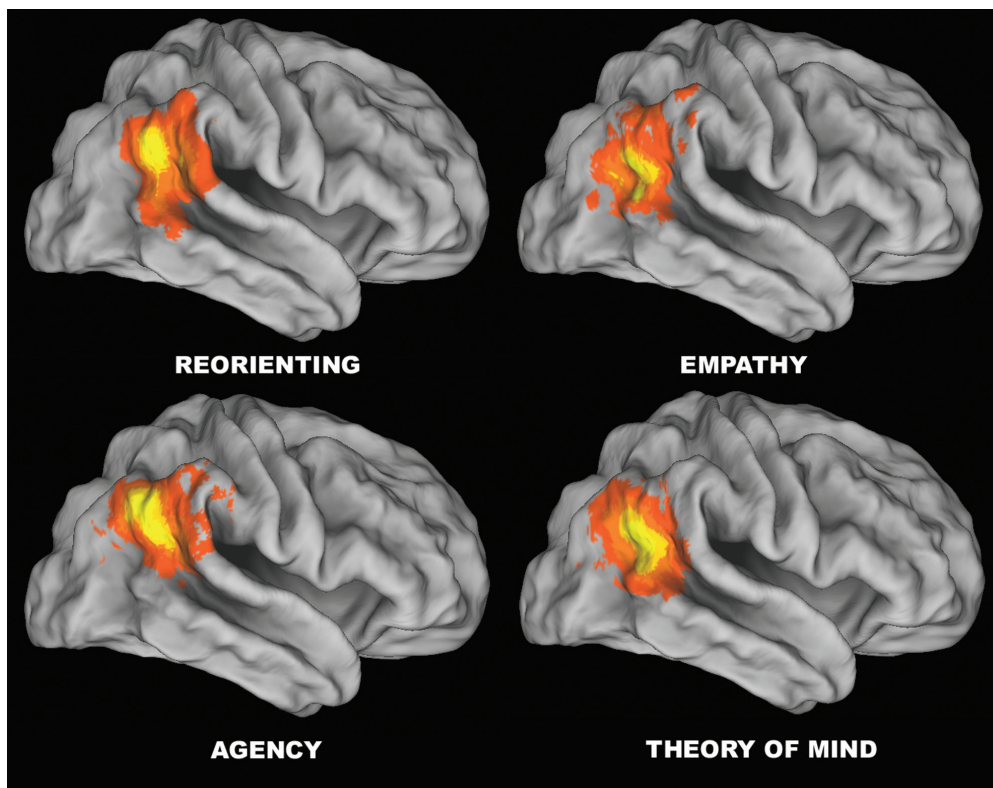


Fig. 1. Activation likelihood estimation maps (ALE) in the right temporoparietal junction projected on a partially inflated lateral view of the PALS-B12 brain atlas. The yellow to orange colors code the probability of activation, with brighter yellow indicating higher activation probability. Note that the activation peaks are localized very closely, whereas the extent of activation is slightly different across the four conditions.

The results from quantitative meta-analyses show a substantial overlap of activation clusters in the right TPJ during both high- and low-level cognitive processes. The most parsimonious interpretation of this overlap would suggest that activation in the TPJ during social cognition may therefore rely on a lower-level computational mechanism involved in generating, testing, and correcting internal predictions about external sensory events. Such an interpretation is consistent with an evolutionary view that higher levels operate on previous levels of organization and should not be seen as independent of, or conflicting with, one another. Evolution has constructed layers of increasing complexity, from nonrepresentational to representational and meta-representational mechanisms, which need to be taken into account for a full understanding of human social cognition.

Meta-analyses are becoming more and more popular in the neuroimaging community, reflecting the need to advance from subjective and qualitative reviews of the literature to quantified measures of activation. Notably, such analyses do not replace or overrule available experimental evidence. Rather, they are experiments in themselves, attempting to integrate and synthesize available “scattered evidence.” The analyses performed for this study are in line with the general heuristic of the meta-analytic approach. This heuristic consists of a dialectic

loop that proceeds from meta-analyzing published or available data to generating new or revising old hypotheses, which are then challenged in new experimental studies. The results clearly support our hypothesis that the TPJ implements a component that is not domain-specific in social cognition but is rather a more general and powerful computational process that operates in many other contexts besides theory of mind.

Nonetheless, some limitations of our study do need to be acknowledged. The analysis approach chosen in this article has several shortcomings that partially apply to all meta-analyses. Sample sizes and effects sizes show considerable variability that is not taken into account explicitly by the ALE approach. Additional imprecision is introduced by differences in scanning resolution and signal-to-noise ratio of the chosen neuroimaging methods and by the lack of a standardized analysis approach for statistical parametric mapping. Differences in voxel resolution, the amount of spatial smoothing, or the chosen statistical threshold certainly add some uncontrollable noise to the meta-analyses and will particularly affect their spatial resolution. In addition, the common reporting standard in the neuroimaging literature is to publish only peak coordinates, resulting in a potential mischaracterization of the actual activation profile of the individual studies. Furthermore, not all sampled papers—irrespective of which condition was

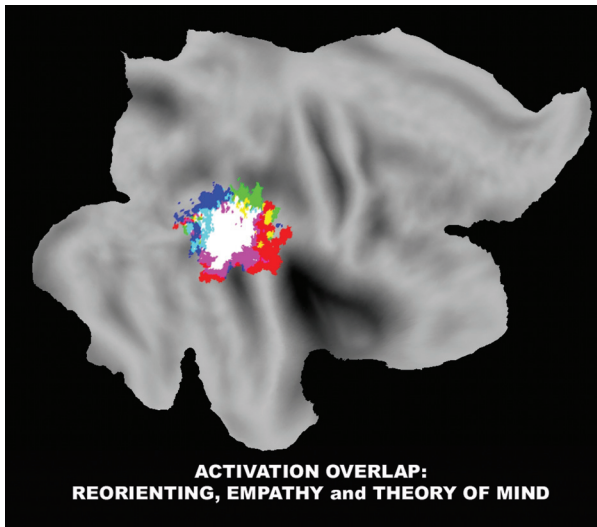


Fig. 2. Overlap of activation between reorienting, empathy, and theory of mind, projected on a flat-map rendering of the PALS-B12 brain atlas. The centered white area indicates the considerable activation overlap between all three conditions. Red = area exclusively activated by reorienting; blue = area exclusively activated by theory of mind; green = area exclusively activated by empathy; purple = overlap between reorienting and theory of mind; yellow = overlap between reorienting and empathy; turquoise = overlap between theory of mind and empathy.

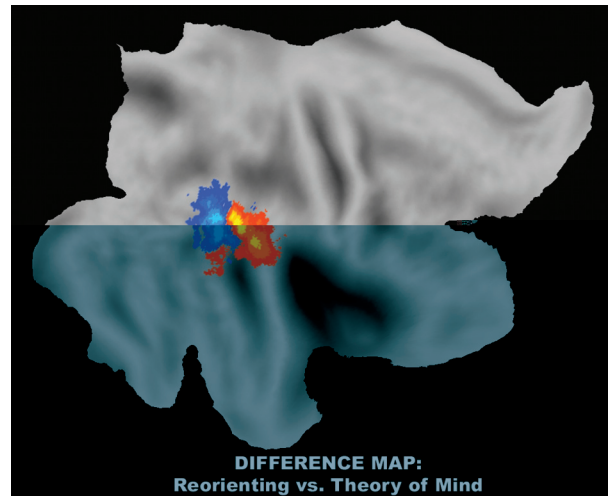


Fig. 3. Activation difference between reorienting and theory of mind. Areas where reorienting led to higher activation probabilities are coded in orange to yellow, whereas areas with higher activation during theory of mind are displayed in light to dark blue. Note that this figure shows graded activation differences—that is, regions in which activation probability was higher during either of the two conditions. The indicated area might nevertheless be activated by both conditions (see Fig. 2).

analyzed—actually reported rTPJ activation. This might be due to a number of reasons, including too high thresholds or the omission of activation reports due to a different focus of the article.

On top of these specific and inherent shortcomings, neuroimaging research suffers from a lack of knowledge about which amount of spatial separation between two clusters justifies the conclusion that they indeed reflect different neural activations. This issue is particularly prevalent in the difference maps for theory of mind and attention. Although these two conditions are statistically separated in image/voxel space, knowledge of brain anatomy suggests that the obtained clusters are in reality very closely located (i.e., on either side of angular gyrus), making it hard to determine whether or not they reflect activation of separate neural networks. This difficulty is complicated further in structure-to-function inferences, in that one of the aims of neuroimaging is to allow conclusions about the functional-cognitive processes involved in the tasks studied (see Henson 2005; Coltheart 2006).

Despite all these shortcomings and caveats, our data provide strong evidence for a high degree of activation overlap in and around the rTPJ region for low-level and high-level cognitive functions. The question therefore is which cognitive processes are implemented in this

area and how they support functions as different as the reorienting of attention and the attribution of agency.

Future research should aim at investigating several experimental designs (spanning from low-level attention reorienting to metacognition) in the same participants. We recommend utilizing tailored high spatial-resolution scanning of the rTPJ to test the hypothesis that reorienting of attention and the detection and processing of uncertainty does significantly contribute to higher-level processes such as theory of mind or empathy. Another challenging aspect, which is certainly more difficult to address than running a new study, yet extremely important, deals with the current conceptualization of mental operations in social neuroscience. Most if not all of the concepts used in social cognition emanate from our folk psychology; we are prisoners of words. Theory of mind, perspective-taking, empathy—these are all complex psychological constructs that cannot be directly mapped to unique single computational mechanisms, and the functions that they attempt to describe are underpinned by a network of areas. By developing a parsimonious account of exactly how and where complex cognitions are instantiated in the brain, we hope to create a clearer understanding of our very concepts themselves. This is certainly one challenging theoretical aspect that social cognition will have to resolve.

APPENDIX
Studies and Coordinates Used for the Meta-Analyses

Study	Condition	Number of Activations	Imaging Method	TALx	TALy	TALz	Original Space
Astafiev SV, Shulman GL, Corbetta M. 2006. Visuospatial reorienting signals in the human temporo-parietal junction are independent of response selection. <i>Eur J Neurosci</i> 23:591–96.	Attention	1	fMRI	51	-51	26	TAL
Baron-Cohen S, Ring HA, Wheelwright S, Bullmore ET, Brammer MJ, Simmons, A, Williams SCR. 1999. Social intelligence in the normal and autistic brain: an fMRI study. <i>Eur J Neurosci</i> 11:1891–8.	ToM	1	fMRI	40	-58	20	TAL
Botvinick M, Jha AP, Blytsma LM, Fabian SA, Solomon PE, Prkachin KM. 2005. Viewing facial expression of pain engages cortical areas involved in the direct experience of pain. <i>NeuroImage</i> 25:312–9.	Empathy	1	fMRI	68	-40	16	TAL
Braver TS, Barch DM, Gray JR, Molfese DL, Snyder A. 2001. Anterior cingulate cortex response conflict: effects of frequency, inhibition and errors. <i>Cereb Cortex</i> 11:825–36.	Attention	1	fMRI	56	-48	24	TAL
Brunet E, Sarfati Y, Hardy-Bayle MC, Decety J. 2000. A PET investigation of attribution of intentions to others with a non-verbal task. <i>NeuroImage</i> 11:157–66.	ToM	1	PET	58	-62	22	TAL
Brunet E, Sarfati Y, Hardy-Baylé MC, Decety J. 2003. A PET study of the attribution of intentions to others in schizophrenia. <i>Neuropsychologia</i> 41:1574–82.	ToM	1	PET	55	-50	19	MNI
Castelli F, Happe F, Frith U, Frith CD. 2000. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. <i>NeuroImage</i> 12:314–25.	ToM	1	PET	60	-56	12	TAL
Chaminade T, Decety J. 2002. Leader or follower? Involvement of the inferior parietal lobule in agency. <i>NeuroReport</i> 15:1975–8.	Agency	1	PET	53	-23	38	MNI

Note: Conversion located peak outside of brain; therefore, x-coordinate was corrected from 57 to 53

(continued)

APPENDIX (continued)

Study	Condition	Number of Activations	Imaging Method	TALx	TALy	TALz	Original Space
Corbetta M, Kincade JM, Ollinger JM, McAvoY MP, Shulman GL. 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. <i>Nat Neurosci</i> 3:292-7.	Attention	3	fMRI	53	-49	30	TAL
Corbetta M, Kincade JM, Shulman GL. 2002. Neural systems for visual orienting and their relationships to spatial working memory. <i>J Cogn Neurosci</i> 14:508-23.	Attention	1	fMRI	57	-45	12	TAL
David N, Bewernick BH, Cohen MX, Newen A, Lux S, Fink GR, and others. 2006. Neural representations of self versus other: visual-spatial perspective taking and agency in a virtual ball-tossing game. <i>J Cogn Neurosci</i> 18:898-910.	Agency	1	fMRI	39	-47	48	TAL
Decety J, Chaminade T. 2003. Neural correlates of feeling sympathy. <i>Neuropsychologia</i> 41:127-38.	Agency	1	fMRI	57	-45	12	TAL
Decety J, Chaminade T, Grèzes J, Meltzoff AN. 2002. A PET exploration of the neural mechanisms involved in reciprocal imitation. <i>NeuroImage</i> 15:265-72.	Empathy	1	PET	53	-49	39	MNI
Decety J, Jackson PL, Sommerville JA, Chaminade T, Meltzoff AN. 2004. The neural bases of cooperation and competition: an fMRI study. <i>NeuroImage</i> 23:744-51.	ToM	1	fMRI	59	-45	35	MNI
Den Ouden HEM, Frith U, Frith CD, Blakemore S-J. 2005. Thinking about intentions. <i>NeuroImage</i> 28:787-96.	ToM	1	fMRI	51	-44	45	MNI
Downar J, Crawley AP, Mikulis DJ, Davis KD. 2000. A multimodal cortical network for the detection of changes in the sensory environment. <i>Nat Neurosci</i> 3:277-83.	Attention	1	fMRI	48	-66	39	MNI
Downar J, Crawley AP, Mikulis DJ, Davis KD. 2001. The effect of task relevance on the cortical response to changes in visual and auditory stimuli: an event-related fMRI study. <i>NeuroImage</i> 14:1256-67.	Attention	2	fMRI	53	-40	16	MNI
Downar J, Crawley AP, Mikulis DJ, Davis KD. 2002. A cortical network sensitive to stimulus salience in a neutral behavioral context across multiple sensory modalities. <i>J Neurophysiol</i> 87:615-20.	Attention	3	fMRI	58	-43	17	MNI
				57	-48	10	MNI
				56	-36	24	TAL
				56	-36	24	TAL
				55	-53	4	TAL

Not classified as TPJ by authors

Note: Conversion located peak outside of brain; therefore, x-coordinate was corrected from 57 to 53

- Farrer C, Franck N, Frith CD, Decety J, Jeannerod M. 2003. Modulating the experience of agency: A PET study. *NeuroImage* 18:324–33.
- Farrer C, Franck N, Frith CD, Decety J, Damato T, Jeannerod M. 2004. Neural correlates of action attribution in schizophrenia. *Psychiatry Res* 131:31–44.
- Farrer C, Frith CD. 2002. Experiencing oneself vs. another person as being the cause of an action: the neural correlates of the experience of agency. *NeuroImage* 15:596–603.
- Fink GR, Marshall JC, Halligan PW, Frith CD, Driver J, Frackowiak RSJ, Dolan RJ. 1999. The neural consequences of conflict between intention and the senses. *Brain* 122:497–512.
- Fletcher PC, Happe F, Frith U, Baker SC, Dolan RJ, Frackowiak RSJ, Frith CD. 1995. Other minds in the brain: a functional imaging study of theory of mind in story comprehension. *Cognition* 57:109–28.
- Gallagher HL, Happe F, Brunswick N, Fletcher PC, Frith U, Frith CD. 2000. Reading the mind in cartoons and stories: an fMRI study of theory of mind in verbal and nonverbal tasks. *Neuropsychologia* 38:1–21.
- Giessing C, Thiel CM, Roesler F, Fink G. 2006. The modulatory effects of nicotine on parietal cortex activity in a cued target detection task depend on cue reliability. *Neuroscience* 137:853–64.
- Greene J, Sommerville RB, Nystrom LE, Darley JM, Cohen JD. 2001. An fMRI investigation of emotional engagement in moral judgment. *Science* 293:2105–8.
- Grezes J, Frith CD, Passingham RE. 2004. Inferring false beliefs from the actions of oneself and others: an fMRI study. *NeuroImage* 21:744–50.
- Hynes CA, Baird AA, Grafton ST. 2006. Differential role of the orbitofrontal lobe in emotional versus cognitive perspective-taking. *Neuropsychologia* 44:374–83.

Agency	1	PET	55	-53	36	MNI
Agency	1	PET	63	-53	25	MNI
Agency	1	fMRI	44	-55	32	MNI
Agency	1	PET	50	-54	38	TAL
ToM	1	PET	42	-50	24	TAL
ToM	1	fMRI	46	-56	26	TAL
Attention	1	fMRI	44	-46	19	MNI
Moral	1	fMRI	50	-57	20	TAL
ToM	1	fMRI	42	-59	27	MNI
ToM	1	fMRI	53	-51	19	TAL

(continued)

APPENDIX (continued)

Study	Condition	Number of Activations	Imaging Method	TALx	TALy	TALz	Original Space
Hynes CA, Baird AA, Grafton ST. 2006. Differential role of the orbitofrontal lobe in emotional versus cognitive perspective-taking. <i>Neuropsychologia</i> 44:374–83.	Empathy	1	fMRI	53	-51	19	TAL
Indovina I, Macaluso E. 2006. Dissociation of stimulus relevance and saliency factors during shifts of visuospatial attention. <i>Cereb Cortex</i> Epub ahead of print.	Attention	1	fMRI	50	-36	28	MNI
Jackson PL, Brunet E, Meltzoff AN, Decety J. 2006. Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain: an event-related fMRI study. <i>Neuropsychologia</i> 44:752–61.	Empathy	1	fMRI	48	-54	28	MNI
Jackson PL, Meltzoff AN, Decety J. 2005. How do we perceive the pain of others: a window into the neural processes involved in empathy. <i>NeuroImage</i> 24:771–9.	Empathy	1	fMRI	40	-47	39	MNI
Kable JW, Chatterjee A. 2006. Specificity of action representations in the lateral occipitotemporal cortex. <i>J Cogn Neurosci</i> 18:1498–517.	Agency	1	fMRI	50	-48	26	MNI
Kincade M, Abrams RA, Astafiev SV, Shulman GL, Corbetta M. 2005. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. <i>J Neurosci</i> 25:4593–604.	Attention	3	fMRI	50	-48	26	TAL
Konrad K, Neufang S, Thiel CM, Specht K, Hanisch C, Fan J, and others. 2005. Development of attentional networks: an fMRI study with children and adults. <i>NeuroImage</i> 28:429–39.	Attention	3	fMRI	51	-51	26	TAL
Lamm C, Batson CD, Decety J. 2007. The neural basis of human empathy—effects of perspective-taking and cognitive appraisal. <i>J Cogn Neurosci</i> 19:1–7.	Empathy	1	fMRI	48	-60	44	MNI
Lawrence EJ, Shaw P, Giampietro VP, Surguladze S, Brammer MJ, David AS. 2006. The role of 'shared representations' in social perception and empathy: an fMRI study. <i>NeuroImage</i> 29:1173–84.	Empathy	1	fMRI	47	-45	41	MNI

Coordinates requested via e-mail; no response received

Lepsien J, Pollmann S. 2006. Covert reorienting and inhibition of return: an event-related fMRI study. *J Cogn Neurosci* 14:127-44.

Leube DT, Knoblich G, Erb M, Grodd W, Bartels M, Kircher TT. 2003. The neural correlates of perceiving one's own movements. *NeuroImage* 20:2084-90.

Macaluso E, Frith CD, Driver J. 2002. Supramodal effects of covert spatial orienting triggered by visual or tactile events. *J Cogn Neurosci* 14:389-401.

Mayer AR, Doflinger JM, Rao SM, Seidenberg M. 2004. Neural networks underlying endogenous and exogenous visual-spatial orienting. *NeuroImage* 23:534-41.

Moll J, Oliveira-Souza R, Eslinger PJ, Bramati IE, Mourao-Miranda J, Andreuolo PA, Pessoa L. 2002. The neural correlates of moral sensitivity: a functional magnetic resonance imaging investigation of basic moral emotions. *J Neurosci* 22:2730-8.

Moriguchi Y, Decety J, Ohnishi T, Maeda M, Mori T, Nemoto K, and others. 2006. Empathy and judging other's pain: an fMRI study of alexithymia. *Cereb Cortex* Epub ahead of print.

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Attention	2	fMRI	56	-52	16	TAL
			55	-49	15	TAL
Agency	1	fMRI	48	-40	19	MNI
Attention	1	fMRI	60	-48	32	TAL
Attention	2	fMRI	54	-51	28	TAL
		fMRI	55	-53	27	TAL
Moral	1	fMRI	45	-60	18	TAL
Empathy	1	fMRI	63	-33	35	MNI
ToM	1	fMRI	52	-46	14	MNI
ToM	1	fMRI	48	-42	19	TAL
ToM	2	fMRI	53	-54	28	MNI
			48	-52	34	MNI

Note: Conversion located peak outside of brain; therefore, x-coordinate was corrected from 57 to 53

(continued)

APPENDIX (continued)

Study	Condition	Number of Activations	Imaging Method	TALx	TALy	TALz	Original Space
Ramrani N, Miall RC. 2004. A system in the human brain for predicting the actions of others. <i>Nat Neurosci</i> 7:85–90.	Agency	1	fMRI	55	-51	27	MNI
Rilling JK, Sanfey AG, Aronson JA, Nystrom LE, Cohen JD. 2004. The neural correlates of theory of mind within interpersonal interactions. <i>NeuroImage</i> 22:1694–703.	ToM	2	fMRI fMRI	48 40	-55 -55	27 32	TAL TAL
Rilling JK, Sanfey AG, Aronson JA, Nystrom LE, Cohen JD. 2004. Opposing BOLD responses to reciprocated and unreciprocated altruism in putative reward pathways. <i>NeuroReport</i> 15:2539–43.	ToM	1	fMRI	42	-52	16	TAL
Ruby P, Decety J. 2001. Effect of the subjective perspective taking during simulation of action: a PET investigation of agency. <i>Nat Neurosci</i> 4:546–50.	Agency Agency Agency	3	PET	48 45 44	-57 -64 -46	38 25 26	MNI MNI MNI
Ruby P, Decety J. 2003. What you believe versus what you think they believe? A neuroimaging study of conceptual perspective taking. <i>Eur J Neurosci</i> 17:2475–80.	ToM	1	PET	44	-66	36	MNI
Ruby P, Decety J. 2004. How would you feel versus how do you think she would feel? A neuroimaging study of perspective taking with social emotions. <i>J Cogn Neurosci</i> 16:988–99.	Empathy	1	PET	59	-53	23	MNI
Ruff CC, Driver J. 2006. Attentional preparation for a lateralized visual distractor: behavioral and fMRI evidence. <i>J Cogn Neurosci</i> 18:522–38.	Attention	1	fMRI	56	-36	16	TAL
Saxe R, Kanwisher N. 2003. People thinking about people—the role of the temporo-parietal junction in theory of mind. <i>NeuroImage</i> 19:1835–42.	ToM	1	fMRI	50	-55	28	MNI
Saxe R, Powell LJ. 2006. It's the thought that counts: specific brain regions for one component of theory of mind. <i>Psychol Sci</i> 17:692–9.	ToM	1	fMRI	52	-52	18	MNI
Saxe R, Wexler A. 2005. Making sense of another mind: the role of the right temporo-parietal junction. <i>Neuropsychologia</i> 43:1391–9.	ToM	1	fMRI	53	-51	25	MNI

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Agency	1	fMRI	53	-40	19	MNI
ToM	1	fMRI	56	-54	19	MNI
Agency	2	fMRI	61	-48	23	MNI
		fMRI	52	-42	24	MNI
Attention	3	fMRI	51	-49	28	TAL
			45	-49	42	TAL
			53	-39	40	TAL
ToM	1	fMRI	53	-46	19	MNI
Empathy	1	fMRI	50	-49	13	MNI
Agency	1	PET	40	-46	40	TAL
Attention	1	fMRI	45	-66	17	MNI
Attention	1	fMRI	59	-47	24	TAL

(continued)

APPENDIX (continued)

Study	Condition	Number of Activations	Imaging Method	TALx	TALy	TALz	Original Space
Vogele K, Bussefeld P, Newen A, Herrmann S, Happe F, Falkai P, and others. 2001. Mind reading: neural mechanism of theory of mind and self-perspective. <i>NeuroImage</i> 14:170–81.	ToM	1	fMRI	58	-56	12	TAL
Voellm BA, Taylor AN, Richardson P, Corcoran R, Stirling J, Mckie S, and others. 2006. Neuronal correlates of theory of mind and empathy: a functional magnetic resonance imaging study in nonverbal task. <i>NeuroImage</i> 29:90–8.	ToM	1	fMRI	44	-75	20	MNI
Voellm BA, Taylor AN, Richardson P, Corcoran R, Stirling J, Mckie S, and others. 2006. Neuronal correlates of theory of mind and empathy: a functional magnetic resonance imaging study in nonverbal task. <i>NeuroImage</i> 29:90–8.	Empathy	1	fMRI	52	-57	19	MNI
Vossel S, Thiel CM, Fink GR. 2006. Cue validity modulates the neural correlates of covert endogenous orienting of attention in parietal and frontal cortex. <i>NeuroImage</i> 32:1257–64.	Attention	1	fMRI	56	-55	17	MNI
Walter H, Adenzato M, Ciaramidaro A, Enrici I, Pia L, Bara BG. 2006. Understanding intentions in social interaction: the role of the anterior paracingulate cortex. <i>J Cogn Neurosci</i> 16:1854–63.	ToM	3	fMRI	56	-49	13	MNI
Williams JHG, Walter GD, Gilchrist A, Perrett DI, Murray AD, Whiten A. 2006. Neural mechanisms of imitation and mirror neuron functioning in autistic spectrum disorder. <i>Neuropsychologia</i> 44:610–21.	Agency	1	fMRI	58	-30	28	MNI

TAL = Talairach & Tourmoux; MNI = Montreal Neurological Institute; fMRI = functional magnetic resonance imaging; PET = positron emission tomography; ToM = Theory of Mind.

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