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Attention to the other's body sensations modulates the ventromedial prefrontal cortex

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Abstract

Theory of Mind (ToM) is involved in experiencing the mental states and/or emotions of others. A further distinction can be drawn between emotion and perception/sensation. We investigated the mechanisms engaged when participants' attention is driven toward specific states. Accordingly, 21 right-handed healthy individuals performed a modified ToM task in which they reflected about someone's emotion or someone's body sensation, while they were in a functional magnetic resonance imaging scanner. The analysis of brain activity evoked by this task suggests that the two conditions engage a widespread common network previously found involved in affective ToM (temporo-parietal junction (TPJ), parietal cortex, dorso-lateral prefrontal cortex (DLPFC), medial- prefrontal cortex (MPFC), Insula). Critically, the key brain result is that body sensation implicates selectively ventromedial prefrontal cortex (VMPFC). The current findings suggest that only paying attention to the other's body sensations modulates a self-related representation (VMPFC).

Key words: ToM; fMRI; emotion; perception; VMPFC

Introduction

Theory of Mind (ToM) is the ability to understand other people by ascribing mental states, beliefs, emotions and intentions to them (e.g. Premack and Woodruff, 1978). Several theories of ToM have been put forward to date (Baron-Cohen, 2001). Among them, the Simulation Theory (Gallese and Goldman, 1998; Ramnani and Miall, 2004) holds that self-representations, awareness and agency are cognitive components of ToM, while the temporoparietal area and the prefrontal cortex have been indicated as the neural correlates of self-other representations and agency (e.g. Decety and Grèzes, 2006). According to this theory, we can 'read' ToM states by imagining, through mental simulation, the same beliefs, states, emotions and intentions of others (e.g. Decety and Grèzes, 2006). A significant portion of ToM, however, is not simulationbased but theory-based: as individuals might employ stereotypes about the behavior/experience of a character described as being of a different gender/group, the inference about others is not based on a simulation.

ToM is multidimensional and includes a cognitive ToM, which corresponds to the knowledge about beliefs of the other, and an affective ToM, which corresponds to knowledge about emotions, through empathic appreciation of the observed person's emotional state (e.g. Shamay-Tsoory and Aharon-Peretz, 2007b). Although many studies focused on the difference between Cognitive and Affective ToM, there is very limited literature attempting to single out effects associated specifically with body sensations from a more general affective processing. Some studies employed modified ToM tasks focused specifically on pain (Bruneau *et al.*, 2012, 2015; Corradi-Dell'Acqua *et al.*, 2014, 2020; Jacoby *et al.*, 2016), however it is unclear whether the effects observed were indeed specifically due to pain or they rather reflected a broader effect of 'somatic sensations'. Saxe and Powell (2006) compared somatic sensations with cognitive ToM but failed to control for affective ToM.

The cognitive and emotional components of ToM are captured, respectively by the first and second factors of the quadrifactorial model of social cognition proposed by Blair and Cipolotti (2000): the cognitive component is assessed by requiring a person to understand the mental states of others (Baron-Cohen *et al.*, 1985; Happé, 1994), while the emotional component is assessed by asking her to attribute specific emotional states to the protagonists of scenes with an emotional content, respectively. The third factor in Blair and Cipolotti's model concerns a person's ability to judge, based on semantics, particular behaviors either as appropriate or violations, while the fourth factor has to do with the adherence to social rules, distinguished into moral and conventional rules.

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It remains to be understood whether the second factor of Blair and Cipolotti's model could extend the general affective processing to body sensations. Observing an actor experience in the first-person perspective or simulating the actor's bodily sensation in attributing specific states activate body sensation (BS) in participants. Indeed, perceptions of others figure as contents of mental simulation (Gallese and Goldman, 1998; Gallese, 2009). For instance, the authors report an activation of the insula—a visceral/sensory cortex—when participants observe actors' disgusted facial expressions (Gallese *et al.*, 2004).

In the present study we set out to investigate the neural correlates of the participants' ability to attribute specific states to others by relying on either emotion or sensation. As ToM is by hypothesis involved in both BS task and emotion task (E), we predicted that TPJ would be activated when participants performed either task.

To test this hypothesis, participants were asked to pay attention in the sentence to either the sensation expressed by the actor's body, or to the emotion supposedly in the actor's mind, using an Italian version of a task (Prior et al., 2003). In the emotion task (E), they were required to decide on the extent to which the actor is feeling a given emotion (e.g. 'How much terrified does she feel?'). In the BS task, instead, participants estimated how much the actor is feeling the sensation in a given body part (e.g. 'How much does she feel the sensation in her face?'). We hypothesized that a participant can solve this task by imagining in first person the bodily sensations of the actor. Our hypothesis is based on the evidence that different emotions are associated with culturally universal bodily sensations (Nummenmaa et al., 2014) They asked 701 participants to color on a silhouette the bodily parts where they felt a sensation while reading emotional words, stories, or watching movies, or facial expressions (Nummenmaa et al., 2013). The authors showed that the different emotions were consistently associated with statistically separable bodily sensation maps. Accordingly, in the BS task we administered, the participant had to pay attention to an actor's body part and decide the extent of actor's bodily sensation through perspective taking which, in turn, is expected to selectively activate areas involved in processing egocentric representations.

A recent meta-analysis from Schurtz et al. (2021), which applied the representation similarity analysis to meta-analytic maps on a wide range of paradigms testing ToM and empathy, showed that the neural response in this task can be modeled on three partially-segregated networks, involved in predominantly cognitive processes, affective processes and combined processes.

Methods and materials

Participants

Twenty-one healthy, right-handed (mean handedness $72.31 \pm 24.55\%$) subjects (9 M, 12 F, aged 22–48 years, mean age 30 ± 6.63 years) (Oldfield, 1971) participated in the study. They were all monolingual native speakers of Italian and had comparable levels of education (mean education 16.09 ± 2.71 years, range 8–18 years). The study was approved by the Ethics Committee of the IRCCS 'Eugenio Medea' Scientific Institute and written informed consent was obtained from each adult participant.

Experimental design Stimuli

We used the same stimuli as in the subtest Test 'Emotion Attribution Test' devised by Prior et al. (2003). In particular, participants were presented with 30 randomly selected short stories of the original 58 describing emotional scenes happening to an actor (see Appendix). The sentences are univocally designed to trigger sadness, fear, embarrassment, disgust, happiness, anger or envy. An example on the scenario is 'Melania si trova in un vicolo. Un uomo sta andando verso di lei con un coltello', i.e. 'Melanie is in an alley. A man is walking towards her with a knife'.

Task and experimental paradigm

The functional magnetic resonance imaging (fMRI) protocol consisted of an event-related experimental design with two tasks. Participants were asked to pay attention to the 'BS' and to the emotion 'E' described by the stimuli.

Participants were instructed to silently read the series of sentences describing a scene as in the subtest Test 'Emotion Attribution Test' devised by Prior et al. (2003) and make an estimation on a 4-level scale (0-1; 2-4; 5-7; 8-10) by pressing the corresponding button. They were explicitly asked to pay attention to either the sensation on the actor's body or to the emotion in the actor's mind. We did not modify the items' presentation. We only added a brief question below each item. When they paid attention to the sensation on the actor's body (BS task) the estimation had to be made on how much the actor is feeling the sensation in a given body part. There was a fixed part of the phrase (e.g. 'How much does she feel the sensation in her face?") and a changing body part (the highlighted part of the sentence above). When they paid attention to the emotion in the actor's mind (E task) the estimation had to be made on how much the actor is feeling a given emotion. There was a fixed part of the phrase (e.g. 'How much terrified does she feel?') and a changing emotion (the highlighted part of the sentence above). The body part labels (i.e. hands, belly, rob, face and legs) were selected according to the stronger body part---emotion associations as reported by the data from the Bodily maps of emotions' study (Nummenmaa et al., 2014) in which participants colored the body part associated with a given emotion. The emotion labels (i.e. happiness, embarrassment, fear, anger, sadness) were selected according to the correct emotion response in the 'Emotion Attribution Test' norming study (Prior et al., 2003). The BS questions (126.83 \pm 34.28 characters) were significantly longer than the E questions $(114.63 \pm 35.3 \text{ characters})$ t(29) = 22.81, P < 0.001).

Instruction lasted 5 s. All experimental trials (n = 60, 30 BS, 30 E) had a duration of 9 s and were followed by a variable intertrial interval, with a duration that was jittered between 3000 and 4000 ms, with incremental steps of 250 ms. In addition, a fixation cross (250 ms) was presented between trials, and 36 null events (i.e. blank screens) perceived as a prolongation of their intertrial period were randomly interspersed among the event trials to increase the power of estimating the BOLD response (Dale and Buckner, 1997).

Visual stimulation was generated by using Presentation (Neurobehavioral Systems Inc., Albany, CA, USA) and presented by using the VisuaStimDigital (Resonance Technology Inc., Los Angeles, CA, USA) Goggle system. Responses were given by pressing four keys of an MRI Compatible Keypad (Resonance Technology Inc., Los Angeles, CA, USA) with the fingers of the right hand. Subjects practiced the task outside the scanner, prior to the magnetic resonance experiment, and utilized the dominant hand to respond.

MRI Acquisition

Images were acquired using a 3T Achieva MR whole-body scanner (Philips, The Netherlands) with a standard 8-channel

head coil. High-resolution anatomical images were acquired using a 3D T1-weighted Turbo-Gradient Echo sequence (TR: 8.388 ms, TE: 3.85 ms, voxel size: 1×1 mm, thickness: 1 mm, number of slices: 190, field of view: $240 \times 190 \times 240$ mm, acquisition matrix: 240×240 , flip angle: 8°). Functional images were obtained using a T2*-weighted Gradient-Echo Echo-Planar Imaging EPI sequence (TR: 2500 ms, TE: 35 ms, voxel size: 1.797 mm × 1.797 mm, thickness: 3 mm, number of slices: 29, field of view: $230 \times 88.33 \times 230$ mm, acquisition matrix: 128×128 , flip angle: 90° , number of volumes: 308). Slices were acquired in the axial plane, parallel to the anterior commissure/posterior commissure (ACPC) line. The total scanning time was 20 min (12 min and 83 s the fMRI task plus the anatomical T1 acquisition).

Data analysis Behavioral data

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Behavioral performance was analyzed using SPSS 21.0 (SPSS, Inc., Chicago, IL) on subjects' reaction times and responses by performing an ANOVA with, as a factor, the task (attention to the body part 'BP' or to the emotion 'E').

fMRI data processing

fMRI preprocessing and statistical analysis were performed using MATLAB18r (The Mathworks, Inc., Natick, MA, USA) and SPM12 (Statistical Parametric Mapping software, SPM; Wellcome Department of Imaging Neuroscience, London, U.K. www.fil.ion.ucl.ac.uk/spm). The first four volumes of each functional dataset were discarded from analysis in order to allow for T1 equilibration effects.

We spatially realigned the images to the reference volume (i.e. the now first/previously seventh acquired volume) and then co-registered to the mean EPI image. The mean EPI image was normalized to the standard single subject template in Montreal Neurologic Institute (MNI) space. A Gaussian kernel of 6 mm fullwidth half-maximum was used for smoothing to meet the statistical requirements of the theory of Gaussian fields according to the General Linear Model (GLM) employed in SPM and to compensate for interindividual variability in macro- and microanatomical structures across subjects (Friston *et al.*, 1995a, 1995b).

For this experiment, three event-types were defined and then used as conditions for the model specification: (i) attention to body part, 'BP', and (ii) attention to emotion, 'E'. A GLM was thus applied to each voxel of the functional dataset. We used an eventrelated analysis and the BOLD response for each event type was modeled with the canonical Hemodynamic Response Function (HRF) and its temporal derivative. For this purpose, we convolved the HRF with an event train of delta functions at each stimulus onset of 0s of duration. A temporal high-pass filter of 1/128 Hz and linear trend removal were employed. The three translation and the three rotation movement parameters obtained from the initial spatially realignment were included as further regressors.

Specific effects were assessed by applying appropriate linear contrasts of the parameter estimates of the four experimental conditions and the baselines resulting in t-statistics for each voxel. The set statistics were then Z-transformed to statistical parametric maps [SPM(Z)] of differences between the experimental conditions and between the experimental conditions and the baseline. [SPM(Z)] statistics were interpreted in light of the probabilistic behavior theory of Gaussian random fields (Friston et al., 1995a, 1995b). For each subject we calculated the following



Fig. 1. (A) Behavioral results: Participants' mean reaction times (ms) on task performance (left panel) and their ratings (right panel). Subjects were significantly slower on the BP task than on the E task. Error bars indicate standard deviations (s.d.). (B) and C) Relative increases in neural activity associated with the BP task (B) and the E task (C) (P < 0.05, corrected at the cluster level; see Table 1) are displayed on a rendered template brain provided by SPM12. (D) Common network activated by the BP and E tasks as revealed by the whole brain analysis. (E) The activation cluster in the left superior medial (and orbital) gyrus at the maximally activated voxel (x = 10, y = 48, z = 2) differentially recruited by the BP (relative to F) contrast.

contrast images: the simple contrasts tasks (BP and E), and the main effect of the task [BP-E] and [E-BP].

Second-level Random Effects Analyses were performed by using a t-test to create an SPM(T) on contrast images obtained from individual participants, in order to obtain significant activations specific for each contrast on a group level. We used a threshold of P < 0.05, corrected for multiple comparisons at the cluster level [using family-wise error (FWE)], with a height threshold at the voxel level of P < 0.001, uncorrected (see Woo *et al.*, 2014). Anatomical localization of the activations was done by using the SPM Anatomy Toolbox 3.0 (Eickhoff *et al.*, 2005).

Results Behavioral data *Accuracy*

The rating significantly differs between tasks [$\underline{E}(1,20) = 74.16$, P < 0.001, 6.82 BS task ± 1.62 vs 8.1 ± 7.6 E] (Figure 1E). Participants rated stronger the intensity of emotions (8.1 ± 7.6 E task)

Table 1. Brain regions showing significant relative increases of BOLD response associated with each comparis	arison of inte	rest
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		MNI coordinates				
Side	Region	x	у	Z	Т	Size (k _E)
Attention-to-	BS Task-related network					
LH	Supramarginal gyrus	-58	-36	26	8.48	2436
RH	Supramarginal gyrus	60	-30	38	5.42	633
RH	Middle temporal gyrus	22	-26	16	6.47	364
LH	Anterior Insula	-38	6	8	6.50	1775
RH	Posterior Insula	42	-12	-4	5.16	777
RH	Superior frontal gyrus (medial segment)	4	48	6	7.26	1201
LH	Superior frontal gyrus	-24	54	22	6.43	273
LH	Inferior frontal gyrus (pars triangularis)	-46	44	0	4.80	207
Attention-to-	Emotion (E) Task-related network					
LH	Angular gyrus	-48	-56	40	7.43	1759
RH	Supramarginal gyrus	66	-32	36	6.63	950
RH	Inferior temporal gyrus	40	-46	-2	6.64	248
RH	Superior temporal gyrus	50	-10	-6	5.54	180
LH	Cerebellum	-38	-80	-32	7.00	315
LH	Anterior insula	-38	6	10	6.46	902
LH	Middle frontal gyrus	-42	26	34	5.98	250
RH	Middle frontal gyrus	28	52	-2	5.24	366
RH	Superior frontal gyrus (medial segment)	6	46	20	4.76	171
Conjunction A	Analysis BS Task ∩ E Task					
LH	Supramarginal gyrus	-64	-38	30	6.46	1689
LH	Angular gyrus	-48	-54	38	6.44	
LH	Anterior insula	-40	4	-2	4.83	709
RH	Supramarginal gyrus	60	-30	38	5.42	616
RH	Angular gyrus	62	-48	32	4.84	
Main effect TA	ASK [BS > E]					
М	Ventromedial prefrontal cortex	10	48	2	5.26	190

For each region of activation, the coordinates in MNI space are given referring to the maximally activated focus within an area of activation as indicated by the highest T-value. LH/RH = left/right hemisphere, M= medial; Size = number of voxels in a cluster.

All the activations are significant at P<0.05 (corrected for multiple comparisons at the cluster level, height threshold P<0.001, uncorrected).

as compared to the intensity level of sensation in the body part (6.82 \pm 1.62, BS task).

Reaction times

Reaction times were significantly longer $[\underline{F}(1,20) = 61.192, P < 0.001]$ in the BS task (5554.49 ± 586.81) than in the E task (4867.52 ± 526.31). This result could be related also to the different lengths of the BS and E questions. We evaluated this hypothesis by performing an analysis of covariance with the length of sentences as a covariate. Results showed that there is a statistically significant difference between adjusted means for the BS task vs the E task (P < 0.0001) once their means had been adjusted for different length of the stimuli.

fMRI data

The attention-to-BS task-related network

Figure 1B shows that the task-related network of areas (P < 0.05, cFWE corrected) involved clusters of activity localized in the right middle temporal gyrus, left supramarginal gyrus, right supramarginal gyrus, left anterior insula, right posterior insula, left superior frontal gyrus, right superior frontal gyrus (medial segment) and left inferior frontal gyrus (pars triangularis).

The attention-to-emotion (E) task-related network

Figure 1C shows that the task-related network of areas (P < 0.05, cFWE corrected) involved clusters of activity were localized in (i) the right middle temporal gyrus, (ii) right superior temporal gyrus, (iii) the left angular gyrus, (iii) the right supramagrinal gyrus, (iv)

the left cerebellum, (v) the left anterior insula, (vi) the middle frontal gyrus bilaterally and (vii) the right superior frontal gyrus (medial segment).

Conjunction analysis: BS task \cap E task

Commonly activated areas (P < 0.05, cFWE corrected) by both tasks were localized in the supramarginal gyrus bilaterally (extending to the angular gyrus), and left anterior insula (see Figure 1D).

Main effect of task: BS task—E task (and vice versa)

The BS task (vs E task) differentially activated (P < 0.05, cFWE corrected) the ventromedial prefrontal cortex (VMPFC) (see Figure 1E). The reverse contrast (E task vs BS task) did not reveal any suprathreshold activation. The analysis comprising character lengths of the BS and E questions as a covariate revealed the same results.

Discussion

Using fMRI with healthy participants we investigated the relative neuronal contribution of bodily sensation or emotion. First, we observed the BS vs E main effect that led to a significant increase in activation in the VMPFC when participants performed the 'attention to the BS task' (vs 'attention to the E'). Extant neuroimaging literature indicates that VMPC is part of the network underlying ToM processes (e.g. Gallagher and Frith, 2003; Amodio and Frith, 2006; Stone *et al.*, 1998; for meta-analyses see Molenberghs et al., 2016; Schurz et al., 2014; Hiser and Koenigs, 2018). Likewise, neuropsychological studies showing that ToM deficits may occur following damage to the VMPFC (e.g. Shamay-Tsoory et al., 2003, 2005, 2007a; Shamay-Tsoory and Aharon-Peretz, 2007b). However, the conjunction analysis performed on both the BS and E tasks failed to return significant results in the VMPFC, suggesting that the differential activation in this area does not reflect a general effect of ToM task. There is indeed agreement that the ToM includes two components: a cognitive component, corresponding to the processing of others' beliefs, and an affective component, relying on emotional knowledge, through empathic appreciation of emotional states of others (e.g. Shamay-Tsoory and Aharon-Peretz, 2007b).

Our result complements previous studies which focused on the Cognitive vs Affective ToM distinction (Saxe and Powell, 2006; Bruneau et al., 2012, 2015; Corradi-Dell'Acqua et al., 2014, 2020; Jacoby et al., 2016), as it adds data singling out effects associated specifically with body sensations from a more general affective perspective. Likewise, we found that the VMPFC was differentially activated during the ToM task when participants estimated the actor's bodily sensations. Estimating the extent to which the actor is feeling a sensation in a given body part, e.g. 'how much the actor is feeling the sensation in the chest?', likely requires processing egocentric representations. According to some patient studies, lesions to the VMPFC reduce the ability to process affective stimuli leaving the processing of cognitive stimuli intact (Shamay-Tsoory et al., 2006), see also (Leopold et al., 2012). In fact, damage to VMPFC may produce deficits in empathy (Barrash et al., 2000; Shamay-Tsoory et al., 2009), facial emotion recognition (Heberlein et al., 2008; Tsuchida and Fellows, 2012) and moral judgments (Young and Koenigs, 2007; Fumagalli and Priori, 2012). Thus the activation of VMPFC we observed in our study may be related to the processing of bodily states in ToM tasks.

The activation of the VMPCF is in line with the view that we use the self as a reference for understanding others (Gordon, 1986) as in tasks eliciting self-related bodily information. There is also neuropsychological evidence showing that perspectivetaking requires remapping of objects and locations coded with reference to the other person's body (e.g. Becchio et al., 2013). Along the same line, we already reported that performing a mental rotation of body shapes (relative to letter shapes) engages egocentric representations that are modified by mental rotation (Tomasino et al., 2016). Specifically, in a mental rotation task, participants imagine their own body into the position of the body stimulus and mentally rotate it until it matches the stimulus orientation. In that study, the contrast body shapes vs letter shapes lead to the activation of the VMPFC (Tomasino et al., 2016). The VMPFC (and the insula) were found to be activated both by interoceptive information and subjective experience of emotion (Terasawa et al., 2013).

Several studies identified the VMPFC as a neural correlate of self-related and perspective-taking processes (e.g. Northoff and Bermpohl, 2004). For instance, an activation of the VMPFC was observed when participants silently read sentences depicting their own ('self' task) or another person's ('other' task) personality traits or social issues ('society' task) (D'Argembeau *et al.*, 2005). An activation very close to the one we reported here was observed in self-referential processing (x = -8, y = 50 and z = -2, away from our coordinates only by 2 mm in x, 2 mm in y and 0 mm in z plane), and not in perspective taking itself (x = -4, y = 52 and z = -1), when participants judged the appropriateness of an adjective for the self vs the other person (D'Argembeau *et al.*, 2007). In other study, in which participants judged how different adjectives are relevant

for the self, an activation in the VMPFC was obtained in association with self-relevant adjectives (at x = -6, y = 53 and z = 6) relative to adjectives considered less self-relevant (Moran *et al.*, 2006). Similarly, an activation in the VMPFC (at x = 0, y = 54 and z = -15) was found while subjects viewed emotionally charged pictures and, post-fMRI measurements, judged the self-relatedness of the stimuli (Schneider *et al.*, 2008). Results showed that activation in the VMPFC was parametrically modulated by the subjects' self-relatedness judgments. Single-neuron recordings in the dorsomedial prefrontal cortex of interacting Rhesus macaques code for details of the interaction, such as identity, context, and interaction history (Báez-Mendoza *et al.*, 2021). The neurons from which the authors recorded were located in the more medial part of the Brodmann's area 24, just above the activation cluster we observed in our study.

Lastly, previous studies comparing affective ToM with pain inferences showed activation in the supramarginal gyrus, in the insula and also in one case also to VMPFC. For instance, Saxe and Powell (2006) found supramarginal activation for inferring somatic sensations vs Cognitive ToM. Other few studies (Bruneau et al., 2012, 2015; Corradi-Dell'Acqua et al., 2014, 2020; Jacoby et al., 2016) compared affective ToM with pain inferences, associating the latter to the insular cortex (especially the posterior/opercular portion), and in one case also to VMPFC. In this perspective, we can speculate that these previous studies on pain inferences reflect, although at a more general level with respect to our BS task, inference of somatic sensations.

We acknowledge a limitation in our study consisting in the lack of a control condition testing Cognitive ToM. In fact, it is unclear whether the network triggered by E and BS tasks reflects purely affective/somatic inference or it also engaged by cognitive ToM processes. However, we are positive that this should not weaken our key result, that is the selective activation of the VMPFC during the BS task, obtained by contrasting different task demands on the same stories, which evoked similar idiosyncratic considerations about the protagonist's thoughts.

Conclusion

When participants performed a ToM task paying attention to the either bodily sensations or emotions activated a core region in the TPJ, parietal cortex, DLPFC, MPFC and insula. By contrast, only when participants paid attention to the bodily sensations, selfrelated bodily representations were selectively activated in the VMPFC.

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Conflict of interest

The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

Author contributions

R.I.R. and B.T. designed the study, C.C. acquired the data; B.T. and C.B. analyzed the data; B.T. and R.I.R. wrote the paper; all authors edited the paper; all authors revised the final version of the manuscript.

Data availability

The datasets analyzed for this study will be made available from the authors upon request.

Reference

- Amodio, D.M., Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. Nature Reviews Neuroscience, 7, 268–77.
- Báez-Mendoza, R., Mastrobattista, E.P., Wang, A.J., Williams, Z.M. (2021). Social agent identity cells in the prefrontal cortex of interacting groups of primates. *Science* (New York, N.Y.), **374**, eabb4149.
- Baron-Cohen, S., Leslie, A.M., Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition*, **21**(1), 37–46.
- Baron-Cohen, S. (2001). Theory of mind and autism: a review. In: Glidden, L.M. editor International Review of Research in Mental Retardation: Autism, Vol. 23, Cambridge, MA: Academic Press, 169–84.
- Barrash, J., Tranel, D., Anderson, S.W. (2000). Acquired personality disturbances associated with bilateral damage to the ventromedial prefrontal region. *Developmental Neuropsychology*, **18**, 355–81.
- Becchio, C., Del Giudice, M., Dal Monte, O., Latini-Corazzini, L., Pia, L. (2013). In your place: neuropsychological evidence for altercentric remapping in embodied perspective taking. Social Cognitive and Affective Neuroscience, 8, 165–70.
- Blair, R.J., Cipolotti, L. (2000). Impaired social response reversal. A case of 'acquired sociopathy'. Brain: A Journal of Neurology, **123**, 1122–41.
- Bruneau, E.G. Pluta, A., Saxe, R. (2012). Distinct roles of the 'shared pain' and 'theory of mind' networks in processing others' emotional suffering. *Neuropsychologia*, **50**(2), 219–31.
- Bruneau, E.G. Jacoby, N., Saxe, R. (2015). Empathic control through coordinated interaction of amygdala, theory of mind and extended pain matrix brain regions. *NeuroImage*, **114**, 105–19.
- Corradi-Dell'Acqua, C., Hofstetter, C., Vuilleumier, P. (2014). Cognitive and affective theory of mind share the same local patterns of activity in posterior temporal but not medial prefrontal cortex. Social Cognitive and Affective Neuroscience, **9**(8), 1175–84.
- Corradi-Dell'Acqua, C., Ronchi, R., Thomasson, M., Bernati, T., Saj, A., Vuilleumier, P. (2020). Deficits in cognitive and affective theory of mind relate to dissociated lesion patterns in prefrontal and insular cortex. Cortex; a Journal Devoted to the Study of the Nervous System and Behavior, **128**, 218–33.
- D'Argembeau, A., Collette, F., Van der, L.M., *et al.* (2005). Selfreferential reflective activity and its relationship with rest: a PET study. *Neuroimage*, **25**, 616–24.
- D'Argembeau, A., Ruby, P., Collette, F., et al. (2007). Distinct regions of the medial prefrontal cortex are associated with self-referential processing and perspective taking. *Journal of Cognitive Neuroscience*, **19**, 935–44.
- Dale, A.M., Buckner, R.L. (1997). Selective averaging of rapidly presented individual trials using fMRI. Human Brain Mapping, 5, 329–40.
- Decety, J., Grèzes, J. (2006). The power of simulation: imagining one's own and other's behavior. Brain Research, **1079**, 4–14.
- Eickhoff, S., Stephan, K.E., Mohlberg, H., et al. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage*, **25**, 1325–35.
- Friston, K.J., Ashburner, J., Frith, C.D., Poline, J.B., Heather, J.D., Frackowiak, R.S.J. (1995a). Spatial registration and normalization of images. *Human Brain Mapping*, **3**, 165–89.
- Friston, K.J., Frith, C.D., Turner, R., Frackowiak, R.S.J. (1995b). Characterising evoked hemodynamics with fMRI. Neuroimage, 2, 157–65.
- Fumagalli, M., Priori, A. (2012). Functional and clinical neuroanatomy of morality. Brain, 135, 2006–21.

- Gallagher, H.L., Frith, C.D. (2003). Functional imaging of 'theory of mind'. Trends in Cognitive Sciences, **7**, 77–83.
- Gallese, V., Keysers, C., Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, **8**, 396–403.
- Gallese, V. (2009). Mirror neurons, embodied simulation, and the neural basis of social identification. *Psychoanalytic Dialogues*, **19**, 519–36.
- Gallese, V., Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, **2**, 493–501.
- Gordon, R.M. (1986). Folk psychology as simulation. Mind & Language, 1, 158–171.
- Happé, F. (1994). An advanced test of theory of mind: understanding of story characters' thoughts and feelings by able autistic, mentally handicapped, and normal children and adults. *Journal* of Autism and Developmental Disorders, **24**, 129–54.
- Heberlein, A.S., Padon, A.A., Gillihan, S.J., Farah, M.J., Fellows, L.K. (2008). Ventromedial frontal lobe plays a critical role in facial emotion recognition. *Journal of Cognitive Neuroscience*, **20**, 721–33.
- Hiser, J., Koenigs, M. (2018). The multifaceted role of the ventromedial prefrontal cortex in emotion, decision making, social cognition, and psychopathology. Biological Psychiatry, 83, 638–47.
- Jacoby, N., Bruneau, E., Koster-Hale, J., Saxe, R. (2016). Localizing Pain Matrix and Theory of Mind networks with both verbal and nonverbal stimuli. NeuroImage, 126, 39–48.
- Leopold, A., Krueger, F., Dal Monte, O., et al. (2012). Damage to the left ventromedial prefrontal cortex impacts affective theory of mind. Social Cognitive and Affective Neuroscience, 7, 871–88.
- Molenberghs, P., Johnson, H., Henry, J.D., Mattingley, J.B. (2016). Understanding the minds of others: a neuroimaging meta-analysis. *Neuroscience and Biobehavioral Reviews*, 65, 276–91.
- Moran, J.M., Macrae, C.N., Heatherton, T.F., Wyland, C.L., Kelley, W.M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience*, 18, 1586–94.
- Northoff, G., Bermpohl, F. (2004). Cortical midline structures and the self. Trends in Cognitive Sciences, **8**, 102–7.
- Nummenmaa, L., Glerean, E., Hari, R., Hietanen, J.K. (2014). Bodily maps of emotions. Proceedings of the National Academy of Sciences of the United States of America, **111**, 646–51.
- Oldfield, R.C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, **9**, 97–113.
- Premack, D., Woodruff, G. (1978). Does the chimpanzee have a theory of mind? Behavioral and Brain Sciences, **1**, 515–26.
- Prior, M., Marchi, S., Sartori, G. (2003). Cognizione Sociale E Comportamento, Volume I, Uno Strumento per la Misurazione. Padova: Upsel Domeneghini Editore.
- Ramnani, N., Miall, R.C. (2004). A system in the human brain for predicting the actions of others. Nature Neuroscience, 7, 85–90.
- 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), 692–9.
- Schneider, F., Bermpohl, F., Heinzel, A., et al. (2008). The resting brain and our self: self-relatedness modulates resting state neural activity in cortical midline structures. *Neuroscience*, **157**, 120–31.
- Schurz, M., Radua, J., Aichhorn, M., Richlan, F., Perner, J. (2014). Fractionating theory of mind: a meta-analysis of functional brain imaging studies. *Neuroscience and Biobehavioral Reviews*, 42, 9–34.
- Schurz, M., Radua, J., Tholen, M.G., et al. (2021). Toward a hierarchical model of social cognition: a neuroimaging meta-analysis and

integrative review of empathy and theory of mind. Psychological Bulletin, **147**(3), 293–327.

- Shamay-Tsoory, S.G., Tomer, R., Berger, B.D., Aharon-Peretz, J. (2003). Characterization of empathy deficits following prefrontal brain damage: the role of the right ventromedial prefrontal cortex. *Journal of Cognitive Neuroscience*, **15**, 324–37.
- Shamay-Tsoory, S.G., Tomer, R., Berger, B.D., Goldsher, D., Aharon-Peretz, J. (2005). Impaired "affective theory of mind" is associated with right ventromedial prefrontal damage. *Cognitive and Behavioral Neurology*, **18**, 55–67.
- Shamay-Tsoory, S.G., Tibi-Elhanany, Y., Aharon-Peretz, J. (2006). The ventromedial prefrontal cortex is involved in understanding affective but not cognitive theory of mind stories. Social Neuroscience, 1, 149–66.
- Shamay-Tsoory, S.G., Aharon-Peretz, J., Levkovitz, Y. (2007a). The neuroanatomical basis of affective mentalizing in schizophrenia: comparison of patients with schizophrenia and patients with localized prefrontal lesions. *Schizophrenia Research*, **90**, 274–83.
- Shamay-Tsoory, S.G., Aharon-Peretz, J., Perry, D. (2009). Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. Brain, **132**, 617–27.
- Shamay-Tsoory, S.G., Aharon-Peretz, J. (2007b). Dissociable prefrontal networks for cognitive and affective theory of mind: a lesion study. Neuropsychologia, 45, 3054–67.
- Stone, V.E., Baron-Cohen, S., Knight, R.T. (1998). Frontal lobe contributions to theory of mind. *Journal of Cognitive Neuroscience*, **10**, 640–56.
- Terasawa, Y., Fukushima, H., Umeda, S. (2013). How does interoceptive awareness interact with the subjective experience of emotion? An fMRI study. *Human Brain Mapping*, **34**, 598–612.
- Tomasino, B., Campanella, F., Fabbro, F. (2016). Medial orbital gyrus modulation during spatial perspective changes: pre- vs. post-8 weeks mindfulness meditation. *Consciousness and Cognition*, **40**, 147–58.
- Tsuchida, A., Fellows, L.K. (2012). Are you upset? Distinct roles for orbitofrontal and lateral prefrontal cortex in detecting and distinguishing facial expressions of emotion. *Cerebral Cortex*, 22, 2904–12.
- Woo, C.W., Krishnan, A., Wager, T.D. (2014). Cluster-extent based thresholding in fMRI analyses: pitfalls and recommendations. *NeuroImage*, **91**, 412–9.

Young, L., Koenigs, M. (2007). Investigating emotion in moral cognition: a review of evidence from functional neuroimaging and neuropsychology. British Medical Bulletin, 84, 69–79.

Appendix

List of items (from the 'Emotion Attribution Test' by Prior et al. (2003), body part (BP) and emotion (ADJ) for the attention to the bodily sensation (BS) task and for the attention to the emotion (E) task.

	FBS	FE How much [ADJ] does she/he feel		
Item n.	How much does she/he feel the sensation in her/his [BP]			
1	Bell	Sad		
6	Rob	Sad		
8	Face	Sad		
31	Bell	Disappointed		
41	Rob	Disappointed		
57	Face	Disappointed		
7	Face	Scared		
11	Rob	Scared		
21	Bell	Scared		
26	Hands	Frightened		
43	Bell	Frightened		
46	Rob	Frightened		
3	Rob	Embarrassed		
14	Bell	Embarrassed		
17	Face	Embarrassed		
44	Face	Ridiculous		
47	Bell	Ridiculous		
52	Rob	Ridiculous		
5	Face	Нарру		
16	Rob	Нарру		
20	Bell	Нарру		
22	Hands	Enraptured		
32	Leg	Enraptured		
42	Face	Enraptured		
12	Hands	Angry		
13	Rob	Angry		
33	Face	Angry		
45	Rob	Bothered		
49	Hands	Bothered		
53	Face	Bothered		