SOCIAL NEUROSCIENCE, 2013
http://dx.doi.org/10.1080/17470919.2012.761160

Routledge
Taylor & Francis Group

Brain systems for visual perspective taking and action perception

Elisabetta Mazzarella[1], Richard Ramsey[2], Massimiliano Conson[1], and Antonia Hamilton[3]

[1]Neuropsychology Laboratory, Department of Psychology, Second University of Naples, Caserta, Italy
[2]Wales Institute of Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, UK
[3]School of Psychology, University of Nottingham, Nottingham, UK

Taking another person's viewpoint and making sense of their actions are key processes that guide social behavior. Previous neuroimaging investigations have largely studied these processes separately. The current study used functional magnetic resonance imaging to examine how the brain incorporates another person's viewpoint and actions into visual perspective judgments. Participants made a left–right judgment about the location of a target object from their own (egocentric) or an actor's visual perspective (altercentric). Actor location varied around a table and the actor was either reaching or not reaching for the target object. Analyses examined brain regions engaged in the egocentric and altercentric tasks, brain regions where response magnitude tracked the orientation of the actor in the scene and brain regions sensitive to the action performed by the actor. The blood oxygen level-dependent (BOLD) response in dorsomedial prefrontal cortex (dmPFC) was sensitive to actor orientation in the altercentric task, whereas the response in right inferior frontal gyrus (IFG) was sensitive to actor orientation in the egocentric task. Thus, dmPFC and right IFG may play distinct but complementary roles in visual perspective taking (VPT). Observation of a reaching actor compared to a non-reaching actor yielded activation in lateral occipitotemporal cortex, regardless of task, showing that these regions are sensitive to body posture independent of social context. By considering how an observed actor's location and action influence the neural bases of visual perspective judgments, the current study supports the view that multiple neurocognitive "routes" operate during VPT.

Keywords: Perspective taking; Action observation; Social cognition; fMRI.

Understanding the goals and intentions of another person is considered a fundamental component of social cognition in humans (Frith & Frith, 2012). Several skills contribute to understanding others, including the ability to take another person's point of view and the ability to make sense of other people's actions. Here, we test whether these two abilities are related in terms of the neural systems involved in each.

The ability to understand the visual experience of another agent, known as visual perspective taking (VPT), is a central process in spatial and social cognition (Frith & Frith, 2012; Zacks & Michelon, 2005). Level 1 VPT consists of knowing "if" another agent can see an object, while level 2 consists of determining "where" an object is located relative to another agent (Flavell, Everett, Croft, & Flavell, 1981). For example, when a child observes his father looking toward a teapot, the child can know that his father can see the teapot (level 1 VPT) or that the teapot is located to the left of his father (level 2 VPT). Level 2 VPT can be performed according to two different spatial reference frames: egocentric and

---

Correspondence should be addressed to: Richard Ramsey, Wales Institute of Cognitive Neuroscience, School of Psychology, Bangor University, Bangor, UK. E-mail: r.ramsey@bangor.ac.uk

The authors E. Mazzarella and R. Ramsey contributed equally to this work.

allocentric/altercentric (Howard & Templeton, 1966). The egocentric point of view codes the object with respect to the observer, while the altercentric point of view codes the object with respect to another person.[1] Thus, taking an altercentric viewpoint can involve "getting inside another person's shoes" in order to imagine an alternative visual experience. Such processes exemplify a striking feature of human social abilities: we are not only able to reason about our own perceptions of the world but we also have some insight into the minds of other people.

In order to imagine an alternative visual experience, one may rely on the ability to mentally transform oneself into a new spatial location (Zacks & Michelon, 2005). Such "perspective transformations" are effortful in the sense that they result in increased reaction times (RTs) and errors compared to zero-degree transformations (Graf, 1994; Kessler & Thomson, 2010; Zacks & Michelon, 2005). Neuroimaging studies have shown that mentally transforming one's own body engages premotor, parietal, and occipitotemporal cortices (Keehner, Guerin, Miller, Turk, & Hegarty, 2006; Lambrey, Doeller, Berthoz, & Burgess, 2012; Wraga, Flynn, Boyle, & Evans, 2010; Wraga, Shephard, Church, Inati, & Kosslyn, 2005; Zacks, Vettel, & Michelon, 2003) and that these responses are similar, but not identical, to those engaged in during mental rotation of objects (Creem et al., 2001; Zacks, 2008; Zacks & Michelon, 2005). These results suggest that mental transformations of bodies and objects engage a partially shared neural circuit.

In addition to mentally transforming one's spatial location, the extra cognitive resources required during perspective transformations, in part, reflect the need to resist interference from one's own perspective (Birch & Bloom, 2004). Inhibition of one's own viewpoint engages lateral prefrontal cortex and has been suggested to be a key process when reasoning about other people's perspectives (Samson, Apperly, Kathirgamanathan, & Humphreys, 2005; van der Meer, Groenewold, Nolen, Pijnenborg, & Aleman, 2011; Vogeley et al., 2001). However, recent results suggest that taking an altercentric perspective is not always effortful and can sometimes be adopted in an easy and effortless manner (Cohen & German, 2009; Kovács, Téglás, & Endress, 2010; Ramsey, Hanson, Apperly, & Samson, in press; Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010). Further, the likelihood of adopting another's perspective can be spontaneously prompted by social context without explicit instruction to consider the other person's viewpoint (Mazzarella, Hamilton, Trojano, Mastromauro, & Conson, 2012; Tversky & Hard, 2009). For example, Tversky and Hard (2009) showed that when participants see a picture of another person grasping an object, they are more likely to adopt the other person's perspective than when the actor is not grasping. This latter result suggests that action observation and VPT are linked and that VPT is influenced by social context (e.g., observing another person's action). Although prior studies consistently demonstrate that observing actions performed by others engages inferior frontal, parietal, and occipitotemporal cortices (for meta-analyses, see Caspers, Zilles, Laird, & Eickhoff, 2010; Grèzes & Decety, 2001), it is not clear how visual perspective judgments and observed actions are linked in the brain. A key question, therefore, which remains underexplored, is how different components of social cognition are integrated in the brain.

The aim of the present study is to uncover brain regions underlying the interaction of VPT and action observation. We used a left–right judgment task in which participants viewed pictures of a round table with an object on top and an actor standing around the table at eight different orientations (40°, 80°, 120°, and 160° clockwise and counterclockwise; see Figure 1). Participants had to decide whether the object was on the left or on the right from their own point of view (egocentric task) or from the actor's point of view (altercentric task). In addition, the observed actor could either be reaching for the object with his hand (reaching) or the actor's hand could by his side (not reaching). This design permits the examination of brain regions sensitive to the interaction between spatial reference frame (egocentric vs. altercentric), actor orientation (40°, 80°, 120°, and 160°), and observed action (reach vs. no reach), which has not been possible in previous neuroimaging studies of VPT or action perception.

Our analysis focuses on three questions (Figure 2). First, we want to establish which brain regions are engaged in each VPT task in our particular paradigm (i.e., egocentric and altercentric)? Consistent with a recent review, we predict both common and distinct brain regions to be involved (Zaki & Ochsner, 2011). Both the VPT tasks involve calculating visuospatial relations between items in the environment, a process likely to engage lateral occipitotemporal, medial, and lateral parietal as well as lateral frontal cortices (Committeri et al., 2004; Lambrey et al., 2012; Vogeley et al., 2004; Zaehle et al., 2007). The egocentric task more than the altercentric task is likely

---

[1] Note that altercentric is termed allocentric in some previous papers. We use the term altercentric to refer to prospectives anchored on another person, leaving the term allocentric for perspectives that are anchored externally but not specifically tied to a person.

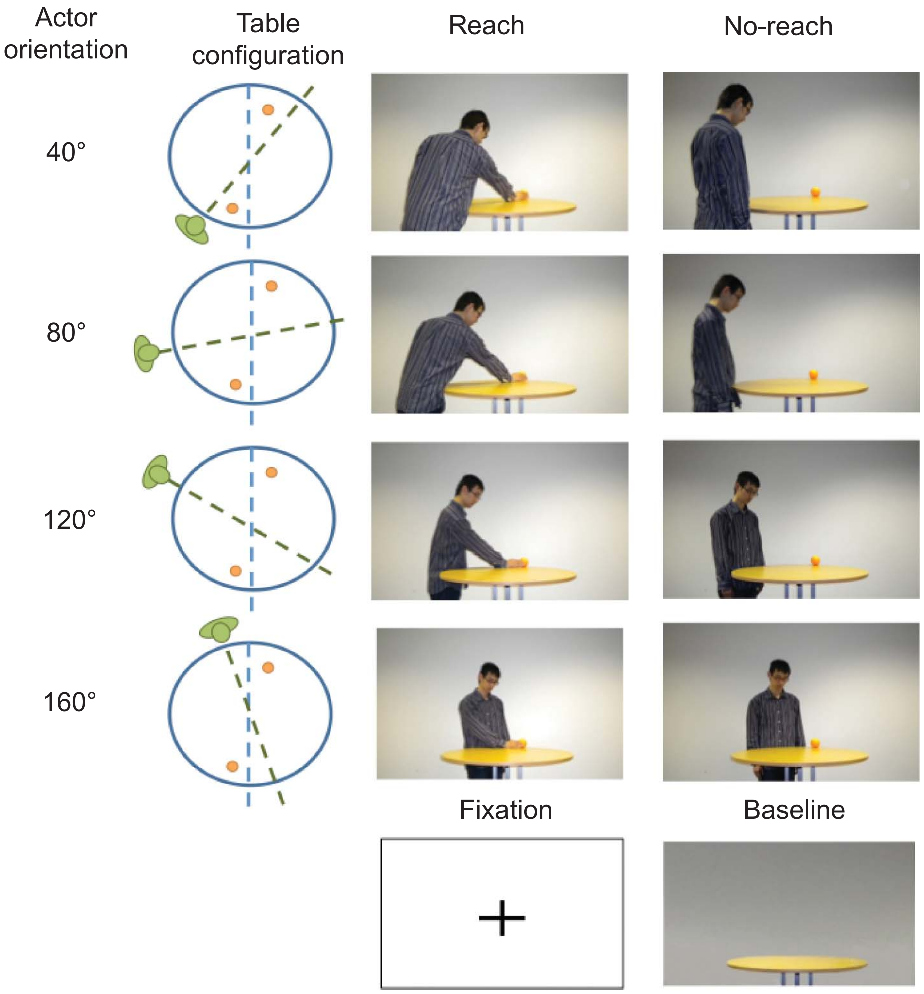


Figure 1. **Stimuli.** This figure shows example images for each of the four-actor orientations and two reaching conditions. The table configuration column illustrates the spatial layout of the table (blue, viewer at 6 pm) and of the actor (green). The object was always at one of the two locations marked with an orange disk; so, if it was on the viewer's left, it would be on the actor's right or vice versa. The distance between the center of the image and the object was constant in every condition. A mirrored set of images with the actor on the right-hand side of the table was also used.

to involve self-related thought processes and therefore engage medial cortical structures (comprising anterior prefrontal, parietal, and posterior cingulate), as well as lateral parietal cortex (David et al., 2006; Vogeley et al., 2004; Zaehle et al., 2007). The inverse contrast will place more demands on processes of mental transformation and self-inhibition, which are likely to engage lateral prefrontal, premotor, occipitotemporal, and lateral parietal cortices (Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006; Committeri et al., 2004; Kockler et al., 2010; Lambrey et al., 2012; Vogeley et al., 2004; Zaehle et al., 2007).

Second, which brain regions are specifically related to the mental transformation component of VPT? To address this question, we will perform parametric analyses, which correlate the Blood oxygen level-dependent (BOLD) response with increasing actor orientation (40°, 80°, 120° and 160°). The majority of previous VPT functional magnetic resonance imaging (fMRI) studies have shown general responses in premotor, parietal, and occipitotemporal brain regions when performing perspective transformations, but these studies did not parametrically relate BOLD responses with the amount of self-rotation (Creem et al., 2001; Creem-Regehr, Neil, & Yeh, 2007; Lambrey et al., 2012; Schwabe, Lenggenhager, & Blanke, 2009; Wraga, Boyle, & Flynn, 2010; Wraga et al., 2005; Zacks et al., 2003). Therefore, the profile of response in these brain regions during perspective transformations remains unspecified; for instance, it is not known whether the response is proportional or independent to the amount of self-rotation. Just two studies have previously related the BOLD response

a. Factorial design		**Factor: Task**	
		Altercentric	**Egocentric**
Factor: Condition	VPT-Reach	AVR	EVR
	VPT-no reach	AVN	EVN
	Plant		EVP
	Baseline	AB	EB

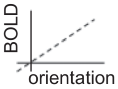
b. Contrasts	
Q1: VPT	Altercentic: (ABR + AVN) > 2 × AB Egocentric: (EVR + EVN) > 2 × EB
Q2: Actor orientation	Alter: parametric modulation by orientation Ego: parametric modulation by orientation Task × orientation interaction 
Q3: Actor reaching	Reach > No-reach Reach by task interaction [AVR > AVN] > [EVR > EVN]

Figure 2. Factorial design and contrasts. (a) This table depicts the 2 × 4 factorial design and lists the acronyms for each condition. (b) The table lists the major contrasts calculated to address each of our three research questions. Abbreviation: VPT, visual perspective taking.

to the magnitude of imagined self-rotation, but these provided inconclusive results (Keehner et al., 2006; Wraga, Flynn et al., 2010). In the present study, we will examine the orientation effects for both egocentric and altercentric VPT. In the altercentric task, stimuli with increased actor orientation demand a greater perspective transformation and should lead to increased BOLD in brain regions which perform this component of VPT. In contrast, the egocentric condition uses the same stimuli but does not require any imagined self-rotation, so should not engage the same regions in the same manner. Comparing parametric analyses of actor orientation between tasks (altercentric and egocentric) will examine these predictions.

Third, are any brain regions modulated by the observation of a reaching actor compared to the observation of a non-reaching actor? We would expect that observation of an action might engage brain regions in lateral occipitotemporal cortex, as well as inferior frontal and parietal cortices, as these regions make up an “action observation network” (Caspers et al., 2010; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Grafton & Hamilton, 2007). The key question concerns whether any components of this network show an interaction between the presence of an action in the stimulus and the spatial perspective adopted to make a VPT judgment. As observed actions bias the adoption of the altercentric perspective (Tversky & Hard, 2009), it could be that regions within the action observation network play a role in biasing altercentric perspective judgments. Addressing these three questions will advance our understanding of the brain systems for perspective taking and action observation, as well as the links between them.

MATERIALS AND METHODS

Participants

Twenty naïve students (11 males, mean age: 27.7), who were all right-handed were paid 15 pounds for participating. They gave their written informed consent in accordance with the requirements of the local medical ethics committee.

Stimuli and procedure

Participants were presented with a photo of a male actor standing at a round table at eight different orientations (40°, 80°, 120°, and 160° clockwise and counterclockwise). A piece of fruit (an orange) was on the table and served as the target object. The location of the orange was always 45 pixels left or right of a fixation cross, which remained on the screen for first 500 ms of each trial. In the “reach” condition the picture showed the actor reaching for the orange with his right hand, while in the “no-reach” condition the actor’s right hand was by the side of his body (Figure 1). Pictures were 600 wide by 400 pixels high and presented with Cogent running under Matlab 6.5 permitting synchronization with the scanner and accurate timing of stimuli presentation. Stimuli were presented on a screen located in front of the scanner, which participants could see through a mirror positioned on the head coil. The distance between the screen and participant's eyes was 2.3 m.

Each participant performed two tasks: egocentric and altercentric. In the egocentric task, participants were asked to decide whether the orange was on their own left or right. In the altercentric task, participants were asked to decide whether the same object was on the actor's left or right. The stimuli were identical in the egocentric and altercentric tasks. In all stimuli, egocentric and altercentric responses opposed each other; for example, if the orange was on the left of the actor, it was on the right of the participant and vice versa (Figure 1). In addition, in the egocentric task, there was an additional control condition, which showed a plant at the same eight orientations instead of the actor. The plant condition could not also be included in the altercentric task because it was not informative to ask participants to take the perspective of the plant.

Responses were given with the right hand on a button box (during scanning) or the computer keyboard (during training). In all cases, the index finger denoted that the object is on the left and the middle finger that the object is on the right. The egocentric and altercentric tasks were presented in separate blocks during scanning. Within both blocks, an identical baseline condition was included to allow within-block comparisons of VPT-task to baseline, which are more powerful and less susceptible to low frequency changes in scanner signal than between-block comparisons (Henson, 2006). The baseline photo depicted a table without any object or person and participants were asked to press both keys when it appeared on the screen. Each trial was five seconds long and started with a fixation point (500 ms), followed by the presentation of one photo. When the participant responded, a fixation-cross appeared on the photo to confirm that a keyhit had been received. The photo then remained on the screen for a variable duration (1000–5000 ms). This ensured that the total stimulus duration was not correlated with the participant's RT, allowing the effects of stimulus orientation to be modelled without confounds from RT.

The procedure for each participant was as follows. First, outside of the scanner, participants completed a practice block of each task (altercentric: 4 orientations (40°, 80°, 120°, and 160°) × 2 conditions (reach and no reach) × 8 repetitions + 16 baseline trials gave 80 trials; egocentric: 4 orientations (40°, 80°, 120°, and 160°) × 3 conditions (reach, no reach, and plant) × 8 repetitions + 16 baseline trials gave 112 trials). They then entered the scanner and completed a "refresher" block of their first condition (altercentric: 40 trials or egocentric: 56 trials). The refresher blocks were included to allow participants to gain more experience with each task and were the same as practice trials performed outside of the scanner, but the number of repetitions was reduced.

During two runs of functional scanning, participants then completed two blocks of their first task (altercentric: 80 trials per block or egocentric: 112 trials per block). While a high-resolution anatomical scan was collected, participants completed a "refresher" block of their second task (altercentric: 40 trials or egocentric: 56 trials). During the final two runs of functional scanning, participants completed two blocks of their second task (altercentric: 80 trials per block or egocentric: 112 trials per block). Altercentric and egocentric trials were organized into separate blocks to avoid task-switching costs, and the order of the two tasks (altercentric first or egocentric first) was counterbalanced across participants.

The experiment was performed in a 3T Phillips Achieva scanner using an 8 channel-phased array head coil with 38 slices per TR (3 mm thickness); TR: 2500 ms; TE: 40 ms; flip angle: 80°; field of view: 24 cm, matrix: 80 × 80. In total, 188 images were collected and stored for the egocentric blocks and 169 images were collected and stored for the altercentric blocks. Data were realigned, unwarped, corrected for slice timing, normalized to the Montreal Neurological Institute (MNI) template with a resolution of 3 × 3 × 3 mm and spatially smoothed (8 mm) using SPM8 software. A design matrix was fitted for each subject, with one regressor for each of the three trial types for the altercentric condition and one regressor for each of the four trial types for the egocentric condition (see Figure 2a for a summary of experimental conditions). In addition, the orientation of the actor (40°, 80°, 120°, or 160°) on each trial was modeled as a parametric regressor on that trial type. In a second design matrix, an additional regressor was added that included mean centered RT as a parametric variable according to the variable impulse model (Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008; Yarkoni, Barch, Gray, Conturo, & Braver, 2009). This second design matrix enabled comparison between results with and without the inclusion of RTs as a covariate (Yarkoni et al., 2009). Each trial was modeled as a boxcar with the duration of that event convolved with the standard hemodynamic response function. SPM8 was used to compute parameter estimates (beta) and contrast images (containing weighted parameter estimates) for each comparison at each voxel.

Three sets of contrasts were calculated to evaluate our three questions. First, for the egocentric and altercentric blocks separately, we compared VPT task (collapsed across reach and no-reach conditions) to the baseline condition. Thus, we evaluated: [(AVR + AVN) > 2 × AB] and [(EVR + EVN) > 2 × EB] (see Figure 2a for abbreviations). To identify brain regions involved in both the egocentric and altercentric tasks, we displayed both contrasts on the same template brain and examined visible overlap, which is equivalent to a formal conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005). In addition, to identify brain regions that show a preferential response to one type of VPT task, we evaluated the interaction between VPT-task and condition, that is, [(AVRN – 2 × AB) > (EVRN – 2 × EB)] and its inverse (where AVRN is altercentric visual perspective reach and no-reach and EVRN is egocentric visual perspective reach and no-reach).

Second, we tested for the effects of actor orientation by examining the parametric modulators in the egocentric and altercentric blocks. This identifies brain regions where BOLD signal increases or decreases linearly with increases in actor orientation. Due to a lack of power, we did not analyze the influence of actor orientation separately based on the actor's laterality (i.e., whether the actor was on the left or right side of the table); instead, we collapsed the orientation analyses across actor laterality. Again, we identified brain regions that were sensitive to actor orientation in both egocentric and altercentric tasks by visualizing the overlap of the two orientation contrasts on the same brain template. We also examined if any brain regions showed a preference to orientation in one VPT-task (A-Orient > E-Orient, and its inverse), as well as for reach compared to no-reach conditions (AVR-Orient > AVN-Orient, and the ego equivalent).

Third, we compared the reach condition to the no-reach condition to test for brain regions engaged in the VPT condition that are also modulated by the actor's reaching action. As before, we first calculated this contrast for each VPT-task separately, that is, (AVR > AVN) and (EVR > EVN). We then examined the visual overlap of these two contrasts to locate brain regions selective for observation of reaching in both tasks. Finally, we calculated the interaction between VPT-task and reach [(AVR – AVN) > (EVR – EVN)] and its inverse. These interaction contrasts identify brain regions that preferentially respond in one type of VPT-task and are modulated by the actor's reaching behavior.

Contrast images for all the participants were taken to the second level for random effects analysis. Correction for multiple comparisons was performed at the cluster level (Friston, Worsley, Frackowiak, Mazziotta, & Evans, 1994), using a voxel-level threshold of $p < .001$ and 20 voxels and a family-wise error (FWE) cluster-level correction of $p < .05$. For each contrast, brain regions surviving the voxel-level threshold are reported in tables with regions surviving the FWE cluster-correction highlighted in boldface font. We only interpret and illustrate responses that either survived whole-brain cluster-correction or those that were consistent with our *a priori* predictions. Brain regions were localized using an online search tool (http://sumsdb.wustl.edu/sums/) and the SPM Anatomy toolbox (Eickhoff et al., 2005). For the purpose of illustration, parameter estimates were extracted from a 10-mm sphere focused on peak coordinates of each contrast and plotted within Figures 4–7. When more than one cluster is visible, white circles are used to highlight which cluster's parameter estimates are displayed.

RESULTS

Behavioral data

Reaction time

RTs on correct trials were averaged over the two scanner blocks for each task and each participant (Figure 3a). These data were submitted to a repeated measures ANOVA with task (egocentric and altercentric), condition (reach and no reach), and orientation (40°, 80°, 120°, and 160°) as within-subjects factors. The results showed a significant main effect of the task, $F(1,19) = 89.870$, $p < .001$, partial $\eta^2 = .825$, with faster RTs in egocentric than altercentric blocks. There were also main effects of condition, $F(1,19) = 9.712$, $p = .006$, partial $\eta^2 = .338$, with slower RTs when the actor is reaching compared to when he is still, and orientation, $F(3,57) = 3.078$, $p = .035$, partial $\eta^2 = .139$. The task × condition $F(1,19) = 3.810$, $p = .066$, partial $\eta^2 = .167$ and task × orientation $F(3,57) = 2.697$, $p = .054$, partial $\eta^2 = .124$ interactions approached significance. There were no condition × orientation or task × condition × orientation interactions ($p > .1$ in both cases).

To explore the task × condition and task × orientation interactions, the RT data were submitted to two further ANOVAs, separated by task (egocentric and altercentric). In both cases, condition (reach and no reach) and orientation (40°, 80°, 120°, and 160°) were within-subjects factors. For the egocentric task, there was a significant main effect of condition

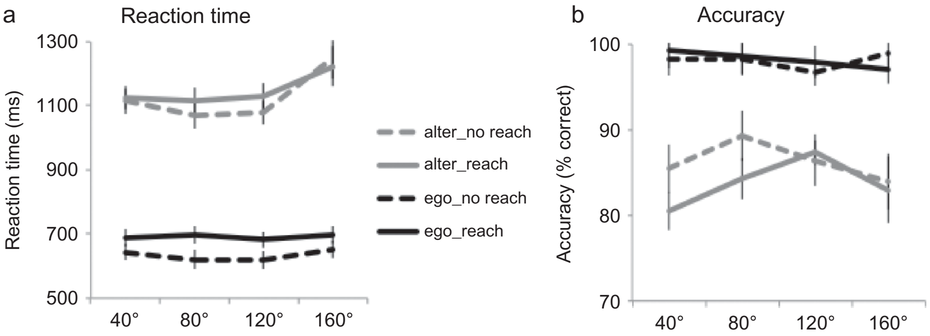


Figure 3. Behavioral results. (a) Mean reaction time for correct trials and (b) mean error rate for each task are illustrated.

$F(1,19) = 24.659, p < .001$, partial $\eta^2 = .565$, showing that participants were slower when the actor is reaching relative to when he is still (Figure 3a). The main effect of orientation and the interaction between condition and orientation were not significant ($p > .4$ in both cases).

For the altercentric task, the main effect of orientation was significant, $F(3,57) = 3.104$, $p = .034$, partial $\eta^2 = .140$, while the main effect of condition and the interaction between condition and orientation were not significant (Figure 3a). *Post hoc* comparisons (paired *t*-tests) between different levels of orientation showed slower RTs at 160° compared to 120° ($t = -2.600; p = .018$) and 80° ($t = -2.266; p = .035$) (Figure 3a). No other comparisons between different levels of orientation were significant ($p > .1$ in all cases).

Accuracy

Accuracy data were analyzed with a repeated measures ANOVA with task (egocentric and altercentric), condition (reach and no reach), and orientation (40°, 80°, 120° and 160°) as within-subjects factors. The results showed a significant main effect of the task, $F(1,20) = 19.353$, $p < .001$, partial $\eta^2 = .492$, with more accurate responses in the egocentric than altercentric blocks (Figure 3b). There were no main effects of condition, orientation and no interactions between any factors ($p > .1$ in all cases).

fMRI data

Our analysis of the functional imaging data aimed to reveal both similarities and differences in the BOLD response associated with the egocentric and the altercentric VPT tasks, as well as the reach and no-reach conditions. Thus, we calculated contrasts for each task separately (altercentric: Table 1; egocentric: Table 2). Further, any significant interactions between VPT-task, orientation, and/or reach are reported in Tables 3 and 4. In what follows, we only describe the contrasts that are relevant to our three main questions, which are summarized in Figure 2b.

Brain regions involved during VPT

Compared with baseline, the altercentric task engaged bilateral inferior occipital gyrus extending into fusiform gyrus and lateral occipitotemporal cortex, intraparietal sulcus (IPS) and dorsal premotor cortex (PMd) (Figure 4a and Table 1). Comparing the egocentric task to baseline showed the engagement of bilateral inferior occipital gyrus extending into fusiform gyrus and lateral occipitotemporal cortex, as well as right IPS (Figure 4b and Table 2). Overlap between the two contrasts was observed in bilateral lateral occipitotemporal cortex and right IPS (Figure 4c).

A test of the interaction between the tasks [(AVRN – 2 × AB) > (EVRN – 2 × EB)] revealed that left anterior IPS extending into middle IPS, as well as posterior parts of inferior frontal gyrus (IFG) and middle frontal gyrus (adjacent to premotor cortex) showed more engagement in the altercentric condition compared to the egocentric condition (Figure 5a and Table 3). Curiously, inspection of the parameter estimates also suggested that baseline responses differed in these regions. This surprising pattern of data is discussed later. The inverse interaction contrast, which tested for greater responses in the egocentric than the altercentric task (compared with baseline), revealed engagement of right anterior superior temporal gyrus/insula and right parahippocampal gyrus (Figure 5b and Table 3).

TABLE 1
Brain regions engaged during the altercentric condition

				MNI co-ordinates		
Region	*BA*	*Number of voxels*	*T*	*x*	*y*	*z*
Altercentric VPT-Task contrasts						
(a) Reach > Baseline						
Right OT		**1024**	**9.76**	**48**	**−70**	**10**
				48	**−73**	**−11**
				45	**−64**	**−17**
Left OT		**1366**	**9.50**	**−51**	**−76**	**1**
				−18	**−94**	**−11**
				−39	**−79**	**−20**
Right middle IPS/SPL	**7**	**227**	**6.77**	**15**	**−67**	**52**
				27	**−79**	**46**
				39	**−46**	**43**
Left SFS	**6**	**211**	**6.26**	**−24**	**−1**	**49**
				−39	**−1**	**49**
Right SFS	**6**	**115**	**5.41**	**24**	**2**	**55**
				36	**2**	**52**
Left IFG/MFG	**45/46**	**94**	**4.95**	**−39**	**20**	**22**
				−54	**23**	**28**
				−42	**5**	**28**
(b) No reach > Baseline						
Left OT		**859**	**8.45**	**−51**	**−76**	**1**
				−21	**−94**	**−11**
				−36	**−49**	**46**
Right OT		**767**	**7.26**	**48**	**−70**	**10**
				48	**−67**	**−5**
				18	**−97**	**−8**
Right medial SFS	**6**	**129**	**6.41**	**27**	**−1**	**55**
				39	**2**	**49**
Left medial SFS	**6**	**174**	**6.20**	**−27**	**−1**	**52**
Right posterior IPS	**7**	**124**	**5.56**	**15**	**−64**	**55**
				27	**−79**	**46**
				18	**−64**	**43**
Right middle IPS	40/7	47	5.31	39	−46	43
(c) Reach and no reach > Baseline						
Left lateral OT extending into IOG/posterior fusiform gyrus and IPS		**1221**	**9.47**	**−51**	**−76**	**1**
				−21	**−94**	**−11**
				−36	**−49**	**46**
Right lateral OT extending into IOG/posterior fusiform gyrus		**954**	**9.33**	**48**	**−70**	**10**
				48	**−73**	**−11**
				18	**−100**	**−8**
Right middle SPL/middle IPS	**7**	**219**	**6.36**	**15**	**−67**	**52**
				27	**−79**	**46**
				39	**−46**	**43**
Left medial SFS/PMd	**6**	**197**	**6.34**	**−27**	**−1**	**52**
Right medial SFS/PMd extending laterally	**6**	**134**	**6.25**	**27**	**−1**	**58**
				39	**2**	**49**
Left anterior IFG/MFG		30	4.25	−51	23	34
				−39	17	22
				−48	20	25
Orientation contrasts						
(d) Orientation (positive)						
Left posterior IFG adjacent to PMv	44	50	6.43	−60	8	22
				−54	11	16
Left IOG/OT		**63**	**6.19**	**−27**	**−94**	**−11**
				−30	**−97**	**1**
				−39	**−85**	**−14**
Left dmPFC/middle cingulate cortex		45	5.36	−6	11	46

(*Continued*)

TABLE 1
(Continued)

Region	BA	Number of voxels	T	*MNI co-ordinates*		
				x	*y*	*z*
Right IOG/OT		**59**	**5.35**	**24**	**−94**	**−11**
				39	**−85**	**−17**
dmPFC/(SMA/preSMA)		25	4.29	3	2	61
				0	11	61
				−9	−1	64
(e) Orientation (negative)						
Bilateral medial IOG/lingual gyrus		**333**	**7.95**	**12**	**−79**	**−14**
				−15	**−88**	**−2**
				−15	**−76**	**−8**
Right SOG/parieto-occipital cortex		23	5.13	24	−82	22
Left MOG		51	5.10	−21	−94	16
(f) Orientation X Reach				−18	−82	22
No suprathreshold clusters						
Reach contrast						
(g) Reach > No reach						
Right lateral OT extending into IOG and anterior fusiform gyrus		**679**	**9.63**	**54**	**−67**	**1**
				45	**−70**	**−2**
				30	**−88**	**−17**
Left lateral OT extending into IOG and anterior fusiform gyrus		**601**	**7.31**	**−51**	**−73**	**−2**
				−33	**−91**	**−17**
				−45	**−49**	**−26**

Notes: Only regions surviving a voxel-level threshold of $p < .001$ and 20 voxels are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed. Boldface font indicates clusters that survive FWE $p < .05$ cluster-correction.

Abbreviations: dmPFC, dorsomedial prefrontal cortex; OT, occipitotemporal cortex; I/M/S OG, inferior/middle/superior occipital gyrus; SMA, supplementary motor area; I/M/S FG, inferior/middle/superior frontal gyrus; PMv/d, ventral/dorsal premotor cortex; SFS, superior frontal sulcus; IPS, intraparietal sulcus; MNI, Montreal Neurological Institute

Brain regions modulated by actor orientation

The effects of actor orientation were modeled as parametric modulators on each VPT-task, collapsed across reach and no-reach conditions. For altercentric and egocentric blocks separately, we evaluated brain regions that showed an increase in BOLD response with increasing angular distance (positive correlation) as well as a decrease in BOLD response with increasing angular distance (negative correlation). In the altercentric task, the positive correlation revealed a response bilaterally in inferior occipital gyrus extending into occipitotemporal cortex, left posterior IFG adjacent to ventral premotor cortex (PMv), as well as dorsomedial prefrontal cortex (dmPFC) extending into middle cingulate cortex (Figure 6b and Table 1d). A negative correlation was found in bilateral medial inferior occipital gyrus. In the egocentric task, the positive correlation revealed responses in bilateral inferior/middle occipital gyrus, parahippocampul gyrus, and right middle IFG (Figure 6c and Table 2d). The negative correlation showed no responses. Overlap between the altercentric and egocentric positive correlations emerged in bilateral inferior occipital gyrus (Figure 6d).

We also tested for differential effects of actor orientation between VPT tasks. The BOLD response in middle cingulate cortex extending into superior frontal gyrus and dmPFC showed a greater positive correlation with actor orientation in the altercentric than egocentric VPT task (Figure 6e and Table 4a). The inverse contrast, which tested for a greater positive correlation with increasing actor orientation in the egocentric than the altercentric VPT task, showed responses in bilateral anterior fusiform cortex, left middle occipital gyrus, right parieto-occipital junction, and right posterior and middle IFG (Figure 6f and Table 4b). The response of right IFG in the latter contrast overlapped with a weaker effect of actor orientation observed in the egocentric orientation analysis (Supplementary Figure S1). No regions showed an interaction between the effects of actor orientation and whether the actor was reaching or not reaching.

TABLE 2
Brain regions engaged during the egocentric condition

				MNI coordinates		
Region	*BA*	*Number of voxels*	*T*	*x*	*y*	*z*
Egocentric VPT-task contrasts						
(a) Reach > *Baseline*						
Right medial IOG/lingual gyrus	**18**	**1039**	**10.05**	**21**	**−94**	**−11**
				45	**−76**	**−14**
				45	**−67**	**−14**
Left IOG and MOG	**18/19**	**881**	**7.73**	**−24**	**−91**	**−14**
				−48	**−79**	**1**
				−42	**−52**	**−20**
Right middle IPS/SPL	**7**	**121**	**5.40**	**18**	**−61**	**55**
				30	**−58**	**52**
				30	**−52**	**46**
(b) No reach > Baseline						
Right OT and fusiform gyrus	**37**	**729**	**8.34**	**45**	**−43**	**−23**
				24	**−97**	**−11**
				51	**−76**	**−5**
Left IOG and MOG	**18/19**	**454**	**6.05**	**−24**	**−91**	**−14**
				−45	**−82**	**4**
				−39	**−85**	**−11**
Right posterior IPS/SPL	7	41	5.03	18	−61	55
(c) Reach and No reach > Baseline						
Right IOG extending into fusiform gyrus and lateral OT	**18/19**	**1029**	**8.34**	**24**	**−97**	**−11**
				48	**−73**	**−8**
				42	**−79**	**−14**
Left IOG extending into fusiform gyrus and lateral OT	**18/19**	**755**	**7.32**	**−24**	**−91**	**−14**
				−48	**−79**	**1**
				−42	**−52**	**−20**
Right middle IPS/SPL	**7**	**123**	**6.01**	**18**	**−61**	**55**
				30	**−52**	**46**
Orientation contrasts						
(d) Orientation (positive)						
Left IOG and MOG	**18/19**	**513**	**6.73**	**−24**	**−91**	**−17**
				−36	**−67**	**−14**
Right MOG				**−39**	**−91**	**−8**
	18/19	**532**	**6.48**	**36**	**−88**	**−2**
				36	**−58**	**−20**
				30	**−85**	**−17**
Medial anterior cerebellum/posterior parahippocampul gyrus		24	4.87	−3	−37	−8
Right middle IFG	45	35	4.65	54	29	10
				45	29	13
(e) Orientation (negative)						
No suprathreshold clusters						
(f) Orientation × reach						
No suprathreshold clusters						
Reach contrast						
(g) Reach > No reach						
Left lateral OT extending into IOG/lingual gyrus	**19/37**	**224**	**6.18**	**−48**	**−67**	**−5**
				−45	**−82**	**−2**
				−24	**−97**	**−8**
Right lateral OT	**19/37**	**167**	**5.94**	**48**	**−73**	**−5**

Notes: Only regions surviving a voxel-level threshold of $p < .001$ and 20 voxels are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed. Boldface font indicates clusters that survive FWE $p < .05$ cluster-correction.

Abbreviations as in Table 1.

TABLE 3
Visual perspective taking task interactions

				MNI coordinates		
Region	*BA*	*Number of voxels*	*T*	*x*	*y*	*z*
(a) [(Allo − Allo-Base) > (Ego – Ego-Base)]						
Left aIPS extending into middle IPS	**40/7**	**131**	**5.19**	**−42**	**−43**	**43**
				−36	**−52**	**43**
				−30	**−61**	**37**
Left posterior IFG adjacent to PMv*	44	64	5.00	−45	5	28
Left posterior MFG/SFS adjacent to PMd		32	3.96	−24	2	58
				−24	−1	49
				−27	−7	43
(b) [(Ego − Ego-Base) > (Allo − Allo-Base)]						
Right anterior STG/insula	**22/38**	**78**	**6.08**	**39**	**−1**	**−11**
				36	**−19**	**−5**
Medial SFG		41	5.60	15	50	43
Left anterior MTG*		53	5.56	−54	−13	−20
				−63	−22	−17
Medial orbitofrontal cortex		38	5.33	9	41	−11
Left lateral posterior MTG/STS*		57	5.27	−66	−37	−2
				−66	−25	−2
Right hippocampus/anterior fusiform/parahippocampal gyrus		45	5.17	21	−43	−2
				36	−55	−5
				30	−49	−8
Right parahippocampal gyrus extending into anterior medial cerebellum	**20/28/36**	**79**	**5.02**	**30**	**−19**	**−29**
				24	**−28**	**−29**
				21	**−43**	**−23**
Right lateral posterior STG		27	5.00	57	−34	1
Right inferior occipital gyrus/lingual gyrus		49	4.87	9	−67	−2
				15	−55	4
Left ventromedial PFC extending into medial OFC		27	4.62	−12	53	−2
				−6	53	−14
PCC/precuneus		47	4.58	−6	−58	37
Right ventromedial PFC		28	4.57	9	56	7
				15	65	13
				12	56	−2
Precuneus/cuneus*		58	4.52	−3	−70	19
				−6	−61	19
Left anterior fusiform gyrus		28	4.29	−33	−34	−23

Notes: Only regions surviving a voxel-level threshold of $p < .001$ and 20 voxels are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed. Boldface font indicates clusters that survive FWE $p < .05$ cluster-correction.

Abbreviations as in Table 1. Additionally, PCC = posterior cingulate cortex.

*Approaching cluster-correction ($p < .01$ FWE).

Brain regions modulated by the observation of a reaching actor

In the altercentric task, the reach condition engaged bilateral occipitotemporal cortex extending into inferior occipital gyrus and anterior fusiform gyrus compared to the no-reach condition (Figure 7a and Table 1g). In the egocentric task, the reach condition engaged bilateral occipitotemporal cortex and left inferior occipital gyrus/lingual gyrus compared to the no-reach condition (Figure 7b and Table 2g). These two contrasts overlapped in bilateral occipitotemporal cortex and left inferior occipital gyrus (Figure 7c). The interaction between VPT-task and reaching [(AVR – AVN) > (EVR – EVN)] as well as its inverse showed no responses.

As the main contrasts of interest found effects in bilateral occipitotemporal regions, we again used an overlap analysis to test how these responses relate to one another. Specifically, we tested for brain regions showing a conjunction of six contrasts: AV > AB; A-orient; AVR > AVN; EV > EB; E-orient; and EVR > EVN. This analysis revealed that bilateral occipital clusters responded for all the contrasts

TABLE 4
Orientation × VPT-task interactions

				MNI coordinates		
Region	*BA*	*Number of voxels*	*T*	*x*	*y*	*z*
(a) Allo_orient > Ego_orient						
Left middle cingulate cortex extending into SFG and dmPFC	6/8	28	4.57	−12	8	49
				−21	11	52
				−3	17	52
(b) Ego_orient > Allo_orient						
Left anterior fusiform gyrus extending into lateral occipitotemporal cortex		**341**	**7.16**	**−36**	**−67**	**−14**
				−36	**−76**	**−11**
				−48	**−73**	**−8**
Right MOG extending into IOG and SOG		**201**	**6.55**	**32**	**−82**	**19**
				36	**−85**	**4**
				33	**−85**	**31**
Right anterior fusiform gyrus extending into lateral occipitotemporal cortex		**266**	**5.47**	**33**	**−52**	**−17**
				30	**−76**	**−17**
				48	**−61**	**−23**
Left MOG		**116**	**5.32**	**−36**	**−88**	**13**
				−21	**−97**	**10**
				−30	**−88**	**22**
Right posterior extending into middle IFG	**44/45**	**79**	**5.21**	**48**	**8**	**25**
				48	**17**	**13**
				51	**29**	**16**

Notes: Only regions surviving a voxel-level threshold of $p < .001$ and 20 voxels are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed. Boldface font indicates clusters that survive FWE $p < .05$ cluster-correction.

Abbreviations as in Table 1.

(Supplementary Figure S2). Therefore, these areas show sensitivity to both VPT tasks compared to baseline, when seeing a reaching actor compared to a non-reaching actor and to the orientation of the observed actor.

We also evaluated all of the contrasts presented above based on a second design matrix, which included RT as an additional regressor (Grinband et al., 2008; Yarkoni et al., 2009). These results were similar in all respects to the results reported above; the only differences were small changes in alpha values. This additional analysis suggests that when RTs have been "covaried out" of the design matrix, there is little influence on the pattern of results. Therefore, we do not report results from this additional analysis.

DISCUSSION

In everyday life, taking another's visual perspective and making sense of their actions are critical processes that guide social behavior. Prior neuroimaging experiments have examined the neural substrates involved in VPT and action perception separately, whereas the current study examined the brain regions underlying the interaction of these social processes. Consistent with prior findings, we found a distributed set of brain regions to be engaged in VPT, with overlapping as well as distinct responses in occipitotemporal, parietal, and frontal cortices for altercentric and egocentric judgments. Localization of brain regions showing parametric modulation of BOLD response with actor orientation provides a novel insight into VPT judgments. The BOLD response in dmPFC was sensitive to actor orientation in the altercentric task, whereas the response in right IFG was sensitive to actor orientation in the egocentric task. These parametric analyses suggest that dmPFC and right IFG may play distinct but complementary roles during VPT, which will be discussed in detail below. Finally, observation of a reaching actor engaged occipitotemporal cortex, as expected, but no specific brain regions showed an interaction between action observation and VPT task. This suggests that the processes linking the observation of other's actions and the adoption of their visual perspective are distributed across the brain rather than in one focal region. Following the structure outlined above, we focus our discussion on the three core questions that we outlined in the introduction, which are summarized in Figure 2b. Before touching on the neuroimaging results, we briefly review the behavioral findings.

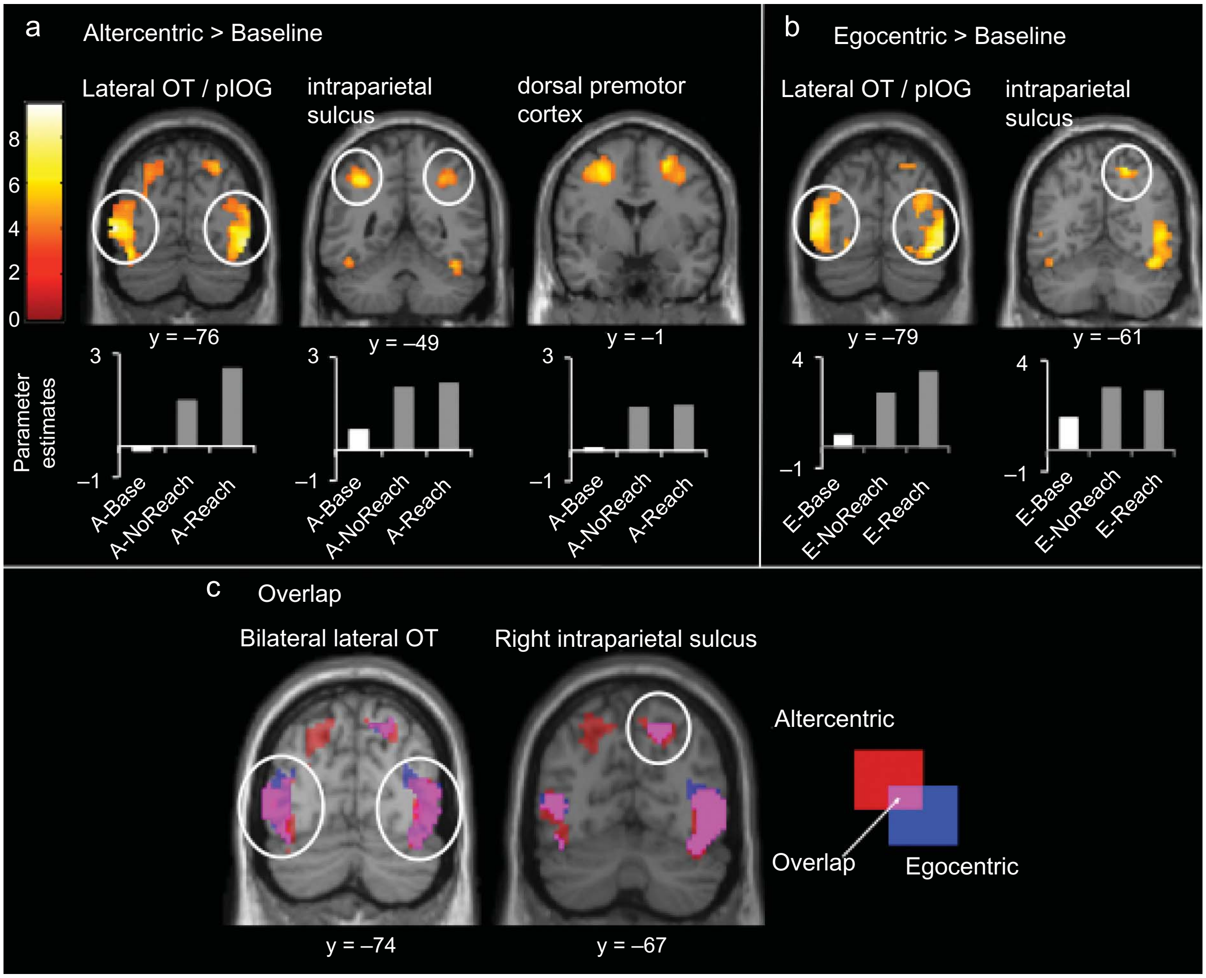


Figure 4. Brain areas activated by altercentric (a) and egocentric (b) tasks compared with baseline, as well as overlap between these two contrasts (c). Abbreviations as Table 1.

Behavioral findings

Participants were faster when taking their own point of view (egocentric perspective) compared to the actor's point of view (altercentric perspective) (David et al., 2006; Kockler et al., 2010; Vogeley et al., 2004). This result is in line with the suggestion that taking another's perspective requires extra cognitive effort when compared with using information gained from one's own viewpoint (Kessler & Thomson, 2010; Shelton & McNamara, 1997). Moreover, we found that in the altercentric task, but not in the egocentric task, RTs showed a dependence on the angle of rotation of the actor: RTs increased with increasing actor's orientation (Kockler et al., 2010). Specifically, this increment was visible only at higher degrees of actor orientation (160° compared to 80° and 120°), while no significant differences were revealed at 40° compared to the other orientations. The absence of significant differences between 40° and higher actor orientations is unexpected. We suggest that the 40° orientation may have been more difficult than expected because the orange was harder to see in the reach-40° photos, where the actor's hand partially occluded the orange.

Participants were also more accurate when performing the egocentric task than the altercentric task, which is consistent with prior work (e.g., Vogeley et al., 2004) and confirms that there is no speed–accuracy tradeoff in our data. The difference in accuracy and RT between conditions supports the suggestion that altercentric tasks are more cognitively demanding than egocentric tasks. Our fMRI analysis is able to take account of this by modeling RT as an additional regressor in our design in such a way that time spent on the task can be accounted for and thus not influence our results (Grinband et al., 2008; Yarkoni et al., 2009).

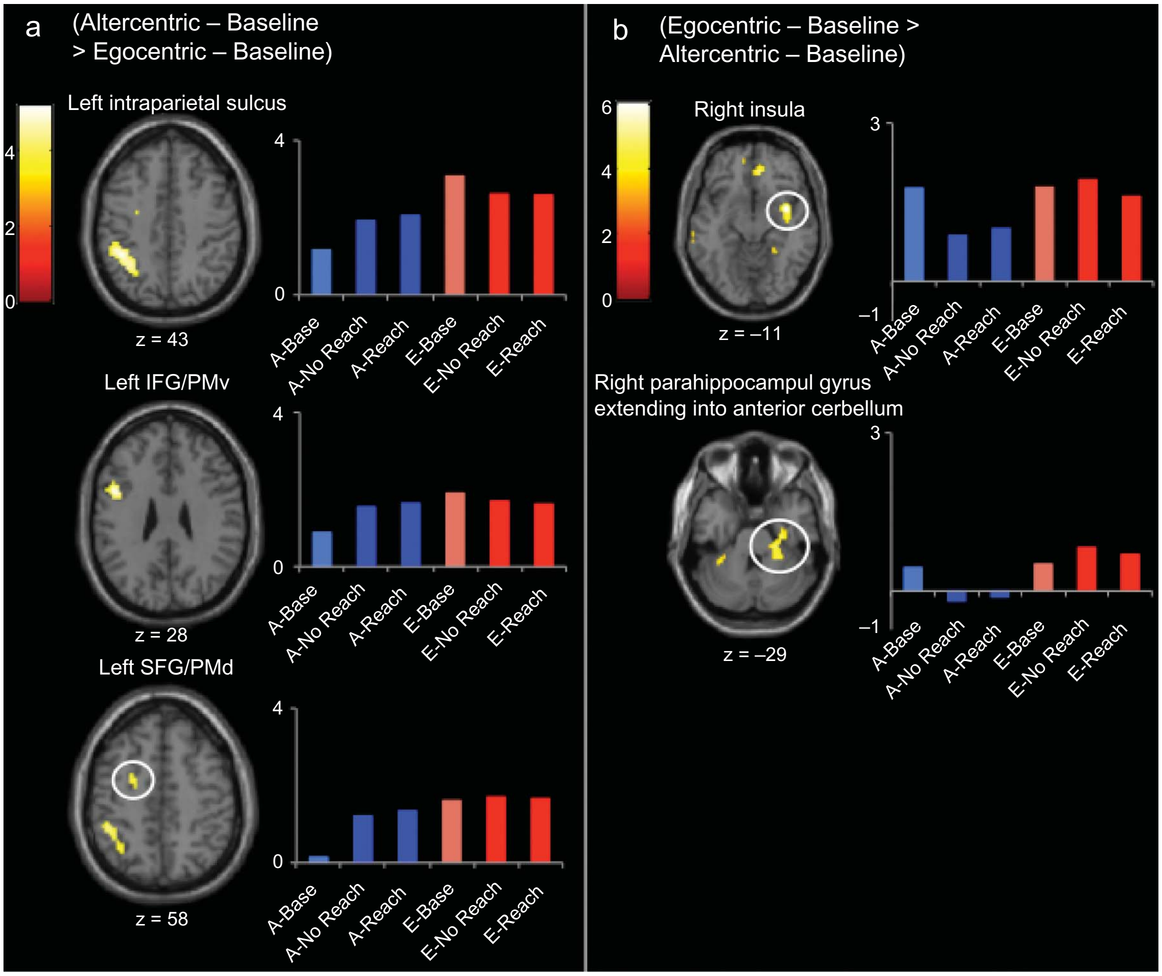


Figure 5. Brain regions showing differential activation in the two VPT tasks. (a) Regions showing greater activity in altercentric VPT relative to baseline, compared with egocentric VPT against baseline. (b) Regions showing greater activity in egocentric VPT relative to baseline, compared with altercentric VPT relative to baseline. Abbreviations as Table 1.

fMRI findings

Which brain regions are involved in egocentric and altercentric VPT?

Previous studies investigating the brain systems involved during VPT have used a variety of tasks, identifying common brain regions engaged in all VPT tasks as well as distinct regions contributing to egocentric and altercentric VPT (Zaki & Ochsner, 2011). In our dataset, occipitotemporal cortex and right superior parietal lobule were engaged in both altercentric and egocentric VPT tasks when compared with baseline. This is consistent with previous reports that compare VPT tasks to a simple baseline condition (Keehner et al., 2006; Macuga & Frey, 2011; Vogeley et al., 2004; Wraga et al., 2005; Zaehle et al., 2007). It suggests that these brain regions subserve common VPT processes that are engaged when making judgments from both egocentric and altercentric spatial perspectives, such as processing visuospatial relations between agents and objects in the environment (Vogeley et al., 2004).

Considering our altercentric task, an interaction between altercentric and egocentric task performance was found in left anterior IPS, as well as posterior parts of IFG and middle frontal gyrus (adjacent to premotor cortex) with greater engagement of these regions during altercentric VPT. In previous studies, lateral frontal and parietal cortices have been linked to altercentric VPT (David et al., 2006; Kockler et al., 2010; Vogeley et al., 2004). These lateral frontoparietal responses could reflect processes involved in mentally transforming one’s spatial location (Wraga, Boyle et al., 2010; Wraga, Flynn et al., 2010), as well as referencing an object in relation to

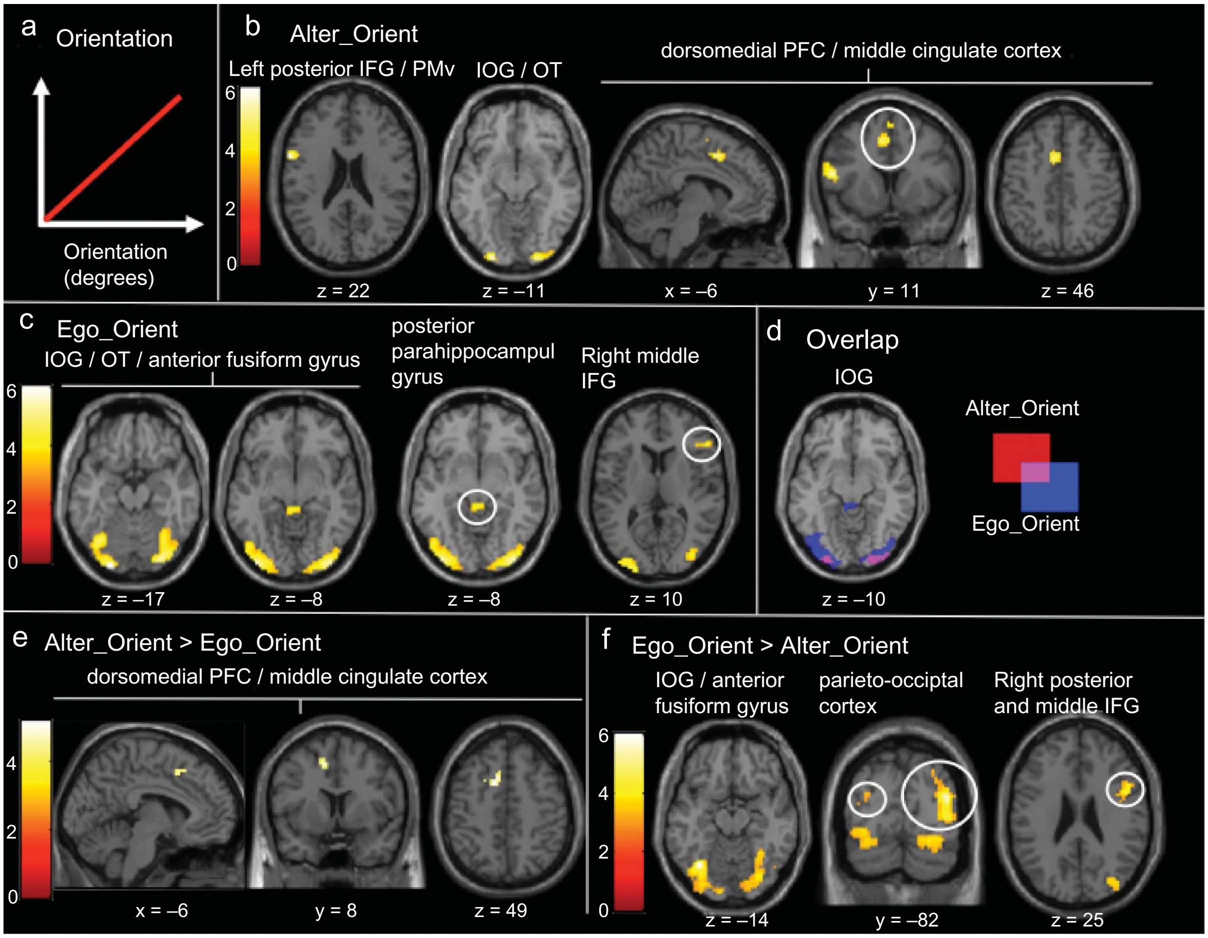


Figure 6. **Effects of actor orientation.** (a) Summary of the relationship tested by this parametric analysis. (b) Regions where BOLD correlates with actor orientation in the altercentric task. (c) Regions where BOLD correlates with actor orientation in the egocentric task. (d) These contrasts overlap in inferior occipital gyrus. (e) dmPFC shows a stronger correlation with actor orientation in the altercentric task than in the egocentric task. (f) Occipital regions and right IFG show a stronger correlation with actor orientation in the egocentric task than in the altercentric task. Abbreviations as in Table 1.

a person's midline (for a review, see Galati, Pelle, Berthoz, & Committeri, 2010). Alternatively, such responses could reflect processes involved in selecting a relevant over an irrelevant visual perspective, which also engages lateral frontoparietal cortex (McCleery, Surtees, Graham, Richards, & Apperly, 2011; Ramsey et al., in press). However, one caveat must be made concerning these results. Close examination of parameter estimates (Figure 5a) suggests that activation during the baseline task (press both keys on seeing a blank table) differed between the egocentric and altercentric blocks. This makes it hard to give a clear interpretation of the greater activation of frontal and parietal cortices in the altercentric VPT task. However, it does demonstrate the importance of using a within-block baseline in fMRI studies (Henson, 2006), rather than making direct comparisons across task blocks that are spaced further apart in time. The latter approach, which has been adopted in some VPT studies, might give misleading results.

Contrasting the egocentric task with the altercentric task revealed an interaction in right anterior insula and right parahippocampal gyrus. Both of these regions showed a deactivation relative to the baseline task during the altercentric task and an increase relative to the baseline task in the egocentric task. This is consistent with previous results. Lambrey and colleagues (2012) studied a task where participants had to imagine themselves moving around a table, or imagine the table rotating. They report stronger activation of the insula and hippocampus when imagining self-rotation. Similarly, Wraga and colleagues (2005) report stronger insula activation in a task requiring self-rotation compared to the one requiring object-rotation. One possible interpretation of these results is in terms of the use of stable landmarks. In a review

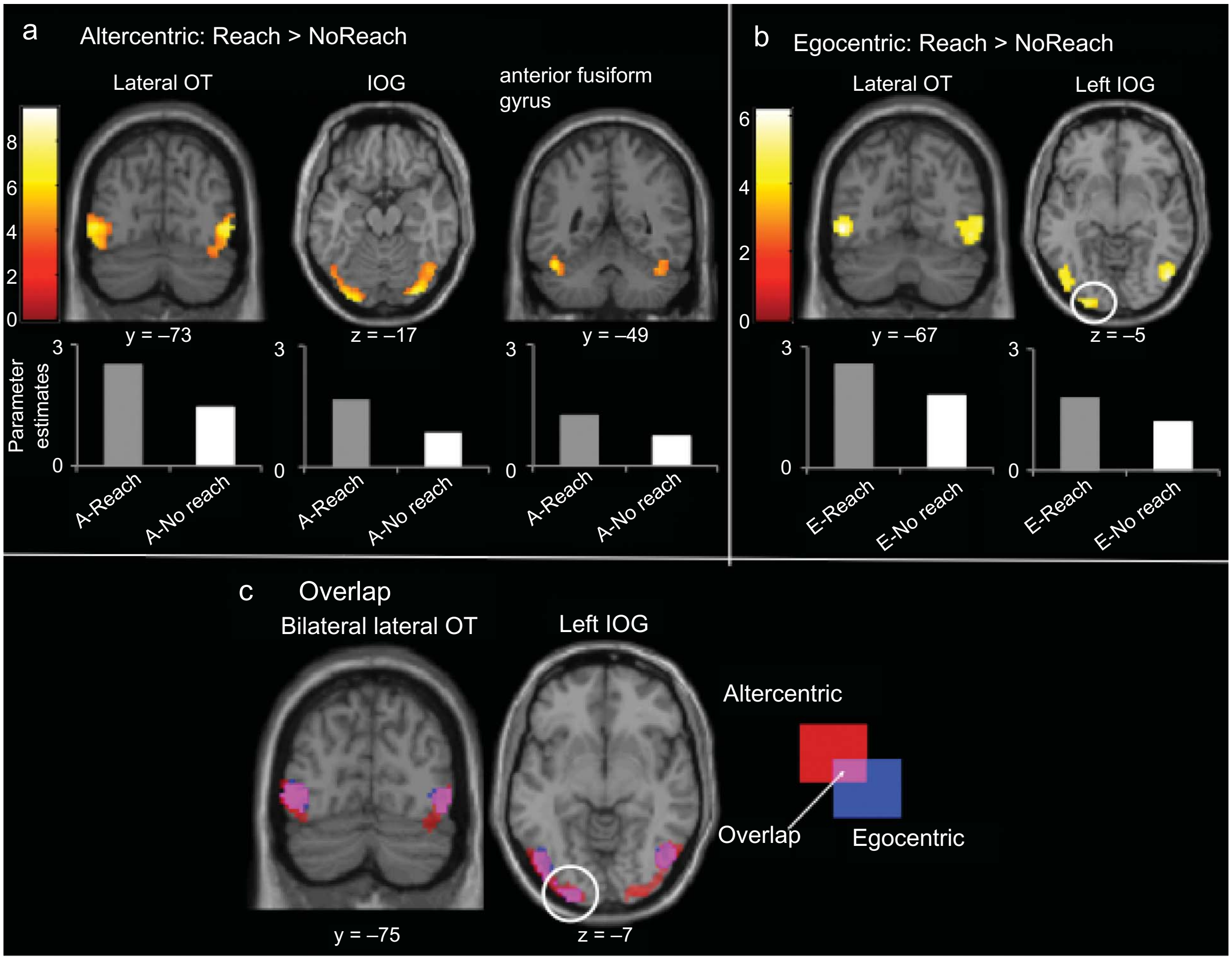


Figure 7. Effects of viewing a reaching actor. Reach > no-reach in the altercentric task (a) and reach > no-reach in the egocentric task (b), both reveal engagement of occipitotemporal regions. There was overlap between these two contrasts in occipitotemporal cortex (c). Abbreviations as Table 1.

of recent fMRI studies, Galati and colleagues (2010) suggest that medial temporal gyri and precuneus are activated whenever a reference to a familiar environment or a stable landmark is required. The egocentric task might place more demands on the use of the table as a stable landmark than the altercentric task, which requires a change of visual perspective. This suggestion is consistent with the view that multiple spatial reference frames are involved in spatial reasoning (Galati et al., 2010) and highlights the consideration of spatial reference frames during VPT judgments (body vs. external) in addition to the target of VPT judgments (i.e., self or other).

Overall, our examination of altercentric and egocentric VPT yields results that are largely consistent with previous studies, despite the differences in stimulus sets and tasks used across research labs. This provides a solid basis for moving on to consider the novel questions of brain systems encoding the actor's orientation and reaching actions.

Which brain regions are sensitive to actor orientation?

Our analysis of the BOLD signal in relation to the position of the actor yielded novel findings. When taking the actor's visual perspective, increasing angular disparity between the participant and actor positively correlated with BOLD signal in bilateral occipitotemporal regions, left IFG adjacent to PMv, and in dmPFC, at the border of the middle cingulate cortex. The response in dmPFC adjacent to middle cingulate cortex also showed a significantly greater orientation response in the altercentric task than in the egocentric task. Since previous fMRI studies examining neural responses that parametrically vary with actor orientation have reported mixed results (Keehner et al., 2006; Wraga, Flynn et al., 2010), the current results provide the most robust evidence to date that demonstrates how dmPFC is involved in mental transformations during VPT. By parametrically varying actor orientation, the result demonstrates that the engagement of dmPFC is related to the varying demands placed on mental self-rotation. This result further delineates the nature of dmPFC involvement during VPT. Rather than responding in a categorical manner during instances of imagined self-rotation, dmPFC is sensitive to the amount of imagined self-rotation required during VPT.

The response in dmPFC is particularly interesting because several previous studies have implicated this brain region in tasks involving motor imagery and perspective transformations. Previous neuroimaging studies have shown that motor imagery (i.e., imagery of oneself performing actions in the absence of overt movement; Jeannerod, 1994) engages dmPFC as well as middle cingulate cortex (for a review, see Munzert, Lorey, & Zentgraf, 2009). The engagement of dmPFC has also been reported in VPT studies when tasks require imagined self-rotation (Creem et al., 2001; Wraga et al., 2005). Self-rotation during VPT has similar properties to motor imagery; in both the cases, one has to imagine the movement of one's own body. We suggest that engagement of dmPFC in both VPT and motor imagery tasks could reflect a common process involving imagery of movements. Further, using connectivity analyses, dmPFC has been shown to exert a suppressive influence on primary motor cortex during motor imagery and self-rotation (Chen, Yang, Liao, Gong, & Shen, 2009; Dinomais et al., 2009; Gao, Duan, & Chen, 2011; Kasess et al., 2008; Solodkin, Hlustik, Chen, & Small, 2004). Therefore, in the current study, as more self-rotation is required with increasing angular disparity between the participant and actor, a greater demand could be placed on suppressing the urge to actually rotate one's body.

Our data also revealed that fusiform and occipital cortices, as well as right IFG are engaged with increasing actor orientation in the egocentric task, when participants must respond from their own visual perspective. The egocentric task does not require mental self-rotation, but may demand that participants inhibit the automatic consideration of the actor's perspective (Cohen & German, 2009; Kovács et al., 2010; Ramsey et al., in press; Samson et al., 2010). Fusiform and occipital responses may be unspecific to VPT and relate encoding of the actor's position in the visual image, as well as the reorienting of attention to the spatial location of the actor (Martinez et al., 1999; Wandell, Brewer, & Dougherty, 2005). In contrast, lateral prefrontal cortex has been linked to a key process in perspective taking: inhibition of irrelevant self (Samson et al., 2005; van der Meer et al., 2011; Vogeley et al., 2001) and other perspectives (McCleery et al., 2011; Ramsey et al., in press). Specifically, Ramsey and colleagues (in press) showed that bilateral lateral frontoparietal cortices are involved in selecting self over other visual perspectives, as well as selecting other over self visual perspectives. These previous results may suggest that the involvement of lateral prefrontal cortex may reflect the need to inhibit an alternative visual perspective in the egocentric task. At higher angular disparities between the participant and the actor, the actor's spatial viewpoint is increasingly discrepant from participants' viewpoint. Greater discrepancy in visual perspective content may lead to more interference to one's own left/right judgment. Thus, in the egocentric task, greater demands could be placed on resisting interference form the irrelevant other's visual perspective as the actor moves around the table (Kovács et al., 2010; Samson et al., 2010).

Based on these data, we suggest that there could be multiple inhibitory mechanisms involved during VPT: "action inhibition" would suppress the tendency to actually move one's body, whereas "perspective content inhibition" would suppress conflicting content of a competing viewpoint. The current data may suggest that these inhibitory processes can be differentially engaged by altercentric and egocentric judgments. The altercentric condition engages a process of mental self-rotation and a concurrent inhibitory mechanism to suppress a tendency to actually move (action inhibition), and there is growing evidence that this is performed in dmPFC and middle cingulate cortex (Chen et al., 2009; Dinomais et al., 2009; Gao et al., 2011; Kasess et al., 2008; Solodkin et al., 2004). In the egocentric condition, there is no need for action inhibition as mental self-rotation is not required. Instead, one has to inhibit the actor's irrelevant visual perspective (perspective content inhibition) and select one's own viewpoint, and evidence suggests that this engages lateral frontal and parietal cortices (McCleery et al., 2011; Ramsey et al., in press). This is consistent with the idea that perspective taking involves multiple neurocognitive "routes," which are engaged flexibly depending on the social context (Perner & Leekam, 2008; Samson & Apperly, 2010). Overall, our examination of BOLD signal in relation to actor orientation provides new insights into how participants imagine a scene from another visual perspective and report on a scene from their own perspective.

One possible limitation of our results in these correlations between actor orientation and BOLD signal is the fact that RT was not always linearly related to actor orientation (Figure 3a). RTs were slower than expected in the 40° orientation, and were not linear overall. As stated above, it is possible that this occurred because it might be harder to see the orange in the reach-40° photos, where the actor's hand partially occluded the orange. The nonlinear pattern of

RT also provides a major advantage in our fMRI data analysis, because we can be confident that the BOLD signal correlation with actor orientation reflects a true "orientation-dependent" process and not a more general effect of the amount of time spent on task in each trial.

Can we localize an interaction between action observation and VPT?

Our third question focused on the relationship between action observation and VPT. Contrasting observation of a reaching actor to observation of a non-reaching actor yielded activation in lateral occipitotemporal cortex, regardless of the VPT task. Cortical areas within occipitotemporal cortex are known to show greater responses to the observation of static human bodies than inanimate objects (Downing, Jiang, Shuman, & Kanwisher, 2001) and it has been argued that these areas code body shape and posture (Downing & Peelen, 2011). Activation was not seen in other parts of the action observation network, including parietal and premotor cortices (Caspers et al., 2010; Cross et al., 2009; Grafton & Hamilton, 2007). This may not be surprising, however, as we used static images as stimuli rather than movies, which provide more consistent BOLD responses.

More fundamental to addressing our third question, no brain regions showed an interaction between the presence of a reaching actor and VPT task. RT data did not yield any interactions between action and the orientation of the actor, and the substantial RT differences between the egocentric and altercentric tasks make it hard to directly compare RT across VPT task. Prior neuroimaging studies have demonstrated differential responses in occipital and sensorimotor cortices when observing an action from a visual orientation that is consistent with one's own movement rather than another person's (Jackson, Meltzoff, & Decety, 2006; Macuga & Frey, 2011). Such studies have shown how "viewing perspective" can influence neural responses during action observation. However, our data did not reveal any clear interactions between viewing a reaching actor and the different VPT tasks. This means that the data do not provide an immediate or definitive brain-based account of why observing a reaching actor might lead one to adopt another person's viewpoint more readily (Mazzarella, Hamilton, Trojano, Mastromauro, & Conson, 2012; Tversky & Hard, 2009).

Further study of links between action observation and VPT could focus on lateral occipital cortex. This area has been linked to the perception of actions from different orientations (Macuga & Frey, 2011), as well as perceiving body shape and posture (Downing & Peelen, 2011). Our data revealed a substantial overlap between different contrasts in lateral occipital regions (Supplementary Figure 2). These regions show greater activity when participants observe a reaching actor compared to a nonreaching actor, when participants perform the VPT task compared to baseline, and when viewing an actor at an orientation away from the participant's viewpoint. This pattern is similar across both the altercentric and egocentric tasks. These overlapping activation patterns could reflect stimulus-driven processes that are common to all conditions in our study, including representing the actor's body shape, posture, and spatial location in each scene. These signals are likely to be critical inputs to anterior brain systems involved in other processes (Ramsey, van Schie, & Cross, 2011), such as mental rotation and inhibitory processes in the case of this study. This view is consistent with a growing move toward distributed but reciprocally connected models of neural processing in the human brain rather than models that attempt to neatly separate perception and cognition into discrete processes (Friston & Price, 2001; Mesulam, 1990). Further study using functional connectivity analysis would be needed to test this possibility.

CONCLUSION

The current study advances on previous investigations of VPT by considering the roles of actor orientation and observed actions in two closely matched tasks within one fMRI study. The novel results from the analysis of actor orientation highlight the differences between altercentric and egocentric VPT. Altercentric tasks rely on imagined self-rotation and engagement of dmPFC while egocentric tasks require inhibition of the other's visual perspective and engagement of lateral prefrontal cortex. Further study will be required to uncover the relationship between observation of action and the tendency to take different perspectives. Such research will contribute to an integrated understanding of different networks of the social brain across a broader variety of tasks.

Supplementary material

Supplementary material (Figure S1 and Figure S2) is available via the 'Supplementary' tab on the article's online page (http://dx.doi.org/doi=10.1080/17470919.2012.761160).

Original manuscript received 6 September 2012
Revised manuscript accepted 18 December 2012
First published online 24 January 2013

REFERENCES

Aichhorn, M., Perner, J., Kronbichler, M., Staffen, W., & Ladurner, G. (2006). Do visual perspective tasks need theory of mind? *Neuroimage*, *30*(3), 1059–1068.

Birch, S. A. J., & Bloom, P. (2004). Understanding children's and adults' limitations in mental state reasoning. *Trends in Cognitive Sciences*, *8*(6), 255–260.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, *50*(3), 1148–1167.

Chen, H., Yang, Q., Liao, W., Gong, Q., & Shen, S. (2009). Evaluation of the effective connectivity of supplementary motor areas during motor imagery using Granger causality mapping. *NeuroImage*, *47*(4), 1844–1853.

Cohen, A. S., & German, T. C. (2009). Encoding of others' beliefs without overt instruction. *Cognition*, *111*(3), 356–363.

Committeri, G., Galati, G., Paradis, A.-L., Pizzamiglio, L., Berthoz, A., & LeBihan, D. (2004). Reference frames for spatial cognition: Different brain areas are Involved in viewer-, object-, and landmark-centered judgments about object location. *Journal of Cognitive Neuroscience*, *16*(9), 1517–1535.

Creem, S., Downs, T., Wraga, M., Harrington, G., Proffitt, D., & Downs, J. (2001). An fMRI study of imagined self-rotation. *Cognitive, Affective, & Behavioral Neuroscience*, *1*(3), 239–249.

Creem-Regehr, S. H., Neil, J. A., & Yeh, H. J. (2007). Neural correlates of two imagined egocentric transformations. *NeuroImage*, *35*(2), 916–927.

Cross, E. S., Kraemer, D. J. M., Hamilton, A. F. D. C., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex*, *19*(2), 315–326.

David, N., Bewernick, B. H., Cohen, M. X., Newen, A., Lux, S., Fink, G. R., . . . Vogeley, K. (2006). Neural representations of self versus other: Visual-spatial perspective taking and agency in a virtual ball-tossing game. *Journal of Cognitive Neuroscience*, *18*(6), 898–910.

Dinomais, M. l., Minassian, A. T., Tuilier, T., Delion, M., Wilke, M., N'Guyen, S., . . . Menei, P. (2009). Functional MRI comparison of passive and active movement: Possible inhibitory role of supplementary motor area. *NeuroReport*, *20*(15), 1351–1355. doi:1310.1097/WNR.1350b1013e328330cd328343

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*(5539), 2470–2473.

Downing, P. E., & Peelen, M. V. (2011). The role of occipitotemporal body-selective regions in person perception. *Cognitive Neuroscience*, *2*, 186–203.

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, *25*(4), 1325–1335.

Flavell, J. H., Everett, B. A., Croft, K., & Flavell, E. R. (1981). Young children's knowledge about visual perception: Further evidence for the level 1-level 2 distinction. *Developmental Psychology*, *17*(1), 99–103.

Friston, K. J., & Price, C. J. (2001). Dynamic representations and generative models of brain function. *Brain Research Bulletin*, *54*(3), 275–285.

Friston, K. J., Worsley, K. J., Frackowiak, R. S. J., Mazziotta, J. C., & Evans, A. C. (1994). Assessing the significance of focal activations using their spatial extent. *Human Brain Mapping*, *1*(3), 210–220.

Frith, C. D., & Frith, U. (2012). Mechanisms of social cognition. *Annual Review of Psychology*, *63*(1), 287–313.

Galati, G., Pelle, G., Berthoz, A., & Committeri, G. (2010). Multiple reference frames used by the human brain for spatial perception and memory. *Experimental Brain Research*, *206*(2), 109–120.

Gao, Q., Duan, X., & Chen, H. (2011). Evaluation of effective connectivity of motor areas during motor imagery and execution using conditional Granger causality. *NeuroImage*, *54*(2), 1280–1288.

Graf, R. (1994). *Self-rotation and spatial reference: The psychology of partner-centred localisations*. Frankfurt: Peter Lang.

Grafton, S. T., & Hamilton, A. F. (2007). Evidence for a distributed hierarchy of action representation in the brain. *Human Movement Science*, *26*(4), 590–616.

Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*(1), 1–19.

Grinband, J., Wager, T. D., Lindquist, M., Ferrera, V. P., & Hirsch, J. (2008). Detection of time-varying signals in event-related fMRI designs. *NeuroImage*, *43*(3), 509–520.

Henson, R. N. A. (2006). Efficient experimental design for fMRI. In K. J. Friston, J. Ashburner, S. Kiebel, T. Nichols, & W. Penny (Eds.), *Statistical parametric mapping: The analysis of functional brain images* (pp. 193–210). London: Elsevier.

Howard, I. P., & Templeton, W. B. (1966). *Human spatial orientation*. Oxford: John Wiley & Sons.

Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *NeuroImage*, *31*(1), 429–439.

Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, *17*(02), 187–202.

Kasess, C. H., Windischberger, C., Cunnington, R., Lanzenberger, R., Pezawas, L., & Moser, E. (2008). The suppressive influence of SMA on M1 in motor imagery revealed by fMRI and dynamic causal modeling. *NeuroImage*, *40*(2), 828–837.

Keehner, M., Guerin, S. A., Miller, M. B., Turk, D. J., & Hegarty, M. (2006). Modulation of neural activity by angle of rotation during imagined spatial transformations. *NeuroImage*, *33*(1), 391–398.

Kessler, K., & Thomson, L. A. (2010). The embodied nature of spatial perspective taking: Embodied transformation versus sensorimotor interference. *Cognition*, *114*(1), 72–88.

Kockler, H., Scheef, L., Tepest, R., David, N., Bewernick, B. H., Newen, A., . . . Vogeley, K. (2010). Visuospatial perspective taking in a dynamic environment: Perceiving moving objects from a first-person-perspective induces a disposition to act. *Consciousness and Cognition*, *19*(3), 690–701.

Kovács, Á. M., Téglás, E., & Endress, A. D. (2010). The social sense: Susceptibility to others' beliefs in human infants and adults. *Science*, *330*(6012), 1830–1834.

Lambrey, S., Doeller, C., Berthoz, A., & Burgess, N. (2012). Imagining being somewhere else: Neural basis of changing perspective in space. *Cerebral Cortex*, *22*(1), 166–174.

Macuga, K. L., & Frey, S. H. (2011). Selective responses in right inferior frontal and supramarginal gyri differentiate between observed movements of oneself vs. another. *Neuropsychologia*, *49*(5), 1202–1207.

Martinez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., . . . Hillyard, S. A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, *2*(4), 364–369.

Mazzarella, E., Hamilton, A., Trojano, L., Mastromauro, B., & Conson, M. (2012). Observation of other's action but not eye gaze triggers allocentric visual perspective. *The Quarterly Journal of Experimental Psychology*, *65*, 2447–2460. doi: 10.1080/17470218.2012.697905

McCleery, J. P., Surtees, A. D. R., Graham, K. A., Richards, J. E., & Apperly, I. A. (2011). The neural and cognitive time course of theory of mind. *The Journal of Neuroscience*, *31*(36), 12849–12854.

Mesulam, M. M. (1990). Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Annals of Neurology*, *28*(5), 597–613.

Munzert, J., Lorey, B., & Zentgraf, K. (2009). Cognitive motor processes: The role of motor imagery in the study of motor representations. *Brain Research Reviews*, *60*(2), 306–326.

Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J.-B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage*, *25*, 653–660.

Perner, J., & Leekam, S. (2008). The curious incident of the photo that was accused of being false: Issues of domain specificity in development, autism, and brain imaging. *The Quarterly Journal of Experimental Psychology*, *61*(1), 76–89.

Ramsey, R., Hanson, P., Apperly, I. A., & Samson, D. (in press). Seeing it my way or your way: Frontoparietal brain areas sustain viewpoint-independent perspective selection processes. *Journal of Cognitive Neuroscience*. doi:10.1162/jocn_a_00345

Ramsey, R., van Schie, H. T., & Cross, E. S. (2011). No two are the same: Body shape is part of identifying others. *Cognitive Neuroscience*, *2*(3–4), 207–208.

Samson, D., & Apperly, I. A. (2010). There is more to mind reading than having theory of mind concepts: New directions in theory of mind research. *Infant and Child Development*, *19*(5), 443–454.

Samson, D., Apperly, I. A., Braithwaite, J. J., Andrews, B. J., & Bodley Scott, S. E. (2010). Seeing it their way: Evidence for rapid and involuntary computation of what other people see. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(5), 1255–1266.

Samson, D., Apperly, I. A., Kathirgamanathan, U., & Humphreys, G. W. (2005). Seeing it my way: A case of a selective deficit in inhibiting self-perspective. *Brain*, *128*(Pt 5), 1102–1111.

Schwabe, L., Lenggenhager, B., & Blanke, O. (2009). The timing of temporoparietal and frontal activations during mental own body transformations from different visuospatial perspectives. *Human Brain Mapping*, *30*(6), 1801–1812.

Shelton, A., & McNamara, T. (1997). Multiple views of spatial memory. *Psychonomic Bulletin & Review*, *4*(1), 102–106.

Solodkin, A., Hlustik, P., Chen, E. E., & Small, S. L. (2004). Fine modulation in network activation during motor execution and motor imagery. *Cerebral Cortex*, *14*(11), 1246–1255.

Tversky, B., & Hard, B. M. (2009). Embodied and disembodied cognition: Spatial perspective-taking. *Cognition*, *110*(1), 124–129.

van der Meer, L., Groenewold, N. A., Nolen, W. A., Pijnenborg, M., & Aleman, A. (2011). Inhibit yourself and understand the other: Neural basis of distinct processes underlying theory of mind. *NeuroImage*, *56*(4), 2364–2374.

Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., . . . Zilles, K. (2001). Mind reading: Neural mechanisms of theory of mind and self-perspective. *Neuroimage*, *14* (1 Pt 1), 170–181.

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.

Wandell, B. A., Brewer, A. A., & Dougherty, R. F. (2005). Visual field map clusters in human cortex. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1456), 693–707.

Wraga, M., Boyle, H. K., & Flynn, C. M. (2010). Role of motor processes in extrinsically encoding mental transformations. *Brain and Cognition*, *74*(3), 193–202.

Wraga, M., Flynn, C. M., Boyle, H. K., & Evans, G. C. (2010). Effects of a body-oriented response measure on the neural substrate of imagined perspective rotations. *Journal of Cognitive Neuroscience*, *22*(8), 1782–1793.

Wraga, M., Shephard, J. M., Church, J. A., Inati, S., & Kosslyn, S. M. (2005). Imagined rotations of self versus objects: An fMRI study. *Neuropsychologia*, *43*(9), 1351–1361.

Yarkoni, T., Barch, D. M., Gray, J. R., Conturo, T. E., & Braver, T. S. (2009). BOLD correlates of trial-by-trial reaction time variability in gray and white matter: A multi-study fMRI analysis. *PLoS ONE*, *4*(1), e4257.

Zacks, J. M. (2008). Neuroimaging studies of mental rotation: A meta-analysis and review. *Journal of Cognitive Neuroscience*, *20*(1), 1–19.

Zacks, J. M., & Michelon, P. (2005). Transformations of visuospatial images. *Behavioral and Cognitive Neuroscience Reviews*, *4*(2), 96–118.

Zacks, J. M., Vettel, J. M., & Michelon, P. (2003). Imagined viewer and object rotations dissociated with event-related fMRI. *Journal of Cognitive Neuroscience*, *15*(7), 1002–1018.

Zaehle, T., Jordan, K., Wüstenberg, T., Baudewig, J., Dechent, P., & Mast, F. W. (2007). The neural basis of the egocentric and allocentric spatial frame of reference. *Brain Research*, *1137*, 92–103.

Zaki, J., & Ochsner, K. (2011). You, me, and my brain; Self and other representations in cognitive neuroscience. In A. Todorov, S. Fiske, & D. Prentice (Eds.), *Social neuroscience: Toward understanding the underpinnings of the social mind*. Oxford: Oxford University Press.