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Taking perspective into account in a communicative task

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ABSTRACT

Previous neuroimaging studies of spatial perspective taking have tended not to activate the brain's mentalising network. We predicted that a task that requires the use of perspective taking in a communicative context would lead to the activation of mentalising regions. In the current task, participants followed auditory instructions to move objects in a set of shelves. A 2×2 factorial design was employed. In the Director factor, two directors (one female and one male) either stood behind or next to the shelves, or were replaced by symbolic cues. In the Object factor, participants needed to use the cues (position of the directors or symbolic cues) to select one of three possible objects, or only one object could be selected. Mere presence of the Directors was associated with activity in the superior dorsal medial prefrontal cortex (MPFC) and the superior/middle temporal sulci, extending into the extrastriate body area and the posterior superior temporal sulcus (pSTS), regions previously found to be responsive to human bodies and faces respectively. The interaction between the Director and Object factors, which requires participants to take into account the perspective of the director, led to additional recruitment of the superior dorsal MPFC, a region activated when thinking about dissimilar others' mental states, and the middle temporal gyri, extending into the left temporal pole. Our results show that using perspective taking in a communicative context, which requires participants to think not only about what the other person sees but also about his/her intentions, leads to the recruitment of superior dorsal MPFC and parts of the social brain network.

Introduction

"Theory of mind" (ToM) or "mentalising" refers to the ability to make inferences about mental states such as beliefs, desires and intentions. The ability to infer mental states enables us to understand and predict other people's behaviour. Extensive research has investigated the development of ToM. The understanding of mental states develops in a step-wise fashion during the first 4 or 5 years of life (Frith and Frith, 2003). At around 18 months, infants start to recognise that looking at an object is a way of directing attention to that object (Baldwin, 1993; Baldwin and Moses, 1994). At around 2 years, children start to develop level 1 visual perspective taking, that is, the ability to infer which objects someone with a different perspective can or cannot see (Flavell et al., 1981; Masangkay et al., 1974). Level 2 perspective taking requires the understanding that people with different viewpoints have different visual percepts of the same object. Level 2 tasks are usually not passed by children before the age of around 4 years (Masangkay et al., 1974). Children at around the age of 4 also begin to pass false belief tasks (Wimmer and Perner, 1983). False belief tasks typically require the ability to attribute to other individuals' beliefs that are different from our own and from reality. The current study was designed to investigate the neural systems involved in using theory of mind (level 1 perspective taking) in an online communicative task. The communicative nature of the task employed here is more ecologically valid than previous theory of mind tasks employed in neuroimaging experiments. The task is based on a paradigm that results in a high number of errors in healthy adults (Keysar et al. 2003) and continues to develop late in adolescence (Dumontheil et al. 2010).

A number of neuroimaging studies have explored mentalising using a variety of stimuli designed to elicit the attribution of mental states, including stories (Aichhorn et al., 2009; Fletcher et al., 1995; Saxe and Kanwisher, 2003), cartoons (Gallagher et al., 2000) and animations (Castelli et al., 2000). Meta-analyses report a highly circumscribed "mentalising network," which includes the posterior superior temporal sulcus (pSTS), the temporoparietal junction (TPJ), the temporal poles and the medial prefrontal cortex (MPFC) (Frith and Frith, 2003; Gallagher and Frith, 2003; Saxe et al., 2004). Lesion studies have consistently demonstrated that damage to the superior temporal lobes (Samson et al., 2004) and PFC (Happé et al., 2001; Rowe et al., 2001; Stuss et al., 2001) impairs mentalising (although see Bird et al., 2004, for non-replication and Blakemore, 2008, for discussion).

The different brain regions within the mentalising network appear to be associated with different roles in the mentalising process. The STS is claimed to be one of the host brain regions not only for ToM, but also for motion processing, audio-visual integration and face

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processing (in more posterior regions in the superior temporal gyrus (STG)), and speech processing (in more anterior regions in the middle temporal gyrus (MTG)) (see Hein and Knight, 2008, for review). ToM activations do not show specificity for any of these clusters and Hein and Knight (2008) suggest that the function played by the STS in a given task depends on the other brain regions that are co-activated, noting that ToM tasks typically activate STS and MPFC in conjunction. The temporal poles are activated during the retrieval of episodic and autobiographic memory and the recognition of familiar faces, scenes and voices (Frith and Frith, 2003) and are associated with the storage and retrieval of facts about specific people or social situations (Frith, 2007). Such knowledge might serve as a "social script" during mentalising to enable the prediction of someone else's mental state by using information about a particular person or previous events. Meta-analyses have divided the MPFC into functionally specific subregions and demonstrate that the medial anterior dorsal section of the MPFC is engaged in mentalising, regardless of whether this involves making inferences about one's own or someone else's mental states (Amodio and Frith, 2006; Gilbert et al., 2006). Within this region, the more superior part of dorsal MPFC tends to be activated when thinking about the mental states of unfamiliar or dissimilar others, while the more ventral part is activated when thinking about the mental states of familiar or similar others, or the self (Mitchell et al., 2006; Van Overwalle, 2009).

Although the MPFC and pSTS/TPJ are consistently activated during mentalising tasks (e.g. Castelli et al., 2000; Frith and Frith, 2003; Gallagher et al., 2002; Gilbert et al., 2007; Saxe, 2006; Saxe and Kanwisher, 2003), studies focusing on perspective taking have failed to activate these regions (Aichhorn et al., 2006; David et al., 2006; Vogeley et al., 2004). In contrast to classic ToM tasks, perspective taking tasks require participants to make visuo-spatial inferences rather than inferences about someone's mental state. These studies typically require participants to adopt a third person's (or avatar's) visual perspective to make spatial judgements, either regarding which object the third person can see (level 1 perspective taking, Vogeley et al., 2004) or the spatial arrangement of objects or persons from the third person's viewpoint (level 2 perspective taking, Aichhorn et al., 2006; David et al., 2006). Aichhorn et al. (2006) suggest that the necessity to make behavioural predictions and to anticipate the consequences of an action, rather than make a purely visual perspective computation, is critical for the recruitment of the pSTS/TPJ and MPFC. The aim of the current study was to test the prediction that level 1 perspective taking would recruit these regions when the social context of the task requires participants to consider another individual's knowledge and intentions during a communicative interaction with that individual.

We adapted a paradigm that has been used in a number of recent behavioural experiments and is thought to test the use of ToM information in the context of a realistic communication situation (Apperly et al., 2009; Barr, 2008; Dumontheil et al., 2010; Keysar et al., 2000, 2003; Nilsen and Graham, 2009; Wu and Keysar, 2007). A number of interesting results have been obtained with this task. Despite the consistent finding that by age 4 most children pass false-belief tasks, it has been demonstrated that the ability to reason explicitly about ToM does not always lead to automatic, online use of ToM information even in healthy adults. Keysar et al. (2000, 2003) report that adults do not reliably use their ToM knowledge to interpret the intentions of others. In Keysar et al.'s task, participants view a 4 × 4 set of shelves, which contains various objects. Participants are instructed to move objects around the shelves by their conversation partner (the "director") who is seated on the other side of the shelves. Some of the objects in the shelves are occluded from the director's viewpoint so that only some of the objects visible to the participant can also be seen by the director. Critical trials require the participant to take the perspective of the director into account when moving the required object. Participants often (~50% of the time) failed to use information about the director's perspective and instead used an egocentric heuristic. We recently adapted Keysar's task in two ways. First, we designed a computerised version of the task. Second, we introduced a matched control condition in which the director was absent and, instead, participants had to act according to a simple rule ("ignore objects with a grey background"). Using this computerised version of the task, we recently replicated Keysar and colleagues' results, showing that adults make large numbers of errors in the Director condition (Apperly et al., 2009). In a second study, we found that adolescents are worse than adults at using ToM-derived information, exhibiting an even stronger egocentric bias (Dumontheil et al., 2010). The Director task differs from other ToM tasks in that it requires participants to have a functioning ToM, and also to use ToM in concert with other cognitive processes such as executive functions, to overcome their egocentric bias and respond quickly and accurately. It is proposed that it is this interaction between theory of mind and executive functions that continues to develop in late adolescence, and is still prone to error in adults (see Dumontheil et al., 2010). Variants of the Director task have now been used in a number of behavioural studies (Wu and Keysar, 2007; Nilsen and Graham, 2009; Barr, 2008).

The aim of the current study was to investigate whether the perspective taking component of the Director task would recruit brain regions involved in social cognition when the social context of the task requires participants to consider another individual's knowledge and intentions during online communication with that individual. This is the first neuroimaging study that has investigated the neural basis of the processes used in the Director task. To make the paradigm suitable for functional magnetic resonance imaging (fMRI), a number of design modifications were made to the tasks developed by Keysar and colleagues. Following Apperly et al. (2009) and Dumontheil et al. (2010), only half the trials involved a director whose perspective participants should take into account when interpreting instructions (*Director: Present vs. Absent*; see Fig. 1). For other trials, there was no director, and participants instead followed simple rules that had to be taken into account when interpreting the very same instructions. Director Present and Director Absent trials were presented in separate blocks, and we hypothesised that a comparison of Director Present and Director Absent conditions would result in activations in regions sensitive to face and bodies, including the STS and extrastriate body area, as well as in regions sensitive to mentalising, such as the MPFC, temporal poles and STS/TPJ. However, the activations associated with this main effect might be attributable to a number of differences between the Director Present and Absent conditions (perspective taking, the presence of bodies and faces and so on). Therefore, we included an additional factor, which was crossed with the Director factor. In this Object factor, we manipulated whether the director's perspective (in Director Present blocks) or the rules (in the Director Absent blocks) ever made any difference to the correct interpretation of the instructions to move objects from one shelf to another (*Object: 1-object vs. 3-objects*). To do this, half of the blocks involved instructions that referred only to a single item, always located in an open shelf (e.g. "Move the turtle right" in Fig. 1). In these 1-object blocks, there was no need to take account of the director's perspective in Director Present blocks (or the rule in Director Absent blocks). The other half of the blocks involved instructions referring to an object that was one of three exemplars in the shelves (e.g., "Move the large ball up" in Fig. 1). For these 3-object instructions the correct target object could be located either in an open or a closed shelf, depending on the perspective of the director issuing the instruction (or on the specifics of the rule in the Director Absent condition). On half of the Director Present 3-objects trials the director's perspective was different from that of the participant; on the other half the director's and the participant's perspectives were the same. This varied on a trial-by-trial basis. Thus, in order to judge whether the director's perspective was the same or different from their own perspective

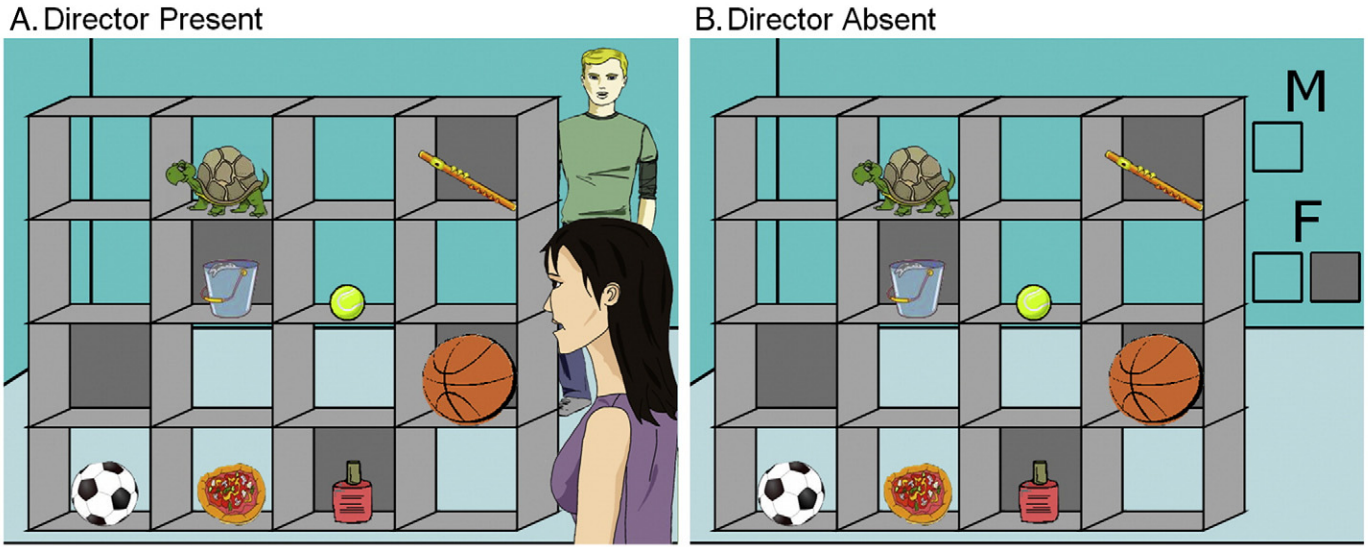

Fig. 1. Examples of a 3-objects trial in the Director Present (A) and the Director Absent (B) conditions. In both conditions in this example, participants hear the instruction: "Move the large ball up," either in a male or in a female voice. In both examples, if the voice is female, the object to be moved would be the basketball, since in the Director Present condition (A) the female Director is standing in front of the shelves and can see all the objects, while in the Director Absent condition (B) the two boxes below the "F" (for "female") indicate that all objects can be moved by the participant. If the voice is male, the object to be moved would be the football, since in the Director Present condition (A) the male Director is standing behind the shelves and therefore cannot see the larger basketball in the occluded slot, while in the Director Absent condition (B) the single clear box below the "M" (for "male") indicates that only objects in open shelves can be moved.

participants had to take account of the director's perspective on every trial. Having done so, it was only when the director's perspective was different to that of the participants' that a correct interpretation of the director's instruction differed from the interpretation participants would have made from their own perspective.

The main focus of the current study was thus the interaction between Director and Object, that is, having to select one of three objects in the context of having to take into account someone else's perspective (as opposed to a simple rule) in order to select the correct object. Our hypothesis was that any effects of Director Present/Absent on brain regions sensitive to mentalising would be modulated by the need to take account of the director's perspective, with greater activation of these regions in 3-objects than 1-object blocks.

Material and methods

Participants

Fourteen right-handed female volunteers (mean age 24.9 years; age range 21.3–30.6 years) took part in this study. All participants spoke English fluently. Informed consent was obtained and the study was approved by the local ethics committee.

Design and stimulus material

Each stimulus consisted of a set of 4×4 shelves (16 shelves) with objects located in half of the shelves. Five shelves had a grey background (see Fig. 1). In every trial, participants were given instructions via headphones from either a male or a female voice to move one of the eight objects to a different slot, either up, down, right or left (note that this was the participant's left or right). To move objects, participants moved a trackball mouse with their thumb and pressed the left mouse button with the index finger of their right hand. On each trial, participants first moved the mouse cursor from the middle of the screen to the identified object, then clicked on the object and dragged it to the appropriate slot, before releasing the mouse button. Response times were measured from the presentation of the visual stimulus to the click of the mouse button. Accuracy was measured on the basis of which object was moved.

A 2×2 factorial within-subject design was used with the factors Director (Present vs. Absent) and Object (1-object vs. 3-objects) varying between blocks.

Director factor

In the *Director Present* (DP) condition, the stimuli showed sets of shelves containing objects, and two directors, one female and one male (see Fig. 1). In the *Director Absent* (DA) condition, the same shelves and objects were presented but no directors. Instead, the letter "F" for female and "M" for male were shown beside the shelves. Below each of the letters there was either one transparent box, which indicated to participants that only objects in open shelves should be moved, or two boxes, one grey and one transparent, which indicated that there was no restriction on the participant's choice and all objects could be moved. Thus, in Fig. 1B, if participants heard the male voice say: "Move the large ball up," they would have to work out that, since the M is above one clear box, they should ignore the basketball in the grey slot and thus move the football. These rules had precisely the same consequences as the position of the director in the Director Present blocks. In Director Present blocks the physical position of the director issuing the instruction varied on a trial-by-trial basis; similarly, in Director Absent blocks the M/F rules changed on a trial-by-trial basis.

Object factor

Instructions in *1-object* blocks (for example, in Fig. 1, "Move the turtle left") referred to a unique object, which was in an open shelf. Instructions in *3-objects* blocks (for example, "Move the large ball up") could refer to an object either in a closed shelf (with a grey background) or in an open shelf that could be described with the same adjectival noun phrase. Which of the possible referents was in fact correct was determined by whether the director was at the back or at the front of the shelves (in DP) or whether the cues indicated that only objects in open shelves could be moved (in DA) (see Supplementary material for discussion of this aspect of the task and associated analyses). This manipulation ensured that in DP 3-objects blocks participants needed to consider the director's perspective (different from their own perspective on 50% of the trials) in order to know on any given trial which was the correct object to move. In DP 1-object blocks the director's perspective never made any difference to the correct interpretation of his or her instructions, and thus participants could use their own perspective to select the appropriate object on all trials. In the DA condition, perspective taking is not involved as participants only reduce their search space according to the rule for the current trial (all shelves or open shelves only) to select the correct object.

There were 48 different object-shelf configurations, each containing eight objects. A set of three exemplars of the same object was used for 3-objects instructions (e.g. three drums). These objects differed in either size (large/small) or position (top/bottom) and were distributed so that the smallest/largest/topmost/bottommost object identified in the instruction was in a closed shelf and the second smallest/largest/topmost/bottommost object and the remaining object were in open shelves. Five additional unique objects were distributed among three grey-backed closed shelves and two open shelves. Those objects in the open shelves could be used for 1-object instructions.

In each trial the visual stimulus and the auditory instruction were presented over a period of 2.2 s. The visual stimulus remained on screen for another 3.8 s. Between each trial a blank screen was presented for 200 ms. The stimuli were presented on a computer screen using Cogent 2000 (www.vislab.ucl.ac.uk/Cogent/index.html) and Cogent Graphics implemented in Matlab 6.5 (Mathworks Inc., Sherborn, MA).

For both Director conditions, standardised instructions were read to participants, and included example stimuli and practice examples in which they had to state which objects should be moved for the different directors and voices. A practice session outside the MRI scanner was then performed to ensure participants understood the task and would perform it correctly in the scanner. The practice session included one block of each of the four conditions. Participants also practiced using the trackball mouse by performing a task requiring to click on a red circle and drag it into a blue square, first outside and then inside the scanner. Participants were required to pass 20 successful trials in each trackball practice session before the start of the fMRI experiment.

There were three scanning sessions. Each session consisted of 16 task blocks with four trials in each block. There were four types of block: Director Present 1-object; Director Absent 3-objects; Director Present 1-object; Director Absent 3-objects. Each of the 48 object-shelf configurations was shown once in each block type, thus resulting in 12 blocks of each block type in total. Task blocks lasted 24.8 s and were preceded by an instruction screen presented for 2 s, which indicated to participants whether they were starting a Director Present or Director Absent block. The order of the four block types was counterbalanced within and between sessions. A fixation baseline block lasting 20 s was conducted after each set of four task blocks; thus there were four fixation blocks per session.

fMRI data acquisition

3D T_1-weighted fast-field echo structural images and multi-slice T_2-weighted echo-planar volumes with blood-oxygen level dependant (BOLD) contrast ($TR = 3$ s; $TE = 50$ ms; $TA = 2.9143$ s) were obtained using a 1.5 T MRI scanner (Siemens TIM Avanto, Erlangen, Germany). Functional imaging data were acquired in three scanning sessions lasting approximately 8 min 40 s each in which 174 volumes were obtained. The first 2 volumes of each session were discarded to allow for T_1 equilibrium effects. Each functional brain volume was composed of 35 axial slices with an in-plane resolution of $3 \times 3 \times 3$ mm, positioned to cover the whole brain. A T1 weighted anatomical image lasting 5 min 30 s was acquired after the first two functional sessions for each participant. The total duration of the experiment was approx. 30 min.

Data analyses

Behavioural data analyses

Response times (RTs) and accuracy in all four conditions were recorded and analysed using 2×2 repeated measures ANOVA to investigate the effects of Director (Director Present vs. Director Absent), and Object (1-object vs. 3-objects), and the interactions between these two factors.

fMRI data preprocessing and analyses

fMRI image preprocessing and analyses were carried out using SPM5 (Wellcome Department of Imaging Neuroscience, London, UK), implemented in MATLAB 6.5 (Mathworks Inc., Sherborn, MA). To correct for movement effects images were realigned with a 4th-degree-B-spline interpolation. These realigned images were then normalised to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain and spatially smoothed by an 8mm FWHM Gaussian kernel.

For each participant the imaging data of the three sessions were treated as separate time series; statistical parametric maps were created and estimated using a general linear model for each time series (Friston et al., 1995). Six boxcar regressors, modelling the blocks of instructions, fixation and the four types of task blocks (Director (2) × Object (2)) were used plus one event-related regressor representing error trials. All regressors were convolved with a canonical haemodynamic response function and, together with regressors representing residual movement-related artefacts and the mean over scans, comprised the full model for each session. The data and model were high-pass filtered to a cut-off of 1/128 Hz.

Parameter estimates calculated from the least mean squares fit of the model to the data were used in four pair-wise contrasts contrasting each block type to the fixation baseline at the individual subject level. These contrasts were then entered into a 2×2 factorial design second-level analysis in which 'participant' was treated as a random effect to make inferences on a population level. Main effects and the interaction between the two factors were specified by appropriately weighted linear contrasts, and determined using the t-statistic on a voxel-by-voxel basis. The main effects of Director (Present vs. Absent) and Object (3-object vs. 1-object) were investigated as well as their interaction. The main interaction of interest [(DP 3-objects − DP 1-object) − (DA 3-objects − DA 1-object)] was inclusively masked ($p < 0.05$) with the contrast [DP 3-objects − DP 1-object].

Statistical contrasts were used to create SPM{Z} maps thresholded at $p < 0.001$ (uncorrected, 10 or more contiguous voxels). Activations that survive family-wise error (FWE) whole brain correction at $p < 0.05$ are indicated, as well as activations within regions for which we had an a priori hypothesis and which survived small-volume correction (SVC; 12 mm radius sphere) at $p < 0.05$. Coordinates used for the SVC were defined by calculating the average of the coordinates reported in mentalising and social cognition studies, and consisted of: [±10, 51, 34] for the MPFC (Burnett et al., 2009; Castelli et al., 2000; Gallagher et al., 2002; Gilbert et al., 2007; Mason et al., 2004; Mitchell et al., 2005); [±43, 8, −34] for the temporal poles (Blakemore et al., 2007; Burnett et al., 2009; Castelli et al., 2000; Gallagher et al., 2000; Ruby and Decety, 2003); [±52, −56, 23] for the posterior superior temporal sulcus/temporo-parietal junction (pSTS/TPJ) (Aichhorn et al., 2009; Castelli et al., 2000; David et al., 2008; Gallagher et al., 2000; Ruby and Decety, 2003; Saxe and Kanwisher, 2003). All coordinates are given in MNI coordinates, and coordinates cited from other studies were transformed from Talairach to MNI coordinates when needed.

Results

Accuracy in session 3 of one participant was significantly lower than the other participants for this session (>2 SD away from the session mean) and was excluded from all analyses.

Behavioural results

Accuracy

Participants answered correctly on 89% of trials overall (SD = 4.8%; range 81–96%). 36% of errors were due to no response. A 2×2 repeated measures ANOVA on accuracy with the factors Director (Present vs. Absent) and Object (3-objects vs. 1-object) showed a significant main effect of Object ($F(1,13) = 14.41$, $p = 0.002$) with a lower accuracy in 3-objects trials than in 1-object trials (see Table 1). The main effect of Director ($F(1,13) = 1.97$) and the interaction between Director and Object ($F(1,13) = 0.33$) were not significant.

Response time

Median RTs were calculated for correct responses only. Participants took on average 3301 ms (SD = 192 ms; range 3005–3727 ms) to make their response, as measured from the time the visual stimulus was presented to the time the mouse button was pressed. A 2×2 repeated measures ANOVA on RT was performed. The object identifier in the instructions for 3-objects trials tended to be longer than for 1-object trials (e.g. large apple vs. turtle), thus little can be concluded from RT differences between these two conditions. However, when collapsing across male and female instructions, the instructions were matched between the Director Present and Absent conditions. The main effect of Director and the interaction between Director and Object are thus meaningful comparisons. Both main effects were significant. Participants were slower in the Director Absent condition than in the Director Present condition ($F(1,13) = 38.97$, $p < 0.001$), and in the 3-objects condition than 1-object condition ($F(1,13) = 238.65$, $p < 0.001$) (see Table 1). There was a significant interaction between Director and Object ($F(1,13) = 10.86$, $p = 0.006$). Post-hoc t-tests indicated that all four conditions differed significantly from each other (all $t > 3.58$ and $p \leq 0.003$). Follow up comparisons indicated that the interaction was driven by a significantly greater effect of Object (3-objects>1-object) in the Director Absent condition than in Director Present condition ($t(13) = 3.29$, $p = 0.006$).

Table 1
Percentage accuracy and RT results (mean and SD) in each condition.

Director	Object	Accuracy (%)	RT (ms)
Director Absent	1-object	90 (6)	2996 (213)
	3-objects	86 (5)	3812 (241)
Director Present	1-object	91 (7)	2865 (208)
	3-objects	88 (6)	3531 (235)

Functional imaging results

Main effect of Director

Comparison between the Director Present and Director Absent conditions resulted in activations in predicted regions, including clusters in the middle/superior temporal gyri bilaterally, extending into the pSTS, in the superior part of the dorsal MPFC and in the left middle temporal gyrus. There was also a cluster in the left cuneus (see Table 2 and Fig. 2).

Conversely, the Director Absent condition activated the left intraparietal sulcus and the right middle frontal gyrus to a greater extent than the Director Present condition (see Table 2).

Main effect of Object

3-Objects trials required participants either to take the director's perspective into account (Director Present condition) or to apply a specific pre-determined rule using visual cues (Director Absent condition) to choose the appropriate object. In 1-object trials, by contrast, the director's perspective, or the rule, were irrelevant as a unique object was available. Comparison of 3-objects and 1-object blocks revealed activity in a large network of brain regions, including the medial part of the superior frontal gyrus, the left superior temporal gyrus, and bilateral activations in the inferior parietal cortex, the middle frontal gyri, the inferior temporal gyri (see Table 2 and Supplementary Fig. 1).

Table 2
Coordinates and Z-values for regions of significant activation in the contrasts of interest ($p < 0.001$ uncorrected, >10 contiguous voxels). The interaction between Director and Object was tested by the contrast [(DP 3-objects − 1-object) − (DA 3-objects − 1-object)] inclusively masked by [DP 3-objects − 1-object]. * and # indicate regions surviving FWE-correction for the whole brain or a small volume (12 mm sphere) respectively. BA: Brodmann area.

	MNI coordinates					
Foci of activation	x	y	z	Z-value	Cluster size	BA
Main effects						
Director Present vs. Director Absent						
L middle temporal gyrus	−46	−70	12	5.07^{*}	896	39
L cuneus	−12	−94	4	4.85^{*}	310	17
R superior temporal gyrus	46	−58	12	$4.54^{\#}$	711	22
L precuneus	−8	−52	44	4.15	148	7
L parahippocampal	−36	−30	−14	3.93	47	36
L superior frontal gyrus	−6	54	44	$3.80^{\#}$	207	9
	−6	54	30	$3.37^{\#}$		
L hippocampus	−32	−14	−22	3.79	26	
L caudate nucleus	−16	20	−2	3.68	34	
R superior frontal gyrus	14	50	48	3.45	35	8
R inferior frontal gyrus	58	28	4	3.32	10	45
Director Absent vs. Director Present						
L intraparietal sulcus	−30	−56	44	4.28	300	7
R middle frontal gyrus	30	54	4	3.37	34	10
3-objects vs. 1-object						
L supramarginal gyrus	−40	−50	44	7.39^{*}	13655	40
L intraparietal sulcus	−28	−56	44	6.71^{*}		7
R superior parietal lobule	22	−68	52	6.57^{*}		7
L precentral gyrus	−46	6	36	5.99^{*}	9421	6
R precentral gyrus	46	6	30	5.89^{*}		6
L superior frontal gyrus	−6	14	48	4.72^{*}		6
L middle frontal gyrus	−44	46	10	5.44^{*}	560	46
R inferior temporal gyrus	42	−56	−14	5.06^{*}	1251	37
L superior temporal gyrus	−42	−50	14	3.84^{*}	85	22
R insula	30	22	6	3.83	71	13
L cerebellum	−6	−76	−20	3.72	140	
L cerebellum	−30	−46	−22	3.39	42	
L thalamus	−10	−16	10	3.50	21	
Interaction						
Director × Object interaction						
L middle temporal gyrus	−48	−12	−18	4.67^{*}	332	21
L middle temporal gyrus	−42	−4	−28	$4.13^{\#}$		
R middle temporal gyrus	46	−6	−26	4.46	74	21
L cingulate gyrus	−10	−8	44	4.23	39	24
L temporal pole	−32	12	−24	4.15	268	38
L superior medial frontal cortex	−10	42	42	$4.03^{\#}$	120	8
	−10	40	34	$3.73^{\#}$		
L inferior frontal gyrus	−48	22	10	3.91	100	45
R anterior cingulate gyrus	22	40	10	3.88	25	32

Interaction between Director and Object

The main focus of the current study was the interaction between Director and Object. Specifically, we hypothesised that the effects of Director Presence/Absence on brain regions sensitive to mentalising would be modulated by the need to take account of the director's perspective in 3-objects blocks, with greater activation of these regions in 3-objects than 1-object blocks. The results indicated that there was a significant interaction between Director and Object [(DP 3-objects − DP 1-object) − (DA 3-objects − DA 1-object), masked inclusively by (DP 3-objects − DP 1-object)], in the left middle temporal gyrus extending towards the left temporal pole, the right middle temporal gyrus, the left superior dorsal MPFC and the left inferior frontal gyrus (see Table 2 and Fig. 3).

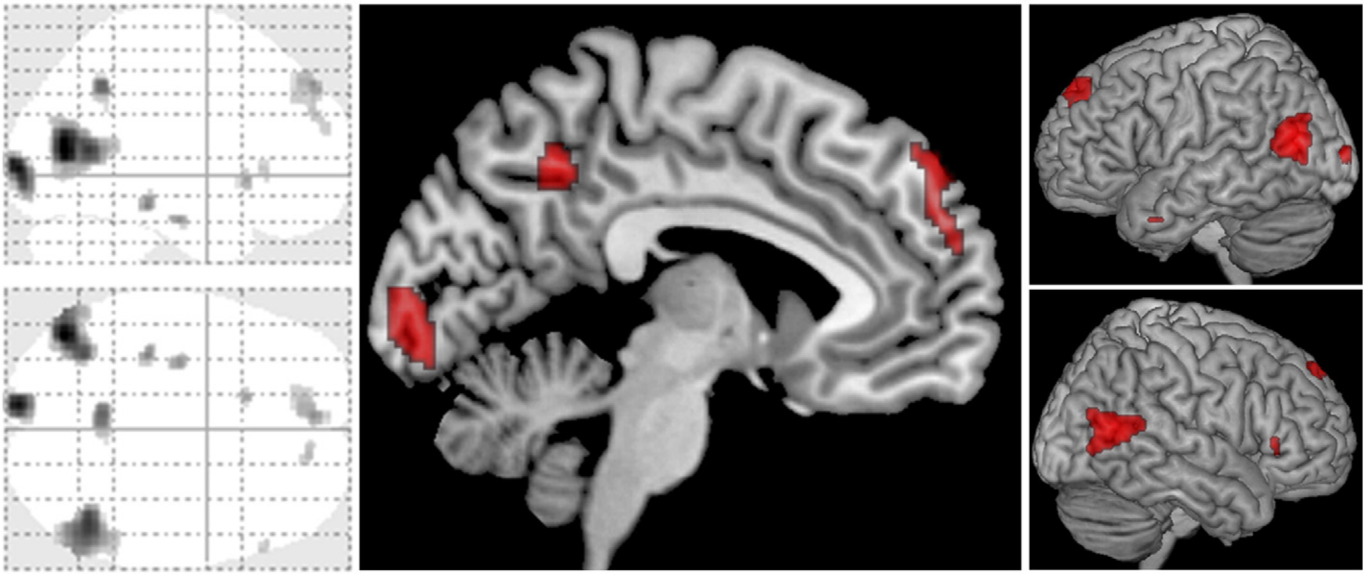

Fig. 2. Regions showing increased blood-oxygenation-level-dependent (BOLD) signal for the Director Present compared with the Director Absent condition ($p<0.001$ uncorrected, >10 contiguous voxels). Left panel: glass brain, sagittal view (top) and transversal view (bottom). Middle panel: sagittal slice at $x=-6$. Right panel: activations rendered on the lateral surface of the brain (top: left hemisphere; bottom: right hemisphere).

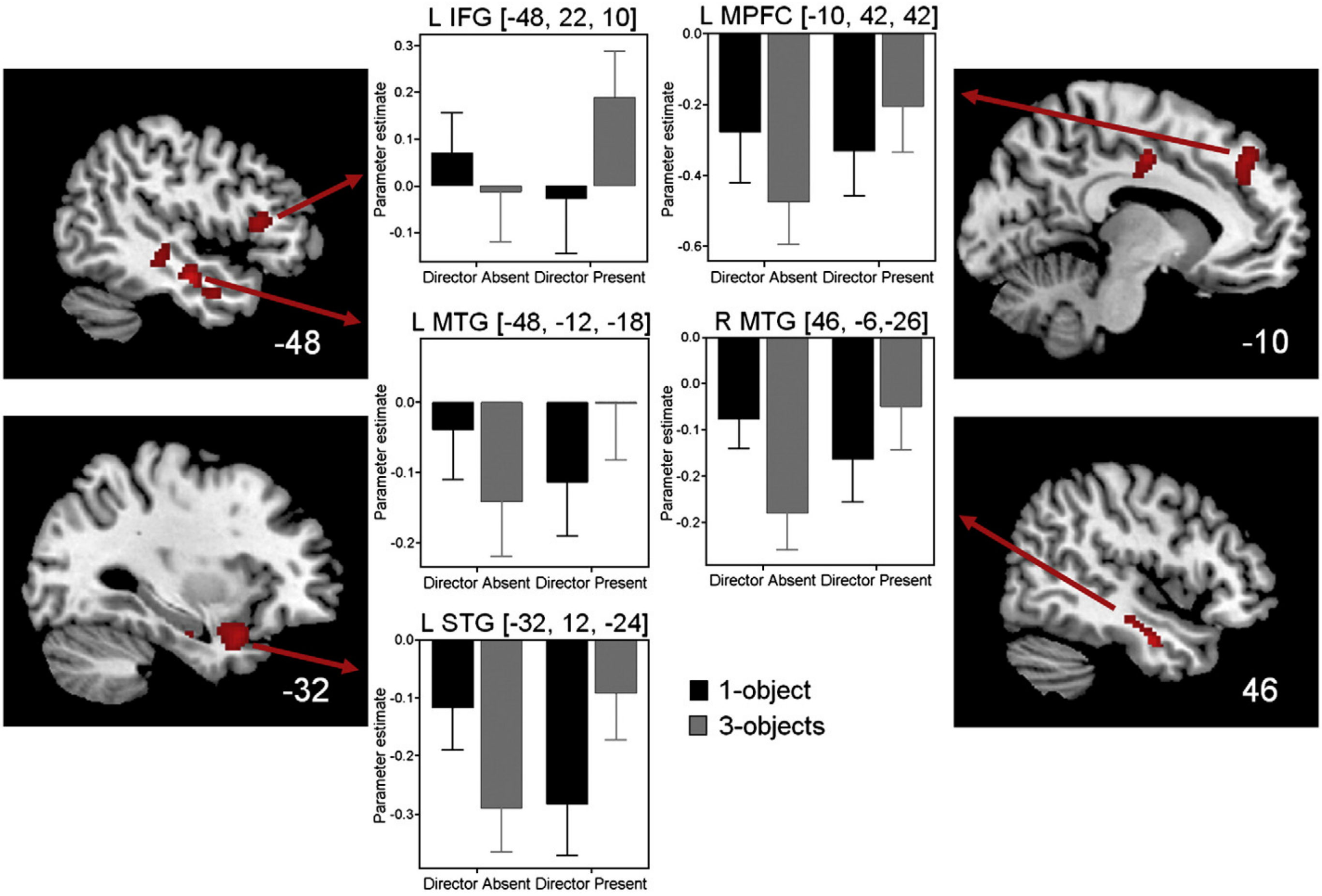

Fig. 3. Sagittal slices at $x=-48$, -32, -10 and 46 showing regions exhibiting an interaction between Director and Object [(DP 3-objects − DP 1-object) − (DA 3-objects − DA 1-object) inclusively masked with (DP 3-objects − DP 1-object)] ($p<0.001$ uncorrected, >10 contiguous voxels). Plotted in the centre are the parameter estimates (relative to fixation baseline) in the 1-object (black) and 3-objects (grey) blocks of the Director Absent and Director Present conditions for the peak voxels in the left inferior frontal gyrus (L IFG), left middle temporal gyrus (L MTG), left superior temporal gyrus (L STG), left medial prefrontal cortex (L MPFC) and right middle temporal gyrus (R MTG). These regions showed an interaction between Director and Object in which the simple effect (DP 3-objects − DP 1-object) was significant at $p<0.05$.

Discussion

In the current fMRI study, we investigated the neural substrates underlying perspective taking in a communicative task. Participants were instructed to move objects in a set of shelves. In the critical condition (Director Present, 3-objects), participants were required to use information about a director's visual perspective, which could differ from their own perspective. This condition contained aspects of visual perspective taking tasks, in which participants have to judge how an object is perceived from a third person's point of view. However, in addition to perspective taking, the situation investigated in this study also involves thinking about the *intentions* of another person. Participants had to adopt the director's perspective to work out which object he/she wanted (or intended) to be moved. In this respect, our task required mentalising. However, the current task differs from most classic mentalising tasks, which often involve the attribution of beliefs to other people in story vignettes or cartoons (e.g., Aichhorn et al., 2009; Apperly et al., 2004; Fletcher et al., 1995; Saxe and Kanwisher, 2003; Vogeley et al., 2001; Wimmer and Perner, 1983). The results of the current study indicate that, when participants were required to use information about another person's perspective in a communication game, parts of the mentalising network, including the MPFC and temporal pole, were recruited, while other social brain regions, notably the TPJ, were not.

Behavioural performance

Participants made more errors in 3-objects than in 1-object trials. This is in line with our previous behavioural study (Dumontheil et al., 2010) and was expected as 3-objects trials require participants to adopt another person's perspective (in the Director Present condition), or to apply a specific rule (in the Director Absent condition), in order to select the correct object out of three similar items. Response times were longer in 3-objects than in 1-object trials, and in the Director Absent than in the Director Present condition. In addition, there was an interaction between the two factors such that the difference in RTs between 3-objects and 1-object trials was larger in the Director Absent than in the Director Present condition. These results suggest that participants found selecting an appropriate object out of three possibilities easier when cued in a more natural way by the position of two individuals than when cued by abstract symbols. This facilitation may relate to the recent findings that humans automatically compute information about what others see in simple tasks (Samson et al., in press). Previous studies similarly found that response times are shorter in conditions requiring participants to think about intentional causality rather than physical causality (den Ouden et al., 2005), and in tasks requiring intentional understanding rather than mechanical understanding (Baron-Cohen et al., 1986).

Main effect of Director

In Director Present blocks two directors were shown, one behind and one in front of the shelves. Participants were instructed to adopt the perspective of the director speaking (male or female) to work out which object needed to be moved. In contrast, in Director Absent blocks, participants had to use a specific rule to perform the task. This rule was indicated by symbols beside the shelves. Due to differences in stimulus material (e.g. persons vs. abstract symbols), as well as the perspective taking involved in the Director Present condition, it was predicted that the comparison of the Director Present and Absent conditions would result in brain regions sensitive to the presence of human bodies and faces as well as brain regions involved in mentalising. Indeed, we observed activations in the superior dorsal MPFC, a region that exhibits higher activation in conditions involving other people, in particular dissimilar others compared to similar others, or the self (Mitchell et al., 2006; Van Overwalle, 2009). This contrast also resulted in activation in posterior parts of the superior and middle temporal sulci, in a region located between (and extending into) the extrastriate body area (EBA), and the pSTS. The EBA is sensitive to the perception and processing of the human body (Aleong and Paus, 2010; Downing et al., 2001, 2006a,b; Grossman and Blake, 2002; Hodzic et al., 2009; Morris et al., 2006; Pitcher et al., 2009). The pSTS is sensitive to the perception of human faces (Frith and Frith, 2003; Hein and Knight, 2008; Liu et al., 2010; Morris et al., 2006; Yovel and Kanwisher, 2005) and is consistently activated in ToM studies. Although ToM tasks typically recruit a slightly more anterior part of the STS (Van Overwalle, 2009), a number of ToM studies have shown peaks of activation as posterior as those in the current study ([−46 −70 12] and [46 −58 12]) during, for example, the inference of somebody else's knowledge (Goel et al., 1995, [−44 −67 18]), thinking about the intention of an actor (Van der Cruyssen et al., 2009, L: [−53 −69 5], R: [54 −55 13]), and intentional actions in stories (Van der Cruyssen et al., 2009, L: [−45 −70 13], R: [54 −55 13]) and cartoons (Saxe and Wexler, 2005, L: [−48 −69 21], R: [54 −54 24]; Völlm et al., 2006, [−54 −60 18], R: [54 −63 15]) (see Van Overwalle and Baetens, 2009, for review).

Notably, there was no evidence that the TPJ was activated in this contrast. The TPJ has been associated with the processing of social false beliefs (Aichhorn et al., 2009; Saxe, 2006; Saxe et al., 2004; Sommer et al., 2007), although its role may extend to reorienting attention towards task-relevant stimuli in non-social tasks (Mitchell, 2008). The Director task used in the current study requires participants to interact with avatars and think about their visual perspective and their intentions, but does not require representation of true or false beliefs, which may explain the lack of activation in the TPJ.

The comparison of Director Present and Director Absent blocks revealed additional activations in the left cuneus and precuneus. Activations in the precuneus are often reported in studies involving mentalising (e.g. Gallagher et al., 2000; Gobbini et al., 2007; Saxe and Kanwisher, 2003; Wolf et al., 2010), perspective taking (Ruby and Decety, 2001) and other social cognition tasks (e.g., Burnett et al., 2009; den Ouden et al., 2005; Elliott et al., 2006; Farrer and Frith, 2002). Cavanna and Trimble (2006) reviewed the functional role of the precuneus and found activation during different abstract cognitive processes, such as visuo-spatial and mental imagery, attention shifts between targets, episodic memory retrieval, processing of the self and during the ‘default mode’ of the brain in a conscious resting state. The authors suggest that the precuneus contributes to the mental representations of the self. Legrand and Ruby (2009) recently showed that a network of brain regions (including the precuneus) involved in self-relatedness evaluation overlaps with regions recruited during resting baselines, others' mind reading, memory recall and reasoning. The precuneus might therefore play a role in the representation of the mind of self and the mind of others.

Main effect of Object

The contrast between 3-objects and 1-object blocks revealed activity in a large network of brain regions including the lateral frontal cortex extending into the medial superior frontal gyrus, the parietal cortex and the temporal cortex bilaterally. These activations could be due to a variety of differences between the two Object conditions. Cognitive demands are higher in the 3-objects blocks, as also demonstrated by lower accuracy in this condition. In the 3-objects blocks, participants have to use cues (position of the directors or symbols) to select one object out of three items and, half the time, have to inhibit their prepotent response towards one object in favour of another object (when the Director was standing behind the shelves, or only objects in open shelves could be moved). In addition, the selection of the appropriate object required participants to focus on either the relative visuo-spatial properties of these objects (large/

small) or the relative locations of these objects (top/bottom), processes that are not required in the 1-object condition.

Interaction between Director and Object

The main focus of the current study was the interaction between Director and Object, that is, having to select one of three objects in the context of having to use someone else's perspective (as opposed to a simple rule) in order to select the correct object. The Director × Object interaction shown in Fig. 3 and Table 2 represents activation in the critical Director Present 3-objects blocks that cannot be accounted for by the additional demands of the 3-objects condition alone, which are controlled for by the orthogonal design. The Director Present 3-objects condition was the only condition in which it was necessary to adopt the perspective of a communication partner and figure out which objects could be seen from his/her point of view and thus which object he/she intended to be moved. On this basis it was predicted that this interaction contrast would reveal increased activations in mentalising regions in the Director Present 3-objects condition. Activations were found in the middle temporal gyri bilaterally, extending to the temporal pole in the left hemisphere, the left superior dorsal MPFC and the left inferior frontal gyrus.

Note that some of the regions observed in this contrast exhibited a pattern of greater activation in the Director Absent 1-object than the Director Absent 3-objects condition, which was a more demanding condition in terms of accuracy and reaction times (see Fig. 3). This pattern of activation could be interpreted in light of the fact that medial prefrontal cortex and regions of the temporal lobes are thought to be part of the default mode network of brain regions, which typically exhibit decreased activation during attention demanding task performance (Fransson, 2006; Gusnard et al., 2001; Shulman et al., 1997; see Schilbach et al., 2008 for a discussion of the default and social brain networks).

Activation of the superior dorsal MPFC has not been reported in previous visuo-spatial perspective tasks (Aichhorn et al., 2006; David et al., 2006; Vogeley et al., 2004). In these tasks, participants were asked to adopt the spatial perspective of another person (third person spatial perspective or 3PP) to judge whether, or how, this other person sees particular objects. These tasks thus differ from the Director task in a number of ways. First, in the Director task participants need to use spatial perspective information implicitly to perform an action, rather than respond to an explicit question about somebody else's spatial perspective. Second, in the Director task, participants perform an additional step in their reasoning to assess, on the basis of the other person's visual perspective, which object he/she was referring to when giving the instruction. Third, the Director task is based on a situation of communication between the participant and the person whose perspective needed to be adopted. On this basis, our hypothesis was that the requirements of the Director task would lead to the additional recruitment of mentalising processes, rather than perspective taking processes only. In fact, comparison of the results of the current study to those of a study that investigated level 1 perspective taking (Vogeley et al., 2004), which is the level involved in the Director task, reveals that it is the main effect of Director Present–Director Absent, rather than the interaction, which showed similar activations to the third person perspective taking–first person perspective taking contrast, with common activations in the precuneus, occipital cortex, and right inferior frontal gyrus.

Activation of the MPFC is consistently reported in mentalising tasks and this region has been suggested to be part of the core mentalising network (Brunet et al., 2000; Fletcher et al., 1995; Gilbert et al., 2007; Goel et al., 1995; Mitchell, 2008; Vogeley et al., 2001; Walter et al., 2004; see Frith and Frith, 2003, and Frith, 2007, for review). Although activations tend to be inferior to the peak activation observed in the current study, the localisation of MPFC activation in mentalising tasks can extend quite superiorly. For example, Goel et al. (1995) observed dorsal MPFC activations during inference of another person's knowledge of an object ([−12 37 37], see Van Overwalle, 2009, for a review of MPFC activations). Activation in the superior dorsal MPFC is also reported in *online* mentalising studies, where participants play a competitive game against another person and need to figure out what the other person is going to do in the upcoming trial and adapt their actions accordingly (e.g. Gallagher et al., 2002; McCabe et al., 2001). In these studies participants are typically told they are playing against a human (intentional opponent) or against a computer (non-intentional opponent), or sometimes alone, when in fact the sequence of trials is the same in all conditions. Superior dorsal MPFC regions similar to the activation observed in the current study ([−10 42 42], [−10 40 34]) are activated when participants think they are playing against humans (Elliott et al., 2006, [−6 51 33]; Fukui et al., 2006, [−8 42 40]; Gallagher et al., 2002, [−10 50 35]; Kircher et al., 2009, [4 52 44]; Rilling et al., 2004, [3 44 24]).

It is interesting to note that the dorsal MPFC activation observed in the current study in the interaction between Director and Object, and in the Director Present vs. Director Absent main effect, is located in the superior dorsal part of MPFC typically recruited when thinking about unfamiliar others rather than familiar others or oneself. In contrast, the ventral MPFC tends to be recruited when thinking about familiar or similar others, or about oneself. For example, Mitchell et al. (2006) found that a very similar region of superior dorsal MPFC to that activated in the current study was more active when participants inferred mental states about dissimilar than similar others ([−9 45 42]). In contrast, the ventral MPFC was more active in the reverse contrast (similar > dissimilar others, [18 57 9]) (see Van Overwalle, 2009 for a review). In the current study, participants were not given any information regarding the directors and thus the directors can be considered as unfamiliar others. The activations observed in the main effect and interaction contrasts thus fit with the proposed dissociation of the MPFC along a self/other, familiar/unfamiliar, similar/dissimilar axis. In summary, the superior dorsal MPFC is recruited when thinking about an unfamiliar other's intentions, and/or adapting one's own behaviour to someone else's intentions/perspective. The results of our study demonstrate that this brain region is also recruited when using another person's visual perspective in a communication situation, and more specifically in a situation where participants may need to reject their own perspective and first intention to move an object and adopt the perspective and intention of someone else.

Director × Object interactions were also found in the middle temporal gyri bilaterally, extending to the temporal pole in the left hemisphere. The temporal poles play a role in the storage and retrieval of facts about particular people or social situations (Frith, 2007) and are activated during numerous mentalising and social cognition tasks (Aichhorn et al., 2009; Akitsuki and Decety, 2009; Blakemore et al., 2007; Burnett et al., 2009; Castelli et al., 2000; Fletcher et al., 1995; Gallagher et al., 2000; Gilbert et al., 2007). On the basis of the anterior temporal lobes' involvement in social and semantic processing, Ross and Olson (2010) propose that these brain regions contribute to the understanding of meaning through access to both general and specifically social conceptual knowledge. This includes knowledge about social descriptors, social rules and social etiquette, and relationships between specific individuals. Ross and Olson suggest that this type of information is critical for understanding another individual's actions and intentions.

Activation close to the peak in the right middle temporal gyrus in this study ([46 −6 −26]) has been found in a range of other studies, for example, when listening to and rating self-judgements (Johnson et al., 2002, [53 −5 −31]), listening to personal autobiographic memories (Fink et al., 1996, [42 −3 −19]), reading social emotions (Takahashi et al., 2004, [48 −6 −33]), thinking about intentions in a communicative context (Walter et al., 2004, [51 −3 27] [54 0 −21]), or comparing thought stories to bodily sensations or appearance stories (Saxe and Powell, 2006). Left temporal regions close to the peak activation found here ([−48 −12 −18]) have been reported by studies contrasting intentional vs. unintentional faces of a partner (Singer et al., 2004, [−51 −9 −15]), and that involved participants making inferences about someone else's knowledge of an object (Goel et al., 1995, [−48 −16 −20]). In a recent review, the MTG/STG regions around the STS were found to support a range of cognitive functions, with posterior STS in the STG supporting motion processing, audio-visual integration and face processing and anterior STS in the MTG supporting speech processing (Hein and Knight, 2008). ToM-specific activations extended along the STS, without left/right or anterior/posterior clustering (Hein and Knight, 2008). As the recruited regions for these functions overlap, the authors argue against a functional subdivision of the STS/MTG/STG and propose that the region's function might be determined by other regions that are co-activated during the task in question.

Interestingly, there was no evidence of an interaction in the pSTS/TPJ in the current study. The pSTS region exhibited only a main effect of Director, with greater activation in the Director Present than Director Absent condition. It is thus possible that this brain region is mainly sensitive to the presence of the directors and participants' awareness that they may need to take into account the perspective of the director when responding, and was not additionally sensitive to whether the participants actually used this perspective information or not (i.e. in the 3-objects blocks).

Conclusion

The aim of this study was to use a novel paradigm to investigate the processing of visual perspective information in a communication context. It was proposed that the use of perspective information would recruit the mentalising network, reflecting the need to consider the intentions of another individual when interacting with them, in addition to their visual perspective. Our communicative task led to the recruitment of dorsal MPFC as well as regions responsive to the perception of human bodies and faces (extrastriate body area, STS) when directors were present compared to when the directors were absent. The use of perspective information to select the correct object when there were three similar objects to choose from (i.e. the interaction) led to further increase in superior dorsal MPFC activation, in a region typically recruited when thinking about unfamiliar others' mental states. In addition, the interaction was associated with increased activity in middle temporal gyri and the left temporal pole, which are typically involved when relying on social scripts or schemas. This study reinforces the importance of distinguishing between cognitive processes (such as visual perspective taking) and their online use in a complex, "realistic" situation (such as a communicative game) to better understand aspects of social cognition.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2010.05.056.

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