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The special case of self-perspective inhibition in mental, but not non-mental, representation

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ABSTRACT

The ventrolateral prefrontal cortex (vlPFC) has been implicated in studies of both executive and social functions. Recent meta-analyses suggest that vlPFC plays an important but little understood role in Theory of Mind (ToM). Converging neuropsychological and functional Magnetic Resonance Imaging (fMRI) evidence suggests that this may reflect inhibition of self-perspective. The present study adapted an extensively published ToM localizer to evaluate the role of vlPFC in inhibition of self-perspective. The classic false belief, false photograph vignettes that comprise the localizer were modified to generate high and low salience of self-perspective. Using a factorial design, the present study identified a behavioural and neural cost associated with having a highly salient self-perspective that was incongruent with the representational content. Importantly, vlPFC only differentiated between high versus low salience of self-perspective when representing mental state content. No difference was identified for non-mental representation. This result suggests that different control processes are required to represent competing mental and non-mental content.

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1. Introduction

Considerable effort has been directed towards determining the roles of the temporoparietal junction (TPJ) and medial prefrontal cortex (mPFC) in Theory of Mind (ToM; for reviews see Carrington and Bailey, 2009; Lieberman, 2007; Mar, 2011; Schurz et al., 2014; Spreng et al., 2009; Van Overwalle, 2009). Quantitative meta-analyses, however, suggest consistent recruitment of several, less examined, regions including the amygdala, precuneus and ventrolateral prefrontal cortex (vlPFC), across a multiplicity of paradigms (see Bzdok et al., 2012; Mar, 2011; Schurz et al., 2014; Spreng et al., 2009). The vlPFC in particular, and more specifically the left inferior frontal gyrus (IFG), has been described as a possible candidate for part of the "core mentalizing network" (Mar, 2011, p.124); however, the functional profile of vlPFC in ToM has been largely unexamined.

Developmental studies provide considerable evidence that both children and adults have difficulty with representing certain ToM states, in terms of suspending self-perspective in favour of someone else's, or selecting from competing perspectives (Birch and Bloom, 2004, 2007; Carlson and Moses, 2001; German and Hehman, 2006). This difficulty can be attributed to the propensity to automatically compute other people's viewpoints, even when we need not (e.g., see Ramsey et al., 2013), and the associated executive processes that accompany managing this. An increasing literature suggests that vlPFC may play a key part in aiding selection between self- and other perspectives. For example, Vogeley et al. (2001) identified that right vlPFC was recruited when participants were required to feature as an agent in a story, whilst making a ToM judgement about a further character in the story. This was suggested to reflect an executive process that was required in the instance of taking someone else's perspective, whilst having to integrate this with their self-perspective. In a single case study of a patient with right frontal damage including right vlPFC, Samson et al. (2005) demonstrated that the patient's success in passing a false belief task was dependent on whether their own knowledge conflicted with that of the agent. In this study, the patient completed two versions of the classic unexpected transfer task. In both versions, the participant had to determine an agent's belief as to the location of an object which, in the absence of that agent, was transferred from its original location to a new location. Samson's adaptation of the task meant that the first version followed a typical format, where the patient was aware of where the object was moved from and to. This condition carried high inhibitory demands as the patient had to suppress their own conflicting knowledge of where the object really was, in favour of the agent's outdated viewpoint. In a novel, low inhibition version of

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the task, the patient again knew that the object had been moved, but was blind to its location, therefore reducing competition between the two knowledge states. This patient's difficulty with the typical, high inhibition false belief task was suggested to reflect their inability to resist interference from self-perspective, not a ToM deficit as such. Using a modified version of the Samson et al. (2005) task, van der Meer et al. (2011) collected fMRI data from neurologically intact adults whilst they watched false belief scenarios designed to make high versus low inhibitory demands. The same participants also completed a classic Go/No-Go task. In high versus low inhibition scenarios, frontal activation was limited to bilateral vlPFC and dorsal mPFC. Similarly, No-Go versus Go trials elicited bilateral vlPFC. Common to high > low inhibition and No-Go > Go was left lateral PFC and right vlPFC. These data led the authors to conclude that inhibition of self-perspective is mediated by bilateral vlPFC when supporting a functioning ToM. Along a similar vein, Rothmayr et al. (2011) asked participants to identify whether an agent looked for the transferred object in a location that was expected, given their true or false belief about its location. They used the same pictorial stimuli to create a separate, novel Go/No-Go task. Contrast masking analyses identified that a largely left lateralised network, including left IFG and the wider lateral PFC, was recruited exclusively in false > true belief versus No-Go > Go trials. A conjunction between the false > true belief and No-Go > Go identified right dorsal mPFC and dorsolateral PFC bilaterally, plus bilateral TPJ and other regions outside of the PFC. On the basis of common neural recruitment during the ToM and inhibitory control tasks, the authors conclude that TPJ, dorsal medial- and lateral PFC support domain general processes common to both ToM and executive control. What is particularly interesting here, however, is that left IFG responded preferentially to conflict in ToM, over a more classical motor-inhibition task. In line with Mar (2011), Spreng et al. (2009), Samson et al. (2005) and Vogeley et al. (2001), this provides a further suggestion that vlPFC serves a role in response inhibition that is specific to ToM

The evidence reviewed suggests that the use of ToM is mediated by executive control. Defining a precise role for inhibition in ToM, however, is complicated by the different elements of control that are required for some, but not all, mental representation tasks. For example, executive control is required for the unexpected transfer task in order to direct a response away from the target object, whether that is because the protagonist falsely believes it to be somewhere else, or because they have a desire to avoid the object. As a result, an amount of control is required to *direct* executive selection resources. Similarly, executive control is also necessary when a perspective difference exists between self- and other, such as is the case for false belief. Here, control is required to *resolve* differences between the content of a representation – own belief versus their belief – as opposed to the contextual features – the true location versus the "false" location or the desired versus the undesired outcome. Hartwright et al. (2012) demonstrated neurocognitive differences between mental representation which required inhibition of a competing contextual feature, such as when switching from one location to another, against representing a mental state which required inhibition of a competing perspective. Representing mental states which contained differing contextual features, but not perspective differences, drew on a number of regions associated with executive function including anterior cingulate cortex (ACC), whereas representing mental states which featured both differing contextual features and perspective differences additionally drew on vlPFC. Thus, lateral prefrontal and medial prefrontal cortices work together to direct selection and resolve competition (Paus, 2001), but the recruitment of either was dependent on the nature of the representational task. Importantly, the manipulation in Hartwright et al. (2012) illustrates that vlPFC and not midline control regions such as ACC, was specifically involved in resolving competing perspectives, which is of primary interest here.

Whilst a role for vlPFC in self-perspective inhibition emerges from the existing literature, little is known about how this region responds to conflict caused by variation in perspectives within mental and other, structurally matched, non-mental representation tasks. Contrasting brain activation associated with mental versus non-mental representation has, however, been a frequent approach to examine ToM (e.g., see review Carrington and Bailey, 2009). The present study therefore sought to examine the role of vlPFC, specifically in the inhibition of self-perspective, during mental (ToM, i.e., belief) and non-mental (non-ToM, i.e., physical) representation. The present study comprises a simple manipulation to an extensively published ToM localizer task, created by Saxe and Kanwisher (2003) (e.g., see Aichhorn et al., 2009; Hartwright et al., 2012; Mitchell, 2007; Perner et al., 2006; Saxe and Powell, 2006; Saxe and Wexler, 2005; Scholz et al., 2009). In the original localizer task, neural activation resulting from reasoning about an agent with a false belief (ToM) is contrasted with that from reasoning about a closely matched, non-mental representation scenario, such as a false photograph or video (non-ToM). This approach is argued to isolate brain regions that might be specialised for ToM. For the present study, the localizer task was modified to include vignettes which feature high and low salience of self-perspective. This contrasts with the original localizer, where self-perspective was generally highly salient. The novel task comprised an orthogonal design whereby representation (belief/physical) and salience of self-perspective (high/low) were manipulated within a single, within-subjects experiment. This factorial design enabled a whole brain analysis to isolate any neural regions that were modulated either by the form of representation required, the salience of self-knowledge, or both. Following on from the quantitative reviews by Spreng et al. (2009) and Mar (2011), alongside neuropsychological evidence from Samson et al. (2005), and neuroimaging data from Vogeley et al. (2001), Rothmayr et al. (2011) and van der Meer et al. (2011), of specific interest was vlPFC, particularly within IFG. It was anticipated that vlPFC would be modulated on the basis of high versus low salience of self-perspective, as a result of the need to inhibit the competing self-perspective.

2. Method

2.1. Participants

Participants were recruited from a University wide Research Participation Scheme. All self-reported that they had not been diagnosed with any social, cognitive or neurological disorder. Twenty one right-handed adults (12 female; age range 19–28, $\bar{X}$ age=22 years) participated in exchange for a small honorarium. The Wide Range Achievement Test – Third Edition (WRAT-3) Reading Scale was administered prior to taking part in the experiment to ensure reading proficiency commensurate with the task.

2.2. Materials and procedure

The task was based substantially on a localizer procedure devised by Saxe and Kanwisher (2003), where the core change was the inclusion of additional vignettes. Stimuli were based on a modified and expanded selection of the localizer stories (Saxe and Andrews-Hanna, n.d.). All of the vignettes were rated for ease of understanding and trialled on a separate group of individuals prior to running the fMRI experiment. Participants read a total of 56 short vignettes which referred to either a mental representation

Table 1
Example vignettes.

Representation	Salience of self-perspective	
	High	**Low**
Mental (belief)	Lorraine dashed out the door and mistakenly left her lunch money on the side table. Thinking it was for a school trip, her daughter put the money upstairs in her purse. Lorraine expects to find her lunch money in her daughter's purse. True False	Liz hurried out the door and mistakenly left her coffee money on the desk. Thinking it was for his school lunches, her son put the money away in the usual safe place. Liz expects to find her coffee money on the desk. True False
Non-mental (physical)	The speed camera captured an image of the bright red car as it sped along the road. The following day, the car was painted a grey colour and the number plates were changed. According to the speed camera image, the car is bright red. True False	The traffic camera snapped an image of the dark blue car as it jumped the traffic lights. The following day, the car was painted a bright colour and the number plates were changed. According to the traffic camera image, the car is a bright colour. True False

(belief), such as an agent with a false belief, or a non-mental representation (physical), such as a false photograph, video or painting (see Zaitchik (1990)). In order to modulate neural regions that support self-perspective inhibition, following a theoretically similar approach to Samson et al. (2005), the original vignettes were modified so that the salience of the participant's perspective – the information describing the true state of affairs – was systematically varied from high to low. Each belief vignette and each physical vignette had a high and low salience version where the contents and structure were closely matched; see Table 1. In high salience vignettes, the occurrence and precise nature of the change of state was made explicit; thus, the viewer held a highly salient perspective on reality. The resulting striking incongruence between participants' own, self-perspective and the representational perspective was anticipated to cause considerable interference when adopting the false, representational perspective, resulting in behavioural and neural consequences (Birch and Bloom, 2004; Birch and Bloom, 2007). In low salience vignettes, the occurrence of the change of state was still made explicit; however, the precise nature of reality was less clearly-specified, making the viewer's perspective of the true state of affairs less salient. It is important to highlight that incongruence between the representational and real state of affairs is again present although, this time, incompatibility between the participant's perspective and the state of reality was intended to be less vivid. As a consequence, it was expected that participants would suffer less interference from their own knowledge point when adopting the false, representational perspective.

The paradigm comprised a 2×2 repeated measures design with two within-subjects factors, representation (belief/physical (B/P)) and salience of self-perspective (high/low (H/L)), collapsed into four equally occurring conditions: BH, BL, PH, PL. Each vignette was displayed in black Arial point 22 font, presented on a grey background. Experimental timings reflected the original localizer task in Saxe and Kanwisher (2003). A single trial comprised a short story, displayed for 10 s, followed for 4 s by a true or false question about the preceding story. This required participants to make a response using a two button box that was placed in their left hand, where the left button was always used to indicate a true statement. The experiment contained an equal number of true/false responses, which were randomised across the experiment. Stories alternated between belief and physical and were interleaved with a 13.5 s rest period comprising a fixation dot. The presentation of high versus low salience was pseudo randomised to prevent more than three repetitions of either saliency variant, and pairs of high/low stories were not repeated within the same block. The word lengths of each type of vignette were equivalent (belief versus physical representation $t(23)=0.073$, $p=0.943$; high versus low salience $t(23)<0.001$, $p=1.000$).

The experiment comprised four blocks of 12 trials of interest, each containing three vignettes of from each condition. This resulted in 12 trials for each of the four conditions. Participants completed four practise trials immediately prior to scanning to orientate themselves with the task. Each block also contained a further two randomly placed anti-strategy trials. Whilst the structure of the story element in these anti-strategy vignettes was identical to the trials of interest, the question phase required participants to answer a true/false question about the true outcome described within the vignette. This prevented participants from adopting a formulaic approach to response preparation (Saxe and Kanwisher, 2003).

2.3. Data acquisition and preprocessing

The data were acquired during a single session using a 3T Philips Achieva scanner, with an 8 channel head coil. The stimuli were presented using Presentation software (v. 14.1; Neurobehavioral Systems, CA), which also recorded the behavioural response data simultaneously. 159 T2*-weighted echo-planar imaging (EPI) volumes were obtained per block of the experiment, each of which consisting of 42 axial slices obtained consecutively in a bottom up sequence, reconstructed voxel size $=3 \times 3 \times 3$ mm^3. Whole brain coverage was achieved with a TR$=2.5$ s, TE$=35$ ms, acquisition matrix$=96 \times 96$, flip angle$=83°$, SENSE factor$=2$, voxel size$=3 \times 3 \times 3$ mm^3. High resolution T1-weighted structural images were acquired following collection of the functional data (3D TFE, sagittal orientation, TR$=8.4$ ms, TE$=3.8$, 175 slices, reconstructed voxel size$=1 \times 1 \times 1$ mm^3).

Preprocessing and statistical analyses of the data were performed using the FMRIB software library (FSL version v.4.1.9; FMRIB, Oxford, www.fmrib.ox.ac.uk/fsl; FEAT version 5.98). Initial preprocessing of the functional data consisted of slice timing and motion correction using rigid body transformations (MCFLIRT; Jenkinson et al., 2002). The blood oxygen level dependent (BOLD) signals were high-pass filtered using a Gaussian weighted filter of 21 s. The BOLD data were then spatially smoothed using a 5 mm full-width-half-maximum kernel. The functional data were registered to their respective structural images and transformed to a standard template based on the Montreal Neurological Institute (MNI) reference brain, using a 7-DoF linear transformation (FLIRT; Jenkinson and Smith, 2001; Jenkinson et al., 2002).

2.4. fMRI data analysis

Four explanatory variables (EVs) of interest – BH, BL, PH, PL – were modelled to reflect the four experimental conditions. Each EV comprised the story and question phase of a single vignette (14 s). Each EV was convolved with a gamma derived hemodynamic response function (HRF) within a general linear model (GLM) framework. The anti-strategy trials and motion parameters were modelled as regressors of no interest. Consistent with prior application of the localizer, all trials were modelled regardless of response accuracy. Higher level modelling was used to aggregate the data across participants and experimental runs within a mixed

effects model. For confirmatory purposes, a whole brain analysis was computed to replicate the original localizer contrast belief > physical, as per Saxe and Kanwisher (2003). To determine whether vlPFC is modulated by varying demands in inhibition of self-perspective, further modelling reflected a 2×2 repeated measures ANOVA with representation (B/P) and salience of self-perspective (H/L) as within subjects factors. As the factorial analysis does not provide directional information about any identified neural relationship, a quadrupled *t*-test was also computed using the same parameters for planned contrasts: BH > BL, BL > BH, PH > PH and PL > PL. These contrasts were specified a priori to address the questions of interest. In the confirmatory analyses of the belief > physical contrast, as computed by Saxe and Kanwisher (2003), the resulting *Z* statistic images were thresholded using a cluster based approach, where $Z > 2.3$, cluster $p_{corr} < 0.001$. For the later factorial and directional analyses, the resulting *Z* statistic images were thresholded with $Z > 2.3$, cluster $p_{corr} < 0.05$. In addition to conducting whole brain analyses, given our strong a priori hypothesis, and due to the published statistical challenges in identifying neural regions that support complex cognitive functions (Lieberman and Cunningham, 2009), pre-threshold masking was used to constrain these analyses to bilateral vlPFC. This was defined as comprising ventrolateral voxels in Brodmann Areas 44, 45 and 47 which had a $\geq$20% probability of falling within either IFG, the frontal operculum or frontal orbital cortices, as classified by the Harvard-Oxford cortical atlas. Results are described according to gross anatomical regions and anterior, mid and posterior vlPFC, approximating BA 47, 45 and 44 respectively (Badre and Wagner, 2007). Mean percent signal change plots of each effect identified by the GLM analyses were created using FSL's Featquery. This enabled a closer examination of how the data contribute to each result (Poldrack and Mumford, 2009).

3. Results

3.1. Behavioural data

The participants' error rates were analysed in a 2×2 repeated measures ANOVA, with representation (B/P) and salience of self-perspective (H/L) as within subjects factors[1] (Fig. 1). Overall, few incorrect responses were made. Whilst, across the whole experiment, participants made numerically fewer errors when making a belief inference versus when making a physical representation judgment, factorial analysis found no significant effect of representation ($F(1,17)=0.46$, $p=0.51$, $\eta^2=0.03$). Almost three times as many errors were made when self-perspective was highly salient, which was supported by a significant main effect of salience ($F(1,17)=10.07$, $p=0.006$, $\eta^2=0.37$). Post hoc comparisons confirmed a significant difference in the number of errors made in high versus low salience (high > low; $SE=0.44$, $p=0.006$). Participants were generally most error prone when making a physical representation judgment and their self-perspective highly salient; however, there was no statistically significant interaction between representation and salience in error rate ($F(1,17)=2.69$, $p=0.12$, $\eta^2=0.14$). Inspection of the error rate for anti-strategy trials determined that the participants were generally performing at ceiling, and thus were not ignoring presented information strategically (mean frequency correct 7.23/8. *SD* 0.89).

[1] Due to an equipment failure, behavioural data from 3 participants were unavailable. These participants were included in subsequent neuroimaging analyses as their inclusion yielded no key differences in the localisation of effects in the raw, unthresholded data.

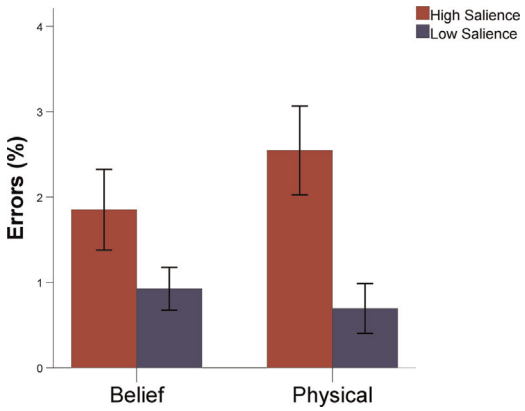

Fig. 1. Mean percentage of errors made per condition. Error rates calculated across the whole experiment. BH=1.85%; BL=0.93%; PH=2.55%; PL=0.69%. Error bars reflect +/−1 SE of the mean.

3.2. Neuroimaging data

3.2.1. Confirmatory analyses

Confirmatory analyses of the belief > physical contrast, as computed by Saxe and Kanwisher (2003), identified regions consistent with ToM and previously published uses of the localizer. This included bilateral TPJ temporal poles, precuneus and mPFC (Table 2; Fig. 2).

3.2.2. Novel task, whole brain analyses

A whole brain, 2×2 repeated measures ANOVA with representation (belief/physical (B/P)) and salience of self-perspective (high/low (H/L)) as within subjects factors identified a main effect of representation (B/P) in nine clusters of activation (Table 3; Supplementary Table i). Manipulation of representation resulted in the largest signal intensities within two large clusters centred on bilateral TPJ. These clusters spanned the parietal and temporal lobes, running in the rostral direction along the lateral and superior temporal sulci to the temporal poles. The right lateralised of these clusters also extended superiorly from the temporal pole to encompass vlPFC. Equally large intensity values were identified in a posterior midline cluster which encompassed the posterior cingulate gyrus, extending in the superior direction to include bilateral precuneus and left lingual gyrus. The largest cluster was centred on bilateral frontal pole and extended laterally to both hemispheres to include bilateral superior frontal and middle frontal gyri. A further cluster was identified in left frontal cortex, which encompassed the frontal pole and vlPFC, comprising inferior to middle frontal gyri. Clusters also included bilateral occipital and cerebellar regions. No main effect of salience of self-perspective (H/L) was identified. However, a significant interaction existed between the two main factors in four clusters of activation. Here, the largest signal intensities were in a left lateralised cluster comprising voxels in pre and post central gyri. A second left lateralised cluster was identified in vlPFC, encompassing inferior to middle frontal gyri. The largest cluster centred on bilateral anterior cingulate cortex, extending to the right hemisphere running posteriorly to include the parahippocampal gyrus and insular cortex. A further cluster centred on right anterior lingual gyrus near the midline, crossing to the contralateral hemisphere to include mostly left lateralised structures including the parahippocampal gyrus, then extending towards the lateral surface to include the temporal pole.

Planned contrasts, computed as a quadrupled *t*-test, identified four clusters of activation where BH > BL and three clusters where PL > PH (Table 3; Supplementary Table i). For belief representation, a largely left lateralised network, encompassing anterior lateral and medial frontal regions, was more active for high versus

Table 2
Cluster peaks for confirmatory whole brain analysis; belief > physical.

Cluster peak	Hemi	Brodmann area	Cluster size (voxels)	MNI coordinates			Z-value
				x	y	z	
Temporoparietal junction	R	21	1204	62	−56	16	9.53
Precuneus	L/R	7	2441	0	−56	34	9.34
Temporoparietal junction	L	21	767	−54	−56	22	8.35
Temporal Pole	R	21	442	56	6	−34	8.26
Middle temporal gyrus, anterior division	L	20	318	−54	0	−36	8.25
Middle temporal gyrus, posterior division	R	20	82	54	−8	−20	6.97
Frontal pole	L	9	59	−14	52	32	6.81
Frontal pole	L/R	10	110	0	62	10	6.62
Cerebellum	L	N/A	33	−28	−80	−40	6.59
Middle frontal gyrus	R	9	20	28	26	34	6.44
Middle temporal gyrus, posterior division	L	21	40	−64	−22	−10	6.43
Middle temporal gyrus, posterior division	R	21	16	66	−26	−10	6.19
Temporal pole	L	20	2441	−38	16	−42	5.68

Note: Result reflects a two sample paired *t*-test, were neural regions listed were more responsive to belief (B) over physical (P) representation. Thresholded voxelwise at $p_{corr} < 0.001$. Brodmann areas are approximate.

low salience of self-perspective. Left vlPFC showed the greatest signal intensities, with activation concentrated around IFG. For physical representation, a network of posterior, bilateral regions, mainly limited to the parietal lobe, were more active for low versus high salience of self-perspective. No neural regions were identified by the contrasts BL > BH and PH > PL.

3.2.3. Novel task, region of interest analyses

For the main analysis within pre-defined voxels of bilateral vlPFC, a 2 × 2 repeated measures ANOVA identified a main effect of representation (B/P) in bilateral vlPFC, where the peak activation was centred on mid vlPFC, the IFG pars triangularis (IFG_{tr}). This cluster extends in the rostral direction to include a small portion of the superior quadrant of anterior vlPFC, and in the caudal direction towards the posterior boundary of the frontal poles. This main effect was driven by a larger percentage signal change in physical versus belief stimuli (Fig. 3A; D red shading). No main effect of salience of self-perspective (H/L) was identified; however, a two-way interaction identified a separate cluster which chiefly comprised left anterior vlPFC (Fig. 3B; D blue shading). This cluster centred on the IFG pars orbitalis (IFG_{or}) and extended in the superior direction to encompass part of mid vlPFC, although this activation was more posterior to the region modulated by the main effect of representation. The signal plot in Fig. 3B and activation map in Fig. 3C together indicate that the interaction was driven by an effect of salience when making a belief representation, where having a highly salient self-perspective recruited more resources in vlPFC than when self-perspective was less salient. The a priori planned contrasts provide further information for interpreting this interaction. Whilst there appears to be a trend towards the opposite effect when representing non-mental information, in fact the quadrupled *t*-tests found that the effect of salience was only present during mental representation in vlPFC. Thus, no other contrasts within this quadrupled *t*-test, including physical high > physical low, survived cluster detection. Voxels contributing to the significant *t*-test for high versus low salience when making a belief inference formed a single cluster, which comprised left mid to anterior vlPFC (Fig. 3C; D green shading). The cluster peak for this significant contrast of belief high > belief low was positioned in IFG_{tr} extending in the caudal direction to encompass voxels identified within the factorial analysis for the effect of representation (Fig. 3D yellow shading), and in the ventral direction to include voxels identified by the factorial interaction effect (Fig. 3D cyan shading). Table 4 details contrasts performed in these analyses and the resulting cluster peaks.

4. Discussion

Prior behavioural literature evidences children's and adults' difficulty with certain ToM states, for example, when required to suspend self-perspective in favour of someone else's (Birch and

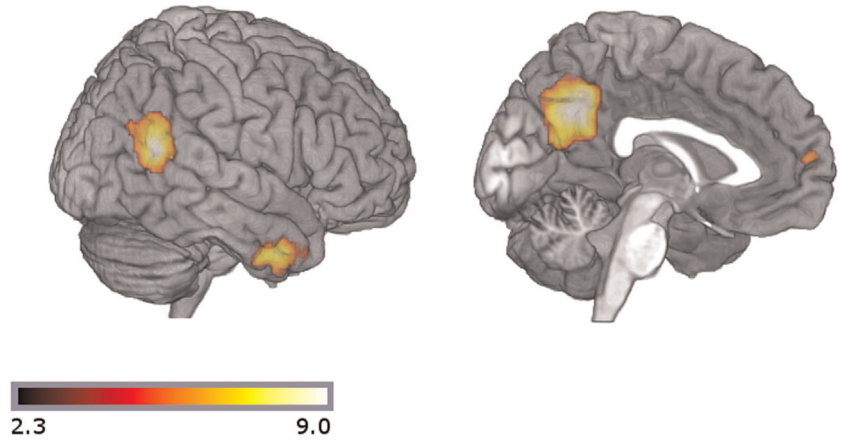

Fig. 2. Activation map for the contrast B > P overlaid onto the MNI brain template. Shows significantly activated voxels where $p_{corr} < 0.001$. Images reflect *Z*-corrected *t*-stat images. Lateral view shows right hemisphere to illustrate right TPJ.

Table 3
Cluster peaks for whole brain, representation by salience analyses

Cluster peak	Hemi	Brodmann area	Cluster size (voxels)	MNI coordinates			Z-value
				x	y	z	
2x2 Repeated Measures ANOVA							
Main effect of Representation (B/P)							
Temporoparietal junction	R	21	8470	62	-56	16	8.21
Temporoparietal junction	L	21	7706	-54	-56	22	8.21
Cingulate Gyrus, posterior division	L	23	5794	-8	-54	26	8.21
Frontal Pole	L	9	11084	-14	52	32	6.71
Inferior Temporal Gyrus, temporo-occipital part	L	20	858	-52	-52	-16	6.21
Frontal Pole	L	45	973	-44	40	4	5.07
Cerebellum	R	–	799	26	-80	-38	4.64
Cerebellum	L	–	*1609*	-20	-90	-44	4.24
Intracalcarine Cortex	L	19	988	-24	-68	4	4.08
Main effect of Salience of Self-Perspective (H/L)							
ns							
Representation * Salience Interaction							
Postcentral Gyrus	L	3	950	-28	-38	40	4.17
Inferior Frontal Gyrus, pars triangularis	L	48	671	-32	30	12	3.98
Cingulate Gyrus, anterior division	R	24	1444	4	28	18	3.92
Lingual Gyrus	R	–	1205	10	-52	-8	3.85
Planned Contrasts (Quadrupled t-test)							
BH > BL							
Inferior Frontal Gyrus, pars triangularis	L	48	2224	-32	30	14	4.54
Lingual Gyrus	R	–	808	8	-48	-2	4.00
Middle Frontal Gyrus	L	8	945	-26	18	50	3.92
Temporal Fusiform Cortex, posterior division	L	30	783	-24	-40	-18	3.74
BL > BH							
ns							
PH > PL							
ns							
PL > PH							
Cingulate Gyrus, anterior division	R	–	2950	8	-6	44	4.31
Supramarginal Gyrus, anterior division	R	2	1274	62	-30	30	4.29
Postcentral Gyrus	L	48	900	-64	-18	18	3.80

Note. Results from ANOVA reflect regions identified using F-contrasts in a 2-way repeated measures factorial analysis with representation (belief/physical, B/P) and salience of self-perspective (high/low, H/L) as within subjects factors. ANOVA results reflect cluster peaks for cortical regions which are modulated by varying representation status (belief/physical) and salience status (high/low). Quadrupled t-test reflects planned contrasts within specific conditions of interest. Brodmann Areas are approximate. ns = non-significant at $Z > 2.3$, $p_{corr} < 0.05$. B = belief, P = physical, H = high, L = low. Supplementary Table i additionally details anatomically unique local maxima for these analyses.

Bloom, 2004, 2007; Carlson and Moses, 2001; German and Hehman, 2006). Converging evidence suggests that vlPFC, and IFG in particular, plays an important part in ToM (Mar, 2011; Spreng et al., 2009), where neuropsychological (Samson et al., 2005) and neuroimaging data (e.g., Hartwright et al., 2012; McCleery et al., 2011; Rothmayr et al., 2011; van der Meer et al., 2011) indicate that this role may reflect an inhibitory mechanism, such as would be required when selecting from competing sources of information like self versus other perspectives. The present study aimed to clarify the nature of inhibition supported by vlPFC, by manipulating how salient participants' own perspectives were, within a single, repeated measures design. Using an extensively published ToM localizer task (Saxe and Kanwisher, 2003), we examined self-perspective inhibition in both mental and non-mental representation. It was anticipated that systematic manipulation of salience of self-perspective would modulate vlPFC, due to resulting varying levels of interference from self-perspective.

In general, the participants performed with high accuracy in mental and non-mental representation, as well as understanding the real state of affairs. No behavioural effect of representation was identified in terms of the number of errors made; thus, adults showed no behavioural cost between assuming a mental, versus a physical, representation of an event. A significant cost was, however, associated with judging the content of mental and non-mental representations when under the influence of a highly salient self-perspective. This corresponds with numerous behavioural data which suggest that self-perspective interferes when making judgments about a naive or misinformed other (see Birch and Bloom, 2004; 2007 for a review). For example, the classic unexpected transfer false belief task illustrates that children under the age of four respond from their own, egocentric perspective (Wimmer and Perner, 1983). Furthermore, adults tend to overestimate the extent to which own knowledge is shared by others, in terms of the outcome of an event (Fischhoff, 2003) or general knowledge (Thomas and Jacoby, 2013). Also adults, like children, suffer interference from their own visual perspective when considering the viewpoint of an agent (Keysar et al., 2003; Surtees and Apperly, 2012). Considered together, the behavioural data presented here add further credence to the view that holding an incompatible perspective with an agent, when realised, is necessarily effortful. What is interesting to note at this point, however, is that the participants' behaviour was not sensitive to any

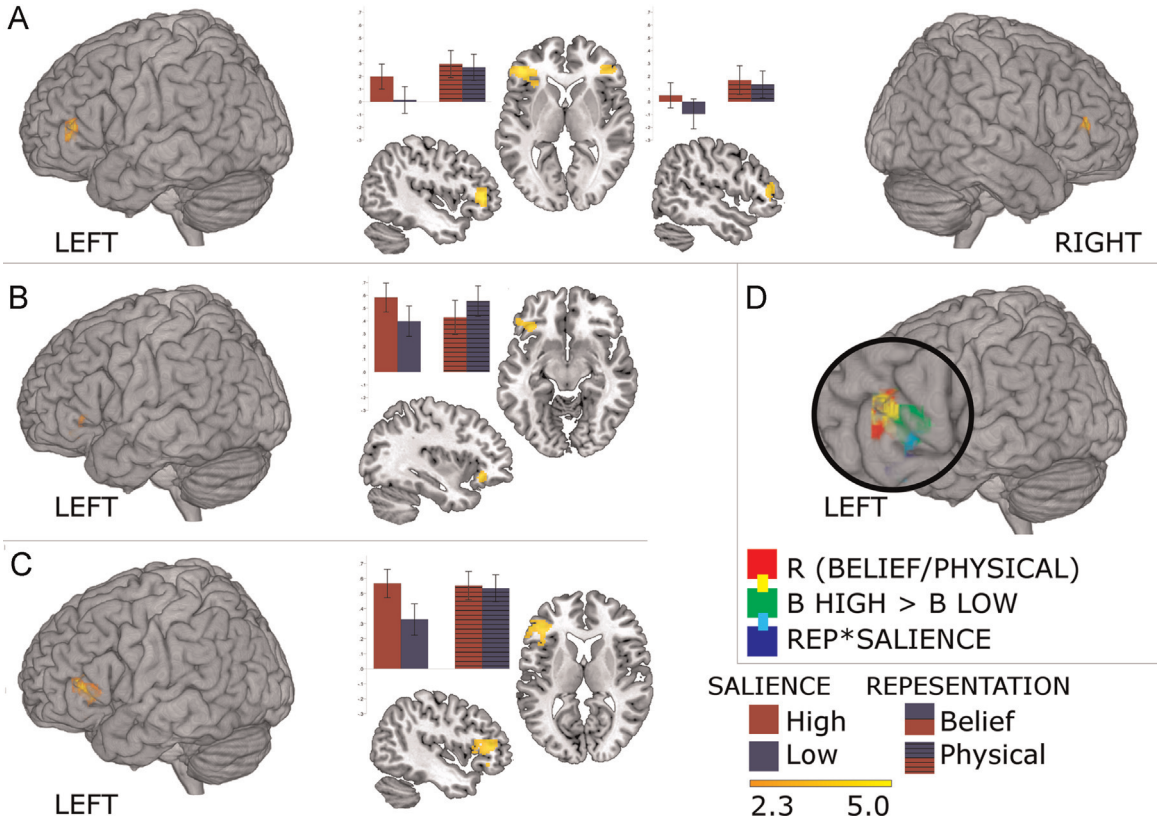

Fig. 3. Activation maps overlaid onto the MNI brain template show significantly activated voxels where $Z > 2.3$, $p_{corr} < 0.05$. Images are displayed in neurological convention, where left is represented on the left side of the image. Slices highlight cluster peaks. Plots reflect group mean percentage signal change in the highlighted cluster for each condition; error bars reflect $+/-1$ SE of the mean (Panel A). Result from 2×2 repeated measures ANOVA, with Representation (B/P) and Salience (H/L) as within-subjects factors. Image reflects a Z-corrected F-stat image of neural regions modulated by the factor of representation (B/P). Slices from left to right, $z=4$, $x=-44$, $x=48$ (Panel B). Image reflects a *Z*-corrected F-stat image of regions modulated by an interaction between representation (B/P) and salience of self-perspective (H/L). Slices $z=-10$, $x=-36$ (Panel C). Image reflects a *Z*-corrected *t*-stat image following a quadrupled *t*-test where BH > BL. Slices $z=10$, $z=-44$ (Panel D). Activation maps are rendered onto a standard brain, showing the left vlPFC. Red shading indicates main factorial effect of Representation (B/P); dark blue indicates representation × salience interaction; green indicates significant result from quadrupled *t*-test where BH > BL. Yellow indicates voxels recruited by both factor of representation (B/P) and quad *t*-test BH > BL; cyan indicates voxels recruited by R × S interaction and BH > BL *t*-test. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

distinction between mental and physical representation, whereas the neural measures, as will be outlined shortly, were sensitive to this factor.

Whilst imperceptible on the basis of the behavioural data, whole brain analyses suggested that different functional processes were engaged following the salience manipulation for mental versus physical representation. Consequently, no main effect of the salience manipulation was identified. The absence of a brain-based main effect may appear in conflict with the behavioural data, but can be understood through the interaction effect revealed in the fMRI analyses. This interaction, when considered alongside the planned directional contrasts, demonstrated that the salience manipulation modulated a frontal–lateral network during mental representation, and midline frontal structures for physical representation. Thus, we conclude that different neural architectures produced the similar behavioural output patterns, as has been observed in many previous studies (see Wilkinson and Halligan, 2004 for a review). In the case of ToM, the present study provides new evidence that, when reasoning about what someone else believes, vlPFC is modulated by how salient one's own, self-perspective is, as greater demand on IFG was associated with representing the belief state of an agent when the participants' own, competing self knowledge was highly salient. Notably, the neural cost of high salience in vlPFC was only identified when making a mental, but not a non-mental, representational judgement. Specifically, the neural interaction effect pinpointed left IFG as responding differently to the salience manipulation for mental versus physical representations. Planned contrasts using a quadrupled *t*-test confirmed this was due to greater resource demand for high versus low salience of self-perspective in belief reasoning, whereas no difference between high or low salience of self-perspective was identified in vlPFC when reasoning about outdated non-mental content, such as photographs, videos and paintings. Importantly, a whole brain analysis, using the approach specified in Saxe and Kanwisher (2003), confirmed that the modifications outlined in the present paradigm had not altered the performance of the localizer. Thus, when contrasting beliefs with physical representation as per the original localizer, the task identified brain areas similar to those in previous studies, in particular TPJ and mPFC. However, the inclusion of novel stimuli and analyses showed an interaction between the type of representation (mental versus non-mental) and how salient self-perspective was in vlPFC. Taken together, the data presented here extend the set of brain regions responding differentially to the contrast between false belief and false photograph stimuli, which have been consistently identified in previous research (e.g., Saxe and Wexler, 2005; Scholz et al., 2009). Below we consider alternative interpretations of these findings.

The rationale for the development of Saxe and colleagues' false belief versus false photograph contrast was to identify brain areas that were selectively active when reasoning about mental states (Saxe and Kanwisher, 2003). Following this reasoning, the natural

Table 4
Cluster peaks for representation by salience analyses within pre-defined vlPFC mask.

Cluster peak	Hemi	Brodmann area	Cluster size (voxels)	MNI coordinates			*Z*-value
				x	*y*	*z*	
2 × 2 Repeated measures ANOVA							
Main effect of representation							
Inferior frontal gyrus, pars triangularis	L	45	605	−44	40	4	5.07
Inferior frontal gyrus, pars triangularis	R	45	280	48	40	10	4.11
Main effect of salience of self-perspective							
ns							
Representation × salience interaction							
Inferior frontal gyrus, pars orbitalis	L	47	246	−36	30	−10	4.49
Planned contrasts (quadrupled *t*-test)							
BH > BL							
Inferior frontal gyrus, pars triangularis	L	45	669	−44	38	10	4.38
BL > BH							
ns	–	–	–	–	–	–	–
PH > PL							
ns	–	–	–	–	–	–	–
PL > PH							
ns	–	–	–	–	–	–	–

Note: Results from ANOVA reflect regions identified using F-contrasts in a 2-way repeated measures factorial analysis with representation (belief/physical, B/P) and salience of self-perspective (high/low, H/L) as within subjects factors. ANOVA results reflect cluster peaks for cortical regions within vlPFC masked region which were modulated by varying representation status (belief/physical) and salience status (high/low) quadrupled *t*-test reflects planned contrasts within specific conditions of interest. Brodmann areas are approximate. ns=non-significant at $Z > 2.3$, $p_{corr} < 0.05$. B=belief, P=photo, H=high, L=low.

conclusion would be that the present data identify a new domain-specific brain region associated with an inhibitory demand during mentalising but not an equivalent inhibitory demand in a non-mentalising context. However, we do not favour this conclusion, for two reasons. Firstly, executive functions, such as inhibition, are typically viewed as domain-general by definition (e.g., Miyake et al., 2000), and this view is supported by a wealth of evidence suggesting that executive demands of diverse tasks are met by drawing upon the same pool of executive resources (e.g., Miller and Cohen, 2001). Secondly, the particular brain region identified in the present study – left IFG – is frequently implicated in diverse non-social tasks that make inhibitory demands (e.g., Badre and Wagner, 2007; Moss et al., 2005; Swick et al., 2008), reducing the likelihood that the present results correspond to domain-specific processes.

A second interpretation of the selective effect of our salience manipulation for representation of mental states is that it is an artefact of inadequate matching between our mental representation and non-mental representation stimuli. For example, Callejas et al. (2011) suggested that the original false belief and false photograph localizer vignettes used by Saxe and colleagues make different demands on working memory and employ different linguistic structures, which might be sufficient to explain away the difference in neural activation for these two classes of stimuli. Left IFG has been implicated in the integration of semantic information in text and, thus, could lead to the view that the present results reflect differing linguistic complexity (Hagoort, 2005). The design of the present task, however, does not favour this explanation for the findings presented here. In the present study, no evidence was found for a behavioural difference between stories with mental and non-mental representational content, although the low observed error rates lead us to make this assertion cautiously. In addition, all of the vignettes were rated for ease of understanding on a separate sample of participants and both these ratings, and the word lengths of each type of vignette were equivalent. Moreover, concerns in the literature about spurious differences between mental- and non-mental vignettes correspond to the high-inhibition vignettes used in the present study, which yielded no difference in activity in left vlPFC. The effect in left vlPFC was an interaction between the representation and salience conditions, which planned contrasts highlighted was driven by a neural difference between high versus low salience of self-perspective in belief reasoning. Thus, it was the salience manipulation *within* the ToM condition that modulated vlPFC, not a feature of difference between mental and non-mental representation per se. It is important to reiterate that the structure of the high/low belief reasoning vignettes were identical (as were high/low for physical); each high salience vignette had a matched low salience version. Thus, we do not believe that our distinctive results in vlPFC are due to incidental differences between the classes of vignette used.

Our favoured interpretation is that belief and photo stimuli are indeed not perfectly matched in their executive demands, but for the theoretically important reason that while both false beliefs and false photographs contain different content from the new state of reality, only false beliefs are “about” reality (Perner et al., 2006; Sabbagh et al., 2006). This “aboutness” relation is a critical feature of mental representations such as beliefs, and a narrow class of other non-mental representations, such as signs, and it is this aboutness relation that allows beliefs in our scenarios to be considered “false” representations of the updated situation, whereas the photographs are more correctly described as accurate representations of an outdated situation. Our data suggest that this aboutness relationship between belief and reality meant that manipulation of the salience of reality in the belief vignettes

changed the degree of interference between participants' representation of belief and reality, resulting in differential recruitment of inhibitory resources in the high- versus low-salience vignettes. In contrast, the absence of this aboutness relationship in the photograph vignettes meant that manipulation of the salience of reality had no effect. Thus, the effect we observe in vlPFC is not the recruitment of a domain-specific resource, nor is it an artefact of poorly-controlled stimuli; it is the recruitment of domain-general inhibitory resources in response to a theoretically important feature of beliefs that is not shared with photographs, videos and drawings.

Although the present study provides significant progress in understanding the role of vlPFC in ToM, important questions remain. Whereas the present study indicated a left lateralised process for the inhibition of self-perspective, a parallel literature has implicated right (Samson et al., 2005; Vogeley et al., 2001) or bilateral vlPFC (van der Meer et al., 2011). Although the laterality of our data are in line with a quantitative meta analysis of ToM (Mar, 2011), additional research is needed to determine if, and how, right vlPFC works in conjunction with left vlPFC to support inhibitory processes in ToM, particularly as left and right vlPFC are thought to support different, but related, mechanisms in inhibitory control (O'Reilly, 2010). The present data speak to an account of vlPFC where the left hemisphere supports controlled retrieval and the right plays a more general role in suppressing irrelevant information. Specifically, the experimental manipulation presented here varied the *level* of salience of self-perspective, rather than the *presence* of it. All conditions therefore contained two competing sources of information: a representational and real state of affairs. As right vlPFC is suggested to suppress irrelevant informational items (Aron et al., 2004) – which was an equal requirement across all of the experimental conditions presented here – right vlPFC would not be identified by the analyses that could be performed on the present data. Left vlPFC, conversely, has been shown to be involved in controlling the retrieval of competing informational items, working in conjunction with semantic information areas, such as the temporal poles (Badre et al., 2005; Badre and Wagner, 2007), which were recruited alongside left IFG in the whole brain interaction effect. In the case of ToM, the temporal poles may access semantic knowledge for ToM. Importantly, a natural propensity towards our own perspective (Birch and Bloom, 2004; 2007) suggests that "self" may serve as one source of reference in situations of limited knowledge. Self-perspective in this case, however, is not informative. Thus, by varying the salience of own perspective, this latter process of left IFG working with the temporal poles could be facilitated, wherein other, relevant semantic knowledge for ToM, beyond "self", can be retrieved. A direct test of this hypothesised relationship between the left IFG and temporal poles in the context of mentalising would be a valuable topic for further work.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2014.12.015.

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