Neuropsychologia 67 (2015) 183–192

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

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

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ARTICLE INFO

Article history:
Received 17 June 2014
Received in revised form
10 November 2014
Accepted 12 December 2014
Available online 16 December 2014

Keywords:
Theory of Mind
Self-perspective inhibition
False belief
Ventrolateral prefrontal cortex
Representation

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.

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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http://dx.doi.org/10.1016/j.neuropsychologia.2014.12.015

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