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Thinking about the thoughts of others; temporal and spatial neural activation during false belief reasoning

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ABSTRACT

Theory of Mind (ToM) is the ability to understand the perspectives, mental states and beliefs of others in order to anticipate their behaviour and is therefore crucial to social interactions. Although fMRI has been widely used to establish the neural networks implicated in ToM, little is known about the timing of ToM-related brain activity. We used magnetoencephalography (MEG) to measure the neural processes underlying ToM, as MEG provides very accurate timing and excellent spatial localization of brain processes. We recorded MEG activity during a false belief task, a reliable measure of ToM, in twenty young adults (10 females). MEG data were recorded in a 151 sensor CTF system (MISL, Coquitlam, BC) and data were co-registered to each participant's MRI (Siemens 3T) for source reconstruction. We found stronger right temporoparietal junction (rTPJ) activations in the false belief condition from 150 ms to 225 ms, in the right precuneus from 275 ms to 375 ms, in the right inferior frontal gyrus from 200 ms to 300 ms and the superior frontal gyrus from 300 ms to 400 ms. Our findings extend the literature by demonstrating the timing and duration of neural activity in the main regions involved in the "mentalizing" network, showing that activations related to false belief in adults are predominantly right lateralized and onset around 100 ms. The sensitivity of MEG will allow us to determine spatial and temporal differences in the brain processes in ToM in younger populations or those who demonstrate deficits in this ability.

Introduction

In everyday interactions, humans make suppositions about the thoughts and beliefs of others to explain or predict their behaviour in a certain context (Baron-Cohen et al., 1985; Schlinger , 2009). This ability to recognize that other people are thinking agents and that their mental lives or thoughts can be different from one's own or from reality is key to social interactions and is referred to as Theory of Mind (ToM) (Premack and Woodruff, 1978). ToM has been recognized as one of the main components of social cognition, which is crucial in navigating human interactions (Vistoli et al., 2011). During development, explicit ToM ability has been shown to emerge between 4 and 5 years of age (see Wellman et al., 2001 for a review) and continues to develop into adolescence (Blakemore, 2012; Lagattuta et al., 2015). Studies of ToM have often used false belief tasks, as false belief understanding is indicative of possession of a ToM and is thus a mechanism for measuring ToM ability (Colle et al., 2007; Dennis et al., 2012; Gweon and Saxe, 2013; Russell, 2005). Conceptually, success on ToM tasks requires decoupling beliefs from reality, where an individual understands that another person's belief can differ from his/her own and reality (Liu et al., 2004; Ruffman, 2014).

Delineating the mechanism of false belief understanding has been a subject of interest in both clinical (Apperly et al., 2007; Gregory et al., 2002; Shamay-Tsoory et al., 2007) and developmental research (Colle et al., 2007; Kobayashi et al., 2007; Slaughter, 2015) that focuses on populations with deficits in ToM ability. Theoretical models outline a set of perceptual and cognitive processes that are required for understanding false belief. These processes include low level perceptual processing of reality, inferring the beliefs of others, and inhibiting one's own beliefs (Leslie et al., 2004; Samson et al., 2007). It has been postulated that successful "mentalizing" requires a specific sequence of neural activations in the brain regions associated with these cognitive processes. For example, Le Bouc et al. (2012) suggested that lower level attention and perceptual neural processing precedes more complex higher order processes such as managing several representations, referred to as metarepresentation (Sommer et al., 2007; van Overwalle, 2009), as well as inhibiting one's own beliefs.

Functional magnetic resonance imaging (fMRI) studies have characterized the brain networks that underlie false belief understanding. In a

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meta-analysis of fMRI studies of social cognition conducted between 2000 and 2007, van Overwalle (2009) concluded that the temporo-parietal junction (TPJ) and temporo-parietal areas are involved in inferring and representing mental states at a relatively perceptual level, whereas the medial prefrontal cortex (mPFC) – given its high degree of interconnectivity with other brain regions such as the superior temporal sulcus (STS) and TPJ – integrates social information and manages several representations across time, allowing for more complex and explicit metarepresentation on an abstract cognitive level. Schuwerk et al. (2013) suggested that the role of the mPFC is particularly important in computing discrepant mental states, as it is selectively active in false belief. In a comparison between false and true belief, Döhnel et al. (2012) found, however, that both false and true belief conditions involved significantly different activations from a non-mental reality state. Interestingly, when false and true belief conditions were compared, the right TPJ (rTPJ) was not differentially involved in either condition. These findings are in contrast to much of the literature, which notes differences between true and false belief understanding (e.g., Meinhardt et al., 2011; Rothmayr et al., 2011; Sommer et al., 2007). The role of the TPJ in inferring the beliefs of others has been further described by Saxe and Wexler (2005) who found that the rTPJ was associated specifically with conditions where the participant had to think about the mental states of others compared to social descriptions of a person in a scenario, suggesting that the TPJ is a core mentalizing region (Saxe and Wexler, 2005). This notion has been supported by other fMRI studies (e.g., Saxe and Kanwisher, 2003; Scholz et al., 2009; Sommer et al., 2007). Support for a dissociation of function of the main ToM regions comes from clinical studies. Le Bouc et al. (2012) found that Alzheimer's patients with neurodegeneration in temporo-parietal regions were more impaired in inferring someone else's belief, whereas patients with behavioural variant frontotemporal dementia were specifically impaired in inhibiting their own mental perspective.

Although spatio-temporal patterns of ToM-related brain activity are critical to understanding its underlying functions, only a few studies have examined the temporal profile of ToM. Meinhardt et al. (2011), using event-related potentials (ERPs), reported that false belief reasoning was associated with a late slow wave (LSW, adults: 600 ms to 900 ms; children 750 ms to 1450 ms) over frontal regions and a late positive complex (LPC, adults and children 300 ms to 600 ms) over parietal regions. The authors suggested that the LPC was similar to another potential, P3, which is associated with activity in the TPJ. Wang et al. (2010) reported that although an early ERP (P200) was not significantly different between a person perception scene and a ToM scene, the LPC was significantly more positive in the ToM condition. ERP studies that compared false belief or mental state reasoning to reasoning about a physical phenomenon or reality, consistently found a LSW component over frontal regions (Liu et al., 2004, 2009; Sabbagh and Taylor, 2000). ERP studies provide information about the general distribution and regions involved in processing mental states, but their poor spatial resolution hinders precise source reconstruction of the ToM-related network regions, such as the TPJ that have been reliably identified in fMRI studies.

Understanding the temporal dynamics of the neural processes involved in ToM would allow us to determine the order and duration of activation in regions involved in processing theories about the minds of others and consequently assess the framework proposed for false belief understanding. Thus, in the present study, we used magnetoencephalography (MEG), as this technique offers the ability to measure neuronal activity directly with millisecond (ms) time resolution while also providing good spatial resolution. As with all non-invasive techniques, neuronal signals are recorded outside the head, thus requiring a solution to the inverse problem for source localization. Various models and assumptions are used to reconstruct the exact sources of these signals (for a review see Hansen et al., 2010). With these approaches MEG affords a measure of temporal activity that is orders of magnitude higher than the time resolution of an fMRI with comparable spatial resolution (5 mm) (Hari and Salmelin, 2012).

We recorded MEG activity during a false belief task, where ToM ability was required, and comparable true belief conditions in which the participant held the same belief as the character in the task.

Although true belief conditions may involve activations of regions in the ToM network (Döhnel et al., 2012), the false belief condition triggers activation of brain areas underlying core cognitive processes required for ToM ability such as decoupling mental states from reality (Meinhardt et al., 2011; Liu et al., 2004) and inhibitory control over one's own mental states (Zhang et al., 2009).

Based on fMRI and ERP literature, we predicted that compared to the true belief condition, the false belief condition will be associated with stronger activations in the ToM network such as parietal regions as early as 300 ms, and specifically the rTPJ which enables orienting and inferring beliefs to others (Rothmayr et al., 2011; Saxe and Kanwisher, 2003), followed by frontal activations involved in inhibition of one's own beliefs (Le Bouc et al., 2012), which are reported in ERP studies from 480 to 900 ms in adults (Meinhardt et al., 2011; Liu et al., 2009; Zhang et al., 2009).

We used the Jack and Jill task developed by Dennis et al. (2012) where an agent is absent in the false belief condition but present in the comparable true belief condition. Therefore, we predicted perceptual differences such as early visual processing of the missing character in false belief compared to true belief that are not related to ToM. Thus, we expected that our sequence of activations would involve regions that are both specific and non-specific to ToM processing, beginning with visual and attention processing of the change in visual scene in the false belief condition followed by activations in the rTPJ, followed by frontal activations.

Methods

Participants

Twenty adults (10 F; 20–35 years, M = 24.9 ± 4.1) were recruited from the general public or were students or staff from various research labs at the Hospital for Sick Children (SickKids). 18 participants were right handed. The two-subtest WASI (Wechsler Abbreviated Scale for Intelligence; Wechsler, 2002) was administered to participants (M = 120.5, SD = 10.1). Informed consent was obtained and participants were compensated for their time. Exclusion criteria included a history of neurological or developmental disorders, head trauma, uncorrected vision problems, colour blindness, the use of psychotropic medications and standard neuroimaging contraindications. The study protocol was approved by SickKids' Research Ethics Board. Written informed consent was obtained from all participants.

Stimuli

The Jack and Jill false belief task of Dennis et al. (2012) was adapted for this study. The size and contrast of the original images were modified to minimize stimulus complexity. Sequences of images showing the cartoon drawings of Jack and Jill, a red hat, a blue hat and a ball were projected in the centre of a screen in the MEG room, at a viewing distance of approximately 80 cm. The projected images were 9.1 × 9.5 cm and subtended 6.8° of visual arc.

Each trial consisted of a sequence of two images followed by a fixation cross. Stimulus duration of the first image was 500 ms, immediately followed by the second image for up to 3000 ms or until the participant responded via button press on the VPIXX 4 button pad (Visual Science Solutions, Saint-Bruno QC), ending the trial. Participants were instructed to respond as quickly as possible when they saw the second image. Once they responded, the image was replaced by a fixation cross at the centre of the screen for 1000 ms ± 100 ms, which was the inter-trial interval (ITI). The time jitter was included to