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Brain Mechanisms Underlying Reading the Mind from Eyes, Voice, and Actions

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Abstract—Evidence from cognitive and social neuroscience research suggests that Theory of Mind (ToM), the ability to attribute mental states to others, is mediated by a group of brain regions collectively known as the ToM network. Nevertheless, there is significant variability in the functional activation of regions within this network across tasks. The goal of the present functional magnetic resonance imaging (fMRI) study was to examine the common and differential neural mechanisms of two aspects of ToM processing (emotion/mental-state recognition and intentional attribution) using three distinct, but complementary ToM tasks (*Reading the Mind in the Eyes* (RMIE), *Reading the Mind in the Voice* (RMIV), and *Intentional Causal Attribution*) in healthy adults. Participant accuracy was significantly worse in the ToM compared to the control condition across all tasks. Brain activation analyses replicated previously reported activation in inferior frontal gyrus (IFG) and middle temporal gyrus extending to posterior superior temporal sulcus (pSTS) in RMIE. Activation in the fusiform gyrus and bilateral middle temporal gyrus extending to temporo-parietal junction (TPJ) was unique to causality task. A region-of-interest analysis revealed shared activation in left IFG for RMIE and RMIV as well as TPJ recruitment specific to the causality task. The role of right TPJ in the causality task was further supported by a percent signal change analysis. A conjunction analysis revealed overlap in left IFG, left precentral gyrus, and left superior frontal gyrus activity across all tasks. These findings highlight common and differential recruitment of ToM regions according to task demand. Published by Elsevier Ltd on behalf of IBRO.

Key words: RMIE, RMIV, intentional causality, theory of mind.

INTRODUCTION

Individuals learn to extract socially salient information from the environment by making inferences about the thoughts, feelings, motives, desires, and intentions of others. This ability, known as Theory of Mind (ToM), is a fundamental cognitive mechanism which allows individuals to acknowledge the thoughts and actions of themselves and others and to form interpersonal connections (Premack and Woodruff, 1978). The formation of ToM has a protracted developmental trajectory with early precursor skills, such as joint attention, emerging before 9 months of age (Baron-Cohen, 1991) and high-order skills, such as false belief, emerging around the age of 4 years (Baillargeon et al., 2010). Traditionally, research on ToM processing has focused exclusively on young children and utilized tasks which appear to be mastered by children between the ages of 4 and 7 years (Apperly, 2012) such as false belief (Wimmer and Perner, 1983; see Wellman et al., 2001 for review), strange stories (Happé, 1994), and social faux pas (Baron-Cohen et al., 1999). Several researchers, however, argue that although children are able to pass classic ToM tasks such as false belief and strange stories at a young age, their performance and nuanced understanding of the mental states and thoughts of others improve throughout childhood (Wellman et al., 2001; Rai and Mitchell, 2004; Calero et al., 2013; Devine and Hughes, 2013) as well as adolescence through young adulthood due, in part, to corresponding increases in cognitive ability (Frischen et al., 2007; Dumontheil et al., 2010; Valle et al., 2015).

In addition to the debate on the developmental progression of ToM, ToM has also been interpreted to reflect a wide range of behaviors and has been studied extensively using behavioral and neuroimaging

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Abbreviations: fMRI, functional magnetic resonance imaging; FOV, field of view; IFG, inferior frontal gyrus; MNS, mirror neuron system; MPFC, medial prefrontal cortex; MTG, middle temporal gyrus; PCC, posterior cingulate cortex; PSC, percent signal change; pSTS, posterior superior temporal sulcus; RMIE, *Reading the Mind in the Eyes*; RMIV, *Reading the Mind in the Voice*; ROI, region of interest; RTPJ, right temporoparietal junction; TBI, traumatic brain injury; TPJ, temporo-parietal junction.

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methods. Neuroimaging studies suggest that ToM may be mediated by a group of brain areas including: medial prefrontal cortex (MPFC), anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), precuneus, superior temporal sulcus (STS), inferior frontal gyrus (IFG), and bilateral temporo-parietal junction (TPJ: Castelli et al., 2002; Saxe and Kanwisher, 2003; Mitchell et al., 2005; Ochsner et al., 2005; Amodio and Frith, 2006; Saxe and Powell, 2006; Kana et al., 2009, 2015; Mahy et al., 2014; Schurz et al., 2014). There is, however, considerable variability in the tasks used to assess ToM which likely results in different activation profiles across regions within the ToM network in response to these paradigms. The overuse and often widely defined nature of the construct of ToM in social neuroscience has led to relatively poor consensus on the involvement of specific brain areas involved in different levels of ToM processing (see Schaafsma et al., 2015 for review). This is further supported by meta-analytic studies of differential activation in core ToM regions which found that only bilateral posterior TPJ and MPFC were commonly activated across all ToM tasks included in the review (see Schurz et al., 2014; Molenberghs et al., 2016 for reviews). A different meta-analysis, however, concluded that the same core brain regions are activated in response to different ToM paradigms, though the consistency of reported activation in each area differed across task (Carrington and Bailey, 2009). Two extensively used ToM tasks, false belief and social animation of geometrical shapes, have been found to differentially recruit the ToM network with more activation in the TPJ, precuneus, and PCC seen in the false belief task compared to activation in posterior superior temporal sulcus (pSTS), inferior parietal lobule (IPL), and fusiform seen in the social animation task (Gobbini et al., 2007). It is evident that the recruitment of ToM regions is task-dependent and requires further characterization. The current study will investigate the neural basis of mental-state detection, and, specifically, will focus on two types of mental state: emotion and intention. Emotion detection will be studied using the Reading the Mind in the Eyes (RMIE; Baron-Cohen et al., 1997, 2001) and the Reading the Mind in the Voice (RMIV; Rutherford et al., 2002) tasks which differ in the sensory modality used to express emotional state, and understanding intention will be studied using an intentional causal attribution (Brunet et al., 2000) task. These tasks were chosen due to their suitability for testing an adult population and the fact that they tap into specific sub-components of ToM which allows for specificity in the examination of ToM processing.

RMIE is a mental-state recognition task, which relies on inferring emotion from eye expressions. Since the inception of the task, RMIE has been used to assess ToM deficits in a number of clinical conditions such as autism (Baron-Cohen, 2001), borderline personality disorder (Fertuck et al., 2009), alcohol dependence (Maurage et al., 2011), traumatic brain injury (TBI; Dal Monte et al., 2014), fetal alcohol spectrum disorders (FASD; Lindinger et al., 2016), Parkinson's disease (Tsuruya et al., 2011), and psychopathy (Richell et al., 2003). Previous studies have found that inferring mental states from eye expressions in the RMIE task primarily activates the posterior STS and IFG (Adams et al., 2010; Gunther Moor et al., 2000). Evidence from research on patients with TBI suggests that lesions to the left IFG result in poorer performance on the RMIE task (Dal Monte et al., 2014). The consistency in reported STS activation across RMIE studies aligns with research on eye gaze perception which suggests that the eyes convey implicit social information and the STS serves as the primary hub of this processing (Frischen et al., 2007). Some studies with younger adolescents have reported activation in the MPFC as well, although this activity decreased from early adolescence to adulthood highlighting the developmental trajectory of brain areas underlying social cognition (Gunther Moor et al., 2012; Overgaauw et al., 2015).

A similar but relatively less investigated task, RMIV, differs from the RMIE task by asking participants to attribute emotion or mental states based on speakers' utterances (Rutherford et al., 2002). A revised version of this task found a positive correlation between RMIE scores and RMIV scores indicating a similar level of sensitivity to ToM in both tasks (Golan et al., 2007). Despite this behavioral correlation, it is not known if there is neural correspondence in the ToM regions recruited for RMIE and RMIV. The third task used in this study, Causality, relies on context-driven intentional attribution by requiring participants to make physical or intentional causal attributions to actions and events. The causality task may be a more interactive and integrative measure of ToM processing and facilitate greater recruitment of core ToM regions. A positron emission tomography (PET) study using this causality task reported activity in MPFC, right IFG, STG, and fusiform gyrus (FG; Brunet et al., 2000); whereas functional magnetic resonance imaging (fMRI) studies showed pSTS at the TPJ as a key region of activity during intentional causal attribution (den Ouden et al., 2005; Blakemore et al., 2007; Kana et al., 2014; Murdaugh et al., 2014).

The three tasks used in our study are qualitatively different (RMIE: mental-state detection from static photographs of the eye region; RMIV: mental-state detection from utterances; Causality: intentional attribution to actions described in comic strip vignettes) and may recruit both overlapping and distinct regions in the ToM network. Given the complexity of the concept of ToM, the tasks used in the present study selectively focus on two components of ToM processing: mental-state detection from static images or utterances, and intentional attribution to action scenarios. Both the RMIE and RMIV tasks require participants to decode the emotional state of another person based on a sample of the face (eye region of the face) or voice of that person. These tasks require participants to infer emotion from a third person, a process which represents one aspect of ToM. In the Causality task, participants are asked to identify a logical ending to a vignette which displays a person completing a goal-oriented action. This paradigm requires participants to understand the beliefs, intentions, and goals of the protagonist based on the social context depicted in the stimuli and is perhaps one aspect of the overall construct of ToM. Emotion or mental-state