



Review

How and where: Theory-of-mind in the brain

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ABSTRACT

Theory of mind (ToM) is a core topic in both social neuroscience and developmental psychology, yet theory and data from each field have only minimally constrained thinking in the other. The two fields might be fruitfully integrated, however, if social neuroscientists sought evidence directly relevant to current accounts of ToM development: modularity, simulation, executive, and theory theory accounts. Here we extend the distinct predictions made by each theory to the neural level, describe neuroimaging evidence that in principle would be relevant to testing each account, and discuss such evidence where it exists. We propose that it would be mutually beneficial for both fields if ToM neuroimaging studies focused more on integrating developmental accounts of ToM acquisition with neuroimaging approaches, and suggest ways this might be achieved.

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1. Introduction

As the field of psychology diversifies, communication among researchers who study the same topic with different methodologies becomes increasingly important. Empirical findings are disseminated within a certain theoretical or methodological framework, potentially creating gaps between literatures that may not be bridged. Such is the current state of theory of mind (ToM) research, where there is little overlap in how developmental psychologists and social neuroscientists study the ways in which people impute mental states to self and other.

Social neuroscience and developmental psychology both prominently feature research on ToM, yet emphasize different facets of this core social cognitive ability. Social neuroscientists tend to focus on *where* in the brain mentalizing resides, while developmental psychologists are centrally concerned with *how* mentalizing is acquired (and *when* it emerges). As a result, much of the adult neuroimaging work has not been explicitly linked to developmental theories; instead, it has focused on identifying ToM-relevant neural regions, and distinguishing groups of individuals such as those with and without autism spectrum disorders in terms of systems or processes recruited. The differing research agendas of these two fields are clearly related and yet, as others have noted (e.g., Apperly, 2008; Saxe, 2006), they remain largely unreconciled.

In this paper we aim to advance the field by attempting to integrate developmental and neuroimaging approaches to ToM. We propose that it would be mutually beneficial for both fields if developmental and social neuroscientists were to more fully consider developmental theories focusing on acquisition of ToM when generating hypotheses, designing studies, and interpreting results. Our review is the first to examine in one place neural evidence for the four major theories of ToM acquisition that have been proposed, although others have compared subsets of the theories (e.g., Apperly, 2008; Wilkinson and Ball, 2012). We take the position that processes specified by each theory may potentially contribute to ToM development and that ultimately neuroimaging research may help generate a new theory that integrates existing approaches. Our primary goal is to compile an up-to-date summary of neuroimaging evidence relevant to theoretical accounts of ToM acquisition so that this growing field may advance conceptually, theoretically, and methodologically. Further, we hope to establish where neuroimaging techniques might be particularly helpful or unhelpful in testing a given theory. It is our

hope that both behavioral and neuroimaging researchers will find this review useful and that it will stimulate future work integrating developmental and neuroimaging approaches.

We begin by briefly reviewing the main theoretical accounts of how ToM is acquired and suggesting the types of neural evidence that would support or pose problems for each theory, describing such evidence where it is available. We consider the following four development accounts of ToM: modularity theories, simulation theories, executive accounts, and theory theory. We draw on developmental evidence whenever possible although the current state of the literature dictates a heavy reliance on findings from adult studies, as neuroimaging studies with children remain scarce. We also draw on the autism literature to the extent it is strongly germane to our argument, although a full consideration of that literature is beyond the scope of the current paper (see Happé and Frith, 2013 for a review of neuroimaging studies in ASD). Finally, we address some of the challenges of using neuroimaging techniques to examine developmental theories of ToM and suggest future research that could close the gap between social neuroscience and developmental approaches.

2. Modularity theories: selectivity

2.1. Definition

Modularity theories (e.g., Fodor, 1983; Leslie et al., 2004; Scholl and Leslie, 1999; Baron-Cohen, 1995, 1998) postulate that ToM development is driven by an innate neural mechanism dedicated to mental state reasoning. Although experience may be important in triggering this mechanism, it cannot revise the mechanism's basic nature. Leslie and his colleagues have proposed the most fully articulated and prominent modularity theory of ToM and therefore we focus on their account. It should be noted, however, that their account represents a relatively strong form of modularity and that accounts stipulating less stringent criteria have been proposed (e.g., see Coltheart, 1999; Carruthers, 2003). The central claims made by Leslie and colleagues are that an innate ToM module (ToMM) is working by the second year of life, and that later age-related improvements in ToM performance in childhood are driven by an inhibitory selection process that becomes increasingly able to handle the executive demands of ToM tasks (Leslie et al., 2004; Scholl and Leslie, 2001; German and Hehman, 2006).

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