



Original Articles

The selfless mind: How prefrontal involvement in mentalizing with similar and dissimilar others shapes empathy and prosocial behavior



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ABSTRACT

Engaging in mentalizing, i.e., reflecting on others' thoughts, beliefs and feelings, is known to facilitate later empathy and prosocial behavior. Activation in dorsomedial prefrontal (dmPFC) areas during mentalizing has been shown to predict the extent of prosocial behavior. It is unclear, however, what cognitive process drives these effects: a simulation process in which the own mental states are used as a proxy for those of others (self-projection) or an effortful other-enhancement process in which one's own perspective is overridden. In this fMRI study we examined the effects of mentalizing with similar and dissimilar others on behavioral and brain measures of empathy and prosocial behavior, to assess which cognitive process mediates the facilitative effects of mentalizing. Participants had to mentalize with two fictitious target persons, one of whom was manipulated to have similar thoughts and beliefs as the participant, while the other had dissimilar mental states. We then assessed participants' behavioral and neural responses during an empathy for pain task and a prosocial behavior task. Similarity between participant and target person increased empathy and affiliation ratings, and mentalizing with dissimilar persons evoked increased activation in ventrolateral prefrontal cortex, the extent of which was inversely related with bias towards the similar person in empathy. Responses in two dmPFC regions were also predictive of later variations in subsequent empathy and prosocial behavior, either predicting overall prosociality and empathic concern (lateral dmPFC), or predicting reduced empathic bias towards the similar person and a lower response to self-related stressors in pain matrix areas (medial dmPFC). This pattern of results suggests that generating and enhancing other-related representations while overcoming one's own perspective, rather than enhanced recruitment of self-projection processes, is driving the facilitative effects of mentalizing on later empathic and prosocial responses.

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1. Introduction

Humans have the capacity, and spontaneous tendency, to reflect on the thoughts, beliefs and feelings of their conspecifics, known as mentalizing. Although the mental states of others cannot be directly observed, making inferences about them greatly increases our ability to predict others' future behavior, which is a crucial advantage for individuals living in complex social groups.

It has been shown that engaging in mentalizing with others may also intensify feelings of empathy for these persons, as well

as the willingness to engage in prosocial behavior towards them. For instance, explicitly instructing participants to take the cognitive or affective perspective of others increases both self-reported empathy and helping behavior (Oswald, 1996). These effects can also be induced by more implicit forms of mentalizing: in a previous fMRI study we have shown that having to take others' affective or cognitive perspective to solve questions about them in a priming task impedes subsequent decisions to harm them in hypothetical moral dilemmas where one individual could be sacrificed to save the lives of several others. These behavioral effects were accompanied by increased activity in brain areas associated with aversive emotions and empathy during the decision phase (Majdandžić et al., 2012). Others have shown that the magnitude of the BOLD response in several parts of the dorsomedial prefrontal cortex (dmPFC), an area reliably associated with mentalizing, during a

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mentalizing task predicts later altruistic helping (Waytz, Zaki, & Mitchell, 2012). This led the authors to conclude that prosociality is associated with a propensity to engage in social-cognitive thought, i.e. the consideration of others' subjective experiences.

However, despite clear evidence for a link between mentalizing and diverse measures of prosocial attitude and behavior, it is unclear what cognitive process, as reflected in medial prefrontal activation during mentalizing, drives these effects. Presumably, mentalizing forces us to perceive others as full-blown individuals with beliefs and desires. Therefore, the effects of harmful or beneficial acts on the mental states of these persons might also be represented in a more salient way. Yet, this altered, more full-blown "mental" representation of others could be achieved in several ways.

One candidate mechanism is based on the hypothesis that mentalizing engages simulation mechanisms in which the self is used as a "template" or anchor for making inferences about others (Epley & Gilovich, 2001; Epley, Keysar, Van Boven, & Gilovich, 2004; Tamir & Mitchell, 2010). That is, inferring someone's thoughts and feelings is achieved by mentally projecting oneself into his or her position, and imagining how one would think and feel then. Support for a role of such self-projection processes in mentalizing comes from behavioral studies showing that people tend to assume that others hold the same opinions (Krueger & Clement, 1994; Ross, Greene, & House, 1977) and have the same knowledge (Epley et al., 2004), as they themselves do. People are worse at understanding others' thoughts and feelings when those mental states differ from their own (Niedenthal, Halberstadt, Margolin, & Innes-Ker, 2000; Wellman, Cross, & Watson, 2001). In addition, self-referential processing (i.e., reflecting on one's own mental states) and mentalizing with others seem to rely on largely overlapping activation patterns, especially in the medial prefrontal cortex, indicating that they involve a common process also on the functional level (Frith & Frith, 1999; Gallagher, Jack, Roepstorff, & Frith, 2002; Gallagher et al., 2000; Jenkins, Macrae, & Mitchell, 2008; Kelley et al., 2002; Mitchell, 2009; Mitchell, Banaji, & Macrae, 2005; Mitchell, Macrae, & Banaji, 2006; Northoff et al., 2006; Zaki & Ochsner, 2011). Activation in several subregions of the medial prefrontal cortex is moreover modulated by the perceived similarity between the self and the person mentalized with (Mitchell et al., 2006). This might be seen as a further indication that mentalizing involves self-projection processes, given the assumption that people will engage in more self-projection when thinking about similar persons, for which the self a priori seems to be a more suitable model.

Evidence on how similarity exactly affects these activation patterns is far from conclusive, though: while involvement of some subareas seems to increase with self-other similarity (Jenkins et al., 2008; Mitchell et al., 2005), other regions show a stronger response for dissimilar persons (Mitchell et al., 2006; Tamir & Mitchell, 2010), or show inconsistent effects across different studies (Mitchell et al., 2006; Tamir & Mitchell, 2010). Yet, in spite of these inconsistencies, it is widely assumed that self-referential simulation processes play at least some role in mentalizing.

Self-projection processes, then, would drive the effects of mentalizing on subsequent prosocial behavior by increasing the extent of "overlap" between mental representations of one's own inner states and those of the target person (Aron, Aron, & Smollan, 1992; Davis, Conklin, Smith, & Luce, 1996; Galinsky, Ku, & Wang, 2005). Such merging of self-other representations may facilitate empathic responses (Chambers & Davis, 2012), since empathy also seems to rely on shared representations: it involves activation of the same neural networks as those involved in the first-hand experience of the affective state (Bernhardt & Singer, 2012; Lamm, Decety, & Singer, 2011; Lamm & Majdandžić, 2015; Rütgen, Seidel, Riečanský, & Lamm, 2015; Rütgen, Seidel, Silani, et al.,

2015; for reviews see Bernhardt & Singer, 2012 and Lamm & Majdandžić, 2015). Enhanced empathy may in turn motivate prosocial behaviors (Batson et al., 1997; Cialdini et al., 1987). Thus, according to this view, the effects of mentalizing on prosocial behavior can be explained on a functional level by the engagement of self-projection processes, with more self-projection being reflected in enhanced recruitment of medial prefrontal areas classically involved in mentalizing.

Yet, reflecting on the mental states of others evidently also involves other processes than basic self-projection mechanisms. From a theoretical point of view, successfully evaluating others' mental states not only requires the ability to mentally project oneself into their position, but also to inhibit one's own perspective if needed, and to enhance a potential alternative perspective. In view of this, it has been proposed that mentalizing involves a two-stage process, in which the own perspective is used as a starting point or "anchor", which then gets adjusted in a serial and effortful process (Epley & Gilovich, 2001; Tamir & Mitchell, 2010). Support for this notion comes from studies showing that assessing perspectives different from one's own is time-consuming, and that time constraints increase egocentric biases (Epley et al., 2004). This adjustment process seems to rely on general self-inhibition abilities (Launay et al., 2015). For instance, the ability to reason about mental states different from one's own is strongly correlated with inhibitory control in children (Carlson & Moses, 2001). Notably, medial prefrontal brain areas tend to show higher activation during mentalizing with dissimilar others, which is consistent with a serial adjustment process from a self-based starting point, with more adjustment requiring stronger involvement of these areas (Tamir & Mitchell, 2010). Along with this self-inhibition process, a representation of the other's perspective should be generated and actively enhanced. This fits with notions that the cognitive operations carried out by the brain network involved in mentalizing can be framed in more general terms as a "fuzzy" mode of processing, characterized by generating and manipulating approximate mental estimates based on inexact, internally retrieved information (Mitchell, 2009). Accordingly, mentalizing can be seen as an instance of a more general cognitive ability in which "past experiences are used adaptively to imagine perspectives and events beyond those that emerge from the immediate environment" (Buckner & Carroll, 2007, p. 49).

Thus, although mentalizing may involve setting an initial, self-based "anchor", it may be the subsequent effortful process of inhibiting this own perspective so as to enhance an alternative perspective that is decisive for its facilitative effects on prosocial behavior. In this view, making the own perspective less salient to "make room" for the other's perspective implies a transition from a self-centered to an other-directed orientation, which may foster empathy and prosocial behavior. This is in line with earlier notions that while empathy entails both self-related emotions (personal distress) and other-related emotions (empathic concern) (Batson, Fultz, & Schoenrade, 1987), the latter seem to better predict altruistic behavior (Batson, Duncan, Ackerman, Buckley, & Birch, 1981; Batson et al., 1989). Notably, this suggestion does not dismiss the possibility that mentalizing involves a form of self-projection; rather, it argues that this initial, automatic self-projection is insensitive to the degree of similarity of the person mentalized with, and is not driving changes in prosocial orientation. Instead, it is the effectiveness of subsequent self-inhibition and other-enhancement that is mediating these effects.

With the present fMRI-study we aimed to clarify which of the abovementioned cognitive processes: (1) self-projection or (2) self-inhibition / other-enhancement, as reflected in increased contributions by prefrontal "mentalizing" areas, is driving the enhancing effects of mentalizing on prosocial behavior, and how these effects are mediated by empathy. To this end, we manipulated

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