



# A developmental perspective on the neural bases of human empathy



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## ARTICLE INFO

### Article history:

Received 14 March 2015

Accepted 30 November 2015

Available online 17 March 2016

### Keywords:

Empathy  
Neural correlates  
Affective sharing  
Perspective-taking  
Development  
Infancy

## ABSTRACT

While empathy has been widely studied in philosophical and psychological literatures, recent advances in social neuroscience have shed light on the neural correlates of this complex interpersonal phenomenon. In this review, we provide an overview of brain imaging studies that have investigated the neural substrates of human empathy. Based on existing models of the functional architecture of empathy, we review evidence of the neural underpinnings of each main component, as well as their development from infancy. Although early precursors of affective sharing and self-other distinction appear to be present from birth, recent findings also suggest that even higher-order components of empathy such as perspective-taking and emotion regulation demonstrate signs of development during infancy. This merging of developmental and social neuroscience literature thus supports the view that ontogenic development of empathy is rooted in early infancy, well before the emergence of verbal abilities. With age, the refinement of top-down mechanisms may foster more appropriate empathic responses, thus promoting greater altruistic motivation and prosocial behaviors.

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## 1. Introduction

The evolution of hominids has no doubt contributed to our physical appearance, but what really makes us human is our minds, especially the complexity of our social skills (Dunbar, 2003). We are, indeed, social animals. Most of our daily lives consist of social interactions, whether they are dyadic, in groups, experienced first-hand, witnessed, or simply imagined. One of the interpersonal faculties that support and promote these everyday social interactions is empathy, the ability to share and understand others' affective states. Recent advances in social neuroscience have provided new insights to this construct by characterizing the neural correlates of empathic responses. Empathy is now often viewed as a complex construct emerging from several interacting components, including bottom-up and top-down processes (Decety & Jackson, 2004; Shamay-Tsoory, 2011). Increasing attention is also given to the relationship between empathy and altruism, as some authors include altruistic motivation as an essential part of the empathic experience (Batson, 2011). Research in developmental psychology and neuroscience has also shed light on the basic building blocks of empathy and their development from birth to adulthood.

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Developmental research brings an interesting perspective on how the different components of empathy interact with each other and emerge at different paces, and how their alteration during early years can affect social abilities.

## 2. Defining empathy

There are many definitions of empathy in the literature, and while there are several common elements among these definitions, some distinctions exist. The domain from which a definition emerges, be it philosophy, psychology, psychiatry or neuroscience, often influences its constitution. Historically, the term “empathy” was first used as a way to describe how we project ourselves into artwork, and then was transposed to social psychology to describe an interpersonal phenomenon. The field of neuroscience, and more specifically neuroimaging, started contributing to the characterization of this complex phenomenon soon after (Jackson, Meltzoff, & Decety, 2005; Singer et al., 2004; Wicker et al., 2003), leading to the development of several models of the functional architecture of empathy (Decety & Jackson, 2004; Decety & Lamm, 2006; Decety, 2010; Engen & Singer, 2013; Preston & de Waal, 2002; Shamay-Tsoory, 2011; Zaki & Ochsner, 2012). Most of these models argue that empathy involves both bottom-up information processing (i.e., automatic processing based on sensory inputs, such as affective resonance) and top-down information processing (i.e., higher-level cognitive processing, such as emotion regulation). For the purpose of this review, we will conceptualize empathy as a multidimensional construct consisting of five main components, based on the different models of the literature: (i) affective sharing: a bottom-up process that leads to vicariously experiencing another person’s emotional state, (ii) self-other distinction: the ability to differentiate the feelings that belong to the self and those that belong to the other, involving a sense of self-awareness and agency, (iii) perspective-taking: deliberately imagining or projecting oneself into another person’s perspective in order to understand her/his feelings, (iv) emotion regulation: a top-down process that allows a down-regulation or up-regulation of one’s own emotions in order to promote an appropriate empathic response, and (v) altruistic motivation: a desire to enhance another person’s welfare or experience that results from the interaction of the four other components. These five components have been associated with distinct but interacting and sometimes overlapping neural circuits, and seem to present different developmental trajectories (Decety & Meyer, 2008).

## 3. Affective sharing

### 3.1. Neural bases of affective sharing

This basic emotional sharing system, also known as affective resonance (Decety & Meyer, 2008), affective arousal (Decety, 2010), emotional contagion (Shamay-Tsoory, 2011), or shared representations between self and other (Decety & Jackson, 2004), is the main bottom-up information process involved in human empathy. At the neural level, it has been proposed that affective sharing relies on a perception–action coupling mechanism, through which the perception of another person’s emotional state automatically activates the perceiver’s representation of this state, and that this representation primes the associated autonomic and somatic responses, unless inhibited (Preston and de Waal, 2002). Pain observation paradigms have been extensively used in the study of the neural bases of affective resonance. Activation of areas known to be involved in self-experienced pain has been observed during vicarious pain exposure, whether through the observation of facial expressions of pain (e.g., Botvinick et al., 2005) or of body parts in painful conditions (e.g., Jackson et al., 2005), or even through a signal indicating that another person was experiencing pain (e.g., Singer et al., 2004). A meta-analysis by Lamm, Decety, and Singer (2011) summarizes findings on shared representations of pain by demonstrating a constant common activation of bilateral anterior insula (AI) and adjacent inferior frontal gyrus (IFG), and the dorsal anterior/anterior medial cingulate cortex (dACC/aMCC) during directly experienced pain and empathy for pain. Empathy for (or the observation of) other basic emotions such as disgust (Wicker et al., 2003), anxiety (Morelli, Rameson, & Lieberman, 2014), and fear (De Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004) has been found to elicit similar neural responses than the emotion per se. Indeed, another meta-analysis has revealed that dACC, aMCC and bilateral AI/IFG are part of a core neural network underlying empathy for different types of emotional stimuli (Fan, Duncan, de Greck, & Northoff, 2011). While the AI has been associated with the representation of interoceptive and emotional information, the ACC has been viewed as its motivational counterpart which selects and prepares the appropriate response (Craig, 2009). The coactivation of these two regions during empathy could thus represent awareness of the feelings of others and the prediction of their affective behavior via the representation of our own feelings (Singer et al., 2004). All the studies suggesting a common activation during emotion observation and self-experienced emotion provide strong support for the shared representations account of affective sharing. However, an overlap of activation at a voxel resolution, reflecting the activity of thousands of neurons, does not indicate an overlap of representations at the neuronal level. Recent studies using more advanced methods of functional magnetic resonance imaging (fMRI) signal analysis are currently searching for the limits of this sharing mechanism, and whether it is related to similar neuronal populations remains to be confirmed (Corradi-Dell’Acqua, Hofstetter, & Vuilleumier, 2011; Krishnan, 2013).

### 3.2. Development of affective sharing

Accumulating behavioral data from developmental studies suggest that the mechanisms underlying affective sharing are already present at birth (Decety, 2010). Humans are born with a capacity to send and receive affective cues and to distinguish

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