Progress in Neurobiology 98 (2012) 38–48

Contents lists available at SciVerse ScienceDirect

Progress in Neurobiology

journal homepage: www.elsevier.com/locate/pneurobio

# A neurobehavioral evolutionary perspective on the mechanisms underlying empathy

Jean Decety[a,b,*], Greg J. Norman[a], Gary G. Berntson[c,d,e], John T. Cacioppo[a,b]

[a] Department of Psychology, The University of Chicago, United States
[b] Department of Psychiatry and Behavioral Neuroscience, The University of Chicago, United States
[c] Department of Psychology, Ohio State University, United States
[d] Department of Psychiatry, Ohio State University, United States
[e] Department of Pediatrics, Ohio State University, United States

ARTICLE INFO

*Article history:*
Received 29 December 2011
Received in revised form 9 April 2012
Accepted 1 May 2012
Available online 11 May 2012

*Keywords:*
Affective neuroscience
Attachment
Caring
Empathy
Evolution
Social neuroscience
Pro-social behavior

ABSTRACT

In mammals, empathy is crucial for living in social groups and caring for others. In this paper, we consider the structural and functional organization of empathy. We propose that empathy subsumes a variety of neurobiological processes and partially dissociable information processing subsystems, each of which has a unique evolutionary history. Even the most advanced and flexible forms of empathy in humans are built on more basic forms and remain connected to core subcortical and neurohormonal mechanisms associated with affective communication, parental care and social attachment processes. Considering empathy within a framework that recognizes both the continuities and the changes within a phylogenetic perspective provides a richer understanding of empathy and related neurobehavioral processes.

## Contents

1. Neuroevolution of empathy-related behaviors . . . 39
2. Evolution of empathy from parenting behavior . . . 41
3. Parental care is rewarding . . . 41
4. Neural circuits associated with the perception of others' distress . . . 42
5. The lack of empathic arousal contributes to callous disregard to others' welfare . . . 43
6. Aspects of empathy specific to humans . . . 44
7. Empathy as an adaptive response . . . 44
8. Conclusions . . . 45
Acknowledgements . . . 46
References . . . 46

Mammalian reproductive fitness and survival depend crucially on the ability of conspecifics to communicate with each other, sharing information about their emotions and intentions and appropriately responding to their offspring or relatives needs. Although organisms can develop a variety of understanding of others, empathy entails more than just understandings or expectations. When individuals empathize, they vicariously feel the emotions of others, which not only promote affective communication but depending on the context and social relationships may motivate to behave pro-socially towards other conspecifics (Decety, 2011).

Empathy has been a focus of speculation in philosophical and psychological investigations throughout written history (Batson, 2009). Recently, the scientific understanding of empathy has blossomed into a vibrant and multidisciplinary field of study

---

*Abbreviations:* ACC, anterior cingulate cortex; AIC, anterior insular cortex; aMCC, anterior midcingulate cortex; fMRI, functional magnetic resonance imaging; mPOA, medial preoptic area; PAG, periaqueductal gray; SMA, supplementary motor area.

[*] Corresponding author at: Department of Psychology, The University of Chicago, United States.

*E-mail address:* decety@uchicago.edu (J. Decety).

0301-0082/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.pneurobio.2012.05.001

appealing to those in developmental and cognitive psychology, evolutionary biology, and affective and social neuroscience (Mason and Ben Ami-Bartal, 2010). Considerable evidence now exists to suggest that empathy has deep evolutionary, neuroendocrine, and neurophysiological underpinnings.

One likely source of empathetic responses in mammals comes from the phylogenetically ancient practice of caring for ones offspring. For example, caregiving to offspring can be observed in birds (Cockburn, 2006), fish (Goodwin et al., 1998), and a minority of reptiles (Clutton-Brock, 1991). Moreover, caregiving of offspring is a characteristic of all mammals (Bell, 2001). While parental care for offspring is not necessary for evolutionary success, in some cases it provided a fitness advantage for the offspring of particular species and the genes that promoted this behavior were passed onto subsequent generations. Over countless generations, mammals developed ever more complex physiological (e.g., lactation) and behavioral (e.g., perceiving the needs of their offspring) processes associated with improving offspring survival (Bell, 2001). The neurobiological and behavioral manifestations of parental care also provide the means through which individuals within a social group are able to care for one another. Kin selection models of social behavior presumes that the pro-social tendencies within groups resulted from the fact that organisms that assist their genetic relatives are better able to propagate a fraction of their own genetic legacy into future generations (e.g., assisting sibling's offspring which share 25% of one's genes) (Wilson, 1975). However, kin selection models of pro-social behaviors within groups do not actually specify how these behaviors are motivated and do not assume that individuals must be able to detect genetic relatedness (Bell, 2001). Thus, any evolved motivational system that increases the fitness of kin will produce the same results in terms of fitness regardless of fact that this motivational system may also apply to non-relatives (Bell, 2010). The ability to model the emotions of non-relatives and react appropriately within in a social group would likely confer some fitness advantages (e.g., better able to communicate and detect distress in group members). For example, the motivational systems that may have originally developed to care for offspring has likely been co-opted and used in the service of facilitating positive relationships between unrelated group members. In humans for example, our relationships with spouses, friends and co-workers are highly valued and require vast amounts of psychological resources to maintain. In fact, the perception that such relationships are threatened engenders profound emotional and physiological stress responses (Norman et al., 2012a). Conversely, feeling well connected with friends and family provides a strong behavioral and physiological buffer that can actually diminish stress responses and result in improved health (Uchino et al., 1996). Therefore, while the motivational components of pro-social behaviors such as empathy may have originally developed in service of parental care, they have now become invaluable tools for the formation and maintenance of strong social bonds between unrelated individuals.

More recently, neuroscientists have begun to examine the neurobiological mechanisms that instantiate empathy, especially in response to signals of distress and pain, and how certain dispositional and contextual factors modulate its experience and behavioral manifestations. Functional neuroimaging studies in humans document a circuit – including the anterior insula, dorsal anterior cingulate cortex, anterior midcingulate cortex, supplementary motor area, amygdala, brainstem, and periaqueductal gray – that responds to the perception of others' distress (Lamm et al., 2011).

While it is important to consider the broad range of species-specific behaviors when dealing with motivated behaviors (e.g., sex, hunger and thirst), a clear evolutionary continuity of behaviors has been conserved across organisms such as parental behavior in mammals (Insel and Young, 2001; Panksepp, 1998). This continuity has important implications for the study of human social behaviors as it allows for the application of animal models to better understand neurobehavioral processes including empathy (Panksepp, 2010). Indeed, as will be discussed in further detail below, human and animal studies have revealed that the perception of distress in others tends to activate a highly conserved neurobiological circuit to produce an aversive response in the observer, which can inhibit aggression and prompt pro-social behavior (Decety and Michalska, 2010; Eisenberg and Eggum, 2009).

Animal research has shown that the ability to share and be affected by the emotional state of another is organized by basic systems subserving attachment-related processes, involving the brainstem, preoptic area of the thalamus, and paralimbic areas (Panksepp, 1998; Watt, 2000). As a result of the importance of social connections for mammalian survival, these attachment systems appear to exploit the well developed physical pain system, borrowing the aversive signals associated with pain to indicate when relationships are threatened (Cacioppo and Hawkley, 2009; Eisenberger, 2011; MacDonald and Leary, 2005). Moreover, higher level cortical structures have been proposed to reflect a system involved in detecting, processing and reacting to the occurrence of salient events regardless of the sensory modality through which these stimuli are conveyed; basic operations by which the neural structures detect stimuli that can represent a potential threat for the integrity of the self (Legrain et al., 2011). Therefore, just as the physical pain system alerts organisms to the presence of a noxious environmental stimulus so too does the social pain system; the experience of social pain alerts an individual to potential threats in their social environment and can induce various coping strategies to attempt to mitigate the threat (e.g., increase motivation to strengthen relationships) (MacDonald and Leary, 2005).

In addition to the pain system mentioned above, the dopaminergic reward system also appears to have been partially co-opted for attachment and caring, and thus plays a role in empathic concern (see Box 1 for definition of concepts). Indeed, mammals are highly motivated to care for their offspring and experience this interaction as a highly rewarding experience (Mayes et al., 2009). Although empathy in humans is assisted by other general high-level cognitive abilities such as executive functions and language, which introduce contextual control and expand the repertoire of behaviors that can be driven by empathy and emotional connection, it also operates on more primitive reward processes and is highly dependent upon these lower level processes to achieve higher order goals associated with affective communication, social attachment, parental care, and motivation to cooperate.

Here we consider the evolutionary origins and neuroarchitectural characteristics of empathy and empathy-related processes in social mammals. We review evidence that empathy-like responses are apparent across a broad range of non-human animals and that empathy subsumes a variety of neurobiological processes and partially dissociable social-cognitive subsystems each having a unique evolutionary history (see Box 2) (Fig. 1).

## 1. Neuroevolution of empathy-related behaviors

At the behavioral level, it is apparent from the descriptions of ethologists that behaviors homologous to empathy and concern can be observed in other mammalian species, and even avian species. For instance, the presence of specific behavioral (e.g., increase alertness, decreased preening behavior) and physiological (eye temperature) changes in hens observing their chicks being exposed to a mildly aversive stimulus indicates a responsive capacity that is distinguishable from the hens' own experiences of the same stimulus (Edgar et al., 2011).