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Current Opinion in Behavioral Sciences

The neural pathways, development and functions of empathy

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Empathy reflects an innate ability to perceive and be sensitive to the emotional states of others coupled with a motivation to care for their wellbeing. It has evolved in the context of parental care for offspring as well as within kinship. Current work demonstrates that empathy is underpinned by circuits connecting the brainstem, amygdala, basal ganglia, anterior cingulate cortex, insula and orbitofrontal cortex, which are conserved across many species. Empirical studies document that empathetic reactions emerge early in life, and that they are not automatic. Rather they are heavily influenced and modulated by interpersonal and contextual factors, which impact behavior and cognitions. However, the mechanisms supporting empathy are also flexible and amenable to behavioral interventions that can promote caring beyond kin and kith.

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Current Opinion in Behavioral Sciences 2015, **3**:1–6

This review comes from a themed issue on **Social behavior**

Edited by **Molly J Crockett** and **Amy Cuddy**

For a complete overview see the Issue and the Editorial

Available online 17th December 2014

http://dx.doi.org/10.1016/j.cobeha.2014.12.001

The scope of empathy

Empathy is best considered in the context of emotional processing, which is an adaptive orienting system that evolved to guide behavior. Empathy is also an interpersonal communication system that elicits response from others, helps to determine priorities within relationships, and holds people together in social groups. Recent research in behavioral, developmental, and social neuroscience has made progress in clarifying the nature of empathy and narrowing down its scope by delineating dissociable facets that are not totally overlapping in functions and mechanisms, but yet interact to support interpersonal relationships [1–3]. These facets include: firstly, affective sharing, which reflects the capacity to share or become affectively aroused by others' emotional valence and relative intensity without confusion between self and other; secondly, empathic concern, which corresponds to the motivation to caring for another's welfare; and thirdly, perspective taking (or cognitive empathy), the ability to consciously put oneself into the mind of another and understand what that person is thinking or feeling.

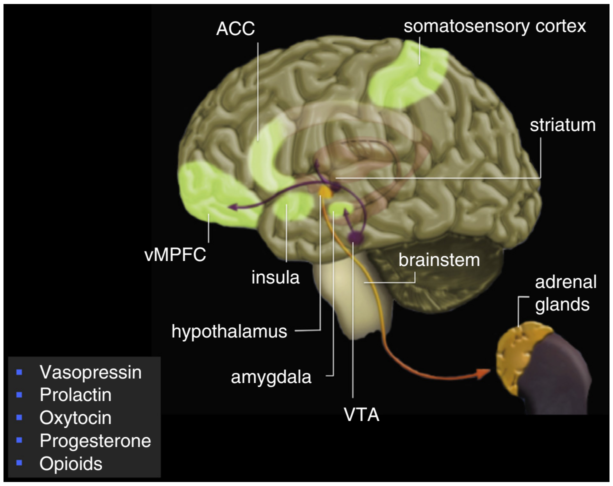
Proximate mechanisms of empathy

Each of these emotional, motivational, and cognitive facets of empathy relies on specific mechanisms, which reflect evolved abilities of humans and their ancestors to detect and respond to social signals necessary for surviving, reproducing, and maintaining well-being. While it is important to consider the broad range of species-specific behaviors when understanding motivated behaviors, there is a clear evolutionary continuity in the proximate mechanisms underlying empathy across mammalian species. These include neural circuits connecting the brainstem, amygdala, hypothalamus, basal ganglia, and orbitofrontal cortex that regulate approach motivation and avoidance motivation [4–6]. These pathways together with neuroendocrine mechanisms, and the behaviors they mediate are highly conserved across mammalian species, as exemplified by a growing body of work with rodents [7,8,9,10••] (Figure 1).

Numerous studies demonstrated that the brainstem, amygdala, insula and orbitofrontal cortex are activated by the perception of others' emotional states, but the extent to which the pattern of brain activity in these regions can predict the type of emotion remains unclear [11]. In the same vein, despite the current enthusiasm for the idea that the experience of emotion and the perception of emotion in others rely on the same neural substrates, meta-analyses of functional neuroimaging studies show a striking dissociation between the two [12].

An impressive body of work, using functional magnetic resonance imaging (fMRI) with both children and adults has reliably demonstrated that when individuals are exposed to facial expressions of pain, sadness, or emotional distress, brain regions involved in the first-hand experience of physical pain are activated [13]. These regions include the anterior cingulate cortex (ACC), anterior insula (aINS), supplementary motor area (SMA), amygdala, somatosensory cortex, and periaqueductal gray area (PAG). Given that regions involved in the first-hand experience of physical pain are also active when

Figure 1



Empathy is implemented by a complex network of distributed, often recursively connected, interacting neural regions including the brainstem, amygdala, hypothalamus, striatum, insula, anterior cingulate cortex, and orbitofrontal cortex, as well as autonomic nervous system (parasympathetic and sympathetic branches which represent antagonist and coordinated regulation of internal states) and neuroendocrine/hormones that are silent regulator of in social behaviors.

viewing or thinking about others in distress, activity in these regions has often being interpreted as 'empathy-related', or as direct evidence that one can 'share' the pain of others. However, a new fMRI study found greater activity in this network when Jewish participants viewed hateful targets (anti-Semitic individuals) compared with likable targets in pain [14••] (Figure 2). Thus, enhanced activity in this network may better be interpreted as increased saliency and relevance to pain-related cues rather than to empathic processing per se. Hence, the shared neural representations in the affective-motivational part of the pain matrix may not be specific to the sensory qualities of pain, but instead seems associated with more general survival mechanisms such as aversion and withdrawal when exposed to danger or threat [15].

Findings from another line of research on the physiological underpinnings of empathy implicate neuropeptides oxytocin and vasopressin in the regulation of various social behaviors including social bonding, attachment, empathic concern, and parental care [16]. Oxytocin in particular plays a modulatory role in empathetic behaviors for both in-group and out-group members [17,18]. However, other studies have shown that oxytocin promotes group bias by motivating in-group favoritism [19]. Thus oxytocin should not be considered as a 'moral molecule', and these apparently conflicting findings may be better understood under the salience hypothesis, which proposes that oxytocin plays a general role in social interaction that includes the facilitation of both positive and negative emotions [20]. The role of oxytocin in facilitating species-typical social and reproductive behaviors is as evolutionarily conserved as its structure and expression, although the specific behaviors that it regulates are quite diverse.

The emergence of empathy

For a long time, infants were assumed to have an innate capacity for empathic distress but not able to experience feelings of concern until the second year of life. This view is now being challenged. In fact, similarly to older children, young infants' self-distress reactions to the distress of another stem from difficulties in regulation arousal, rather than from confusion between self and other [21••,22•]. A neurodevelopmental study with electroencephalography and event-related potentials (EEG/ERPs) in which children aged 3–9 years were shown stimuli depicting physical injuries to people [23] demonstrated both an early automatic component (N200), which reflects empathic arousal, and a late-positive potential (LPP), indexing cognitive reappraisal, with the latter showing an age-related gain.

Empathic concern in humans has been documented as early as 6–8 months of age and continues to develop until adulthood. Not only do very young children make pain attributions, but studies on comforting behavior demonstrate that they also respond to a variety of distress cues, and they direct their comforting behavior in ways that are appropriate to the target's distress [21••]. For example, moderate levels of empathic concern (indicated by facial expressions, vocalizations, and gestures reflecting concern) and attempts to explore and comprehend the others' distress are already present at 8 and 10 months [24]. Furthermore, in these studies, children often comforted the target in appropriate ways, and demonstrated pain attribution in conjunction with their comforting behavior by recognizing what the target was distressed about. Two-year-old children are not motivated to help by a desire to benefit themselves via reciprocity or because they are interested in engaging with the task, but rather by a desire to see the person be helped [25]. Additionally, contextual appraisal plays a role very early in development as demonstrated by a study with three-year-olds, who showed reduced empathic concern and subsequent behavior toward a 'crybaby' (i.e. an individual who was exaggeratedly distressed after being very mildly inconvenienced), than toward a person who was distressed after being more seriously harmed [26]. In children aged 3–6 years old, empathic concern leads to prosocial resource allocation both by promoting sharing and decreasing envy [27]. As children grow up and become increasingly sophisticated social actors, they can learn to regulate their empathy so that it is more likely to occur toward familiar, close, or deserving individuals [28]. For instance, experiencing a natural disaster, like an earthquake, significantly affects children's altruistic giving [29•]. Overall, infants' fundamental motivation for connectedness is clearly manifested