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Comparative perspectives of empathy development: Insights from chimpanzees and bonobos

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Abstract

Empathy – the sharing and understanding of others' emotions and thoughts – is considered a defining feature of what it means to be human. Although empathy underpins many of our social interactions and is thought to be evolutionarily ancient, its origins remain relatively obscure. Here, we present research investigating socio-emotional development in our closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*), to identify the origins of empathy, across ontogenetic and evolutionary timescales. Research on consolation, a form of comforting behaviour, indicate that sensitivity to others' emotional states is present early in great ape life, and that individuals consistently differ from one another in this trait. Mirroring effects shown for human infants, orphan juvenile apes show more disordered socio-emotional functioning and reduced empathy as compared to mother-reared peers. These findings suggest a deep evolutionary and ontogenetic basis of empathy and some striking similarities in socio-emotional development between humans and great apes.

Key words

Consolation, sympathetic concern, emotion contagion, great apes, mammals, developmental disturbances, perspective taking

Introduction

Empathy, broadly defined as the sharing and understanding of other's emotions and thoughts, is a cornerstone of sociality. Through sharing and understanding others' states, empathy enables us to socially connect with others, to predict their behaviours and to respond to them appropriately. Despite the importance of empathy for everyday social functioning and widespread interest in the concept, surprisingly little is known about its origins, in particular about how particular forms of empathy have evolved within our own species and how empathy first develops in infancy. In order to address such questions, it is necessary to retrace its steps by identifying earlier points of emergence of empathy across both developmental and evolutionary time scales. Doing so enables us to reconstruct its basis, understand how its components interact, and establish how it could have evolved (de Haan & Gunnar 2009).

As our closest living relatives, great apes provide a unique opportunity to identify the evolutionary foundations of human empathy. Moreover, exploring when and how socio-emotional skills such as empathy develop in great apes enables us to further refine our understanding of empathy's ontogenetic trajectory across species. In the following chapter, we discuss and review recent comparative work that investigates evidence for empathic responding and its development in our closest living relatives, the chimpanzees and bonobos. We examine the proposal that an orientation to the emotional needs of others is present from a young age in great apes but becomes more discerning and cognitively sophisticated with age and experience, as it does in humans. Such a view challenges the claim that empathy is a uniquely-human capacity and instead highlights its deep evolutionary foundations and patterns of overlapping ontogeny.

The concept of empathy

The term empathy was first proposed in 1903 by Lipps, and originates from the German *Einfühlung*, which translates as 'feeling-into'. Lipps argued that our ability to experience others' emotions is achieved via a form of automatic 'inner mirroring' that enables projection of the self into the other. Although there remains controversy about how to define empathy (Batson, 2009; Cuff et al., 2016; de Waal & Preston, 2017), most definitions retain, at least to some extent, Lipps' concept of inner mirroring as a core component, upon and to which subsequent components are built and related. In this regard, empathy is considered as a multi-faceted capacity involving both affective and cognitive components (de Waal & Preston, 2017; Preston & de Waal, 2002, see chapter by KATELAAR, this volume). The *affective* components, which include processes such as emotion contagion and motor mimicry, enable the sharing or experiencing of others' states, whereas *cognitive* components, such as cognitive appraisal, perspective-taking, and self-other awareness (Decety & Lamm, 2006; de Waal & Preston, 2017; Preston & de Waal, 2002), enable the individual to understand others' states, by taking their perspective. Interconnected is the process of emotion regulation, which enables effective management of one's own internal states (Eisenberg et al., 1994). Taking this approach, de Waal and Preston (2017) define empathy as "emotional and mental sensitivity to another's state, from being affected by and sharing in this state to assessing the reasons for it and adopting the other's point of view". Through integration of cognitive and affective skills, individuals can come to experience another's emotional state, understand it as separate from their own, and respond to it appropriately, such as by showing concern or providing assistance (Decety & Lamm, 2006). While the dual component approach is a useful conceptualisation, there remains active debate about whether these cognitive and affective components can be dissociated, or, rather, whether they represent an integrated system (Shamay-Tsoory et al., 2009)

Current debates on empathy typically contrast a *top-down view,* which focuses on empathy as a mentalistic mind-reading process, with a *bottom-up* view, which considers empathy as a layered process, where more complex forms of cognition and affect are built upon a more evolutionary ancient core. A top-down perspective assumes that great apes and other animals cannot show empathy given their limitations in the cognitive and affective skills required to separate the emotions of self and other, to adequately regulate their emotions, and to take others' perspectives (Baron-Cohen, 2005; Hoffman, 2002). These cognitive and affective skills are needed since failing to maintain the boundaries between the emotions of self and other can result in personal distress, which in turn prevents empathic concern and negatively affects prosocial behaviours (Batson et al., 1987; Eisenberg et al., 1989). Early experiments were thought to support this proposed difference; for example, several studies indicate that chimpanzees are indifferent to others' welfare (Silk et al 2005; Vonk et al., 2008) and lack the ability or motivation to help others in need (Tennie et al., 2016). Other studies, however, have shown that both chimpanzees and bonobos do show evidence of caring about the well-being of others in that they seek prosocial outcomes or produce benefits for others, even at a cost to themselves (de Waal & Suchak, 2010; Horner et al., 2011; Tan et al., 2017)

From a theoretical standpoint, given the close phylogenetic relationship between humans and great apes, and the large overlaps in our social organisation and cognition, it seems more parsimonious to assume the evolutionary principle of continuity, which posits that complex traits evolve gradually, usually as elaborations of pre-existing simpler traits. Using the analogy of a Russian doll, de Waal (2008) argues that more complex forms of empathy, such as *sympathetic concern* and *targeted helping* - are built upon a more automatic Perception-

Action Mechanism (Preston & de Waal, 2002), whereby another's affective state is represented in the self's own experience through an automatic mirroring of sensory and motor responses, known as sensori-motor coupling (de Waal, 2008). Sympathetic concern refers to concern about another's state, and the attempts to ameliorate this state; whereas targeted helping refers to assistance and care, based on an appreciation of others' needs or circumstances (de Waal, 2008). Thus, while evolution and, similarly, ontogeny, may add layers of complexity in empathic responding, the fundamental cognitive and affective building blocks appear to be already present in many non-human animals (Batson, 2009).

In terms of empirical evidence for the building blocks of empathy within animals, many studies reveal evidence for motor mimicry in great apes and other animals, such as rapid facial mimicry in play faces (Kret et al., 2014; Palagi et al., 2014). There is some experimental evidence for targeted helping (Melis et al 2011; Yamamoto et al., 2012) and wide observational evidence of sympathetic concern, discussed below (e.g., Clay & de Waal 2013a, b; Cordoni et al., 2006; de Waal & Aureli, 1996; Fraser et al., 2008; Romero & de Waal, 2010).

Research in other taxa suggests that empathic capacities may occur widely across the animal kingdom. For example, studies have revealed evidence for affective concern towards others' in distress in a wide array of mammals, including rodents, monkeys, elephants, dogs, horses and wolves as well as some avian species such as ravens (Burkett et al., 2016; Custance & Mayer, 2012; Cozzi et al., 2010; Fraser & Bugnyar, 2010; Palagi et al., 2014; Plotnik & de Waal, 2014). MacLean (1985) proposed that empathy first evolved within the context of mammalian parental care, which has since become incorporated into a broader adaptation for group living. However, the fact that we find suggestive evidence for empathy in non-mammals, indicates that its evolutionary origins may be older than this. For social species that cooperate and/or show extended parental care, empathy enables individuals to quickly respond to one another's states, which facilitates the regulation of social interactions, coordination of shared goals, and for collective responses to danger (de Waal, 2008; de Waal & Preston, 2017). Consistent with this view, in both humans and animals, empathic responding falls along an 'empathy gradient' where empathy is predicated by or biased towards social closeness; being lowest between weakly-bonded individuals, higher between tightly-bonded ones, and highest among kin (de Waal & Preston, 2017; Palagi et al., 2014)

Consolation in chimpanzees and bonobos

Observing the natural behaviour of animals, the discipline known as ethology, provides a key opportunity to examine their underlying cognitive skills, including for capacities such as empathy. For ethologists interested in the evolutionary origins of empathy, observing how animals spontaneously respond to social conflicts, in particular in response to the outbursts of distressed victims, have provided some of the most convincing evidence thus far of empathy in great apes and other animals. In the immediate aftermath of a conflict in great apes, for example, uninvolved bystanders sometimes spontaneously approach distressed victims to offer them affiliative contacts such as to groom, gently touch, hug or even kiss them (see Figure 1; de Waal & van Roosmalen, 1979; Fraser et al., 2008; Romero & de Waal, 2010). Given the close resemblance between these apparently comforting bystander affiliative contacts to the acts of reassurance seen in humans, it is not surprising that these post-conflict reunions have been labelled *consolation* since the first time they were systematically studied (de Waal & van Roosmalen, 1979). Following the pioneering work by de Waal and van Roosmalen (1979) on chimpanzees, research has revealed evidence for consolation in great apes (chimpanzees, bonobos and gorillas) in a wide variety of conditions across captivity, sanctuaries, and the wild (Clay & de Waal, 2013, a, b; de Waal & Aureli, 1996; Fraser et al., 2008; Koski & Sterck, 2007; Kutsukake & Castles, 2004; Palagi et al., 2004; Palagi, Cordoni, & Tarli, 2006; Romero & de Waal, 2010; Webb et al., 2017; Wittig & Boesch, 2003).

The term consolation is a functional label implying that the friendly contact offered by bystanders functions to alleviate the distress of the recipient i.e. consolation should be offered to those that are in need of emotional comfort. This spontaneous orientation towards someone in distress implies that consolation involves a direct emotional response to the victim’s state, as well as a motivation to ameliorate it.. Though the underlying mechanisms motivating consolation remain elusive, there is reliable evidence that consolation is effective in relieving the recipient’s distress (reviewed in de Waal & Preston, 2017). The fact that consolation is targeted towards distressed individuals and is effective in reducing their distress suggests that consolation may also involve a cognitive ability to appreciate others’ needs as being separate from one’s own and potentially, the capacity to appraise the reason for their distress. For this reason, consolation is considered a marker of sympathetic concern (see Summary Box). Nevertheless, appraising the reasons causing their distress may not always be necessary for an empathy response; for example, in a recent study of monogamous prairie voles (*Microtus ochrogaster*), pair-mates showed increased grooming toward their mate (but not to strangers) that had experienced an unobserved stressor, with their grooming providing effective social buffering (Burkett et al., 2016).

Research has further revealed that patterns in chimpanzee responses towards others in distress follow predictions derived from an empathy-based hypothesis. In humans, expressions of empathy are facilitated by similarity, familiarity, and social closeness (de Waal & Preston, 2017). Similarly, research on consolation in great apes consistently reveals a bias towards social closeness based on kinship and affiliation (Clay & de Waal, 2013a; Fraser et al., 2008; Kutsukake & Castles, 2004; Romero et al., 2010; Webb et al., 2017; but see Koski & Sterck, 2007). In chimpanzees, consolation is more commonly provided by females than males (Romero et al., 2010) which appears consistent with trends in humans, including during infancy (e.g., Knafo et al., 2008; Volbrecht et al., 2007; Zahn-Waxler et al., 1992) Nonetheless, there was no evidence for sex differences in consolation in another study of chimpanzees (Webb et al., 2017) or bonobos (Clay & de Waal, 2013a), a topic therefore that warrants further investigation.

Consolation across ape development: evolutionary homologies

Research on human development has shown that consolation and other empathy-based behaviours emerge early in life but increase with age, both in terms of the frequency and type of targets (Light & Zahn-Waxler, 2011; Davidov et al., 2013). There are also stable individual differences (e.g., Eisenberg et al., 1999), with higher empathy predicting various aspects of social and emotional competence (e.g., Allemand, Steiger, & Fend, 2015). Though children first show comforting behaviours as they approach their second year (Decety, 2011; Zahn-Waxler et al., 1992), the foundations for other-orientated empathic responding appear present from a much earlier age. For example, in a study of 8 to 16-month-old infants' responses to others' distress, personal distress responses were rare, whereas orientation and gaze towards the distressed other, rather than the mother, were more common (Roth-Hanania, Davidov & Zahn-Waxler, 2011). In this way, even though not yet mobile or fully equipped with the socio-cognitive capacities to take others' perspectives or understand their needs, infants already appear to be attentive towards the arousal states of others. While this study did not control for infant attention to distress in unfamiliar people compared to in their mothers, the initial orientation towards others' distress appears to represent the basis upon which more sophisticated forms of emotion responding can develop.

While research into emotion development in great apes is still in its infancy, there is increasing evidence of homologous patterns. In a recent longitudinal study, Webb and colleagues (2017) analysed a long-term dataset spanning nearly a decade of observations on over 3,000 conflict and post-conflict interactions in two captive groups of chimpanzees. The inclusion of forty-four chimpanzee subjects comprising all age-classes allowed for systematic investigations of individual differences in consolation tendency: namely, because consolation was sampled across the full developmental spectrum from infancy to adulthood, analyses could test whether such differences were relatively stable across developmental periods. Findings revealed that individual variation in consolation was strikingly consistent over time and context— i.e., an individual with high consolation tendencies relative to its peers when younger was likely to be a high consoler relative to peers when older. Thus, as in humans, empathy-driven behaviours in great apes are not only present from a young age, they also appear to form part of a stable personality disposition. As with research on humans across different developmental time-points, consolation tendencies were positively related to individuals' Composite Sociality Index scores, an index of social integration that comprises measures of grooming and social proximity. A similar result has also been shown for bonobos, as discussed below. Thus, akin to patterns reported in the human developmental literature, empathy appears to predict important measures of social competence in our primate relatives.

From a developmental standpoint, both chimpanzees and bonobos show striking and consistent age-related changes in consolation behaviour (Clay & de Waal, 2013a; Webb et al., 2017). Namely, infants and juveniles show the strongest propensity to console in their social groups, exhibiting significantly higher rates of consolation as compared to adolescent and adult counterparts (see Figure 1). These results are important for three reasons. First, they challenge the view that consolation, or indeed other forms of empathic responding, necessarily depend on sophisticated cognitive mechanisms, such as cognitive appraisal and perspective taking. Second, they demonstrate that young apes, as with young human infants, are already sensitive to the emotions of others and are able to respond to them appropriately (Clay & de Waal, 2013a, b, Webb et al. 2017). Finally, this apparent age-based decline in consolation in chimpanzees and bonobos contrasts with patterns typically reported in the human developmental literature (Eisenberg & Strayer 1990; Hoffman, 2008), suggestive of a potential increase in empathic responding in our own species across development, as compared to that of our close relatives.

Some future research directions

It is possible, for instance, that while humans share the basic capacity for empathy with great apes, the emotional and socio-cognitive scaffolding provided to human infants by their caregivers promotes the onset of unique forms of self-other awareness that facilitate more complex forms of emotional perspective taking. A key caregiver behaviour, apparently universal across human societies (Broesch et al., 2016), is that of 'affect mirroring', which refers to contingent and amplified emotional responses made by the caregiver toward the infant's emotional state. Affect mirroring is said to represent a kind of social 'bio-feedback' whereby caregivers' contingent responses provide feedback to the infant about their internal states which they can thus externalise and relate to objects and events in the world (Gergley & Watson, 1996; 1999). Through this social bio-feedback process, infants can learn to engage in reciprocal emotional exchanges, thus separating self from other and associating physiological sensations with external events. The rich and highly interactive nature of affect mirroring in humans may represent a key divergence point from other species which could explain species differences in human empathy development. Such a hypothesis is theoretically important but remains untested, as no systematic data have yet been collected on great apes. Investigating evidence for affect mirroring in great apes is thus a topic ripe for future research.

Alternatively, the observed developmental decline in consolation in both bonobos and chimpanzees may point to other explanations. First, it is possible that the behavioural expression of empathy in great apes transforms over the course of development, where such expressions becomes increasingly refined or filtered with age (rather than reflecting a decline in empathy per se, see also chapter by KIM, this volume). For example, it is worth speculating that empathy's socially biased nature (i.e. empathic responding being biased towards individuals that are perceived to be socially close, familiar or similar to the actor) increases with age, in which case we would expect older individuals, as compared to their younger counterparts, to console fewer but more high-quality social partners. However, we do not yet know whether this explanation could account for the reported developmental patterns in great apes, nor to what degree, nor via what mechanisms (e.g., increased social learning opportunities, heightened cognitive control, or other factors). Interestingly, socioemotional selectivity theory (Carstensen, 1995), which has recently been extended from humans to study social networks in other primate species (Almeling et al., 2017), invites us to hypothesize that great ape consolation networks may too become progressively smaller and more tailored with age.

Second, such findings may also call for a re-evaluation of the methodologies that have led to such assumptions about empathy in our own species. Specifically, it is possible that the variety and often contrasting use of methodologies that have been employed to study empathy in different age-groups in humans have biased conclusions. Namely, the tendency to rely on self-report measures in human adults contrasts markedly with the reliance on observed behavioural expressions in younger children. In particular, if the behavioural measures that are often used in young children are directly compared to the self-report methodologies that are often used in adults, developmental increases in human empathy may reflect the social desirability of the empathy response as much as any changes in empathy itself. Thus, future longitudinal and cross-sectional research with humans should strive to investigate the same or similar measures of empathy across the widest plausible range of developmental stages. Similarly, future ape research on the development of empathy would benefit from a more comprehensive approach, with the simultaneous evaluation of a range of empathy responses in different social contexts.

There are also evidently similar issues to face when making species comparisons. In order to address such issues of comparability, Cordoni et al (2016) carried out an ethological study on pre-school children using the same observational methodology used for non-human primates. The study revealed many similarities in patterns of consolation observed in great apes and human children, which included the timing of consolation as well as the fact that children offered comfort to others at a young age. As in the great apes, consolation by children seems to be a spontaneous and immediate response towards distress in others and also appears effective in reducing victim anxiety. Thus, when data on humans and great apes are collected using similar procedures and operational definitions, striking similarities in the sympathetic response can emerge. Nonetheless, longitudinal work that tracks a similar set of behavioural responses across a wider range of development stages will provide new comparative developmental perspectives on empathy’s trajectory in humans and great apes.

A note on developmental disturbances

As with humans, comparative research also highlights the importance of the mother-offspring relationship and stability of caregiving for the development of socio-emotional functioning, including empathy (Bard, 1994, 1996, 2012; Bard et al., 2014; Clay et al., 2015; van Leeuwen et al, 2016). In a seminal series of studies (Cross & Harlow 1965; Harlow 1965), Harlow and colleagues separated infant rhesus monkeys from their mothers and examined the effects of deprivation on socio-emotional development. The results paralleled what has been demonstrated for deprived human children: lack of stable caregiving early in life has a significant negative impact on subsequent socio-emotional functioning (de Bellis, 2005; van Ijzendoorn et al., 2009, see chapter by PLATE, this volume). Building on this work, Clay and de Waal showed consistent impairments in the socio-emotional functioning of orphaned juvenile bonobos being cared for within a sanctuary setting as compared to their age-matched counterparts (Clay & de Waal 2013a, b). Mother-reared juveniles were more likely to console victims of social conflicts than age-matched orphans, as well as showing generally higher levels of sociability, social competence and lower levels of social anxiety. For instance, there was a direct positive correlation between how juveniles handled their own distress and how they responded to distress witnessed in others: individuals quicker to recover from their own distress as victims (mother-reared) were more likely to console others. Overall, such results are consistent with the human developmental literature in demonstrating a tight interplay between emotional and social skills while highlighting the critical role of early experience for empathy development (Eisenberg, 2002; Eisenberg & Fabes 2006; Murphy et al., 1999; Zahn-Waxler et al., 1985; see chapters by CONNER and KETELAAR, this volume).

Conclusion

In sum, comparative research with great apes has revealed some striking overlaps in the form, function and apparent ontogeny of empathy. Such research has prompted new and interesting questions concerning the expression of empathy as well as its developmental and evolutionary foundations. Overall, the apparent similarity to findings from human research is telling, providing further support not just for shared affect in our closest relatives, but also for key aspects of socioemotional development across species. That empathy-related responding emerges early in life, demonstrates relative stability over the lifespan, and predicts social integration, allows for the conclusion that like humans, great apes exhibit marked ‘empathetic personalities’ which are shaped by learning and experience across the lifespan.

--- SUMMARY BOX ---

Methodological approaches to study empathy in our Pan relatives

Diverse methodologies have been developed and employed to measure the affective and cognitive signatures of empathy in primates. A number of studies have focused on yawns as a possible form of motor mimicry putatively related to empathy, although see Massen & Gallup 2017. In such studies, yawn contagion has been measured naturalistically (by observing whether spontaneously-occurring yawns trigger further yawns in nearby groupmates; e.g., see Palagi et al., 2014) or induced experimentally (by showing subjects videos of conspecific yawns, e.g., see Campbell & de Waal, 2011). As in humans (see Xu et al., 2009; Norscia & Palagi, 2011), both approaches have revealed that affective contagion in chimpanzees and bonobos is biased by social closeness, thus suggestive of an underlying empathy mechanism. Studies on rapid facial mimicry provide even further support, for example an experimental study revealed that both humans and chimpanzees are more likely to rapidly mimic the pupil size of conspecifics than those of the other species (i.e. human and chimpanzee), corroborating the similarity bias posited by the empathy hypothesis (Kret et al., 2014). These and related methodological techniques tap into empathy’s affective core by measuring the spontaneous matching between observers’ and targets’ affective states.

Empathy’s cognitive dimension in great apes has traditionally been investigated via **targeted helping paradigms**, which examine whether individuals can comprehend the target’s specific goals or circumstances and act accordingly. For instance, chimpanzees are known to select the appropriate tool from a tool set to transfer to a partner in need (Yamamoto et al., 2012) and thereby help in situations wherein they cannot selfishly benefit (see also: Melis et al., 2011, Tan & Hare 2013, Tan et al., 2017). Additional evidence for empathic perspective-taking abilities stems from anecdotal accounts of animals orienting their help to another’s particular predicament, such as reports of bonobos rescuing group members from drowning (reviewed in de Waal, 2008).

Sympathetic concern emerges when emotional contagion is combined with some appraisal of the other’s situation (de Waal, 2008). As emphasized here, consolation – or uninvolved bystanders approaching to comfort distressed victims of aggression – is the best-documented marker of sympathetic concern in other primates. Consolation is typically studied by comparing the frequency and timing of friendly contacts received by victims following an aggressive conflict with those of similar friendly contacts during non-conflict situations or controls (Veenema, Das, & Aureli, 1994). This comparison allows one to correct for baseline levels of affiliation and thereby ensure that consolatory contacts are not just a mirror of the general affiliation tendencies within the dyad. Although consolation is typically studied following conflicts, there is some evidence that bystanders offer comfort following spontaneous distress (e.g., bonobos: Clay & de Waal, 2014b) and perhaps even over extended timeframes subsequent to distressing events such as the death of a group member (e.g., chimpanzees: Goldsborough et al., 2019). In the latter study, chimpanzees consoled a bereaved mother through reassurance behaviours (e.g., mouth- and body-kisses) on the day of and after the stillbirth of her infant, and through increased grooming in the following month. As the range of social contexts and methodological approaches to study empathy-driven responses widens, so too will our understanding of this phenomenon across species.

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Figure 1. Photograph depicting a juvenile bonobo offering consolatory contact to a distressed victim. Photo taken at Lola ya Bonobo Sanctuary, DR Congo by Zanna Clay