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Empathy as a driver of prosocial behaviour: highly conserved neurobehavioural mechanisms across species

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Empathy reflects the natural ability to perceive and be sensitive to the emotional states of others, coupled with a motivation to care for their well-being. It has evolved in the context of parental care for offspring, as well as within kinship bonds, to help facilitate group living. In this paper, we integrate the perspectives of evolution, animal behaviour, developmental psychology, and social and clinical neuroscience to elucidate our understanding of the proximate mechanisms underlying empathy. We focus, in particular, on processing of signals of distress and need, and their relation to prosocial behaviour. The ability to empathize, both in animals and humans, mediates prosocial behaviour when sensitivity to others' distress is paired with a drive towards their welfare. Disruption or atypical development of the neural circuits that process distress cues and integrate them with decision value leads to callous disregard for others, as is the case in psychopathy. The realization that basic forms of empathy exist in non-human animals is crucial for gaining new insights into the underlying neurobiological and genetic mechanisms of empathy, enabling translation towards therapeutic and pharmacological interventions.

1. Introduction

There has been substantial progress in recent years towards a comprehensive understanding of evolutionary processes that drive social behaviours across species and the neurobiological architecture that supports them. One phenomenon that connects individuals, and which has received a lot of attention from both the social and biological sciences and the public, is empathy. It is generally believed that empathy shapes the landscape of our social lives by motivating prosocial and caregiving behaviours, inhibiting aggression, and facilitating cooperation between members of a similar social group.

The purpose of this article is to provide an integrative perspective on the mechanisms underlying empathy and how these mechanisms constitute a causal force in motivating prosociality towards other conspecifics. In particular, multi-level integrative analyses in social neuroscience provide a mechanistic understanding of empathy and its motivational role in caring for others. Drawing from theoretical and empirical work in animal behaviour, developmental science, and affective and clinical neuroscience, we argue that empathy is an ability common to humans and many other animals, which has evolved primarily to support a range of prosocial behaviours, from parental care to helping.

Importantly, not all prosocial behaviours are motivated by empathy. Cooperation, for instance, is a fundamental aspect of all biological systems from bacteria to primates, and seems to follow a very simple rule: natural

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selection favours cooperation, if the benefit of the altruistic act, b, divided by the cost, c, exceeds the average number of neighbours, k, which means $b/c > k$. In this case, cooperation can evolve as a consequence of 'social viscosity' [1], and not as a consequence of empathy explicitly. Additionally, it has been argued that morality is distinct from empathy. In fact, empathy can conflict with morality and justice by introducing partiality because these two abilities rely on different ultimate and proximate mechanisms [2,3]. While empathy is a powerful motivator for caring and helping behaviours in many species, we distinguish the experience of empathy from consequent behaviours. This is an important issue because we are neither claiming that empathy is the only source of prosociality nor that empathy and prosocial behaviour should be conflated. Discussions about the role of empathy in prosocial behaviour are plagued by disagreement and misunderstanding. In particular, there are endless debates as to whether non-human animals have the capacity to share the feelings experienced by conspecifics, as well as whether this affective experience can be a causal factor in eliciting a behavioural response to benefit another [4]. These controversies often depend on loose definitions and diverse use of the concept of empathy.

2. Empathy

(a) What is empathy?

'Empathy' in the literature is used to refer to a collection of heterogeneous phenomena [5–7], to the extent that some authors are now suggesting dropping its usage because it sows confusion [8]. For many scholars, 'empathy' is feeling what others feel, and thus 'empathy' overlaps with the concept of 'emotional contagion'. For others 'empathy' is referring to a more complex cognitive capacity such as intentionally adopting the subjective perspective of another individual in order to understand what she feels and thinks, a definition largely overlapping with 'theory of mind', 'social cognition' and 'perspective taking'. A complete taxonomy of empathy-related phenomena is outside the scope of this paper. Here we consider empathy as an induction process that reflects an innate ability to perceive and be sensitive to the emotional states of others, which can be, but not necessarily is, coupled with a motivation to care for their well-being [9]. Empathy does not require complex cognitive capacities such as theory of mind (ToM), or a conscious awareness of one's feelings and others' feelings, but it does entail a basic ability to discriminate between self-generated versus externally-caused stimulation. This self–other distinction is implicit [10] and was articulated by Gibson's idea [11] that any organism has an implicit sense of one's own body situated and acting in the environment. Self-perception is inseparable from perception and action in the environment. From an evolutionary perspective, this proposal also implies that this ability to distinguish between self and the external world is not restricted to humans, as any organism that perceives and acts in the environment in a flexible, goal-oriented way is an agentive entity in the environment. This ecological self has been extensively documented in neonates, and does not depend on reciprocal communication and shared experience with others [12].

This minimal definition allows us to examine both the extent to which empathy and its potential outcomes (such as helping or comforting) are present across species, and the neurobiobehavioural mechanisms that support its operation in human and non-human animals. Thus, we do not see the utility of defining empathy as an overarching category containing all associated concepts such as emotional contagion, imitation, sympathy and compassion. Naturally, in humans, empathy can be activated in a variety of different ways. It can be elicited by controlled cognitive processes like those activated by imagination or reading fiction. Theory of mind, language and executive functions do greatly expand the range of cognitions and behaviours that can be driven by empathy [13]. In this paper, we focus on empirical findings from studies with humans and non-human animals that demonstrate common proximate biological mechanisms underlie the reactions to, and processing of, the distress cues of conspecifics, as a paradigmatic case for empathy across species.

(b) Why empathy has evolved

Affective signalling and communication between conspecifics contribute to inclusive fitness in many ways, including facilitation of coordination and cooperation. This type of information transfer increases defences against predators, bonds individuals to one another and improves caregiving for offspring and other individuals within a social group [14,15]. In addition, in many species, nurturance is functionally required for survival. Despite the diversity in parental-care strategies across large evolutionary distances, the underlying neural pathways for responding to infants, especially signals of vulnerability and need, seem to be universally present and conserved across species [16]. Importantly, caregiving produces social preferences which can be viewed as consequences of the caring emotion/motivation that promotes social bonding between carer and recipient.

It has been proposed that a system of infant care was co-opted during evolution to extend to other conspecifics [17]. The social attachment system was gradually built up from more primitive regulation systems, like those involved in place attachment, thermoregulation and physical pain [18]. Parental care and protection of young is essential for the survival and flourishing of offspring, and thus promotes their fitness. In mammals, the neural circuits controlling affiliative and caring behaviours are highly conserved, and are modulated by intrinsic and socio-environmental factors [16]. The ability to perceive and respond with care to the suffering and distress of others stems from evolutionarily ancient subcortical circuits (brainstem, amygdala, hypothalamus and basal ganglia) and neuro-hormonal mechanisms associated with affective sensitivity, attachment and parental care [19]. Empathy-related behaviours have co-opted these primitive homeostatic processes involved in reward and pain systems in order to facilitate various social attachment processes. In humans and primates, the prolonged dependence of offspring made it particularly necessary and beneficial for mothers to detect signs of suffering and distress in their offspring. Mothers who were good at detecting such signals went on to rear more surviving offspring, and over time a communication system developed in which children's stylized distress signals triggered maternal care.

If empathy has its evolutionary origins in nurturance, then individuals of species that have evolved parental care and proximate mechanisms to be sensitive to their offspring's signals of need and distress should express similar behaviours. This is indeed the case with birds where often both males and females provide parental care. For example, members of a graylag geese flock that observed a conflict involving either their partner or a family member experienced more distress (measured by an increase in heart rate)—consistent with an empathic response [20]. Additionally, it has been found that members of breeding pairs perform affiliation behaviours following conflicts, which suggests that pair-bonded rooks may actually be consoling their partner when s/he is distressed [21]. In ravens, bystanders to a conflict may console victims with whom they share a valuable relationship, thus alleviating the victims' post-conflict distress [22].

This evolutionary perspective is compatible with the nested brain-mind hierarchies model proposed by Panksepp [18]. This model posits that human emotions spread across conspecifics, and at times these shared emotions facilitate empathy, which promotes prosocial behaviours and altruism. Primary emotional states, which are potential sources of empathy when experienced in relation to another individual, are integrated with cognitive functions such as learning, memory and regulation to produce an adaptive interpersonal response.

(c) The mechanisms underlying the experience of empathy

One salient aspect of the evolutionary representation of neurobiological function is in the relation between the neuropeptide oxytocin (OT) and mammalian social and affiliative behaviours including empathy [18]. Predecessors of OT are present in the earliest phyla of animal evolution [23], yet OT in its current form coincides with the evolution of placentation. However, OT is not a peptide unique to mammals. OT-like neuropeptides have played special roles in social affiliation and reproduction ever since the peptides first evolved (450 Ma), and exert widespread influences on affiliative behaviours across a variety of vertebrate classes [24]. For instance, studies have demonstrated that endogenous activation of oxytocic receptors in the brain is necessary for the natural formation of pair bonds in zebra finches [25], as has previously been shown in prairie voles [26]. An analysis of the role of OT suggests that its peripheral role is in smooth-muscle contraction, specifically in uterine contractions and lactation, and has been co-opted to serve in organizing and coordinating maternal care and mother–offspring bonding. These bonds, in turn, promote male–female bonding, family relationships, friendships and group living [27,28]. Some of the same characteristics that are basic to the mother–infant bond and are associated with OT are also important components of these relationships, such as social recognition, attachment and social cooperation. OT has a crucial role in solidifying attachment to a sexual partner (pair-bonding), inhibiting aggression and supporting affiliative behaviour [28]. In humans, OT increases emotion recognition accuracy [29], as well as trust [30], generosity [31] and cooperation [32]. The OT receptor genotype was directly associated with self-reported empathy [33–35] and prosocial behaviour [36,37].

The extent to which animals are affected by the distress of conspecifics has been robustly demonstrated in many species including avian [38] and rodent [39]. Rats and mice exhibit a stress response and fear learning when they observe a conspecific getting shocked [40]. This effect is also observed when mice encounter a conspecific who was recently shocked, even when they did not witness the shock itself [41]. Furthermore, rodents show social modulation of emotional responses and learning. In one such study, pain sensitivity in mice was increased by the presence of other mice displaying pain behaviours [42]. Observing pain behaviours in conspecifics only augments pain behaviour when the target mouse is their cage mate. Female mice express greater freezing behaviour when exposed to the pain of a close relative than when exposed to the pain of a more distant relative, suggesting that it serves an adaptive function [43]. To investigate whether pain behaviour can serve the function of soliciting a primitive form of empathy, Langford *et al.* [44] used a social approach paradigm to test mice in various dyadic or triadic conditions. Some conditions involved restrained mice that were in pain (as a result of intraperitoneal injection of acetic acid) and test mice that were free to approach or avoid the restrained mice. Results showed a sex-specific effect wherein female test mice approached a familiar same-sex conspecific in pain more frequently than they approached an unaffected conspecific. The frequency of contact by the test mouse was negatively correlated with the pain behaviour of the jailed mouse, suggesting that the proximity of a familiar unaffected conspecific has analgesic properties for the test mouse. The authors argued that the proximity of a familiar other provides this analgesic social buffer. The existence of a social buffering phenomenon, and its neural substrate, is well established across a variety of species [45]. Moreover, socially isolated mice display significantly higher levels of mechanical pain sensitivity as well as depressive-like responses following peripheral nerve injury as compared to their pair-housed counterparts, potentially through a mechanism involving OT [46].

Neurodevelopmental differences in the spatio-temporal dynamic in response to the distress of others can be detected very early in ontogeny. In one study using electroencephalography and event-related potentials (EEG/ERPs), children aged 3–9 years were shown stimuli depicting physical injuries to people. The authors demonstrated that even children this young show both an early automatic component (N200), which reflects empathic arousal, and a late-positive potential, indexing cognitive reappraisal, with the latter showing an age-related gain [47]. One cross-sectional developmental functional MRI study tested participants ranging from 7 to 40 years of age while they watched video clips of individuals being physically injured [48]. Younger participants showed a stronger response in the amygdala (a region involved in processing emotionally salient stimuli), anterior insular cortex (aINS), anterior cingulate cortex (ACC) and ventromedial prefrontal cortex (vmPFC) when they observed others in distress. The early engagement of the amygdala, insula and vmPFC during the perception of others' distress and pain is consistent with the timing of their structural maturation. These reciprocally interconnected regions, which underlie rapid and prioritized processing of emotion signals and are involved in affective arousal and somatovisceral resonance, come online much earlier in ontogeny than other neural structures, especially regions of the prefrontal cortex implicated in emotion regulation. These latter regions of the prefrontal cortex with their reciprocal connections with the limbic system and basal ganglia are vital for more advanced forms of empathy, like those linked with perspective-taking and moral decision-making. These neural regions continue to develop until late in adolescence (figure 1).

Numerous neuroimaging studies in humans have documented the reliable activation of a neural network (aka the pain matrix) involved in first-hand experience of pain. This pain matrix includes the ACC, aINS, supplementary motor area, periaqueductal gray area (PAG) and the amygdala (e.g. [48–52]). This network has been shown to be recruited in response to watching facial expressions of pain, body parts being injured, imagining the suffering of others or simply when observing a signal indicating that someone will receive a painful stimulation (Lamm *et al*. [53] for a meta-analysis). Activation of the pain matrix may not be specific to the sensory qualities of pain, but instead might be associated with more general survival mechanisms such as aversion and withdrawal when exposed to danger and threat [54]. Concern for another's distress requires the involvement of several brain areas that are distinct from the pain matrix. Among these areas is the vmPFC, a region reciprocally connected with ancient affective systems in the brainstem, amygdala and hypothalamus. The vmPFC integrates affective and value-based information necessary for caregiving behaviours [55,56]. The vmPFC, together with the ventral striatum, amygdala and insula, is a part of a domain-general valuation system that processes significant and motivating information, and guides (both social and non-social) decision-making [57]. A recent neuroimaging study found that individuals high in dispositional empathic concern engaged in costly altruism, and this relationship was supported by neural activity in the ventral tegmental area, caudate and vmPFC [58]. Thus, caring for others piggybacks on older evolutionary motivational mechanisms associated with parental care.

Conversely, a lack of sensitivity to others' distress can be the product of abnormal neural responses, measurable as early as childhood [59]. Disregard for others in distress assessed during toddlerhood/early childhood is a strong predictor of antisocial behaviour in middle childhood and adolescence [60]. Functional MRI and EEG studies have reported that children and adolescents with psychopathic traits and conduct problems show reduced neural activity in response to stimuli depicting physical distress in the ACC, alNS and amygdala, structures typically implicated in affective responses to others' pain [61–63]. Recent research with psychopaths has similarly documented atypical neural processing of others' distress cues [64]. Psychopathy is a personality disorder associated with a constellation of traits including lack of guilt, remorse and empathy, lack of attachment to others, narcissism, superficial charm, dishonesty, reckless risk-taking and impulsive antisocial behaviour [65]. In a series of recent studies, brain activation patterns elicited by dynamic stimuli—individuals in physical distress and facial expression of pain—were compared between incarcerated psychopaths and incarcerated controls [66,67]. Individuals with psychopathy exhibited significantly less activation in the vmPFC, lateral orbitofrontal cortex and PAG relative to controls. Psychopaths fail to experience distress cues as aversive—an experience that is a critical component in the mechanism underlying empathy [65,68]. Diffusion tensor imaging demonstrates that psychopathy is associated with reduced fractional anisotropy in the right uncinate fasciculus, the major white matter tract connecting ventral prefrontal and anterior temporal cortices [69]. This pathway is believed to play a critical role in social-affective function and decision-making. Atypical functional and anatomical connectivity between the amygdala and insula and vmPFC has been reported in individuals with psychopathy, and accounts for their decreased sensitivity to negative affects of others [70].

To be motivated to be concerned about another's welfare, one needs to be affectively and empathically aroused and to anticipate the cessation of mutually experienced personal distress [71]. Overall, clinical and social neuroscience research lends strong support to the notion that emotion reactivity in general, particularly the sharing of another's distress, plays a pivotal role in facilitating prosocial behaviour. The affective experience of discomfort that occurs while witnessing others in pain or distress facilitates the urge to help.

3. Empathy and prosocial behaviour

(a) What is prosocial behaviour?

Prosocial behaviour refers to any action performed by one organism to alleviate another's need or improve their welfare [72]. From rescue behaviour in ants [73], to helping in elephants, prosocial behaviour is indeed ubiquitous throughout the animal kingdom [74,75]. Prosocial behaviour increases the fitness of the receiver and carries some cost to the benefactor [76]. There are some arguments that prosocial behaviour is not 'prosocial' because it also provides a fitness benefit to the benefactor. From an evolutionary perspective, there is no reason that prosocial behaviour should be discounted as they do not appear selflessly motivated. Labelling behaviour 'prosocial'—even when including behaviours motivated by empathy—only when they are 'selfless' acts, is missing the ultimate cause of their selection. Prosocial and altruistic behaviours have been selected because they benefit the fitness of the individual's genes through inclusive fitness [74]. It should, therefore, come as no surprise that animals, as well as humans, deploy their prosocial behaviours preferentially towards their kin and those group members that will probably reciprocate. Furthermore, it follows that prosocial behaviour is highly sensitive to social context and interpersonal relationships. Though increased fitness is the ultimate explanation or cause of prosocial behaviours, the proximate mechanisms that facilitate their expressions need not be similar across species and types of behaviours.

It is also critical to distinguish prosocial behaviour from empathy. While some forms of prosocial behaviours (i.e. helping and consolation) can be the outcome of empathy, many other forms of prosocial behaviours (i.e. sharing) are not necessarily associated with nor elicited by empathy [77,78]. Thus, it is more appropriate to consider prosocial behaviour as a multidimensional construct rather than a global concept, as it is traditionally viewed [79]. Much is to be gained by recognizing and studying the different facets of prosocial behaviour [80]. Most of contemporary research in humans confirms early findings that there are weak or non-significant correlations among various forms of prosocial behaviour [81].

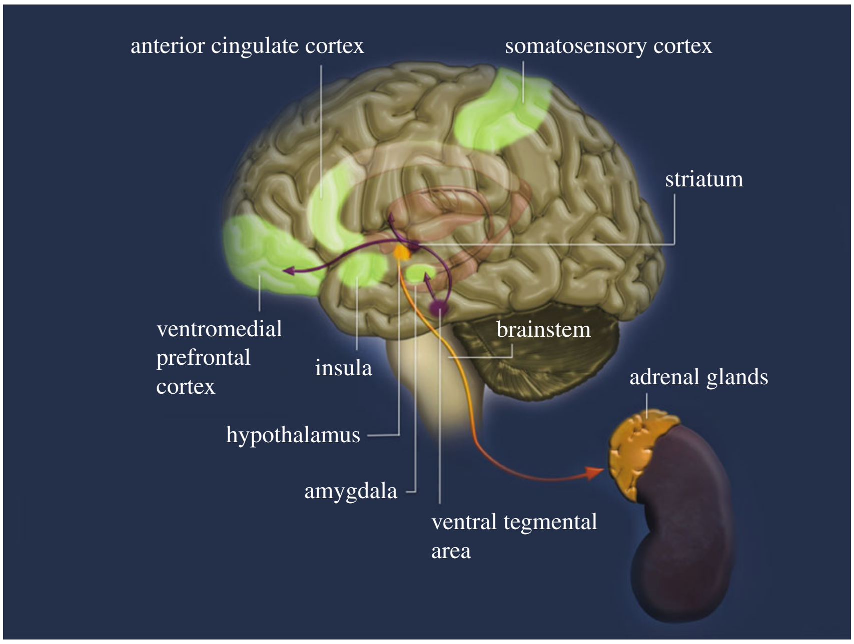

Figure 1. In humans, empathy is supported by a network of distributed, often recursively connected, interacting neural regions including the brainstem, amygdala, hypothalamus, striatum, insula, ACC and orbitofrontal cortex, as well as autonomic nervous system (parasympathetic and sympathetic branches which represent antagonist and coordinated regulation of internal states) and neuroendocrine processes implicated in social behaviours and emotional states. Thus, the experience of empathy and motivation to care for others emerge from the interaction of multiple areas in conjunction with the autonomic nervous system and the neuroendocrine system. (Online version in colour.)

(b) Development and genetic underpinnings of empathy and prosocial behaviour

At as early as six months, some infants manifest directed other-oriented behaviours to peers expressing distress, while rarely becoming distressed themselves [82]. Infants have been shown to more robustly express empathy around eight months [83,84]. Preverbal infants show rudimentary empathic concern toward others, as indexed by their evaluation of characters' interactions. In one study, 10-month-olds manifested sympathetic responses, evidenced by preferentially reaching for victims as opposed to aggressors or neutral objects, after observing third-party social interactions involving aggression [85]. Children between the ages of 1 and 2 years express comforting behaviours toward those in distress and may go so far as to give up their own favourite objects as an empathetic action [10,86]. Toddlers show early signs of internally motivated helping behaviour—for instance, 14- to 18-month-olds fetch desired objects that appear out of reach for an experimenter and help to complete household chores. Children also help by informing, where children as young as 12 months point towards objects that an experimenter is searching for [81]. From early in ontogeny children have genuine concern for the welfare of others and show signs of empathy and prosociality in ways that experience, socialization and cognitive construction cannot account for alone [87,88]. A study using measurements of pupil dilation found that the motivation for young children's helping behaviour is simply that the person in need should be helped [89]. The early emergence of prosocial behaviours and empathy in ontogeny thus reflects a biological predisposition to act upon empathic motivations. At 2 years of age, children are most responsive to the distress of their mothers but show some sensitivity toward unfamiliar persons [90]. Their prosocial interventions take a variety of forms, including sharing, helping and comforting victims in distress. Importantly, these prosocial behaviours and signs of empathic concern are unrelated to self-distress. Prosocial behaviour in 5- to 6-year-old children is significantly correlated with ratings of the emotional state of the protagonist but not with their own emotional state, suggesting that empathic concern rather than personal distress was the primary influence on prosocial behaviour [91]. Children's prosocial behaviours increase with age, regardless of their socio-economic environment, even when facing adversity such as an earthquake [92,93].

Empathy and prosocial behaviour are genetically influenced. A meta-analysis of twin studies found that genetic factors exert a moderate effect on individual variability in empathy [94]. Genetic factors also explain a moderate amount of the individual variance in prosocial behaviour [86,95,96]. Importantly, however, both genetics and environmental factors contribute to the association between prosocial behaviour and empathy [86]. The established effect of genetics allows for the identification of specific genes and polymorphisms that are part of the proximal biological mechanism that underlies empathy and prosocial behaviour. One of the most prominent and studied candidates for proximal biological mechanism is OT. This nonapeptide is synthesized in the hypothalamus and exerts peripheral as well as central influence. Genetic studies of the hormone have focused on the single receptor for oxytocin (OXTR). The association between this gene and empathy has been primarily investigated in adults, with findings pointing to an association between the rs53576 single nucleotide polymorphism (SNP) and empathy [35]. Prosocial behaviour is also associated with the OXTR. The association between prosocial behaviour and OXTR has been shown to be mediated by empathic concern and perspective-taking, which are important components of human empathy [97].

Of particular interest are two studies relating polymorphisms in the OXTR to social cognition and prosocial behaviour in children. In a family-based design study, [98] social cognition (including joint attention, empathy, cooperation and self-recognition) in 18-month-olds was associated with OXTR SNP (rs11131149) and haplotypes including that SNP. Another study focused on prosocial behaviour in young children (3–5 years old). Prosocial behaviour was measured by three different tasks, and ToM was also measured [99]. The study specifically examined the rs53576 SNP and found that children who were homozygous for the G allele (GG) exhibited more prosocial behaviours than did those with one or two copies of the A allele (AA). GG carriers also displayed better ToM ability than did AA individuals. Further tests showed differences between genotypes in helping and comforting, albeit not in sharing. The results demonstrated that OXTR rs53576 was related to individual differences in ToM and was associated with prosocial behaviour even at younger ages.

Taken together, these studies suggest that feelings of distress in response to others' negative emotional experiences do not lead to other-oriented concern. They also support the notion of a developmental and a genetic link (via the OT system) between empathy and prosocial behaviour. These associations suggest that the same or a closely related proximal mechanism is at the root of both empathy and prosocial behaviour, adding further support to the account of a linked evolution of empathy and prosocial behaviour.

(c) How empathy motivates prosocial behaviour

Affective processing has evolved as a mechanism to promote certain behaviours and inhibit others in a way that maximizes odds for surviving and thriving. The systems that give rise to positive and negative affect support approach and avoidance behaviours. For instance, fear can induce avoidance from dangerous situations. Anger, a social emotion, supports aggression, a behaviour that is often adaptive in an environment with limited resources. In the same vein, empathy plays a critical role in promoting prosocial behaviour and helps to reduce others' distress and to reduce aggression. Like several classic models in social psychology (e.g. [100]), we propose a process model in which several steps distinguish between the initial event necessitating help, and the actual help given. In our view, the core mechanism leading from others' distress to performing a prosocial behaviour towards them is empathy (figure 2). Witnessing another's distress (step 1) can lead to an aversive affective arousal combined with a physiological stress response (step 2). When appropriate, a prosocial drive is triggered (step 3), which, depending on the context, can lead to prosocial behaviour. In contrast with the classic tension-reduction model [101] which proposes a return to homeostasis as the main driver for helping others in distress, and thus that the ultimate goal is to reduce one's own aversive empathic arousal [5], we posit that helping and caring are inherently rewarding.

Many studies have shown that witnessing another's distress can lead to an aversive affective arousal, and a physiological stress response. Studies with humans document that the perception of another in pain or emotional distress activates neural structures that are also involved in processing of the first-hand experience of pain [53]. Markers of stress, such as elevated cortisol, are observed in people who are exposed to others' pain [102]. Placebo analgesia reduces empathic responses [103], demonstrating that the same circuit is used for processing self and other's pain. Some pharmacological studies of anxiolytics support the role of affective resonance in prosocial decision-making. The benzodiazepine Lorazepam increases utilitarian choices [104] and the beta-adrenergic blocker propranolol reduces racial bias [105]. The modulation of social behaviour with these drugs may be due to their effect on OT and arginine vasopressin release in the brain rather than a systemic inhibition of hypothalamic–pituitary–adrenal axis activity [106,107].

An other-oriented response that leads to successful helping requires resilience to stress or fear that may be experienced in situations of need (e.g. when helping someone that is wounded). Trait resilience will determine whether the observer will approach the distressed other or engage in avoidance and escape strategies. Prosocial drive is experienced when an empathic response is coupled with a motivation to act. However, high cost or lack of perceived ability to help can reduce the motivation and prevent action.

Furthermore, by terminating the observed distress of others, an individual experiences a personal relief from tension. Prosociality is not primarily motivated by a drive to return to homeostasis. Helping can also be experienced as rewarding, an effect referred to as the 'warm glow'. People report helping as pleasurable. One fMRI study demonstrated that donating to a charity activates the same mesolimbic reward circuit as receiving a monetary reward [108]. Helping others through direct actions or charitable contributions produces a positive affect marked by fMRI activation in the nucleus accumbens (NAcc), a critical brain area in the reward pathway [109]. Additionally, helping can demonstrate fitness and strength, increasing individual dominance, which is also an individual benefit to empathic behaviours [110].

Most research on empathy and helping behaviour in non-human animals has been done with apes and rodents, and these studies show that many of the effects observed in humans with respect to empathy and prosocial behaviour are also present in different animal species. The role of affiliation and attachment in modulating prosocial behaviour is exemplified in a study that examined post-conflict interactions and found that bonobos across age and sex classes spontaneously offered consolation to distressed parties, with bystanders significantly more likely to console relatives or closely bonded partners [111]. Additionally, mother-reared individuals were significantly more involved in post-conflict interactions than orphans. This highlights the role of rearing and early attachment in emotional development across species, and suggests that individuals who have been reared in a species-typical way by their own species are better equipped both to comfort others and to reconcile conflicts when they arise.

The same neurobiological systems involved in human social processing are implicated in rodent sociality. These systems include OT, vasopressin, dopamine and serotonin [112]. In mice, social reward is dependent on combined activity of serotonin and OT in the NAcc, a brain region that processes reward and value [113]. Research with sheep [114], birds [115] and even fish [116] suggests that OT and the opioid system play a crucial role in parenting and social behaviour across the phylogeny [18,27,117].

In humans, the ability to share others' distress is a critical component in eliciting prosocial behaviour. Increasing evidence suggests that the same is true for rats. A number of empirical studies with rodents have shown that rats are motivated to alleviate the distress of a conspecific. For instance, rats that learned to press a lever to obtain food stop doing so if their action is paired with the delivery of

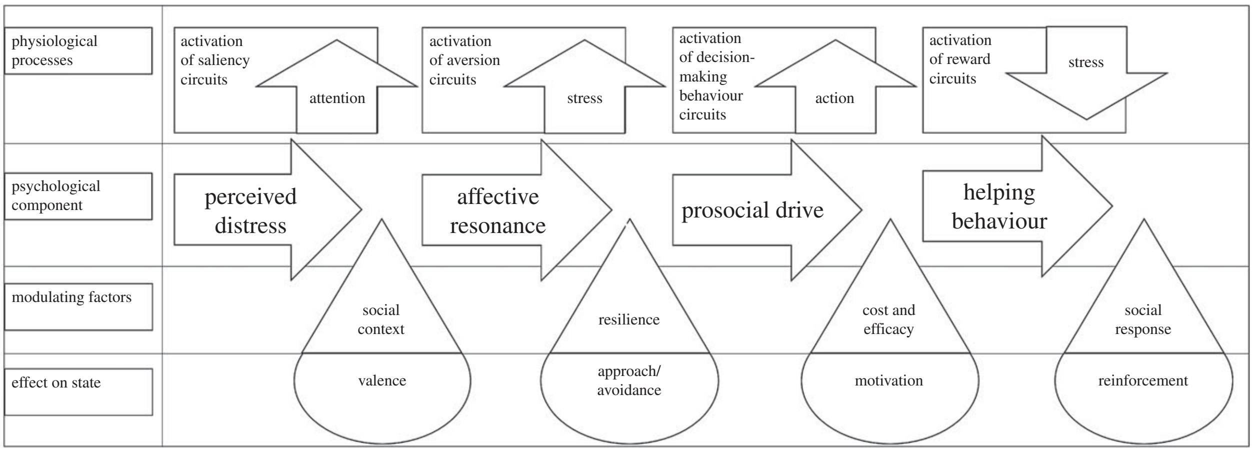

Figure 2. Empathically motivated prosocial behaviour in non-human animals begins with the perception of another conspecific's cues of need or distress, causing an orienting response and activation of attentional processes. The social context (e.g. kinship, relationship) influences the valence and intensity of the affective response. The observation of an affiliated other in distress causes a negative tension, aka stress. The other's distress is experienced as aversive to the observer, recruiting neural circuits related to aversion, including the brainstem, amygdala, ACC and insula, and a systemic stress response is initiated. In individuals with low resilience, or high stress reactivity, emotional distress can be overwhelming and lead to avoidance rather than approach behaviour. Signals of distress are a powerful call to action, experienced as a prosocial drive. In humans, perceiving or even imagining another in distress may also lead to empathic concern and caring, and comprises the basic motivating factors for behaviour directed at improving the well-being of the other. Activation of neural circuits involved in approach, caregiving and social decision-making processes are engaged, including the basal ganglia, hypothalamus and vmPFC. A high cost or lack of perceived ability to help successfully can reduce the motivation for helping. Successful helping is followed by the reduction of distress, and return to homeostasis in the victim, and by proxy in the helper. The social response from the victim is experienced as rewarding, and causes activation of reward circuits involving the striatum and NAcc that reinforce the behaviour and increase likelihood of its re-occurrence in the future.

an electrical shock to a visible neighbouring rat [39]. Rats will press a bar to lower another rat that is suspended in mid-air, which is interpreted as relieving the suspended animal's distress [118]. Rats helped distressed conspecifics that had been soaked with water, and chose to help the cage mate before obtaining a food reward ([119] but see [120]). Moreover, rats prefer a mutual reward to a selfish reward [121] and this prosocial choice is motivated by food-seeking behaviour on the part of the other rat [122]. Rats will intentionally free a cage mate locked in a restrainer even when social reward was prohibited [123]. The same study found that when liberating a cage mate was pitted against a highly palatable food (chocolate chips) contained within a second restrainer, rats opened both restrainers and typically shared the chocolate with the freed cage mates. These manifestations of prosociality are motivated by affective arousal caused by the conspecific's distress. Administration of the anxiolytic midazolam to either the free or trapped rat significantly reduced door-opening for a trapped cage mate but not for a restrainer containing chocolate chips. Moreover, corticosterone responses in both the free and trapped rats were abolished by successful door-opening [124]. A new study combining mice and human subjects demonstrated that empathy for strangers is blunted by social stress, and that blocking glutocorticoid synthesis or glucocorticoid or mineralocorticoid receptors enhances empathy in the same situation [125]. Thus, while the stress response plays an important role in motivating helping, the relationship between stress and empathy is not straightforward. Rather, it is likely that moderate stress arousal sets the optimal conditions for helping.

(d) Social and contextual modulators of empathy and prosocial behaviour

While empathy and prosocial behaviour toward in-group members increases thriving and group survival, these behaviours can be maladaptive when manifested toward members of other social groups, especially in situations where resources are limited. Thus, the empathic response has evolved to be highly selective, and is modulated by the social context. In both human and non-human animals, empathy and its motivational role in prosocial behaviour is highly influenced by the social context, particularly the relationship, familiarity, kinship and group membership of a conspecific [2,126]. This is supported by neurobiological findings documenting that the neural response elicited by the perception of others in distress is either strengthened or weakened by interpersonal relationships, implicit attitudes and group preferences across species. In humans, activity in the neural network including the ACC, aINS and PAG is significantly enhanced when individuals view their loved-ones in physical pain as compared to strangers [127]. In another study, participants were significantly more sensitive to the pain of individuals who had contracted AIDS as the result of a blood transfusion as compared to individuals who had contracted AIDS as the result of their illicit drug addiction, as evidenced by higher subjective ratings of pain and greater neuro-hemodynamic activity in the ACC, aINS and PAG, although the actual intensity of the facial expressions was strictly similar across all videos clips and categories of targets [128]. Another fMRI study reported a modulation of empathic neural responses by racial group membership [129]. The neural response in the ACC to viewing others in pain decreased remarkably when participants viewed faces of racial out-group members relative to racial in-group members. This effect was comparable in Caucasian and Chinese subjects and suggests that modulations of empathic neural responses by racial group membership are similar in different ethnic groups. Reduced skin conductance, a measure of autonomic arousal, decreases when participants view out-group members in distress as compared to in-group members [130]. Using ERPs, painful stimuli elicited greater modulation for in-group targets in early perceptual stages (N 100), but not in late cognitive stages of neural responses in empathy for pain. This suggests an automatic, early effect of race in empathy that appears to be driven by salient physical features of the stimuli and is related to affective resonance [131]. Conversely, an fMRI study demonstrated that the failures of an in-group member are painful, whereas those of a rival out-group member give pleasure—a feeling that may motivate harming rivals [132]. In that study, participants who reported greater rival-specific aggression not only reported more pleasure but also exhibited greater ventral striatum activity (a subcortical region involved in reward and pleasure) in response to watching rivals fail, even against a third party.

As in humans, empirical work with animals demonstrates kin and in-group preferences in the detection and reaction to signs of distress. In particular, it has been observed that rodents do not react indiscriminately to other conspecifics in distress. Female mice had higher fear responses (freezing behaviour) when exposed to the pain of a close relative than when exposed to the pain of a more distant relative [43]. Another investigation found that the act of a female mouse approaching a dyad member in physical pain led to less writhing from the mouse in pain. These beneficial effects of social approach were seen only when the mouse was a cage mate of the mouse in pain rather than an unfamiliar mouse [44]. While rats were helpful to trapped strangers of their own strain [133], they did not release strangers of an unfamiliar strain. Yet two weeks of pair-housing with a member of the other strain were sufficient to induce door-opening for strangers of that strain. This finding suggests that the in-group bias that exists in humans is biologically rooted, and is in line with evidence showing that in humans, social experience can influence empathy for strangers [125] and out-group members [134–136]. Although kin selection is a powerful force due to the adaptive value of prosocial behaviour, a recent study demonstrated that it is social bonds, and not solely genetic relatedness, that can motivate helping strangers. Rat pups were fostered from birth by rats from another strain. As adults, fostered rats helped strangers of the fostering strain but not rats of their own strain [133].

4. Conclusion

Empathy is often viewed as a complex cognitive ability specific to humans. However, theoretical and empirical research demonstrate that even the most advanced forms of empathy in humans are built on more rudimentary neurobehavioural processes that have been selected for over the course of evolution to facilitate affective communication, social attachment and parental care. The sharing of vicarious negative arousal provides a strong signal that can promote empathic concern and caring behaviours, but is strongly modulated by both intrinsic and extrinsic factors. This phylogenic account parallels the ontogeny of empathy in humans. In their first year, infants show an innate capacity to be affected by the distress of others and express concern for their well-being. This concern, in both human and non-human animals, requires only a minimal capacity for mindreading and self-awareness.

There is, however, a caveat to the theoretical perspective that the mechanisms underlying empathy are similar between humans and non-human species and that empathy is distinct from its outcomes such as caring or helping. Such claims are quite easy to be substantiated in humans who can reflect on their own feelings, report on their subjective experiences, and be subjected to diverse experimental manipulations with various techniques from reaction times to functional imaging. It is much more difficult and challenging to disentangle empathy from prosocial behaviour in non-human animals, as the latter is often necessary to inform the presence of the former.

Basic forms of empathy and similar underlying biological and genetic mechanisms have been identified in non-human animals and humans alike. This translational neuro-evolutionary model from social neuroscience enables the development of novel strategies for conflict resolution and interventions in developmental psychopathologies. Moreover, as demonstrated above and previously acknowledged by Darwin [137], empathy motivates some types of prosociality, which are part of the natural behavioural repertoire of many animals. It is paramount to demystify the concept of empathy to be able to study it from a biological perspective.

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