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Empathy and Prosocial Behaviours. Insights from Intra- and Inter-species Interactions

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Abstract It has been suggested that "sharing the same body" between the observer and the observed subject allows for a direct form of understanding and emotional attuning by a process of simulation. Then, what happens when we don't share the same body? The aim of the present paper is to review available evidence of intra- and inter-species empathic and prosocial behaviours, with respect to within-human, within-animals and cross-specifies interactions. Similarities and differences will be evaluated using a comparative perspective, and some possible moral and ethical implications for human-animal interactions will be discussed. According to Charles Darwin's work, the perceived differences between human and animal empathy could be more quantitative than qualitative, suggesting a common affective core which allows both categories to mirror and tune to conspecifics' feelings, where in the case of humans it can be integrated with more complex cognitive processes.
KEYWORDS: Empathy; Emotion; Prosocial Behaviours; Intra- and Inter-species Interaction.

Riassunto *Empatia e comportamenti prosociali. Evidenze dalle interazioni intra- e interspecie* – Si è ipotizzato che la "condivisione di correlati corporei" tra soggetto osservante e soggetto osservato permetta una forma diretta di comprensione e sintonizzazione emotiva mediante un processo di simulazione. E quindi, che cosa accade quando non condividiamo lo stesso corpo? Scopo di questo lavoro è fornire una rassegna delle evidenze disponibili circa i comportamenti empatici e prosociali intra- e inter-specie, in relazione alle interazioni tra umani, tra animali e inter-specie. Similarità e differenze saranno valutate secondo un'ottica comparativa e verranno discusse alcune possibili implicazioni morali ed etiche sul piano delle interazioni tra umani e animali. Secondo quanto suggerito da Charles Darwin, le differenze percepite tra l'empatia umana e quella animale potrebbe essere più di tipo quantitativo che qualitativo, deponendo a favore di un comune nucleo affettivo che permetterebbe a entrambe le categorie di riflettersi e sintonizzarsi con i sentimenti dei propri conspecifici, dove, nel caso degli umani, questo nucleo potrebbe essere integrato con processi cognitivi più complessi.
PAROLE CHIAVE: Empatia; Emozione; Comportamenti prosociali; Interazioni intra- e inter-specie.

Introduction

EMPATHY IS A FUNDAMENTAL MOTIVATION for prosocial behavior and knowledge of the processes underlying this capacity is crucial to understanding why and how we engage in prosocial behaviours.[1] The ability to perceive and understand others' mental

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states and moods is critical to reinforcing and maintaining our social bonds. Thus, empathy and altruism are most commonly considered forms of compassion that human beings express toward one another. What is not clear, however, is the extent to which non-human animals can feel empathy.

Although researchers on human empathy have recently published many new articles, the current interest in the topic draws on a line of animal research that began almost half a century ago, while human studies began first in the 1970s with young children and continued, in the 1980s, with adults. Finally, since the 1990s, researchers began placing humans in brain scanners to monitor them while viewing pictures or videos depicting others in pain or distress, to find out about the neural correlates of empathy and compassion.[2] Ethologists and sociobiologists have identified many behaviors within other species that may be viewed as prosocial or altruistic, as well as behaviors reflecting apparent concern for others, even if a possible comparison between human and animal empathy still needs to be elucidated.

Research suggests that we more readily empathize with those to whom we feel closer and more similar. In fact, there is less evidence of altruism across species, even if behaviors reflecting apparent concern for others seem to occur between different species as well. For example, animal owners sometimes report that their pets show emotional concern for others. The recent spate of research on animal assisted therapy attests to the capacity of animals to provide comfort to persons suffering from a variety of physical and emotional problems.

In intra-human studies several factors that can increase the perception of similarity, and consequently empathy, have been investigated, with cultural similarity, sentience or social circumstance being the most influential.[3] The perception of similarity has also been thought to underlie empathic behaviors towards animals: it has been theorized by many philosophers that the amount of empathy shown towards animals may indicate a more general capacity for empathy and related prosocial behaviors.[4] Furthermore, the link between human-human and human-animal relationships is being given increasing attention by empirical research and suggests that the lack of empathy demonstrated by some individuals is a general deficit not simply restricted to its expression towards other human beings.[5] Preliminary self-report empathy research currently supports a relationship between human- and animal-orientated empathy.[6] However, there is a need for improved objectivity in these measures.

Therefore, the aim of the present paper is to discuss empathic and prosocial behaviors in human studies, taking into account the main behaviors which can be considered as explicit markers of empathic attitudes. A second major intent is to systematically review the available literature on empathic-like behaviours in non-human animals, with particular attention to resonance mechanisms, affiliative behaviours and pain sharing. Then, possible insights on cross-species empathy will be furnished with respect to both humans' and animals' attitudes. Finally, some moral and ethical implications about human-animal relationship will be considered.

Intra-species interactions: Empathy within humans

Empathy is an aspect of social cognition that concerns our interactions with the people around us. Indeed humans perceive and represent themselves in a very different and specific way in respect to non-human objects and events. Despite the diverse terminology used by different authors, there is wide agreement that empathy involves three primary elements: the cognitive ability to adopt the perspective of another person, the presence of monitoring and self regulatory mechanisms that keep track of the origins of own and other emotions, and the affective response to another person's emotional state, that often entails the capacity to share this state.[7]

These aspects may be experienced independently from one another, and may be expressed at different levels of complexity within the empathic experience, from mimicry to sympathy. Affective components include the ability to monitor and regulate own and other's emotional processes[8] and coincide with the ability to share and imitate them.

A basic resonance mechanism is thought to lie underneath the emotional empathic response and includes: the capacity to know what the other person is feeling, by monitoring external cues such as emotional facial expressions; to have the intention to respond compassionately to another person's distress; to mimic what another person is feeling by responding with similar emotional behavior.[9] These aspects together with their functional relevance and their neural substrates have been extensively illustrated by simulation[10] and emotional contagion[11] theories. Interestingly, unlike other components that require intentional processing, such as cognitive perspective-taking and, in part, emotion regulation, these phenomena can occur automatically and without awareness.[12]

In this light, empathy seems related to the ability to comprehend emotions and feelings of others, where resonance mechanisms permit a direct form of understanding between the observer and the observed. But how can we understand and learn about these feelings?

It has been observed that the perceptual ability to attend to socially relevant stimuli, including facial expressions of emotions, is a central mechanism, together with motivational and attentional components.[13] This ability allows us to acquire information about the intentions and future actions of others, to support effective social communication and to develop the motivation for prosocial and cooperative behaviour.[14]

Empathy and the detection of emotional cues

Consistent evidence suggests a close relationship between the experience of emotional empathy and the ability to recognize emotions from facial expressions.[15] Previous studies demonstrated that the degree of emotional empathy was linked to sensitivity to facial expressions.[16] In a recent study[17] Balconi and Bortolotti found trait empathy affected the degree of subjective responsiveness to facial cues, where subjects with higher empathy scorings were also more accurate in responding to emotional faces. Moreover, viewing another's emotional expression automatically triggers that emotion in oneself, and elicits unintentional mimicry of that expression.[18] Current findings involving people with disorders of emotional experience, such as autism, schizophrenia and major depressive disorder, assume that these populations may have abnormal psychophysiological responses to emotional cues and anomalous empathic behaviours.[19]

Thus, different degrees of empathic experiences may also affect psychophysiological responses:[20] facial muscle reactions are thought to be related to emotional responses and their electrical activity is thought to be related to emotional empathy. Previous studies demonstrated that individuals with a greater autonomic tendency to reciprocate facial expressions score higher on an empathy questionnaire.[21] Interestingly, Balconi proved that facial expression detection and autonomic mimicry reaction to emotional faces (measured by electromyography; EMG) are strictly related.[22]

Empathy-related brain networks

These mechanisms are supported by cognitive and emotive competences and could be based on specific neural networks.[23] Neuroimaging studies on emotion have revealed a very wide range of areas activated in response to emotional cues, specifically the medial prefrontal cortex (MPFC) for general emotional processing,[24] the dorsolateral prefrontal cortex (DLPFC) for decisions and supportive behaviours[25] and the sensorimotor cortex[26] when a subject simulates perceived emotions.

The MPFC has been shown to be involved in empathic responsiveness and regulation of facial recognition in response to an emotional task.[27] Studies on clinical populations, such as schizophrenic subjects, have revealed a significant relationship between the impairment of comprehension of emotional cues, empathic behavior, and structural abnormalities of this area.[28]

It has been recently demonstrated by Balconi and colleagues[29] that the ability to recognise facial expressions of emotion and facial mimicry are modulated by prefrontal functioning: in fact, the use of the TMS technique allowed researchers to prove its relevance in empathic mechanisms by temporally inhibit MPFC. Participants were required to empathise with the situation by entering into the picture's feelings: the four emotions portrayed were anger, fear, happiness, and neutral. Results showed an impaired performance on both facial expression recognition and mimicry when TMS stimulation resulting in inhibition of the MPFC was carried out.

Besides MPFC, the contribution of DLPFC has also proved crucial for empathic responses, with respect to prosocial behaviors: electrophysiological studies, in fact, have shown the presence of a clear ERP marker, the N200 effect, correlated with a predisposition to intervene, support and help other people, with a main cortical localization within the frontal sites.[30] Moreover, it has been recently found that excitatory rTMS stimulation on DLPFC can induce a facilitatory effect on engagement in prosocial behaviours.[31]

Finally, sensorimotor cortices has been implicated in empathic behaviors: simulation models of emotion recognition, in fact, suggest that understanding another's emotions requires that individuals map the observed state onto their own representations.[32] According to theories of embodied cognition, in fact, visual mechanisms alone are insufficient to elicit simulating responses associated with the observed emotion.[33] On the other hand, there is growing evidence that sensorimotor activity plays a crucial role in facial emotion recognition by linking emotion perception with representations of somatic states previously engendered by emotions.[34]

In fact, the ability to monitor emotional cues and behavioral empathic responsiveness was shown to be partially compromised in the case of frontal activity disruption, highlighting the central role of the sensorimotor system in empathic social skills. These findings demonstrate that regions in the sensorimotor circuits guarantee a correspondence between emotional recognition and the ability to provide an empathic response, by allowing the simulation of that emotional behavior with recourse to previous somatic states.

Thus, the abovementioned evidence may suggest the existence of inter-individual differences in emphatic cerebral activations.[35] These differences in neural activity appear to correlate with measures of behavioral trait empathy assessed behaviorally through questionnaires. Interestingly an increase in autonomic responsiveness recorded through Heart Rate (HR) measure and Skin Conductance Response (SCR) was also observed as a function of empathic measures, with high empathic subjects being more responsive to empathy-related situations than low empathic subjects.[36] Thus, autonomic measures could be interpreted as a functional mechanism for mirroring and understanding the emotional conditions displayed by other people, while sharing similar emotional and somatic responses.[37]

Intra-species interactions: Empathy within animals

Empathy is a social phenomenon that has for decades attracted the interest of philosophers and psychologists and, more recently of neuroscientists and evolutionary biologists. Non-human empathy, in fact, is receiving growing attention, even if the presence of observable examples of emotional contagion in animals has only been mentioned in the literature, while objective experimental evidence is beginning to emerge.[38]

Moreover, the influential paper of Preston and de Waal published in 2002[39] contributed to empathy being considered as a phylogenetically continuous ability, ranging across animals with more basic and automatic reactions in response to the emotions of others, to perspective-taking. The authors, in fact, proposed a sequence of progressively complex levels of empathy across animals that parallels the development of empathy in humans. Evidence in this field suggests that empathic and sympathetic concern may even have emerged on a pre-human basis, in that some species, especially primates, show consolation-like and prosocial behaviours.[40] Social species like humans and primates need to regulate group interactions between members to coordinate travel, communicate about danger, assist group mates in need and facilitate cohesion and emotional balance, so that the capacity to interpret behavioral signals and react to the emotional state of the other seems favorable.[41]

These mechanisms have been described with reference to the social brain hypothesis, which states that primates with bigger neocortices are better able to catch social signals.[42] However, growing evidence is suggesting the presence of empathy-related responses also in other mammals and birds, despite the absence of a large neocortex; this fact raises the hypothesis that other mechanisms are involved in sharing the affective state of a conspecific.[43] Nevertheless, whereas human pro-social behavior is often driven by empathic concern for another, it is unclear whether other animals can experience a similar motivational state.

Despite the difficulty of establishing the capacity for empathy in animals, recent evidence suggests that many species are sensitive to suffering in others. A possible definition of empathy with respect to non-human animals can be described as a situation in which an animal perceives a reciprocal state of feeling in another animal and identifies with its concerns. In this context, empathy can be recognized when an animal seems to be sympathizing with another animal's mental state, and can be seen in helping or prosocial situations.[44]

The advantageous role of empathy is sustained in a theoretical model described by Preston and de Waal[45] which proposed that empathy is linked to all facilitation behaviors relying on perception-action, including imitation, coordination and unconscious mimicry. According to the Perception-Action model (PAM), the observation of another's emotional states automatically and unconsciously activates neural representations of congruent states in the observer. The more similar and socially close two individuals are, the easier the tuning with the partner.[46] This consideration explains why, in this context, empathy is considered essential for directional cooperation in achieving a shared goal and in some social interactions.[47]

The evolution of empathy is thought to go back to mammalian maternal care. Whether a human or a rat, a mother must be in tune with behavioral indicators of hunger, danger, or discomfort in her offspring. Sensitivity to emotional signals confers clear adaptive value also to the dyad as well as the group of conspecifics; this fact would explain observed sex differences (see herein for details).[48] As previously discussed current evolutionary evidence suggests that empathy is a multilayered phenomenon with different intermediate forms, ranging from motor mirroring and mere agitation at the distress of others to complex forms of perspective taking.[49] While subtle, complex and cognitive forms of empathy exist, any empathic process relies to some extent on personal distress and emotional contagion.[50]

Despite the arguments against the presence of empathy in non-human animals,[51] there is growing evidence for the presence of behaviours which appear to be driven by empathy in the context of contagious yawning (CY), affiliative behaviours towards distressed individuals, and modulation of pain sensitivity. In the following paragraphs these contexts will be exhaustively discussed.

Contagious yawning

Contagious Yawning (CY) is a useful candidate behaviour to explore basic forms of empathy across species and different types of social systems. In fact, it is present in both humans and non-human animals and it seems related to empathy and affective tuning.[52] In fact, describing the phenomenon of contagious yawning (CY) first in humans, within a comparative perspective, the susceptibility to contagion has been theoretically and empirically related to our capacity for empathy: yawning when seeing other people yawn is associated with activations in neural networks related to action simulation, social behavior and empathy,[53] such as the ventromedial prefrontal cortex[54] and the mirror neuron system,[55] though its role in yawn contagion remains unclear.

Moreover, CY has been reported to occur more frequently in individuals with higher scores on questionnaires evaluating empathy[56] and less in clinical populations characterized by impaired empathic abilities, like autistic and schizotypic patients.[57] Additionally, it has been demonstrated recently that the social-emotional bond between individuals influences the occurrence, frequency, and latency of yawn contagion. Cross-cultural observations in humans have shown the CY effect to be stronger in response to the yawns of kin, then friends, then acquaintances, and lastly strangers.[58] Thus, although contagious yawning is not an emotional reaction itself, its occurrence has been clinically, psychologically, neurobiologically, and behaviorally linked to our capacity for empathy.[59]

Different theories have tried to explain the possible functions of yawning:[60] communication theories propose yawning as a way to synchronize group behaviors or communicate tiredness or stress. Arousal theories propose, instead, that yawning should help subjects maintain their attention levels and promote maintenance of vigilance and shared attention.[61] Because of its relevance to evolutionary biology and its evident expression, this phenomenon has been the focus of recent investigations in non-human species:[62] in fact, humans are not the only species affected by contagious yawning. Chimpanzees, bonobos,[63] gelada baboons[64] and domestic dogs,[65] have been reported to yawn in relation to a conspecific yawning. In contrast, no CY has been demonstrated in tortoises,[66] a solitary species, lending some empirical support to the notion that CY serves to coordinate and synchronize group behaviour.[67]

Palagi and colleagues in a study with gelada baboons found that contagious yawning seems unrelated to external stressful events and that it is more frequent between socially close individuals. Moreover they demonstrated CY to be more common between individuals with higher levels of affiliation, thus suggesting that the roots of empathy may be present in non-human primates. Moreover, yawn contagion was present only in adults.

This is particularly interesting in that also humans show a developmental increase in susceptibility to yawn contagion, with children displaying a substantial increase at the age of four, together with the development of related cognitive abilities such as the identification of others' emotions.[68] Finally, adult females showed an additional feature, that is the capability to match the type of yawn. These findings fit the empathy-based hypothesis of contagious yawning since similarity, familiarity, and closeness are known to facilitate empathy.[69]

Although empathic abilities outside the human domain were previously thought to be present only in primates and animals with a large neocortex, some new evidence suggests that simpler forms exist in other animal species. Romero and colleagues[70] using a highly standardized observational approach under naturalistic settings found that yawning is contagious in wolves and that, according to the empathy-based hypothesis, the susceptibility to yawn contagion is biased toward close social partners.

The importance of this study relies in the fact that it is the first to demonstrate intraspecies contagious yawning in a carnivore species, suggesting that this ability might be deeply rooted in the Mammalia class for within-species social communication, which can be transferred to animal-human interactions (see below). Again, sex differences were observed, with female wolves responding quicker than males when the initial yawner was a close associate, suggesting a higher ability for female wolves to react to the emotional stimulus.

Affiliative behaviors

Following the discovery that chimpanzees often kiss and embrace shortly after a fight within the group,[71] numerous studies have documented reconciliation-like behaviours in non-human primates. Specific methodologies allow comparing post-conflict observations with baseline behaviours to determine how species members behave before and after antagonism. Such comparisons show that primates are generally attracted to previous opponents, seeking friendly contact. This kind of consolation reduces the recipient's arousal and follows the same sex difference reported in humans, with female apes providing comfort more often than males.[72]

In research conducted on empathy between chimpanzees[73] O'Connell found that these animals show empathy of varying types and levels, and across a wide spectrum of situations. Of particular interest is understanding the perspective of another individual to support it and even rescue it from life-threatening circumstances, suggesting the possession of second order intentionality. Studying titi monkeys, Clyvia and colleagues[74] reported an intriguing finding about the presence of empathetic responses towards an individual of a different group. Thus, if empathy is more likely to occur when there is social proximity between individuals, it does not mean that unrelated individuals do not have the perception of mental and emotional states of other individuals.

As already stated, empathy is thought to be unique to higher primates; nevertheless Bates and colleagues[75] described elephants as showing a rich social organization and displaying a number of behaviours that have the potential to reveal signs of empathic understanding, such as coalition formation, the offering of protection and comfort to others, retrieving and "babysitting" calves, aiding individuals that would otherwise have difficulty in moving, and removing foreign objects attached to others. These capabilities demonstrate that elephants can diagnose animacy and goal directedness, and understand the physical competence, emotional state and intentions of others, even if they differ from their own.

Also, Ben-Ami Bartal and colleagues[76] tested empathically motivated pro-social behavior in rats, positioning a free individual besides a cagemate trapped in a restrainer. After several attempts, the free rat learned to intentionally and quickly open the restrainer and free the cagemate, in response to its conspecific's distress, thus providing strong evidence for the biological roots of empathically motivated helping behaviour. More interestingly, when liberating a cagemate was pitted against chocolate contained within a second restrainer, rats opened both restrainers and typically shared the chocolate; they also freed cagemates when social contact was prevented, while they did not open empty or object-containing restrainers. This study proves that rats can behave pro-socially when they perceive a conspecific experiencing nonpainful psychological restraint stress, acting to end that distress through deliberate action, in the absence of training or social reward, and even when in competition with highly desired food.

Modulation of pain sensitivity

In a paper by Russell Church entitled *Emotional Reactions of rats to the Pain of Others*,[77] he describes that, after training a rat to obtain food by pressing a lever, if it saw another rat in a neighboring cage receiving a shock from an electrified cage floor, the first rat would interrupt its activity. The bigger question is whether the rat was worried about their companions or just afraid that something bad might happen to it, as well.

Nearly fifty year later, Langford and colleagues[78] reported the modulation of pain sensitivity in mice produced by exposure to their cagemates in pain. Pairs of mice were placed in two transparent Plexiglas cylinders, so that they could see each other, and were injected with acetic acid, which is known to cause a mild stomachache and characteristic stretching movements. The researchers found that an injected mouse showed increased pain behaviors if its partner displayed the same behaviour, especially for mouse pairs who were cage mates.

Moreover, when familiar mice were given noxious stimuli of different intensities, their pain behavior was influenced by their neighbor's status bidirectionally. Overlooking the huge ethical implications that such studies should raise, this research showed that rodents can recognize and show emotional reactions to the pain of conspecifics, and that their pain sensitivity can be altered by social factors.

Inter-species interactions: Can animals feel empathy for humans?

Contagious yawning and affiliative behaviors

Most studies on yawn contagion in non-human animals have demonstrated the intraspecific effect of yawn contagion. However, studies on primates and dogs have also been able to demonstrate cross-species contagious yawning. Madsen and colleagues[79] examined whether emotional closeness affected the strength of contagion in orphaned chimpanzees observing unfamiliar and familiar humans, demonstrating the existence of cross-species contagious yawning. Specifically, viewing a human yawn elicited yawning in 48 per cent of juvenile chimpanzees, while infants were immune to contagion. In fact, like humans and dogs,[80] chimpanzees are subject to a developmental increase in susceptibility to yawn contagion.

Following recent studies suggesting that contagion yawning in humans, and some other primates, is empathy-related, some authors have considered the possibility that the same mechanism may underlie contagious yawning in dogs, with increasing interest of researchers in the field of animal cognition. Joly-Mascheroni and colleagues[81] have been the first to demonstrate that the observation of yawns elicits yawning in a non-primate species like dogs, and to suggest the possibility of contagious yawning between different species.

In this study the presentation of human yawning elicited yawns in 72 per cent of the dogs tested, which is higher than the rate reported in humans (45-60%) and chimpanzees (33%). The presence of contagious yawning in dogs suggests that this phenomenon is not restricted to primate species, and may indicate that dogs possess the capacity for at least a basic form of empathy. Since yawning is known to modulate the level of arousal,[82] it may help coordinate interactions as well as communication between humans and dogs.

Madsen and Persson explored the ontogeny of dogs' susceptibility to yawn contagion and demonstrated that, like humans, they show a developmental increase in susceptibility to yawn contagion, with consistent evidence of contagion starting from 7 months. Romero and colleagues also demonstrated that human yawning can elicit CY in domestic dogs, and that the social bond, associated with empathy, mediates its occurrence; indeed dogs yawn more frequently when watching the familiar model than the unfamiliar one, demonstrating once again the correlation with the level of emotional proximity.

Similar findings have been found by Silva and colleagues with the presentation of a mere sound of a human yawn.[83] Results suggest that dogs possess unique social skills in interacting with humans, which may derive from the process of domestication.[84] It has been shown that they can follow human gaze and pointing,[85] show sensitivity to others' knowledge states[86] and match their actions to observed human ones.[87]

Silva and De Sousa[88] suggested three main reasons for why dogs may be able to empathize with humans. First, dogs originated from wolves, which are highly social animals that maintain cooperative activities and that have some capacity for empathy towards familiar conspecifics. Second, biological changes produced during domestication may have allowed dogs to use their inherited empathic capacities to synchronize with humans and predict their behavior more flexibly than their ancestors. Third, the selection for increasingly complex cognitive capacities may have led to more complex forms of empathy that now resemble certain traits of human emotional communication.

Besides contagious yawning, which reflects automatic and involuntary behaviors elicited by affective resonance and tuning mechanisms, further evidence of voluntary prosocial acts has been provided especially by human-dog experiments. Their affectional bond is particularly evident and relies on the fact that dogs appear empathically well-tuned to human emotions.[89] They seem to celebrate our joy and commiserate with our sorrow. Although owners often report empathic behaviors in their pets, systematic empirical confirmation remains elusive.[90] Even if, as previously discussed, it has been found that dogs contagiously yawn in response to a human yawning,[91] such behavior seems very different from empathically responding to human emotional displays such as distress.

In an attempt to solve this query, Custance and Mayer[92] performed an experiment where dogs were exposed to their owner or a stranger while he was talking, humming or feigning to cry. They succeeded in showing that dogs behave in an upset manner when people fake distress and cry. In fact, the majority of dogs showed comfort-offering and responded differently when both their owner and the stranger were crying, in contrast with humming or talking conditions. This behavior strongly suggests sympathetic concern.

Inter-species interactions: Can humans feel empathy for animals?

The majority of previous human studies attempting to characterize empathy-related responses did not separate empathy towards humans from that towards animals. Furthermore, in some studies, scenes showing animals were treated as a neutral condition.[93] Nevertheless many people have a strong emotional attachment to their pets and half of pet owners consider their pet as much a part of the family as any member of the household.[94]

Literature on attachment measures showed very similar results for human infants' and dogs' behaviors with their mother or owner during high and low stress conditions.[95] Similar neurobiologic mechanisms of bonding have been found in human-human and owner-dog pairs, with increased levels of oxytocin, beta-endorphin, prolactin, beta-phenylethylamine, and dopamine in pet owners and their dogs during[96] and after[97] a positive interaction. Nevertheless, neural substrates underlying the human-pet relationship are largely unknown.

A recent paper by Stoeckel and colleagues[98] examined brain activation patterns by means of fMRI when mothers viewed images of their own child and dog, or an unfamiliar child and dog, with the aim of comparing the functional neuroanatomy of human-pet bonds with that of maternal-child bonds. The authors reported substantial overlap in brain activation patterns elicited by images of both a mother's own child and dog in regions involved in reward (medial Orbito-Frontal Cortex, mOFC; putamen),[99] emotion and affiliation, together with similar pleasantness (valence) and excitement (arousal) ratings for their child and dog compared to unfamiliar pictures.

Moreover the amygdala was activated by both the own child and dog images; it is thought to be a critical region for bond formation, and it may be involved in providing the emotional tone and incentive salience that directs attention to the needs of the child and dog, which is critical for the formation of these pair bonds. Such similarities between the human-dog and the human-infant relationship have been described within the framework of human attachment theory, developed to explain the role of the human infant-caregiver relationship in development, to ensure safety, security and survival.

In this context the attachment bond has been also extended to adult-adult caregivers, peer, and romantic relationships,[100] and it may be applied to the formation and maintenance of people's relationship with their pets.[101] Anyway, while a common brain network involved in reward, emotion, and affiliation was activated when mothers viewed images of their child and dog, a specific activation emerged in response to images of their child, localized in the dopamine, oxytocin, and vasopressin-rich midbrain, a key region involved in reward and affiliation. This result replicates previous reports of maternal midbrain activation to stimuli related to their child.[102] This area was not involved during the observation of subjects' own dog, indicating that, in humans, it is essential for the formation and maintenance of pair bonds that sustain and propagate our species. On the other hand, own-dog images elicited greater activation in the fusiform gyrus compared to viewing own child. This region is central to visual and face processing and social cognition.[103]

Considering the primacy of language for human-human communication, facial cues may be a more central device for dog-human interaction, by helping owners identify their dog, use gaze direction to communicate, and interpret emotional states.[104] To conclude, despite the presence of similarities in the perceived emotional experience and brain function associated with the mother-child and mother-dog bonds, there are also key differences that may reflect variance in the evolutionary course and function of these relationships.

An overlapping of brain region activation when viewing human and animal images has also been found in the case of suffering: Franklin and colleagues,[105] in fact, asked their human participants to observe images of humans and animals in pain. They found that many of the same brain regions known to be involved in human empathy were active when perceiving both human and animal suffering, including the anterior cingulate gyrus and anterior insula.

Anyway, despite these similarities, direct comparisons also revealed distinct patterns of activation in response to pictures of humans versus animals, suggesting that different neural mechanisms may underlie how we derive our empathic responses to humans and animals: human suffering yielded significantly greater medial prefrontal (MPFC), inferior parietal and posterior cingulate activation, which are known to be implicated in taking a third-person perspective of others' situations[106] and distinguishing between one's own emotions and the emotions of those who are suffering.[107] On the other hand, observing dog versus human suffering led to increased activation in the anterior insula (AI), the inferior frontal gyrus (IFG) and the precuneus.

The AI is important in the affective nature of empathy, suggesting that perceiving animal suffering elicits greater emotional responses than human suffering. The IFG, instead, is active in mentalizing and empathy-related tasks using picture-based stimuli.[108] This may reflect the greater effort needed to understand the actions of scenes including dogs than to perceive human suffering, which can require more perspective-taking mechanisms. Also, the IFG is involved in attention allocation as part of the ventral attention system and is important in allocating attention upon detecting salient stimuli and unexpected changes in the environment.[109] Then, another possible explanation is that dog suffering, being less familiar, captures attention to a greater degree than human suffering.

These results indicates that there are many overlapping regions in humans' empathic responses to viewing animal and human suffering, particularly in areas classically associated with empathic responses; also, they indicate the presence of different and specific neural substrates, suggesting that the way we develop our empathic responses to the suffering of dogs or humans may be different. More interestingly, many of the cited regions differentially recruited for the two conditions were significantly active for both conditions if compared to baseline, indicating that although they represent potentially different networks for similar empathic responses, they are not mutually exclusive, but rather differentially predominant. This suggests that empathy is not simply a response we save for humans alone, but can also be extended to familiar animals.

Perceived closeness and similarity, in fact, is thought to affect how much empathy is attributed to suffering animals. Plous[110] has examined human responses to suffering in animals with particular interest in the use of animals for human gain. In his research, he found that animals perceived as more similar to humans were also judged as being more capable of perceiving pain, and the viewing of pictures depicting them in pain elicited greater skin conductance responses (SCR), indicating that perceiving suffering in those animals aroused more anxiety than perceiving suffering in animals judged as being less similar to humans. A couple of years later Hills[111] investigated the relationship between empathy towards animals and the attribution of animal mind, which refers to the belief that an animal is capable of thinking and feeling. Six different emotional scenarios were presented with printed text to farmers, urban dwellers, and animal rights activists: results showed that animals that were closer phylogenetically to humans (mammals) were rated higher in terms of the belief that they possessed a mind than more distant animals (cold-blooded animals and invertebrates).

In 2008 Westbury and Neumann[112] performed an experiment in which participants were exposed to ecological real-life film stimuli depicting humans, primates, quadruped mammals and birds in victimized circumstances while their SCR was recorded. Participants also completed a subjective trait empathy questionnaire. The authors hypothesized that a linear pattern of responses across increasing phylogenetic relatedness would be found for each of the subjective and psychophysiological measures of empathic responding, with respect to the similarity hypothesis. Consistent with Preston and de Waal's[113] interpretation of proximal empathic mechanisms (the PAM of empathy), the predicted linear pattern of empathy-related responses as a function of phylogenetic similarity was supported for both subjective empathy ratings and SCR. Bird stimuli tended to elicit less self-reported scorings than the mammalian stimuli, while SCR decreased as a function of phylogenetic distance. Moreover, high trait empathy participants gave higher subjective empathy ratings and exhibited greater corrugator electromyographic activity than moderate and low trait empathy participants. These results provide evidence that human feelings of empathy tend to generalize easily towards animals perceived to be similar, such as other mammals, but starts to decline in response to non-mammals.

As previously discussed, empathic behaviors can be traced back to group life preservation, but also to nurturance and offspring protection. In this framework, innate releasing stimuli like infants could be particularly salient and elicit stronger empathy-related responses than older individuals, in particular during negative contexts. Prguda and Neumann[114] presented their participants with images of both infant and adult human and wild non-human animals (non-human primates, quadruped wild mammals, and wild birds) depicted in negative, victimizing situations. Subjective empathy and arousal ratings were greater for human infants but this did not extend to the non-human infants. Psychophysiological measures did not differ across species, but HR was lower during infant than adult stimuli presentations, while a pattern of HR deceleration followed by an acceleration and subsequent deceleration was observed for infant stimuli. Such a pattern pertains to orienting behaviors, enhanced attention and information intake.[115]

Also, this study confirmed previous findings that more empathic individuals produce significantly higher subjective empathy ratings than the lower empathy individuals, suggesting that empathetic responding at the inter-species level may shed further light on human empathetic processes in general.

Moral and ethical issues related to human-animal interactions

According to what has been discussed above, it seems that the degree of empathy shown towards animals may indicate a more general capacity for empathy and prosocial behavior. This is particularly interesting for our discussion in that it has been theorized by many philosophers that a humane treatment of non-human animals is an indicator of general moral propensity and ethical conduct. This hypothesis has recently found support by empirical studies demonstrating a link between intra-human and human-animal violence.[116] However, little research has investigated how human empathic responding extends towards non-human animals.

This association suggests that a lack of empathy could be a general deficit, and not simply restricted to expression towards other human beings:[117] in fact, from criminal record studies we know that offenders who engage in animal abuse are also more likely to have a history of violent[118] and concomitant anti-social behaviors, such as drug, public disorder and property offenses.

Even if the subjective attitude held toward suffering individuals does not completely coincide with empathic behaviours, it can be used to explore empathic responses with respect to these and other ethical issues. Filippi and colleagues[119] explored brain activations related to dietary preferences based on avoidance of animal product consumption for ethical reasons. In detail, they scanned vegetarians, vegans and omnivores while perceiving negatively valenced images of injured and dead animals in comparison to threatening images of violence in humans.

Vegetarians and vegans guided by ethical issues were selected for this study as a possible example of people with humane concern for animals, and they have been thought to show different neural representation of conditions of abuse and suffering, thanks to different motivational factors and beliefs. Results showed that people with greater interest in animals consistently display higher engagement of empathy-related areas while observing negative scenes, independently of the species of the individuals involved, which is characterized by an increased recruitment of the ACC and the IFG. Moreover, they show a higher engagement of empathy-related areas while observing negative scenes regarding animals rather than humans, with the additional recruitment of the amygdala, for the regulation of intense emotions, the MPFC and the Posterior Cingulate Cortex (PCC).

These regions are frequently observed in conditions involving representation of the self and self values and the PCC, in particular, is also thought to be involved in memory and visuospatial processing in relation to emotions and social behavior. These results reveal that distinct brain responses are evoked by emotionally significant pictures of humans and animals in people with particular concern for animals, suggesting that different motivational factors underlying preferences and moral attitudes could reflect specific regulatory processes due to complicity in the suffering of animals.

Starting from these results and the assumption that vegetarians and vegans show increased empathic responses to animal suffering because of their propensity to identify with them, Filippi and colleagues[120] hypothesized that they could also show brain responses to animals behaviors performed by humans, monkeys, and pigs, different from omnivores. To prove this the authors showed participants oral communicative actions (OCA) vs biting. Results showed an increased functional connectivity between regions of the fronto-parietal and temporal lobes during observation of mouth actions performed by humans and, to the same degree, animals, in people with more animal-oriented empathy.

During human scenes they showed an increased activity of the right amygdala, which contributes to the analysis of body movements for perception of actions through its connections with the Superior Temporal Sulcus (STS) and the frontal cortex,[121] thus assigning emotional salience to sensory inputs. Therefore, its increased activity suggests a different analysis of dispositions and intentions of other people in these individuals. Besides these shared network activation, vegetarians and vegans also showed specific pattern of brain response: vegetarians showed an increased recruitment of the right medial frontal gyrus (MFG) and right posterior insula, which contributes to social perception, to social cognitive processes (such as inferences about others[122]), and to interoception, perception and emotion,[123] respectively. Interestingly, the insula also modulates connections between the MNS and the limbic system during social mirroring, and the ability to empathize with others.[124]

Vegans, on the other hand, recruited the left MFG, Inferior Frontal Gyrus (IFG; pars opercularis) and MTG (posterior portion), which are part of the MNS. Such a system includes Broca's area, which is involved in language processing in humans. These results indicate the presence of different portions of empathy-related networks in people with special attitudes towards animals, which contribute to the modulation of social interactions with other individuals.

Nevertheless, despite their particular pattern of brain activation while processing animal mouth actions, the activity of this system remains higher also for conspecifics. Also, phylogenetical proximity with humans can modulate MNS recruitment in these subjects, as suggested by the between-group differences observed for monkey, but not pig OCAs.

Discussion and conclusion

Starting from a systematic review of human studies it was possible to describe empathy as a multifaceted and multilayered phenomenon which ranges from relatively simple processes such as behavioural or physiological emotional tuning, to more complex events which involve interaction between emotional and cognitive perspective taking systems.[125] In any case, a basic resonance mechanism is thought to underlie the emotional empathic response and includes (1) the capacity to know what the other person is feeling, (2) to mimic corresponding emotional behavior, together with (3) the intention to respond compassionately to another person's distress.[126] These phenomena can occur automatically and without awareness.[127] These three main points will be discussed with respect to both intra-human and intra-animal interactions.

With respect to the first point, consistent evidence suggests a close relationship between trait empathy and the degree of subjective responsiveness to facial cues, with higher empathic subjects producing more accurate responses to emotional faces.[128] Moreover, consistent with the second point, viewing another's emotional expression automatically triggers that emotion in oneself, and elicits facial muscle reactions especially for high empathic subjects,[129] together with increased autonomic responsiveness.[130] Thus, autonomic measures could be interpreted as a mechanism for mirroring and understanding the emotional condition displayed by other people, while sharing similar emotional and somatic responses.[131] Finally, it has been found that the decision to engage in prosocial behaviors is associated with measures of behavioral trait empathy assessed through questionnaires.

Since animals cannot furnish verbal responses, more indirect ways to measure empathic attitudes should be found: being part of a more general process of emotional contagion, a number of researchers have proposed that humans and some other species show a specific phenomenon of affective tuning, contagious yawning. This is a useful candidate behaviour to explore basic forms of empathy across species in that it is present in both humans and non-human animals. It is more frequent in high empathic subjects and it is related to empathy-related brain areas. Thus, although it is not an emotional reaction itself, its occurrence has been clinically, psychologically, neurobiologically, and behaviorally linked to our capacity for empathy;[132] also, it is thought to represent the commonest, developmentally earliest, and phylogenetically oldest process by which emotional empathy can arise.[133] Because of its relevance to evolutionary biology CY has been the focus of recent investigations in non-human species which have demonstrated that chimpanzees,[134] bonobos,[135] gelada baboons,[136] wolves[137] and domestic dogs,[138] yawn in relation to a conspecific yawning.

Besides CY, which reflects automatic and involuntary behaviors elicited by affective resonance and tuning mechanisms, further evidence of voluntary prosocial acts has been provided that many species are sensitive to suffering in others. The extent to which animals are affected by the distress or pain of conspecifics probably depends on the ethological characteristics and the socializing attitudes of the species. Prosocial attitudes have been proved to be present in primates,[139] rats,[140] mice[141] and elephants,[142] while no CY has been demonstrated in solitary species.[143] When we inquire into the presence of empathic competencies in animals, distinctions between species must be taken into account. Consolation behaviors, coalition formation, offering of protection and comfort are only some of the available examples in the literature on animal-animal empathy.

Interestingly, empathy is more likely to occur when there is perceived social proximity between individuals. This is also applicable to animal-human interaction, in that the available literature on the theme shows that dogs-human bonds are particularly strong since they rely on the domestication process. Evidence proves that dogs show comfort-offering in the presence of people crying, which strongly suggests sympathetic concern. Moreover it has been found that dogs[144] and primates[145] can catch a human's yawn.

Finally, and once again, evidence suggests that, because of the similarity hypothesis, human feelings of empathy also tend to generalize easily towards animals perceived to be similar, such as other mammals, but starts to decline in response to non-mammals. Although the majority of available human studies did not separate empathy towards humans from that towards animals when we consider human empathic attitudes towards animals we must take into account that many people have a strong emotional attachment to their pets.

Available literature showed the presence of similarities between the human-infant and the human-animal relationship, which can be interpreted as useful for the formation and maintenance of people's relationship with their pets.[146] Moreover, results indicate that there are many overlapping regions of activation in humans' brain responses while viewing animal and human suffering, particularly in areas classically associated with empathic responses.[147]

However, according to Gallese and colleagues,[148] "sharing the same body" between the observer and the observed permits a direct form of understanding by a process of simulation in the mirror neuron system. If so, what happens when we don't share the same body? With respect to cross-species interactions perceived social proximity seems to be crucial for animals expressing empathic attitudes and for humans with high animal-oriented empathy, with a series of moral and ethical implications.

To conclude, previous attempts to measure empathic responsiveness in animals have suffered from a lack of terminological agreement over precise definitions of empathy and emotional empathy. By now it is shared knowledge that empathy is a phylogenetically continuous ability, ranging across animals from more basic and automatic reactions in response to the emotions of others, up to at least basic forms of perspective-taking in primates.[149] In fact, evidence in this field suggests that empathic and sympathetic concern may even have emerged from a pre-human basis with a series of adaptive advantages.

From this perspective it seems that, according to Charles Darwin's work, the perceived differences between human and animal empathy could be more quantitative than qualitative, suggesting a common affective core which allows both categories to mirror and tune to conspecifics' feelings, where in the case of humans it can be integrated with more complex cognitive processes.

Notes

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