

Mammalian empathy: behavioural manifestations and neural basis

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Abstract | Recent research on empathy in humans and other mammals seeks to dissociate emotional and cognitive empathy. These forms, however, remain interconnected in evolution, across species and at the level of neural mechanisms. New data have facilitated the development of empathy models such as the perception–action model (PAM) and mirror-neuron theories. According to the PAM, the emotional states of others are understood through personal, embodied representations that allow empathy and accuracy to increase based on the observer's past experiences. In this Review, we discuss the latest evidence from studies carried out across a wide range of species, including studies on yawn contagion, consolation, aid-giving and contagious physiological affect, and we summarize neuroscientific data on representations related to another's state.

Empathy

Any process that emerges from the fact that observers understand others' states by activating personal, neural and mental representations of that state, including the capacity to be affected by and share the emotional state of another; assess the reasons for the other's state; and identify with the other, adopting his or her perspective.

In lay parlance as well as the scientific literature, the term empathy refers to both the sharing of emotions between individuals and the adopting of another's point of view. This capacity allows individuals to quickly relate to another's state, which is essential in species that provide extensive parental care and work cooperatively towards common goals¹. A mentalistic definition of empathy, closer to theory-of-mind, is also common, and describes how empathy allows one to access another's mind by simulating how one would feel in his or her shoes². For example, Baron-Cohen³ describes empathy as a "leap of imagination into someone else's headspace". Definitions that favour cognition over emotion, however, exclude young children and most non-human species, which, nonetheless, are affected by the emotional states of others, and provide striking care and aid as a result.

The notion that empathy is an affective fusion with another individual's state, rather than a cognitive deduction, had already been proposed in early 20th century philosophy⁴. Lipps⁵, who gave us the concept of *Einfühlung* (German for 'feeling into'), emphasized the almost involuntary nature of this response, which he regarded as possible without extensive learning, association or reasoning. It took a century, however, for the quick spontaneous nature of human affective empathy to be confirmed by empirical research. In this Review, we propose a definition that balances the emotional and cognitive sides, and use empathy as an 'umbrella' term for all processes that emerge from the fact that observers understand others' states by activating their own personal, neural and mental representations of that state^{1,6}.

This umbrella term includes obvious instances of affective resonance, such as when an observer feels contagiously distressed by the target's distress or mimics their emotions. However, such outward signs are not required, as shared neural representations do not need to produce downstream bodily responses⁷. This phenomenon exists for all states, but we focus on distress because of the preponderance of relevant data and the clear application to helping behaviour. Empathic accuracy exists on a continuum that is dependent upon the observer's attention, motivation to understand and relevant personal past experiences. Empathy can but does not always lead to helping. Conversely, helping can emerge from many routes aside from empathy and shared affect. As higher-level processes such as simulation, theory-of-mind and cognitive empathy require observers to activate their own representations of the target's state from the top down, they are included under the umbrella term empathy, even if they require additional cognitive and executive processes.

Arranging related yet distinguishable phenomena into a single concept reflects the evolutionary view according to which complex organs and capacities arise incrementally. They evolve in layers, with each new layer being built on top of and dependent on older ones without ever replacing them, as in the so-called Russian-doll model (FIG. 1). There exists a tendency to treat each aspect separately and dwell on the distinctions, but in doing so we lose sight of the functionally integrated whole. Accordingly, empathy is defined here as emotional and mental sensitivity to another's state, from being affected by and sharing in this state to assessing the reasons for it and adopting the other's point of view.

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Theory-of-mind

The ability to attribute mental states to others, such as knowledge, intentions and beliefs.

Affective empathy

Also known as emotional empathy. Empathy that is directly affected by the emotional state of another by matching or 'feeling with' it, as a result of perceiving this state.

Cognitive empathy

Empathy derived from a top-down process in which the observer imagines how the target feels, even if the target is not present or their feelings cannot be directly observed.

Empathic perspective-taking

The capacity to take another's affective perspective: for example, understanding their specific situation and needs, separate from one's own, which still requires access to personal representations of the other's state.

False-belief task

A crucial theory-of-mind task that determines whether an observer knows what another knows, even if this knowledge is incongruent with the observer's own.

Targeted helping

Assistance and care based on a cognitive appreciation of the other's specific need or circumstances.

Tinbergian framework

A series of 'why' questions that we may ask about any observed behaviour, as proposed by Niko Tinbergen. The questions concern different levels of causation: for example, why did a behaviour evolve (what are its benefits), why does the behaviour occur (what caused it) and what is the behaviour's phylogenetic origin?

Emotional contagion

Emotional state matching between a target and an observer.

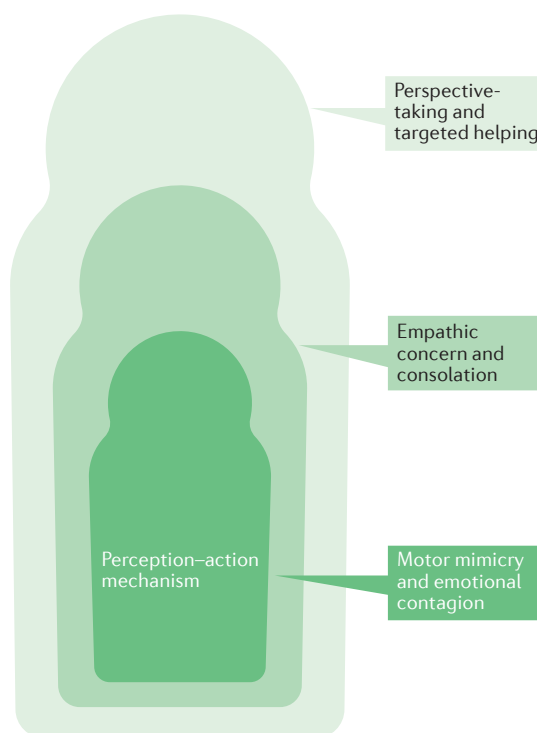


Figure 1 | The Russian-doll model of the evolution of empathy. Various components of the empathic response, which have been added layer upon layer during evolution, remain functionally integrated. At its core is the perception–action mechanism, which induces a similar emotional state in the observer as in the target. Its most basic expressions are motor mimicry and emotional contagion. The doll's outer layers, such as empathic concern and perspective-taking, build upon this core socio-affective basis while increasingly requiring emotion regulation, self–other distinction and cognition. Even though the doll's outer layers depend on prefrontal functioning, they remain fundamentally linked to the core perception–action mechanism. Adapted with permission from: de Waal, F. B. M. in *Feelings & Emotions: The Amsterdam Symposium* (eds Manstead T., Frijda, N. & Fischer A.) 379–399 (Cambridge Univ. Press, 2003).

Thus defined, empathy is common in our species, starts early in life⁸, and shows neural and physiological correlates as well as inheritability⁹. Whereas emotional responses to the emotions of others are commonplace in many species^{10,11}, the best evidence for empathic perspective-taking, which we have distinguished as cognitive empathy¹², comes from intensely social animals that have a high degree of encephalization, such as humans, apes, elephants and dolphins. Some species show signs of theory-of-mind in a false-belief task¹³, while others perform targeted helping that demonstrates an appreciation of another's specific predicament. For example, dolphins may lift an incapacitated companion to the surface so that they can breathe and chimpanzees may bring down fruits from a tree to an elderly female who has lost her climbing abilities¹⁴. Chimpanzees seem to understand the needs and desires of others because after having judged another's situation they will find the specific tool that the

other requires and hand it to them¹⁵. Similarly, capuchin monkeys vary their food-sharing with what they know about their partner's previous food consumption¹⁶. There is no a priori reason to exclude perspective-taking in smaller-brained species, and studies on rodent aid-giving are indeed suggestive of related capacities (see below). The shared vocabulary adopted here for expressions of empathy in both humans and other animals reflects the Darwinian assumption that if related species show similar responses under similar circumstances, the underlying proximate processes are probably homologous (that is, derived from a common ancestor) rather than analogous (that is, independently evolved).

The first review of this framework was presented in 2002 (REF. 1) and was based on evidence available at the time that came from across different species and levels of analysis. According to the perception–action model (PAM), individuals understand and have a sense of others' emotions because the nervous system evolved to map others' states onto their own individual representations for experiencing those states¹. As such, when an observer attends to another's state, he or she spontaneously accesses information about the other (the 'target'), their feelings, the situation and other related concepts through a distributed associative process. The fact that observers understand others using their own individual representations, which are developed through experience, explains why empathy and accuracy increase with familiarity and similarity with the other and their situation. Extensive empirical support for the PAM has accumulated since it was first presented, and thus an update is warranted. In fact, so much research has been performed since 2002 that we cannot comprehensively review it here. We focus on summarizing the most robust and central findings and debates, and often cite review articles to avoid selective citation. We place empathy within the Tinbergian framework according to which every behavioural phenomenon can be investigated from different yet complementary angles, such as 'why' these mechanisms were selected during evolution, and 'how' behavioural and neural mechanisms regulate their expression^{17,18}.

The existence of empathy outside of our own species is hardly a novel idea. Even while avoiding the term itself, early studies on altruistic behaviour often employed paradigms suggesting that the emotional contagion of pain or distress is a motivating factor. Altruism is defined as an act that benefits another individual at a cost to the self. Having trained rats to obtain food by pressing a lever, Church¹⁹ found that if the same action delivers an electric shock to a visible second rat, the first rat will temporarily cease lever-pressing, thus foregoing its rewards. Entitled "Emotional reactions of rats to the pain of others", Church's 1959 paper inspired a flurry of research, which initially assumed a conditioning explanation. Later, it turned out that such behaviour did not require prior experience with the protocol. For example, Rice and Gainer²⁰ found that rats spontaneously help distressed companions that have been hoisted off of the cage floor by lowering them back down. Monkeys tested in the same era showed even more dramatic responses, such as macaques refusing to pull a chain that delivers food

Consolation behaviour
Reassurance behaviour directed at a distressed party, such as a victim of aggression (also see the definition of 'empathic concern').

Empathic concern
Also known as sympathetic concern. Concern about another's state, and attempts to ameliorate this state (also see the definition of 'consolation behaviour').

to themselves if doing so also shocks a visible conspecific²¹. Subjects sometimes went more than a week with only minimal food to avoid shocking another monkey, and this effect was augmented by prior shock experience but did not require it²². Such sacrifices relate to the tight social linkage among macaques and the fact that these responses were more pronounced between familiar than unfamiliar individuals²².

Early research stressed the untrained, spontaneous nature of helping and its social bias in order to counter explanations that were based on conditioning and associative learning. If the avoidance of aversive stimuli (such as distress vocalizations) or the seeking of extrinsic rewards was the sole reason for altruistic behaviour, there would be no reason for a familiarity bias and effects should be similar between strangers, yet with few exceptions familiarity promotes altruism. In addition, when Miller *et al.*²³ compared macaque responses to images of fearful conspecifics versus negatively conditioned non-social stimuli,

the aversion was stronger to the former. None of these early results supported explanations based on learning and conditioning, even though these processes do have a role in empathy and altruism. The assumption of a basic empathy mechanism is in fact more parsimonious than is any learning-based explanation, which would need to be rather demanding in its range of proposed contingencies.

With regards to our closest relatives, the apes, observations of empathic responses go back to early last century. Yerkes²⁴ reported "sympathetic behaviour" by a bonobo towards a sickly companion, and Ladygina-Kohts²⁵ described similar tendencies for her juvenile chimpanzee. By the 1970s, these responses were defined as consolation behaviour and were systematically documented in naturalistic settings²⁶. The way in which apes comfort others in distress (for example, embracing, touching and kissing) (FIG. 2) is morphologically similar to how young children express so-called empathic concern for family members who have been instructed to feign pain or discomfort^{8,27}.






		Behaviour	Definition	Mechanisms	Non-human species
a		Mirroring	Rapid face matching and movement mapping	Motor mimicry	<ul style="list-style-type: none">• Chimpanzees• Orangutans• Gelada baboons• Macaques
b		Yawn contagion	Yawning in response to another's yawns	Motor mimicry	<ul style="list-style-type: none">• Chimpanzees• Macaques• Canines• Budgerigars
c		State matching	Sharing the emotional state of another	Emotional contagion	<ul style="list-style-type: none">• Mice• Voles• Chickens
d		Consolation	Comforting a distressed party	Empathic concern that is based on emotional contagion and requires self-regulation	<ul style="list-style-type: none">• Chimpanzees• Bonobos• Macaques• Canines• Elephants• Voles• Mice• Rooks
e		Learned helping	Liberating another or relieving its pain	Aiding that is motivated by emotional contagion, and requires self-regulation and trial-and-error learning	<ul style="list-style-type: none">• Macaques• Rats
f		Targeted helping	Help adapted to the specific need or situation of another	Aiding that is motivated by emotional contagion, and requires self-regulation and perspective-taking	<ul style="list-style-type: none">• Apes• Capuchin monkeys• Dolphins• Elephants

Figure 2 | Behavioural manifestations of animal empathy. The table summarizes behavioural patterns that are considered to be expressions of empathy in non-human vertebrates, ranging from motor mirroring and yawn contagion to targeted helping. Most of these behaviours have been characterized by experimental research, whereas others have been documented observationally (see the references cited in the main text). The mechanisms and the non-human species in which these behaviours have been observed are shown. From top to bottom, the images show the following: two gelada baboon juveniles with playfaces (that is, they are showing rapid facial mimicry) (part **a**); a yawning wolf (part **b**); prairie vole

mates matching each other's physiological stress level (part **c**); a juvenile bonobo wrapping her arms around another who has just lost a fight to provide consolation (part **d**); a rat that has learned to liberate another rat that was trapped in a container (part **e**); and an adult chimpanzee showing targeted helping by assisting a juvenile's descent from a tree (part **f**). The images in parts **a–f** are courtesy of Pier Francesco Ferrari, University of Parma, Italy; Teresa Romero, University of Lincoln, UK; Zack Johnson, Georgia Institute of Technology, USA; Zanna Clay, Durham University, UK; and Inbal Ben-Ami Bartal, University of California, Berkeley, USA.

Even infants younger than 1 year old exhibit significant attention and concern for a peer in distress^{28,29}, which contrasts with long-held stereotypes that human infants do little more than cry contagiously when others cry.

Behavioural manifestations

Behavioural studies of empathy in mammals and other animals follow one of three approaches. The first focuses on motor mimicry, which is one of many behaviours that reveal an underlying perception–action mechanism (as described in the PAM). The second approach measures resonating physiological and behavioural responses to the emotions of others, such as pain contagion. The third is to focus on altruistic behaviour, such as consolation behaviour and the helping of others in need, which are often motivated by shared affect between an observer and a target along with an evaluation of the target's situation. All three areas have seen recent progress, as summarized in FIG. 2.

Motor mirroring. Motor mimicry is a natural consequence of a neural system that maps another individual's bodily and facial expressions onto the observer's own representations for action. This perception–action mechanism permits the adaptive synchronization of states between targets and observers, such as in the rapid facial mimicry described in humans³⁰ and other primates^{31,32}. Supporting a possible causal link with empathy, humans who report being more emotionally empathic in daily life are the most accurate mimics of others' facial expressions³³. A typical example of motor mimicry is yawn contagion, which can be studied with experimental protocols in which subjects watch videos of yawning conspecifics or through naturalistic observations of the spreading of yawns across a group. Yawn contagion has been found in species as diverse as humans, non-human primates, canines and birds^{34–37}. As with empathy more broadly, yawn contagion is biased towards socially close others, which cannot be explained by attention as controlled studies report either similar or greater attention to unfamiliar yawn stimuli^{34,38}.

Even though monkeys are sometimes said to lack true imitation³⁹, they do mimic human facial and hand gestures⁴⁰, and they socially prefer partners who mimic them⁴¹. In the wild, monkeys copy one another's feeding techniques, resulting in 'cultural' behavioural variation⁴². In the laboratory, monkeys replicate the motor actions of a group member in, for example, the way in which they open a box⁴³. Anthropoid apes show additional capacities in that they imitate with an understanding of cause and effect⁴⁴. However, even in apes, motor mimicry and shared representations probably provide the foundation for such behaviour: for example, when an observing ape spontaneously synchronizes his movements with those of a conspecific model demonstrating tool use⁴⁵. Studies of ape imitation indicate that it is not merely about emulating a beneficial outcome because 'ghost' demonstrations of the correct outcome without an actual conspecific demonstrating the required actions are ignored. For imitation to occur, apes need to see a conspecific perform the action sequence⁴⁶, which suggests the crucial role of bodily identification and motor mimicry.

Emotional contagion. Following the tradition of Church and Miller from the mid-20th century, researchers have recently confirmed the existence of contagious affect in rodents. For example, the pain of one rodent may increase the pain response of an observing conspecific, and this effect is highly influenced by familiarity with the suffering target^{47,48}. Moreover, this effect is blocked by the presence of strangers, who induce a glucocorticoid stress response that suppresses the natural motivating contagion of distress in rodents and humans⁴⁹. Contagious emotional responses are at least partially conveyed by the transfer of negative physiological states between the target and the observer. For example, both prairie voles⁵⁰ and humans⁵¹ match the hormonal stress response of a stressed target. In humans, this effect correlates with self-reported empathic concern and perspective-taking in daily life⁵¹.

Contagious anxiety in observers probably follows an inverted-U-shaped function, with moderate activation facilitating a response but high activation inhibiting it⁵². Emotion self-regulation may be key to keeping the activation at a moderate level. Thus, a bonobo's ability to overcome its own distress correlates with the frequency with which it offers consolation to others who are in distress⁵³. As emotion self-regulation is compromised in bonobos that are orphaned early in life⁵³ — as also reported for human orphans⁵⁴ — fully developed empathy may require an affectionate upbringing.

Altruistic helping. It has been claimed that humans are the only truly altruistic species, and that other animals are self-interested and only care about return benefits (for examples, see REFS 55,56). This view erroneously conflates evolution and motivation. Although the evolution of altruism is indeed explained by kin selection and reciprocal altruism — both of which emphasize the eventual return benefits from helping — this explanation does not consider the role of motivation. Animals do not know about genetic benefits such as inclusive fitness. There is also not much evidence indicating that they anticipate future return favours from their acts, as in reciprocal altruism. One cannot be motivated by what one does not know. There is no conflict, therefore, between the assumption that altruistic behaviour evolved for self-serving reasons and the suggestion that it reflects a spontaneous motivational impulse that originates — at least in humans and other mammals — from empathy with the recipient's need, pain or distress⁶. Tinbergen¹⁸ encouraged researchers to separate why a behaviour evolved (the ultimate reason for its existence) from how it is instantiated in the individual (its proximate causation). Theories regarding these issues are different yet compatible as they occupy separate levels of analysis.

The view that humans are uniquely altruistic is also inconsistent with the increasing amount of evidence indicating that even rodents are affected by the pain of familiar conspecifics and offer help. For example, monogamous voles show a contagious stress response to familiar partners, and this is mediated by stress and anxiety induced in the observer; they also groom stressed partners, and this seems to have a calming effect as it reduces anxiety-related behaviour⁵⁰. Rats learn by

Perception–action mechanism

Spontaneous activation of an individual's own personal representations for a target, their state and their situation when perceiving the target's state.

Emotion self-regulation

Control over one's own emotions to promote adaptive responding, including response delay, recovery from upsets and selective attention.

trial-and-error how to free a trapped conspecific by opening a door^{57,58}, and this is again mediated by shared anxiety but impeded by excessive stress in the observer⁵⁷.

The transfer of negative affect from a target to an observer is also thought to motivate another important prosocial behaviour in primates: consolation. Defined as comforting body contact aimed at distressed others, consolation was first described in the great apes^{26,53,59,60}, but has since also been found in some macaque species⁶¹, canines⁶², elephants⁶³, rodents⁵⁰ and corvids⁶⁴. In primates, responses such as placing an arm around another or grooming a victim of aggression have been shown to reduce behavioural indicators of anxiety, such as self-scratching and self-grooming^{60,65}, while also reducing heart rate⁶⁶.

In line with the PAM¹, these studies support the crucial role of caught distress and arousal in prosocial behaviour, which nonetheless must be kept within limits to facilitate a prosocial response. The same mechanism probably underlies rescue attempts by rodents, dogs, elephants, primates and humans, given that all of these species possess mammalian brains that have highly conserved characteristics. Although many acts that are defined by biologists as altruistic (for example, alarm calls and defence of the hive) do not require emotional empathy, there is a category of directed altruism in mammals that does seem to depend on an affective sensitivity to another's state and situation^{6,14}.

There is little support for the main alternative hypothesis, which is that helping behaviour is driven by tangible rewards. For example, rats prefer to release a trapped cage mate over accessing attractive food for themselves^{57,58,67}. They share any available rewards after the rescue and perform helping responses even if a subsequent reunion with the target (which could be rewarding) is blocked⁵⁷. Both human children and chimpanzees spontaneously assist a human experimenter, but children given an extrinsic reward for helping actually help less than do those who are merely praised or not rewarded at all^{68,69}. Thus, aid can be given in direct response to another's need or distress in a manner that is independent of extrinsic rewards.

Taken together, altruistic and consoling responses seem to arise from the transfer of emotion from the target to the observer, which in turn motivates the observer to approach and console the target, thus reducing the negative state of both parties (FIG. 3). The central role of affect transfer in helping behaviour was demonstrated in rats in the above helping paradigm, in an experiment that showed that the administration of the anxiolytic midazolam reduced rats' helping responses without impairing the instrumental act required to obtain food⁶⁷. Affect transfer provides a built-in reward to helping because it gives the observer a stake in another's well-being, producing both shared pain and vicarious relief or joy when the pain is ameliorated; this is accompanied by the "warm glow" that humans feel after doing a good deed⁷⁰ or the vicarious rewards that monkeys seem to gain from prosocial behaviour^{6,71,72}.

Blurring the line between the self and the other at the proximate level undermines the usefulness of a dichotomy between selfish and altruistic motives^{6,73}. As expressed by Hoffman⁷⁴, "empathy may be uniquely well suited for bridging the gap between egoism and altruism,

since it has the property of transforming another person's misfortune into one's own feeling of distress". This is the beauty of the empathy mechanism and makes its operation similar to most activities that are required for mammalian survival (for example, eating, breeding and nursing), which are all inherently rewarding. If the same intrinsic rewards apply to helping behaviour, this is no reason to denigrate the response or to refuse to call it 'altruistic'. Evolutionary biology already assumes that altruistic tendencies yield long-term net benefits.

Altruistic behaviour is far from limited to mammals, yet it remains unclear whether the same mechanism underlies helping in non-mammals. This is quite possible in other vertebrates (see below), but it is less likely that homologous, neural perception-action mechanisms underpin the well-documented altruism of invertebrates such as social insects. Through convergent evolution, genetically distant species often arrive at functionally similar, analogous behaviours while using different mechanisms. However, even if the sophisticated rescue of trapped conspecifics by ants is not based on emotional or cognitive empathy^{75,76}, it has been suggested that contagious ant alarm and digging is induced in nearby conspecifics by the release of a volatile chemical from the mandible of a trapped ant⁷⁷. If true, the mechanism in ants may not be as different from the PAM as one might think, as their helping response is still triggered by the transfer of a physiological state from target to observer, and thus represents a pheromonal analogy to the perception-action mechanism of mammals.

The evolution of empathy. Offspring care most likely strengthened the evolution of empathy because of the selection pressure to develop a rapid, motivating emotional connection between helpless neonates and their caregivers^{8,12,78}. Signalling their state through smiling and

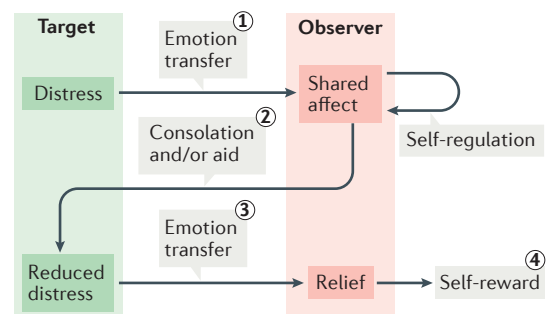


Figure 3 | From affect transfer to altruism. As shown in multiple animal studies, empathy may promote aid-giving behaviour between conspecifics^{8,57,58}. First, the target's distress induces stress or distress in the observer through emotional transfer (step 1). The observer needs to downregulate its own distress in order to effectively attend to the target, such as through helping or consolation (step 2). The resulting reduction of the target's distress as a result of being helped is then transferred back to the observer, ameliorating the observer's caught distress (step 3); this reduction constitutes an intrinsic reward for performed altruism (step 4).

Directed altruism
Helping or comforting behaviour directed at an individual in need, pain or distress.

Convergent evolution
A process in which unrelated species independently evolve similar traits or capacities in response to similar environmental pressures.

Ideomotor action

An action that is covertly mimicked when another's action or movement of an object is being observed, such as moving your arm when you watch someone bowl or tilting your head in synchrony with a pendulum swing.

Motor imitation

Re-enactment by the observer of a target's motor movements or facial expressions.

Affordances

Motor or action properties of objects that are activated by their percepts, which are intrinsic to the mental representation of the object.

Simon effect

A behavioural effect in which motor actions are facilitated when they are consistent with the spatial location of the stimulus, and slowed when they are inconsistent or opposing the location.

crying, human infants prompt caregivers into action. Equivalent signals operate in other animals in which reproduction requires feeding, cleaning and warming of the young. Parents that paid close attention to the emotional signals from their offspring probably out-reproduced the indifferent ones, and this selective advantage applies at least to mammals and birds. The signals of the young are not just responded to but induce an agitated state in observers, suggesting that parents become distressed at the perception of offspring distress⁷⁹. Transferred negative affect provides a natural motivation to act^{1,12}. In addition, neuropeptide systems that subserve offspring care are homologous across mammals and facilitate altruism in humans (for a review, see REF. 78). Given this origin, the capacity to be motivated to help distressed and vulnerable targets should occur in a wide variety of vertebrates that show social attachment and parental care, including rodents⁸⁰, birds⁸¹ and possibly reptiles⁸². Given the highly conserved nature of neuropeptide systems, an even older origin of empathy could be envisioned, particularly in species that show social attachments⁸³.

Once the neural underpinnings of an empathic 'offspring care system' existed, they could serve outside of the rearing context and have a role in the wider social fabric. They could be activated by the perception of a distressed adult conspecific, such as in rodent consolation behaviour⁵⁰. For every species, the reach of empathy varies with its social organization, creating differences across solitary, pair-bonded, cooperatively hunting or group-living animals, not because the empathy mechanism works differently, but because species and their ecology place different

demands on it (for an example, see REF. 84). The fact that mammals retain distress vocalizations into adulthood hints at the continued survival value of care-inducing signals, such as those that prompt primates to carefully lick and clean the wounds of unrelated conspecifics⁸⁵.

Despite the fact that the spread of emotion from one individual to another occurs spontaneously, empathy is still subject to appraisals, filters and inhibitions⁸⁶ that prevent it from being expressed when it would be maladaptive. For example, chimpanzees are capable of brutally killing each other^{87,88}, as are humans. Social species must be able to suppress their empathic response to another's pain when, for example, it is better for the observer to flee, keep a safe distance or confront a potential adversary. Conflicting individual goals will prevent the activation of shared representations from proceeding to compassion, concern or altruistic action, but they are still needed to at least initially decode the target's state. Conversely, in humans and other species, the empathic response is increased by similarity, familiarity and social closeness (for examples, see REFS 1,47,89), and this is consistent with where evolutionary theory expects it to occur: that is, in close interdependent social relationships that involve either genetic relatedness or reciprocation. Thus, the empathy mechanism is biased in precisely the way that is predicted by the current evolutionary models of cooperation⁶.

Neural basis

The PAM¹ offers a proximate explanation for how we can 'feel into' others' states. The PAM derives from a perception–action theory of motor behaviour that reveals overlapping representations for performing and observing actions, as exemplified in phenomena such as ideomotor action, motor imitation, affordances and the Simon effect⁹⁰. Applied to emotional phenomena, attending to another's distress is assumed to activate observers' own distributed representations for the target and their state and situation — including related feelings, memories and associations — in a connectionist manner.

A few key early studies offered the first notable neuroscientific evidence for the PAM. First, mirror neurons were recorded in macaque monkeys that responded similarly to performed and observed actions, and these recordings provided cellular-level evidence for perception–action coding in the brain⁹¹ (BOX 1). Extending this to humans, a subsequent imaging study found premotor activity in the brains of participants who simply observed pictures of tools (for example, hammers) or silently named the use of the tool in their mind⁹². Finally, emotional evidence for using personal representations to perceive another's affect came from a brain-lesion study in which patients were most impaired at decoding another's facial expressions of emotion when they had somatosensory damage⁹³. Since these results were summarized in the original theoretical review paper¹, many studies have further tested this view through a variety of methods, including positron emission tomography, functional neuroimaging (functional MRI (fMRI)), psychophysiology, electromyography, transcranial magnetic stimulation and electroencephalography (for reviews, see REFS 94–96).

Box 1 | Mirror neurons as part of the 'bigger picture'

The extension of mirror neurons to social-cognitive phenomena^{135,136} has received both attention and criticism. Mirror cells cannot fully explain empathy, but their relevance should not be dismissed. Mirror neurons per se only represent a small subset of monkey F5 inferior premotor cells⁹¹ and, thus, must be part of a larger coding scheme. Yet, even these single cells represent motor plans and goals, which are bidirectionally connected to the resulting sensations⁹⁰, allowing primates to infer goals from simple observed acts. Extended to emotional phenomena, observing an affective posture or expression can feed back from peripheral motor representations to activate associated emotional states. After the discovery of mirror neurons in macaques⁹¹, their existence was confirmed in human patients¹³⁷. Given that mirror cells were found in humans outside of traditional 'mirror regions', mirroring may be a generalized neural coding strategy. In addition, some human cells are activated during execution but are inhibited during observation, which may assist in self–other distinction¹³⁸.

Brain areas that constitute the wider 'mirror system' — namely, the inferior frontal gyrus (IFG; also known as Brodmann area 44) and rostral posterior parietal cortex (rPPC) — clearly participate in the imitation of motor acts, expressions and empathy. These human mirror regions are homologous with the macaque mirror regions F5, and PF and PFG (which are subdivisions of the rostral inferior parietal lobule). These human regions are also interconnected with the insula and show activation in functional MRI (fMRI) studies of empathy and imitation^{136,139}. The role of the IFG is supported by a meta-analysis that found consistent activation of the IFG and adjacent anterior insula during empathic pain¹¹⁸. The ventromedial prefrontal cortex can integrate such affective signals to guide emotional decisions¹³⁴. Both mirror theories and the perception–action model (PAM) presume that motor acts and affective states can transfer from a target to an observer in a bottom-up, goal-relevant manner through shared representations for perception and action. However, the PAM explains a wider range of phenomena and empathic biases through its focus on distributed, person-specific representations that are formed through experience⁷.

Bottom-up

Describes a neural and mental process that is stimulus-driven on the basis of directly observed information without requiring explicit cognitive processes or capacities. Empathy arises from bottom-up processes that are shared across species such as motor mimicry, emotional contagion and state matching.

Research has confirmed the existence of overlapping neural signatures for experiencing and observing affective states, including happiness, anger, fear, disgust, sadness^{97–99} and — most often — pain (for a review, see REF. 100). The data are largely consistent, logical and supportive of the PAM. However, there is controversy in the field that originates from divergent views of what ‘overlap’ between representations means (for example, it might be mistaken for signatures that are ‘identical’ or ‘without distinct properties’). In addition, controversy persists regarding the role of mirror neurons or mirror systems in empathy. Mirror theories are similar to the PAM in that both rely on shared representations for perception and action. However, the PAM focuses more on distributed representations that include relevant feelings, memories and associations that are related to the target, and to the target’s state and situation. Even if mirror theories are sometimes maligned because of popularized media accounts about them, they should not be dismissed, but rather understood in conjunction with information about neural coding strategies and the function of the inferior frontal gyrus (IFG) in the perception and production of language, gesture,

expression and empathy (BOX 1). There are more studies in this rich field than can be described here, but we summarize the main findings and controversies below, focusing on the implications for the PAM.

Levels of empathy in the brain. Even though the PAM emphasizes the spontaneous activation of the observer’s representations for the target’s state⁷, it is not limited to reflexive processes such as mimicry and emotional contagion, but also addresses complex forms of empathy, including the effects of attention, regulation, experience and culture. Perception–action processes are indeed more noticeable during contagion and mimicry. However, the PAM is a proximate-level theory that presumes a shared, distributed, neural representation for the self and other that is engaged whenever the state of another individual is decoded, even if the shared property is not always obvious to or felt by the observer.

If observers attend to another’s state, this produces empathy and accuracy in a highly graded fashion that increases with personal and contextual factors, and can be inhibited in many different ways (for example, avoiding attention, focusing on the response and motor inhibition at multiple levels of the system). As representations are person-specific and developed through experience, they are fundamentally sensitive to the observer’s unique history, which explains why empathy and accuracy increase with the relevance of the target’s state to the observer’s own past experiences, and to their similarity and familiarity; these effects occur across species (as discussed above). As a result of this graded quality, one cannot make binary statements about experiences that are ‘the same’ or ‘different’, or in which empathy or accuracy either does or does not exist^{7,101}.

Observers must process the target’s state using whatever relevant representations they possess — at least initially — as part of the process of basic information decoding. Degrees of ‘understanding’ that result from this process range from a rudimentary sense that the other feels ‘bad’ to a highly tailored, accurate understanding of that specific state and its entailments^{98,102}. There is also information about the target in the observer’s activated representation, which makes it possible for the observer to understand dissimilar others on the basis of specific knowledge about them. Finally, shared representations do not always lead to felt resonance, compassion or help, particularly when the observer’s goals conflict with those of the target; this explains the importance of interdependence for prosocial outcomes.

Whereas neuroscience has shown that there are distinct brain correlates for emotional and cognitive empathy (for examples, see REFS 103–106), and clinicians observe distinct emotional or cognitive empathy impairments in clinical disorders^{107,108}, these distinctions do not undermine the shared-representations model. It is sometimes useful to bifurcate empathy into affective and cognitive components, but this does not deny shared processes. Shared processing is required for both bottom-up and top-down forms of empathy because it is the distributed affective representation that imbues the percept with content and meaning, and this is needed for all forms of empathy (FIG. 4).

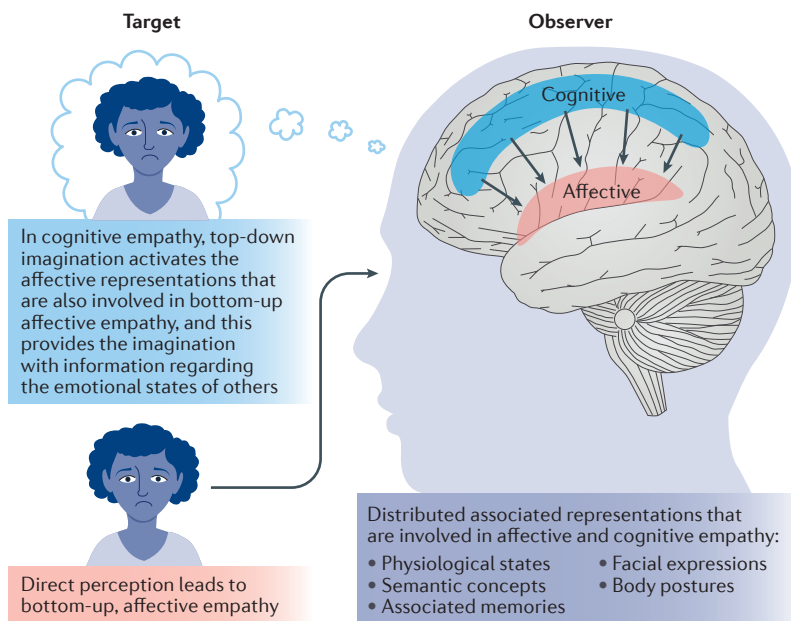


Figure 4 | Both cognitive and affective empathy access distributed, person-specific affective representations. Bottom-up, affective empathy (red box) occurs when an observer directly perceives the emotional state (such as a sad facial expression) of the target. This naturally activates distributed, personal representations of the target’s state in the observer (purple box). These representations have developed over time with experience in the observer’s life and include associated memories, semantic concepts, and bodily states and expressions. When empathy proceeds in a top-down, cognitive manner (blue box), the neural regions that support working memory, executive function, emotion regulation and visuospatial processes instead access the affective empathy representations from the top-down (indicated by the arrows). Thus, although the stimulation emerges from inside the mind rather than from the outside world, the affective regions and the associated representations are shared between cognitive and affective processes. Thus, subtractions of affective from cognitive forms of empathy reveal greater brain activity in the blue regions than in the red regions. However, the cognitive process must still access the affective regions and their shared associated representations (purple) to provide the imagination or simulation with content and meaning.

Top-down

Describes a neural and mental process that requires a conscious, cognitive evaluation to take into account information that is not directly observable, such as taking another's perspective or reasoning about their state on the basis of conceptual knowledge. These processes participate in more advanced forms of empathy that are more sophisticated in humans and with age, but they are not required to simply understand how someone feels.

This initial decoding phase of processing is mostly brief and not subjectively experienced, except in rare cases of sustained resonance. Moreover, their shared properties cannot be demonstrated using procedures designed to emphasize differences, such as the fMRI subtraction method or even multi-voxel pattern analysis. By analogy, our concept of a chair includes the affordance of sitting in a chair, which can be associated with motor activity when viewing chairs. However, it does not follow from this that our neural correlates for viewing chairs and tree stumps are indistinguishable, or that either will always be accompanied by subjectively felt pressure on our backsides.

When human subjects are presented with different tasks, concepts, instructions or stimuli, we obviously expect differences in brain activity. For example, emotional empathy tasks engage brain regions that are associated with affective and motor-motivational processes to a greater extent (for example, the insula, anterior cingulate cortex (ACC), thalamus, amygdala, fusiform gyrus, somatosensory and motor cortices, and ventromedial prefrontal cortex (VMPFC)). Cognitive empathy and perspective-taking tasks engage executive, working memory and visuospatial processes to a greater extent (for example, the dorsolateral PFC (DLPFC), dorsomedial PFC (DMPFC), superior temporal gyrus (STG), temporoparietal junction (TPJ), superior parietal lobule (SPL) and inferior parietal lobule (IPL)) (FIG. 5). In addition, the frontal activity observed

during theory-of-mind tasks is more medial when the task is more affective (for example, involving the orbito-frontal cortex and/or VMPFC) and more lateral when it is more cognitive (involving the DLPFC) (for examples, see REFS 103–106). ‘Mentalizing’ per se — that is, thinking about what the other thinks or believes, or taking their perspective — is particularly associated with activation of the STG and TPJ^{106,109,110}. The amygdala is not always implicated in empathy because it habituates quickly to repeated stimuli, but it is engaged by tasks that involve salient states such as fear and distress, or learning associations between these states and outcomes^{111–113}.

However, just because neural regions are engaged to different extents, or are engaged more reliably in one task than in another, does not mean that they are completely ‘separate’ and do not share properties. Researchers need to focus on the inherent relationship between the task, instructions and analysis strategy and their resulting neural correlates. Even if we argue against oversimplified claims about neural distinctiveness or overlap, it is true that we need to study the precise way in which representations overlap versus the precise way in which they are distinct, particularly at the scale of neurons and their distributed interconnections.

Empathic pain. Owing to its ease of study, physical pain is the most common context for testing shared representations between the self and the other. Typically,

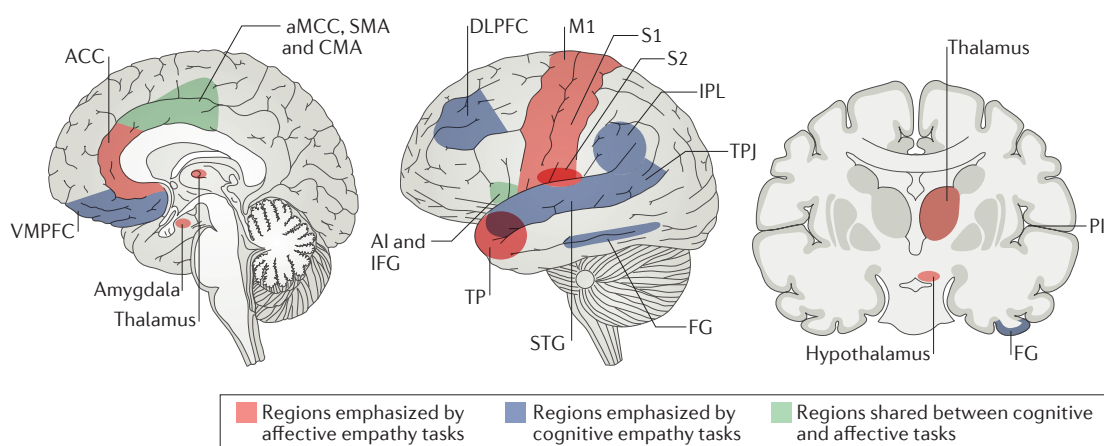


Figure 5 | Neural regions that participate in human empathy. The figure shows a medial sagittal view (far left), a left lateral side view (centre) and a coronal view (far right) of the human brain, and indicates the relative locations and roles of brain areas that are involved in human empathy. Affective representations are required to imagine how another person feels. Depending on the task, however, the observed neural activity will emphasize bottom-up, affective brain areas or top-down, cognitive ones. Regions that are more associated with affective empathy tasks — such as direct perception of the emotion or pain of another person — are shown in red: the anterior cingulate cortex (ACC) including perigenual and subgenual regions of the ACC, amygdala, thalamus, hypothalamus, primary motor cortex (M1), premotor cortex, the primary and secondary somatosensory cortices (S1 and S2), and the temporal pole (TP). Brain regions that are more associated with higher-level, top-down forms of empathy — such as imagining how you would feel in the place of another or taking their perspective — are shown in blue: the dorsolateral prefrontal cortex (DLPFC), inferior parietal lobule (IPL), temporoparietal junction (TPJ), superior temporal gyrus (STG) and fusiform gyrus (FG). Two regions that are commonly activated in both affective and cognitive tasks are shown in green: the anterior insula (AI) and the anterior middle cingulate cortex (aMCC), which extends dorsally into the supplementary motor area (SMA) and cingulate motor area (CMA). Neural locations are approximated so that the regions can be viewed in just three images (for example, the FG is normally too medial to be seen in the lateral image, the amygdala is shown in the medial view as emerging from behind the visible midline slice in right temporal cortex, and differences in laterality by region and task are not represented). IFG, inferior frontal gyrus; PI, posterior insula; VMPFC, ventromedial PFC.

participants view images of injury to another (for example, a hand closed in a door or cut with a knife) or symbols that are associated with the application of a noxious stimulus to another (for example, an electrical shock or a hand submerged in ice-cold water). In other phases of the experiment, the same participants receive a noxious stimulus to their own body. Neural activity is operationalized as ‘empathic pain’ when the same brain region is activated during pain to the self and pain to the other. Data from these studies strongly support the PAM in that pain representations are shared but not identical, and are widely distributed and highly specific to the state, task and the observer’s prior experiences. Almost all studies find that both experiencing pain (‘self pain’) and perceiving another’s pain (‘other pain’ or ‘empathic pain’) activate the anterior insula and cingulate cortex (from the posterior ACC (pACC) to the anterior middle cingulate cortex (aMCC))^{114–117}. A meta-analysis has confirmed early empirical reports, and found that viewing either pain or symbols of pain to the other consistently activate the bilateral anterior insula (merging into the IFG), and the pACC or aMCC¹¹⁸.

There is also pharmacological evidence that one’s own pain influences how one processes the pain of others. Acetaminophen decreases self pain and empathic pain for physical and social forms of distress¹¹⁹. Analgesia reduces self pain and empathic pain, and this is accompanied by reduced pain ratings and alterations in the pain related P2 type event-related potential¹²⁰. Even placebo analgesia reduces empathic pain and associated activity in the anterior insula and aMCC, and this effect can be blocked by the opioid antagonist naltrexone¹²¹. Moreover, demonstrating that pain

effects are influenced by personal experience, patients with congenital insensitivity to pain (CIP) — who do not experience peripheral pain — are also impaired at detecting others’ pain and can feel indifferent to it, although their performance can be improved by trait concern for others¹²² (BOX 2).

The precise meaning of the ‘empathic pain’ network is debated (see REFS 118, 123–126). Generally, researchers assume that the anterior insula and aMCC do not represent the sensation of physical pain, such as the feeling of a prick on your arm or a burn on your fingertip. Instead, these regions are thought to encode something about the salient, aversive or arousing properties that pain shares with other experiences. Even the earliest reports of empathic pain suggested that it represents affective rather than sensory components¹¹⁴. Similarly, a recent meta-analysis found that the bilateral anterior insula and the dorsal ACC (dACC)–aMCC–supplementary motor area (SMA) were reliably activated during empathy for pain and for basic emotions¹²⁵. Moreover, self and other experiences activate the left anterior insula and aMCC for three distinct negative experiences (pain, disgust and economic unfairness)¹²⁶. In addition, patients with CIP still show anterior insula and aMCC activity when observing others’ pain, which suggests that the activation does not derive from peripheral sensations¹²⁷ (BOX 2).

Of course, introspection alone is sufficient to tell us that empathic pain does not usually make people feel the precise peripheral sensation that they witness being experienced by another. People do not look at their own hand when they see someone touch a hot stove or say “Ouch!”. They are more likely to feel an aversive sickening feeling in their stomach and wrinkle their nose in disgust while turning away and exclaiming “Ooh!” or “Ugh!”. Their experiences differ from those of the other. As such, they must also differ at the level of the brain while sharing affective properties as well.

Although the representations in the anterior insula are unlikely to be specific or exclusive to felt pain (at least in this anterior region), they probably represent feeling states that are more like the internal ‘gut’ feelings that are experienced in a wide variety of intense states, including disgust, pain, dread, anxiety, stomach aches and even desire. The anterior insula is known to represent interoceptive states across species¹²⁸, and patients with CIP who have spared anterior insula activation in response to empathic pain do experience internal sensations such as headaches and stomach aches¹²⁷. The aMCC is assumed to respond to any unexpected outcome that requires a fast or reissued response, including pain, non-pain negative states, cognitive-motor errors and even unexpected rewards (see REFS 71, 129–131). This motor-motivational view of the aMCC is consistent with other proposals^{71, 125, 131} and with the caregiving model of altruism⁷⁸. These interpretations are consistent with the core principle of the PAM that the brain integrates sensation and action more than linguistic and disciplinary categories tend to.

Even if the anterior insula and aMCC are not specific to felt pain, one should not conversely infer that empathy ‘never’ includes bodily sensations or peripheral

Box 2 | The mysterious case of empathic pain in patients who do not feel any

Functional MRI (fMRI) has shown that the anterior insula and anterior middle cingulate cortex (aMCC) are activated in patients with congenital insensitivity to pain (CIP) during empathic pain^{122, 127}. Does this mean that empathy does not require a similar experience or access to personal representations of pain? The data tell a different story.

Patients with CIP are actually impaired at perceiving others’ pain and empathizing with them, and this impairment scales with their pain insensitivity. In one study, patients with CIP “frequently suspected other people of exaggerating their pain and often considered others — including their friends or spouse — as ‘sissies’” (REF. 122). Some patients showed no reaction to others’ pain at all, in experiments or real life¹²². Patients with CIP also rate others’ pain as less aversive, they have a less intense empathic pain response in the left anterior insula and inferior frontal gyrus, and the aMCC, and they lack the aMCC response to others’ facial pain. In short, patients with CIP are impaired at empathizing with others’ pain.

Patients with CIP also do not have a deficit for all types of pain, only peripheral pain, and some somatic pain (for example, headaches and migraines) remains intact¹²². These intact representations allow them to relate to the noxious, aversive, motivating properties of pain that are represented in the anterior insula and aMCC. Patients with CIP also learn how to interpret pain cues, allowing them to pass easy behavioural tests such as rating facial pain on a three-point scale¹²².

Therefore, data from patients with CIP support the perception–action model by showing that it is harder to feel concerned about another’s state in the absence of a highly relevant, elaborate representation of the same state from personal experience. It also supports the view that the brain uses whatever representations are available to understand others, in a way that scales with the relevance of the observer’s experiences⁷. Experience with one’s own pain thus influences one’s ability to empathize with another’s.

stimulation. Ideomotor actions and spontaneous mimicry demonstrate the effector-specific, peripheral effects of the underlying neural perception–action process⁹⁰. In the emotional domain, the somatosensory cortices are activated during a variety of empathy tasks — including those involving pain¹⁰⁴, facial emotion recognition⁹³ and emotional empathy¹⁰⁵ — thus indicating a role for sensation in observing emotions, particularly when the task emphasizes sensation. The anterior insula — which is consistently activated during empathic pain (see above) — is also active during observed and imitated facial emotion¹³², felt and observed disgust^{97,133}, and the feeling of ‘butterflies in the stomach’ while anticipating risk¹³⁴. Thus, there are times when sensations have a more prominent role in empathic emotion perception, particularly when the sensation is made salient by the stimuli and task instructions. For example, rating pain intensity on the target’s limb activates more sensory areas than does rating pain aversiveness or viewing facial pain expressions without knowing the cause¹²⁴. Tasks that focus attention on the location of the injury activate more sensory activity (for example, in S1, S2 and the SMA), whereas tasks that ask subjects to ‘place themselves into the shoes of the other’ recruit more visuospatial, executive and working-memory processes (mentalizing; for example, the STG, TPJ, IPL, DMPFC and VMPFC)^{100,118,124}. By carefully linking neural regions to the focus of the task and the experience of the subject, the many seemingly puzzling results from different studies begin to make sense.

Conclusion

Our scientific understanding of empathy has greatly improved within the past two decades owing to a huge amount of research into how this capacity evolved, exists across species, and is instantiated in the body and brain.

Research supports an evolutionary, perception–action view in which observers spontaneously imitate, mimic and ‘feel into’ the states of those they attend to through a neural process by which the targets’ states are mapped onto the observers’ distributed learned and personal representations for the target, state and situation. This shared component of self and other representations explains the strong biases for similarity, familiarity and past experience that are found across species.

All species may not possess complex capacities to put themselves into another’s ‘shoes’ in the same goal-directed manner as is seen in humans, but most caregiving mammals that live in interdependent social groups are affected by the pain and distress of familiar others in ways that may propel them to act on their behalf. For some species, there is experimental evidence of well-developed empathic perspective-taking and targeted helping. Shared representations of affective states are activated from the top down in more cognitive forms of empathy, which recruit additional executive and visuospatial processes. However, the literature overestimates distinctions between emotional and cognitive empathy, following traditional practices to dichotomize in science and philosophy. Despite each having unique features, affective and cognitive empathy both require access to the shared representations of emotion that provide simulations with content and an embodied meaning.

Future research must examine empathy and its mechanisms in a wider variety of species, even beyond the mammals, to better understand the underlying mechanisms and how empathy shifts with social ecology. In addition, neuroscience must move beyond oversimplified claims of ‘same’ or ‘different’ processes, and apply a more phenomenological approach that contextualizes results within the tasks, instructions and analyses employed.

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