

Review

Neural basis of prosocial behavior

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The ability to behave in ways that benefit other individuals' well-being is among the most celebrated human characteristics crucial for social cohesiveness. Across mammalian species, animals display various forms of prosocial behaviors – comforting, helping, and resource sharing – to support others' emotions, goals, and/or material needs. In this review, we provide a cross-species view of the behavioral manifestations, proximate and ultimate drives, and neural mechanisms of prosocial behaviors. We summarize key findings from recent studies in humans and rodents that have shed light on the neural mechanisms underlying different processes essential for prosocial interactions, from perception and empathic sharing of others' states to prosocial decisions and actions.

Behaving to benefit others

Are humans predisposed to help and care for others or are we inherently selfish? This fundamental question about human nature has been debated by philosophers for centuries and is frequently brought into public attention through extraordinary examples of altruistic behaviors, such as heroic acts of first responders. In accordance with the view that evolutionary success relies on the survival of one's own genes in subsequent generations, most animal behaviors, from feeding to mating and fighting, are driven by one's own survival and reproductive needs and serve the purpose of benefiting oneself [1]. The existence of behaviors that benefit other individuals – known as prosocial behavior – has long puzzled evolutionary biologists since Darwin [2]. What mechanisms may enable humans and other species to behave to benefit others, even at a cost to the self? Research through the lens of modern neuroscience can help provide insights into the biological basis and evolutionary roots of our 'good nature'. Here, we discuss the phenomenon of prosocial behavior across species and its proximate and evolutionary mechanisms. We further highlight recent findings from human and rodent research on the neural basis of prosocial behavior.

The concept of prosocial behavior

Within the realm of social interactions, diverse forms of behaviors take place in a context- and goal-dependent manner [3], and can be broadly grouped by characteristics along two wide spectrums – from affiliative to antagonistic and from self- to other-benefitting (Figure 1A). Affiliative behaviors involve generally positive and friendly interactions, including those that foster the development and maintenance of social relationships [4,5]. Compared with other social behaviors, prosocial behaviors are not only affiliative, but also associated with the motivation and/or consequence of benefitting others [6–9]. Prosocial behavior is a powerful force that enhances social cohesiveness and promotes the physical and emotional well-being of social species [8,10].

In the human and non-human primate literature, 'prosocial behavior' typically refers specifically to behaviors that benefit others, although various studies have put different emphasis on the intentional/motivational and consequential aspects of this behavior [6]. In rodents, while most studies have used 'prosocial behavior' to refer to other-benefitting behavior [11–15] (which is in line with the definition in primates), some studies have used this term more broadly as general sociability or general affiliative, non-agonistic social behavior (such as social approach and

Highlights

Both humans and animals display prosocial behaviors, such as comforting, helping, and resource sharing, to improve the well-being of others. Prosocial actions across species share core behavioral features and may have common proximate and evolutionary mechanisms.

Functional neuroimaging and brain stimulation studies in humans have implicated several cortical and subcortical areas in various aspects of prosocial behavior, including attribution of others' emotional and mental states, encoding of subjective values, cognitive control, and reward processing.

Application of systems-neuroscience approaches in genetically tractable rodent models enables interrogation at high spatiotemporal precision of the neural coding and control of prosocial behavior. This provides new insights into specific neuronal populations and neural circuits causally regulating comforting and helping behaviors.

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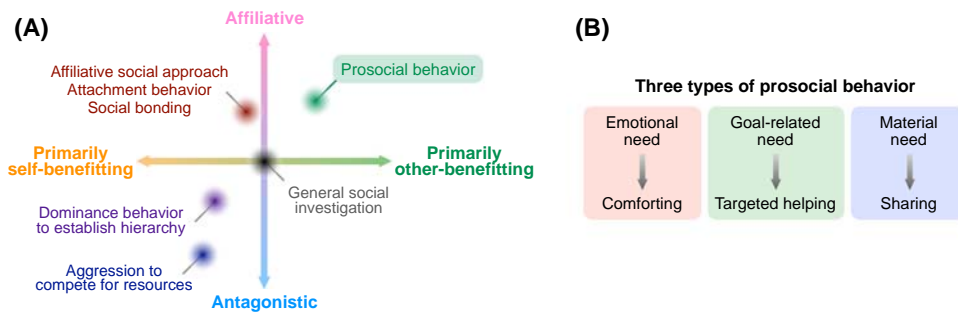


Figure 1. Categorization of prosocial behaviors. (A) Diverse forms of social behaviors are distributed along two spectrums: whether they are affiliative or agonistic and whether they primarily serve to benefit the self or others (axis scales are arbitrary). Prosocial behavior represents a specific category of social behavior – it is not only affiliative, but is also driven by the motivation of benefitting another and/or results in improvement of another's welfare. (B) Prosocial behaviors can be broadly categorized based on the type of negative state or need that elicits them: (i) comforting – induced by others' emotional distress; (ii) targeted helping – induced by others' difficulty to complete a goal-related action; and (iii) sharing – induced by others' material needs or desires.

investigation) [16–18]. We suggest that 'prosocial behavior' be used in rodents consistent with its usage in primates, to denote an affiliative behavior that occurs in response to a negative state and/or unmet need in another individual and helps to alleviate this negative state and/or fulfill the need of the recipient [6,8,19]. This definition encompasses behaviors such as comforting, targeted helping, and resource sharing, which are induced by another's negative emotional state or unmet need and serves to support the recipient's emotions, goals, or material needs (Figure 1B). Cooperation represents a form of reciprocal prosocial behavior in which individuals achieve common goals or mutual benefits by working together or returning previously received favors. Prosocial behavior can be distinguished from general sociability, such as basic social approach and investigation, or other types of general affiliative social behavior (Figure 1A). Although these non-agonistic social behaviors can be associated with immediate social reward and long-term reproductive benefit to the recipient, they are usually not induced by a specific negative state or need in the recipient and are mainly driven by and serve the actor's own survival or reproductive needs.

Prosocial behavior across species

While humans display some of the most complex known forms of prosocial behaviors, prosocial actions in humans and other species share core behavioral features and motivational drives and may have an evolutionary origin in offspring-directed caring behavior.

Behavioral manifestations

Human prosocial behaviors manifest in diverse forms, such as helping, emotional support, sharing, donating, volunteering, cooperation, and acts of bravery or heroism [7,8]. These behaviors can be broadly categorized into several classes – comforting in response to emotional distress, helping in response to needs to achieve goals or evade harm, and sharing in response to material desires [8] (Figure 1B). However, real-world scenarios often involve simultaneous presentation of multiple types of negative states and may lead to co-occurrence of different types of prosocial responses [21].

In young children, different types of prosocial behaviors show different ages of onset and developmental trajectories [8,20], with goal-related helping emerging as early as 14 months [22], sharing shortly after the second year [23], and comforting roughly after the third year [20].

This may reflect the differential dependence of various prosocial behaviors on different social-cognitive abilities for recognizing others' states and/or devising a solution. Furthermore, prosocial behaviors appear to show age-related increases across the early years, possibly due to social-cognitive and emotional maturation [24].

Research in non-human primates showed that chimpanzees and bonobos can help others to achieve their goals, such as transferring appropriate tools to conspecifics and helping others to obtain food, even in the absence of immediate reward to the helpers [25,26]. Some species have also been observed to share food [27–29] and console distressed conspecifics [9]. However, the display of prosocial behavior in non-human primates differ across species and types of behavior, and in some species, certain types of prosocial behavior have not been observed [25,30].

Helping, sharing, and comforting behaviors have also been documented in various non-primate species with wide-ranging levels of cognitive capacities and distinct social structures. For instance, elephants help to push others out of a mud hole or riverbed [31], vampire bats share food with fasted group members [32], and several species (e.g., elephants, canids, and corvids) show comforting behavior towards distressed conspecifics [9].

Recent studies also suggest that rodents can display prosocial behaviors (Box 1). Monogamous prairie voles display robust comforting behavior toward distressed partners [14]. This behavior, however, is apparently absent in non-monogamous meadow voles [14], raising the question of whether comforting in rodents is restricted to species with pair bonds like prairie voles. Interestingly, mice were recently also shown to exhibit comforting behavior [15], suggesting that this behavior exists more broadly in rodent species with different social structures. Rats, in addition to comforting, were shown to display simple forms of helping and cooperation [11,120]. These phenomena share the key features of prosocial behavior – they are elicited by a distressed or needy state of another, and help to relieve that state in the recipient. Thus, while complex prosocial behaviors that involve more advanced cognitive skills may be restricted to humans, basic forms of prosocial behaviors may date back to evolutionarily more ancient species.

Motivational drives

An important proximate mechanism thought to motivate prosocial behaviors is empathy, a concept that consists of both affective and cognitive components: affective empathy refers to the ability to perceive and vicariously experience another's emotional states, whereas cognitive empathy is the capacity to understand and adopt another's perspective [9,33,34]. Affective empathy is conserved across many species, from rodents to humans [9,35]. Relatedly, aspects of affective empathy emerge early in development. In humans, the ability to be aroused by others' distress appears in infants, without the advanced cognitive abilities required for the cognitive components of empathy [36,37]. Examples of other species that display affective empathy include great apes, which exhibit basic forms of emotional contagion and sympathetic concern [33], and rodents, which show social transfer of emotions and physiological states, such as pain [38,39], fear [12], and stress [40].

Through empathic sharing, witnessing another's distress may cause a similar aversive state in oneself (Figure 2, steps 2 and 3), such as increased stress hormone levels or negative emotions when observing others in stress or pain [34,41]. Perception of another's negative state and empathic sharing may in turn generate a prosocial drive that results in aide or comforting actions towards another (Figure 2, step 4). Indeed, it has been observed that empathic experience precedes many (but not all) prosocial actions [7] and that empathy positively correlates with

Box 1. Prosocial behavior in rodents

Comforting

Comforting behavior is defined as an increase in affiliative social contact toward distressed conspecifics, which provides a stress-relieving effect (social buffering) [8,9]. In various animal species, including rodents, one of the most common forms of affiliative social touch is allogrooming, which can provide a pleasant and soothing experience for the recipient [134]. Comforting behavior was observed in monogamous prairie voles and mandarin voles, wherein naïve bystanders display increased allogrooming towards distressed partners compared with unstressed ones [14,112]. Interaction with naïve bystanders leads to social buffering in stressed animals [14]. The bystanders also show empathic sharing in this paradigm [14,112]. A recent study demonstrated that mice also respond to distressed conspecifics with increased allogrooming, leading to social buffering [15]. Other studies also reported increased allogrooming and/or allolicking towards socially defeated, sick, or pain-experiencing conspecifics in mice and rats [115,135,136].

Targeted helping

- Helping to release a trapped conspecific

Several studies have shown that rats are able to learn to open the door to a restrainer to help free a trapped cagemate but do not open empty or object-containing restrainers [11,13]. This behavior appears rewarding and is unlikely to be driven solely by a self-oriented desire for social interaction [11,13] (but also see [137]). Supporting the notion that empathic experience is required for motivating this behavior, administration of an anxiolytic impaired door opening when the restrainer contained a cagemate, but not when it contained food [45]. This behavior can be modulated by social factors such as familiarity between animals and the presence of bystanders [11]. Other studies have also shown that rats can learn to open a door to liberate a cagemate from a pool of water [11].

- Helping to deliver a reward to another

Two studies have shown that when rats are provided with a choice that results in a food reward only to themselves and another choice that delivers an additional reward for a partner, they prefer to deliver mutual food rewards over self-reward only [117,119].

- Helping to avoid an aversive experience to another

After rats are trained to press two levers, pairing the preferred lever with observation of foot-shocks to another rat significantly reduced preference for that lever, indicating that harm to others is a negative reinforcer [118]. One interesting question is whether this phenomenon reflects a passive avoidance of a negative stimulus or a proactive behavior to relieve others' distress.

- Cooperation (mutual helping)

Rats have been shown to exhibit cooperative behaviors through reciprocation of food or allogrooming [120]. Rats can also temporally coordinate their behaviors to obtain mutual rewards [121,122]. A comparative study found that the tree shrew, which is phylogenetically closer to primates than rats, exhibits stronger cooperative abilities, whereas mice demonstrate less cooperation [122].

prosocial behavior [42–44]. In addition, reducing emotional contagion of stress in rats through administration of an anxiolytic impairs prosocial helping [45]. In a study in humans where participants witnessed another individual express pain in response to an apparent (videotaped) hand swat, disrupting the activity of the hand region in primary somatosensory cortex interfered with prosocial decision to reduce others' pain [46]. However, while a certain level of emotional arousal in the observer may motivate prosocial behavior, the inability to control empathy-induced emotional changes (self-regulation) may cause excessive self-stress, which leads to self-protective behavior (e.g. avoidance) and hinders prosocial behavior [45,47,48] (step 5, Figure 2).

The association between empathy and prosocial behavior can be modulated by other factors, such as cost–benefit relationship and perceived ability to help [7,35]. Importantly, while empathy may be a motivator for prosocial behaviors, the experience of empathy and the ensuing active prosocial responses are distinct processes that should not be conflated. In humans, additional considerations, such as social and personal standards and morality, could also promote prosocial behaviors [7,35].

Furthermore, acting to improve another's state could in turn lead to personal relief or joy in the helper (Figure 2, step 8) [9,35,49,50]. For example, charitable donations are associated with a

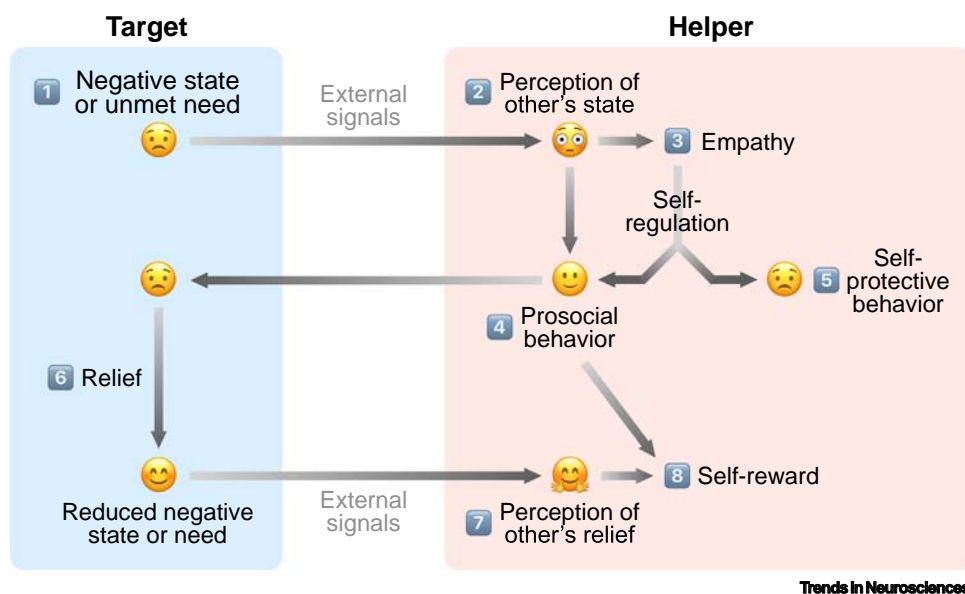


Figure 2. Different processes involved in prosocial interactions. Prosocial interaction is a multi-stage process that starts with the communication of others' negative states or unmet needs through external cues (step 1). Perception of others' states (step 2) can elicit empathic experience (step 3). Perception and sharing of others' states motivate the observer to make prosocial decisions and issue prosocial interventions (step 4). This process involves evaluation and integration of self-, other-, and context-related information as well as self-regulation of emotions. Failure to regulate one's own emotional response to others' negative states may lead to excessive self-stress, which promotes self-protective behavior and reduces prosocial response (step 5). Helper's prosocial interventions can lead to alleviation of the target's negative state (step 6), which may then be signaled back to the helper (step 7). Prosocial behavior *per se* or the perceived improvement in others' well-being is often associated with a rewarding experience to the helper (step 8).

positive feeling known as the 'warm glow' [51], and people report higher positive affect after acting kindly towards others [49]. The positive experience resulting from the intrinsic reward associated with prosocial behavior or the perception of improvements in others' states may help reinforce prosocial behavior [35,49].

Evolutionary mechanisms

The fact that animals can enact other-benefitting behaviors may appear inconsistent with the idea that behaviors are selected for because they promote the fitness of individuals' own genes. To resolve this apparent paradox, several evolutionary mechanisms have been proposed to explain how prosocial behaviors towards relatives or unrelated individuals could lead to a reproductive advantage. One line of thought relates to the 'inclusive fitness' theory. By acting to benefit related individuals, animals may increase the transmission of their genes that are shared among relatives [2]. Other perspectives highlight the point that helping other individuals (whether related or unrelated) may provide evolutionary advantages if it leads to reciprocation of the favor (reciprocal altruism), or if a group with more prosocial individuals is more likely to out-compete another group with more 'selfish' individuals [7].

It has been proposed that prosocial behavior may have an evolutionary origin in caring for helpless newborn offspring, a phenomenon that is ubiquitous across mammals [9,52]. Although offspring caring is primarily driven by animals' own reproductive need, both types of behaviors involve a target in distress or need that presents a salient stimulus to the observer, who then responds with aide or consolation to relieve the target's negative state. From rodents to humans, mothers show robust emotional and behavioral responses to distress cues from offspring [52], akin to

the empathic arousal and behavioral interventions in prosocial situations. In some animal species, offspring caring can also be displayed by non-mother females and/or males, and can be extended to unrelated newborns, suggesting that mechanisms subserving offspring caring can be extended beyond the mother–offspring relationship [52]. Indeed, across multiple primate species including humans, the extent of cooperative maternal care predicts proactive prosociality [53]. Investigating whether and how prosocial and parental behaviors are regulated by shared or divergent neural mechanisms may provide additional insights into their evolutionary relationship.

Neural mechanisms of prosocial behavior

As described above, prosocial interactions involve a multi-step process (Figure 2). Below, we first briefly summarize the mechanisms of the two important steps (steps 2–3) that often precede prosocial behavior – perception of others' states and empathic sharing (see [9,12,40,54–58] for comprehensive reviews). We then review state-of-the-art research on the neural mechanisms underlying prosocial decisions and actions (step 4). The subsequent steps, such as how the helper's prosocial behavior influences the recipient's state (e.g., social buffering), are not a focus of this review (see [59–62] for additional discussions).

We summarize studies in both humans and rodents, which represent two major branches of research that have provided complementary insights. While human studies have implicated various brain areas in complex prosocial decisions, the specific neurons and neural circuits involved are difficult to delineate in human studies, due to the limited spatial resolution of noninvasive techniques for recording and perturbing neural activity. In parallel, substantial progress has been made in applying systems-neuroscience approaches in rodent models [63] to interrogate the neural encoding and causal mechanisms of prosocial behavior at the levels of neural circuits and genetically defined cell types.

Mechanisms mediating perception of others' affective states

Perception of other's mental state is a prerequisite step for eliciting prosocial behavior (Figure 2, step 2). Emotional and mental states are conveyed through multiple channels. In humans, visual, vocal, and tactile cues are among the frequently encountered mediators in this context [54,56]. Processing of emotional facial expressions engages cortical areas that process dynamic facial features, such as the inferior occipital gyrus and superior temporal sulcus (STS) [54,56,64]. The amygdala also contains single neurons that encode subjective judgements of facial emotions [54,56]. Additionally, the perception of vocal cues involves mid-temporal regions known as 'voice areas' that respond more strongly to emotional vocalizations compared with neutral vocalizations [56]. Moreover, the affective experience induced by gentle tactile stimulations may involve the posterior insula and the posterior STS [56,59]. Lastly, information from different sensory modalities can be integrated at different processing stages and may transition from largely perceptual representations to modality-nonspecific conceptual representations [56].

In rodents, olfactory cues play a major role in emotional communication. Stressed animals can release volatile chemicals that lead to fear, stress, and anxiety-related responses in receiving animals [40,65]. Odors from mice in altered emotional states also elicit approach, avoidance, or comforting behavior of the observer [15,66,67]. Additionally, visual and auditory cues are also involved in the perception and discrimination of others' emotional states, such as pain, stress, and relief [38,66–69]. In addition to the sensory modalities involved, studies have identified several brain areas that mediate the perception of other's emotional states, including the central amygdala (CeA) [66], the medial amygdala (MeA) [15], the paraventricular nucleus of the hypothalamus [70], the insula and its projection to the nucleus accumbens (NAc) [71,72], and the medial prefrontal cortex (mPFC) [67]. In addition, the neuropeptide oxytocin, which plays a pivotal role in social cognition [73], acts in the CeA and insula to regulate emotion perception and discrimination [66,71].

Mechanisms of shared experience (empathy)

The perception of others' states may further elicit an empathic experience in the self (Figure 2, step 3). In humans, the neural correlates of empathy have been mainly investigated using functional neuroimaging in affective and cognitive empathy tasks, during which empathic experience is usually self-reported. Many studies have focused on empathic pain, due to the robustness of pain in inducing empathy. The anterior insula (AI) and dorsal anterior cingulate cortex/anterior midcingulate cortex (dACC/aMCC) are activated during both direct and vicarious pain experiences and are thought to encode the negative affect associated with self and empathic pain [9,57,74]. These regions are also recruited during vicarious experience associated with other aversive stimuli, such as disgust and anxiety, and positive stimuli, such as reward [57,74,75]. Several other brain areas associated with processing of social, emotional, and sensorimotor information, such as the thalamus, amygdala, and somatosensory and motor cortices, can also be engaged, depending on the specific task [9,75,76].

Interestingly, self and other experience of emotions and sensations appear to recruit some overlapping brain regions (e.g., areas in the insular, cingulate, and somatosensory cortices), suggesting that self and empathic experience may involve shared neural substrates [9,57,77]. Indeed, reduction in self pain resulting from pain medications, the placebo effect, or congenital pain insensitivity also attenuates empathic pain, indicating a functional overlap between neural substrates of self and empathic pain [9,57]. However, whether self and empathic experience recruit the same neurons in these brain areas is still unclear and these processes also activate some non-overlapping brain regions [57,78]. Whether empathic experience emerges directly from a shared representation of self and others' states is still debated.

Cognitive empathy in humans has been studied using paradigms such as false beliefs, trait judgments, social animations, and inference of intentions [79,80]. These tasks activate areas such as the dorsomedial and ventromedial PFC (dmPFC/vmPFC), temporoparietal junction (TPJ), inferior parietal lobule (IPL), precuneus, cingulate and paracingulate areas, superior temporal cortex, and anterior temporal lobe [79–81]. How information is encoded in various brain regions and how their differential functions give rise to affective and cognitive empathy remain to be further investigated.

As self-report of empathy is not feasible in animals, rodent studies rely on behavioral and physiological measures as proxies of empathy. In the observational fear paradigm, for instance, an animal observing a conspecific receiving foot-shocks displays freezing behavior, reflecting vicarious fear [12]. The ACC is required for experience-independent observational fear (observer is naïve to the stressor) and its function relies on somatostatin-positive interneurons and the $\text{Ca}_v1.2$ Ca^{2+} channel subunit [69,82,83]. The basolateral amygdala (BLA) and mediodorsal thalamus may function downstream of the ACC in mediating this function [84,85]. A lateral amygdala-MeA circuit also regulates observational fear [86]. Observational fear can also occur through an ACC-independent mechanism when the observer has prior experience with the stressor (experience-dependent), which involves the dorsal and ventral hippocampus and the BLA [84]. Besides observational fear, the ACC also controls the social transfer of pain through its projections to the NAc [39].

Mechanisms of prosocial decisions and actions

Humans

Investigation of the neural mechanisms of human prosocial behaviors have mainly focused on decision-making in various experimental paradigms that model sharing, helping, and cooperation, such as neuroeconomic games (Box 2). Across different prosocial contexts, decision-making likely entails the attribution and/or sharing of others' emotional and mental states, which may then

Box 2. Experimental paradigms for studying prosocial behavior in humans and non-human primates

In humans, neuroeconomic games have been widely used as experimental paradigms to study prosocial decision-making [133].

The prisoner's dilemma game and the public goods game examine cooperation in a pair of players or larger groups. In the prisoner's dilemma, the total payoff is the greatest when both cooperate and the lowest when both defect. However, a player earns the most if they defect and their partner cooperates. In the public goods game, an individual chooses how to split their earnings between a private pot and a public pot. Earnings in the public pot are multiplied and split among the participants. Total earnings are maximized when all cooperate, but a single player earns the most if they defect while others cooperate.

The trust game assesses trust and reciprocity/trustworthiness during cooperation. A 'trustor' is endowed with a sum of money and decides how much of this money to invest in a 'trustee'. This investment is multiplied and transferred to the trustee, and the trustee can either defect and keep the money or reciprocate and return part of the multiplied investment to the trustor.

In the ultimatum game, a 'proposer' is endowed with a sum of money and chooses what proportion of the money to share with a 'responder'. The responder then decides either to accept the offer, in which case both players earn the amount proposed, or reject the offer, in which case neither player earns anything. The dictator game is similar to the ultimatum game except that the responder has no choice but to accept the offer. These games evaluate the proposer's willingness to make monetary offers and the responder's reaction to the fairness of the offers.

Healthy human subjects behave in ways that indicate the ability of prosocial decision-making in these games [133]: rather than adopting a strategy of maximizing self-interest, they are able to make fair offers, cooperate, trust, and reciprocate. Other paradigms, such as charitable donation, helping, and prosocial learning, have also been developed (e.g., [94,95,97,108]).

In non-human primates, several experimental paradigms have been developed to examine the preference between self and mutual reward [25] and the ability of targeted helping, such as helping others to obtain objects out of reach, transferring appropriate tools to others, opening locked doors for others to obtain food, and releasing inaccessible rewards to others [25]. In addition, the prisoner's dilemma game has been used to study the neural encoding of self and other's behavioral decisions during cooperation [90], and a reward allocation task has been used to examine the neural recording of self- and other-regarding decision preference [110].

produce a motivation to act prosocially according to others' needs and intentions (Figure 2, step 4). To decide which behavioral option to choose, individuals need to assign values to the expected outcomes of different options for self and others and select an option of optimal joint value. These processes can be modulated by contextual and social factors such as norms and group identity.

Consistent with the notion that understanding and sharing of others' states can facilitate prosocial decisions, several empathy-related brain regions are associated with other-benefitting decisions [43,87–89]. For example, activity in the AI and TPJ predicts the amount of charitable donations [43], activity in the dmPFC tracks monetary donations and time spent helping others [87], and activation in the rostral ACC is associated with the decision to cooperate [88]. The functional roles of these brain regions in promoting prosocial decisions remain to be elucidated. Interestingly, in monkeys, single neurons in the dorsal ACC predict others' future decisions during cooperation and disruption of dorsal ACC activity reduces cooperation [90].

In prosocial decision-making, individuals need to assign subjective values to the expected outcomes of different options to select the option of optimal value. These subjective values are computed based on assessment and integration of values to both self and others [91,92]. Several brain areas, such as the mPFC, ACC, and ventral striatum, have been implicated in representing self- and/or other-regarding values during prosocial interactions [91,93–97]. In addition, attribution of others' values recruits mentalizing-related brain areas, such as the TPJ, precuneus, and IPL, which may mediate inference of others' intentions or anticipation of others' responses

[95–97]. For instance, the vmPFC and dmPFC preferentially encode self- and other-regarding values, respectively, in a prosocial learning task [94]. In a prosocial choice task, responses in the vmPFC and ventral striatum correlate with self-regarding values, whereas TPJ activity correlates with other-regarding values [95]. How self- and other-regarding values are compared and integrated to generate an overall value is not well understood. Some evidence suggests that the mPFC and ACC may also encode relative values and joint values [91,93,95].

In humans, rules and norms (such as fairness) influence prosocial decisions. Previous studies suggest an important role of the lateral PFC (lPFC) in norm/rule compliance [91]. Single-neuron recording in monkeys showed that lPFC neurons can encode rules [98]. Neuroimaging in humans found that the lPFC shows higher activity during decision-making in the presence of stronger rules compared with weaker rules and that lPFC activity correlates with rule-complying decisions [99]. Furthermore, brain stimulations in the lPFC alter norm compliance [100,101]. The lPFC may exert cognitive control of impulsive decisions that violate norms [91], or it may modulate the subjective values of different options by integrating information about rules and norms, such that norm/rule-conforming decisions are assigned higher subjective values [92].

Group membership based on different social identities also impacts prosocial behaviors; humans tend to share with, help, and cooperate with in-group targets more than out-group targets [102,103]. These effects may be due to a weakened ability to empathize with out-group individuals compared with in-group members [104,105], or because benefitting in-group members may be assigned higher values and is subjectively more satisfying [106,107].

Prosocial behavior is thought to be a motivated and rewarding process [49,50]. Accordingly, prosocial decisions are often accompanied by activation of brain areas linked to motivation and reward processing, such as the striatum and ventral tegmental area [88,108,109]. Important open questions include (i) how the motivation for prosocial decisions is generated following perception of others' states, (ii) how prosocial decisions lead to a rewarding experience, and (iii) how this reward signal reinforces prosocial decisions. In monkeys, the ACC is necessary for forming prosocial preferences through vicarious reinforcement [110]. It is possible that connections between empathy-related and reward-related regions link improvement in another's states to a rewarding experience to the helper to facilitate prosocial learning.

Rodents

While human studies have identified brain regions recruited during complex prosocial decision-making, recent studies in rodents began to uncover specific neuronal populations and neural circuits that control the expression of prosocial actions, including comforting and simple forms of helping and cooperation (Box 1).

In rodent comforting behavior, perception of others' emotional distress induces increased affiliative social contact, such as allogrooming by an observer, which helps to relieve the target's distress [14,15]. A recent study identified the MeA as a key node that may link the perception of others' distress with the expression of comforting behavior [15] (Figure 3C). In mice, olfactory cues play a potent role in communicating emotional states [40] and eliciting allogrooming [15]. The MeA is an important hub that receives social sensory inputs from the olfactory systems [111]. *In vivo* calcium imaging showed that MeA neurons respond differentially to stressed versus unstressed animals both at single-cell and population levels, suggesting that the MeA is involved in the detection of conspecific stress [15]. Interestingly, an intersectional genetic approach identified a tachykinin (Tac1)-expressing subpopulation of MeA GABAergic neurons that control allogrooming – optogenetic activation of these neurons elicits time-locked allogrooming towards

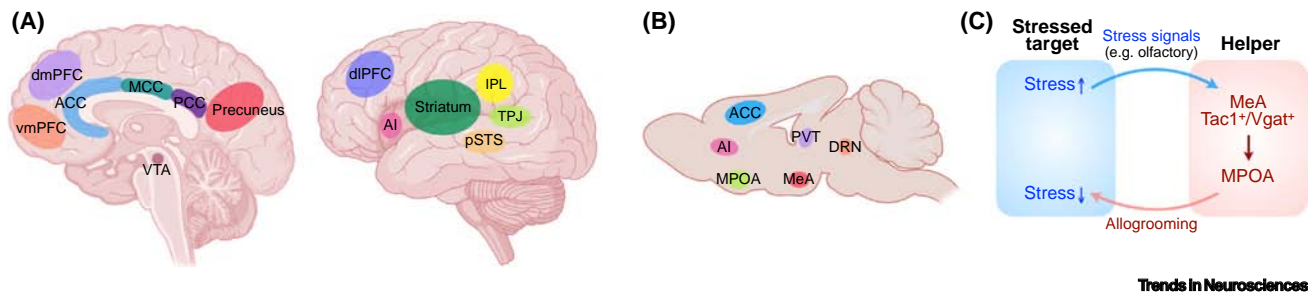


Figure 3. Main brain areas involved in prosocial decisions and actions in humans and rodents. (A) Prosocial decision-making in humans has been shown to recruit brain areas involved in attribution of others' emotional and mental states, evaluation of subjective values, norm representation and compliance, and reward processing. (B) Brain areas shown to regulate prosocial behaviors in rodents. (C) Regulation of comforting behavior by the MeA-MPOA circuit in mice. In mice, olfactory cues play an important role in communicating emotional distress. Conspecific stress leads to activation of MeA neurons. MeA tachykinin (Tac1)-expressing GABAergic neurons (Tac1⁺/Vgat⁺ neurons) promote allogrooming behavior towards distressed partners through their projections to the MPOA, leading to a reduction of stress in the target [15]. Abbreviations: ACC, anterior cingulate cortex; AI, anterior insula; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; DRN, dorsal raphe nucleus; IPL, inferior parietal lobule; MCC, midcingulate cortex; MeA, medial amygdala; MPOA, medial preoptic area; PCC, posterior cingulate cortex; pSTS, posterior superior temporal sulcus; PVT, paraventricular nucleus of the thalamus; TPJ, temporoparietal junction; vmPFC, ventromedial prefrontal cortex; VTA, ventral tegmental area.

stressed animals, while optogenetic inhibition suppresses allogrooming [15]. These bidirectional, time-locked effects support a direct role of these neurons in promoting this behavior. Furthermore, these MeA neurons project to the medial preoptic area (MPOA) and optogenetic activation of this MeA-MPOA circuit drives allogrooming. These findings provide direct evidence that allogrooming can be induced by manipulating the activity of a molecularly defined neuronal population and circuit. Interestingly, MeA neurons activated during sniffing of stressed animals partially overlap with neurons recruited during allogrooming [15], suggesting a potential direct link between the perception of other's stress state and the control of allogrooming.

While the MeA-MPOA circuit appears to directly control allogrooming, other brain regions involved in the perception and sharing of emotions may also modulate comforting behavior. Indeed, injection of an oxytocin antagonist into the ACC, which is involved in empathy, blocks allogrooming towards stressed partners in monogamous voles [14,112], suggesting that oxytocin signaling in the ACC is necessary for this behavior. Inhibition of serotonergic dorsal raphe neurons that project to the ACC decreases both allogrooming and general sociability in voles [113], although whether the effect on allogrooming is due to changes in general sociability is unclear [113]. Moreover, the paraventricular nucleus of the thalamus (PVT), which is involved in regulating state-dependent arousal under stressful or aversive contexts [114], is required for allogrooming/allolicking towards sick conspecifics [115]. As the effect of activating the ACC or PVT has not been reported, whether these regions play an instructive role in driving comforting behavior remains unclear. The functional relationships between the MeA, ACC, and PVT pathways in comforting behavior is also an important open question [114,115].

Comforting behavior is expected to reduce the recipient's emotional distress. Indeed, close social contacts with naïve partners reduce anxiety-related behaviors in stressed prairie voles and mice [14,15] and more allogrooming by partners is correlated with more reduction in stress-induced synaptic changes in mice [116]. This social buffering effect is thought to involve a subtype of C-tactile afferents and the endogenous opioid system that may mediate the pleasant experience associated with gentle tactile stimuli [59]. In addition, comforting can also reduce stress in the observer [14], possibly through vicarious sharing of the recipient's relieved state.

Another important element of prosocial actions in rodents, in addition to comforting, is helping behavior. It was shown that rats can help to liberate a trapped conspecific by learning to open a door

to a restrainer, help another to obtain a food reward, help a conspecific to avoid an aversive experience, and cooperate [13,117–122] (Box 1). In rats, blockade of oxytocin receptor in the ACC delayed learning of door opening to release trapped rats, suggesting a requirement for oxytocin signaling in the ACC in mediating this prosocial learning [123]. In addition, similar to the ingroup bias in human prosocial behavior, rats can learn to free individuals from a familiar strain but not those from an unfamiliar strain. This ingroup bias correlates with higher neural activity (i.e., higher c-Fos expression) in several brain areas, in particular the NAc-projecting ACC neurons [124]. It is unclear whether the ACC-to-NAc projection has a causal role in this ingroup bias and whether its differential activation between the groups modulates a particular step of this interaction (i.e., perception or sharing of emotions, initiation or reinforcement of helping). Furthermore, the AI also influences conspecific-liberation behavior: while heroin self-administration in rats suppresses this behavior, chemogenetic activation of the AI reverses this effect [125]. The exact role of the AI in emotional sharing and in initiating and reinforcing this behavior remains to be further elucidated.

The neural mechanisms underlying other types of helping behaviors are also starting to be explored. Inhibition of the ACC, in line with this brain region's role in empathic sharing, decreased avoidance of a lever that is paired with harm to another rat [118]. In addition, lesion of the BLA reduced helping behavior to deliver rewards to another rat [126]. Furthermore, neural activity in the rat orbitofrontal and prefrontal cortices encodes the occurrence of cooperation and differential roles of individuals (as an initiator or follower) during cooperation [122]. Still much remains to be learned about how neural dynamics in various brain regions encode different variables during these prosocial interactions and how these activities contribute to prosocial behaviors.

Conceptual questions in understanding the neural mechanisms of prosocial behaviors

Disambiguating mechanisms for different stages of prosocial interaction

One important brain area that has emerged from both primate and rodent studies is the ACC, which appears to be involved in both empathic processes and prosocial decisions and actions. This raises the question of whether the ACC facilitates prosocial behavior simply because it mediates the initial empathic sharing, or by playing an additional, different role in regulating the subsequent prosocial behavior. If the ACC exerts separate functions in these two processes, are these functions mediated by shared or different sets of neurons and downstream circuits? These questions also apply to other brain areas that influence both empathy and prosocial behavior. Examining and manipulating the activity of select neuronal populations during specific stages of prosocial interaction may help discriminate between these different possibilities.

Unique and converging mechanisms across prosocial contexts

As the display of prosocial behavior is highly dependent on the context of interaction (e.g., the nature of another's negative state and the type of prosocial behavior elicited), the underlying neural mechanisms may differ across contexts. Nevertheless, an important common step is to transform signals conveying another's state into a prosocial command. Does this transformation occur through separate neural pathways for different types of prosocial behaviors and sensory modalities or are there common hubs where information regarding others' states converges in different contexts? The ACC, which has been shown to influence several types of prosocial behavior (e.g., comforting, helping, cooperation [14,90,123]), might serve as such a hub. By contrast, the MeA, which in rodents receives olfactory cues communicating others' stress state and controls allogrooming, may represent an example where this transformation occurs in a comforting-specific manner. Examination of the neural coding of states of others and subsequent behavioral decisions across different prosocial contexts will provide additional insights into their shared and divergent mechanisms.

Multi-brain framework for prosocial interactions

Finally, prosocial interaction, like other social interactions, is essentially a dynamic feedback loop that couples behaviors and internal neural processes across the interacting partners, but studies so far have mostly focused on single individuals (e.g., the helper). An intriguing future direction would be to apply a multi-brain framework and monitor neural activity across multiple brains simultaneously [127–129]. By considering interacting individuals as embedded in an integrated system, this approach can provide a new angle for understanding how emergent neural properties across individuals may encode and shape prosocial interactions.

Concluding remarks

Recent studies of prosocial behavior using modern neuroscience tools have advanced our understanding of the brain mechanisms of this evolutionarily conserved phenomenon. Functional neuroimaging in humans has been instrumental in revealing the neural correlates of various cognitive processes during complex prosocial decision-making, such as brain areas involved in the attribution of others' emotional and mental states, evaluation of self- and other-regarding outcomes, and compliance to rules and norms. Complementarily, the emergence of genetically tractable rodent models of prosocial behaviors has enabled interrogation of the neural representations and causal circuit mechanisms of these behaviors using techniques for high-resolution monitoring and manipulation of neural activity. These studies have also shed light on neural mechanisms that may be shared between rodents and humans, such as the roles of the ACC, insula, amygdala, and the reward system. Future research should investigate the neural representation of social information and behavioral decisions during prosocial interactions at both single-cell and population levels and map additional nodes, cell types, and connections to further delineate the neural circuits that functionally regulate prosocial behaviors (see [Outstanding questions](#)). Collectively, insights garnered from these lines of research will contribute to a deeper understanding of the biological basis of human generosity and kindness and facilitate the study of dysregulation of prosocial behavior in mental disorders [130–133].

Acknowledgments

We thank members of the Hong lab for comments. This work was supported in part by NIH grants R01-NS113124, R01-MH130941, and UF1-NS122124, and awards from Packard, McKnight, Vallee, Mallinckrodt, and Keck Foundations. Figure 3A, B was created using [BioRender.com](#).

Declaration of interests

The authors have no competing interests to declare in relation to this work.

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Outstanding questions

Major gaps remain in our understanding of the neural encoding of prosocial behavior. How is prosocial interaction represented in different brain areas at single-cell and population levels? How is information communicated and integrated across different brain regions to coordinate prosocial decisions and actions? How do inter-brain neural dynamics and emergent neural properties across interacting individuals relate to different behavioral features during prosocial interaction?

The neural circuitry that functionally regulates prosocial behaviors needs to be further dissected. How does the medial amygdala, for instance, control prosocial comforting behavior through downstream brain areas? Does the ACC influence comforting behavior purely by regulating empathy, or are these separate functions that might be mediated by different neuronal populations or downstream circuits? How are other types of prosocial behavior such as helping and cooperation controlled by neural circuits? How do prior experience and social factors (e.g., group membership) modulate circuit functions to influence prosocial behavior?

Given the potential evolutionary link between prosocial behavior and offspring care, do different hormones, neuropeptides, and neuronal populations involved in parental and reproductive behaviors also influence prosocial behavior? Do parental states and sex hormones contribute to individual differences and sex differences in prosocial behavior?

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