

# Prosocial Helping Behavior: Conceptual Issues and Neural Mechanisms

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## ABSTRACT

Prosocial helping behavior, characterized by voluntary actions taken to benefit others, plays a vital role in promoting cooperation and maintaining social bonds across human and animal social groups. In this review, we examine key conceptual issues surrounding prosocial behavior, focusing specifically on targeted helping and comforting actions. We outline the behavioral paradigms used to study these two types of prosocial behaviors and summarize recent insights into their underlying neural mechanisms. Drawing on findings across species and with an emphasis on rodent models, we discuss how these behaviors are regulated by molecularly and anatomically defined neural systems and how distinct neuronal populations and circuits may differentially regulate targeted helping and comforting behaviors. Lastly, we discuss the clinical relevance of this research by addressing the implications of prosocial deficits in psychiatric disorders.

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## PROSOCIAL HELPING BEHAVIOR

Prosocial behavior, which refers to actions taken to help and benefit others, is vital to promoting cooperation and maintaining social bonds in both human and animal social groups (1). Prosocial behavior is fundamentally about recognizing and addressing the needs of others, whether those needs are physical, emotional, or psychological. Depending on specific needs, prosocial behavior can be categorized into three distinct types: targeted helping, sharing, and comforting (2). Targeted helping behaviors address instrumental needs by providing practical assistance; sharing resources fulfills material needs; and comforting behaviors alleviate emotional distress through support and empathy. These actions play a crucial role in fostering group cohesion and individual well-being across species.

While previous studies typically used the term “prosocial behavior” to refer to behavior that benefits others, it can sometimes refer more broadly to general sociability or general affiliative, nonagonistic social behavior such as social approach and interaction. To prevent potential misinterpretations, in this review we refer to prosocial behavior as “prosocial helping behavior.” This term specifically refers to voluntary actions taken to help and benefit others by addressing their various needs, emphasizing that these behaviors are active choices to assist or support others. This term aims to highlight the voluntary, other-oriented nature of these actions and distinguishes them from general, positive social interactions that are not primarily other-benefitting behaviors. It is also distinguished from “targeted helping behavior,” which is one form of prosocial helping behavior that is aimed at addressing others’ goal-directed needs by providing practical assistance, such as opening the door for someone or helping others to retrieve an object.

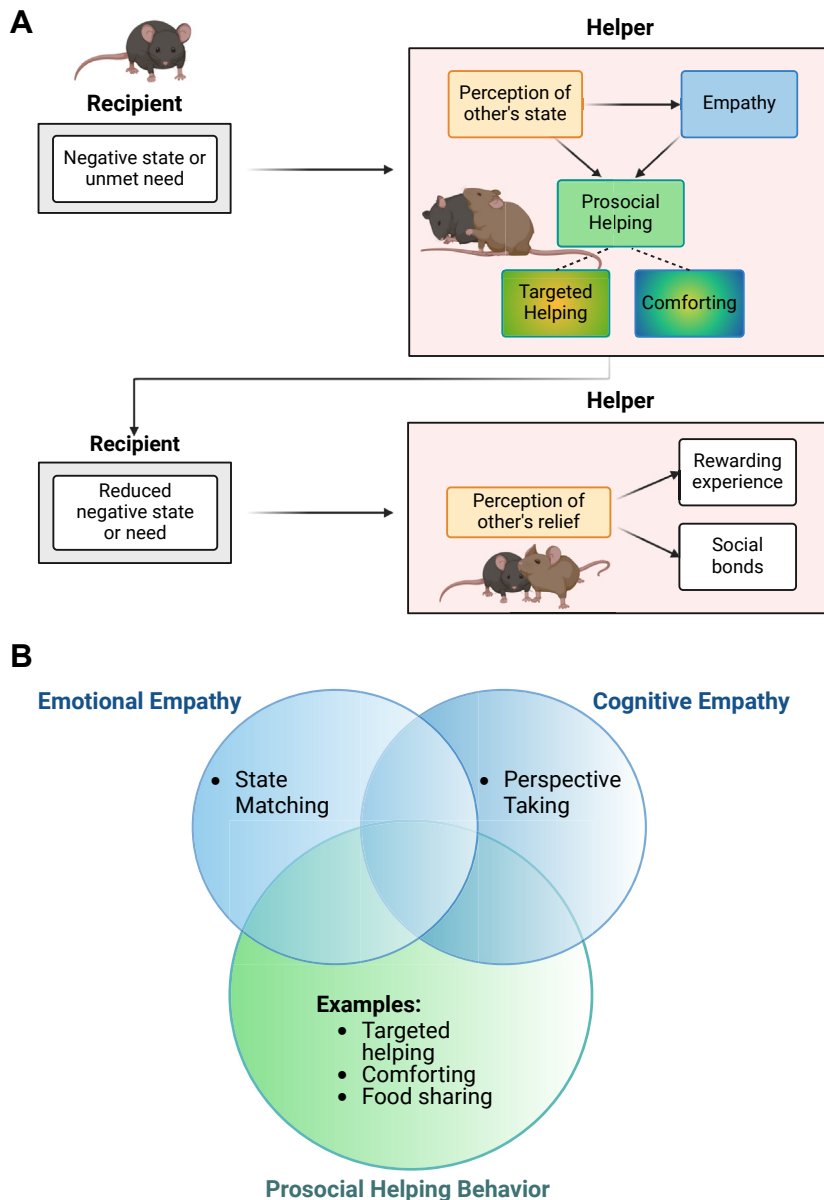
## WHAT CONSTITUTES PROSOCIAL HELPING: INTENTIONS VERSUS OUTCOMES

While prosocial helping behavior is typically characterized by a subjective intention to help, defining this intention can be challenging. Even in humans, the motivations behind a behavior may not always be clear. For example, a person may donate to a charity for genuinely altruistic reasons, or they may do so primarily for tax benefits or social recognition. Some researchers define prosocial helping behavior based primarily on the observable outcomes or consequences of the behavior regardless of the underlying intentions or motives (3). If the behavior results in a measurable benefit to the recipient, it can be considered prosocial helping behavior. This outcome-based approach makes it easier to define prosocial helping behavior in real-world situations and is particularly useful when studying animal models, where assessing intent is often difficult. This consequentialist view focuses on the result rather than the intention. For example, if a chimpanzee shares food with another member of its group, it would be considered prosocial helping behavior regardless of whether the sharing was motivated by empathy, reciprocity expectations, or simply a desire to stop the other’s begging.

While prosocial helping motivations typically lead to positive outcomes (Figure 1A), they can sometimes have unintended negative consequences, such as in-group bias or misguided interventions. This complex relationship between intentions and outcomes emphasizes the need for comprehensive studies of neural mechanisms and contextual factors.

## EMPATHY VERSUS PROSOCIAL HELPING BEHAVIOR

Although empathy and prosocial helping behavior are closely related, they are distinct concepts that should be carefully differentiated. Empathy refers to the process through which individuals recognize, comprehend, and resonate with the



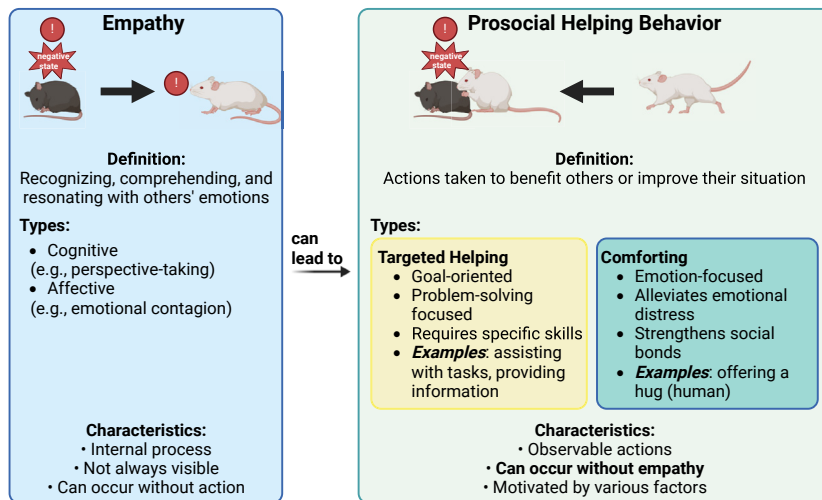
**Figure 1.** Conceptual framework of prosocial helping behavior, empathy, and their interactions. **(A)** The process of prosocial helping behavior: A recipient's negative state or unmet need triggers a helper's perception and sometimes an empathic response, leading to prosocial helping actions (targeted helping or comforting). The outcome includes reduced negative state for the recipient and potential rewards for the helper, including strengthened social bonds. **(B)** Relationship between empathy and prosocial helping behavior: Venn diagram illustrating the overlap between emotional empathy (state matching), cognitive empathy (perspective taking), and prosocial helping behavior. Examples of prosocial helping behavior include targeted helping, comforting, and food sharing.

emotional experiences and viewpoints of others (4). This process involves both cognitive elements such as perspective taking and affective components including emotional contagion and sympathy (Figure 1B). Empathy allows us to form a mental representation of another's emotional state and, to some degree, experience it ourselves. In contrast, prosocial helping behavior encompasses the concrete actions that are taken to benefit others or improve their situation. Prosocial helping behavior is directly observable and measurable and ranges from simple acts of kindness to more complex forms of assistance and support. While prosocial helping behavior is action-oriented and visible, empathy is often internal and may sometimes only be inferred through physiological or neural responses to others' distress.

Empathy often serves as a key motivator for prosocial behavior. Prosocial helping behavior typically requires recognition of others' distress or unmet needs through various external signals (Figure 1A). When an individual witnesses another's distress, empathic sharing can trigger a similar aversive state, such as increased stress hormones or negative emotions (5). This empathic experience often generates a prosocial helping drive, leading to actions that are aimed at targeted helping or comforting others (1). While empathy provides the emotional and cognitive foundation for understanding others' needs, it is prosocial helping behavior that transforms this understanding into tangible benefits for those in need.

Although prosocial helping behavior is often viewed through an empathy-centric lens, the two can occur independently.

## Neural Mechanisms of Prosocial Helping Behavior



**Figure 2.** Conceptual distinctions between empathy and prosocial helping behavior. Empathy involves recognizing, comprehending, and resonating with others' emotions, encompassing both cognitive (e.g., perspective taking) and affective (e.g., emotional contagion) components. It is an internal process that may occur without visible action. In contrast, prosocial helping behavior refers to concrete actions taken to benefit others, primarily manifesting as targeted helping (goal oriented, problem-solving focused) or comforting (emotion focused, alleviating distress). While empathy can inspire prosocial helping behavior, the latter specifically involves taking action to address others' needs and improve their conditions.

Empathy does not always lead to action, and prosocial helping can occur without empathic engagement (6,7). For example, an individual may experience strong empathic emotions without engaging in targeted helping behavior. Conversely, prosocial helping actions can occur in the absence of deep empathic feelings and be motivated instead by social norms, reciprocity, or other factors (8). For example, food sharing among nonhuman primates does not necessarily require the sharer to match the recipient's emotional state (Figure 2) (9). From this perspective, prosocial helping behaviors can be studied without assuming that they are dependent on empathic capacities.

While empathy typically promotes prosocial helping actions, excessive emotional arousal without effective self-regulation can lead to self-protective behaviors, such as avoidance, which may inhibit helping responses (10–12). Furthermore, factors such as cost-benefit analysis, perceived ability to help, and personal moral standards can modulate this relationship (1). Humans may actively avoid empathic experiences when they anticipate that empathy will lead to costly helping behaviors, emotional exhaustion, or conflicts with their desired outcomes in competitive situations (13). Conversely, individuals are motivated to increase their empathic engagement when it might strengthen social ties or be consistent with socially desirable outcomes. This motivation helps explain why humans and potentially other social species may self-select into situations that minimize empathic responses and, by extension, reduce the likelihood of engaging in costly prosocial behavior.

### TARGETED HELPING VERSUS COMFORTING BEHAVIOR

Both targeted helping and comforting behaviors are prosocial helping actions that are aimed at improving the well-being of others in response to the perceived distress of others in need. Despite these similarities, they also tend to serve distinct purposes and manifest in different contexts, and they

may involve different underlying emotional and cognitive processes.

Targeted helping typically involves direct action to help someone achieve a goal or overcome an obstacle. It is goal oriented and problem-solving focused, and it often requires specific skills or resources to address concrete issues or fulfill particular needs (1,2,14) (Figure 2). Examples include assisting with tasks, providing information, rescuing from danger, or treating physical injuries.

In contrast, comforting behavior is primarily emotion-focused and is aimed at alleviating emotional distress or providing support to others through social proximity, tactile stimulation, or other sensory cues (15) (Figure 2). It strengthens social bonds and promotes group cohesion, with effects that are mainly psychological, providing reassurance and a sense of security (15). Comforting behaviors may include offering a hug, providing verbal reassurance, or simply being present with someone who is upset.

Thus, while targeted helping behavior often requires more complex cognitive processes, such as understanding specific needs, planning appropriate actions, and executing them, comforting behavior may rely more on emotional mirroring and instinctive responses to distress signals. Both behaviors can include empathy and social understanding, but they engage these capacities in different ways. It is important to note that while targeted helping and comforting behaviors are distinct, they often co-occur in real-world situations (Figure 1B). For example, practical assistance may be accompanied or followed by emotional support, demonstrating how these behaviors can complement each other to address both physical and emotional needs. (Figure 2).

### NATURALISTIC TARGETED HELPING AND COMFORTING BEHAVIOR ACROSS SPECIES

#### Targeted Helping

Targeted helping and comforting behaviors are widespread across various species. Primates assist injured group

members (16), while elephants help others overcome environmental obstacles (17). In marine environments, cetaceans aid sick pod members (18,19), and on land, meerkats act as sentinels and share parental care (20). Vampire bats engage in food sharing (21), and corvids not only provide food but also defend cooperatively (22,23). Even insects rescue wounded nestmates (24).

A common helping behavior among species is the tendency to alleviate pain and tend to injuries (25). Pain typically elicits instinctive responses such as self-licking of the injury site, which not only alleviates discomfort but also reduces infection risk and promotes healing through enzymes and beneficial components in saliva (26–31). In social contexts, an individual's pain or injury serves as a salient signal that may elicit targeted helping responses from others (1,32). While humans often provide physical assistance to treat wounds, a wide range of animal species, from primates to rodents, engage in communal wound licking. This targeted helping response differs from general comforting behavior (32), presenting a specific need that requires goal-oriented action directed toward the injury site. Recent research has demonstrated that this ethologically relevant behavior also occurs in mice, offering insights into its fundamental biological mechanisms (32).

### Comforting

Many different species display behaviors that are meant to console others. For example, primates console injured group members (16), while canids provide solace to distressed pack members (22). A key component in this comforting process is gentle social touch such as allogrooming, which has been shown to reduce stress in distressed animals (1,15,33–35). Prairie voles increase allogrooming toward familiar conspecifics that have experienced a stressor (33). This behavior parallels consolation patterns observed in humans and nonhuman primates, suggesting a potentially shared mechanism across species (22). Initially, the observation of this behavior in monogamous prairie vole species, but not promiscuous vole species, led to the hypothesis that comforting behaviors in rodents were limited to monogamous species (33). However, recent research has demonstrated that laboratory mice also engage in allogrooming to assist distressed partners and that this behavior produces a comforting effect by reducing the stress level of the recipient mice (36). This finding challenges the notion that social behavior in mice is only driven by reproductive and territorial instincts, thus highlighting the broader prevalence of comforting behaviors across species (35–37). While allogrooming can also manifest as a dominance display leading to alopecia in subordinate animals (38), the anxiolytic effects of allogrooming observed in rodents suggest that it plays a significant role in stress relief.

## BEHAVIOR PARADIGMS FOR STUDYING TARGETED HELPING

### Naturalistic Targeted Helping Behavior

To understand targeted helping behavior, an important approach is to study behavior that occurs in naturalistic

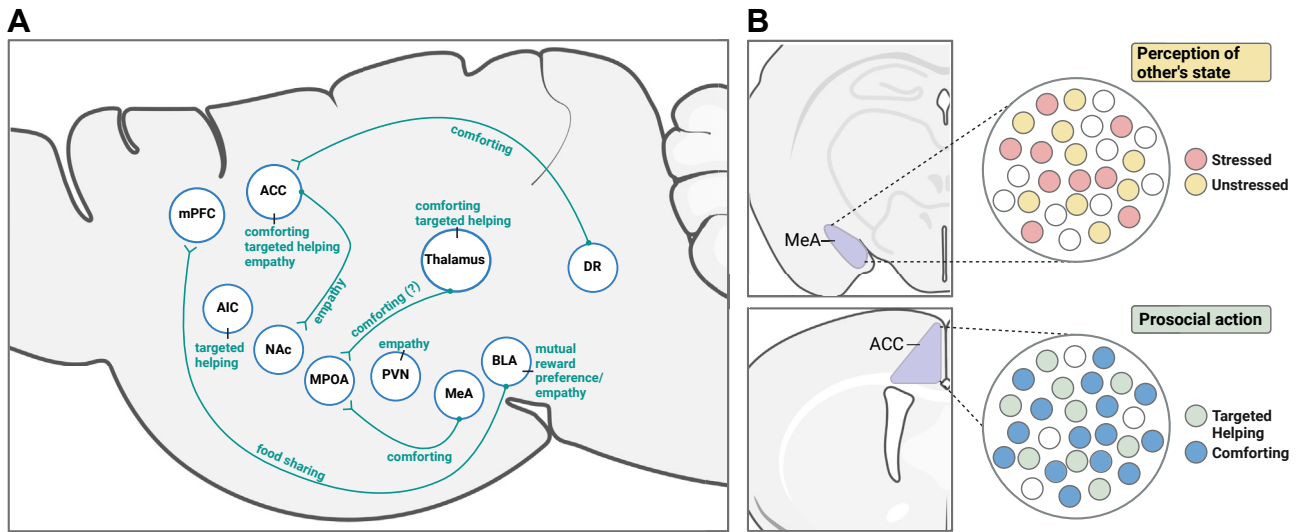
settings. Naturalistic targeted helping behaviors are instinctive and do not require prior experience or training of animals to carry out an artificial behavior. As discussed above, mice exhibit a specific form of targeted allolicking, where they lick the injury site of other mice (31,32). Targeted allolicking appears to be a proactive behavior, likely influenced by various sensory cues such as observing self-licking by the injured animal or detecting chemical and tactile signals (31,32). Compared to the social transfer of pain, where an animal increases its own pain sensitivity after interacting with another in pain (39), targeted allolicking seems to be a direct response to visible injury. This behavior is an untrained, natural response aimed at helping others cope with pain, reflecting a naturalistic form of prosocial targeted helping behavior (26).

### Operant Tasks Used to Assess Targeted Helping Behavior

An alternative approach to studying targeted helping is to train animals to associate their prosocial motivation with an operant action, such as pressing a lever. For example, rats can be trained to press a lever to release another rat from confinement (40), deliver food to a conspecific (41), or avoid causing harm to others (42). Releasing another rat from confinement has been extensively studied. After a rat learns this task, it consistently chooses to release the confined rat (40). It is not fully clear to what extent innate and learned components contribute to this behavior or what the underlying motivations are because the rat's actions could be driven by a desire for social interaction rather than purely empathic concern even in the absence of direct social contact. When given multiple options, rats show a preference for socializing with free conspecifics over targeted helping of restrained ones (43). Furthermore, this task may be influenced by additional factors such as neophilia or the learning process, as evidenced by rats' tendency to return to restraining tubes over time and continue door-opening behaviors even when they are ineffective (44). A study of mice suggests that their rescue-like behavior toward constrained cagemates is driven more by social interest and curiosity rather than empathy or prosocial helping motivations (45).

### Measuring Benefits in Recipient Animals

The study of prosocial helping behavior in animals has traditionally been focused on the helper, but it is also important to examine the benefits for the animal that receives help or comfort (15), because prosocial helping interaction is a dynamic feedback loop between individuals rather than isolated actions. Gentle social touch, such as allogrooming, can have significant anxiolytic and rewarding effects on the recipients. For example, receiving gentle, massage-like stroking can lower heart rate, decrease anxiety behaviors, and reduce plasma corticosterone levels following stress in humans and rodents (15,46,47). By examining recipients of prosocial helping behavior, researchers can uncover new dimensions of animal social interactions and stress management, potentially leading to a better understanding of similar mechanisms in humans.



**Figure 3.** Neural substrates of prosocial helping behavior and empathy. **(A)** Representation of brain regions involved in empathy, targeted helping, and comforting behaviors. Various interconnected areas contribute to different aspects of prosocial actions and empathic processes. **(B)** Distinct neural encoding in the medial amygdala (MeA) for perception of stressed and unstressed states and in the anterior cingulate cortex (ACC) for different prosocial actions (targeted helping and comforting). This demonstrates specialized neural populations for processing social information and executing prosocial helping behaviors. AIC, anterior insular cortex; BLA, basolateral amygdala; DR, dorsal raphe nucleus; mPFC, medial prefrontal cortex; MPOA, medial preoptic area; NAc, nucleus accumbens; PVN, paraventricular nucleus of the hypothalamus.

### NEURAL MECHANISMS OF TARGETED HELPING AND COMFORTING

In the following sections, we examine specific brain regions, genetically defined cell types, and the circuits and neural encoding mechanisms that drive targeted helping and comforting behaviors. We also discuss both the distinct and overlapping mechanisms that are involved in targeted helping and comforting (Figure 3).

#### Brain Regions Involved in Human Empathy and Prosocial Behavior

The neural mechanisms that drive how humans respond to others' distress and engage in helping behaviors emerge from the interplay of multiple brain systems. This process begins with the amygdala, which acts as an initial responder, activating when a person encounters signs of distress, from infant cries to fearful expressions (48–50). This signal is further processed by the anterior cingulate cortex (ACC) and anterior insula, regions that share neural pathways with those activated during our own pain. This connection is so fundamental that placebo analgesia, which reduces our personal pain, also weakens our empathic response to others' distress by decreasing activation in these areas (51).

Our capacity for empathy shows flexibility, particularly in social contexts. When we encounter distress in people who we consider outsiders, especially during competition, the ACC and anterior insula show reduced activity, although this response can be modified through intervention (13).

Distinct regions regulate empathic care and distress. For example, when we provide care toward others, reward regions such as the ventromedial prefrontal cortex (PFC) and ventral striatum activate, while our experience of others' distress

engages sensorimotor mirroring systems (52). A meta-analysis of functional magnetic resonance imaging studies revealed 3 distinct categories of prosocial decision making with unique neural signatures: cooperative decisions engaging reward-related regions such as the striatum and ventral tegmental area, equitable decisions activating value and cognitive control regions including the ventromedial and dorsolateral PFC, and altruistic decisions recruiting empathy-related regions such as the anterior insula and ACC (53,54). The somatosensory cortex guides prosocial behavior execution (55), while the septal area processes prosocial responses (56). Adding to these findings, activation in the bed nucleus of the stria terminalis (BNST) during empathy tasks predicts real-world helping behavior, particularly toward strangers, demonstrating how these neural systems translate into prosocial actions (57).

#### Neural Circuits That Underlie Naturalistic Comforting (Allogrooming) and Targeted Helping Behavior (Allolicking)

Recent studies have revealed that naturalistic prosocial behaviors such as allogrooming and allolicking in rodents are regulated by a hierarchical network of both subcortical and cortical circuits. At the subcortical level, the medial amygdala (MeA), a heterogeneous structure within the social brain network, plays a crucial role in initiating these behaviors through its integration of chemosensory information (58,59). MeA neurons show differential responses to stressed versus unstressed animals and activate during allogrooming, suggesting a direct link between distress perception and comforting behaviors (15,36). In particular, optogenetic activation of GABAergic (gamma-aminobutyric acidergic) tachykinin-expressing ( $Tac1^+$ ) neurons projecting to the medial preoptic area selectively elicits allogrooming toward stressed mice (36).

Other subcortical regions, such as the thalamus, contribute to these prosocial helping behaviors. The posterior intralaminar thalamic nucleus controls allogrooming in female rats via medial preoptic area projections (60), although this has not been tested in a prosocial behavior context. Similarly, the paraventricular thalamus regulates both allogrooming and anxiety-like behaviors in helpers (61), with particular involvement in allogrooming/allolicking that is directed toward sick conspecifics (61,62).

While these subcortical regions process fundamental sensory and emotional information, cortical areas also provide regulation of prosocial responses. The ACC has emerged as a key coordinator of these behaviors, containing distinct neuronal populations that separately control allolicking and general allogrooming (32). Chemogenetic and optogenetic manipulations have demonstrated the ACC's role in bidirectionally regulating both behaviors. These behaviors are encoded by largely non-overlapping neuronal populations, suggesting dedicated neural circuits for different forms of prosocial helping (32). One open question is whether allolicking and general allogrooming behaviors are regulated by distinct projections from the ACC.

Neuromodulatory systems coordinate activity in both cortical and subcortical regions. Serotonergic projections from the dorsal raphe to the ACC mediate allogrooming in mandarin voles (63), although chronic stress can impair this consolation behavior through effects on serotonin, oxytocin (OXT), and dopamine receptors in the ACC (64). Paradoxically, in mice, an increase in serotonin in the ACC reduces observational fear and pain responses (65). The OXT system is particularly important, as demonstrated by studies showing that OXT receptor antagonism in the ACC reduces comforting in prairie voles (33). Notably, there are sex differences in these mechanisms. OXT receptor deficiency reduces allogrooming in females but not males (66), although males generally show a higher frequency of allogrooming behavior (36).

Other hormonal systems also contribute to these behaviors in multiple brain regions. Testosterone modulates comforting behavior through the arginine vasopressin (AVP) system in the ACC, with castration increasing consoling behavior and testosterone administration reducing it, effects that can be reversed by AVP receptor antagonism (67). Additionally, both the BNST and MeA contain receptors for OXT and AVP that may translate environmental cues into prosocial behaviors (68).

### Neural Circuits That Regulate Operant Tasks for Prosocial Motivation

The ACC not only controls naturalistic prosocial behaviors such as allogrooming and allolicking but also guides prosocial decision making in operant tasks, as evidenced by its necessity for rats to avoid actions that harm conspecifics (42). When given a choice between 2 levers that offer equal rewards but differ in effort, rats switched to the higher-force lever to prevent another rat from being shocked, although this behavior was dependent on previous shock experience (42). The learning of targeted helping behaviors is modulated by OXT signaling in the ACC because administering an OXT receptor antagonist in the ACC delays the acquisition of helping responses (69).

The basolateral amygdala (BLA) and its cortical connections are particularly important for social reward preferences and decision making. BLA projections to the prelimbic cortex (PLC) are crucial for developing preferences for sharing food with conspecifics, while reciprocal projections from the PLC to the BLA influence self-interested decision making (41). The BLA is also necessary for expressing mutual reward preferences in rats (70), suggesting its role in weighing social versus individual benefits.

The anterior insular cortex (AIC) has emerged as another key region for targeted helping behavior in rats. Inhibiting the AIC disrupts helping responses, such as assisting another animal to escape a stressful context (71). When the AIC was inhibited, observers helped less frequently, and this reduction in aid corresponded with increased distress calls from the targets. The AIC also plays a role in maintaining prosocial behavior in challenging conditions, and activation of AIC neurons can reverse the decline in prosocial helping behavior (helping trapped cagemates) that is caused by heroin self-administration (72), suggesting potential therapeutic applications for treating social deficits in addiction.

Studies of “opener” rats—i.e., rats who consistently help release trapped cagemates—have revealed increased neural activity in multiple regions during prosocial motivation (73). Notably, they also show higher OXT receptor messenger RNA expression in the nucleus accumbens and upregulation of several transcription control pathways (73). The effectiveness of OXT in shaping these helping behaviors depends on the social relationship between the helper and the recipient (74), and OXT receptors are necessary for door-opening helping behavior in prairie voles (75), highlighting the importance of social context and species-specific mechanisms in prosocial motivation.

The OXT system plays a vital role in social cognition, bonding, and affiliation (76). Paraventricular nucleus of the hypothalamus (PVN) OXT neurons projecting to the nucleus accumbens mediate social reward processing in mice (77), while early-life social touch enhances PVN OXT neuronal firing and social approach through interaction with substance P systems (78). Whether these pathways influence targeted helping remains unknown; they may either directly mediate prosocial behavior or function as attentional modulators enhancing social cue salience (79). Research has disproportionately focused on OXT over AVP (76); both systems show sex-dependent effects on prosocial behavior, although the precise mechanisms and species-specific differences require further investigation.

### Specificity of Circuits in Prosocial Helping Behavior

While certain mechanisms required for general social behavior, such as the ability to perceive social sensory cues that identify other individuals, are also necessary for prosocial helping, these may not fully or directly explain how prosocial helping behavior is controlled. The ultimate question is what mechanisms are specifically or uniquely involved in prosocial helping behavior. Addressing this question requires identifying neural populations, circuits, or mechanisms that specifically control prosocial helping behavior as opposed to general social behavior. This approach involves 1) testing the

behavioral specificity of neuronal manipulations, 2) manipulating circuits in finer neuronal populations, and 3) performing neural recording with single-cell resolution. For example, it is important to determine whether inhibiting a population of neurons broadly suppresses all social behaviors or specifically affects prosocial helping. Likewise, does activating a particular group of neurons selectively elicit behaviors such as allogrooming? Given that a brain region typically contains heterogeneous populations of neurons that are involved in multiple behaviors, identifying circuits specific to prosocial helping may necessitate focusing on particular neuronal populations and circuits, defined by molecular markers or neural connectivity. For example, single-cell RNA sequencing has revealed that the MeA consists of diverse neuronal cell types, which are characterized by distinct neuromodulator expressions (80). Optogenetic activation of GABAergic Tac1<sup>+</sup> neurons in the MeA, but not somatostatin or cholecystinin neurons, selectively drives allogrooming in a time-locked manner (36), providing the first evidence that a molecularly defined neural circuit can be selectively activated to promote allogrooming directed toward stressed animals. Further research is needed to identify additional mechanisms specifically required for prosocial helping behavior.

### Distinct Representation of Targeted Helping Versus Comforting

Are there distinct mechanisms that control targeted helping and comforting behaviors? Recent research has unveiled insights into the distinct neuronal populations within the ACC that are responsible for controlling different prosocial helping actions, such as targeted helping or comforting others (32). Remarkably, these neural substrates appear to be largely non-overlapping, suggesting a high degree of specialization even within a single brain area. Furthermore, similar actions directed toward oneself versus others engage separate groups of neurons, hinting at a neural basis for distinguishing self-care from prosocial helping behaviors. This work suggests that distinct mechanisms may be involved in regulating different forms of prosocial helping behavior (e.g., comforting vs. targeted helping) as well as different aspects of the same behavior.

### PROSOCIAL HELPING BEHAVIOR AND PSYCHIATRIC DISORDERS

Prosocial behavior deficits are observed across numerous psychiatric and neurological conditions, including autism spectrum disorder (ASD), psychopathy, schizophrenia, bipolar disorder, depression, anxiety, attention-deficit/hyperactivity disorder (ADHD), posttraumatic stress disorder, and obsessive-compulsive disorder (81–91), as well as neurological diseases and addiction (92–96). These deficits extend beyond empathy impairments; individuals with ADHD show empathy-independent social communication deficits (89), while antisocial disorders and ASD share social reward-processing difficulties despite different prosocial impairment patterns (91). Mechanisms vary from impaired social attention (97) to complex disruptions in emotional processing and perspective taking, as is seen in borderline personality disorder (BPD) (98). Prosocial behavior has bidirectional health impacts,

protecting against anxiety/depression (88) and enhancing immunity (99), although effects vary across individuals, with sex-specific impacts on depression risk (100).

These disorders share overlapping neural substrates in social cognition and attention circuits, which suggests common network dysfunction. Fronto-parietal attention network dysregulation affects social focus across conditions (101), while ACC-thalamus circuits have been implicated in ASD, schizophrenia, and psychopathy (102–104). Individuals with psychopathy show reduced amygdala, insula, and ACC activity during empathy tasks; individuals with BPD exhibit hyperactive amygdala and altered insula-prefrontal responses (105,106); and individuals with depression present with ACC-insula changes and reduced ventral striatum activation during prosocial behavior (107,108).

Given this shared neural architecture across disorders, a key question emerges about the relationship between social experience and these circuits' function. Social isolation may reduce prosocial behavior (109), likely through changes in the neural circuits that regulate social responses. However, the relationship appears to be bidirectional; for example, engaging in prosocial actions, such as gift-giving and writing appreciative notes, can reduce feelings of loneliness and improve mood (110). Despite these findings, we lack a mechanistic understanding of how prosocial behavior is related to the homeostatic control of social interaction (111). Moreover, whether prosocial behavior itself is regulated in a homeostatic manner remains an open question for future investigation.

Research across clinical conditions has also revealed important dissociations between empathic capacity and prosocial helping behavior. For example, individuals with major depressive disorder may have intact empathy but show reduced prosocial helping behavior due to diminished ventral striatum activation (107,108), suggesting impaired reward processing for prosocial actions. Similarly, while individuals with BPD may experience intense empathic reactions through hyperactive shared representation networks (105,106), their ability to translate this into appropriate helping behavior may be compromised by impaired decision-making processes (98). Additionally, children diagnosed with ASD are often as prosocial as their peers but may express it differently, which highlights the importance of understanding and validating autistic-specific expressions of prosocial behavior rather than measuring against purely neurotypical norms (112,113).

### FUTURE DIRECTIONS AND CONCLUSIONS

A critical open question in the field is: To what extent are the neural mechanisms underlying prosocial helping behaviors distinct from those governing general social behaviors? How do specific brain regions and circuits differentiate between prosocial helping actions such as targeted helping and comforting and other forms of social interaction? The key mechanism for controlling prosocial helping behavior likely lies in the neural basis of the decision-making process occurring between perceiving another's need and initiating a prosocial helping action. This involves understanding how the brain weighs costs and benefits, integrates emotional responses with cognitive processes, regulates personal distress, and

incorporates contextual information and values to guide prosocial helping decisions and translate them into actions.

Although current experimental paradigms, particularly in rodent studies, have predominantly focused on need-based helping scenarios, there is a growing recognition that we must expand our understanding to distinguish between need-based helping, generalized sociality, and empathy-driven behaviors. This broader perspective is crucial because prosocial behaviors can arise from various motivational factors that extend beyond empathy, including the anticipation of social rewards, the expectation of reciprocity, and naturalistic behavioral responses, suggesting a more complex and nuanced understanding of prosocial helping behavior.

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### ARTICLE INFORMATION

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