



Neural, cognitive, and evolutionary foundations of human altruism

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This article considers three forms of altruism from both a psychological and a neural perspective, with an emphasis on homologies that can be observed across species and potentially illuminate altruism's evolutionary origins. Kin-based altruism benefits biological relatives and, according to the theory of inclusive fitness, is ultimately beneficial to the altruist from a genetic standpoint. Kin selection adequately explains some altruistic behavior, but it is not applicable to much human altruism. Little is known about the neural processes that support it, but they may include cortical regions involved in processing autobiographical memory and the identities of familiar others. Reciprocity-based altruism is performed in expectation of future rewards and is supported by dopaminergic cortico-striatal networks that guide behavior according to anticipated rewards. Care-based altruism is aimed at improving the well-being of distressed and vulnerable individuals and is closely linked to empathic concern. This form of altruism is thought to rely on the subcortical neural systems that support parental care, particularly structures densely populated with receptors for the hormones oxytocin and vasopressin, including the amygdala, stria terminalis, and striatum. The amygdala may be a particularly important convergence point for care-based altruism because of its dual role in responding both to cues that signal infantile vulnerability and those that signal distress. Research on altruism continues to converge across disciplines, but more research linking molecular-level neural processes to altruistic behavior in humans and other species is needed, as is research on how various forms of altruism intersect. © 2015 Wiley Periodicals, Inc.

How to cite this article:

WIREs Cogn Sci 2016, 7:59–71. doi: 10.1002/wcs.1377

INTRODUCTION

Altruism is a behavior that improves the welfare of another individual at the expense of the altruist.^{1,2} This definition captures a wide variety of human and nonhuman behaviors, from a heroic rescuer saving a drowning child to a mother rat who sacrifices her own caloric resources to nurse her young. Although these behaviors may appear wildly different

in scope and specifics, even seemingly divergent behaviors performed for the good of others may be unified by common psychological and neural mechanisms.

Research on altruism has historically proceeded along separate lines within distinct academic fields, including biology, psychology, and economics.³ Increasingly interdisciplinary work across these fields, however, has led to a more unified understanding of the processes that support altruism. In particular, attempts to reconcile psychological and biological explanations for altruism have helped to connect the ultimate biological forces that drive the emergence of altruistic behavior in a species and the proximate psychological forces that motivate altruistic behavior in an organism (Box 1).

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Conflict of interest: The author has declared no conflicts of interest for this article.

BOX 1

IS IT *REALLY* ALTRUISM?

Altruism remains a highly contentious psychological phenomenon. It is common for people to argue that all altruistic behavior is actually selfish, in part due to two persistent misunderstandings: about ultimate versus proximate causes⁴ and about intended versus foreseen effects.⁵ Some who argue that all altruism is selfish believe this to be the case because the altruist's genes may benefit from the behavior, as in the case of kin selection or caring for one's offspring. All evolved behaviors must be assumed to yield evolutionary benefits or they would not exist, and the same must be true for altruism. But genetic selfishness should not be confused with psychological selfishness. An organism that acts intentionally to sacrifice its own fitness for another is altruistic, regardless of potential genetic advantages. This is because any behavior can simultaneously be driven by ultimate (genetic) and proximate (psychological) causes.⁴ Another argument is that intentionally altruistic acts are really selfish because the altruist ultimately derives satisfaction from them. Thus, the altruist somehow benefits from the act; but this argument confuses foreseen outcomes with intended outcomes.⁵ A person who gives change to a needy stranger or rescues a drowning child undoubtedly finds the behavior rewarding, just as successfully performing any goal-directed behavior is rewarding. The fact that hedonic reward can be foreseen does not mean that achieving hedonic reward was the goal of an action. The results of empirical studies generally contradict the idea that hedonic reward is the proximate goal of altruistic behavior.⁶

But altruism remains one of the central mysteries of the biological and social sciences. As Darwin⁷ commented, 'It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those which were the most faithful to their comrades, would be reared in greater number than the children of selfish and treacherous parents of the same tribe. He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature' (p. 157). Organisms whose behavior promotes their successful survival and reproduction pass along their genes in greater proportions to

subsequent generations. The types of behaviors that most obviously promote survival and reproduction, such as acquiring resources and fending off threats, tend to be selfish.⁸ Altruistic behavior by definition disadvantages altruists, who in sacrificing their own self-interest reduce their fitness relative to those who act selfishly.

Nevertheless, an impressive array of altruistic behaviors is found among social species.^{1,9} Ground squirrels shriek alarm calls to their colony-mates upon spotting a predator, thereby improving the colony-mates' odds of escaping while at the same time drawing the predator's attention to themselves.^{10,11} Vampire bats regurgitate blood for colony-mates who might otherwise risk starvation.¹² Male turkeys support other males' courtship displays to improve those males' odds of successfully reproducing.¹³ And of course humans display a wide variety of altruistic behaviors.¹⁴⁻¹⁶ These behaviors, by which an individual risks his or her own energy, safety, or fitness to improve other individuals' welfare seem contradictory to basic biological principles.

KIN SELECTION

Two models of altruistic behavior emerged to resolve this seeming conundrum in the mid-twentieth century. The first is *kin selection*,^{17,18} which hinges on the concept of inclusive fitness. Inclusive fitness dictates that an altruistic behavior can evolve if its beneficiaries are closely related enough to the altruist to compensate the altruist for the risk he or she engenders. So an altruistic act's benefit to a full sibling must be more than twice as great as the risk it poses to the altruist. If the beneficiary is a half sibling, the benefit must be more than four times as great as the risk.¹⁹ This model most clearly explains altruistic behaviors like provisioning and defense of the colony among eusocial species such as honeybees and mole rats, among which members of a colony are the progeny of a single queen and so share strong genetic overlap.^{20,21}

What appears to be preferential altruism toward kin is also commonly observed among species that are not eusocial, including humans.^{10,11,13,22} In the laboratory, human participants report a preference for helping kin over non-kin in response to hypothetical scenarios, especially those that involve life-or-death situations.²³ Real-world life-or-death situations may also favor altruism toward kin. Living organ donation requires donors to undergo significant inconvenience, discomfort, and a small risk of serious injury or death to provide a life-saving organ

like a kidney to another person.²⁴ Perhaps unsurprisingly, the vast majority of living kidney donations (as many as 65%) are made to biologically related individuals, with far fewer donations made to individuals who are not biologically related.²⁵ Humans' and other species' tendency to exhibit preferential treatment toward individuals who are similar to themselves may also reflect preferential altruism toward individuals with stronger genetic overlap.^{18,26–29}

Proximally, kin selection must rely on specialized mechanisms for identifying and detecting biological kin.²² These mechanisms may include those required to evaluate whether a target was observed in association with one's own mother during the perinatal period, or whether the target was frequently present when the perceiver was receiving parental care, both of which are markers of siblinghood. Both variables predict self-reported altruistic behaviors toward siblings, including the number of favors previously performed for the sibling and willingness to donate a kidney to the sibling in the future.²² At the neural level, the mechanisms that may be involved in identifying kin are not well understood, but coordinated activity among cortical regions involved in social recognition (such as the fusiform face area) and multi-modal autobiographical memory (such as the precuneus) may be involved.^{30,31}

Kin selection is in some ways a problematic model for describing human altruism, however.^{18,19,32} On the one hand, a large proportion of human helping behavior across cultures is clearly aimed at benefiting close genetic relatives, including offspring, siblings, and parents. On the other hand, it is difficult to calculate whether such behaviors yield the adaptive outcomes required for true kin selection. This is in part because humans, unlike eusocial species, are much less strongly genetically related to other members of their social groups, and they do not relinquish reproduction to a single colony member. And of course their behavior is more flexible, cognitively complex, and influenced by culture.¹⁶ As a result, it is often difficult to disentangle the various ultimate and proximate motives that drive helping behaviors toward kin, which can include habit, social learning, conformity to cultural norms, and indirect self-benefit.³³ In addition, kin selection theory does not explain altruism that benefits distantly related or unrelated individuals, as much human altruism does.

RECIPROCAL ALTRUISM

An alternate model for explaining altruistic behavior toward non-kin is *reciprocal altruism*.³⁴ The premise of reciprocal altruism is that individuals will be more

likely to perform costly or altruistic behaviors for others who have helped them previously, or who they anticipate will help them in the future. As a result, reciprocal altruism is most commonly observed in closed systems of individuals who encounter one another frequently or comprise a mutually dependent social group.¹² This form of altruism is pervasive among human societies, and may have been essential to the survival of early hunter-gatherers.³⁵

Reward Expectancy

Neurocognitively, reciprocal altruism appears to be driven by reward expectancy, which is mediated in part by activity in the striatum and ventromedial prefrontal cortex.³⁶ In the ventral striatum, the release of the neurotransmitter dopamine corresponds to enhanced expectation of reward.³⁷ Information about rewards expected and received is communicated between the striatum and ventromedial prefrontal cortex to guide decision-making.^{38–40} Changes in reward expectancy arising from this process may in some cases be conscious and explicit, but in many cases (perhaps most) they are not.

The role of these regions has been demonstrated in neuroimaging studies using an iterated Prisoner's Dilemma paradigm to model reciprocal altruism.^{41,42} In this paradigm, players maximize their own gain within a round if they defect on their partner. But because defecting is typically met with retaliation, cooperation improves players' outcomes across multiple rounds by increasing the odds that their partner will cooperate in the next round. Mutual cooperation leads to the highest payoffs over multiple iterations of the game.⁴³ The paradigm models reciprocal altruism because players achieve the greatest mutual long-term gains by sacrificing their own short-term gains in any single round. In keeping with the striatum's role in tracking expected reward, activation in this region is lowest during rounds in which a player defects. This is despite the fact that defecting results in higher gains within that round. The ventral striatum is more active when the player cooperates (even if the player's partner defects). This is consistent with the idea that activation in this region does not correspond to rewards already received, because cooperating when one's partner defects yields the lowest payoff of all. This region is preferentially active following cooperation because cooperating typically results in higher payoffs in future rounds. In addition, the strength of striatal activation in any given round predicts the likelihood that the player will *continue* cooperating in future rounds,

suggesting that activation in this region positively reinforces cooperation. This may be because it increases the immediate reward value of mutual cooperation or because it provides a learning signal.^{41,44}

Serotonin

These processes may be modulated by the neurotransmitter serotonin, low levels of which decrease the value of delayed rewards relative to immediate rewards.⁴⁵ As a result, pharmacologically lowering serotonin levels decreases cooperation in the Prisoner's Dilemma, whereas elevating serotonin levels increases cooperation.^{46,47} The effects of serotonin on reciprocal altruism may be mediated by the ventromedial prefrontal cortex, a region in which activity is modulated by serotonin.⁴⁸ Depleting serotonin can result in similar patterns of neurocognitive impairment, like increased impulsiveness, as are observed in people with ventromedial prefrontal lesions.^{49,50} Serotonergic modulation of activity in the ventromedial prefrontal cortex may promote reciprocal altruism by increasing the subjective value of the long-term rewards that result from mutual cooperation.^{36,47} Together, these findings reinforce the view that reciprocal altruism is a fundamentally utilitarian phenomenon that requires the ability to use—either explicitly or implicitly—representations of delayed rewards to inhibit the tendency to acquire smaller short-term rewards.

Striatal mediated reward-expectancy seems unlikely to account for all instances of altruism, however, particularly altruism for which reciprocity is not expected. Human altruism often takes the form of care or protection provided in response to the distress of vulnerable individuals. Examples range from sharing low-cost resources with strangers in need, such as giving directions or spare change, to lifesaving heroic rescues, such as the famous case of the 'Subway Superman' Wesley Autrey, who saved a young man named Cameron Hollopeter from certain death on the New York City Subway tracks.⁵¹ Altruism in response to vulnerability or distress in strangers is not utilitarian, and is unlikely to be performed in anticipation of reciprocity, as those who are very vulnerable are generally not capable of performing altruistic acts in return.³⁴ Instead, altruistic care in response to the distress of vulnerable individuals is thought to emerge from systems that evolved to support parental care.^{2,16}

CARE-BASED ALTRUISM

Intensive care of vulnerable offspring is an essential behavior in mammals, which typically

bear *altricial*, or highly dependent, young. The survival of mammalian offspring requires that their parents (usually mothers) provide them with constant care and remain vigilant to cues that their well-being may be threatened.⁵² The emergence some 220 million years ago of the earliest mammals who were motivated to provide their offspring with such care has been described as a 'star hour,' or a transformational moment in the evolution of vertebrate behavior, because it enabled the possibility of care-based altruism.⁵³

Parental care is such an ordinary phenomenon that we often fail to think of it as altruism.⁵⁴ But it clearly meets the definition, which is a behavior that improves the welfare of another individual at the expense of the altruist. Parental care may involve, depending on the species, providing young with food, cleaning them, warming them, retrieving them to the nest, and defending them from predators.² These behaviors often require significant sacrifice to parents' own safety, resources, and reproductive opportunities. Caring for offspring genetically benefits parents, of course. But among social mammals, parental care is often and enthusiastically extended to distantly related or unrelated infants as well, a behavior known as *alloparenting*.⁶

Alloparenting

Alloparenting is observed in species ranging from rodents to primates to humans.⁵² Rats, for example, will exhibit equally intense devotion to and defense of their own pups and unrelated pups in their nest.⁵⁵ Mother deer respond with comparable behaviors to the distress vocalizations not only of unrelated infant deer, but infant marmots, seals, and even humans.⁵⁶ Over a century ago, McDougall⁵⁷ suggested that altruistic responses to distress in one's own offspring might also emerge (in somewhat weaker form) in response to distress in other's offspring and even other adults, providing a basis for altruism more generally:

Tender emotion and the protective impulse are, no doubt, evoked more readily and intensely by one's own offspring, because about them a strongly organized and complex sentiment grows up. But the distress of any child will evoke this response in a very intense degree in those in whom the instinct is strong... By a further extension of the same kind the emotion may be evoked by the sight of any very young animal, especially if in distress... In a similar direct fashion the distress of any adult (towards whom we harbour no hostile sentiment) evokes the emotion... (p. 61, 63).

Similar themes have been elaborated more recently by many investigators.^{2,16,52,58–61} Why would care be extended beyond direct offspring? Care of vulnerable offspring may represent such a powerful impulse, and one that is so essential to the survival of social mammals, as to generate altruistic responding to anything resembling an infant in distress. Supporting this link, the degree of alloparental care provided by adults of a given primate species is the single best predictor of altruistic behavior between adults of that species.⁶

Like many other primates, humans have lived in small, mutually interdependent groups for most of their evolutionary existence.⁵² Within these groups, a tendency for adults to provide nurturant care for the offspring of siblings, the offspring of unrelated group members, and even needy or vulnerable adult group members may have increased the fitness of all group members.⁶² This pattern is consistent with multilevel selection theory, also known as group selection.³ According to multilevel selection theory, selection can occur at the level of the gene, individual, or group. Under some circumstances, altruism could be selected if it yielded group-level benefits that outweighed individual-level costs.⁶² Although multilevel selection theories are sometimes viewed in opposition to other theories of altruism, like kin selection, recent analyses suggest that they may actually be strongly compatible.⁶³

That humans do experience the urge to care for unrelated children, even those who are strangers to them, can be observed in many contexts today, including the adoption and fostering of children, the use of child-related imagery to boost charitable giving, even the urge to care for pets and dolls, particularly those with infantile appearances.¹⁶ This urge is experienced by both sexes in our species, which is unusual among mammals, and may reflect the unusually intensive care required by human infants.⁶⁴

Care-based altruism is most effectively elicited not by infantile features alone, but by infantile features paired with indications of emotional distress.^{2,65} As it happens, the nonverbal cues used by many species, including humans, to signal distress tend to incorporate features of infants. Fearful vocalizations are typically high pitched, as are infant vocalizations, and fear-related postural displays typically make the individual appear smaller or otherwise more juvenile.^{58,66–68} Unlike most species, humans also rely heavily on facial expressive behavior for emotional communication.⁶⁹ And human facial expressions of fear also appear to serve to mimic characteristics of infants.^{70,71} Fearful expressions are perceived to look infantile, and perceivers rate them

as looking babyish, round, submissive, and weak. This is true even when digital manipulations prevent the expressions from being explicitly recognized as conveying fear.⁷⁰ The babyish appearance of fearful expressions—with their widened eyes, raised brows, and a flattened brow ridge—may stimulate associations between individuals expressing fear and human infants.^{59,70} As a result, fearful expressions may elicit parental responses via similar mechanisms as do actual infants.

Empathic Concern

Proximally, the mental state that promotes altruistic care in response to vulnerability and distress is empathic concern, sometimes called simply ‘empathy’ or, alternately, sympathy, concern, caring, or compassion.^{1,16} Empathic concern is typically defined as the other-oriented, tender state experienced in response to another individual’s distress that promotes altruistic behaviors aimed at relieving the distress.^{1,16} A wealth of research has established the relationship between empathic concern and altruism. In one classic paradigm, study participants watched an obviously distressed stranger receiving electrical shocks, then had the opportunity to volunteer to receive the remaining shocks in her place. Participants induced to feel more empathic concern were more likely to volunteer to receive the shocks even when an alternative was offered.⁷²

Empathic concern may be powerful enough to override other self-interested or normative motivations. For example, inducing empathic concern in the laboratory can upend the pattern of responses typically observed in the Prisoner’s Dilemma. During games in which participants learn of their partner’s response before submitting their own response, participants will almost always (in upward of 95% of cases) defect if their partner defects first.⁷³ But if participants are first induced to feel empathic concern for their partner, they will cooperate with her 45% of the time even after she defects, and even though cooperating conflicts with their material self-interest as well as with social norms like fairness and distributive justice.¹⁶

It is important to distinguish empathic concern from other phenomena also commonly described as ‘empathy,’ such as Theory of Mind, which is sometimes called *cognitive empathy*, and empathic accuracy, which is sometimes called *emotional empathy*.^{1,74,75} Cognitive empathy is the identification of others’ high-level cognitive states, including their focus of attention, intentions, and beliefs.^{76,77} This is the form of empathy impaired by autism

spectrum disorders.⁷⁶ Cognitive empathy is reliant on activity in higher-level perceptual and cognitive brain areas including the medial prefrontal cortex and temporoparietal junction, and it is not closely linked either to altruism or to antisocial behaviors like aggression.^{75,78} On the other hand, emotional empathy, which is the low-level representation or identification of another's emotional state, can be linked to altruism.^{15,79} Emotional empathy probably relies primarily on activity in the cortical and subcortical structures responsible for generating the target emotion. Hence empathy for pain involves activation in dorsal anterior cortex and the anterior insula, which are involved in affective and motivational components of experiencing pain,⁸⁰ but empathy for fear relies on activation in the amygdala, which is the structure most directly involved in the experience of fear.⁸¹

It must be emphasized that emotional empathy is not synonymous with empathic concern.^{81,82} Emotional empathy refers to *understanding* another's emotional state, not *caring* about that state—these are distinct processes. But some forms of emotional empathy are important precursors for empathic concern. This is most demonstrably true regarding emotional empathy for fear, as individuals who are highly sensitive to others' fear—who can, for example, accurately identify it from others' facial expressions—also tend to be highly altruistic.^{15,79,83} Conversely, psychopaths, who lack empathic concern, also lack emotional empathy for others' fear—but not for emotions like anger or disgust.^{84,85}

The Neural Basis of Care-Based Altruism

At the neural level, care-based altruism appears to be driven by mechanisms that overlap heavily with the mechanisms driving parental care.² These are comprised primarily of subcortical structures containing receptors for the neurohypophyseal hormone oxytocin.^{86,87} This hormone is produced only in mammals, and its emergence is closely tied to the emergence of mammalian parental care.⁸⁸ It is by no means the only hormone involved in parental care (others include vasopressin and prolactin, as well as gonadal hormones that prime the effects of neurohypophyseal hormones^{87,89,90}), but oxytocin is the hormone most robustly associated with parental care.⁹¹

Parental care is frequently studied in rats because of how dramatically pregnancy changes female rats' responses to rat pups. Female rats who have not previously been pregnant find rat pups actively aversive. They go out of their way to avoid them or may even cannibalize them.⁸⁷ But around the time a rat is ready to bear young for the first

time, her behavior toward pups radically transforms. Now she not only does not avoid pups, but she will make sacrifices to maintain contact with them. In one study (described in detail by Preston²), rat mothers continually pressed a bar for hours when the bar presses allowed them to access and retrieve a succession of unrelated rat pups.⁹² In another, new rat mothers chose contact with rat pups over injections of a powerfully enjoyable drug (cocaine).⁹³

Oxytocin

This shift in maternal orientation is driven primarily by changes in the oxytocin system during and after parturition. Toward the end of pregnancy and the onset of lactation, the hypothalamic neurons that manufacture oxytocin proliferate, as do oxytocin receptors in brain areas such as the amygdala, bed nucleus of the stria terminalis, and septum.^{94,95} Both the density of receptors and the amount of oxytocin produced appear to support the provision of maternal care. The density of oxytocin receptors in certain brain regions strongly predicts variation in the quality of maternal care at baseline.⁸⁶ And when oxytocin receptors are blocked chemically, maternal behaviors drop off.⁹⁶ Genetic manipulations that eliminate oxytocin receptors also reduce maternal behaviors,⁹⁷ but circulating levels of oxytocin are important as well.⁹⁸ Oxytocin injected directly into the brains of virgin rats causes them to spontaneously exhibit the full suite of maternal behaviors in response to unrelated pups, including retrieving pups to the nest and crouching over them, which simultaneously provides pups with warmth, protection, and nursing access.^{99,100} Intranasal administration of oxytocin is also effective, and can generate maternal care and alloparental care for unrelated young in a variety of species.^{101–103} Exposure to infant-related sensory stimuli can also in itself trigger increased production of oxytocin,¹⁰⁴ which may explain why simple continuous exposure to infants typically results in increasing levels of care over time, even among virgin female rats.¹⁰⁵

Where does oxytocin act in the brain to produce these effects? Oxytocinergic messages are projected from the paraventricular and supraoptic nucleus of the hypothalamus to other subcortical structures that include the amygdala, bed nucleus of the stria terminalis, striatum, and brainstem.^{106,107} In both humans and nonhuman animals, the amygdala appears to be a central locus of oxytocin's effects.^{86,106,107} The amygdala is richly populated with oxytocin receptors, particularly in the central nucleus.⁸⁶ This is the primary output nucleus of

the amygdala, which coordinates fear-related autonomic and behavioral responses via its projections to the hypothalamus and periaqueductal gray, respectively.¹⁰⁸

Within the central nucleus, oxytocin is expressed primarily in the lateral division, and increases in oxytocin production increase neuronal excitability in this region.¹⁰⁹ This may seem paradoxical, as oxytocin has anxiolytic effects.^{110,111} In neuroimaging studies oxytocin reduces overall amygdala activity in response to distress cues like fearful facial expressions or infant cries.^{112–114} But neurons in the lateral division of the central nucleus include ‘off’ neurons that are preferentially active in response to appetitive stimuli (and only appetitive stimuli) such as cocaine or morphine.¹¹⁵ These neurons function to downregulate activity in the medial division of the central amygdala.¹⁰⁹ The role of these ‘off’ neurons may be to inhibit fear responding in the context of appetitive stimuli.

Infants themselves are powerfully appetitive stimuli.¹¹⁶ The characteristic features of an infant’s body and face have been conserved across species precisely because they are so appealing.^{117,118} In humans, the appeal of infant faces has been demonstrated using a lever task in which neutral infant faces elicited behavioral approach, whereas neutral adult faces did not.⁵⁹ In this study, participants viewing infant faces could pull a lever toward themselves (approach) more quickly than they could push it away from themselves (avoidance), a response likely driven by dopaminergic reward systems in the striatum that are highly responsive to infant faces, particularly those considered classically ‘babyish.’¹¹⁶ Interestingly, similar approach-based behavioral responses are observed in response to adults’ fearful expressions, corroborating the babyish qualities of these expressions.^{59,119}

Infants’ appeal also increases as oxytocin levels rise. Infant faces are rated as more appealing following a dose of intranasal oxytocin, whereas the same is not true for adult faces, which are actually seen as less appealing following oxytocin.¹²⁰ Increased oxytocin levels may potentiate the appetitive qualities of sensory stimuli related to infants, whether it be the smell, appearance, or vocalizations of actual infants, or stimuli that mimic these features of infants.⁸⁶

Convergent Roles of the Amygdala

The two key features of care-based altruism, then—responses to distress and responses to infant cues—appear to converge in the amygdala. In addition to its role in supporting parental care, the amygdala is

also a critical region for perceiving others’ distress—particularly fear-related cues like facial and vocal expressions.^{121,122} Individuals with complete bilateral amygdala lesions are impaired in recognizing facial and vocal expressions of fear, as are psychopathic individuals who exhibit both amygdala dysfunction and minimal empathic concern.^{84,85,123} This may reflect the fact that the amygdala is the structure most directly involved in the experience of fear and it may therefore be essential for empathic simulation of others’ fear.⁸¹

This may be why higher-than-average levels of fear responsiveness and amygdala reactivity are associated with heightened altruistic responding (although excessive self-focused anxiety is associated with reduced altruistic behavior¹²⁴). Rats bred for high levels of anxiety provide better care to their pups than do low-anxiety rats,¹⁰⁷ and this enhanced maternal care is associated with increases in the amount of oxytocin released in hypothalamus and the central nucleus of the amygdala.⁹⁸ High levels of fear-sensitivity in humans also are associated with increased altruistic behavior as well as enhanced amygdala reactivity.^{79,125–127} Higher fear sensitivity may reflect a more responsive amygdala that is better equipped to respond empathically to others’ distress.

Supporting this, extraordinarily altruistic adults are more sensitive than average to others’ fear. A recent study investigated neural and cognitive correlates of extraordinary altruism by assessing neural structure and functioning in a population of altruistic kidney donors, all of whom had donated a kidney to a stranger.¹⁵ Relative to controls, altruists exhibited a stronger amygdala response to fearful facial expressions, and were relatively better at identifying fearful expressions as well. Their amygdalae were also 8% larger than those of controls (in contrast to psychopaths, who have relatively small amygdalae).¹²⁸ Importantly, however, altruists’ amygdalae were not *generally* more responsive than controls—their amygdala response to angry expressions was actually reduced. Their increased sensitivity was only in response to fear.

Together, these findings suggest that when indications of vulnerability and distress are paired—whether in the form of actual infant distress cries or infantile-looking fearful expressions—the information converges in the amygdala, perhaps in the lateral division of the central nucleus, stimulating oxytocin-mediated inhibition of behavioral and autonomic fear responding via the central nucleus’s efferent projections, and potentiating motivated altruistic care.^{86,106,114,129} The provision of care appears to be

coordinated via connections between the central amygdala and regions that include the hypothalamus, periaqueductal gray, stria terminalis, and dopaminergic cortico-striatal networks.^{2,95} Oxytocin activity in regions of sensory cortex may also play a role in responding to infant-related sensory cues like distress cries.¹³⁰

UNRESOLVED QUESTIONS

Although research on altruism continues to converge across disciplines, investigations of the various forms of altruism remain somewhat siloed. A major as-yet unresolved question concerns how altruistic behaviors based on kin, cooperation, and care intersect, as they surely do.

Although the study of reciprocal altruism has focused primarily on the role of dopaminergic striatal reward systems, the study of care-based altruism has focused primarily on the role of oxytocinergic limbic structures. It is likely, however, that these regions interact to support both forms of altruistic behavior. Care systems may modulate the tendency to cooperate in reciprocal altruism paradigms and real-world settings. Care may moderate the tendency to cooperate as a first move in the absence of any baseline information about one's partner, given oxytocin's role in promoting trust.¹³¹ Care may also modulate retaliatory behavior following defection. If a partner is portrayed as vulnerable and distressed, retaliation plummets, suggesting that when the urge to provide care for a vulnerable individual is triggered, it may overwhelm the urge to maximize personal gain.⁷³ This is consistent with evidence of mutual inhibition between striatal networks that promote approach and reward learning and limbic networks that promote avoidance and fear-learning.¹³²

But the interaction between systems that support care-based altruism and reciprocal altruism must be more complex than this, as striatal reward mechanisms are also thought to support motivated care-based behavior once the urge to provide altruistic care has been generated.² These interactions may occur at multiple levels. Subcortically, lesions to the hypothalamic neurons that project to the dopamine-producing ventral tegmental area inhibit maternal behavior.¹³³ But dopaminergic and oxytocinergic pathways also converge in the medial prefrontal cortex, and this convergence may play an important role in reinforcing the rewarding aspects of parental care.¹⁰⁶

Less empirical information is available regarding interactions between kin-based and care-based

altruism. Under normal circumstances, the two forms of altruism may be complementary, such that altruism is more likely the more closely related and infantile a target is. This would result, appropriately, in a person's own infant receiving more intense care than her older child, but the older child receiving more intense care than unrelated peers. But tensions between these systems could arise as well. Responding to the distress of an unrelated individual to the disadvantage of one's own kin is an obvious example, and one that arises in the real world, particularly in the case of so-called 'pathological altruism.' Wesley Autrey, for example, left his own young daughters alone on a subway platform to save a stranger.⁵¹ Any risky, altruistic act on behalf of a stranger runs a similar risk of advantaging a stranger over family if harm does befall the altruist and causes family members distress. This may explain why such behavior is sometimes described as pathological.¹³⁴

Because multiple altruistic motivations almost certainly co-occur with some frequency, better understanding of the interactions among them would likely help to illuminate complex human behaviors as well as the neural and psychological basis of each form of altruism in isolation.

Conclusion

Altruism is a central organizing principle among group-living mammals, and there are few species for which this is more evident than humans. Altruistic behavior is ubiquitous in human social interactions, whether it be kin-based, cooperation-based, or care-based, or some combination of these types. Kin-based altruism involves altruism toward biological relatives, whose survival and reproduction will ultimately benefit the genes of the altruist. This form of altruism likely relies on neurocognitive systems that enable the recognition of siblings and other close genetic relatives. Cooperation-based altruism involves sacrificing immediate gains to benefit another in anticipation of future reward, and is supported by dopaminergic striato-cortical pathways, which are also likely moderated by serotonin. Care-based altruism co-opts systems that originally developed to support parental care. In social species, these systems also support alloparental care, or care for others' young. Alloparenting likely represents the direct origin of care-based altruism, which is elicited by signs of vulnerability and distress. This form of care is supported by oxytocinergic limbic structures like the amygdala. Although these forms of altruism surely interact, little is known at this point about how these interactions

might occur. However, a recent surge in academic interest in altruism and an increasing emphasis on cross-disciplinary explorations of the topic are

promising signs that the understanding of the neural and psychological bases of altruism will continue progressing rapidly.

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