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Beyond nature and nurture: a context-dependent, mechanism-specific framework for altruism

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Abstract

Altruism and prosocial behavior are foundational to moral development. Yet, the extent to which these tendencies are innate or acquired through experience remains a central debate across psychology, neuroscience, and evolutionary biology. Existing research for innate explanations argues that prosocial behaviors are seen across different species, linked to specific variants, associated with neural activity in areas like the medial prefrontal cortex and anterior cingulate cortex, and present in infants before childcare learning environments significantly influence them. On the other hand, socialization research in support of a learned origin displays how parenting styles, cultural values, socioeconomic status, and school environments all shape the extent of our prosocial behaviors. Despite this extensive literature, framing altruism as either nature- or nurture-driven overlooks its multifacetedness. This review synthesizes evidence across disciplines and argues that the nature-versus-nurture framework alone is insufficient to explain prosocial behavior. Instead, it proposes a context-dependent, mechanism-specific model in which altruism is understood as a set of distinct but interacting processes, including kin-based, reciprocity-based, empathy-driven, and norm-based behaviors. By reframing altruism as a collection of contextually activated mechanisms rather than a single underlying trait, this framework offers a new theoretical approach for interpreting seemingly conflicting findings across disciplines and generates falsifiable predictions for future research. To facilitate empirical evaluation, the review also outlines a testable experimental framework capable of distinguishing among these mechanisms and assessing their selective activation across contexts.

Keywords

Altruism, Prosocial behavior, Context-dependent altruism, Mechanism-specific framework, Regime-based model, Nature versus nurture, Empathy, Reciprocity, Social norms, Kin selection

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1. Introduction

The extent to which human morality is biologically determined versus socially constructed is a long-standing uncertainty, especially within the context of choosing prosocial/altruistic behavior. Prosociality is the voluntary action of performing an action that benefits another. Altruism takes this concept one step further, in which the doer of the action may incur a cost and/or will not gain a personal advantage (1). If altruism is largely innate, it suggests that humans may be biologically predisposed to cooperation, with these tendencies emerging early in development. If altruism is primarily learned, it could imply that social environment, cultural norms, and other life experiences shape helping behavior.

A wide range of disciplines has contributed to this debate. Evolutionary biologists turn to the helping behavior exhibited by nonhuman animals, which suggests that prosociality predates human evolution and was selected by natural selection as a beneficial trait (2). Theories such as kin selection and Hamilton's rule also provide frameworks for understanding the dynamics between fitness and costs when an individual performs this self-disadvantageous behavior (3). Their work is complemented by behavioral genetics and neuroscience, which demonstrate that genes and brain volume shape individual differences in behavior (4). On the other hand, social psychologists turn to the heavy influence of parenting, school, and cultural contexts on other moral behaviors such as aggression, obedience, and fear (5,6). Developmental psychology provides evidence for both perspectives, as they debate the extent to which infants are influenced by their surroundings (7).

Despite substantial research, a consensus has not been reached about whether intrinsic or extrinsic factors play a greater role in the display of a prosocial behavior. One reason for this is that altruism has been treated as a single construct despite being measured across different contexts. Each type of altruistic behavior arises from different cognitive or affective processes; for example, the mechanism behind helping a kin-related individual is different from the one that causes one to respond to someone in distress. Thus, this review seeks to synthesize evidence from the nature-versus-nurture literature, identify conceptual limitations in treating altruism as a single trait, and propose a context-dependent, mechanism-specific framework in which prosocial behavior emerges from distinct mechanisms that are selectively activated across different contexts. Though prosociality/altruism are distinct concepts, they are used interchangeably in this review because many empirical studies do not distinguish "pure" altruism from helping/cooperative behavior. By integrating findings across fields and reframing altruism, this paper aims to provide a more precise account of prosocial behavior and identify directions for future research that move beyond treating altruism as a single trait.

2. Discussion

2.1 Is altruism innate?

2.1.1 *Evolutionary perspective*

The evolutionary origin of altruistic behavior in humans can be traced to behaviors observed in related primate species. As seen in cooperative breeding species such as marmosets *(Callithrix jacchus)* and cotton-top tamarins *(Saguinus oedipus)*, food sharing is common among

genetically unrelated individuals (8). Tamarins in particular were shown to share more food with individuals that had previously shared food with them, suggesting an ability to distinguish between cooperative and non-cooperative social partners (9). Similar observations have been reported in non-cooperative breeders such as bonobos (*Pan paniscus*) and tufted capuchin monkeys (*Cebus apella*), although capuchins were more likely to help another conspecific when a reward was available to themselves, indicating that their prosocial behavior may be contingent on expected personal benefits (10–12).

Interestingly, chimpanzees *(Pan troglodytes),* the most closely related primate species to humans, show variable prosociality. They demonstrate the ability to help both humans and unrelated individuals retrieve out-of-reach items and utilize cognitively advanced, targeted helping to help others with specific goals using visual cues (13–15). Wild Tai forest chimpanzees also provide extensive care to orphans through adoption (16). However, other studies conducted in captive settings have shown contrasting results, with selfishness prevailing over mutualistic or altruistic behaviors, and prosocial responses observed only when given significant vocal cues (17–19). These observations have led many to suggest that cooperative behavior may have emerged later in human evolution than was originally assumed. However, only being responsive to a signalling cue, some argue, does not rule out the prosociality of chimpanzees and may suggest species-dependent uniqueness (20). Taken together, these findings support the view that altruistic behavior has deep evolutionary roots in primates, although the timing, origins, and mechanisms underlying its emergence remain unclear.

Non-primate animals exhibit prosocial behavior, suggesting that cooperative behavior has independent evolutionary origins. Rats prefer mutualistic rewards and can respond prosocially when they see a conspecific in distress, though whether they are motivated by empathy or social experience remains debated (21–24). Eusocial communities like the Mediterranean desert-dwelling ants *(Cataglyphis piliscapa)* make valiant efforts to free trapped individuals for the hypothesized reasons of maintaining colony size to maintain an appropriate number of workers to forage (25). Moreover, non-breeding subordinate purple-crowned fairy-wrens (*Malurus coronatus*) were more likely to defend nests from predators when they had a greater probability of inheriting the breeding position, indicating that cooperative behavior may be shaped by anticipated future fitness benefits. In other words, anti-predator response is enacted more frequently when the wren has a higher chance of producing its own kin, which aligns with the kin selection theory (26). Beyond naturally cooperative species, prosocial behavior has also been documented in more competitive species, such as archerfish, suggesting that helping behaviors may arise across a broader range of ecological and social environments than previously assumed (27).

In the discussion of the evolutionary origins of altruism, it is important to acknowledge Hamilton’s rule, which posits that altruism is favored when the action is performed on an individual who is more closely related, so that copies of the altruist's genes are more likely to be passed down to future generations. This has

been observed in several human studies in which people have indicated, through surveys, that they are more willing to act altruistically toward closer relatives than toward distantly related individuals (28,29). While many examples discussed thus far involve helping unrelated individuals, these behaviors illustrate that the evolutionary maintenance of altruism is not limited to immediate personal gain. Consistent with Hamilton's broader insight that costs and benefits determine the evolutionary viability of helping behavior, actions such as food sharing and cooperative assistance can provide long-term fitness advantages through enhanced social cohesion, reciprocal interactions, and increased survival within social groups.

2.1.2 *Ontogenetic studies*

Studies of infants have frequently been invoked as evidence for the innate origins of altruism, as prosocial tendencies can be observed early in development, before environmental and social influences are thought to have fully shaped behavior. As early as 5 days old, newborns were more attentive to videos of prosocial interactions than to to those of antisocial interactions, suggesting a preference for prosociality despite limited life experience (30). Similar social cognitive processing via the visual system was observed in six-month-olds, with changes in pupil dilation from baseline when they witnessed a person's happiness or distress (31). Notably, two-year-olds showed no significant difference in pupil dilation when they themselves could help a person in distress compared with when they saw a third party assisting. This is highly indicative of children's genuine interest in others' welfare, as their physiological responses showed that they wanted the person to receive help, even if they were not the ones providing it (32). This interpretation is further supported by findings that parental encouragement had little influence on helping behavior, suggesting that young children's prosocial actions may not be driven primarily by the pursuit of social approval or external reinforcement (33). Together, these findings reveal that infant studies provide compelling evidence for innate altruistic tendencies.

2.1.3 *Genetic causes*

The genetic underpinnings of altruistic tendencies have primarily been found to regulate the oxytocin–vasopressin–dopaminergic neural and neuroendocrine systems. For example, researchers have observed that individuals who made more empathetic decisions in an ultimatum game underwent a significant increase in oxytocin levels from baseline (34). Many have highlighted the role of variants in the oxytocin receptor (OXTR) gene, which encodes oxytocin, a key modulator of social behavior. More copies of the major allele (G) in the rs11131149 marker were associated with higher social cognition (greater cooperation, empathy, and joint attention) at 18 months (35). In adults, several OXTR SNPs were associated with greater allocation of funds in laboratory-based economic games such as the Dictator Game and the Social Value Orientations Task (36). These studies suggest that OXTR variants affect prosociality across multiple stages of human development. The effects of these SNPs may also be gender-specific, such as the association between rs2254298 and prosocial tendencies being observed only in males, which may be due to their larger hypothalamic grey matter volume (37).

Additionally, a less-studied genetic marker, the arginine vasopressin 1a (AVPR1a) receptor, which is involved in the affiliative behavior of voles, also appears to influence prosociality in humans. Individuals with longer AVPR1a RS3 repeats allocated more money in the Dictator Game and reported higher scores on two self-report measures of human altruism (38). Moreover, individuals with short androgen receptor (AR) alleles were found to be more generous in economic games, underscoring the role of hormone receptors in prosocial behavior (39). Collectively, evidence involving the OXT, AVPR1a, and AR genes underscores the genetic complexity of altruistic behavior and illustrates how inherited genetic variation can contribute to individual differences in prosocial tendencies.

2.1.4 *Neural correlates of altruistic behavior*

Various areas of the brain are activated when making prosocial decisions, especially the fronto-limbic system. The medial prefrontal cortex (MPFC) is engaged in understanding others' mental states, especially in registering situational distress (40). Those with greater dorsal MPFC activity reported being more amenable to understand others' thoughts and desires; they were also more likely to be generous and to exert greater effort to help others (41). In conjunction, the ventral MPFC has been shown to evaluate the value of a reward given to another by midbrain dopamine neurons, whose firing rates increase with reciprocated cooperation (42,43). This area also integrates information from the posterior superior temporal cortex (PSTC), which helps an individual perceive the agency of their actions (44).

Located behind the MPFC is another area implicated in altruistic decision-making, the anterior cingulate cortex (ACC). Rhesus monkeys that had lesions to the ACC no longer exhibited a previously observed prosocial preference for rewarding another monkey with juice, suggesting that the ACC plays a critical role in linking decisions to outcomes that benefit others (45). Humans show a similar dependence on the ACC in predicting the value of a reward for another, specifically in the anterior cingulate cortex gyrus (ACCg) (46). This ability of the ACCg was then associated with empathy; individuals with high emotion contagion/empathy had an ACCg that only activated when assessing rewards for others, and high activity in ACCg was associated with reacting to someone's pain (47,48). Individuals exhibiting greater other-oriented empathic concern were more likely to engage in altruistic decision-making and tended to do so more quickly, consistent with the notion that empathy-driven helping may involve relatively rapid affective processing (49).

While there is a consensus on the functions of the MPFC and ACC, the roles of other brain areas are more debated. Some regard the ventral tegmental area (VTA) as being involved in helpful behavior, based on higher activation of the area in highly empathetic individuals (40). It was also found to operate in conjunction with the bilateral striatum in providing the "warm glow" effect, a reward-reinforcement mechanism during altruistic acts (50). Although this mechanism has been interpreted as evidence that rewarding prosocial actions reinforces future helping behavior, others argue that it may instead reflect the VTA's broader role in processing self-relevant rewards and motivating self-benefiting decisions (51).

In addition to neuronal circuitry, neuroanatomical differences present within altruists have also been explored. Altruistic kidney donors showed better responses to fearful facial expressions, consistent with the finding that they also showed enhanced volume in the right amygdala (AMY), an area of the brain that processes emotions (52). Similarly, greater gray matter volume in the right temporoparietal region was associated with a greater willingness to engage in altruistic actions despite increasing personal costs (Figure 1) (53).

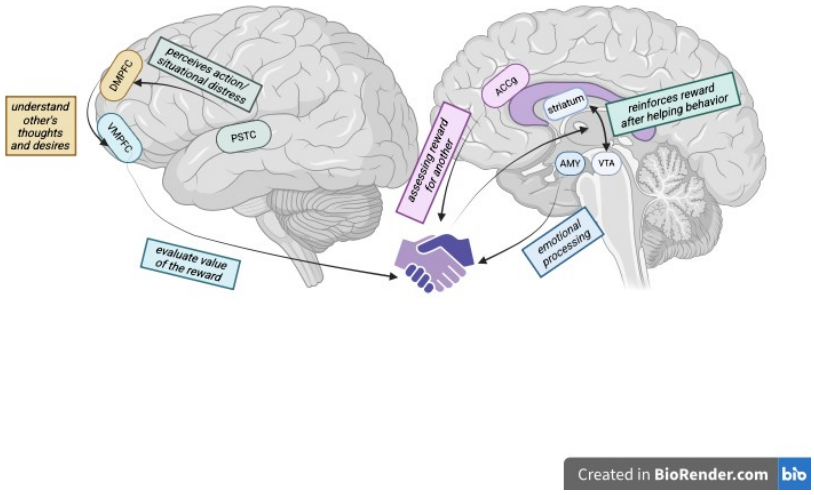

Figure 1. Areas of the brain that are activated during prosocial/altruistic behavior. (Created with Biorendr.com)

2.2 Is altruism learned?

2.2.1 *Ontogenetic studies*

Several studies of infants suggest that early learning experiences significantly shape their altruistic behavior and that not all altruistic behavior is innate. For example, reciprocal playing may help one and two-year-olds recognize that people are responsive to each other's needs (54). Children who were modeled helping behavior by adults were more likely to exhibit similar behavior, such as by learning how to respond to communicative cues about their desires (55,56). Responsiveness to facial cues, such as fear, however, was found to be independent of maternal engagement in seven-month-olds (57). Together, these findings suggest that there may be differences in how verbal and communicative cues are processed during early development.

2.2.2 *The effect of parenting*

Parenthood can influence prosociality in humans during early childhood development. Preschool children whose fathers played active roles in housework, childcare, and playtime exhibited more prosocial behavior because they consistently saw models of helpful behaviors and sharing (58). Modeling prosociality and enforcing expectations of child behavior as part of authoritative parenting also contribute to children exhibiting more cooperative behaviors

than those who experienced authoritarian parenting, in which the focus is on fear of punishment rather than genuine kindness (59). Furthermore, children who experienced harsh discipline or had parents who showcased negative expressiveness through threats and lack of attentiveness were more likely to be less prosocial and more conduct-disordered (60,61). Thus, parents who model prosocial behavior are more likely to have children who exhibit it, underscoring the importance of adopting positive parenting styles.

2.2.3 *The effect of school and workplaces*

Beyond the family environment, early childcare and educational settings serve as important contexts in which prosocial norms, behaviors, and social expectations are learned and reinforced. Teachers serve as role models of positive social exchanges and foster spaces for people to form friendships through daily activities (58,62). With children spending most of their time in school, the setting has proven to be a successful place to implement interventions that promote prosocial behavior. This, in turn, decreases aggression and improves students' learning experiences (63). Beyond school-age, leadership in communal spaces promotes prosocial behavior. For example, in a study of working adults in a professional setting, employees were more likely to engage in prosocial behavior when they perceived their leaders as humble or supportive (64). Together, these studies show that the behavior of people in authority greatly influences whether an individual exhibits altruism.

2.2.4 *The effect of cultural values*

Values that are more prominent in some cultural groups affect the development of prosocial behavior. Collectivist societies, typically found in Asian and South American cultures, tend to be more prosocial, as interpersonal relations, family-oriented values, and social obligation are emphasized compared to individualistic societies found in Western cultures (65,66). For example, a study comparing Indonesian and Australian older adults found that Indonesian participants were more likely to discuss the potential risks and obligations associated with prosocial acts, suggesting that helping behavior in collectivist cultures may be viewed more as a deliberate moral responsibility than as an intuitive response (67). Another example of the influence of collectivism is imitative altruism, in which children from collectivist societies are more likely to imitate altruistic behavior because they are taught to obey elders. In contrast, children in individualistic societies are more likely to emphasize autonomy. This was highlighted in a study that found children from rural Indian villages to be more generous than those from a city in the United States after watching their parents model donations (68). Children from collectivist societies are also more likely to respond to fearful faces, suggesting that certain cultures emphasize responsiveness to distress more than others (69). These findings support the notion that sociocultural contexts affect how others practice and perceive prosociality.

2.2.5 *The effect of economic status*

Economic status has been shown to influence altruistic and prosocial behavior, although the relationship appears to vary across contexts and stages of development. In the Dictator Game, one participant receives a resource and can choose how much, if any, to allocate to another participant who cannot reciprocate, making it a useful paradigm for studying prosocial behavior in the absence of direct personal gain. Using this

task, one study found that children were less generous when sharing involved resources they valued more highly, even when they understood principles of fairness (70). This finding suggests that prosocial behavior is shaped not only by moral reasoning but also by perceived personal costs, highlighting the role of resource valuation in helping decisions. Similarly, another study that used the Dictator Game found that young children from higher socioeconomic backgrounds shared more resources than their peers from lower socioeconomic backgrounds, suggesting that greater access to resources and social norms around sharing can shape prosocial choices (71,72). In contrast, other findings from a study of college students indicate that socioeconomic status did not directly predict prosocial behavior; instead, it is mediated by parent-child attachment and emotion regulation self-efficacy (73). Overall, these findings indicate that economic status influences altruistic behavior indirectly rather than determining behavior uniformly.

2.2.6 *The influence of pet ownership*

Interactions with animals, particularly household pets, may be an environmental factor influencing the development of altruistic personality traits and prosocial behavior. Generally, caring for a pet involves a full understanding of recognizing non-verbal behavior, which has the effect of promoting empathy and concern for others. A study found that adult humans who rated their emotional attachment to their pets as higher also rated their empathic concern and prosocial behavior as higher (74). These findings indicate that pet ownership is likely to support the development of prosocial behavior by providing everyday and normalized opportunities for empathy and responsibility.

2.2.7 *Neural correlates of prosocial learning*

The Reinforcement Learning Theory states that prediction errors drive learning. In the context of prosocial behaviors, it can be argued that individuals need to learn how their actions affect others. A study exploring prosocial learning found that the ventral striatum distinguished between selfish and selfless behaviors, whilst the ACC was highly activated when an individual learned to benefit another person. However, the authors found that more empathic people's ACCs showed greater signaling sensitivity. This suggests that individual neuronal differences may contribute to prosociality (75).

2.3 Analysis of the innate and learned approaches

Taken together, the literature reviewed here reveals both the strengths and limitations of the nature-versus-nurture framework for understanding altruistic and prosocial behavior. Proponents of the innate nature of altruism argue that it has been observed across species, from primates to non-mammals, and that individual differences in behavior are due to variants in the OXT, AVPR1a, and AR genes and to differences in the neuroanatomy of the limbic system. In contrast, proponents of the learned origins of prosocial behavior emphasize the roles of parenting, educational environments, cultural values, and socioeconomic conditions in shaping helping behavior. Given the substantial evidence supporting both perspectives, a critical evaluation of their respective strengths and limitations is necessary to better understand the origins of prosociality (Figure 2).

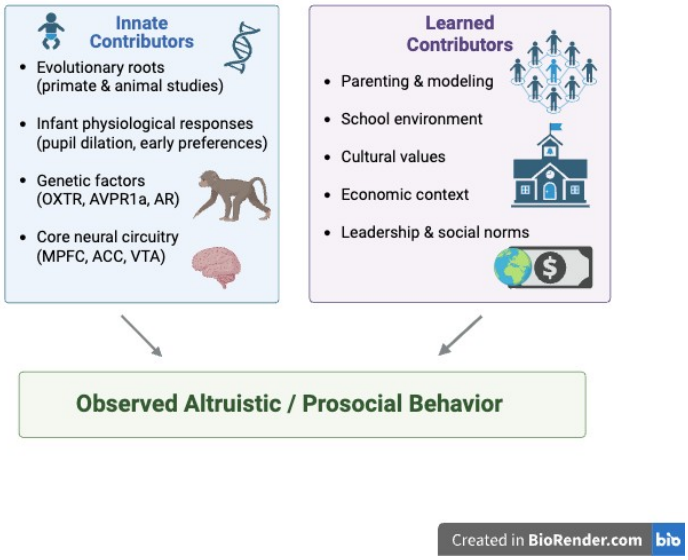

Figure 2. Studied contributors of prosocial/altruistic behavior. (Created with Biorendr.com)

Although helping behaviors observed across a wide range of species support the evolutionary roots of altruism, caution must be exercised when interpreting such actions, as human concepts of kindness and morality can be readily anthropomorphized. One debate centers on whether behaviors explained by kin selection—where helping is directed toward genetically related individuals—should be considered genuine altruism or simply an evolutionary strategy for increasing inclusive fitness. Some scholars argue that altruism, in its strictest sense, requires helping individuals without regard to genetic relatedness, placing it in tension with kin selection theory (76). However, substantial evidence demonstrates that many animals assist unrelated conspecifics and, in some cases, even individuals of other species, suggesting that prosocial behavior cannot be explained solely by kin-directed mechanisms (8,9,13–16,21–24).

Studies of infants have been cited in support of both innate and learned explanations of prosocial behavior. Proponents of an innate origin argue that the emergence of prosocial tendencies early in development suggests the presence of biologically prepared social capacities. For example, infants have been shown to distinguish between prosocial and antisocial interactions as early as 5 days after birth, implying the existence of rudimentary mechanisms for evaluating social behavior (30). In contrast, advocates of the learned perspective contend that early developmental environments play a critical role in shaping prosocial tendencies. This view is rooted in the concept of *tabula rasa*, the idea that knowledge and behavior are largely acquired through experience, making socialization and early learning particularly influential during infancy (57). However, evidence that genetic and neurobiological factors influence behavior from the earliest stages of life challenges a strict *tabula rasa* perspective and instead suggests that humans possess predispositions that interact with environmental experiences throughout

development. Consequently, the evidence reviewed here indicates that the innate and learned aspects of prosocial behavior are not competing explanations but interdependent influences that jointly shape altruistic tendencies (77).

The interplay between genetic and environmental influences is perhaps most clearly illustrated in twin studies of prosocial behavior. Because monozygotic (MZ) twins share nearly all of their genetic material, whereas dizygotic (DZ) twins share, on average, only half, differences in similarity between the two groups can be used to estimate genetic and environmental contributions to behavior. One study found that traits such as sharing and empathic concern showed evidence of genetic influence, as MZ twins were more similar than DZ twins. However, kindness appeared to be shaped more strongly by non-shared environmental factors, including individual experiences and social contexts unique to each twin (78). Furthermore, the effects of shared environmental influences, such as parental negativity, were found to vary depending on the behavioral characteristics of the twins themselves, highlighting the complex interaction between genetic predispositions and environmental experiences (79).

The relative contributions of genetic and environmental influences to prosocial behavior across development remain a subject of debate. Some researchers argue that genetic influences become more pronounced with age, whereas the effects of shared environmental factors diminish over time. One explanation is that individuals increasingly select and shape environments that align with their genetically influenced dispositions, while the influence of peers gradually becomes more significant than that of parents during adolescence and adulthood (80). In contrast, other studies suggest that genetic influences are strongest during early childhood, with substantial effects observed up to 36 months of age, whereas environmental factors become increasingly important later in development as children accumulate experiences and learn to respond empathetically to others (81). Taken together, these findings suggest that the balance between genetic and environmental influences may shift throughout development, rather than remaining constant across the lifespan.

Given these complexities, the evidence reviewed here suggests that framing altruism solely as a product of nature or nurture may be an oversimplification. The genetic and environmental influences discussed throughout this review are deeply intertwined and appear to exert their effects in ways that depend on developmental, social, and situational context. Consequently, a more useful framework may be one that conceptualizes altruism not as a single trait whose origins must be determined, but as a collection of context-dependent mechanisms whose expression emerges from the interaction between biological predispositions and lived experience.

3. Toward a mechanism-specific, regime based framework of altruism

3.1 From traits to mechanisms: a regime-based model

This literature review highlights a limitation in the current view of altruism; it is not a single, latent variable but rather a multifaceted trait that has been poorly defined in current studies. The cognitive processes that compel an individual to help kin, respond to others' distress, or reciprocate another's action are distinct; aggregating them to understand altruism yields inconsistent findings. Therefore, it is imperative to distinguish between these various approaches to truly understand the mechanisms of altruistic behavior.

Rather than viewing altruism as the result of the additive influences of genetics and the environment, we propose a regime-based framework in which altruistic behavior is generated by distinct mechanisms that are selectively activated depending on context. We identify four primary regimes:

[1] Kin-based behavior is driven by evolutionary influences that prompt one to prefer genetically related individuals (26).

[2] Reciprocal behavior is based on the results of repeated actions; it involves an individual using strategic thinking to expect help in return (82).

[3] Empathy-driven behavior arises from a response to someone's distress(83).

[4] Norm-based driven behavior requires one to acknowledge rule violations and be willing to incur costs to ensure fairness (84).

Within this framework, behavior at any given moment is generated by the dominant active mechanism. By distinguishing underlying mechanisms from their behavioral expressions, the model addresses a key source of circularity in prior accounts, in which the same variables are often used both to define altruism and to explain its emergence.

3.2 A non-circular framework for identifying altruistic mechanisms

A central challenge for any mechanism-based model is determining which mechanism is active in a given situation without inferring it from the very behavior it is intended to explain. For example, attributing a helping action to empathy solely because helping occurred is circular reasoning if empathy is simultaneously being invoked as the explanation for that behavior. To avoid this problem, mechanism identification must rely on evidence that is independent of the behavioral outcome itself. Accordingly, the present framework proposes three complementary approaches for identifying active mechanisms without circular inference.

First, experimental contexts can be structured to selectively activate one mechanism while minimizing competing explanations. In the kin condition, helping should be directed toward a close relative in the absence of repeated interactions or salient social norms (28,29). In the reciprocity condition, repeated exchanges and the prospect of future benefits should make reciprocal motivations most relevant (9,54). In the empathy condition, behavior should be evaluated in response to visible distress, allowing helping to be attributed to empathic concern rather than strategic incentives (47,48,83). Finally, norm-based behavior should be assessed in situations where individuals can incur personal costs to enforce fairness or uphold social expectations, thereby isolating norm-driven motivations (84).

Second, each mechanism may exhibit a distinct cognitive signature that can be measured through reaction times, physiological indicators, and self-reported motivations. Empathy-driven helping is expected to be relatively rapid and accompanied by heightened emotional arousal, whereas reciprocity-based decisions are likely to involve greater deliberation due to the need to evaluate future returns and repeated interactions. These signatures could complement existing neuroscience research by providing independent evidence for mechanism identification rather than relying solely on behavioral outcomes (42,43,47,48). Likewise, norm-based behavior may be reflected in a willingness to incur personal costs to enforce fairness, while kin-based behavior is expected to be guided more strongly by relatedness and familial affiliation than by adherence to broader social norms.

Third, experimental manipulations can be used to selectively attenuate specific mechanisms, thereby strengthening inferences about the mechanisms driving observed behavior. For example, increasing cognitive load may reduce the influence of reciprocity-based decision-making by limiting the capacity for strategic deliberation. Likewise, interventions that suppress or regulate emotional responses may diminish empathy-driven helping, while removing salient social norms or opportunities for norm enforcement may reduce norm-based behavior. Although no manipulation can completely isolate a single mechanism, these approaches can help distinguish among competing explanations and provide converging evidence regarding the dominant mechanism operating in a given context. Together, these strategies enable a more rigorous and non-circular identification of the processes underlying prosocial behavior (Table 1).

Table 1. Testable predictions of a regime-based framework of altruistic behaviors

	Kin-Based Behavior	**Reciprocity-Based Behavior**	**Empathy-Driven Behavior**	**Norm-Based Behavior**
Dissociation Across Conditions	Kin preference	Strategic cooperation	Emotion-driven	Costly punishment
Process-Level Differentiation	Relatedness-sensitive decisions	Slower, deliberative responses	Fast, affect-driven responses	Rule-sensitive decisions
Variable Irrelevance	Norm framing	Emotional distress	Future payoff	Kin relation

3.3 A new experimental framework

To operationalize this framework, we propose an experimental paradigm that systematically varies social context while holding the underlying decision structure constant (see Appendix). Across all conditions, participants repeatedly decide whether to incur a personal cost to benefit another individual. The identity of the recipient and the situational context are manipulated to selectively activate different mechanisms. In the kin condition (K), the recipient is a close family member and interactions are limited to a single encounter. In the reciprocity condition (R), participants interact repeatedly with the same individual, creating opportunities for future exchange. In the empathy condition (E), the recipient is presented as being in visible distress or need,

whereas in the norm condition (N), the situation involves a violation of fairness or a social rule. For each condition, behavioral outcomes, reaction times, and post-decision motivational reports should be recorded. By maintaining a common decision structure while varying contextual cues, this design enables direct within-subject comparisons across mechanisms and generates clear, falsifiable predictions regarding the context-dependent nature of prosocial behavior.

3.4 Implications

This framework reframes the nature-versus-nurture debate by moving beyond the question of whether altruism is innate or learned and instead examining how different prosocial mechanisms are activated under specific conditions. In this view, genetic and environmental factors do not directly determine altruistic behavior; rather, they influence the likelihood that an individual will engage a particular behavioral regime when confronted with a given social context.

4. Conclusion

Investigating the origins of altruism provides evidence against simplistic philosophical arguments about whether humans are "naturally selfish" or "naturally good," and instead suggests a more dynamic account of human behavior. Evidence supporting evolutionary, genetic, developmental, and environmental influences arises from different processes that often operate under different circumstances. This review sought to shift the question from "How altruistic is an individual?" to "Under which conditions does an individual exhibit prosocial behavior, and which mechanisms are engaged in those contexts?"

In doing so, this review advances a context-dependent, mechanism-specific framework of altruism that reconceptualizes prosocial behavior not as the expression of a single underlying trait, but as the outcome of distinct mechanisms—including kin-based, reciprocity-based, empathy-driven, and norm-based processes—that are selectively activated by situational context. By reframing altruism as a collection of contextually triggered behavioral regimes rather than a unitary construct, this framework offers a falsifiable explanation for why findings across evolutionary biology, genetics, neuroscience, developmental psychology, and social psychology often appear fragmented or contradictory. Importantly, the framework generates clear empirical predictions regarding the selective relationship between individual predispositions and specific helping contexts, providing a testable foundation for future research. To facilitate such testing, the Appendix translates the theoretical framework into a concrete research program by proposing a non-circular experimental paradigm, mechanism-specific measurement strategy, and predicted dissociation pattern capable of empirically validating or falsifying the model. This transition from conceptual synthesis to testable prediction represents a key contribution of the present review, as it moves beyond explaining existing findings and provides a practical roadmap for future investigation.

Future research could use longitudinal studies to examine how altruistic behavior is shaped by genetic and environmental influences within the same sample of children, which would help clarify how different mechanisms emerge and interact across development. The proposed framework also provides a basis for experimental studies capable of distinguishing

among competing mechanisms and testing whether prosocial behavior is best understood as a unified disposition or as a set of context-dependent processes. Implications of understanding the origins and mechanisms of altruism extend beyond prosocial behavior itself and may help researchers contend with phenomena such as psychopathy, including which aspects are biologically predisposed and which are influenced by environmental factors such as trauma and prenatal stress (85). This discourse also holds practical implications for societal structures, as schools, families, and communities which may be able to cultivate and construct policy around specific forms of prosocial behavior during developmentally sensitive periods if the relevant mechanisms are better understood (86).

Ultimately, this work does not resolve the nature-versus-nurture debate. Rather, it suggests that the debate may be incomplete when framed around altruism as a single construct. Instead, altruistic behavior may be best understood as a multifaceted phenomenon emerging from the interaction of innate predispositions, learned experiences, and context-dependent mechanisms. Beyond synthesizing evidence across disciplines, this review contributes a falsifiable theoretical framework and an accompanying experimental blueprint through which its central claims can be rigorously evaluated. By moving beyond the assumption of a unitary altruistic trait and toward a mechanism-specific understanding of prosocial behavior, this framework offers both a new theoretical lens and a concrete empirical pathway for future research.

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Appendix: Formal experimental framework

Part 1: Behavioral experiment ~300 participants

To enable non-circular identification of the mechanisms underlying altruistic behavior, the experimental design maintains a constant decision structure across all trials, rather than varying task conditions to induce specific mechanisms. In each trial, participants are presented with a scenario in which multiple cues are simultaneously available—for example, the recipient may vary in relational proximity (e.g., sibling vs. stranger), emotional state (distressed vs. neutral), and potential for future interaction (one-shot vs. repeated). Participants then make a binary or graded decision about whether to incur a cost to help the recipient. Crucially, mechanism identification is not inferred from the behavioral outcome alone but from independent process-level and attributional measures collected alongside the decision. Immediately after each choice, participants report their primary motivation (e.g., "because they are family," "because they were in distress," "because they may help me later," or "because it is the right thing to do"), allowing for self-attributed mechanism classification. To mitigate the limitations of self-report, these responses are complemented by process measures, such as reaction time (fast, affect-driven vs. slower, deliberative decisions), and attention allocation (e.g., focus on emotional cues vs. payoff information), which provide converging evidence of the underlying cognitive process. By combining constant scenarios, competing cues, and multiple independent indicators, this design enables identification of the operative mechanism on a per-decision basis, avoids circular inference, and allows for direct testing of whether different mechanisms dominate under different contextual configurations.

Part 2: Survey (same ~300 participants)

Please indicate how much you agree with each statement on a scale from 1 (Strongly Disagree) to 5 (Strongly Agree). There are no right or wrong answers.

SECTION A: Empathy (E) – affective + cognitive sensitivity
(captures responsiveness to others' distress, not "helping" directly)
1. I often feel emotionally affected when I see someone in distress.
2. When someone is upset, I can easily imagine how they feel.
3. I find it hard to ignore people who are suffering.
4. I tend to notice subtle emotional expressions in others.
5. Seeing someone cry makes me feel uncomfortable or concerned.

SECTION B: Reciprocity Orientation (R) – strategic expectation
(captures belief in and reliance on future return)
6. I am more willing to help someone if I think they might help me in the future.
7. Helping others usually pays off in the long run.
8. I consider how my actions today might affect how others treat me later.
9. I am less likely to help if I know I will never see the person again.
10.I keep track of whether people return favors.

SECTION C: Norm Sensitivity (N) – rule-based reasoning
(captures internalization of "should," independent of emotion)
11.People should follow fairness rules even when it is personally costly.
12.I feel bothered when others break social rules, even if it doesn't affect me.
13.It is important to do what is right, even when no one is watching.
14.I would feel guilty if I didn't act according to my moral principles.
15.Rules exist for a reason and should generally be followed.

SECTION D: Kin Preference (K) – relational bias
(captures prioritization of close others, not general altruism)
16.I feel a stronger responsibility to help family members than strangers.
17.I would be more willing to sacrifice for someone close to me than for a stranger.
18.Family obligations should come before helping others.
19.I feel more connected to the well-being of my close relatives than to others.
20.I would prioritize helping someone I know over someone I don't.

SECTION E: Cost Sensitivity (C) – constraint variable (important control)
(this is critical—often missing in papers)
21.I hesitate to help if it would cost me time or resources.
22.I carefully consider the personal cost before helping someone.
23.I am less likely to help if it inconveniences me.
24.Even small costs can discourage me from helping others.
25.I prefer to help only when it is easy to do so.

SECTION F: Attention checks (important for validity)

26.Please select “Agree” for this statement.
27.I am currently paying attention to the survey.

SECTION G: Behavioral self-perception (for comparison only)
28.I consider myself a helpful person.
29.I often go out of my way to help others.

Compute mean scores:
Ei = mean(1–5)
Ri = mean(6–10)
Ni = mean(11–15)
Ki = mean(16–20)• Ci = mean(21–25)

High Ei → predicts behavior only in empathy condition
High Ri → predicts behavior only in repeated interaction
High Ni → predicts punishment in norm condition
High Ki → predicts kin bias only

The results from the above survey will be primarily intended to show that each trait predicts behavior selectively, not globally. This supports regime activation, not trait altruism. Compute Cronbach’s alpha for each Empathy, Reciprocity, Norms, Kin, Cost and report (for example) that “All scales showed acceptable internal consistency ($\alpha > 0.7$)”. Run a Repeated-measures ANOVA (or simple comparison): AiK,AiR,AiE,AiN to show that conditions actually differ and that context changes behavior. Run simple regressions (one per condition) to show that each trait predicts behavior which is significant (coefficient magnitudes) only in its matching condition. This would mean that “Each trait predicted behavior selectively within its corresponding condition, but not significantly across conditions. This dissociation demonstrates that prosocial behavior is not governed by a single underlying trait, but by distinct mechanisms that are contextually activated.”

Table A1. Selective prediction pattern

Trait	K Condition	R Condition	E Condition	N Condition
K (Kin)	**Yes**	No	No	No
R (Reciprocity)	No	**Yes**	No	No
E (Empathy)	No	No	**Yes**	No
N (Norm)	No	No	No	**Yes**

The “selective prediction pattern” table serves as the central empirical test of the regime-based framework by demonstrating a dissociation between stable individual traits and context-dependent behavioral expression. In this table, each row represents a trait—an independently

measured, relatively stable predisposition obtained from the survey component of the study (Part 2), such as kin preference, reciprocity orientation, empathy sensitivity, or norm adherence—while each column represents an experimentally manipulated condition from the behavioral task (Part 1), i.e., a specific decision context designed to make one mechanism salient (e.g., kinship, repeated interaction, distress, or rule violation). Thus, traits reflect *who an individual is predisposed to be*, whereas conditions define *the situational context in which a decision is made*. The key result is that each trait predicts behavior only within its corresponding condition (e.g., empathy predicts helping in the empathy condition but not in reciprocity or norm conditions), producing a diagonal pattern of significance. This selective mapping shows that traits do not operate as general, global drivers of altruism; instead, they function as latent biases that increase the likelihood of a particular mechanism being activated when the relevant context is present. In contrast, conditions do not measure traits but instantiate environments that determine which mechanism is expressed. The resulting dissociation—traits predicting behavior selectively rather than universally—provides direct evidence against a single-trait model of altruism and supports the claim that prosocial behavior arises from distinct, context-triggered mechanisms rather than a unified underlying disposition.