

# Prosocial Behavior and Depression: a Case for Developmental Gender Differences

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## Abstract

*Purpose of Review* Prosocial behavior and depression are related constructs that both increase during adolescence and display gender-specific effects. The current review surveys literature examining the association between depressive symptoms and prosociality, measured with behavioral economic paradigms, across development and proposes a theoretical model explaining a mechanism through which adolescent girls have higher risk for depression than boys.

*Recent Findings* Relative to healthy controls, prosocial behavior is reduced in adults with major depressive disorder (MDD) but may be increased in adolescents with MDD. The relationship between non-clinical levels of depressive symptoms and prosocial behavior remains to be studied experimentally; however, self-reported prosocial behavior is negatively associated with depressive symptoms in non-clinical adolescents, which may suggest a shift in the relation of prosocial behavior and depressive symptoms across the non-clinical (i.e., negative) to clinical range (i.e., positive).

*Summary* The effect of gender on these developmental and clinical status shifts has not been studied but could have important implications for understanding the emergence of higher rates of depression in girls than boys during adolescence. We propose that girls are at heightened risk for

depression due to higher social-evaluative concern and other-oriented prosocial motivation that emphasize the needs of others over the self, leading to more altruistic prosocial behavior (despite personal cost) and a higher burden that enables depressive symptoms.

**Keywords** Prosocial behavior · Depression · Gender · Adolescence · Behavioral economic theory · fMRI

## Introduction

Disruptions to social processing and decision-making are features of major depressive disorder (MDD) that may precede diagnosis [1]. Indeed, prosocial behavior, defined most simply as a voluntary action intended to benefit others, has been shown to correlate negatively with depressive mood in non-clinical samples [2–6]. This finding supports the theory that people engage in prosocial behavior because they take pleasure in helping others [7], which, in turn, increases their happiness [8]. However, previous literature has largely ignored the motivations behind prosocial behavior when reporting associations with depressive symptoms. Prosocial motivation includes other-oriented (i.e., selfless; altruistic) and self-oriented (i.e., selfish; egoistic) motives, which can lead to similar behavioral outcomes under certain circumstances. However, individuals who are motivated by the needs of others are more likely to behave prosocially even when there is the potential for personal cost [9], which can create substantial burden [10•] and lead to higher depressive symptoms [11]. Therefore, the association between prosocial behavior and depressive symptoms maybe more nuanced than previously assumed.

Important developmental and gender differences in prosocial behavior may affect its relationship to depressive

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symptomatology. Compared to adulthood, adolescence is characterized by heightened peer affiliation and salience of social information, rooted in the development of endocrine, neural, and social systems [12]. In fact, prosocial behavior increases across adolescence and then decreases and plateaus in early adulthood [13]. Moreover, the adolescent period is marked by a substantial increase in the onset of depressive disorders, which predominantly impacts girls versus boys [14]. The onset of puberty triggers not only a rise in sex hormone levels, such as testosterone, which not only differentiate girls and boys but also triggers a re-organization of neural oxytocin binding sites, representing a refinement of the social brain [15]. These endocrine changes contribute to the maturation of neural networks involved in key aspects of prosocial behavior, including reward, cognitive control, and social cognition neural networks [16, 17]. The convergence of puberty, brain development, and social development places adolescents in a context where prosociality becomes more important for affiliation but may include a cost for individuals who sacrifice their own needs for those of others, increasing the risk for depressive symptoms.

Due to the increased relevance of peers and relationships to define self-identity and self-worth, adolescents, particularly female adolescents, display more social-evaluative concern or concern with negative social evaluation [18]. In females, heightened psychological investment in relationships manifests in more worry about judgment of peers, closer interpersonal connections, and more self-reported prosocial behavior [19]. Importantly, adolescent girls are more likely to report other-oriented concerns (e.g., fear of disapproval from peers), while boys are more likely to report self-oriented prosocial motivations (e.g., helping others to achieve a sense of self-satisfaction) [20]. These gender differences in motivation for prosocial behavior may help to explain the higher prevalence of depression in girls than boys, beginning in adolescence. Indeed, social-evaluative concern, specifically concern about disapproval from peers, is not only linked with altruistic prosocial behavior [21•] but also predicts depressive symptoms [18]. Thus, other-oriented motivations for prosocial behaviors in adolescent girls may underlie the link between these behaviors and depressive symptoms.

Importantly, the associations between prosocial behavior and depressive symptoms may be more complex in individuals diagnosed with MDD, as social functioning tends to decline during episodes [22]. Patients with MDD often display anhedonia—the inability or reduced ability to feel pleasure—and may not readily experience the pleasure accompanying prosociality, which will result in less helping behavior. Alternatively, individuals with MDD may seek opportunities to behave prosocially if they want to relieve negative symptoms of depression. In addition, individuals with MDD, particularly females, often display excessive interpersonal dependence—a reliance on other people for emotional and social

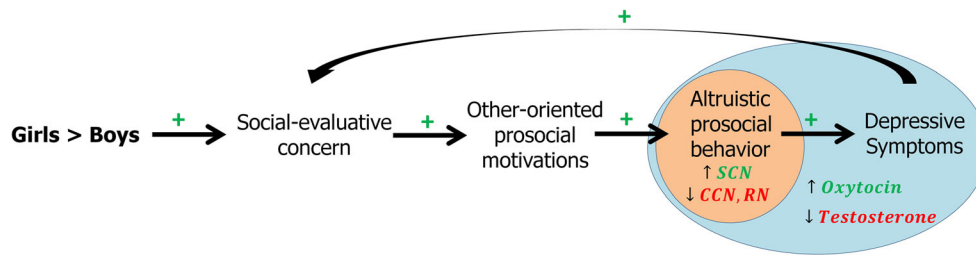
support—in response to loneliness and fear of rejection [23]. Therefore, individuals with MDD may display either more or less prosocial behavior than healthy controls, which may depend on the gender of the individual.

We present a theoretical model based on the emergence of gender differences in motivations for prosocial behavior that may explain adolescent gender differences in the risk for depressive symptoms (Fig. 1). Specifically, we propose that higher social-evaluative concern in girls translates into more other-oriented prosocial motivations, leading to more altruistic prosocial behavior. Engaging in altruistic prosocial behavior that prioritizes the needs of others over the self can, in turn, lead to burden that perpetuates the expression of depressive symptoms. In a current state of depression, adolescent girls may fear rejection further and demonstrate more social-evaluative concern, which perpetuates the cycle. Importantly, this proposed mechanism is not exclusive to females, but it may be less common in males since they tend to report less social-evaluative concern, other-oriented prosocial motivation, altruistic prosocial behavior, and fewer depressive symptoms.

The current manuscript will review studies that measure prosocial behavior, using behavioral economic paradigms, in relation to depression, defined as both depressive symptoms and MDD diagnosis. The behavioral economic approach combines mathematical theory and rigorous experimental paradigms from game theory (and may also include neural activity measured with neuroimaging methods—e.g., neuroeconomics) to predict effects of cognitive and emotional factors (e.g., social-evaluative concern) on (prosocial) individual choices [24] including those that are costly to the individual. Research conducted in adults and adolescence (defined as 12–19 years old) will be presented to delineate developmental differences in prosocial behavior in MDD and non-clinical populations. The neural correlates of prosocial behavior and the relationships between prosocial behavior and gender, testosterone, and oxytocin will be discussed as well. Finally, a discussion of the reviewed literature in the context of the proposed theoretical model will be included and future directions will be provided.

## Operationalizing Prosocial Behavior

Behavioral economic paradigms offer an ecologically valid means to study complex social behaviors—such as altruistic punishment, cooperation and reciprocity—by modeling interactions between two or more individuals in a variety of contexts (reviewed by [25•]). The behavioral economic paradigms most frequently studied in the context of depression include the Ultimatum Game, the Trust Game, and the Prisoner's Dilemma (reviewed by [26•]). Other types of prosocial games include the Dictator and Public Goods Games (Table 1). Manipulation of task conditions to promote



**Fig. 1** Theoretical model of adolescent gender differences in depressive symptom expression. Girls experience heightened social-evaluative concern, which supports increased other-oriented prosocial motivations and altruistic prosocial behavior, which is further supported by engagement of the social cognitive network and reduced engagement of

the reward and cognitive control networks. The burden created by prioritizing the needs of others at the expense of the self may then perpetuate depressive symptoms, which are further supported by higher oxytocin and lower testosterone levels. *SCN* social cognition network, *CCN* cognitive control network, *RN* reward network

or discourage prosocial outcomes is common; however, only the most basic task parameters will be discussed below.

The Ultimatum Game is used to measure altruism. Briefly, player 1 (*proposer*) proposes how to divide a fixed amount of money and player 2 (*responder*) decides to accept or reject this proposal without negotiation. If the proposal is accepted, the proposed split is realized, but if it is rejected neither player receives money. Proposing a more generous split of the money, although potentially confounded by strategic concerns and risk aversion (e.g., determining the lowest possible offer while avoiding rejection), is indicative of higher prosociality. Responders typically reject unfair proposals even though they stand to benefit from accepting any offer. More fair-minded (i.e., justice-oriented) individuals tend to reject unfair offers and accept zero payment for both themselves and the proposer as a form of punishment (i.e., altruistic punishment) meant to encourage the proposer to make more fair offers in subsequent trials played against the responder and/or other future responders. Altruistic punishment may be interpreted as prosocial behavior or a failure of self-control (to inflict punishment).

The Trust Game is used to study reciprocal exchanges: first, a *trustor* decides if and how much money to invest in a *trustee* and if invested the money is multiplied by some factor; second, the trustee has the option to return any proportion of the multiplied amount to the trustor. Both parties stand to gain more money by reciprocating trust, and typically both the

trustor and trustee choose to invest and return money, respectively. The trustor’s behavior is more reflective of trust and risk aversion, and the trustee’s behavior indicates degree of altruism, reciprocity, and trustworthiness; more trust and reciprocity reflect more prosocial behavior. The trustee’s choice to return a portion of an investment (or not) mirrors the choice of the proposer in the Dictator Game. In the Dictator Game, the *proposer* makes an offer to be split between himself/herself and a *receiver*, who has no choice but to accept the offer. Even though the proposer faces no monetary repercussions for unfair behavior, they tend to make fair offers, which serves as a measure of altruism.

Finally, the Prisoner’s Dilemma and Public Goods Games are used to measure cooperative behavior. In the Prisoner’s Dilemma, two players are confronted with the same option to cooperate or defect and there are four possible outcomes for a given trial. Payout for a trial is determined by the interaction between both players, such that the largest payout for a player occurs when he or she defects and the partner cooperates and the worst outcome occurs when the player cooperates while the partner defects. The largest payout is brought upon by mutual cooperation, while mutual defection yields a smaller payout to each player. More cooperation represents higher prosociality. In the Public Goods Game, multiple players decide how many tokens to privately put into a public pot. The amount in the pot is multiplied by a factor (greater than 1 and less than the number of players) and evenly divided among

**Table 1** Behavioral economic operationalization of prosocial behavior

	Role	Prosocial action	Construct(s) measured
Dictator Game	Proposer	Allocation of funds	Altruism
Ultimatum Game	Proposer	Allocation of funds	Altruism/risk aversion
	Responder	Rejection of unfair offers	Altruistic punishment/ Self-control failure
Trust Game	Trustor	Allocation of funds	Trust/risk aversion
	Trustee	Reciprocation	Reciprocity/trustworthiness
Prisoner’s Dilemma	Proposer	Cooperation	Cooperation
Public Goods Game	Proposer	Allocation of funds	Altruism/cooperation

players. In addition, players keep the tokens they do not contribute. Total payoff is maximized when everyone in the group contributes all of their tokens. Those who contribute below average are termed defectors or free riders, in contrast to cooperators who make above-average contributions to the public pot.

## Adult Prosocial Behavior and Depression

Recent studies examining linear associations between prosocial behavior and depressive symptoms in non-clinical adults report mixed results (Table 2). Positive associations between depressive symptoms and prosocial behavior, as indicated by more cooperation in the Prisoner's Dilemma [27, 28] and Public Goods Game [28], have been reported. However, Brendan Clark and colleagues [28] also show that depressive symptoms are not correlated with behavior on the Trust or Ultimatum Games. Furthermore, another study reports that higher depression scores are negatively correlated with cooperation on the Prisoner's Dilemma [29]. Only one study reported a full range of participant depressive symptoms [27]; therefore, the association between prosocial behavior and depressive symptoms may be underestimated. Overall, there is no clear association between depressive symptoms and prosocial behavior in healthy adults, which stands in contrast to previous research that has used self-report measures of prosocial behavior showing a negative association [6].

Studies comparing prosocial behavior of adults with MDD and healthy or non-clinical adults also demonstrate mixed results, although on balance studies tend to report that MDD is associated with less prosocial behavior (Table 2). Using the Prisoner's Dilemma, Pulcu and colleagues [30] report less cooperation by adults diagnosed with MDD compared to healthy controls. Similarly, Zhang and colleagues [31] show that adults with MDD engage in less reciprocity during a Trust Game than non-clinical adults. Finally, using the Ultimatum

Game, Radke and colleagues [32] show that adults with MDD reject more (fair and unfair) offers in the role of responder, compared to healthy controls. However, five studies show no difference in prosocial behavior by adults with MDD compared to healthy or non-clinical controls using a variant of the Dictator Game [30], the Prisoner's Dilemma [33•], an Ultimatum Game in the role of proposer [30] and responder [30, 34] and a Trust Game in the roles of trustor and trustee [35•, 36]. Shao and colleagues [35•] also measured the correlation between reciprocity and depressive symptoms in adults with MDD; however, the association was not statistically significant. Finally, three other studies report more prosocial behavior (measured with the Ultimatum Game) in adult patients with MDD compared to healthy and non-clinical controls in both the roles of proposer [37] and responder [37–39]. However, latter studies measured altruistic punishment (i.e., rejection of unfair offers), which may also represent failures of self-control. Therefore, the data are in favor of a negative or null effect of MDD diagnosis on prosocial behavior.

In sum, non-clinical adults do not show a significant association between prosocial behavior and depressive symptoms, but the onset of MDD seems to alter prosocial behavior, such that adults with MDD demonstrate less prosociality than healthy controls. A state of depression may heighten sensitivity to social signals and rejection, which encourages individuals to retreat to avoid rejection [40]. In contrast, it is possible that anhedonia plays a role in decreasing the salience of prosocial behavior. Although causality cannot be determined without longitudinal investigation of these factors, prosocial neural activation studies provide some support for the latter interpretation.

## Neural Correlates of Prosocial Behavior in Adult MDD

Several studies report aberrant activation of reward and cognitive control networks in adults with MDD during behavioral economic paradigms designed to engage prosocial behavior. The reward network includes the ventral striatum, which mediates (social) reward processing, reinforcement, and motivational salience [41], while the cognitive control network includes the dorsolateral prefrontal cortex (DLPFC) and mediates executive functions, including inhibitory control (of selfish behavior) [42]. Gradin and colleagues [33•] report weaker activation of the reward network during prosocial behavior (i.e., cooperation during the Prisoner's Dilemma) and weaker activation of the cognitive control network during prosocial behavior (i.e., defection by self or partner), in patients with MDD, compared to healthy controls. The same group replicate part of these findings using the Ultimatum Game in the role of responder: patients with MDD show weaker activation of the reward network during prosocial behavior, compared to

**Table 2** Associations between prosocial behavior measured with behavioral economic paradigms and depressive symptoms or major depressive disorder diagnosis (MDD)

	Adolescents (number of studies)	Adults (number of studies)
Non-clinical <sup>a</sup> (↑ Depressive symptoms)	? Prosocial (0) <sup>c</sup>	↔ Prosocial (3) <sup>c</sup>
MDD–control <sup>b</sup>	↑ Prosocial (2)	↔/↓ Prosocial (11)

<sup>a</sup> Refers to sample whose mental health status was not assessed with clinical interviewing

<sup>b</sup> Includes healthy and non-clinical control samples; healthy mental status of healthy controls was confirmed with clinical interviewing

<sup>c</sup> Studies using self-report measures of prosocial behavior report a negative association with depressive symptoms

healthy controls. Furthermore, activation of the ventral striatum was negatively correlated with anhedonia [34•], lending support to the interpretation that MDD diagnosis, via anhedonia, decreases the salience and rewarding properties of prosocial behavior, which may, in turn, discourage future prosocial behavior. Finally, using a modified Trust Game in the role of trustee, Shao and colleagues [35•] found reduced activity of the cognitive control network during prosocial behavior in patients with MDD compared to non-clinical controls. In sum, adults with MDD show reduced activation of the reward network during prosocial behavior, which may indicate blunted rewarding properties of prosocial behavior, and weaker activation of cognitive control network during prosocial behavior, suggesting a failure to inhibit selfish behavior.

### Adolescent Prosocial Behavior and Depression

Studies to date have not assessed the link between depressive symptoms and prosocial behavior in adolescents with non-clinical levels of depression using behavioral economic paradigms (Table 2). However, adolescent prosociality has been studied extensively with self-report measures; studies that examine the relation between self-reported prosocial behavior and depressive symptoms generally report a negative correlation. Indeed, longitudinal studies show that depressive symptoms negatively predict prosocial behavior in adolescents [2–5]. Importantly, there is also some evidence that more prosocial behavior leads to fewer depressive symptoms in healthy youth [3]. Thus, it is plausible that behavioral economic paradigms would find a similar negative association in healthy adolescents. Indeed, the only functional magnetic resonance imaging (fMRI) study to have measured the association between prosociality and depression during adolescence found that more robust activation of the ventral striatum during prosocial behavior directed at family (using a variant of the Dictator Game) predicted fewer depressive symptoms 1 year later (gender differences were not reported) [43•]. Notably, the association between depressive symptoms and prosocial behavior was not reported [43•]. These findings stand in contrast with our proposed model; however, the discordant findings between non-clinical adult studies using experimental and self-report measures [6, 27–29] may indicate that individuals' actual prosocial behavior does not align with self-reported behavior. Thus, it is possible that non-clinical adolescents display a positive association between prosocial behavior measured experimentally and depressive symptoms. However, more research using behavioral economic paradigms during the adolescent period is needed to confirm any association between depressive symptoms and prosocial behavior.

A limited number of studies have examined differences in prosocial behavior between youth with MDD and healthy

controls using behavioral economic paradigms (Table 2). McClure and colleagues [44] show that MDD and anxiety patients respond more cooperatively than healthy controls following partner cooperation (but not defection) on the Prisoner's Dilemma. A study by Harlé and colleagues corroborates this finding by showing that individuals with MDD accept more unfair offers on the Ultimatum Game despite reporting a more negative reaction to unfair offers, compared to healthy controls. Accepting unfair offers is typically considered a rational choice; however, the choice to accept an unfair offer benefits the proposer and can still be considered a prosocial choice. Indeed, in patients with MDD, this pattern of responding can reflect a fear of being socially rejected by a proposer after refusing the proposer's unfair offer [22]. Thus, in contrast to the adult literature, these studies tentatively suggest that youth with MDD behave more prosocially than their healthy counterparts; however, this effect may be partially attributed to anxiety. To our knowledge, there are no studies measuring differences in prosocial behavior via self-report between adolescents diagnosed with MDD and healthy or non-clinical controls. Overall, these findings support our theoretical model, such that potential fear of rejection and heightened social-evaluative concern during a depressive episode fuel other-oriented prosocial motivations and subsequent prosocial behavior, perpetuating the cycle of depressive symptoms (Fig. 1).

### Summary

Adults with MDD display less prosocial behavior than healthy controls, potentially via anhedonia and blunted reward system activation, as well as weaker recruitment of the cognitive control network, leading to poor inhibition of prosocial behavior. Similarly, an accumulating literature has begun to indicate a negative association between self-reported depressive symptoms and prosocial behavior, such that more depressive symptoms predict less prosocial behavior and more prosocial behavior predicts less depressive symptoms in adolescence (although neither effect has been confirmed experimentally). The latter mechanism is supported by an fMRI study reporting that stronger ventral striatal brain response during prosocial behavior, albeit not prosocial behavior per se, predicts fewer depressive symptoms in non-clinical adolescents [43•]. By contrast, recent work suggests that clinically significant depressive illness in adolescents may associate with *more* prosocial behaviors than in healthy controls [44, 45]. The shift from negative to positive associations between prosocial behavior and depressive symptoms following MDD onset may reflect a disease state-dependent shift in mechanism or strategy supporting prosocial behavior. However, as proposed by our theoretical model (Fig. 1), the influence of gender, oxytocin, and testosterone on prosocial behavior and depressive

symptoms must be considered in order to determine the direction of the effect (positive or negative) of prosocial behavior on depressive symptoms (or vice versa).

## Gender

Gender differences in prosocial behavior using behavioral economic paradigms only emerge under certain conditions [46•]. Framing the experimental context with social and emotional conditions tends to increase prosocial behavior in women. For instance, reducing social distance (i.e., playing with a friend versus stranger) increases prosocial behavior in women, but not men [47]. In contrast, framing prosocial behavior to be consistent with self-interests by introducing a delay in decision making that promotes reflection [48, 49] or by explicitly stating how prosocial behavior benefits the individual [50] can make men, but not women, behave less prosocially [46•]. Importantly, gender differences are absent in adulthood if social interactions are conducted with a stranger or a computer program [51•, 52], suggesting that prosocial behavior is generally the same for men and women under baseline conditions, but begins to differ when context and motivation for social behavior is manipulated.

Although many studies using self-report measures, observation, and teacher/peer ratings indicate that adolescent girls are more prosocial than boys [53], studies using behavioral economic paradigms report mixed findings. Critically, the majority of adolescent studies have not examined gender differences directly [54, 55•, 56–61]. A study using the Prisoner's Dilemma reports that adolescent girls are more cooperative than boys [62•]. Using the Trust Game, another study shows that adolescent boys display more trust behavior (trustor) than girls, but no gender differences in reciprocity (trustee) are found [63•]. Notably, in this study, more girls identify as “prosocials” than “proselfs,” and prosocial individuals are more likely to be trusting and trustworthy [63•], indicating that adolescent boys may be trusting because they are actually less risk averse. Other studies in healthy adolescents have reported no gender difference in prosocial behavior using a Public Goods Game [64•] and a Trust Game in the role of trustee [65]. Similar to adulthood, this discrepancy in findings might be explained by differential sensitivity to experimental cues by girls compared to boys; however, this remains to be empirically tested in adolescents.

## Oxytocin and Testosterone

Oxytocin and testosterone are implicated in prosocial behavior and depression [66•]. Oxytocin is a neuropeptide produced in the hypothalamus and released by the posterior pituitary to facilitate social behavior. In addition, oxytocin is positively

associated with depression [66•]. Neural oxytocin binding sites are re-distributed from the postnatal period through adulthood, with one shift in distribution occurring after the onset of puberty, representing a refinement of the social brain [15], which may indicate that oxytocin plays a larger role in prosocial behavior and depression following puberty. In contrast, testosterone is a steroid that is primarily produced in the testes and adrenal glands. Testosterone has many behavioral effects, including increasing aggression and (broadly) decreasing prosocial behavior. During puberty, testosterone increases dramatically, especially in boys, which could help explain gender differences in prosocial behavior.

The great majority of studies report that oxytocin is positively associated with prosocial behavior, but this effect varies based on individual factors and task conditions. For instance, oxytocin tends to increase prosocial behavior directed at individuals belonging to an in-group [67–72]; in some cases, oxytocin is negatively related to prosocial behavior directed to individuals of an out-group [73] or in response to betrayal [74]. Importantly, some studies report no associations between prosocial behavior and oxytocin [75–77], indicating that this relationship is complex and requires further study. Indeed, some of this complexity may be accounted for by gender differences. Studies reporting that oxytocin increases or is positively associated with prosocial behavior also show that this effect is particularly robust for female children [78] and adults [79–81], compared to males. However, not all studies report gender differences in the effect of oxytocin on prosocial behavior [75, 76]. In general, however, oxytocin signals the presence of a socially relevant stimulus that requires attention and ultimately promotes social affiliation [66•]. The association between oxytocin and prosocial behavior has not been measured during adolescence, although one study shows that adolescent males with higher salivary oxytocin levels report fewer conduct problems [82], which can be cautiously interpreted as more prosocial behavior. Finally, one study reported elevated oxytocin levels in adolescents with treatment-resistant MDD, compared to non-treatment resistant and healthy control adolescents [83•]. However, the association between prosocial behavior and oxytocin in pubertal patients with MDD remains to be studied.

In contrast to oxytocin, testosterone is generally associated with less prosocial behavior and fewer depressive symptoms [66•]. Recent studies using behavioral economic paradigms indicate that higher testosterone is typically associated with less prosocial behavior in males [84–88]—although not always [89, 90]. However, if the prosocial behavior is directed at someone belonging to the participant's in-group (e.g., a friend), higher testosterone is associated with more cooperative behavior in males [84, 91, 92]. In women, the link between testosterone and prosocial behavior is mixed, with studies reporting a negative association [93], in one case following mild stress [87] and a positive association [93, 94], in one case only when

reciprocating generosity [93]. Although the association between testosterone in prosocial behavior per se has not been studied across adolescence, there is a positive relationship between testosterone and antisocial behavior that intensifies across adolescence in males, but not females, which may be informed by social experiences and higher fetal exposure to testosterone [95]. A negative association between testosterone and depression has been reported [96]; however, to our knowledge, the association between testosterone and prosocial behavior in relation to depression has not been studied previously.

In sum, oxytocin is generally positively associated with prosocial behavior and depressive symptoms; however, gender differences in the effect of oxytocin on prosocial behavior in MDD have yet to be determined. Testosterone appears to increase proself behavior when there is a potential social challenge or threat (i.e., members of an out-group), but it may increase prosocial behavior in the absence of threat or when status or reputation maybe well served by prosocial actions. Therefore, the combination of high oxytocin and low testosterone may lead to more depressive symptoms and prosocial behavior, particularly if that behavior is directed at a member of an in-group, such as a friend. The combination of (1) gender-specific effects of oxytocin on prosociality favoring more prosocial behavior in females compared to males and (2) the inverse association between prosociality and testosterone favoring less prosocial behavior in males, who have higher levels of testosterone than females, may facilitate more altruistic prosocial behavior in adolescent girls compared to boys, which increases personal burden and risk for depressive symptoms.

## Conclusions

The literature presented here support a developmental dissociation between prosociality and depression, such that adults with MDD demonstrate less prosocial behavior and adolescents with MDD demonstrate more prosocial behavior, compared to healthy and non-clinical controls. Furthermore, these associations may be different in non-clinical populations. In non-clinical adults, there is no relation between depressive symptoms and prosocial behavior, which stands in contrast with studies measuring prosocial behavior via self-report that indicate a negative association. In non-clinical adolescents, a negative association between depressive symptoms and prosocial behavior has been reported by studies using self-report measures of prosocial behavior, but this association has not been studied using behavioral economic paradigms.

The lack of studies using behavioral economic paradigms to study prosocial behavior in non-clinical adolescent samples makes it difficult to conclusively determine whether clinical

status of an individual affects the associations between prosocial behavior and depressive symptoms. However, if we assume that behavioral economic paradigms will replicate the effects obtained with self-report measures of prosocial behavior then it may be the case that prior to MDD diagnosis, adolescents benefit from the protective effects of prosocial behavior; however, after diagnosis, they may seek relief from their negative emotional state or avoid social rejection by engaging in more prosocial behavior. An alternative interpretation is that social-evaluative concern and other-oriented motivations inform altruistic prosocial behavior and play a larger role in shaping risk for depression in non-clinical adolescents that continues after MDD diagnosis. It may be that for a subset of individuals, such as adolescent girls, a positive association between depression and prosocial behavior (measured experimentally) exists due to the cost associated with heightened social-evaluative concern. Once in a state of MDD, social-evaluative concern is reinforced and perpetuates more altruistic prosocial behavior (Fig. 1). Future research considering prosocial motivations driving behavior will be needed to distinguish between these possibilities.

Consideration of factors that interact with depression and have biological underpinnings, such as gender, brain activation, oxytocin, and testosterone, will be crucial to achieve full comprehension of the relationship between prosocial behavior and depression. A focus on reward, cognitive control, and social cognition brain networks, and the interactions between oxytocin and testosterone across development would be most fruitful. Studies that directly assess adolescent gender differences (in contrast to statistically controlling for gender) in neural activity during prosocial behavior are needed. Manipulating behavioral economic task conditions can assist with isolating context-related differences between male and female prosocial behavior. For instance, comparing prosocial behavior that is directed at individuals with varying degrees of closeness (i.e., strangers versus friends) may lead to gender differences and may also elucidate the effects of oxytocin and testosterone on prosocial behavior, as these hormones are both sensitive to the in-group versus out-group distinction. Moreover, manipulating social desirability (e.g., popularity) of prosocial targets may differentiate between self- versus other-oriented prosocial motivations, such that other-oriented individuals (e.g., girls) might behave prosocially towards all targets, even at a personal cost, whereas more self-oriented individuals (e.g., boys) would restrict prosocial behavior towards the most desirable peer in order to gain favor or some other personal benefit. Most importantly, longitudinal assessments of the effects of prosocial behavior, specifically altruistic prosocial development, on depressive symptoms are needed. By elucidating this relationship, we stand to uncover behavioral risk factors and markers of MDD that will be much more amenable for use in prevention and intervention efforts.

## Compliance with Ethical Standards

**Conflict of Interest** Dr. Gabriela Alarcón and Dr. Erika E. Forbes declare that they have no conflicts of interest.

**Human and Animal Rights and Informed Consent** This article does not contain any studies with human or animal subjects performed by any of the authors.

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- Declercq CH, Boone C, Emonds G. When do people cooperate? The neuroeconomics of prosocial decision making. *Brain Cogn*. 2013;81(1):95–117. doi:10.1016/j.bandc.2012.09.009. **This is a review about the neuroeconomics of prosocial behavior that covers theory of social decision making, including economic (i.e., extrinsic) and social (e.g., trust) incentives and the neural systems engaged in costly prosocial behavior. Literature supporting the interpretation that (1) the reward network generates motivation to cooperate (or not), (2) the cognitive control network processes extrinsic incentives to inform prosocial**



- motivation, and (3) the social cognition network processes social and threat signals that affect prosocial motivation is discussed. The function of these networks during altruistic punishment is also discussed
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