Pathways for engaging in prosocial behavior in adolescence

Published in:
Advances in Child Development and Behavior

Publication status and date:
Published: 01/01/2022

DOI (link to publisher):
10.1016/bs.acdb.2022.03.003

Document Version
Publisher's PDF, also known as Version of record

Citation for the published version (APA):
Crone, E. A., Sweijen, S. W., Te Brinke, L. W., & van de Groep, S. (2022). Pathways for engaging in prosocial behavior in adolescence. *Advances in Child Development and Behavior*, *63*, 149-190. https://doi.org/10.1016/bs.acdb.2022.03.003

CHAPTER SIX

Pathways for engaging in prosocial behavior in adolescence

Eveline A. Crone[a,b,*], Sophie W. Sweijen[a], Lysanne W. te Brinke[a], and Suzanne van de Groep[a]

[a]Erasmus School of Social and Behavioral Sciences, Erasmus University Rotterdam, Rotterdam, The Netherlands

[b]Department of Developmental and Educational Psychology, Leiden University, Leiden, The Netherlands

*Corresponding author: e-mail address: crone@essb.eur.nl

Contents

Abstract

Adolescent development is often regarded as a period of social sensitivities, given that brain development continues into the early 20s in interplay with social experiences. In this review, we present adolescence as a unique window for prosocial development; that is, behavior that benefits others. We present evidence for multiple pathways of neural sensitivity that contribute to key developmental processes related to prosocial behaviors, including valuing, perspective taking, and goal-flexibility. Yet, these processes are dependent on several contextual factors including recipients, audience effects, and strategic motivations. Next, we present intervention findings suggesting that prosocial

Advances in Child Development and Behavior, Volume 63
ISSN 0065-2407
https://doi.org/10.1016/bs.acdb.2022.03.003

experiences within these various contexts are crucial for adolescents developing into engaged and contributing members of society. These findings suggest a new interpretation of the elevated socio-affective sensitivity and emerging socio-cognitive development in adolescence, focusing on opportunities rather than risks.

1. Introduction

One of the hallmarks of adolescence is developing meaningful relationships outside the family context to eventually become an engaged and contributing member of society (Fuligni, 2019). As such, adolescence is an important transition period between the dependency on parents and other caregivers of childhood, and the mature social goals and independence of adulthood. The development of prosocial behavior, defined as behavior intended to benefit others, is of crucial importance for taking social responsibilities and developing mature social relationships (Carlo & Padilla-Walker, 2020). These behaviors may lead to extension of relationships with family members and friends to contributing to needs of more distant others (e.g., helping unknown others) and to society (e.g., engaging in community service).

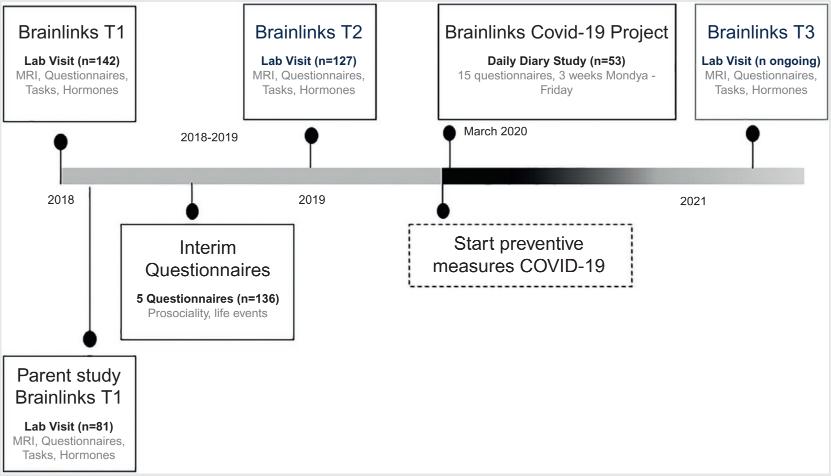
Adolescence represents a developmental time window typified by strong needs for exploration, forming new relationships, increasing intimacy, and rapid adjustment to changing social contexts (Blakemore & Mills, 2014; Steinberg, 2008). Adolescence starts with the onset of puberty, approximately at the age of 9–10-years in girls and 10–11-years in boys, although differences are observed between countries and cultures (Crone & Dahl, 2012). The onset of puberty is characterized by a rise in gonadal hormones, which are released through the hypothalamus-pituitary-gonadal axis, and have large influence on bodily characteristics and brain development (Goddings et al., 2014; Shirtcliff, Dahl, & Pollak, 2009). Pubertal development (also referred to as early to mid-adolescence) lasts until approximately age 15–16-years (with differences between cultures). The prolonged period of mid- to late adolescence continues until individuals have achieved mature social and personal responsibilities and is culturally dependent (Steinberg, 2008). The period of adolescence has extended considerably in the last century, as individuals rely on parents longer and have more possibilities for personal development and identity formation (Arnett, Zukauskiene, & Sugimura, 2014).

Prosocial behavior refers to behavior that benefits others, which can be non-costly (e.g., helping) or costly (e.g., sharing) (Carlo & Padilla-Walker, 2020). It is well established that prosocial behavior changes during adolescence and young adulthood. However, the exact developmental patterns are still debated. Some studies show increases in prosocial behavior during adolescence (Fu, Padilla-Walker, & Brown, 2017; Padilla-Walker, Carlo, & Memmott-Elison, 2018), whereas others find decreases or stabilization (Malti et al., 2015). This has recently been interpreted as evidence that prosocial behavior should be regarded as a multi-dimensional construct, comprising many behaviors such as cooperating, helping, and giving. It depends on socio-affective and socio-cognitive developmental processes, (i.e., valuing, perspective-taking, and goal flexibility) and on multiple contextual processes (i.e., the target or recipient of prosocial behavior and the situational context), such as whether prosocial behavior is observed by others (i.e., audience effects; Carlo & Padilla-Walker, 2020).

In this review article, we will provide a comprehensive perspective on prosocial development suggesting that the development of prosocial behavior depends on mutual socio-affective and socio-cognitive maturation, as is evident from behavioral and neural pathways. The review is organized around the common themes of the Brainlinks study, an experimental accelerated longitudinal cohort and intervention study on prosocial development that includes adolescents between ages 9–22-years (see Box 1 for a description and Appendix 1 for the meta-data). First, we will summarize evidence for the structural development of the human brain during adolescence, suggesting that this may be a time during which the developing individual is particularly sensitive to environmental influences. Second, we will present a possible model to describe the pathways of multi-dimensionality of prosocial behavior, illustrated with examples of recent empirical developmental behavioral and neuroimaging studies (including, but not limited to results from the Brainlinks study). Third, we will show behavioral evidence for malleability of prosocial behavior in intervention designs according to the presented model. Finally, we will show that a comprehensive understanding of pathways of prosocial behavior, including sensitivity to environmental influences, will be of importance for valuing the contribution of young people to benefit self and other, as well as to adaptation and resilience of the society at large.

BOX 1 The Brainlinks study

The Brainlinks study located in the Netherlands aims to examine the multi-dimensionality of prosocial development in adolescence. The project includes (a) an accelerated longitudinal design with neuroimaging, behavioral, and questionnaire measures acquired in 3 waves across a time window of 5 years (see figure); and (b) a behavioral intervention study. We present the full project's meta-data in the Appendix 1.



The goal of the longitudinal study is to examine the processes described in this review (vicarious gains/cooperation, giving/sharing, trust/reciprocity), which reflect prosocial processes of increasing complexity. Contextual manipulations involve the target of prosocial behavior, audience effects on giving and strategic giving manipulations. The key aims of the project are:

(i) Combining neural development with behavioral development
(ii) A longitudinal design allowing for testing within-person change
(iii) A multidimensional approach of prosocial behavior allowing for the examination of state and trait dimensions, and possible underlying latent variables, as well as associations within individuals over time
(iv) A detailed assessment of environmental factors that may shape prosocial development

Prior studies have pointed to an important role of the family in shaping prosocial behaviors in adolescence. The study therefore includes an enrichment wave (following wave 1) in which a selection of mothers and fathers performed a selection of the same measures as the adolescents, including a neuroimaging vicarious reward task for children and a self-concept task for parenting.

BOX 1 The Brainlinks study—cont'd

An additional aim of the study includes a separate naturalistic and micro-trial intervention study for enrichment of prosocial experiences, with partly overlapping measures as the longitudinal study. These study dimensions will reveal the effects of environmental factors hindering or fostering prosocial development. An unexpected event was the start of the pandemic between wave 2 and wave 3 of the longitudinal study. For this reason, the study has an enrichment of three-weeks daily diary measures collected in between these waves.

2. A cognitive neuroscience perspective on adolescent development

By the time children enter puberty, the human brain has already gone through massive developments (Gilmore, Knickmeyer, & Gao, 2018; Lee et al., 2019). Yet, numerous longitudinal structural neuroimaging studies have revealed that adolescent development involves additional widespread changes in the structure of the brain (Mills et al., 2016; Tamnes et al., 2017). Longitudinal research examining changes in brain structure over time within individuals has shown that cortical white matter increases approximately linearly with age throughout childhood and adolescence until the early twenties (Paus, 2010). In addition, cortical gray matter, which reflects neuronal density and the number of connections between neurons, follows an inverted-U shape over development, peaking at different ages depending on the region (Tamnes et al., 2017). Therefore, gray matter loss is often considered an index of the time-course of maturation of a brain region (Lee et al., 2014).

Within the cortex, gray matter reduction is most protracted for medial and lateral prefrontal cortex (PFC), and the junction between temporal cortex and parietal cortex (temporal-parietal junction: TPJ). Here, cortical gray matter loss continues until the early 20s (Mills, Goddings, Clasen, Giedd, & Blakemore, 2014). The development of subcortical brain regions, which are evolutionarily older parts of the brain, is also subject to both linear and non-linear changes, such that some subcortical regions (such as the caudate and the putamen) linearly decrease in size, whereas other subcortical regions (such as the amygdala and the hippocampus) show an increase in size at the onset of puberty, which stabilizes in adolescence and adulthood (Herting et al., 2018; Wierenga et al., 2018). Both cortical and subcortical brain development are driven by both age- and puberty-specific changes

(Goddings et al., 2014). The relation between structural brain volume changes and changes in behavior, however, is currently not yet well understood. In addition, very little is known about how experience-dependent changes influence or shape brain development in adolescence. Recent studies show initial evidence for an important contribution of social experiences on brain development, by showing a longitudinal relationship between gray matter thickness of the medial PFC and TPJ, and friendship quality (Becht et al., 2020). More direct evidence for the hypothesis that brain development is sensitive to environmental influences comes from genetic twin modeling. In a recent study in 7–8-year-old monozygotic and dizygotic twins, it was found that gray matter of all social brain regions is heritable, but that especially the gray matter thickness of TPJ was sensitive to shared environmental influences (Van der Meulen et al., 2020). Taken together, structural brain imaging findings illustrate a formative change in gray matter thickness and surface area during childhood and the teenage years, with initial evidence that some of the regions that show the most protracted development are more sensitive to environmental influences.

One way to further understand the relation between brain development and behavior is by using event-related functional magnetic resonance imaging (fMRI) studies. fMRI gives insight into neural regions that are involved in processing events or decision-making by detecting changes in blood oxygenation and flow that occur in response to neural activity (Logothetis, 2008). Known for its excellent spatial resolution, fMRI enables the examination of both cortical and subcortical brain regions, which are both assumed to play an important role in social behaviors (Blakemore & Mills, 2014; Crone & Dahl, 2012; Logothetis, 2008). An additional advantage of fMRI is that it allows for the measurement of processes that may be hard to capture on a behavioral level, such as initial tendencies, feelings, and other processes that are not necessarily expressed verbally or behaviorally (Lieberman, Straccia, Meyer, Du, & Tan, 2019). To date, studies have reported separate developmental pathways for socio-affective processes, with a focus on the subcortical ventral striatum (VS), and socio-cognitive developmental processes, with a focus on cortical brain regions including the medial PFC, the TPJ, and the superior temporal sulcus (STS), and the lateral prefrontal cortex (DLPFC) (Fig. 1). We will summarize these processes below in a pathway model, followed by empirical examples.

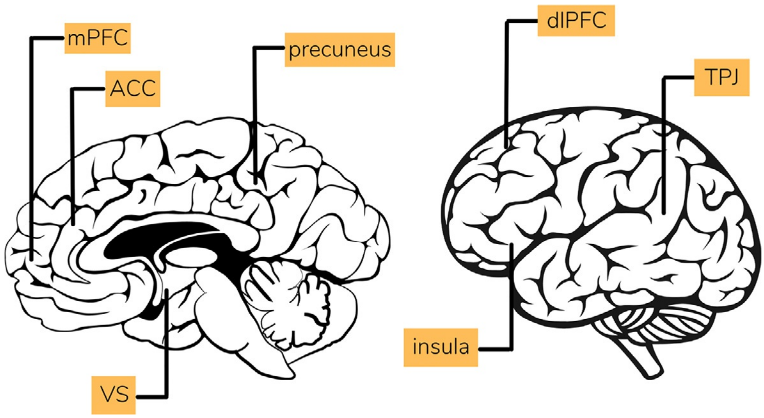


Fig. 1 Brain regions involved in various aspects of prosocial behavior, displayed are the ventral striatum (VS), insula, anterior cingulate cortex (ACC), medial prefrontal cortex (mPFC), precuneus, temporal parietal junction (TPJ), the superior temporal sulcus (STS) and the dorsolateral prefrontal cortex (dlPFC).

3. Capturing the complexity of prosocial development in a multiple-pathway model

The complexity of prosocial development can best be understood by decomposition of the various processes involved in behaviors that benefit self and others (Tamir & Hughes, 2018). Here, we differentiate between socio-affective and socio-cognitive processes which are thought to follow separable developmental time courses. Adolescence is one of the periods in life well known for its rise in emotional reactivity, both in terms of frequency and intensity (Dahl, Allen, Wilbrecht, & Suleiman, 2018). The dynamic characteristic of emotional reactivity is thought to peak in mid-adolescence, suggesting that adolescents can experience emotions more strongly than children and adults (Ernst, 2014; Larson, Moneta, Richards, & Wilson, 2002).

These changes in emotional reactivity and reward processing co-occur with a protracted development of socio-cognitive perspective taking. Whereas it has been well conceptualized that the basic socio-cognitive building blocks for prosocial behavior, such as theory of mind, develop in early childhood, recent studies have supported the notion that more complex social-cognitive behaviors, such as perspective taking and goal-flexibility, emerge in adolescence (Dumontheil, Apperly, & Blakemore, 2010; Fett et al., 2014; van den Bos, Westenberg, Van Dijk, & Crone, 2010).

Traditionally, the heightened emotional reactivity and protracted development of socio-cognitive functions have been linked to maladaptive adolescent behaviors such as alcohol and substance abuse, anxiety, and depression (Paus, Keshavan, & Giedd, 2008). These behaviors are known to increase considerably in adolescence with peaks in risk-taking and social anxiety around age 16–17-years (Blote, Kint, Miers, & Westenberg, 2009). This is also the time when most affect-driven psychiatric disorders manifest themselves for the first time, such as anxiety, depression, substance abuse, and schizophrenia (Lee et al., 2014; Paus et al., 2008).

Existing models, however, have often ignored how this normative development of emotional reactivity and protracted development of socio-cognitive functions have adaptive functions, creating opportunities to understand people's views and motivations (i.e., perspective taking) and aiding rapid adaptation to different contexts (i.e., goal flexibility; (Crone & Dahl, 2012)). Recent evidence suggests that the very same emotional reactivity that creates sensitivities for potential negative developmental trajectories (including risk for substance abuse, delinquency, social anxiety, or depression) may under other circumstances create opportunities for positive developmental trajectories—such as by fostering social sensitivity, cooperation, sharing, and helping (Telzer, Fuligni, Lieberman, & Galvan, 2014). One possibility is that increased emotional reactivity in mid-adolescence is associated with heightened reward valuing in prosocial contexts (Telzer, 2016).

Indeed, brain imaging research has allowed for empirical evaluations of prosocial developmental processes by relating neural activity to prosocial behaviors, resulting in three important findings. The first finding pertains to the ventral striatum, a region involved in many different types of reward and learning signals. This region is especially well known for its role in processing a variety of basic rewards (Haber & Knutson, 2010). The ventral striatum has anatomical and functional connections to the orbitofrontal cortex, also referred to as ventral medial prefrontal cortex (Lieberman et al., 2019), and together this network of brain regions has been interpreted as having a crucial role in updating reward values (Delgado et al., 2016). Studies in adults have reported that ventral striatum activity does not only correspond with monetary rewards, but also with feelings of inclusion (Tamir & Hughes, 2018), cooperation (Rilling & Sanfey, 2011), and fairness, suggesting that the ventral striatum is also sensitive to social rewards

(Tabibnia, Satpute, & Lieberman, 2008). This social reward sensitivity is therefore thought to also underlie prosocial motivations, as it reinforces behaviors that benefit others and strengthens social relationships (Fett, Gromann, Giampietro, Shergill, & Krabbendam, 2014). Second, based on research in adults, there is converging evidence from functional neuroimaging studies for a crucial role of the medial PFC, TPJ, and STS (also referred to as the "social brain" network) in situations that require individuals to consider about thoughts and intentions of others, such as helping and trusting others (Amodio & Frith, 2006; Lieberman et al., 2019; Rilling & Sanfey, 2011). These forms of perspective-taking play an important role in motivations that underlie prosocial actions (Crone & Fuligni, 2020). Third, various studies have demonstrated that the dorsolateral prefrontal cortex (DLPFC) plays an important role in goal-flexibility related to balancing between the needs of self and others, for example by inhibiting selfish impulses (Achterberg, van Duijvenvoorde, Bakermans-Kranenburg, & Crone, 2016) or by engaging strategic actions (van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2009). Together, these processes, which rely on brain regions that develop during adolescence (Blakemore & Mills, 2014), are thought to work in concert when acting prosocially toward various targets and in various contexts.

Two additional processes related to prosocial behavior that are sensitive to individual differences in adolescence are empathy and norm processing. Empathy refers to the communication of an emotional state from one individual to another and is associated with multiple cooperating brain regions, from mirror neurons to cognitive control (Decety & Holvoet, 2021). A recent literature review outlines evidence that empathy in its basic form develops in childhood through interactions with the environment, with an important role for the family context (Brownell, Svetlova, Anderson, Nichols, & Drummond, 2013). These basic empathic abilities are important building blocks for more complex socio-cognitive processes such as perspective taking, which develop further in adolescence (Decety & Holvoet, 2021; Van der Graaff, Carlo, Crocetti, Koot, & Branje, 2018). Norm processing develops considerably in childhood years, with strong social equity norms around the ages of 8–9-years (Meuwese, Crone, de Rooij, & Guroglu, 2015). In adolescence, these equity norms become replaced by more complex norms that require higher levels of perspective-taking (understanding intentions or others) and goal flexibility (taking into account the broader social context) (Guroglu, van den Bos, & Crone, 2014; van den Bos et al., 2010). Prior studies in adults revealed a unique set of brain regions that are responsive to norm violations specifically; the anterior cingulate cortex (ACC) and the bilateral insula (Rilling & Sanfey, 2011). These regions are typically engaged when individuals perform actions that go against their personal norms (Guroglu, van den Bos, van Dijk, Rombouts, & Crone, 2011). Even though empathic concern and norm processes appear to be relatively stable in adolescence in terms of developmental processes, empirical studies typically show large individual differences (Meuwese et al., 2015; Stern & Cassidy, 2018; Van der Graaff et al., 2018), possibly suggesting relatively larger susceptibility to the environment, which Is why we take these processes into account in our model of prosocial development (Decety & Holvoet, 2021).

In the next sections, we implement this model in three steps: (i) we evaluate a multiple-pathway neuroscientific model of prosocial development by relating neuroscience discoveries to developmental changes in key dimensions of prosocial development and their sensitivity to various contextual factors; (ii) we test the role of environmental support factors by reviewing experimentally controlled and naturalistic service learning programs aimed at fostering socio-affective and/or socio-cognitive processes that contribute to prosocial development in adolescence. This approach will allow us to evaluate the important question: (iii) When and how do changes in socio-affective and socio-cognitive development result in opportunities for prosocial development and which factors facilitate opportunities for positive, prosocial development?

4. Developmental neural pathways of prosocial behavior

Although originally regarded as a generalized construct, recent studies have elucidated that prosocial behavior is an umbrella term consisting of many different types of other-benefitting behaviors. These studies have shown that different types of prosocial behaviors do not always correlate within individuals, and often have unique antecedents and developmental patterns (Carlo & Padilla-Walker, 2020; Padilla-Walker et al., 2018). In the next sections, we examine developmental changes in four key dimensions of prosocial development which are increasing in complexity: (i) socio-affective valuing of rewards for others through vicarious gains and cooperation, (ii) socio-cognitive understanding of needs when helping, (iii) combining socio-affective and socio-cognitive building blocks during giving and sharing, and (iv) understanding long-term consequences for others when trusting or reciprocating trust.

The various forms of prosocial behavior are also situated within a multitude of contexts, including variations in the target/recipient of prosocial behavior (e.g., family, friends, community), the visibility of prosocial behavior (e.g., being observed online or by an audience), the strategic context (power of the recipient), and the needs and time periods of prosocial behavior (e.g., targets in need, COVID-19). In the subsequent section, we describe studies that aim to decompose contextual influences on prosocial behavior, which allows us to examine these various domains in more detail (Luo, 2018). These processes will be examined by reviewing behavior and fMRI studies including children, adolescents and adults.

4.1 Valuing rewards for others through vicarious gains and cooperation

One motivation for prosocial actions can be the pleasure of receiving rewards for others (Harbaugh, Mayr, & Burghart, 2007; Morelli, Knutson, & Zaki, 2018). A way to operationalize this is through vicarious rewards, that is, rewards that are received for another individual, either in a mutual gaining context or gaining only for others. Typically, these rewards are non-costly as they do not come at the expense of self.

It is well known that the ventral striatum is a reward center in the brain that responds strongly to receiving rewards for self (Haber & Knutson, 2010). A significant number of studies has found that, relative to children and adults, activity in ventral striatum is heightened during adolescence when receiving rewards for self, suggesting more emotional reactivity in response to reward (Casey, 2015; Galvan, 2010). This result has been replicated several times using a variety of gambling paradigms, such as passive gambling tasks (Galvan et al., 2006; Van Leijenhorst et al., 2010), active gambling tasks (Van Leijenhorst et al., 2010), social risk taking tasks (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011), and probabilistic learning tasks (Cohen et al., 2010), and was confirmed in a meta-analysis (Silverman, Jedd, & Luciana, 2015). Although prior studies have mostly relied on monetary rewards to elicit striatal reactivity, recent work shifted to other forms of rewards, showing that the ventral striatum response appears to be highly sensitive to social factors, especially in adolescence (Chein et al., 2011). One hypothesis is that emotional reactivity in adolescence in terms of ventral striatum activity to vicarious rewards can account for changes in the emotional valuing of prosocial activities (Telzer, 2016; Telzer, Fuligni, Lieberman, & Galvan, 2013). Indeed, prior research in adults showed that the ventral striatum is most responsive to rewards for close others relative to distant others (Morelli et al., 2018), and when there is higher social identification with the group (Hackel, Zaki, & Van Bavel, 2017). Together, these studies show that in adults the ventral striatum may be an important marker for the "warm glow" of receiving rewards for others (Harbaugh et al., 2007; Rilling & Sanfey, 2011). Below, we summarize studies that have examined whether adolescence is a time of heightened reward activity, not only for self but also for others.

In studies focusing on adolescence, vicarious rewards have been examined for family members, friends, unknown others such as peers, and broader community partners (e.g., charity). First, in a cross-sectional study vicarious neural reward responses were examined for family members, specifically mothers. Adolescents aged 10–27-years gained money for self or for their mother, and a neural peak ventral striatum in mid-adolescence was observed when vicariously gaining for mothers (Braams & Crone, 2017). Vicarious gains may be an important factor in valuing the outcome of cooperation, which refers to a group of individuals working together toward a similar goal. To examine the relation between neural activity in the ventral striatum for vicarious gains in the family context in more detail, a second study examined vicarious gains in a Prisoner Dilemma format (Brandner, Guroglu, & Crone, 2020). The Prisoner Dilemma Game is a cooperation game where two players each decide simultaneously whether to cooperate or defect. In case of mutual cooperation, both players receive a moderate size reward (Rilling et al., 2002). An experimental behavioral part of the study in 9–18-year-old adolescents revealed differential developmental trajectories for cooperation with parents (increasing with age) and unknown others (peaking in mid-adolescence followed by a decrease in adulthood) (Brandner, Guroglu, van de Groep, Spaans, & Crone, 2021; see also Box 1). A false-choice fMRI version of the Prisoner Dilemma Game administered to the same participants showed that ventral striatum activity scaled with reward values for self, but the ventral striatum was also responsive to vicarious rewards for parents (see Fig. 2A; Box 1). In contrast, no such vicarious reward response was observed when gaining for unknown peers (Brandner et al., 2020, 2021). Together, these findings show evidence for vicarious neural gains for family members, with some evidence that this activity is heightened in mid-adolescence (Braams & Crone, 2017) and scales with pleasure of winning for mothers (Brandner et al., 2021).

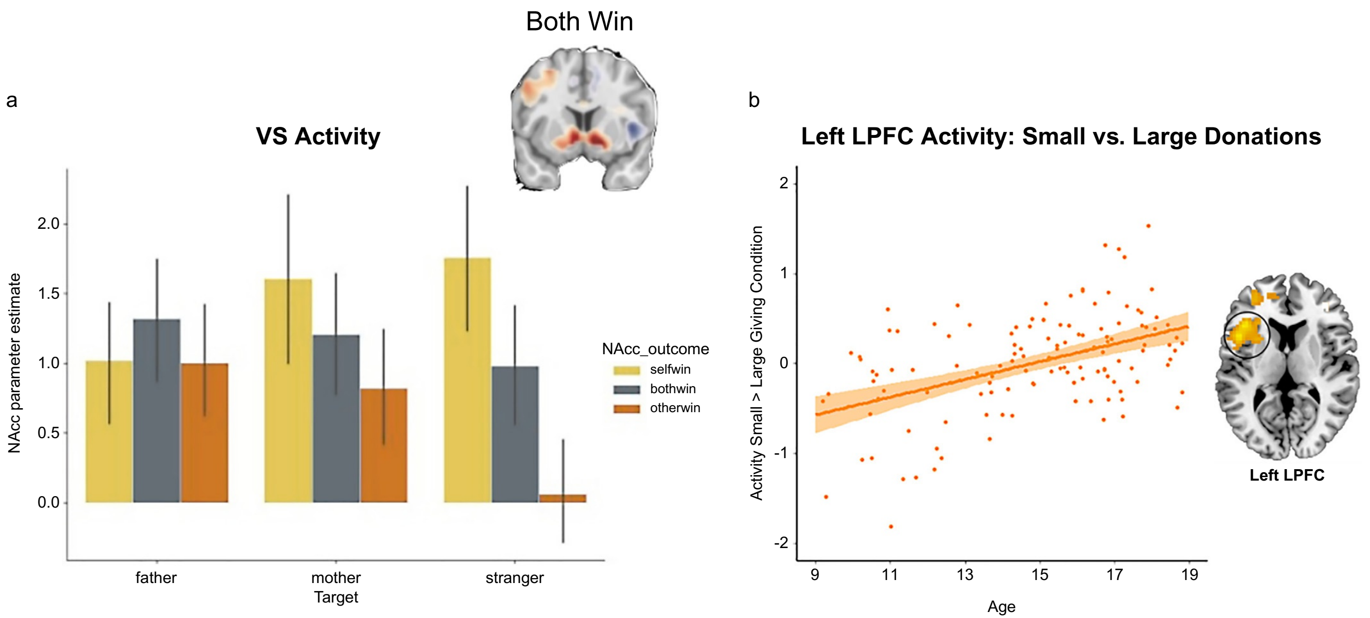


Fig. 2 Example of neural activity in a social-affective vicarious reward task (Brandner et al., 2021) and socio-cognitive giving task (van de Groep et al., 2022) based on the first wave of the Brainlinks study (Box 1). (A) Results showing heightened ventral striatum activity when gaining for family members, but not for strangers in adolescence. (B) Young adolescents engage the dlPFC stronger for large donations whereas older adolescents engage dlFPC more for small donations.

Second, a longitudinal study examined whether vicarious gains for friends elicited a similar developmental pattern of neural activity as rewards for self. For this study, 8–29-year-old participants reported who was their best friend on three longitudinal waves separated by 2 years. This allowed for the distinction between adolescents with stable best friends (same friend across 3 waves) and unstable best friends (different best friend across 3 waves). For adolescents with stable best friends, there was a peak in neural activity in mid-adolescence for vicarious rewards for friends as well as for rewards for self. In contrast, no such developmental pattern was observed for adolescents with unstable best friends, although for unstable best friends, ventral striatum activity correlated with experienced friendship quality (Schreuders, Braams, Crone, & Guroglu, 2021). These findings show evidence for vicarious neural gains for close friends in adolescence.

Third, vicarious rewards can be gained also for more distant prosocial partners with whom the participant does not have a direct connection. One such recipient can be a charity, which typically receives prosocial actions because of the observed need and because charities are considered societal trustworthy recipients (Harbaugh et al., 2007). Using a similar Prisoner Dilemma Game format, one recent study including adolescents aged 11–21-years showed that when gaining vicariously for charity, on the group level charity gains were not associated with increased activity in the ventral striatum (Spaans, Peters, & Crone, 2019). However, it was found that adults who scored higher on self-reported empathy (Spaans, Peters, & Crone, 2019) and that adolescents who scored higher on perspective taking and donation behavior (Spaans, Peters, & Crone, 2020), showed higher activity in the ventral striatum when vicarious gaining for charity, possibly suggesting that they feel a closer connection to the charity. Together, these findings show that ventral striatum activity is related to the relationship with the recipient, with higher activity when the target is experienced as closer or when the recipient is deserving, such as in the case of charity.

Finally, to examine whether vicarious rewards were related to behavioral adaptations, prior studies examined vicarious gains in a learning paradigm. In one functional neuroimaging study, it was examined whether behavioral learning rates and neural prediction errors in a probabilistic learning task for self and unknown peers differed across 9–21-year-old adolescents (Westhoff, Blankenstein, Schreuders, Crone, & van Duijvenvoorde, 2021). A prior study in adults already showed that prediction errors for unknown peers were related to activity in the ventral striatum, but only activity in the subgenual ACC, a region bridging the ventral striatum and the vmPFC, was correlated to self-reported empathy (Lockwood, Apps, Valton, Viding, & Roiser, 2016). In a similar study including adolescents and adults, it was found that learning rates were higher in younger adolescents (indicating more immediate adaptation) when learning for peers. At the neural level, ventral striatum activity was higher for prediction errors for self than for peers across adolescence, but activity in vmPFC showed an age-related increase when learning for others (Westhoff et al., 2021). An intriguing question for future research is therefore to examine how vicarious gains and learning rates develop for close others, such as family and friends.

Taken together, in a vicarious reward setting, adolescents show neural peaks in activity when receiving rewards for close others such as mothers and stable friends, but not for more distant others such as charity, unstable best friends, or unknown peers. In case of more distant others, ventral striatum activity correlates more strongly with perspective taking (charity), friendship quality (unstable friends), and prediction errors (unknown others).

4.2 Helping: Social-cognitive perspective taking

When prosocial behaviors involve an action to contribute to the needs of others, this can be defined as helping. In its simplest format, helping behavior is non-costly as it does not need to involve giving up resources to provide assistance to others. Helping does, however, involve an understanding of the needs of others (Carlo & Padilla-Walker, 2020; Decety & Holvoet, 2021).

Prior studies have examined helping behavior in the context of needs of unknown peers in a prosocial Cyberball Game. The traditional Cyberball game involves a three player ball tossing game where one of the players is excluded, leading to negative feelings and loss of control (Boyes & French, 2009). In the prosocial Cyberball game, there are four players where the participant observes that two players exclude a third player from the ball tossing game. The participant has the possibility to help the excluded player by increasing the number of ball tosses toward them, thereby compensating for their exclusion (Riem, Bakermans-Kranenburg, Huffmeijer, & van IJzendoorn, 2013). In a behavioral study, it was found that adolescents between ages 9–17-years compensate for exclusion, but compensation was higher for adolescents who reported more empathy (Vrijhof et al., 2016). In an fMRI study including adults, it was observed that tossing to the excluded player was associated with increased activity in the ventral striatum and temporal parietal junction (van der Meulen, van IJzendoorn, & Crone, 2016). A similar set of studies in children, in contrast, showed either no robust neural activity in three studies including children ages 7–10-years (van der Meulen et al., 2017) or increased activity in the precuneus when compensating exclusion in 7–8-year-old (van der Meulen, Steinbeis, Achterberg, van IJzendoorn, & Crone, 2018). A different study comparing 12–17-year-old adolescents with 22–30-year-old adults showed that adults more often helped excluded others than adolescents, which was accompanied by more activation in the TPJ and medial prefrontal cortex in adults (Tousignant, Eugene, Sirois, & Jackson, 2018).

Together, these studies suggest that helping excluded unknown peers is associated with activation in different neural regions depending on the age of the participants, specifically showing increased activity in the TPJ in adults relative to children and adolescents (Tousignant et al., 2018; van der Meulen et al., 2016). Even though it has not yet been examined how friends are compensated during adolescence, a prior behavioral study showed that participants only help unknown peers when they are being excluded by unknown others, but not when they are excluded by their friends (Spaans, Will, van Hoorn, & Guroglu, 2019). Thus, the extent to which adolescents show helping behavior depends on the development of perspective taking and the context in which help is needed, such as whether the excluded target is a family member, friend, or unknown other.

4.3 Giving: Socio-affective and socio-cognitive building blocks

Giving is a costly prosocial act in which an individual distributes valuable resources between themself and someone else (Cutler & Campbell-Meiklejohn, 2019). There is accumulating evidence from studies in adults that this behavior is driven by both socio-affective and socio-cognitive processes, which are represented in intuitive and deliberative neural systems, respectively (Feng, Luo, & Krueger, 2015; Luo, 2018). The intuitive, socio-affective system includes regions such as the ventral striatum, vmPFC, and anterior insula, which play a role in the processing of reward valuing and norm violations, respectively (Luo, 2018). The more deliberate socio-cognitive system includes regions such as the dLPFC, TPJ, and STS) (Cutler & Campbell-Meiklejohn, 2019; Feng et al., 2015; Luo, 2018). Below, we give an overview on the role of these affective and cognitive brain systems in giving behavior, which often requires adolescents to take the target of giving and situational demands into perspective.

One way to operationalize giving behaviors is by utilizing economic games, which are structured experiments which model interdependent situations (Cutler & Campbell-Meiklejohn, 2019; Gummerum, Hanoch, & Keller, 2008) (see Fig. 3). The Dictator Game is the most basic economic game, in which one individual decides upon a certain split of valuable resources (Engel, 2011). The target or recipient of this division has no power over this decision, hence the name Dictator Game. Although economic games were initially developed with the idea that individuals would show self-interested, rational (i.e., homo-economical) behavior, studies in adults and adolescents alike quickly showed that individuals tend to give away 20–30% of their resources to unknown others, even in situations where there are no extrinsic or future rewards associated with this decision (Urbina & Ruiz-Villaverde, 2019). Neuroimaging studies have often utilized variations of the Dictator Game to study giving behavior as its structured nature enables the quantification of this complex behavior. This allows for the comparison of neural activity associated with varying levels of generosity. These studies, which have mostly been performed in adults, have elucidated that, compared to selfish decisions, giving elicits activation in various regions, including the nucleus accumbens, mPFC, and dlPFC (Cutler & Campbell-Meiklejohn, 2019).

Giving in the Dictator Game: One study in 8–16 year-old children and adolescents operationalized giving by comparing four conditions: costly giving, non-costly giving, costly-rewards, and non-costly rewards to unknown peers (Do, McCormick, & Telzer, 2019). Comparing costly giving to costly- and non-costly rewards revealed no differences in neural activation. In contrast, comparing costly to non-costly giving revealed activation in the precuneus and inferior temporal gyrus. A subsequent analysis examined costly prosocial versus non-costly prosocial choices in a subsample of youth that made sufficient prosocial decisions. This analysis revealed a quadratic peak in neural activation in the pSTS, temporal pole and inferior frontal gyrus (IFG) in early adolescence when comparing costly giving to costly rewards; and in pSTS, dlPFC, and IFG activation when comparing costly versus non-costly giving. Overall, these results suggest elevated activation in socio-cognitive systems of the brain in early/mid-adolescence, particularly in relatively prosocial individuals, possibly reflecting higher goal-flexibility.

In a recent study from our own group (van de Groep et al., 2022; van de Groep, Zanolie, & Crone, 2020a; for more details see Box 1), we designed a variation of the Dictator Game in which individuals could give away coins in either a small or large giving condition, to control for the number of

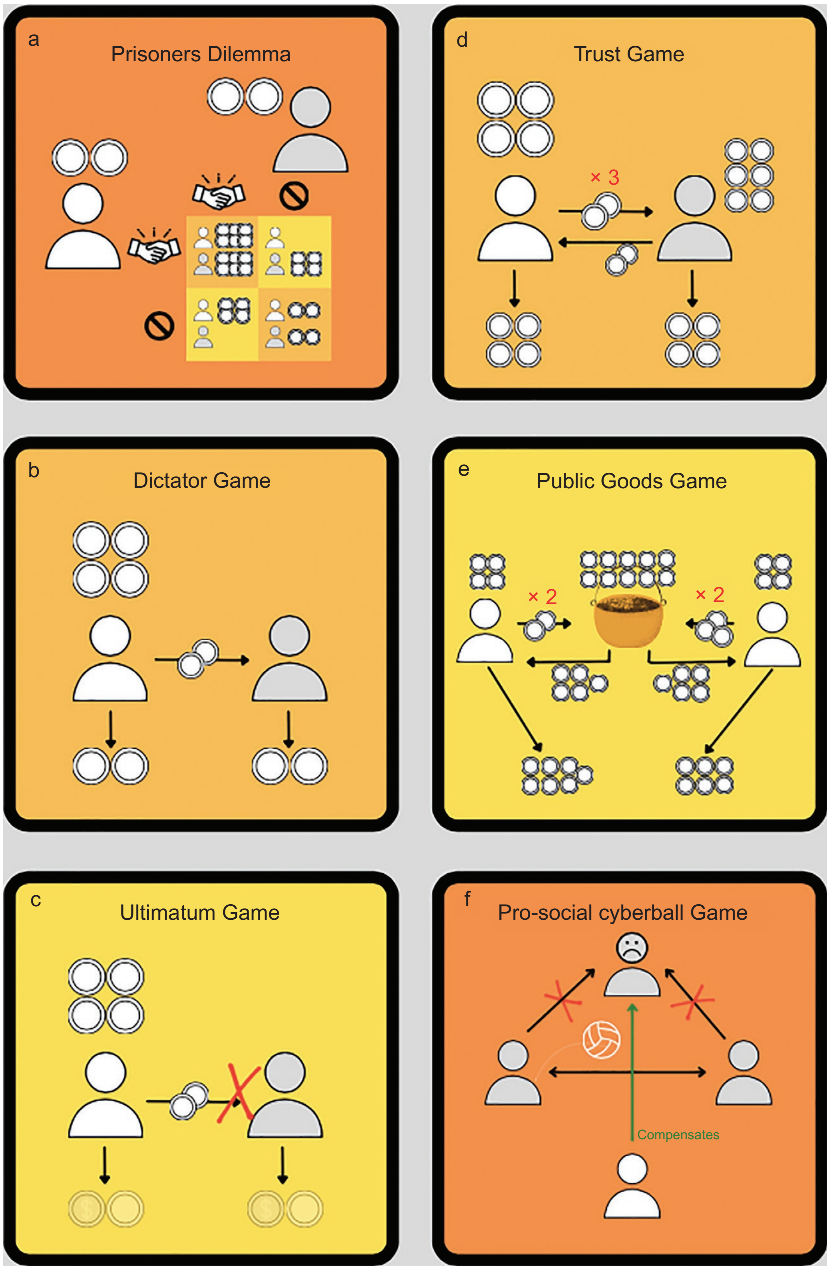


Fig. 3 See figure legend on opposite page.

prosocial choices. In the small giving condition, individuals could give away 1, 2, or 3 out of 7 coins. In the large giving condition, individuals could give away 4, 5 or 6 out of 7 coins. This design allowed us to compare small versus large size giving conditions, but also relative generosity within these giving conditions. Importantly, this design also allowed for voluntary decisions within the small and large giving conditions, as voluntary decisions give the best indication of generosity (Gagné, 2003). The results of the first wave of this longitudinal study ($N = 128$, ages 9–19) revealed that adolescents gave more in the small compared to large size giving condition. Giving very small or very large amounts was associated with increased activity in the mPFC and anterior insula, suggesting a general response to giving size. In addition, age comparisons revealed that older adolescents showed increased lateral and anterior PFC activation for small size giving (van de Groep et al., 2022) (see Fig. 2B; Box 1). These results were interpreted to suggest a role for the mPFC and anterior insula in saliency detection and norm processing, and show a developmental shift from stronger activity in the anterior and lateral PFC for large (high-costly) giving to small (low-costly) giving. These studies fit well with recent studies comparing Ultimatum Game giving (i.e., strategic) with Dictator Game giving. The Ultimatum Game is a game with the same structure as the Dictator Game but where the second player has the possibility to reject the offer, in which case both players receive nothing. Comparing this additional strategic element of the Ultimatum Game versus the Dictator Game resulted in elevated activity

Fig. 3 Example of economic games that are often used to examine prosocial behavior. (A) The Prisoner Dilemma Game is a cooperation game where a mutual cooperation choice leads to mutual benefit. (B) The Dictator Game is an economic game where a player can divide resources between themselves and a second player. (C) The Ultimatum Game is an economic game that is similar to the Dictator Game, but with the possibility of the second player to reject in which case both players receive nothing. (D) The Trust Game is a two-player exchange game, where the first player can decide on the division of resources, or can trust the second player in which case resources are increased. The second player has the option to reciprocate (the prosocial choice) in which case both players moderately benefit, or to defect in which case the second player benefits most. (E) The Public Goods Game is a multi-player economic game where all players contribute resources to a common good, which is then increased by a multiplier and shared among the players. The prosocial game is to contribute. (F) The Prosocial Cyberball Game is a helping paradigm where the participant has the possibility to compensate (i.e., help) a player who is being excluded by other players in a ball tossing game.

in lateral PFC for strategic giving, which increases between ages 6–12-years (Steinbeis, Bernhardt, & Singer, 2012, see also Guroglu et al., 2011).

Taken together, costly and strategic giving involve both socio-affective and socio-cognitive neural systems in deciding upon giving size (i.e., generosity). These studies show possible evidence for higher goal flexibility as demonstrated by increased lateral PFC activity in early to mid-adolescence (Do et al., 2019; van de Groep et al., 2022).

Giving to various targets: Giving to unknown others tells only part of the story of human generosity, as most of our interactions are with people we know (Guroglu et al., 2014). Several studies have focused on relational giving, such as giving to family and friends.

One study showed that neural activation related to giving to one's family depended on their culture (Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010). Whereas Latino and White participants showed similar levels of generosity toward their family, they showed distinct patterns of activity within the mesolimbic reward system. Latino participants showed more reward activity when contributing to their family, while White participants showed more reward activity when they gained money for themselves. Reward activity was measured as activity in the ventral and dorsal striatum, as well as the ventral tegmental area. These results show that characteristics of the benefactor and target of giving interact to shape giving decisions.

Other studies have examined giving to peers, such as a recent study that examined giving to real-life friends, disliked peers, neutral peers, and unfamiliar peers in mid-adolescence (Schreuders, Klapwijk, Will, & Guroglu, 2018). Here, adolescents showed highest levels of giving to friends, and lowest levels for disliked peers. Giving to friends compared to disliked peers was associated with activation in the putamen and posterior middle temporal gyrus, and giving to friends compared to unfamiliar peers was associated with activation in the superior parietal lobule and precentral gyrus. However, these studies did not examine age-related differences in neural activation in relational giving.

In our own study we aimed to examine age-related differences in neural activation pertaining to giving to friends and unfamiliar peers (van de Groep et al., 2022, see also Box 1). To this end, we employed the aforementioned variation of the Dictator Game in which participants could divide seven coins between friends and unfamiliar peers, in either a small or large giving condition. Here, we observed that individuals gave more to friends than to unfamiliar peers. This differentiation was greater in older compared to younger adolescents. Giving to friends was associated with activation in the right insula, bilateral TPJ, right lateral PFC, and right SMA, but no age-related differences were observed in neural activity for friends compared to unfamiliar peers. One region, the precuneus, showed an interaction between giving size and target, such that activation was lowest for large-size giving to unfamiliar peers, suggesting that adolescents were less likely to engage in perspective taking during these decisions compared to decisions that involved small-size giving and giving to friends. Overall, these results suggest that age-related differences in giving in adolescence may be specific to friends, a target whose importance greatly increases during this period in life (Van Hoorn, Van Dijk, Guroglu, & Crone, 2016). However, it remains an empirical question whether and how this bias in giving to friends is reflected in the brain. Answering this question may require a different methodology, such as longitudinal analyses or functional connectivity analyses.

Finally, neuroimaging studies have investigated the extent to which neural activity is modulated by in-group to out-group giving. These studies in young adults (Telzer, Ichien, & Qu, 2015) and adolescents (Do & Telzer, 2019) have shown that youth give more to in-group members (i.e., have an in-group bias). In young adults, this was accompanied by increased activation in the ventral striatum. Moreover, a greater sense of group identity was associated with heightened activation in the VLPFC, ACC, TPJ, and dmPFC when contributing to out-group compared to in-group members, suggesting that this requires additional self-control and perspective taking related processing (Telzer et al., 2015). The 8–16-year-old adolescents were more likely to give when there was a greater discrepancy between outcomes for others over oneself (i.e., higher reward inequity). No differences in general corticostriatal activation were observed for giving to in-versus out-group members, but adolescents showed greater connectivity between the ventral striatum and posterior STS when considering relatively inequitable decisions that benefited out-group peers (Do & Telzer, 2019). This study observed no age differences, suggesting that in-group versus out-group biases and the associated brain processes already exist from childhood onwards.

Giving in situational context: Giving can require individuals to take into account other social situational demands in addition to the target. One example is whether decisions are being observed by a peer audience. One study in adolescents, in which 12–16-year-olds played a public goods game (i.e., they divided valuable resources between themselves and a group) shows that adolescents gave more to the group (at their own expense) when they were being observed, and even more when they received evaluative feedback from peers (Van Hoorn, Van Dijk, Guroglu, & Crone, 2016). Peer presence was associated with activation in the mPFC, TPJ, precuneus, and STS, suggesting socio-cognitive and perspective taking related processing. In this study, younger adolescents were more generous, but peer presence effects did not differ as a function of age. Finally, adolescents' TPJ activity was associated with generosity. This is in line with another study which observed that individual differences in TPJ recruitment while viewing others' prosocial behaviors were associated with adolescents' own charitable giving (Tashjian, Weissman, Guyer, & Galvan, 2018), suggesting an important role for the TPJ in balancing the needs of self and others. In our own work, we also examined Dictator Game giving decisions for friends and unfamiliar peers in audience and anonymous contexts: in half of the trials, decisions would be completely anonymous, whereas in the other half, decisions would be observed by peers later in time (van de Groep et al., 2022; see also Box 1). Adolescents were more generous in the audience condition, and the difference in activation in the insula for friends compared to unfamiliar others was amplified in the audience but not anonymous condition, suggesting that peer presence can increase social concern or saliency for friends.

All in all, the current literature on giving shows that giving in adolescence is highly dependent on the social context, including the target and situation. Studies that examined relative generosity and social contextual factors, such as target and peer presence, reveal that giving is associated with neural activation in regions involved in both socio-affective (i.e., ventral striatum, mPFC, and insula) and socio-cognitive processes (i.e., TPJ, lateral PFC, STS). This suggests that giving decisions are shaped by balancing feelings (e.g., related to reward or saliency) and cognition (e.g., perspective taking, goal flexibility) associated with outcomes for self and others (Crone & Fuligni, 2020). There is evidence that adolescents recruit these regions differently than adults. Sometimes, adolescents show reduced activity in the TPJ when performing a prosocial task, for example when helping (Tousignant et al., 2018). However, in other situations adolescents show elevated activity in the lateral PFC, for example when giving (Do et al., 2019). We hypothesize that these differences reflect higher goal flexibility in adolescents relative to adults, with flexible recruitment of PFC, TPJ and STS, depending on whether situations require exploration, perspective taking, and forming new social connections (Casey, 2015; Crone & Dahl, 2012).

4.4 Trust/reciprocity: Contribution of multiple processes

Trust and reciprocity are two important, potentially costly, prosocial processes that are more complex than giving behavior, as they require an interaction between a trustee and trustor (Rilling & Sanfey, 2011). As a result, trust and reciprocity require advanced and mature levels of perspective taking and strategic thinking, processes that still develop in adolescence and young adulthood. Trust, defined as decisions favoring outcomes for other individuals aiming at future cooperation and self-gain, is important for the development of positive relationships, whereas reciprocity, defined as a mutual exchange (e.g., reciprocating trust shown by another individual), is important for maintaining these relationships (Lahno, 1995). Trust and reciprocity behavior are therefore types of prosocial behaviors that are more oriented toward long term relationships. Developing trust and reciprocity behavior helps adolescents to successfully navigate a complex social world, which aids them to develop new social relations based on values such as cooperation and sharing.

An economic game that is often used to study trust and reciprocity is the Trust Game (Berg, Dickhaut, & McCabe, 1995). In the Trust Game, two players are involved in dividing a certain number of resources. The first player (trustor) chooses how to divide the initial number of resources between themselves and the second player (trustee). The given number of resources by the trustor is multiplied and given to the trustee. The trustee then decides how much they want to give back to the trustor. Studies examining trust and reciprocity using the Trust Game have shown age-related increases between childhood and adolescence in trust decisions (van den Bos et al., 2010). However, other studies have shown a general stability in trust and a decrease in reciprocity (van de Groep, Meuwese, Zanolie, Guroglu, & Crone, 2018). The exact developmental patterns seem highly dependent on the level of perspective taking required (van de Groep et al., 2018; van den Bos et al., 2010), and, in case of iterative games, on the behavior of the other players (Fett, Gromann, et al., 2014; Westhoff, Molleman, Viding, van den Bos, & van Duijvenvoorde, 2020).

Trust and reciprocity behavior are more strategic than other types of prosocial behaviors, because of the second player involved in the social context. Deciding whether to show trust and reciprocity toward another individual is dependent on socio-cognitive processes, such as perspective taking, risk calculation, and outcome monitoring (Burke, van de Groep, Brandner, & Crone, 2020). Just like giving, trust and reciprocity decisions involve both socio-affective and socio-cognitive processes. However, given the additional socio-cognitive demands of such a strategic task, it was found that an especially important role is reserved for the more socio-cognitive developmental processes, including underlying brain networks such as the dlPFC, TPJ and STS. Indeed, a prior study demonstrated an age-related increase in dlPFC when receiving trust, as well as an increase in TPJ during reciprocity, which requires perspective taking (van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2011).

Although most studies using the Trust Game have focused on trust and reciprocity toward unknown others, recent evidence demonstrates that these behaviors depend on the target. A recent study using an iterative Trust Game with partners of varying levels of trustworthiness demonstrated that adolescents show higher levels of trust and reciprocity choices when the other individual is more trustworthy (i.e., in a cooperative context) relative to a less trustworthy interaction partner (Fett, Gromann, et al., 2014). These findings illustrate that adolescents learn over time whom to trust, which was associated with increased activity in the TPJ and the precuneus, regions previously associated with perspective taking (Carter & Huettel, 2013). In addition, it has been observed that adolescents show higher levels of trust and reciprocity toward friends compared to unknown, neutral, and disliked peers (Guroglu et al., 2014).

Whereas previous studies mainly focused on trust and reciprocity choices toward targets that differentiated in closeness and trustworthiness, such as family, friends, and unknown others (Guroglu et al., 2014), currently less is known about this prosocial behavior oriented toward more distant others and society. Adolescence is an important developmental period for expanding the social world and acquiring societal values (Crone & Fuligni, 2020). Given that this also touches upon adolescents' fundamental need to contribute (Fuligni, 2019), the development of trust and reciprocity behavior toward society may be formative for adolescents (Fuligni, 2020). Future studies may therefore investigate how the social context, particularly who the other is, moderates the developmental pattern of trust and reciprocity behavior during adolescence. Another Important future direction Is to study the role of flexible goal recruitment, as reflected by flexible PFC, TPJ and STS recruitment, when considering whether to engage in prosocial behavior such as showing trust and reciprocity to others (see Box 1).

5. Environmental influences on prosocial behavior

Given the separable developmental time courses of socio-cognitive and socio-affective processes, and described differences in antecedents of prosocial behaviors, it may be expected that during adolescence, some aspects of prosocial behavior are specifically sensitive to environmental influences. We recently showed that, even though prosocial behaviors are relatively stable across time in early and late adolescence, socio-affective (i.e., empathy) and socio-cognitive (i.e., perspective taking) processes are differentially related to prosocial behaviors such as giving, altruism, and emotional support (te Brinke, van de Groep, van der Cruijsen, & Crone, n.d.). This leads to the question whether individuals are more sensitive to environmental influences in adolescence, during periods of higher social-affective reactivity and goal flexibility. In this section, we first present intervention findings, examining whether prosocial experiences are important for wellbeing, contribution to society, and forming meaningful relationships with others. In the second part of this section, we examine how prosocial behaviors are shaped by family, peer, and societal contexts.

5.1 Intervention effects

Several studies have examined whether prosocial behavior can be fostered during adolescence using intervention designs. Meta analyses show that, overall, these interventions have positive effects on both participating adolescents and their environments (Curry et al., 2018; Mesurado, Guerra, Richaud, & Rodrigues, 2019; Shin & Lee, 2021). Studies that aim to promote prosocial behavior in children, adolescents and/or adults by instructing them to perform "Acts of Kindness" (e.g., greet unknown peers in the hallway, spend money on someone else) show a small to medium positive effect of these prosocial actions on the wellbeing of the actor (Curry et al., 2018). Moreover, intervention programs that aim to improve the prosocial behavior of children and adolescents, have a moderate positive effect on prosocial behavior outcomes (Mesurado, Guerra, et al., 2019). Finally, a meta-analysis examining the effects of prosocial behavior interventions on adolescents, also found a small to moderate positive effect on prosocial behavior outcomes (Shin & Lee, 2021). Intervention effects do not appear to be moderated by age or grade levels (Curry et al., 2018;

Mesurado, Guerra, et al., 2019). There are, however, large differences in the focus, duration, and targets of these interventions. In the next part, we will therefore discuss these programs.

A first difference between intervention programs is their relative focus on socio-affective and/or socio-cognitive skills. Interventions that aim to enhance socio-affective skills such as empathy, frequently use a combination of experience- and practice-based learning skills (i.e., experiencing empathy through videos or real-life experiences, engaging in prosocial activities). An example of an intervention program that focuses on socio-affective skills is the "Roots of Empathy" program (Schonert-Reichl, Smith, Zaidman-Zait, & Hertzman, 2012). This 9-month program is implemented by elementary school teachers and includes a monthly classroom visit by an infant and his/her parent(s) whom the class "adopts" at the beginning of the school year. Research shows that this intervention has a positive effect on the peer nominated prosocial behavior of 8–12 year-old children. No direct effects on empathy were observed (Schonert-Reichl et al., 2012). Another socio-affective skills intervention is the "Caring for Life" curriculum, which is found to promote teacher-reported prosocial behavior among Chinese elementary school students (Samuels, 2018). In contrast, the intervention program "Try volunteering"—an 8-week program that stimulates adolescents to start volunteer work—has a positive effect on empathy among 13–16 year-olds (Truskauskaitė-Kunevičienė, 2016). The self-administered online "Hero" intervention that stimulates socio-affective skills, such as empathy, emotion recognition, and forgiveness, is found to be effective in promoting prosocial behavior toward family members and unknown others, but direct effects on the targeted socio-affective skills were not assessed (Mesurado, Distefano, Robiolo, & Richaud, 2019). Lastly, an 11-day online prosocial intervention that included motivational videos and daily prosocial behavior exercises was found to have positive effects on both empathy and prosocial behavior among 16–25 year-olds (Baumsteiger, 2019).

In contrast, other interventions have a stronger focus on socio-cognitive skills such as perspective taking. These interventions frequently include skill-based learning strategies, such as exercises that aim to increase adolescents' recognition of the needs and perspectives of others. For example, CEPIDIA, an Italian prosocial behavior intervention, includes five domains of skill-based learning strategies: perspective taking, prosocial values, emotion-regulation, interpersonal-communication, and civic-engagement (Caprara et al., 2014). During early adolescence, this program is found to be effective in promoting helping behavior toward friends and unknown others, both directly after the intervention and at an 18-month follow-up (Caprara et al., 2014; Caprara, Luengo Kanacri, Zuffianò, Gerbino, & Pastorelli, 2015). Moreover, an intervention that targets perspective taking and empathy (and thereby socio-cognitive and socio-affective processes), was found to have positive effect on both perspective taking capacities and prosocial behavior in a sample of 10–12 year-old children (Etxebarria et al., 1994).

A second difference between intervention programs is their relative focus on peer- or adult-based delivery of the intervention. A peer-based intervention approach stems from the finding that adolescents, in contrast to younger children, frequently resent or reject adult-driven interventions because these interventions do not align with their desire to feel respected and to be accorded status (Yeager, Dahl, & Dweck, 2018; Yeager, Fong, Lee, & Espelage, 2015). Several intervention programs have been developed that aim to enhance prosocial behavior via positive peer network influences (Veenstra & Laninga-Wijnen, 2021). For example, the Meaningful Roles intervention aims to increase opportunities for prosocial behavior by providing adolescents specific school jobs (i.e., pupil responsibilities). These school jobs are embedded in a context of frequent verbal and written recognition for prosocial behavior from peers (Ellis, Volk, Gonzalez, & Embry, 2016). Moreover, a cooperative-play intervention, which stimulates positive peer influence, was found to increase prosocial behavior among 10–11 year-olds (Garaigordobil, 2008). An important question for future research is to examine the relative effectiveness of peer- versus adult-delivered prosocial behavior interventions. It may be expected that peer-led interventions are most effective when they focus on implicit peer influence (i.e., imitation and social norms) and target popular peers as role models (Veenstra & Laninga-Wijnen, 2021).

A third difference is whether interventions focus on intra-personal or intra-societal prosocial behavior. In the experience-, skill-based, and peer-delivered interventions that we described above, the desired outcomes were often an increase in intra-personal prosocial behavior, for example behaviors directed to peers (e.g., helping peers in the classroom; (Caprara et al., 2014)) or unknown others (e.g., volunteering; (Truskauskaitė-Kunevičienė, 2016)). However, research from the civic engagement literature shows that interventions that aim to enhance prosocial behaviors toward larger societal goals, may also yield positive effects. Civic engagement refers to prosocial and political contributions to community and society (Wray-Lake, DeHaan, Shubert, & Ryan, 2019). An example of a civic engagement intervention is the action-oriented "Generation Citizen curriculum," in which students choose a local issue that they wish to tackle, learn strategies and skills to take action, and develop an implementation plan (Ballard, Cohen, & Littenberg-Tobias, 2016; Pope, Stolte, & Cohen, 2011). This program is found to be effective in promoting civic self-efficacy; meaning that after following the program, middle and high school students had stronger beliefs in their ability to make a difference in their community, and believed that their voice would be heard if they would speak up about an issue in their community (Ballard et al., 2016). An interesting direction for future research is to examine the interrelatedness of prosocial development and civic engagement in relation to the formative phase of adolescence.

5.2 Shaping prosocial behaviors by family, peer, and societal contexts

In the previous section, it was demonstrated that interventions can modify prosocial behaviors. Adolescents' prosocial behavior intentions, however, do not develop in isolation. Both family members, peers, and broader societal experiences contribute to these developmental patterns (see Fig. 4B). Research shows that parental volunteering is a strong predictor of adolescent volunteering (Andolina, Jenkins, Zukin, & Keeter, 2003; McGinley, Lipperman-Kreda, Byrnes, & Carlo, 2010; Smetana & Metzger, 2005). Moreover, 12–20 year-old adolescents volunteer more frequently when their family is characterized by strong civic orientation values and open communication (van Goethem, van Hoof, van Aken, Orobio de Castro, & Raaijmakers, 2014), and 13–17 year-old adolescents who perceive higher levels of support from their parents are found to behave more prosocially 1 year later (Malonda, Llorca, Mesurado, Samper, & Mestre, 2019). Family influence on prosocial behavior also appears to continue during late adolescence and early adulthood. For example, a study among 18–25 year-olds showed that parenting practices (i.e., parental support and challenge) were positively related to prosocial behavior toward friends and family members (Mesurado & Richaud, 2018). Thus, family members can have a positive impact on adolescents' prosocial development, both through modeling (i.e., parental volunteering) and socialization (i.e., supportive parenting).

Research on peer influences shows that adolescents are also more likely to set prosocial goals or show prosocial behavior, when their (close) friends also value or engage in these behaviors (Barry & Wentzel, 2006; van Goethem et al., 2014). Moreover, 13–17 year-old adolescents who receive

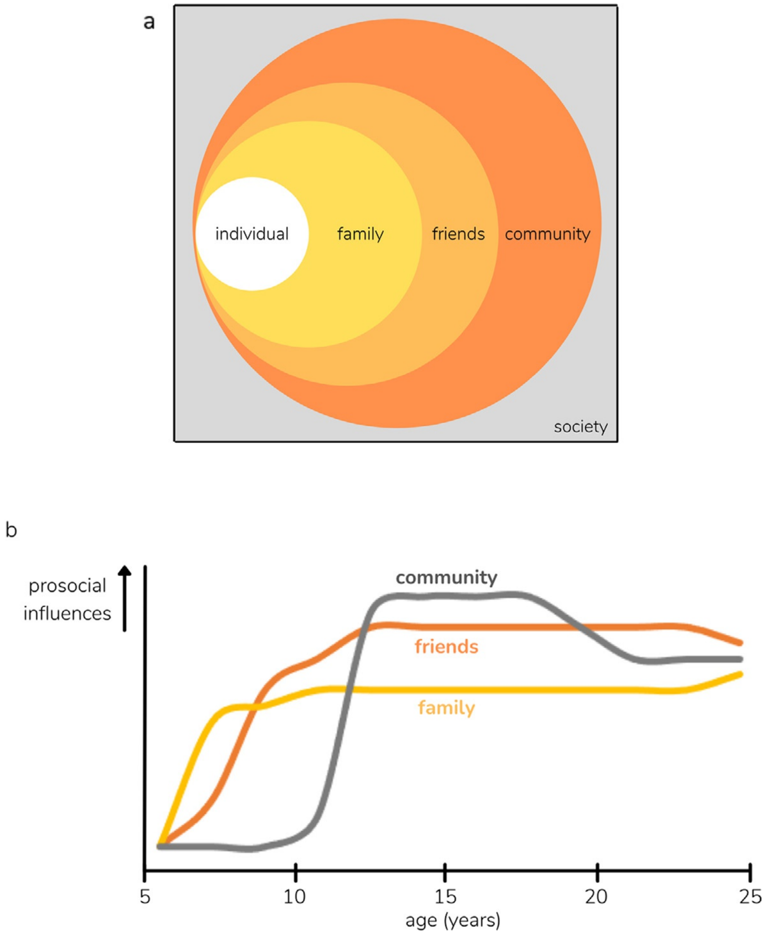


Fig. 4 (A) Example of the various contexts in which adolescents engage and that may shape their prosocial motivation and behavior. (B) Conceptual model showing the developmental pathways for influences on prosocial behavior by family, friends or community targets. Family should be interpreted as influences by parents, and friends should be interpreted as (dyadic) friendships. Community should be interpreted in terms of peer networks, school and neighborhood activities. We expect that influences experiences in one domain shape influences in other domains.

higher levels of support from their friends act more prosocial 1 year later (Malonda et al., 2019). Aside from indirect peer influences (i.e., modeling and socialization), adolescents' prosocial behavior can also be directly influenced by peers. For example, 12–16 year-old adolescents who received manipulated 'prosocial feedback' from friends, are found to give more in a

Public Goods game (Van Hoorn, Van Dijk, Meuwese, Rieffe, & Crone, 2016). A separate study showed that prosocial influence effects are larger in adolescence than in adulthood (Foulkes, Leung, Fuhrmann, Knoll, & Blakemore, 2018), Finally, an experimental study examined the effect of peer influence on prosocial behavior of 12–15 year-olds with an experimental "Chat Room" paradigm. The results showed that adolescents' prosocial intentions were higher after viewing peers behaving prosocially. This effect was moderated by peer status. Specifically, the effects of peer influence were stronger when adolescents interacted with high-status – in comparison to low-status peers (Choukas-Bradley, Giletta, Cohen, & Prinstein, 2015).

There is convincing evidence that family and peer influence shape prosocial behavior. However, prosocial behavior may also be influenced by societal factors (Fig. 4A), such as government or municipal influences, although these are more difficult to study. A recent large societal change was the sudden start of the Covid-19 pandemic. Researchers examined in experimental and survey designs whether these large societal changes affect the behaviors of children, adolescents, and adults. One study showed that 10–12 year-old adolescents who had more face-to-face and virtual societal connections were more willing to help unknown peers during the pandemic (Sabato, Abraham, & Kogut, 2021). In a recent study including adolescents ages 10–25 years, we examined the frequency with which adolescents provided emotional support in the beginning and during the pandemic (Sweijen et al., n.d.). It was found that providing emotional support peaked in mid-adolescence, consistent with prior studies (Blankenstein, Telzer, Do, van Duijvenvoorde, & Crone, 2020). We also observed emotional support increasing during the pandemic, possibly because adolescents created new opportunities to help others after an initial hard lockdown. Finally, the study made use of a giving paradigm, using modifications of the Dictator Game, where the targets were medical doctors (deserving targets), Covid-19 patients, individual with poor immune systems (needing targets), friends, and unknown others. Adolescents gave most to needing and deserving targets, fair splits to friends and least to unknown partners, consistent with a prior study (van de Groep, Zanolie, Green, Sweijen, & Crone, 2020). Giving to needing and serving targets was higher in adolescence compared to adulthood (Sweijen et al., n.d.).

An interesting direction for future research will be to examine how influences by immediate interactions (parents, peers) and larger societal influences (government regulations) influence the trajectories of prosocial development. The Covid-19 crisis is not the only crisis that affects adolescents; they are also confronted with rapidly changing climates and increasing societal inequalities. As stated by Armstrong-Carter and Telzer (2021), positive eco-friendly actions and climate activism should be considered important forms of prosocial behavior in the 21st century, because these behaviors contribute positively to the planet and the lives of others.

6. Conclusions and future directions

This review set out to examine the question: When and how do changes in emotional reactivity and socio-cognitive development result in opportunities for prosocial development and which factors facilitate opportunities for positive, prosocial development? We demonstrated that prosocial behavior is a multidimensional construct (Carlo & Padilla-Walker, 2020), where age patterns are related to the emergence of developmental processes as well as increasing sensitivity to social and contextual factors.

In terms of developmental processes, we reviewed evidence showing socio-affective neural reactivity to rewards for close others, consistent with the hypothesis that valuing rewards for self and others relies on the same neural system, including the dopamine-rich ventral striatum and the vmPFC (Telzer, 2016). There is some evidence for heightened activity in the ventral striatum in mid-adolescence for vicarious rewards for close friends and for mothers (Braams & Crone, 2017; Schreuders et al., 2021), but these developmental patterns are not consistent across studies (Brandner et al., 2021) and warrant further investigation, including the relation with warmth of the relationship or influences of childhood experiences (Decety & Holvoet, 2021). Socio-cognitive developmental processes such as perspective taking and goal flexibility show consistently protracted changes during adolescence; including changes in the medial PFC, TPJ and dlPFC (Do et al., 2019; van de Groep et al., 2022). Together, the reviewed studies provide consistent support for a model showing dynamic changes in socio-affective and socio-cognitive changes during adolescence.

We argue that the emergence of these developmental processes interacts with contextual processes. First, we showed that individuals give more to in-group compared to out-group members, and more to close, familiar others compared to unknown others (van de Groep, Zanolie, & Crone, 2020b). Although in-group biases materialize early in life, recent studies showed that differentiation between targets further increases over the course of adolescence (Guroglu et al., 2014). Second, from childhood to adolescence, individuals move from simple decisions such as equal splits in childhood, to more nuanced decisions that incorporate the social situation and require perspective taking in adolescence, such as differentiating between the target of giving (Do & Telzer, 2019). Third, giving decisions are influenced by whether individuals are observed by others (audience effects) (van de Groep, Zanolie, & Crone, 2020a) and these influences may make adolescents also sensitive to prosocial peer interventions (Van Hoorn, Van Dijk, Guroglu, & Crone, 2016; Veenstra & Laninga-Wijnen, 2021). Future studies should examine how this working model may aid in developing interventions that shape prosocial behavior toward family, school or neighborhood. These interventions should also examine how developing prosocial behavior may influence the need of adolescents to contribute (Fuligni, 2019) and the need to experience purpose and meaning (Yeager et al., 2018).

There are several methodological questions that require more emphasis in future research. The reviewed studies examined adolescents in relatively isolated lab environments. In future studies it will be important to test actual online or offline interactions. Further, we used a decomposition method, but in future studies it will be interesting to test the multidimensionality of prosocial behavior to examine how (latent) processes interact with each other within individuals. We showed in Box 1 an example of a large longitudinal study from our group that allows for the test of these relations. Finally, it should be noted that we reviewed relatively simple economic games formats where participants were confronted with resources to share with others. In future research, it should be examined how the various contexts test not only the motivation ("willingness") and developmental processes ("capacity"), but also the resources to give to others ("possibility") of adolescents.

Future studies should examine prosocial behavior in relation to the challenges that adolescents face today and with the tools that adolescent use to influence their environment. Adolescents face complex societal challenges that require a vision that goes beyond country borders (climate changes, pandemics, global inequalities) (Orben, Tomova, & Blakemore, 2020) but adolescents also have the tools to influence at larger scales using digital networks (Armstrong-Carter & Telzer, 2021). It was previously found that reward sensitivity in mid-adolescence predicts both intentions to be rebellious as well as prosocial behavior (Blankenstein et al., 2020). Possibly, adolescents, who traditionally have been categorized as a risk group, may have a large drive to influence society by combining rebelliousness with prosocial behaviors, providing a possible pathway to a socially cohesive and cooperative society with the ability to tackle tomorrow's global challenges (Do, Guassi Moreira, & Telzer, 2017).

Acknowledgments

E.A.C. is supported by an "innovative ideas" grant of the European Research Council (ERC CoG PROSOCIAL 681632 to E.A.C.). We thank Iris Langereis for helping with the illustrations.

Declaration of interest

None.

Appendix 1

		Longitudinal neuroimaging study						Intervention study			
		T1 - Adolescents	T1 - Parent study	T1.5	T2	COVID-19 daily diary study	T3	T1	T2	T3	
		May - Oct 2018	Oct 2018 - March 2019	Every 2 months between T1 and T2	Aug 2019 - Jan 2020	March - April 2020	October 2021 -	October 2021	ongoing	ongoing	
Measurements	**Respondents**										**Comments**
Prosocial behavior											
Neurobiological measures											
Cooperation	Child, Parent(s)	x	x								
Giving	Child	x			x		x				
Trust and Reciprocity	Child						x				
Behavioral experiments											
Social Dilemma	Child, Parent(s)	x	x				x				
Naturalistic Helping Task	Child	x									
Charity Dictator Game	Child	x			x		x				
Societal Trust Game	Child									x	
Pandemic Dictator Game	Child					x				x	Five targets: unfamiliar peer, friend, individual with poor immune system, individual with COVID-19, medical doctor
Questionnaires											
Opportunities for Prosocial Actions (OPA)	Child	x		5x	x	15x	x	x	x	x	At COVID-19 daily diary study, only the subscale emotional support was administered. At the intervention study, a revised version was administered
Prosocial Tendencies Measure Revised (PTM-R)	Child, Parent(s)	x	x		x	15x	x	x			At COVID-19 daily diary study, only the subscales Dire and Altruism were administered. At the intervention study, only the subscale Altruism was administered.
Social Value Orientation (SVO)	Child, Parent(s)	x	x		x	2x	x				
Digital Prosocial Behavior	Child				x		x				
Contributions to society - General	Child				x	x	x	x	x	x	At the intervention study, a revised version was administered
Contributions to society - Crisis	Child					x					
Pandemic Questionnaire - Helping	Child					x					
Online Prosocial Behavior Scale	Child						x				
Need for Useful Contributions - Revised measure	Child						x	x	x	x	
Motives for Prosocial Behavior	Child							x	x	x	
Personal Characteristics											
Neurobiological measures											
Delay Discounting For Self and Other	Child				x						
Behavioral experiments											
Stop-Signal Task (Impulsivity)	Child	x			x		x				
Balloon Analogue Risk Task (Risk-taking)	Child	x									
WISC/WAIS similarities (verbal IQ)	Child	x									
WISC/WAIS block design (Visual/Spatial IQ)	Child	x									
Three Minute Test (Reading Fluency)	Child	x									
Questionnaires											
Demographics	Child, Parent(s)	x	x		x	x	x				
Self Control Scale	Child	x			x		x				
Adolescent Risk-taking Questionnaire	Child	x			x		x				
Positive Risk-taking Scale	Child				x		x				
Rosenberg Self-esteem Scale	Child	x			x		x				
Interpersonal Reactivity Index	Child	x			x	4x	x	x	x	x	Only subscales Empathic Concern and Perspective Taking were administered. At the intervention study, the subscale empathic concern was only administered at T1
Social Desirability Response Set	Child	x			x	x	x				
Emotion Awareness Questionnaire (revised)	Child	x			x		x				
HEXACO	Child, Parent(s)	x	x								
Religious Background and Behaviors Questionnaire (RBBQ)	Child, Parent(s)	x	x		x		x				
Adult Temperament Questionnaire (ATQ)	Parent	x	x		x		x				
Pandemic Questionnaire - Perceived Risk	Child					15x					
Pandemic Questionnaire - Selfish behavior	Child					15x					
Risk Taking (1 question, scale 0 - 100)	Child					2x					
Childhood Narcissism Scale	Child						x				
Feeling useful	Child				x		x				
The Brief Sensation-Seeking Scale	Child							x			
Social Tendencies											
Questionnaires											
Social Reward Questionnaire (adolescent version)	Child	x			x		x	x			At the intervention study, only the subscale Prosocial Interactions was administered
Social Comparison Orientation	Child	x			x						
Intrasexual Competition	Child	x									
Olweus Bully/Victimization Questionnaire	Child	x									
Inclusion of Other in Self	Child	x	x		x		x				
Experiences in Close Relationships Revised	Child	x	x	5x	x	x	x				
Friendship Quality Scale	Child	x			x		x				
Romantic Relationships, Gender Identity, and Sexual Orientation	Child	x			x						
Self in a Social Context-Social Connectedness Scale	Child							x	x	x	
Strenghts and Difficulties Questionnaire	Parent(s)	x			x						
Social Responsiveness Scale	Parent(s)	x			x						
Family-related Measures											
Sibling Relationship Questionnaire	Child	x									
Family Adaptability and Cohesion Evaluation Scale (FACES)	Child, Parent(s)	x	x		x		x				
Leuven Adolescent Perceived Parenting Scale (LAPPS)	Child, Parent(s)	x	x		x		x				
Physical/physiological measures											
Neurobiological measures											
Structural MRI scan	Child, Parent(s)	x			x		x				
Resting State MRI scan	Child, Parent(s)	x			x		x				
Diffusion Tensor Imaging scan	Child, Parent(s)	x			x						
Hormonal measures											
Testosterone	Child, Parent(s)	x			x		x				
Estradiol	Child, Parent(s)	x			x		x				
Oxytocin	Child, Parent(s)	x									
DHEA	Child, Parent(s)	x			x		x				
Cortisol	Child, Parent(s)	x									
Progesterone	Child, Parent(s)	x									
Questionnaires											
Pubertal Development Scale	Child	x			x		x				
Menstrual Cycle Questionnaire	Child	x			x						
Life Events											
Questionnaires											
LEC-5 (Life Event Checklist)	Parent(s)		x								
Child and Adolescent Survey of Experiencs (CASE)	Child			5x	x						
Pandemic Questionnaire - Home Isolation	Child					15x					
Pandemic Experiences	Child						x				
Mood/Wellbeing											
Questionnaires											
Profile of Mood Scale (POMS)	Child			5x		15x		x	x	x	At COVID-19 daily diary study, only the subscales Vigor and Tension were administered. At the intervention study, only the subscales Vigor and Depression were administered
Pandemic Questionnaire - Stress	Child					15x					
Multidimensional Wellbeing Paradigm	Child						x	x	x	x	At the intervention study, a shortened version was administered

References

Achterberg, M., van Duijvenvoorde, A. C., Bakermans-Kranenburg, M. J., & Crone, E. A. (2016). Control your anger! The neural basis of aggression regulation in response to negative social feedback. *Social Cognitive and Affective Neuroscience*, *11*(5), 712–720. https://doi.org/10.1093/scan/nsv154.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews. Neuroscience*, 7(4), 268–277. https://doi.org/10.1038/nrn1884.

Andolina, M. W., Jenkins, K., Zukin, C., & Keeter, S. (2003). Habits from home, lessons from school: Influences on youth civic engagement. *Political Science and Politics*, *36*(3), 275–280. https://doi.org/10.1017/S104909650300221X.

Armstrong-Carter, E., & Telzer, E. H. (2021). Advancing measurement and research on Youths' prosocial behavior in the digital age. *Child Development Perspectives*, *15*(1), 31–36. https://doi.org/10.1111/cdep.1239.

Arnett, J. J., Zukauskiene, R., & Sugimura, K. (2014). The new life stage of emerging adulthood at ages 18-29 years: Implications for mental health. *Lancet Psychiatry*, *1*(7), 569–576. https://doi.org/10.1016/S2215-0366(14)00080-7.

Ballard, P. J., Cohen, A. K., & Littenberg-Tobias, J. (2016). Action civics for promoting civic development: Main effects of program participation and differences by project characteristics. *American Journal of Community Psychology*, *58*, 377–390. https://doi.org/10.1002/ajcp.12103.

Barry, C. M., & Wentzel, K. R. (2006). Friend influence on prosocial behavior: The role of motivational factors and friendship characteristics. *Developmental Psychology*, *42*(1), 153–163. https://doi.org/10.1037/0012-1649.42.1.153.

Baumsteiger, R. (2019). What the world needs now: An intervention for promoting prosocial behavior. *Basic and Applied Social Psychology*, *41*(4), 215–229. https://doi.org/10.1080/01973533.2019.1639507.

Becht, A. I., Wierenga, L. M., Mills, K. L., Meuwese, R., van Duijvenvoorde, A., Blakemore, S. J., et al. (2020). Beyond the average brain: Individual differences in social brain development are associated with friendship quality. *Social Cognitive and Affective Neuroscience*, *16*(3), 292–301. https://doi.org/10.1093/scan/nsaa166.

Berg, J., Dickhaut, J., & McCabe, K. (1995). Trust, reciprocity, and social history. *Games and Economic Behavior*, *10*, 122–142.

Blakemore, S. J., & Mills, K. L. (2014). Is adolescence a sensitive period for sociocultural processing? *Annual Review of Psychology*, *65*, 187–207. https://doi.org/10.1146/annurev-psych-010213-115202.

Blankenstein, N. E., Telzer, E. H., Do, K. T., van Duijvenvoorde, A. C. K., & Crone, E. A. (2020). Behavioral and neural pathways supporting the development of prosocial and risk-taking behavior across adolescence. *Child Development*, *91*(3), e665–e681. https://doi.org/10.1111/cdev.13292.

Blote, A. W., Kint, M. J., Miers, A. C., & Westenberg, P. M. (2009). The relation between public speaking anxiety and social anxiety: A review. *Journal of Anxiety Disorders*, *23*(3), 305–313. https://doi.org/10.1016/j.janxdis.2008.11.007.

Boyes, M. E., & French, D. J. (2009). Having a cyberball: Using a ball-throwing game as an experimental social stressor to examine the relationship between neuroticism and coping. *Personality and Individual Differences*, *47*(5), 396–401.

Braams, B. R., & Crone, E. A. (2017). Peers and parents: A comparison between neural activation when winning for friends and mothers in adolescence. *Social Cognitive and Affective Neuroscience*, *12*(3), 417–426. https://doi.org/10.1093/scan/nsw136.

Brandner, P., Guroglu, B., & Crone, E. A. (2020). I am happy for us: Neural processing of vicarious joy when winning for parents versus strangers. *Cognitive, Affective, & Behavioral Neuroscience*, *20*(6), 1309–1322. https://doi.org/10.3758/s13415-020-00839-9.

Brandner, P., Guroglu, B., van de Groep, S., Spaans, J. P., & Crone, E. A. (2021). Happy for us not them: Differences in neural activation in a vicarious reward task between family and strangers during adolescent development. *Developmental Cognitive Neuroscience*, *51*, 100985. https://doi.org/10.1016/j.dcn.2021.100985.

Brownell, C. A., Svetlova, M., Anderson, R., Nichols, S. R., & Drummond, J. (2013). Socialization of early prosocial behavior: Parents' talk about emotions is associated with sharing and helping in toddlers. *Infancy*, *18*, 91–119. https://doi.org/10.1111/j.1532-7078.2012.00125.x.

Burke, S. M., van de Groep, S., Brandner, P., & Crone, E. A. (2020). Neurocognitive developmental changes in trust and reciprocity across adolescence. In K. Cohen Kadosh (Ed.), *Developmental cognitive neuroscience*. Oxford: Oxford University Press.

Caprara, G. V., Kanacri, B. P. L., Gerbino, M., Zuffianò, A., Alessandri, G., Vecchio, G., et al. (2014). Positive effects of promoting prosocial behavior in early adolescence: Evidence from a school-based intervention. *International Journal of Behavioral Development*, *38*(4), 386–396. https://doi.org/10.1177/0165025414531464.

Caprara, G. V., Luengo Kanacri, B. P., Zuffianò, A., Gerbino, M., & Pastorelli, C. (2015). Why and how to promote adolescents' prosocial behaviors: Direct, mediated and moderated effects of the CEPIDEA school-based program. *Journal of Youth and Adolescence*, *44*(12), 2211–2229. https://doi.org/10.1007/s10964-015-0293-1.

Carlo, G., & Padilla-Walker, L. (2020). Adolescents' prosocial behaviour though a multidimensional and multicultural lens. *Child Development Perspectives*, *14*(4), 265–272.

Carter, R. M., & Huettel, S. A. (2013). A nexus model of the temporal-parietal junction. *Trends in Cognitive Sciences*, *17*(7), 328–336. https://doi.org/10.1016/j.tics.2013.05.007.

Casey, B. J. (2015). Beyond simple models of self-control to circuit-based accounts of adolescent behavior. *Annual Review of Psychology*, *66*, 295–319. https://doi.org/10.1146/annurev-psych-010814-015156.

Chein, J., Albert, D., O'Brien, L., Uckert, K., & Steinberg, L. (2011). Peers increase adolescent risk taking by enhancing activity in the brain's reward circuitry. *Developmental Science*, *14*(2), F1–10. https://doi.org/10.1111/j.1467-7687.2010.01035.x.

Choukas-Bradley, S., Giletta, M., Cohen, G. L., & Prinstein, M. J. (2015). Peer influence, peer status, and prosocial behavior: An experimental investigation of peer socialization of adolescents' intentions to volunteer. *Journal of Youth and Adolescence*, *44*(12), 2197–2210. https://doi.org/10.1007/s10964-015-0373-2.

Cohen, J. R., Asarnow, R. F., Sabb, F. W., Bilder, R. M., Bookheimer, S. Y., Knowlton, B. J., et al. (2010). A unique adolescent response to reward prediction errors. *Nature Neuroscience*, *13*(6), 669–671. https://doi.org/10.1038/nn.2558.

Crone, E. A., & Dahl, R. E. (2012). Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nature Reviews. Neuroscience*, *13*(9), 636–650. https://doi.org/10.1038/nrn3313.

Crone, E. A., & Fuligni, A. J. (2020). Self and others in adolescence. *Annual Review of Psychology*, *71*, 447–469. https://doi.org/10.1146/annurev-psych-010419-050937.

Curry, O. S., Rowlans, L. A., Van Lissa, C. J., Zlotowitz, S., McAlaney, J., & Whitehouse, H. (2018). Happy to help? A systematic review and meta-analysis of the effects of performing acts of kindness on the well-being of the actor. *Journal of Experimental Social Psychology*, *76*, 320–329. https://doi.org/10.1016/j.jesp.2018.02.014.

Cutler, J., & Campbell-Meiklejohn, D. (2019). A comparative fMRI meta-analysis of altruistic and strategic decisions to give. *NeuroImage*, *184*, 227–241. https://doi.org/10.1016/j.neuroimage.2018.09.009.

Dahl, R. E., Allen, N. B., Wilbrecht, L., & Suleiman, A. B. (2018). Importance of investing in adolescence from a developmental science perspective. *Nature*, *554*(7693), 441–450. https://doi.org/10.1038/nature25770.

Decety, J., & Holvoet, C. (2021). The emergence of empathy: A developmental neuroscience perspective. *Developmental Review*, *62*, 100999.

Delgado, M. R., Beer, J. S., Fellows, L. K., Huettel, S. A., Platt, M. L., Quirk, G. J., et al. (2016). Viewpoints: Dialogues on the functional role of the ventromedial prefrontal cortex. *Nature Neuroscience*, *19*(12), 1545–1552. https://doi.org/10.1038/nn.4438.

Do, K. T., Guassi Moreira, J. F., & Telzer, E. H. (2017). But is helping you worth the risk? Defining prosocial risk taking in adolescence. *Developmental Cognitive Neuroscience*, *25*, 260–271. https://doi.org/10.1016/j.dcn.2016.11.008.

Do, K. T., McCormick, E. M., & Telzer, E. H. (2019). The neural development of prosocial behavior from childhood to adolescence. *Social Cognitive and Affective Neuroscience*, *14*(2), 129–139. https://doi.org/10.1093/scan/nsy117.

Do, K. T., & Telzer, E. H. (2019). Corticostriatal connectivity is associated with the reduction of intergroup bias and greater impartial giving in youth. *Developmental Cognitive Neuroscience*, *37*, 100628. https://doi.org/10.1016/j.dcn.2019.100628.

Dumontheil, I., Apperly, I. A., & Blakemore, S. J. (2010). Online usage of theory of mind continues to develop in late adolescence. *Developmental Science*, *13*(2), 331–338. https://doi.org/10.1111/j.1467-7687.2009.00888.x.

Ellis, B. J., Volk, A. A., Gonzalez, J. M., & Embry, D. D. (2016). The meaningful roles intervention: An evolutionary approach to reducing bullying and increasing prosocial behavior. *Journal of Research on Adolescence*, *26*(4), 622–637. https://doi.org/10.1111/jora.12243.

Engel, C. (2011). Dictator games: A meta study. *Experimental Economics*, *14*(4), 583–610.

Ernst, M. (2014). The triadic model perspective for the study of adolescent motivated behavior. *Brain and Cognition*, *89*, 104–111. https://doi.org/10.1016/j.bandc.2014.01.006.

Etxebarria, I., Apodaka, P., Eceiza, A., Ortiz, M. J., Fuentes, M. J., & Lopez, F. (1994). Design and evaluation of a programme to promote prosocial-altruistic behaviour in the school. *Journal of Moral Education*, *23*(4), 409–425. https://doi.org/10.1080/0305724940230403.

Feng, C., Luo, Y. J., & Krueger, F. (2015). Neural signatures of fairness-related normative decision making in the ultimatum game: A coordinate-based meta-analysis. *Human Brain Mapping*, *36*(2), 591–602. https://doi.org/10.1002/hbm.22649.

Fett, A. K., Gromann, P. M., Giampietro, V., Shergill, S. S., & Krabbendam, L. (2014). Default distrust? An fMRI investigation of the neural development of trust and cooperation. *Social Cognitive and Affective Neuroscience*, *9*(4), 395–402. https://doi.org/10.1093/scan/nss144.

Fett, A. K., Shergill, S. S., Gromann, P. M., Dumontheil, I., Blakemore, S. J., Yakub, F., et al. (2014). Trust and social reciprocity in adolescence—A matter of perspective-taking. *Journal of Adolescence*, *37*(2), 175–184. https://doi.org/10.1016/j.adolescence.2013.11.011.

Foulkes, L., Leung, J. T., Fuhrmann, D., Knoll, L. J., & Blakemore, S. J. (2018). Age differences in the prosocial influence effect. *Developmental Science*, *21*(6), e12666. https://doi.org/10.1111/desc.12666.

Fu, X., Padilla-Walker, L. M., & Brown, M. N. (2017). Longitudinal relations between adolescents' self-esteem and prosocial behavior toward strangers, friends and family. *Journal of Adolescence*, *57*, 90–98. https://doi.org/10.1016/j.adolescence.2017.04.002.

Fuligni, A. J. (2019). The need to contribute in adolescence. *Perspectives on Psychological Science*, *14*(3), 331–343. https://doi.org/10.1177/1745691618805437.

Fuligni, A. J. (2020). Is there inequality in what adolescents can give as well as receive? *Current Directions in Psychological Science*, *29*(4), 405–411. https://doi.org/10.1177/0963721420917738.

Gagné, M. (2003). The role of autonomy support and autonomy orientation in prosocial behavior engagement. *Motivation and Emotion*, *27*(3), 199–223.

Galvan, A. (2010). Adolescent development of the reward system. *Frontiers in Human Neuroscience*, *4*, 6. https://doi.org/10.3389/neuro.09.006.2010.

Galvan, A., Hare, T. A., Parra, C. E., Penn, J., Voss, H., Glover, G., et al. (2006). Earlier development of the accumbens relative to orbitofrontal cortex might underlie risk-taking behavior in adolescents. *The Journal of Neuroscience*, *26*(25), 6885–6892. https://doi.org/10.1523/JNEUROSCI.1062-06.2006.

Garaigordobil, M. (2008). Assessment of the effects of a cooperative play programme for children aged 10–11 years on social adaptation and on the perception that parents, teachers and peers have of children's prosocial behaviours. *Infancia y Aprendizaje*, *31*(3), 303–318. https://doi.org/10.1174/021037008785702974.

Gilmore, J. H., Knickmeyer, R. C., & Gao, W. (2018). Imaging structural and functional brain development in early childhood. *Nature Reviews. Neuroscience*, *19*(3), 123–137. https://doi.org/10.1038/nrn.2018.1.

Goddings, A. L., Mills, K. L., Clasen, L. S., Giedd, J. N., Viner, R. M., & Blakemore, S. J. (2014). The influence of puberty on subcortical brain development. *NeuroImage*, *88*, 242–251. https://doi.org/10.1016/j.neuroimage.2013.09.073.

Gummerum, M., Hanoch, Y., & Keller, M. (2008). When child development meets economic game theory: An interdisciplinary approach to investigating social development. *Human Development*, *51*(4), 235–261.

Guroglu, B., van den Bos, W., & Crone, E. A. (2014). Sharing and giving across adolescence: An experimental study examining the development of prosocial behavior. *Frontiers in Psychology*, *5*, 291. https://doi.org/10.3389/fpsyg.2014.00291.

Guroglu, B., van den Bos, W., van Dijk, E., Rombouts, S. A., & Crone, E. A. (2011). Dissociable brain networks involved in development of fairness considerations: Understanding intentionality behind unfairness. *NeuroImage*, *57*(2), 634–641. https://doi.org/10.1016/j.neuroimage.2011.04.032.

Haber, S. N., & Knutson, B. (2010). The reward circuit: Linking primate anatomy and human imaging. *Neuropsychopharmacology*, *35*(1), 4–26. https://doi.org/10.1038/npp.2009.129.

Hackel, L. M., Zaki, J., & Van Bavel, J. J. (2017). Social identity shapes social valuation: Evidence from prosocial behavior and vicarious reward. *Social Cognitive and Affective Neuroscience*, *12*(8), 1219–1228. https://doi.org/10.1093/scan/nsx045.

Harbaugh, W. T., Mayr, U., & Burghart, D. R. (2007). Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science*, *316*(5831), 1622–1625. https://doi.org/10.1126/science.1140738.

Herting, M. M., Johnson, C., Mills, K. L., Vijayakumar, N., Dennison, M., Liu, C., et al. (2018). Development of subcortical volumes across adolescence in males and females: A multisample study of longitudinal changes. *NeuroImage*, *172*, 194–205. https://doi.org/10.1016/j.neuroimage.2018.01.020.

Lahno, B. (1995). Trust, reputation, and exit in exchange relationships. *Journal of Conflict Resolution*, *39*(3), 495–510.

Larson, R. W., Moneta, G., Richards, M. H., & Wilson, S. (2002). Continuity, stability, and change in daily emotional experience across adolescence. *Child Development*, *73*(4), 1151–1165.

Lee, F. S., Heimer, H., Giedd, J. N., Lein, E. S., Sestan, N., Weinberger, D. R., et al. (2014). Mental health. Adolescent mental health—Opportunity and obligation. *Science*, *346*(6209), 547–549. https://doi.org/10.1126/science.1260497.

Lee, S. J., Zhang, J., Neale, M. C., Styner, M., Zhu, H., & Gilmore, J. H. (2019). Quantitative tract-based white matter heritability in 1- and 2-year-old twins. *Human Brain Mapping*, *40*(4), 1164–1173. https://doi.org/10.1002/hbm.24436.

Lieberman, M. D., Straccia, M. A., Meyer, M. L., Du, M., & Tan, K. M. (2019). Social, self, (situational), and affective processes in medial prefrontal cortex (MPFC): Causal, multivariate, and reverse inference evidence. *Neuroscience and Biobehavioral Reviews*, *99*, 311–328. https://doi.org/10.1016/j.neubiorev.2018.12.021.

Lockwood, P. L., Apps, M. A., Valton, V., Viding, E., & Roiser, J. P. (2016). Neurocomputational mechanisms of prosocial learning and links to empathy. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(35), 9763–9768. https://doi.org/10.1073/pnas.1603198113.

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature*, *453*(7197), 869–878.
Luo, J. (2018). The neural basis of and a common neural circuitry in different types of pro-social behavior. *Frontiers in Psychology*, *9*, 859. https://doi.org/10.3389/fpsyg.2018.00859.
Malonda, E., Llorca, A., Mesurado, B., Samper, P., & Mestre, M. V. (2019). Parents or peers? Predictors of prosocial behavior and aggression: A longitudinal study. *Frontiers in Psychology*, *10*, 2379. https://doi.org/10.3389/fpsyg.2019.02379.
Malti, T., Averdijk, M., Zuffiano, A., Ribeaud, D., Betts, L. R., Rotenberg, K. J., et al. (2015). Children's trust and the development of prosocial behavior. *International Journal of Behavioral Development*, *40*(3), 262–270.
McGinley, M., Lipperman-Kreda, S., Byrnes, H. F., & Carlo, G. (2010). Parental, social and dispositional pathways to Israeli adolescents' volunteering. *Journal of Applied Developmental Psychology*, *31*(5), 386–394. https://doi.org/10.1016/j.appdev.2010.06.001.
Mesurado, B., Distefano, M. J., Robiolo, G., & Richaud, M. C. (2019). The Hero program: Development and initial validation of an intervention program to promote prosocial behavior in adolescents. *Journal of Social and Personal Relationships*, *36*(8), 2566–2584. https://doi.org/10.1177/0265407518793224.
Mesurado, B., Guerra, P., Richaud, M. C., & Rodrigues, L. M. (2019). Effectiveness of prosocial behavior interventions: A meta-analysis. In *Psychiatry and neuroscience update* (pp. 259–271). Springer.
Mesurado, B., & Richaud, M. C. (2018). The relationship between parental variables. *Journal of Happiness Studies*, *18*(3), 843–860. https://doi.org/10.1007/s10902-016-9748-7.
Meuwese, R., Crone, E. A., de Rooij, M., & Guroglu, B. (2015). Development of equity preferences in boys and girls across adolescence. *Child Development*, *86*(1), 145–158. https://doi.org/10.1111/cdev.12290.
Mills, K. L., Goddings, A.-L., Clasen, L. S., Giedd, J. N., & Blakemore, S.-J. (2014). The developmental mismatch in structural brain maturation during adolescence. *Developmental Neuroscience*, *36*, 147–160.
Mills, K. L., Goddings, A. L., Herting, M. M., Meuwese, R., Blakemore, S. J., Crone, E. A., et al. (2016). Structural brain development between childhood and adulthood: Convergence across four longitudinal samples. *NeuroImage*, *141*, 273–281. https://doi.org/10.1016/j.neuroimage.2016.07.044.
Morelli, S. A., Knutson, B., & Zaki, J. (2018). Neural sensitivity to personal and vicarious reward differentially relates to prosociality and well-being. *Social Cognitive and Affective Neuroscience*, *13*(8), 831–839. https://doi.org/10.1093/scan/nsy056.
Orben, A., Tomova, L., & Blakemore, S. J. (2020). The effects of social deprivation on adolescent development and mental health. *The Lancet Child & Adolescent Health*, *4*(8), 634–640. https://doi.org/10.1016/S2352-4642(20)30186-3.
Padilla-Walker, L., Carlo, G., & Memmott-Elison, M. K. (2018). Longitudinal change in adolescents' prosocial behavior toward strangers, friends, and family. *Journal of Research on Adolescence*, *28*(3), 698–710. https://doi.org/10.1111/jora.12362.
Paus, T. (2010). Growth of white matter in the adolescent brain: Myelin or axon? *Brain and Cognition*, *72*(1), 26–35. https://doi.org/10.1016/j.bandc.2009.06.002.
Paus, T., Keshavan, M., & Giedd, J. N. (2008). Why do many psychiatric disorders emerge during adolescence? *Nature Reviews. Neuroscience*, *9*(12), 947–957. https://doi.org/10.1038/nrn2513.
Pope, A., Stolte, L., & Cohen, A. (2011). Closing the civic engagement gap: The potential of action civics. *Social Education*, *75*(5), 265–268.
Riem, M. M., Bakermans-Kranenburg, M. J., Huffmeijer, R., & van IJzendoorn, M. H. (2013). Does intranasal oxytocin promote prosocial behavior to an excluded fellow

player? A randomized-controlled trial with Cyberball. *Psychoneuroendocrinology*, *38*(8), 1418–1425. https://doi.org/10.1016/j.psyneuen.2012.12.023.
Rilling, J., Gutman, D., Zeh, T., Pagnoni, G., Berns, G., & Kilts, C. (2002). A neural basis for social cooperation. *Neuron*, *35*(2), 395–405. https://doi.org/10.1016/s0896-6273(02)00755-9.
Rilling, J. K., & Sanfey, A. G. (2011). The neuroscience of social decision-making. *Annual Review of Psychology*, *62*, 23–48. https://doi.org/10.1146/annurev.psych.121208.131647.
Sabato, H., Abraham, Y., & Kogut, T. (2021). Too lonely to help: Early adolescents' social connections and willingness to help during COVID-19 lockdown. *Journal of Research on Adolescence*, *31*(3), 764–779. https://doi.org/10.1111/jora.12655.
Samuels, W. E. (2018). Nurturing kindness naturally: A humane education program's effect on the prosocial behavior of first and second graders across China. *International Journal of Educational Research*, *91*, 49–64. https://doi.org/10.1016/j.ijer.2018.08.001.
Schonert-Reichl, K. A., Smith, V., Zaidman-Zait, A., & Hertzman, C. (2012). Promoting children's prosocial behaviors in school: Impact of the "roots of empathy" program on the social and emotional competence of school-aged children. *School Mental Health*, *4*(1), 1–21. https://doi.org/10.1007/s12310-011-9064-7.
Schreuders, E., Braams, B. R., Crone, E. A., & Guroglu, B. (2021). Friendship stability in adolescence is associated with ventral striatum responses to vicarious rewards. *Nature Communications*, *12*(1), 313. https://doi.org/10.1038/s41467-020-20042-1.
Schreuders, E., Klapwijk, E. T., Will, G. J., & Guroglu, B. (2018). Friend versus foe: Neural correlates of prosocial decisions for liked and disliked peers. *Cognitive, Affective, & Behavioral Neuroscience*, *18*(1), 127–142. https://doi.org/10.3758/s13415-017-0557-1.
Shin, J., & Lee, B. (2021). The effects of adolescent prosocial behavior interventions: A meta-analytic review. *Asia Pacific Education Review*, *22*(3), 565–577. https://doi.org/10.1007/s12564-021-09691-z.
Shirtcliff, E. A., Dahl, R. E., & Pollak, S. D. (2009). Pubertal development: Correspondence between hormonal and physical development. *Child Development*, *80*(2), 327–337. https://doi.org/10.1111/j.1467-8624.2009.01263.x.
Silverman, M. H., Jedd, K., & Luciana, M. (2015). Neural networks involved in adolescent reward processing: An activation likelihood estimation meta-analysis of functional neuroimaging studies. *NeuroImage*, *122*, 427–439. https://doi.org/10.1016/j.neuroimage.2015.07.083.
Smetana, J. G., & Metzger, A. (2005). Family and religious antecedents of civic involvement in middle class African American late adolescents. *Journal of Research on Adolescence*, *15*(3), 325–352. https://doi.org/10.1111/j.1532-7795.2005.00099.x.
Spaans, J. P., Peters, S., & Crone, E. A. (2019). Neural reward-related reactions to monetary gains for self and charity. *Cognitive, Affective, & Behavioral Neuroscience*, *19*(4), 845–858. https://doi.org/10.3758/s13415-018-00672-1.
Spaans, J. P., Peters, S., & Crone, E. A. (2020). Neural reward related-reactions to monetary gains for self and charity are associated with donating behavior in adolescence. *Social Cognitive and Affective Neuroscience*, *15*(2), 151–163. https://doi.org/10.1093/scan/nsaa027.
Spaans, J. P., Will, G. J., van Hoorn, J., & Guroglu, B. (2019). Turning a blind eye? Punishment of friends and unfamiliar peers after observed exclusion in adolescence. *Journal of Research on Adolescence*, *29*(2), 508–522. https://doi.org/10.1111/jora.12401.
Steinbeis, N., Bernhardt, B. C., & Singer, T. (2012). Impulse control and underlying functions of the left DLPFC mediate age-related and age-independent individual differences in strategic social behavior. *Neuron*, *73*(5), 1040–1051. https://doi.org/10.1016/j.neuron.2011.12.027.
Steinberg, L. (2008). *Adolescence*. McGraw-Hill.

Stern, J. A., & Cassidy, J. (2018). Empathy from infancy to adolescence: An attachment perspective on the development of individual differences. *Developmental Review*, *47*, 1–22.

Sweijen, S. W., van de Groep, S., Green, K. H., te Brinke, L., Buijzen, M., de Leeuw, R. N. H., & Crone, E. A., n.d., Daily prosocial actions during the COVID-19 pandemic contribute to giving behavior in adolescence. https://psyarxiv.com/7cptg/, (preprint).

Tabibnia, G., Satpute, A. B., & Lieberman, M. D. (2008). The sunny side of fairness: Preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). *Psychological Science*, *19*(4), 339–347. https://doi.org/10.1111/j.1467-9280.2008.02091.x.

Tamir, D. I., & Hughes, B. L. (2018). Social rewards: From basic social building blocks to complex social behavior. *Perspectives on Psychological Science*, *13*(6), 700–717. https://doi.org/10.1177/1745691618776263.

Tamnes, C. K., Herting, M. M., Goddings, A. L., Meuwese, R., Blakemore, S. J., Dahl, R. E., et al. (2017). Development of the cerebral cortex across adolescence: A multisample study of inter-related longitudinal changes in cortical volume, surface area, and thickness. *The Journal of Neuroscience*, *37*(12), 3402–3412. https://doi.org/10.1523/JNEUROSCI.3302-16.2017.

Tashjian, S. M., Weissman, D. G., Guyer, A. E., & Galvan, A. (2018). Neural response to prosocial scenes relates to subsequent giving behavior in adolescents: A pilot study. *Cognitive, Affective, & Behavioral Neuroscience*, *18*(2), 342–352. https://doi.org/10.3758/s13415-018-0573-9.

te Brinke, L. W., van de Groep, S., van der Cruijsen, R., & Crone, E. A., n.d. Variability and Change in Adolescents' Prosocial Behavior Across Multiple Time Scales. doi: 10.31234/osf.io/cqntp (web archive link), (preprint).

Telzer, E. H. (2016). Dopaminergic reward sensitivity can promote adolescent health: A new perspective on the mechanism of ventral striatum activation. *Developmental Cognitive Neuroscience*, *17*, 57–67.

Telzer, E. H., Fuligni, A. J., Lieberman, M. D., & Galvan, A. (2013). Ventral striatum activation to prosocial rewards predicts longitudinal declines in adolescent risk taking. *Developmental Cognitive Neuroscience*, *3*, 45–52. https://doi.org/10.1016/j.dcn.2012.08.004.

Telzer, E. H., Fuligni, A. J., Lieberman, M. D., & Galvan, A. (2014). Neural sensitivity to eudaimonic and hedonic rewards differentially predict adolescent depressive symptoms over time. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(18), 6600–6605. https://doi.org/10.1073/pnas.1323014111.

Telzer, E. H., Ichien, N., & Qu, Y. (2015). The ties that bind: Group membership shapes the neural correlates of in-group favoritism. *NeuroImage*, *115*, 42–51. https://doi.org/10.1016/j.neuroimage.2015.04.035.

Telzer, E. H., Masten, C. L., Berkman, E. T., Lieberman, M. D., & Fuligni, A. J. (2010). Gaining while giving: An fMRI study of the rewards of family assistance among white and Latino youth. *Social Neuroscience*, *5*(5–6), 508–518. https://doi.org/10.1080/17470911003687913.

Tousignant, B., Eugene, F., Sirois, K., & Jackson, P. L. (2018). Difference in neural response to social exclusion observation and subsequent altruism between adolescents and adults. *Neuropsychologia*, *116*(Pt. A), 15–25. https://doi.org/10.1016/j.neuropsychologia.2017.04.017.

Truskauskaitė-Kunevičienė, I. (2016). Direct and mediated long-term effects of the positive youth development intervention program try volunteering on empathy and prosocial behavior. *Social Inquiry into Well-being*, *2*(2), 8.

Urbina, D. A., & Ruiz-Villaverde, A. (2019). A critical review of homo economicus from five approaches. *American Journal of Economics and Sociology*, *78*(1), 63–93.

van de Groep, S., Meuwese, R., Zanolie, K., Guroglu, B., & Crone, E. A. (2018). Developmental changes and individual differences in trust and reciprocity in adolescence. *Journal of Research on Adolescence*, *30*(1), 192–208. https://doi.org/10.1111/jora.12459.

van de Groep, S., Zanolie, K., Burke, S. M., Brandner, P., Fuligni, A. J., & Crone, E. A. (2022). Growing in generosity? The effects of giving magnitude, target, and audience on the neural signature of giving in adolescence. *Developmental Cognitive Neuroscience*, *54*, 101084. https://doi.org/10.1016/j.dcn.2022.101084.

van de Groep, S., Zanolie, K., & Crone, E. A. (2020a). Familiarity and audience effects on giving: A functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, *32*(8), 1577–1589. https://doi.org/10.1162/jocn_a_01568.

van de Groep, S., Zanolie, K., & Crone, E. A. (2020b). Giving to friends, classmates, and strangers in adolescence. *Journal of Research on Adolescence*, *30*(Suppl. 2), 290–297. https://doi.org/10.1111/jora.12491.

van de Groep, S., Zanolie, K., Green, K. H., Sweijen, S. W., & Crone, E. A. (2020). A daily diary study on adolescents' mood, empathy, and prosocial behavior during the COVID-19 pandemic. *PLoS One*, *15*(10), e0240349. https://doi.org/10.1371/journal.pone.0240349.

van den Bos, W., van Dijk, E., Westenberg, M., Rombouts, S. A., & Crone, E. A. (2009). What motivates repayment? Neural correlates of reciprocity in the trust game. *Social Cognitive and Affective Neuroscience*, *4*(3), 294–304. https://doi.org/10.1093/scan/nsp009.

van den Bos, W., van Dijk, E., Westenberg, M., Rombouts, S. A., & Crone, E. A. (2011). Changing brains, changing perspectives: The neurocognitive development of reciprocity. *Psychological Science*, *22*(1), 60–70. https://doi.org/10.1177/0956797610391102.

van den Bos, W., Westenberg, M., Van Dijk, E., & Crone, E. A. (2010). Development of trust and reciprocity in adolescence. *Cognitive Development*, *25*, 90–102.

Van der Graaff, J., Carlo, G., Crocetti, E., Koot, H. M., & Branje, S. (2018). Prosocial behavior in adolescence: Gender differences in development and links with empathy. *Journal of Youth and Adolescence*, *47*(5), 1086–1099. https://doi.org/10.1007/s10964-017-0786-1.

van der Meulen, M., Steinbeis, N., Achterberg, M., Bilo, E., van den Bulk, B. G., van IJzendoorn, M. H., et al. (2017). The neural correlates of dealing with social exclusion in childhood. *Neuropsychologia*, *103*, 29–37. https://doi.org/10.1016/j.neuropsychologia.2017.07.008.

van der Meulen, M., Steinbeis, N., Achterberg, M., van IJzendoorn, M. H., & Crone, E. A. (2018). Heritability of neural reactions to social exclusion and prosocial compensation in middle childhood. *Developmental Cognitive Neuroscience*, *34*, 42–52. https://doi.org/10.1016/j.dcn.2018.05.010.

van der Meulen, M., van IJzendoorn, M. H., & Crone, E. A. (2016). Neural correlates of prosocial behavior: Compensating social exclusion in a four-player Cyberball game. *PLoS One*, *11*(7), e0159045. https://doi.org/10.1371/journal.pone.0159045.

Van der Meulen, M., Wierenga, L. M., Achterberg, M., Drenth, N., Van IJzendoorn, M. H., & Crone, E. A. (2020). Genetic and environmental influences on structure of the social brain in childhood. *Developmental Cognitive Neuroscience*, *44*, 100782. https://doi.org/10.1016/j.dcn.2020.100782.

van Goethem, A. A. J., van Hoof, A., van Aken, M. A. G., Orobio de Castro, B., & Raaijmakers, Q. A. W. (2014). Socialising adolescent volunteering: How important are parents and friends? Age dependent effects of parents and friends on adolescents' volunteering behaviours. *Journal of Applied Developmental Psychology*, *35*(2), 94–101. https://doi.org/10.1016/j.appdev.2013.12.003.

Van Hoorn, J., Van Dijk, E., Guroglu, B., & Crone, E. A. (2016). Neural correlates of prosocial peer influence on public goods game donations during adolescence. *Social Cognitive and Affective Neuroscience*, *11*(6), 923–933. https://doi.org/10.1093/scan/nsw013.

Van Hoorn, J., Van Dijk, E., Meuwese, R., Rieffe, C., & Crone, E. A. (2016). Peer influence on prosocial behavior in adolescence. *Journal of Research on Adolescence*, *26*(1), 90–100.

Van Leijenhorst, L., Gunther Moor, B., Op de Macks, Z. A., Rombouts, S. A., Westenberg, P. M., & Crone, E. A. (2010). Adolescent risky decision-making: Neurocognitive development of reward and control regions. *NeuroImage*, *51*(1), 345–355. https://doi.org/10.1016/j.neuroimage.2010.02.038.

Van Leijenhorst, L., Zanolie, K., Van Meel, C. S., Westenberg, P. M., Rombouts, S. A., & Crone, E. A. (2010). What motivates the adolescent? Brain regions mediating reward sensitivity across adolescence. *Cerebral Cortex*, *20*(1), 61–69. https://doi.org/10.1093/cercor/bhp078.

Veenstra, R., & Laninga-Wijnen, L. (2021). Peer network studies and interventions in adolescence. *Current Opinion in Psychology*, *44*, 157–163. https://doi.org/10.1016/j.copsyc.2021.09.015.

Vrijhof, C. I., van den Bulk, B. G., Overgaauw, S., Lelieveld, G. J., Engels, R. C., & van IJzendoorn, M. H. (2016). The prosocial Cyberball game: Compensating for social exclusion and its associations with empathic concern and bullying in adolescents. *Journal of Adolescence*, *52*, 27–36. https://doi.org/10.1016/j.adolescence.2016.07.005.

Westhoff, B., Blankenstein, N. E., Schreuders, E., Crone, E. A., & van Duijvenvoorde, A. C. K. (2021). Increased ventromedial prefrontal cortex activity in adolescence benefits prosocial reinforcement learning. *Developmental Cognitive Neuroscience*, *52*, 101018. https://doi.org/10.1016/j.dcn.2021.101018.

Westhoff, B., Molleman, L., Viding, E., van den Bos, W., & van Duijvenvoorde, A. C. K. (2020). Developmental asymmetries in learning to adjust to cooperative and uncooperative environments. *Scientific Reports*, *10*(1), 21761. https://doi.org/10.1038/s41598-020-78546-1.

Wierenga, L. M., Bos, M. G. N., Schreuders, E., Vd Kamp, F., Peper, J. S., Tamnes, C. K., et al. (2018). Unraveling age, puberty and testosterone effects on subcortical brain development across adolescence. *Psychoneuroendocrinology*, *91*, 105–114. https://doi.org/10.1016/j.psyneuen.2018.02.034.

Wray-Lake, L., DeHaan, C. R., Shubert, J., & Ryan, R. M. (2019). Examining links from civic engagement to daily well-being from a self-determination theory perspective. *The Journal of Positive Psychology*, *14*(2), 166–177. https://doi.org/10.1080/17439760.2017.1388432.

Yeager, D. S., Dahl, R. E., & Dweck, C. S. (2018). Why interventions to influence adolescent behavior often fail but could succeed. *Perspectives on Psychological Science*, *13*(1), 101–122. https://doi.org/10.1177/1745691617722620.

Yeager, D. S., Fong, C. J., Lee, H. Y., & Espelage, D. L. (2015). Declines in efficacy of anti-bullying programs among older adolescents: Theory and a three-level meta-analysis. *Journal of Applied Developmental Psychology*, *37*, 36–51. https://doi.org/10.1016/j.appdev.2014.11.005.