


## Behavioral and Neural Pathways Supporting the Development of Prosocial and Risk-Taking Behavior Across Adolescence

Neeltje E. Blankenstein   
*Leiden University and Leiden Institute for Brain and Cognition*

Eva H. Telzer and Kathy T. Do  
*University of North Carolina at Chapel Hill*

Anna C.K. van Duijvenvoorde, and Eveline A. Crone  
*Leiden University and Leiden Institute for Brain and Cognition*

This study tested the pathways supporting adolescent development of prosocial and rebellious behavior. Self-report and structural brain development data were obtained in a three-wave, longitudinal neuroimaging study (8–29 years,  $N = 210$  at Wave 3). First, prosocial and rebellious behavior assessed at Wave 3 were positively correlated. Perspective taking and intention to comfort uniquely predicted prosocial behavior, whereas fun seeking (current levels and longitudinal changes) predicted both prosocial and rebellious behaviors. These changes were accompanied by developmental declines in nucleus accumbens and medial prefrontal cortex (MPFC) volumes, but only faster decline of MPFC (faster maturity) related to less rebellious behavior. These findings point toward a possible differential susceptibility marker, fun seeking, as a predictor of both prosocial and rebellious developmental outcomes.

Adolescence is often described as the most important transition period for developing into an adult with social competence and mature social goals (Blakemore & Mills, 2014; Crone & Dahl, 2012). Yet, there are many paradoxes when describing typical adolescent behavior. For instance, adolescents are described as notorious risk takers, characterized by “rebellious behaviors” such as substance use, and with a preferred focus on short-term rewards rather than long-term consequences of their decisions (Dahl, 2004; Hall, 1904; Steinberg, 2008). Experimental and self-report studies have confirmed this adolescent rise in risk-taking behaviors (Burnett, Bault, Coricelli, & Blakemore, 2010; Defoe, Dubas, Figner, & van Aken, 2015), which are more pronounced in social contexts, such as in the

presence of friends (Gardner & Steinberg, 2005; Knoll, Magis-Weinberg, Speekenbrink, & Blakemore, 2015). However, in parallel, most individuals also develop social competence during adolescence, with rises in perspective taking and in considering the needs of others (Blakemore & Mills, 2014). Indeed, adolescents show increases in prosocial behaviors, especially toward their friends (Guroglu, van den Bos, & Crone, 2014), and show increases in social perspective taking (Dumontheil, Apperly, & Blakemore, 2010). Adolescence has therefore been described as a developmental period of both risks and opportunities (Crone & Dahl, 2012; Do, Guassi Moreira, & Telzer, 2017). Although it is key to our understanding of how these behaviors develop in tandem in adolescence, the relation between risk-taking and prosocial tendencies in adolescence has been overlooked (Telzer, Fuligni, Lieberman, &

---

This study was supported by an innovative ideas grant of the European Research Council (ERC-2010-StG-263234 awarded to Eveline A. Crone) and a travel grant of the Leiden University Fund (Den Dulk/Moermans fund, awarded to Neeltje E. Blankenstein).

Conflict of interest: The authors declare that they have no conflict of interest, financial, or otherwise.

Correspondence concerning this article should be addressed to Neeltje E. Blankenstein, Department of Developmental and Educational Psychology, Leiden University, Wassenaarseweg 52, 2333 AK Leiden, The Netherlands. Electronic mail may be sent to [n.e.blankenstein@fsw.leidenuniv.nl](mailto:n.e.blankenstein@fsw.leidenuniv.nl).

© 2019 The Authors

Child Development published by Wiley Periodicals, Inc. on behalf of Society for Research in Child Development.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

0009-3920/2020/9103-0034

DOI: 10.1111/cdev.13292

Galvan, 2013). Therefore, a critical question concerns whether risk-taking (specifically, rebellious behaviors) and prosocial tendencies are related constructs over adolescent development, and which processes predict these seemingly paradoxical behaviors. Understanding the mechanisms that underlie or differentiate these two seemingly disparate behaviors may help to identify pathways for reducing risks and/or promoting opportunities often inherent in adolescence (Crone & Dahl, 2012).

One possible mechanism that may account for increases in the occurrences of both risk-taking and prosocial tendencies is elevated reward sensitivity (Crone & Dahl, 2012; van Duijvenvoorde, Peters, Braams, & Crone, 2016; Telzer, 2016). It has been well conceptualized that reward sensitivity is correlated with risk-taking behavior such as alcohol consumption, and functional neuroimaging work has shown that heightened activation of the ventral striatum (a subcortical region that plays a primary role in reward sensitivity) during receipt of reward correlates with alcohol use (Braams, Peper, van der Heide, Peters, & Crone, 2016). To date, it remains unclear whether behavioral sensitivity to rewards also drives prosocial tendencies, although prior functional neuroimaging studies have established that heightened ventral striatum activation is also observed during positive, other-oriented behavior such as giving to others (Telzer, 2016; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010). Furthermore, gaining for others also results in functional activity of the ventral striatum (Varnum, Shi, Chen, Qiu, & Han, 2014), and this activity is heightened in adolescents when gaining for close family members (Braams & Crone, 2017). If sensitivity to rewards is related to both risk-taking and prosocial tendencies, then an important question concerns whether adolescence is a window for stronger reward reactivity that may, in some instances, lead adolescents to develop stronger risk-taking tendencies, whereas in other instances, lead adolescents to develop stronger prosocial tendencies, also referred to as differential susceptibility (Schriber & Guyer, 2015). Alternatively, the same window of reward sensitivity may also result in adolescents who show *both* risk-taking behavior as well as prosocial tendencies, also referred to as “prosocial risk takers” (Do et al., 2017). Thus, in this study we address whether the development of behavioral reward sensitivity underlies risk-taking and/or prosocial tendencies, as well as a combination of these traits.

Two other processes that have previously been related to prosocial behavior are social cognitive perspective taking and empathic concern, specifically the

intention to comfort others (Overgaauw, Rieffe, Broekhof, Crone, & Guroglu, 2017). First, the development of perspective taking has been well described, such that perspective-taking abilities increase across adolescence (Humphrey & Dumontheil, 2016), and adolescents who show better perspective-taking skills report more prosocial behavior (Tamnes et al., 2017). In addition, in adolescence, functional activation in the medial prefrontal cortex (MPFC; a region part of the “social brain network,” involved in social cognitive processing and mentalizing; Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014) has been found to be heightened during prosocial behavior in the presence of peers (Van Hoorn, Van Dijk, Güroğlu, & Crone, 2016). Second, the empathic intention to comfort others increases across age (10–15 years) in girls and declines in boys, and has been related to lower levels of bullying behavior (Overgaauw et al., 2017). Thus, the development of perspective-taking abilities and the intention to comfort others has been shown to promote prosocial behavior, and may also have a buffering effect against antisocial tendencies (Overgaauw et al., 2017). However, it is not yet known if perspective taking and intention to comfort also relate to risk-taking behavior. Therefore, an additional question concerns whether individuals’ development of perspective taking and the intention to comfort others are related to prosocial and/or risk taking in adolescents.

Finally, in addition to the development of reward sensitivity and social skills, the development of brain structures that may accompany the development of these behaviors is relatively understudied. Between conception and childhood, the number of neurons in the brain increase and peak in early childhood. This increase co-occurs with synaptic pruning, a process in which excess synapses are eliminated in order to strengthen other synaptic connections within a specific brain region, resulting in fewer synapses for the same amount of work (Huttenlocher, 1990). Synaptic pruning increases across adolescence in a nonlinear fashion, most extensively in regions involved in cognitive regulation and higher order social cognition (Tamnes et al., 2017) and in subcortical regions (Goddings et al., 2014). This process results in more fine-tuned brain regions that yield more efficient cognitive and social processing and improved performance with age (Blakemore, 2008). Indeed, structural brain development, capturing the most consistent within-individual patterns of change, has been associated with a number of developmental outcomes such as identity formation and social functioning (Becht et al., 2018; Blakemore & Mills, 2014; Tamnes et al., 2018), yet how structural development relates to prosocial and/or risk-taking behaviors is less well known.

In two recent studies, the nucleus accumbens, a region of the ventral striatum involved in reward sensitivity (Sescousse, Caldú, Segura, & Dreher, 2013), decreased in volume during the course of adolescent development (Herting et al., 2018; Wierenga et al., 2018). A separate study showed that this volume decrease was related to greater behavioral reward sensitivity (Urosevic, Collins, Muetzel, Lim, & Luciana, 2012). However, the relation between this structural decrease and risk-taking tendencies is not yet known. In addition, MPFC volume has consistently been linked to social perspective taking (Blakemore & Mills, 2014) and prosocial behavior (Thijssen et al., 2015; Wildeboer et al., 2017). Alternatively, functional MRI studies have consistently found that greater activation in this region is related to choice valuation and reward outcome processing of risky (i.e., gambling) decisions in adolescence (Blankenstein, Schreuders, Peper, Crone, & van Duijvenvoorde, 2018; Van Duijvenvoorde et al., 2015), but the relation between the structural development of MPFC and risk taking is less well understood. Taken together, in addition to reward sensitivity, social perspective taking, and intention to comfort, the structural development of brain regions related to these processes nucleus accumbens (NACC and MPFC) may provide additional insights into developmental outcomes, namely risk-taking and prosocial tendencies.

### *The Current Study*

This study set out to test four questions in the Braintime sample, a large longitudinal neuroimaging study with three biannual measurement waves (e.g., Peters & Crone, 2017; Schreuders et al., 2018). First, we examined the occurrence of two important developmental outcomes in adolescence, risk-taking behavior and prosocial behavior, and how they are related in adolescents and young adults between ages 12 and 30 years at the final measurement wave. We made use of self-report findings because previous studies have shown that these are most trait-like and take into account the history of individuals (Peper, Braams, Blankenstein, Bos, & Crone, 2018). We were especially interested in the question whether risk-taking behavior and prosocial behaviors were positively related (possibly reflecting individuals who are “prosocial risk takers”; Do et al., 2017), negatively related (those who are risky are less prosocial and vice versa), or not related (indicating they do not covary meaningfully within individuals). A frequency measure of rebellious behavior was used as an index of risk taking (Gullone, Moore,

Moss, & Boyd, 2000), given that these types of behaviors were most related to risk-taking tendencies in real life, such as alcohol consumption and smoking. In addition, a frequency measure of prosocial actions was used as an index of prosocial tendencies, as this measure examined occurrences of actual prosocial behaviors rather than intentions (Overgaauw et al., 2017). Given that both traits have previously been related to age and gender, these factors were included and controlled for in the analyses, because the focus in this study was on individual differences in trajectories of change.

A second question in this study concerned whether reward sensitivity related to rebellious behavior and prosocial behavior using the Behavioral Activation Scale (BAS)-subscales of the Behavioral Inhibition Scale (BIS)/BAS questionnaires (drive, fun seeking, reward responsiveness; Carver & White, 1994). In addition to reward sensitivity, we examined the contributions of perspective taking, as assessed with the perspective taking subscale of the Interpersonal Reactivity Index (IRI; Davis, 1983), and the intention to comfort others, as assessed with the empathic concern questionnaire for children and adolescents (Overgaauw et al., 2017). We hypothesized that reward sensitivity, perspective taking, and intention to comfort would be related to prosocial behavior and that reward sensitivity would also be related to rebellious behavior. Furthermore, we explored associations perspective taking, intention to comfort, and rebellious behavior.

Third, we examined in the same individuals whether the developmental trajectory of reward sensitivity and perspective taking across the three measurement waves would predict the outcome measures rebellious behavior and prosocial behavior at the final wave. In previous research, it was demonstrated that not only the initial levels (intercepts) but also the trajectory of change (slopes) is informative for predicting developmental outcomes (e.g., Becht et al., 2018). Therefore, longitudinal measurements are crucial to examine whether trajectories of change are predictive for developmental outcome measures. Because our variable of intention to comfort was only available at the final wave, this question was not addressed for this measure.

Finally, we examined whether the development of volumes of the nucleus accumbens and MPFC predicted the outcomes of prosocial and rebellious behavior. Again, for brain measures the trajectory of change is presumed to be more informative than the mean levels, and therefore we determined both mean levels (intercepts) as well as trajectories of change (slopes) to use as predictors for rebellious

and prosocial outcomes above the behavioral indices (Foulkes & Blakemore, 2018).

## Method

### Participants

Participants were part of the Braintime study, a longitudinal study conducted in the Netherlands in 2011 (Time Point 1: T1), 2013 (T2), and 2015 (T3). At T1, data from 299 participants were collected (153 female, 8–25 years), at T2 287 participants (149 female, 10–27 years), and at T3 275 participants (143 female, 12–29 years). IQ was estimated at T1 and T2, and did not correlate with age (Braams, van Duijvenvoorde, Peper, & Crone 2015). From all Braintime participants, 81.2% had European parents and at least three European grandparents, 4.7% had European parents and fewer than three European grandparents, and 7.7% were from diverse ethnic backgrounds. For 6.4% this information was missing. In total, across all time points, there were 15 participants (5%) who reported they currently used medicine for a neuropsychiatric disorder (such as anxiety, depression, or AD(H)D). To include as many participants in our analyses as possible, these participants were included in this study (excluding these participants did not qualitatively affect our results). Table 1 depicts an overview of the number of observations per measure on each time point.

### Self-Report Measures

#### Outcome Measures

**Rebellious behavior.** To measure participants' risk-taking behavior at T3 (age range 11.94–28.72 years), we examined the Rebellious subscale

of the Adolescent Risk-Taking Questionnaire (Gul-lone et al., 2000). This scale assesses the frequency with which individuals displayed risky behaviors such as "Staying out late" and "Getting drunk" with five items ( $\alpha = .880$ ), on a scale ranging from 1 (*never*) to 5 (*very often*). Data of this subscale have previously been reported in Blankenstein et al. (2018) in a subset of the current sample.

**Prosocial behavior.** We assessed participants' prosocial behavior at T3 (age range 11.94–28.72 years) with 27 items using a questionnaire referred to as the Opportunities for Prosocial Actions scale (unpublished measure;  $\alpha = .924$ ) assessing the frequency of prosocial actions toward friends and peers within the last few months. Example items include "Sacrifice your own goals to help a friend or peer with theirs," "Helped a friend find a solution to their problem," and "Gave money to a friend or peer because they really needed it." The full list of items is displayed in Supporting Information. The items covered a broad range of prosocial actions such as helping, giving, altruistic tendencies, and providing emotional support. Participants indicated how often they displayed these behaviors, ranging from 1 (*not something i do*) to 6 (*very often*).

#### Predictor Variables

**Behavioral Inhibition/Behavioral Approach Questionnaire.** We used the BAS scales of the BIS/BAS questionnaire (Carver & White, 1994) to obtain indices of participants' approach behavior. BAS scales were available at each time point (age ranges: T1: 8.01–25.95; T2: 9.92–26.6; T3: 11.94–28.72 years). The BAS subscales are Drive (the tendency to persist in pursuit of goals,  $\alpha_{T3} = .725$ ; four items), Fun Seeking (the desire for rewards and the willingness to approach rewards;  $\alpha_{T3} = .546$ ; four items), and

Table 1  
Number of Observations Per Time Point, and Intraclass Correlations (ICC) With 95% CI

Variable	N (female)			ICC T1, T2, T3 (95% CI)
	T1	T2	T3	
Prosocial behavior	—	—	263 (142)	—
Rebellious behavior	—	—	226 (116)	—
EMQ Intention to Comfort	—	—	274 (143)	—
IRI Perspective Taking	31 (16)	286 (148)	262 (141)	.76 (.54, .89)
BAS Drive	277 (145)	286 (148)	262 (141)	.60 (.50, .68)
BAS Fun Seeking	277 (145)	286 (148)	262 (141)	.58 (.48, .66)
BAS Reward Responsiveness	277 (145)	286 (148)	262 (141)	.60 (.50, .68)
Nucleus accumbens	238 (129)	226 (119)	219 (120)	.94 (.92, .96)
Medial prefrontal cortex	238 (129)	226 (119)	219 (120)	.96 (.77, .99)

Note. EMQ = Empathy Questionnaire; IRI = Interpersonal Reactivity Index; BAS = Behavioral Activation Scale.

Reward Responsiveness (the response to rewards and reward anticipation;  $\alpha_{T3} = .609$ ; five items). Participants indicated on a 4-point scale the degree to which statements applied to them, ranging from 1 (*very true*) to 4 (*very false*). Example items include “When I want something I usually go all-out to get it” (Drive), “I’m always willing to try something new if I think it will be fun” (Fun Seeking), and “When I get something I want, I feel excited and energized” (Reward Responsiveness). We recoded the items such that higher scores indicate more approach behavior. T3 data of a subset of the current sample are reported in Blankenstein et al. (2018), and longitudinal trajectories of these subscales are reported in Schreuders et al. (2018).

*Interpersonal Reactivity Index: Perspective taking.* At T1, we presented participants aged 18 and older (range 18.44–25.95 years) with the Perspective Taking subscale of the IRI (Davis, 1983). At T2 and T3, we administered this scale to all participants (age ranges: T2: 9.92–26.6; T3: 11.94–28.72 years). The Perspective Taking subscale measures the spontaneous tendency to adopt another person’s point of view in daily life, with seven items ( $\alpha_{T3} = .775$ ). Example items include “I sometimes try to understand my friends better by imagining how things look from their perspective” and “When two peers disagree, I try to see both sides.” Participants gave their responses on a scale ranging from 1 (*does not describe me well*) to 5 (*describes me very well*).

*Empathy Questionnaire for Children and Adolescents: Intention to Comfort scale.* At T3 (age range: 11.94–28.72 years), we introduced the Intention to Comfort subscale of the Empathy Questionnaire [EMQ] for Children and Adolescents (Overgaauw et al., 2017). This subscale includes five items ( $\alpha = .599$ ) and measures the extent to which someone feels inclined to actually help or support a person in need. Participants were asked to rate to what extent the description was true for them on a 3-point scale: 1 (*not true*), 2 (*somewhat true*), and 3 (*true*). Examples include “If a friend is sad, I like to comfort him,” and “I want everyone to feel good.”

Finally, in Supporting Information (Table S1) we report Cronbach’s alpha’s for all behavioral measures at T3 for the whole sample and across three separate age groups. Measures were overall equally reliable across age.

### Brain Imaging

We used a 3T Philips Achieva MRI scanner for structural neuroimaging. All images were visually inspected after processing (using the longitudinal

pipeline) for accuracy (e.g., Becht et al., 2018; Mills & Tamnes, 2014). Scans of poor quality were excluded, and high-quality scans were reprocessed through the longitudinal pipeline (single time points were also processed longitudinally). This procedure of quality control was repeated until only acceptable scans were included. See Table 1 for the number of scans included per time point (age ranges: T1: 8.01–25.95; T2: 9.92–26.6; T3: 11.94–28.72 years). Scan acquisition parameters and a detailed description of the structural analyses are described in Bos, Peters, van de Kamp, Crone, and Tamnes, 2018; and Wierenga et al., 2018.

### Regions of Interest

We derived the measure of gray matter volume for the NACC using the volumetric segmentation procedure. We used the average of left and right NACC in our analyses. Gray matter volume was obtained using the surface-based reconstructed image. We defined the MPFC by combining the following subregions: superior frontal, rostral anterior cingulate, and caudal anterior cingulate of the Desikan–Killiany–Tourville atlas (Klein & Tourville, 2012).

### Individual Estimations Intercepts and Slopes From Longitudinal Measures

From the longitudinal measures (IRI Perspective Taking, BAS scales, brain structure) we estimated starting points and rates of change (i.e., intercepts and slopes) for each participant. To do so, we ran regression analyses for each participant individually, in which we predicted the longitudinal variables across time points from age at T1 (or the first time point for which data were available). This resulted in an estimation of an intercept and a linear slope for each participant (except for participants who had data on only one time point, for which slopes could not be estimated). Because there were only three waves, only linear slopes were estimated (Becht et al., 2018). These estimates of individual intercepts and linear slopes were used in subsequent analyses predicting the outcome variables prosocial and rebellious behavior.

Note that in Supporting Information we report which developmental trajectories best described the longitudinal measures (i.e., Perspective Taking, BAS scales, and brain structures), on a group level. Developmental trajectories of BAS scales and NACC volume are already described in Schreuders et al. (2018) and Wierenga et al. (2018), respectively,

whereas the longitudinal development of IRI Perspective Taking and MPFC have not yet been reported. In brief, IRI Perspective Taking followed a cubic developmental pattern across age, described best as an adolescent-emergent pattern of Perspective Taking increasing into adulthood, and higher levels of Perspective Taking in girls than in boys (see also Figure 1A below). MPFC volume was best described by a declining cubic effect of age, and greater volumes in boys than in girls (Figure 1B). In Supporting Information an elaborate description of these results is provided. In addition, in Supporting Information we describe the age patterns as they were observed for cross-sectional behavioral predictors (i.e., BAS scales at T3, Perspective Taking at T3, and EMQ Intention to Comfort).

### Analysis Plan

First, to address whether prosocial and rebellious behavior were negatively related, positively related, or not related, we ran a partial correlation analysis on these measures, controlling for age (linear and quadratic) and gender. Gender was dummy-coded (0 [female] or 1 [male]) in all analyses. Second, in our cross-sectional analyses (data from the final wave), we tested which predictors (i.e., intention to comfort, perspective taking, BAS scales) best described prosocial behavior and which predictors

best described rebellious behavior (controlling for age and gender). We also tested to which extent these predictors were specific for prosociality, controlling for rebelliousness (i.e., patterns of behavior in the upper right and lower right quadrants of the conceptual model by Do et al., 2017; see Figure 2) and vice versa (i.e., upper left and lower left quadrant). In addition, to test which predictors best described a combination of prosocial and rebellious behavior, we created an interaction variable of these traits. Here we tested which predictors best described a combination of high levels of rebelliousness and prosociality (upper right quadrant, also referred to as “prosocial risk takers”; Do et al., 2017). Next, in our longitudinal analyses, we tested whether longitudinal change (i.e., linear slopes) predicted additional variance above initial levels (i.e., intercepts) of our behavioral predictors on prosocial and rebellious behavior, and on their interaction (similar to the cross-sectional analyses). Finally, we tested if structural brain development (i.e., intercepts and slopes) of NACC and MPFC predicted additional variance above the behavioral indices (i.e., above their intercepts and slopes).

For each regression model we checked whether statistical assumptions of multiple regression were met. We checked for the normality residuals, the absence of multicollinearity, and the assumption of homoscedasticity. There was no evidence of violations of statistical

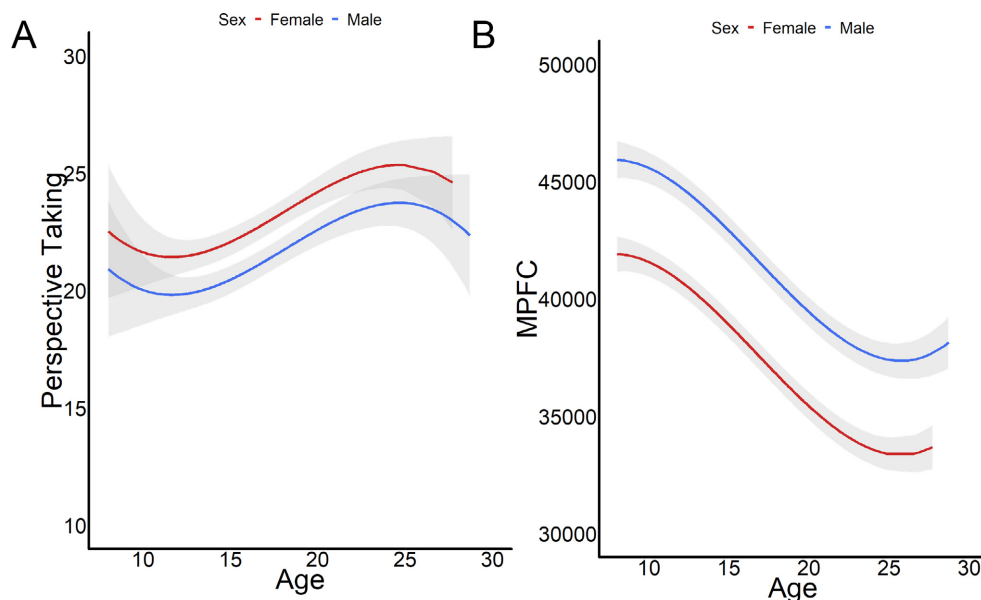


Figure 1. Developmental trajectories of (A) Perspective Taking and (B) medial prefrontal cortex (MPFC; in cubic millimeters). Red lines indicate female, blue lines indicate male, and gray areas mark the 95% CI. Developmental trajectories of Behavioral Activation Scales and NACC are described in Schreuders et al. (2018) and Wierenga et al. (2018), respectively.

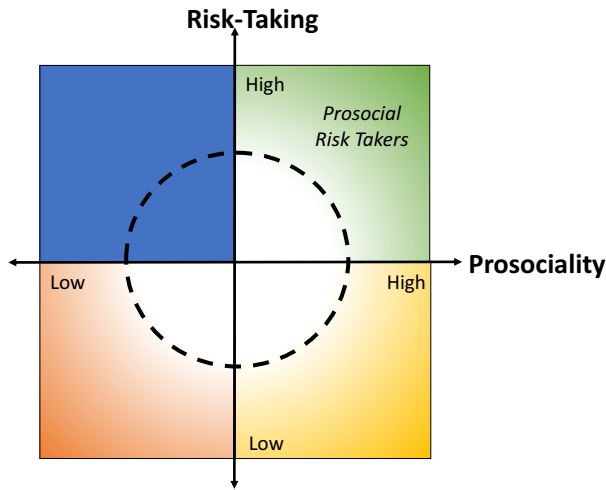


Figure 2. Theoretical model depicting the intersection between risk-taking and prosocial tendencies. Reprinted from Do et al. (2017, p. 267), Copyright (2016), with permission from Elsevier.

assumptions, as indicated by normally distributed residuals (through inspection of histograms and Q-Q plots of residuals), no multicollinearity (as indicated by Variance Inflation Factor values below 10), and no heteroscedasticity (as indicated by scatter plots of residuals vs. predicted values).

### Results

#### Age Patterns Outcome Measures at the Final Wave

Below we report the results of the analyses on predictors of the outcome measures Rebellious and

Prosocial behavior. In this section, we first describe the age patterns of these outcome measures. The age patterns of the predictor variables at T3 are described in Supporting Information.

For Rebellious and Prosocial behavior, we tested for linear, quadratic, and cubic effects of age, as well as gender effects, on Rebellious and Prosocial behavior assessed at the final wave (see Figures 3A and 3B). Rebellious behavior was best described by a quadratic age effect,  $R^2 = .40$ ,  $F(2, 223) = 73.96$ ,  $p < .001$ ; age linear:  $b = 0.25$ ,  $SE = 0.02$ ,  $p < .001$ ; age quadratic  $b = -.02$ ,  $SE = 0.004$ ,  $p < .001$ . Prosocial behavior was best described by a quadratic age effect and a main effect of gender,  $R^2 = .15$ ,  $F(3, 259) = 15.52$ ,  $p < .001$ ; age linear:  $b = 0.01$ ,  $SE = 0.02$ ,  $p = .38$ ; age quadratic  $b = -.008$ ,  $SE = 0.003$ ,  $p = .003$ , gender:  $b = -.56$ ,  $SE = 0.09$ ,  $p < .001$ ; No Age  $\times$  Gender Effects were observed. Given these nonlinear age effects, in all subsequent analyses we controlled for age (linear and quadratic) and gender.

#### Cross-Sectional Relations Among Behavioral Measures at the Final Wave

First, we tested the association between the outcome measures Rebellious and Prosocial behavior, controlling for age (linear and quadratic) and gender. A partial correlation showed that these outcome measures were positively correlated (partial  $r = .197$ ,  $p < .01$ ; see Figure 3C). Table 2 depicts the correlations between age (linear and quadratic; no cubic effects were observed), gender, the outcome measures (rebellious and prosocial behavior), and the behavioral predictors at T3. Both zero-order

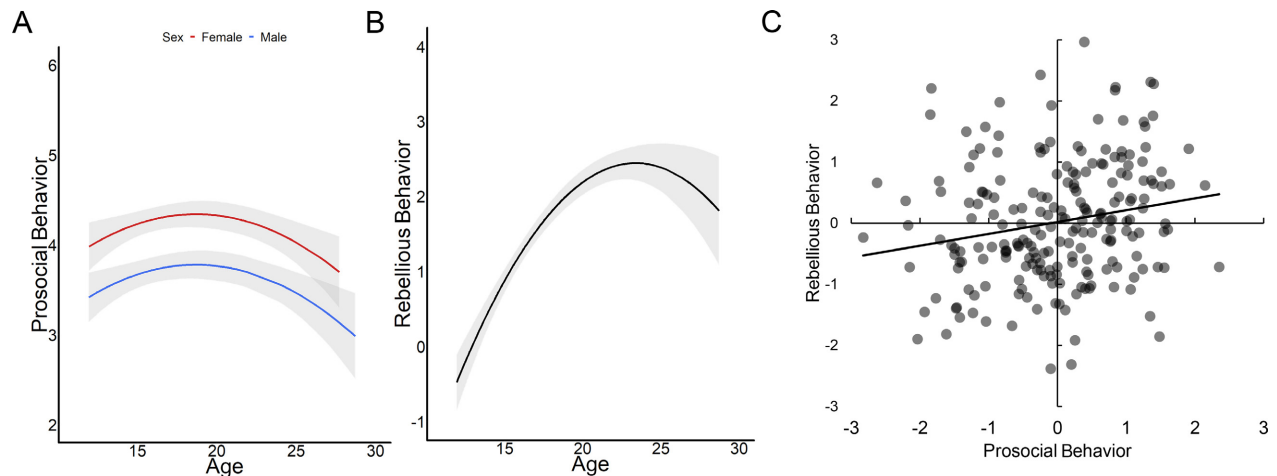


Figure 3. Developmental patterns of (A) prosocial behavior and (B) rebellious behavior, assessed at the final wave. The red line indicates female, the blue line indicates male, and the black line indicates no gender effect. Gray areas mark the 95% CI. (C) The positive association between prosocial and rebellious behavior, controlled for age (linear and quadratic) and gender.

correlations are provided (above the diagonal) as well as partial correlations (controlled for age [linear and quadratic] and gender; below the diagonal).

Next, we predicted the outcome measures from the other behavioral measures at T3 (BAS scales, Perspective Taking, and Intention to Comfort) while controlling for age and gender. To explore which behavioral predictors best described the dependent variables, we used stepwise regressions. Age (linear and quadratic) and gender were always included in the model to control for their effects.

*Prosocial Behavior*

Prosocial behavior was best explained by IRI Perspective Taking, EMQ Intention to Comfort, and BAS Fun Seeking,  $R^2 = .240$ ,  $F(6, 249) = 13.090$ ,  $p < .001$ , Intention to Comfort:  $b = 0.449$ ,  $SE = 0.177$ ,  $p = .012$ ; Perspective Taking:  $b = 0.042$ ,  $SE = 0.013$ ,  $p = .001$ , Fun Seeking:  $b = 0.053$ ,  $SE = 0.025$ ,  $p = .031$ ; see Table 3. All regression coefficients were positive, indicating that higher levels of the predictor variables were related to higher levels of Prosocial behavior. When adding ARQ Rebellious behavior to the model (after trimming the model from the nonsignificant predictors Drive and Reward Responsiveness), similar effects were observed, although effects of Fun Seeking and Intention to Comfort no longer reached significance (Perspective Taking:  $b = 0.047$ ,  $SE = 0.014$ ,  $\beta = .226$ ,  $p = .001$ ; Fun Seeking:  $b = 0.049$ ,  $SE = 0.028$ ,

$\beta = .110$ ,  $p = .086$ ; Intention to Comfort:  $b = 0.310$ ,  $SE = 0.206$ ,  $\beta = .098$ ,  $p = .14$ , not depicted in Table 3).

*Rebellious Behavior*

Next, we predicted Rebellious behavior from the independent variables. Rebellious behavior was best explained by BAS Fun Seeking, in which higher levels of Fun Seeking were related to higher levels of Rebellious behavior,  $R^2 = .46$ ,  $F(4, 208) = 43.90$ ,  $p < .001$ ;  $b = 0.140$ ,  $SE = 0.033$ ; see Table 3. When adding Prosocial behavior to the model, this effect of Fun Seeking remained significant ( $b = 0.127$ ,  $SE = 0.033$ ,  $\beta = .198$ ,  $p < .001$ , not depicted in Table 3).

*Prosocial × Rebellious Behavior*

Finally we predicted the combined effect of Prosocial and Rebellious behavior from the other behavioral predictors. This combined variable was created as follows. We first regressed Prosocial behavior and Rebellious behavior onto age linear, quadratic, and gender. Second, we saved the standardized residuals of these regressions, to which we added a constant so that all values were positive values. Third, we multiplied these terms, thus creating a combined interaction variable (Prosocial × Rebellious) controlled for any effects of age and gender. We used multiplication instead of addition to rate participants who scored more

Table 2  
Correlation table (Pearson's r) of Associations Between Age (Linear and Quadratic; No Cubic Effects Were Observed), Gender, and Behavioral Variables at T3

	1	2	3	4	5	6	7	8	9	10
1 Age linear										
2 Age quadratic (above age linear)	—									
3 Gender	—	—								
4 Rebellious behavior	—	—	—							
5 Prosocial behavior	—	—	—	—						
6 BAS Drive	—	—	—	—	—					
7 BAS Fun Seeking	—	—	—	—	—	—				
8 BAS Reward Responsiveness	—	—	—	—	—	—	—			
9 IRI Perspective Taking	—	—	—	—	—	—	—	—		
10 EMQ Intention to Comfort	—	—	—	—	—	—	—	—	—	

Note. Values above the diagonal represent zero-order correlations. Values below the diagonal represent partial correlations (controlled for age (linear and quadratic) and gender). BAS = Behavioral Activation Scale; IRI = Interpersonal Reactivity Index; EMQ = Empathy Questionnaire.  
<sup>a</sup>Positive values indicate boys scored higher than girls, negative values indicate girls scored higher than boys. \* $p < .05$ . \*\* $p < .01$ . \*\*\* $p < .001$ .



Table 3  
Coefficient Statistics for the Cross-Sectional Stepwise Regressions on Prosocial Behavior, Rebellious Behavior, and the Interaction Variable

Dependent variable Predictor	Prosocial <sup>a</sup>			Rebellious <sup>b</sup>			Prosocial × Rebellious <sup>c</sup>		
	<i>b</i>	<i>SE</i>	$\beta$	<i>b</i>	<i>SE</i>	$\beta$	<i>b</i>	<i>SE</i>	$\beta$
(Constant)	1.44**	0.56	—	1.35	0.41	—	3.52***	4.15	—
Age linear	−0.01	0.02	−.047	0.23***	0.02	.69	—	—	—
Age quadratic	−0.01	0.003	−.126	−0.02***	0.004	−.31	—	—	—
Gender	−0.43***	0.10	−.263	−0.02	0.12	−.009	—	—	—
BAS Fun seeking	0.05*	0.03	.123	0.14***	0.03	.22	1.25***	0.27	.30
IRI Perspective taking	0.04***	0.01	.203	—	—	—	0.31*	0.13	.16
EMQ Intention to comfort	0.45*	0.18	.155	—	—	—	—	—	—

Note. — = not applicable.

<sup>a</sup>Change statistic of adding behavioral variables above age and gender:  $\Delta R^2 = .014$ ,  $\Delta F(1, 249) = 4.690$ ,  $\Delta p = .031$ . <sup>b</sup>Change statistic of adding behavioral variables above age and gender:  $\Delta R^2 = .05$ ,  $\Delta F(1, 208) = 17.84$ ,  $\Delta p < .001$ . <sup>c</sup>Effects of age (linear and quadratic) and gender have been regressed out. Change statistic of final model:  $\Delta R^2 = .025$ ,  $\Delta F(1, 210) = 6.00$ ,  $\Delta p = .015$ . \* $p < .05$ . \*\* $p < .01$ . \*\*\* $p < .001$ .

extreme on both measures higher than participants who scored high on only one of the measures. Higher values indicate relatively more rebellious as well as more prosocial behavior (“prosocial risk-takers”), whereas lower values indicate relatively lower rebellious and prosocial behavior. We ran a stepwise regression with this interaction variable as the dependent variable and the behavioral predictors as independent variables. This interaction variable was predicted by BAS Fun Seeking and IRI Perspective Taking,  $R^2 = .122$ ,  $F(2, 210) = 14.59$ ,  $p < .001$ ; Fun Seeking  $b = 1.252$ ,  $SE = 0.272$ ,  $p < .001$ ; Perspective Taking:  $b = 0.312$ ,  $SE = 0.127$ ,  $p = .015$ ; see Table 3, with higher levels of Fun Seeking and Perspective Taking related to higher values of this combined variable.

These findings suggests that Fun Seeking positively relates to both Prosocial and Rebellious behavior. Note that partial correlations among Fun Seeking, Rebellious Behavior, and Prosocial behavior limited to a mid-to-late adolescent group (15–22 years) revealed similar findings as reported above (see Table S5).

Together, these cross-sectional findings set the stage for testing our hypotheses on longitudinal associations between these behavioral measures and Prosocial and Rebellious behavior. From these analyses, IRI Perspective Taking and BAS Fun Seeking appeared consistent predictors for prosocial and rebellious behavior. We therefore aimed to investigate whether these variables had longitudinal predictive value as well. Hence, we proceeded with these variables in the subsequent analyses.

### Longitudinal Predictions of Prosocial and Rebellious Behavior

Next, we predicted Prosocial behavior, Rebellious behavior, and the combined variable Prosocial × Rebellious from the longitudinal Perspective Taking and BAS Fun Seeking data. That is, we tested whether initial levels of Perspective Taking and BAS Fun Seeking (i.e., intercepts; see Methods for further specification) predicted variance above age (linear and quadratic) and gender. Next, we tested whether the rate of change in these variables (i.e., linear slopes) predicted additional variance above intercepts and age (linear and quadratic) and gender. Coefficients and significance levels of the predictors are presented in Table 4.

#### Prosocial Behavior

For prosocial behavior, we observed that BAS Fun Seeking intercept and Perspective Taking intercept predicted additional variance above age and gender, and additionally, that the slopes predicted additional variance above intercepts,  $R^2 = .23$ ,  $F(7, 251) = 10.69$ ,  $p < .001$ ; Fun Seeking intercept:  $b = 0.07$ ,  $SE = 0.032$ ,  $p = .045$ , Fun Seeking slope  $b = 0.23$ ,  $SE = 0.102$ ,  $p = .024$ ; Perspective Taking intercept:  $b = 0.06$ ,  $SE = 0.014$ ,  $p < .001$ , Perspective Taking slope:  $b = 0.07$ ,  $SE = 0.028$ ,  $p = .013$ . That is, greater longitudinal increases in BAS Fun Seeking and Perspective Taking predicted higher levels of prosocial behavior at T3, above initial levels of BAS Fun Seeking and Perspective Taking. When including Rebellious behavior in

Table 4

Coefficient Statistics for the Regressions With Longitudinal Predictors, on Prosocial and Rebellious Behavior and the Interaction Term Prosocial  $\times$  Rebellious

Predictor	Prosocial <sup>a</sup>			Rebellious <sup>b</sup>			Prosocial $\times$ Rebellious <sup>c</sup>		
	<i>b</i>	<i>SE</i>	$\beta$	<i>b</i>	<i>SE</i>	$\beta$	<i>b</i>	<i>SE</i>	$\beta$
(Constant)	2.30***	0.49	—	-0.06	0.65	—	2.53	5.06	—
Age linear	-0.01	0.02	-.05	0.24***	0.02	.69	—	—	—
Age quadratic	-0.006*	0.003	-.14	-0.02***	0.004	-.31	—	—	—
Gender	-0.48***	0.09	-.30	-0.05	0.13	-.022	—	—	—
Fun Seeking intercept	0.07*	0.03	.15	0.17***	0.04	.27	1.37***	0.36	.34
Fun Seeking slope	0.23*	0.10	.17	0.60***	0.14	.31	5.07***	1.13	.40
Perspective Taking intercept	0.06***	0.01	.27	-0.005	0.019	-.02	0.30*	0.15	.15
Perspective Taking slope	0.07*	0.03	.16	0.03	0.04	.05	0.50	0.30	.12

Note. — = not applicable.

<sup>a</sup>Change statistic of adding slopes above intercepts:  $\Delta R^2 = .04$ ,  $\Delta F(2, 251) = 5.86$ ,  $\Delta p = .003$ . <sup>b</sup>Change statistic of adding slopes above intercepts:  $\Delta R^2 = .05$ ,  $\Delta F(2, 202) = 9.84$ ,  $\Delta p < .001$ . <sup>c</sup>Change statistic of adding slopes above intercepts:  $\Delta R^2 = .10$ ,  $\Delta F(2, 205) = 11.91$ ,  $\Delta p < .001$ . \* $p < .05$ . \*\* $p < .01$ . \*\*\* $p < .001$ .

the model, the effects of BAS Fun Seeking intercept and slope were no longer significant (intercept:  $p = .25$ , slope:  $p = .12$ , not depicted in Table 4).

#### Rebellious Behavior

For Rebellious behavior, we observed that greater increases in BAS Fun Seeking were related to higher levels of Rebellious behavior at T3, above initial levels of BAS Fun Seeking and age and gender,  $R^2 = .47$ ,  $F(7, 202) = 25.94$ ,  $p < .001$ ; intercept:  $b = 0.17$ ,  $SE = 0.043$ ,  $p < .001$ , slope:  $b = 0.60$ ,  $SE = 0.138$ ,  $p < .001$ . No effects of Perspective Taking were observed. When including Prosocial behavior in the model, these findings remained significant.

#### Prosocial $\times$ Rebellious Behavior

Finally, we tested whether the intercepts and slopes of Fun Seeking and Perspective Taking predicted the interaction variable Prosocial  $\times$  Rebellious. Here, the model with intercepts only was not significant ( $p = .088$ ), but adding slopes revealed a significant effect of Fun Seeking intercept ( $b = 1.37$ ,  $SE = 0.36$ ,  $p < .001$ ) Fun Seeking slope ( $b = 5.07$ ,  $SE = 1.125$ ,  $p < .001$ ), a small effect of Perspective Taking intercept ( $b = 0.30$ ,  $SE = 0.15$ ,  $p = .038$ ), but no significant effect of Perspective Taking slope ( $p = .10$ ).

#### Longitudinal Predictions of Prosocial and Rebellious Behavior: Behavior and Brain

Finally, we tested whether development of brain structures predicted Prosocial and Rebellious

behavior at T3. That is, we reran the behavioral longitudinal analyses on Prosocial and Rebellious behavior, and added intercepts and slopes of NACC and MPFC above the behavioral predictors. Only for Rebellious behavior did we observe a small but significant effect of MPFC slope above the behavioral predictors,  $R^2 = .48$ ,  $F(11, 170) = 14.23$ ,  $p < .001$ ,  $\Delta R^2 = .02$ ,  $\Delta F(2, 170) = 2.96$ ,  $\Delta p = .055$ ;  $b = -.001$ ,  $SE = 0.000$ ,  $\beta = -.16$ ,  $p = .023$ , indicating that greater reductions in MPFC volume were associated with lower levels of rebellious behavior at T3. When including Prosocial behavior in the regression model, this effect remained significant. Finally, the regressions on Prosocial behavior and the interaction variable yielded no significant findings.

Finally, an alternative approach is to test whether brain volume changes support improved Perspective Taking and/or Fun Seeking, which in turn predict Prosocial and Rebellious behavior. To this end we tested models in which we added the brain measures (intercepts and slopes) before adding the behavioral predictors (intercepts and slopes). These analyses revealed highly similar results and thus confirmed all our prior findings.

## Discussion

This study set out to test the behavioral and neural predictors leading to prosocial and risk-taking behaviors in adolescents and young adults using a three-wave longitudinal design. The results showed three main conclusions. First, prosocial and rebellious behavior were positively correlated. Second,

perspective taking and intention to comfort uniquely predicted more prosocial behavior. However, current levels, as well as longitudinal change, in fun seeking behavior were positive predictors of both prosocial and rebellious behavior. Finally, these findings co-occurred with pronounced decreases in volumes of the nucleus accumbens and MPFC, of which greater declines in MPFC predicted less rebellious behavior. These findings are interpreted in the context of current conceptualizations of adolescent development as a period of both risks and opportunities (Crone & Dahl, 2012; Do et al., 2017), and the need to better understand individual differences in developmental trajectories in behavioral and brain development to predict developmental outcomes (Foulkes & Blakemore, 2018).

#### *Developmental Trajectories*

What predicts who will become prosocially oriented and who will show rebellious behavior? In this study we tested this question using occurrences of prosocial and rebellious behaviors as outcome measures. First we investigated the developmental patterns of these measures. Consistent with prior work showing that risk-taking behavior increases and peaks during adolescence (Gullone et al., 2000; Steinberg, 2007), we found that rebelliousness similarly increases from early adolescence to late adolescence before declining into adulthood. Research on the development of prosocial behavior however is mixed (for an overview, see Do et al., 2017). We observed a quadratic effect of age on a broad measure of prosocial behavior, peaking in mid-to-late adolescence, suggesting that, like rebelliousness, prosocial development follows a nonlinear age pattern that converges during late adolescence, although future studies should test if different age patterns are observed for different domains within prosocial behavior (such as helping and donating behavior). Our findings converge on the hypothesis that the development of rebellious and prosocial tendencies peak during late adolescence relative to earlier or later ages (Do et al., 2017), thus highlighting late adolescence as both a window of vulnerability and opportunity.

Next we observed that the seemingly paradoxical measures prosocial and rebellious behavior were in fact positively correlated (even when controlling for age), suggesting that the same developmental processes may result in both types of behaviors (Schriber & Guyer, 2015). Therefore, in addition to examining the dichotomy of rebellious and

prosocial behavior, we aimed to examine individuals who are characterized by similar levels of both rebellious and prosocial tendencies. Indeed, cross-sectionally, we observed that higher levels of fun seeking were related to both more prosocial and more rebellious behaviors, as well as their interaction. Previous studies already reported relations between approach tendencies and greater risk taking (Steinberg, 2007), but this study demonstrated that the same fun seeking tendencies may also be related to prosocial tendencies, and the combination of prosocial and rebellious behaviors. These findings fit with the hypothesis that adolescent development may be a tipping point for how interacting social-affective systems may influence trajectories of development (Crone & Dahl, 2012; Schriber & Guyer, 2015).

Finally, in these cross-sectional analyses we examined associations between prosocial and rebellious behavior and indices of social functioning: perspective taking (the development of this longitudinal predictor is discussed below) and intention to comfort. Intention to comfort was measured at the final wave in ages 12–30 and showed no significant age effects, suggesting that this trait remains stable across adolescence. This echoes prior work with 10- to 16-year-olds in which limited age effects were observed in boys and none in girls (Overgaauw, Guroglu, Rieffe, & Crone, 2014). Consistent with prior studies, we found that higher levels of intention to comfort and social perspective taking at the final wave were uniquely related to more prosocial behavior, but these measures were not related to rebellious behavior. The relations among empathic tendencies, perspective taking, and prosocial behaviors have been well documented (Eisenberg, 2000; Overgaauw et al., 2014; Tamnes et al., 2018), and previous studies also reported relations between emotionality and prosocial behavior (Eisenberg et al., 1994).

From our longitudinal analyses, we observed that prosocial and rebellious behavior were not only predicted by initial levels of perspective taking and fun seeking (i.e., intercepts) but also the change over time (i.e., linear slopes). Consistent with previous longitudinal studies, we observed that IRI perspective taking and BAS Fun Seeking emerged in adolescence, following a cubic increasing developmental slope (Hawk et al., 2013; Urosevic et al., 2012; see also Schreuders et al., 2018). In particular, those individuals who showed the greatest increase in perspective taking and fun seeking during adolescent development showed more prosocial

behavior at the final measurement. In addition, individuals who showed the largest increase in fun seeking during adolescent development showed more rebellious behavior at the final measurement. The common contribution of fun seeking to both prosocial and rebellious behavior suggests that developmental increases in this fun seeking tendency may be a differential susceptibility marker in adolescence that may contribute to different types of behaviors (Do et al., 2017; Schriber & Guyer, 2015; Telzer, 2016). That is, specifically the tendency to approach a possibly rewarding event in the spur of the moment, may lead individuals to develop prosocial behaviors in some instances, whereas in other instances it may lead individuals to develop rebellious behaviors. Finally, these findings are consistent with the suggestion that change measures are informative for detecting development (Crone & Elzinga, 2015).

An important question was the extent to which these predictors were specific for individuals displaying mostly prosocial or rebellious behaviors. Previous studies have mainly focused on the development of either prosocial development or risk-taking development, but this may have led to an oversight of individuals who develop these behaviors in parallel. The analyses that examined rebellious behavior controlling for prosocial behaviors showed that fun seeking was a consistent factor in predicting rebellious outcomes. However, when examining the relation between prosocial behavior while controlling for rebellious behavior, the relation with fun seeking was no longer significant, suggesting that some of this variation was driven by rebellious individuals. Yet, change in fun seeking did predict the combined variable of high prosocial and high rebellious behavior, suggesting that this particular change may be predictive for individuals who may be conceived as “prosocial risk takers” (Do et al., 2017). Together, these findings tentatively support the view of a differential susceptibility marker (fun seeking) that may predict developmental outcomes in the domains of prosocial and rebellious behaviors (Do et al., 2017), although more research is needed to confirm these findings. For instance, a way to more formally study predictive factors of subgroups of prosocial risk takers is to actually identify subgroups of participants who display different combinations of prosocial and rebellious behavior, using a latent profile analysis, and use membership to these subgroups as an outcome variable. This approach may be a useful addition to future studies including larger samples.

### *Brain Development and the Relation With Developmental Outcomes*

Previous studies have consistently reported that brain regions that are important for approach behaviors and social functioning show pronounced changes in gray matter volume (Mills, Goddings, Clasen, Giedd, & Blakemore, 2014; Mills, Lalonde, et al., 2014). We previously reported a developmental decline in NACC volume in participants included in the current data set (Wierenga et al., 2018). This study further confirmed a similar decline in volume of MPFC, consistent with previous studies (Mills, Lalonde, et al., 2014), and extended this to three subregions in the MPFC (superior frontal, rostral anterior cingulate, and caudal anterior cingulate, reported in Supporting Information). Previous studies have demonstrated the importance to distinguish between subregions in the MPFC (Pfeifer & Peake, 2012). Here, we demonstrated that all three subregions of the MPFC showed cubic developmental patterns with relatively rapid decline during mid to late adolescence. The results are comparable to previous studies that have demonstrated gray matter volume declines in prefrontal and parietal cortex across several adolescent samples from multiple sites (including the current sample; Tamnes et al., 2017).

The question of how individual patterns of brain development predicted occurrences of prosocial and rebellious behaviors was addressed by adding NACC and MPFC volume intercepts and slopes to the regression models. Only MPFC slope was related to the behavioral outcome measures, such that greater decreases in MPFC were negatively related to rebellious behavior. More specifically, stronger declines in volume, or faster maturation, was related to lower levels of rebellious behavior at the final measurement wave. This finding fits well with prior functional neuroimaging studies. For instance, MPFC functional activation has consistently been found during high-risk decision making, and with reward outcome processing following risky decisions during adolescence (Blankenstein et al., 2018; Van Leijenhorst et al., 2010). However, even though statistically significant, the effect was modest. It is currently unclear if this has predictive value, and future studies should confirm if this relation also exists in other samples. Furthermore, adding brain volume measures to the model after controlling for age, gender, perspective taking, and fun seeking intercepts and slopes possibly accounted for little additional variance (although adding brain volume measures before the

behavioral predictors resulted in similar findings). In future studies it will be important to test these relations in new samples, but the current findings provide an important starting point for a possible role of the MPFC in these processes.

It was unexpected that relations were only observed for MPFC and not for NACC. Prior studies found relations between NACC volume and behavioral approach measures, such that adolescents with greater baseline NACC volumes showed more behavioral approach tendencies over time (Urosevic et al., 2012). Functional activation in the NACC is also consistently observed as an important marker for reward reactivity in studies examining experimental and self-reported risk-taking behaviors as well as prosocial behaviors (Telzer, Fuligni, Lieberman, & Galvan, 2014). Future studies may also complement these findings with functional MRI measures specifically targeting prosocial and rebellious behaviors, in addition to longitudinal structural MRI measures in relation to self-report measures. For example, recent reviews show that especially for subcortical brain regions, functional activation is more state dependent (Herting, Gautam, Chen, Mezher, & Vetter, 2017), whereas studying volume changes over time does not capture these moment-to-moment fluctuations. Future research could examine more daily fluctuations in brain responses to fun seeking and perspective taking contexts, and test the relation with prosocial and rebellious outcomes as measured with self-report and experimental measures. In addition, it has been found that greater functional connectivity between ventral striatum, and the MPFC is heightened under different conditions of social evaluation, which may promote motivated social behavior (Bault, Joffily, Rustichini, & Coricelli, 2011; Somerville et al., 2013). An interesting next step is to relate longitudinal changes in functional connectivity of subcortical and cortical brain regions to longitudinal changes in prosocial and risk-taking behaviors.

#### *Limitations and Future Directions*

This study has several strengths, including a longitudinal design with three waves spanning ages 8–29 years, relatively large sample sizes, and the inclusion of behavior and brain measures. The age coverage in this study is more extended than in previous adolescent research, which is important when focusing on developmental outcomes. However, the study also has several limitations and open questions that should be addressed in future research. First, not all measurements were available at each time point.

Specifically, the intention to comfort questionnaire was only available at the final wave and IRI perspective taking was only available at the second and final wave for the majority of participants. The greater contribution of BAS fun seeking may therefore be related to more measurement waves (available at all waves). Relatedly, an interesting avenue for future research is to relate longitudinal changes in the predictor variables to changes in prosocial and rebellious behavior, which in this study were assessed at the final wave only. Second, this study made use of self-report measures, because previous studies showed that these have more stability than experimental tasks. The selection of measures in this study all had sufficient reliability and intraclass correlations values, increasing the strength of the results. However, although the items assessing prosocial behavior covered a broad range of prosocial actions such as helping, giving, altruistic tendencies, and providing emotional support, the items measuring risk taking (i.e., rebellious behavior) covered risky behaviors that may often occur within a social context (e.g., getting drunk). Given that risk taking is a multifaceted construct (Peper et al., 2018) and may differ across social, financial, and health-safety domains (van Duijvenvoorde et al., 2017), future studies may test whether similar findings can be observed across domains. Relatedly, questionnaires do not capture the variations in behavior under different experimental contexts and may be sensitive to social desirability, and may not show measurement invariance across age. Therefore, an important avenue for future research is to develop experiments with good test-retest reliability, which assess prosocial and rebellious behaviors, and possibly test the specific role of fun seeking tendencies in these dynamic situations. Recent work on measurement invariance of the BIS/BAS questionnaire from 6- to 45-years-old showed that the Fun seeking scale of the BIS/BAS questionnaire had inconsistent factor loadings (Pagliaccio et al., 2008). Although Fun Seeking at least had comparable internal consistency across age in the current sample (see Supporting Information), this highlights the importance of replicating our finding of fun seeking as a common predictor of both prosocial and rebellious behavior, using both self-report *and* experimental measures. Third, in our analyses on contributions to prosocial and rebellious behavior we controlled for age (linear and quadratic) but did not examine age-specific associations. Future research, preferable using larger sample sizes, may further unravel whether our findings are specific to or differentially pronounced in different phases of adolescence and across boys and

girls. Nonetheless, the finding that fun seeking related to both prosocial and rebellious behavior was confirmed in a sample of mid-to-late adolescents (15–22 years; reported in Supporting Information). Although outside the scope of this study, future work may further test whether age moderates any of the observed associations. Finally, there was no assessment of environmental influences on behavioral outcomes. This is an important next step for a test of developmental susceptibility, to examine if the same sensitivity can lead to multiple developmental outcomes, depending on how environmental influences interact with sensitivity measures.

### Conclusions and Broader Implications

This study tested the association between prosocial and rebellious behavior, and developmental pathways leading to these behaviors, in adolescent development. The results confirmed that seemingly paradoxical prosocial and rebellious behavior are positively associated, and show an important contribution of fun seeking to these behavioral outcomes, where both current levels, as well as longitudinal changes, predicted these outcomes. These findings suggest that fun seeking may be a differential susceptibility marker for diverse adolescent outcomes (Do et al., 2017; Schriber & Guyer, 2015; Telzer, 2016). Furthermore, there was preliminary evidence that faster adolescent brain development (i.e., faster maturity), specifically of the MPFC, predicted less rebellious behavior, contributing to the current question how structural brain development relates to adolescent behaviors (Foulkes & Blakemore, 2018). These findings point toward a more differentiated perspective on adolescent development, where similar sensitivity markers may lead to multiple developmental outcomes.

### References

- Bault, N., Joffily, M., Rustichini, A., & Coricelli, G. (2011). Medial prefrontal cortex and striatum mediate the influence of social comparison on the decision process. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 16044–16049. <https://doi.org/10.1073/pnas.1100892108>
- Becht, A. I., Bos, M. G., Nelemans, S. A., Peters, S., Vollebergh, W. A., Branje, S. J., . . . Crone, E. A. (2018). Goal-directed correlates and neurobiological underpinnings of adolescent identity: A multimethod multisample longitudinal approach. *Child Development*, *89*, 823–836. <https://doi.org/10.1111/cdev.13048>
- Blakemore, S. J. (2008). The social brain in adolescence. *Nature Reviews Neuroscience*, *9*, 267. <https://doi.org/10.1038/nrn2353>
- 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., Schreuders, E., Peper, J. S., Crone, E. A., & van Duijvenvoorde, A. C. K. (2018). Individual differences in risk-taking tendencies modulate the neural processing of risky and ambiguous decision-making in adolescence. *NeuroImage*, *172*, 663–673. <https://doi.org/10.1016/j.neuroimage.2018.01.085>
- Bos, M. G., Peters, S., van de Kamp, F. C., Crone, E. A., & Tamnes, C. K. (2018). Emerging depression in adolescence coincides with accelerated frontal cortical thinning. *Journal of Child Psychology and Psychiatry*, *59*, 994–1002. <https://doi.org/10.1111/jcpp.12895>
- 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*, 417–426. <https://doi.org/10.1093/scan/nsw136>
- Braams, B. R., van Duijvenvoorde, A. C., Peper, J. S., & Crone, E. A. (2015). Longitudinal changes in adolescent risk-taking: A comprehensive study of neural responses to rewards, pubertal development, and risk-taking behavior. *Journal of Neuroscience*, *35*(18), 7226–7238. <https://doi.org/10.1523/JNEUROSCI.4764-14.2015>
- Braams, B. R., Peper, J. S., van der Heide, D., Peters, S., & Crone, E. A. (2016). Nucleus accumbens response to rewards and testosterone levels are related to alcohol use in adolescents and young adults. *Developmental Cognitive Neuroscience*, *17*, 83–93. <https://doi.org/10.1016/j.dcn.2015.12.014>
- Burnett, S., Bault, N., Coricelli, G., & Blakemore, S. J. (2010). Adolescents' heightened risk-seeking in a probabilistic gambling task. *Cognitive Development*, *25*, 183–196. <https://doi.org/10.1016/j.cogdev.2009.11.003>
- Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS scales. *Journal of Personality and Social Psychology*, *67*, 319. <https://doi.org/10.1037/0022-3514.67.2.319>
- Crone, E. A., & Dahl, R. E. (2012). Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nature Reviews Neuroscience*, *13*, 636–650. <https://doi.org/10.1038/nrn3313>
- Crone, E. A., & Elzinga, B. M. (2015). Changing brains: How longitudinal functional magnetic resonance imaging studies can inform us about cognitive and social-affective growth trajectories. *Wiley Interdisciplinary Reviews: Cognitive Science*, *6*(1), 53–63. <https://doi.org/10.1002/wcs.1327>
- Dahl, R. E. (2004). Adolescent brain development: A period of vulnerabilities and opportunities. Keynote address. *Annals of the New York Academy of Sciences*, *1021*, 1–22. <https://doi.org/10.1196/annals.1308.001>

- Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology, 44*, 113. <https://doi.org/10.1037/0022-3514.44.1.113>
- Defoe, I. N., Dubas, J. S., Figner, B., & van Aken, M. A. (2015). A meta-analysis on age differences in risky decision making: Adolescents versus children and adults. *Psychological Bulletin, 141*(1), 48–84. <https://doi.org/10.1037/a0038088>
- 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>
- Dumontheil, I., Apperly, I. A., & Blakemore, S. J. (2010). Online usage of theory of mind continues to develop in late adolescence. *Developmental Science, 13*, 331–338. <https://doi.org/10.1111/j.1467-7687.2009.00888.x>
- Eisenberg, N. (2000). Emotion, regulation, and moral development. *Annual Review of Psychology, 51*, 665–697. <https://doi.org/10.1146/annurev.psych.51.1.665>
- Eisenberg, N., Fabes, R. A., Murphy, B., Karbon, M., Maszk, P., Smith, M., . . . Suh, K. (1994). The relations of emotionality and regulation to dispositional and situational empathy-related responding. *Journal of Personality and Social Psychology, 66*, 776–797. <https://doi.org/10.1037/0022-3514.66.4.776>
- Foulkes, L., & Blakemore, S. J. (2018). Studying individual differences in human adolescent brain development. *Nature Neuroscience, 21*, 315–323. <https://doi.org/10.1038/s41593-018-0078-4>
- Gardner, M., & Steinberg, L. (2005). Peer influence on risk taking, risk preference, and risky decision making in adolescence and adulthood: An experimental study. *Developmental Psychology, 41*, 625–635. <https://doi.org/10.1037/0012-1649.41.4.625>
- 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>
- Gullone, E., Moore, S., Moss, S., & Boyd, C. (2000). The Adolescent Risk-Taking Questionnaire: Development and psychometric evaluation. *Journal of Adolescent Research, 15*, 231–250. <https://doi.org/10.1177/0743558400152003>
- 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>
- Hall, G. S. (1904). *Adolescence: Its psychology and its relation to physiology, anthropology, sociology, sex, crime, religion, and education*. Prentice-Hall, NJ: Englewood Cliffs.
- Hawk, S. T., Keijsers, L., Branje, S. J., Graaff, J. V., Wied, M., & Meeus, W. (2013). Examining the Interpersonal Reactivity Index (IRI) among early and late adolescents and their mothers. *Journal of Personality Assessment, 95*, 96–106. <https://doi.org/10.1080/00223891.2012.696080>
- Herting, M. M., Gautam, P., Chen, Z., Mezher, A., & Vetter, N. C. (2017). Test–retest reliability of longitudinal task-based fMRI: Implications for developmental studies. *Developmental Cognitive Neuroscience, 33*, 17–26. <https://doi.org/10.1016/j.dcn.2017.07.001>
- Herting, M. M., Johnson, C., Mills, K. L., Vijayakumar, N., Dennison, M., Liu, C., . . . Tamnes, C. K. (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>
- Humphrey, G., & Dumontheil, I. (2016). Development of risk-taking, perspective-taking, and inhibitory control during adolescence. *Developmental Neuropsychology, 41* (1–2), 59–76. <https://doi.org/10.1080/87565641.2016.1161764>
- Huttenlocher, P. R. (1990). Morphometric study of human cerebral cortex development. *Neuropsychologia, 28*, 517–527. [https://doi.org/10.1016/0028-3932\(90\)90031-I](https://doi.org/10.1016/0028-3932(90)90031-I)
- Klein, A., & Tourville, J. (2012). 101 labeled brain images and a consistent human cortical labeling protocol. *Frontiers in Neuroscience, 6*, 171. <https://doi.org/10.3389/fnins.2012.00171>
- Knoll, L. J., Magis-Weinberg, L., Speekenbrink, M., & Blakemore, S. J. (2015). Social influence on risk perception during adolescence. *Psychological Science, 26*, 583–592. <https://doi.org/10.1177/0956797615569578>
- 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. <https://doi.org/10.1159/000362328>
- Mills, K. L., Lalonde, F., Clasen, L. S., Giedd, J. N., & Blakemore, S. J. (2014). Developmental changes in the structure of the social brain in late childhood and adolescence. *Social Cognitive and Affective Neuroscience, 9*, 123–131. <https://doi.org/10.1093/scan/nss113>
- Mills, K. L., & Tamnes, C. K. (2014). Methods and considerations for longitudinal structural brain imaging analysis across development. *Developmental Cognitive Neuroscience, 9*, 172–190. <https://doi.org/10.1016/j.dcn.2014.04.004>
- Overgaauw, S., Guroglu, B., Rieffe, C., & Crone, E. A. (2014). Behavior and neural correlates of empathy in adolescents. *Developmental Neuroscience, 36*, 210–219. <https://doi.org/10.1159/000363318>
- Overgaauw, S., Rieffe, C., Broekhof, E., Crone, E. A., & Guroglu, B. (2017). Assessing empathy across childhood and adolescence: Validation of the Empathy Questionnaire for Children and Adolescents (EmQueCA). *Frontiers in Psychology, 8*, 870. <https://doi.org/10.3389/fpsyg.2017.00870>
- Pagliaccio, D., Luking, K. R., Anokhin, A. P., Gotlib, I. H., Hayden, E. P., Olino, T. M., . . . Barch, D. M. (2008). Revising the BIS/BAS Scale to study development:

- Measurement invariance and normative effects of age and sex from childhood through adulthood. *Psychological Assessment*, 28(4), 429. <https://doi.org/10.1111/j.1542-474X.2008.00219.x>
- Peper, J. S., Braams, B. R., Blankenstein, N. E., Bos, M. G., & Crone, E. A. (2018). Development of multifaceted risk taking and the relations to sex steroid hormones: A longitudinal study. *Child Development*, 89, 1887–1907. <https://doi.org/10.1111/cdev.13063>
- Peters, S., & Crone, E. A. (2017). Increased striatal activity in adolescence benefits learning. *Nature Communications*, 8(1), 1983. <https://doi.org/10.1038/s41467-017-02174-z>
- Pfeifer, J. H., & Peake, S. J. (2012). Self-development: Integrating cognitive, socioemotional, and neuroimaging perspectives. *Developmental Cognitive Neuroscience*, 2(1), 55–69. <https://doi.org/10.1016/j.dcn.2011.07.012>
- Qu, Y., Galvan, A., Fuligni, A. J., Lieberman, M. D., & Telzer, E. H. (2015). Longitudinal changes in prefrontal cortex activation underlie declines in adolescent risk taking. *Journal of Neuroscience*, 35, 11308–11314. <https://doi.org/10.1523/jneurosci.1553-15.2015>
- Schreuders, E., Braams, B. R., Blankenstein, N. E., Peper, J. S., Güroğlu, B., & Crone, E. A. (2018). Contributions of reward sensitivity to ventral striatum activity across adolescence and early adulthood. *Child Development*, 89, 797–810. <https://doi.org/10.1111/cdev.13056>
- Schriber, R. A., & Guyer, A. E. (2015). Adolescent neurobiological susceptibility to social context. *Developmental Cognitive Neuroscience*, 19, 1–18. <https://doi.org/10.1016/j.dcn.2015.12.009>
- Sescousse, G., Caldú, X., Segura, B., & Dreher, J.-C. (2013). Processing of primary and secondary rewards: A quantitative meta-analysis and review of human functional neuroimaging studies. *Neuroscience & Biobehavioral Reviews*, 37, 681–696. <https://doi.org/10.1016/j.neubiorev.2013.02.002>
- Somerville, L. H., Jones, R. M., Ruberry, E. J., Dyke, J. P., Glover, G., & Casey, B. J. (2013). The medial prefrontal cortex and the emergence of self-conscious emotion in adolescence. *Psychological Science*, 24, 1554–1562. <https://doi.org/10.1177/0956797613475633>
- Steinberg, L. (2007). Risk taking in adolescence new perspectives from brain and behavioral science. *Current Directions in Psychological Science*, 16, 55–59. <https://doi.org/10.1111/j.1467-8721.2007.00475.x>
- Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review*, 28, 78–106. <https://doi.org/10.1016/j.dr.2007.08.002>
- Tamnes, C. K., Herting, M. M., Goddings, A. L., Meuwese, R., Blakemore, S. J., Dahl, R. E., . . . Mills, K. L. (2017). Development of the cerebral cortex across adolescence: A multisample study of inter-related longitudinal changes in cortical volume, surface area, and thickness. *Journal of Neuroscience*, 37, 3402–3412. <https://doi.org/10.1523/JNEUROSCI.3302-16.2017>
- Tamnes, C. K., Overbye, K., Ferschmann, L., Fjell, A. M., Walhovd, K. B., Blakemore, S.-J., & Dumontheil, I. (2018). Social perspective taking is associated with self-reported prosocial behavior and regional cortical thickness across adolescence. *Developmental Psychology*, 54, 1745–1757. <https://doi.org/10.1037/dev0000541>
- 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. <https://doi.org/10.1016/j.dcn.2015.10.010>
- 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, 6600–6605. <https://doi.org/10.1073/pnas.1323014111>
- 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, 508–518. <https://doi.org/10.1080/17470911003687913>
- Thijssen, S., Wildeboer, A., Muetzel, R. L., Bakermans-Kranenburg, M. J., El Marroun, H., Hofman, A., . . . White, T. (2015). Cortical thickness and prosocial behavior in school-age children: A population-based MRI study. *Social Neuroscience*, 10, 571–582. <https://doi.org/10.1080/17470919.2015.1014063>
- Urosevic, S., Collins, P., Muetzel, R., Lim, K., & Luciana, M. (2012). Longitudinal changes in behavioral approach system sensitivity and brain structures involved in reward processing during adolescence. *Developmental Psychology*, 48, 1488–1500. <https://doi.org/10.1037/a0027502>
- van Duijvenvoorde, A. C. K., Blankenstein, N. E., Crone, E. A., & Figner, B. (2017). Towards a better understanding of adolescent risk taking: Contextual moderators and model-based analysis. In M. E. Toplak & J. A. Weller (Eds.), *Individual differences in judgment and decision-making: A developmental perspective* (pp. 8–27). New York, NY: Psychology Press.
- Van Duijvenvoorde, A. C. K., Huizenga, H. M., Somerville, L. H., Delgado, M. R., Powers, A., Weeda, W. D., . . . Figner, B. (2015). Neural correlates of expected risks and returns in risky choice across development. *Journal of Neuroscience*, 35, 1549–1560. <https://doi.org/10.1523/JNEUROSCI.1924-14.2015>
- Van Duijvenvoorde, A. C., Peters, S., Braams, B. R., & Crone, E. A. (2016). What motivates adolescents? Neural responses to rewards and their influence on adolescents' risk taking, learning, and cognitive control. *Neuroscience & Biobehavioral Reviews*, 70, 135–147. <https://doi.org/10.1016/j.neubiorev.2016.06.037>
- Van Hoorn, J., Van Dijk, E., Güroğlu, B., & Crone, E. A. (2016). Neural correlates of prosocial peer influence on public goods game donations during adolescence. *Social*



- Cognitive and Affective Neuroscience*, 11, 923–933. <https://doi.org/10.1093/scan/nsw013>
- 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, 345–355. <https://doi.org/10.1016/j.neuroimage.2010.02.038>
- Varnum, M. E., Shi, Z., Chen, A., Qiu, J., & Han, S. (2014). When "your" reward is the same as "my" reward: Self-construal priming shifts neural responses to own vs. friends' rewards. *NeuroImage*, 87, 164–169. <https://doi.org/10.1016/j.neuroimage.2013.10.042>
- Wierenga, L. M., Bos, M. G. N., Schreuders, E., Vd Kamp, F., Peper, J. S., Tammes, C. K., & Crone, E. A. (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>
- Wildeboer, A., Thijssen, S., Muetzel, R. L., Bakermans-Kranenburg, M. J., Tiemeier, H., White, T., & van IJzendoorn, M. H. (2017). Neuroanatomical correlates of donating behavior in middle childhood. *Social Neuroscience*, 13, 541–552. <https://doi.org/10.1080/17470919.2017.1361864>

### Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's website:

**Appendix S1.** Supporting Information