Risky business? Behavioral and neural mechanisms underlying risky decision-making in adolescents

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Chapter 6

Behavioral and neural pathways supporting the development of prosocial and risk-taking behavior across adolescence

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Abstract

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 three). First, prosocial and rebellious behavior assessed at wave three were positively correlated. Perspective taking and empathy 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) was related to less rebellious behavior. These findings point towards a possible differential susceptibility marker, fun seeking, as a predictor of both prosocial and rebellious developmental outcomes.

Key words: prosocial, risk-taking, brain, adolescence, longitudinal

Introduction

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, 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 (Burnett, Bault, Coricelli, & Blakemore, 2010; Defoe, Dubas, Figner, & van Aken, 2015), which is 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 towards 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). While 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, & Galvan, 2013). Therefore, a critical question concerns whether risk-taking 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; Telzer, 2016; van Duijvenvoorde, Peters, Braams, & Crone, 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 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 activity in 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 a subgroup of 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 perspective taking and empathic concern (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, activation in the medial prefrontal cortex (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, empathy increases across age (10-15 years) in girls, and declines in boys, and specifically the empathic intention to comfort others 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 empathy 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 behaviors 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. Structural brain development, which follows the most consistent within-individual patterns of change, has been associated with a number of developmental outcomes such as identity formation (Becht et al., 2018) but 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 correlated with 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, the medial prefrontal cortex (MPFC) 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 linked this region to choice valuation and reward outcome processing of risky 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 empathy, the structural development of brain regions related to these processes (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. 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 (reflecting a subgroup of '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. Given that both traits have previously been related to age and gender, these factors were included and controlled for in the analyses, given that 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 BAS-subscales of the 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 (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 between 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. Therefore, longitudinal measurements are crucial to examine whether trajectories of change are predictive for developmental outcome measures. Because our variable of empathy 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 medial prefrontal cortex 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 risk-taking and prosocial outcomes above the behavioral indices (Foulkes & Blakemore, 2018).

Methods

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). 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 the current 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 (Gullone et al., 2000). This scale assesses the frequency with which individuals displayed risky behaviors such as 'Staying out late', and 'Getting drunk, with 5 items (α = .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 (α = .924) assessing the frequency of prosocial actions towards 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 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 Behavioral Inhibition / Behavioral Activation questionnaire (BIS/BAS; Carver & White, 1994) to obtain indices of participants' approach behavior. BAS

Table 1. **Number of observations per time point, and intraclass correlations (ICC) with 95% confidence intervals (CI).**

	N (female)			ICC T1, T2, T3 (95% CI)
Variable	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)

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, α_{T3} = .725; four items), Fun seeking (the desire for rewards and the willingness to approach rewards; α_{T3} = .546; four items), and Reward Responsiveness (the response to rewards and reward anticipation; α_{T3} = .609; five items). Participants indicated on a four-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 Interpersonal Reactivity Index (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

(α_{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 for Children and Adolescents (EmQue-CA; (Overgaauw et al., 2017). This subscale includes five items (α = .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 three-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’.

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., Mills & Tamnes, 2014; Becht et al., 2018). Scans of poor quality were excluded, and high quality scans were reprocessed though 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, & Tamnes, 2018; 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 was 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 the supplements 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, while 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 the supplementary materials an elaborate description of these results is provided.

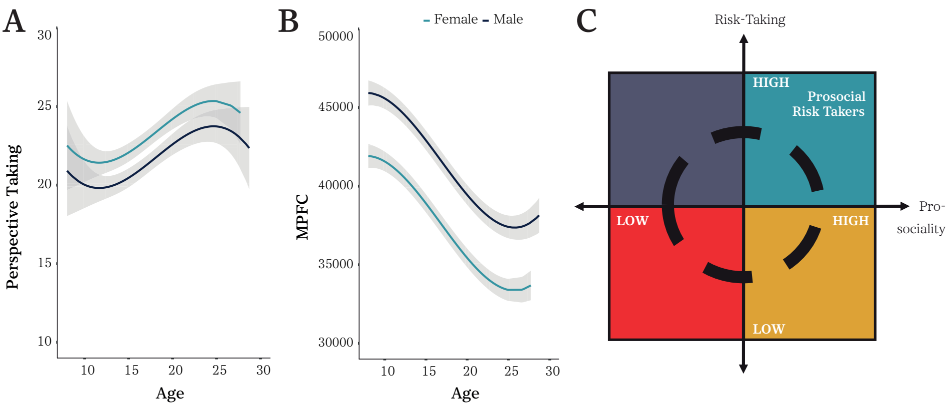

Figure 1. *Developmental trajectories of Perspective Taking* ***(A)*** *and Medial prefrontal cortex* ***(B),*** *in cubic millimeters. Light blue lines indicate females, dark blue lines indicate males, and grey areas mark the 95% confidence interval. Developmental trajectories of BAS scales and NACC are described in Schreuders et al. (2018) and Wierenga et al. (2018), respectively.* ***C.*** *Theoretical model depicting the intersection between risk-taking and prosocial tendencies. Adapted (with permission) from Do et al., 2017.*

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 and gender. Second, in our cross-sectional analyses (data from the final wave), we tested which predictors (i.e., empathy, 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 1C) and vice versa (i.e., upper left and lower left quadrant). In addition, to test if and which predictors best described a combination of prosocial and rebellious behavior we created a combined 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).

Results

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 and gender. A partial correlation showed that these outcome measures were positively correlated (*partial* $r = .259$, $p < .001$; see Figure 2). 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 and Gender were always included in the model to control for their effects. Table 2 depicts the correlations between the outcome measures (rebellious and prosocial behavior) and the behavioral predictors at T3, controlled for age and gender.

Table 2. Partial correlations between behavioral variables at T3, controlled for age (linear) and gender.

		1	2	3	4	5	6	7
1	Rebellious behavior	-						
2	Prosocial behavior	.259***	-					
3	BAS Drive	.119	.115	-				
4	BAS Fun Seeking	.318***	.175**	.468***	-			
5	BAS Reward Responsiveness	.084	.133*	.378***	.321***	-		
6	IRI Perspective Taking	.097	.261***	.037	.050	.097	-	
7	EMQ Intention to Comfort	.086	.234***	.070	.170**	.078	.237***	-

* *p* < .05, ** *p* < .01, *** *p* < .001

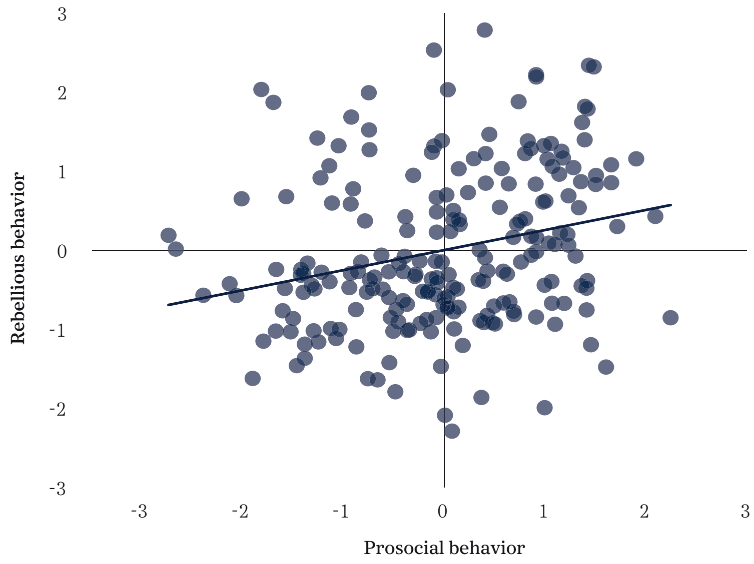

Figure 2. *The positive association between prosocial and rebellious behavior, controlled for age and gender.*

Table 3. Coefficient statistics for the cross-sectional stepwise regressions.

	Prosocial			Rebellious			Prosocial * Rebellious		
Predictor	**b**	**SE**	**β**	**b**	**SE**	**β**	**b**	**SE**	**β**
(Constant)	1.66**	.58	-	-3.70***	.504	-	.106	.523	-
Age	-.03	.01	-.115	.18***	.019	.535	-.044*	.019	-.156
Gender	-.43***	.10	-.264	-.05	.129	-.022	-.130	.134	-.066
Fun Seeking	.06*	.02	.137	.17***	.035	.265	.078*	.036	.147
Perspective Taking	.05***	.01	.219	-	-	-	-	-	-
Empathy	.45*	.18	.156	-	-	-	-	-	-

$p < .05$, $**p < .01$, $***p < .001$.

Prosocial behavior

Prosocial behavior was best explained by IRI Perspective Taking, EMQ Intention to Comfort, and BAS Fun Seeking ($R^2 = .228$, $F(5, 250) = 14.798$, $p < .001$, $\Delta R^2 = .018$, $\Delta F(1, 250) = 5.855$, $\Delta p = .016$; Intention to Comfort: $b = .452$, SE = .177, $p = .011$; Perspective Taking: $b = .045$, SE = .013, $p < .001$, Fun Seeking: $b = .059$, SE = .024, $p = .016$; see Table 3). All regression coefficients were positive, indicating that higher levels of the predictor variables were related to higher levels of Prosocial behavior. Note that when adding ARQ Rebellious behavior to the model (after trimming the model from the non-significant predictors Drive and Reward Responsiveness) the effects of BAS Fun Seeking and Perspective Taking remained significant (Fun Seeking: $b = .056$, SE = .028, $\beta = .126$, $p = .049$; Perspective Taking: $b = .053$, SE = .014, $\beta = .257$, $p < .001$) while this was not the case for Intention to comfort ($p = .13$).

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 ($R^2 = .38$, $F(3, 209) = 43.39$, $p < .001$, $\Delta R^2 = .07$, $\Delta F(1, 209) = 23.58$, $p < .001$; $b = .169$, SE = .035, $p < .001$; see Table 3). When adding Prosocial behavior to the model, this effect of BAS Fun Seeking remained significant ($b = .147$, SE = .035, $\beta = .230$, $p < .001$).

*Prosocial * Rebellious behavior*

Finally we predicted the combined effect of Prosocial and Rebellious behavior from the other behavioral predictors. This combined variable was creating by Z-transforming Rebellious and Prosocial behavior and then multiplying them, thus creating an

Table 4. Coefficient statistics for the regressions with longitudinal predictors.

	Prosocial			Rebellious		
Predictor	**b**	**SE**	**β**	**b**	**SE**	**β**
(Constant)	2.595***	.481	-	-3.913***	.688	-
Age	-.028*	.013	-.126	.178***	.019	.523
Gender	-.481***	.095	-.295	-.060	.134	-.025
Fun Seeking intercept	.068*	.032	.155	.179***	.045	.291
Fun Seeking slope	.078**	.028	.192	.727***	.144	.372
Perspective Taking intercept	.059***	.014	.290	.007	.020	.025
Perspective Taking slope	.078**	.028	.179	.057	.040	.089

**p* < .05, ***p* < .01, ****p* < .001.

*No significant findings were observed for the interaction variable Prosocial * Rebellious.*

interaction variable (Prosocial * Rebellious). Higher values indicate relatively more rebellious, as well as more prosocial behavior ('prosocial risk-takers'), while lower values indicate relatively lower rebellious and prosocial behavior. This interaction variable was predicted by BAS Fun Seeking only (R^2 = .045, $F(3, 209) = 3.29$, p = .022, ΔR^2 = .021, $\Delta F(1, 209) = 4.69$, Δp = .032; b = .078, SE = .036, p = .032; Table 3), with higher levels of Fun Seeking related to higher values of this combined variable.

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 both 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 interaction 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 and gender. Next, we tested whether the rate of change in these variables (i.e., linear slopes) predicted additional variance above intercepts and age 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= .22, F(6,252) = 11.56 p < .001, ΔR^2= .05, ΔF(2, 252) = 7.56, Δp = .001; Perspective Taking intercept: b = .06, SE = .014, p < .001, Fun Seeking intercept: b = .07, SE = .032, p = .038, Perspective Taking slope: b = .08, SE = .027, p = .006, Fun Seeking slope b = .262, SE = .102, p = .011). 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 the model, the effects of BAS Fun Seeking intercept and slope were no longer significant (intercept: p = .27, slope: p = .099).

Rebellious behavior

For Rebellious behavior, we observed that greater increases in BAS Fun Seeking was related to higher levels of Rebellious behavior at T3, above initial levels of BAS Fun Seeking and age and gender (R^2= .40, F(6, 203) = 22.79, p < .001, ΔR^2 = .083, ΔF(2, 203) = 14.09, Δp < .001, intercept: b = .179, SE = .045, p < .001, slope: b = .727, SE = .144, p < .001). No effects of Perspective Taking were observed. When including Prosocial behavior in the model these findings remained significant.

*Prosocial * Rebellious behavior*

Finally, we tested whether the intercepts and slopes of Fun Seeking and Perspective Taking predicted the interaction variable Prosocial * Rebellious. Here, no significant findings were observed.

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= .46, F(12, 169) = 11.99, p < .001, ΔR^2 = .05, ΔF(2, 169) = 8.06, Δp < .001; b = -.001, SE = .000, β = -.253, p = .025), 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.

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 empathy 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 medial prefrontal cortex, of which greater declines in medial prefrontal cortex 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, and we aimed to gain a better understanding of subtypes of individuals, rather than using the dichotomy of separable outcomes. This approach was driven by the observation that the seemingly paradoxical measures prosocial and rebellious behavior were in fact positively correlated, suggesting that the same developmental processes may result in both types of behaviors (Schriber & Guyer, 2015). Indeed, cross-sectionally, we observed that higher levels of fun seeking were related to both prosocial and rebellious behaviors, as well as their interaction. Previous studies already reported relations between approach tendencies and risk taking (Steinberg, 2007), but the current 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). Furthermore, consistent with prior studies, high levels of empathy and social perspective taking uniquely predicted prosocial behavior, but these measures were not related to rebellious behavior. The relations between empathy, perspective taking, and prosocial behaviors have been well documented (Eisenberg, 2000; Overgaauw, Guroglu, Rieffe, & Crone, 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 subgroups of prosocial or rebellious individuals. 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. Finally, change in fun seeking was not related to a combined variable of high prosocial and high rebellious behavior, suggesting that this particular change may not be predictive for a specific subgroup of ‘prosocial risk takers’. 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.

Brain development and the relation with developmental outcomes

Prior studies have consistently reported that brain regions important for approach behaviors and social functioning show pronounced changes in gray matter (Mills, Goddings, Clasen, Giedd, & Blakemore, 2014; Mills et al., 2014). We previously reported a developmental decline in NACC volume in participants included in the current data set (Wierenga et al., 2018). The current study further confirmed a similar decline in volume of MPFC, consistent with prior work(Mills et al., 2014), and extended this to three subregions in the MPFC (superior frontal, rostral anterior cingulate, and caudal anterior cingulate, see supplement). 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 declines during mid to late adolescence. The results are comparable to prior work that has 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 wave. This finding fits well with prior functional neuroimaging studies, showing that longitudinal declines in functional coupling between MPFC and ventral striatum were associated with decreases in self-reported risk taking (Qu, Galvan, Fuligni, Lieberman, & Telzer, 2015). In addition, 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 exists in other samples. Furthermore, adding brain volume to the model after controlling for age, gender, perspective taking, and fun seeking intercepts and slopes, possibly accounted for little additional variance. 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 (Urosevic et al., 2012). Functional activation in the NACC is also consistently observed as an important marker for reward reactivity in studies examining both 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. 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.

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 empathy questionnaire was only available at the final wave and 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). Second, the current study made use of self-report measures, because previous studies showed that these have more stability than experimental tasks (Peper et al., 2018). The selection of measures in this study all had sufficient reliability and ICC values, increasing the strength of the results. However, questionnaires do not capture the variations in behavior under different experimental contexts and may be sensitive to social desirability. 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. Third, in our analyses we controlled for age and 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 males and females. 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 towards a more differentiated perspective on adolescent development, where similar sensitivity markers may lead to multiple developmental outcomes.

Supplementary materials

Mixed model building procedure for longitudinal measures

To test which developmental trajectories best described the longitudinal measures (Perspective Taking, BAS, and brain structures), we used a mixed-models approach in R using the *nlme* package (R Core Team, 2014; Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2013). For all measures, we tested for linear, quadratic, and cubic effects of age, reflecting an age-related increase or decrease, a non-linear adolescent-specific U- or inverted-U pattern, and a non-linear adolescent emerging or declining pattern, respectively. Age was a polynomial predictor, and because the data were nested within participants we included a random intercept for participants in our models (see also Schreuders et al., 2018). Finally, after determining which age pattern best described the data, we tested whether Gender (dummy-coded 0 (female) or 1 (male)) improved model fit. In the case of a main effect of Gender, we also tested for Age*Gender interaction effects. We used the Akaike Information Criterion (AIC; Akaike, 1974) to compare model fits and the log-likelihood ratio to assess significance of model improvement. We also report the Bayesion Information-Criterion values (BIC; Schwarz, 1978). Model fit summaries are depicted in Table S1.

Longitudinal developmental trajectories

Here we describe the longitudinal trajectories of the behavioral and neural predictors. The developmental trajectory of the BAS scales have previously been described in Schreuders et al. (2018). In brief, BAS Drive shows a cubic age effect for males and a linear increase in girls; BAS Fun Seeking shows a cubic effect of age (depicting an adolescent-emergent pattern of fun seeking across development), but no effect of Gender; and BAS Reward Responsiveness shows a cubic effect of age and a main effect of Gender (with higher levels in girls than in boys).

The longitudinal development of IRI Perspective Taking has not yet been reported. The best-fitting model included a cubic effect of age and a main effect of Gender, 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 Figure 1A in the main manuscript and Table S1 and Table S2 below). No Age * Gender interaction effect was observed.

The developmental trajectory of nucleus accumbens volume is described in (Wierenga et al., 2018) and shows a linear decrease with age, and greater volumes in boys than in girls. The development of MPFC volume has not yet been reported. MPFC volume was best described by a declining cubic effect of age and a main effect of Gender (with boys having greater volumes than girls; Figure 1B in the main manuscript; Table S1, Table S2). Developmental trajectories of the MPFC subregions (i.e., superior frontal, rostral anterior cingulate, and caudal anterior cingulate of the Desikan-Killiany-Tourville atlas) also show similar cubic effects of age and a main effect of Gender (Figure S1, Table S3). Finally, no Age * Gender interaction effects were observed in any of the brain structures.

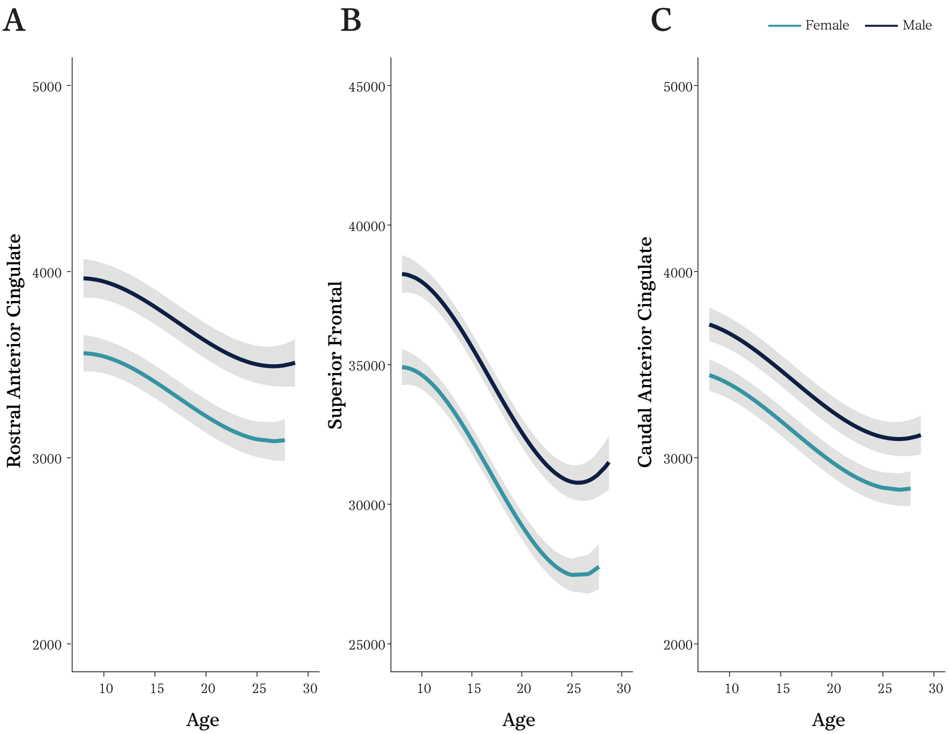

Figure S1. *Developmental trajectories of MPFC subregions (in cubic millimeters).* ***A.*** *Rostral anterior cingulate.* ***B.*** *Superior frontal.* ***C.*** *Caudal anterior cingulate. Light blue lines indicate females, dark blue lines indicate males, and grey areas mark the 95% confidence interval.*

Table S1. AIC and BIC values for Null, Linear, Quadratic, and Cubic models to describe the relation with age and each of the longitudinal measures.

	Null		Linear	
Dependent variable	**AIC**	**BIC**	**AIC**	**BIC**
Perspective Taking	3130.85	3143.93	3098.27	3115.71
MPFC total	12727.04	12740.6	12239.42	12257.52
Rostral anterior cingulate	9388.46	9402.04	9153.16	9171.27
Superior frontal	12525.85	12539.43	12042.69	12060.80
Caudal anterior cingulate	9326.06	9339.64	8851.66	8869.77

Bold values indicate best fit measures.

Table S2. Coefficient statistics for the longitudinal mixed-model results of Perspective Taking and the combined MPFC.

	Perspective Taking		MPFC	
Predictor	**b**	**SE**	**b**	**SE**
(Constant)	36.52 ***	9.09	35591.76 ***	1806.29
Age Linear	-3.08 *	1.55	1798.58 ***	321.63
Age Quadratic	.19 *	.09	-149.81 ***	18.72
Age Cubic	-.004 *	.001	2.97 ***	.35
Gender	-1.61 ***	.37	4010.11 ***	426.62

**p < .05, **p < .01, ***p < .001.*

Quadratic		Cubic		Cubic + Gender	
AIC	BIC	AIC	BIC	AIC	BIC
3099.92	3121.73	3095.40	3121.57	**3079.16**	**3109.69**
12233.52	12256.15	12167.24	12194.40	**12092.21**	**12123.90**
9154.61	9177.24	9136.59	9163.75	**9103.10**	**9134.78**
12036.86	12059.50	11969.49	11996.65	**11891.87**	**11923.56**
8840.53	8863.16	8808.85	8836.00	**8789.78**	**8821.47**

Table S3. Coefficient statistics for the longitudinal mixed-model results of MPFC subregions.

	Rostral anterior cingulate		Superior frontal		Caudal anterior cingulate	
Predictor	b	SE	b	SE	b	SE
(Constant)	3241.76 ***	169.15	29081.75 ***	1612.86	3301.60 ***	126.95
Age Linear	90.09 **	29.42	1637.58 ***	287.85	62.72 **	21.74
Age Quadratic	-7.42 ***	1.71	-135.09 ***	16.75	-6.73 ***	1.27
Age Cubic	.14 ***	.03	2.68 ***	.31	.139 ***	.02
Gender	402.52 ***	65.61	3334.98 ***	348.14	272.07 ***	58.35

**p* < .05, ***p* < .01, ****p* < .001.