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Transitioning from childhood into adolescence: A comprehensive longitudinal behavioral and neuroimaging study on prosocial behavior and social inclusion

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ABSTRACT

Acting prosocially and feeling socially included are important factors for developing social relations. However, little is known about the development of neural trajectories of prosocial behavior and social inclusion in the transition from middle childhood to early adolescence. In this pre-registered study, we investigated the development of prosocial behavior, social inclusion, and their neural mechanisms in a three-wave longitudinal design (ages 7–13 years; $N_{T1} = 512$; $N_{T2} = 456$; $N_{T3} = 336$). We used the Prosocial Cyberball Game, a ball tossing game in which one player is excluded, to measure prosocial compensating behavior. Prosocial compensating behavior showed a linear developmental increase, similar to parent-reported prosocial behavior, whereas parent-reported empathy showed a quadratic trajectory with highest levels in late childhood. On a neural level we found a peak in ventral striatum activity during prosocial compensating behavior. Neural activity during social inclusion showed quadratic age effects in anterior cingulate cortex, insula, striatum, and precuneus, and a linear increase in temporo-parietal junction. Finally, changes in prosocial compensating behavior were negatively associated with changes in ventral striatum and mPFC activity during social inclusion, indicating an important co-occurrence between development in brain and social behavior. Together these findings shed a light on the mechanisms underlying social development from childhood into adolescence.

1. Introduction

The formation of long-lasting social relationships with others is a fundamental part of human development. The transition from childhood into adolescence is characterized by extensions in the social environment, such as an increase in time spent with peers in addition to family (Crone and Dahl, 2012), and larger social circles with more emphasis on contributions to the needs of others (Fuligni, 2018). In order to engage in meaningful social interactions it is necessary to gain social competence, defined as the ability to fulfill both others' and own social needs (Rubin and Rose-Krasnor, 1992).

Fulfilling others' social needs can be achieved by showing prosocial behavior, defined as voluntary acts to help another individual (Eisenberg et al., 2006). Prosocial behavior is an important foundation for reciprocal relationships, in particular for adolescents, who spend relatively more and qualitatively different time with their peers compared to younger children (Blakemore and Mills, 2014; Crone and Achterberg, 2022; Crone et al., 2022; Nelson et al., 2016). Various studies have demonstrated that prosocial behavior rapidly develops during early childhood (Malti and Dys, 2018; Warneken and Tomasello, 2006). This

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development is thought to co-occur with increases in socio-cognitive and –affective skills, such as perspective taking and empathic reasoning (Crone and Dahl, 2012; Eisenberg et al., 2005; Lehmann et al., 2022; Steinbeis and Over, 2017). However, findings on the development of prosocial behavior beyond early childhood are inconsistent, with research showing linear increases in one form of prosocial behavior (i.e., cooperation) but decreases in another form of prosocial behavior (i.e., helping (Do et al., 2017; Güroğlu et al., 2014; Malti et al., 2016)). Moreover, increases in socio-cognitive skills such as perspective taking can explain individual differences in prosocial behavior (van de Groep et al., 2020) but are not consistently associated with increases in prosocial helping behavior (Eisenberg et al., 2005). This raises the question what mechanisms might drive changes in various prosocial behaviors in the transition from childhood to adolescence.

One such mechanism might be neural development, as development in prosocial behavior has been shown to co-occur with the development of the social brain (Blakemore, 2008; Frith and Frith, 2003). This neural network includes brain regions that support both socio-cognitive processes such as perspective-taking (i.e., temporo-parietal junction (TPJ), posterior superior temporal sulcus (pSTS), precuneus, and medial prefrontal cortex (mPFC (Blakemore, 2008)), as well as socio-affective processes such as the processing of salient emotional events (i.e., anterior insula (AI), dorsal anterior cingulate cortex (dACC) and ventral striatum (VS) (Davey et al., 2010; Eisenberger et al., 2003)). Neuroimaging studies have shown changes in social brain function during the transition from adolescence into adulthood (Blakemore, 2012; Blakemore and Mills, 2014). Research on neural correlates of mentalizing or perspective taking in particular shows that activation in the mPFC decreases from adolescence into adulthood (Blakemore, 2012), whereas posterior regions such as pSTS/TPJ showed an increase in activation from adolescence into adulthood (Blakemore et al., 2007; Güroğlu et al., 2011; Tousignant et al., 2017). In contrast, relatively little is known about the development of the social brain from middle childhood into early adolescence, with only few studies focusing on this particular period in development. For example, work by Richardson et al. (2018) reported increased anti-correlation between socio-affective brain and socio-cognitive regions between the ages of 3–12 years. Interestingly, other work reported changes in social brain activity over the course of pre- to mid-adolescence in the absence of age-related changes in prosocial behavior (Do et al., 2019). As such, these findings indicate that understanding neural changes may lead to new insights in the mechanisms of prosocial development. With the current study we aimed to expand our understanding of the functional development of the social brain, by focusing on the transition from middle childhood into early adolescence.

Prior seemingly mixed findings on behavioral and neural correlates of prosocial behavior might be explained by differential effects of prosocial actions in fulfilling the needs of self and others, such as whether the prosocial behavior is costly or non-costly for self (Dunfield et al., 2011; El Mallah, 2019). In our prior research, we examined prosocial behavior in the Prosocial Cyberball Game, a four-player social interaction ball tossing game where participants observe two players excluding the fourth player (Riem et al., 2013). In both 7–9-year-old children and adults we observed that participants compensated for observed social exclusion by more often tossing the ball to the excluded player, which is considered non-costly prosocial behavior (van der Meulen et al., 2017; van der Meulen et al., 2018, 2016). This finding of prosocial compensating behavior is in line with earlier work on prosocial compensation towards excluded individuals (Masten et al., 2010, 2011; Moor et al., 2012; Vrijhof et al., 2016; Will et al., 2013). In addition, prosocial compensating behavior was associated with increased activity in the posterior cingulate cortex/precuneus in childhood (van der Meulen et al., 2018), and with activation in the ventral striatum and TPJ in adolescents and adults (Tousignant et al., 2017; van der Meulen et al., 2016; Will et al., 2015). Moreover, increased neural activation was observed in the 7–9-years old child sample when participants were themselves included (compared to being excluded), with pronounced activation in the bilateral insula and dACC (van der Meulen et al., 2018). Research in adults corroborates the findings that experiencing positive social events is associated with increased activation of dACC, bilateral insula and VS (Achterberg et al., 2018b; Davey et al., 2010; Eisenberger et al., 2003; Guyer et al., 2011). On a behavioral level, being socially included may increase the opportunity to partake in meaningful social interaction, and to develop and maintain a social network. Indeed, adolescents who in daily life are more socially included by their peers are more likely to show non-costly prosocial behavior compared to socially excluded adolescents (Will et al., 2016). In addition, socially included adolescents show stronger activation in pSTS/TPJ and anterior insula when dividing coins between self and others than socially excluded adolescents (Will et al., 2016), possibly indicating that socially included adolescents pay more attention to others when making social decisions (Fink et al., 2014; Slaughter et al., 2015). Together these findings emphasize the close connection of focusing on others' needs and own needs in social contexts. Therefore, here we addressed the interplay of showing prosocial behavior and feeling socially included.

The goals of this study were I) to investigate developmental trajectories of prosocial behavior from middle childhood into adolescence using a non-costly prosocial compensating behavior task and II) to investigate developmental trajectories of the neural correlates of prosocial behavior and feeling socially included using fMRI. An increased understanding of within-individual longitudinal transition as well as group-level development of prosocial behavior and associated neural activation is expected to shed light on how children become socially competent adolescents. Therefore, we modeled longitudinal changes in prosocial behavior, social inclusion, and associated neural activation using three waves of the longitudinal Leiden Consortium on Individual Development study, spanning middle childhood to early adolescence (ages 7–14 years, Crone et al. (2020)).

Our first pre-registered aim (see van der Meulen et al., 2021) was to investigate the behavioral developmental trajectories of non-costly prosocial behavior from middle childhood into early adolescence. We used the Prosocial Cyberball Game as a measure of prosocial compensating behavior and of feeling socially included. To further examine prosocial behavior in a broader social context and test whether our findings could be extended to other aspects of prosocial behavior, we additionally investigated developmental trajectories of parent-reported prosocial behavior. We expected that prosocial behavior would increase from middle childhood into adolescence, driven by an increase in socio-cognitive and socio-affective skills (Crone and Dahl, 2012; Eisenberg et al., 2005). Our second pre-registered aim was to describe the developmental trajectories of neural responses to prosocial behavior in regions of the social brain. We hypothesized that neural activation of the social brain (i.e., TPJ, precuneus, mPFC, pSTS, AI, dACC, VS) would increase from middle childhood to early adolescence. In addition to our preregistered analyses on prosocial behavior, we also explored the developmental trajectories of neural responses to social inclusion, to examine whether neural activation during prosocial behavior and social inclusion showed similar developmental trajectories. We preregistered regions of interest and specifically focused on patterns of neural activity in regions associated with prosocial behavior, i.e., the precuneus, mPFC, and pSTS and TPJ, and regions associated with social inclusion, i.e., the anterior insula, dACC and VS (Blakemore, 2008; van der Meulen et al., 2018, 2016). Our final pre-registered aim was to investigate the co-occurrence of individual developmental trajectories of prosocial behavior with markers of neural development (i.e., individual linear slopes of neural activity in regions of interest). We expected that markers of neural development, specifically the precuneus, mPFC, pSTS, TPJ and VS, would be positively associated with individual rates of development of prosocial behavior (Blakemore et al., 2007; Güroğlu et al., 2011). However, for anterior insula and dACC specifically we expected negative associations between neural and behavioral development, based on earlier work showing that individuals who engaged in more prosocial behavior showed less neural activity in anterior insula and dACC (Do et al., 2019; Schreuders et al., 2018; van der Meulen et al., 2018).

2. Methods

2.1. Participants

Participants in this study took part in the middle childhood cohort of the longitudinal twin study of the Leiden Consortium on Individual Development (L-CID; see Crone et al. (2020) for details on the study and its procedures). For recruitment families with same-sex twins born between 2006 and 2009 were invited to participate. Twin pairs aged 7–9 at the time of the first wave of data collection (T1), fluent in Dutch or English, and without visual or physical impairments that could hinder their performance in behavioral tasks, were included in the study. Written informed consent was obtained from both parents and/or caregivers, as well as from participants once they turned 12. The study and its procedures were approved by the Dutch Central Committee for Human Research (CCMO; protocol number NL50277.058.14). In total, 514 children (257 twin pairs) participated in the middle childhood cohort of the L-CID study. For the present study, we included data collected during the lab visits at wave 1 (T1; $n = 512$), wave 3 (T2; $n = 456$) and wave 5 (T3; $n = 336$). Between T1 and T2, there was a mean time interval of 2.06 ± 0.15 years (range: 0.99 – 3.01 years). Between T2 and T3, there was a mean time interval of 2.45 ± 0.27 years (range: 1.95 – 3.25 years). See Table 1 for demographic information at each wave. Because our aim was to study development in a population sample, we also included participants diagnosed with a psychiatric disorder ($n = 19$ at T3). Diagnoses, as established by medical experts, were reported by the parents. IQ was estimated at T1 via the subscales Block Design and Similarities of the Wechsler Intelligence Scale for Children, 3rd version (WISC-III); Wechsler (1991). Estimated IQ was within the normal range (range = 72.5 - 137.5). Results from T1 were previously published (see Achterberg et al., 2018; Achterberg and van der Meulen, 2019, Achterberg et al., 2018b; van der Meulen et al., 2018).

We aimed to include as many participants as possible in each analysis, and therefore our analyses were performed on the largest available samples, resulting in a *behavioral sample*, a *neuroimaging sample* and a *questionnaire sample.* We checked whether participants who were excluded in parts of the analysis differed in age, sex, IQ, and diagnosed psychiatric disorders as measured at T1. Demographic information was not available for one family at T1, as they entered the study at a later moment. Therefore, their characteristics were not taken into account for these comparisons. Reasons for exclusion were not completing the session for various reasons or movement in the fMRI session (see Fig. 1 for an elaborate overview). Note that the demographical comparisons were performed on the included versus excluded participants in the total sample ($n = 512$), whereas Fig. 1 reports the exclusion numbers in the sample at that specific time point (T1: $n = 512$, T2: $n = 456$, T3: $n = 336$). In our *behavioral sample* we observed that participants who were excluded at T1 ($n = 6$) were more often male than female (X^2=6.36, $p < .05$) compared to those included at T1. At T2, excluded participants ($n = 61$) were older ($M = 8.19$, $SD = 0.61$) than included participants ($M = 7.91$, $SD = 0.67$; $t(80.70)=3.32$, $p < .005$). Participants excluded from the behavioral sample at T3 ($n = 178$) did not differ from included participants in terms of age, sex, IQ, and psychiatric disorders. In the *neuroimaging sample* we observed that participants excluded at T1 ($n = 241$) were younger ($M = 7.87$, $SD = 0.66$) than included participants ($M = 8.00$, $SD = 0.67$; $t(504.59)=-2.18$, $p < .05$), and excluded participants were also more often male than female (X^2=11.72, $p < .005$). At T2 excluded participants ($n = 240$) did not differ from included participants in terms of age, sex, IQ, and psychiatric disorders. At T3 participants excluded from the neuroimaging sample ($n = 322$) had a lower IQ ($M = 102.51$, $SD = 11.90$) than included participants ($M = 105.41$, $SD = 11.31$; $t(413.07)=-2.75$, $p < .01$). Finally, in the *questionnaire sample* we observed that participants excluded at T1 ($n = 26$) were younger ($M = 7.56$, $SD = 0.55$) than included participants ($M = 7.96$, $SD = 0.67$; $t(29.20)=-3.61$, $p < .05$), and excluded participants were more often male than female ($X^2 = 8.65$, $p < .005$). At T2, excluded participants ($n = 71$) had a lower IQ ($M = 100.35$, $SD = 12.33$) than included participants ($M = 104.10$, $SD = 11.59$; $t(91.06)=-2.40$, $p < .05$), and were older ($M = 8.11$, $SD = 0.64$) than included participants ($M = 7.92$, $SD = 0.67$; $t(96.61)=2.34$, $p < .05$). At T3 excluded participants ($n = 162$) were lower in IQ ($M = 102.04$, $SD = 11.55$) than included participants ($M = 104.30$, $SD = 11.80$; $t(319.90)=-2.05$, $p < .05$). Given these differences between included and excluded participants we tested whether observed effects of age would remain significant after controlling for main and interaction effects of sex and IQ.

Table 1
Demographic information of the L-CID middle childhood cohort.

	T1	T2	T3
N	512	456	336
Mean age (SD)	7.94 (0.67)	9.98 (0.70)	12.41 (0.76)
Female	51.2 %	52.50 %	52.40 %
Estimated IQ at T1 (SD	103.58 (11.76)	103.81 (11.62)	104.28 (11.91)
Diagnosed psychiatric disorders	2.2 %	3.6 %	5.7 %
ADHD and/or ADD	*9*	*9*	*9*
ASD	*1*	*3*	*4*
GAD	*1*	*2*	*2*
ADHD and/or ADD & DCD		*1*	*1*
PTSS		*1*	
DCD			*1*
OCD			*1*
Tourette's syndrome			*1*

2.2. Procedure

Data were collected during annual visits, alternating between lab and home visits. Between the second and the third wave, approximately 40 % of the sample received a video-feedback intervention to promote positive parenting and sensitive discipline (VIPP-TWINS, see Euser et al., 2016). The other 60 % received a series of phone calls as a control condition. As a sensitivity check, we tested whether observed effects of age would remain significant after controlling for main and interaction effects of VIPP above other covariates sex and IQ.

The lab visits at T1, T2, and T3 all consisted of a similar set-up (see Achterberg and van der Meulen (2019) for details). In short, twin children visited the lab with their primary parent (i.e., the parent that spent most time with the children at the start of the study). After a practice session children performed the Prosocial Cyberball Game during the MRI session. First-born and second-born children of each twin pair were randomly assigned to either start with the MRI session or start with other tasks. Both parents completed questionnaires via Qualtrics prior to or during the visit.

2.3. Behavioral measures

2.3.1. Prosocial cyberball game

We measured prosocial compensating behavior and neural correlates using the Prosocial Cyberball Game (PCG) (based on Riem et al. (2013); previously described in van der Meulen et al. (2018)). In this four-player virtual ball-tossing game participants were instructed to toss the ball to three other players. Players 1, 2, 3 were represented by the figures at the left, top, and right of the screen, respectively. The participant was represented by the figure at the bottom of the screen (see Fig. 2). The ball could be tossed to the other players by pressing a button. We asked participants to imagine the social settings of the game by thinking about what the other players and the setting would look like. Participants played the PCG in two rounds: a Fair Game and an Unfair Game. During the Fair Game (120 trials) all players received the ball an equal number

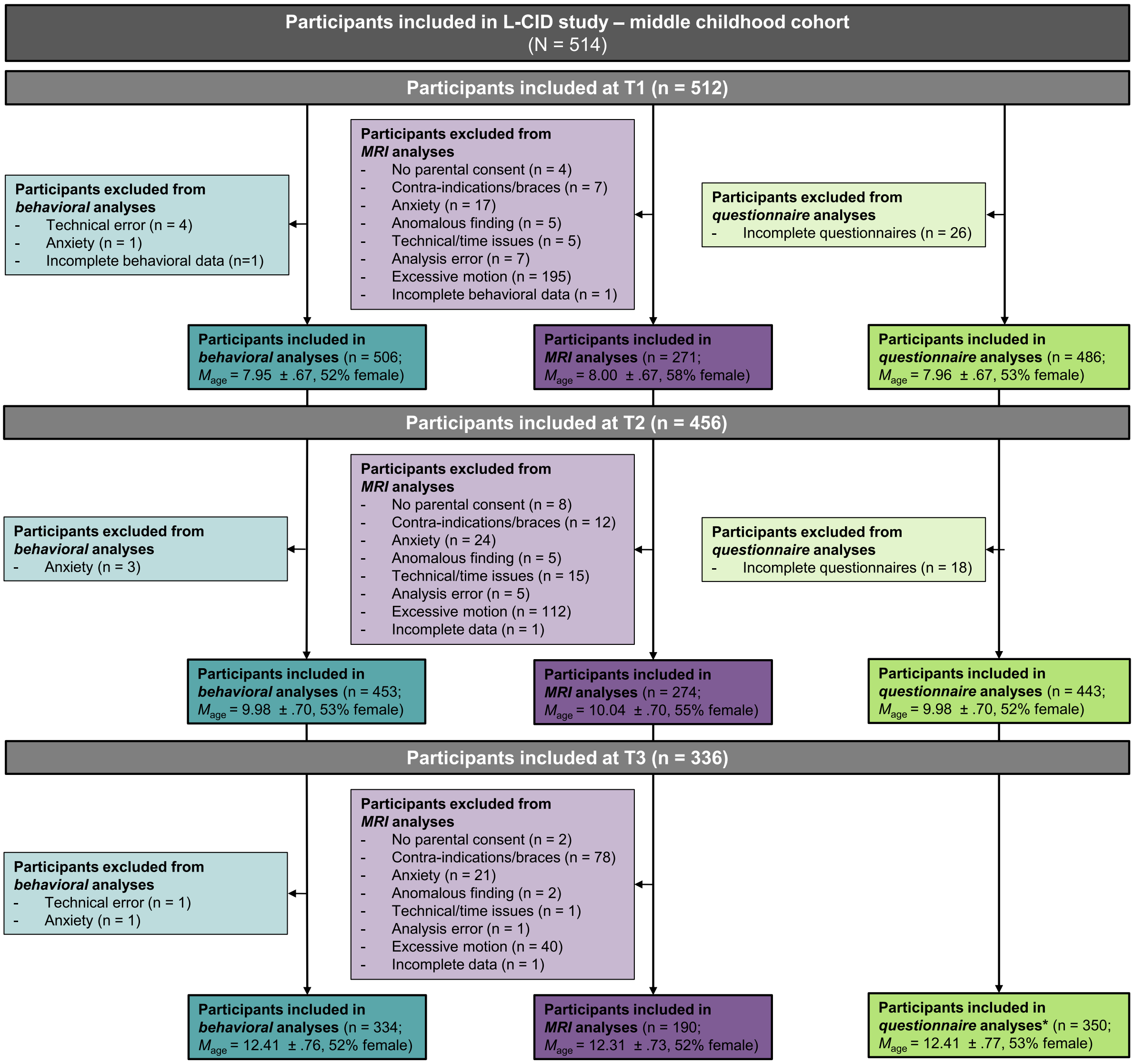

Fig. 1. Flowchart of participant inclusion. The sample used for behavioral analyses is shown on the left (in blue), the sample used for neuroimaging (MRI) analyses is shown in the middle (in purple) and the sample used for questionnaire analyses is shown on the right (in green). Details on participant exclusion are provided in light colored boxes.

Note: At T3 an additional 14 participants were only included in the questionnaires, but did not attend the lab visit. Therefore, no behavioral or MRI data were collected for these participants.

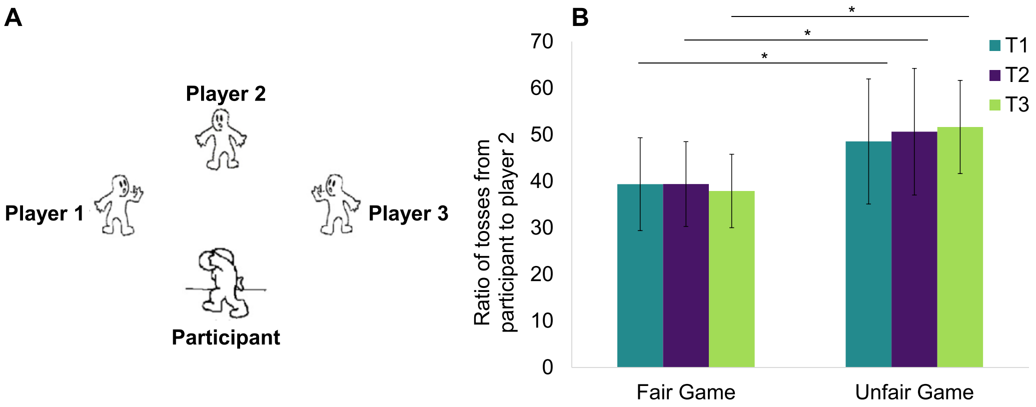

Fig. 2. (A) Visualization of play situation and players in the Prosocial Cyberball Game. (B) Ratio of tosses of the participant to Player 2 in the Fair Game and Unfair Game of the Prosocial Cyberball Game across the three waves.

Note. Significant differences between Fair and Unfair Game are indicated with an asterisk (*).

of times, thus creating a fair play situation for all players. At T1 the Fair Game was administered on a laptop, at T2 and T3 the Fair Game was administered during the fMRI session. During the Unfair Game (168 trials), virtual player 2 was excluded by virtual players 1 and 3, thus creating an unfair play situation for player 2. The Unfair Game started with either player 1 or player 3 tossing the ball once to player 2. After that, these players no longer tossed the ball to player 2. The Unfair Game was split in two identical blocks with a short rest in between, and was administered during the fMRI session at all waves. Trials in both Fair and Unfair Game consisted of a ball toss with a duration of 2000 ms, followed by an intra-trial interval jitter (1000–2000 ms). In trials where the participant was tossing, the intra-trial interval was overwritten by the actual response time of the participant. For an example trial see Fig. 2**.**

Our variable of interest in the PCG is prosocial compensating behavior to excluded Player 2, defined as the difference in ratio of tosses to Player 2 in the Unfair Game compared to the Fair Game. This ratio was calculated by dividing the number of tosses to Player 2 by the total number of tosses to all players (van der Meulen et al., 2016). Participants showed no differences in behavior between the first and second half of the Unfair Game at all time points, and therefore the scores were combined in one assessment of the Unfair Game. To account for individual differences in tosses to Player 2 in the two games, we calculated a difference score between the percentage of tosses to Player 2 in the Unfair Game minus the percentage of tosses to Player 2 in the Fair Game (for all statistics see **Supplementary Table S1**). The resulting score was used as an index of prosocial compensating behavior in further analyses. As preregistered, participants with incomplete data (defined as missing more than 20 % of trials in the Unfair Game) on one of the waves were considered missing for that specific wave (also see Fig. 1).

2.3.2. Parent-reported prosocial behavior

We used the parent-report version of the Prosocial subscale of the Strengths and Difficulties Questionnaire (SDQ; Goodman, 1997) and the Empathic and Prosocial Response subscale of the My Child Questionnaire (MC; Kochanska et al., 1994) as a composite measure of parent-reported prosocial behavior. The SDQ subscale consists of 5 items that were answered on a 3-point Likert scale (0 = not true to 2 = certainly true) and includes items such as “My child is considerate of other people’s feelings”. The MC subscale consists of 13 items that were answered on a 5-point Likert scale (0 = not true to 4 = true) and includes items such as “My child will try to comfort or reassure another in distress”. We asked both the primary parent and the other parent to complete the questionnaires.

Following the procedure used in van der Meulen et al. (2020) we calculated two new subscales based on the items from the original questionnaires. This resulted in a subscale for parent-reported prosocial behavior and a subscale for parent-reported empathy (see **Supplementary Materials**). Higher scores (range 0–4) indicated more prosocial behavior and more empathy, respectively. As preregistered, participants with incomplete data (defined as neither parent having completed the questionnaire) on one of the waves were considered missing for that specific wave (also see Fig. 1).

2.4. Neural measures

2.4.1. fMRI data acquisition

The same Philips Ingenia MR 3.0T scanner was used to collect data during the three waves (also see van der Meulen et al., 2018). We used a standard 32-channel whole-head coil. The functional scans were acquired using a T2*-weighted echo-planar imaging (EPI). The first two volumes were discarded to allow for equilibration of T1 saturation effects (TR = 2.2 s; TE = 30 ms; sequential acquisition, 37 slices; voxel size = 2.75 × 2.75 × 2.75 mm; Field of View = 220 × 220 × 112 mm; flip angle = 8°). After the functional runs, a high-resolution 3D T1-weighted anatomical image was collected (TR = 9.8 ms, TE = 4.6 ms, 140 slices; voxel size = 1.17 × 1.17 × 1.2 mm, and FOV = 224 × 177 × 168 mm). At T3, the T1-weighted anatomical scan was acquired before the functional scans. Foam inserts were used within the head coil to restrict head movement. Stimuli were displayed on a screen that was visible via a mirror attached to the head coil.

2.4.2. fMRI preprocessing

All data were analyzed with SPM12 (Wellcome Department of Cognitive Neurology, London), following the processing described in van der Meulen et al. (2018). In short, processing steps included correction for slice timing acquisition and differences in rigid body motion, spatial normalization to T1 templates (based on the MNI305 stereotaxic space) using 12-parameter affine transform mapping together with non-linear transformation with cosine basis functions, resampling to 3 × 3 × 3 mm voxels, and spatial smoothing (6 mm full width at half maximum (FWHM) isotropic Gaussian kernel). Data of participants were excluded from the neuroimaging analyses when participants moved more than 3 mm in any volume in any direction (x,y,z).

2.4.3. fMRI first-level analyses

Individual participant’s fMRI data at each time point were analyzed using a general linear model (GLM). Different events in Unfair Game were determined by the tossing of the ball, with the start of each ball toss (i.e., from and to the participant, excluded player and other two players) modeled as separate regressors with a zero-duration event. Six motion regressors were included as covariates of no interest in the first level analysis. High-pass filtering was implemented in the design using a residual forming matrix with a cosine basis set of regressors and a filter cutoff at 128 s. Serial correlations in the time series data were accounted for using an autoregressive AR(1) model on the data and GLM design matrix. The least-squares parameter estimates of height of the best-fitting canonical hemodynamic response function were used in pairwise contrasts. The resulting subject-specific images were included in the whole-brain analyses.

2.4.4. fMRI whole-brain analysis

As no fMRI data were available for the Fair Game of the PCG at T1, our whole-brain second-level analyses focused on the Unfair Game of the PCG. As described in our preregistration, to study neural correlates of prosocial compensating behavior across the three waves we compared the events of the participant compensating for the observed exclusion by tossing the ball to excluded player 2 (“Compensating”) to the participant tossing the ball to players 1 and 3 (“Tossing to excluders”). We performed a whole-brain analysis on this contrast to check whether there was activation in other regions than our previously determined ROIs. We also explored the neural correlates of feeling socially included by comparing the events of the participant receiving the ball from players 1 and 3 (“Inclusion”) to the participant not receiving the ball from players 1 and 3 (“Exclusion”). In keeping with our prior studies (van der Meulen et al., 2017, 2018), in the social inclusion contrast we did not include ball tosses from the excluded player (player 2), as being included by the excluders (the majority of the group) may be related to other motives or may feel more as social inclusion compared to being included by the person who is excluded themselves (player 2). Neural responses were considered significant when they exceeded a cluster-corrected threshold of $p < .05$ FWE-corrected, with a primary threshold of $p < .001$ (Woo et al., 2014).

2.4.5. fMRI ROI analysis

We selected regions of interested (ROIs) that were independent from the current study, to ensure that our selection was not biased towards one of the waves in our longitudinal study. Our final selection of ROIs is therefore based on previous work showing associations with socio-cognitive processes (i.e., TPJ, mPFC, and precuneus (based on the meta-analysis of Schurz et al., 2014), and pSTS (based on Lahnakoski et al., 2012)) and socio-affective processes (dACC and anterior insula (based on the meta-analysis of Lamm et al., 2011) and VS (based on the meta-analysis of van Hoorn et al., 2019)). We used the Marsbar ROI toolbox (Brett et al., 2002) to create 8 mm spheres around reported peak coordinates in MNI space (see Table 2, for visualization see Fig. 6). For coordinates that were closely located together (i.e., TPJ and pSTS), ROIs without overlapping voxels were created. Parameter estimates were extracted from the ROIs for further analyses. To investigate neural correlates of prosocial compensating behavior we used the condition difference between "Compensating" – "Tossing to excluders". To explore neural correlates of social inclusion we used the condition difference between "Inclusion" – "Exclusion". As neural activation was highly correlated between left and right hemisphere for bilateral regions (i.e., TPJ, pSTS, anterior insula, and VS; all $r > 0.67$ for the prosocial contrast, all $r > 0.63$ for the inclusion contrast) and we had no specific hypotheses for left versus right hemispheric effects, we performed our analyses for these regions collapsed across hemispheres. As preregistered, participants with anomalous findings, excessive movement (>3 mm in any volume), or incomplete behavioral data on one of the waves were considered missing for that specific wave (also see Fig. 1).

2.5. Mixed-effects model building procedure

In both behavioral data or neuroimaging data (parameter estimates) outliers (z-values $> |3.29|$) were winsorized (Tabachnick and Fidell, 2013). We inspected intra class correlations (ICCs) to assess homogeneity of the data for the two behavioral measures of prosocial behavior and the parameter estimates of the ROIs. We calculated ICCs in SPSS (version 27.0), using a two-way mixed model with absolute agreement. Average measures were reported (see Table 3). Values above 0.01 were considered sufficient (Ordaz et al., 2013).

Our first aim was to describe the developmental trajectory of prosocial behavior and neural activity from middle childhood into early adolescence. We tested which developmental trajectories best described our behavioral and neural measures with a mixed-effects model approach, using the lme4 package (Bates et al., 2015) in R (R Core Team, 2015). This approach allowed for flexible analysis of longitudinal data. Separate mixed-effects models were ran with each of our behavioral and neural measures as dependent variable. To overcome the nested nature of the data (i.e., longitudinal design, twin design) we included random effects for individual subjects (childID) as well as family groups (familyID) in every model. Using the following model-building procedure, we first ran a null-model with a random intercept to encompass individual differences in starting points, specified in R as:

$$Dependent\ variable \sim (1|childID) + (1|familyID).$$

We then tested age-related linear increases in the outcome variable by adding a polynomial predictor for age as a fixed effect, specified in R as:

$$Dependent\ variable \sim poly(Age, 1) + (1|childID) + (1|familyID).$$

Table 2
Overview of peak coordinates (in MNI space) for selected ROIs (created in 8 mm spheres).

ROI	x	y	z
dACC	6	18	30
left anterior insula	−40	22	0
right anterior insula	39	23	−4
left VS	−6	12	−6
right VS	9	9	−9
Left TPJ	−53	−59	20
Right TPJ	56	−56	18
Left pSTS	−58	−42	12
Right pSTS	58	−44	14
Precuneus	4	−55	34
mPFC	−1	56	24

Table 3
Intra-class correlations for behavioral and neural measures.

Behavior		
Prosocial compensating behavior	.10 [−0.08, 0.25]	
Parent-reported prosocial behavior	**.84 [.81, 0.87]**	
Parent-reported empathy	**.84 [.80, 0.86]**	
ROI parameter estimates	**Compensating - Tossing**	**Inclusion - Exclusion**
dACC	−0.19 [−0.69, 0.18]	.08 [−0.16, 0.30]
insula	−0.14 [−0.62, 0.21]	.02 [−0.30, 0.29]
ventral striatum	.27 [−0.01, 0.49]	.05 [−0.32, 0.34]
TPJ	.21 [−0.12, 0.45]	.22 [−0.11, 0.46]
pSTS	.12 [−0.25, 0.39]	.26 [−0.05, 0.49]
precuneus	.17 [−0.18, 0.42]	.14 [−0.20, 0.40]
mPFC (ROI)	.15 [−0.21, 0.42]	**.30 [.01, 0.52]**

Values represent intra-class correlations, with 95 % confidence intervals between square brackets. Significant ICCs are indicated in bold font.

Next, we exploratively ran a model to test for quadratic effects of age, specified in R as:

$$Dependent\ variable \sim poly(Age, 2) + (1|childID) + (1|familyID).$$

We compared these three models to determine the best fitting developmental pattern, before adding a random slope of age to the best fitting model (example provided for model with linear age term), specified in R as:

$$Dependent\ variable \sim poly(Age, 1) + (1 + age|childID) + (1|familyID).$$

For the models with neural activation as outcome variable we added a random slope of age on family level instead of child level, to facilitate model convergence. Only if the model fit was improved by adding random slopes we included the random slopes in subsequent steps. In the next step of our model-building procedure we added main and interactive effects of sex (dummy coded as 0 = male, 1 = female) and IQ in order to examine age effects when accounting for sex and IQ, specified in R as:

$$Dependent\ variable \sim poly(Age, 1) * sex * IQ + (1 + age|childID) + (1|familyID).$$

Finally, for the best fitting model we investigated whether the observed effects of age would remain significant after controlling for a main effect of VIPP condition, specified in R as:

$$Dependent\ variable \sim poly(Age, 1) * sex * IQ + VIPP\ condition + (1 + age|childID) + (1|familyID).$$

We used Akaike information criterion (AIC) and Bayesian information criterion (BIC) to compare the null model to less parsimonious models, with lower AIC and BIC values indicating better model fit. When models were very similar in fit (i.e., only the AIC or the BIC value was lower), the best-fitting model was selected using log-likelihood ratio tests.

Finally, for our additional aim to investigate the co-occurrence of trajectories of neural and behavioral development, we extracted growth parameters (i.e., individual linear slopes) of neural activity for each ROI and of prosocial compensating behavior for each participant. To this end, individual intercepts and slopes were created in R by fitting a linear age model per participant separately (using the lm function in R). From each individual linear age model, we saved the regression intercept and regression coefficient as intercept and slope. These individual intercepts and slopes (i.e., growth parameters) were used in subsequent analyses. We then tested a separate mixed-model for each ROI, with the extracted slopes of neural activity as a fixed effect (neural development), family as a random effect, and slopes of prosocial behavior as outcome variable (prosocial development), specified in R as:

$$Prosocial\ development \sim neural\ development + (1|familyID).$$

If neural development was found to be significantly associated with prosocial development, we subsequently tested the association while controlling for effects of sex and IQ. Any deviations from the preregistered analyses are described in the **Supplementary Materials**.

3. Results

Pearson's correlations were calculated between all measures for the three waves, and a colored correlation matrix can be seen in Fig. 3. We observed no significant associations between prosocial compensating behavior and parent-reported prosocial behavior and empathy. Parent-reported prosocial behavior and empathy however showed significant positive associations at each wave (T1; $r = 0.35$, T2; $r = 0.39$, T3; $r = 0.31$, all $p's < 0.001$).

3.1. Longitudinal trajectories of prosocial behavior

For each measure we separately tested whether age showed a linear or quadratic relationship with prosocial behavior (in the Prosocial Cyberball Game or as reported by parents) and neural activation. AIC and BIC values for all models are listed in Table 4, full model statistics for the best fitting model are reported in **Supplementary Table S3**.

3.1.1. Prosocial compensating behavior

Here we report the best fitting models for prosocial behavior. The scores for prosocial compensating behavior reveal that, on average, participants tossed more balls to player 2 during the Unfair Game than during Fair Game ($M_{T1} = 9.19$, $SD_{T1} = 14.28$; $M_{T2} = 11.27$, $SD_{T2} = 15.86$; $M_{T3} = 13.76$, $SD_{T3} = 11.16$). The linear mixed model procedure revealed a linear effect of age ($b = 1.01$, $SE = 0.21$, $p < .001$) on prosocial compensating behavior (for visualization see Fig. 4, for full model statistics see **Supplementary Table S3**), which revealed an increase of prosocial compensating behavior with increasing age. There was no quadratic effect of age.

3.1.2. Parent-reported prosocial behavior

To test whether our findings are limited to one aspect of prosocial behavior, we additionally investigated developmental trajectories of parent-reported prosocial behavior and empathy. The linear mixed model comparison procedure for parent-reported prosocial behavior revealed a linear effect of age ($b = 0.02$, $SE = 0.01$, $p < .05$, including a random linear slope of age and controlled for a main effect of sex), showing an increase of prosocial behavior with increasing age. There was no quadratic effect of age. The same analysis for parent-reported empathy revealed a significant quadratic effect of age ([linear age] $b = 0.42$, $SE = 0.12$, $p < 0.001$, [quadratic age] $b = -0.02$, $SE = 0.01$, $p < .001$, including a random linear slope of age), showing that empathy increased in middle childhood and then decreases in early adolescence (for visualization see Fig. 4, for full model statistics see **Supplementary Table S3**). The quadratic trajectory of parent-reported empathy was confirmed in sensitivity analyses in two age-split samples. In the sample with participants younger than 10 years, there was a linear increase across age ($b = 0.06$, SE $= 0.03$, $p = .021$), whereas in the sample of participants older than 10 years, there was a linear decrease across age ($b = -0.09$, SE $= 0.03$, $p = .004$).

3.2. Longitudinal trajectories of neural activation

3.2.1. Whole-brain results

First, we examined the whole-brain analysis for the prosocial contrast (Compensating > Tossing) at the three waves. We found no significant pattern of activation during prosocial behavior at T1, nor at T2. The analysis for T3 resulted in significant activation in a cluster that

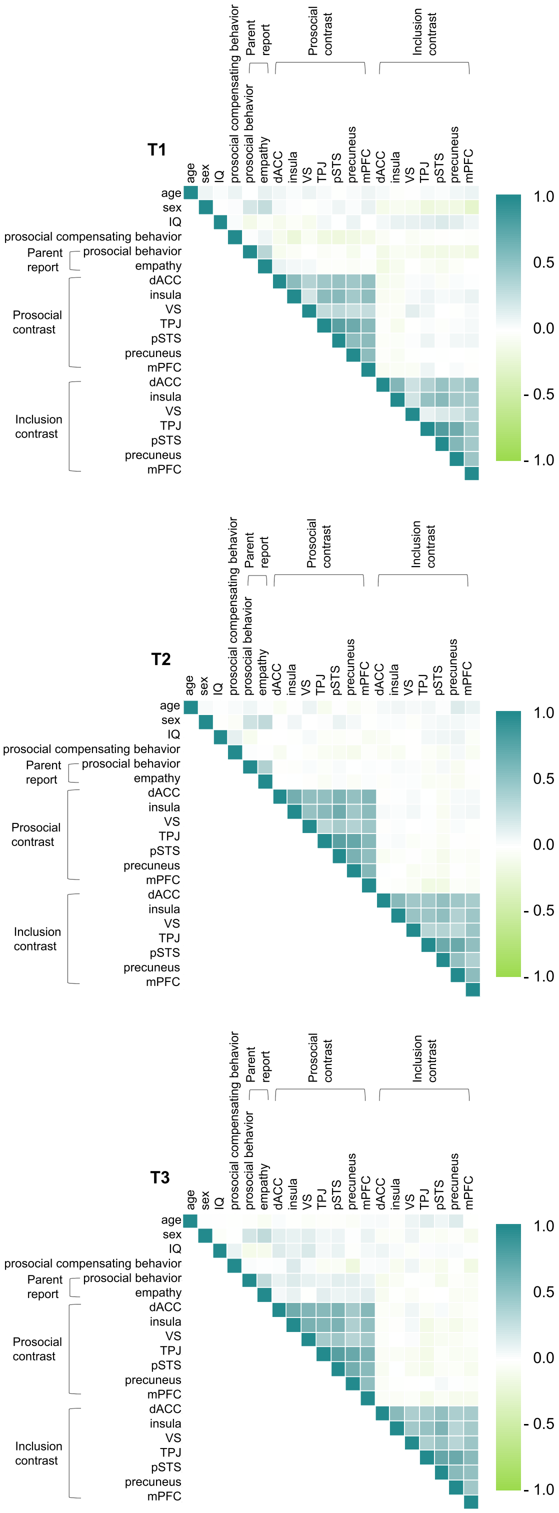

Fig. 3. Correlation matrix of all variables on T1, T2, and T3. For the brain regions, prosocial contrast refers to Compensating > Tossing, and inclusion contrast refers Inclusion > Exclusion.
dACC = dorsal anterior cingulate cortex, VS = ventral striatum, TPJ = temporal parietal junction, pSTS = posterior superior temporal sulcus, mPFC = medial prefrontal cortex.

Table 4
AIC and BIC values for all mixed-models to describe effects of age, and to control for effects of sex, IQ, and VIPP condition.

	Null-model		+ Linear age		+ Quadratic age		+ Random slope of age (varying over participants)		+ Interaction sex * IQ		+ Main effect of VIPP condition	
	AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC	AIC	BIC
Prosocial Cyberball Game												
Prosocial compensating behavior	10,532	10,553	**10,510**	**10,536***	10,511	10,542	10,512	10,548[a]	10,510	10,566[a]	10,516	10,557[a]
Parent-reported questionnaires												
Prosocial behavior	1262.3	1282.9	1252.4	1278.2*	1253.8	1284.7	1226.1	1262.2[a]	**1201.4**	**1268.4**[a,c]	1232.3	1304.4[ac]
Empathy	2465.2	2485.9	2466.6	2492.3	2432.6	2463.5*	2412.3	2453.5[b]	**2376.8**	**2464.4**[b,c]	2380.3	2483.3[b,c]
Parameter estimates ROI												
Prosocial contrast												
dACC	**3649.6**	**3668.0**	3648.4	3671.4	3649.7	3677.3						
insula	**3439.7**	**3458.1**	3441.2	3464.1	3441.7	3469.3						
ventral striatum	3179.1	3197.5	3172.5	3195.5*	3169.1	3196.6*	**3117.6**	**3154.3**[b]	3122.7	3200.8[b,c]	3122.5	3173.1[b,c]
TPJ	**3540.3**	**3558.7**	3542.3	3565.3	3544.2	3571.8						
pSTS	**3384.9**	**3403.3**	3384.3	3407.2	3386.2	3413.7						
precuneus	**4179.6**	**4198.0**	4181.3	4204.3	4182.3	4209.9						
mPFC	**3551.8**	**3570.1**	3553.7	3576.7	3555.3	3582.9						
Inclusion contrast												
dACC	3600.6	3619.0	3587.3	3610.3*	3524.2	3551.8*	**3513.9**	**3550.6**[b]	3521.5	3599.6[b,c]	3517.1	3567.7[b,c]
insula	3224.0	3242.4	3214.2	3237.2*	3186.8	3214.4*	**3181.7**	**3218.5**[b]	3191.1	3269.2[b,c]	3182.9	3233.5[b,c]
ventral striatum	2974.4	2992.8	2961.7	2984.7*	2952.7	2980.2*	**2940.4**	**2977.1**[b]	2948.4	3026.5[b,c]	2946.1	2996.6[b,c]
TPJ	3266.4	3284.8	3263.8	3286.8*	3263.6	3291.2	3262.6	3294.8[a]	3263.7	3314.3[a]	**3261.1**	**3297.9**
pSTS	**3092.6**	**3111.0**	3094.4	3117.4	3094.7	3122.3						
precuneus	3918.4	3936.8	3914.4	3937.4*	3906.3	3933.8*	**3897.8**	**3934.6**[b]	3903.6	3981.7[b,c]	3901.8	3952.3[b,c]
mPFC	**3190.7**	**3209.1**	3191.0	3214.0	3192.3	3219.9						

* n addition to AIC/BIC, log likelihood ratio test indicated that this model had a better fit to the data than the more parsimonious model.

[a] This model included a linear age term.

[b] This model included a quadratic age term.

[c] This model included a random linear slope of age (varying over participants).

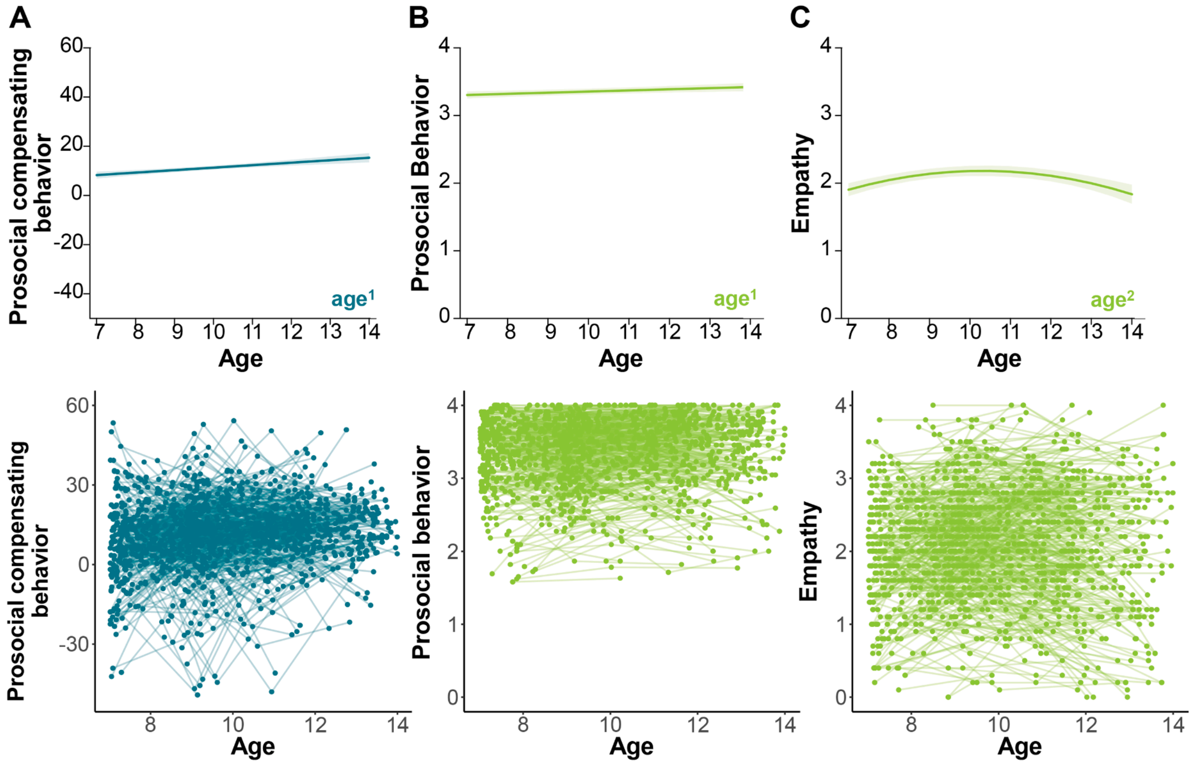

Fig. 4. Effects of age (upper panels) and raw data (lower panels) for (**A**) prosocial compensating behavior, (**B**) parent-reported prosocial behavior, and (**C**) parent-reported empathy. For age effects, solid lines represent predicted values of the best fitting model, ribbon represents the 95 % confidence interval. For raw data, dots represent a data point and connected dots represent one participant.
Note. Age^1 indicates a significant linear effect of age, age^2 indicates a significant quadratic effect of age.

included medial prefrontal cortex (mPFC) and a cluster in the visual cortex (see **Supplementary Table S4** for an overview of the whole brain results).

We also explored the whole-brain analysis for the inclusion contrast (Inclusion > Exclusion) at the three waves. At T1 we found two large clusters; a cluster spanning the dACC, bilateral insula, ventral striatum and supplementary motor area, and a cluster in the visual cortex. At T2 we found four clusters, including a cluster in the dACC and a cluster that included the left insula. At T3 we found five clusters, including a large cluster spanning the dACC and bilateral insula, and two clusters in the middle frontal region (see **Supplementary Table S4**). Results from the whole brain contrasts are visualized in Fig. 5, whole-brain results at an uncorrected threshold are shown in **Supplementary Figure S1**. As the whole-brain analyses revealed a cluster of activation in the mPFC that was slightly different from our a-priori selected mPFC, we additionally performed our ROI analyses on the whole-brain mPFC cluster to explore developmental trajectories. Results of the mPFC cluster derived from the whole brain analyses are reported in the **Supplementary Files** (including **Supplementary Figure S5**) and did not result in different effects compared to the a-priori selected mPFC.

3.2.2. *Prosocial behavior*

As preregistered, we used the same model building procedure to test for developmental trajectories of neural activity in seven ROIs during prosocial behavior. For visualization, condition effects in the prosocial contrast across the three waves are shown in **Supplementary Figure S2**. For activity in the prosocial contrast (Compensating – Tossing), we found a quadratic effect of age for ventral striatum ([linear age] $b = 1.25$, $SE = 0.48$, $p < .05$, [quadratic age] $b = -0.06$, $SE = 0.02$, $p < .05$, including a random slope of linear age, also see Fig. 6). This was best described as a quadratic peak in late childhood (around 10–11 years): a gradual increase in activity during middle childhood, followed by a stabilization in early adolescence. For the other ROIs, no linear or quadratic effect of age was found.

3.2.3. *Social inclusion*

Exploratively, we also tested developmental trajectories of neural activity when feeling socially included on the same seven ROIs. For visualization, condition effects in the inclusion contrast across the three waves are shown in **Supplementary Figure S3**. Here we observed a quadratic effect of age with random linear slopes for dACC ([linear age] $b = -6.58$, $SE = 0.63$, $p < .001$, [quadratic age] $b = 0.31$, $SE = 0.03$, $p < .001$), bilateral insula ([linear age] $b = -3.15$, $SE = 0.49$, $p < .001$, [quadratic age] $b = 0.15$, $SE = 0.02$, $p < .001$), ventral striatum ([linear age] $b = -1.75$, $SE = 0.40$, $p < .001$, [quadratic age] $b = 0.08$, $SE = 0.02$, $p < .001$), and precuneus ([linear age] $b = -2.68$, $SE = 0.78$, $p < .001$, [quadratic age] $b = 0.14$, $SE = 0.04$, $p < .001$, also see Fig. 6**,** for model statistics see **Supplementary Table S3**). For dACC, bilateral insula, and ventral striatum we found a quadratic dip in late childhood: a decrease of neural activity in middle childhood, followed by an increase in activity in early adolescence. For precuneus we also observed a quadratic dip in middle childhood: a gradual decrease in activity in middle childhood, followed by a steeper increase in activity in early adolescence. Finally, we observed a linear effect of age for TPJ (controlled for a main effect of VIPP condition), showing an increase in TPJ activity with age. Finally, we found no linear or quadratic effects of age for mPFC and pSTS.

3.3. *Co-occurrence in longitudinal trajectories*

Finally, to investigate whether trajectories of neural and behavioral development co-occur, we tested whether growth parameters of neural activity were associated with growth parameters of prosocial compensating behavior. First, we tested the association between neural activity in the prosocial contrast (Compensating – Tossing) and prosocial compensating behavior. Here we found no significant association between changes in neural activity and changes in prosocial compensating behavior in any of the seven ROIs (for model comparison see **Supplementary Table S5**). The model that fitted best for the slopes of prosocial compensating behavior was a null-model.

Next, we also explored the association between neural activity in the inclusion contrast (Inclusion – Exclusion) and prosocial compensating behavior. We observed a significant negative association between changes in neural activity in ventral striatum ([Intercept] $b = 0.62$, $SE =$

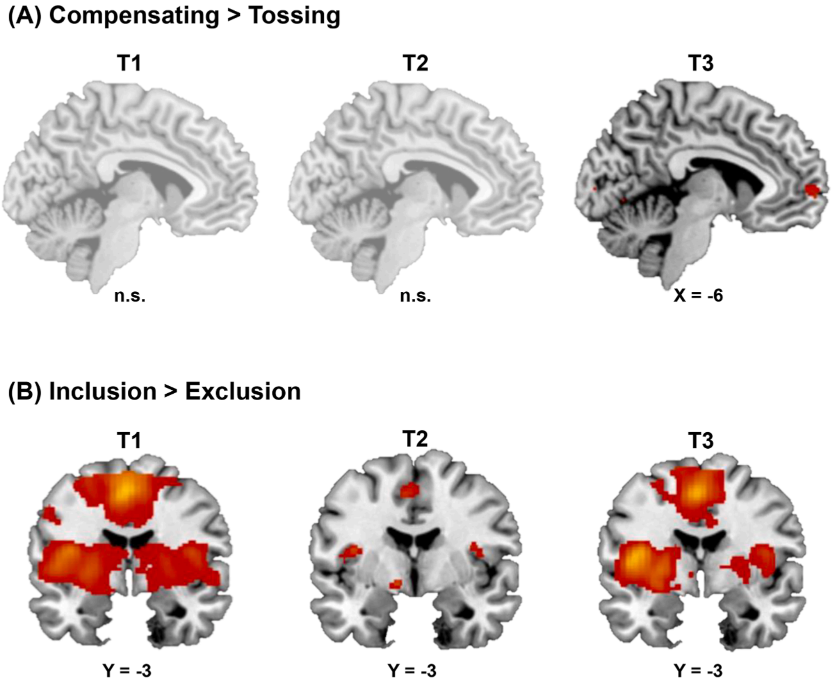

Fig. 5. Whole brain contrasts for (A) Compensating > Tossing and (B) Inclusion > Exclusion across the three waves. Results are reported at a cluster-corrected threshold of $p < .05$ FWE-corrected, with a primary threshold of $p < 0.001$. n.s. = not significant.

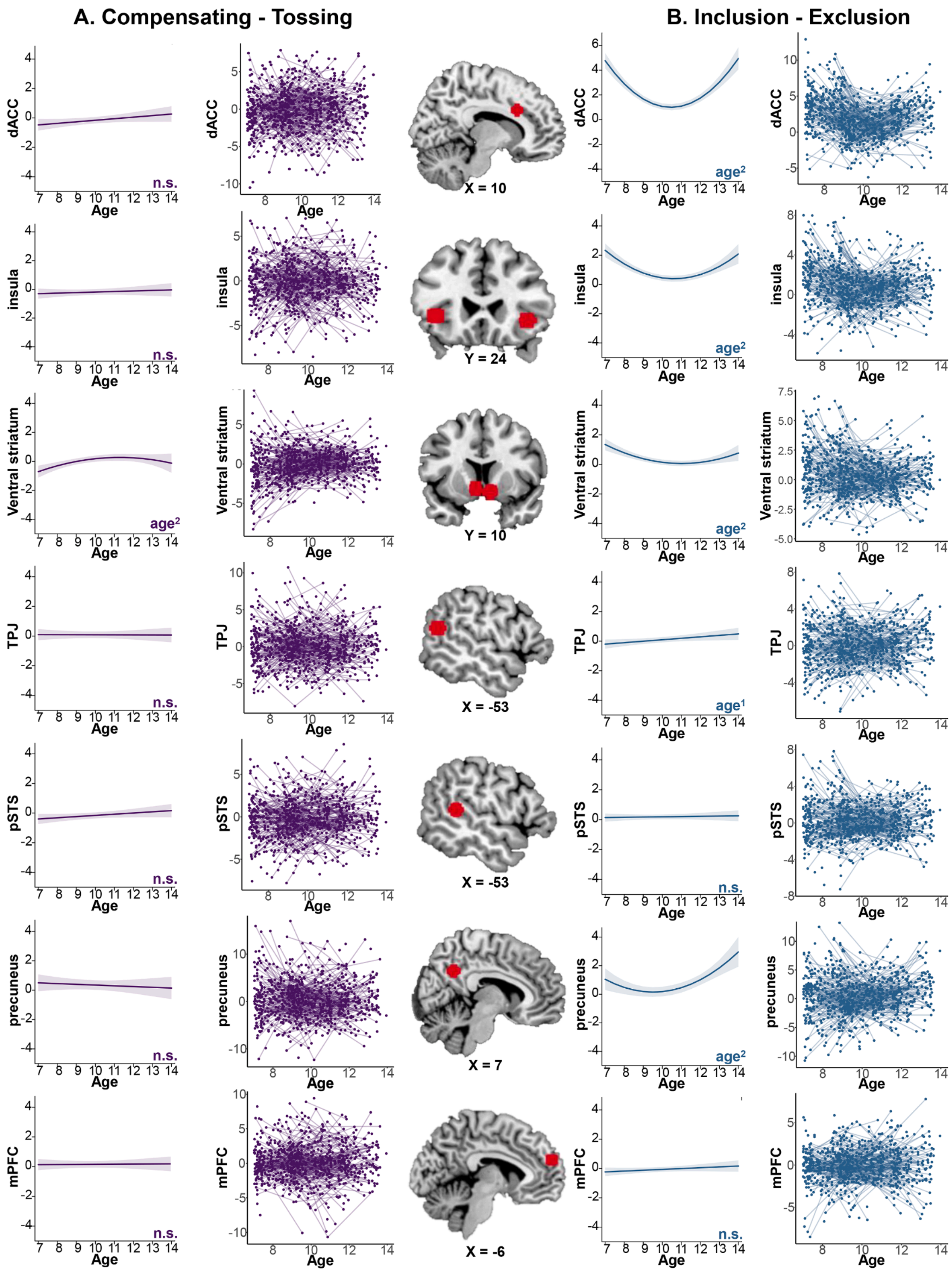

Fig. 6. **(A)** Age effects (left panel) and raw data (right panel) in the prosocial contrast (Compensating – Tossing). **(B)** Age effects (left panel) and raw data (right panel) in the inclusion contrast (Inclusion – Exclusion). For age effects, solid lines represent predicted values of the best fitting model, ribbon represents the 95 % confidence interval. For raw data, dots represent a data point and connected dots represent one participant. dACC = dorsal anterior cingulate cortex; TPJ = temporo-parietal junction; pSTS = posterior superior temporal sulcus; mPFC = medial prefrontal cortex. Values on the Y-axis represent the difference in parameter estimates in the analyzed conditions.
Note. Age^1 indicates a significant linear effect of age, age^2 indicates a significant quadratic effect of age, n.s. indicates no significant effect of age. Plots with age effects are zoomed in to more clearly illustrate the observed effects.

0.34, $p = .07$, 95 % CI [−0.05, 1.28]; [slope VS activity] $b = -0.93$, $SE = 0.35$, $p < .05$, 95 % CI [−1.62, −0.24], $\eta^2_p = 0.03$) and changes in prosocial compensating (for predicted data see Fig. 7, for raw data see **Figure S4**). That is, a stronger longitudinal decrease in ventral striatum activity during social inclusion was associated with a stronger longitudinal increase in prosocial compensating behavior. We also observed a significant negative association between changes in neural activity in mPFC ([Intercept] $b = 0.86$, $SE = 0.33$, $p < .05$, 95 % CI [.21, 1.50];

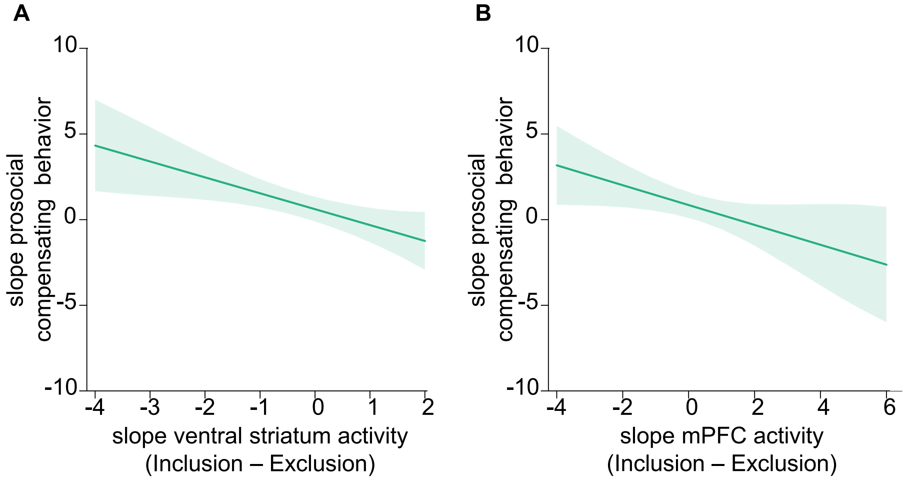

Fig. 7. Slope-slope association between **(A)** ventral striatum activity during inclusion and prosocial compensating behavior and **(B)** mPFC activity during inclusion and prosocial compensating behavior. For ventral striatum as well as for mPFC, a stronger longitudinal decrease in neural activity during inclusion across development was associated with a stronger longitudinal increase in prosocial compensating behavior. Solid lines represent predicted values of the best fitting model, ribbon represents the 95 % confidence interval.

[slope mPFC activity] $b = -0.58$, $SE = 0.28$, $p < .05$, 95 % CI [−1.13, −0.03], $\eta_p^2 = 0.02$) and changes in prosocial compensating (for predicted data see Fig. 7, for raw data see **Figure S4**). That is, a stronger decrease in mPFC activity during social inclusion was associated with a stronger increase in prosocial compensating behavior. No significant associations were observed between changes in neural activity and changes in prosocial compensating behavior in the five other ROIs. The model that fitted best for the slopes of prosocial compensating behavior was a null-model (for model comparisons see **Supplementary Table S5**).

4. Discussion

The transition from childhood to adolescence is a time of continually changing and increasingly complex social landscapes. This pre-registered study examined the behavioral patterns and underlying neural processes associated with the transition from middle childhood to adolescence, an important but relatively understudied developmental phase (Pfeifer et al., 2011). Our results showed three important conclusions. First, both non-costly prosocial compensating behavior and parent-reported prosocial behavior increase with age, whereas parent-reported empathy shows a peak around late childhood (ages 10–11). Second, we found non-linear age effects on neural activity during prosocial behavior (peak in ventral striatum activity) and during social inclusion (dips in dACC, insula, ventral striatum, and precuneus activity) and a linear increase in TPJ activity. Finally, we found post-hoc exploratory suggestions for co-occurrence between changes in social brain activation and changes in prosocial behavior, suggesting that these developmental processes are related. Specifically, a stronger longitudinal decrease in neural activity in ventral striatum and mPFC during inclusion was associated with a stronger longitudinal increase in prosocial compensating behavior. In the discussion, we first review the effects of age on prosocial behavior and social brain activity, followed by an interpretation of the individual differences in brain-behavior trajectories.

4.1. Developmental trajectories

How do children transition into socially competent adolescents? Our first step in addressing this question was by investigating the behavioral patterns of prosociality in the transition from childhood to adolescence. Conceptually, prosocial behavior can be expected to increase with development alongside increases in socio-cognitive and –affective skills, such as perspective taking, mentalizing, moral reasoning, empathy and affect processing (Eisenberg et al., 2005; Crone and Dahl, 2012; Steinbeis and Over, 2017; Lehmann et al., 2022). In line with these findings we found developmental increases in non-costly prosocial behavior as well as in parent-reported prosocial behavior. Despite similar developmental patterns, the correlation between experimental task behavior and parent-reported behavior was not significant. This might reflect that prosocial behavior is sensitive to contextual effects (such as the target to whom prosociality is directed or the state of the individual) as intraclass coefficients were also relatively low, suggesting context-dependent changes at the individual level (Dunfield et al., 2011; El Mallah, 2019; van Ijzendoorn et al., 2010). In contrast, parent-reported prosocial behavior showed relatively high intraclass stability of time and may reflect some stable response bias or more stable parental observations over a larger variety of contexts and longer time periods (Knafo and Plomin, 2006). Interestingly, parent-reported empathy showed a different developmental trajectory than parent-reported prosocial behavior, even though the two constructs are closely related. This possibly showcases their unique biological and environmental influences (van der Meulen et al., 2020). Concretely, the developmental pattern of parent-reported empathy increased in late childhood and decreased in early adolescence. This finding is consistent with other work showing quadratic developmental trajectories of empathy (Lam et al., 2012), even though other studies have also reported an absence of developmental changes in empathy, highlighting mostly individual differences independent of age (Blankenstein et al., 2020; Grühn et al., 2008)). Our more fine-grained developmental analysis of middle childhood may suggest the transition from childhood to adolescence to be an important period for the separable developments of prosocial and empathic behaviors (Crone et al., 2022).

The next goal was to unravel two important building blocks for prosocial behavior using neural analyses, focusing on being socially included and prosocially compensating others who are excluded. Both are considered important dimensions of self-other processes that are involved when responding to needs of others in a social context. We were specifically interested in the unique neural developmental patterns associated with the transition from childhood into adolescence, in regions that have previously been implicated in socio-cognitive processes such as perspective-taking (i.e., TPJ, pSTS, precuneus, mPFC), and in socio-affective processes such as emotional processing (i.e., anterior insula, dACC and VS). In our exploratory analyses towards neural activity during social inclusion, on a whole-brain level we found consistent activation in dACC, insula, and ventral striatum in middle childhood and early adolescence (most pronounced at T1 and T3, respectively), whereas activation patterns in late childhood (T2) were less defined. Indeed, the ROI analyses confirmed quadratic effects of age for dACC, bilateral insula, ventral striatum, and precuneus, with less neural activity in late childhood when feeling socially included, followed by increasing activity in early adolescence. The dACC and bilateral insula have often been associated with the processing of salient social feedback (Davey et al., 2010; Menon and Uddin, 2010), with ventral striatum in particular being associated with reward processing (Delgado, 2007). The finding that these regions show comparable developmental trajectories may indicate the existence of a salience network that may possibly respond to positive social influences over time. Future studies may use network modeling to test whether these regions with similar developmental trajectories are indeed related over time. Moreover, precuneus and TPJ have often been implicated in mentalizing (Blakemore, 2008; Güroğlu et al., 2009; Will et al., 2015), but here we found precuneus and TPJ are also involved in feeling socially included. Most notably, activity in both regions follows a developmental trajectory that suggests increasing activity from early adolescence onwards. Possibly, the involvement of regions traditionally implicated in mentalizing are also involved when thinking about a larger social context that involves feeling socially included by other individuals. It should be noted that receiving the ball (in the social inclusion contrast) versus observing a ball toss (in the social exclusion contrast) involves different task demands, and therefore it is possible that neural activation during social inclusion could also reflect increased attentional demands or action preparations. Future studies should include a subjective measure of feelings of inclusion to help disentangle these possible underlying processes.

Next, we addressed whether similar patterns were observed for prosocial compensation. However, the findings for neural activity during prosocial behavior show different developmental trajectories than those of social inclusion. On a whole-brain level, we observed activation in mPFC in early adolescence (T3), but we found no significant activation during prosocial behavior in middle and late childhood (T1 and T2). Note that we previously reported significant activation in a cluster in posterior cingulate cortex/precuneus during prosocial behavior also at the first time point (T1) in a cross-sectional study (see van der Meulen et al., 2018), at a cluster-corrected threshold. We now analyzed the neuroimaging data in SPM12, instead of SPM8, which resulted in a slightly different selection of participants with regards to excessive motion, leading to minor differences in our findings. Indeed, uncorrected threshold in the **Supplements** reveal clusters of activation in PCC/precuneus and mPFC at T1 and T3. The ROI analyses for mPFC did not confirm a significant developmental increase in activity in mPFC for prosocial compensating. It is possible that developmental changes in neural activation during prosocial compensation occur later in adolescence. Together, these findings highlight that mPFC may be more sensitive to individual differences than to general age patterns in the included age ranges (7–14 years), but this hypothesis should be tested in more detail in future studies including a wider age range extending into late adolescence.

Furthermore, we found that activity in ventral striatum during prosocial behavior shows a quadratic trajectory of change, with a gradual increase in activity during middle childhood followed by a stabilization in early adolescence. This pattern fits earlier work using the Prosocial Cyberball Game, where no ventral striatum activity was reported in middle childhood (van der Meulen et al., 2018) and ventral striatum showed increased activity in early adulthood (van der Meulen et al., 2016). Possibly, ventral striatum is most strongly involved in prosocial compensating behavior during adolescence and early adulthood, which mirrors the previously reported pattern of increased ventral striatum activity for reward during adolescence (Braams et al., 2015; Schreuders et al., 2018). However, this study did not include data from older adolescents, and therefore, this question remains to be investigated in future research. Finally, previous work has demonstrated that heightened ventral striatum activity during prosocial behavior is associated with decreases in risk taking behavior over time (Telzer et al., 2013). Future studies should investigate whether individuals who show an earlier peak in ventral striatum activity for prosocial behavior are relatively less likely to engage in risky behavior, compared to those who experience a late peak in ventral striatum activity.

Finally, we explored the co-occurrence between behavioral and neural trajectories of change, to further study the close interplay of social inclusion and prosocial behavior. Our findings revealed a negative association between changes in prosocial behavior and changes in ventral striatum and mPFC activity during social inclusion. That is, stronger decreases in neural activity in ventral striatum and mPFC during inclusion were associated with stronger increases in prosocial compensating behavior, and vice versa. The ventral striatum has been implicated as important region in the neural reward system (Delgado, 2007). The involvement of ventral striatum in this brain-behavior association might therefore speculatively indicate that individuals who over time experience less strong personal reward feelings during social inclusion (possibly indicated by decreased ventral striatum activity) show an increase in prosociality over time. This could possibly reflect a change from self-motivation to other-motivations. Including a measure of feelings of personal reward in future studies is needed to shed light on this possible interpretation. Even though we observed no relations between insula or dACC activity and prosocial behavior as expected (Schreuders et al., 2018; van der Meulen et al., 2018), these regions were co-activated in the social inclusion contrast, and therefore may be part of the larger inclusion processing network. A similar finding was observed for mPFC in this brain-behavior association. Even though we observed no effect of age on mPFC activity on a group level, individual changes in mPFC activation showed a negative association with individual changes in prosocial compensating behavior. Again, individuals who are less focused on personal social inclusion over time may show stronger increases in prosociality, and vice versa. These preliminary findings should be examined in more detail in future studies but suggest that social inclusion of self and prosocial behaviors towards others may be related processes (also see Crone and Fuligni, 2020). Together, if replicated, these findings on brain-behavior associations would increase our understanding of within-group variance in adolescent neural and behavioral social development (also see Foulkes & Blakemore, 2018).

The findings of the current study may help in theory building about the functions of the developing social brain (Blakemore, 2008; Frith and Frith, 2003). First, this study reveals already pronounced linear and non-linear changes in social brain functions in the age range of 7–14 years old. This development fits well with the processes that characterize the transition from middle childhood into adolescence (DeFries et al., 1994; Del Giudice et al., 2009), such as increased awareness of own mental states (Mah and Ford-Jones, 2012) and internalization of social norms and values (McAuliffe et al., 2017). Whereas previously social brain regions involved in mentalizing (mPFC, precuneus, STS and TPJ) have been examined relatively separately from reward and salience brain regions (dACC, insula, ventral striatum), the current study suggests a similar role for these regions in the development of prosocial behavior. Both activity in mPFC and ventral striatum during social inclusion showed a longitudinal relation with prosocial compensating behavior. The converging role of the mPFC and ventral striatum in the processing of social inclusion and their association with prosocial behavior fits well with the hypothesis that mPFC might serve as a hub region (working together with ventral striatum, amongst others) for the integration of neural processes that underlie social cognition (Crone et al., 2020; Crone and Fuligni, 2020). A previous study reported that functional connectivity between mPFC and ventral striatum declines during adolescence and adulthood (van Duijvenvoorde et al., 2016), therefore an important direction is to investigate the collaborative role of mPFC and ventral striatum in social cognition in future studies. Finally, we observed no pronounced developmental trajectories for the other social brain regions (dACC, insula, TPJ, pSTS, and precuneus) during prosocial behavior. This might indicate that these regions show larger individual variability in neural activity over time, which might be influenced by previous personal experiences (e.g., van Harmelen et al., 2014; van Schie et al., 2017). To further investigate this, future studies could take environmental and social factors into account.

4.2. Strengths and limitations

This study had several strengths. First, the longitudinal design of the L-CID study and its large sample size allowed us to investigate behavioral patterns and underlying neural processes across three waves. More specifically, our study covered development from middle childhood to early adolescence, a relatively understudied developmental phase. Second, we used a multi-method approach to prosocial behavior, thereby measuring prosocial behavior in a very specific experimental setting as well as including parent reports. Future research might further expand upon these findings by including additional measures of prosocial behavior, such as donating or sharing. Additionally, several limitations should also be noted. First, we only inspected findings from the Unfair Game of the Prosocial Cyberball Game (as no neuroimaging data was available for the Fair Game at T1), whereas prior studies also included Fair Game comparisons (Tousignant et al., 2017; van der Meulen et al., 2016). Further insight in the neural processes underlying prosocial compensating behavior might be gained by investigating the Fair Game in addition to the Unfair Game across multiple waves. Second, parent-reported prosocial behavior showed ceiling effects, that may possibly reduce observed age-effects. Additionally, it is possible that the decrease in parent-reported empathy in early adolescence reveals a separate component of social behavior. For example, it may reflect that parents evaluate empathy in the family context whereas the PCG may capture prosocial behavior to unknown others outside the family context. Third, our participants were twins, and although we took this dependency into account, their social context and therefore their reactions to social situations were maybe less comparable to non-twin siblings and singletons (Thorpe and Danby, 2006). Additionally, it should be noted that we observed low intra-class correlations for neural activity, which reflects low test-retest reliability concerns for the field of developmental neuroscience in general (Herting et al., 2018). Given the two-year interval between waves, it is possible that low ICCs reflect actual changes in development in addition to low reliability in fMRI measures. Future studies should aim to disentangle these two components by replicating the current study with shorter and longer time intervals. Finally, given that the neural analyses on the social inclusion contrast were examined in non-preregistered exploratory analyses, we emphasize the need for replication of the slope-slope associations. Additionally, although extracting individual slopes has been used and recommended in prior research (e.g., Blankenstein et al., 2020; Pfister et al., 2013; van der Cruijsen et al., 2023), it is limited by the method not taking into account the broader distribution that the subjects are drawn from. Therefore, we recommend the use of different modeling frameworks in future research.

5. Conclusion

In conclusion, our results provide three important insights. First, prosocial behavior increases from middle childhood into adolescence, whereas empathy shows a distinctly different developmental trajectory. Second, neural activity during social inclusion and prosocial behavior shows that the social brain shows noticeable functional development during the transition from middle childhood into early adolescence, which might serve as an underlying mechanism for the large-scale social changes that characterize this period in human development. Finally, co-occurrence between development in brain and behavior suggests that neural processing of own social inclusion may be associated with prosocial behavior over time, and that individuals who show signs of decreased self-focus (as shown in decreased mPFC and ventral striatum activity) may be the ones who seem more willing to show prosocial behavior towards others. Taken together, these findings highlight the importance of social inclusion and prosocial behavior in children's social development, which can contribute to our understanding of how children grow up to be socially competent adolescents.

Data and code availability

Study materials and code that support the findings of this study will be made available after acceptance in DataverseNL through https://doi.org/10.34894/ZCX8WS. Data is not publicly available, because data cannot be fully anonymized. Data will become available upon request after signing a formal data sharing agreement. Unthresholded statistical maps of group level MRI data for the reported contrasts are available in NeuroVault through https://neurovault.org/collections/SMDVTLJH/.

CRediT authorship contribution statement

Mara van der Meulen: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Simone Dobbelaar:** Investigation, Formal analysis, Writing – review & editing. **Lina van Drunen:** Investigation, Writing – review & editing. **Stephan Heunis:** Resources, Writing – review & editing. **Marinus H. van IJzendoorn:** Methodology, Writing – review & editing, Funding acquisition. **Neeltje E. Blankenstein:** Methodology, Formal analysis, Writing – review & editing. **Eveline A. Crone:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

None.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.120445.

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