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Social exclusion and punishment of excluders: Neural correlates and developmental trajectories

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A B S T R A C T

Social exclusion is a distressing experience and can result in a reduction of prosocial behavior. In this fMRI study we examined the neural networks involved in social exclusion and subsequent fairness considerations across adolescent development. Participants from 3 age groups (10–12, 14–16 and 19–21 year olds) participated in the study and performed two tasks; first, participants played Cyberball to induce feelings of social inclusion and exclusion, followed by a Dictator game in which participants were asked to divide coins between themselves and the players who previously included or excluded them. Results revealed a network of regions associated with social exclusion, which involve the medial prefrontal cortex (mPFC)/ventral anterior cingulate cortex (vACC), subgenual ACC and the lateral PFC, as well as the insula and the dorsal ACC. Although social exclusion generated strong distress for all age groups, 10–12 year olds showed increased activity in the subgenual ACC in the exclusion game, which has been associated in previous studies with negative affective processing. Results of the Dictator game revealed that all age groups selectively punished the excluders by making lower offers. These offers were associated with activation in the temporoparietal junction (TPJ), superior temporal sulcus (STS) and the lateral PFC. Age comparisons revealed that adults showed additional activity in the insula and dorsal ACC when making offers to the excluders. The results are discussed in the light of recent findings on neural networks involved in social exclusion and the development of social brain regions.

Introduction

Humans are strongly motivated to be included by others and to establish a sense of belonging. Indeed, social exclusion has been found to be highly distressing and to result in feelings of hurt (Baumeister and Leary, 1995; Eisenberger et al., 2003; Van Beest and Williams, 2006). The notion that social exclusion leads to strong negative feelings is further supported by neuroimaging studies which have shown that social exclusion elicits activity in brain regions involved in affective processing and physical pain (see Eisenberger and Lieberman, 2004).

Using Cyberball (Williams and Jarvis, 2006), a paradigm in which participants get ostracized by two other players during a ball-tossing game, it was shown that activation in the dorsal anterior cingulate cortex (dACC), a region involved in the experience of physical pain, correlates positively with self-reported distress during exclusion, whereas activation in the ventrolateral prefrontal cortex (vlPFC) correlates negatively with distress (Eisenberger et al., 2003). In subsequent studies, it was shown that a broader network of areas is engaged during social exclusion, including the insula, medial prefrontal cortex (mPFC), ventral ACC (vACC), subgenual ACC, and the posterior cingulate cortex (e.g., Bolling et al., 2011; DeWall et al., 2010; Kross et al., 2007; Lieberman and Eisenberger, 2009; Sebastian et al., 2011).

Given the strong need for social belonging, social exclusion is likely to influence subsequent behavior and coping. Indeed, behavioral studies have shown that social exclusion leads to an increase in reaffilitive behavior in new social encounters to enhance the opportunity for inclusion (Bernstein et al., 2008; Lakin et al., 2008). Further, studies reported a link between social exclusion and a reduction of prosocial behavior (Twenge et al., 2001, 2007), and showed that behavioral responses are modulated by prior interactions; people are more willing to cooperate with others who previously included them and act less prosocially to people who excluded them (Hillebrandt et al., 2010; Maner et al., 2007). These findings indicate that humans have the need to regain a sense of control after being excluded and act less cooperative towards the excluders, which may reflect a desire to punish the excluders.

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Prior neuroimaging studies have shown that fairness considerations in decision-making, as measured with a variety of economic games, are associated with activation in different neural networks (see Rilling and Sanfey, 2011). First, brain regions involved in social decision-making overlap with the (social) pain network, including the insula and dACC. In particular, these regions are believed to be responsive to social norm violations and to mediate aversive responses to inequity (Rilling and Sanfey, 2011; Sanfey et al., 2003). Second, brain regions are reported which are important for understanding the intentions of others, such as the temporoparietal junction (TPJ), and regions implicated in cognitive and emotional control, including regions of the PFC (Güroğlu et al., 2010; Sanfey et al., 2003; Van den Bos et al., 2011). Thus, it is to be expected that these networks are also involved in fairness considerations towards individuals who have previously excluded the participant. The first goal of this study was to identify the neural networks which are sensitive to social exclusion and subsequent punishment behavior.

While social exclusion is a significant social threat for all ages (Baumeister and Leary, 1995), adolescence is believed to be characterized by a heightened sensitivity to rejection by peers (e.g., Sebastian et al., 2010a). The transition into adolescence is marked by an increase in peer orientation, filling the need for peer acceptance (Steinberg and Morris, 2001). In addition, it has been suggested that adolescent changes in social orientation co-occur with structural and functional changes in the brain (e.g., Blakemore, 2008; Nelson et al., 2005). To date, only a handful of studies examined adolescents' neural responses to peer rejection (e.g., Gunther Moor et al., 2010; Masten et al., 2009; Sebastian et al., 2011). One study by Sebastian et al. (2011) demonstrated that activity in the vlPFC was higher in adults compared to adolescents during the exclusion game of Cyberball, suggesting that adults might be better able to regulate the negative feelings associated with exclusion. In another study using Cyberball in 12–13 year olds, Masten et al. (2009) showed that activity in the subgenual ACC corresponds with greater exclusion-related distress, whereas activity in the ventral striatum correlated negatively with distress; a pattern of neural activity suggested being unique to adolescents. Thus, prior studies have suggested that the neural mechanisms, which are responsive to social exclusion, differ between adolescents and adults, but the developmental time course remains poorly understood. The second goal of this study was therefore to extend these prior studies by testing the impact of social exclusion on brain activity across a broader age range, and to test whether adolescents and adults differ in the way they respond to negative peer interactions in a subsequent allocation game.

To achieve the goals of this study, participants performed two tasks in a fixed order in the MRI scanner. First, participants played Cyberball, which started with an inclusion game of fair play, followed by an exclusion game. Each game was played with two novel age-matched peers. The second task was designed to test whether fairness judgments would be modulated by previous encounters with those people who included or excluded the participants. Both tasks were administered in three age groups aiming to test for different phases across adolescent development: 10–12 year olds, 14–16 year olds and 19–21 year olds.

Characteristic for prior fMRI studies using Cyberball is that they used a block design, which provided an index of the overall exclusion experience and the overall inclusion experience. In the current study brain responses were distinguished for events on which participants did not receive the ball within the inclusion and the exclusion game (see also Crowley et al., 2010), and events on which participants received the ball. An advantage of this design is that it removes potential motor responses associated with playing the ball and that it enables us to test whether neural responses associated with ‘not receiving the ball’ would be sensitive to the context of the game. In particular, it has previously been suggested that the exclusion game may elicit a reaction of violated expectations of fair play, as well as exclusion-related distress (Eisenberger and Lieberman, 2004; Somerville et al., 2006, 2010). We anticipated that rejection events in general would be associated with activity in brain regions involved in the affective processing of negative social events, such as the mPFC/vACC, subgenual ACC, and the vlPFC. These regions are also reported in Cyberball studies with alternating blocks of inclusion and exclusion, which have reduced the possibility of expectation violations (Bolling et al., 2011; Sebastian et al., 2011). Second, we hypothesized that the continuous experience of being excluded (exclusion game) would elicit stronger activity in the dACC and the insula; both regions are believed to be implicated in expectancy violations, pain processing and negative affect (e.g., Eisenberger and Lieberman, 2004; Etkin et al., 2011; Shackman et al., 2011; Somerville et al., 2006).

Cyberball was immediately followed by a Dictator game, in which participants were instructed to divide coins between themselves and the players of the inclusion game, players of the exclusion game and two novel players. Previous studies have shown that people tend to punish social norm violations (Singer et al., 2006) and are less willing to cooperate with people who have previously rejected them (Hillebrandt et al., 2010; Maner et al., 2007). Accordingly, we predicted that participants would select lower offers with higher self-gain to the players who previously excluded them and more fair offers to the players they encountered during fair play. Furthermore, we hypothesized that punishment of excluders would engage regions implicated in social-decision making, including the TPJ, dACC, insula and the lateral PFC (Rilling and Sanfey, 2011).

With regard to Cyberball, we predicted that social exclusion would result in feelings of hurt in all age groups (Sebastian et al., 2010a) that would be most pronounced in early adolescence, possibly related to the onset of puberty which is associated with a reorganization of the brain (e.g., Forbes and Dahl, 2010; Nelson et al., 2005). Further, we predicted that this increased sensitivity to peer rejection would be accompanied by increased activity in brain regions associated with the experience of negative affect (e.g., subgenual ACC: Masten et al., 2009), and/or less activation in brain regions involved in affect regulation (e.g., vlPFC: Sebastian et al., 2010b, 2011). With regard to the Dictator game we hypothesized that early adolescents would show a higher tendency to punish the excluders. This hypothesis comes from studies suggesting that with increasing age adolescents are better able to control their negative emotions related to exclusion (Sebastian et al., 2011), and to take into account the perspectives of others (e.g., Güroğlu et al., 2009; Van den Bos et al., 2010). In addition, there is evidence that brain regions involved in social-decision making, including the TPJ and regions of the PFC, show a protracted development, suggesting an increased involvement of these regions with advancing age (Van den Bos et al., 2011).

Methods

Participants

Fifty-three healthy, right-handed volunteers were included in the study. Data of two additional participants (10-year-old boy, 11-year-old girl) were excluded from the analyses due to excessive head movement (>3 mm). To examine developmental changes in distinct phases of adolescent development, we recruited participants from three age groups: twenty-two 10–12 year olds (early adolescence; 15 female; mean age = 11.8, $SD = .87$), sixteen 14–16 year olds (mid adolescence; 8 female; mean age = 15.74, $SD = .74$) and fifteen 19–21 year olds (young adults; 8 female; mean age = 20.38, $SD = .85$). A chi-square analysis confirmed that gender distribution did not differ between age groups (X^2 (2) = .15, $p = .48$). All participants reported to be healthy with no history of neurological or psychiatric disorders. For participants younger than 18 years parents filled out the Child Behavior Checklist (CBCL; Achenbach, 1991) to confirm the absence of psychiatric symptoms. Participants and primary caregivers (for minors) gave informed consent for the study and received fixed payment for participation. All procedures were approved by the Medical Ethics Committee of the University Medical Center.

To assess pubertal development, a picture-based interview about puberty was administered to participants in the two youngest age groups (PBIP; Shirtcliff et al., 2009). Results revealed a significant difference in puberty levels between participants aged 10–12 ($M=2.52$, $SD=.75$) and participants aged 14–16 year old ($M=4.18$, $SD=.63$; $t(1,36)=52.29$, $p<.001$), confirming that the two age groups reflect distinct phases of adolescent development. All participants completed the WAIS or WISC intelligence subscales similarities and block design (Wechsler, 1991, 1997) to obtain an estimate of their intellectual functioning (IQ). There were no significant differences in IQ between the different age groups, $F(2,52)=.38$, $p>.6$.

Design and procedure

Participants performed two tasks in the MRI scanner using a fixed order. First, participants played Cyberball, which started with an inclusion game followed by an exclusion game to induce feelings of social inclusion and exclusion, respectively. Cyberball was immediately followed by a Dictator game in which participants were asked to divide coins between themselves and the players of the inclusion game, players of the exclusion game and two novel players. In Fig. 1 a schematic overview of the experimental procedure is presented.

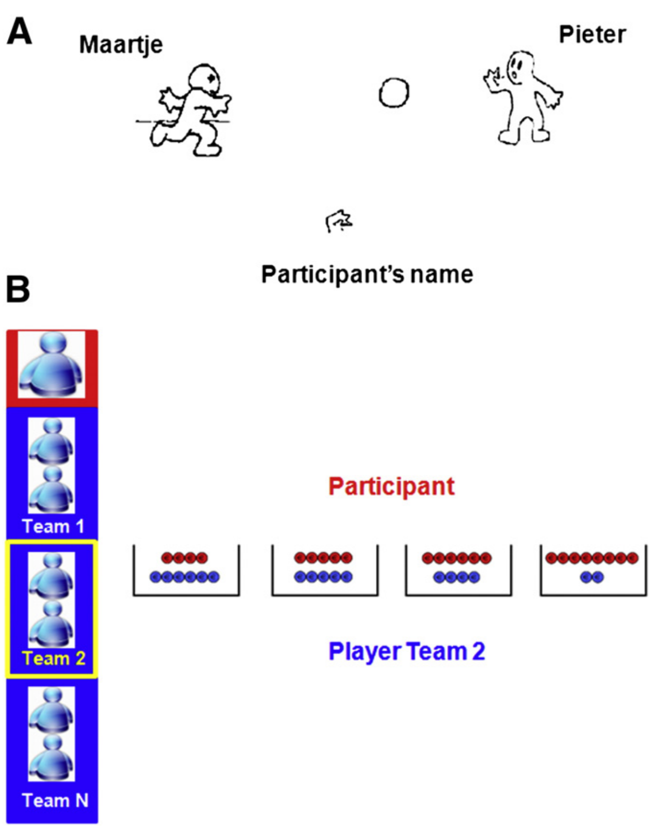

Fig. 1. Schematic presentation of the experimental procedure. A) Visual display of Cyberball: Participants are displayed as a cartoon hand at the bottom of the screen and the two other players as icons in the upper corners of the screen. B) Visual display of the Dictator game: On each round participants were asked to divide 10 coins between themselves and a player of Team 1 (includers), Team 2 (excluders), or Team N (two novel age-matched peers) (here Team 2). Participants could choose between four distributions (4–6, 5–5, 6–4, and 8–2), visually presented as buckets (red coins for the participant, blue coins for the other player).

Cyberball

Before playing Cyberball participants were presented with an instruction screen explaining that they would play an online virtual ball-tossing game with two age-matched peers. In addition, participants were led to believe that this was a study about the relation between mental visualization and task performance and that they had to try to imagine the ball-tossing game as vividly as they could (e.g., Van Beest and Williams, 2006). The experimenter repeated the instructions using the intercom device in the MRI scanner.

During Cyberball participants saw an animated ball-tossing game. The two other players were depicted as animated cartoon icons in the upper corners of the screen accompanied by two fictitious names (one male and one female player). In reality, the actions of these players were determined by the computer. Participants were displayed as an animated hand at the bottom of the screen labelled with their own name (Fig. 1). Participants started with an inclusion game in which they received the ball in 33% of the throws (i.e., fair play). Once receiving the ball, participants could throw the ball to one of the players by pressing a button on a left or right response box using their index fingers. The inclusion game was followed by an exclusion game in which participants received the ball only once at the beginning, but then got ostracized. Before the start of the exclusion game, participants were instructed that they would play a similar ball-tossing game with two novel players, which was made explicit by two other fictitious names.

Both Cyberball games consisted of a total of 30 ball tosses and were administered in two separate runs that lasted for approximately 5 min each. While the duration of each ball toss was fixed to 2 s, a random jitter interval (between 100 and 4000 ms) was added to account for the reaction time of a real player. To further increase credibility, both games started with a loading screen notifying that 'the computer was trying to connect to the other players'. The fictitious names used in the Cyberball games were counterbalanced between participants.

Dictator game

Cyberball was followed by a separate single-run Dictator game. Participants were instructed that this was an online game in which they could divide coins between themselves and one of the players of three teams; players with whom they had played the first Cyberball game (Team 1), players which whom they had played the second Cyberball game (Team 2), and a team of 2 novel players (Team N). In addition, participants were informed that they would play multiple rounds against each team in a random order and that at the end of the experiment the computer would randomly select one offer for each team, which would be converted to real money outcomes.

On each round, participants could choose from four distributions: four coins for themselves and six for the other (4–6), five for themselves and five for the other (5–5), six for themselves and four for the other (6–4) and eight for themselves and two for the other (8–2). The distributions were visually presented as buckets and the location of the four buckets differed randomly across trials. On each round participants were informed whether they were playing against a player of Team 1, Team 2 or Team N, which was made explicit in two ways; 1) the opposing team was displayed in yellow on the left side of the screen and 2) the label 'Player of Team 1'/'Player of Team 2'/'Player of Team N' appeared in the center of the screen (Fig. 1).

Each round of the Dictator game started with a fixation cross (jittered between 600 and 8000 ms), followed by the presentation of the four buckets and announcement of the opposing team. The duration of each trial was 7 s, but participants were required to give a response within a 6 s timeframe. If they failed to respond within the given timeframe, the message 'Too late!' was presented for 1 s. Responses could be made by pressing a button with the index and middle fingers of both hands. Following the response, the bucket that was selected by the participant was underlined for the remaining length of the trial. Participants played 10 rounds for each team in a random order, yielding a total of 30 trials. The task lasted for approximately 5 min in total.

Need satisfaction and mood ratings

After each Cyberball game participants were asked to complete a set of 16 questions assessing their mood and need satisfaction during the game. The same questions were also administered out of the scanner after they had completed the Dictator game, but then they were asked to assess their current mood and need satisfaction. Participants received eight items of the Need Threat Scale (Van Beest and Williams, 2006), which included ratings of self-esteem, belonging, meaningful existence and control (two questions for each need), and eight mood items (feeling good/bad, happy/sad, relaxed/tense, and friendly/unfriendly) (Sebastian et al., 2010a). After the exclusion game of Cyberball participants also completed four questions assessing their intentions to punish the excluders (how much do you want to punish, to harm, to help or to injure the players?). All items were rated from 1 ('not at all') to 5 ('very much').

fMRI data acquisition

Prior to scanning, participants were familiarized with the scanner environment using a mock scanner. Scanning was performed using a 3.0-Tesla Philips Achieva scanner at the University Medical Center. Head motion was restricted using foam inserts that surrounded the head. Functional data were acquired using T2*-weighted Echo-Planar Images (EPI) (TR = 2.2 s, TE = 30 ms, slice-matrix = 80 × 80, slice-thickness = 2.75 mm, slice gap = 0.28 mm, field of view (FOV) = 220) during three functional runs. The two first volumes of each run were discarded to allow for equilibration of T1 saturation effects. After the functional runs, high-resolution T2-weighted images and high-resolution T1-weighted anatomical images were obtained.

fMRI data analysis

Data were analyzed using SPM5 (Wellcome Department of Cognitive Neurology, London). Images were corrected for differences in timing of slice acquisition, followed by rigid body motion correction. Preprocessing further included normalization to EPI templates and spatial smoothing with an 8-mm full-width half-maximum Gaussian kernel. The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basic functions, and resampled the volumes to 3 mm cubic voxels. Movement parameters never exceeded 1 voxel (<3 mm) in any direction for any subject or scan. Average head movement (in mm) for each functional run was as follows; 1) inclusion game: .07 for 19–21 year olds, .07 for 14–16 year olds, and .11 for 10–12 year olds, 2) exclusion game: .08 for 19–21 year olds, .10 for 14–16 year olds, and .15 for 10–12 year olds, and 3) dictator game: .08 for 19–21 year olds, .11 for 14–16 year olds and .16 for 10–12 year olds. Even though movement was higher in the youngest age group for each functional run (all $ps < .05$), the total amount of movement was minimal; the maximum movement parameter never exceeded 3 mm for all scans.

Statistical analyses were performed on individual participants' data using the general linear model in SPM5. The fMRI time series data were modelled by a series of events convolved with a canonical hemodynamic response function (HRF). Contrary to previous neuroimaging studies using a block design for Cyberball, BOLD responses were distinguished for events on which participants did not receive the ball for both the inclusion and the exclusion game, and events on which participants received the ball. The onset of ball movement was used to model the data with zero duration. For the inclusion game ball tosses were divided into 3 conditions: 'receiving the ball', 'not receiving the ball' and 'playing the ball'. For the exclusion game all ball tosses were qualified as 'not receiving the ball', except for the first two trials (1 trial of receiving the ball, 1 trial of playing the ball). In a second model the 28 'not receiving the ball' events of the exclusion game were divided into three blocks (resp. 8, 10, and 10 trials). For the analyses of the Dictator game the onset of each round was modelled as a separate event with zero duration. Analyses distinguished three conditions related to decisions of the participants for the opposing teams: Team 1, Team 2 and Team N. For the purpose of this study, we focused our analyses on brain areas that were differentially sensitive to making an offer to Team 1 or Team 2.

For both experimental paradigms, modelled events were used as covariates in a general linear model, along with a basic set of cosine functions that high-pass filtered the data. The least-squares parameter estimates of height of the best-fitting canonical HRF for each condition were used in pair-wise contrasts. At the group level, contrasts between conditions were computed by performing one-tailed *t*-tests, treating participants as a random effect. Age-related differences were explored by conducting voxelwise ANOVAs with age group as a between-subjects factor. First, we tested for linear age-related trends by performing conjunction analyses (linear decrease $[1\ -1\ 0] \cap [0\ 1\ -1]$ and their inverse). Next, it was examined whether activation differed specifically in one age group relative to the other two age groups (groups modelled as $[2\ -1\ -1]$, $[-1\ 2\ -1]$, $[-1\ -1\ 2]$ and their inverse). We further tested for individual differences in neural activity by conducting regression analyses with self-report ratings and behavioral responses as regressors. In addition, we tested for individual differences by extracting BOLD activity in regions of interest (ROIs) from the main contrasts across all participants. Unless otherwise indicated, all fMRI analyses were conducted at the commonly used threshold of $p < .001$ uncorrected, with a 10 voxel threshold. We also examined whether results remained significant using FDR correction ($p < .05$, >10 voxels). The Marsbar toolbox for SPM5 (Brett et al., 2002) was used to extract BOLD activity in ROIs. All brain coordinates are reported in MNI atlas space.

Results

Need satisfaction and mood

Self-report ratings were administered at three time-points; immediately following the inclusion game, the exclusion game and after the Dictator game. These ratings were analyzed using repeated-measures ANOVAs with condition (inclusion, exclusion, and post Dictator game) as within-subjects factor. Separate analyses for each of the four needs (belonging, control, self-esteem, and meaningful existence) resulted in main effects of condition for all needs, with lower need satisfaction after the exclusion game (all $ps < .001$). Next, the ratings on the four needs were averaged to create an overall index of need satisfaction at each time-point (see Table 1). Results on these overall ratings revealed a main effect of condition, $F(2,100) = 283.67$, $p < .001$), showing lower need satisfaction (i.e., greater need threat) after the exclusion game. No main effect of age or interaction with age group was found.

Similar analyses were conducted on the mood ratings. Again, results revealed main effects of condition for all mood constructs (good/bad, happy/sad, tense/relaxed, and friendly/unfriendly), with lower mood ratings after the exclusion game (all $ps < .001$). Further, the ratings on the mood constructs were averaged to create an overall index of mood at each time-point (see Table 1). Results on overall mood ratings revealed a main effect of condition, $F(2,98) = 117.64$, $p < .001$, showing lower mood after the exclusion game. No main effect of age or interaction with age group was found.

Table 1
Means of overall need satisfaction and mood ratings for each age group after the inclusion game, exclusion game and following the Dictator game (SD in parentheses). Lower scores indicate lower need satisfaction and lower mood (scale from 1 to 5).

	Need satisfaction	Mood
10–12 year olds		
Inclusion	3.62 (0.74)	4.26 (0.46)
Exclusion	1.76 (0.31)	2.75 (0.81)
Post Dictator game	4.23 (0.59)	4.52 (0.44)
14–16 year olds		
Inclusion	3.56 (0.72)	4.18 (0.47)
Exclusion	1.63 (0.68)	2.83 (0.76)
Post Dictator game	3.97 (0.48)	4.05 (0.55)
19–21 year olds		
Inclusion	3.81 (0.76)	4.13 (0.48)
Exclusion	1.78 (0.41)	3.09 (0.67)
Post Dictator game	3.98 (0.48)	4.33 (0.35)

Behavioral results Dictator game

We submitted the number of offers to a repeated-measures ANOVA with offer type (4–6, 5–5, 6–4, and 8–2) and team (Team 1, Team 2, and Team N) as within-subject factors and age group as between-subjects factor. Results revealed a main effect of offer type, $F(3,150) = 29.85$, $p < .001$, and a significant interaction between team and offer type, $F(6,300) = 41.74$, $p < .001$. No interactions with age group were found. As can be seen in Fig. 2, players from Team 1 and Team N mostly received fair offers (5–5), while the players who previously excluded the participants (Team 2) received more unfair offers (8–2). Post-hoc analyses on each offer type separately confirmed this by revealing main effects of team on 5–5 and 8–2 offers, as well as on 4–6 offers (all $ps < .001$). Only for 6–4 offers, the interaction between team and age group reached significance, $F(4,100) = 2.51$, $p < .05$. As can be seen in Fig. 2, all age groups most often selected the 8–2 offer when allocating coins to the excluders, but adults also selected the 6–4 offer for players of Team 2. The results of the self-report ratings assessing the participants' intentions to punish the excluders are reported in the Supplementary material.

fMRI results Cyberball

Neural activity during Cyberball across age groups

First, brain regions were examined that were recruited during Cyberball across ages. The first contrast compared brain activity for 'not receiving the ball' during the inclusion game relative to 'receiving the ball' during the inclusion game [no ball-inclusion game > ball-inclusion game]. Results revealed a network of regions, including the mPFC/vACC, subgenual ACC, bilateral inferior frontal gyrus (or vlPFC), and the left middle temporal gyrus. Interestingly, a largely overlapping network of regions was recruited by the contrast that compared brain activity for 'not receiving the ball' during the exclusion game relative to 'receiving the ball' during the inclusion game [no ball-exclusion game > ball-inclusion game] (Fig. 3A) (all regions remained significant after FDR correction $p < .05$). These results suggest that these brain regions are sensitive to 'not receiving the ball' regardless of the context of the game. It should be noted here that the subgenual ACC and the ventral ACC/mPFC are labelled as different regions based on the literature of subregions of the ACC (e.g., Vogt, 2005). The subgenual ACC refers to the cluster of activation located underneath the genua of the corpus callosum. Activity in the vACC/mPFC lies more anterior in the brain, and given its larger extent of activation this region encompasses both the vACC and vmPFC (see also Sebastian et al., 2011; Somerville et al., 2006, 2010).

Subsequently, we compared brain activity during 'not receiving the ball' in the exclusion game compared to 'not receiving the ball' in the inclusion game. For this contrast [no ball-exclusion game > no ball-inclusion game] activation was found in the right insula (Fig. 3B). Further, results revealed that activity in this region correlated negatively with the difference score for need satisfaction following exclusion relative to inclusion ($r = -.30$, $p = .028$), revealing that activity in the insula was higher during the exclusion game in those participants who reported higher levels of distress after this game. Finally, we tested whether brain regions were differentially sensitive to the continuous experience of 'not receiving the ball' at the beginning of the exclusion game compared to at the middle and end of the game. For this purpose, the 28 trials of 'not receiving the ball' were divided into three blocks (resp. 8, 10, and 10 trials). The contrasts [first > middle block] and [first > last block] resulted in activation in the ACC, right IFG/insula and left IFG (Fig. 3C). No regions were differentially sensitive for the middle and last block of the game. All significant clusters (uncorrected and FDR corrected) are reported in Table S1 (Supplementary material).

Age differences during Cyberball

Age-related changes in brain activity were tested by performing linear and non-linear ANOVAs with age group as between-subjects factor. No task-relevant regions showed a peak in 14–16 year olds or adults, or a linear change with age. The ANOVA testing for a peak in 10–12 year olds [2 −1 −1] resulted in activation in a posterior region of the subgenual ACC, extending into the ventral striatum, for the contrast [no ball-exclusion game > ball-inclusion game; peak at: 3, 18, −3]. Fig. 4 shows that 10–12 year olds activated this region more on events of not receiving the ball during the exclusion game than older adolescents and

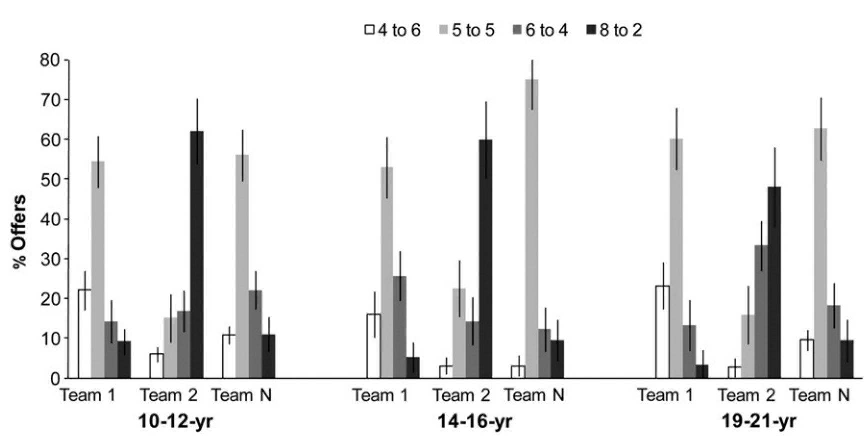

Fig. 2. Behavioral results of the Dictator game. Percentages of offer types (4–6, 5–5, 6–4, and 8–2) for each team (Team 1, Team 2, and Team N) displayed for each age group.

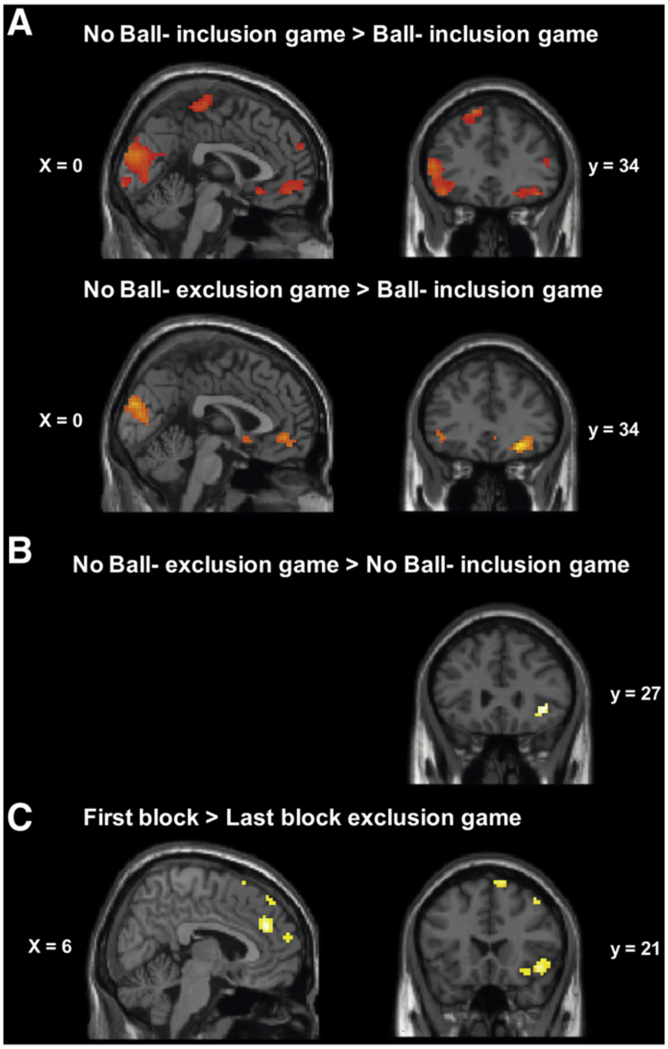

Fig. 3. Whole-brain results for the Cyberball game across participants. All images are thresholded at $p<.001$ uncorrected, >10 voxels. A) Contrasts No Ball-inclusion game > Ball-inclusion game and No Ball-exclusion game > Ball-inclusion game. B) Contrast No Ball-exclusion game > No Ball-inclusion game. C) First block > Last block of 'No Ball' trials during the exclusion game.

adults. Similar results in an overlapping region were found for the ANOVA testing for a peak in 10–12 year olds [2 −1 −1] for the contrast [no ball-exclusion game > no ball-inclusion game; peak at: 0, 21, −3]. The coordinates of activation overlap with subgenual ACC activity reported in adolescents in another study using Cyberball (Masten et al., 2009). All areas of activation are listed in Table S2 (Supplementary material).

Whole-brain regression: individual differences

To further examine how subjective distress correlated with neural activity during Cyberball, whole-brain regression analyses were conducted. For both contrasts focusing on brain activity during events on which participants did not receive the ball during the exclusion game [no ball-exclusion game > ball-inclusion game; no ball-exclusion game > no ball-inclusion game], a negative correlation was found between activity in the posterior insula (peak at: 30, −21, 18; see Table 3S and figure in Supplementary material) and the overall index of need satisfaction after the exclusion game. Thus, the posterior insula was more active during the exclusion game in those participants who reported lower need satisfaction after this game.

Similar regression analyses were conducted to test whether neural activity during Cyberball correlated with subsequent punishment behavior towards the excluders. For the contrast [no ball-exclusion game > ball-inclusion game], a positive correlation was found between activity in the left IFG (peak at: −48, 27, −12; see Table 3S and figure in Supplementary material) and the percentage of 8–2 offers for players of Team 2. That is, activity in the left IFG (or vlPFC) was higher during the exclusion game in those participants who subsequently offered fewer coins to the excluders.

fMRI results Dictator game

Neural activity during the Dictator game across age groups

First, brain regions were examined that were differentially sensitive to making an offer for the players who previously included (Team 1) or excluded the participants during Cyberball (Team 2). In the behavioral data, a team × offer type interaction was found; players of Team 2 received more 8–2 offers, whereas the player of Team 1 mostly received a fair split. The current fMRI analysis collapsed across different offer types for each team. The contrast that compared brain activity for Team 2 > Team 1 across all participants revealed increased BOLD responses in the left TPJ, right superior temporal sulcus (STS) and bilateral IFG (Fig. 5A). That is, these regions were more sensitive to making an offer for players who previously excluded the participants. All areas of activation are listed in Table S4 (Supplementary material). The opposite contrast [Team 1 > Team 2] did not result in significant clusters of activation.

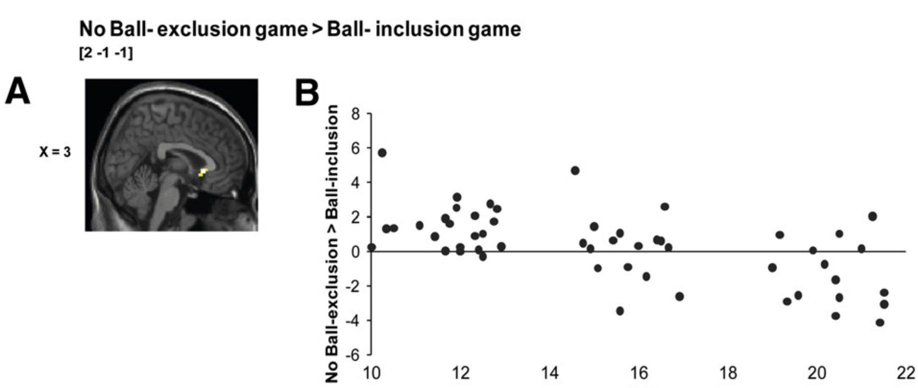

Fig. 4. Age differences in brain activity during the Cyberball game. A) Activation in the subgenual ACC (3, 18, −3) that shows a peak in 10–12 year olds [2 −1 −1] for the contrast [No Ball-exclusion game > Ball-inclusion game] at $p<.001$, 10 voxel threshold. B) Scatterplot of contrast values for age and activity in the subgenual ACC.

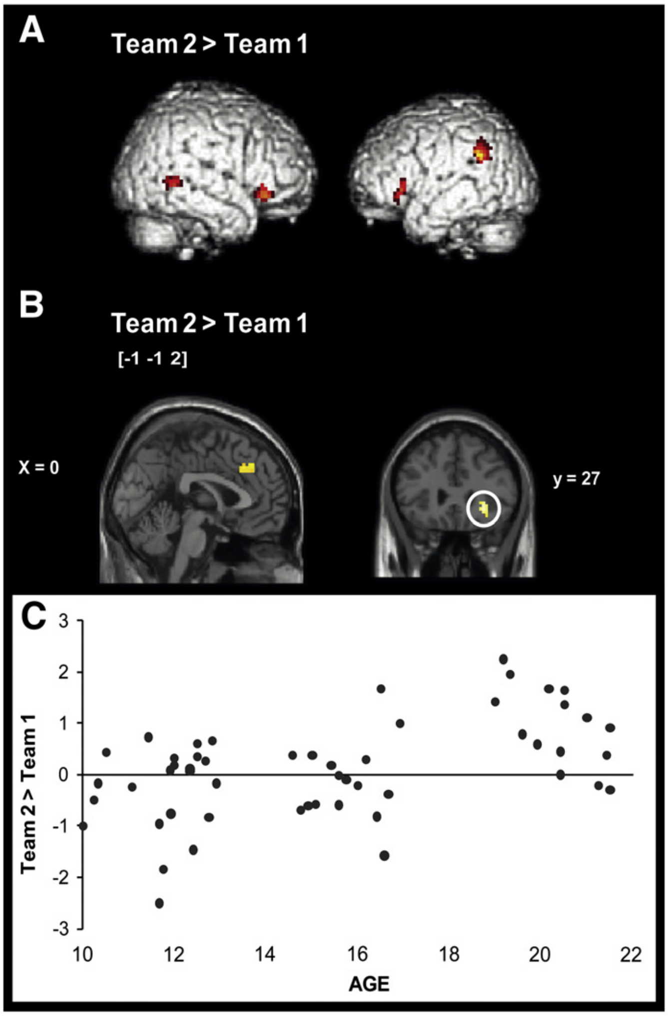

Fig. 5. Neuroimaging results for the Dictator game. A) Whole-brain results for the contrast [Team 2>Team 1] across participants (at $p<.001$, 10 voxel threshold). B) Activation in the right insula (30, 27, −6; at $p<.001$, > 10 voxels) and the dACC (0, 33, 36; at $p<.002$, >10 voxels) that shows a peak in 19–21 year olds [−1 −1 2]. C) Scatterplot of contrast values for age and activity in the right insula.

Age differences in the Dictator game

Age-related differences in brain activity were tested by ANOVAs with age group as between-subjects factor on the contrast [Team 2>Team 1]. The ANOVA testing for a peak in adults [−1 −1 2] resulted in clusters of activation in the right anterior insula (peak at: 30, 27, −6; Figs. 5B and C) and the left temporal pole (peak at: 33, 21, −18). When we lowered the threshold to $p<.002$ (uncorrected), we also found activity in the dACC (peak at: 0, 33, 36; Fig. 5B). These findings demonstrate that adults additionally recruited this network when making an offer to the excluders. All areas of activation are listed in Table S5 (Supplementary material). No regions were found that showed a peak in activity in 10–12 or 14–16 year olds, or a linear change with age.

Whole-brain regression: individual differences

The final question concerned the relation between neural activity on the contrast [Team 2>Team 1] and individual differences in behavior towards players of Team 2. A whole brain regression with the percentage of 8–2 offers per individual as predictor revealed a negative correlation in the dACC (peak at: −6, 15, 39). A similar analysis with the percentage of 6–4 offers for Team 2, resulted in a positive correlation in an overlapping region of the dACC (peak at: 6, 21, 39). No relations were found with percentages of 5–5 or 4–6 offers (Table 6S, Supplementary material). Together, these analyses showed that activation in the dACC was higher in those participants who generally acted more prosocial (less 8–2 offers/more 6–4 offers) towards the excluders. To further examine these correlations within each age group, we created functional ROIs from the whole group regression analyses and plotted these for each age group (Fig. 6). These scatter plots reveal a negative correlation between activity in the dACC and the percentages of 8–2 offers for all age groups (all $ps<.05$) (Fig. 6A). The positive correlation between activity in the dACC and the percentages of 6–4 offers was only significant for adults ($p<.05$; Fig. 6B).

Discussion

The goal of this study was to identify the neural networks that are sensitive to social exclusion and subsequent fairness considerations, and to test for developmental differences. By administering a Dictator game following Cyberball, we were able to examine whether fairness judgments were modulated by previous encounters with those people who included or excluded the participants. Self-report ratings showed that all participants reported greater distress after exclusion, which sets the stage for examining subsequent punishment behavior.

Cyberball

Using an event-related design of Cyberball, the current study examined neural responses associated with rejection events of not receiving the ball, instead of the overall experience of an exclusion block. Across all participants, events on which participants did not receive the ball compared to receiving the ball were associated with activation in the mPFC/vACC, subgenual ACC, and the vlPFC. The location of activity overlaps with neural responses during exclusion blocks of 'classic' (i.e., fixed order) Cyberball studies (e.g., Eisenberger et al., 2003; Masten et al., 2009), and studies with alternating blocks of inclusion and exclusion (Bolling et al., 2011; Sebastian et al., 2011). Prior studies pointed to a role of these regions in the regulation of negative affect (vlPFC: Eisenberger et al., 2003), affective information processing (vACC/mPFC, subgenual ACC: Masten et al., 2009; Somerville et al., 2006), and self-referential processing (mPFC: Amodio and Frith, 2006). It should be noted here that the pattern of activation was observed in both the inclusion and exclusion game, which may suggest that these regions are recruited by single events of not being involved in a specific interaction, irrespective of feelings associated with the larger context of the game (i.e., inclusion or exclusion). This hypothesis needs further testing in future research.

The next question we aimed to address was whether there are brain regions that were sensitive to the continuous experience of not receiving the ball which generally leads to high levels of distress associated with being excluded. Indeed, we observed that a subset of areas was specifically sensitive to events of not receiving the ball in the context of the exclusion game. That is, activity in the insula was generally stronger for rejection events during the exclusion game compared to the inclusion game, and the insula, vlPFC and a more dorsal region of the ACC were more recruited at the beginning of this game. It is possible that the first experience of being excluded elicits strong aversive responses associated with violated expectations of fair play, which may diminish after multiple rejection events in a row. Indeed, the insula and the dACC are commonly reported during exclusion blocks of Cyberball (e.g., DeWall et al., 2010; Eisenberger et al., 2003) and are believed to be implicated in negative affect, expectancy violations and pain (see Etkin et al., 2011; Rilling and Sanfey, 2011; Shackman et al., 2011). It has previously been suggested that both social distress and expectancy violation may act as complementary processes of a neural alarm system (see Eisenberger

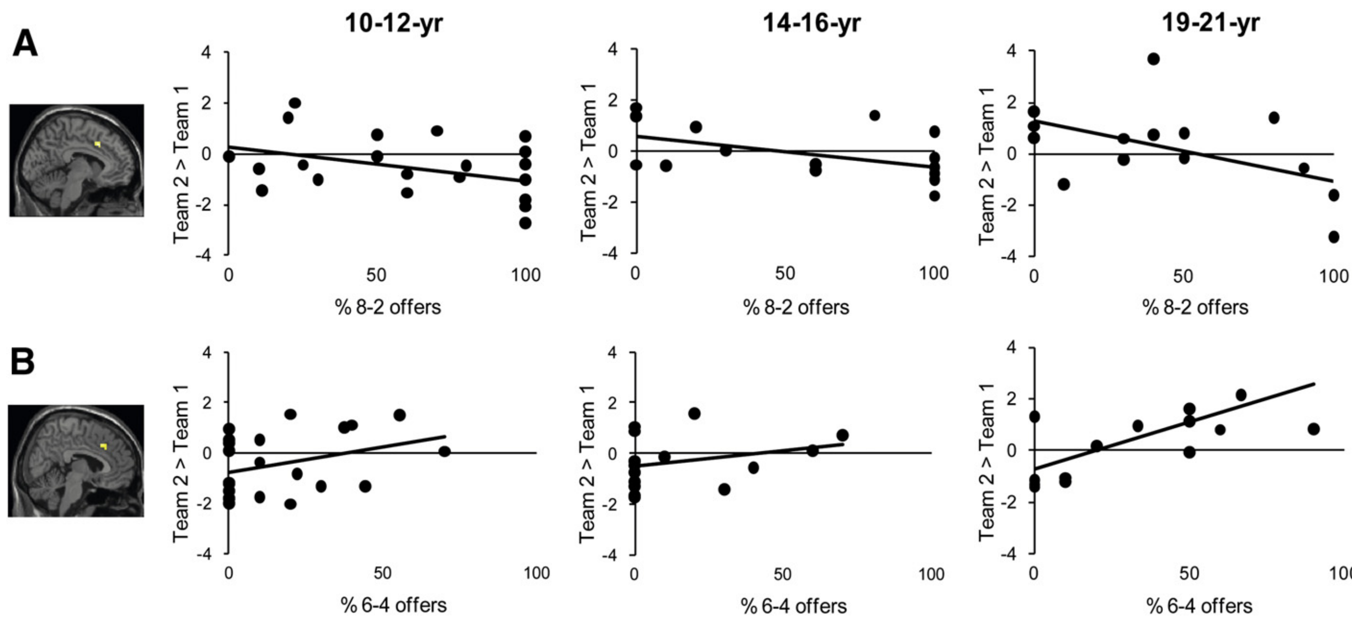

Fig. 6. Scatterplots representing the correlations between contrast values [Team 2>Team 1] and percentage of 8–2 (A) and 6–4 offers (B) for the excluders in the dACC. ROIs were extracted from the whole brain regression analyses across participants. Scatterplots are presented separately for each age group.

and Lieberman, 2004), which may be particularly involved in the continuous experience of not receiving the ball.

Together, the neural regions that were sensitive to single-trial rejection events in the current study overlap considerably with the regions previously associated with exclusion blocks of Cyberball, and may provide additional insight in the processes that are involved in social exclusion. Further, results revealed that several regions were specifically recruited during single-trial rejection events in the exclusion game, suggesting that the larger context of the game may alter the processing of these single rejection events. In line with this notion, self-report ratings showed that participants reported greater distress after the exclusion game, pointing to a strong negative impact of social exclusion. In addition, it was observed that activity in the insula was higher for rejection events in the exclusion game in those participants who reported greater distress after this game.

An unresolved issue in the current study is that we did not replicate previously observed associations between brain activity and self-reported distress associated with Cyberball (i.e., vlPFC, dACC, and subgenual ACC), apart from activity in the insula (Masten et al., 2009). It is possible that the event-related design of Cyberball might be less optimal for relationships with self-report ratings, since these ratings capture affective responses associated with the overall exclusion experience and the overall inclusion experience that are assessed after the game, instead of single trials of not receiving the ball. For future research it would be of interest to collect continuous self-report ratings of emotion during scanning (e.g., Goldin et al., 2005), or autonomic measurements, such as heart rate.

Dictator game

The experience of the exclusion game clearly affected subsequent fairness considerations; players who previously excluded the participants received lower offers with more self-gain for the participants, whereas players who previously included the participants received more fair offers. It is possible that social exclusion might have caused participants to adopt a strategy to selectively punish the excluders to avoid further exploitation or to protect the self from being hurt (Hillebrandt et al., 2010; Maner et al., 2007; Twenge et al., 2007), and might have given a justification for maximizing their own gains. It should be noted that the current study does not provide an answer to the question whether participants would be willing to punish the excluders to their own cost (e.g., Fehr and Gächter, 2002).

The brain regions which were active during making an offer for the excluders were highly comparable to the previously described 'social brain network', and included the left TPJ, right STS and bilateral vlPFC. Prior studies showed that the TPJ and the STS are involved in perspective-taking and theory of mind (e.g., Gallagher and Frith, 2003; Pelphrey et al., 2003), and the vlPFC in the regulation of negative affect (see Rilling and Sanfey, 2011). All these processes may be involved in the decision to punish the excluders and to maximize own gains. For instance, it is possible that participants are more engaged in switching attention between their own perspectives and that of the other, which may be involved in justifying their decision to punish the excluders based on their previous interactions with them (Mitchell, 2008). Finally, we explored whether neural activity during Cyberball correlated with subsequent offers towards the excluders. Results revealed that activity in the left vlPFC on events of not receiving the ball during the exclusion game was higher in those participants who offered fewer coins to the excluders. This finding may suggest that activity in the left vlPFC during social exclusion is predictive for subsequent punishment behavior to regain a sense of control.

Developmental differences

An important aim of this study was to test for age-related differences in the experience of peer rejection and to test whether age groups differ in the way they allocate money after negative peer interactions. First, all participants reported greater distress after the exclusion game showing that social exclusion is a significant social threat across age groups. This finding contradicts prior results, which reported stronger negative feelings in adolescents (Sebastian et al., 2010a, 2011). The lack of increased exclusion-related distress in adolescents is possibly related to the inclusion of both genders, whereas in previous studies only females were included. Indeed, it has been reported that peer acceptance and rejection may be especially salient in adolescent girls (e.g., Guyer et al., 2009). The current study did not have enough participants to distinguish between boys and girls, and exploratory collapsed analyses did not result in gender differences across age groups. Nonetheless, this is an issue that needs to be explored with larger samples.

A comparison of neural activity revealed a strong overlap between age groups in regions that are sensitive to rejection events of not receiving the ball, in both the inclusion and exclusion context, suggesting that these neural networks mature early in life. Age-related differences were found in a small section of the subgenual ACC. Specifically, this region was found to be strongly engaged in 10–12 year olds in the context of the exclusion game, and overlapped with the subgenual ACC activity reported in a previous Cyberball study in adolescents using a block design (Masten et al., 2009). In this study it was reported that activity in the subgenual ACC during social exclusion correlated with greater exclusion-related distress in 12–13 year olds, which was also found to be predictive for future depression in the same sample of adolescents (Masten et al., 2009, 2011). Further evidence for a role of the subgenual ACC in negative emotions comes from adult studies, showing a link between heightened activity in the subgenual ACC and higher levels of sadness and depression (e.g., Chen et al., 2007; Vogt, 2005). Together, these results may suggest that early adolescents display increased activity in brain regions associated with negative affect during social exclusion, which may not always be observable in self-reported distress. Future studies should test in more detail whether greater responsivity in the subgenual ACC could reflect developmental differences in affective responses to peer rejection or in the ability to regulate negative affect (see Masten et al., 2011).

The question then arises whether adults and adolescents differ in behavior and neural activity in subsequent allocation games with excluders. Although all age groups most often selected the harsh punishing offer (8–2) when allocating money to the excluders, adults selected the milder punishing offer (6–4) more often than both 10–12 and 14–16 year olds. Possibly, adults take less advantage of the possibility to punish the other players. Alternatively, they may feel it is less justified to maximize their own gains in this context. These two explanations should be tested in future research. Further, it should be noted that this age effect was only present in follow-up comparisons and therefore should be replicated in future studies.

Neuroimaging results revealed that all groups activated the social brain network when making an offer to the excluders, but that adults additionally recruited the right insula, left temporal pole and the dACC. In particular, the insula and the dACC are believed to be key regions of the brain involved in resolving conflict when allocating money between self and others (Rilling and Sanfey, 2011), and are sensitive to norm violations (Güroğlu et al., 2010; Van den Bos et al., 2009). Results of the current study further showed that activity in the dACC was more pronounced in those participants who acted more prosocial towards the excluders, as reflected by a higher number of 6–4 or less 8–2 offers. It is possible that the exclusion experience may have shifted the personal norms from inequity aversion to a willingness to punish the excluders, resulting in activation in the dACC when acting more prosocial. Furthermore, this explanation fits well with the results for adults, showing that adults more often selected the milder punishing offer (6–4) towards the excluders compared to younger participants. It should be noted here that the increased activity in the dACC in adults when making an offer towards the excluders may be linked to their higher number of 6–4 offers. As such, age-related differences in neural activity could be related to behavioral differences that vary with age.

An unexpected finding was the absence of age-related differences in activity in prefrontal regulatory regions (i.e., vlPFC) during social exclusion, as reported in the Cyberball study by Sebastian et al. (2011) (see also Sebastian et al., 2010b). The lack of this effect may reflect differences in task structure and design. In their study, short blocks of inclusion and exclusion were repeatedly presented in a pseudorandom order and analysed using a block design. Notably, in their study participants were over-included, which may have had an impact on the intensity of social exclusion, increasing the need for affect regulation. Further, this study did not find evidence for an age-related increase in involvement of the TPJ and the PFC during social-decision making (e.g., Van den Bos et al., 2011). Several possibilities may account for these differences. First, the focus of prior studies using allocation games was mainly on responder behavior, whereas the focus of the current study was on the behavior of the proposer. Second, prior studies typically involved interactions with unknown, neutral players which could lead to more ambiguity in social interactions. The current study may have facilitated perspective-taking skills because participants allocated money to someone they had previous encounters with.

Conclusions

Together, the current results demonstrate that a broad network of brain regions can be recruited by single-trial rejection events. Although there was a strong overlap between age groups in regions that are sensitive to not receiving the ball, early adolescents displayed increased activity in the subgenual ACC in the exclusion context, which has been associated in previous studies with negative affect. As expected, participants selectively punished the excluders by making lower offers. There was consistent activation in the social brain network when making offers for the excluders, but adults showed additional activity in brain regions associated with norm-violations. In future research it would be of interest to test whether relationships in real life similarly modulate fairness considerations.

The current study brings us a step closer towards an understanding of the developmental time course of the neural mechanisms involved in social exclusion and subsequent punishment behavior. For future research it is important to test for individual differences, for instance by comparing neural responses between popular and unpopular adolescents. A recent study by Masten et al. (2010) demonstrated that spending more time with friends during adolescence is related to less activity in brain regions involved in affective processing in a social exclusion experience two years later. Future research could benefit from longitudinal designs to track how chronic peer rejection has an impact on neural responses involved in peer interactions. Ultimately, this field of research has the potential to make significant contributions to an understanding of the development of psychopathology in adolescence.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2011.07.028.

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