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Gambling for self, friends, and antagonists: Differential contributions of affective and social brain regions on adolescent reward processing

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ABSTRACT

Adolescence is a time of increasing emotional arousal, sensation-seeking and risk-taking, especially in the context of peers. Recent neuroscientific studies have pinpointed to the role of the ventral striatum as a brain region which is particularly sensitive to reward, and to 'social brain' regions, such as the medial prefrontal cortex (mPFC), the precuneus, and the temporal parietal junction, as being particularly responsive to social contexts. However, no study to date has examined adolescents' sensitivity to reward across different social contexts. In this study we examined 249 participants between the ages 8 and 25, on a monetary reward-processing task. Participants could win or lose money for themselves, their best friend and a disliked peer. Winning for self resulted in a mid- to late adolescent specific peak in neural activation in the ventral striatum, whereas winning for a disliked peer resulted in a mid- to late adolescent specific peak in the mPFC. Our findings reveal that ventral striatum and mPFC hypersensitivity in adolescence is dependent on social context. Taken together, these results suggest that increased risk-taking and sensation seeking observed in adolescence might not be purely related to hyperactivity of the ventral striatum, but that these behaviors are probably strongly related to the social context in which they occur.

Adolescence is a period of increased risk-taking and sensation-seeking, especially in the presence of peers (Steinberg, 2004). Excessive risk-taking can have adverse effects, such as injury due to risky driving or excessive alcohol use. An important component of risk-taking involves anticipation and processing of rewards. It is well known that reward processing is associated with activation in the ventral striatum (VS) (Delgado, 2007; Sescousse et al., 2013). Prior developmental studies have further shown that activity in the VS is elevated in adolescence (Ernst et al., 2005; Galvan et al., 2006; Van Leijenhorst et al., 2010a). However, these studies reported mixed results with respect to the specificity of the VS response to rewards, possibly due to different task demands and differences in selection of age groups (Richards et al., 2013). Especially the VS response to anticipation of rewards has yielded mixed findings. Although some studies have found elevated VS responses in adolescence in response to anticipation of gains (Galvan et al., 2006; Van Leijenhorst et al., 2010a), other studies have reported an under activation of the VS in response to anticipation of rewards (Bjork et al., 2004, 2010; Geier et al., 2010).

Adolescence is also a period of re-orientation towards the peer group, coupled with an increasing importance of friendships (Rubin et al., 2008). Despite the pronounced changes in this social orientation towards peers, less is known about how similar reward processing for self and others is. Telzer et al. (2010) previously showed that gaining money for family results in increased activation in the ventral striatum. This activity was stronger for those adolescents who derived greater fulfillment from helping their family. Thus, there seems to be a link between gaining for relevant others and activity in the VS. Also, Varnum et al. (2014) showed that when adult participants were primed for an interdependent self-construal, winning for friends resulted in as much striatum activation as when participants won for themselves. These findings led to the hypothesis that receiving rewards for friends would also result in VS activity and we tested whether this response was stronger in mid adolescence relative to childhood and adulthood.

Several previous studies have suggested that processing of rewards and thinking about friends depend on separate but interacting brain networks in adults (Braams et al., 2013; Fareri et al., 2012). Specifically, processing of rewards is associated with VS activation, whereas thinking about friends or significant others results in activation in a set of cortical midline structures (medial prefrontal cortex and precuneus) as well as the temporal–parietal junction (Güroğlu et al., 2008), regions also referred to as the 'social brain network' (Blakemore, 2008; Van Overwalle, 2009; Young et al., 2010). In a neuroimaging study with adult participants, we found that the social brain areas were more active when playing a simple heads-or-tail gambling game for another person relative to playing the game for yourself, independent of the outcome of the game (reward or loss). In contrast, VS activity was dependent on the beneficiary, such that VS activity was higher when winning for self and

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friends, but not when winning for disliked others (Braams et al., 2013). Self-report ratings of how much participants liked to win and lose for the two other players exhibited the same pattern, with highest ratings for winning for friend, followed by losing and winning for the disliked other and lowest ratings for losing for the friend. Similarly, a study by Fareri et al. (2012) showed that sharing with a friend resulted in more VS activation compared to sharing with a confederate or a computer, suggesting that VS activation is dependent on social context. In this study, mPFC activation was also higher when sharing with a friend compared to the other two players.

Developmental studies have reported differences in recruitment of the social brain areas in adolescence compared to adulthood. Adolescents appear to recruit the more anterior regions, such as mPFC, more than adults, whereas adults recruit more posterior regions, such as temporal regions, more than adolescents (Blakemore, 2008). Elevated activation in the mPFC has been found in mid-adolescence, in response to socially demanding contexts, such as thinking about others' intentions or distinguishing between social and basic emotions (Blakemore, 2008; Burnett et al., 2009; Goddings et al., 2012). However, it is not yet known whether mPFC activity decreases from childhood to adulthood or whether mPFC shows peak sensitivity in mid-adolescence.

Based on developmental studies pointing out an elevated response in the striatum (Galvan et al., 2006; Van Leijenhorst et al., 2010a) and social sensitivity in adolescents (Chein et al., 2011), and findings from neuroimaging studies in adults pointing out the context sensitivity of the VS activity (Braams et al., 2013; Fareri et al., 2012), we examined adolescent specific differences in the VS when participants received rewards for themselves, their friend, and a disliked other (i.e. antagonist). First, we predicted that adolescents would show elevated VS responses to rewards when playing a gambling game in comparison to children and adults (replicating Galvan et al., 2006; Van Leijenhorst et al., 2010a). Second, we investigated the role of social factors on reward processing in the VS and how this changes during adolescence, by having the participants perform a gambling game for themselves, as well as for their best friend and an antagonist. Based on the prior neuroimaging study in adults showing higher VS activity when playing for self and friends relative to antagonists (Braams et al., 2013), we predicted a similar pattern for the younger age groups. Furthermore, we expected self-report ratings indicating how much participants liked to win and lose for the different players to correspond with the VS activity. Given the importance of friendships in adolescence (Rubin et al., 2008), the current study had a special focus on the role of friendship quality on VS activity. Therefore, we examined the relation between self-reported friendship quality and VS responses to winning for friends. We predicted a stronger VS response to playing for a friend for participants who reported a better friendship quality. Finally, we tested whether the social brain network, which was previously found to be most active when playing for friends and antagonists in adults (Braams et al., 2013), would show hypersensitivity in adolescence.

Materials and methods

Participants

Final inclusion consisted of 249 participants between the ages of 8 and 25 who were members of the general public, recruited through schools and local advertisements. An additional 14 participants were excluded for not finishing the task or technical problems during data collection, and an additional 36 participants were excluded for excessive head motion (more than 3 mm in any direction) which is common in developmental neuroimaging studies (approximately 12%) (Galvan et al., 2012; Poldrack et al., 2002). When only participants who moved less than 1/2 voxel were included in the analysis, the results were comparable (see the supplemental material for a description of these results). Descriptives of the age and division of gender of the final sample can be found in Supplemental Table 1. For some of the analyses, indicated where appropriate, the total sample was divided into 9 age groups, such that each group represented participants of the same age in years. The 8- and 9-year-olds were grouped together because of the relatively smaller sample size of these age groups. Results of the adult group (ages 18–25) have been reported separately in an earlier study (Braams et al., 2013).

An approximation of IQ was determined by two subscales, similarities and block design, of the Wechsler Intelligence Scale for Adults (WAIS-III) or the Wechsler Intelligence Scale for Children (WISC-III) (Wechsler, 1997). Estimated IQ for all participants fell within the normal range ($M = 109$, $SD = 10$). Informed consent from adult participants and from the parents of under aged participants was obtained before the start of the study. Participants were screened for MRI contra indications and were free of neurological and psychiatric disorders. All procedures were reviewed and approved by the university medical ethical committee. Participants received an endowment (€60 for adults, €25 for participants aged 12–17 and €20 for participants younger than 12) for their participation in a larger scale study.

Experimental design

Gambling task

Participants performed a gambling task in which they could choose heads or tails and win (or lose) money when the computer selected the chosen (or not chosen) side of the coin. Therefore, probability of winning or losing was 50% on each trial. The number of coins that could be won or lost on each trial was varied. Three variations were included: trials in which five coins could be won or two coins could be lost, trials on which three coins could be won or three coins could be lost and trials on which two coins could be won or five coins could be lost. The reason for presenting three variations was to keep the participants engaged in the task (see also Braams et al., 2013). To maximize statistical power we collapsed across these variations.

Before the start of the experiment, the participants were told that they would play the gambling task for themselves, for their same-sex best friend and for another participant from the study. The participant's best friend and the other participant were not present at the time of the experiment. Participants were explained that one of the three players (self, friend or other) would be paid the money that was earned for that person during the task. Care was taken that the participants understood that the money won during the game was not hypothetical. We asked the participants to fill out a Friendship Quality Questionnaire about their best friend, prior to the experiment, and the name of the best friend was used in the best friend condition during the game. To manipulate the liking of the other participant that they would play the gambling game for, a cover story was used. This cover story was as follows: "*You will play a game with another participant in the study, who will participate after you. You can divide 10 euros between yourself and the next participant. You can split the amount as you like, but the next participant will decide whether the division is accepted or not. If the division is not accepted, you will both receive nothing.* [Participant makes offer]. *You will now receive the offer from a prior participant and you can decide whether you want to accept the division or not.* [Participant receives unfair division of 9 coins for the proposer and 1 coin for the participant, and makes a choice to accept or reject]. *We will now practice the gambling game that you will play in the scanner. You will play this game for yourself, for* [name of participant who made unfair offer] *and for* [name of best friend]." The average offer made by the participants in the division (also known as an Ultimatum Game) was 4.7 euros out of 10 euros ($SD = .08$). The average rejection rate of the 9–1 offer made by the antagonist was 73%. One-way ANOVAs with age group as independent variable showed no significant differences between age groups, neither for the height of the offer nor for the rejection rate (all p's $> .05$). This cover story with an unfair ultimatum game offer allowed us to create an antagonist as the third player (Braams et al., 2013; Sanfey et al., 2003; Singer et al., 2006). To validate that the participants liked the

antagonist less than their friend, we asked them to rate how much they liked the antagonist at the end of the experiment. The ratings were average 4.9 ($SD = 2.1$) on a 10-point scale. Participants were told that at the end of the experiment one of the three players would be randomly selected to receive the total amount of money won for that player in the game. In reality, at the end of the experiment 50% of the participants received the gain for themselves, and 50% of the participants received the gain for their best friend. The amount earned was 4, 5 or 6 euros.

The task (see Fig. 1) consisted of two event-related runs, both lasting approximately seven minutes. In total 90 trials were presented, 30 trials for self, 30 trials for the best friend and 30 trials for the antagonist. Each trial started with the presentation of the stimulus during which the name of the player and the coins at stake were presented for 4000 ms. The choice to play for heads or tails was made within this time interval by pressing the right index finger for heads and the right middle finger for tails. The stimulus was followed by a fixed delay of 1000 ms during which a blank screen was presented, followed by an outcome screen that displayed gain or loss. This screen was presented for 1500 ms. The trial ended with a variable jitter of 1000–13,200 ms. Trial sequence and timing was optimized using OptSeq (Dale, 1999); see also (http://surfer.nmr.mgh.harvard.edu/optseq/). Over all age groups participants chose on average to play half of the time for heads and half of the times for tails ($M_{choice\ heads} = 49.7\%$, $SD_{choice\ heads} = 11.8\%$). There was no developmental difference in these choices.

Ratings for winning and losing

After the scan, participants rated how much they liked winning and losing for each player separately. Ratings were made on a scale from one to ten with anchors 'not at all' and 'very much'. All participants provided a rating for winning and losing for the friend and the antagonist; the 8–17 year-old participants also provided a rating for winning and losing for themselves.

Friendship quality

To assess friendship quality with the best friend, participants filled out the modified version of the Friendship Quality Scale (FQS); (Bukowski et al., 1994) before the scanning session. The modified scale consisted of 20 items assessing positive, an example item is 'I can trust and rely upon my friend', as well as negative friendship quality, an example item is 'My friend can bug or annoy me even though I ask him not to'. Participants were asked to indicate how true each item is for their relationship with the best friend by providing a rating on a 5-point scale ranging from (1) 'not true at all' to (5) 'very true'. A total of 7 items were recoded; higher scores indicate higher friendship quality. Reliability of the scale was high (Cronbach's alpha .80). The FQS is divided into two subscales that measure positive as well as negative friendship quality. The range of scores for the positive scale is between 13 and 65. The range of scores for the negative scale is between 7 and 35. Mean score for the positive scale was 55.5 (*SD* 6.23), mean score for the negative scale was 11.4 (*SD* 3.8). There were no age differences in friendship quality scores, neither for the positive scale ($F(9,234) = .844$, $p = n.s.$) nor for the negative scale ($F(9,234) = 1.08$, $p = n.s.$).

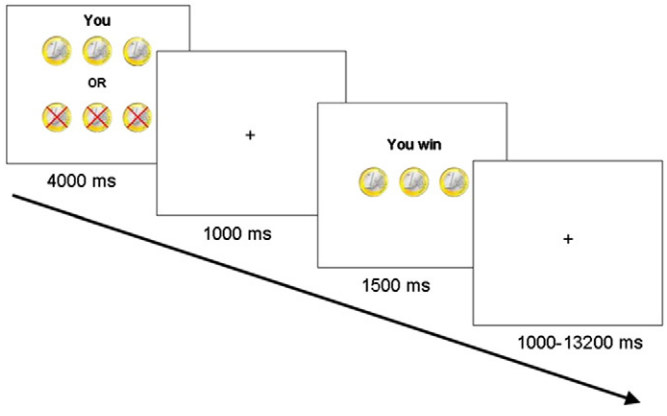

Fig. 1. Example of a trial. On stimulus onset participants were presented with a screen indicating how much they could win or lose and for whom they were playing on that trial. During this time they chose to play for heads or tails by pressing the corresponding button. After 4000 ms a fixation cross was presented for 1000 ms, after which the outcome screen was presented for 1500 ms. The outcome screen indicated how many coins the participant had won or lost and for whom. A trial ended with a fixation cross shown for a variable delay between 1000 and 13,200 ms.

Procedure

Participants were prepared for the testing session in a quiet laboratory. They were familiarized with the MRI scanner with a mock scanner as well as by listening to recordings of the scanner sounds. Next, they provided and received the Ultimatum Game offer. After explanation of the task and the different players, participants performed 6 practice trials. At the end of the experiment, participants provided ratings for how much they liked winning and losing for each player (i.e. self, best friend, antagonist). Participants filled out the friendship quality scale online at home, before the test date. The WISC-III or WAIS-III was administered after the scanning session.

MRI data acquisition

Scanning was performed on a 3 Tesla Philips scanner, using a standard 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, 8 slices of 2.75 mm, field of view 220 mm, 80 × 80 matrix, in-plane resolution 2.75 mm). A high-resolution 3D T1-FFE scan for anatomical reference was obtained (TR = 9.760 ms; TE = 4.59 ms, flip angle = 8°, 140 slices, 0.875 × 0.875 × 1.2 mm^3 voxels, FOV = 224 × 168 × 177 mm^3). After the functional runs, a high resolution 3D T1-weighted anatomical image was collected (TR = 9.751 ms, TE = 4.59 ms, flip angle = 8°, 140 slices, 0.875 mm × 0.875 mm × 1.2 mm, and FOV = 224.000 × 168.000 × 177.333). Visual stimuli were displayed onto a screen in the magnet bore and could be seen by the participant via a mirror attached to the head coil. Head movement was restricted by using foam inserts inside the coil.

fMRI preprocessing and statistical analysis

All data was analyzed with SPM8 (Wellcome Department of Cognitive Neurology, London). Images were corrected for differences in rigid body motion. Structural and functional volumes were spatially normalized to T1 templates. Translational movement parameters never exceeded 1 voxel (<3 mm) in any direction for any participant or scan. Average head movement was 0.91 mm. Movement was correlated with age such that younger participants moved significantly more than older participants ($r = -.29$, $p < .001$). However, all participants moved less than 3 mm (1 voxel) during the whole length of the experiment and the results did not change when using more strict inclusion criteria (see Supplement). The normalization algorithm used a 12-parameter affine transform together with a nonlinear transformation involving cosine basis functions and resampled the volumes to 3 mm cubic voxels. Templates were based on the MNI305 stereotaxic space (Cocosco et al., 1997). Functional volumes were spatially smoothed with an 8 mm FWHM isotropic Gaussian kernel.

Statistical analyses were performed on individual subjects data using the general linear model in SPM8. The fMRI time series were modeled as a series of zero duration events convolved with the hemodynamic response function (HRF) and its temporal derivative. Trial onset and feedback onset were modeled as events of interest with null duration. Trials on which the participants failed to respond were modeled separately as covariate of no interest and were excluded

from further analyses. The trial functions were used as covariates in a general linear model; along with a basic set of cosine functions that high-pass filtered the data, and a covariate for session effects. The least-squares parameter estimates of height of the best-fitting canonical HRF for each condition were used in pair-wise contrasts. The resulting contrast images, computed on a subject-by-subject basis, were submitted to group analyses.

At the group level two ANOVAs were computed. To investigate responses on trial onset we computed a one-way within-subject ANOVA with three levels (Self, Friend, Antagonist). To investigate responses related to reward processing we computed on feedback onset a 3 (Person: Self, Friend, Antagonist) × 2 (Outcome: Win, Lose) repeated measures ANOVA. Task-related responses were considered significant when they exceeded a threshold of $p < .05$, FWE corrected, and consisted of at least 10 contiguous voxels. In Supplemental Table 2 we report all coordinates for the analyses at trial onset and in Supplemental Table 3 for all analyses at feedback onset at the $p < .05$ FWE corrected threshold. The main effect of gender as well as interaction effects of gender with the other factors were tested on whole brain level both for stimulus onset and feedback onset and resulted in no significantly activated clusters. Therefore, gender is not taken into account in the main analyses.

To test for specific patterns of neural responses related to age, regression analyses with age as independent variable were performed. On trial onset regression analyses were performed for the contrast person–baseline for each of the three persons separately. Baseline refers to the non-modeled fixation time. On feedback onset regression analyses were performed on the contrast winning–losing for each person separately. We hypothesized a quadratic regression pattern, based on previous literature (Galvan et al., 2006; Van Leijenhorst et al., 2010b). The quadratic model was mean age centered ($M_{age} = 15.0$). We hypothesized that the peak in striatum activation would be around ages 14–16, based on prior studies by Galvan et al. (2006), Van Leijenhorst et al. (2010a, 2010b), for a review see Richards et al. (2013). In these whole brain analyses, we used an uncorrected threshold of $p < .001$ to avoid Type 2 errors (Lieberman and Cunningham, 2009). To correct for multiple comparisons, we performed a small volume correction on the clusters identified in the whole brain analysis. Anatomical masks of the regions identified in the whole brain analysis were used as masks for the small volume correction. The threshold used for the small volume corrections was $p < .05$, FWE corrected. For exploratory reasons we also performed linear regression analyses, but these were not a specific focus of this study (see Supplemental Table 4).

Region of interest analysis

We used the MarsBaR toolbox (Brett et al., 2002) (http://marsbar.sourceforge.net/) for SPM8 to perform region of interest (ROI) analyses to further illustrate patterns of activation in the clusters found with whole brain analyses. Functional regions of interest were masked with anatomical regions when appropriate (see below). Ventral striatum was masked with an anatomical mask of the caudate nucleus, except when otherwise specified. Greenhouse–Geisser corrected p-values for the ANOVAs are reported when appropriate.

Results

Behavioral ratings

To test whether the subjective pleasure values for winning and losing differed per condition a repeated measures ANOVA was conducted with two within-subjects factors: Person (three levels: Self, Friend, Antagonist) and Outcome (two levels: Win, Lose). Age groups were added as a between-subjects factor.

The ANOVA showed significant main effects of Outcome ($F(1205) = 365.67$, $p < .001$, $\eta^2 = .62$) and Person ($F(2,410) = 25.47$, $p < .001$, $\eta^2 = .10$). Furthermore, the interaction effect of Person × Outcome was significant ($F(2,410) = 214.13$, $p < .001$, $\eta^2 = .51$). Follow-up paired samples t-tests showed that all ratings were significantly different from each other (all t's > 2.2, all p's < .027). Winning for Self (M = 8.2, SD = 1.9) and Friend (M = 7.7, SD = 1.7) were rated as most pleasurable, whereas losing for Friend (M = 3.5, SD = 2.0) and losing for Self (M = 3.1, SD = 2.0) were rated lowest. Losing (M = 5.5, SD = 2.4) and winning for the Antagonist (M = 4.9, SD = 2.2) were rated intermediately (see Fig. 5C). There was also an Outcome × Age group interaction ($F(8,205) = 2.4$, $p = .018$, $\eta^2 = .03$), such that with increasing age, the difference between ratings for winning and losing decreased. However, there was no interaction between Outcome, Age and Person, showing that the Person differentiation was similar across ages.

fMRI analyses

Trial onset

The first fMRI analysis concerned neural responses on trial onset, when the participant was informed of the person they were playing for on that trial and made a choice to play for heads or tails. A repeated measures ANOVA with within-person factor Person (three levels: Self, Friend and Antagonist) yielded a robust main effect of Person in the bilateral striatum (MNI 9 15 0; −12 12–6), the bilateral TPJ (MNI 51–57 27; MNI −51 −66 30), medial prefrontal cortex (MNI −6 57 27) and precuneus (MNI 0–57 24). To further investigate the direction of this activity under different conditions we performed ROI analyses on the regions derived from the ANOVA. Paired samples t-tests showed that bilateral VS was more active for self than for the friend and the antagonist (all t's > 5.3, all p's < .001). Also, activation in both regions was higher for the friend than for the antagonist (all t's > 2.7, p's < .006). The network of bilateral TPJ, mPFC and precuneus was more active in both the friend and the antagonist conditions than in the self condition (all t's > 2.9, all p's < .004; see Fig. 2). Activity for antagonist was higher in the mPFC ($t(248) = 2.1$, $p = .034$) and right TPJ ($t(248) = 4.9$, $p < .001$) than in the friend condition, whereas activity in the left TPJ and precuneus did not differ for friend and antagonist conditions (all t's < 1.5, *n.s.*).

Age related effects. To test for age related differences we used whole-brain regression analyses. Specifically, to test for an adolescent specific peak in activation a whole brain quadratic regression with age was performed for trials on which the participants played for themselves compared to baseline. A small volume correction on the resulting VS clusters was performed. The whole brain quadratic regression was significant in the left VS at an uncorrected threshold when testing whole brain ($p < .001$ uncorr, 10vox, MNI −6 9–3, $t(247) = 3.77$) and at an FWE corrected threshold when using small volume correction (see Figs. 3A and B). No age related effects in activity in the VS were found for friend, also not at an uncorrected threshold. For antagonist a caudate cluster ($p < .001$ uncorr, 10vox, MNI −15 −3 6, $t(247) = 3.72$) was found at an uncorrected threshold, but this cluster did not survive small volume correction (see Supplemental Table 5 for a full description of resulting clusters).

Feedback onset

The second fMRI analysis concerned neural responses to winning and losing at feedback onset. A repeated measures ANOVA with factors Outcome (two levels: Win, Lose) and Person (three levels: Self, Friend, Antagonist) revealed a main effect of Outcome in bilateral VS (MNI 9 12–3; MNI −9 12–3) and mPFC (MNI 0 51–3) and a main effect of Person in bilateral TPJ (MNI −51 -66 33; MNI 54–63 33), mPFC (MNI −3 60–3) and the precuneus (MNI −3 −57 36) (see Fig. 4). In addition to these main effects there was an interaction of Person × Outcome in the bilateral VS (MNI 15 18–3; −12 15–6; see Fig. 5) and mPFC (MNI −9 48–3) (see Supplemental Fig. 1).

To investigate directionality of the effects we performed ROI analyses on the areas described above. The VS, identified in the main effect

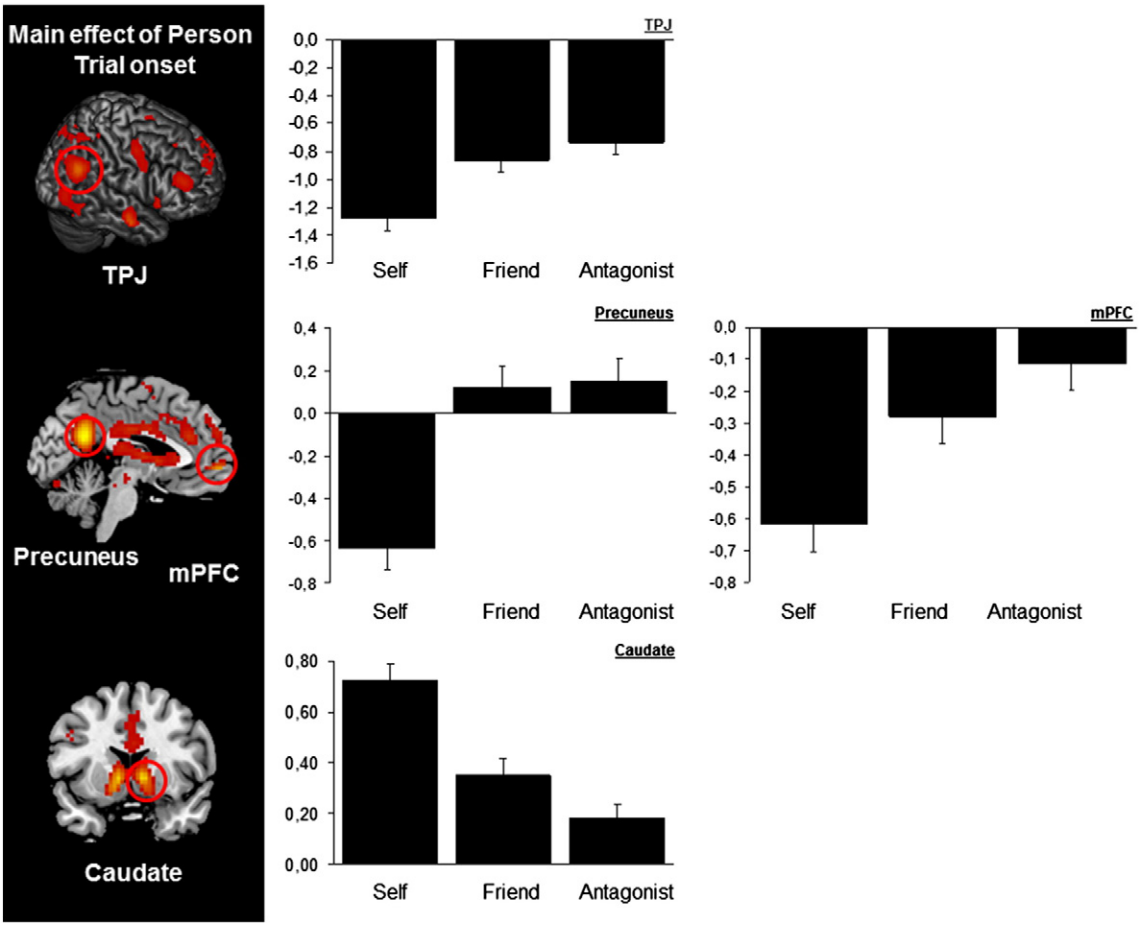

Fig. 2. Areas identified in the main effect of Person of the within person ANOVA with factor Person (three levels: Self, Friend, Antagonist) performed on trial onset. Graphs represent follow up ROI analyses performed on the right TPJ (MNI 51–57 27), Precuneus (MNI 0–57 24), mPFC (MNI −6 57 27) and Caudate (MNI 9 15 0) areas indicated with red circles.

of Outcome, was more active during winning than losing (all *t*'s (248) > 8.5, $p < .001$, $\eta^2 > .22$). All areas in the network identified in the Main effect of Person were more active in the friend and antagonist conditions than in the self condition (all *t*'s (248) > 7.2, $p < .001$, $\eta^2 > .17$), but friend and antagonist did not differ from each other in the precuneus, mPFC and left TPJ (*t*'s(248) < 1.4, *n.s.*). In the right TPJ there was more activation for antagonist than friend ($t(248) = 3.1$, $p = .002$, $\eta^2 = .04$).

The ROI analyses performed on the VS identified in the Person × Outcome interaction on whole brain level showed a similar pattern for self and friend, with more activation of the VS during winning compared to losing (*t*'s(248) > 7.8, $p < .001$, $\eta^2 > .20$). Playing for the antagonist showed a reversed pattern of results, significant at trend level, such that losing for the antagonist was associated with more activation of the VS than winning ($t(248) = 1.8$, $p = .07$, $\eta^2 = .01$) (see Fig. 5). A similar pattern was found in the mPFC as for the VS (see Supplemental Fig. 1).

Age related effects. To test for adolescent specific peak in activation, we performed whole brain quadratic regression analyses. On the contrast winning > losing for self, there was a significant quadratic relationship between age and striatum activation for both the left and right VS ($p < .001$ uncorr, 10vox, VS Left: MNI −18 9–6, $t(247) = 3.83$; VS Right: MNI 18 15–9, $t(247) = 3.85$, significant at FWE

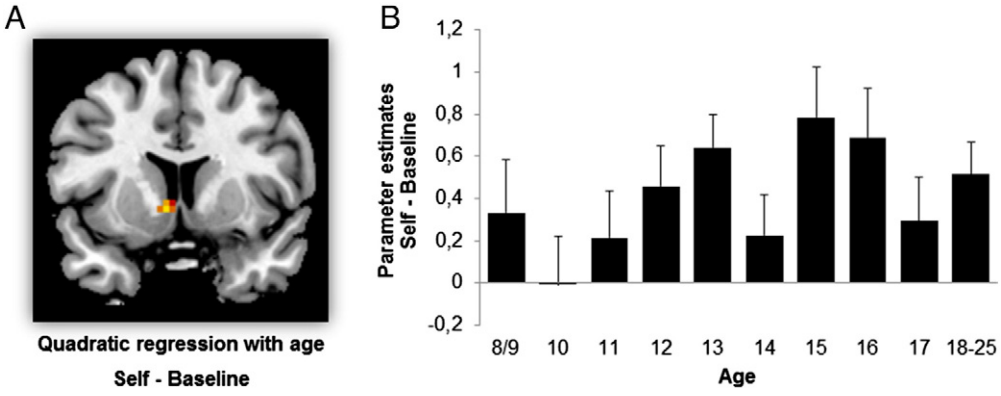

Fig. 3. A — Whole brain quadratic regression on the contrast Self–Baseline, modeled at trial onset. B — Parameter estimates for 10 age groups for the whole brain quadratic regression on the contrast Self–Baseline modeled at trial onset.

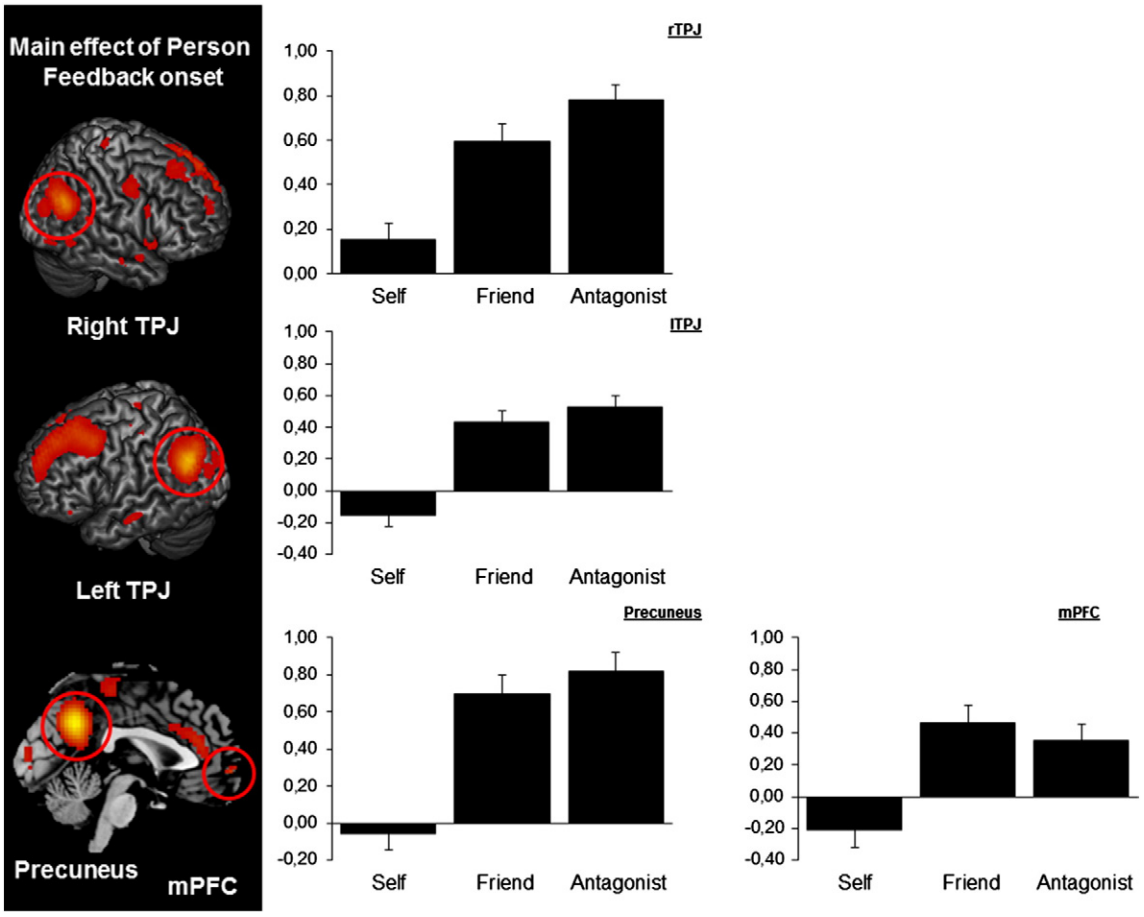

Fig. 4. Areas identified in the main effect of Person of the within person ANOVA with factors Person (three levels: Self, Friend, Antagonist) and Outcome (two levels: Win, Lose) performed on feedback onset. Graphs represent follow up ROI analyses performed on bilateral TPJ (MNI −51 −66 33; MNI 54–63 33), mPFC (MNI −3 60–3) and the precuneus (MNI −3 −57 36), indicated with red circles.

threshold when using small volume correction, see Figs. 6A and B, and Supplemental Table 5). Whole brain quadratic regressions did not show significant clusters of activation for contrast values between winning > losing for friend. On the contrast winning > losing for antagonist, there was a significant quadratic relationship between age and activation in medial prefrontal cortex ($p < .001$ uncorr, 10vox, MNI −6, 36, 3, $t(247) = 4.02$; significant at FWE threshold when using small volume correction, see Figs. 6C and D, and Supplemental Table 5). This analysis shows that mPFC activation is elevated in mid- to late adolescence compared to children and adults when winning versus losing for the antagonist.

Correlations with self-report measures

To investigate how self-reported pleasure ratings of winning and losing were related to neural responses we performed correlation analyses on ROIs derived from the whole brain Person × Outcome ANOVA on feedback onset. A positive correlation was found between the contrast value for winning–losing for self, derived from the VS clusters identified in the whole Person × Outcome ANOVA, and the difference on the ratings of the questions 'how much did you like to win for yourself' and 'how much did you like to lose for yourself' (r's > .19, p's < .006). A similar correlation was found for the contrast winning–

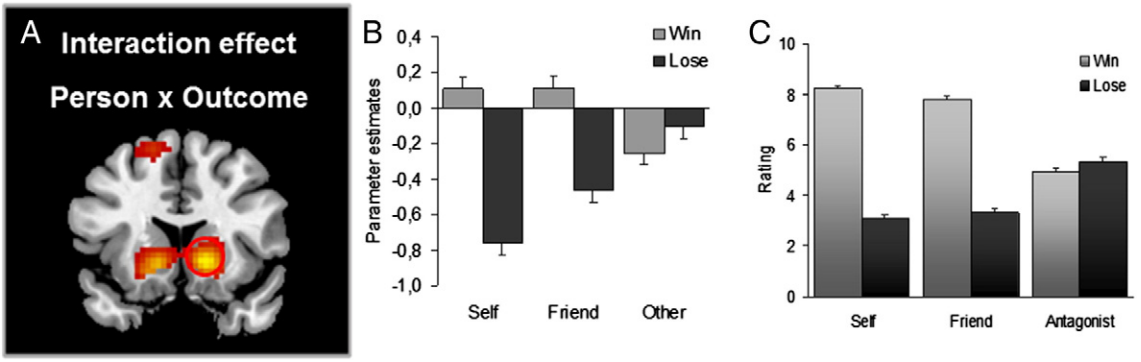

Fig. 5. A — Caudate clusters identified for the Person × Outcome interaction effect of the within person ANOVA with factors Person (three levels: Self, Friend, Antagonist) and Outcome (two levels: Win, Lose) performed on feedback onset. B — Follow up ROI analyses performed on the right caudate cluster identified in the Person × Outcome interaction. C — Self-report ratings for winning and losing for each of the persons.

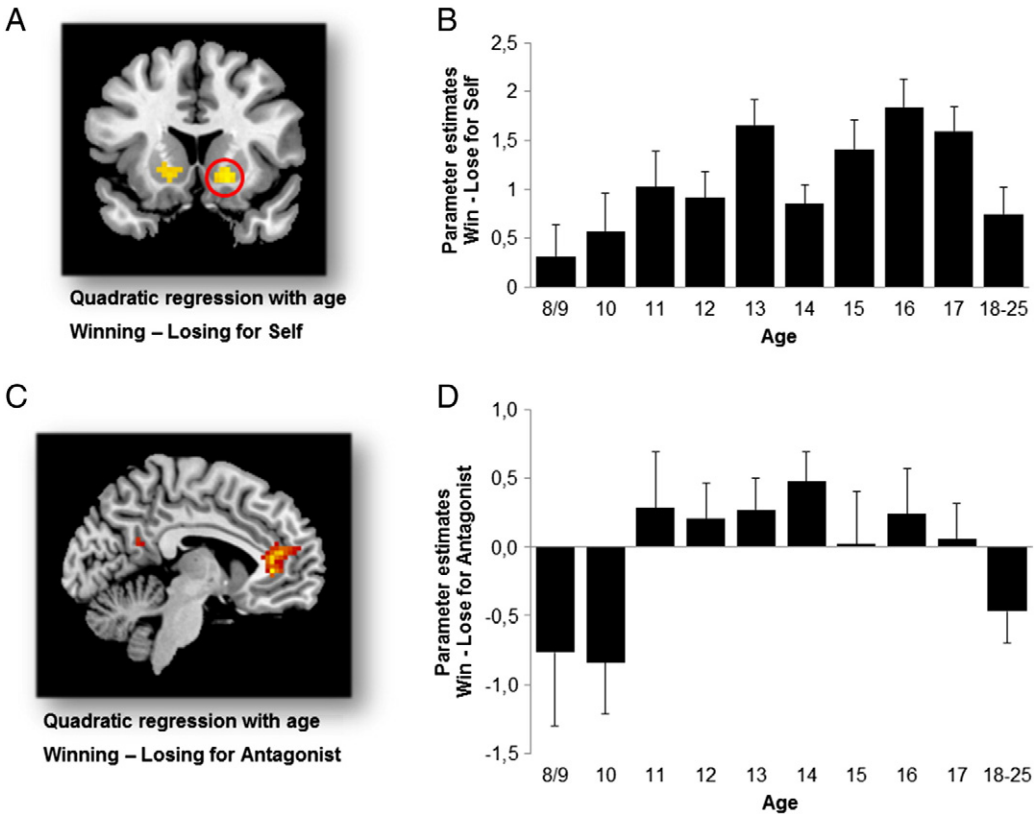

Fig. 6. A — Whole brain quadratic regression on the contrast winning > losing for Self, modeled at feedback onset. B — Parameter estimates for winning > losing for Self for the right ventral striatum cluster derived from the whole brain quadratic regression in panel A. C — Whole brain quadratic regression on the contrast winning > losing for Antagonist, modeled at feedback onset. D — Parameter estimates for winning > losing for Antagonist for the mPFC cluster derived from the whole brain quadratic regression in panel C.

losing for antagonist and the difference on the ratings for winning and losing for the antagonist (r's > .20, p's < .001). These findings confirm that the VS is implicated in the subjective feelings of pleasure when winning and losing money. For friend no such relationship was found.

Correlation analyses for the FQS showed that positive friendship quality was positively related to the contrast value winning–losing for friend in bilateral caudate for females (r's > .23, p's < .01; see Supplemental Fig. 2), but not for males (r's < .05, *n.s.*). When males and females were collapsed, the correlation was not significant.

Discussion

The current study aimed to investigate developmental patterns of neural responses to rewards in a social context in a large sample with a continuous age range between 8- and 25-years-old. Reward related neural responses have been associated with heightened risk-taking behavior during adolescence (Galvan, 2010), which is hypothesized to be related to the social context (for instance peer presence) (Steinberg, 2008). Here we investigated the social context related components of reward related activation. Our main findings are threefold: First, the results show that striatum responses to rewards are dependent on the beneficiary across age groups (see also Braams et al., 2013). Second, we found evidence for the hypothesized peak in striatum activation during adolescence which was specific to playing for self (Somerville et al., 2010). Third, there was a mid to late adolescent peak in medial prefrontal cortex activity when winning versus losing for antagonists. The discussion is organized in line with these three main findings.

Consistent with earlier findings in the adult sample (Braams et al., 2013), the results show that striatum responses to rewards are dependent on the beneficiary across age groups. Responses to rewards for self and friend showed a similar pattern, all participants showed robust activation in VS when winning versus losing for self and best friends whereas responses for an antagonist showed a reversed pattern. Furthermore, striatum activation was positively correlated with self-report measures of pleasure of winning for self and antagonist, thereby confirming the assumed relation between receiving rewards and pleasure responses in the ventral striatum (Delgado, 2007). These results are in line with previous research showing that social information influences striatum responses (Braams et al., 2013; Fareri et al., 2012; Güroğlu et al., 2008; Mobbs et al., 2009). Furthermore, the current findings concur with previous findings by Telzer et al. (2010) who showed that gaining for family also results in activity in the VS. Interestingly, Telzer et al. (2013) showed that those adolescents who had stronger activity in the VS when gaining for family showed larger declines in risk-taking two years later, suggesting that activity in the VS to close other's gains may be an indicator for positive development and may be protective against future risk-taking.

These findings set the stage for examining developmental differences in the ventral striatum and the social brain network in response to rewards for self, friends and antagonists. As in prior developmental studies (Galvan et al., 2006; Richards et al., 2013; Van Leijenhorst et al., 2010a), we found evidence for the hypothesized peak in striatum activation during mid to late adolescence (Somerville et al., 2010). Importantly, this peak was not only found on feedback onset, but also on trial onset. This finding indicates that VS responses in adolescence are elevated for both receipt of rewards as well as anticipation of outcomes.

However, the peak in VS responses was observed only when playing for self and not when playing for friends or antagonists, showing that this is a context dependent neural sensitivity. Given the importance of friendships in adolescence (Hartup and Stevens, 1997), we predicted that winning for friends would be more salient in mid-adolescence. The results did not confirm an adolescent peak in reward responses for friends, but showed dependency on friendship quality. That is to say, for girls we found a positive relationship with the self-reported

quality of the friendship with the friend they were playing for and neural activity in the ventral striatum when winning for their friend. However, this relationship was not found for boys. Possibly, girls experience friendships in a different way than boys (Dwyer et al., 2010). Previous studies have pointed out that girls tend to share and disclose more information with their best friend leading to more intimate friendships than boys. Boys are often more oriented towards a group of peers, whereas girls are more oriented towards the dyadic friendship (Rubin et al., 2008). Possibly this difference in friendship is reflected in striatal activity when gaining money for the best friend, but this question should be addressed in future studies.

When examining developmental differences in the social brain network (medial prefrontal cortex, precuneus, TPJ), we found that this network was selectively more active when playing for friends and antagonists, but not when playing for self, consistent with the notion that these areas are important for thinking about others (Blakemore, 2008). Additionally, the results revealed a mid to late adolescent peak in the medial prefrontal cortex when winning versus losing for antagonists. Previously, this area has been implicated as being important when thinking about relevant others (Blakemore, 2008; Braams et al., 2014; Van Overwalle, 2009; Young et al., 2010). Furthermore, activation in the medial prefrontal cortex has previously been implicated in mentalizing, or thinking about self relative to relevant others (Frith and Frith, 2012). According to one hypothesis, the ventral area of medial prefrontal cortex is important for evaluating self versus other-related information (Mitchell et al., 2005; Murray et al., 2012). Specifically, this area is more active when thinking about self and close others than distant unknown others (Murray et al., 2012). This hypothesis would indicate that rewards for disliked others are more relevant for self-other evaluation in mid-adolescence. Future studies should test this hypothesis in more detail. Yet, another hypothesis suggests that the ventral prefrontal cortex is active when there are higher cognitive demands for evaluating social information (Flagan and Beer, 2013). This more social-cognitive information processing hypothesis predicts that any information that requires more evaluation results in increased activation of ventral medial prefrontal cortex. This social–cognitive explanation suggests that the increased ventral medial PFC activation when gaining money for disliked others is related to increased social–cognitive evaluation in mid adolescence. One possible explanation would be that in adolescence there is higher need for peer acceptance (Sebastian et al., 2011) and understanding intentions of others (Blakemore, 2008). This explanation concurs with a prior study by Somerville et al. (2013) that also showed peak activity in mid-adolescence (relative to children and adults) in ventral medial prefrontal cortex when participants felt that they were being evaluated by peers. Future studies should test whether it is more important for adolescents to be accepted by dissimilar others compared to children and adults.

Our findings are consistent with results of Somerville et al. (2013) who also reported peak activity in medial prefrontal cortex activity. These are the first studies reporting adolescent specific activity in medial PFC, as previous studies that reported a developmental decrease in medial prefrontal cortex activity typically did not include a younger control group (Blakemore et al., 2007; Burnett et al., 2009). This peak activity pattern might suggest that social reorientation may have a unique effect on brain function not only in limbic areas, but also in higher social cognition areas, such as the medial prefrontal cortex. Previous work has shown that adolescents are influenced by their peers when taking risks. The current study provides new insights into how adolescents process rewards for friends and disliked others. However, real world risk-taking usually takes place in a context in which adolescents are in the presence of friends or where friend influence decisions directly (Steinberg, 2004). An interesting direction for future studies will be to investigate how the presence of friends influences neural responses to reward related outcomes for self and friends (Chein et al., 2011). Furthermore, the task used in this study is a passive gambling task in which the participants cannot actively take or avoid risks. Future studies could examine reward related neural responses to actively taking risks and assess whether participants distinguish between beneficiaries in level of risk-taking.

Conclusion

Taken together, this study shows that striatum activation peaks in mid-adolescence and that striatum activation is influenced by social context. In addition, we observed that medial prefrontal cortex shows a similar adolescent peak in sensitivity when playing for disliked others. This is the first study confirming the hypothesized peak in both striatum and social brain activation during adolescence in a large sample with a continuous age range spanning from childhood to early adulthood. These results have major significance given that risk-taking is one of the main causes for injury in adolescence. Increased activation of the striatum has been proposed to be the mechanism behind this risk-taking, whereas this study shows that the social context is most likely of equal importance.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2014.06.020.

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