The neurocognitive development of social decision-making

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4. Changing brains, changing perspectives: The neurocognitive development of reciprocity

Adolescence is characterized by the emergence of advanced forms of social perspective-taking and substantial changes in social behavior. Yet, little is known about how changes in social cognition are related to changes in brain function during adolescence. This study investigated the neural correlates of social behavior in three phases of adolescence using fMRI while participants played the second player in a Trust Game. With age, adolescents were increasingly sensitive to the perspective of the other player as indicated by their reciprocal behavior. These advanced forms of social perspective-taking were associated with increased involvement of the left temporal parietal junction (TPJ) and the right dorsolateral prefrontal cortex (DLPFC). In contrast, young adolescents showed more activity in the anterior medial prefrontal cortex (aMPFC), a region previously associated with self-oriented processing and mentalizing. These findings suggest that the asynchronous development of these neural systems may underlie the shift from self towards other-oriented thought.

4.1 Introduction

"*When I was a boy of 14, my father was so ignorant I could hardly stand to have the old man around. But when I got to be 21, I was astonished at how much the old man had learned in seven years."* (Arnett, 2000)

This quote by Mark Twain (1835-1910) illustrates the importance of understanding changes in perspective-taking across adolescence. Although this phenomenon has attracted attention for centuries, the question how these changes arise is still as debated today as it was 100 years ago. For example, it is well known that early in adolescence, individuals are still more inclined towards self-oriented thought and actions (Eisenberg, Carlo, Murphy, & Van Court 1995; Elkind, 1985), whereas later in adolescence individuals become more inclined towards thinking about others, taking social responsibility and controlling their impulses (Steinberg, 2009). Additionally, recent studies have shown that functional changes occur in 'social brain' regions (for a review see Blakemore, 2008). It is, however, not yet known how changes in brain function contribute to specific changes in social behavior and perspective-taking. Understanding the emergence of social behavior and perspective-taking in adolescence is of high importance to society, as it is the critical transition period during which children gradually become independent individuals.

Recently, reciprocal exchange in social interaction has been examined with a simple economic exchange game; the Trust Game (Berg, Dickhaut, & McCabe, 1995) (see Figure 4.1). In the Trust Game two players can share a certain amount of money. The first player can choose to divide the money equally between herself and the second player, or to give it all to the second player with the advantage that the amount then increases in value. The second player has the choice to reciprocate and share the increased amount of money with the first player (act prosocial), or to defect and exploit the given trust by keeping most of the money for herself (act proself). This game touches on a central issue in the development of social perspective-taking; it requires the ability to understand intentions of and benefits for others.

Prior studies with adults using functional magnetic resonance imaging (fMRI) demonstrated different neural circuits for the receipt and the display of prosocial behavior in the Trust Game (King-Casas et al., 2005; Krueger et al., 2008; van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2009b). In particular, when the second player receives trust from the first player, a network of areas including the temporal parietal junction (TPJ) is activated. Several meta-analyses have shown that in social contexts the TPJ is important for shifting attention between own and other perspectives and inferring intentions (Mitchell, 2008; van Overwalle, 2009). It has therefore been suggested that within the context of the trust game, receiving trust might result in a shift in perspective from self to the other (King-Casas et al., Krueger et al., 2008, van den Bos et al., 2009b).

In contrast, a different network is activated when the second player decides to either reciprocate or exploit trust. In particular, anterior medial prefrontal cortex (aMPFC) activity has been reported when individuals exploit trust and maximize own gains (van den Bos et al., 2009b). This region has also been reported to be important for first players when they trust another individual, with the expectation of increasing their own pay-off (McCabe et al., 2001). It is suggested that the aMPFC activity in context of the Trust Game reflects the evaluation of own outcomes or thinking about one's reputation (Frith & Frith, 2008).

Thus, the TPJ and the aMPFC, which together have been described as part of the 'social brain' network (van Overwalle 2009), seem to have separable roles in reciprocal behavior. Importantly, these regions work in concert with brain circuits which are important for regulation of thought and action such as the dorsolateral prefrontal cortex (DLPFC) (Miller & Cohen, 2001). In particular, the DLPFC was found to be important for the control of selfish or self-oriented impulses in several economic games (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; Rilling et al., 2007). Importantly, DLPFC is one of the brain regions that shows the most protracted structural as well functional development (Crone, 2009).

One of the predictions that follows from these prior studies is that adolescent development of perspective-taking in social decision-making is associated with different recruitment of aMPFC, TPJ and DLPFC. Our specific hypotheses about the neural developmental brain changes related to social behavior were informed by studies showing developmental changes in the brain during childhood and adolescence. In prior studies using simple tasks that involve thinking about different social scenarios, young adolescents showed less activity in TPJ, but increased activity in aMPFC compared to adults (Blakemore et al., 2007; Pfeifer, Lieberman, & Dapretto, 2007; Wang, Lee, Sigman, & Dapretto, 2006).We predicted that defecting (a self-oriented act) would be associated with increased aMPFC activity, given its role in thinking about self-motives relative to intentions and goals of others. Under the hypothesis that especially in early adolescence individuals are more inclined towards self-oriented thought and action (Eisenberg et al., 1995; Elkind, 1985), we predicted higher defection in early adolescents and more activity in self-related brain areas (aMPFC), relative to mid adolescents and adults. Furthermore, under the hypothesis that adolescents show late changes in intention consideration (Blakemore, 2008), we predicted that activity in TPJ when receiving trust would increase between early adolescence and adulthood. Finally, based on developmental studies that demonstrated increased activity in cognitive control and emotion regulation tasks with increasing age (Crone et al., 2006; Steinberg, 2005), we expected that DLPFC would be increasingly engaged during adolescence in intention consideration and reciprocity.

To test these hypotheses, we examined behavioral choices and neural responses of second players in the Trust Game in three age groups selected based on adolescent developmental stage; pubertal early adolescents (12-14 years), post-pubertal mid adolescents (15-17 years) and young adults (18-22 years). Based on our own and other behavioral studies with economic games, we expected an increase in the general level of reciprocity with age (Sutter & Kocher, 2007; van den Bos, van Dijk, Westenberg, & Crone, 2009a).

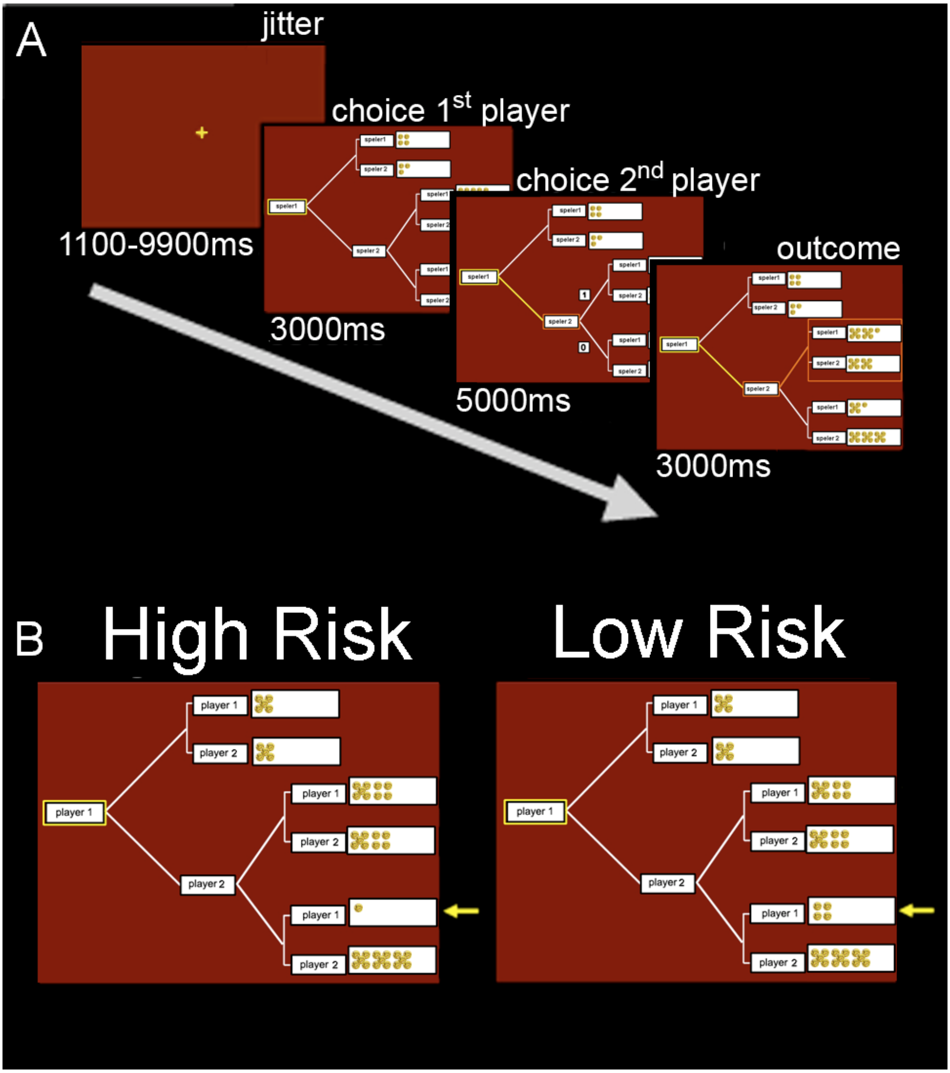

Figure 4.1: A: Each trial started with a 3-second display of the two choice alternatives for the first player; trust or no trust. After 3 seconds the trust or no-trust decision was shown to the participant. When the first player chose not to trust, the no-trust outcome was visually highlighted for 3- sec and the trial ended. For those trials on which the first player chose to trust, participants were instructed to make their decision within a 5-second window. The 5-sec decision-display was followed by either a 3-sec display of the outcome of their decision (reciprocate or defect) or a “too late” screen in case the participant did not respond within 5 seconds. In case of trust the total amount of money increased with a factor between 1.8 and 2.2.

To further test the ability to understand others' intentions, we added a task condition in which we manipulated the amount that the first player could lose by trusting the second player (the participant) (Malhotra, 2004; van den Bos et al., 2009a, 2009b, see Figure 4.1). In the analyses the trials on which the first player could lose a relatively large amount were labeled high-risk choices, and the trials on which the first player could lose only a small amount were labeled low-risk choices. Higher level of reciprocity in the high-risk context is hypothesized to reflect the recognition of the positive intentions of the first player, relative to the low-risk context (Malhtora, 2004; Pillutla, Malhotra, & Murnighan, 2003). As a consequence, this additional manipulation enabled us to obtain a behavioral measure of social perspective-taking within the task, with the expectation of larger risk-related reciprocity differentiation (RDS) for the older participants who are more capable of identifying intentions and integrating perspectives (van den Bos et al., 2009a).

4.2 Methods

4.2.1 Participants

Sixty-two healthy right-handed paid volunteers (30 female, 32 male; ages 12-22, M = 16.2, SD = 2.9) participated in the fMRI experiment. Eight participants were excluded from the fMRI analysis because they had an unreliable number of observations in one of the conditions ($n<4$). Age groups were based on adolescent development stage, resulting in groups composed of early adolescence/pubertal (12- to 14-year-olds, N=21, 11 females), mid adolescence/post-pubertal, (15- to 17-year-olds, N=15, 7 females) and young adults (18- to 22-year-olds, N=18, 9 females). A chi square analysis indicated that the gender distribution was similar across age groups (X2 (2) = .114, p = .94). The data from the adults were also reported in another study (van den Bos et al., 2009b). Participants gave informed consent for the study, and all procedures were approved by the medical ethical committee of the Leiden University Medical Center (LUMC).

Participants completed the Raven Standard Progressive Matrices (R-SPM) for an estimate of their reasoning skills (Raven, 1941), and the Tanner scale (Tanner, 1975) for an estimate of their stage of pubertal development (see Table S4.1). There were no significant differences in IQ between the different age groups (F (2, 51) = .62, p = .54), and the Tanner stage development demonstrated a significant difference in puberty levels between age groups 12-14 (M = 2.95, SE = .24) and 15-17 (M = 4.11, SE = .22, t(1,33) = 3.89, $p < .001$).

4.2.2. Task Procedure

The procedure for the Trust Game was similar to the previously reported imaging study with adults (van den Bos et al., 2009b, see Figure 4.1). Participants were instructed that in an earlier phase of the study, other individuals had been assigned the roles of first player, and that they would complete the study in the role of second player inside the scanner. Furthermore, they were instructed that both the participant and the other players were financially rewarded based on the choices made during experiment. In each round of the experiment, participants were paired with a different, anonymous player who was matched for age and gender. At the end of the experiment the computer randomly selected the outcome of 5 trials and the sum of these trials determined the participants' payoff.

Unknown to the participant the decisions of the first player were not the decisions of real other participants, but were preprogrammed to reflect the behavioral pattern that was displayed in an earlier study (van den Bos et al, 2009a). In total, the task consisted of 145 trials; 96 trust trials and 49 no trust trials. The trials were divided over 4 blocks of 8.5 minutes each. The trials were presented in pseudo-random order with a jittered interstimulus interval (min=1.1-sec, max=9.9 sec, mean= 3.37 sec).

Before the experiment participants received a written explanation of the task, filled out a questionnaire and played 12 "practice" rounds. None of the participants failed this test.

4.2.3. fMRI Data Acquisition and Analysis

Data were acquired using a 3.0T Philips Achieva scanner at the LUMC. T2*-weighted EPIs (TR= 2.2 sec, TE= 30ms, 80 x 80 matrix, FOV = 220, 35 2.75mm transverse slices with 0.28mm gap) were obtained during 4 functional runs of 232 volumes each. A high-resolution T1-weighted anatomical scan was obtained from each participant after the functional runs. Data were analyzed using SPM2 (Wellcome Department of Cognitive Neurology, London). The functional time series were realigned, normalized to EPI templates, and spatially smoothed using a 8 mm full-width half-maximum Gaussian kernel. There were no significant differences in movement parameters between age groups ($F(2, 51) = 1.03$, $p = .36$).

Statistical analyses were performed on individual participants' data using the general linear model in SPM2. The fMRI time series data were modeled by a series of events convolved with a canonical haemodynamic response function (HRF). The start of the first player's choice display, no-trust and trust outcomes were modeled as 0-duration events. The trust outcomes were divided into reciprocate and defect decisions. These 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 run effects. The least-squares parameter estimates of height of the best-fitting HRF for each condition were used in pairwise contrasts. At the group level, contrasts between conditions were computed by performing one-tailed t-tests on these images, treating participants as a random effect. Results were considered significant at an uncorrected threshold $p > .001$ and $k > 10$ voxels.

We further performed voxelwise ANOVAs to identify regions that showed age related differences in relation to social decision-making. The developmental patterns in the behavior and fMRI data we constrained to a specific set of contrasts that captured developmental trends (linear increase [-1 1 0] ∩ [0 -1 1], early increase [-2 1 1], late increase [-1 -1 2], and their inverse) in the trust vs. no trust and defect vs. reciprocate comparisons. For the age analyses we used a more stringent threshold of $p < .0002$, using a Bonferroni correction for multiple comparisons ($p < .001 / 6$).

We used the MARSBAR toolbox for SPM2 (Brett et al., 2002) to extract BOLD activity time series in Regions of Interest (ROI) to further characterize patterns of activity. We created ROIs of the regions that were identified in the functional mask of whole brain analyses.

4.3 Results

4.3.1. Behavioral Results

Increasing effect of intentions on behavior. On average participants reciprocated about half of the trials (*M* = 53%), but there were large individual differences in behavior (*SD* = 17%, Min = 12%, Max = 87%; see Figure 4.2A). As predicted, the analyses of risk showed that participants reciprocated more when the risk for player 1 was high compared to when it was low ($F(2, 51) = 25.22$, $p < .001$, see Figure 4.2B). Even though there were no age related differences in mean reciprocal choices ($F(2, 51) < 1$, $p = .66$; see Figure 4.2A), there was an age x risk interaction for percentage of reciprocal choices ($F(2, 51) = 5.44$, $p < .007$, see Figure 4.2B). As expected, a post hoc Tukey test confirmed that all groups differed significantly from each other in RDS score at $p < .05$. Furthermore, only for the older adolescents and adults there was more reciprocity for high-risk than for low-risk trials (both *p*'s < .01), whereas the youngest adolescent group did not differentiate between high- and low-risk trials ($p = .8$, Figure 4.2B).

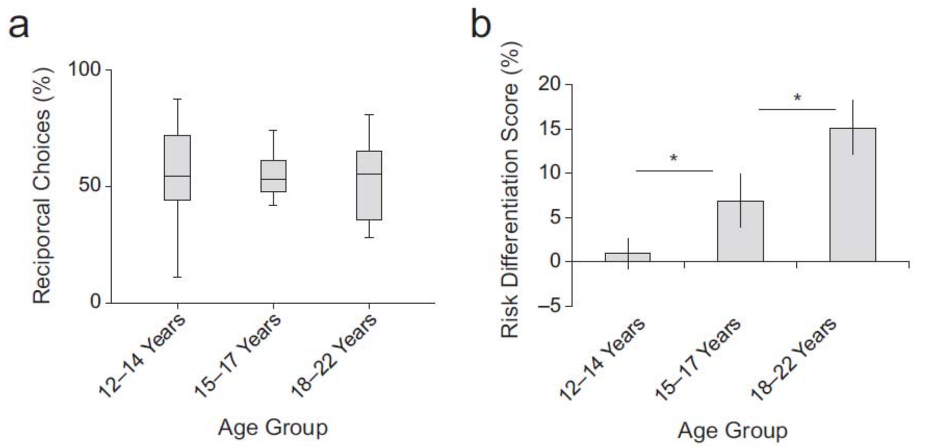

Figure 4.2: A) Average level of reciprocity for the total duration of the experiment displayed separately for each age group. Error bars represent standard deviation. Testing for outliers at 95% confidence interval did not yield any outliers for any of the age groups. **B)** The risk differentiation score (high-risk reciprocity – low-risk reciprocity) for each age group. This graph shows that the RDS increased with age, a post hoc Tukey test revealed that all groups differed significantly from each other ($p < .05$). Error bars are standard errors.

4.3.2 fMRI Results

*Receiving Trust***.** To identify the neural correlates of receiving trust, which was hypothesized to be associated with consideration of the intentions of the other, we compared the [Trust – No Trust] contrast across all participants. This analysis revealed increased activity in a large network of areas associated with cognitive control; the DLPFC, parietal cortex and dorsal medial frontal cortex/anterior cingulate cortex (ACC) (see Table 1). Subsequently, we tested the hypothesis of age related changes in activity related to receiving trust by performing mixed linear and non-linear ANOVAs with age group as between participant factor. As anticipated, the conjunction contrast [-1 1 0] ∩ [0 -1 1] demonstrated age related changes in left TPJ. Additionally, the contrast [-1 -1 2] revealed activity in right DLPFC (see Figure 4.3, Table 4.1). Time-series analyses of l-TPJ showed heightened activity for both reciprocate and defect choices compared to no-trust trials, however this difference was not significant in early adolescence, whereas it was present for late adolescents and greatest for the young adults (see Figure 4.3). In contrast, the time series analysis for DLFPC revealed heightened activity for reciprocate and defect choices relative to no-trust trials only for the young adults. The correlations between individual risk difference scores (RDS) and activity in these areas ($r = .37$, $p < .006$ for l-

TPJ and $r = .45$, $p < .001$ for r-DLPFC, see Figure S4.1) strengthens the hypothesis of a relation between l-TPJ and r-DLPFC function and intention identification and perspective-taking.

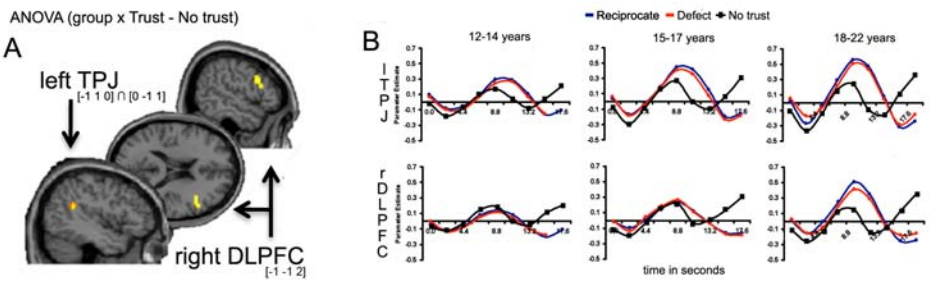

Figure 4.3: Age differences in l-TPJ and r-LPFC activity associated with receiving trust. **A)** Activation maps with the clusters that show significant linear [-1 1 0] ∩ [0 -1 1] and non-linear [-1 -1 2] increases in trust related activation with age. **B)** Showing the time-course of activation in the l-TPJ and the r-DLPFC related to defect, reciprocate and no trust. Along the x-axis 0 seconds indicates 1) the onset of the choice for the participant in case of trust, or 2) the outcome of the experiment in case of no trust.

*Defect vs. Reciprocate***.** Next, we investigated the neural correlates of proself versus prosocial motivated acts, by examining differences in neural activity for reciprocate and defect choices following trust outcomes. As expected, the [Defect – Reciprocate] contrast across all participants revealed increased BOLD response in the aMPFC (Figure 4.4 and Table 4.1). Additional activity was found in the left anterior Insula and the right inferior frontal gyrus. Consistent with our previous findings (van den Bos et al., 2009b), the opposite contrast [Reciprocate – Defect] did not result in significant changes in neural activity.

To further investigate whether there were age related changes in [Defect - Reciprocate] activity, we performed linear and non-linear ANOVAs with age group as between subjects factor on the [Defect – Reciprocate] contrast. The contrast [-2 1 1] revealed an age related change which was specific for the aMPFC (see Figure 4.4 and Table 4.1). These findings demonstrate that the differential engagement of the aMPFC increases between early and mid adolescence and then remains stable in mid to late adolescence/early adulthood.

The time-series of the aMPFC region revealed increased activity compared to baseline for defect choices in all age groups. Closer inspection of the activation patterns revealed that early adolescents also demonstrate heightened activity for reciprocal choices compared to baseline. Thus, consistent with the hypothesis of heightened aMPFC activity in early adolescence, we demonstrate a *decrease* in aMPFC activity related to reciprocal choices with age. This was further confirmed by a significant negative age correlation for reciprocate > fixation (r = .56, *p* < .02). No such correlation was observed for defect > fixation (r = .06, *p* = .72).

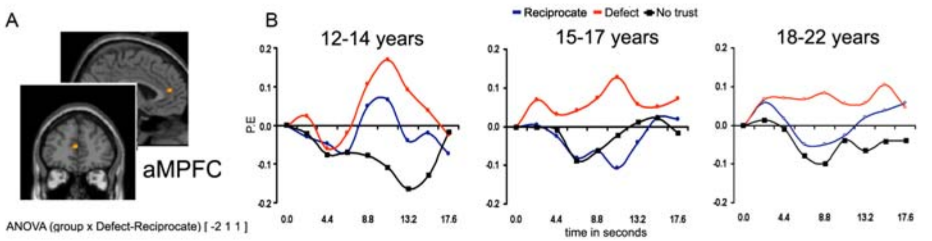

Figure 4.4: Age differences in aMPFC activity associated with defect vs. reciprocate decisions. **A)** Activation maps with the clusters that show an early increase [-2 1 1] in the difference in defect vs reciprocate activation. **B)** Showing the time-course of activation in the l-TPJ and the r-DLPFC related to defect, reciprocate and no trust. Along the x-axis 0 seconds indicates 1) the onset of the choice for the participant in case of trust, or 2) the outcome of the experiment in case of no trust.

Table 4.1: Brain Regions revealed by whole brain contrasts.

Anatomical region	L/R	vxls	Z	MNI coordinates		
				x	y	z
Receiving Trust						
[Trust - No Trust]						
Superior Parietal Lobule	R	71	4.14	21	-66	54
Precuneus	L	121	4.18	-30	-45	42
Caudate / Dorsal Striatum	L/R	431	5.20	-15	0	15
ANOVA [Trust - No Trust] [-1 1 0] ∩ [0 -1 1]						
TPJ	L	44	4.06	-44	-46	29
ANOVA [Trust - No Trust] [-1 -1 2]						
DLPFC	R	56	4.01	44	16	21
Choice Type						
[Defect – Reciprocate]						
anterior Medial Prefrontal Cortex	L/R	774	4.89	0	42	6
Visual Cortex	L/R	733	8.82	6	-93	12
Insular Cortex	L	63	4.82	-36	24	-12
Inferior Frontal Gyrus	R	27	3.95	62	21	0
[Reciprocate – Defect]						
Visual Cortex	L/R	490	7.72	6	-73	6
ANOVA [Defect – Reciprocate] [-2 1 1]						
anterior Medial Prefrontal Cortex	L/R	78	5.84	2	42	15

MNI coordinators for main effects, peak voxels reported at *p* < .001, at least 12 contiguous voxels. Age contrasts were corrected for multiple comparisons; *p* < .001 / 6. For each ROI, the center of mass is reported.

Individual differences. A final question concerned the relation between neural activity and the average level of prosocial behavior displayed in the task. A whole-brain regression analyses on the [Defect – Reciprocate] contrast with average reciprocity per individual as predictor revealed activation in bilateral anterior Insula, dorsal anterior cingulate cortex (dACC) and r-DLPFC (Table S4.2, Figure 4.5). Higher reciprocity was thus associated with more activation in these areas when defecting, and higher defection was associated with more activation in these areas when reciprocating.

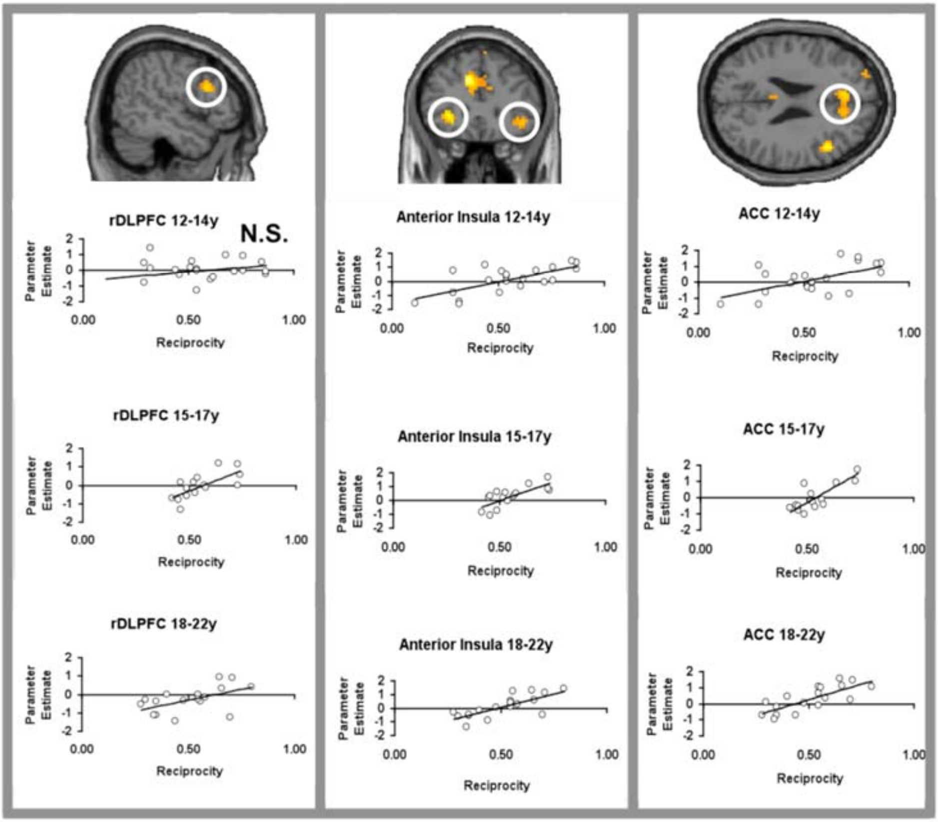

Figure 4.5: Activation maps for the regression analysis on the [Defect – Reciprocate] contrast with average level of reciprocity as covariate for all participants, threshold at p < .001. Separate scatter plots representing the correlations between the [Defect-Reciprocate] parameter estimate and average reciprocity for each age group separately, all based on the ROIs extracted from the whole group regression analysis.

4.4 Discussion

We investigated adolescence as a transitional period, during which linear as well as non-linear changes in social reasoning and associated brain circuitry take place (Casey et al., 2008). Indeed, analyses of age differences demonstrate that the regions implicated in social behavior followed asynchronous developmental patterns, with faster maturation of aMPFC but late maturation of l-TPJ and r-DLPFC. This asynchronous pattern of functional brain development may bias adolescents towards different social behavior in daily life (Casey et al., 2008; Paus, Keshavan, & Giedd, 2008; Steinberg, 2005).

The behavioral data are consistent with prior observational studies which marked adolescence as a transition period for social behavior (Eisenberg et al., 1995, 2005). Interestingly, these results highlight that adolescence is not necessarily characterized by general increases of prosocial behavior, but rather by an increase in the sensitivity to the perspective of others in social decision-making (see also Blakemore 2008; Kohlberg, 1981; Selman 1980). That is, increased consideration of consequences for others (i.e., increased RDS) was accompanied by both an *increase* in reciprocity on high-risk trials and a *decrease* of reciprocity for low-risk trials, and importantly the youngest adolescents did not show sensitivity to the perspective of the other. Alternatively, the age related increase in risk differentiation could be the result of increased inequity aversion (Fehr & Schmidt 1999). Both explanations are consistent with the notion of advanced forms perspective-taking in adolescence.

Our reasoning that receiving trust was associated with more active deliberation of the motives of others was further supported by increased activity in the l-TPJ, an area that is implicated in taking the perspective of others and inferring intentions (Mitchell, 2008; van Overwalle, 2009). In support of the hypothesized shift in attention from self to the other during adolescence, we observed an increase in the engagement of the l-TPJ with age. Moreover, the suggested role of the l-TPJ in shifting perspective from self to other was further supported by the correlation between l-TPJ activity and the behavioral index of perspective-taking (RDS); the more participants differentiated between the low an high-risk context, the more active the l-TPJ was after receiving trust. In addition, the pattern of activation of the l-TPJ, and the absence of an effect of risk on behavior for the youngest adolescents, suggests that in early adolescence focus of attention is not (yet) on the outcomes and intentions of others, and that there are still changes between mid adolescence and young adulthood in the focus on the other. These findings are in line with prior social scenario reading studies, which also demonstrated an increase in the l-TPJ activity between ages 10-18 and 22-32-years (Blakemore et al., 2007). Furthermore, recent studies revealed that TPJ is correlated with self reports of altruism (Tankersley et al.,

2007) and charitable giving (Hare et al., 2010), consistent with the presumed role of shifting attention from self to others in a social context.

Besides activity in the l-TPJ, we found that young adults, when receiving trust, showed increased activity in the r-DLPFC, an area previously found to be involved in tasks requiring cognitive control (Miller & Cohen, 2001) and the control of selfish or self-oriented impulses in context of social dilemmas (Rilling et al., 2007). This activity may indicate a regulatory role of r-DLPFC in social exchange as it was more active for adults for the non-preferred response alternative (Knoch et al., 2006). Consistent with studies which employed cognitive control paradigms (Crone et al., 2006) our results indicated an increase in the engagement of the r-DLPFC with age. Apparently, over the course of adolescence not only the development of the l-TPJ, but also the r-DLPFC contributes to a refinement in social behavior, which is supported by the finding that activity in the r-DLPFC also correlated with the ability to infer intentions of others (risk difference score). Thus, the differential involvement of l-TPJ and r-DLPFC marks mid adolescence (15-17-years) as an important transition period for intention consideration and social behavior, during which not all children are yet recruiting the associated brain regions to the same extent as adults, but during which emerging intention consideration is on its way.

If the changes in social behavior are associated with increased consideration of the outcomes for the other, what then motivated adolescents to act selfish? What are the neural correlates of self-oriented behavior? These questions were tackled by the comparison of defect and reciprocate choices which revealed increased activity in the aMPFC for defect choices in young adults and mid adolescents. Given the role of the aMPFC in processing self-referential and self-relevant events (for a review see van Overwalle, 2009), these findings suggest that participants were more involved in self-oriented thought when they defect and thus maximize personal outcome. The question then arises; how does this region support self-oriented acts in early adolescence; do adolescents show increased activity for defect choices? Intriguingly, this was not the case. When acting pro-self (i.e., when defecting), early adolescents showed similar activity in aMPFC as mid adolescents and young adults. When reciprocating, however, young adolescents also showed activity in aMPFC. This activity was not found in mid adolescents and adults. One of the fascinating questions for future research is to test the hypothesis that even when reciprocating young adolescents are engaged in self-referential thoughts. Prior research has demonstrated that in late childhood/early adolescence, social interaction is considered from an egocentric perspective (Eisenberg et al., 1995; Elkind, 1985). Possibly it is not until mid adolescence that a prosocial act becomes more automatic and less self-engaged.

Although meta-analyses of social cognition for adults (Lieberman, 2007; van Overwalle 2009) and adolescents (Blakemore, 2008) have indicated the importance of the aMPFC in self referential processes, other research has implicated this region in mentalizing, or thinking about what others are thinking about you (Amodio & Frith, 2006). In particular, in the context of social interactions the role of the aMPFC has been related to considering one's reputation (Frith & Frith, 2008). Future studies should unravel which of these aspects of self-referential processing is changing in early to mid adolescence.

This study brings us a step closer towards understanding why Mark Twain started to understand his father better when he was 21 than when he was 14. Most likely this was associated with increased perspective-taking skills subserved by interacting brain regions important for social reasoning. Future research could benefit from analyzing connectivity between these areas to better understand how these regions contribute to social behavior (Burnett & Blakemore, 2009). Finally, prior studies have shown that the combined use of neuroimaging and game theoretical paradigms can further the understanding of the neural underpinnings of psychopathology (Chiu et al., 2009).Therefore, the current findings on normative social development can also be the basis for understanding the development of psychopathology in adolescence (Paus et al., 2008).

4.5 Supplementary Material

Table S4.1. Group scores for IQ, reaction times (RT), head movement and gender distribution (SD = Standard Deviation; mm= millimeter). None of the group differences are significant (all *p*'s > .5)

Group differences			
	12-14 years	15-17years	18-22years
Raven IQ (SD)	121.2 (5.2)	121.5(6.2)	119.2(8.1)
RT in seconds (SD)	1.6(0.6)	1.7(0.6)	1.8(0.5)
Movement (mm)	0.75	0.76	0.73
Female (Male)	11(10)	7(8)	9(9)

Table S4.2. : Brain Regions revealed by regression analysis

Anatomical region	L/R	voxels	Z	MNI coordinates		
				x	y	z
Regression [Defect – Reciprocity] w/ avg. reciprocity			Z			
anterior Cingulate Cortex	L/R	335	4.70	-9	27	36
anterior Insula	R	241	5.12	33	21	0
	L	133	4.72	-33	24	0
Superior parietal cortex	R	150	4.04	21	-66	54
DLPFC	R	84	4.38	48	18	24

MNI coordinates for main effects across all participants, peak voxels reported at $p < .001$, at least 12 contiguous voxels.

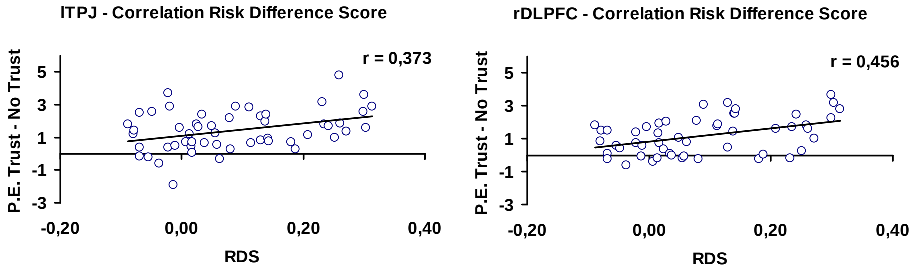

Figure S4.1: Plots showing the correlation between parameter estimates for the Trust - No Trust contrast and the risk differentiation scores (RDS), in the l-TPJ and the r-DLPFC.