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Changing Brains, Changing Perspectives: The Neurocognitive Development of Reciprocity

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Abstract

Adolescence is characterized by the emergence of advanced forms of social perspective taking and significant changes in social behavior. Yet little is known about how changes in social cognition are related to changes in brain function during adolescence. In this study, we investigated the neural correlates of social behavior during three phases of adolescence, carrying out functional magnetic resonance imaging of participants' brains while they were Player 2 in the Trust Game. We found that 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 behavior were associated with increased involvement of the left temporo-parietal junction and the right dorsolateral prefrontal cortex. In contrast, young adolescents showed more activity in the anterior medial prefrontal cortex, 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 thinking about self to thinking about the other.

Keywords

Trust Game, reciprocity, development, perspective taking, fMRI

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> 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. (Mark Twain, quoted by Arnett, 2004, p. 210)

This quote by Mark Twain (1835–1910) illustrates the importance of understanding changes in one's perspective from adolescence to adulthood. Although this phenomenon has attracted attention for centuries, just 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 more inclined toward self-oriented thought and actions (Eisenberg, Carlo, Murphy, & Van Court 1995; Elkind, 1985), whereas later in adolescence, individuals become more inclined to think about others, take social responsibility, and control their impulses (Steinberg, 2009). In addition, studies show that functional changes occur in social brain regions during adolescence (see Blakemore, 2008, for a review). However, it is not yet known exactly 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 this is the critical transition period during which children gradually become independent individuals.

Reciprocal exchange in social interaction has been examined via a simple economic exchange game, the Trust Game (Fig. 1; Berg, Dickhaut, & McCabe, 1995). In the Trust Game, two players can share a certain amount of money. The first player (Player 1) can choose to divide the money equally between himself or herself and the second player (Player 2) or to give it all to Player 2; the advantage of giving all the money to Player 2 is that the amount increases in value. If Player 1 decides to divide the money equally, the game ends. However, if Player 1 decides to give the money to Player 2, Player 2 subsequently has the choice to reciprocate and share the increased amount of money with Player 1 (act in a prosocial manner) or

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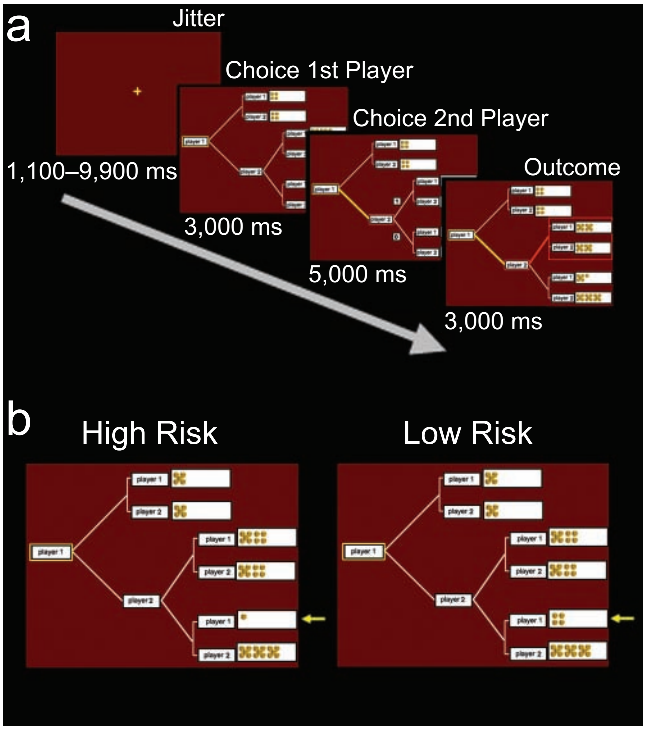

Fig. 1. Diagram of the sequence of a Trust Game trial (a) and examples of a high-risk trial and a low-risk trial (b). The diagram in (a) shows the sequence of a Trust Game trial in which Player 1 decided to trust and Player 2 decided to reciprocate. The paths highlighted in yellow and orange indicate the decisions of the players. A fixation cross (with jittered duration) was presented before each trial. Risk was defined as the amount that Player 1 could lose if he or she trusted Player 2 (the participant) and Player 2 decided to defect. All possible outcomes were known by both players at the start of each trial. Thus, in the examples shown here, Player 1 risked losing four coins in the high-risk trial and just one coin in the low-risk trial.

to defect and exploit the given trust by keeping most of the money for himself or herself (act in a proself manner). This game touches on two central issues in the development of social perspective taking: It requires the ability to understand the intentions of others and to understand benefits for others.

Figure 1a shows the sequence of a Trust Game trial in which Player 1 decided to trust Player 2 and Player 2 decided to reciprocate. Each trial began with 3-s display of the two choice alternatives for the first player: trust or no trust (in cases of trust, the total amount of money increased by a factor of 1.8 to 2.2, which varied across trials). After 3 s, the trust or no-trust decision was shown to the participant. For trials on which Player 1 chose to trust (as illustrated in Fig. 1a), the name of the participant was highlighted, and Player 2 was instructed to make a decision within a 5-s time period. The 5-s decision display was followed by either a 3-s display in which the outcome of the decision (reciprocate or defect) was highlighted or a “too late” screen if the participant did not respond within 5 s. If Player 1 chose not to trust, the no-trust outcome was visually highlighted for 3 s, and the trial ended.

Studies of adults using functional magnetic resonance imaging (fMRI) demonstrate 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, 2009). In particular, when Player 2 receives trust from Player 1, a network of areas including the temporo-parietal junction (TPJ) is activated. Several meta-analyses have concluded that in social contexts, the TPJ is important for shifting attention between one’s own and other perspectives and for 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 the self to the other (King-Casas et al., 2005; Krueger et al., 2008, van den Bos et al., 2009).

In contrast, a different network is activated when Player 2 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., 2009). This region has also been reported to be important for Player 1 when he or she trusts another individual, with the expectation of increasing his or her own payoff (McCabe, Houser, Ryan, Smith, & Trouard, 2001). It has been suggested that the aMPFC activity in the context of the Trust Game reflects the evaluation of one’s 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), appear to have separable roles in reciprocal behavior. It is important to note that these regions work in concert with brain circuits that are involved in the regulation of thought and action, such as the dorsolateral prefrontal cortex (DLPFC; Miller & Cohen, 2001). In particular, the DLPFC has been 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). Furthermore, the DLPFC is one of the brain regions that shows the most protracted structural as well as functional development (Crone, 2009).

One of the predictions that follows from these prior studies is that adolescent development of perspective-taking behavior in social decision making is associated with different degrees of recruitment of the aMPFC, TPJ and DLPFC. Our specific hypotheses about neural development related to social behavior were informed by studies showing developmental changes in the brain during childhood and adolescence. Studies using simple tasks that involve thinking about different social scenarios indicate that young adolescents show less activity in the TPJ, but increased activity in the aMPFC in comparison with 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 the hypothesized role of this brain region in thinking about self-motives relative to the intentions and goals of others. On the basis of the hypothesis that young adolescents in particular are more inclined toward self-oriented thought and action (Eisenberg et al., 1995; Elkind, 1985), we predicted that early adolescents would defect more often and would exhibit more activity in self-related brain areas (aMPFC), relative to mid adolescents and adults. Furthermore, on the basis of the hypothesis that adolescents show late changes in the consideration of other individuals' intentions (Blakemore, 2008), we predicted that activity in the TPJ when receiving trust would increase between early adolescence and adulthood. Finally, given developmental studies demonstrating increased activity in cognitive-control and emotion-regulation tasks with increasing age (Crone, Wendelken, Donohue, van Leijenhorst, & Bunge, 2006; Steinberg, 2005), we expected that the DLPFC would be increasingly engaged during adolescence, particularly during intention consideration and reciprocity.

To test these hypotheses, we examined the behavioral choices and neural responses of participants assigned the role of Player 2 in the Trust Game. Participants belonged to three age groups, which were selected on the basis of the developmental stages of adolescence: pubertal early adolescents (12–14 years), postpubertal mid adolescents (15–17 years), and young adults (18–22 years). On the basis of our own studies (e.g., van den Bos, van Dijk, Westenberg, & Crone, 2010) and other behavioral studies with economic games (e.g., Sutter & Kocher, 2007), we expected an increase in the general level of reciprocity with age.

To further test the ability to understand the intentions of others, we added a task condition in which we manipulated the amount that Player 1 could lose by trusting the participant, Player 2 (Fig. 1; Malhotra, 2004; van den Bos et al., 2009, 2010). In our analyses, the trials on which Player 1 could lose a relatively large amount of money were labeled high-risk trials, and the trials on which Player 1 could lose only a small amount of money were labeled low-risk trials. A higher level of reciprocity in the high-risk context, relative to the low-risk context, is hypothesized to reflect the recognition of the positive intentions of Player 1 (Malhotra, 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. We expected to observe larger risk-related reciprocity differentiation for older participants, who are more capable of identifying intentions and integrating perspectives (van den Bos et al., 2010).

Method

Participants

Sixty-two healthy right-handed paid volunteers (30 female, 32 male; ages 12–22 years, *M* = 16.2 years, *SD* = 2.9 years) 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 pubertal, early adolescents (12- to 14-year-olds, $n = 21$; 11 females, 10 males), postpubertal mid adolescents (15- to 17-year-olds, $n = 15$; 7 females, 8 males), and young adults (18- to 22-year-olds, $n = 18$; 9 females, 9 males). A chi-square analysis indicated that the gender distribution was similar across age groups, $\chi^2(2, N = 54) = 0.114$, $p = .94$. (We have reported the data from the adults in another study; van den Bos et al., 2009). Participants gave their informed consent for the study, and all procedures were approved by the medical ethical committee of the Leiden University Medical Center.

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 S1 in the Supplemental Material available online). There were no significant differences in IQ between the different age groups, $F(2, 51) = 0.62$, $p = .54$, and the Tanner scores demonstrated a significant difference in puberty levels between the 12- to 14-year-olds ($M = 2.95$, $SE = 0.24$) and the 15- to 17-year-olds ($M = 4.11$, $SE = 0.22$), $t(1, 33) = 3.89$, $p < .001$.

Task procedure

The procedure for the Trust Game that we used in our study (Fig. 1) was similar to that used in our imaging study with adults (van den Bos et al., 2009). Participants were instructed that in an earlier phase of the study, other individuals had been assigned the role of Player 1, and that they would complete the study, inside the fMRI scanner, in the role of Player 2. Furthermore, participants were instructed that both players would be financially rewarded on the basis of the choices they had made during the experiment. In each round of the experiment, participants were paired with a different, anonymous player who allegedly was of the same age and gender. At the end of the experiment, the computer randomly selected the outcome of five trials, and the sum of the monetary outcomes on these trials determined the participant's payoff.

Unbeknownst to the participants, the decisions of Player 1 were not the decisions of real participants, but were preprogrammed to reflect the behavioral pattern that was displayed in our earlier study (van den Bos et al., 2010). In total, the task consisted of 145 trials: 96 trust trials (i.e., trials on which Player 1 trusted Player 2) and 49 no-trust trials (i.e., trials on which Player 1 did not trust Player 2). The trials were divided into four blocks of 8.5 min each. The trials were presented in pseudorandom order with a jittered interstimulus interval (minimum = 1.1 s, maximum = 9.9 s, *M* = 3.37 s). Before the experiment, participants received a written explanation of the task, filled out a questionnaire and played 12 practice rounds, so that we could be sure all participants understood the task.

fMRI data acquisition and analysis

Data were acquired using a 3.0-T Achieva scanner (Philips Medical Systems, Amsterdam, The Netherlands) at the Leiden

University Medical Center. T2*-weighted echo-planar images (EPIs): repetition time (TR) = 2.2 s, echo time (TE) = 30 ms, 80 × 80 matrix, field of view (FOV) = 220. Thirty-five 2.75-mm transverse slices with a 0.28-mm gap were obtained during four functional runs of 232 volumes each. A high-resolution T1-weighted anatomical scan was obtained from each participant after the functional runs were carried out. Data were analyzed using the imaging software SPM2 (Statistical Parametric Mapping 2; Wellcome Department of Cognitive Neurology, London, England). The functional time series were realigned, normalized to EPI templates, and spatially smoothed using an 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 hemodynamic response function (HRF). The start of Player 1's choice display, no-trust outcomes, and trust outcomes were modeled as events of 0-s duration. 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 square parameter estimates of height of the best-fitting 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 on these images, treating participants as a random effect. Results were considered significant at an uncorrected threshold of $p < .001$, with a minimum cluster size of 12 voxels.

We further performed voxel-wise analyses of variance (ANOVAs) to identify regions that showed age-related differences in relation to social decision making. The developmental patterns in the behaviors and fMRI data were constrained to a specific set of contrasts that captured developmental trends across the three age groups—early increase: [−2 1 1]; late increase: [−1 −1 2]; and the conjunction of [−1 1 0] and [0 −1 1] to test for a linear increase. For the fMRI analyses, these contrasts were tested in the trust-versus-no-trust and defect-versus-reciprocate comparisons. For these age analyses, we used a more stringent threshold of $p < .0002$, using a Bonferroni correction for multiple comparisons, $p < .001/6$.

We used the Marseille boîte à région d'intérêt (MarsBaR) toolbox for SPM2 (Brett, Anton, Valabregue, & Poline, 2002) to extract blood-oxygen-level-dependent (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.

Results

Behavioral results

On average, participants reciprocated in about half of the trials ($M = 53\%$), but there were large individual differences in behavior ($SD = 17\%$, minimum = 12%, maximum = 87%; see Fig. 2a). As predicted, the analyses of risk showed that participants reciprocated more when the risk for Player 1 was high than when the risk for Player 1 was low, $F(2, 51) = 25.22$, $p < .001$ (see Fig. 2b). Even though there were no age-related differences in the mean percentage of reciprocal choices,

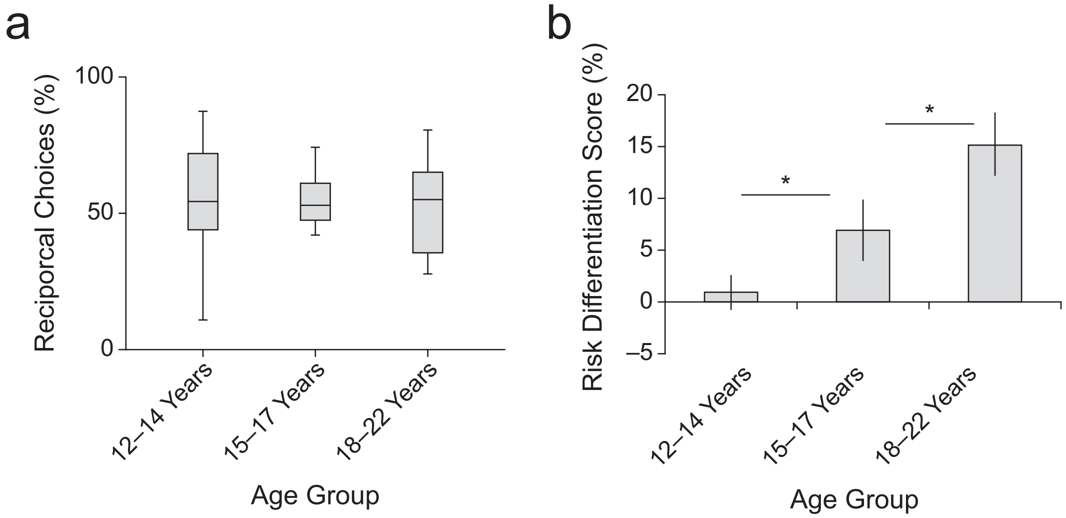

Fig. 2. Participants' reciprocal choices: (a) average percentage of trials on which participants in each age group chose to reciprocate and (b) risk differentiation score (high-risk reciprocity minus low-risk reciprocity) for each age group. In (a), the top and bottom of each box indicate the 75th and 25th percentiles (the upper and lower quartiles, respectively), and the band near the middle of the box is the 50th percentile (the median); the whiskers represent the lowest data point still within 1.5 interquartile range of the lower quartile and the highest data point still within 1.5 interquartile range of the upper quartile. In (b) the error bars represent standard errors of the mean. Asterisks indicate significant differences between groups ($p < .05$).

$F(2, 51) < 1$, $p = .66$ (see Fig. 2a), there was an Age × Risk interaction, $F(2, 51) = 5.44$, $p < .007$ (see Fig. 2b). As expected, a post hoc Tukey test confirmed that all groups differed significantly from each other in risk differentiation score (RDS; percentage of reciprocity on high-risk trials minus percentage of reciprocity on low-risk trials), $p < .05$. Furthermore, there was more reciprocity for high-risk trials than for low-risk trials (both ps < .01) only in older adolescents and adults; the youngest adolescent group did not differentiate between high-risk and low-risk trials ($p = .8$; Fig. 2b).

fMRI results

Receiving trust. To identify the neural correlates of receiving trust, which we 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 (see Table 1): the DLPFC, parietal cortex, and dorsal medial frontal cortex/anterior cingulate cortex (ACC). Subsequently, we tested the hypothesis that age-related changes in activity are related to receiving trust, by performing mixed linear and nonlinear ANOVAs with age group as the between-participants factor. As anticipated, the conjunction contrast, [−1 1 0] ∩ [0 −1 1], demonstrated age-related changes in the left TPJ.

In addition, the [−1 −1 2] contrast revealed activity in the right DLPFC (see Fig. 3 and Table 1). Time-series analyses of left TPJ showed heightened activity for both reciprocate choices and defect choices compared with no-trust trials. However, this difference was not significant in early adolescence, whereas it was present in late adolescence and greatest in young adults (see Fig. 3). In contrast, the time-series analysis for DLPFC revealed heightened activity for reciprocate and defect choices relative to no-trust trials only for the young adults. The correlations between individual RDS and activity in these areas ($r = .37$, $p < .006$, for left TPJ; $r = .45$, $p < .001$, for right DLPFC; see Fig. S1 in the Supplemental Material available online) strengthen the hypothesis that left TPJ and right DLPFC function is related to intention identification and perspective taking.

Defect versus 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 (Fig. 4 and Table 1). Additional activity was found in the left anterior insula and the right inferior frontal gyrus. As in our previous study (van den Bos et al., 2009), the opposite contrast, reciprocate > defect, did not reveal in significant changes in neural activity.

To further investigate whether there were age-related differences in the defect > reciprocate contrast, we performed linear and nonlinear ANOVAs with age group as the between-subjects factor. The [−2 1 1] contrast revealed an age-related

Table 1. Brain Regions of Interest Revealed by Whole-Brain Contrasts

Contrast and anatomical region	Hemisphere	Number of voxels	*Z* score	MNI coordinates *x*	*y*	*z*
Trust versus no-trust conditions						
Trust > no trust						
Superior parietal lobule	Right	71	4.14	21	−66	54
Precuneus	Left	121	4.18	−30	−45	42
Caudate/dorsal striatum	Left, right	431	5.20	−15	0	15
(Trust > no trust) ANOVA: [−1 0 1]						
Temporo-parietal junction	Left	44	4.06	−44	−46	29
(Trust > no trust) ANOVA: [−1 −1 2]						
Dorsolateral prefrontal cortex	Right	56	4.01	44	16	21
Defect versus reciprocate choices						
Defect > reciprocate						
Anterior medial prefrontal cortex	Left, right	774	4.89	0	42	6
Visual cortex	Left, right	733	8.82	6	−93	12
Insular cortex	Left	63	4.82	−36	24	−12
Inferior frontal gyrus	Right	27	3.95	62	21	0
Reciprocate > defect						
Visual cortex	Left, right	490	7.72	6	−73	6
(Defect > reciprocate) ANOVA: [−2 1 1]						
Anterior medial prefrontal cortex	Left, right	78	5.84	2	42	15

Note: The threshold for main effects was $p < .001$, with a minimum cluster size of 12 contiguous voxels. Age contrasts were corrected for multiple comparisons, $p < .001/6$. For each region of interest, the Montreal Neurological Institute (MNI) coordinates of the peak voxel are reported. ANOVA = analysis of variance.

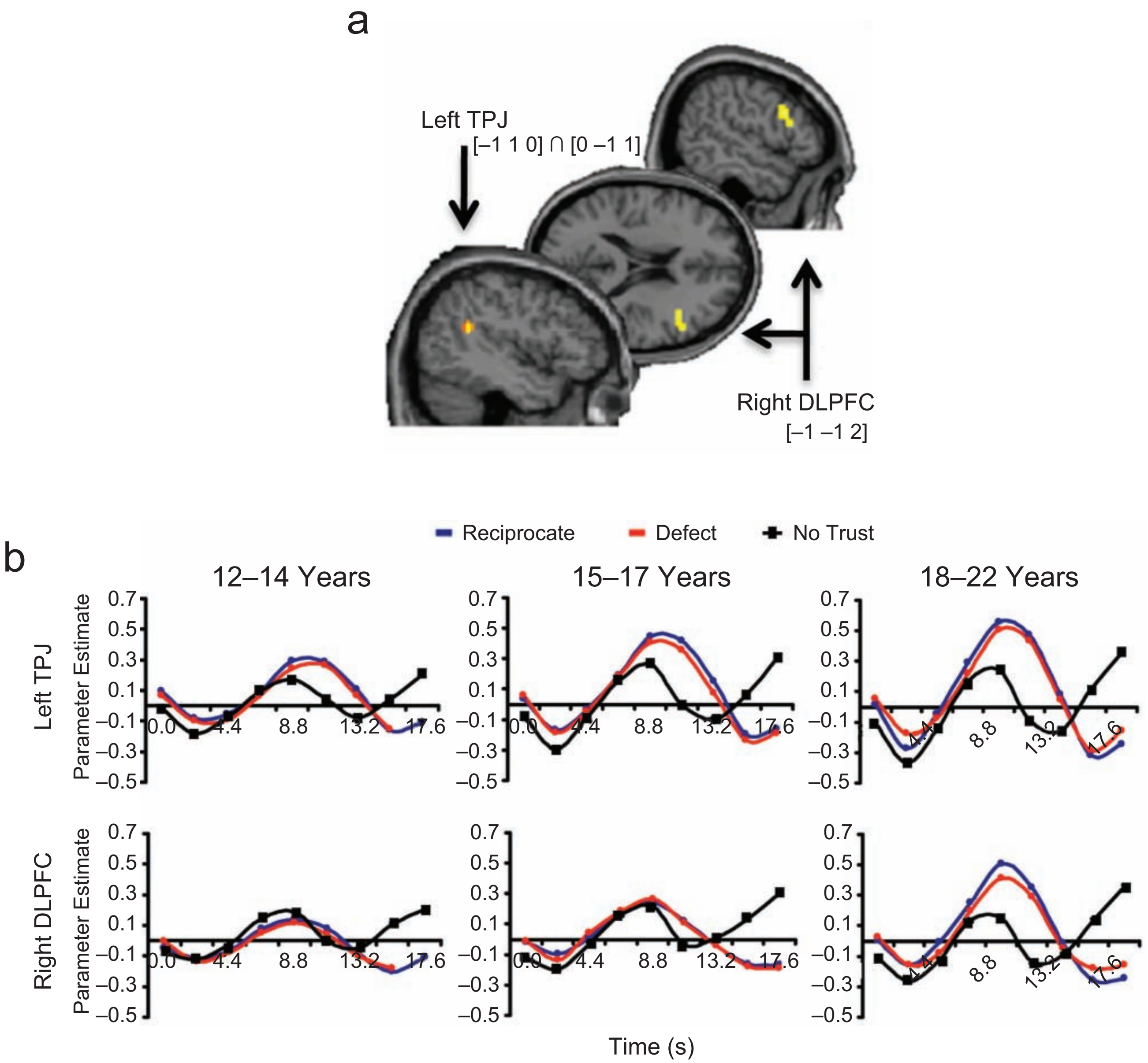

Fig. 3. Age differences in activity associated with receiving trust in the left temporo-parietal junction (TPJ) and right dorsolateral prefrontal cortex (DLPFC). In the functional magnetic resonance images (a), yellow clusters indicate significant linear, $[-1\ 1\ 0] \cap [0\ -1\ 1]$, and nonlinear, $[-1\ -1\ 2]$, increases in trust-related activation with age. The graphs (b) show the parameter estimates in the left TPJ and the right DLPFC for the defect, reciprocate, and no-trust conditions as a function of time, separately for each age group. On the *x*-axis, 0 s indicates either the onset of the participant's choice (trust) or the outcome of the experiment (no trust).

change that was specific to the aMPFC (see Fig. 4 and Table 1). These findings demonstrate that the differential engagement of the aMPFC increases between early and middle adolescence, and then remains stable into early adulthood.

The time series for the aMPFC region revealed increased activity compared with 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 with baseline. Thus, our results are consistent with the hypothesis of heightened aMPFC activity in early adolescence: The aMPFC activity related to reciprocal choices decreased with age. This was further confirmed by a significant negative age correlation for the reciprocate > fixation contrast (r = –.56, p < .02). No such correlation was observed for the defect > fixation contrast (r = .06, p = .72). Thus, aMPFC activity related to reciprocal choices decreased with age, whereas there were no age-related changes in aMPFC activity related to defect choices.

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 analysis on

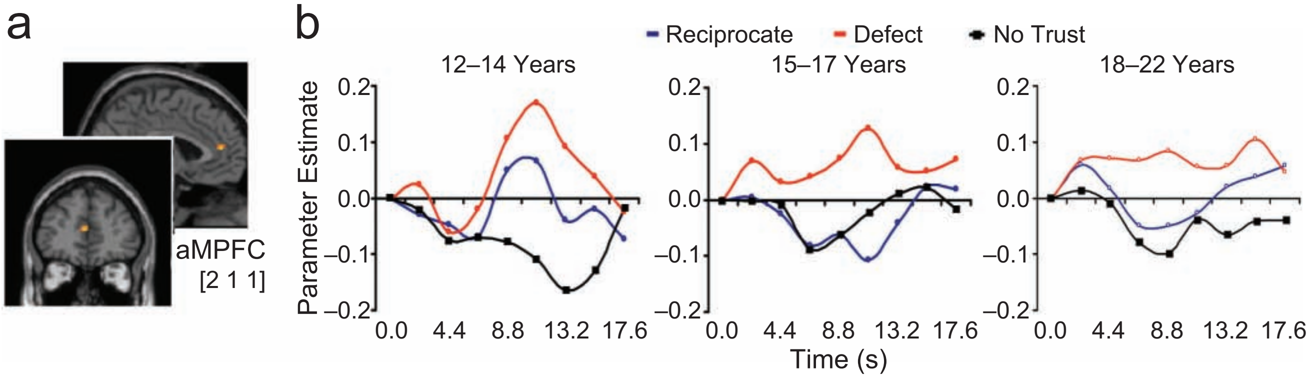

Fig. 4. Age differences in activity associated with defect versus reciprocate decisions in the anterior medial prefrontal cortex (aMPFC). In the functional magnetic resonance images (a), yellow clusters indicate an early age-related increase, [-2 1 1], in the difference between defect and reciprocate activation. The graphs (b) show parameter estimates in the aMPFC for the defect, reciprocate, and no-trust conditions as a function of time, separately for each age group. On the *x*-axis, 0 s indicates either the onset of the participant's choice (trust) or the outcome of the experiment (no trust).

the defect > reciprocate contrast with average reciprocity per individual as the predictor revealed activation in bilateral anterior insula, dorsal ACC, and right DLPFC (see Fig. 5 and Table S2 in the Supplemental Material available online). Higher reciprocity was thus associated with more activation in these areas during defection, and higher defection was associated with more activation in these areas during reciprocation.

Discussion

We investigated adolescence as a transitional period, during which linear as well as nonlinear changes in social reasoning and associated brain circuitry take place (Casey et al., 2008). Our analyses of age differences demonstrated that the regions implicated in social behavior followed asynchronous developmental patterns, with faster maturation of the aMPFC but late maturation of the left TPJ and the right DLPFC. This asynchronous pattern of functional brain development may underlie adolescent-specific social behavior in daily life (Casey et al., 2008; Paus, Keshavan, & Giedd, 2008; Steinberg, 2005).

Our behavioral findings are consistent with observational studies marking 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 in prosocial behavior, but rather is characterized by an increase in 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 in reciprocity on low-risk trials. It is important to note that the youngest adolescents did not show sensitivity to the perspective of the other player. Alternatively, the age-related increase in risk differentiation that we observed could have been the result of increased inequity aversion (Fehr & Schmidt, 1999). Both explanations are consistent with the notion that advanced forms of perspective taking in adolescence contribute to changes in social behavior.

Our reasoning that receiving trust was associated with more active deliberation of the motives of others was further supported by increased activity in the left TPJ, an area implicated in taking the perspective of others and inferring the intentions of others (Mitchell, 2008; van Overwalle, 2009). We observed an increase in the engagement of the left TPJ with age, a finding that supports the hypothesized shift in attention from self to the other during adolescence. The suggested role of the left TPJ in shifting perspective from self to the other was further supported by the correlation between left TPJ activity and the behavioral index of perspective taking (RDS): The more participants differentiated between the low-risk context and the high-risk context, the more active the left TPJ was after participants received trust. In addition, the pattern of activation of the left TPJ, and the absence of an effect of risk on behavior for the youngest adolescents, suggests that in early adolescence the 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 agree with those of studies in which participants read social scenarios, which have demonstrated an increase in the left TPJ activity between the ages of 10 to 18 and 22 to 32 (e.g., Blakemore et al., 2007). Furthermore, recent studies reveal that TPJ activity is correlated with self-reports of altruism (Tankersley, Stowe, & Huettel, 2007) and charitable giving (Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010), findings consistent with the presumed role of TPJ in shifting attention from self to others in a social context.

We also found that young adults, when receiving trust, showed increased activity in the right 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 the context of social dilemmas (Rilling et al., 2007). This activity may indicate a regulatory role of right DLPFC in social exchange, as we found that this area was more active in adults with the nonpreferred response alternative (Knoch et al., 2006). Consistent with studies that employed

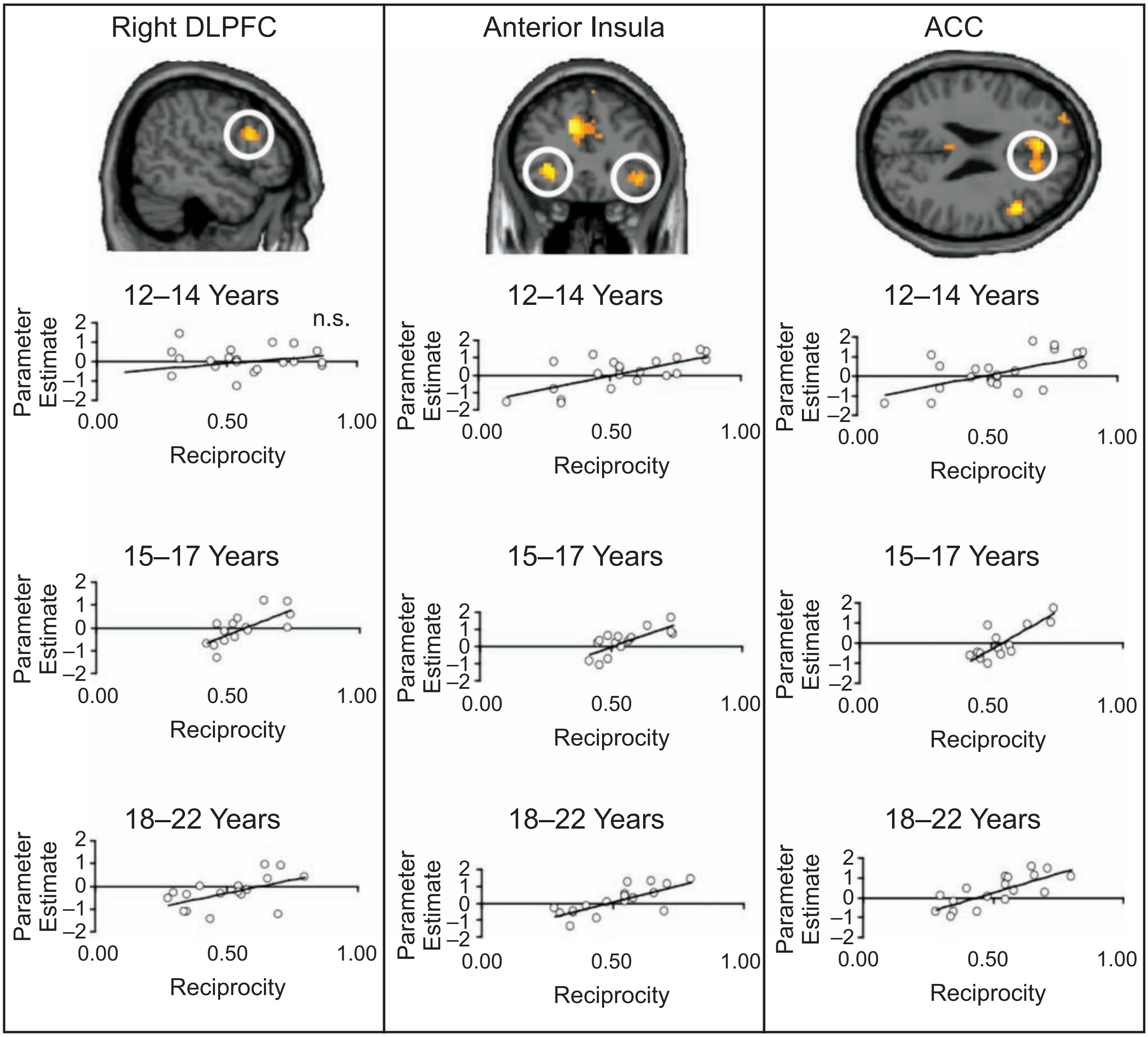

Fig. 5. Functional magnetic resonance imaging activation of the right dorsolateral prefrontal cortex (DLPFC; left column), the anterior insula (middle column), and the anterior cingulate cortex (ACC; right column) for the regression analysis on the defect > reciprocate contrast (average level of reciprocity was a covariate for all participants, threshold at $p < .001$). The three scatter plots in each column represent the correlations between the defect > reciprocate parameter estimate and average reciprocity for each age group; all correlations are based on the regions of interest extracted from the whole-group regression analysis.

cognitive-control paradigms (Crone et al., 2006), our results indicated an increase in the engagement of the right DLPFC with age. It is apparent that over the course of adolescence, the development of not just the left TPJ but also the right DLPFC contributes to a refinement in social behavior. This conclusion is supported by our finding that activity in the right DLPFC also correlated with the ability to infer the intentions of others (RDS). Thus, the differential involvement of left TPJ and right 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 intention consideration is emerging.

If the observed changes in social behavior were associated with increased consideration of the outcomes for the other, what motivated adolescents to act selfishly? What are the neural correlates of self-oriented behavior? We approached these questions by comparing defect and reciprocate choices. This analysis 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 may be more involved in self-oriented thought when they defect than when they reciprocate, and thus maximize personal outcome.

How, then, does this region support self-oriented acts in early adolescence? When acting in a proself manner (i.e., when defecting), early adolescents showed aMPFC activity similar to that of mid adolescents and young adults. However, young adolescents also showed activity in aMPFC when reciprocating, and this activity was not found in mid adolescents and adults. An interesting avenue for future researchers is to test the hypothesis that even when reciprocating, young adolescents are engaged in self-referential thoughts. Prior research suggests that in late childhood and early adolescence, social interaction is considered from an egocentric perspective (Eisenberg et al., 1995; Elkind, 1985). It is possible that a prosocial act does not become more automatic and less self-engaged until mid adolescence.

Although meta-analyses of social cognition for adults (Lieberman, 2007; van Overwalle 2009) and adolescents (Blakemore, 2008) indicate the importance of the aMPFC in self-referential processes, other studies implicate 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 undergo change between early adolescence and mid adolescence.

We hope that this study clarifies Mark Twain's statement about understanding his father better when he was 21 than when he was 14. It is most likely that this increase in understanding was associated with increased perspective-taking skills that relied on the development of interacting brain regions important for social reasoning, such as the aMPFC and the TPJ. Future research studies could benefit from analyzing connectivity between these regions to better clarify how these regions contribute to social behavior (Burnett & Blakemore, 2009). Finally, 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).

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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