The neurocognitive development of social decision-making

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5. Dissociable brain networks involved in development of fairness considerations

In this functional magnetic resonance imaging study, we examined developmental changes in the brain regions involved in reactions to unfair allocations. Previous studies on adults suggested that reactions to unfairness are not only affected by the distribution itself but also by the ascribed intentionality of the proposer. In the current study, we employed the mini Ultimatum Game (Falk, Fehr, & Fischbacher, 2003) to examine responder behavior to unfair offers of varying degrees of intentionality. Sixty-eight participants from four age groups (10-, 13-, 15-, and 20-year-olds) carried out the task while fMRI data were acquired. Replicating previous findings in adults, participants of all ages showed activation in the bilateral insula and dorsal anterior cingulate cortex (dACC) during rejection of unintentional but acceptance of intentional unfair offers. Rejection of unintentional unfair offers involved increasing activation with age in the temporoparietal junction and the dorsolateral prefrontal cortex. These findings provide evidence for an early developing insula-dACC network involved in detecting personal norm-violations and gradually increasing involvement of temporal and prefrontal brain regions related to intentionality considerations in social reasoning. The results are discussed in light of recent findings on the development of the adolescent social brain network.

5.1 Introduction

Fairness consideration is a key component of social interactions and involves the comparison between outcomes for self and other. People prefer equitable distribution of resources and react strongly to inequitable distributions, which has also been termed as inequity aversion (Fehr & Schmidt, 1999). In this sense, fairness forms a socially shared norm. Violations of norms, behaviors that deviate from the norm, are generally perceived to be aversive, where people want to be nice to those who treat them fairly and hurt others who do not treat them fairly (Fehr & Schmidt, 1999). However, assessment of behaviors that deviate from the norm goes paired with a second process assessing its intentionality (Falk et al., 2008; Fehr & Schmidt, 1999). For example, Blount

(1995) showed that behavioral reactions to unfairness are strongly modulated by the ascription of intentionality: people react less negative to disadvantageous inequity when they feel the inequity was not intentional. This process of intentionality understanding requires the ability to mentalize about other individuals’ goals and intentions. In human development, behavioral studies have suggested that inequitable distribution of resources (i.e., unfairness) is aversive from an age as early as 7-8 years (Fehr et al., 2008), followed by increased understanding of intentionality in adolescence (Güroğlu et al., 2009; Selman, 1980; van den Bos et al., 2010). The goal of this study was to examine the development of the neural correlates of intentionality understanding related to fairness considerations.

Neuroscientific studies have identified separable brain regions involved in these different aspects of fairness considerations. These studies typically employ the Ultimatum Game (Güth et al., 1982), where two players are given a stake to share. The first player (the proposer) makes an offer that the second player (the responder) can accept or reject. Acceptance of the offer results in sharing the stake between the two players as proposed, whereas rejection of the offer yields both players to go empty-handed. On the one hand, functional magnetic resonance studies using the Ultimatum Game suggest that bilateral insula activation might reflect the detection of norm violations following unfair proposals (Güroğlu et al., 2010; Sanfey et al., 2003). In addition, transcranial magnetic stimulation and neuroimaging studies suggest that the dorsolateral prefrontal cortex (DLPFC) might be important for overriding self-interest (accepting unfair offers in an Ultimatum Game) and thereby enable participants to act upon their inequity aversion, or violation of the fairness norm (Knoch et al., 2010; Knoch et al., 2006a; van 't Wout et al., 2005).

On the other hand, considering others’ intentions involves the activation of the temporoparietal junction (TPJ) (Frith & Frith, 2007; van Overwalle, 2009). Activity in this region has been related to switching attention between different perspectives (Mitchell, 2008) and is also involved in competitive games (Assaf et al., 2009; Halko et al., 2009; Polezzi et al., 2008) and charitable giving (Hare et al., 2010). A neuroimaging study with adults showed that the insula, DLPFC and TPJ had dissociable patterns of activation during a fairness game which allowed for the separation of processes involved in fairness considerations (Güroğlu et al., 2010). In sum, neuroimaging findings suggest that the insula might be involved in detecting social norm violations, the DLPFC in the regulation social behavior (e.g., rejection of unfair offers), and the TPJ in intentionality considerations.

Brain regions such as TPJ and DLPFC show protracted structural development (Gogtay et al., 2004), suggesting that the ability to understand intentions and the control of selfish impulses mature relatively late. Indeed, recent behavioral and neuroimaging studies provide support for the development of perspective taking (Dumontheil et al., 2009) and the contribution of the TPJ to social reasoning across adolescence (Sebastian et al., 2008; van den Bos et al., 2011). In previous behavioral research, we demonstrated that the ability to judge fairness develops at an early age, whereas the ability to understand intentions does not develop fully until late adolescence (Güroğlu et al., 2009).

Accordingly, we hypothesized that that the slow emergence of intentionality consideration in fairness judgments is associated with protracted development of the DLPFC and TPJ. Using the mini-Ultimatum game, we examined intentionality understanding in unintended versus intended unfair offers. We predicted that responses to unintended unfair offers would require increased intentionality consideration and regulation of social behavior, and therefore would be associated with increased DLPFC and TPJ activation that emerges gradually over adolescence. Further, we hypothesize that TPJ activity might be increased during the rejection of unintentional offers, because the participants might then make additional considerations about what the proposer might think about their rejection, which is generally not considered to be the socially acceptable decision (Güroğlu et al., 2009).

5.2 Methods

5.2.1 Participants

Sixty-eight participants from four age groups took part in the study: 10-year-olds (N = 17, M age = 10.4, SD = 0.86; 6 females), 13-year-olds (N= 15, M age = 13.4, SD = 0.51; 8 females), 15-year-olds (N= 13, M age = 15.4, SD = 0.51; 5 females), and 20-year-olds (N= 23, M age = 20.4, SD = 1.67; 13 females). Gender distribution was similar across age groups ($\chi2(3) = 2.39$, $p = .50$). The data from the young adults have been previously reported (Güroğlu et al., 2010). All participants were healthy and right-handed volunteers without neurological or psychiatric impairments. All participants provided informed consent; participants younger than 18 years-old were accompanied by their parents who also provided consent. A radiologist reviewed all anatomical scans; no anomalies were found.

In order to obtain an estimate of intelligence, 10-year-olds completed two subscales (Block design and Similarities) of the Wechsler Intelligence Scale for Children (WISC; Wechsler, 1991), 13- and 15-year-olds completed the same subscales of the (revised) adult version, the Wechsler Adult Intelligence Scale (WAIS-R; Wechsler, 1997) and 20-year-olds completed the Raven Standard

Progressive Matrices (Carpenter et al., 1990). The scores were converted to Intelligence Quotient (IQ) estimates and participants had average IQ (M = 107.93, SD = 11.53); there were no significant age differences (F (3, 66) = 1.69, p = .18) and IQ scores did not correlate with behavioral performance in terms of rejection rates of unfair offers (all r (67) < 0.14, p > 0.27).

5.2.2 Task description

Participants played the role of the responder in the modified version of the Ultimatum Game (UG) which incorporates intentionality considerations (Güroğlu et al., 2009; Güroğlu et al., 2010). In this version, the first player (proposer) is presented with a fixed set of two distributions for sharing the stake (here 10 coins) with the responder (i.e., the second player). There were three conditions in the game; in each condition one of the distributions was an unfair distribution of the stake with 8 coins for the proposer and 2 coins for the responder (i.e., 8/2 offer). The three conditions were termed depending on the alternative offer pitted against the 8/2 offer: a) 5/5 offer (fair-alternative), b) 2/8 offer (hyperfair-alternative), and c) 8/2 offer (no-alternative).

Participants practiced the task (24 trials) on a computer before the scanning session and subsequently they played 168 trials of the game with anonymous age and gender matched partners. These 168 trials consisted of 126 trials of unfair offers (42 per condition, 3 conditions: fair-, hyperfair-, and no-alternative) and 42 alternative offers (21 for fair- and hyperfair-alternative conditions each). The trials were presented in three blocks of 42 trials lasting about 8.3 min each.

Each trial started with the presentation of the fixation cross followed by the presentation of the set of offers available to the proposer, where the offer made by the proposer was encircled in red, and the Yes and No buttons (see Figure 5.1). Participants could accept or reject the offer by pressing a button using the index and middle fingers of their right hand. If they failed to respond within 5000 ms, a screen displaying ‘Too late!’ was presented for 1000 ms. Upon responding, the response was presented on the screen until the end of the 6000 ms. Trials were randomized and presented with a jittered interstimulus interval (mean = 1530 s, min = 550 ms, max = 4950 ms; optimized with OptSeq2, surfer.nmr.mgh.harvard.edu/optseq/, developed by (Dale, 1999)).

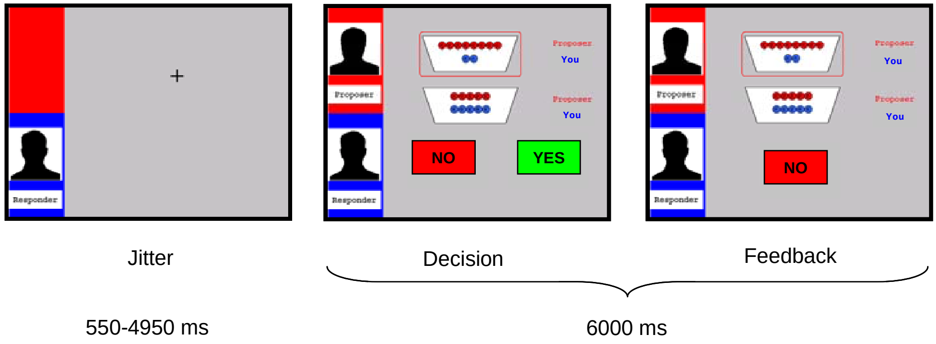

Figure 5.1: Visual display of events presented in the scanner task. Trials started with a jittered fixation screen lasting 550-4950 ms. The left panel in the decision screen displayed the name of the proposer in red (here 'proposer') and the name of the responder (here 'responder'). Two offers each containing red and blue coins indicate the share for the proposer and the responder, respectively (here 8/2 vs 5/5) and the offer made by the proposer was encircled in red (here 5/5). The responder was a maximum response time of given 5000ms to select Yes or No to accept or reject the offer. Upon response, the feedback screen displayed the given response (here 'Yes') until 6000 ms after the start of the trial.

Each trial was played with a new player to avoid learning and reputation effects. Only the first name and the first letter of the surname of the players were displayed on screen to ensure anonymity. Participants were told that the offers of the proposers had already been obtained in a previous part of the study and that at the end of the session the computer would randomly select ten trials that would determine their total earnings. In order to emphasize the interactive character of the game with consequences for them and the other players, participants were explained that the proposers' earnings would be contingent upon their decisions. At the end of the session, a screen was presented indicating the pay-off (five euros for each participant). In reality, the offers presented to the participants were computer simulated but were based on behavior reported in prior experiments (Güroğlu et al., 2009). After the scan session, none of the participants expressed doubts about the cover story.

5.2.3 MRI data acquisition

The scanning session was carried out at the university medical center using a 3.0T Philips Achieva. Using E-Prime software, stimuli were projected onto a screen at the head of the scanner bore and participants viewed the stimuli by means of a mirror mounted on the head coil assembly. The scanning sessions consisted of four types of scans in the following order: i) localizer scan, ii) T2*-weighted echo-planar imaging (EPI) sequence measuring the bold-oxygen-level-dependent (BOLD) signal (TR= 2.2 sec, TE= 30ms, slice-matrix= 80 x 80, slice-thickness=2.75mm, slice gap = 0.28mm gap, field of view (FOV) = 220 mm), iii) high-resolution T1-weighted anatomical scan, and iv) high resolution T2-weighted matched-bandwidth high-resolution anatomical scan with the same slice prescription as the EPIs. Each of the three blocks of functional runs consisted of 200 volumes; the first two scans were discarded to allow for equilibration of T1 saturation effects.

5.2.4 MRI data analysis

SPM5 software (www.fil.ion.ucl.ac.uk) was used for image preprocessing and analyses. Slice-time correction, realignment, spatial normalization to EPI templates, and spatial smoothing using a 8mm full-width half-maximum 3D Gaussian kernel were carried out. The youngest age group moved significantly more than the other three age groups (main effect of Age $F(3, 67) = 3.21$, $p < .05$, followed by posthoc Tukey comparisons). However, the total amount of movement was minimal: the maximum movement parameters were below 1.81 mm for all participants and all scans. The functional time series were modeled by a series of events convolved with a canonical haemodynamic response function (HRF). The moment of stimulus presentation with zero duration was used to model the data. For the purposes of this study, the unfair offers (8/2 offers) were modeled separately based on context (3 levels: fair-, hyperfair-, or no-alternative) and response (2 levels: accept or reject). Contrast images for each individual were used in the second-level random effects model to run full-factorial analysis of variance and one-tailed post hoc t-tests. We further conducted regression analyses to test for brain-behavior relations using mean rejection levels per condition. Unless otherwise indicated, the fMRI analyses were conducted at the commonly used (Sanfey et al., 2003; Tabibnia et al., 2008) threshold of $p < .001$ uncorrected with a voxel threshold of 10 functional voxels. Results are reported in the MNI305 stereotaxic space.

5.2.5 Region-of-interest (ROI) analyses

In order to further examine the effects obtained in the whole-brain full factorial ANOVAs, Region of Interest (ROI) analyses were conducted using the MARSBAR tool in SPM5 (Brett et al., 2002). These analyses were conducted in predetermined brain regions of interest, including the insula, the DLPFC and the TPJ.

5.3 Results

5.3.1 Behavioral results

A repeated-measures ANOVA was conducted with context (3 levels: fair-, hyperfair-, and no-alternative) as the within subjects factor, age (4 levels: 10-, 13-, 15-, and 20-year-olds) as between subjects factor and rejection rates of unfair offers as the dependent variable. There was a main effect of context (F (2, 128) = 67.67, $p < .001$) as well as a context x age interaction (F (6, 128) = 3.00, $p < .01$) (see Figure 5.2). Rejection rates of unfair offers in the fair-alternative condition were highest, followed by the hyperfair-alternative (M = .79, SD = .25 and M = .73, SD = .27, respectively; F (1, 67) = 3.04, p = .05), and lowest rejection rates were observed in the no-alternative condition (M = .35, SD = .36; F (1, 67) = 73.58, $p < .001$).

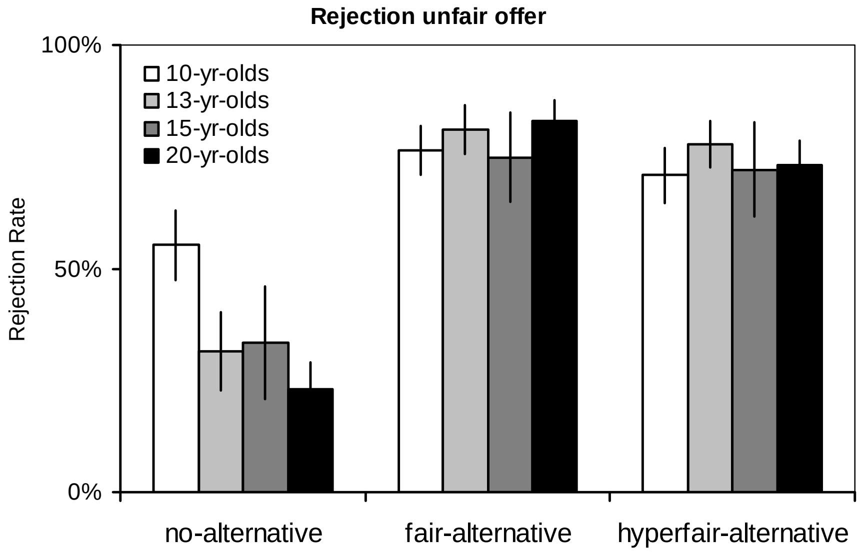

Figure 5.2: Display of means and standard deviations of rejection rates of unfair offers in the three conditions for the four age groups.

Tukey post-hoc analyses exploring the age x context interaction showed that rejection rates of unfair offers did not differ across age groups in the fair- and hyperfair-alternative conditions (both F (3, 64) < .37, p > .78) whereas they did in the no-alternative condition (F (3, 64) = 2.90, $p < .05$). Youngest participants rejected unfair offers in the no-alternative condition more often than oldest participants did (M = .55, SD = .32 and M = .23, SD = .27, respectively). Thirteen and 15-year-olds rated in between and did not differ from either age group (M = .32, SD = .34 and M = .33, SD = .45, respectively).

5.3.2 fMRI results

Response x Intentionality Interaction across ages. First, we examined developmental differences in the role of intentionality (i.e., context) in responses to unfairness[9]. Whole brain analyses conducted with a 2 x 3 x 4 full factorial ANOVA with response (2 levels: accept / reject) and context (3 levels: fair- / hyperfair- / no-alternative) as the within subject factors and age (4 levels: 10-, 13-, 15-, and 20-year-olds) as the between subject factor yielded no three-way interaction between response, context and age. There was a response x intentionality interaction across all age groups ($F(2,350) = 7.34$, FDR $p < .05$, 10 voxel threshold) in the dorsal ACC (MNI -3, 27, 36) and bilateral insula/inferior frontal gyrus (IFG; MNI (42, 24, -6 and -36, 15, -9), see Figure 5.3A). To further examine the interaction effect, ROI analyses were conducted in the three regions involved in the interaction. These post hoc analyses showed that the activation in both the bilateral insula/IFG and dorsal ACC were higher during rejection than acceptance of unfair offers in the no-alternative condition (all F (1, 48) > 8.95, $p < .004$), but higher during acceptance than rejection of unfair offers in the fair- and hyperfair-alternative conditions (all F (1, 49) > 7.79, $p < .007$ and F (1, 52) > 8.86, $p < .004$, respectively). These effects were found for all age groups, suggesting that these areas are sensitive to the response x intentionality interaction independent of age (see Figure 5.3B). In previous studies these brain regions are shown to play a role in personal norm violations, that is, related to behaviors that are not frequently displayed by the individual (Güroğlu et al., 2010; van den Bos et al., 2009). The role of these areas in personal norm violations was further supported by brain-behavior correlations. BOLD activity for the reject > accept contrast correlated negatively with mean rejection levels of unfair offers in the no-alternative (left insula $r = -.35$, $p < .05$), fair-alternative (right insula $r = -.32$, $p < .05$) and hyperfair-alternative condition (left insula $r = -.46$, $p = .001$, right insula $r = -.39$, $p < .01$, and dACC $r = -.44$, $p = .001$). In other words, participants who often accepted unfair offers (i.e., had low rejection rates) showed high levels of insula and/or dACC activity when they rejected these offers and vice versa.

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[1] Main effects of response and intentionality were also explored. Examination of the main effect of response yielded significant activation in bilateral Insula (MNI -33, 18, -15 and 51, 15, 6; p< .001, 10 voxel threshold) for the Acceptance > Rejection contrast. There were no regions involved in the Rejection > Acceptance contrast (see Supplementary Table 1). Examining the main effect of intentionality, we only found activation in the occipital lobe (MNI 21, -96, 6; p< .001, 10 voxel threshold) for the fair-alternative > no-alternative condition. See supplementary table for main effect of offer type (unfair > fair offers) per intentionality condition.

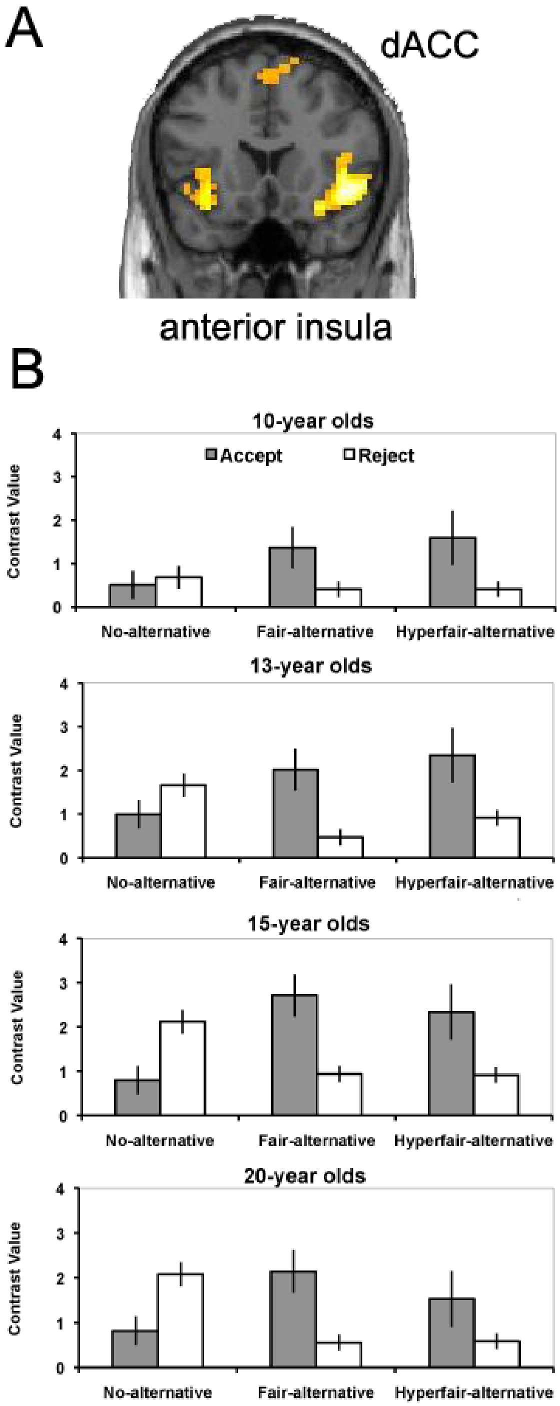

Figure 5.3: A) Results of the whole brain 2 (response) x 3 (context) interaction, showing the dACC [MNI -3, 27, 36] and bilateral insula/IFG [MNI 42,23, -6] at p < .001 10 voxel threshold. **B)** Contrast values in the right insula for acceptance and rejection of unfair offers in the three conditions for the four age groups. Results for left Insula and dACC showed similar patterns of activity but are not shown.

Age differences in rejection in the no-alternative condition.

In order to examine developmental patterns in unintended versus intended unfair proposals we focused our analyses on brain areas that were specifically involved in rejection of unfair offers in the no-alternative condition with age included as a regressor in two separate contrasts.

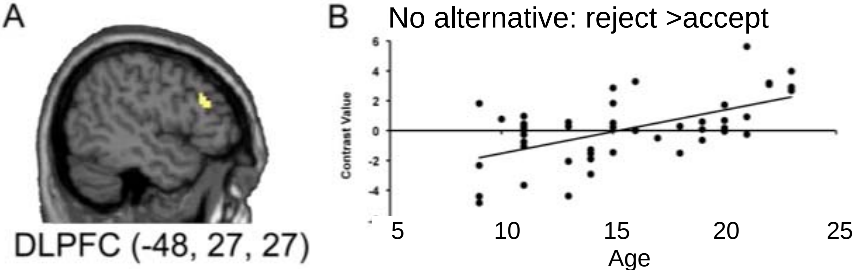

Figure 5. 4: A) Activation in the left dorsolateral prefrontal cortex (DLPFC; MNI -48, 27, 27) with positive correlation with age in the rejection no-alternative > acceptance no-alternative contrast; p < .001, 10 voxel threshold. **B)** Plot of contrast values for age and activity in left DLPFC for the rejection no-alternative > acceptance no-alternative contrast.

For the rejection > acceptance contrast in the no-alternative condition, brain activity in the DLPFC (MNI -48, 27, 27) correlated positively with age (r = .57; T(60) = 3.23; see Figure 5.4A and 5.4B). Other areas of activation are listed in Table 5.1. There were no negative correlations with age and no brain areas were correlated with age for the rejection versus acceptance contrasts in the hyperfair- and fair-alternative conditions. Thus, the age related increase in the DLPFC response was specific for no-alternative rejection relative to no-alternative acceptance trials. When no-alternative rejection behavior was added as covariate to the contrast, the DLPFC effect remained, showing that the effects are specific to age and cannot be solely explained on the basis of behavioral differences.

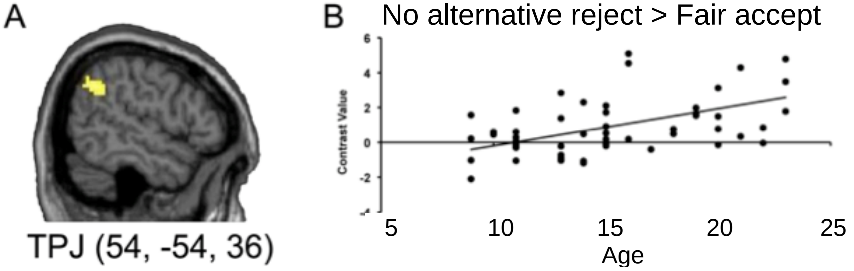

Figure 5.5: A) Activation in the right temporoparietal junction (TPJ; MNI 54, -54, 36) with positive correlation with age in the rejection no-alternative > rejection fair-alternative contrast; p < .001, 10 voxel threshold. B) Plot of contrast values for age and activity in right TPJ for the rejection no-alternative > rejection fair-alternative contrast.

Second, age was added as a regressor in the rejection no-alternative > rejection fair-alternative and rejection no-alternative > rejection hyperfair-alternative contrasts. Both contrasts resulted in positive correlations between BOLD activity and age in the TPJ (MNI 54, -54, 36 and 57, -48, 33, respectively; r = .51 and r = .50, respectively; T (53) = 3.25; see Figure 5.5A, 5.5B and Table 5.1). Other areas of activation are listed in Table 1. There were no negative correlations with age. Thus, age related increase in TPJ response was again specific for the no-alternative rejections relative to other types of rejections.

Mediation Analyses

To further investigate the relation between age, rejection rates in the no-alternative condition, and brain activity in DLPFC and TPJ we have performed mediation analyses. According to Baron and Kenny (1986), mediation can be established by demonstrating that (a) there is a direct effect of the independent variable (i.e., age) on the dependent variable (i.e., punishment), (b) there is a significant effect of the independent variable on the proposed mediator (i.e., anger), (c) the proposed mediator is correlated with the dependent variable after controlling for the independent variable, and (d) the effect of the independent variable on the dependent variable drops significantly when the mediator is included in a simultaneous regression (Baron & Kenny, 1986). First we investigated the mediation effect of DPLFC activity. As can be seen in Figure 5.5A, almost all the Baron and Kenny requirements are met. First, there is a significant effect of age on rejection rate ($\beta = -.02$), $t(49) = -2.01$, $p < .05$, and on the proposed mediator, contrast value [DLPFC reject – accept] ($\beta = .29$), $t(49) = 4.8$, $p < .001$. Second, DLPFC activity was borderline significantly correlated with rejection rate when controlling for age ($\beta = -.05$), $t(49) = -2.0$, $p = .05$. Third, the direct effect of age on rejection rate was no longer significant ($\beta = -.006$), $t(49) = -.54$, $p = .6$, when controlling for DLPFC activity. Finally, a Sobel test indicated that this reduction in significance was marginally significant, suggesting at least partial mediation (Sobel $z = -1.81$, $p = .07$).

Next we investigated the mediation effect of TPJ activity. As can be seen in Figure 5.5B, all the Baron and Kenny requirements are met again. First, there is a significant effect of age on rejection rate ($\beta = -.03$), $t(55) = -2.59$, $p < .02$, and on the proposed mediator, contrast value [TPJ reject_no-alternative – reject fair-alternative] ($\beta = .21$), $t(55) = 4.3$, $p < .001$. Second, TPJ activity was significantly correlated with rejection rate when controlling for age ($\beta = -.07$), $t(55) = -2.3$, $p < .03$. Third, the direct effect of age on rejection rate was no longer significant ($\beta = -.1$), $t(55) = -1.13$, $p = .26$, when controlling for TPJ activity. Finally, a Sobel test indicated that this reduction was significant, suggesting full mediation (Sobel $z = -1.9$, $p < .05$).

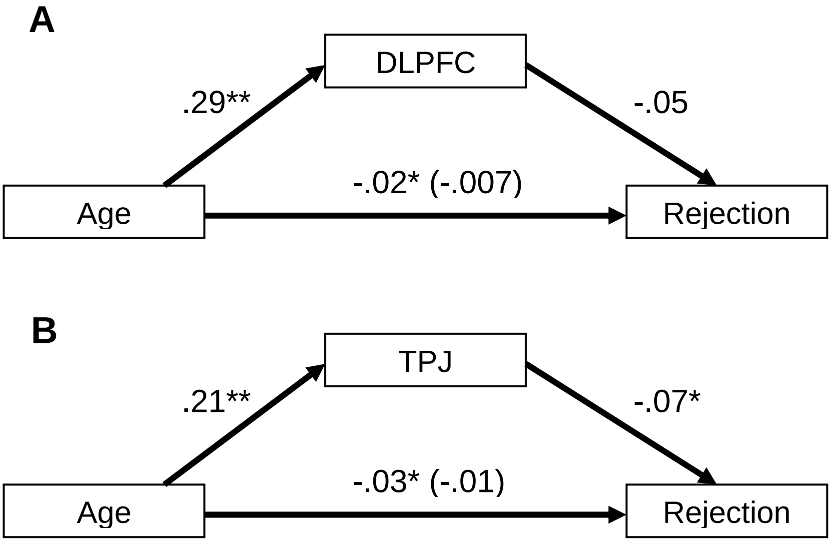

Figure 5.5 (**A**) Beta coefficients in the model testing for the mediation effect of neural activation in DLPFC for the rejection no-alternative > acceptance no-alternative contrast for the link between age and rejection of unfair offers in the no-alternative condition. (**B**) Beta coefficients in the model testing for the mediation effect of neural activation in TPJ for the rejection no-alternative > rejection fair-alternative contrast for the link between age and rejection of unfair offers in the no-alternative condition. ** $p < .01$, * $p < .05$.

5.4 Discussion

The goal of this study was to gain a better understanding of the emergence of intentionality understanding in fairness considerations. Using the mini Ultimatum Game we were able to distinguish between responses to unfair offers of varying degrees of intentionality. Consistent with prior behavioral studies, participants rejected unfair proposals when the alternative for the proposer was a fair division (Güth et al., 1982). This behavior has previously been reported across age groups and shows that fairness perceptions already play an important role in social decisions in late childhood and early adolescence (Fehr et al., 2008; Güroğlu et al., 2009; Sutter, 2007). However, the gradual emergence of intention-consideration in late childhood and adolescence was demonstrated by a decrease in rejection rates for unintentional unfair offers over the course of adolescence, with lowest rejection rates in adulthood. The results of this study thus provide further support for improving intentionality understanding across adolescence (Güroğlu et al., 2010).

Importantly, we demonstrated that two different brain networks involved in fairness considerations develop at different rates and contribute to behavior in separate ways. First, a norm-violation network, including the anterior insula and the dorsal ACC, which develops relatively early in childhood, and second, a social brain network, including DLPFC and TPJ, which develops gradually over the course of adolescence, play a role in social decision-making involving fairness considerations. The developmental patterns of these networks set the stage for the interpretation of brain maturation during fairness considerations.

Early maturation of the norm violation network

Consistent with prior studies, anterior insula and dorsal ACC were differentially sensitive to acceptance and rejection responses, depending on the norm regarding the participant's behavior in the particular context, as defined by intentionality (Güroğlu et al., 2010). Namely, the activation of this network was related to acceptance of intentional unfair offers (i.e., in the context of a fair alternative where normative behavior would be to reject), but also to rejection of unintentional unfair offers (i.e., in the context of no alternative where normative behavior would be to accept). It should be noted here that the *norm violation* here is not to be confused with the detection of a social norm violation, which would be responses to unfair offers in general. Our findings show that perception of an unfair offer and the performed 'normative behavior' is highly context dependent. In this sense, the way we refer to norm violations is closer to *personal norms*, which are self-based standards of behavior in specific situations and differ from general attitudes or social norms referring to internalized self-expectations (Schwartz, 1977; Schwartz & Fleishman, 1978). This interpretation is strengthened by the correlations between brain activation and individual task behavior. That is, the dACC and insula network response when rejecting an unfair offer where the proposer had no alternative was even stronger for individuals who mostly accepted these offers. This role of the insula in personal norm violations is also supported by the relation between insula activity during social norm violations and individual differences in Machiavellianism (Spitzer et al., 2007) and social value orientation (van den Bos et al., 2009). Furthermore, the general function of this network in detecting deviations from the personal norm is supported by several studies showing its involvement in betrayals of trust (van den Bos et al., 2009) as well as in non-social norm violations such as risk prediction errors (Montague & Lohrenz, 2007; Singer et al., 2009). In this sense, the neural network including the anterior insula and dorsal ACC is related to behavior that deviates from personal standards that are shaped by what one normally does within a particular context, that is, accepting an unfair offer in the no-alternative context and rejecting an unfair offer in the fair- and hyperfair-alternative contexts.

One limitation of the current study, and of social decision-making studies in general, is the relative low number of trials involved in the analysis. We should note that the analyses involving the acceptance of unfair offers in the fair- and hyperfair-alternative conditions may be suffering from low power, particularly in adults. The average number of trials for these conditions was relatively low (8.67 and 11.19, respectively). Although we have replicated our findings in an analysis which controlled for the number of trials, this is an issue that needs to be addressed in future research.

Notably, the norm-violation effects in the insula and dorsal ACC were observed for all age groups, showing that norm-violation are already detected by this network in young children. Indeed, behavioral studies have reported that already at age 7-8-years there is a strong preference for social norms of strict equity (Fehr et al., 2008) and a basic understanding of fairness (Güroğlu et al., 2009). It has been known for a long time that the rules for appropriate behavior are learned at a young age, as is shown by children's concepts of social rules (Piaget, 1956). The current findings indicate that children also rely on the insula / ACC network when judging their own social behavior in a particular context. These findings further suggest that the brain network related to fairness considerations including contextual information mature relatively early. However, the late maturing social brain network seems to incorporate extra information regarding intentionality into the decision-making process.

Late development of the social brain network

A crucial aspect of fairness considerations relates to our judgments of others' intentionality. Prior work has demonstrated that understanding intentions is associated with activation in the TPJ (Assaf et al., 2009; Halko et al., 2009; Polezzi et al., 2008; van Overwalle, 2009). These regions have also been implicated in inference of mental states (Hampton et al., 2008) and redirection of our focus of attention to others (Mitchell, 2008). In the current study, we hypothesized that TPJ was specifically associated with the considerations of unfair offers when the proposer did not have an alternative. Whereas children and adolescent showed similar activation of the insula and dorsal ACC as adults when rejecting no-alternative offers, TPJ involvement emerged gradually across adolescence. The intentions of the proposer are least clear in the no-alternative condition, which makes it likely that this condition exerts the highest mentalizing and intention consideration demands. Furthermore, the increased involvement of TPJ was specific for rejection of unfair offers in the no-alternative condition. Whereas rejection of an unfair offer in the fair-alternative condition can be readily justified, this is not the case in the no-alternative condition. The consideration of self-interest and the related desire to reject an unfair offer, combined with the simultaneous (and automatic) consideration for lack of intentionality of the offer in this condition might also lead to feelings of guilt. Possibly, TPJ activation is related to these feelings of guilt towards others (Takahashi et al., 2004). This hypothesis needs further testing in future research.

In a pioneering set of studies, Blakemore and colleagues (Blakemore, 2008; Dumontheil et al., 2009; Sebastian et al., 2008) showed that the TPJ is less active in adolescents than adults during tasks requiring mentalizing. The current findings are consistent with these previous studies, and show that TPJ involvement is context-dependent. Furthermore, older adolescents are increasingly better able to take context, and thus intentionality-related information, into account while making decisions.

Besides TPJ, DLPFC was also more active during rejection of unintentional unfair offers in adults than in children, with an intermediate pattern for adolescents. In prior research, the slow maturation of DLPFC has been related to the emerging ability to control thoughts and actions (Bunge & Wright, 2007; Crone, 2009). Considering that the social norm is to accept unfair offers when there was no alternative, the increased DLPFC activation for rejection may indicate that adults override the tendency to accept (Knoch et al., 2006b). The negative correlation in children may indicate the opposite tendency; children may be inclined to reject unfair proposals (regardless of intentionality) and acceptance of unfair offers may require increased control. This interpretation should be tested in future research.

Finally, mediation analyses importantly demonstrated the mediating role of neural activity in the link between age and rejection rates of unfair offers. As such, these findings contribute to an understanding of the developmental mechanisms underlying age related changes in behavior. Our results suggest that age related differences in neural activation are partially responsible for behavioral differences that vary with age. Future longitudinal studies that incorporate structural brain development in the social brain network are crucial for further understanding of the mechanisms underlying development.

A new direction in understanding the development of fairness considerations

Two advantages of the current approach in examining development of social decision-making relative to prior reports is that we 1) included participants of four age groups, which is uncommon in fMRI studies, but allows for more precise measurement of developmental change (Galvan, 2010), and 2) related changes social brain network activation to real social behavior. Prior studies on the development of the social brain network have typically involved comparisons of two groups (adolescents versus adults) whereas our approach allowed us to assess gradual changes over time. In addition, relative to prior studies, the current approach reveals that it is important to relate thinking about fairness and moral scenario's to actual social behavior in context, as behavior in the current task was modulated by intentionality considerations.

In sum, the current approach demonstrated development of the dissociable brain networks contributing to social decision-making across childhood, adolescence and adulthood. Regions associated with norm-violations showed a different developmental trajectory in their involvement in social decision-making than regions associated with perspective taking and intentionality consideration. The latter finding strengthens the claim that detection of norm-violations related to inequity and intentionality considerations are dissociable components of fairness consideration.

Finally, in future studies it is important to distinguish between different interaction partners in social interactions. In prior fMRI work in adults, it was demonstrated that interactions with friends was related to differential activation of a set of regions, including the ventral medial prefrontal cortex, the striatum and the amygdala (Güroğlu et al., 2008), and these regions may work together with the norm-detection and social brain networks reported here (e.g., Hare et al., 2010). Considering age differences in the social brain network (Blakemore, 2008), it is important in future research to understand how quality of relationships modulate the development of brain activation in social interactions across adolescence.