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Impulse Control and Underlying Functions of the Left DLPFC Mediate Age-Related and Age-Independent Individual Differences in Strategic Social Behavior

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SUMMARY

Human social exchange is often characterized by conflicts of interest requiring strategic behavior for their resolution. To investigate the development of the cognitive and neural mechanisms underlying strategic behavior, we studied children's decisions while they played two types of economic exchange games with differing demands of strategic behavior. We show an increase of strategic behavior with age, which could not be explained by age-related changes in social preferences but instead by developmental differences in impulsivity and associated brain functions of the left dorsolateral prefrontal cortex (DLPFC). Furthermore, observed differences in cortical thickness of lDLPFC were predictive of differences in impulsivity and strategic behavior irrespective of age. We conclude that egoistic behavior in younger children is not caused by a lack of understanding right or wrong, but by the inability to implement behavioral control when tempted to act selfishly; a function relying on brain regions maturing only late in ontogeny.

INTRODUCTION

Throughout centuries and across cultures, humans have engaged in social exchange of goods ranging from food to money (Henrich et al., 2001). Such bargaining situations often produce a conflict of interest of the exchanging parties where both parties aim to maximize their own outcomes and reach mutually satisfactory results (Güth et al., 1982). These conflicts emerge early in life. Think of, for example, a child with multiples of a trading card who wants to swap for a much-desired item missing from his/her collection. The child is required to engage in behavioral control in order to make an acceptable offer and get what he/she wants. Therefore successful bargaining requires strategic behavior (Camerer, 2003). Visibly selfish and antisocial acts typically lead to retaliation and preclude the possibility of future prosocial exchange (Axelrod and Hamilton, 1981; Fehr and Gächter, 2000), further highlighting the importance of behaving in ways that satisfy one's own needs while being acceptable to others. Strategic social behavior, therefore, ensures sustained goodwill for present and future interactions.

So far, descriptions of the emergence and development of other-regarding preferences in humans indicate significant changes during childhood (Beneson et al., 2007; Harbaugh et al., 2003; Murningham and Saxon, 1998). Typically, behavior shifts from a more self-oriented way of sharing resources to a tendency to increasingly take the payoffs of others into account. For instance, it has been shown that inequity aversion increases between the ages of 3–8 years (Fehr et al., 2008). Similarly, sharing increases over the course of childhood (Beneson et al., 2007). Some evidence for rudimentary strategic considerations in children comes from studies reporting increases in sharing under threat of punishment compared to no threat of punishment (Harbaugh et al., 2003; Murningham and Saxon, 1998). To date, however, there are neither reports of age-related changes in the degree of strategic behavior through development nor explanatory accounts of the underlying cognitive or neuronal mechanisms of such age-related differences in social behavior.

To fill this gap, we conducted two behavioral experiments and one functional and structural imaging (MRI) study comparing children of different ages engaged in two different economic exchange games: the Ultimatum Game and the Dictator Game (henceforth UG and DG). In the UG, two anonymous individuals, a proposer and a responder, need to negotiate the division of a set amount of money between them. The proposer can offer a split of the sum, which the responder can accept or reject. In case of acceptance, the money is divided between the players as proposed. However, if the responder rejects, neither player obtains anything (Figure 1A). Thus, the proposer needs to be able to consider the sanctioning threat and exercise increased behavioral control in order to act strategically when making the offer. The DG is different in that the responder can only accept. Therefore, the proposer's offers purely reflect generosity and fairness preferences. Moreover, given that the behavior cannot be punished, less behavioral control is necessary to be able to maximize one's own outcome. The difference in offer size between UG and DG thus provides an elegant measure of strategic behavior.

The developmentally determined differences in maturational time course of different areas of the human brain can be used to make predictions about the possible neural mechanisms

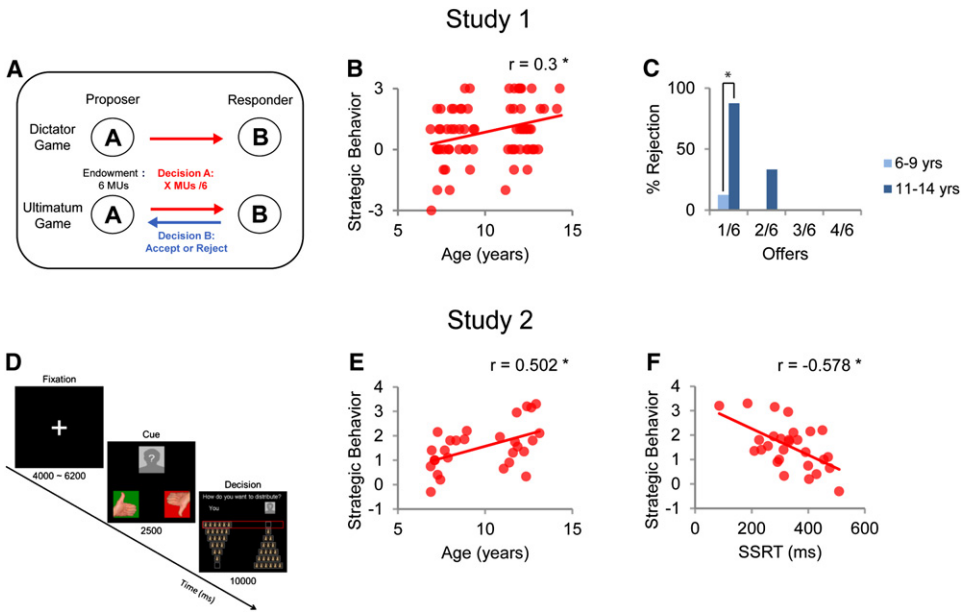

Figure 1. Behavioral Data of Proposer and Responder Decisions over Both Studies

(A) Study 1 (behavioral) design. Participants were assigned to play either as proposer or responder in a one-shot DG and UG.

(B) There was an increase in strategic behavior with age ($r = 0.3$, $p = 0.009$; ρ (Spearman's rho) = 0.256, $p < 0.027$).

(C) Rejection rates across subject groups. Older children rejected unfair offers of 1/6 MU more often than younger children ($\chi^2 = 9.0$; $p = 0.01$).

(D) Study 2 (behavioral and fMRI) design. Participants were scanned in the role of the proposer. Each trial was preceded by a jitter followed by a decision-cue after which subjects had 10 s to decide how they wanted to share the six MUs by shifting a red bar to the desired distribution.

(E) There was an increase in strategic behavior with age ($r = 0.502$, $p = 0.006$; $\rho = 0.514$, $p = 0.005$).

(F) There was an increase in strategic behavior with better performance on a measure of impulse control (SSRT; $r = -0.578$, $p = 0.001$).

See also Figures S1 and S2 and Table S1.

that may underlie the emergence of different cognitive functions and associated behaviors during ontogeny. For example, evidence from structural MRI data suggests that, in particular, lateral prefrontal cortices are among the brain regions taking longest to fully mature, developing well into early adulthood (Gogtay et al., 2004; Giedd et al., 1999; Shaw et al., 2008; Sowell et al., 2003, 2004). Interestingly, functional MRI (fMRI) studies in adults have revealed that dorsolateral portions of the prefrontal cortex (DLPFC) are functionally implicated in cognitive control (Miller and Cohen, 2001), more specifically in self-control (Hare et al., 2009), as well as in bringing about norm-related behavior (Sanfey et al., 2003) and in making strategic decisions (Spitzer et al., 2007). Importantly, it has been shown that temporarily disrupting the function of right DLPFC by means of repetitive transcranial magnetic stimulation (rTMS) increases the willingness to accept unfair offers, but leaves fairness judgments unchanged (Knoch et al., 2006). Similarly, disruption of left DLPFC during intertemporal choice leads to more impulsive behavior as indicated by increased choices of immediate rewards over larger delayed rewards, while valuation judgments of the same rewards remain stable (Figner et al., 2010). This suggests that DLPFC plays a key role in the implementation of self-control and might also be crucial for possible age-related changes in strategic social behavior.

We specifically aimed to test the hypothesis that late maturing cortical areas such as DLPFC are critical for age-related differences in the implementation of fair behavior when this requires the control of prepotent, predominantly selfish impulses. Assuming that such strategic behavior resembles the ability to forgo the impulse of keeping all resources to oneself in order to make an acceptable offer to the other, this should also be linked to more general impulse control abilities. To be able to test for such a relationship, we made use of a well-established measure of impulse control and response inhibition, the stop-signal reaction time task (SSRT, Logan et al., 1997). Moreover, alternative explanations for age-related changes in social behavior were also tested for, including the possibility of age-related differences in the knowledge of what constitutes fairness (beliefs in what the other will do or should have done), social abilities (such as simulating the actions of another), empathic concern and perspective taking, as well as risk preferences and general intelligence.

A further hypothesis we set out to test was whether individual differences in brain structure would be predictive of individual differences in strategic behavior and impulse control irrespective of any age-related changes that might occur in those regions. Extensive literature has shown a link between individual differences in brain structure and performance on a broad range of cognitive and motor tasks, providing evidence both for the effects of behavioral training on brain structure (Draganski et al., 2004), as well as predispositional effects of brain structure on behavior (Thompson et al., 2001). To date, however, there are

no studies reporting a relationship between individual differences in brain structure and individual differences in social decision making.

To realize these goals, we first conducted one purely behavioral study in a large sample of children (Study 1: n = 146; age range: 6.9–14.4 years; mean: 10.4 years) and another behavioral study combined with fMRI in a smaller sample of children (Study 2: n = 28; age range: 6.9–13.1 years; mean age: 9.8 years). In each of these studies, every participant made decisions in both the DG and UG.

The present study's focus was on behavioral changes in strategic social behavior and associated behavioral and neural mechanisms during childhood. Given ethical and methodological constraints on MRI studies of very young children, as well as the pronounced nonlinear changes in brain structure and function throughout adolescence (Shaw et al., 2008; Uhlhaas et al., 2009), the lower age bound was fixed at 6 years and the upper age bound at 13 years, the latter constituting the end of late childhood and the onset of adolescence.

In Study 1, children were assigned either the role of the proposer (n = 75; age range: 6.9–14.3; mean age: 10.3) or of the responder (n = 71; age range: 7.0–14.4; mean age: 10.6) and played both games, which were counterbalanced across subjects (Figure 1A). In Study 2, only proposer decisions were investigated in children when playing both games (Figure 1D). To test whether the same neural structures relevant for bringing about age-related changes in strategic behavior in childhood continue to play a role in adulthood, we additionally studied the proposer's decisions by means of fMRI in a group of adults (n = 14; age range: 20.7–35.1 years; mean age: 24.1). These will be reported alongside the child data.

RESULTS

Kolmogorov-Smirnov tests did not indicate any deviation from normality in the age distribution of the child sample (Kolmogorov-Smirnov Z = 0.923; p = 0.361), justifying a unified parametrical statistical framework for all current analyses. To further cross-validate the presently reported age effects, we also used nonparametric Spearman rank order correlations, which will also be reported wherever necessary using Spearman's ρ.

Behavioral Data

Proposers were given six monetary units (MUs), which could be exchanged for gifts at the end of the experiment. Analyzing the proposer behavior in Study 1 and 2 consistently revealed that offers were larger in the UG than in the DG (Study 1: $t_{74} = 5.52$, $p < 0.001$; Study 2: $t_{27} = 8.84$, $p < 0.001$, Figures S1A and S2A available online). In both studies, age did not correlate with offers in the DG, but with offers in the UG (Study 1: $r = 0.672$, $p < 0.001$; $\rho = 0.693$, $p < 0.001$; Study 2: $r = 0.728$, $p < 0.001$; $\rho = 0.715$, $p < 0.001$). More importantly, in both studies age correlated positively with strategic behavior (i.e., the difference in offer size between UG and DG; Study 1: $r = 0.3$, $p = 0.009$; $\rho = 0.256$, $p < 0.027$; Figure 1B; Study 2: $r = 0.502$, $p = 0.006$; $\rho = 0.514$, $p = 0.005$; Figure 1E). Analysis of reaction times (RTs) in Study 2 showed that reactions in the UG (mean ± SE = 1,254 ± 100 ms) took longer than in the DG (1,004 ± 72 ms; $t_{27} = 3.39$, $p = 0.002$), but that neither RTs in the DG nor UG, nor the difference between them was correlated with age. These results extend previous findings of age-related changes in social exchange behavior (Harbaugh et al., 2003; Murningham and Saxon, 1998) and demonstrate an increase in strategic social behavior with age during childhood reliably observed in two independent studies.

Further analyses support the hypothesis that age-related changes are based on the development of behavioral control abilities rather than social norm understanding and social abilities. Indeed, when performing a median-split on age in Study 1 to analyze the responder behavior, we observed that younger children were more willing to accept unfair offers of one MU than older children ($\chi^2_1 = 9.0$, $p = 0.01$; Figure 1C). Astonishingly, these age-related differences in rejection behavior occurred despite comparable fairness judgments across age; that is, children of different ages showing already an equal understanding of which offer was fair and which not (see Figure S1C). Responders were also asked to rate how they had felt when seeing the offer on three scales asking for happiness, sadness, and anger ranging from "very" to "not at all." Again, there were no differences in rated emotions on any of the three scales between the two age groups, neither when accepting offers (happiness: $F[1,52] = 1.05$; $p = 0.309$; sadness: $F[1,52] = 3.23$; $p = 0.078$; anger: $F[1,52] = 0.09$; $p = 0.766$; Figure S1D) and more importantly nor when rejecting offers (happiness: $F[1,10] = 2.03$; $p = 0.185$; sadness: $F[1,10] = 0.47$; $p = 0.509$; anger: $F[1,10] = 0.00$; $p = 0.987$; Figure S1E).

Another indicator for age-related differences in behavioral control were findings from Study 2, where the degree of strategic behavior was correlated with behavioral control as measured by SSRT scores ($r = -0.578$, $p = 0.001$; Figure 1F) as well as age ($r = -0.558$, $p = 0.002$; $\rho = -0.563$; $p = 0.002$).

Importantly, strategic behavior in both studies was unrelated to performance on measures of perspective taking, empathic concern, risk taking, or general intelligence (see Experimental Procedures for details on the measures and Tables S1) and no age differences could be found on fairness judgments (Figures S1B and S2B), proposers' beliefs about the responders' decision (Figure S2C), or what proposers indicated they would have done in the role of responder (Figure S2D). Thus, in two independent studies, we show that the degree of strategic behavior increases with age and demonstrate that this is linked to age-related differences in the ability to implement behavioral control and not to developmental differences in social preferences, knowledge about social norms or beliefs about the others, social skills such as cognitive or affective perspective taking, risk preferences, or general cognitive abilities.

Analysis of the proposer behavior in adults revealed that offers were larger in the UG than in the DG ($t_{13} = 7.75$, $p < 0.001$, Figure S2E), showing that adults also demonstrate strategic behavior.

MRI Data

In the analyses of the imaging data of Study 2, we opted for a region of interest (ROI) approach (Kriegeskorte et al., 2009). We conducted a coordinate-based meta-analysis on six previous studies (Hare et al., 2009; Sanfey et al., 2003; Spitzer

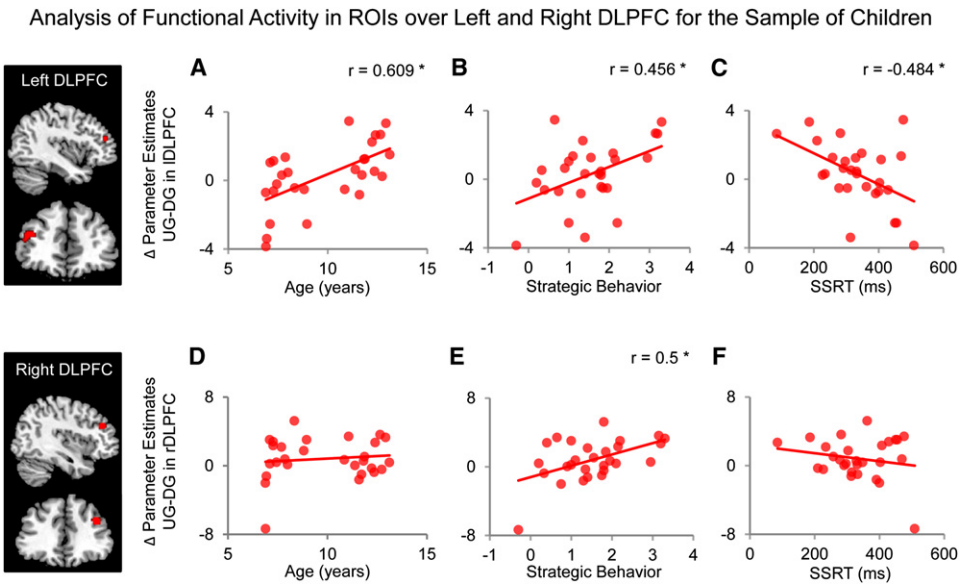

Figure 2. Analysis of Functional Activity in ROIs over Left and Right DLPFC

(A) With increasing age, there was an increase in activation in lDLPFC when making offers in UG compared to DG ($r = 0.609$, $p = 0.001$; $\rho = 0.632$; $p = 0.001$).
(B) The more strategically subjects behaved, the greater the increase in activation in lDLPFC when making offers in UG compared to DG ($r = 0.456$, $p = 0.015$).
(C) The better subjects were at impulse control, the stronger the activation in lDLPFC associated to strategic behavior ($r = -0.484$, $p = 0.009$).
(D) There was no link between age and activation in rDLPFC when making offers in UG compared to DG.
(E) The more strategically subjects behaved, the greater the increase in activation in rDLPFC when making offers in UG compared to DG ($r = 0.5$, $p = 0.007$).
(F) There was no link between impulse control and activation in rDLPFC when making offers in UG compared to DG.
See also Tables S1–S5.

et al., 2007; Güroglu et al., 2010, 2011; Tabibnia et al., 2008, for details see Experimental Procedures) to focus on brain regions that have consistently been shown to play a role in behavioral control in economic and social decision making. We identified two ROIs, one in left DLPFC (lDLPFC: $x = -40$, $y = 44$, $z = 18$; Figure 2A) and one in right DLPFC (rDLPFC: $x = 39$, $y = 37$, $z = 27$; Figure 2D) as the focus of subsequent analyses. In addition to the reported ROI analysis, we also performed whole-brain analyses reported in Tables S2–S5. Whereas we limit discussion of the findings to results significant at corrected thresholds, for the sake of completeness, we also report results at uncorrected thresholds ($p < 0.001$) in the tables, but without heeding these any further. Bonferroni corrections for comparison across multiple ROIs were also applied (with two ROIs, the new α-level is at 0.025).

Functional Data

Functional activity was averaged over all voxels for each ROI. There were no significant differences in activity between decisions made during the UG and the DG in either lDLPFC or rDLPFC (main contrast of UG-DG: Table S2). Activity in lDLPFC was positively correlated with age ($r = 0.609$, $p = 0.001$; $\rho = 0.632$; $p = 0.001$; Figure 2A), strategic behavior ($r = 0.456$, $p = 0.015$; Figure 2B), and negatively with SSRT scores ($r = -0.484$, $p = 0.009$; Figure 2C). Activity in rDLPFC on the other hand was positively correlated with strategic behavior only ($r = 0.5$, $p = 0.007$; Figure 2D), and not with age ($r = 0.114$, $p = 0.564$; $\rho = 0.143$, $p = 0.467$; Figure 2E) or with SSRT scores ($r = -0.118$, $p = 0.338$; Figure 2F). When correcting for age, activity in lDLPFC no longer correlated with strategic behavior ($r = 0.219$, $p = 0.271$) nor with SSRT scores ($r = -0.22$, $p = 0.27$), whereas activity in rDLPFC still correlated positively with strategic behavior ($r = 0.516$, $p = 0.006$) but not with SSRT scores ($r = -0.151$, $p = 0.453$). Findings from these ROI analyses converged with results obtained from whole-brain analyses identifying peaks in lDLPFC when correlating activity in the contrast UG-DG with age, as well as strategic behavior and performance on the SSRT and in rDLPFC when correlating activity in the contrast UG-DG with strategic behavior (correlation of activity in contrast UG-DG with age, strategic behavior, performance on SSRT: Tables S3–S5). This convergence of findings between the ROI and the whole-brain analyses suggests that the selected independent ROIs, mostly based on adult studies, are well suited for capturing meaningful age effects in a sample of children.

The same analysis in adults revealed that individual differences in strategic behavior were correlated with activity in lDLPFC ($r = 0.607$, $p = 0.021$; Figure 4A) and rDLPFC ($r = 0.669$, $p = 0.009$; Figure 4C), which, in turn, also converged with findings from whole-brain analyses (main contrast of UG-DG and correlation of activity in contrast UG-DG with strategic behavior: Tables S2 and S4). Even though there were no differences in our predefined ROIS of left and right DLPFC when computing the contrast UG-DG, other regions of bilateral DLPFC were still preferentially engaged (Table S2), thus replicating previous findings, at least in the adult sample (Spitzer et al., 2007).

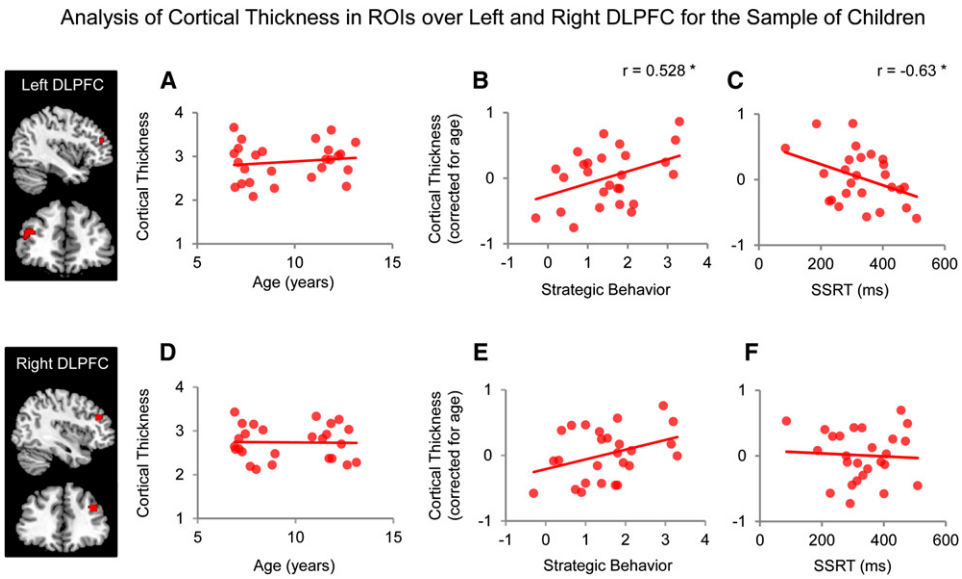

Figure 3. Analyses of Cortical Thickness in ROIs over Left and Right DLPFC for the Sample of Children

(A) There was no decrease in cortical thickness in lDLPFC with age.

(B) When correcting for age-related cortical thickness effects, there was an increase in thickness in lDLPFC with increasing strategic behavior ($r = 0.528$, $p = 0.007$).

(C) When correcting for age-related cortical thickness effects, there was an increase in thickness in lDLPFC with increasing impulse control ($r = -0.63$, $p = 0.001$).

(D) There was no decrease in cortical thickness in rDLPFC with age.

(E) When correcting for age-related cortical thickness effects, there was no significant increase in thickness in rDLPFC with increasing strategic behavior.

(F) There was no association between age-corrected cortical thickness in rDLPFC and impulse control.

See Figure S3.

Structural Data (Cortical Thickness)

In addition, we analyzed cortical thickness as a measure of brain structure in each individual (see Experimental Procedures for details). Performing a whole-brain assessment of cortical thickness in children, we observed widespread thinning with increased age in bilateral prefrontal, cingulate, supramarginal, paracentral, and medial occipital regions (family-wise error [FWE] < 0.05, Figure S3). Although there was a small negative relationship between age and cortical thickness in our ROIs, effects failed to reach significance ($p > 0.3$ in both lDLPFC and rDLPFC; Figures 3A and 3D). Given that studies on structural brain development typically include samples of a greater age range (Gogtay et al., 2004; Sowell et al., 2003), we also looked at age-related cortical thinning over the entire range of children and adults in our two ROIs. Indeed, this revealed significant thinning in both lDLPFC ($r = -0.385$, $p = 0.014$; $\rho = -0.412$, $p = 0.008$;) and rDLPFC ($r = -0.428$, $p = 0.006$; $\rho = -0.322$, $p = 0.043$; Figure S4), confirming previous results (Gogtay et al., 2004; Sowell et al., 2003, 2004).

We also assessed whether cortical thickness predicts individual differences in strategic behavior and impulse control, irrespective of any age-related cortical thinning. After statistically controlling for age effects, we found that thickness in lDLPFC correlated positively with both strategic behavior ($r = 0.528$, $p = 0.007$; Figure 3B) and negatively with SSRT scores ($r = -0.630$, $p = 0.001$; Figure 3C). Considering age-corrected cortical thickness of rDLPFC, on the other hand, we neither observed correlations with strategic behavior ($r = 0.347$, $p = 0.089$; Figure 3D) nor with SSRT scores ($r = -0.049$, $p = 0.816$; Figure 3E). This latter finding suggests that greater thickness of lDLPFC is related to both increased strategic behavior and impulse control, irrespective of age.

In the sample of adults, analysis of the cortical thickness revealed no correlation with age in either lDLPFC or rDLPFC ($p > 0.3$). Interestingly, like in the sample of children, analysis of an age-corrected relationship between cortical thickness and individual differences in strategic behavior in the sample of adults revealed a significant positive correlation in lDLPFC ($r = 0.663$, $p = 0.014$; Figures 4B) but not in rDLPFC ($r = 0.159$; $p = 0.587$; Figure 4D). These data provide a striking convergence with the age-corrected cortical thickness in the children, showing that greater thickness in lDLPFC is linked to increased strategic behavior.

Commonality Analysis

In a final integrative step, using commonality analyses we assessed the relative shared and unique predictive contributions of age and impulsivity, as well as functional and structural data of both left and right DLPFC to explain individual differences in strategic behavior in our child sample (Figure 5; Table S7). This analysis represents a synthesis in that we took all predictors of interest and tested for shared and unique variance components of these predictors to account for individual differences in strategic behavior. The analyses were performed separately for lDLPFC and rDLPFC (for details see Experimental Procedures; Figure S4). When including lDLPFC, we found that individual

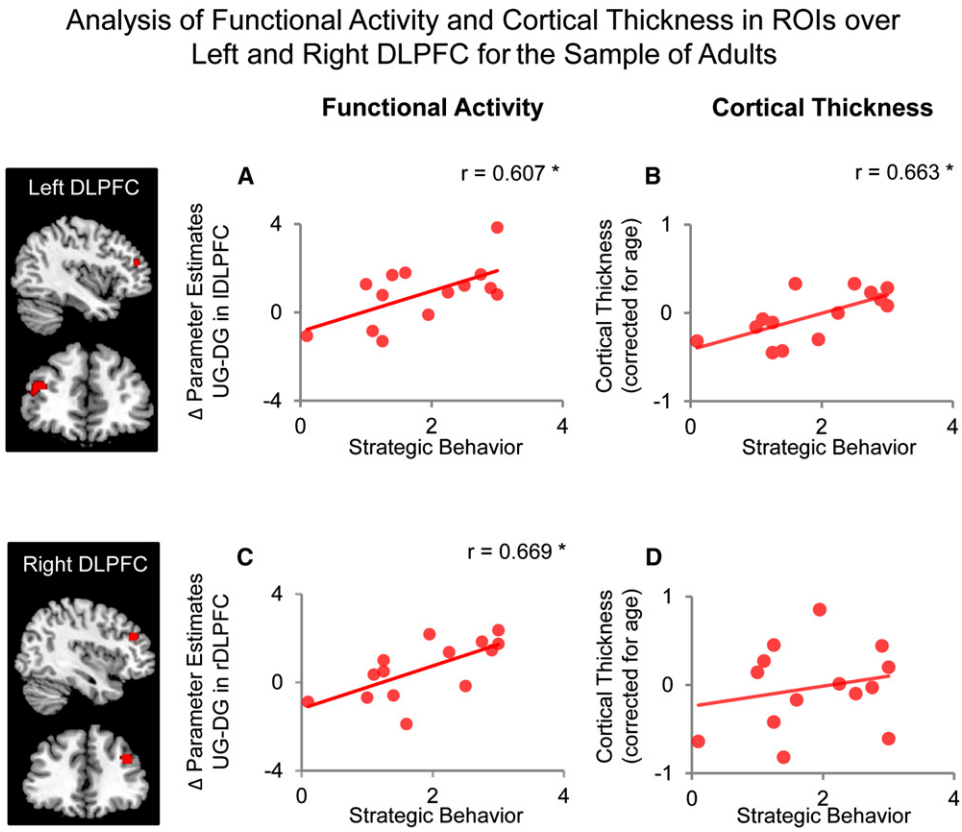

Figure 4. Analyses Functional Activation and Cortical Thickness in ROIs over Left and Right DLPFC for the Sample of Adults

(A) The more strategically subjects behaved, the greater the increase in activation in lDLPFC when making offers in UG compared to DG (r = 0.607, p = 0.021).
(B) There was an increase in cortical thickness in lDLPFC with increasing strategic behavior (r = 0.663, p = 0.014).
(C) The more strategically subjects behaved, the greater the increase in activation in rDLPFC when making offers in UG compared to DG (r = 0.669, p = 0.009).
(D) There was no increase in cortical thickness in rDLPFC with increasing strategic behavior.
See also Tables S1–S5.

differences in strategic behavior were best explained by the shared variance component of age, impulsivity and functional activity in lDLPFC (20.58%, Figure 5A, and see also Figures 1E and 2A–2C), as well as by the shared variance component of impulsivity and cortical thickness in lDLPFC (12.12%, Figure 5A, and see also Figures 3B and 3C). Considering rDLPFC, strategic behavior was optimally predicted by the shared variance between age and impulsivity (15.82%, Figure 5B), as well as the unique variance of impulsivity alone (12.19%, Figure 5B). This means that the shared variance of age, impulsivity and functional activation of lDLPFC constitutes a significant contributor to explaining individual differences in observed strategic behavior in children aged 6–13 years. In addition to this age-related component, further variance can be explained by individual differences in impulsivity and associated differences in cortical thickness of lDLPFC.

Reproducibility Analysis with an Additional Measure of Strategic Behavior

To demonstrate the robustness of our effects, we obtained an additional measure for strategic behavior, by calculating the difference between the proposer's offers in the UG and their beliefs about the smallest acceptable offer for the responder. Making greater offers than one believes the other to find minimally acceptable constitutes another instance of strategic social behavior, in that one attempts to increase the probability of offer acceptance.

Behavioral Data

There was a high correlation between the two measures of strategic behavior in both children (r = 0.79, p = 0.0001) as well as adults (r = 0.622, p = 0.017). In addition, we could replicate the correlation between strategic behavior and age (r = 0.498, p = 0.007; ρ = 0.477; p = 0.01) as well as behavioral control as measured by SSRT scores (r = −0.46, p = 0.014).

Functional Brain Data

By using this additional measure of strategic behavior in the sample of children, we could further replicate significant correlations with activity in lDLPFC (r = 0.435, p = 0.021) but not with activity in rDLPFC (r = 0.31, p = 0.1). In the sample of adults, correlations were marginally significant with activity in lDLPFC (r = 0.519, p = 0.057) as well as rDLPFC (r = 0505, p = 0.065). Whole-brain correlations of the functional data with this measure of strategic behavior revealed peaks almost exclusively in lDLPFC and rDLPFC (Table S6).

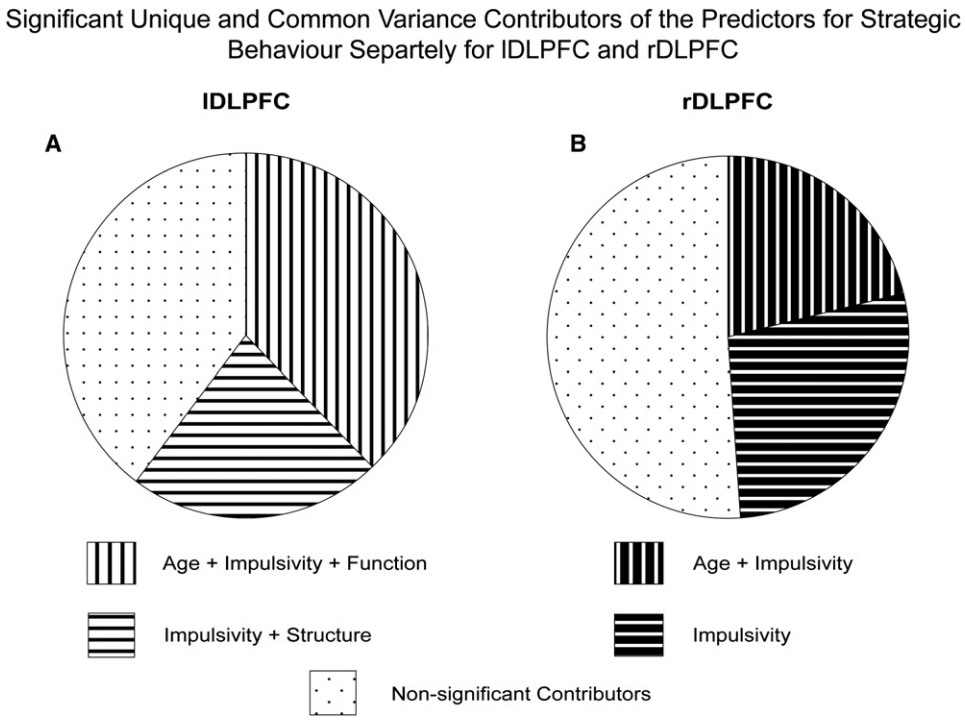

Figure 5. Commonality Analysis of Four Predictors

The four predictors were age, impulsivity, functional activity (function), and cortical thickness (structure) for either right or left DLPFC in explaining variance in strategic behavior. For full details on the variance explained by each of the 15 components making up significant as well as nonsignificant contributors, see Table S7.

(A) When including the lDLPFC, the total explained variance of strategic behavior was 54.19%. The shared variance of age, impulsivity, and function (20.58%) and the shared variance of impulsivity and structure (12.12%) were significant predictors of strategic behavior.

(B) When including the rDLPFC, the total explained variance of strategic behavior was 57.01%. The unique variance of impulsivity (12.19%) and the shared variance of age and impulsivity (15.82%) were significant predictors of strategic behavior.

See also Figure S4.

Structural Brain Data

In the sample of children, there were marginally significant correlations with age-corrected cortical thickness in lDLPFC ($r = 0.41$, $p = 0.042$) and none in rDLPFC ($r = 0.275$, $p = 0.184$). For the adults, however, the correlations were not significant in lDLPFC ($r = 0.342$, $p = 0.253$) or in rDLPFC ($r = 0.222$, $p = 0.465$).

DISCUSSION

The goal of the present study was to investigate the development of strategic social behavior during childhood and the specific cognitive and neural mechanisms which give rise to observed age-related changes. Given the importance of late-maturing brain regions such as DLPFC in implementing fair behavior (Sanfey et al., 2003; Knoch et al., 2006; Spitzer et al., 2007), we hypothesized that these areas would also be critically involved in bringing about increased social strategic behavior as a function of improved impulse control with increasing age. We used two game-theoretical-based paradigms derived from economics that differed only in their demands for strategic behavior. In both games, proposers could decide on how to split their endowment with the responders, but in one game (the Ultimatum Game, UG) they could incur punishment in the form of the responder rejecting the offer, and in the other game (the Dictator Game, DG) no such punishment option was available to the responder.

We observed that when rejection of the offers was possible, proposers were willing to share more than when it was not possible, indicating strategic behavior to avoid punishment. More importantly, however, strategic behavior, operationalized as the difference between offers in UG versus DG, increased with age, which was shown and replicated in two independent studies. Crucially, we also observed age-related increases in performance on an impulse control measure (Logan, 1994), which, in turn, also correlated with the degree of strategic behavior. No age differences could be found on other relevant tasks included in an extensive battery of tests, such as social preferences of fairness, beliefs, and simulations of the responder's behavior or risk preferences. Furthermore, individual differences in strategic behavior did not show any significant correlations with specific social skills such as empathy or theory of mind, or general cognitive skills such as fluid intelligence. These findings provide strong behavioral evidence in support of the hypothesis that there is an observed age-related increase in strategic social behavior in social exchange tasks during childhood that arises out of improved behavioral control abilities.

Further support for this hypothesis is provided by analysis of the responder behavior in Study 1. Younger children were more willing to accept unfair offers than older children, despite comparable ratings of how fair and unfair these offers were considered. Thus, even though fairness norms of the younger children are comparable to those of older children, acting on them when confronted with valuable and, therefore, tempting options seems more difficult for younger children. This finding is particularly striking, in the light of the evident discrepancy between what younger children say they would do in case of a poor offer (over 85% reject) and how they actually behave (only 12.5% reject). That there were also no differences in emotional experience between the two age groups when seeing offers that were subsequently rejected (as shown by comparable ratings on scales measuring anger, sadness, and happiness) indicates that children of all ages cared equally about the offers made. This also speaks against the possible hypothesis that younger children might in fact be better at regulating emotional responses to unfair offers (i.e., anger), in turn, leading to increased acceptance. These data stand in contrast to the interpretation offered by Sanfey et al. (2003), arguing for a role of experienced emotion in producing responder behavior. Rather our findings imply that the difficulty of younger children to implement fairness norms in the face of strong incentives against doing so can best be accounted for by poorer impulse and behavioral control. This provides again support for the hypothesis that both age-related changes in proposer and responder behavior can be best explained by developmental improvements in control abilities during childhood.

Our fMRI data analysis focused on changes in ROIs in lDLPFC and rDLPFC that were derived from a meta-analysis of previous fMRI studies assessing self- and behavioral control in decision making (Hare et al., 2009; Sanfey et al., 2003; Spitzer et al., 2007; Güroglu et al., 2010, 2011; Tabibnia et al., 2008). In our sample of children, functional activity of both lDLPFC and rDLPFC correlated positively with strategic behavior. In addition, both lDLPFC and rDLPFC were also correlated with strategic behavior in the sample of adults, which suggests that these structures continue to be important in implementing this behavior well into adulthood. However, only lDLPFC was significantly correlated with age and impulse control abilities in the child sample. Particularly this last finding suggests that age-related changes with regards to the functional implementation of strategic behavior occur selectively in left and not right DLPFC, which, in turn, is also linked to individual differences in impulse control. Importantly, however, while there is evidence that right DLPFC is involved in strategic behavior, this does not appear to change as a function of age or impulse control.

We also analyzed brain structural markers as predictors for differences in strategic behavior using the measurement of cortical thickness. These measures allow for the study of gray matter variations across thousands of vertices on the folded cortical surface (Fischl and Dale, 2000). They may thus offer a more direct and biologically meaningful marker of brain structure than the technique of voxel-based morphometry, which may often be confounded by sources of registration error and partial volume effect (Ashburner and Friston, 2001; Bookstein, 2001). In our sample of children, whole-brain cortical thickness analysis revealed marked and multilobar age-related thinning, encompassing large clusters in bilateral prefrontal, cingulate, supramarginal, paracentral, and medial occipital regions. Findings were consistent across several surface based smoothing kernels chosen, indicating high degrees of robustness of effects across different spatial scales. Even though cortical thickness in our circumscribed ROIs of lDLPFC and rDLPFC, did not show such marked age effects when testing only within the narrow age range of the child sample, the inclusion of the adult sample into the analysis indeed revealed age-related thinning in our ROIs over lDLPFC and rDLPFC replicating previous results which were usually based on samples covering a large and arguably more densely sampled age-range (Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 2003, 2004). Our relatively narrow age-range as well as comparably small sample of children are likely also among the reasons why age-related cortical thinning in our ROIs was not associated with strategic behavior. In addition, collecting a greater range of structural parameters, providing for instance indicators for the development of white matter, might help to find a structural brain basis for the age-related changes observed in strategic behavior.

We performed a separate regression analyses focusing on the relationship between cortical thickness of lDLPFC and rDLPFC and strategic behavior independent of age. After statistically controlling for age effects prior to analysis, we observed positive correlations between cortical thickness of lDLPFC, but again not rDLPFC, with both strategic behavior and impulse control in the sample of children. Importantly, the association of increased age-corrected cortical thickness of lDLPFC and greater strategic behavior was replicated in the sample of adults, providing a striking convergence of brain-behavior correlations. These results may reflect cortical plasticity dependent on individual differences in the daily practice of behavioral control functions, which are required for social strategic behavior. Similarly, previous studies demonstrated an association between the degree of changes in brain structure and the acquisition of specific skills, as shown in the domains of motor training (Draganski et al., 2004), spatial navigation (Maguire et al., 2000), language acquisition (Mechelli et al., 2004), and memory capacity (Engvig et al., 2010). The present findings extend previous data in the domain of social decision making and constitute a crucial role for individual differences in cortical thickness in explaining variations observed in the extent of strategic behavior in children as well as in adults. The range of possible cellular processes, which could explain the presently observed increase in cortical thickness with increased strategic behavior and impulse control include synaptogenesis, dendritic branching, and dendritic spine density, as well as neurogenesis or an increase of glial cells (Gross, 2000; Markham and Greenough, 2004). However, the use of noninvasive neuroimaging techniques such as MRI in awake humans cannot tell us which of these possible neurobiological mechanisms may underlie observed effects. Animal studies using similar paradigms will be needed to understand the exact neurobiological mechanisms underlying neuronal plasticity in the domain of social decision making.

Alternatively, the observed association between cortical thickness in areas known to be crucial for impulse control and

individual differences in the capacity for strategic behavior could also reflect differential effects of genes on cortical structure (Lenroot et al., 2009), which, in turn, predispose toward greater impulse control and strategic social behavior. This interpretation is supported by previous findings reporting that cortical thickness in late developing regions, such as the prefrontal and temporal neocortical regions is highly heritable, especially at later maturational stages (Lenroot et al., 2009). Longitudinal developmental and training studies, allowing a reliable assessment of subject-specific effects, could help to further clarify the origin of this effect. Nevertheless, these findings constitute the first evidence of an association between measures of individual differences in cortical thickness in prefrontal regions and decision making in the context of social exchange in children and adults.

Interestingly, we were able to replicate most of the key findings with an additional measure for strategic behavior, as made up of the increase in offer size during the UG compared to one's beliefs about the smallest offer acceptable for the responder. This suggests a considerable robustness of the present findings across different measures testing for effects of strategic behavior.

Given that several predictor variables had been shown to account for variance in strategic behavior, we conducted a commonality analysis to test for the predictor variables' unique and shared contributions in explaining the observed variance in strategic behavior. This analysis is, therefore, an important integrative and synthesizing step that brings together age and measures of impulse control, as well as brain structure and function. We observed that age-related changes in strategic behavior could best be explained by individual differences in a cognitive process related to impulse control and are subserved by functions of the lDLPFC. In addition to these linear age-dependent changes, cortical thickness of the very same region of lDLPFC also accounts for age-independent components in strategic behavior, which are again associated to measures of impulsivity. The fact that age-dependent functional activation and age-independent cortical thickness of lDLPFC in children, as well as age-independent cortical thickness of lDLPFC in adults, account for strategic behavior provides a striking convergence on the crucial role of lDLPFC in implementing this behavior.

As indicated by the commonality analysis, age-related cortical thinning in our ROIs was not related to the observed age-related changes in functional activation. Even though the direct link between structural and functional neural correlates is still poorly understood (Poldrack, 2010), especially from a developmental perspective (although for first attempts, see Lu et al., 2009), this suggests, that other age-dependent aspects of brain maturation, not included in the present study, might be responsible for the observed age-related changes. Several studies have shown that white matter structure changes substantially through development (Lebel and Beaulieu, 2011; Giedd et al., 1999) as a function of increases in axonal diameter and increasing myelination (Lebel and Beaulieu, 2011; Benes et al., 1994). It has been argued that these changes can help to establish interregional cortical processing (Salami et al., 2003), which can, in turn, influence functional activation in specific cortical regions (Fornari et al., 2007; Hagmann et al., 2010). Future work should focus on including a wide range of functional and structural imaging methods capable of tracking all facets of age-dependent changes in the brain, thereby enabling the mapping of developmentally determined biological substrates of observed changes in functional activation and associated changes in behavior and cognition.

The present study reports age-related inter-hemispheric differences in functional involvement of DLPFC during strategic behavior in the presently tested age range. Whereas both left and right DLPFC are equally involved in bringing about strategic behavior, left DLPFC seems to require further age-dependent specification and thus accounts for most of the variance in age-related differences observed in strategic behavior. This finding is also echoed in other studies on the development of social behavior, such as reciprocal fairness during late childhood into early adulthood (Güroglu et al., 2011) and the development of response inhibition, where both adults and children recruited right, but only adults additionally recruited left prefrontal cortical areas (Bunge et al., 2002). The present data are consistent with evidence of differential functional specification of individual cortical regions in spite of comparable structural maturation (Johnson, 2000; Chiron et al., 1997). We would probably expect that if it were possible to test even younger children with functional as well as structural MRI techniques, results might have even revealed age-related differences in functional recruitment of rDLPFC.

The hemispheric difference reported in the present paper with regards to age-specific involvement is striking in so far as recent studies report an exclusively causal role for rDLPFC and not lDLPFC in bringing about behavioral control as responder in the UG in adults (Knoch et al., 2006). However, there is now also evidence of specific left lateral involvement of DLPFC when implementing behavioral control in economic decisions (Hare et al., 2009; Figner et al., 2010), suggesting that hemispheric differences in the context of decision making cannot easily be reconciled within a single explanatory framework. More work will have to be carried out, using a range of different tasks requiring behavioral control within the same set of subjects and of a large age range in order to test for the stability of such reports, as well as a possible functional specialization of right and left DLPFC in social decision making.

The present developmental approach focused on changes observed in behavior and brain during childhood. In addition, we also tested a small sample of adults to see whether patterns of behavior-brain correlations continue to hold later in life. This was the case both for an association between strategic behavior and functional activity as well as cortical thickness and suggests that we could report age-related changes in cortical areas that continue to be relevant for the implementation of the same behavior in adulthood. A life-span approach testing throughout childhood and adolescence into adulthood, however, was beyond the scope of the present paper. Future investigations should attempt to adopt this approach and, in fact, there are currently several promising attempts to do so already (Güroglu et al., 2011; Burnett et al., 2011).

In the present paper, we demonstrated an age-related increase in strategic decision making between ages 6 and 13 years and showed that these age-related changes in

bargaining behavior can best be accounted for by age-related differences in impulse control abilities and underlying functional activity of left but not right DLPFC. These data are complemented by the evident inability of younger children to reject unfair offers even though they are aware of the unfairness of the offer and agree that such unfair behavior should, in principle, be rejected. Thus, the difficulty that younger children experience in comparable social situations can be explained by poor behavioral control rather than by a lack of social norm understanding, differences in fairness- or risk preferences, and other social abilities such as mentalizing or empathic abilities, or general intelligence.

More generally, our findings suggest that the primary reason for egoistic or antisocial behavior in normally developing children may not result from ignorance of what is right or wrong, but more from an inability to implement this behavior when in a concrete situation with strong self-serving incentives. This inability seems to have its root in the late maturation of the prefrontal cortices, subserving the capacity for impulse and behavioral control. These findings represent a critical advance in our understanding of the development of social behavior with far-reaching implications for educational policy and research and highlight the importance of helping children act on what they already seem to know, as well as training the regulation of impulse and self-control. Such interventions could set the foundation in ontogeny for increased prosociality and altruism in the future.

EXPERIMENTAL PROCEDURES

Study 1 (Behavioral)

One hundred forty-six children (69 males, 77 females) from a school outside of Zurich (Schule Kaltbrunn, Kanton St. Gallen) participated in the study. Seventy-five were assigned the role of the proposer (34 males) and 71 the role of the responder (35 males). Children underwent a series of tasks, including the Dictator Game and the Ultimatum Game (DG and UG) either as proposer or as responder, a risk game (the Devils game; Slovic, 1966) as well as completing an empathy questionnaire for children (Litvack-Miller et al., 1997). For details see Supplemental Information.

Study 2 (Behavioral and MRII)

Participants

Children. Thirty-one children participated in the MRI experiment. Three had to be excluded due to excessive head movement or difficulty in understanding the task, leaving 28 subjects to be studied (14 female; range, 6.9–13.1; mean, 9.8).

Adults. Fourteen adults also took part in an MRI experiment (7 female; range: 20.7–35.01; mean, 24.1), with an identical setup as that of the children.

All subjects or the subject's parents gave informed consent and the study was approved by the ethics committees of the University of Zurich and of the Canton of Zurich (E68/2008).

Procedure

Scanning was performed within one single session, beginning with the structural scan, followed by the functional scan and ending with a postimaging questionnaire. The following description of the imaging procedure and analysis was identical for children and adults.

The study was carried out at the Laboratory for Social and Neural Systems Research. There were two sessions. Children came in the company of their parents and partook in a structural scan, as well as extensive behavioral tests in the first session and in the functional scan and some postimaging questions in the second session. At most, seven days passed between the two scanning sessions for any of the children. The following will report the behavioral and the imaging parts separately.

Behavioral Part. An extended battery of behavioral tests was carried out following the structural scan in the first session for children. This included the stop-signal-reaction-time task (SSRT; Logan et al., 1997), the Colored Progressive Matrices (CPM, Raven et al., 2003), a risk game (the Devil's Game; Slovic, 1966), and an empathy questionnaire (Davis, 1980; Litvack-Miller et al., 1997). After the functional session, all subjects answered questions on a postimaging questionnaire. For specific details on all tasks, please see Supplemental Information.

Experimental Paradigm during the Functional Imaging Session. Subjects played 20 trials of both DG and UG, which were presented in blocks of ten trials for each game. Game order was counterbalanced across subjects (for more details see Supplemental Information).

Imaging Part

MRI Acquisition. Brain images were acquired on a 3 Tesla Philips Intera Whole-body Scanner (Philips Medical Systems, Best, The Netherlands) at the Laboratory for Social and Neural Systems Research located at the University Hospital Zurich, equipped with an 8-channel Philips SENSitivity Encoded (SENSE) head coil. Structural image acquisition entailed 301 T1-weighted transversal images with a slice thickness of 1.2 mm reconstructed to 0.6 mm (TR, 7.6 ms; TE, 3.6 ms, flip angle, 3°, field of view [FOV], 250 mm; matrix size, 228 × 227). For the functional imaging, a SENSE T2*-weighted echo-planar imaging (EPI) sequence was used. Thirty axial slices were acquired covering the whole brain with a slice thickness of 3 mm and an interslice gap of 0.5 mm (TR, 1,568 ms; TE, 30 ms, flip angle = 90°, FOV = 240 mm; matrix size, 128 × 128). A total of 624 volumes were acquired over four runs with 156 volumes in each run. Each run began with five "dummy" volumes that were discarded from further analysis.

Functional Image Processing and Analysis. Images were analyzed using SPM5 (Wellcome Department of Imaging Neuroscience, London, UK) on the basis of an event-related model (Josephs et al., 1997). To correct for head movements, functional volumes were realigned to the first volume (Friston et al., 1995a), spatially normalized to a standard template with a resampled voxel size of 3 × 3 × 3 mm and smoothed using a Gaussian kernel with a full width at half maximum (FWHM) of 10 mm. Following previous studies which looked at BOLD response in children and comparing this to that of adults, we normalized all images to the same adult brain template (Burgund et al., 2002; Kang et al., 2003), a method shown to be valid for pediatric imaging. A high-pass temporal filter with cutoff of 128 s was applied to remove low-frequency drifts from the data.

Statistical analysis was carried out according to the general linear model (Friston et al., 1995b, see Supplemental Information for details). Regressors were defined separately for decisions made in UG and DG, and for null trials. Results at the whole-brain level are reported at $p < 0.001$ uncorrected unless indicated otherwise (see Tables S2–S6). Where applicable, we corrected for multiple comparisons to ensure FWE of maximally 0.05 using random field theory.

ROI Analyses. We obtained ROIs by performing a coordinate-based analysis using the Activation Likelihood Estimation (ALE) approach (Eickhoff et al., 2009). This was achieved by focusing the data analysis on regions that are consistently implicated in behavioral control in the context of social and economic decision making. To this end, we took studies investigating behavioral control in the context of social and economic decision making. This entailed five studies looking at behavior in the context of economic exchange games and taking the coordinates of peak activations when contrasting conditions with higher behavioral control with those of lower behavioral control (i.e., rejection versus acceptance as the responder in the UG; Sanfey et al., 2003; Güroglu et al., 2010, 2011; Tabibnia et al., 2008); giving under sanctioning threat versus no sanctioning threat; Spitzer et al., 2007). In addition, we included one further study that explicitly looked at behavioral control in the context of economic decision making by looking at choices of foods in dieters and nondieters (Hare et al., 2009). The six studies contained a total of 60 foci. These foci were analyzed using the GingerALE software (version 2.0.1, http://www.brainmap.org/ale/). The algorithm takes account of the sample size of each contrast and uses random effects analysis (Eickhoff et al., 2009). The resulting map was thresholded at $p = 0.05$ (with a minimum of 450 mm^3 cluster extent) corrected for multiple comparisons by means of the false discovery rate approach. Data was subsequently extracted using the Marsbar toolbox (Brett et al., 2009).

Cortical Thickness. FreeSurfer was used to generate models of the cortical surface from the T1-weighted images and to measure cortical thickness (Version 4.5.0; http://surfer.nmr.mgh.harvard.edu). The processing steps have been described in detail elsewhere (Han et al., 2006; Fischl and Dale, 2000). For whole-brain analysis, thickness data were smoothed using a surface-based 20 mm FWHM Gaussian kernel prior to statistical analysis. For ROI-based thickness analysis, we intersected coregistered volumetric labels with cortical surface models to generate surface-based labels, in which unsmoothed mean thickness was measured.

Statistical analyses of cortical thickness data were performed using the SurfStat (http://www.math.mcgill.ca/keith/surfstat) toolbox for Matlab (R2007a, The Mathworks, Natick, MA) (Worsley et al., 2009). We first tested for age-related cortical thinning across the entire cortical surface. Findings from this analysis were controlled at FWE < 0.05 using random field theory for nonisotropic images (Worsley et al., 1999; see Figure S3). Correcting for age effects, we also correlated strategic behavior and impulsivity with cortical thickness at each vertex, which did not survive stringent statistical thresholds. All findings were reproducible at different surface-based blurring kernels, ranging from 10 to 30 mm FWHM. In a separate analysis, we fitted the same linear models on mean cortical thickness in the predefined ROI.

Commonality Analysis. Commonality analyses were performed to assess unique and shared variance contributions of our experimental variables in the prediction of strategic behavior (Nimon et al., 2008). Each analysis included four predictor variables: age (1); impulsivity as measured by scores on the SSRT (2); functional activation of DLPFC in the contrast UG-DG (3); and cortical thickness of the DLPFC (4). The last two variables were gathered by means of the ROI analyses and performed for left and right DLPFC separately. We chose to conduct two commonality analyses, one including function and structure of lDLPFC and another including function and structure of rDLPFC. Restricting the analysis to one DLPFC region at a time was justified by the fact that the output of the shared variance contributors increases exponentially with the number of predictor variables. Indeed, performing the analysis on six predictor variables would have yielded 61 contributors in total, rendering a meaningful analysis virtually impossible. In addition, patterns of left and right DLPFC structure and function differed considerably regarding their correlation with age, impulsivity and strategic behavior. As a result, we chose to perform the analyses separately (for details see Supplemental Information).

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures, seven tables, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.neuron.2011.12.027.

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REFERENCES

Ashburner, J., and Friston, K.J. (2001). Why voxel-based morphometry should be used. Neuroimage *14*, 1238–1243.

Axelrod, R., and Hamilton, W.D. (1981). The evolution of cooperation. Science *211*, 1390–1396.

Benes, F.M., Turtle, M., Khan, Y., and Farol, P. (1994). Myelination of a key relay zone in the hippocampal formation occurs in the human brain during childhood, adolescence, and adulthood. Arch. Gen. Psychiatry *51*, 477–484.

Beneson, J.F., Pascoe, J., and Radmore, N. (2007). Children's altruistic behaviour in the dictator game. Evol. Hum. Behav. *28*, 168–175.

Bookstein, F.L. (2001). "Voxel-based morphometry" should not be used with imperfectly registered images. Neuroimage *14*, 1454–1462.

Brett, M., Anton, J., Valabregue, R., and Poline, J. (2009). Region of interest analysis using an SPM toolbox. Neuroimage *16*, 2.

Bunge, S.A., Dudukovic, N.M., Thomason, M.E., Vaidya, C.J., and Gabrieli, J.D.E. (2002). Immature frontal lobe contributions to cognitive control in children: evidence from fMRI. Neuron *33*, 301–311.

Burgund, E.D., Kang, H.C., Kelly, J.E., Buckner, R.L., Snyder, A.Z., Petersen, S.E., and Schlaggar, B.L. (2002). The feasibility of a common stereotactic space for children and adults in fMRI studies of development. Neuroimage *17*, 184–200.

Burnett, S., Bault, N., Coricelli, G., and Blakemore, S. (2011). Adolescents' heightened risk-seeking in a probabilistic gambling task. Cogn. Dev. *25*, 183–196.

Camerer, C.F. (2003). Behavioural studies of strategic thinking in games. Trends Cogn. Sci. (Regul. Ed.) *7*, 225–231.

Chiron, C., Jambaque, I., Nabbout, R., Lounes, R., Syrota, A., and Dulac, O. (1997). The right brain hemisphere is dominant in human infants. Brain *120*, 1057–1065.

Davis, M.H. (1980). A multidimensional approach to individual differences in empathy. JSAS Catalog of Selected Documents in Psychology *10*, 85.

Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., and May, A. (2004). Neuroplasticity: changes in grey matter induced by training. Nature *427*, 311–312.

Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., and Fox, P.T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. Hum. Brain Mapp. *30*, 2907–2926.

Engvig, A., Fjell, A.M., Westlye, L.T., Moberget, T., Sundseth, O., Larsen, V.A., and Walhovd, K.B. (2010). Effects of memory training on cortical thickness in the elderly. Neuroimage *52*, 1667–1676.

Fehr, E., and Gächter, S. (2000). Cooperation and punishment in public goods experiments. Am. Econ. Rev. *90*, 980–994.

Fehr, E., Bernhard, H., and Rockenbach, B. (2008). Egalitarianism in young children. Nature *454*, 1079–1083.

Figner, B., Knoch, D., Johnson, E.J., Krosch, A.R., Lisanby, S.H., Fehr, E., and Weber, E.U. (2010). Lateral prefrontal cortex and self-control in intertemporal choice. Nat. Neurosci. *13*, 538–539.

Fischl, B., and Dale, A.M. (2000). Measuring the thickness of the human cerebral cortex from magnetic resonance images. Proc. Natl. Acad. Sci. USA *97*, 11050–11055.

Fornari, E., Knyazeva, M.G., Meuli, R., and Maeder, P. (2007). Myelination shapes functional activity in the developing brain. Neuroimage *38*, 511–518.

Friston, K., Ashburner, J., Frith, C., Poline, J.-B., Heather, J., and Frackowiak, R. (1995a). Spatial registration and normalization of images. Hum. Brain Mapp. *2*, 165–189.

Friston, K., Holmes, A., Worsley, K., Poline, J.-B., Frith, C., and Frackowiak, R. (1995b). Statistical parametrical maps in functional imaging: a general linear approach. Hum. Brain Mapp. *2*, 189–210.

Giedd, J.N., Blumenthal, J., Jeffries, N.O., Castellanos, F.X., Liu, H., Zijdenbos, A., Paus, T., Evans, A.C., and Rapoport, J.L. (1999). Brain development during childhood and adolescence: a longitudinal MRI study. Nat. Neurosci. *2*, 861–863.

Gogtay, N., Giedd, J.N., Lusk, L., Hayashi, K.M., Greenstein, D., Vaituzis, A.C., Nugent, T.F., 3rd, Herman, D.H., Clasen, L.S., Toga, A.W., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. Proc. Natl. Acad. Sci. USA *101*, 8174–8179.

Gross, C.G. (2000). Neurogenesis in the adult brain: death of a dogma. Nat. Rev. Neurosci. *1*, 67–73.

Güroglu, B., van den Bos, W., Rombouts, S.A.R.B., and Crone, E.A. (2010). Unfair? It depends: neural correlates of fairness in social context. Soc. Cogn. Affect. Neurosci. *5*, 414–423.

Güroglu, B., van den Bos, W., van Dijk, E., Rombouts, S.A.R.B., and Crone, E.A. (2011). Dissociable brain networks involved in development of fairness considerations: understanding intentionality behind unfairness. Neuroimage *57*, 634–641.

Güth, W., Schmittberger, R., and Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. J. Econ. Behav. Organ. *3*, 367–388.

Hagmann, P., Sporns, O., Madan, N., Cammoun, L., Pienaar, R., Wedeen, V.J., Meuli, R., Thiran, J.-P., and Grant, P.E. (2010). White matter maturation reshapes structural connectivity in the late developing human brain. Proc. Natl. Acad. Sci. USA *107*, 19067–19072.

Han, X., Jovicich, J., Salat, D., van der Kouwe, A., Quinn, B., Czanner, S., Busa, E., Pacheco, J., Albert, M., Killiany, R., et al. (2006). Reliability of MRI-derived measurements of human cerebral cortical thickness: the effects of field strength, scanner upgrade and manufacturer. Neuroimage *32*, 180–194.

Harbaugh, W.T., Krause, K., and Liday, S.G. (2003). Bargaining by Children. Working paper.

Hare, T.A., Camerer, C.F., and Rangel, A. (2009). Self-control in decision-making involves modulation of the vmPFC valuation system. Science *324*, 646–648.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Gintis, H., McElreath, R., and Fehr, E. (2001). In search of Homo economics: experiments in 15 Small-Scale Societies. Am. Econ. Rev. *91*, 73–79.

Johnson, M.H. (2000). Functional brain development in infants: elements of an interactive specialization framework. Child Dev. *71*, 75–81.

Josephs, O., Turner, R., and Friston, K. (1997). Event-related f MRI. Hum. Brain Mapp. *5*, 243–248.

Kang, H.C., Burgund, E.D., Lugar, H.M., Petersen, S.E., and Schlaggar, B.L. (2003). Comparison of functional activation foci in children and adults using a common stereotactic space. Neuroimage *19*, 16–28.

Knoch, D., Pascual-Leone, A., Meyer, K., Treyer, V., and Fehr, E. (2006). Diminishing reciprocal fairness by disrupting the right prefrontal cortex. Science *314*, 829–832.

Kriegeskorte, N., Simmons, W.K., Bellgowan, P.S., and Baker, C.I. (2009). Circular analysis in systems neuroscience: the dangers of double dipping. Nat. Neurosci. *12*, 535–540.

Lebel, C., and Beaulieu, C. (2011). Longitudinal development of human brain wiring continues from childhood into adulthood. J. Neurosci. *31*, 10937–10947.

Lenroot, R.K., Schmitt, J.E., Ordaz, S.J., Wallace, G.L., Neale, M.C., Lerch, J.P., Kendler, K.S., Evans, A.C., and Giedd, J.N. (2009). Differences in genetic and environmental influences on the human cerebral cortex associated with development during childhood and adolescence. Hum. Brain Mapp. *30*, 163–174.

Litvack-Miller, W., McDougall, D., and Romney, D.M. (1997). The structure of empathy during middle childhood and its relationship to prosocial behavior. Genet. Soc. Gen. Psychol. Monogr. *123*, 303–324.

Logan, G.D. (1994). On the ability to inhibit thought or action: a user's guide to the stop signal paradigm. In Inhibitory Processes in Attention, Memory and Language, D. Dagenbach and T.H. Carr, eds. (San Diego: Academic Press), pp. 189–236.

Logan, G.D., Schachar, R.J., and Tannock, R. (1997). Impulsivity and inhibitory control. Psych. Sci. *8*, 60–64.

Lu, L.H., Dapretto, M., O'Hare, E.D., Kan, E., McCourt, S.T., Thompson, P.M., Toga, A.W., Bookheimer, S.Y., and Sowell, E.R. (2009). Relationships between brain activation and brain structure in normally developing children. Cereb. Cortex *19*, 2595–2604.

Maguire, E.A., Gadian, D.G., Johnsrude, I.S., Good, C.D., Ashburner, J., Frackowiak, R.S.J., and Frith, C.D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. Proc. Natl. Acad. Sci. USA *97*, 4398–4403.

Markham, J.A., and Greenough, W.T. (2004). Experience-driven brain plasticity: beyond the synapse. Neuron Glia Biol. *1*, 351–363.

Mechelli, A., Crinion, J.T., Noppeney, U., O'Doherty, J., Ashburner, J., Frackowiak, R.S., and Price, C.J. (2004). Neurolinguistics: structural plasticity in the bilingual brain. Nature *431*, 757.

Miller, E.K., and Cohen, J.D. (2001). An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. *24*, 167–202.

Murningham, J.K., and Saxon, M.S. (1998). Ultimatum bargaining by children and adults. J. Econ. Psychol. *19*, 415–445.

Nimon, K., Lewis, M., Kane, R., and Haynes, R.M. (2008). An R package to compute commonality coefficients in the multiple regression case: an introduction to the package and a practical example. Behav. Res. Methods *40*, 457–466.

Poldrack, R.A. (2010). Interpreting developmental changes in neuroimaging signals. Hum. Brain Mapp. *31*, 872–878.

Raven, J., Raven, J.C., and Court, J.H. (2003). Manual for Raven's Progressive Matrices and Vocabulary Scales (San Antonio, TX: Pearson Assessment).

Salami, M., Itami, C., Tsumoto, T., and Kimura, F. (2003). Change of conduction velocity by regional myelination yields constant latency irrespective of distance between thalamus and cortex. Proc. Natl. Acad. Sci. USA *100*, 6174–6179.

Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E., and Cohen, J.D. (2003). The neural basis of economic decision-making in the Ultimatum Game. Science *300*, 1755–1758.

Shaw, P., Kabani, N.J., Lerch, J.P., Eckstrand, K., Lenroot, R., Gogtay, N., Greenstein, D., Clasen, L., Evans, A., Rapoport, J.L., et al. (2008). Neurodevelopmental trajectories of the human cerebral cortex. J. Neurosci. *28*, 3586–3594.

Slovic, P. (1966). Risk-taking in children: age and sex differences. Child Dev. *37*, 169–176.

Sowell, E.R., Peterson, B.S., Thompson, P.M., Welcome, S.E., Henkenius, A.L., and Toga, A.W. (2003). Mapping cortical change across the human life span. Nat. Neurosci. *6*, 309–315.

Sowell, E.R., Thompson, P.M., Leonard, C.M., Welcome, S.E., Kan, E., and Toga, A.W. (2004). Longitudinal mapping of cortical thickness and brain growth in normal children. J. Neurosci. *24*, 8223–8231.

Spitzer, M., Fischbacher, U., Herrnberger, B., Grön, G., and Fehr, E. (2007). The neural signature of social norm compliance. Neuron *56*, 185–196.

Tabibnia, G., Satpute, A.B., and Lieberman, M.D. (2008). The sunny side of fairness: preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). Psychol. Sci. *19*, 339–347.

Thompson, P., Cannon, T.D., Katherine, L.N., van Erp, T., Poutanen, V., Huttunen, M., Lönnqvist, J., Standertskjöld-Nordenstam, C., Kaprio, J., Khaledy, M., et al. (2001). Genetic influences on brain structure. Nat. Neurosci. *4*, 1–6.

Uhlhaas, P.J., Roux, F., Singer, W., Haenschel, C., Sireteanu, R., and Rodriguez, E. (2009). The development of neural synchrony reflects late maturation and restructuring of functional networks in humans. Proc. Natl. Acad. Sci. USA *106*, 9866–9871.

Worsley, K.J., Andermann, M., Koulis, T., MacDonald, D., and Evans, A.C. (1999). Detecting changes in nonisotropic images. Hum. Brain Mapp. *8*, 98–101.

Worsley, K.J., Taylor, J.E., Carbonell, F., Chung, M.K., Duerden, E., Bernhardt, B., Lyttelton, O., Boucher, M., and Evans, A.C. (2009). SurfStat: a Matlab toolbox for the statistical analysis of univariate and multivariate surface and volumetric data using linear mixed effects models and random field theory. Neuroimage *47*, S102.