



Universiteit
Leiden
The Netherlands

Acceptance, rejection, and the social brain in adolescence : toward a neuroscience of peer relations

Will, G.J.

Citation

Will, G. J. (2015, June 4). *Acceptance, rejection, and the social brain in adolescence : toward a neuroscience of peer relations*. Retrieved from <https://hdl.handle.net/1887/33102>

Version: Corrected Publisher's Version

License: [Licence agreement concerning inclusion of doctoral thesis in the Institutional Repository of the University of Leiden](#)

Downloaded from: <https://hdl.handle.net/1887/33102>

Note: To cite this publication please use the final published version (if applicable).

Cover Page



Universiteit Leiden



The handle <http://hdl.handle.net/1887/33102> holds various files of this Leiden University dissertation

Author: Will, Geert-Jan

Title: Acceptance, rejection, and the social brain in adolescence : toward a neuroscience of peer relations

Issue Date: 2015-06-04

CHAPTER 6

A NEUROCOGNITIVE PERSPECTIVE ON THE DEVELOPMENT OF SOCIAL DECISION-MAKING

This chapter is accepted for publication as:

Will, G.-J. & Güroğlu, B. (in press). A neurocognitive perspective on the development of social decision-making. In M. Reuter & C. Montag (Eds.), *Neuroeconomics*. Berlin, Germany: Springer-Verlag.

ABSTRACT

In this chapter we review evidence for the hypothesis that developmental changes in the abilities to control impulses and to take other people's perspective are crucial in understanding age-related changes in social behavior. Studies that have examined the developmental roots of prosocial behavior and (strategic) fairness using experimental economic games show that other-oriented concern and a preference for fairness emerge early in development. Continued development of intentionality understanding and strategic behavior in bargaining situations suggest that perspective taking and cognitive control undergo extended development and continue to contribute to changes in social behavior well into adolescence. Furthermore, functional developmental neuroimaging studies have shown that these behavioral changes are accompanied by an increased recruitment of brain regions implicated in impulse control (e.g. dorsolateral prefrontal cortex) and perspective taking (e.g. temporo-parietal junction). Together these studies show that developmental changes in impulse control and perspective taking and their underlying neural circuitry are associated with progressively more strategic thinking and an increased incorporation of other's perspectives into social decision-making across development.

6.1 INTRODUCTION

Beginning early in ontogeny humans show levels of sociality that surpass those of other species (Tomasello & Vaish, 2013). For example, 1-year-old toddlers help others to achieve a goal by pointing toward, or picking up, objects that are needed to successfully complete an action without any explicit request or reward (Warneken & Tomasello, 2006). Despite the early emergence of key social tendencies, social behavior continues to develop and grow in complexity across childhood and adolescence. Children expand their behavioral repertoire with social tactics, such as teasing and deception, and they increasingly learn to take other people's feelings into account in their social responses (Burnett & Blakemore, 2009a). For instance, whereas preschoolers mainly use deception to their own benefit, school-aged children increasingly start to use deception to protect other's feelings (e.g. telling 'white lies') (Talwar, Murphy, & Lee, 2007).

Developmental changes in social behavior are thought to be supported by developmental changes in general cognitive functions like impulse control and specific social cognitive functions such as the ability to adopt another person's perspective (e.g. perspective taking). Controlling impulses is of crucial importance for the regulation of social behavior and continues to develop across childhood and adolescence (Davidson, Amso, Anderson, & Diamond, 2006; Rueda, Rothbart, McCandliss, Saccomanno, & Posner, 2005). Children acquire a core component of perspective taking when they develop an understanding that other people's mental states might differ from their own (Wellman et al., 2001). Even though this 'theory of mind' emerges before adolescence, more advanced forms of perspective taking needed to act on the understanding of other people's mental states continue to develop during adolescence (Dumontheil, Apperly, & Blakemore, 2010; Selman, 1980). This rather protracted development of both impulse control and perspective taking is likely to contribute to developmental changes in social behavior across adolescence and into adulthood. This implication is central in the neurobiological models of social development which posit that continued structural development of the brain is associated with functional changes in brain networks implicated in cognitive control and social cognition, which in turn contribute to developmental changes in social behavior (Blakemore, 2008; Crone & Dahl, 2012; Nelson, Leibenluft, McClure, & Pine, 2005).

In this chapter we review evidence for the hypothesis that the gradual development of impulse control and perspective-taking skills are associated with progressively more strategic thinking and an increased incorporation of other's intentions in social decision-making. In the following sections, we first describe why paradigms from behavioral economics provide valuable tools to study developmental changes in social behavior and its underlying mechanisms (6.2). Subsequently, we describe the age-related behavioral changes in these games (6.3), followed by evidence linking these behavioral changes to children's developing abilities to control

selfish impulses and to take other people's perspective (6.4). Next, we focus on functional neuroimaging studies showing that social decision-making in adults relies on separable, but interacting, networks in the brain (6.5). Finally, we review recent neuroimaging studies demonstrating differential development of the brain networks involved in social decision-making (6.6), supporting the proposition that increased intentionality understanding and strategic motivations in social decision-making are associated with developmental changes in these networks.

6.2 WHY USE ECONOMIC GAMES TO STUDY SOCIAL DEVELOPMENT?

To investigate the psychological and neural mechanisms underlying social decision-making, psychologists and neuroscientists have turned to game theoretical paradigms derived from behavioral economics (Rilling & Sanfey, 2011). These paradigms offer a context of social interactions where the decisions people make have actual consequences for their own and their interaction partner's outcomes. Two of these games, namely the Ultimatum Game and the Dictator Game, have proven to be valuable tools to study concerns about fairness. In these two-player exchange games one player (i.e., the proposer) is given a set of valuable rewards, such as money, candy or stickers and is given the opportunity to propose a split of the rewards between themselves and a second player. In the Ultimatum Game the second player (i.e., the responder) can either accept or reject the proposal. If the proposal is accepted, both players receive their part of the stake as proposed. In case of rejection, neither of the players receives anything (Güth et al., 1982). The Dictator Game is different in the sense that the responder (i.e., the recipient in this case) does not have the power to reject the proposal and thus passively receives the amount of rewards that the first player transfers (Forsythe et al., 1994).

Game theoretical models assume that humans are rational decision-makers who act to maximize personal outcomes (Camerer, 2003). Accordingly, game theory predicts that Ultimatum Game proposers would make the smallest offer possible and that responders would accept any offer greater than zero. However, findings show that (adult) proposers and responders do not follow the game theoretical predictions: proposers offer most often an equal split and responders usually reject offers smaller than 20% of the stake (Camerer, 2003). In the Dictator Game, there is no possibility for reciprocation or retribution for the recipient, so game theory would predict that proposers would keep the entire set of rewards to themselves. Interestingly, proposers in the Dictator Game rarely act in accordance with these predictions. Adult humans transfer on average 20 to 30% of the stake to anonymous others with 50% of the stake typically being one of the most frequently occurring offers (Forsythe et al., 1994; Hoffman, McCabe, Shachat, & Smith, 1994). These deviations from the game theoretical predictions suggest that

people not only have an interest in maximizing their own payoffs but also have a concern for the other person's outcomes. Importantly, whereas the positive offers in the Dictator Game reflect other-regarding concern, the comparatively larger offers in the Ultimatum Game suggest that strategic considerations aimed at reducing the possibility of rejection also play a role in decisions about fairness. In addition, the consistently found rejections of unfair Ultimatum Game offers suggest an aversive response to receiving less than the proposer (known as 'disadvantageous inequity aversion') and rejection of the offer possibly provides the responder with a way of correcting such inequity (Fehr & Schmidt, 1999).

Using these games for developmental research offers several advantages (Gummerum, Hanoch, & Keller, 2008). First, an important advantage is that the same paradigm can be used across a wide age range (from children as young as 3 years old to adults), enabling meaningful comparisons between different age groups. Second, the structured nature of the games makes it possible to quantify complex social behavior, which makes them useful for neuroimaging research. Third, these games allow for experimental manipulations where subcomponents of social decision-making, such as understanding another person's intentions and controlling selfish impulses, can be disentangled. Such subcomponents of decision-making might be differentially sensitive to developmental change. For example, emotional reactions to unfairness might mature earlier than an understanding of an interaction partner's intentions, which might depend on slowly developing cognitive functions. Psychological and neural mechanisms underlying such sub processes can further be investigated by relating age-related and age-independent individual differences in behavior and neural activation to external measures of cognitive control (e.g. inhibition tasks) or perspective taking (e.g. theory of mind tasks). By doing so, one can examine how different cognitive functions and their underlying neural substrates are involved in developmental changes in social behavior.

6.3 DEVELOPMENT OF A PREFERENCE FOR FAIRNESS

Concern for another person's wellbeing has strong developmental roots and emerges at very young ages. Twelve- to 18-month old infants willingly engage in instrumental helping of an adult who has dropped (Warneken & Tomasello, 2006) or misplaced (Liszkowski, Carpenter, & Tomasello, 2008) an object that is needed to complete an action and during the second year of life toddlers start to comfort others in distress (Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992). Nonetheless, infants and toddlers are much more reluctant to show prosocial behavior when it is costly, i.e. when they have to give up some of their own possessions to benefit another person (Svetlova, Nichols, & Brownell, 2010). Developmental studies employing the Dictator Game have shown that although children tend to keep most of

the resources to themselves, the size of their donations increase with age between the ages of 3 and 8 (Benenson, Pascoe, & Radmore, 2007; Blake & Rand, 2010; Smith, Blake, & Harris, 2013) and no longer differs from donations made by adults after age 9 (Gummerum, Keller, Takezawa, & Mata, 2008; Güroğlu et al., 2009; Steinbeis et al., 2012).

Interestingly, this developmental increase in costly sharing is not due to developmental differences in explicit knowledge about what constitutes a fair (i.e., in most cases equal) distribution of resources. Infants as young as 15 months already expect resources to be distributed equally as indicated by prolonged eye gazes in situations when resources are distributed unequally between two recipients compared to situations where both recipients receive an equal amount of resources (Schmidt & Sommerville, 2011; Sloane, Baillargeon, & Premack, 2012). A recent study showed that, although 3 year-olds do not differ from 8-year-olds in their judgments about what constitutes an equal division of rewards, they still tend to keep more than half of the rewards to themselves in a Dictator Game and the willingness to give away half of the rewards increases between the ages of 3 to 8 (Smith et al., 2013). Furthermore, converging evidence from developmental investigations of rejections of unequal distributions confirms that the willingness to incur costs to avoid unequal outcomes (“I’d rather receive nothing than less than the other”) increases between age 3 and 8 (Blake & McAuliffe, 2011). Also when distributing resources, 8-year-olds appear not to choose a distribution that favors a peer; even when this has no consequences for their own outcomes (Fehr et al., 2008; Shaw et al., 2013; Shaw & Olson, 2012). Taken together, these findings suggest that a developing sense of fairness makes children increasingly enforce equality when this is costly, but that it does not make them necessarily more generous or tolerant of higher outcomes for a peer.

Investigations of proposer behavior in the Ultimatum Game show that not only a prosocial concern about the other person’s profits or equal outcomes plays a role in fairness considerations, but also that strategic considerations aimed at reducing the possibility of rejection come into play. That is, adults tend to offer higher shares of the stake (closer to an equal split of the rewards) when the second player can punish unfair offers (e.g. by rejecting them in an Ultimatum Game) (Fehr & Fischbacher, 2004b; Spitzer, Fischbacher, Herrnberger, Grön, & Fehr, 2007). As such, the difference in Ultimatum Game and Dictator Game offers provides a measure of strategic social behavior. During late childhood (age 7–10), children start making higher Ultimatum Game proposals compared to Dictator Game allocations, but their Ultimatum Game proposals are still smaller than those proposed by adults (Harbaugh, 2003). During adolescence, the difference between Ultimatum Game and Dictator Game offers becomes progressively greater, suggesting a developmental increase in strategic behavior across adolescence (Güroğlu et al., 2009; Leman et al., 2009). The results from these studies also demonstrate that the increasing discrepancy between Ultimatum Game and Dictator Game offers is driven by increasingly higher Ultimatum Game offers and that Dictator Game offers made by children in late childhood do not differ from adult Dictator Game offers (Güroğlu et al., 2009; Steinbeis et

al., 2012). Taken together these studies show that a prosocial tendency to share resources with another person emerges early in development, but social behavior seems to become increasingly strategic across childhood and adolescence.

6.4 IMPULSE CONTROL AND PERSPECTIVE TAKING

Strategic bargaining depends on the notion that unfair Ultimatum Game proposals can be punished, while Dictator Game proposals cannot. Recently, it was demonstrated that strategic bargaining assessed as the difference between Ultimatum Game and Dictator Game

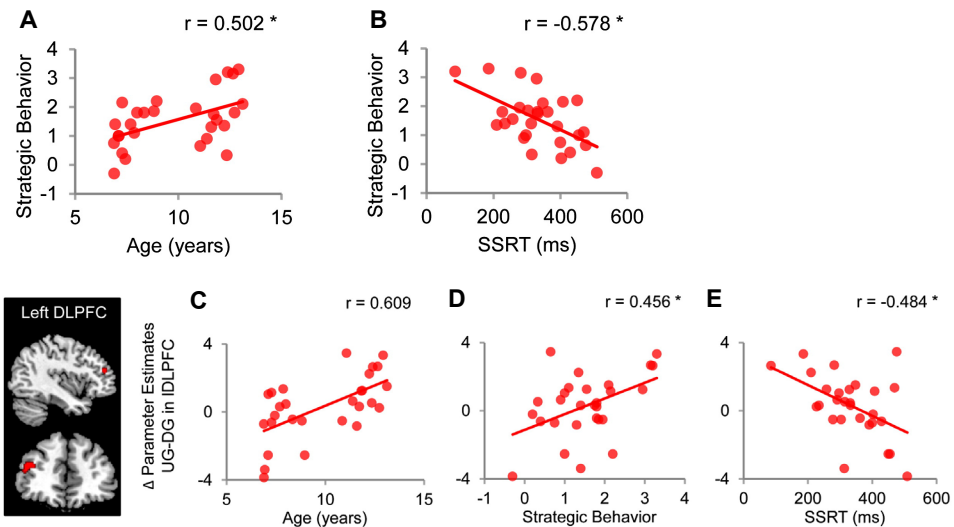


Figure 6.1 Age-related changes in strategic behavior and recruitment of the left dorsolateral prefrontal cortex (dlPFC): (A) Strategic behavior (Ultimatum Game (UG) proposals – Dictator Game (DG) proposals) increased with age; (B) More strategic behavior was associated with better performance on a measure of impulse control (lower stop-signal reaction times [SSRTs] represent enhanced impulse control); (C) Older children recruited the left dlPFC to a larger extent when making offers in the UG compared to the DG; (D) More strategic behavior was associated with higher activation in left dlPFC when making offers in the UG compared to the DG; (E) Higher levels of impulse control were associated with higher activation levels in left dlPFC when making offers in the UG compared to the DG. Adapted from Steinbeis et al. (2012) reprinted with permission.

offers is associated with the developing capacity to control impulses (Steinbeis et al., 2012). The difference between the number of rewards transferred in the Ultimatum Game and in the Dictator Game increased between the ages of 6 and 14 (see **Figure 6.1A**). Furthermore,

irrespective of age, children and adults who were better at controlling a prepotent motor response in a stop-signal reaction time (SSRT) task, also showed more strategic behavior (see **Figure 6.1B**). These findings suggest that strategic social behavior relies on the capacity to implement behavioral control over a selfish impulse of keeping all resources to oneself in situations where selfish behavior can be punished.

In addition, it has been argued that proposers have to take the responder's perspective in order to infer what kind of offers is likely to be rejected (Singer, 2006; Singer & Fehr, 2005). Indeed, 4-5 year old children who passed a false-belief task (a task to probe the acquisition of a theory of mind), more often proposed a fair offer in the Ultimatum Game than same-aged peers who failed to pass this task (Takagishi et al., 2010). Furthermore, children with deficits in perspective taking such as children with autism spectrum disorders tend to propose self-serving unfair offers in the Ultimatum Game (Sally & Hill, 2006). Interestingly, a prosocial tendency to share at least some part of one's resources with a peer in a Dictator Game is no different in children with autism spectrum disorders, suggesting that perspective-taking abilities are especially important when social interactions have a strategic component.

Further evidence for a role of perspective taking in decisions about fairness comes from studies that have shown that identical unfair Ultimatum Game offers (in terms of monetary outcomes) are rejected at different rates, depending on the alternative offer that was available to the proposer (Falk, Fehr, & Fischbacher, 2003). Specifically, an unfair offer is less often rejected when the proposer had no better alternative (e.g., a less unfair distribution of the stake) compared to cases where the proposer indeed had a fair alternative to share the stake equally. This suggests that responders not only judge the fairness of an offer by its absolute value or the relative profits in comparison with the proposer's profits, but also in terms of the proposer's intentions behind an unfair offer. Several studies examining developmental differences in responses to unfair Ultimatum Game offers with varying alternative options indeed showed interesting age differences in such intentionality understanding in fairness considerations (Güroğlu et al., 2009; Sutter, 2007). A comparison of four age groups in distinct phases of development (9 year-old pre-adolescents, 12 year-old early adolescents, 15 year-olds mid-adolescents and 18-year-old late adolescents/young adults) showed that rejection rates of an unfair offer where the proposer had no other alternative decreased between the ages of 9 and 18. Furthermore, 9-year-olds rejected monetarily identical unfair offers regardless of whether the proposer had a fair alternative, no alternative or an even more unfair alternative. With increasing age, adolescent proposers and responders flexibly adapted their bargaining behavior in accordance with the alternative that is available to an unfair distribution, suggesting an age-related increase in the incorporation of the proposer's intentionality behind an unfair offer ("it is unfair, but there was no better alternative") into the decision-making process (Güroğlu et al., 2009).

The role of perspective taking in social decision-making has also been investigated using

another economic game called the Trust Game (Berg, Dickhaut, & McCabe, 1995). In the Trust Game the first player (the trustor) is given the choice of either splitting the stake with a second player (the trustee) or transferring the entire endowment to the trustee and let the trustee split the stake. When the trustor decides to trust the trustee by transferring everything, the stake is multiplied (usually by 3 or 4). The trustee can reciprocate trust by sharing this higher stake equally, or defect trust and keep all the money. Developmental studies have shown that the frequency of trusting the second player continues to increase during adolescence (Sutter & Kocher, 2007; van den Bos et al., 2010). Furthermore, young adults and older adolescents show higher levels of reciprocity than early adolescents and children (van den Bos et al., 2010). Moreover, these age differences are most pronounced in situations where the trustor takes a larger risk of losing money by trusting the second player (van den Bos et al., 2010). Trust-decisions become riskier when the amount of money that can be lost in case of defection increases. In adults, riskier trust-decisions are met by higher levels of reciprocity, which possibly reflects a recognition of the trustor's positive intentions and an appreciation of the risk the trustor took by investing in the trustee (Malhotra, 2004; Pillutla, Malhotra, & Murnighan, 2003). Van den Bos and colleagues (2010) showed that 9-year-olds did not reciprocate more when the trustor took a larger risk than when he/she took a relatively lower risk. This 'risk-dependent' reciprocity gradually increased across adolescence, again suggesting a continuing increase in the sensitivity to other people's intentions well into adulthood.

Taken together, behavioral studies employing different economic exchange paradigms consistently show that cognitive development related to both impulse control and perspective taking play a crucial role in understanding age-related changes in social behavior. In the following sections, we will review results from neuroimaging studies that provide converging evidence for the role of impulse control and perspective taking in social decision-making.

6.5 NEURAL NETWORKS INVOLVED IN SOCIAL DECISION-MAKING

Neuroimaging studies have elucidated a role for three distinct, but interacting, brain networks in social decision-making: a basic affective network, a cognitive regulatory network, and a mentalizing network (see **Figure 6.2**) (Rilling & Sanfey, 2011). We will first briefly summarize findings that provide support for the notion that these three networks contribute to social decision-making. Subsequently, we will review the evidence from developmental functional magnetic resonance imaging (fMRI) studies that show that these networks are differentially sensitive to developmental change. Findings from these studies support the hypothesis that asynchronous development of these systems is associated with age-related increases in strategic social behavior and intentionality understanding in social interactions.

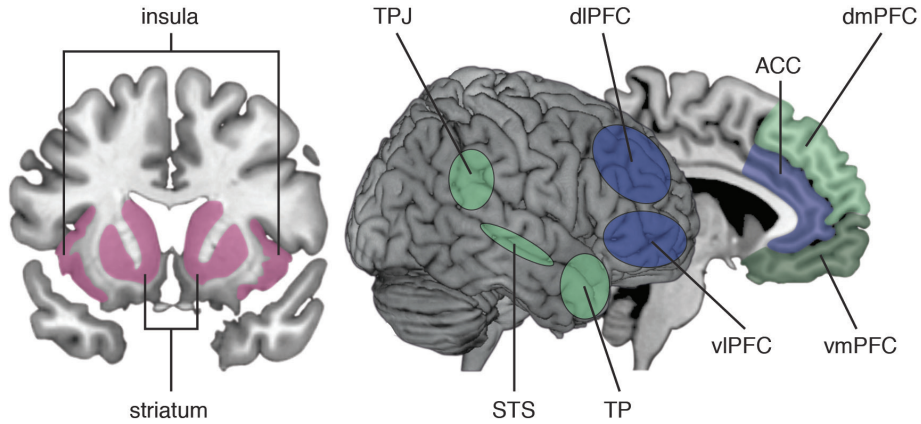


Figure 6.2. Schematic representation of brain networks involved in social decision-making: basic affective network (pink), cognitive-regulatory network (blue), and mentalizing network (green). TPJ = temporo-parietal junction; STS = Superior Temporal Sulcus; TP = temporal pole; dlPFC = dorsolateral Prefrontal Cortex; vlPFC = ventrolateral Prefrontal Cortex; ACC = Anterior Cingulate Cortex; dmPFC = dorsomedial Prefrontal Cortex; vmPFC = ventromedial Prefrontal Cortex.

First, neural structures implicated in the processing of basic positive and negative affect, such as the anterior insula (AI) (Sanfey et al., 2003), ventral striatum (Tabibnia, Satpute, & Lieberman, 2008) and the amygdala (Haruno & Frith, 2010) are involved in biasing social decisions, i.e. whether certain social stimuli should be approached (associated with a positive emotional signal) or avoided (associated with a negative emotional signal). For example, increased activation of the AI, a brain region that is involved in encoding representations of the physiological state of the body and negative affect such as disgust, anger and sadness, has been associated with unreciprocated trust (Rilling et al., 2008) and receiving unfair offers in an Ultimatum Game (Sanfey et al., 2003). Interestingly, the AI is activated not only when people receive unfair offers, but also when people observe someone else receiving an unfair offer (Corradi-Dell'Acqua et al., 2013) and when people have to divide resources unequally themselves (Hsu, Anen, & Quartz, 2008). In contrast, activation of the ventral striatum, a region important for processing rewards, has been associated with mutual cooperation in a prisoner's dilemma (Rilling et al., 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004b) and receiving an equal split of the stake in the Ultimatum Game (Tabibnia et al., 2008). Based on such findings, it has been argued that brain structures involved in basic emotion processing might play a role in signaling pleasantness (ventral striatum) and unpleasantness (AI) of social interactions and consequently might give rise to the maintenance or elimination of such interactions.

Second, brain regions that are involved in the processing of basic positive and negative affect interact with a cognitive regulatory network including the dorsal anterior cingulate cortex (dACC) and regions in the prefrontal cortex (PFC), such as the ventrolateral prefrontal cortex (vlPFC) and the dorsolateral prefrontal cortex (dlPFC) (Rilling & Sanfey, 2011). Activation in this cognitive regulatory network has been associated with cognitive control over selfish impulses and allows individuals to act in a goal-directed manner when there is a conflict between self-interest and social norms (Knoch et al., 2006; Sanfey et al., 2003). For example, activation in lateral regions of the PFC has been associated with strategic bargaining (Spitzer et al., 2007) and temporarily disrupting activity in the dlPFC using repetitive transcranial magnetic stimulation decreases rejection rates of unfair offers in an Ultimatum Game, while leaving explicit fairness judgments unaffected (Knoch et al., 2006). These findings suggest that control-related brain regions are of crucial importance for the regulation of (strategic) social behavior.

Third, when making social decisions, affective and cognitive regulatory regions interact with a third system, namely the mentalizing network. The mentalizing network includes the left and right temporo-parietal junction (TPJ), superior temporal sulci, ventral and dorsal regions of the medial PFC and the temporal poles (Frith & Frith, 2010; Saxe, Carey, & Kanwisher, 2004). Regions in this network are consistently identified in tasks that probe reasoning about other people's mental states (i.e., mental state reasoning or mentalizing), for instance when people have to infer other people's thoughts, beliefs or desires (Blakemore, den Ouden, Choudhury, & Frith, 2007; Saxe & Kanwisher, 2003). Moreover, taking other people's perspective in economic exchange has repeatedly been associated with activation in regions of the mentalizing network, such as the TPJ (Güroğlu et al., 2010) and the dorsomedial PFC (Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004a; van den Bos et al., 2009).

6.6 UNDERSTANDING CHANGING SOCIAL BEHAVIOR FROM A DEVELOPMENTAL NEUROSCIENCE PERSPECTIVE

Longitudinal research examining changes in brain structure over time has shown that different brain regions reach maturity at different ages (Giedd et al., 1999; Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 2003). That is, sensorimotor regions in the occipital and parietal lobes reach maturity first, followed by other parts of the cortex in a posterior to anterior direction. In particular, the dlPFC and the TPJ are among the brain regions latest to fully mature, developing well into early adulthood, which in turn might (partially) explain a similar protracted developmental pattern in their associated functions, such as impulse control (dlPFC) and perspective taking (TPJ). Indeed, models of functional brain development have posited

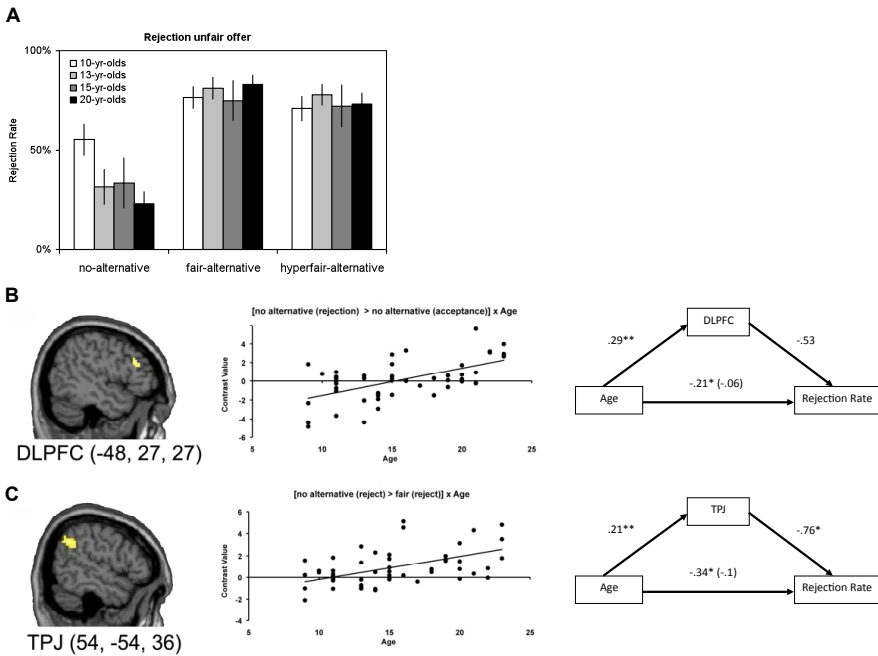


Figure 6.3 Age-related changes in intentionality understanding in fairness are mediated by age-related increases in recruitment of the dorsolateral prefrontal cortex (dlPFC) and the temporo-parietal junction (TPJ): (A) Rejection rates of unfair offers when the proposer could not make a fair offer decrease with age; (B) Rejection of unfair offers when the proposer could not make a fair offer is associated with increased recruitment of the dlPFC (B) and TPJ (C); the age-related changes in behavior are mediated by neural activation in these regions. Adapted from Güroğlu et al. (2011) reprinted with permission.

that structural brain development might underlie emerging contributions of late maturing brain networks to social behavior (Blakemore, 2008; Crone & Dahl, 2012). Importantly, whereas affective networks including subcortical brain structures might reach maturity during childhood or puberty, regions of the cognitive regulatory network and the mentalizing network show continued structural changes well into the second and third decades of life (Goddings et al., 2013; Mills, Lalonde, Clasen, Giedd, & Blakemore, 2012). This interplay between structural and functional brain development could underlie a developmental asynchrony between earlier maturing affective reactions to unfairness (associated with activity in basic affective network) and continued development of strategic considerations and intentionality understanding in social decision-making (associated with later maturing cognitive regulatory and mentalizing networks).

To investigate developmental changes in the neural networks involved in fairness-related decision-making Güroğlu and colleagues (2011) examined the neural correlates of

intentionality understanding in reactions to unfairness in four phases of development: 10 year-olds, 13 year-olds, 16 year-olds and a young adults aged 20. Their results showed that age was positively associated with TPJ and dlPFC activity when participants were confronted with an unfair offer where the proposer had no alternative to making an unfair offer (see **Figure 6.3A**). Rejection rates of such unfair offers decreased across adolescence, which again suggests that with age, adolescents become increasingly sensitive to the proposer's intentions behind an unfair proposal. Furthermore, mediation analyses showed that age-related decreases in rejection rates in this 'no alternative' condition were fully mediated by activation in the dlPFC (**Figure 6.3B**) and the TPJ (**Figure 6.3C**). Moreover, no developmental differences were observed in dACC and bilateral AI activation during reactions to unfair proposals. Together these findings suggest that the detection of violations of fairness norms and underlying neural responses in the AI and dACC mature prior to entering adolescence and that the continued development of intentionality understanding in decisions about fairness across adolescence is accompanied an age-related increase in neural activity in brain regions important for perspective taking (i.e., TPJ) and impulse control (i.e., dlPFC).

The importance of the emerging contribution of dlPFC to the development of strategic social behavior was elegantly demonstrated by Steinbeis and colleagues (2012) in a study where they asked children (ages 6-13) to be a proposer in both the Ultimatum Game (where unfair offers can be punished) and a Dictator Game (where there is no sanction to unfair offers). They showed that activity in both left and right dlPFC when making Ultimatum Game proposals compared to Dictator Game proposals correlates positively with two measures of strategic behavior: 1) the difference between Ultimatum Game and Dictator Game offers (**Figure 6.1D**) and 2) the difference between Ultimatum Game offers and the proposers' beliefs about the smallest acceptable offer to the responder. Moreover, they also showed that activity in the left dlPFC when making Ultimatum Game proposals compared to Dictator Game proposals increases between the ages of 6 and 13 (**Figure 6.1C**).

The involvement of brain regions in both the cognitive regulatory network (e.g. dlPFC) and the mentalizing network (e.g. the dorsomedial prefrontal cortex and the TPJ) in perspective taking in social interactions has also been studied using the Trust Game. Neuroimaging studies with adult participants have demonstrated the involvement of the dorsomedial prefrontal cortex (dmPFC) in decisions to trust (Rilling et al., 2004a), as well as in decisions to defect (McCabe, Houser, Ryan, Smith, & Trouard, 2001; van den Bos et al., 2009). Given the importance of the dmPFC in for self-referential thinking (Amodio & Frith, 2006), it has been suggested that these findings reflect an increased attention to one's own outcomes because both decisions involve maximization of payoffs (i.e., trust decisions lead to a multiplication of the stake and defect decisions lead to sure gains). Decisions to trust another person have also been shown to coincide with TPJ activation, which increases with age into adulthood (Fett, Gromann, Giampietro, Shergill, & Krabbendam, 2013). In addition, TPJ activity has also been associated

with receiving trust, in particular in situations in which people received trust from a trustor who took a larger risk by trusting them (van den Bos et al., 2009), suggesting that the TPJ is involved in shifting attention to the trustor's perspective when evaluating the risk he/she took.

To investigate the development of the neural correlates of reciprocity and the role of perspective taking herein, van den Bos and colleagues (2011) examined trustee behavior in three different age groups (early adolescents aged 12–14 years; mid adolescents aged 15–17 years; and young adults aged 18–22 years). They showed that receiving trust (compared to receiving no trust) was associated with increased activation in the left TPJ and right dlPFC and that activation in these regions increased linearly with age. Importantly, higher levels of risk taken by the trustor were associated with higher levels of activation of the TPJ and the dlPFC during reciprocity choices. Moreover, they showed that participants of all ages activated the dmPFC during defection, but that early adolescents also activated the dmPFC when they reciprocated trust. This latter result corroborates findings from developmental functional neuroimaging studies that show an age-related decrease in dmPFC activity during mentalizing in theory of mind tasks across adolescence (Blakemore et al., 2007; Moriguchi, Ohnishi, Mori, Matsuda, & Komaki, 2007) and an age-related increase in functional specificity of the TPJ to processing information about people's mental states compared to other forms of social information (Gweon, Dodell-Feder, Bedny, & Saxe, 2012; Saxe, Whitfield-Gabrieli, Scholz, & Pelphrey, 2009). It has been suggested that the age-related shift in the relative contributions of the dmPFC and the TPJ to social reasoning might tip early adolescents toward more self-oriented choices (associated with higher mPFC activation) and late adolescents toward more other-oriented choices (associated with higher TPJ activation) (Crone, 2013).

6.7 CONCLUSIONS AND FUTURE DIRECTIONS

In this chapter we reviewed evidence for the notion that the abilities to control impulses and to take others' perspectives when making social decisions undergo extended development, and that these behavioral changes can be traced to brain networks involved in social decision-making developing at different rates. Much of this evidence comes from studies employing experimental paradigms with economic games, which have proven to be valuable tools for studying the development of social behavior and in particular for successfully dissecting sub processes involved in social decision-making. Behavioral studies show that other-oriented concern and a preference for fairness have strong developmental roots. Greater sensitivity to others' intentions and more strategic behavior in bargaining situations provide evidence that continued development in perspective taking and impulse control contribute to changes in social behavior that occur across adolescence. Finally, these behavioral changes are accompanied by an increased recruitment of regions involved in impulse control (e.g. dlPFC) and perspective

taking (e.g. TPJ) in decisions where perspectives of interaction partners have to be effectively weighed against self-interest and social norms.

While elucidating developmental differences in recruitment of the dlPFC and TPJ and their involvement in social decision-making is a crucial first step, many fundamental questions remain unanswered. First, it is important not only to understand how the different brain regions (such as the TPJ or the dlPFC) are differentially recruited across development, but also how these regions interact and communicate with one another. For example, increased functional connectivity between regions of the mentalizing network (e.g. pSTS/TPJ) and brain structures implicated in the computation of reward (e.g. ventral MPFC) has been associated with higher levels of prosocial behavior in adults (Hare, Camerer, Knoepfle, & Rangel, 2010). Functional connectivity in the cognitive regulatory network (Fair et al., 2008) and the mentalizing network (Burnett & Blakemore, 2009b; Klapwijk et al., 2013) changes across adolescence, suggesting that developmental changes in functional connectivity may further contribute to changes in social behavior.

Second, the majority of developmental functional neuroimaging studies are based on cross-sectional data sets with participants of different ages. Although cross-sectional studies are an excellent first step to demonstrate developmental *differences*, there is a great need for longitudinal studies of social brain development. Longitudinal designs rule out the role of possible cohort differences and can give us insight on actual developmental *changes* within participants. One of the major questions in the field of developmental neuroimaging centers around the specific contributions of maturational processes relative to environmental or societal influences on the development of (social) behavior. For example, children who are accepted by their peers during childhood express higher levels of prosocial behavior and show advanced development of empathy and theory of mind compared to children who are rejected by their peers (Slaughter et al., 2002). Longitudinal studies can provide insights on how developmental trajectories of individual characteristics (such as long-term peer acceptance or rejection by peers) are related to social cognitive development and how they relate to developmental trajectories of both brain structure and function. An increased understanding of this intricate interplay between a dynamic social context and a maturing brain will be crucial for developing interventions that can help children and adolescents in navigating their increasingly complex social worlds.

