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[–] **Abstract and Keywords**

Adolescence can be seen as a period of pronounced cognitive advancements accompanied by significant changes in emotional and social behavior. Adolescents become more self-conscious and more focused on their social behavior and emotions. Recent studies have explored these changes in terms of brain maturation, brain function, and cognitive, emotional, and social development. This chapter examines the development of emotion and social reasoning in adolescence and how it is mediated by functionally different brain networks. It looks at brain maturation vis-à-vis developmental changes in reward processing, risk-taking, and social reasoning and proposes a working hypothesis that integrates neuroimaging data with behavioral studies. It also discusses use of the Ultimatum Game to probe social decision-making processes, along with the role of the insula, temporaparietal junction, and dorsolateral prefrontal cortex in the development of emotion processing and social reasoning in adolescents.

Keywords: emotion, social reasoning, adolescence, brain maturation, reward processing, risk-taking, Ultimatum Game, insula, temporaparietal junction, dorsolateral prefrontal cortex

Introduction

George had always been a happy, easygoing boy who liked to play sports and was pleasant to his friends and family. In the last few years he had lost interest in playing sports and spent more time on his computer chatting with friends. His parents complained that he talked less to them than he used to. On some days he was easy to talk to, whereas on other days it seemed like they did everything wrong. At the last family gathering, George was constantly listening to his iPod, and together with his cousins he had some beers in the back yard, even though his parents told him not to. Interestingly, George himself did not understand why he engaged in these risky activities, and he felt uneasy about his looks and the way he acted. Even though it may seem like George was going through a major transformation, these changes are more easily captured under the interesting, unavoidable, and intriguing stage in development: adolescence.

Adolescence is a highly important transition phase between childhood and adulthood, marked by significant physical, social, cognitive, and emotional changes (Dahl & Gunner, 2009; Steinberg, 2008). The onset of adolescence is characterized by the start of pubertal maturation around the age of 10 years, during which children undergo rapid physical growth and experience the onset of sexual maturation (Shirtcliff, Dahl, & Pollack, 2009). One of the more salient achievements in adolescence is a steady increase in self-regulation. During adolescence, children increasingly master the ability to control their behavior for the benefit of future goals (Best, Miller, & Jones, 2009; Crone, Bunge, van der Molen, & Ridderinkhof, 2006; Cragg & Nation, 2008; Huizinga, Dolan, & van der Molen, 2006). (p. 123) Developmental studies have converged on the conclusion that increased capacity for self-regulation may be associated with maturation of the prefrontal cortex (PFC) and its connections to other brain areas (Gogtay et al., 2004). Prior studies showed that the regions important for mental flexibility and performance

adaptation, including the PFC, parietal cortex, and anterior cingulate cortex (ACC), become increasingly engaged across childhood and adolescence (Crone, Zanolie, van Leijenhorst, Westenberg, & Rombouts, 2008; van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008). These studies are consistent with results from a wider range of cognitive control paradigms, which have reported that developmental changes in cognitive control functions are associated with more focal and increased magnitude of activation in brain regions important for cognitive control in adults, including the lateral PFC, parietal cortex, and ACC (for a review, see Chapter 4 in this book). Self-regulation is thought to be central to human cognition, and therefore adolescence can be seen as a period of significant cognitive advancements.

These advances in self-regulation abilities in adolescence, however, are accompanied by pronounced changes in emotional and social behavior. The main developmental task during adolescence is the formation of self-identity with a particular focus on social relationships. Adolescents are increasingly self-conscious and become more focused on their social behavior and emotions, which is accompanied by more complex peer relationships. Scientists have began to examine and understand these changes in terms of brain maturation, brain function, and cognitive, emotional, and social development, which has led to biological models that provide a framework for understanding changes in development that are specific for adolescence.

This chapter will highlight these new insights with a focus on brain maturation vis-à-vis developmental changes in reward processing, risk-taking, and social reasoning. We will propose a working hypothesis that integrates brain imaging data with behavioral studies and that may provide a unifying approach toward understanding this erratic period in life.

Emotion, Reward Processing, and Risk-Taking

The emerging self-regulatory abilities in adolescence work in concert or in competition with emotions that become more intense and erratic in adolescence and that affect emotional functioning and social reasoning. Since Stanley Hall defined *adolescence* as the period of storm and stress in development in the early 1900s, many scientists have been puzzled by adolescent-specific changes in emotion and social reasoning, as these are often unpredictable and subject to individual differences (Arnett, 1992).

Affective behaviour in adolescence has been widely studied using risk-taking paradigms, which is typically measured as choice behavior that can result in short-term gain but long-term loss. Learning to make good decisions and avoid excessive risks is one of the most important abilities to be acquired during development. In order to make good decisions, we have to be able to control our impulses, judge the probability that we will be successful, and weigh the risk involved against the potential benefit. Adolescents perform well on risk-taking tasks that require the simple evaluation of probabilities (van Leijenhorst, Westenberg, & Crone, 2008). Developmental studies have demonstrated that adolescents become better at delaying gratification (Scheres et al., 2006), and the ability to weigh short-term against long-term benefits has been shown to improve throughout adolescence (Crone & van der Molen, 2004; Hooper, Luciana, Conklin, & Yarger, 2004).

It has been suggested that the heightened sensitivity to rewards is associated with increased sensitivity and vulnerability of subcortical brain regions in adolescence, which is most likely the result of biological changes that affect brain functioning (Casey, Getz, & Galvan, 2008). Specifically, gonadal hormones associated with the onset of puberty may have a modulating effect on subcortical brain regions, resulting in increased approach and/or avoidance behavior, whereas cortical development and function follows a developmental pattern independent of hormonal changes (Steinberg et al., 2008). There is compelling evidence from animal models that gonadal hormone changes in puberty induce a (second) organizational period that serves to guide the remodeling of the adolescent brain in sex-appropriate ways (Sisk & Zehr, 2005; Spear, 2009). Results derived from rodent studies indicate a remodeling of the dopaminergic system within the affective subcortical brain network which involves an initial postnatal rise starting in preadolescence and a subsequent reduction of dopamine receptor density in the striatum and prefrontal cortex. As a result, dopaminergic activity increases significantly in early adolescence and is higher during this period than before and after it (Sisk & Zehr, 2005; Spear, 2009). (p. 124) Given the important role of dopamine in the brain's reward circuitry, this redistribution of dopamine receptors may increase reward-seeking behavior in puberty and thus affect executive and self-regulatory functions.

This model has received initial support from empirical studies in which functional brain activation in children,

adolescents, and adults was compared using risk or reward-seeking paradigms. Consistent with the assumption that risk-taking is associated with increased self-regulation and control, a set of studies by Ernst and colleagues demonstrated protracted development of brain regions important for self-regulation and cognitive control in risk-taking studies across adolescence (Ernst & Fudge, 2009; Ernst, Pine & Hardin, 2006; Eshel, Nelson, Blair, Pine, & Ernst, 2007). Eshel et al. (2007) examined behavioral and neural responses in a Wheel-of-Fortune task, in which participants chose between high-probability and low-probability gambles. A risky choice was defined as a choice from a low-probability option that could result in high reward, whereas a non-risky choice was defined as a choice from a high-probability option that would result in a smaller reward. The behavioral results demonstrated that adolescents were more willing to choose the risky option than the adults. When taking risks, increased activation in lateral PFC and ACC was observed, but this activation was more pronounced for adults than for adolescents. Thus, it may be that adolescents recruit prefrontal control areas to a lesser extent than adults when they take risks.

In a different set of studies, risky-choice evaluation was found to be associated with not only protracted development of PFC but also heightened sensitivity of brain regions important for reward processing. The heightened reward sensitivity was demonstrated in an fMRI experiment by Galvan et al. (2006) in which participants ranging in age from 7 to 29 years performed a task in which they could win small, medium-size, or large rewards. Using a pirates cartoon task, Galvan et al. asked participants to press the button at the location where a pirate appeared, which was then followed by a monetary reward (finding the treasure). Three different pirates resulted in three different reward magnitudes (small, medium, large). In response to receiving rewards, individuals in mid-adolescence (13–17 years) showed enhanced responses in the nucleus accumbens, which is part of the neural reward circuitry, relative to children (7–11 years) and adults (23–29 years). This region had previously been shown to play an important role in processing rewards and motivating behavior in adults (Knutson, Adams, Fong, & Hommer, 2001; McClure, Berns, & Montague, 2003). In addition, Galvan et al. correlated real-life risk-taking indices, such as the Cognitive Appraisal of Risk Activities Scale and Connor's Impulsivity Scale, to neural activation in the pirates task described above. They demonstrated that those individuals who are likely to engage in risky activities in real-life show enhanced neural responses to reward in the nucleus accumbens (Galvan, Hare, Voss, Glover, & Casey, 2008). The authors interpreted this effect as indicating that those individuals who are prone to risky behavior are at further risk in adolescence when neural systems underlying risky behavior go through developmental changes (see also Ernst et al., 2005).

It should be noted that the opposite results have also been reported. Bjork et al. (2004) reported that adolescents show underactivation in the nucleus accumbens when faced with potential rewards, and no age differences were observed when study participants were receiving reward. According to these authors, adolescents need more stimulation to get the same rewarding experience as that of adults. We performed two studies in our laboratory which aimed to further investigate this apparent inconsistency. Our hypothesis was that it matters what the task demands are, given that the Galvan et al. study required simple reward prediction and outcome processing, whereas the Bjork et al. study required more complex reward prediction. In a first study, we took out all behavioral demands and asked participants to perform a passive slot machine game. Here we found that when faced with slot machine rewards, mid-adolescents show heightened activation in the nucleus accumbens to rewards, more so than early adolescents and adults. We concluded that the elevated reward sensitivity in adolescence is a relatively basic sensitivity and that this neural response occurs independently of whether participants need to perform accurately to receive the reward (van Leijenhorst et al., 2010a).

Click to view larger

Figure 8.1 Enhanced neural activation in the striatum following reward in the cake gambling task. Between–age group contrasts show elevated activation in the caudate nucleus in adolescents aged 12–14 and 16–17 relative to that in children aged 8–10 and adults aged 19–26 (age–reward interaction). Images are displayed for each age group at *p* < .005 uncorrected (van Leijenhorst et al., 2010).

Subsequently, we examined whether and how adolescents were sensitive to outcomes after taking a risk. First, we were interested in examining whether the elevated reward sensitivity reported in two passive gambling tasks (Galvan et al., 2006; van Leijenhorst et al., 2010a) would also be found when adolescents were actively judging

probabilities and taking risks, followed by outcomes. We were also interested in understanding the specificity of this elevated sensitivity, as adolescence has often been broadly defined, whereas there are pronounced (p. 125) differences between phases of development (Giedd et al., 2006). For this reason, participants from four age groups (8–10, 12–14, 16–17, 19–26 years) were asked to play a risk-taking task (referred to as the cake gambling task) while functional MRI data were collected. The behavioral data demonstrated that all participants were sensitive to rewards, and increased risk-taking was observed when more rewards were at stake. The neuroimaging data demonstrated that, in individuals of mid- and late adolescence (12–14 and 16–17 years), there was increased neural response in the striatum to rewards that followed risky gambles (see Figure 8.1; van Leijenhorst et al., 2010b). The elevated neural response in the striatum was reported in several studies and was found specifically for mid- and late adolescence. Future studies should examine how these changes are related to task performance, for example, by predicting performance on the basis of observed neural activation.

Intriguingly, the same pattern of subcortical hypersensitivity in adolescence has been observed for negatively valenced stimuli. Using an emotional go/no-go task, Hare and colleagues (2008) asked 7- to 12-year-old children, 13- to 18-year-old adolescents, and 19- to 32-year-old adults to respond or inhibit their responses, based on the valence of a presented face. These faces could have fearful, calm, or happy expressions. All participants showed activation in the amygdala following the presentation of fearful faces, but this neural activation was increased in adolescents relative to that in children and adults. Greater amygdala activation was associated with lower trait anxiety scores, confirming that the amygdala response was associated with level of anxiety. These findings extended earlier results by Monk et al. (2003), who demonstrated that adolescents ages 9 to 17 have greater activation in the amygdala, relative to that in adults ages 25 to 36, to fearful than to neutral faces. In addition, a study by Guyer et al. (2008) also found that 9- to 17-year-old adolescents have an elevated amygdala response to fearful faces, and that adults have increased amygdala–hippocampus connectivity when viewing fearful faces. The latter effect was interpreted in the context of a strengthening with age of memory storage and retrieval for emotionally salient stimuli.

Taking these findings together, it is clear that the slowly maturing PFC hypothesis cannot explain all changes in affective behavior; developmental changes in adolescence are associated with competition between at least two brain networks. The first, evolutionary older system builds on subcortical structures that have been linked to the processing of emotion, such as the amygdala and the nucleus accumbens; whereas a second, evolutionary younger system builds on cortical brain areas, including the PFC and the parietal cortex (Adolphs, 2003). Developmental changes in risk-taking are most likely associated with different developmental trajectories of these systems (Casey et al., 2008; Rivers, Reyna, & Mills, 2008; Steinberg, 2008). The slow development of brain regions important for cognitive control and self-regulation, together with the faster development of brain regions subserving reward sensitivity, may result in a fragile balance between emotional impulses and cognitive control.

Social Reasoning

Although the fragile-balance hypothesis provides a starting point for understanding erratic behaviour in adolescence, it is clear that emotional impulses toward rewards, risks, and aversive stimuli are not the only factor in explaining adolescent behavior. One of the more evident changes in adolescence is that adolescents form and interact in an increasingly complex social environment. During adolescence, friendships change and peers become increasingly important. Not only do adolescents spend more time in the presence of peers, but the opinions of peers also become more important (Harris, 1995). (p. 126) Indeed, in an experimental study on the influence of peers on risk-taking, adolescents showed high sensitivity to the presence of peers by making a disproportionately greater number of risky decisions when they were with their peers (Gardner & Steinberg, 2005).

The increased sensitivity to rewards in the presence of peers led us to hypothesize that basic approach and avoidance sensitivities in adolescence may also account for sensitivity to social context. For example, it has been demonstrated that brain regions responding to feelings of envy and schadenfreude are also those that respond to physical pain and reward/pleasure, respectively (Takahashi et al., 2009). We hypothesized that increased capacity for making inferences about mental states of others influences choice behavior in adolescents, which may be associated with additional brain systems that come online during adolescence (Blakemore, 2008). We propose that heightened sensitivity in adolescence to social evaluation and reasoning results from heightened sensitivity in subcortical limbic regions, together with slow maturation of brain regions important for intention

understanding.
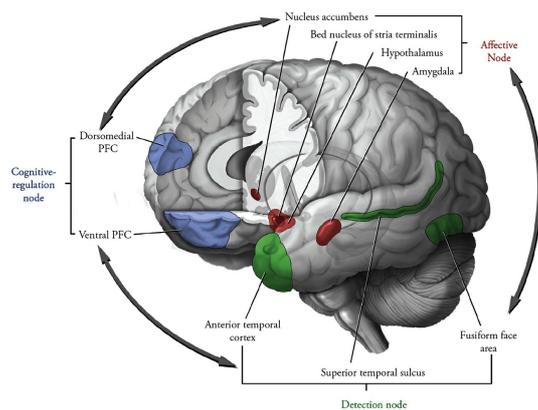
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Figure 8.2 The social information processing network (Nelson et al., 2005). Reprinted with permission from Cambridge University Press.

Recently, brain models used to explain the emotion–cognitive balance in the developing brain have been extended by taking into account brain networks that facilitate our understanding of others and mentalizing about intentions. One of these models is the Social Information Processing Network (SIPN) model, which focuses specifically on developmental changes across adolescence (see Figure 8.2; Nelson, Leibenluft, McClure, & Pine, 2005). The SIPN model incorporates physiological and hormonal changes at puberty with developmental changes in brain circuits to explain normal and pathological social behavior across adolescence. The model is based on three basic nodes: the detection node, the affective node, and the cognitive node. The detection node is composed of brain areas such as the inferior occipital and temporal cortex (including the fusiform face area and the intraparietal gyrus), related to the perception and categorization of a stimulus based on its "social" properties. The function of this node is to determine the extent to which one can socially interact with the stimulus, depending on what the stimulus is doing or intending to do. Once a stimulus has been detected and categorized as being, for example, animate and (p. 127) social, the affective node, composed of the reward–punishment related brain areas such as the striatum, amygdala, hypothalamus, and the orbitofrontal cortex, is activated in order to determine the emotional valence of the stimulus. The emotional significance attached to the stimulus is crucial for the subsequent response, which is regulated by the third, cognitive, node. This cognitive node, composed of the PFC as well as the paracingulate and the temporal cortex, is more complex in terms of its broader regulatory function. It plays a role in perceiving the thoughts, goals, and feelings of others (i.e., the theory of mind [TOM]; see Chapter 13 in this book), executing control over prepotent responses, and planning and executing goal-directed behavior.

Nelson and colleagues (2005) have proposed that the hormonal and neural changes within the SIPN model are intermittently related to the socioemotional and behavioral changes across adolescence. Whereas the detection node matures quite early in life, the affective node experiences major changes with the onset of puberty. As in previously named models (e.g., Casey et al., 2008; Ernst et al., 2006), the hormonal changes during puberty alter regulation of the neurotransmitter systems involving oxytocin, vasopressin, serotonin, and dopamine, resulting in changes in social and emotional responsiveness. The changes in the affective node are reflected in social behavior in adolescence, particularly in terms of emotional responses to social stimuli such as increased reward sensitivity (Steinberg, 2007, 2008). Finally, the cognitive node is characterized by a prolonged trajectory of maturation that extends into late adolescence. The ventral and medial prefrontal regions and the superior temporal cortex, which underlie TOM-related functioning, mature across adolescence (Choudhury, Blakemore, & Charman, 2006). The late development of the prefrontal and temporal brain regions might explain the increase in executive functioning and perspective-taking skills into late adolescence and early adulthood (Blakemore & Choudhury, 2006; Blakemore, den Ouden, Choudhury, & Frith, 2007).

In a set of experiments, we tested this hypothesis, with a special focus on perspective-taking and regions previously implicated in mentalizing about one's own and others' intentions. Studies with healthy participants confirmed the role of mentalizing brain regions, such as the medial prefrontal cortex (MPFC) and the posterior superior temporal sulcus (pSTS)/temporaparietal junction (TPJ), during social emotion processing (Burnett, Bird, Moll, Frith, & Blakemore, 2009). The increasing perspective-taking skills that enable incorporation of intentionality

understanding are of great importance in social decision-making processes across adolescence. We tested these social emotions, which accompany decision-making processes in social interactions, by studying the development of interpersonal concepts such as fairness, trust, and reciprocity. Economic game paradigms, including the Ultimatum Game (UG) and the Trust Game (TG), prove efficient in this investigation because of their feasibility in simple two-person interactions that can also be simulated in neuroimaging studies.

Ultimatum Game and the Role of Insula, TPJ, and DLPFC

In the UG, a proposer has the opportunity to divide a certain stake (e.g., 10 dollars) between him- or herself and another player. After the proposer has made an offer, the responder has two possibilities: accept the offer, in which case the stake will be divided as proposed by the first player, or reject the offer made by the proposer, which results in both players going empty handed. Thus, the UG provides the opportunity to examine the role of self-interest relative to fairness. That is, according to economic principles, the responder should never reject, because then both players would not receive anything. However, unfair splits are often rejected, indicating that choices are based not only on self-interest only but also on feelings of fairness and the aversion of inequity (De Dreu, Lualhati, & McCusker, 1994; van Dijk & Vermunt, 2000).
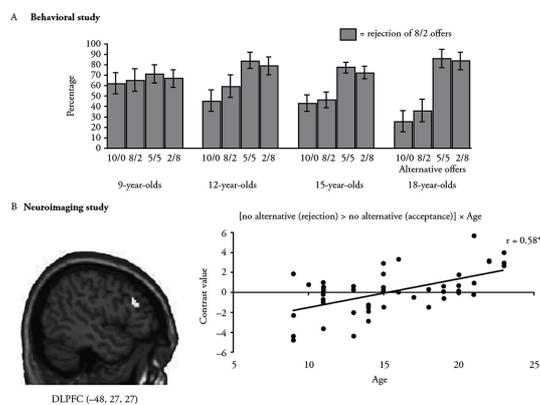
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Figure 8.3 A. In the mini-Ultimate Game, there is a steady age-related increase in the ability to understand intentionality (Güroğlu et al., 2009). **B**. In the no-alternative condition (8/2 vs. 8/2 offer), an age-related difference emerges in recruitment of dorsolateral prefrontal cortex (DLPFC) such that the older adolescents and the adults show increased activation for reject > accept (Güroğlu et al., 2011).

We were interested in understanding how adolescents are sensitive to fairness and the increasing role of perspective-taking abilities in judging fairness, as well as the neural underpinnings. In order to better incorporate intentionality understanding and perspective-taking skills, we used an alternative version of the UG, referred to as the mini-UG (Falk, Fehr, & Fischbacher, 2003). In this setup, proposers had to choose between two predetermined distributions of the stake (10 coins) and select one of the two offers; the responders, in turn, were informed about the available options for the proposers and could decide whether to accept or reject that offer (Güroğlu, van den Bos, & Crone, 2009). We manipulated intentionality by using four conditions against which an unfair distribution of the stake (i.e., 8/2 distribution, with 8 coins for self versus 2 coins for the responder) was pitted: (1) hyperunfair alternative (i.e., 10/0 distribution), (2) no alternative (i.e., 8/2 distribution), (3) fair alternative (i.e., (p. 128) 5/5 distribution), and (4) hyperfair alternative (i.e., 2/8 distribution). Intention understanding was studied by examining the proportion trials on which responders rejected an unfair 8/2 division when this offer was pitted against one of the four alternatives. The behavioral findings showed that 9-year-olds did not make any differentiation between intentionality conditions: rejection rates of unfair 8/2 offers were independent of the alternative distribution available to the proposer (see Figure 8.3A). Intentionality considerations were already incorporated into decision-making by age 12 such that rejection of unfair offers was lower in the hyperunfair- and no-alternative conditions than in the fair- and hyperfair-alternative conditions. However, there was a linear age-related increase in acceptance of unfair 8/2 offers when the proposer did not have a better alternative (8/2 vs. 8/2). In other words, changes in fairness considerations in social interactions were related to the development of intentionality understanding and perspective-taking skills across adolescence (Güroğlu et al., 2009).

In an fMRI study including adults, we demonstrated that the mentalizing brain regions, such as the medial PFC and

TPJ, as well as subcortical brain areas, such as the insula and ventral striatum, were differentially sensitive to the social-context manipulations (Güroğlu, van den Bos, Rombouts, & Crone, 2010). The results replicated prior reports showing high insula activation during UG performance, especially when participants made choices that were against the norm (acceptance of unfair 8/2 offers when the proposer has a fair alternative, and rejection of unfair 8/2 offers when the proposer has no alternative). Of most interest was the role of the TPJ in intention understanding, which was most evident in the no-alternative condition. That is, rejecting an unfair 8/2 offer when the proposer had no alternative was associated with elevated activation in the TPJ, a region thought to be related to mentalizing and the shifting of attention from self to other (Decety & Lamm, 2007; Mitchell, 2008). Thus, the UG manipulations were successful in identifying brain regions sensitive to violation of personal norms and to intention understanding and perspective-taking.

Next, these data were complemented with fMRI data from children (mean age = 10), early-adolescent (p. 129) individuals (mean age = 13), and mid-adolescent individuals (mean age = 15) relative to young adults (mean age = 20) (Güroğlu, van den Bos, van Dijk, Rombouts, & Crone, 2011). Similar to what was found in the adult data, the insula was involved in UG performance, such that the insula was sensitive to the violation of personal norms, in children and adolescents. Again, the no-alternative condition, which is though to rely most on perspective-taking skills, yielded an interesting age–response interaction. This time, the most striking age differences were observed in dorsolateral prefrontal cortex (DLPFC), a brain region thought to be important for response selection and impulse control (Miller & Cohen, 2001) and which has previously shown to be highly sensitive to developmental change (Bunge & Wright, 2007), as well as in the TPJ. In the current paradigm, mid-adolescent individuals and young adults demonstrated higher DLFPC and TPJ activity during rejection of unfair 8/2 offers than when accepting these offers (see Figure 8.3B; Güroğlu et al., 2011). We interpreted these findings as showing that adolescent development is associated with increased cognitive control (as indicated by increased DLPFC activation) and increasing intentionality understanding (as indicated by increased TPJ activation).

Trust Game and the Role of MPFC, TPJ, and DLPFC

One brain region that has been implicated in mentalizing about self and other is the MPFC, although the role of the MPFC in development is not yet well understood. In a study where participants were asked to identify irony in cartoon drawings, children engaged the mPFC more than adults, whereas there was a shift toward activation in posterior regions in adults (Wang, Lee, Sigman, & Dapretto, 2006). Others have also reported increased MPFC activation in adolescents relative to that in adults (Blakemore, 2008; Pfeifer, Lieberman, & Dapretto, 2007). The heightened activation in MPFC in adolescence has been interpreted as increased self-referential processing in adolescence, based on prior literature showing that MPFC is mainly sensitive to self-oriented thoughts (Amodio & Frith, 2006).

We tested this hypothesis using a social decision-making paradigm in which self-referential thoughts and actions are most evident. This set of studies made use of the Trust Game (TG), in which one player (the trustor) is given a sum of money that he or she can divide between him- or herself and a second player, or the first player can decide to trust the money to the second player. In the latter case, the money is tripled and the second player has the possibility of reciprocating the trust by splitting the money between him- or herself and the trustor, or to keep all the money. If a second player does not reciprocate, this decision might be interpreted as self-serving. We tested the role of MPFC when trust was not reciprocated in the participants aged 12–14 years, 15–17 years, and 18–25 years while they played the TG as the second player (i.e., as trustee). As anticipated, abandonment of trust resulted in elevated activation in anterior MPFC (aMPFC) in adults and older adolescents. In contrast, in young adolescents (12–14 years), the aMPFC was increased for both the trust-abandoned and trust-reciprocated trials, which could be interpreted as broader self-referential processing (van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2009, 2010). These findings were accompanied by elevated activation in TPJ and DLPFC for older adolescents and adults relative to that in younger adolescents when receiving trust.

Similar results were found in another study that examined the neural correlates of perspective-taking and intentionality understanding. In this study, the posing of questions regarding intentional causality of situations compared to physical causality resulted in higher MPFC activity in adolescents than adults (Blakemore et al., 2007). These findings present converging evidence suggesting that the brain networks supporting understanding of intentionality and higher order perspective-taking develop across adolescence and shift from anterior (aMPFC) to

posterior brain regions (pSTS/TPJ).

Conclusion

In this chapter, we discussed the development of emotion and social reasoning in adolescence and their mediation by functionally different brain networks. Current models of adolescent brain development suggest slow development of prefrontal and parietal cortex regions, which are important for impulse control and intention understanding, together with elevated sensitivity of subcortical brain regions (Blakemore, 2008; Casey et al., 2008; Nelson et al., 2005). This claim is supported by longitudinal studies demonstrating protracted development of cortical brain regions in terms of gray matter volume (Gogtay et al., 2004), by animal research suggesting that gonadal hormones induce increases in dopaminergic activity that influence affective subcortical brain systems (Quevedo, Benning, Gunnar, & Dahl, 2009; Sisk & Zehr, **(p. 130)** 2005; Spear, 2009), and by recent functional MRI studies providing initial evidence for this fragile balance between reward processing and social reasoning (Galvan et al., 2006; Güroğlu et al., 2009; van Leijenhorst et al., 2009).

In this chapter, we have demonstrated that adolescence is a time period of significant improvement in self-regulation, but it is also marked by vulnerabilities to affective input or social context. Although steady improvements are observed between childhood and adulthood in the ability to perform cognitive tasks, the developmental changes in emotion regulation and social competence have been found to follow complicated nonlinear age patterns. In particular, functional neuroimaging studies have shown that adolescent development is typically characterized by immature PFC activity (important for cognitive control and intelligent behavior) and enhanced responses in subcortical affective systems (important for emotional responses). Such activity suggests an intensification of emotional experience and an immature capacity of affective regulation and self-control in adolescence (Galvan et al., 2006; Hare et al., 2008). In future studies, it will be important to also examine within-subject changes and to identify early on those adolescents who are at risk for vulnerability to real-life risks (Galvan et al., 2008) or psychiatric disorders (Paus, Keshvan, & Giedd, 2008).

We suggest that the development of emotional functioning in adolescence and the underlying neural architecture that subserves these changes can also be applied to the domain of social reasoning. Previous studies examining changes in social functioning have used complex tasks that are difficult to disentangle and that leave open the question the means by which functional maturation of brain regions subserves the development of social reasoning. In this chapter, we illustrated how an experimental approach in which relatively simple social interaction games are presented in different conditions allows us to draw conclusions about specific changes in development. We also demonstrated the involvement of distinguishable brain networks which make differential contributions to the development of social reasoning. Thus, models of emotion development can be articulated further by taking into account the role of social factors in development. The task for future research is to gain converging evidence from behavioral, hormonal, neuroimaging, and connectivity analyses, which may provide a working model for the functionally segregated and emerging connectivity between brain regions that may account for adolescent development, as well as developmental changes in various aspects of emotional and social processing.

Most studies examining social decision-making processes focus on simulations of social interactions with anonymous others. Findings from economic-game paradigms such as the Ultimatum Game and the Trust Game rely on single-shot exchanges with interaction partners, neglecting the relationship aspect of real-life social interactions. Repetition of such interactions builds relationships over time that are closely related to many aspects of socioemotional well-being (Baumeister & Leary, 1995). Patterns of brain activity related to social interactions with familiar partners might be related to specific relationship characteristics that develop over time. This interplay between relationships and neural activity has been neglected because of the difficulties related to simulating real-life social interactions within the scanner. One example of such an attempt is a study implementing a social-interaction simulation task to examine the neural correlates of friendships (Güroğlu et al., 2008). In this study, emotion processing as well as empathy-related brain networks were particularly activated during social interactions with friends. Future studies need to focus on examining the mechanisms related to relationship patterns in order to better understand the neural basis of social behavior.

One of the challenges for future research is to further understand why, when, and how behavior is more erratic in adolescence than during other stages in life. Future studies should focus on the interplay between developmental,

cognitive, emotional, and social neuroscience studies in order to examine how brain development contributes to the emergence of the many complex skills we use in daily life. In addition, future studies should identify not only the risks but also the opportunities of this highly potential developmental period in life.

Acknowledgments

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