The neurocognitive development of social decision-making

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9. Summary and Future Directions

9.1 Introduction

The research described in this thesis concerned the development of functionally defined brain networks underlying important aspects thought to drive developmental changes in adolescent social decision-making. Developmental theories suggest that the changes in adolescent social decision-making are related to increasing capacities for: (1) perspective-taking (Eisenberg et al., 1995; Elkind, 1985), and (2) the regulation of social behavior (Steinberg, 2009). More recently it has been shown that these developmental changes in social decision-making are paralleled by substantial changes in brain structure (Giedd et al., 1999). Neurodevelopmental models hypothesize that changes in brain structure and social behavior are mediated via changes in brain function (Blakemore, 2008; Johnson, 2011).

Current neuroscientific models of interactive social decision-making suggest that there are multiple systems that contribute to social behavior; a specific 'social brain' network involved in understanding others' beliefs and intentions, and brain networks with a more general role in the monitoring and adaptation of behavior (Sanfey, 2007). Additionally, there is evidence that there are developmental changes in the activation patterns within these networks across adolescence (Blakemore, 2008; Sommerville & Casey, 2010)

The experiments in this thesis set out to test the hypothesis that the age-related changes in perspective-taking and self-regulation are associated with developmental changes in respectively the 'social brain' network, and the networks involved in the monitoring and regulation of behavior.

The first empirical study described in **Chapter 2** had two main goals: (1) to develop a new version of the Trust Game that enabled us to examine the developmental trajectory of trust and reciprocity during adolescent development, and (2) to examine the extent to which these processes are sensitive to social perspective-taking skills as measured by the risk and benefit manipulations. Participants of four age groups between 9 and 25 years participated in this study. For this study, a child friendly Trust Game paradigm was designed to capture individual and developmental differences in perspective-taking. To examine the role of perspective-taking, experimental manipulations were added to the original Trust Game that revealed whether participants were taking the intentions of others, and consequences for others, into account (cf. Pillutla et al., 2003; Malhotra, 2004). All participants played multiple rounds of the Developmental Trust Game, in the roles of player 1 and 2, with a different anonymous other player each round. As anticipated, the results demonstrated that during development there was a general increase of both trust and reciprocity. The results of this study also demonstrated that developmental differences in trust and reciprocity depended on the extent to which the other person's perspective was taken into account. Although all age groups were more willing to trust when the risk was low rather than high, there were age related changes in sensitivity to the benefit of the other player in trust decisions; only the oldest participants were more willing to trust when the benefit for player 2 was high. Similarly, all age groups, except the youngest, were more willing to reciprocate when the benefit was high. However, only from mid adolescence onwards were participants also more willing to reciprocate when the risk for player 1 was high. The age differences in sensitivity to risk and benefit for trust and reciprocity support the hypothesis that besides a general increase of prosocial behavior, considering the outcomes for the other becomes important in social decision-making during adolescent development.

Chapter 3 describes the second empirical study with the Developmental Trust Game. The goal of this study was to investigate the neural correlates of reciprocity motives in brain regions that have previously been associated with mentalizing (aMPFC, TPJ), affective processes (ventral striatum and insula) and regulation of selfish impulses (ACC, DLPFC) in social behavior. This study was inspired by the previous findings that decisions to reciprocate trust are not only motivated by personal outcome considerations but also involve considerations of the intentions of others, and the general tendency of individuals to value the outcome of others (McClintock and Allison, 1989; de Dreu and van Lange, 1995; van Lange et al., 1997). In this study, young adults between 18 and 22 years of age were the second player in the Developmental Trust Game while fMRI data were collected.

As expected, the behavioral results showed that participants reciprocated more when the first player took a high risk to trust, indicating that participants took the consequences for the other into account. The imaging analyses revealed that two important areas of the social brain network, the aMPFC and right TPJ (Frith and Frith, 2003) have separable functions in reciprocal behavior. Consistent with previous studies, the aMPFC was more active when participants defected compared to when they reciprocated (Gallagher et al., 2002; Decety et al., 2004). This result is consistent with the hypothesis that the aMPFC is important for self-referential processing (Northoff et al., 2006; Ochsner, 2008). In contrast to the aMPFC, the right TPJ was not sensitive to the type of choice but was sensitive to the risk manipulation when reciprocating. This result indicates that the right TPJ is involved in the shifting attention from the self to the other (Lamm et al., 2007), i.e. perspective-taking.

Further analyses showed that the ACC and the right DLPFC were most active when social impulse control was required; both these areas were activated when participants reciprocated even though the benefit of being trusted was low. In other words, when the external incentive to reciprocate was low, the ACC and the right DLPFC were more engaged in reciprocal decisions.

Finally, further analyses demonstrated that activity in the insula was sensitive to individual differences in social value orientation. The insula was more active when prosocial participants defected and more active when proself participants reciprocated. Additionally, the insula showed sensitivity to the risk manipulation; it was more active on those trials where participants chose to reciprocate when the risk that the first player took was low. Taken together, these results indicate that the insula was most active when a norm was violated (which can be a reciprocate norm for prosocial individuals or a defect norm for proself individuals, Singer et al., 2006; Montague and Lohrenz, 2007).

Chapter 4 aimed at understanding the neurodevelopmental differences in the brain areas involved in reciprocal exchange and perspective-taking. To test the neural correlates of reciprocating behavior during adolescence, a neuroimaging study was performed with the Developmental Trust Game that included adolescents and adults between ages 12 and 22 years. Using the same Developmental Trust Game the developmental changes in neural correlates of perspective-taking in reciprocal behavior were investigated.

The results of this study revealed that with age, adolescents were increasingly sensitive to the perspective of the other player as indicated by their reciprocal behavior in the different risk conditions. Furthermore, these advanced forms of perspective-taking were associated with an increased involvement of the left TPJ when being trusted. In contrast, the aMPFC was more active for the youngest participants. These results are consistent with recent developmental studies that indicated that there is an age related shift in relative contribution of the aMPFC and the TPJ during theory-of-mind tasks (e.g. reading stories, thinking about others; Wang et al., 2006; Pfeifer et al., 2007; Blakemore, 2008). Additionally, these results support the hypothesis that this shift in balance from aMPFC to TPJ is related to a decrease in self-referential thought and an increased focus of attention on the other in social decision-making.

This study also revealed that young adults, when receiving trust, showed increased activity in the right DLPFC, an area previously found to be involved in tasks requiring cognitive control (Miller & Cohen, 2001) and the control of selfish or self-oriented impulses in the context of social dilemmas (Rilling et al., 2007). More importantly, there was an age related increase in DLPFC activity that was also related to advanced forms of perspective-taking, suggesting improved regulation of social behavior with increasing age.

Finally, this study again showed that the insula was sensitive to personal norm violations. However, in contrast to the changes in the social brain network, activity in this area did not show developmental differences, indicating this network matures at an earlier age.

In the subsequent chapter (**Chapter 5**) the neuro-developmental changes in another type of social decisions were investigated; fairness considerations. This research was inspired by prior behavioral studies that demonstrated that there are important developmental changes in perspective-taking related to fairness considerations until late adolescence (Sutter, 2007). For example, in a study using the mini-Ultimatum Game the youngest participants (9 years) were more likely to reject than to accept unfair offers, even when the proposer could not have chosen otherwise. In contrast, older participants (18 years) were more likely to accept unfair offers in that situation (Güroğlu et al., 2009).

The developmental neuroimaging study using the mini-Ultimatum Game investigated the neural correlates of age differences in fairness considerations in participants between ages 10 and 20. Consistent with prior behavioral studies, participants rejected unfair proposals when the alternative for the proposer was a fair division (Güth et al., 2008). This behavior has previously been reported in children and adults, and shows that inequity aversion motivates fairness judgment already in late childhood and early adolescence (Fehr et al., 2008; Güroğlu et al., 2009). However, children demonstrated high rejection rates for unfair offers even when the proposer did not have a fair alternative, and this rejection rate gradually dropped over the course of adolescence. These results indicate that there was an increasingly important role for taking the perspective of the other person in fairness judgments. Furthermore, the imaging analyses revealed that TPJ activity was associated with intention considerations, and that there was an age related increase in TPJ activation. Additionally, besides the TPJ, the DLPFC was also more active in adults than in children, when considering unintentional unfair offers. Finally, participants of all ages showed activation in the bilateral insula related to norm violations.

In sum, consistent with the results of the study with the Developmental Trust Game, these findings provide evidence for an early developing affective network involved in detecting norm-violations and a gradually increasing involvement of temporal and prefrontal brain regions related to intentionality considerations and the regulation of social behavior.

The study described in **Chapter 6** had two main goals: (1) to examine the development of trust relationships between late childhood and young adulthood, and (2) to examine the developmental trajectory of emotions evoked by non-cooperative behavior of others, and to what extent these emotions may lead to altruistic punishment. To investigate developmental changes in adaptive social behavior we used a repeated Trust Game paradigm in which participants, between 11 and 25 years old, interacted with three different players for several rounds (King-Casas et al., 2005). Unbeknownst to the participant the other players were computer players, preprogrammed to display different levels of trustworthiness (low, medium and high). During the repeated interactions the participants were in the role of the first player, thus, each round they had to decide whether or not to trust the other.

The data showed that adult participants often chose to trust in the first round, indicating that they expected others to reciprocate (e.g. Berg et al., 1995). In contrast, children showed a lower level of initial trust; most of them started with not trusting the other. However, for all age groups the strategy of the other player influenced the percentage of trust choices; over time all participants learned who to trust and who to distrust. Interestingly, our analyses also revealed developmental changes in strategies and adaptive behavior; all participants played a tit-for-tat type of strategy, but the children used the strictest form of tit-for-tat strategy compared to the other age groups. Further analyses revealed that children differed from adults and adolescents especially in showing higher levels negative reciprocity, thus being more sensitive to violations of trust.

Next, we investigated the relation between trust violations and participants' emotional reactions and their level of punishment. As expected, the different levels of trustworthiness displayed by the other players evoked different levels of both anger and punishment. Participants of all age groups were most angry at the player that violated trust the most and punished accordingly. Additionally, the results showed that with increasing age the amount of both anger and punishment decreased, and that age differences in trust were fully mediated by feelings of anger. Together these results indicate that the stability of adult trust relationships might be the result of an age related increase in regulation of negative affect towards violations of trust.

The studies in chapters 7 and 8 were inspired by (1) recent neuroimaging studies of social interactions that have shown that brain areas that are involved in performance monitoring are also involved in tracking and predicting the social behavior of self and other players in multi-round Games (Delgado et al., 2005; King-Casas et al., 2005; Behrens et al., 2009), and (2) developmental studies showed that monitoring and regulating behavior based on feedback signals undergoes pronounced developmental improvements between late childhood and early adulthood (Crone & van der Molen, 2004; Hooper et al., 2004). Therefore, further understanding of the age related changes in the neural mechanisms of adaptive behavior is useful for understanding developmental changes in the fundamental systems that are shown to support adaptive social behavior in multiple interactions.

In **Chapter 7** we used functional magnetic resonance imaging (fMRI) to examine the neural developmental changes when processing positive and negative feedback signals in a probabilistic decision-making task. This study was inspired by several previous studies that suggested that the neural mechanism underlying adaptive learning based on feedback signals undergo developmental changes until early adulthood (Crone et al., 2008; van Duivenvoorde et al., 2008). The study was specifically set up to test whether this developmental difference is related to valence or informative value of the feedback by examining neural responses to negative and positive feedback while applying probabilistic rules. Healthy volunteers between ages 8 and 22 years old participated in the study.

Behavioral analyses revealed that all participants learned to choose the correct rules (high probability stimuli A&C) more often than the alternative rules (low probability stimuli B&D) (Frank et al., 2004; Klein et al., 2007). After approximately 40 trials, participants adapted a performance pattern consistent with ‘probability matching behavior’, and this behavioral phase, consisting of the last 60 trials, was the focus of the first set of analyses. Although probability matching behavior occurred in all age groups and there were no age differences in overall accuracy, there were age differences in win-stay, lose-shift strategies. Sequential analyses revealed that the children applied a less optimal shifting strategy after negative feedback.

These age differences in decision-making strategy were paralleled by changes in functional brain activity. All participants, regardless of age, showed increased recruitment of DLPFC when choosing the alternative rule compared to the correct rule. However, children, but not adults, showed more activation in DLPFC after positive feedback when choosing the alternative rule. In contrast, adults, but not children, showed more activation in DLPFC after negative feedback when choosing the alternative rule. Thus, consistent with prior studies, these developmental differences indicate a shift from focus on positive to a focus on negative feedback with age (Crone et al., 2008; van Duivenvoorde et al., 2008; Somsen, 2007). Taken together, these findings suggest that developmental differences in neural responses to feedback in the DLPFC are not related to valence per se, but that there is an age related change in processing learning signals with different informative value.

Chapter 8 describes a follow up study that concerned the neural mechanisms that underlie developmental differences in adaptive probability learning. In this study, based on the same data and participants as Chapter 7, we used a reinforcement learning model to investigate neurodevelopmental changes in the representation and processing of learning signals during the complete task. In order to capture age related changes in learning from positive and negative feedback separately, we use a reinforcement learning model (Sutton & Barto, 1999) with separate learning rates for positive and negative feedback (Kahnt et al., 2009). The individually estimated trial-by-trial prediction errors generated by this reinforcement model were subsequently used to test whether developmental differences in learning reflect functional differences in the representation of prediction errors or developmental changes in the propagation of prediction errors as measured by functional fronto-striatal connectivity (Park et al., 2010).

The model-based analyses of learning behavior showed that, with age, there is a decrease in the learning rate for negative feedback. This finding indicates that with increasing age, the impact of negative feedback on the future expected value decreases. Subsequent analyses of imaging data revealed that, consistent with previous studies, trial-by-trial prediction errors generated by the reinforcement learning model correlated with activity in a network of areas including the ventral striatum, mPFC and the amygdala (Pagnoni et al., 2002; McClure et al., 2003; O'Doherty et al., 2003; Cohen & Ranganath, 2005). The analyses did not reveal any age related differences in prediction errors. In contrast, age related differences in feedback adjustment were associated with increased ventral striatum connectivity with the VMPFC. The pattern shifted from stronger connectivity after negative feedback for the youngest participants towards stronger connectivity after positive feedback for the oldest participants. These findings suggest that developmental changes in adaptive behavior are not due to differences in the computation of the learning signal, but rather related to changes in how the learning signal is subsequently used in adaptive behavior.

9.2 Conclusions and Future Directions

How can these results contribute to our understanding of the relation between the development of prosocial behavior and functional brain development? Since the specific implications of the studies have been discussed in detail in the respective chapters the general discussion will take a broader perspective, focusing on theoretical and methodological points that open avenues for future inquiries.

Child's play – Games as a proxy for social development

The first important finding of the studies presented here is that the two economic games, the Trust and Ultimatum Game, capture the increased capacity of perspective-taking in relation to changes in social behavior during adolescence (Güroğlu et al., 2009; van den Bos et al., 2010). Additionally, the study employing the iterative Trust Game revealed that children use a stricter tit-for-tat strategy compared to the other age groups, especially showing increased levels of anger and retribution following trust violations. These results support the hypothesis that developmental differences in social decision-making are related to differences in capacity to regulate social feedback.

Second, the studies also yielded novel insights in the development of social behavior. As Eisenberg has shown in an extensive meta-analysis (1987), there was only a mildly positive correlation between age and prosocial behavior. Hence, many studies did not find this relationship. This raises the question to what extent age related changes in display of prosocial behavior are context-dependent. The results of the collection of studies presented in this thesis, show that economic games can be useful to further investigate this question. For instance, the study with the Developmental Trust Game suggests that from mid-adolescence onwards there is no general increase in prosocial behavior but rather a 'sophistication' of prosocial behavior. Although trust and reciprocal behavior were at a stable level at mid-adolescence, there were still changes in the effect of the outcome manipulations until late adolescence. Thus, with age, prosocial behavior becomes more context dependent, leading to more prosocial behavior in one situation but less in another. Similarly, the analyses of multiple interactions showed that children and adults showed similar responses when trust was reciprocated, but that children were more sensitive to violations of trust. These are examples of how economic games can reveal how the differences in social behavior across development are dependent on the context.

Taken together, economic games are useful extensions of the researchers' toolbox for experimental research on the development of social behavior. In future studies, economic games can further contribute to structured investigation of prosocial behavior of children, adolescents, and adults.

Neurocognitive development

The imaging studies demonstrated asynchronous developmental patterns in the 'social brain' network. In general, the pattern demonstrated a faster maturation of the aMPFC but late maturation of the TPJ. Additionally, the results showed increased involvement of the regulatory network (e.g. DLPFC), and an early maturation of the network involved in monitoring norm violations (e.g. insula). Importantly, these changes were related to developmental changes in behavior as assessed by the various social decision-making tasks. As such, the results support the hypothesis that social development is related to developmental changes in different brain networks, especially those underlying perspective-taking and self-regulation. These findings provide further support for the theoretical perspective that poses that social development is driven by increased capacities for perspective-taking and self-regulation. The following sections will: (1) reflect on the possible nature of the changes in the respective networks in light of theoretical perspectives and frameworks of brain development, and (2) point out two general directions that can advance our understanding of developmental changes in brain function.

Changing brains, changing perspectives

The analyses of the 'social brain' network identified two different developmental patterns for the aMPFC and TPJ. The aMPFC shows a pattern of local specialization, that is, in early adolescence this area is engaged in both reciprocal and defect choices, whereas from mid adolescence onwards it is only engaged in defect choices. The pattern of activity of the TPJ in both the Trust and Ultimatum Game suggests that this area gradually becomes more involved in the decision process until young adulthood. Therefore the increase in prosocial behavior might be the result of two separate processes, an early decrease in self-focus and a gradual increase in other-focus.

However, the framework of interactive specialization proposes that the developmental shift from aMPFC to TPJ may be the result of the strengthening of connections between these areas (Johnson et al., 2009). Because at younger ages the network is not fully developed young adolescents might rely more on self-reflective processes associated with the aMPFC. Findings by Blakemore and colleagues support this hypothesis; in a series of studies they showed that during adolescent development there was a developmental shift from aMPFC to TPJ activation, and at the same time an increase in connectivity strength between the aMPFC and the TPJ (Burnett et al., 2008; Burnett & Blakemore, 2009). These studies involved a passive perspective-taking task: it therefore remains to be determined whether this change in connectivity is related to the developmental changes in social behavior. Future studies using behavioral paradigms, or re-analyses of current data-sets, are needed to investigate the role of connectivity in order to further address the nature of functional brain changes underlying social decision-making.

The regulation of social behavior

The social interaction paradigms also indicated developmental changes in the regulatory network, the DLPFC in particular. The study with the Developmental Trust Game showed that with increasing age the DLPFC gradually becomes more engaged in the decision process, showing significant relations with behavioral measures from mid-adolescence onwards. Furthermore, the data from both social interactions studies indicate that the DLPFC is engaged in situations when participants violate personal norms or behavioral tendencies. Taken together, these results fit with the theoretical accounts that the increased capacity for self-regulation is particularly driven by the gradual increase in strength of the regulatory processes to adapt social behavior (Steinberg, 2009).

The second part of this thesis had a more detailed focus on the development of the networks that underlie the monitoring and regulation of behavior in a probabilistic learning task. This section will reflect on how these results support earlier conclusions on the role of regulation in social development, but also expand on them in various ways. Finally, new hypothesis on the development of self-regulation in context of social behavior will be generated.

The initial analyses showed that the DLPFC is already involved at a young age when processing feedback in context of applying probabilistic rules. However, there was a qualitative shift in the pattern of activation, which may reflect age related changes in strategy differences and attention regulation. On the other hand, analyses of the relation between activity in the regulatory network and shifting behavior showed a very similar pattern as in the social interaction studies: there was an age related increase in the correlation between activity and behavior until young adulthood. Thus, the pattern that emerges from these data is that the DLPFC is already engaged at a young age in processing feedback from the environment, while with increasing age the relation between DLPFC activity and behavioral adaptation becomes stronger.

In subsequent analyses a reinforcement learning model was used to further explore the processes involved in adaptive behavior. These analyses revealed that age related changes in connectivity strength between the striatum and the medial PFC was related to the tendency to adjust behavior following positive or negative feedback. Taken together, these results show that age related changes in adaptive behavior are the related to developmental differences in several sub-processes involved in monitoring and regulation, which are associated with the DLPFC/parietal cortex and striatum/mPFC networks.

Interestingly, the developmental pattern of behavior in the probabilistic learning paradigm was in one aspect very a similar to the behavior in the multiple round Trust Game, namely that children were more sensitive to negative feedback than adults. Based on this similarity in behavior, and given that the DLPFC/parietal cortex and striatum/medial PFC networks have been identified to be involved in numerous adult studies with (multiple) social interactions (Delgado et al., 2005; King-Casas et al., 2005; Behrens et al., 2009), it can be hypothesized that the reported developmental changes in brain activation will also contribute to the ability to regulate social behavior.

Consequently, it follows that the increased capacity for self-regulation of social behavior is not only due to an increased capacity to adapt future behavior, but the result of developmental changes in several sub-processes involved in self-regulation. One of the most interesting directions for future developmental studies would therefore be combining a multi round Trust Game with neuroimaging, to explore this hypothesis in more detail. The results of such studies may reveal in more detail which sub-processes of self-regulation contribute to developmental changes in social behavior.

Detecting norm violations

Finally, a very robust finding in all the social interactions studies is that all participants, almost independent of age, are sensitive to violations of social norms regarding fairness and reciprocity. This was reflected in the early maturation of the pattern of activation in the bilateral anterior insula, and by behavior in the tasks (e.g rejecting unfairness and reciprocating trust). These results suggest knowledge of these social norms is already present at the start of adolescence. Indeed, in case of fairness norms there is evidence that this already present by very young children (e.g. Fehr et al., 2008). However, the behavioral study showed that the youngest participants ages 9-10 did not always behave according to the basic norm of reciprocity, for example, when it was not in their own benefit.

Overall, these results suggest that children are already aware of social norms at a young age but predominantly react to them when it is in their own benefit. This fits well with research on the development of moral reasoning (Kohlberg, 1981) and prosocial behavior (Eisenberg et al., 1995, 2005) that suggests that young children mainly refer to selfish or hedonistic reasons when thinking about social dilemmas. By showing the early maturation of norm-violation related activity, the neuroimaging results further corroborate developmental theories that suggest that moral development during adolescence is not a process of learning and internalizing social norms (Keller & Edelstein, 1993), but rather a process of becoming more skilled in reasoning and applying these norms (Kohlberg, 1981; Eisenberg et al., 1995, 2005). In future studies it would be interesting to expand the age range to younger populations who have not yet internalized these norms, or to investigate populations that are learning novel norms (such as at a student fraternity). One possible outcome is that in the early learning phase, norms are represented in the DLPFC/parietal network that is known to be involved in rule representation (Bunge, et al., 2009).

Multiple systems: connecting the dots

The question that remains is: how do these different networks interact? How does the information that a norm is violated, and our estimation of the intentions of the other, connect to reach a decision? Here the framework of interactive specialization points us towards a way of understanding this question in terms of brain function (Johnson, 2011). Besides the connectivity strength between brain areas within a network, the interactive specialization framework also emphasizes the importance of connectivity strength between specialized networks. In case of social behavior this could be an improved coordination between the networks that represent social norms (e.g., recognizing behavior that transgresses a norm), and the networks that are involved in taking the perspective of the other (e.g. recognizing that norm-transgressing behavior is not intentional). In support of this hypothesis, a recent study with adults showed that the functional connectivity strength between areas of the ‘social brain’ network (TPJ) and the affective network (VMPFC) was associated with the amount of money participants were willing to donate to charity (Hare et al., 2010). This suggests that besides an internal shift in connectivity within the ‘social brain’ network, developmental changes in social behavior may also be the result of strengthening of the connectivity between functional networks. Although there is no direct evidence for such a developmental pattern in the studies described in this thesis, both social interaction studies report increasing co-activation of the DLPFC and the TPJ, which might indicate a stronger functional connectivity between different networks.

To improve our understanding of the development of complex social behavior it would be beneficial to develop integrative models that describe the relation between the functional networks involved in social decision-making. The challenge for these models is not just to recognize the involvement of multiple functional networks but also to understand how these interact, for instance using network analyses (e.g. Fair et al., 2008). To conclude, measuring functional connectivity both *within* and *between* areas or networks can advance our understanding of how these different functional networks contribute to the development of social behavior.

Computational models of social decision-making

Another promising methodological development that may contribute to our understanding of the relation between the development of cognitive processes and brain function is the use computational models (Frank et al., 2009; Poldrack, 2010). Current experimental designs allow only a limited view on the computational processes that underlie individual differences or developmental changes in behavior (Huizinga et al., 2006; Corrado & Doya, 2007). Over the past decade computational models of reward-based decision-making in combination with neuroimaging techniques have proven successful at identifying computational sub-processes and their neural implementations (for review see Rushworth & Behrens, 2008). The study in chapter 8 showed that these relatively simple models could also advance the understanding of the development of the neural mechanisms underlying monitoring and regulation of behavior based on feedback.

Recently, several studies have successfully extended these models to include processes involved in social interactions, such as predicting the mental states of others (Chang et al., 2010; Behrens et al., 2008; Hampton et al., 2008). Using these models the experimenters were able to correlate activity in brain regions with different model parameters, demonstrating dissociations between social and non-social functional processing. Additionally, these models can contribute to the understanding of how social values might interact with more basic computational processes in decision-making.

Taken together, this work shows that computational modeling in combination with neuroimaging can support stronger interpretations than what is possible using neuroimaging alone (Poldrack, 2010). Furthermore, in the past decade there has been a steady growth in the use of computational models to understand the development of cognitive functions (e.g., Mareschal, 2007; Munakata and McClelland, 2003). However, these models have not yet been integrated with neuroimaging studies of cognitive development. Future developmental studies could benefit from using computational models to gain more detailed insight in the processes that underlie changes in social behavior.

Quo vadis?

The previous part focused on (1) how the current results speak to the previous theoretical perspectives on the relation between social and brain development, and (2) how (methodologically) advancing these studies may contribute to a better understanding of the nature of social development. However, these studies also laid groundwork for asking more challenging new questions. The next section will sketch several of those future directions in relation to the impact of internal and external influences on the development of social behavior, and how these studies can be better embedded in theoretical perspectives on social development.

Genetic and environmental influences on social behavior

Besides the developmental differences in the behavior regarding social norms, the results described in this thesis have also shown that there are large individual differences in social value orientation. These individual differences were reflected, for example, in insula activation and were similar for all age groups. Indeed, earlier studies have shown that besides developmental changes in prosocial behavior there are individual differences in prosocial attitudes that are already present at a young age and remain fairly consistent over the course of development (Eisenberg et al., 1995). One of the long standing questions for developmental and social psychology regards the exact nature of individual and developmental differences in prosocial behavior, and to what extend these are influenced by differences in genes and social environment (Lenroot et al., 2009). Currently many studies have shown that individuals differences in both genetic variables (Rueda et al., 2005) and environment (Diamond et al., 2007) are strongly associated with cognitive functioning. However, the question that remains is how these genetic and environmental differences have an impact on brain structure and function, and subsequently individual differences in behavior. For instance, it would be very interesting to be able to point out the sources, in terms of genes or environment, of the differences in neural activation between age groups that are reported in this thesis. An exciting avenue for future developmental research would therefore be combining genetics, economic games and neuroimaging to investigate the neural components of these ‘hard-wired’ differences in prosocial behavior, and to what extent neural differences are related to environmental variables. Note that, ultimately understanding how internal (e.g. genetic differences) and external (e.g. social economic status) factors interact and contribute to different developmental trajectories, rather than outcomes, requires longitudinal neuroimaging studies (Paus, 2010).

Hormonal changes

An example of an internal factor influencing developmental changes in behavior, that is specific to adolescence, is the influence of pubertal hormones. Numerous human and animal studies have indicated that puberty is marked by fundamental modifications in both the hypothalamic-pituitary-gonadal (HPG) and hypothalamic-pituitary-adrenal (HPA) axes (Romeo, 2005). These pubertal shifts in HPG and HPA function result in very different levels of gonadal and adrenal steroid hormones during puberty relative to childhood and are thought to have a significant impact of brain structure and function (Ernst et al., 2008). Interestingly, these hormonal changes have also been suggested to be a driving force of developmental changes in (appetitive) social behavior (Forbes & Dahl, 2010; Nelson et al., 2005; Spear, 2000). A comprehensive perspective on social development should therefore incorporate the effects of puberty related hormonal changes. The use of economic games can be a good starting point to systemically examine the effects of puberty on social behavior. Interesting directions for future research would be the relation between pubertal hormones and: (1) developmental changes in the interactions between different sex peers (Collins, 2003), and (2) the structural and functional development of sub-cortical structures (Ernst et al., 2008; Blakemore et al., 2010).

The structure-function relationship

Linked to the previous points is the relation between brain structure and function. Although, the studies in this thesis were inspired by the changes in brain structure that take place during adolescence, they did not directly examine this topic itself. Further exploration of this relation in developmental populations can contribute to increased understanding of how internal and external factors influence brain function by re-shaping the brain. For instance, it can help determining to what extent observed age differences in brain activation reflect hard developmental constraints (e.g., anatomical constraints on signal transmission speed within certain connections). Recently, several studies have shown that that there are still significant developmental changes in structural connectivity until young adulthood (Schmithorst & Yuan, 2010), and that there are direct relations between structural connectivity and brain function (e.g Cohen, 2009, Camara et al., 2008). The multimodal analysis of structural and functional connectivity is therefore an interesting framework for understanding the relation between structural and functional development, and how network architecture shapes and constrains the development of social behavior (Honey et al., 2007; 2009).

Ecological validity

Finally, in every day life only a very small fraction of social interactions is with anonymous others. An interesting next step will therefore be to experimentally control for the relationship between the players, for instance by making use of sociometric questionnaires to identify peer relations (see Güroğlu et al., 2008). Second, behavior and neural activity associated with social interaction games may be more strongly related to real world behavior (Rilling & Sanfey, 2010), for instance, by using experience sampling methods (Eisenberger et al., 2007). Third, future developmental studies could benefit from combining the use of games with more traditional measures (e.g. self-reports and structured interviews) of perspective taking and moral reasoning, in order to further embed the behavior in economic games in the context of existing developmental theories.

Conclusion

To conclude, this thesis describes a set of studies that have integrated research in developmental, social, and cognitive psychology, experimental economics and neuroscience. The collection of studies presented here provides to a comprehensive and multidisciplinary perspective on the development of prosocial behavior. The application of economic games yielded novel behavioral results and provided evidence for the hypothesis that developmental changes in social behavior are related to specific changes the different neural networks underlying social decision-making.

Additionally, several directions for future research were highlighted that aim at increasing our understanding of the processes and nature of developmental changes in the brain that underlie the development of social behavior. Two promising directions which can be directly applied are: (1) network/connectivity analyses, and (2) the application of computational models. The challenge for the future will be to develop an integrative model that can accommodate evidence from anatomical, functional and psychological analyses, and may account for developmental changes and individual differences in social decision-making.