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Developmental changes of neuronal networks associated with strategic social decision-making



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ABSTRACT

Objectives: One of the important prerequisites for successful social interaction is the willingness of each individual to cooperate socially. Using the ultimatum game, several studies have demonstrated that the process of decision-making to cooperate or to defeat in interaction with a partner is associated with activation of the dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC), anterior insula (AI), and inferior frontal cortex (IFC). This study investigates developmental changes in this neuronal network.

Methods: 15 healthy children (8–12 years), 15 adolescents (13–18 years) and 15 young adults (19–28 years) were investigated using the ultimatum game. Neuronal networks representing decision-making based on strategic thinking were characterized using functional MRI.

Results: In all age groups, the process of decision-making in reaction to unfair offers was associated with hemodynamic changes in similar regions. Compared with children, however, healthy adults and adolescents revealed greater activation in the IFC and the fusiform gyrus, as well as the nucleus accumbens. In contrast, healthy children displayed more activation in the AI, the dorsal part of the ACC, and the DLPFC. There were no differences in brain activations between adults and adolescents.

Conclusion: The neuronal mechanisms underlying strategic social decision making are already developed by the age of eight. Decision-making based on strategic thinking is associated with age-dependent involvement of different brain regions. Neuronal networks underlying theory of mind and reward anticipation are more activated in adults and adolescents with regard to the increasing perspective taking with age. In relation to emotional reactivity and respective compensatory coping in younger ages, children have higher activations in a neuronal network associated with emotional processing and executive control.

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1. Introduction

Social skills such as social cooperation, social interaction, social decision-making, and empathy are important prerequisites for psychosocial adjustment across an individual's life span (Ishii-Kuntz, 1990; Rubin, Bukowski, & Parker, 2006). These skills develop with age (Güroğlu, van den Bos, van Dijk, Rombouts, & Crone, 2011; Parker, Rubin, Erath, Wojslawowicz, & Buskirk, 2006). Children, adolescents, and adults differ in their ability to register, comprehend, and empathize with feelings of others (Auyeung, Allison, Wheelwright, & Baron-Cohen, 2012; Rubin et al., 2006). Moreover, developmental changes are observed for cooperation behavior as well as for strategic, cognitive and affective decision-making processes (Crone, Jennings, & Van der Molen, 2004; Hooper, Luciana, Conklin, & Yarger, 2004). Children are more reward-driven or risk-taking compared to adults, who decide more conservatively and rationally (Paulsen, Platt, Huettel, & Brannon, 2011; Sutter, 2007). Moreover, children and adolescents are less effective in analyzing the intentionality of partners' behavior and their mental states during social interaction

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(Güroğlu, van den Bos, & Crone, 2009; Sutter, 2007). For example, using a children version of the Iowa Gambling Task, Crone and van der Molen (2007) demonstrated less effective decision making in children and adolescents when learning to make advantageous choices in social interactions. It seems likely that children rarely use complex reasoning rules during decision-making compared to adults (Huizenga, Crone, & Jansen, 2007). And finally, Steinbeis, Bernhardt, and Singer (2012) revealed age related increases in strategic decision making associated with strategic reasoning, behavioral and impulse control. Based on these findings, it can be expected that social interaction and strategic decision-making may be influenced by the developmental process, and these developmental effects are associated with the maturation of related brain functions.

Game-theory based models are often used to investigate neuronal networks of social interaction and decision-making. Game theory examines the decision-making process in situations in which the success of one person not only depends on their own behavior, but also on the actions of others (Colman, 1995; Heifetz, 2012). One of the most studied games in neuroeconomic experiments is the ultimatum game (UG; Güth, Schmittberger, & Schwarze, 1982), in which two players have to decide how to divide a given amount of something (e.g. a sum of money). The first player (proposer) makes an offer to split the amount, and the second player (responder) can either accept or reject this. If the responder accepts this allocation, the money is split according to the proposal. However, if the second player rejects, both players receive nothing. The UG is used to examine the fundamental mechanisms of social decision-making.

In different studies, the UG has been employed to investigate neuronal mechanisms of decision-making (Braams et al., 2013; Corradi-Dell'Acqua, Civai, Rumiati, & Fink, 2013; Gospic et al., 2011; Güroğlu, van den Bos, Rombouts, & Crone, 2010; Güroğlu et al., 2011; Harle, Chang, van 't Wout, & Sanfey, 2012; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Tabibnia, Satpute, & Lieberman, 2008; White, Brislin, Meffert, Sinclair, & Blair, 2013; White, Brislin, Sinclair, & Blair, 2013). Sanfey et al. (2003) studied behavioral and neuronal responses to fair and unfair offers to find explanations for the conflict between cognitive and emotional motives. The authors found greater activation in the anterior insula (AI) and the anterior cingulate cortex (ACC) for unfair offers. These results have been replicated in a great number of studies (Braams et al., 2013; Corradi-Dell'Acqua et al., 2013; Gospic et al., 2011; Güroğlu et al., 2010, 2011; Tabibnia et al., 2008; White, Brislin, Meffert, et al., 2013; White, Brislin, Sinclair, et al., 2013). Güroğlu et al. (2009) used a modified version of the UG to investigate developmental changes associated with fairness consideration and perspective taking. Varying the degrees of intentionality of the proposer, they analyzed four age groups of children and adolescents and found developmental differences of responder behavior with an age-related increase in perspective taking. According to their study the ability to recognize unfairness develops early, but the ability to understand others' intentions does develop until late adolescence (Güroğlu et al., 2009). In a follow-up study, Güroğlu et al. (2011) used the same procedure in a magnetic resonance scanner and examined age-related neural activity associated with this growing understanding. They concluded that there is an early developed network including the insula and the ACC, which is responsible for detecting norm violations. The activity in the second network containing the dorsolateral prefrontal cortex (DLPFC) and temporo-parietal junction (regions which are related to intentionality and theory-ofmind), increases with age. This aspect of brain maturation should explain the differences on a behavioral level (Güroğlu et al., 2011).

In the present study, we used a modified-multiround version of the UG to investigate developmental changes of neuronal networks responsible for strategic decision-making of the responder. In classical UG studies, the offers have been made by different partners in order to exclude the influence of reputation building. In such a way, the receiver did not have a chance to influence the flow of interaction with the proposer by accepting or rejecting offers. Moreover, by playing with different partners the receiver does not have to anticipate the next proposer behavior and adjust his/her own behavior depending on the proposer's strategy. In the singleshot UG (with different proposers) there is substantially less social interaction and consideration of social context in the process of decision making than in the multiround repetitive UG. Based on these considerations, we expected that the responder would try to influence the behavior of the proposer strategically by pursuing and influencing offers of the partner by giving acceptance (positive feedback) or rejection (negative feedback) of offers (Steinbeis et al., 2012). This kind of strategic social behavior is aimed at strengthening future positive interactions between the game partners. For this, the ability to anticipate decisions and recognize mental states of others is necessary (Theory of Mind; Weiland, Hewig, Hecht, Mussel, & Miltner, 2012). Mentalizing about others' cognition and emotions allows empathizing with the position of the proposer and this may lead to strategic considerations of the responder (Weiland et al., 2012). Because the reciprocal social interaction is possible by playing against a human partner, we expect to observe differences in strategic decision making between UG with a human proposer and UG with a computer (for example differences in decisions over time; Sanfey et al., 2003). Additionally, we want to examine whether there is an influence of age on the strategic decision making in the UG. And finally, we expect that the developmental differences in behavior between children, adolescents and adults in the strategic decision making should be associated with agedependent activation pattern of neuronal networks responsible for the reciprocal social interaction and strategic decision. Based on results of the previous studies (Güroğlu et al., 2011; Steinbeis et al., 2012), we suggest that younger children should make more emotionally-driven decisions with the greater involvement of the early developed network sensitive to norm violations including ACC and AI. With increasing age, we expect a greater activation in the network underlying brain functions of theory of mind, cognitive empathy and social reciprocal interaction (temporo-parietal junction and inferior frontal cortex) as well as cognitive reasoning (dorsolateral prefrontal cortex; see Frith & Frith, 2003, 1999; Gallagher et al., 2000; Güroğlu et al., 2011; Steinbeis et al., 2012; van der Meer, Groenewold, Nolen, Pijnenborg, & Aleman, 2011).

2. Materials and methods

2.1. Participants

According to self ratings, 15 healthy children (age range: 8–12, mean: 10.2 ± 1.37 SD; 2 female, 13 male), 15 healthy adolescents (age range: 13–18, mean: 15.5 ± 1.46 SD; 9 female, 6 male), and 15 healthy young adults (age range: 19–28, mean: 24.8 ± 2.65 SD; 9 female, 6 male) were recruited using advertisements in a local newspaper. The cut off between groups of children and adolescents was set on 12 years in agreement with multiple previous studies (see for example Güroğlu et al., 2009; Stracciolini, Casciano, Levey Friedman, Meehan, & Micheli, 2013; Sudupe Moreno, 2013; Van den Bosch et al., 2012). All subjects had normal or corrected-to-normal vision. The study was performed according to the Declaration of Helsinki and was approved by the local ethics committee. Participants or their parents (in the case of children) gave their written informed consent.

2.2. UG

Using the classical UG (for a detailed description see Sanfey et al., 2003), the proposer decides how a certain amount of money (e.g. 10 cents into 5:5 or 7:3) is to be divided up. The responder can accept or reject the offers of the proposer. If the offer is accepted, the money is split as proposed. In contrast, if the responder rejects, both players receive nothing. The UG was performed in the MR scanner. Each participant was in the role of the responder and, in contrast to the study of

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