Theory of Mind Development in Adolescence and its (Neuro)cognitive Mechanisms

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Meinem Großvater

Fritz Richter, 1929-2012

In liebevoller Erinnerung und Dankbarkeit
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For all three studies, Nora C. Vetter set up the experimental design, collected the data, conducted the statistical analyses, wrote the first version of the manuscript and implemented comments of co-authors.
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Abstract

Theory of Mind (ToM) is the ability to infer others’ mental states and thus to predict their behavior (Perner, 1991). Therefore, ToM is essential for the adequate adjustment of behavior in social situations. ToM can be divided into: 1) cognitive ToM encompassing inferences about intentions and beliefs and 2) affective ToM encompassing inferences about emotions (Shamay-Tsoory, Harari, Aharon-Peretz, & Levkovitz, 2010). Well-functioning skills of both ToM aspects are much-needed in the developmental period of adolescence because in this age phase peer relationships become more important and romantic relationships arise (Steinberg & Morris, 2001). Importantly, affective psychopathological disorders often have their onset in adolescence. ToM development in adolescence might be based on underlying cognitive mechanisms such as the ability to inhibit one’s own thoughts in order to understand another person’s thoughts (Carlson & Moses, 2001). Another possible mechanism relates to functional brain development across adolescence (Blakemore, 2008). Therefore, neurocognitive mechanisms may underlie ongoing ToM development in adolescence. First studies indicate an ongoing behavioral and functional brain development of ToM (e.g. Blakemore, 2008). However, ToM development in adolescence and how this might relate to underlying (neuro)cognitive functions remains largely underexamined.

The major aims of the current thesis were first to answer the overall question whether there is an ongoing development of ToM in adolescence. This question relates to both behavioral and functional brain development. As a second major aim, the present work sought to elucidate possible (neuro)cognitive mechanisms of ongoing ToM development across adolescence. Specifically, these cognitive mechanisms might be basic cognitive functions as well as executive functions. Additionally, the present work aimed at exploring potential (neuro)cognitive mechanisms through an integration of both behavioral and functional brain studies.

The current experimental work spans three cross-sectional studies investigating adolescents (aged around 12-15 years) and young adults (aged around 18-22 years) to examine for the first time both the behavioral (studies I and II) and functional brain development of ToM (study III) in adolescence and its underlying (neuro)cognitive mechanisms. In all three studies, more complex, advanced ToM tasks were employed to avoid ceiling effects. Study I was aimed at investigating if cognitive and affective ToM continues to
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Develop in adolescence and at exploring if basic cognitive variables such as verbal ability, speed of processing, and working memory capacity underlie such development. Hence, two groups of adolescents and young adults completed tasks of ToM and basic cognitive abilities. Large age effects were revealed on both measures of ToM: adolescents performed lower than adults. These age differences remained significant after controlling for basic cognitive variables. However, verbal ability covaried with performance in affective ToM. Overall, results support the hypothesis of an ongoing development of ToM from adolescence to adulthood on both cognitive and affective aspects. Results may further indicate verbal ability being a basic cognitive mechanism of affective ToM.

Study II was designed to further explore if affective ToM, as measured with a dynamic realistic task, continues to develop across adolescence. Importantly, this study sought to explore executive functions as higher cognitive mechanisms of developing affective ToM across adolescence. A large group spanning adolescents and young adults evaluated affective mental states depicted by actors in video clips. Additionally, participants were examined with three subcomponents of executive functions, inhibition, updating, and shifting following the classification of Miyake et al. (2000). Affective ToM performance was positively related to age and all three executive functions. Specifically, inhibition explained the largest amount of variance in age related differences of affective ToM performance. Overall, these results indicate the importance of inhibition as key underlying mechanism of developing an advanced affective ToM in adolescence.

Study III set out to explore the functional brain development of affective ToM in adolescence by using functional magnetic resonance imaging (fMRI). The affective ToM measure was the behavioral developmentally sensitive task from study II. An additional control condition consisted of the same emotional stimuli with the instruction to focus on physical information. This study faced methodical challenges of developmental fMRI studies by matching performance of groups. The ventromedial prefrontal cortex (vMPFC) was significantly less deactivated in adolescents in comparison to adults, which might suggest that adolescents seem to rely more on self-referential processes for affective ToM. Furthermore, adolescents compared to adults showed greater activation in the dorsolateral prefrontal cortex (DLPFC) in the control condition, indicating that adolescents might be distracted by the emotional content and therefore needed to focus more on the physical content of the stimulus. These findings suggest affective ToM continues to develop on the functional brain level and reveals different underlying neurocognitive strategies for adolescents in contrast to adults.
In summary, the current thesis investigated whether ToM continues to develop in adolescence until young adulthood and explored underlying (neuro)cognitive mechanisms. Findings suggest that there is indeed an ongoing development of both the cognitive and affective aspect of ToM, which importantly contributes to the conceptual debate. Moreover, the second benefit to the debate is to demonstrate how this change may occur. As a basic cognitive mechanism verbal ability and as an executive functioning mechanism inhibition was revealed. Furthermore, neurocognitive mechanisms in form of different underlying neurocognitive strategies of adolescents compared to adults were shown. Taken together, ToM development in adolescence seems to mirror a different adaptive cognitive style in adolescence (Crone & Dahl, 2012). This seems to be important for solving the wealth of socio-emotional developmental tasks that are relevant for this age span.

Keywords:
adolescence, cognitive and affective theory of mind, emotion, basic cognitive abilities, verbal ability, executive functions, inhibition, functional magnetic resonance imaging (fMRI), pediatric neuroimaging, ventromedial prefrontal cortex (vMPFC)
1 General Introduction

“A travelling salesman found himself spending the night at home with his wife when one of his trips was accidentally cancelled. The two of them were sound asleep, when in the middle of the night there was a loud knock at the front door. The wife woke up with a start and cried out, “Oh my God! It’s my husband!” Whereupon the husband leapt out of bed, ran across the room and jumped out the window” (Schank & Abelson, 1977, p. 59).

Socio-emotional competencies are important for everyday social interactions and promote development (Burt, Obradovic, Long, & Masten, 2008). These competencies, such as understanding others’ thoughts, beliefs, and emotions all pertain to the ability of Theory of mind (ToM, Premack & Woodruff, 1978). ToM enables us to infer others’ goals and predict their behavior (Perner, 1991). Therefore, ToM is essential for the adequate adjustment of our own behavior in social situations. This is nicely depicted by the example above of the travelling salesman, who fails to correctly infer his wife’s thoughts and therefore acts inadequately.

Since this ability is central for human development, there has been a long-lasting debate about how and when humans develop ToM (Onishi & Baillargeon, 2005; Wellman, Cross, & Watson, 2001). The emergence of ToM functioning has been observed in childhood (Wellman et al., 2001). However, whether there is an ongoing ToM development after childhood until the beginning of adulthood is mainly unknown. This period characterizes the transitional age phase of adolescence, which can roughly be defined as ranging from early (11 to 13 years) over middle adolescence (14 to 17) until late adolescence/ emerging adulthood (18-22) (Arnett, 2000; Steinberg, 2008). It is astonishing why ToM development is rather under-examined in adolescence, since it is an highly important age range for socio-emotional development (Lerner & Steinberg, 2004). As is known not only anecdotally, adolescents experience a higher relevance of peer relationships, greater self-consciousness (Steinberg & Morris, 2001) and an increased risk taking (Lerner & Steinberg, 2004). Moreover, psychopathological disorders affecting socio-emotional abilities often have their onset in adolescence (Paus, Keshavan, & Giedd, 2008). These lines of evidence lend credibility to the hypothesis that adolescence might be an important period for ongoing ToM development. Clearly, studies are warranted to focus on that aspect.

ToM development in childhood might be based on underlying cognitive mechanisms (Carlson & Moses, 2001). This follows the logic that first, cognitive abilities have to be
acquired in childhood to be able to process inferences about thoughts of others and thus to solve ToM tasks. It is therefore important to investigate which specific cognitive mechanisms seem to drive ToM development. Basic cognitive functions such as verbal ability have been shown to be related to ToM development in childhood (Astington & Jenkins, 1999). Furthermore, higher cognitive functions, i.e. executive functions, might relate to ToM development (Cole & Mitchell, 2000). For example, the cognitive ability to inhibit one’s own thoughts when inferring thoughts of others seems to be important for ToM functioning (Apperly, 2012). There has been a large body of childhood studies on cognitive mechanisms of ToM development (Perner & Lang, 1999). In contrast, adolescence has been largely spared by investigations on cognitive mechanisms of ToM development and thus needs to get into the focus of research.

Another possible mechanism underlying ToM development has to do with the fact that adolescence is accompanied by major physical changes beyond pubertal changes leading to sexual maturation. These additional major changes have been recently demonstrated in form of a massive structural brain development in adolescence (Giedd, 2008a; Gogtay et al., 2004; Lebel & Beaulieu, 2011). Specifically key brain areas for ToM processing such as the medial prefrontal cortex (MPFC) show a protracted development. This structural brain development is thought to underlie ToM development (Blakemore, 2008). Indeed, first fMRI studies on ToM have shown that the MPFC also continues to develop functionally. These findings suggest continued functional brain development of ToM in adolescence, that is a different functional brain processing of ToM stimuli in contrast to adults (Blakemore, 2012). Therefore, besides basic cognitive and executive function mechanisms, there may be neurocognitive mechanisms related to ongoing ToM development across adolescence.

With regard to the large gap in the literature demonstrated above, the present thesis first sought to investigate whether there is an ongoing development of ToM in adolescence by comparing adolescents and young adults both on the behavioral level and the level of brain functioning by use of fMRI (Figure 1). Second, in consideration of the relationship of cognitive abilities and ToM in childhood and first promising studies indicating ongoing ToM development on the brain functioning level, the current thesis aimed at elucidating possible cognitive and neurocognitive mechanisms of such development (Figure 1). Importantly, previous studies on neurocognitive mechanisms regarding the level of brain functioning have been largely unrelated to studies on cognitive mechanisms. In light of this gap between both
research traditions, the current thesis tried to combine both approaches to investigate adolescent ToM and its underlying mechanisms.

The following sections will first explain the concept of ToM (Section 1.1) and summarize previous research on ToM development in childhood and until adolescence (Section 1.2). Next, the supposed mechanisms of ToM development in adolescence will be discussed, that is, first, cognitive mechanisms (Section 1.3), and second in Section 1.4 with regard to the functional brain development (1.4.1) neurocognitive mechanisms (Section 1.4.2) will be reviewed. With respect to this theoretical background, Chapter 2 introduces the aims and research questions of the three empirical studies of the current thesis. The empirical studies comprise, first, a study on ToM development and its basic cognitive mechanisms (Chapter 3), second, a related study on ToM development in adolescence and its executive functioning mechanisms (Chapter 4), and third, an fMRI investigation on the neurocognitive mechanisms of ToM development in adolescence (Chapter 5). Lastly, Chapter 6 summarizes and discusses the obtained empirical results with regard to the research aims, considers their implications, and gives an outlook for future research.

Figure 1: Overview of the topics of this thesis. Numbers I-III indicate empirical studies of this thesis aimed at investigating the specific aspect.
1.1 Concept of ToM: cognitive and affective aspects

ToM is the ability to attribute mental states such as thoughts, beliefs, and emotions to oneself and others, and to be aware that others’ mental states may differ from one’s own (Perner, 1991). ToM therefore enables us to explain and predict but also manipulate others’ behavior (Doherty, 2008). Actually, the term “theory of mind” was introduced by a seminal paper of Premack and Woodruff (1978) asking whether primates have a ToM. Indeed, ToM is a core mental functioning, which seems to be unique to humans (Call & Tomasello, 2008). This concept has inspired human developmental psychology from about the 1980’s on. An impairment of ToM can be observed characteristically in the neurodevelopmental disorder of autism. Autism is typically related to severe problems regarding social interaction, including difficulties to explain and predict others’ behavior from mental states (Frith, 2001).

ToM is a construct with a diverse conceptual background (e.g., Baron-Cohen, 1997; Brothers & Ring, 1992). The conceptual definition of ToM within this thesis will be specified here. The current conceptual use follows a recent framework by Shamay-Tsoory et al. (2010). This framework has been adopted widely in the current ToM literature in fields such as aging (e.g. Duval et al., 2011), clinical (e.g., Mier et al., 2010), or neuroimaging research (e.g., Kalbe et al., 2010). According to this framework, ToM is a multidimensional construct (Amodio & Frith, 2006) that comprises two processes: cognitive ToM and affective ToM (Baron-Cohen & Wheelwright, 2004; Shamay-Tsoory et al., 2010). While cognitive ToM is the ability to understand ‘cold’ mental states, i.e. infer others’ thoughts and beliefs, affective ToM is the ability to understand ‘hot’ mental states, i.e. infer others’ emotions (Shamay-Tsoory et al., 2010). This conceptual distinction is corroborated by evidence from patients with brain lesions of the MPFC, one well-known region for ToM processing (Van Overwalle, 2009). Findings suggest that the MPFC seems to be dissociable with regard to the two ToM aspects: While deficits on affective ToM tasks (e.g., recognizing emotions) have been observed in patients with lesions in the ventral part of the MPFC (vMPFC), deficits on cognitive ToM tasks (e.g., recognizing others’ thoughts) have been shown in patients with lesions in the dorsal part of the MPFC (dMPFC) (Shamay-Tsoory, Tiber, Berger, Goldsher, & Aharon-Peretz, 2005; Shamay-Tsoory, Tiber-Elhanany, & Aharon-Peretz, 2006; Shamay-Tsoory & Aharon-Peretz, 2007; Stone, Baron-Cohen, & Knight, 1998). The conceptual distinction of ToM into cognitive and affective ToM is depicted in Figure 2, A and B. Additionally, the conceptual differentiation of ToM and ‘empathy’ is shown (Figure 2, B and C). Indeed, some authors refer to the same process, which is described by ‘affective ToM’ as
‘cognitive empathy’ (Figure 2B; Walter, 2012). In contrast, ‘affective empathy’ comprises a different process, namely to re-feel the emotions of others (Shamay-Tsoory, 2011, Figure 2C). Affective empathy is not required for affective ToM, i.e. to infer cognitively other’s emotions.

Figure 2: Conceptual differentiation of cognitive and affective ToM and the distinction from empathy. The focus of the current thesis lies on ToM and its cognitive and affective abilities (on the left to the dotted line). The ability of cognitive ToM (A) enables the right character to infer the thought of the left one (e.g., that he / she thinks of the box). The ability of affective ToM (B) enables the right character to not only infer the thought but also the emotional state of the left character (e.g., the left character is happy because the sun shines). In contrast, ‘affective empathy’ (C) comprises to re-feel the emotions of others (Shamay-Tsoory, 2011), that is, the right character feels the same emotion as the left character. Note that the depicted positive emotion is just an example and could be any positive or negative emotion.

The introduced distinction of the two ToM aspects will be important for the current thesis. Cognitive and affective aspects of ToM will be investigated in study I. However, the thesis has a specific focus on affective ToM (study II and III) since this is the part of ToM, which seems to show a more protracted development as will become clear in the following sections.

1.2 ToM Development

Besides very early emerging (Farroni, Csibra, Simion, & Johnson, 2002) precursory abilities such as detecting others’ eye gaze direction (Vetter, 2008) ToM does not seem to belong to human’s cognitive repertoire from the start. ToM skills are developmental achievements, which are gained in sequence. New approaches indicate that implicit precursory ToM abilities might emerge already in infancy (Onishi & Baillargeon, 2005). However, traditionally, research has focused on the emergence of ToM in childhood (Baron-
Cohen, Leslie, & Frith, 1985; Perner, 1991). Another newer perspective is the lifespan investigation of ToM. Some data exists on development in adulthood suggesting a decrease of ToM abilities across middle adulthood (e.g., Pardini & Nichelli, 2009). Moreover, current research in old age aims at elucidating if and why ToM abilities decrease in aging individuals (Happe, Winner, & Brownell, 1998; Henry, Phillips, Ruffman, & Phoebe, 2012; Sullivan & Ruffman, 2004). However, the classic focus of research remains on cognitive ToM in childhood and an important paradigm, the false-belief task (see 1.2.1.1). In contrast, the development beyond children’s false belief understanding has been mainly spared. Several authors have referred to this lack of research (not without some humor, e.g., "Is there developmental life after false belief understanding?", Carpendale & Lewis, 2006). Research of ToM in the specific age span of adolescence until young adulthood has just recently started. Methodically, one reason for the current paucity of research in this important age phase might be the lack of suitable paradigms, which target more advanced forms of ToM (Blakemore, 2008). The following section (1.2.1) first summarizes ToM development in childhood until around the beginning of adolescence. This provides a relevant background for ToM studies in adolescence since it introduces paradigms and developmental trajectories of the two concepts of cognitive (1.2.1.1) and affective ToM (1.2.1.2) in childhood. This section is followed by a review of the few existing studies on ToM development across adolescence (1.2.2), again differentiated in cognitive (1.2.2.1) and affective ToM (1.2.2.2).

1.2.1 ToM Development until Adolescence

As has been indicated in 1.2, most research on ToM development focused on childhood before the adolescent years. Specifically, research on cognitive ToM concentrates on the preschool years, since this seems to be the age span when ToM abilities emerge, i.e. when the first relevant developmental steps are made (1.2.1.1). Later developments of cognitive ToM are observed in school-aged children (1.2.1.1.). This is also the age span when affective ToM seems to emerge (1.2.1.2). In contrast to cognitive ToM, less research exists on affective ToM as will become clear in 1.2.1.2.

1.2.1.1 Cognitive ToM

A first important conceptual milestone of cognitive ToM development marks the emergence of first-order cognitive ToM (Wimmer & Perner, 1983) First-order cognitive ToM requires mastery of the first-order false belief task, which is a standard paradigm employed by hundreds of developmental studies (for a review see Wellman et al., 2001). Studies using this
paradigm consistently show that across cultures and different task variations first-order cognitive ToM is obtained at around four years (Wellman et al., 2001). A typical first-order false belief task introduces two characters, e.g., Sally and Anne (Baron-Cohen et al., 1985) via pictures, a film clip or a play with dolls: Sally hides her ball in a blue box and then leaves. When Sally is away, Anne enters the room, moves the ball to a green box and then leaves. Finally, Sally re-enters and the participating child is asked where Sally thinks her ball is (prototypical question for the participant: ‘What does person A think?’). Children who appreciate that Sally believes her ball is in the blue box and will look there - despite the child’s own knowledge of the ball’s current location in the green box - are assumed to have acquired the concept of first-order cognitive ToM. Extending first-order cognitive ToM is the inference of what the other person thinks about the thoughts of a third person (prototypical question for the participant: ‘What does person A think person B thinks?’). This ability is tested by second-order false belief tasks. Taking the Sally-Anne task, for example, a third person is introduced: Scott is together with Sally and sees how she puts the ball into the blue box. They leave the room together. Then, Anne changes the location of the ball. Unbeknownst to Scott, Sally comes back and finds the ball in the new location. The participating child is asked where Scott thinks Sally thinks the ball is. Inferring correctly that Scott has a false belief about Sally’s thoughts (i.e. she knows where the ball is but Scott does not know this) hallmarks a more elaborate second-order cognitive ToM. It emerges later in childhood between six to seven years (Baron-Cohen, 1989; Perner & Wimmer, 1985). In contrast to first-order cognitive ToM, literature on second-order cognitive ToM is small (for a review see Miller, 2009).

However, research beyond second-order cognitive ToM is even more limited. Therefore, conceptually, it still needs to be shown whether there is a late developing form of ToM and how this might look like. Methodically, adequate paradigms are lacking. A later development seems to be an advanced cognitive ToM, which is the understanding of higher-order mental states. This advanced ToM seems to be based on second-order cognitive ToM. One example is the higher-order mental state of a ‘self-representational lie’, which is a form of a white-lie, (i.e. protecting the self in front of the others in the form “I did not really want this toy”). To understand such mental states, it is important to appreciate that the speaker wants the other persons to believe what he or she said. This implies an inference of second-order mental states (‘What does person A think person B (here: myself) thinks?’, Banerjee, 2002). Methodically, to test advanced cognitive ToM, the most established paradigm is a social stories task, which includes several stories depicting everyday situations (Channon & Crawford, 2000; Happé,
The task for each story is to explain the indirect statement of the main character, which requires inferring the characters’ mental states (e.g., a white-lie or irony). For example: “George went shopping at a supermarket and left the store with many bags when a man bumped into him. The bags dropped on the ground and George said to the man ‘Thanks a lot mate.’” Subsequently, the participant is asked, “Why did George say that?” Using the social stories paradigm, two lines of empirical evidence suggest that there is a form of advanced ToM, which is more complex and develops later than second-order cognitive ToM. First, while autistic subjects seem to pass second-order cognitive ToM, they often show deficits on advanced ToM measures (e.g., Happé, 1994). Indeed, social stories tasks have been constructed originally to detect subtle deficits of ToM functioning in autism. Second, healthy control groups in two clinical studies performed worse in social stories tasks in comparison to second-order false belief tasks (Meristo et al., 2007; Sobel, Capps, & Gopnik, 2005). Moreover, 12 year-olds did not perform at ceiling in a social stories task (O’Hare, Bremner, Nash, Happe, & Pettigrew, 2009), which suggests that there might be an ongoing development beyond this age. Taken together, conceptually, these findings might indicate that there is a form of advanced cognitive ToM. Secondly, the studies suggest that such advanced cognitive ToM continues to develop in adolescence.

1.2.1.2 Affective ToM

Surprisingly, in contrast to cognitive ToM, only a handful of studies have investigated the emergence and development of affective ToM. First empirical evidence suggests that affective ToM begins to develop around the same age as second-order cognitive ToM that is around six to seven years. For example, children from six years on understood false beliefs about emotions (Gross & Harris, 1988; Jingxin, Jiliang, & Wenxin, 2006; but see Parker, MacDonald, & Miller, 2007 for an earlier understanding). This rather late development might indicate children first have to gain an understanding of others’ beliefs in order to appreciate that beliefs guide others’ emotions (Rieffè, Terwogt, & Cowan, 2005). The ability to recognize social emotions (Hareli & Parkinson, 2008) such as surprise, embarrassment, guilt, or pride requires one person to infer others’ thoughts about another person’s thoughts. That means it seems to rely on an understanding of second-order false-belief (Bennett & Matthews, 2000). Corroborating this notice, understanding social emotions develops from an age of about seven years on, i.e. at an age after second-order false-belief understanding has emerged or is emerging (Hadwin & Perner, 1991; Nelson & Russell, 2012; Ruffman & Keenan, 1996). Later, affective ToM seems to continue to develop in the form of advanced affective ToM,
which is indicated by two often used paradigms: First, the faux pas test, which comprises short stories depicting social faux pas, i.e. embarrassing social blunders (Baron-Cohen, O'Riordan, Stone, Jones, & Plaisted, 1999). An example for the faux pas test is the following story: “Jill had just moved into a new house. She went shopping with her Mum and bought some new curtains. When Jill had just put them up, her best friend Lisa came round and said, ‘Oh, those curtains are horrible, I hope you’re going to get some new ones.’ Jill asked, ‘Do you like the rest of my bedroom?’ The participant subsequently had to identify the faux pas by answering the question “Did someone say something that they shouldn’t have said?” The faux pas test is increasingly solved from the age of eight to 10 years (Banerjee, Watling, & Caputi, 2011; Baron-Cohen et al., 1999). This late age range suggests that advanced affective ToM might develop after an understanding of second-order cognitive ToM (Baron-Cohen et al., 1999; Meristo et al., 2007). Second, the ‘Reading the mind in the eyes test’, which depicts affective mental states in pictures of person’s eye regions, seems to be understood from around eight to 10 years, an age range which lies again after second-order cognitive ToM (Eyes test; Baron-Cohen, Wheelwright, Spong, Scahill, & Lawson, 2001). Taken together, this evidence indicates that development of more complex aspects of affective ToM might develop after an understanding of second-order cognitive ToM. Therefore, specifically advanced affective ToM seems to have a prolonged developmental trajectory, which might go well into adolescence.

### 1.2.2 ToM Development in Adolescence

As has been depicted in section 1.2.1, recent findings suggest prolonged advanced ToM development beyond childhood. Furthermore, socio-emotional challenges during adolescence are observed such as increased risk-taking, higher relevance of the peer group and first romantic relationships (Lerner & Steinberg, 2004). In light of this evidence, it is surprising that it remains an open issue whether ToM further develops between adolescence and young adulthood. Only recently, within the last five to maximum seven years, studies have begun to investigate ToM in this age span. The results of these few studies on cognitive ToM (1.2.2.1) and affective ToM (1.2.2.2) are described in the following.

#### 1.2.2.1 Cognitive ToM

First studies suggest ongoing development of specific aspects of advanced cognitive ToM across adolescence. In one study about perspective taking, stimuli consisted of short everyday scenarios, and the participant (aged 8 to 36 years) indicated his or her first person perspective
or the protagonist’s third person perspective regarding a situation (Choudhury, Blakemore, & Charman, 2006). Adolescents’ differences in reaction time between these two perspectives were larger than adults’ whose reaction times were comparable across both first and third person perspective. These results were interpreted in terms of less efficient perspective taking in adolescents compared to adults. In another study, participants were presented with a set of shelves containing objects (Dumontheil, Apperly, & Blakemore, 2010). In this communicative online game, a virtual character could only see some of the shelves, while others were occluded from his viewpoint. The character instructed participants to sequentially move specific objects, which required putting themselves into his perspective. Adolescents aged 14 to 17 performed less accurately than adults aged 19 to 27. Taken these two studies together, advanced cognitive ToM abilities may still improve across adolescence until young adulthood. However, studies only focused on the specific aspect of perspective taking. Besides these two studies, evidence remains limited since advanced cognitive ToM measures such as social stories tasks have only been employed in studies on autism (Miller, 2009). In one such study, performance on a social stories task correlated positively with increasing age in a (rather small) adolescent control group (Kaland, Smith, & Mortensen, 2007). However, whether adolescents perform lower in this task than young adults has not been investigated yet. Taken together, it is unresolved if these preliminary results will hold in advanced ToM tasks besides perspective taking comparing adults with adolescents. Following up on this question, study I investigates cognitive ToM in adolescents compared to adults with a more advanced stories task paradigm.

1.2.2.2 Affective ToM

For advanced affective ToM, research seems to be similarly or even more scarce. Two studies suggest an ongoing development of different aspects of advanced affective ToM. In the first study, the time to decide the appropriateness of emotions following descriptions of situations decreased in adolescents from 13 to 19 years (Keulers, Evers, Stiers, & Jolles, 2010). In the second study, adolescents aged 11 to 16 years performed worse in comparison to adults aged 24 to 40 years in choosing the appropriate ending of short stories depicting character’s responses to their companion’s emotions (Sebastian et al., 2012). Accordingly, advanced affective ToM abilities seem to still increase across adolescence. However, while one study focused on thinking time only and provided no measure of accuracy, the other examined only 15 participants per group, which is sufficient for the goal of a neuroimaging study but behaviorally sparse. Besides these two studies, evidence only stems from few
studies on psychopathologic development with healthy adolescents as a control group (for a review see Miller, 2009). These adolescent control groups did not seem to perform at ceiling in the Eyes test at mean age of 11 years (Dorris, Espie, Knott, & Salt, 2004) respectively mean age of 15 years in both the Eyes and faux pas test (Botting & Conti-Ramsden, 2008), suggesting that there may be room for further improvement until young adulthood. However, methodically, all of these studies have employed the Eyes task in a child version, in which already 8-10 year-old children perform well. Although a more complex adult version exists (Baron-Cohen et al., 2001), it has not been employed in adolescents. Therefore, it is unclear, when adult-level performance is reached by adolescents. Taken together, it remains to be shown whether healthy adolescents differ from young adults on affective ToM performance in accuracy measures in more complex tasks. This was the aim of studies I and II of the current work.

1.3 Cognitive Mechanisms

Section 1.2 showed that both cognitive and affective ToM might continue to develop in adolescence until adulthood. However, for developmental psychology in general and most importantly for suggesting developmental theories, not only that there is a change in behavior is essential but also how and why this change occurs (Salthouse, 1991). How developmental changes occur is explained by change mechanisms underlying behavioral differences of age groups. A developmental theory tries to explain why developmental changes occur (Salthouse, 1991). Especially for the descriptive pattern of ToM development in adolescence, underlying change mechanisms are still under debate. Since ToM requires cognitive processes, it has been suggested that one potential set of change mechanisms are cognitive mechanisms. To solve more complex ToM tasks, an adolescent might need elaborate cognitive abilities. Two important domains of cognitive functions are (1) basic cognitive functions such as verbal ability, speed of processing, or working memory capacity, and (2) executive functions. These cognitive constructs are related to each other since executive functions might orchestrate basic cognitive processes during goal-oriented problem-solving (Neisser, 1967). In the following two sections, these two relevant cognitive constructs, which might be related to ToM development in adolescence, will be defined, and evidence of the relationship will be presented.
1.3.1 Basic Cognitive Functions

The first type of cognitive function mechanisms which may underlie ToM development across adolescence are basic cognitive functions. Specifically, the current focus lies on verbal ability, speed of processing and working memory capacity since these measures seem to have a prolonged developmental trajectory across adolescence and have been suggested to be related to ToM development (Davis & Pratt, 1995; de Sonneville et al., 2002; Milligan, Astington, & Dack, 2007). This section summarizes the theoretical and empirical background that suggests these three basic cognitive functions underlie ToM development in adolescence. It has to be noted, however, that almost all of the literature investigates cognitive ToM (mostly by use of the false belief task). Therefore, the distinction of these two processes will be abandoned within section 1.3.1.

1.3.1.1 Verbal ability

Verbal ability, the basic cognitive ability to use and understand language, might be related to ToM in two possible ways. First, one interpretation of the role of verbal ability in ToM is that linguistic resources may be required for the cognitive processes of ToM throughout development, i.e. also in adulthood (Smith, Hermelin, & Tsimpili, 2003). For example, syntactic structures for sentence understanding might be relevant for ToM (Newton & de Villiers, 2007). Another hypothesis is that verbal ability might support the expression of ToM in childhood, e.g., with getting to know the conversational use of mental state words (Astington & Baird, 2005). Thus it might be no longer relevant in adults. A recent meta-analysis revealed that the correlation of verbal ability and ToM (mostly measured by false-belief tasks) yielded a moderate effect size for children until the age of seven (Davis & Pratt, 1995; Milligan et al., 2007). The direction of the relationship suggests that verbal ability is causal for ToM development: Early language predicted later false belief more strongly than the reverse (Milligan et al., 2007). Moreover supporting this direction, training on verbal ability improved false-belief understanding in preschoolers (Hale & Tager-Flusberg, 2003). Verbal ability also seems to play a role for higher-order ToM. For example, it has been suggested, that verbal ability affects the expression of second-order ToM (Lockl & Schneider, 2007). Advanced ToM tasks and verbal ability have also been shown to be correlated (Filippova & Astington, 2008). However, while these studies have investigated the relationship of ToM and verbal ability in childhood, the developmental period of adolescence has been spared. Two lines of evidence support a continuing relationship of ToM and verbal
ability in adolescence. First, verbal ability continues to improve during adolescence (Clark et al., 2006; Levin et al., 1991). Second, verbal ability has been shown to be related to advanced ToM in young adults (Ahmed & Miller, 2011). Specifically, verbal fluency predicted performance of affective (faux pas) and cognitive (social stories) ToM (Ahmed & Miller, 2011). An examination of the relation of verbal ability and cognitive and affective ToM in adolescence remains open.

1.3.1.2 Speed of processing

Furthermore, speed of processing might represent a second important basic cognitive resource underlying development of ToM. In daily communication, information about mental states is expressed continuously and may thus put high demands on an individual’s processing capacity. Slow processing of social cues might have serious negative impact on social interaction and its development. For example, if too much time and attention are spent interpreting one facial expression, other facial expressions of greater affective importance may be missed during this time interval (Nowicki & Cooley, 1990). Corroborating this suggestion, speed of emotion recognition in children aged seven to 10 years was slower than that of adults, partly associated with lower accuracy (de Sonneville et al., 2002). The relationship of speed of processing and affective or cognitive ToM across adolescence still awaits investigation. It is important to note in this regard that speed of processing is still under development in adolescence; 12 and 13-year-olds have been shown to respond more than one standard deviation slower than young adults (Kail, 1991). Further, from a neuropsychological perspective, the increase in cognitive speed throughout adolescence might be mirrored in the ongoing process of myelination, the formation of the myelin sheath around axons, which speeds neuronal transmission (Mabbott, Noseworthy, Bouffet, Laughlin, & Rockel, 2006).

1.3.1.3 Working memory capacity

Finally, the third basic cognitive mechanism of ToM might be working memory capacity\(^1\) (Baddeley, 2003). ToM requires individuals to keep relevant social information in mind and flexibly evaluate and process this information concurrently. A relationship of working

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\(^1\) The current work distinguishes between working memory capacity as a basic cognitive function and updating as a (higher-order) executive function. Here, working memory capacity (e.g., in complex span tasks such as counting span used in study I) encompasses the ability to simply add new information to the memory set without any further operation to substitute (update) the information. In contrast, updating (such as in the letter memory task used in study II) requires to flexibly and continuously monitor and modify the content of the working memory store with regard to current task requests (Carretti, Belacchi, & Cornoldi, 2010; Morris & Jones, 1990).
memory capacity and ToM, mostly measured with false belief tasks, has been indicated in preschoolers (Davis & Pratt, 1995; Gordon & Olson, 1998; Keenan, Olson, & Marini, 1998). Keenan et al. (1998, p. 81) noted “it is likely that working memory has some role in the developing ability to express those concepts, and perhaps in the ability to form newer, more complex theories of mind”. For working memory capacity the relationship with affective and cognitive ToM across adolescence is largely unknown.

Taken together, there is a lack of research on the relation between these three basic cognitive abilities and the development of affective and cognitive ToM across adolescence. Therefore, the current study I was aimed at elucidating this relationship.

1.3.2 Executive Functions

As has been indicated in section 1.3.1, there is some evidence of a relation of basic cognitive functions and ToM in adolescence. Moreover, it seems to be even more plausible, that more complex cognitive abilities might show a stronger relation with adolescent ToM development. This second type of possible cognitive function mechanisms of ToM development across adolescence are executive functions. Executive functions are higher-level cognitive processes that are important for goal-directed thoughts and actions (Zelazo, Müller, Frye, & Marcovitch, 2003). According to a structural equation model analysis, three clearly separable but moderately correlated executive functions have been suggested: inhibition, updating, and shifting (Miyake et al., 2000). This structure has been corroborated by studies on adults and adolescents (Duan, Wei, Wang, & Shi, 2010; Friedman et al., 2006; Miyake et al., 2000). Inhibition is the ability to deliberately suppress pre-potent, but currently irrelevant responses. Updating requires monitoring of information and replacing irrelevant information with newer task-relevant information in working memory. Shifting encompasses the ability to flexibly shift back and forth between multiple tasks or mental sets. Evidence suggesting the relationship of executive functions and ToM in adolescence is summarized in the following.

It is plausible that all three executive function facets are required for ToM processing. First one’s own dominant perspective has to be inhibited in order to understand the others’ mental state. Second, the relevant information has to be updated in working memory to appreciate current and past information of a person’s mental state. Third, it is crucial to shift between one’s own and the other’s perspective. Indeed, several studies have shown a positive correlation of preschool children’s cognitive ToM and executive functions with an overall strong effect size of 1.08 (see the meta-analysis of Perner & Lang, 1999). Specifically,
research has found inhibition (Carlson & Moses, 2001; Cole & Mitchell, 2000), updating (Davis & Pratt, 1995; Gordon & Olson, 1998), and shifting (Cole & Mitchell, 2000) to be associated with children’s cognitive ToM, almost exclusively operationalized with false belief tasks. The direction of this relationship suggests executive functions lead to a better ToM. For example, children’s executive functions longitudinally predicted ToM performance (Hughes, 1998). While these findings indicate a robust relationship between executive functions and cognitive ToM development, the relationship of affective ToM and executive functions remains unresolved.

Moreover, specifically affective ToM might be related to ongoing development of executive function in adolescence since affective ToM develops relatively late in contrast to cognitive ToM as has been shown in section 1.2. However, the role of executive functions in affective ToM development in adolescence is unclear. This is surprising, given that affective ToM and its cognitive mechanisms are most relevant for this age span. The regulation of one’s own automatic and pre-potent emotions and thoughts is required for affective ToM (Ochsner & Gross, 2005). A lack of regulation in affective situations might be demonstrated by heightened risk taking in adolescence (Steinberg, 2005). Thus, adolescence has been labeled a critical or sensitive period in the development of regulation of affect and behavior (Steinberg, 2005). Corroborating this notice, affective psychopathology often has its onset in adolescence (Paus et al., 2008). Therefore, a continuing development of regulatory mechanisms, i.e. executive functions, might drive the development of affective ToM across adolescence.

One line of evidence that supports this prediction stems from recent studies, suggesting executive functions and affective ToM might be (still) related in young adults. For example, performance on the Eyes test (Baron-Cohen et al., 2001) was impaired by simultaneous performance of an inhibition task (Bull, Phillips, & Conway, 2008). Further, different aspects of executive functions were related to performance on the Eyes test and the Faux pas test (Ahmed & Miller, 2011).

However, the supported relation of ToM and executive functions in adolescence might be supported by the fact that in this age span executive functions continue to develop (e.g. Luna, Garver, Urban, Lazar, & Sweeney, 2004). Specifically, updating has been found to increase linearly until age 15 (Gathercole, Pickering, Ambridge, & Wearing, 2004) or even until age 19 (Luna et al., 2004). Further, shifting was found to increase into adolescence (Huizinga, Dolan, & van der Molen, 2006) and even into young adulthood (Rubia et al., 2006). Finally, several
studies also show an increase in inhibition across adolescence (Adleman et al., 2002; Luna et al., 2004; Velanova, Wheeler, & Luna, 2008). This prolonged behavioral development is thought to be mirrored in differential neural activity in adolescents in comparison to adults, mainly in the dorsolateral prefrontal cortex (DLPFC; see Luna, Padmanabhan, & O'Hearn, 2010 for a recent review). The DLPFC is a region, which is important for processing executive functions (Carter & van Veen, 2007).

Taken together, this evidence suggests that a possible mechanism of affective ToM development across adolescence might be executive functions. Since no study has yet investigated this relationship, the current study II followed up on this question.

### 1.4 Neurocognitive Mechanisms

As has been indicated in section 1.3, cognitive mechanisms might underlie ToM development in adolescence. However, it is still under debate which specific cognitive abilities are mechanisms of ToM development. A complementary second set of potential change mechanisms, closely related to cognitive mechanisms, might help to explain developmental changes. These are neurocognitive mechanisms.

The methodical approach to explore these mechanisms is the investigation of functional brain processes. To this end, the methodology of fMRI might help both in elucidating neural descriptive development and in revealing possible neurocognitive mechanisms across adolescence. This is because fMRI allows detecting neural processes while adolescents solve the task in the scanner and compare them to adults’ neural processes.

Nevertheless, the pediatric application of MRI in children and adolescents is a quite recent advance (Gaillard, Grandin, & Xu, 2001; Luna, Velanova, & Geier, 2010). This is due to the great sensitivity of MRI to movement artifacts, which are specifically likely in younger populations such as adolescents (Luna et al., 2010). However, by use of new technologies, mock scanners, and child-friendly scanner environments many research groups to date are able to examine younger subjects (Schlund et al., 2011). Moreover, although there has been an increase of methodical expertise for the analysis of developmental fMRI data (see special issue of Human Brain Mapping, Volume 31, Issue 6, 2010), methodical standards are still under debate. For example, it is unclear how best to deal with the problem of unequal performance between groups (Church, Petersen, & Schlaggar, 2010). Matching participants with similar performance has been suggested (Schlaggar et al., 2002) but has only been
employed in a few child studies so far (e.g., Braet et al., 2009). This method seems to be a
fruitful approach for studies of adolescent and adult groups and the current topic of ToM. The
fMRI study (study III) of this thesis sought to employ this approach and therefore to face
methodical challenges related with developmental studies.

Besides these methodical advances, there has been a conceptual progress, which is highly
relevant for ToM development across adolescence. This recent advance is related to the
finding of a massive structural brain development across adolescence, which might be related
to functional brain development (Blakemore, 2008). This structural brain development has
been revealed by longitudinal and cross-sectional MRI studies (Gogtay et al., 2004; Sowell et
al., 2003; Tamnes et al., 2010). Specifically, the volume of grey matter seems to develop in an
inverted U-shaped pattern, increasing during childhood, reaching its peak around puberty
onset and decreasing again until young adulthood (Casey, Jones, & Hare, 2008). It has been
suggested that this process of neural plasticity might foster the development of ToM during
adolescence (Burnett, Sebastien, Kadosh, & Blakemore, 2011). Especially these brain regions
involved in ToM processing, including the prefrontal and superior temporal cortex, undergo
the most pronounced and protracted transformation (Gogtay et al., 2004). These structural
findings across adolescence have inspired first studies to investigate functional brain
development of ToM processing in this age span as will be shown in the next section.

1.4.1 Functional brain development of ToM

Functional changes regarding ToM, which might be observed in adolescents in comparison
to adults, might indicate that ToM is processed differently, i.e. is still developing in
adolescence. Recently, fMRI studies have started to investigate ToM development across
adolescence, mainly focusing on cognitive ToM (Blakemore, 2012). However, affective ToM
remains largely under-examined. This is surprising, given that behaviorally affective ToM
seems to show a prolonged developmental trajectory. Therefore, one specific aim of this thesis
(study III) was to investigate the functional processing of affective ToM. Accordingly, the
following review will specifically focus on affective ToM.

Results of the specific neural region differing between adolescents and adults might reveal
ongoing development of underlying cognitive processes. In this regard, the MPFC has
consistently been shown to functionally differ in ToM processing between adolescents and
adults (Blakemore, 2012). The MPFC is an important region for ToM processing in adults
(Amodio & Frith, 2006; Gallagher & Frith, 2003). Interpretations of this finding suggest
different neural processing strategies between adolescents and adults. However, interpretations regarding neural strategies rest on the specific type of activation (e.g., deactivation). These interpretations will be specified in section 1.4.2. Developmental findings on cognitive ToM consistently indicate an increased activity in the dorsal part of the MPFC, the dMPFC in adolescents in comparison to adults (Blakemore, 2008). These studies employed cognitive ToM tasks such as the evaluation of self-knowledge (Pfeifer et al., 2009), intentions (Blakemore, den Ouden, Choudhury, & Frith, 2007), or trust (van den Bos, van Dijik, Westenberg, Rombouts, & Crone, 2011).

However, for affective ToM, the specific neural region under development is rather unclear. Evidence from adult lesion studies suggests that the vMPFC is specifically relevant for affective ToM. Concurrently, patients with vMPFC lesions appear to be impaired on recognizing affective mental states such as emotions (Heberlein, Padon, Gillihan, Farah, & Fellows, 2008), or a faux pas (Shamay-Tsoory et al., 2006; Shamay-Tsoory & Aharon-Peretz, 2007; Stone et al., 1998). Further evidence for the involvement of the vMPFC in affective ToM stems from anatomical (Bandler, Keay, Floyd, & Price, 2000; Price, 2007) and functional studies (Hynes, Baird, & Grafton, 2006). However, it is still unclear if the vMPFC specifically shows ongoing development for affective ToM across adolescence since previous findings are heterogeneous. While one study on affective ToM development in adolescence observed dMPFC involvement (Wang, Lee, Sigman, & Dapretto, 2006), another found both the dMPFC and the vMPFC (Gunther Moor et al., 2012), and a third one observed increased activity of the vMPFC (Sebastian et al., 2012). Divergent findings might be due to methodical problems such as different age groups across studies or too simplistic paradigms (Crone, Poldrack, & Durston, 2010). Overall, neural development of affective ToM across adolescence requires further investigation. The finding of an ongoing functional brain development of affective ToM would also be able to corroborate findings from behavioral studies in fostering the result of an overall ongoing affective ToM development. Therefore, the aim of study III was to investigate this aspect of ToM more thoroughly. Methodically, challenges placed by developmental fMRI studies such as matching performance will be faced.

### 1.4.2 Integrating behavioral and functional brain studies

Recently, several authors have argued for an integration of behavioral and functional brain findings of development (Crone & Ridderinkhof, 2011; Pfeifer & Allen, 2012). Moreover,
new theoretical frameworks like the Interactive Specialization Theory (Johnson, 2011) suggest that the integration might help in exploring cognitive mechanisms underlying development. Cognitive theories could profit from the conceptual inclusion of neural data (Johnson, 2011). Therefore, the investigation of the development of neural processes of ToM across adolescence is not only another methodical approach, but adds conceptual depth to the behavioral findings.

Still, most of the findings remain to be discussed within their own research tradition only. This might be due to the methodical challenges and interpretational caveats for neuroimaging data (Crone & Dahl, 2012c; Pfeifer & Allen, 2012; Poldrack, 2011). However, first attempts have been made to interpret findings on developmental fMRI studies across adolescence with regard to possible underlying cognitive mechanisms. For both affective and cognitive ToM development across adolescence, as has been indicated in section 1.4.1, the overall pattern of findings seems to be a stronger activation (here of the MPFC) in adolescents in comparison to adults (Blakemore, 2008, 2012). For this neural pattern, which has been found across diverse developmental domains such as cognitive control (Durston & Casey, 2006) one general and widely accepted interpretation is the focalization hypothesis (Durston et al., 2006). This hypothesis states that neural activity, which is more diffuse in adolescents, changes to a more focal neural activity in adults. With increasing age a reduced magnitude and extent of activation of areas not critical to the task is observed. Additionally, the magnitude but not the extent of activation in task-central regions increases until adulthood. Closely related to the focalization hypothesis is the concept of neural efficiency: whereas more effortful computation is required in the “immature”, e.g., adolescent brain rather effortless and more automatic processing is observed in the adult brain. However, recently, this interpretation has been criticized (Crone & Dahl, 2012a; Pfeifer & Allen, 2012) since new evidence does not seem to support it. For example, increasing spatial extent and a greater distribution of areas has been found for adults in emotional and cognitive challenge (Strang, Pruessner, & Pollak, 2011).

The finding of greater neural activity in adolescents has been found across different developmental research topics, however, as indicated above is not uncontroversial. A partly contrasting result has been observed specifically for ToM development in adolescence; this result remains challenging to explain: when analyzing the neural response profiles in both affective and cognitive ToM studies in detail, the MPFC seems to be deactivated for ToM in adults but to a lesser extent for adolescents (Blakemore, den Ouden, Choudhury, & Frith, 2007; Sebastian, 2012). One possible explanation refers to the MPFC as a region that is part
of the default-mode network (Greicius, Krasnow, Reiss, & Menon, 2003; Raichle et al., 2001): Deactivations of default-mode network regions suggest less self-related thoughts (Buckner et al., 2008). Thus, in adolescents, less deactivation might implicate *more self-related thoughts* when solving the ToM task. However, this finding still needs to be replicated, and the interpretation of the deactivation pattern is complex.

Another interpretation of data on neural ToM development might imply that there is a change across adolescence in the *modulation of ToM by executive functions* (Blakemore, 2008). This interpretation rests on a study, which showed that dependent on the instruction to attend to emotional or non-emotional features of emotional faces, neural activity was differentially affected in adolescents and adults (Monk et al., 2003). Specifically, adolescents’ activity was modulated by the emotional content of the stimulus while adults’ activation was related to task demands. Although this is an interesting interpretation, this specific finding still calls for replication.

Taken together, importantly, these attempts to integrate findings from behavioral and functional brain studies on adolescent ToM development are only preliminary. Partly, these interpretations contradict each other such as the focalization/neural efficiency hypothesis and the interpretation of less deactivation. However, although speculative, the interpretations provide new perspectives on underlying mechanisms of adolescent ToM development. Given these first promising attempts, the present work aimed to fill the gap on ToM research in adolescence from two perspectives - the behavioral and functional brain level - and tried to integrate the findings with regard to potential mechanisms.
2 Outline and Central Questions

The previous introductory chapter 1 summarized the current theoretical and empirical state of the art both on the behavioral and the level of functional brain imaging on ToM development across adolescence. Additionally, potential (neuro)cognitive mechanisms of ToM development were outlined suggested by both areas of research. However, as has been emphasized, the field is still in its infancy. Thus, major questions regarding ToM development across adolescence remain to be answered. First, the current thesis set out to answer the overall question whether there is an ongoing development of ToM across adolescence. This major question relates to both behavioral and functional brain development. As a second major question, the present work sought to elucidate possible (neuro)cognitive mechanisms of ongoing ToM development across adolescence. Specifically, these cognitive mechanisms might be basic cognitive functions as well as executive functions. Additionally, the present work aimed at exploring potential (neuro)cognitive mechanisms through an integration of both behavioral and functional brain studies. The current experimental work spans three cross-sectional studies investigating adolescents and young adults to examine for the first time both the behavioral and brain functional development of ToM across adolescence and its underlying (neuro)cognitive mechanisms. Studies I and II focused on the behavioral level, study III investigated the functional brain development. In study I, large samples of adolescents and adults were compared on both cognitive and affective ToM measures, and basic cognitive functions were explored as possible mechanisms. Study II comprised a large population of both adolescents and adults, focused on affective ToM development and explored executive functions as possible underlying mechanisms. Finally, study III was an fMRI study, which compared an adolescent and an adult age group on an affective ToM measure, which was adapted from study II.

2.1 Does ToM continue to develop in adolescence?

The first overall question whether ToM continues to develop across adolescence can be divided into the following two sub-questions on behavioral (2.1.1) and functional brain (2.1.2) development:

2.1.1 Does ToM continue to develop on the behavioral level?

It still remains an open question whether there is a behavioral development of ToM in adolescence. The descriptive pattern of both affective and cognitive ToM development across
adolescence has only recently been investigated by a handful of studies. Specifically, very few studies to date have investigated cognitive ToM in adolescence and concentrated on the aspect of perspective taking only. Therefore, the current study I aimed at investigating whether there is an ongoing development of cognitive ToM on a new aspect, namely understanding complex social stories. Moreover, affective ToM has been suggested to show a specifically prolonged behavioral trajectory, making it particularly interesting to investigate adolescents. However, to date, only two studies have targeted ongoing affective ToM development across adolescence (Keulers et al., 2012; Sebastian et al., 2012). Therefore, both studies I and II aimed at investigating the ongoing development of affective ToM more thoroughly. New aspects of affective ToM were investigated spanning understanding emotions expressed in the eye region as well as evaluating dynamic facial emotions. The latter aspect is specifically interesting since it is ecologically valid, a feature which is lacking in most previous studies on affective ToM.

Methodically, this question was targeted by specific conceptual and methodical improvements with regard to previous literature. First, both cognitive and affective aspects of ToM were investigated within the same sample (study I). Moreover, to avoid ceiling effects in all studies advanced ToM paradigms were employed. Further, the focus was on accuracy measures in both studies and more narrow age groups of adolescents and adults were investigated (study I).

2.1.2 Does ToM continue to develop on the level of brain function?

Functional brain studies to date have posed the question whether functional ToM processing continues to develop in adolescence. Although some studies have shown continued MPFC development for cognitive ToM, affective ToM development seems rather under-investigated. Specifically it remains open if there is a neural region continuing to develop for the processing of affective ToM. The vMPFC, which is an important region for affective ToM in adults, has been suggested by first studies. However, findings remain inconsistent (Sebastian et al., 2012; Wang et al., 2006). Therefore, study III sought to elucidate if there is an affective region showing ongoing development, and if so, whether it is the vMPFC.

Methodically, since the affective ToM paradigm in study II proved to be developmentally sensitive, this dynamic paradigm was adapted to fMRI purposes and employed in study III. This enabled comparability between behavioral and functional brain development. Importantly, it enabled to face a methodical challenge regarding developmental fMRI studies,
i.e. to employ developmentally sensitive paradigms to be able to systematically compare performance and subsequently match groups regarding performance (Schlaggar et al., 2002).

### 2.2 What are (neuro)cognitive mechanisms of ToM development in adolescence?

The second overall question, what might be (neuro)cognitive mechanisms underlying ToM development in adolescence was targeted by two sub-questions. First of all, in the current behavioral studies it was asked whether two types of cognitive functions underlie ToM development, i.e. basic cognitive and executive functions (2.2.1). Second, functional brain findings might contribute to the investigation of cognitive mechanisms (Johnson, 2012) by revealing possible underlying neural processing strategies (e.g. Durston, 2006). Therefore, an integration of behavioral findings and functional brain findings was aimed at (2.2.2).

#### 2.2.1 What are basic cognitive and executive functioning mechanisms?

It is in question if possible cognitive mechanisms of ToM development across adolescence might be basic cognitive functions and/or executive functions. However, no study to date has systematically investigated these possible mechanisms. First results suggest *basic cognitive functions* might be mechanisms of cognitive ToM development in childhood. To extend these findings to adolescence, study I was set out to systematically test basic cognitive functions, specifically verbal ability, working memory capacity, and speed of processing as potential mechanisms underlying cognitive and affective ToM development across adolescence. Moreover, it remains open, which mechanisms underlie affective ToM with its prolonged developmental trajectory. No study has yet systematically investigated the influence of the three aspects of executive functions inhibition, updating, and shifting following the conceptualization of Miyake et al. (2000) on affective ToM in adolescence. Therefore, study II aimed at elucidating the role of each of these three potential executive functioning mechanisms on affective ToM development across adolescence.

#### 2.2.2 Can mechanisms be concluded from the integration of behavioral data and functional brain processes?

Finally, the current work sought to explore if specific cognitive mechanisms are revealed by closer inspection and interpretation of functional brain processes. Although this was an exploratory aim, it followed the recent call for more integration of behavioral and functional
brain findings (e.g., “A final useful direction is to foster greater integration of theories and empirical findings from developmental (...) research conducted outside the cognitive neurosciences“, Pfeifer & Allen, 2012, p. 326). Given that there are some theories to interpret functional brain data with regard to cognitive mechanisms such as the focalization hypotheses (Durston, 2006), the aim was to explore these interpretations. Vice versa, the findings from the two possible sources of cognitive basic and executive function mechanisms were aimed to be compared and discussed with the neuroimaging data. Interpretations can only remain speculative; however, they possibly enable perspectives for future studies.
3 Study I – ToM Development in Adolescence and its Basic Cognitive Mechanisms

3.1 Introduction

Social cognition, the ability to understand intentions, beliefs, and emotions, is one of the core abilities of interpersonal functioning. It is essential in everyday life as it allows us to predict other people's behavior and to adjust behavior adequately. Central research topics in social cognition are theory of mind (Perner, 1991; Premack & Woodruff, 1978) and emotion recognition (Adolphs, 2003). Theory of mind requires the ability to understand others' mental states. Emotion recognition, on the other hand, is the ability to decipher emotional expressions of others. Importantly for present purposes, both theory of mind and emotion recognition show marked developmental changes across childhood; yet, possible ongoing development across adolescence is less well documented.

Theory of mind studies have focused on the emergence of children's understanding that others' mental states may differ from their own. Prior research showed that children begin to develop a theory of mind at the age of four years (Wellman et al., 2001). About the age of six years, this ability starts to become more elaborated with the development of a higher order theory of mind (Perner & Wimmer, 1985), which is necessary to understand complex mental states like irony (Happé, 1994). A protracted development of higher order theory of mind has been found at about eight to 10 years (Rieffe et al., 2005) when children begin to understand social faux pas (Baron-Cohen et al., 1999). Whether there is an ongoing development of theory of mind skills beyond this age is a topic of the current research.

The ability to distinguish and respond to basic emotions, such as happiness and sadness, already starts to develop at a remarkably young age of just a few months (Nelson, 1987). Throughout childhood, basic emotion recognition gradually improves (Herba & Phillips, 2004) with a large increase between five and 10 years of age (Gao & Maurer, 2010). More complex, so-called belief-based emotions such as embarrassment, guilt, or pride (which are closely connected to mental states, such as intentions or beliefs; Baron-Cohen et al., 2001) are recognized earliest from an age of about seven years on (Hadwin & Perner, 1991).

Surprisingly, the development of theory of mind and emotion recognition beyond childhood remains largely underexamined. Particularly, there is a lack of data on how these skills develop across adolescence (see also Blakemore & Choudhury, 2006; Moriguchi,
Ohnishi, Mori, Matsuda, & Komaki, 2007). This absence of research is especially remarkable as adolescence represents a phase of major physical (i.e., pubertal) but also cognitive and socio-emotional changes that constitute the transition from a dependent child to an autonomous adult. During this period, adolescents become more self-conscious (Steinberg & Morris, 2001) and develop more complex peer relationships and peer interactions, which require adequate social awareness and behavior (Lerner & Steinberg, 2004).

Recent developmental neuroscience research also supports the prediction of ongoing developmental changes in theory of mind and emotion recognition across adolescence. Specifically, magnetic resonance imaging (MRI) studies show that the brain regions involved in social cognition, including the prefrontal and temporal cortex, undergo the most pronounced and protracted transformation (Gogtay et al., 2004) across adolescence. It has been suggested that this process of neural plasticity might foster the development of social cognition during adolescence (Blakemore, 2008). Functional MRI studies have also shown differential neural activity in tasks of social cognition in adolescence in comparison to adulthood (Moriguchi et al., 2007). In particular, higher activity in adolescents versus adults in a key brain area for social cognition, the medial prefrontal cortex, was observed in a range of studies (Blakemore, 2008). Regarding facial emotion processing, there is evidence for a greater amygdala activity in adolescents versus adults during passive viewing of fearful faces (Guyer et al., 2008).

Behavioral research has initially confirmed protracted development of social cognition in adolescence. For instance, a continued improvement in recognizing facial displays of emotion throughout childhood until early adolescence (i.e., 10–12 years, Kolb, Wilson, & Taylor, 1992; 13 years, Rosenberg-Kima & Sadeh, 2010) or even until adulthood has been reported (Williams et al., 2009). This prolonged development is mainly for negative facial expressions such as fear, anger, sadness, and disgust. Importantly, however, the development of recognition of more elaborated complex or belief-based emotions has not been investigated above the age of 10 years. Therefore, we sought to investigate the ability of complex emotion recognition of adolescents and to compare it with that of young adults.

Recently, studies started to investigate the development of different aspects of theory of mind across adolescence. In a first study, participants were asked to take their own versus another's perspective in everyday scenarios (Choudhury et al., 2006). Adolescents' differences in reaction times between these two perspectives were greater than adults' differences. This
was interpreted in terms of less efficient perspective taking. Another study presented situations and their consequences (Keulers et al., 2010) and found a decrease in the time participants took to decide the appropriateness of the resulting emotion throughout adolescence. Moreover, within groups of adolescents selected as controls in autism studies, age correlated positively with performance on a theory of mind story test (Kaland et al., 2005; Kaland et al., 2007). It has also been shown that an adult control group had a higher accuracy than an older children's group on an advanced theory of mind story test (Happé, 1994). Hence, theory of mind abilities may improve across adolescence. However, this has mostly only been shown by use of reaction times (Choudhury et al., 2006; Keulers et al., 2010).

Taken as a whole, the descriptive pattern of the development of social cognition in adolescence remains underspecified. Moreover, studies often only focus on one specific aspect, like perspective taking or recognition of basic emotions. It has been suggested that one reason for the current paucity of research might be the lack of appropriate developmental tests for this age group; that is, tests that are more elaborated and therefore avoid ceiling effects (Thomas, De Bellis, Graham, & LaBar, 2007). Consequently, the first aim of the current study is to examine age differences in the domain of social cognition covering both theory of mind and emotion recognition using those tests that prior research has shown to be most sensitive for the age groups of interest. Here, we are focusing on accuracy measures since this aspect has previously been underexamined.

For the domain of theory of mind, we will apply the Story Comprehension test (Channon & Crawford, 2000) that consists of rather difficult social stories that resemble real-life situations (see also Happé et al., 1994). The current study is the first to employ it to compare adolescents' and adults' theory of mind abilities. In contrast to previous tests mostly using Ekman faces, for emotion recognition the “Reading the Mind in the Eyes” test (Baron-Cohen et al., 2001) will be employed. This established test sensitively assesses the ability to recognize complex emotions and taps into aspects of theory of mind, requiring the correct attribution of mental states. It has been shown to be sensitive enough to measure an age-related decline in accuracy from young to old-aged adults (Pardini & Nichelli, 2009). To our knowledge, the current study is the first to employ the “Reading the Mind in the Eyes” test to assess adolescents' versus adults' abilities to recognize complex emotions.

As a second aim, we will investigate the influence of puberty on theory of mind and emotion recognition. While adolescence is defined socioculturally, puberty is defined as the
process of physical changes leading to sexual maturation. Some previous studies suggest a pubertal “dip” that is slowed performance in an emotion perception task in pubertal as opposed to pre- and postpubertal adolescents (McGivern, Andersen, Byrd, Mutter, & Reilly, 2002). Also in the recognition of faces mid-pubertal girls performed worse than pre- or postpubertal girls in an early study (Diamond, Carey, & Back, 1983). This dip can be interpreted either in terms of underlying changing brain mechanisms (McGivern et al., 2002), that is, grey matter volume peak at the onset of puberty, or as a change in social interest due to one's awareness of own pubertal changes (Diamond et al., 1983). In contrast to studies employing facial stimuli, theory of mind studies have not found a pubertal dip but an increase of speed across adolescence (Choudhury et al., 2006; Keulers et al., 2010). Noteworthy however, only Diamond et al. and Keulers et al. measured pubertal phase quantitatively. Given previous evidence, we predict that tasks involving facial emotions (i.e., Eyes test) might be more sensitive to a possible pubertal dip in performance than tasks measuring theory of mind (i.e., Story Comprehension).

Our third aim is to investigate whether age effects on social cognition tasks are influenced by the development of more basic cognitive abilities. It is important to establish whether adolescent changes in social cognition may reflect well-documented developmental changes in cognitive-processing resources such as working memory, processing speed, and verbal ability. Working memory (Baddeley, 2003) was investigated because continued development of working memory has been found throughout adolescence (Gathercole et al., 2004; Luna et al., 2004). Also, tasks of social cognition require the individual to keep relevant social information in mind and, at the same time, to flexibly evaluate and process this information. Studies in preschoolers indicate a relationship between working memory capacity and theory of mind abilities (Davis & Pratt, 1995; Gordon & Olson, 1998). Hence, working memory might play a role in adolescents' development of social cognition.

Similarly, speed of processing might represent a second basic cognitive resource covarying with the development of social cognition in adolescence. Effective social cognition not only depends on processing accuracy but also on processing speed as social interactions generally proceed rapidly. De Sonneville et al. (2002) investigated speed in a facial emotions task in older children in comparison to adults. They found slower speed of processing in children, which was partly associated with lower accuracy of emotion recognition. Moreover, 12- and 13-year-olds have been shown to respond more than a full standard deviation slower than
young adults (Kail, 1991). Thus, speed of processing might represent an important factor for the development of social cognition in adolescence.

Furthermore, verbal abilities were expected to potentially covary with social cognition measures. The role of language development in theory of mind has been shown in a recent meta-analysis (Milligan et al., 2007) with various aspects of language (e.g., semantics, general language) predicting theory of mind reasoning. The importance of language for theory of mind performance has been corroborated by a training study (Hale & Tager-Flusberg, 2003). Moreover, an elaborated verbal understanding of complex emotional words might be essential for correct processing of emotion recognition.

The major aim of the current study was (a) to measure the development of social cognition in adolescents in comparison to young adults. Given that social relationships change significantly during adolescence and that brain areas related to social cognition change both structurally and functionally, we predict an ongoing development in social cognition during adolescence. The second aim (b) was to explore a possible pubertal dip in social cognition. Here, we predicted a dip in emotion recognition associated with puberty but not in theory of mind. Further, we explored (c) whether the developmental effects on social cognition are independent from individual differences in cognitive abilities: working memory, processing speed, and verbal ability. We predicted that all three variables might influence age-related differences.

3.2 Method
3.2.1 Participants

The sample consisted of 120 participants: Sixty adolescents (23.3% male) aged 12 to 15 years ($M = 13.86, SD = 0.92$) and 60 young adults (18.3% male) aged 18 to 22 years ($M = 20.23, SD = 0.99$). All participants spoke German as their first language. Exclusion criteria (assessed by parental report for adolescents) were any psychiatric disorders such as autism spectrum disorder, attention deficit/hyperactivity disorder, depression, mania, or schizophrenia. Informed consent was obtained before participation from each participant and from either a parent or guardian for participants under 18. The study had been approved by the university ethics committee. Adolescent participants were recruited via flyers or personal advertisement in high schools and football clubs and adult participants via flyers at the university. Adolescents were in seventh and eighth grade, mostly attended a German high-
school type preparing for university and received monetary compensation. Adult participants comprised university undergraduate psychology students in their first year and participated for course credit. Groups did not differ with respect to gender, $\chi^2 (1, N=120) = 1.2, p = .274$. Further, groups did not differ regarding measures of socioeconomic parental background such as reported household education: mother's education: $\chi^2 (1, N=117) = 0.185, p = .667$; father's education: $\chi^2 (1, N=116) = 0.327, p = .568$; or numbers of books in their parent's house: $\chi^2 (1, N=120) = 0.443, p = .351$, being a proxy for parental cultural capital (De Graaf, De Graaf, & Kraaykamp, 2000). In accordance with the suggestions from the Wechsler Abbreviated Scale of Intelligence (WASI, Wechsler, 1999) was used to estimate general cognitive ability. Vocabulary and Matrices subtests from the Wechsler Adult Intelligence Scale for adult participants (WAIS, German adaptation, von Aster, Neubauer, & Horn, 2007) and the Wechsler Intelligence Scale For Children for adolescent participants (WISC-IV, German adaptation, Petermann & Petermann, 2007) were applied. Both age groups were comparable in their age-corrected verbal: $t(118) = -0.67, p = .541; M_{adolescents} = 13.70, SD_{adolescents} = 2.27; M_{adults} = 13.95, SD_{adults} = 1.9$, and nonverbal abilities: $t(118) = 0.66, p = .508; M_{adolescents} = 12.82, SD_{adolescents} = 2; M_{adults} = 12.58, SD_{adults} = 1.85$.

### 3.2.2 Materials

#### 3.2.2.1 Social cognition

#### 3.2.2.1.1 Theory of Mind

Seven out of twelve short vignettes of the Story Comprehension test (Channon & Crawford, 2000) translated into German by a professional translator were presented to participants and stayed continuously on view until the next story was presented. Pilot tests have shown that the excluded vignettes were not appropriate for cultural context or the age groups included in the study (for example, the story concerning queues at bus stops in Great Britain was excluded). Participants explained the statements of the main character in various everyday situations that was written down by the experimenter. This required the recognition of mental states of the characters. The story types included pretence, white lie, irony, threat, and dare. For example: “George went shopping at a supermarket and left the store with many bags when a man bumped into him. The bags dropped on the ground and George said to the man ‘Thanks a lot mate.’” Subsequently, the participant is asked, “Why did George say that?” Two blind independent raters classified the answers as correct, partly correct, and incorrect according to previously specified scoring guidelines, which were adopted from Channon and
Crawford and modified according to pilot data. A response was classified as correct (2 points) if words or actions of the story character were interpreted accurately and completely, as partly correct (1 point) if the interpretation was correct but not complete, or as incorrect (0 points) if the mental state was not recognized. Good agreement was reached (intraclass correlation coefficient = .90) between the two raters.

3.2.2.1 Emotion recognition

The “Reading the Mind in the Eyes” test with photographs showing eye regions was employed (adult version; Baron-Cohen et al., 2001; in a German translation by Bölte et al., 2005). It consists of seven complex emotions presented twice and all other 22 emotions presented once, that is, 36 items in total. Examples of correct adjectives are reflective, serious, and thoughtful. In each trial, four adjectives were presented. Participants selected out of these four adjectives (different distractors were presented for each item) the one that best describes the complex emotion of the person. Items were presented on a computer screen (using Presentation software) in a fixed order. There was no time limit, but participants were told to answer as accurately and fast as possible. A handout with all 74 emotional adjectives (containing distractors and target words) was provided at the beginning of the task. Participants had to indicate any words that they did not understand, which the experimenter then explained before starting the test procedure.

3.2.2.2 Pubertal development

The self-report questionnaire Pubertal Developmental Scale (PDS; Petersen, Crockett, Richards, & Boxer, 1988) employed in a German version (Watzlawik, 2009) was used to measure pubertal status in the adolescent age group. Three questions were assessed (for boys: body hair growth, voice change, facial hair growth; for girls: body hair growth, breast development, and menarche) with a four-point scale from one (maturation not started) to four (maturation completed). Menarche was measured dichotomously as “yes” (four points) or “no” (one point). The scores were classified in five stages: (1) prepubertal, (2) early pubertal, (3) midpubertal, (4) late pubertal, and (5) postpubertal. Following the procedure of Keulers et al. (2010) the five pubertal stages were recoded in three stages: prepubertal (1, 2), pubertal (3), and postpubertal (4, 5), in order to get an approximately equal distribution of the number of participants over the three pubertal stages.
3.2.2.3 Basis cognitive abilities

3.2.2.3.1 Working memory

In the Counting Span Test (Engle, Tuholski, Laughlin, & Conway, 1999), participants were required to count aloud the number of dark blue circles in a display that also contained light blue circles and dark blue squares. The amount of dark blue circles in each display was to be memorized until, after two to five counting displays, participants were prompted to recall them in order. The number of targets per display varied from three to nine. The number of color distractors (light blue circles) and the number of shape distractors (dark blue squares) also varied. Three practice trials and eight test trials were administered; memory load varied between two and five items. The partial-credit unit scores (i.e. the mean proportions of elements within a trial that were recalled correctly, PCU, see Conway et al., 2005) were chosen as dependent variables because of their high internal consistency.

3.2.2.3.2 Speed of processing

In the Identical Pictures Test (Ekstrom, French, Harman, & Dermen, 1976) participants had to compare simple line drawings. A target line drawing was presented on the left side and participants were required to identify the target drawing out of five similar drawings on the right side. Participants were instructed to press the response button associated with the identical drawing. A time limit of 90 s was imposed, and participants were instructed to solve as many problems correctly as possible from a maximum of 90 problems. The test was preceded by one practice item. The number of problems that were correctly solved within the given time served as the dependent variable.

3.2.2.3.3 Verbal ability

As described above, according to WASI (Wechsler, 1999) the Vocabulary subtests from the WAIS for adults (WAIS, German adaptation, von Aster et al., 2007) and from the WISC for adolescents (WISC-IV, German adaptation, Petermann & Petermann, 2007) were applied.
3.3 Results

3.3.1 Age Effects

For both tests of social cognition as well as for working memory and speed of processing, analyses of variance (ANOVAs) were performed including age group as a between-subjects variable.

3.3.1.1 Theory of mind

3.3.1.1.1 Story Comprehension Test

For the adolescent group, mean proportion of correct responses was lower ($M = 0.56$, $SD = 0.16$) than that of adults ($M = 0.65$, $SD = 0.17$). The ANOVA also revealed a significant effect of age group, $F(1,118) = 9.37$, $p < .01$, $\eta^2 = .074$. The model explains 7.4 % of variance ($r^2 = .074$). Analyzing single stories (see Table 1), significant differences between the age groups only emerged for complex mental states (e.g., elaborated white lies and irony). Analyses on the subgroup of female participants only also revealed a significant age group difference on both measures of social cognition.

Table 1: Mean Proportion of Correct Responses and Standard Deviations of Each Story for Story Comprehension Test.

<table>
<thead>
<tr>
<th>Story Number</th>
<th>Adolescents ($N=60$)</th>
<th>Adults ($N=60$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$M$ (SD)</td>
<td>$M$ (SD)</td>
</tr>
<tr>
<td>Story 1 (pretence)</td>
<td>.52 (.33)</td>
<td>.55 (.34)</td>
</tr>
<tr>
<td>Story 2 (threat)</td>
<td>.53 (.30)</td>
<td>.52 (.33)</td>
</tr>
<tr>
<td>Story 3 (irony)</td>
<td>.79 (.30)</td>
<td>.83 (.26)</td>
</tr>
<tr>
<td>Story 4 (dare)</td>
<td>.47* (.30)</td>
<td>.59 (.33)</td>
</tr>
<tr>
<td>Story 5 (white lie)</td>
<td>.37** (.33)</td>
<td>.60 (.33)</td>
</tr>
<tr>
<td>Story 6 (excuse)</td>
<td>.64 (.38)</td>
<td>.66 (.39)</td>
</tr>
<tr>
<td>Story 7 (elaborated irony)</td>
<td>.63* (.46)</td>
<td>.80 (.36)</td>
</tr>
</tbody>
</table>

* Means for the adolescent group differ significantly from the adult group mean ($p < .05$).
** Means for the adolescent group differ significantly from the adult group mean ($p < .01$).
3.3.1.2  Emotion recognition

3.3.1.2.1  Eyes Test

Also for this test, the adolescent group scored lower in mean proportion of correct responses ($M = 0.63$, $SD = 0.12$) than the adult group ($M = 0.74$, $SD = 0.08$). The ANOVA showed that the effect of age group was significant, $F(1,118) = 35.83$, $p < .001$, $\eta^2 = .23$. The model explains 23.3 % of variance ($r^2 = .233$). Analyses on the subgroup of female participants only also revealed a significant age group difference on both measures of social cognition.

3.3.1.3  Working memory

Comparison of the groups regarding working memory performance with an ANOVA revealed no significant effect of age group, $F(1,118) = 1.5$, $p = .223$, partial $\eta^2 = .013$, indicating similar working memory capacity in adolescents ($M = 0.78$; $SD = 0.14$) and adults ($M = 0.81$; $SD = 0.14$). The model explains 1.3 % of variance ($r^2 = .013$).

3.3.1.4  Speed of processing

The ANOVA showed that the effect of age group was significant, $F(1,118) = 33.78$, $p < .001$, partial $\eta^2 = .223$, indicating slower processing in adolescents ($M = 31.92$; $SD = 4.15$) in comparison to adults ($M = 36.88$; $SD = 5.16$). The model explains 22.3 % of variance ($r^2 = .223$).

3.3.2  Influence of puberty on social cognition

3.3.2.1  Theory of Mind

For Story Comprehension and the comparison of the three pubertal groups, the ANOVA revealed no significant effect of pubertal stage, $F(2,57) = 0.84$, $p = .437$, partial $\eta^2 = .029$, indicating similar Story Comprehension performance across pubertal stages. The model explains 2.9 % of variance ($r^2 = .029$). Performance on Story Comprehension increased slightly across the three pubertal stages (Figure 3). No pubertal dip was observed. Even when controlling for age there was significant influence of pubertal stage on both measures of social cognition.
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Figure 3: Accuracy for pubertal clusters on the Story Comprehension test. Story C. = Story Comprehension; prepubertal adolescents: n = 9; pubertal adolescents n = 18 and postpubertal adolescents = 33. Error bars denote SEM.

Figure 4: Accuracy for pubertal clusters on the Eyes test. Prepubertal adolescents: n = 9; pubertal adolescents n = 18 and postpubertal adolescents = 33. Error bars denote SEM.

3.3.2.2 Emotion recognition

Comparison of the three pubertal groups regarding Eyes test performance with an ANOVA revealed no significant effect of pubertal stage, $F(2,57) = 1.52$, $p = .228$, partial $\eta^2 = .051$, indicating similar Eyes test performance across pubertal stages. The model explains 5.1 % of variance ($r^2 = .051$). Performance on the Eyes test increased slightly across the three pubertal stages (Figure 4). No pubertal dip was observed. Even when controlling for age there was significant influence of pubertal stage on both measures of social cognition.
3.3.3 Controlling for Basic Cognitive Abilities

First of all, correlations were performed with basic cognitive variables and social cognition (see Table 2). There was no significant correlation of neither the Eyes test nor Story Comprehension and speed of processing or working memory. However, there was a significant correlation of verbal ability and the Eyes test in the adult group.

Table 2: Correlation Matrix for the adolescent and the adult group.

<table>
<thead>
<tr>
<th>Measure</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Story C.</td>
<td>.10</td>
<td>.12</td>
<td>.08</td>
<td>-.04</td>
<td>.25</td>
<td>.14</td>
<td></td>
</tr>
<tr>
<td>2. Eyes test</td>
<td>-.19</td>
<td>.10</td>
<td>.16</td>
<td>.20</td>
<td>.20</td>
<td>.20</td>
<td></td>
</tr>
<tr>
<td>3. Working memory</td>
<td>.16</td>
<td>-.07</td>
<td>.04</td>
<td>-.01</td>
<td>-.25</td>
<td>-.17</td>
<td></td>
</tr>
<tr>
<td>4. Speed</td>
<td>-.01</td>
<td>.11</td>
<td>.21</td>
<td>-.06</td>
<td>.31*</td>
<td>.37**</td>
<td></td>
</tr>
<tr>
<td>5. Verbal ability</td>
<td>.16</td>
<td>.26*</td>
<td>.05</td>
<td>.14</td>
<td>-.24*</td>
<td>.15</td>
<td></td>
</tr>
<tr>
<td>6. Age</td>
<td>-.11</td>
<td>-.08</td>
<td>-.22</td>
<td>-.18</td>
<td>-.04</td>
<td>.56***</td>
<td></td>
</tr>
<tr>
<td>7. Puberty</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

Intercorrelations for adolescents are presented above the diagonal, and for young adults are presented below the diagonal. Story C. = Story Comprehension test. Spearman’s Rho was calculated for correlations with puberty.

***p < .001; **p < .01; *p < .05; p = .05; *p = .056; p = .06

To control for the influence of basic cognitive abilities, analyses of covariance (ANCOVAs) were conducted for each measure of social cognition as the dependent variable including working memory, speed of processing, and verbal ability as covariates and age group as the between-subjects factor. Additionally, given that the majority of participants were female, gender was also included as a covariate. The ANCOVA for the Eyes test revealed that verbal ability was a significant covariate, $F(1,115) = 5.79, p = .018$, partial $\eta^2 = .048$. Neither working memory, $F(1,115) = 0.026, p = .87$, partial $\eta^2 = 0$, speed of processing, $F(1,115) = 1.61, p = .2$, partial $\eta^2 = .014$, nor gender of participant, $F(1,115) = 3.50, p = .064$, partial $\eta^2 = .03$, had a significant influence on Eyes test performance. While covarying for these measures, there remained a highly significant main effect of age group, $F(1,115) = 21.43, p <$
.001, partial $\eta^2 = .16$, indicating that the age group differences in Eyes test were not attributable to more basic cognition nor to gender of participant. The ANCOVA for the Story Comprehension test revealed that neither verbal ability, $F(1,115) = 0.29, p = .059$, partial $\eta^2 = .003$, nor working memory, $F(1,115) = 2.12, p = .15$, partial $\eta^2 = .018$, speed of processing, $F(1,115) = 0.01, p = .92$, partial $\eta^2 = 0$, nor gender of participant, $F(1,115) = 2.08, p = .15$, partial $\eta^2 = .018$, were significant covariates. There remained a main effect of age group, $F(1,115) = 6.09, p < .05$, partial $\eta^2 = .05$.

3.4 Discussion

3.4.1 Overview

For the first time, the present study investigated possible age differences between adolescents and young adults in two major areas of social cognition (theory of mind and emotion recognition) within one sample. Furthermore, the relation of possible age differences with working memory, speed of processing as well as verbal abilities was explored. Overall, as expected, results strongly suggest ongoing development in both measures of social cognition across adolescence. Concerning theory of mind, the Story Comprehension test indicated significant differences between the age groups. When analyzing single stories a differential pattern emerged: Age differences were only found for more complex concepts of mental states (e.g., white lie). For emotion recognition, the Eyes test yielded highly significant improvement from adolescence to adulthood. Regarding our exploratory aim, we did not find any evidence for a pubertal dip in performance of social cognition. Individual differences in basic cognitive abilities and gender did not influence age differences in social cognition.

3.4.2 Age differences in social cognition

Present data extend previous developmental studies that have suggested a prolonged development in specific areas of social cognition, particularly in theory of mind (Keulers et al., 2010) and basic emotion recognition (de Sonneville et al., 2002). The current study is the first to show late development in theory of mind — besides perspective taking — in the evaluation of complex social stories and on the other hand in the recognition of more elaborated emotions. Furthermore, it is the first time that this is shown within the same sample.
For theory of mind, current findings clearly demonstrate a prolonged development during adolescence. This nicely dovetails with a study of O'Hare, Bremner, Nash, Happé, and Pettigrew (2009) whose oldest age group (12.0 to 12.11) still showed ongoing development in the overall score of a similar task measuring the understanding of social stories. The current study is one of the very few in the field of the development of an elaborated theory of mind that shows an ongoing development beyond the beginning of puberty until early adulthood.

Concerning age differences in the emotion recognition measure, our results are in line with previous evidence indicating ongoing development of emotion recognition from adolescence to adulthood (Thomas et al., 2007). In the literature, this has been mainly found for negative facial expressions. Extending previous research that mostly focused on basic emotions (Rosenberg-Kima & Sadeh, 2010; Williams et al., 2009), the present study was able to show that adolescents might still be limited in deciphering complex emotions that are closely connected to mental states (Baron-Cohen et al., 2001). It has been argued that, possibly, the ongoing development of visual perception skills of facial expressions is related to a lower performance of adolescents in emotion recognition tasks (Gao, Maurer, & Nishimura, 2010). Future research should investigate this issue. A limitation of the present study — which is shared by many other developmental studies — might be that the emotion recognition test only used adult faces. Possibly, adding adolescent faces may boost performance of adolescents. Future studies should examine the effect of faces of different age groups.

No age group differences emerged for stories assessing basic (pretence, threat, and excuse) theory of mind concepts, but there were developmental improvements in understanding more complex (white lie, dare) concepts (see also O’Hare et al., 2009). Further, while basic understanding of irony seems to be already present in adolescents, elaborated irony showed age effects. This suggests that understanding different aspects of irony might continue to develop across adolescence, which corroborates findings from other studies (Pexman & Glenwright, 2007; Wang et al., 2006). The largest age effect emerged from Story 5 describing a socially desirable white lie in the context of a romantic relationship. Given that forming romantic attachments constitutes one of the key developmental tasks for adolescence, it will be important to further delineate the reasons for those age effects.

In all main analyses, the unequal gender distribution was controlled for. Therefore, it is unlikely that our results have been affected by this unequal distribution. However, there was a trend towards better emotion recognition in females, which corroborates previous findings.
(Baron-Cohen et al., 2001). Another more recent study has shown female superiority in emotion recognition (Hall & Matsumoto, 2004). It can only be speculated about the underlying mechanisms such as socialization or underlying brain circuitry (Hall & Matsumoto, 2004). Prospective research should focus on the influence of gender on tasks of social cognition in different age groups, with larger and more equal sample sizes of males and females.

### 3.4.3 Influence of puberty on social cognition

For neither theory of mind nor emotion recognition was a dip in performance for pubertal in comparison to pre- and postpubertal adolescents found. This is in contrast to studies finding a pubertal dip in facial (emotion) measures (Diamond et al., 1983; Thomas et al., 2007). However, the current study directly measured puberty with a self-report questionnaire while Thomas et al. used age as a proxy for puberty onset. Moreover, the lack of findings of a pubertal dip for theory of mind are in accordance with the study of Keulers et al. (2010), which did not find slower reaction time during puberty. Contrary, Keulers et al. found a linearly increasing speed similar to our finding of a correlation of age and theory of mind performance across adolescence. The present results are the first to extend the finding of an increasing performance over puberty to accuracy measures of theory of mind assessed with social stories. Moreover, the current study is the first to test for a pubertal dip on both emotion recognition and theory of mind in the same sample. Nevertheless, the pubertal groups are rather small, thus future studies are needed to investigate systematically the influence of puberty assessing larger sample sizes.

### 3.4.4 Covariates of age differences in social cognition

With respect to possible covariates of these age effects, the ongoing development in the current social cognition tasks was unrelated to development of working memory and speed of processing. In both of the social cognition tasks, the presentation was not time limited, and instructions focused on accuracy of performance, so this may have reduced the influence of processing speed. Both of the social cognition tasks here are static, and the information was available for as long as participants wished to view it. In more realistic situations in which we analyze mental states or emotions, the information is likely to be more fleeting and dynamic and, therefore, may place heavier demands on speed and memory resources.
After controlling for working memory, speed of processing, and verbal ability, age differences in both measures of social cognition remained significant. This confirms that the age effects on the social cognition tests were unlikely to be caused by improvements in more basic cognitive skills. Although all emotion words were presented before actual testing as well as unclear words were explained beforehand, verbal ability covaried significantly with performance in emotion recognition. This is in accordance with developmental studies of theory of mind and verbal ability (Milligan et al., 2007). Given that the task of emotion recognition puts high demands on participants' vocabulary, not only for theory of mind but also for complex emotion recognition, a well-functioning verbal ability might be important. Interestingly, verbal ability could not explain the observed age difference in theory of mind. Possibly, the simple verbal description of the stories' course required less fine-grained verbal understanding than the more elaborate, subtle emotional words without additional context in the emotion recognition task. Further research is needed to explore the influence of verbal abilities on age differences in (mostly verbal) tests of social cognition.

3.4.5 Conclusions

Social cognition with its important components—theory of mind and emotion recognition—represents a core ability in adolescents' everyday life. The high developmental demands in adolescence regarding the formation of complex peer relationships and exploring the possibilities and constraints of social interaction require efficient social cognition. Furthermore, investigating this transitional age range in terms of social cognition is important in understanding problematic social behavior in adolescence, such as risk taking (Steinberg, 2005). Our results show that adolescents have not yet reached adult levels of social cognition skills. Further, our data indicate that between 15 and 18 years development of social cognition is taking place. Hence, further studies should investigate the development from young adolescence to young adulthood with fine-grained age groups taking puberty into account. Moreover, we found that verbal ability was partly associated with developmental trends in emotion recognition but that strong age effects persisted even when taking this into account. Further characterizing the developmental trends and possible neurocognitive correlates in other domains, for example, executive functions will be an important goal for future developmental research.

Our result of an ongoing behavioral development of social cognition in adolescence might also be related to the neural development of the social brain. From a conceptual perspective,
our findings are in line with recent models derived from neuroimaging studies showing significant structural and functional brain development in adolescence. Especially brain regions involved in processing socially relevant information are assumed to be still developing in the age group investigated. Moreover, a recent study indicated a relation between social interaction and the volume of structures of the social brain in adolescents aged 11 to 13 years (Whittle et al., 2009). Possibly, social interaction might help form the social brain in adolescents. However, at present this remains rather speculative. Similarly, whether neural maturation underlies the ongoing development of social cognition in adolescence is still an open question (Blakemore, 2008). Thus, the complex interplay of the developing social brain and age differences in social cognition across adolescence awaits further exploration.
4 Study II – ToM Development in Adolescence and its Executive Functioning Mechanisms

4.1 Introduction

Adolescence is characterized by major challenges in the socio-emotional domain (Steinberg & Morris, 2001). Peer relationships become more important and romantic relationships arise during this period requiring the development of more elaborate socio-emotional skills (Lerner & Steinberg, 2004). These skills encompass interpreting others’ mental states such as beliefs, desires, and emotions. To interpret others’ mental states a well-functioning theory of mind (ToM) is necessary (Perner, 1991). ToM is a multidimensional construct which can be divided into two components: (1) affective ToM encompassing inferences about emotions (i.e. ‘hot’ aspects) and (2) cognitive ToM encompassing inferences about knowledge and beliefs (i.e. ‘cold’ aspects of ToM; Baron-Cohen & Wheelwright, 2004; Shamay-Tsoory et al., 2010).

Cognitive ToM is a prerequisite for affective ToM according to a model by Shamay-Tsoory et al. (2010). First, the development of a functioning cognitive ToM is required to understand others’ perspective and to infer their mental states. Second, empathy is required to understand the emotions of another person. Only the integration of these two processes enables a functioning affective ToM (Shamay-Tsoory et al., 2010), which therefore represents a specific and cognitively challenging higher order aspect of affective processing (Coricelli, 2005; Mier et al., 2010). In line with this notion, initial behavioral evidence shows that cognitive ToM seems to develop earlier than affective ToM (Ruffman & Keenan, 1996) as children first have to gain an understanding of others’ beliefs in order to appreciate that beliefs guide others’ emotions (Rieffe et al., 2005). This raises the possibility that affective ToM might show a more extended developmental trajectory than first or second-order cognitive ToM. While the emergence and early ontogeny of cognitive ToM has been widely investigated (Wellman et al., 2001) only a handful of studies exist on the development of affective ToM. The understanding of emotions such as surprise begins to develop between the age of seven to nine years (Ruffman & Keenan, 1996), while the more complex abilities involved in understanding social faux pas show development between nine and eleven years (Baron-Cohen et al., 1999).

ToM development throughout adolescence until young adulthood is largely understudied, which particularly accounts for affective ToM (Blakemore, 2008). Only two studies have
investigated possible ongoing development of affective ToM in adolescence. The time required to think about the appropriateness of emotions decreased throughout adolescence (Keulers et al., 2010). Further, adolescents made more errors than adults in choosing the appropriate ending of vignettes depicting a character’s response to her companion’s emotions (Sebastian et al., 2012).

These behavioral findings are corroborated by emerging evidence of a protracted neural development of cognitive (for a review see Blakemore, 2008) and affective ToM across adolescence (Gunther Moor et al., 2012; Sebastian et al., 2012). Accordingly, the medial prefrontal cortex (MPFC) is a key brain area implicated in ongoing ToM development throughout adolescence. Specifically, the ventral MPFC is supposed to be related to affective ToM whereas the dorsal MPFC has been mainly associated with an ongoing development for cognitive ToM (Abu-Akel & Shamay-Tsoory, 2011; Blakemore, 2008). These findings are in accordance with lesion studies which support this double-dissociation of affective and cognitive ToM in the MPFC (Shamay-Tsoory et al., 2006).

Taken together, these neuroimaging findings as well as initial evidence from two behavioral studies suggest ongoing development of affective ToM across adolescence. However, the first behavioral study (Keulers et al., 2010) focused on thinking time only and provided no measure of accuracy and the second (Sebastian et al., 2012) was a neuroimaging study with only 15 participants each in the adolescent and adult age group. Further, previous research has used static, non-naturalistic task material lacking important dynamic features of emotions. Thus, the first aim of the present study was to test for age-related variance in affective ToM across adolescence using the “facial scale” of the Cambridge Mindreading Face-Voice Battery (Golan, Baron-Cohen, & Hill, 2006) presenting complex emotional mental states. It consists of film clips depicting actors’ face and upper body, which approximates real-life social interactions and thus enables the presentation of affective mental states requiring motion (e.g. insincerity). This instrument is suitable for the investigated age group since it was designed to detect subtle deficits in affective ToM in adults with high-functioning autism (Golan et al., 2006). The depicted emotions are complex and situation-based (Golan et al., 2006). In contrast to basic emotions, the depicted emotions might not be extractable at first sight and by use of emotion recognition only (Coricelli et al., 2005; Mier et al., 2010). Therefore, the task requires the individual to take over the other’s perspective (cognitive ToM). Affective ToM is conceptualized as the integration of cognitive ToM and empathy (Shamay-Tsoory et al., 2010). Thus, tasks assessing affective ToM require both
emotion recognition processes as well as higher level understanding of cognitive ToM and lastly empathy. Moreover, according to the model by Shamay-Tsoory et al. (2010) cognitive ToM might be a prerequisite for the affective ToM task used.

In addition to the developmental trajectory of affective ToM, the cognitive processes driving these changes are of interest for cognitive and social developmental research. One major candidate for these cognitive processes that have been discussed are executive functions (EF; Zelazo et al., 2003). EF involve higher level cognitive processes that are important for goal-directed actions. In preschool children, EF have been shown to play an important role in cognitive ToM performance (Carlson & Moses, 2001). According to a meta-analysis, correlations among EF and ToM in young children yield a strong effect size of 1.08 (Perner & Lang, 1999).

However, no study has yet investigated the protracted development of affective ToM and how this might relate to the ongoing development of EF during adolescence. This is surprising, given that executive functioning in affective situations seems to still be under development during adolescence as evidenced by heightened risk taking and sensation-seeking behavior (Steinberg, 2005). Therefore, adolescence has been labeled a critical or sensitive period in development of regulation of affect and behavior (Steinberg, 2005). Regulation of one’s own automatic and pre-potent emotions and thoughts is required for affective ToM (Ochsner & Gross, 2005). A better understanding of the normative development of the role of EF in affective ToM will help to elucidate the complex relationship of cognitive and socio-emotional abilities during this turbulent age period. Moreover, it is important to delineate the range of normal adolescent changes in these abilities in typical samples (Paus et al., 2008), given that this age range is a critical period for the development of psychopathology.

Further, the prediction that the EF-ToM relation may extend to affective ToM development across adolescence comes from two lines of research. First, recent studies show a substantial development of EF across adolescence (e.g. Luna et al., 2004). Neural correlates of this EF development were also observed, mainly in the dorsolateral prefrontal cortex (see Luna et al., 2010 for a recent review). The age period of adolescence is of specific interest for this type of research since adolescents have already developed basic abilities of affective ToM, while the ongoing sophistication of more complex affective ToM abilities might be driven by ongoing EF development (Apperly, Samson, & Humphreys, 2009). Moreover, Apperly and colleagues...
have argued that studies beyond childhood can inform accounts on the role of EF in the emergence of ToM (Apperly et al., 2009). EF and ToM might be related in later phases of the lifespan (such as in adolescence like in the present study). This generates the prediction that the relation between EF and ToM in childhood holds since EF are an essential part of the mature ToM abilities that children are developing (Apperly et al., 2009). Developing more sophisticated EF skills may further enhance one’s ability to deal with others’ emotional states more smoothly and therefore lead to improved social functioning.

Moreover, a second line of research directly indicates association of these two constructs in young adult samples. For example, participants’ performance decreased in a stories task with affective ToM components when working simultaneously on an updating task (McKinnon & Moscovitch, 2007). Performance on a visual task of affective ToM (Eyes test; Baron-Cohen et al., 2001) was selectively impaired by simultaneous performance of an inhibitory demanding task but not an updating task (Bull et al., 2008). In another study different aspects of EF related to performance on different affective ToM measures (Ahmed & Miller, 2011). However, most studies have not investigated systematically dissociable EF facets and instead have focused on either global composite measures of EF (Ahmed & Miller, 2011) or a single component of EF (McKinnon & Moscovitch, 2007). Following Miyake et al. (2000) EF can be conceptualized as three distinguishable subcomponents: (1) inhibition of prepotent responses, (2) updating information in working memory, and (3) shifting between tasks. Therefore, it is advantageous to measure all three distinguishable components of EF. Thus, from a conceptual perspective, the present study aimed at systematically delineating the role of these three specific EFs in affective ToM in an adolescent sample. Since affective ToM seems to be an integrative process relying on both cognitive ToM and empathy (Shamay-Tsoory et al., 2010), possibly additional complex cognitive processes (i.e. executive functions) are required to integrate and coordinate cognitive resources. Various EFs could play a role in affective ToM in the following ways: working memory might allow one to maintain and manipulate information in mind about a person’s current as well as past emotional states, inhibition might allow an individual to inhibit her own mental state to put herself in the emotional shoes of another person, and shifting might be important in order to flexibly shift between one’s own current emotional perspective and that of another.

To date, there are no studies investigating the links between affective ToM and EF in adolescence. Hence, the present study had two aims. (1) To examine age-related variance in a realistic affective ToM measure across adolescence in a large sample. We predict that
affective ToM will continue to develop across adolescence. (2) To examine the influence of inhibition, updating, and shifting in explaining age-related variance and individual differences in affective ToM. We predicted that all three EFs might explain age-related variance in affective ToM. This is corroborated by studies finding increasing inhibition (Velanova et al., 2008), updating (Gathercole et al., 2004), and shifting (Luna et al., 2004) across adolescence.

4.2 Method

4.2.1 Participants

The sample consisted of 139 participants (23% male, 77% female) aged 12.08 to 22.92 years ($M = 17.02, SD = 3.40$). All participants spoke German as their first language. School-aged participants mostly attended high schools preparing for university and did not differ from university students with respect to age-corrected verbal and nonverbal abilities: Vocabulary subtest, $t(137) = -.77, p = .441$; $M_{\text{high school}} = 13.70, SD_{\text{high school}} = 2.23$; $M_{\text{university}} = 13.97, SD_{\text{university}} = 1.9$, and Matrices subtest, $t(136) = .54, p = .588$; $M_{\text{high school}} = 12.74, SD_{\text{high school}} = 2$; $M_{\text{university}} = 12.57, SD_{\text{university}} = 1.75$. Further, these age groups did not differ in terms of their parents’ level of education: mother’s education: $\chi^2(1, N = 132) = .214, p = .726$; father’s education: $\chi^2(1, N = 130) = .407, p = .59$. Exclusion criteria were established by self-report (or parental report for participants under 18) and comprised any psychiatric disorders such as autism spectrum disorder, attention-deficit hyperactivity disorder, depression, mania, or schizophrenia. Participants were recruited via flyers or personal advertisement in high schools, sport-clubs, and at the university. Written informed consent was obtained before participation from each participant and from either a parent or guardian for participants under 18. Participants received monetary compensation or course credit (undergraduate psychology students). All procedures were approved by the University Ethics Committee.

4.2.2 Materials

4.2.2.1 Affective theory of mind

4.2.2.1.1 Faces Test

The Faces Test represents the “facial scale” of the Cambridge Mindreading Face-Voice Battery (Golan et al., 2006). It was translated into German by a professional translator and run on a computer using the experimental software E-Prime (Version 2, Psychology Software Tools, Inc.). Silent clips of male and female adult actors of different age groups (young,
middle-aged, and old adults) that expressed complex emotions in the face and torso (from the shoulders upward) were presented on a LCD screen 23.6 inches away from participants. Film clips varied from three to five seconds and faded after presentation. Participants subsequently selected which of four numbered adjectives (different adjectives for each film clip) best described the emotion of the person via button press. Examples of correct adjectives are resentful, subdued, empathic, and vibrant. After participant’s button press the next film clip was presented. No feedback was given during the task. Response time was unrestricted and adjectives stayed on screen until participant’s response. Participants were told to answer as accurately as possible. Due to technical problems, one item of the original test was not shown. Therefore, the task comprised 49 items that were presented in a random order (preceded by two practice items). A handout containing definitions of all adjectives was provided at the beginning of the task to minimize mistakes due to misunderstanding vocabulary.

Internal consistency was calculated for the Faces test which yielded acceptable consistency (Cronbach’s alpha = .60; Evers, 2001). Golan et al. (2006) showed that the Faces test highly correlated with the Eyes test \( r = .74, p < .01 \), which is a standard measure of affective ToM. Furthermore, the Faces test correlated with the Reading the mind in the voice test \( r = .49, p < .01 \) and with the parallel constructed vocal scale of the Cambridge Mindreading Face-Voice Battery \( r = .57, p < .01 \). The Faces test additionally correlated negatively with the Autism Spectrum Quotient \( r = -.47, p < .01 \). Therefore, it can be concluded that there is good construct validity.

4.2.2.2 Basic cognitive abilities

4.2.2.2.1 Nonverbal and verbal ability

In order to get an estimate of basic cognitive ability for both verbal and nonverbal domains, the following subtests of the Wechsler Adult Intelligence Scale (WAIS, German adaptation, von Aster et al., 2007) and the Wechsler Intelligence Scale for children (WISC-IV, German adaptation, Petermann & Petermann, 2007) were conducted according to participant’s age: Vocabulary and Matrices subtests (see Wechsler, 1999). These two subtests were collected as quick estimators, similar to other studies (Ahmed & Miller, 2001; Sebastian et al., 2012). The Vocabulary subtest reflects expressive vocabulary. It was chosen since knowledge of words may play an especially important role in the Faces test and since the test shows the highest correlation with the subindex verbal comprehension (WIE: \( r = .90 \); WISC-IV: \( r = .92 \); von Aster et al., 2007; Petermann & Petermann, 2007). The Matrices subtest is a marker for
nonverbal fluid intelligence and was chosen since this subtest has the highest correlation with the subindex perceptual organization (WIE: $r = .84$; WISC-IV: $r = .83$, Aster et al., 2007; Petermann & Petermann, 2007). Response time for both tasks was unrestricted. Reliability of these subtasks was acceptable or good (Vocabulary test $r = .76$, Matrices test $r = .92$ taken from WAIS; von Aster et al., 2006). Construct validity of both the WAIS (von Aster et al., 2006) and WISC-IV (Petermann & Petermann, 2007) has been well established.

4.2.2.3 Executive functions

The specific tests of EF were selected since they have been suggested to tap into the three main components of EF (Miyake et al., 2000). Further, these tasks have shown acceptable to good reliability in similar age groups, i.e. inhibition $r = .90$, updating $r = .76$, shifting $r = .97$ (Friedman et al., 2006). The tasks have been validated in terms of their prediction of other cognitive skills (Miyake et al., 2000). Moreover, studies have shown that performance in these tasks seems to increase across adolescence for antisaccade (Luna et al., 2004; Velanova et al., 2008), letter memory (Tamnes et al., 2010) and similar tasks to color shape (Luna et al., 2004; Velanova et al., 2008). All tasks were presented on a LCD screen with a sitting distance of approximately 23.6 inches. Participants were asked to be as accurate as possible on each task but were not given instructions about speed.

4.2.2.3.1 Inhibition

To assess inhibitory control the antisaccade task was used (adapted from Miyake et al., 2000). During each trial (total 92 trials) of this task, participants were required to focus on a fixation point on the center of the screen that was presented for a variable and unpredictable amount of time (1-3 s intervals). A visual cue (black square) then appeared on one side (e.g. left) of the screen. Shortly after presentation of the cue (225 ms), a target stimulus (arrow inside an open square) was briefly presented (100 ms) on the opposite side (e.g. right) of the screen and then masked. Participants were instructed to identify the direction of the arrow (left, right, or up) by pressing one of three response buttons. For this purpose participants were asked to shift their gaze to the side opposite the visual cue. The cues and targets were both presented 3.7 in. away from the fixation point and the participants were seated 23.6 in. from the computer monitor (thus, the visual angle from fixation point to target was approximately 9°). The proportion of correct responses (i.e., trials in which participants correctly identified the direction of the arrow) was the dependent variable.
4.2.2.3.2 Updating

The letter-memory task was used to measure the updating component of EF (adapted from Miyake et al., 2000). In this task, a list of letters was presented serially for 1500 ms per letter. Participants were asked to recall the last three letters of each list and to enter them on the keyboard. List length varied between 5 and 9 letters and was unknown to participants in advance, therefore this task required constant updating of working memory contents throughout the trial. Participants performed 12 trials and had to remember the last three letters of each trial, resulting in a total of 36 letters recalled. Mean proportion of correctly recalled letters across 12 trials was used as the dependent variable.

4.2.2.3.3 Shifting

The color-shape task (Friedman et al., 2006), using geometric objects, was employed to measure shifting (adapted from Miyake et al., 2000). Participants had to classify objects by color (green or red) or by shape (circle or triangle) via button press. An external cueing paradigm was used, that is the task to be executed was written above the stimuli and was present until a response was made. First, there were two single-task blocks of 26 trials each for the color task and the shape task, respectively. Afterwards participants performed the mixed block of 82 trials where tasks were pseudorandomly mixed. Following Miyake et al. (2000), as the dependent variable unspecific switch costs were used, computed as the difference in mean reaction time (RT) between the mixed-task block and the two single-task blocks. RT measures were computed on correct trials only.

4.3 Results

Before analyses, univariate outliers with values more than three standard deviations above or below the mean were excluded. There was only one participant with an outlier total score in the inhibition task. This participant was excluded from further analyses. Descriptive data for the basic cognitive abilities, EF tests, and the affective ToM measure are presented in Table 3. Participants’ nonverbal and verbal age-corrected abilities were in a normal to above-average range.
Table 3: Descriptive statistics of Vocabulary and Matrices test, Executive Functions and Affective ToM.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Min</th>
<th>Max</th>
<th>Mean</th>
<th>SD</th>
<th>Skewness</th>
<th>Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vocabulary test</td>
<td>8</td>
<td>18</td>
<td>13.83</td>
<td>2.07</td>
<td>-.13</td>
<td>-.24</td>
</tr>
<tr>
<td>Matrices test</td>
<td>8</td>
<td>17</td>
<td>12.65</td>
<td>1.87</td>
<td>-.06</td>
<td>-.28</td>
</tr>
<tr>
<td>Inhibition</td>
<td>0.54</td>
<td>0.99</td>
<td>0.81</td>
<td>0.10</td>
<td>-.35</td>
<td>-.40</td>
</tr>
<tr>
<td>Updating</td>
<td>0</td>
<td>1</td>
<td>0.67</td>
<td>0.20</td>
<td>-.40</td>
<td>-.40</td>
</tr>
<tr>
<td>Shifting</td>
<td>215</td>
<td>1693</td>
<td>959</td>
<td>271</td>
<td>.26</td>
<td>.12</td>
</tr>
<tr>
<td>Affective ToM</td>
<td>0.43</td>
<td>0.88</td>
<td>0.66</td>
<td>0.10</td>
<td>-.14</td>
<td>-.26</td>
</tr>
</tbody>
</table>

For both Vocabulary and Matrices test scores are age-corrected (M = 10, SD = 3). For inhibition, updating, and affective ToM scores are given as the proportion of correct responses. For shifting the difference in mean RT (in milliseconds) between the mixed block and the two task-pure blocks is shown.

First, correlations with age were computed for all cognitive variables assessed (see Table 4). As expected there was no correlation with age in the age-corrected normative scores in Vocabulary subscale or Matrices subscale. Thus, basic cognitive ability was age appropriate across the sample included in the present study. Age correlated significantly with all three EF measures: inhibition, updating, and shifting. Age also correlated with performance in affective ToM in the predicted direction (r = .59). Age accounted for 35% of the variance in affective ToM.

Second, correlational analyses were conducted assessing the single contributions of the EF tests and Vocabulary and Matrices test to inter-individual variability in affective ToM (see Table 4). Analyses revealed reliable correlations of affective ToM with all three EF tests in the expected direction, from shifting (lower shifting costs related to better affective ToM performance) to updating to the highest correlation for inhibition. In addition, verbal, but not fluid ability was related to performance in affective ToM. The correlations were not affected by controlling for gender.
Table 4: Correlation Matrix of Verbal and Nonverbal Ability, Executive Functions, Affective ToM, and Age.

<table>
<thead>
<tr>
<th>Measure</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Vocabulary test</td>
<td>.20*</td>
<td>- .07</td>
<td>.07</td>
<td>- .16</td>
<td>.20*</td>
<td>.01</td>
<td></td>
</tr>
<tr>
<td>2. Matrices test</td>
<td>.01</td>
<td>.11</td>
<td>.11</td>
<td>.03</td>
<td>- .07</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Inhibition</td>
<td>.32***</td>
<td>- .25**</td>
<td>.44***</td>
<td>.43***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Updating</td>
<td>- .22*</td>
<td>.33***</td>
<td>.49***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Shifting</td>
<td>- .23**</td>
<td>- .31***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Affective ToM</td>
<td>.59***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Age</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*** \( p < .001 \); ** \( p < .01 \); * \( p < .05 \). Significant negative correlations with shifting indicate that better shifting ability (i.e. lower unspecific shifting costs) correlates with the other measures.

4.3.1 Decomposing the Age Effect in Affective Theory of Mind

In our final analysis, we aimed at delineating the relative contribution of the various cognitive resources to the age effect observed in affective ToM on a multivariate level. We conducted a hierarchical linear regression analysis for accuracy in the Faces test controlling first for individual differences in Vocabulary test (\( \beta = .23, t = 3.32, p < .01 \)) and Matrices test (\( \beta = .01, t = 0.18, p = .86 \)). As expected from the correlational analyses, the Vocabulary test provided a significant (but small) contribution of 4.5% to the observed variance in affective ToM, whereas the Matrices test did not explain any variance (total model step 1: \( R^2 = .045, F(2,133) = 3.10, p < .05 \), estimated power = 0.6). In a second step, EF tests were entered into the equation. From the three EF tests the only significant predictive measure was inhibition (inhibition, \( \beta = .26, t = 3.56, p < .01 \); updating, \( \beta = .01, t = 0.17, p = .86 \); and shifting, \( \beta = .02, t = .29, p = .77 \)). Including the three measures of EF significantly enhanced the prediction and added 26% of explained variance to the model (total model step 2: \( R^2 \) change = .26, \( F(5,130) = 11.27, F \) change = 16.03, \( p < .001 \), estimated power = 1.0, resulting in a total \( R^2 = .30, p < .001 \)). Third, age was entered in the final step into the equation predicting affective ToM (\( \beta = .48, t = 5.88, p < .001 \)). Age further significantly improved prediction, accounting for about 15% of the observed variance in affective ToM (total model step 3: \( R^2 \) change = .148, \( F(6,129) = 17.60, F \) change = 34.63, \( p < .001 \), estimated power = 1.0, resulting in a total \( R^2 = .50 \)).
.450, \( p < .001 \)). Gender did not account significantly for variance in the Faces test in the regression analysis. Taken together, considering the beta weights of the final regression model with all predictors included (i.e., beta values reported above), inhibition emerged as an important and the only significant EF predictor of the affective ToM task.

### 4.4 Discussion

#### 4.4.1 Overview

The first aim of the present study was to investigate the development of affective ToM across adolescence with a new ecologically valid paradigm consisting of film clips depicting affective mental states. Ongoing development of affective ToM was found: Affective ToM and age were strongly correlated. Even after controlling for EF and basic cognitive abilities, age still explained a significant amount of variance in the Faces test. The second aim was to systematically investigate the role of inhibition, updating, and shifting in explaining age-related variance in affective ToM across adolescence. To our knowledge, the current study is the first to investigate the relationship of EF and affective ToM throughout adolescence until young adulthood. Related to our second aim, all three EFs correlated with affective ToM performance and explained a large portion of the variance. Specifically, the highest correlation was found between inhibition and affective ToM. Also in the final regression model with all predictors included, inhibition emerged as an important single EF predictor beyond age, updating, shifting, and Vocabulary test performance.

Given that 35% of variance in the Faces test was explained by age, the current study provides further evidence for ongoing affective ToM development across adolescence. This result extends findings from two recent studies (Keulers et al., 2010; Sebastian et al., 2012), to a larger sample using a more realistic affective ToM task. Further, the result underlines the importance of measuring affective ToM with more naturalistic and complex paradigms to avoid ceiling effects since most of previous studies employed rather simple tasks of affective ToM, (e.g. the child version of the Eyes test; Gunther Moor et al., 2012).

Present findings reveal a close relation between EF and the development of affective ToM. Since affective ToM seems to be an integrative process relying on both cognitive ToM and empathy (Shamay-Tsoory et al., 2010), possibly additional complex cognitive processes (i.e., executive functions) are required to integrate and coordinate cognitive resources. Inhibition correlated most strongly with affective ToM. This finding is consistent with previous evidence
showing that an affective ToM task (the Eyes test) and inhibition were related in young adults (Ahmed & Miller, 2011), or showed dual task interference (Bull et al., 2008). For developing a more complex affective ToM adolescents and young adults need cognitive processes such as inhibition. This underlines the claim made by Apperly et al. (2009) that it is essential to study ToM not only in younger children but also during its extended developmental course (i.e. adolescence or young adulthood). Furthermore, it points to the importance of systematically differentiating among the role of the sub-processes of EF: inhibition, updating, and shifting.

Particularly inhibition might be involved in affective ToM tasks such as the Eyes or Faces test since social attributes, for example attractiveness might be automatically activated and have to be inhibited (Bull et al., 2008). Moreover, it has been argued that inhibition facilitates memory retrieval by suppressing immediate responses long enough to search memory and provide well-thought out answers (Lorsbach, Katz, & Cupak, 1998). This seems plausible since the videos last several seconds requiring to inhibit the first spontaneous guess and to consider the whole sequence.

The specific role for inhibition might also be in line with evidence of the brain regions involved in affective ToM and inhibition. The core region for affective ToM, the vMPFC, seems to code the emotional value of stimuli and select actions on this basis (Ochsner & Gross, 2005). Moreover, inhibition seems to be necessary to modulate the signal encoded in vMPFC (Hare, Camerer, & Rangel, 2009). Inhibitory processes are associated with dorso-lateral PFC activity. Therefore, the behavioral association of inhibition and affective ToM might possibly be related to the neural orchestration of the two underlying regions during emotionally-laden decision-making. Interestingly, Sebastian et al. (2012) found ongoing development of affective ToM on the neural level; the vMPFC showed a stronger activity in adolescents in contrast to adults. Further research is needed to investigate affective ToM development throughout adolescence both at the behavioral and neural level.

Furthermore, the Vocabulary test predicted a small amount of variance of affective ToM performance. This might possibly be since the task required the understanding of complex verbal descriptions of emotions. This is in accordance with evidence of the vital role of language in the development of ToM in children (Astington & Jenkins, 1999) and young adults (Ahmed & Miller, 2011). Most previous studies have employed affective ToM tasks that depend on the understanding of linguistic emotional terms (Ahmed & Miller, 2011; Bull et al., 2008; McKinnon & Moscovitch, 2007). Since verbal abilities continue to develop in
adolescence, future studies should develop and employ more age-adapted tasks that have a lower verbal load. Similarly, basic cognitive functions might also play a role in affective ToM development. However, a recent study has found no relationship of processing speed and affective ToM development (Vetter, Leipold, Kliegel, Phillips, & Altgassen, 2012).

Similar to most of the previous developmental literature a limitation of the current study is the correlational approach investigating the relationship of ToM and EF. However, in the current study we first aimed to test the three sub-components of executive functions systematically. In a future study it would be interesting to test the role of inhibition in a dual-task paradigm in the same age group. A further limitation of the current study is the unequal gender distribution. However, in additional analyses gender was controlled for and had no significant impact on the outcome of the results. Therefore, it is unlikely that our results have been affected by this unequal distribution. Nevertheless, future research should replicate our findings with gender matched samples. Given that ongoing development of inhibition and affective ToM in adolescence may relate to problematic behaviors such as risk taking (Steinberg, 2005) it is important to examine this issue more directly in future studies. Finally, the present study is limited by not including a cognitive ToM task modeled in parallel to the affective ToM task which would allow for direct comparison between the two components of ToM and to examine the role of EF in both aspects of ToM. Importantly, a parallel task would allow for investigation of whether there is a difference between affective and cognitive ToM requiring EF, specifically inhibition. Currently, in the available literature there is no existing instrument which has a comparable design and task difficulty that allows for such direct comparisons between both affective and cognitive ToM and would be appropriate for the investigated age group with avoidance of ceiling effects. Hence, future research should be aimed at constructing tasks that will enable those comparisons and follow up on the present findings.

4.4.2 Conclusions

Recently, Apperly and colleagues postulated that it is crucial to examine the role of EF in ToM in older children and adults (Apperly et al., 2009) in order to investigate whether there is an ongoing development of ToM after childhood and what role EF plays in this development. The current study adopted this approach in a sample of adolescents and young adults. Our findings suggest an extended development of affective ToM across adolescence and demonstrate processing overlaps between EF and affective ToM in this age span. Inhibition
was found to play the most important role in affective ToM out of the three facets of EF measured. Future studies are needed to investigate the ongoing development of cognitive and affective ToM and disentangle the order of development, perhaps using longitudinal designs. To further explore the relation between ToM and EF, more research in different age groups is warranted. Moreover, future investigations of affective ToM at the neural level will help to shed light on this specific subcomponent of ToM.
5 Study III – ToM Development in Adolescence and its Neurocognitive Mechanisms

5.1 Introduction

Theory of Mind (ToM), the ability to infer others’ mental states (Frith & Frith, 2003; Perner, 1991) can be divided into: 1) cognitive ToM encompassing inferences about ‘cold’ mental states such as intentions and beliefs and 2) affective ToM encompassing inferences about ‘hot’ mental states, i.e. emotions (Shamay-Tsoory et al., 2010). Well-functioning skills of both ToM aspects are much-needed in the developmental period of adolescence (Steinberg & Morris, 2001). Surprisingly, studies have only recently begun to shed light on the development of cognitive and affective ToM across adolescence (Blakemore, 2008). Ongoing refinement of cognitive and affective ToM across adolescence has been indicated by first studies, mostly in reaction time measures (Choudhury et al., 2006; Keulers et al., 2010). An improvement in accuracy has been demonstrated for the first time on both cognitive and affective ToM within the same sample of adolescents (Vetter et al., 2012). Moreover, this study indicates greater age differences between adolescents and adults for affective ToM compared to cognitive ToM. Greater age differences of affective ToM were observed in decoding emotions from others’ eye region and from dynamic facial expressions (Vetter et al., 2012; Vetter, Altgassen, Phillips, Mahy, Kliegel, in press). The latter paradigm was the “facial scale” of the Cambridge Mindreading Face-Voice Battery (Golan et al., 2006) presenting complex emotional mental states. By using this developmentally sensitive and ecological valid measure of affective ToM development in adolescence, the current functional magnetic resonance imaging (fMRI) study investigates the neural basis of affective ToM development across adolescence.

The adult neural ToM network (Van Overwalle, 2009) has consistently been shown to comprise the posterior superior temporal sulcus (pSTS; Puce, Allison, Bentin, Gore, & McCarthy, 1998), the temporal poles (TP, Frith & Frith, 2003), the temporo-parietal junction (TPJ, Frith, 2007; Gallagher & Frith, 2003; Saxe & Kanwisher, 2003), and the medial prefrontal cortex (MPFC, Abu-Akel & Shamay-Tsoory, 2011; Van Overwalle, 2009).

With respect to affective ToM, especially the ventral MPFC (vMPFC) has been observed. Strongest evidence comes from findings of vMPFC-lesioned patients showing deficits specifically for affective ToM. Concurrently, these patients appear to be impaired on
recognizing affective mental states such as emotions (Heberlein et al., 2008), a faux pas or irony (Shamay-Tsoory et al., 2006; Shamay-Tsoory & Aharon-Pe'etz, 2007; Stone et al., 1998). Corroborating these findings anatomically, the vMPFC has strong connections with affect-processing regions such as the amygdala (Bandler et al., 2000; Price, 2007). However, functional neuroimaging studies appear to support the importance of vMPFC for affective ToM only partly. Whereas Hynes, Baird & Grafton (2006) found differential vMPFC activity for affective ToM, other authors observed activity in the dorsal MPFC (dMPFC; Völlm et al., 2006) or a cluster reaching from dorsal to ventral MPFC (Sebastian et al., 2012).

With respect to developmental findings on affective ToM processing, results of neural regions showing a stronger activation in adolescents in comparison to adults are threefold: while one study observed dMPFC involvement (Wang et al., 2006), another found both the dMPFC and the vMPFC (Gunther Moor et al., 2012) and a third one observed an activation of the vMPFC (Sebastian et al., 2012). Moreover, additional regions were found such as the right pSTS (Wang et al., 2006) or the right TP (Gunther Moor et al., 2012). Thus, until now there is no clear-cut picture as to which neuronal structures underlie the continued development of affective ToM.

Heterogeneous findings of the aforementioned developmental studies might be due to two possible reasons. First, studies employed children’s tasks, which may not be performance-sensitive for adolescents. For example, Wang et al. (2006) used children’s cartoons asking whether the ending was meant sincere or ironic and found ceiling effects in accuracy. Supporting this notion, significant behavioral differences between adolescents and adults were only observed in one study that used more complex social material: adolescents performed lower in a vignette paradigm, in which participants had to choose the correct reaction of one character to her companion’s affective state (Sebastian et al., 2012).

Second, another reason for the heterogeneous results in the neuroimaging literature on affective ToM development seems to be large differences between investigated age spans: While Wang et al. (2006) included children from nine to 14 years, Sebastian et al. (2012) investigated adolescents from 11 to 16 years. Thus, these studies recruited adolescent groups with a wide age range of five years. However, it is desirable to trace developmental changes in narrow age ranges given the gross developmental changes in brain structure observed during adolescence (Giedd, 2008b). This was done by Gunther Moor et al. (2012) who
differentiated between early (10 to 12 years) and middle adolescents (14 to 16 years) in narrow age clusters.

The current study aimed at extending previous findings by addressing these two methodological challenges. First, the targeted paradigm has proven to be developmentally sensitive since performance differences in adolescents and adults have been shown (Vetter et al., in press). Moreover, the method of performance matching was applied. Controlling for performance systematically has become a demand of neurodevelopmental studies (Church et al., 2010; Schlaggar et al., 2002). Otherwise, it is unclear whether neural differences are due to age or just due to performance differences (Ernst & Mueller, 2008). Adolescent participants were matched to adults with similar performance leading to comparable performance across age groups (Braet et al., 2009; Schlaggar et al., 2002). While in other developmental areas performance matching has been employed successfully (Braet et al., 2009; Schlaggar et al., 2002), to our knowledge, the current study is the first in the area of developing ToM employing a performance-matching strategy. Second, narrow age ranges for both the adolescent (12-14 years) and the adult group (19-25 years) were chosen. By using a developmentally-sensitive affective ToM task in narrow age groups, and by using a performance matching procedure, the aim of the current fMRI study was to further explore age related changes in functional activity associated with affective ToM processing in adolescence relative to adulthood.

5.2 Method

5.2.1 Participants

Originally, 32 adolescent and 20 adult female volunteers were recruited via flyers (pre-university education and undergraduate university students). We measured only females since structural and functional brain development is related to gender (Giedd, 2008c). Adolescents received monetary compensation for participation and university students participated for course credit. Informed consent was obtained from each participant and additionally for adolescents from one of their legal guardians. The study was approved by the local ethics committee.

Three adolescents and one adult were excluded due to excessive movement and one adolescent and one adult due to technical problems. This resulted in 28 adolescent and 18 adult participants with no record of neurological or psychiatric illness. All participants were
right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), spoke German as their first language and had normal or corrected to normal vision. Performance in terms of accuracy in the affective ToM condition differed significantly across groups, \( t(44) = -2.76, p < .01; M_{\text{adolescents}} = 79.83, SD_{\text{adolescents}} = 10.58; M_{\text{adults}} = 87.27, SD_{\text{adults}} = 5.24. \) In order to achieve equal performance on the affective ToM task in both groups, adolescents with the highest performance in the affective ToM task were chosen to match performance of the adult age group (Table 5). The performance-matched groups contained 18 adolescents (range 12.07-14.61 years) and 18 adults (range 19.1-25.77 years; Table 6). According to the Pubertal Development Scale (Petersen et al., 1988) used in a German version (Watzlawik, 2009), 22.2% of the adolescent sample was midpubertal and 77.7% late pubertal. Groups did not differ with respect to socioeconomic status and age-corrected verbal and nonverbal abilities (see Table 6).

5.2.2 Stimuli, design and procedure

We developed an affective ToM task adapted from the “facial scale” of the Cambridge Mindreading Face-Voice Battery (Golan et al., 2006) and added a physical control task. The facial scale has been employed behaviorally with adolescents of the target age group to ensure that it covered the dynamic range of performances in the adolescent group (Vetter et al., in press). Silent film clips of different actors expressing affective mental states in the face and torso (from the shoulders upward) were presented (Figure 5). In the affective ToM task, participants were instructed to choose the adjective that best describes the actor’s affective mental state out of four affective adjectives. Different target and distractor adjectives were used for each film clip. Examples of adjectives are resentful, uneasy, and subdued. In the physical control task, participants were instructed to report on either the color of the actor’s T-shirt, on his or her hair color, or on his or her skin color.

Forty-eight film clips were shown once for the affective ToM and the same 48 film clips were shown once for the physical control task. In the physical control condition each question (color of T-shirt, hair or skin) was given 16 times. The film clips were controlled systematically in terms of gender and age group of the actor; there were three age groups (adolescents, young adults, middle to old-aged adults) so that 16 actors (8 females, 8 males) per stimulus age-group were depicted. The film clips were presented in a pseudorandom order to assure that an individual film clip was not immediately repeated.
Table 5: Means (Standard Deviations) for Percentage of Correct Responses and Reaction Times (RT).

<table>
<thead>
<tr>
<th></th>
<th>Adolescents</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M      (SD)</td>
<td>M      (SD)</td>
</tr>
<tr>
<td>Percentage correct</td>
<td></td>
<td></td>
</tr>
<tr>
<td>affective ToM</td>
<td>85.53 (5.55)</td>
<td>87.27 (5.24)</td>
</tr>
<tr>
<td>physical control</td>
<td>84.37 (3.93)</td>
<td>88.08 (6.5)</td>
</tr>
<tr>
<td>RT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>affective ToM</td>
<td>2649 (398)</td>
<td>2517 (301)</td>
</tr>
<tr>
<td>physical control</td>
<td>1971 (201)</td>
<td>1810 (190)</td>
</tr>
</tbody>
</table>

RT is given in milliseconds for correct-only trials.

Table 6: Means (Standard Deviations) for Sample Characteristics.

<table>
<thead>
<tr>
<th></th>
<th>Adolescents</th>
<th>Adults</th>
<th>Age group comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(N=18 females)</td>
<td>(N=18 females)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M     (SD)</td>
<td>M     (SD)</td>
<td>t</td>
</tr>
<tr>
<td>Age</td>
<td>13.70 (0.77)</td>
<td>21.24 (1.55)</td>
<td></td>
</tr>
<tr>
<td>Verbal ability</td>
<td>13.89 (2.11)</td>
<td>14.67 (2.22)</td>
<td>-1.08</td>
</tr>
<tr>
<td>Nonverbal ability</td>
<td>12.11 (2.03)</td>
<td>11.94 (1.62)</td>
<td>.27</td>
</tr>
<tr>
<td>Socioeconomic status</td>
<td>14.08 (5.11)</td>
<td>15.39 (3.78)</td>
<td>-.87</td>
</tr>
</tbody>
</table>

Verbal and nonverbal ability was measured with the subtests of the Wechsler Adult Intelligence Scale for adult participants (WAIS, German adaptation, von Aster et al., 2007) and the Wechsler Intelligence Scale For Children for adolescent participants (WISC-IV, German adaptation, Petermann & Petermann, 2007). For both verbal and nonverbal ability scores are age-corrected ($M = 10, SD = 3$). Calculation of socioeconomic status included parents' school education, professional education, recent professional status and family income following the procedure suggested by Winkler and Stolzenberg (2009). Scores for mothers and fathers were averaged into a family-based measure of socioeconomic background. The score ranges from 3 to 21, with higher values indicating higher socioeconomic status.
Figure 5: Example trials for the affective ToM and the physical control condition.

Each trial (see Figure 5) began with the instruction screen displayed for 1.5 s consisting of a cue word (“emotion” for the affective ToM condition respectively “body” for the physical control condition). The cue word “body” signaled to concentrate on the three physical features of the person leaving open which physical component would be demanded until the choice screen, that specified the question, was presented. This was to assure that the participant concentrated on the film clip continuously since she had to consider three different features. After the instruction screen, exponentially jittered inter-stimulus intervals (ISIs) were employed varying randomly from two to six seconds (Serences, 2004). This enabled the separation of the neural response of the instruction from that of the film clip. The ISI was followed by the film clip lasting 5.5 s and by the choice screen presented for 6.5 s. During the presentation of the choice screen, the participant gave an answer via button press. After the button press participant’s choice was highlighted with a color change of the selected word, which remained colored until the end of the 6.5 s period. There was no feedback given to the participant. Each trial varied from 15.5 to 19.5 s and the whole functional run lasted about 30 min. Behavioral data was collected by ResponseGrips (©NordicNeuroLab) with two buttons for each hand. The correct response alternative was equally distributed among the buttons. Task presentation and recording of the behavioral responses was performed using Presentation® software (version 11.1, Neurobehavioral Systems, Inc., Albany, CA).

The scanning session was preceded by a short introductory session outside the scanner, followed by a practice session inside the scanner (including 8 additional film clips not included in the main task). Additionally, adolescent participants were made familiar with the scanning environment by use of a mock scanner (Galvan, Van Leijenhorst, & McGlennen, 2012). A hand-out was provided before the scanning session containing all affective mental state adjectives to ensure that all adjectives were known to the participants. Participants were
instructed to read them thoroughly and report if they did not know any of them. The experimenter then gave standardized definitions.

Moreover, partial trials (Ollinger, Shulman, & Corbetta, 2001; Serences, 2004) were employed for separately estimating the hemodynamic response to neural events occurring in a fixed sequence (i.e. film clip followed by the choice screen). Therefore, six additional film clips followed by a fixation cross, presented twice per condition were employed. However, analysis concentrated on the film clip.

5.2.3 Statistical analysis of behavioral data

Statistical analyses were performed using SPSS for Windows (Version 18) applying mixed model repeated measures ANOVAs with a 2 x 2 factorial design: age group (adolescents, adults) as the between-subjects factor and condition (affective ToM, physical control) as the within-subjects factor. The percentage of correct responses and the reaction times (RTs) were used as the dependent variables and a threshold of p < .05 was applied.

5.2.4 Functional imaging

5.2.4.1 Image acquisition

Scanning was performed with a 3 T whole-body MR tomograph (Magnetom TRIO, Siemens, Erlangen, Germany) equipped with a 12-channel head coil. For functional imaging, a standard Echo Planar Imaging (EPI) Sequence was used (repetition time (TR): 2410 ms; echo time (TE): 25 ms; flip angle: 80°). fMRI scans were obtained from 42 transversal slices, tilted up 30° clockwise from the anterior commissure–posterior commissure line to improve signal in the orbitofrontal cortex and minimize susceptibility artifacts. A thickness of 2 mm (1 mm gap), a field of view (FOV) of 192 x 192 mm and an in-plane resolution of 64 x 64 pixels resulted in a voxel size of 3 x 3 x 3 mm. Only marginal sections of the most superior part of the parietal cortex and the most inferior part of the cerebellum were omitted. Moreover, a 3D T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) image data set was acquired (TR = 1900 ms, TE = 2.26 ms, FOV = 256 x 256 mm, 176 slices, 1 x 1 x 1 mm voxel size, flip angle = 9°). Images were presented via magnet-compatible goggles (VisuaStim™, Resonance Technology, CA, USA or NNL goggles, Nordic Neurolab, Bergen, Norway).
5.2.5 Statistical analysis of fMRI data

5.2.5.1 Preprocessing

Functional images were preprocessed and statistically analyzed using Statistical Parametric Mapping (SPM 8, Wellcome Department of Imaging Neuroscience, London, UK). For each participant, functional images were first slice-time corrected by using the middle slice as reference, then realigned to the mean image by 6-degree rigid spatial transformation (Friston et al., 1995), spatially normalized (Ashburner & Friston, 1999) to the standard space defined by the Montreal Neurological Institute (MNI) EPI template and smoothed with a Gaussian kernel of 8 mm at full-width half maximum. Adolescents and adults did not differ regarding movement parameters.

5.2.5.2 Statistical Analysis

In the first-level analysis, a fixed effects analysis was computed for each subject on the basis of the general linear model within each voxel of the whole brain. The analysis focused on amplitude changes in the hemodynamic response function associated with affective ToM processing in the experimental film clip condition contrasted with processing physical appearance in the control film clip condition (Figure 5). The general linear model included as the main regressor of interest the film clip in the two conditions modeled with its duration of 5500 ms. Additionally, the instruction period was modeled with 1500 ms as a regressor of no interest. Furthermore, the response phase was split into three separate regressors of no interest. This enabled to estimate the underlying psychological processes more accurately since they were assumed to differ. These regressors comprised the choice screen (duration = reaction time), the button press (event with no duration) and the color change of choice feedback (duration = 6500 ms minus reaction time). All regressors were modeled as boxcar functions convolved with a canonical hemodynamic response function (except the button press modeled as a stick function). Additionally, the six subject-specific movement regressors, which were derived from the rigid-body realignment, were included as covariates of no interest. Each component of the model served as a regressor in a multiple regression analysis. A high-pass filter with cut-off 128 s was applied to remove the low frequency physiological noise (Henson, 2006). Also an AR(1) model was employed for the residual temporal autocorrelation (Henson, 2006). Statistical parametric maps (SPMs) were generated for each subject by t-statistics derived from contrasts utilizing the HRF. Four contrasts of interest were computed within each subject: affective ToM minus baseline (contrast 1), physical control
minus baseline (contrast 2), affective ToM minus physical control (contrast 3), physical control minus affective ToM (contrast 4). The first-level contrast images from the weighted beta-images were introduced into second-level whole brain random-effects analysis to allow for population inference. The present study focused on analyzing age-related differences in functional activity in brain regions related to affective ToM processing, that is, brain regions that would show a significant group by condition interaction effect. Therefore, an ANOVA was computed using a $2 \times 2$ flexible factorial model with the factors group (adolescents, adults) and condition (using contrasts 1 and 2). For the main effect of group a full factorial model was used. We analyzed the group (adolescents, adults) by task (affective, physical control) interaction. We further explored the response profile in regions showing significant interactions - in order to avoid circular analysis - by performing an independent split-half analysis to extract percent signal change (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). The split half analysis first divided data into (1) an odd run (i.e. all odd trials of the experiment) and (2) an even run (i.e. all even trials of the experiment). A mask of the resulting cluster in the odd run was created. Applying this mask percent signal change was extracted with rfxplot (Glaescher, 2009) in the even run. The resulting set of significant voxel values constituted an SPM map. The SPM maps were thresholded at $p \leq .001$ (uncorrected voxel-level). We report regions that survive a statistical threshold of $p \leq .05$ (corrected for multiple tests on the cluster threshold criterion) or, where we had an a priori hypothesis for their activation we used $p < .001$ uncorrected. All brain coordinates are reported in MNI atlas space.

5.3 Results

5.3.1 Behavioral results

Behavioral results are displayed in Table 5. Regarding response accuracy, the ANOVA revealed no main effects of condition ($F(1,34) = .029, p = .87$) or group ($F(1,34) = 3.37, p = .08$), and no significant group by condition interaction ($F(1,34) = 0.94, p = .34$). For RT as dependent variable the ANOVA showed no main effect of group ($F(1,34) = 3.17, p = .08$) and no significant group by condition interaction ($F(1,34) = 0.09, p = .77$). However, there was a significant main effect of condition ($F(1,34) = 211.61, p < .001$). Post hoc t-tests revealed that this was driven by slower reaction times in the affective ToM condition compared with the physical control condition ($t(15.74), p < .001$) across both groups.
5.3.2 fMRI results

There was no main effect of group in the full factorial model. However, there was a main effect of condition for affective ToM > physical control (Table 7). Activity across both groups was observed in bilateral TPJ / pSTS, extending bilaterally to middle and anterior STS as well as to the TP. Furthermore, the following structures were activated bilaterally: the inferior frontal gyrus, the parahippocampal gyrus extending to the amygdala, the cuneus, and the cerebellum. In addition, the left thalamus was activated. Functional activity was also observed bilaterally in the ventral striatum and the right superior frontal gyrus. Importantly, both the vMPFC and dMPFC were activated.

There was a significant interaction of group (adolescents vs. adults) x condition (affective ToM vs. physical control) in the whole brain analysis in two clusters in the vMPFC (first cluster: x,y,z = 10 50 -12, k = 9, t = 3.66, p = .026 small volume correction with a 10 mm sphere; second cluster x,y,z = 2 40 -18, k = 7, t = 3.59, p = .028 small volume correction with a 10 mm sphere; Figure 6A). Analyses of percent signal change showed a replication of vMPFC activation in the odd trials (x,y,z = -4 36 -20, k = 78, t = 4.33, p = .085 cluster-level corrected, Figure 6B). Percent signal change analysis of this mask in the even trials revealed that the vMPFC was deactivated across both conditions and groups (Figure 6C). An exception was adolescent affective ToM with almost no deactivation (-.0001). Post hoc t-tests conducted on the percent signal change values in the even trials showed that the interaction was driven by the adolescent group, showing significantly more deactivation during the physical control than during the affective ToM condition, \( t(17) = 4.38, p < .001 \) while, adults’ activation in this area did not differ between conditions, \( t(17) = 1.44, p = .168 \) (Figure 6C). Further, a significant difference of affective ToM between adults and adolescents emerged, in that adults compared to adolescents showed more deactivation in the affective ToM condition, \( t(34) = 2.52, p < .05 \) (Figure 6C). There was no difference between adults’ and adolescents’ activation in this area for physical control, \( t(34) = 0.45, p = .656 \).

For the reverse interaction group (adults vs. adolescents) x condition (physical control vs. affective ToM) one significant cluster resulted in the right dorsolateral PFC (DLPFC, x,y,z = 48 8 44, k = 237, t = 5.26, p < .05 corrected cluster level, Figure 7A). Analyses of percent signal change showed a replication of DLPFC activation in the odd run (x,y,z = 48 8 48, k = 83, t = 4.16, p = 0.076, Figure 7B). Percent signal change analysis of this mask in the even
<table>
<thead>
<tr>
<th>Brain region</th>
<th>L/R</th>
<th>BA</th>
<th>peak voxel (mm)</th>
<th>t-value</th>
<th>Cluster corrected p-value</th>
<th>Cluster size</th>
</tr>
</thead>
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<tr>
<td>Ventromedial prefrontal cortex</td>
<td>L</td>
<td>11</td>
<td>0 -40 -18</td>
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<td>Dorsomedial prefrontal cortex</td>
<td>L</td>
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<td>5.92</td>
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<td>-48 26 -4</td>
<td>15.74</td>
<td>&lt; 0.001</td>
<td>14606</td>
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<td></td>
<td>R</td>
<td>45</td>
<td>58 26 12</td>
<td>8.71</td>
<td>Part of same cluster</td>
<td></td>
</tr>
<tr>
<td>Temporal Pole</td>
<td>L</td>
<td>38</td>
<td>-48 14 -26</td>
<td>11.81</td>
<td>Part of same cluster</td>
<td></td>
</tr>
<tr>
<td></td>
<td>R</td>
<td>38</td>
<td>48 14 -32</td>
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<tr>
<td>Anterior STS</td>
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<td>10.84</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>R</td>
<td>21</td>
<td>54 4 -22</td>
<td>10.32</td>
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<td></td>
</tr>
<tr>
<td>Middle STS</td>
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<td>48 -36 2</td>
<td>10.46</td>
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<td></td>
</tr>
<tr>
<td></td>
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<td>-56 -40 4</td>
<td>8.16</td>
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<td>Posterior STS / TPJ</td>
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<td>-60 -48 8</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>R</td>
<td>22</td>
<td>64 -50 12</td>
<td>6.76</td>
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<tr>
<td>Parahippocampal gyrus</td>
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<td></td>
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<tr>
<td></td>
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<td>20 -16 -16</td>
<td>6.53</td>
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<td></td>
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<tr>
<td>Ventral striatum</td>
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<tr>
<td></td>
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<td>10 0</td>
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</tr>
<tr>
<td>Thalamus</td>
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<td>-2</td>
<td>-6 8</td>
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<tr>
<td>Fusiform Gyrus</td>
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<tr>
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<td>20 -92 -4</td>
<td>7.79</td>
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</tr>
<tr>
<td></td>
<td>L</td>
<td>-20</td>
<td>-76 -38</td>
<td>11.72</td>
<td>&lt; 0.001</td>
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<td>Superior frontal gyrus</td>
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<td>6</td>
<td>8 14 72</td>
<td>6.50</td>
<td>&lt; 0.001</td>
<td>656</td>
</tr>
</tbody>
</table>

Brodman areas (BAs) are approximate. Some clusters showed activation in multiple brain regions and BAs. L = left hemisphere, R = right hemisphere, STS = superior temporal sulcus, TPJ = temporo-parietal junction.
**Figure 6:** Result of the interaction group (adolescents vs. adults) x condition (affective ToM vs. physical control) in the ventromedial prefrontal cortex (vMPFC) in the whole run (A). Result of the interaction condition x group in the odd trials (B). The shape of the interaction using the mask of the resulting cluster from (B) was further explored in the even trials extracting percent signal change (C).

**Figure 7:** Result of the interaction group (adults vs. adolescents) x condition (physical control vs. affective ToM) in the dorsolateral prefrontal cortex (DLPFC) in the whole run (A). Result of the interaction condition x group in the odd trials (B). The shape of the interaction using the mask of the resulting cluster from (B) was further explored in the even trials extracting percent signal change (C).
trials revealed that the DLPFC was activated across conditions and groups, except a
deactivation in the adult physical control task (Figure 7C). Post hoc t-tests conducted on the
percent signal change values in the even trials showed that the interaction was driven by the
difference of affective ToM and physical control in both age groups, with a greater response
during physical control than during affective ToM in adolescents, \( t(17) = -4.04, p < .01 \) and the
reverse, namely a greater response during affective ToM in contrast to physical control in
adults, \( t(17) = 2.7, p < .05 \) (Figure 7C). There was no difference between adults’ and
adolescents’ activation in this area for affective ToM, \( t(34) = 0.72, p = .477 \), but for the control
task, namely that adolescents had a significantly greater response than adults in this area,
\( t(34) = 4.10, p < .001 \) (Figure 7C).

5.4 Discussion

This study aimed at investigating the neural development of affective ToM processing
during adolescence using a dynamic and developmentally sensitive paradigm. Further, we
controlled performance via post-hoc performance matching. Consistent with previous ToM
studies (for a recent meta-analysis see Mar, 2011), processing the affective ToM film clips
across groups resulted in ToM-network activation including the ventral and dorsal MPFC, the
bilateral pSTS/TPJ, the TP, the inferior frontal gyrus, the thalamus and the parahippocampal
gyrus. Moreover, the vMPFC finding is in accordance with both fMRI (Hynes et al., 2006;
Sebastian et al., 2012) and lesion studies (Heberlein et al., 2008; Shamay-Tsoory et al., 2006;
Shamay-Tsoory & Aharon-Peretz, 2007; Zald & Andreotti, 2010) and the dMPFC finding is in
line with Sebastian et al. (2012). Most importantly, developmental changes in neural
activation were observed in the vMPFC, which was significantly less deactivated in
adolescents in comparison to adults selectively in the affective ToM condition. Additionally,
we found an interaction in the right DLPFC, which was driven by a higher activation for
physical control than for affective ToM in adolescents versus the opposite pattern for adults.

5.4.1 Developmental differences in brain activations

5.4.1.1 Activation of the vMPFC varies between groups for affective ToM

Results show that vMPFC is similarly deactivated in both conditions for adults. However,
in adolescents we observed significantly less deactivation for affective ToM in contrast to
physical control. It has been suggested that the vMPFC generates affective meaning (Roy,
Shohamy, & Wager, 2012). Specifically, this integrative region recombines complex
information from sensory systems, long-term memory and interoceptive cues into future-oriented models of the self and drives decision-making (Roy et al., 2012). This interpretation fits with Shamay-Tsoory et al. (2007, 2010), who also describe the vMPFC as a highly integrative region of cognitive and affective information. The current task might require the integration of sensory input by the film clip with past experience of affective ToM states into an affective meaning, which might facilitate decision making regarding the correct affective state. The observed group difference in vMPFC activity indicates developmental differences in this integration process. The specific neural pattern of deactivation with less deactivation in the ToM condition for adolescents fits with previous findings of less MPFC deactivation for ToM in adolescents (Blakemore et al., 2007; Sebastian et al., 2012). Specifically, the observed vMPFC deactivation corroborates previous findings (Sebastian et al., 2012) with a carefully controlled experimental design. The vMPFC is a well-known part of the default mode network (Greicius et al., 2003; Mantini & Vanduffel, 2012; Raichle, 2010; Raichle et al., 2001). Deactivations of regions in the default mode network might indicate less self-referential thoughts in favor of stimulus-based attention (Buckner, Andrews-Hanna, & Schacter, 2008). Self-reference might be specifically important for ToM since one’s own mental states seem to be a basis for inferring others’ mental states (Nickerson, 1999). This was corroborated by Jenkins, Macrae, and Mitchell (2008) showing that self-related thoughts and thoughts of similar others are processed in the vMPFC. Interpreting the current findings, in the affective ToM condition adults seem to detach from self-relevant thoughts in order to focus on the others’ emotions. Contrary, adolescents might process affective ToM in a more self-referential way (Wagner, Haxby, & Heatherton, 2012). In adolescents, the affective meaning of the stimulus (Roy et al., 2012) might have a higher impact for the self and therefore trigger self-related thoughts. Also, for self-knowledge retrieval greater activation has been found in the vMPFC in adolescents in comparison to adults, which has been interpreted as mirroring greater on-line self-reflective processes (Pfeifer et al., 2009). Furthermore, in a task presenting faces of peers, an increasing vMPFC activation across adolescence was associated with the expectation to be liked by the peer (Gunther, Van Leijenhorst, Rombouts, Crone, & van der Molen, 2010). In general, a greater egocentrism and ongoing self-development in adolescence has been shown behaviorally (Elkind, 1967; Lapsley, 1991) and neurally (Pfeifer & Peake, 2012). In context with this literature, current results might indicate that there is an ongoing development of self-other interactions in adolescence.
5.4.1.2 Adolescents’ stronger modulation of DLPFC resources for the physical control task

The DLPFC has been suggested to be implicated in cognitive control, specifically attentional (Carter & van Veen, 2007; MacDonald, Cohen, Stenger, & Carter, 2000), or self-control (Hare et al., 2009). Most importantly for the present study, the DLPFC seems to be an important region integrating emotion and cognition (Gray, Braver, & Raichle, 2002; Pessoa, 2008). For instance, this region has been shown to be modulated by the affective valence of stimuli in tasks of working memory (Perlstein, Elbert, & Stenger, 2002) and inhibition (Goldstein et al., 2007), and to reflect both emotional and working memory task components (Gray et al., 2002). Moreover, the DLPFC has been associated with regulating emotions, i.e. controlling emotional memories (Anderson et al., 2004) and controlling thoughts during emotional reappraisal (Ochsner et al., 2004). Thus, the DLPFC seems to be part of a control network associated with cognitive as well as with emotional information processing. The integration of cognition and emotion seems to be specifically important for affective ToM (Shamay-Tsoory et al., 2010). The present study observed that adolescents activate this region significantly more for the physical control condition compared to the affective ToM condition, while adults do so for the affective ToM condition relative to the physical control condition. Thus, adults might rely more on the integration of emotion and cognition for the emotional compared to the non-emotional stimulus information while adolescents may engage in more integrative processes for the non-emotional compared to the emotional stimulus information. Furthermore, adolescents compared to adults showed more DLPFC activation in the physical control condition. Possibly, adolescents might be more distracted by the emotional stimulus information and therefore needed to focus more on the processing of the physical information required in the control task. This interpretation of a distraction by emotions is in line with Monk et al. (2003) who found greater activation in the anterior cingulate cortex in adolescents for emotional stimulus material when attending to a non-emotional feature. By contrast, adults showed a greater neural modulation in the orbitofrontal cortex for emotional versus non-emotional stimulus information. These findings were interpreted as resulting from adults’ greater neural modulation of relevant brain areas based on attentional demands in contrast to adolescents’ greater modulation based on emotional content. Taken together, the DLPFC finding suggests that the integration of emotion and cognition seems to have a prolonged developmental trajectory in adolescence. These neural findings corroborate results of a behavioral study using the same type of affective task (Vetter et al., in press). Performance in the affective task could be predicted by performance in a cognitive task. The cognitive task...
was the antisaccade task (adapted from Miyake et al., 2000), which has also been shown to activate the DLPFC (Dillon & Pizzagalli, 2007).

5.4.2 Conclusions

The current fMRI study together with the previous behavioral study (Vetter et al., in press) is the first to show ongoing development on both the behavioral and neural level using the same type of affective ToM task. Findings suggest that affective ToM continues to develop throughout adolescence. This has been shown using a performance-sensitive task and subsequent control of performance achieved by performance matching. Less deactivation in the vMPFC for adolescents in comparison to adults has been observed. This activation pattern might indicate the importance of self-relevant processes during affective ToM processing in adolescents. Further, these findings might implicate that adolescents used different neural strategies when performing the task than adults. Future studies could aim at investigating the relationship of the developing self and affective ToM. Further, adolescents’ DLPFC activation indicates an ongoing development of the integration of emotion and cognition. Interestingly, heightened sensitivity in the DLPFC in children with low resistance to peer influence has been shown for emotionally stimuli (Grosbras et al., 2007). The relevance of others’ emotions and its cognitive regulation with specific regard to peer interactions as a key developmental aspect in adolescence could be aimed at in future studies. Overall, one possible reason for the observed functional development might be the prolonged structural development, i.e. synaptic pruning of the prefrontal cortex (Giedd, 2008). Specifically, vMPFC and DLPFC undergo grey matter reduction in the course of adolescence (Gogtay et al., 2004; Sowell, Thompson, & Toga, 2004). Future studies could directly investigate this relationship.
6 General Discussion

The major aims of the current thesis were first, to investigate ongoing development of ToM across adolescence and second, to explore possible (neuro)cognitive mechanisms of this development. Both major aims can be differentiated into more detailed research questions. The two questions regarding the first major aim were 1) to investigate an ongoing development of ToM across adolescence on the behavioral level and 2) on the level of brain function. Furthermore, questions relating to the second major aim were 3) to explore cognitive mechanisms in terms of basic cognitive and executive functions and 4) to infer (neuro)cognitive mechanisms via the integration of behavioral data and functional brain processes. The results of the three empirical studies aimed at answering these questions are summarized in the following section (6.1). Subsequently, these results will be discussed and integrated with special regard to the research aims (6.2). Closing the discussion of the current thesis are implications and an outlook for future research (6.3).

6.1 Summary of empirical findings

Study I of the current thesis was aimed at investigating if cognitive and affective ToM continues to develop in adolescence and at exploring if basic cognitive variables such as verbal ability, speed of processing, and working memory capacity underlie such development. This was of particular interest since no study to date has shown ongoing development in adolescence on both aspects of ToM and how this might relate to basic cognitive functions. Hence, two groups of adolescents and young adults completed tasks of cognitive and affective ToM and verbal ability, speed of processing, and working memory capacity. Large age effects were revealed on both measures of ToM: adolescents performed lower than adults. These age differences remained significant after controlling for basic cognitive variables. However, verbal ability covaried with performance in affective ToM. Exploratory analyses indicated no influence of pubertal phase on ToM. Overall, results support the hypothesis of an ongoing development of ToM from adolescence to adulthood on both cognitive and affective aspects, which might be rather independent of individual differences in basic cognitive abilities.

Study II was designed to further explore if affective ToM, as measured with a dynamic task, continues to develop across adolescence. Importantly, this study sought to explore executive functions as mechanisms of developing affective ToM across adolescence. A large group spanning adolescents and young adults was examined with an affective ToM task and three subcomponents of executive functions inhibition, updating, and shifting following the
classification of Miyake et al. (2000). In the affective ToM task adolescents and young adults evaluated affective mental states depicted by actors in video clips. Affective ToM performance was positively related to age and all three executive functions. Specifically, inhibition explained the largest amount of variance in age related differences of affective ToM performance. Moreover, verbal ability predicted a small but significant amount of variance suggesting that verbal ability is related to development of affective ToM in adolescence. Overall, these results indicate the importance of inhibition as key underlying mechanism of developing an advanced affective ToM in adolescence.

Study III set out to explore the neural development of affective ToM in adolescence by using fMRI. The affective ToM measure was the behavioral task from study II, which had been proven to be developmentally sensitive. In addition to the affective ToM condition, a control condition was introduced that consisted of the same emotional stimuli with an instruction to focus on physical information. This study faced methodical challenges of developmental fMRI studies by using narrow age groups and, most importantly, matching performance of both groups. The vMPFC was significantly less deactivated in adolescents in comparison to adults in the affective ToM condition, which might suggest that adolescents seem to rely more on self-referential processes for affective ToM. Furthermore, adolescents compared to adults showed greater activation in the DLPFC in the control condition, indicating that adolescents might be distracted by the emotional stimulus information and therefore needed to focus more on the processing of the physical information. These findings suggest affective ToM continues to develop on the functional brain level and reveals different underlying cognitive processes for adolescents in contrast to adults for both conditions.

6.2 Discussion and integration of the main empirical findings
The studies of the present work contribute significantly to research on ToM in adolescence in highlighting that there is indeed development in this relevant area for adolescent socio-emotional functioning. Furthermore, current results indicate underlying (neuro)cognitive mechanisms for this development. Following up on these issues, the next sub-sections will discuss in detail how the current findings relate to the research questions of this thesis.

6.2.1 Continued ToM development in adolescence
Given the previous main focus of ToM research on the emergence of ToM in childhood, the question if there is an ongoing development of ToM from adolescence to young adulthood
has not been answered yet. Therefore, the first main contribution of the current thesis to ToM literature is to show an ongoing ToM development on two levels of investigation: the behavioral (studies I and II) and brain functional level (study III). The current work also contributes methodically to the present field of research by demonstrating how age-adequate elaborate paradigms may indeed reveal ongoing development on a more advanced ToM in adolescents. Additionally, another approach of the current thesis is the careful implementation of methodical requirements for developmental fMRI studies, e.g., by matching performance. A detailed discussion of conceptual and methodical research progress of the current work will be provided in the following two sections on behavioral (6.2.1.1) and brain functional ToM development (6.2.1.2).

### 6.2.1.1 Continued ToM development on the behavioral level

Studies I and II clearly support the notion of an ongoing development of ToM across adolescence. Using advanced cognitive (study I) and affective ToM measures (studies I and II) an increase in ToM ability across adolescence was shown. Specifically, study I demonstrates that the adolescent group performed significantly lower than the young adult group on both cognitive and affective ToM. Moreover, findings of study I extend previous studies on cognitive ToM that only focused on the aspect of perspective taking (Choudhury et al., 2006; Dumontheil et al., 2010) revealing ongoing development in a new aspect, i.e., understanding social stories. Additionally, study I demonstrated ongoing development in social stories beyond 14 to 15 years. This extends findings of a similar task showing that 12-year-olds were not at ceiling (O’Hare et al., 2009) and suggests that even after age 15 cognitive ToM seems to develop. Interestingly, age differences between adolescents and young adults were only found for more complex concepts of mental states (e.g., white lie, dare) corroborating the notion that adolescent cognitive ToM still develops in rather complex as compared to basic concepts (e.g., pretense, excuse). Focusing on the correlations with age, there is a trend of increasing performance of cognitive ToM over the narrow age span of 12 to 15 years. This might suggest that even in such a short time period cognitive ToM skills improve. Summarizing evidence from study I, this is the first time that an ongoing cognitive and affective ToM development until young adulthood is shown within the same sample. Moreover, a larger effect size may indicate more pronounced changes in affective ToM as compared to cognitive ToM. This is in accordance with the suggestion that affective ToM might show a specifically prolonged developmental trajectory (Ruffman & Keenan, 1996).
Corroborating findings on affective ToM from study I, study II demonstrated ongoing affective ToM development over a large group of adolescents and young adults on a dynamic realistic task. Thus, importantly, both studies I and II suggest an ongoing affective ToM development across adolescence. Therefore, the current studies extend findings from recent affective ToM investigations (Keulers et al., 2010; Sebastian et al., 2012) to accuracy measures in larger samples. Moreover, study II indicates that affective ToM development extends into young adulthood (at least until the age of 22). Interestingly, in the study of Golan et al. (2006) originally employing the same affective ToM task, there was no correlation with age in an overall older adult group (until around the age of 50). Thus, possibly affective ToM might not increase into middle adulthood. However, this question needs to be addressed in future studies.

Methodically, the results of both studies I and II underline the importance of measuring cognitive and affective ToM with more naturalistic and complex paradigms. This avoids ceiling effects and enables to detect performance differences even in adolescents and young adults. The affective ToM task of study II resembles real-life social interaction, which is a feature lacking in previous studies. It therefore represents a new developmentally sensitive and ecologically valid measure. Both ToM measures employed in study I (Stories test and Eyes test) are common in the field of autism research, where the research aims are similar to the current aims: to detect subtle differences in ToM ability with sensitive paradigms (Baron-Cohen et al., 2001; Happé, 1994). Surprisingly though, the current work is one of the first to use them to investigate adolescents’ ToM abilities. The Eyes test was employed in an adult version with complex mental states, which seems to be more developmentally sensitive than the child version that previous studies used where no age differences were found (e.g., Gunther Moor et al., 2012). Another important advantage is the focus on accuracy performance differences instead of previous studies measuring reaction time. Solving advanced ToM tasks correctly might require more important and everyday-like abilities than being faster in rather laboratory-based perspective taking measures.

6.2.1.2 Continued ToM development on the level of brain function

The aim of study III was to investigate a possible ongoing development of affective ToM across adolescence on the functional brain level by using fMRI. Previous studies delivered inconclusive results. Indeed, such development was found: The vMPFC was significantly less deactivated in adolescents in comparison to adults selectively in the affective ToM condition.
This finding importantly adds to the current small developmental fMRI literature by suggesting that the vMPFC is a core region for affective ToM development. Fitting to this interpretation, the vMPFC seems to generate affective meaning (Roy & Wager, 2012). The vMPFC is supposed to be an integrative region, which recombines complex information from several channels (Roy & Wager, 2012) as well as integrates cognitive and affective information (Shamay-Tsoory & Aharon-Peretz, 2007; Shamay-Tsoory et al., 2010). The Faces task might require the integration of the sensory input by the film clip with past experience of affective ToM states into an affective meaning. Findings might indicate a developmental difference in this integration process. Taken together, study III further supports findings from studies I and II in showing an ongoing development of affective ToM, here on the functional brain level.

An additional finding was a higher activity of the DLPFC in the physical control condition versus the affective ToM condition in adolescents in comparison to adults. This might suggest that in addition to a differential activation in the affective ToM condition, there is an ongoing development in processing the control task. The physical control task includes observing emotional mental states but requires focusing on physical aspects. This might be specifically challenging for adolescents.

Methodically, the fMRI study III profited from studies I and II by using a realistic affective ToM task, which enabled for the first time to show ongoing development on the functional brain level in a developmentally sensitive task in adolescence. Moreover, using the same measure helped to assure comparability across behavioral and functional brain studies: the finding of an ongoing affective ToM development was replicated. Additionally, study III made important methodical contributions to the developmental neuroscience literature on ToM. Although the control of performance differences is essential to be able to compare groups regarding functional brain differences, the method of performance matching has only been employed in a few studies on other topics so far (Braet et al., 2009; Schlaggar et al., 2002). It is the first time that performance was matched, and therefore controlled, in the developmental ToM area. A further discussion of methodical and conceptual implications of performance matching is provided in section 6.3.2. Moreover, the narrow age range of the sample is a methodical advantage. Since the brain continues to develop functionally and structurally in adolescence (Giedd, 2008), rather homogeneous groups in terms of age are important. Most previous studies have used wide age ranges, e.g., adolescents differing five years in age (Sebastian et al., 2012; Wang et al., 2006, but see Gunther Moor et al., 2012). Another
methodical advantage of the current fMRI paradigm is the systematic distribution of three age groups of actors in the video clips and the inclusion of adolescent actors, which has been neglected by most previous studies. This is important since there might be an own peer bias, i.e., adolescents might be better in judging their own peer’s emotions (Anastasi & Rhodes, 2005; Chung & Thomson, 1995). The current study III sought to control this possible distorting influence.

**Summarizing all three studies**, ongoing cognitive and affective ToM development from adolescence until young adulthood could be demonstrated. Moreover, an ongoing affective ToM development was replicated on both levels in similar samples as well as similar paradigms. Thus, it seems to be rather robust. Evidence on cognitive and affective ToM development previously stood in stark contrast between the behavioral and the brain functional level. Whereas several studies consistently demonstrated ongoing (cognitive) ToM development on the brain functional level in the MPFC (Blakemore et al., 2007; Pfeifer, 2009; van den Bos et al., 2011) “there is no strong evidence that performance in (ToM) tasks changes during adolescence” (Blakemore, 2008, p. 270). Now, the current work bridges the gap between inconclusive brain functional and behavioral findings by detecting ToM development on both the behavioral and brain functional level with more advanced ToM tasks. The current results demonstrate how the conceptual question of a possible ongoing development can profit from the parallel investigation on the behavioral and brain functional level.

### 6.2.2 (Neuro)cognitive mechanisms of ToM development in adolescence

The previous chapter 6.2.1 delineated how the current work substantially adds to research on descriptive development of ToM abilities in adolescence. This means that there is a change in behavior has been successfully demonstrated (Salthouse, 1991). Additionally, for completing the picture for developmental theories, the question of how this change occurs (Salthouse, 1991) has been followed by all three studies of the current work. Thus, the second focus of the current work concerns possible change mechanisms underlying the behavioral differences of adolescents and young adults. The most important potential set of change mechanisms in this regard are cognitive mechanisms including basic cognitive functions or executive functions. The current work indicates that of the three tested basic cognitive functions (verbal ability, speed of processing, working memory capacity), verbal ability seems to be a mechanism of affective ToM development (6.2.2.1.1). Moreover, current findings
show for the first time that all three executive functions updating, shifting, and (most strongly) inhibition seem to be mechanisms of affective ToM development in adolescence (6.2.2.1.2). Furthermore, the current work has demonstrated *that* changes occur on the level of brain functioning. It has been suggested that the observation of functional developmental brain changes enable to infer possible *neurocognitive mechanisms*. These neurocognitive mechanisms might contribute fruitfully to interpreting behavioral cognitive mechanisms. The following two sections provide a detailed discussion of the findings of cognitive (6.2.2.1) and neurocognitive mechanisms (6.2.2.2).

### 6.2.2.1 Cognitive mechanisms

#### 6.2.2.1.1 Basic cognitive functions

As basic cognitive functions verbal ability, speed of processing, and working memory capacity were investigated. Studies I and II indicate that affective ToM is related to verbal ability. *Verbal ability* seems to be important for children’s ToM (Milligan et al., 2007). However, literature is still inconclusive on the question if verbal ability is necessary only for the emergence of ToM in childhood (Austingon & Baird, 2005), or if more mature ToM skills in the ongoing developmental course still rely on verbal ability or not (Dungan & Saxe, 2012; Newton & de Villiers, 2007). Supporting the notion of a continued relationship, a deficit in cognitive ToM has been indicated to be compensable through elaborate language, e.g., in high-functioning autism (Smith et al., 2003). Overall, current results importantly add to this question. Current studies I and II show that in adolescence, at least for more complex ToM tasks, there is (still) a reliance on verbal ability. *Study I* suggests that verbal ability is related to ongoing affective ToM development in adolescence since verbal ability was a significant covariate on age group differences in the Eyes test. Additionally, *study II* corroborates this finding in showing that verbal ability predicted some part of the variance of performance in the affective ToM task. Therefore, findings of the vital role of verbal ability for cognitive ToM in childhood (Austingon & Jenkins, 1999; Milligan et al., 2007) were extended to the age range of adolescence and to the aspect of affective ToM. The amount of explained variance by verbal ability - after accounting for age - for both affective ToM tests was around 5%. Interestingly, this is half of the overall explained variance of 10% in the meta-analysis of child studies and ToM performance (Milligan et al., 2007). This may indicate that verbal ability has a smaller importance for ToM in adolescence in comparison to childhood.
In contrast to previous studies, the relationship of verbal ability and cognitive ToM (Stories test) has not become significant. Possibly, the verbal description of the stories’ course might require less sophisticated verbal understanding than is measured in the vocabulary task (measured with WAIS/ WISC-IV). In contrast, the task of studies I and II of understanding subtle emotional words for social emotions, i.e. advanced affective ToM, might put high demands on participants’ vocabulary. Corroborating this notion, similar to task demands of the affective ToM task, a precise understanding of specific words is required in the employed vocabulary task. On the other hand, social stories might relate to other verbal ability measures. It is still not clear which specific aspect of verbal ability (syntax, semantic or as in vocabulary) might be related to which aspect of ToM (Milligan et al., 2007). Future studies might test several aspects of verbal ability systematically. It might also be helpful to develop both verbal and nonverbal tasks to find out if the verbal reliance is task-specific, or if verbal ability might support ToM performance independent of the verbal load of the task.

Additionally, the current studies indicate that the relationship of affective ToM and verbal ability extends into young adulthood (mean age 20 years). However, other studies on the relationship in (young) adulthood are inconclusive (Ahmed & Miller, 2011; Dungan & Saxe, 2012; Golan et al., 2006; Newton & de Villiers, 2007). Studies have used verbal shadowing and either supported a reliance of cognitive ToM on verbal ability in 18 to 35-year-olds (Newton & de Villiers) or found no relationship (Dungan & Saxe, 2012). For affective ToM, Ahmed and Miller support current findings of a relationship with verbal ability in a young adult sample with the Eyes test. If this relationship extends into middle adulthood is still unclear; e.g. Golan et al. (2006) did not find a correlation for the Faces test and verbal ability. Whether the relationship of affective ToM and verbal ability holds for middle adulthood (beyond the early 20’s) could be investigated in future studies.

Neither speed of processing nor working memory was related to either ToM aspect. Therefore, it seems that these basic cognitive functions do not play a role in explaining a change in adolescents’ ToM ability. Alternatively, the lacking finding for speed of processing might also be due to the presentation of stimuli, which was not time limited, or due to the instruction, which focused on accuracy. Future studies could employ ToM tasks that rely on speed to test this possibility. Moreover, working memory might not be related since both ToM tasks were static and thus did not require holding information in mind. The lacking finding of a relation of working memory and ToM will further be discussed (in the last paragraph of 6.2.2.1.3.).
6.2.2.1.2 Executive functions

Study II revealed significant correlations of affective ToM with all three executive functions: inhibition, updating, and shifting. Inhibition plays a special role in this regard. Not only did the highest correlation emerge between inhibition and affective ToM, but also in the final regression model with all predictors included, inhibition was the only significant predictor of affective ToM. It could be argued that the strong relationship of inhibition and affective ToM might actually be related to more general maturational or cognitive processes. However, inhibition remained a significant predictor when age, verbal ability and nonverbal ability were included into the equation.

Overall, these findings are in line with child studies, which found a relationship of cognitive ToM performance and executive functions (Carlson & Moses, 2001; Carlson, Moses, & Breton, 2002; Carlson, Moses, & Claxton, 2004; Carlson, Mandell, & Williams, 2004; Cole & Mitchell, 2000). However, current findings extend child studies; first in showing a relationship of executive functions with affective ToM, and second in disentangling the role of all three subcomponents of executive functions (following Miyake et al., 2000). Regarding the correlations with affective ToM, both inhibition and updating correlated moderately while shifting correlated only weakly. This is in accordance with child studies showing consistently that inhibition and updating correlated with ToM (Carlson & Moses, 2001; Davis & Pratt, 1995; Gordon & Olson, 1998) while a correlation with shifting was found only in few studies (e.g. Cole & Mitchell, 2000). It has to be noted, however, that most studies did not compare all three aspects of executive function simultaneously and thus, e.g., did not measure shifting (e.g. Carlson & Moses, 2001; Davis & Pratt, 2005). Future studies should systematically measure all three aspects in different age groups to corroborate these preliminary findings of less importance of shifting for ToM. Shifting might be less relevant for affective ToM, since understanding emotions might not require shifting back and forth from one’s own to the other’s emotional perspective. In contrast, updating might be required to hold in mind emotional information and monitor and adjust one’s memory with current, newer information of emotional mental states. Inhibition might be relevant to suppress processing irrelevant information when understanding emotions.

Importantly, the current study shows that executive functions might not only be relevant for children’s ToM as has been shown in past studies, but indicates an extended relationship to ToM over the course of adolescence until young adulthood. This is corroborated by adult
studies. For updating, the relation to ToM in young adults has also been demonstrated by McKinnon and Moscovitch (2007). The study used a dual-task approach and found that parallel updating requirements lowered performance in a social stories task. Moreover, in another study inhibition led to dual task interference on the Eyes task in a study of young adults (Bull et al., 2008). Taken together, with the exception of the study of Bull et al. (2008), however, most adult studies did not systematically investigate the role of inhibition, updating, and shifting on ToM. Therefore, more research is needed to investigate the specific influence of these executive function subcomponents on ToM. This is important since there is a conceptually diverse understanding of executive functions, and it is desirable to shed more light on the higher-order cognitive functions being underlying mechanisms of ToM. Moreover, in future research, to extend correlative findings in study II, dual-task studies could be used as has been done in adult studies. These studies could measure more directly the relationship of executive functions and ToM and might focus on the role of inhibition and ToM in adolescents following current results.

Having a closer look on the strong influence of inhibition, there are several possibilities why it might be involved in affective ToM tasks such as the Eyes or Faces test. For example, it might be important to inhibit one’s own spontaneous impression in order to focus on the four choices. Bull et al. (2008) systematically tested this possibility by showing participants the four choices before they saw the pictures of the Eyes test so participants knew the possible emotional states beforehand. However, this resulted again in lower performance in the dual task condition with inhibition. Therefore, the suppression of first impression might not be the reason for interference of inhibition and affective ToM. Possibly inhibition might be involved because social attributes such as attractiveness might be automatically activated and have to be inhibited (Bull et al., 2008). Another interpretation might be that a simple recognition process might be involved in the form of “did I see the person before?”, which has to be inhibited. These interpretations may be tested systematically in future studies.

Besides the possibility that inhibition as a cognitive mechanism could directly influence ToM, an indirect relation might also be possible. For example, Hughes and Leekam (2004) suggest that children with better executive functions might likely have good social and communication skills, which might lead to more opportunities for observing social interaction and learning about other people’s minds. This might also hold for the current age group of adolescents: if a person has a well-functioning inhibition, he or she might have more (successful) social interactions and therefore develop a better affective ToM. Future studies
could directly examine the role of social interactions, executive functions and ToM in adolescence, especially since it is an age period with great peer relevance. An example might be to observe social interactions or to measure them e.g. with friendship questionnaires and relate these measures to executive functions and ToM.

Summarizing all three studies, it was shown that possibly higher cognitive functions, i.e. executive functions, seem to be more important for an ongoing ToM development across adolescence than basic cognitive functions. Of these executive functions, inhibition seems to be most important. Moreover, verbal ability as a basic cognitive ability seems to explain a small part of variance of ToM performance.

One question of studies I and II remains, namely why working memory capacity as a basic cognitive ability (measured with counting span, a complex span task) was not related to affective ToM (study I) while updating (measured with the letter memory task) as a higher cognitive ability was related to affective ToM (study II). In contrast to complex span working memory tasks, which require to simply add information, updating tasks measure the ability to flexibly modify the content of the working memory store, i.e. replace older, no longer relevant information with newer more relevant information (Carretti et al., 2010; Morris & Jones, 1990). Therefore, this additional executive demand of updating might be crucial for updating being a mechanism of ToM development in adolescence. Moreover, in study I working memory did not differ between adolescents and adults, while updating in study II did, indicating that updating might still develop in adolescents in contrast to working memory capacity. However, research is inconclusive concerning how complex span and updating tasks of working memory capacity differ. Whereas some studies showed a strong relationship of the two constructs (Schmiedek, Hildebrandt, Lovden, Lindenberger, & Wilhelm, 2009), others have shown a weak correlation (Kane, Conway, Miura, & Colflesh, 2007). If indeed the constructs measure a similar underlying concept (Schmiedek et al., 2009), i.e., working memory capacity, then current results might be due to the different affective ToM tasks. Possibly, the Faces task of study II required more overall working memory capacity/updating, because the film clips disappeared and subsequently the four choices showed up whereas in the Eyes test of study I the four choices remained on view together with the photograph stimulus until participant’s reaction. Future studies are warranted to further disentangle the role of working memory capacity and updating in developing ToM.
6.2.2.2 Neurocognitive mechanisms and the integration of behavioral data and functional brain processes

Regarding the interpretation of neural activation in terms of underlying cognitive mechanisms, the current work revealed two major findings: 1) the specific neural pattern with less deactivation in the ToM condition for adolescents in the vMPFC, 2) a higher activity of the DLPFC in the physical control vs. affective ToM condition in adolescents. Although the interpretation is complex and has to be carried out with caution, the following neurocognitive mechanisms might be indicated by these neural findings:

The first neural finding can be interpreted as indicating a greater self-referential process for adolescents in comparison to adults. Deactivations of the vMPFC as a well-known part of the default mode network (Greicius et al. 2003, Mantini & Vanduffel, 2012, Raichle et al. 2001, 2010) might indicate less self-referential thoughts in favor of stimulus-based attention. The current results therefore suggest that while adults seem to detach from self-relevant thoughts in order to focus on the others’ emotions, adolescents might process affective ToM with more involvement of self-related thoughts. In adolescents, the affective meaning of the stimulus (Roy et al., 2012) might have a higher impact for the self and therefore trigger self-referential thoughts. In general, a greater egocentrism and on-going self-development in adolescence has been shown both behaviorally (Elkind, 1967; Lapsley, 1991) and on the functional brain level (for a review see Pfeifer & Peake, 2012). In context with this literature, the current results might indicate that there is an on-going development of self-other interactions in adolescence. When attending to affective mental states of others, greater self-relevant thoughts might be triggered in adolescents.

For the interpretation of the second neural finding of a greater DLPFC activation for adolescence in the control condition, it is relevant that the DLPFC has been observed to be an important region to integrate emotion and cognition (Gray et al., 2002; Pessoa, 2008). Moreover, the integration of emotion and cognition seems to be specifically important for affective ToM (Shamay-Tsoory et al., 2010). Therefore, adolescents may engage in more integrative processes for the non-emotional compared to the emotional stimulus information. In contrast, adults might rely to a greater extent on the integration of emotion and cognition for the emotional compared to the non-emotional stimulus information. Possibly, adolescents might be more distracted by the emotional stimulus information and therefore needed to focus more on the processing of the physical information required in the control task. This
interpretation of a distraction by emotions is in line with Monk et al. (2003) who found greater activation in the anterior cingulate cortex in adolescents for emotional stimulus material (fearful versus neutral faces) when attending to a non-emotional feature (nose width). These findings were interpreted as resulting from adolescents’ greater neural modulation based on emotional content. Taken together, the DLPFC finding suggests that the integration of emotion and cognition seems to have a prolonged developmental trajectory in adolescence. These functional brain findings corroborate results of study II using the behavioral Faces task. Faces task performance was predicted by inhibition as measured by the antisaccade task. The antisaccade task has previously been shown to activate the DLPFC (Dillon & Pizzagali, 2007).

These two interpretations suggest additional mechanisms besides those from studies I and II, which might be related to affective ToM development across adolescence. First, the self-referential processes might play a stronger role in adolescents; second, the control of emotional situations, which have cognitive requirements, might be specifically difficult for adolescents. Taken together, a specific adolescent “cognitive style” (Crone & Dahl, 2012). This “cognitive style” seems to be functional in adolescence (Crone & Dahl, 2012). In this developmental period there are a lot of social challenges such as the importance of peer relationships and emerging romantic relationships. Crone and Dahl (2012) suggest that these challenges may have favored a specific cognitive style of adolescents, which is more sensitive to social-affective stimuli and more flexible in comparison to adults. With regard to the current results, a different processing in the vMPFC of affective stimuli, possibly related to more self-involvement might promote social-affective learning. Moreover, the higher DLPFC activity might indicate stronger processing of a cognitive task in light of affective stimuli in adolescents, implying flexible processing. Importantly, for the findings related to a possible different cognitive style in adolescents, no claims can be made whether they led to a better or worse performance, since the groups were matched in this regard. Speculatively, the cognitive style has led to a better performance, thus enabling adolescents to solve complex tasks. In line with Crone & Dahl (2012), these findings do not imply that the adult brain functions in an optimal or normative fashion and the adolescent brain still has “deficits”. The interpretation of a different cognitive style shows that generalizations of functional brain differences between adolescents and adults might be too simplistic (Pfeifer & Allen, 2012). Albeit the often-cited focalization theory (Durston et al., 2006) is appealing, it might not capture task- respectively topic-specific conclusions as has been shown here on the topic of affective ToM. Instead, it
makes an overall assumption of a “less mature”, i.e. inefficient adolescent brain in comparison to the adult brain.

However, developmental cognitive neuroscience is a new field with specific methodical challenges. Therefore, all these interpretations can only remain speculative since drawing conclusions from brain processes to underlying cognition has to be treated with caution (problem of reverse inference, Poldrack, 2010). Future research is clearly needed to investigate possibilities of building theories from developmental functional brain differences. The combination of behavioral findings as well as brain functional and structural findings will help in this regard.

Taken all three studies together, besides the findings of a significant relationship of cognitive variables, age still had an important influence on variance of affective ToM. Therefore, the two cognitive mechanisms verbal ability and inhibition only partly underlie the age differences. This means, although two of the examined cognitive variables explain variance, as expected age-related variance remains partly unexplained. Therefore, possibly other mechanisms, which were not targeted by the behavioral studies may account for another part of the remaining variance. The fMRI study revealed possible additional sources of variance. Taken together, the increase of affective ToM performance can be explained by underlying cognitive mechanisms of verbal ability and executive functions, specifically inhibition (see Figure 8). Additionally, neurocognitive mechanisms of greater self-relevance and more cognitive effort in light of emotional distraction from a cognitive task may be underlying this behavioral change of ToM. A limitation here is that these two parts of mechanisms were not drawn from a single study but arise from different studies. Thus, future studies are warranted to directly test these aspects in a single fMRI study, possibly by adding an inhibitory second (dual-) task and/or add stimuli differing in self-relevance.
Overall, an increase of performance on ToM tasks was found in adolescence until young adulthood. As underlying mechanisms current studies indicate specific cognitive and neurocognitive mechanisms. Neurocognitive mechanisms might suggest an overall different “cognitive style” in adolescents (Crone & Dahl, 2012), which does not mean that adolescent cognition and functional brain processing is immature or less functional in comparison to adults. Instead, this cognitive style might be functional for the specific challenges in adolescence.

6.3 Implications and outlook

The present work makes important contributions to the emerging field of research on adolescent ToM and its underlying (neuro)cognitive mechanisms: An ongoing development of ToM in adolescence until young adulthood was shown and relevant (neuro)cognitive mechanisms of development were pointed out. Additionally, conceptual and methodical implications for future research may follow up on the current work, which are targeted in 6.3.1, 6.3.2, and 6.3.3. Furthermore, questions remain, which are closely related to the main topics of the current thesis. They have been targeted or are currently investigated by related studies of this thesis: First, the role of puberty on ToM (6.3.4) was explored as an additional question by study I of this thesis. Second, exploring the role of ToM and age differences in the estimation of others’ economic behavior (6.3.5) was the aim of a related study to this

**Figure 8**: Overview of the main findings of this thesis. Overall, an increase of performance on ToM tasks was found in adolescence until young adulthood. As underlying mechanisms current studies indicate specific cognitive and neurocognitive mechanisms. Neurocognitive mechanisms might suggest an overall different “cognitive style” in adolescents (Crone & Dahl, 2012), which does not mean that adolescent cognition and functional brain processing is immature or less functional in comparison to adults. Instead, this cognitive style might be functional for the specific challenges in adolescence.
thesis. Third, the role of structural development as a possible mechanism of functional brain development regarding ToM (6.3.6) is explored in a follow-up project of study III. Finally, the applied perspective of the current research will be discussed (6.3.7).

### 6.3.1 Current findings and their conceptual fit to present models of ToM

Taken together, conceptually, the current work nicely dovetails with the framework of Apperly (2012) to view ToM not only as a body of conceptual knowledge but also as a cognitive process. The classical view of ToM focuses rather on a conceptual knowledge: a child is said to have a ToM if it has the knowledge that other people might have different thoughts, usually at the age of four years. This is methodically proven by successful performance in the false belief task (Wellman et al., 2001). However, since newer infant studies have shown that specific (precursory) ToM abilities seem to be present from a very early age on (e.g. Onishi & Baillargeon, 2005; for a review see Sodian, 2011), this view does not hold exclusively. On the other older age end as compared to the age of successful false belief performance, the current study supports the view of ToM developing over the course of adolescence. Therefore, ToM can not only be seen as a conceptual knowledge, which is acquired at around the age of four years. ToM is also a cognitive process that develops from infancy, over childhood and adolescence until adulthood and most probably across the whole life span. ToM being a cognitive process is also underlined by the reliance of ToM on other cognitive processes such as inhibition and verbal ability. The major body of research has concentrated on the circumstances, when children acquire a ToM and has pointed out the role of executive functions in this development (e.g. Perner and Lang, 1999). However, executive functions seem to play a role not only in the first steps of ToM development but also in its extended developmental course, i.e. in adolescence as has been shown with this thesis. Moreover, several studies have demonstrated a crucial role of executive functions in adults (Bull et al., 2008; McKinnon & Moscovitch, 1999). Taken together, these adult findings as well as the findings of the current thesis on adolescents support new models of ToM, claiming that there might be two conceptual systems of ToM (Apperly & Butterfill, 2009; Sodian, 2011). The first system relates to rather simple problems and is cognitively less demanding, efficient and more automatic – but on the other hand limited and inflexible. This system is already present in young children. For example, in the Stories task, several more simple stories (e.g. pretence) were solved by adolescents and adults equally. However, the second system is more cognitively demanding but also more flexible and relates to more complex problems. In the current study, this might be e.g. mirrored in the more elaborate stories and
the more complex affective ToM tasks, which were solved better by adults than adolescents. This cognitive demand might be mirrored on the reliance of affective ToM tasks on basic cognitive (verbal ability) and executive functioning processes. According to Sodian (2011) the two core systems themselves do not enable ToM, i.e. a representational understanding of the mind but ToM develops gradually and depends on language and executive functions. Thus, the current thesis corroborates these theoretical claims in showing that an advanced ToM develops gradually in adolescence and that this development relies on language and executive functions. This interpretation fits to Apperly’s (2012) suggestion that advanced ToM tests measure the flexible, pragmatically appropriate and context-sensitive use of ToM. Therefore, the second flexible system of ToM seems to continue to develop in adolescence. This thesis fills the gap between research on children and adults and therefore theoretically underlines accounts, that state that the second more flexible ToM use is related to cognitive mechanisms and continues to develop in adolescence (Apperly, 2012). Adolescence is a specifically interesting age span to investigate ToM both conceptually and methodically. Adolescents have acquired a basic functioning ToM and even in more advanced tasks they seem to perform quite well as has been shown in studies I and II of the current thesis. However, they still perform lower than young adults on both cognitive and affective ToM. Therefore, for the investigation of an ongoing advanced development of ToM and its underlying mechanisms adolescence could be considered as a model age span.

6.3.2 Underpinning the concept of cognitive and affective ToM

Conceptually, findings of the current thesis underpin the framework that differentiates between cognitive and affective ToM by Shamay-Tsoory et al. (2010). Methodically, current results are in line with Ahmed and Miller (2011) suggesting that no composite scores of ToM should be employed in ToM research. The current thesis stresses that specifically no composite scores of cognitive and affective ToM should be used. Present studies might indicate that cognitive and affective ToM are different processes by two findings. First, in study I cognitive ToM and affective ToM were not correlated. Second, it was shown by this thesis that the different concepts of ToM seem to rely on different cognitive resources corroborating findings of Ahmed and Miller (2011). In the current work, while cognitive ToM was only at trend related to verbal ability in study I, in both studies I and II affective ToM was related to verbal ability. This might indicate that affective ToM is more complex, respectively needs more verbal resources than cognitive ToM. Overall, since affective ToM seems to be an integrative process relying on both cognitive ToM and empathy (Shamay-Tsoory et al., 2010),
possibly additional cognitive processes (i.e., verbal ability, executive functions) are required to integrate and coordinate cognitive resources. However, since executive functions were only investigated with affective ToM, these conceptual questions need to be targeted by future studies. To further elucidate the questions how cognitive and affective ToM might be different regarding underlying (neuro)cognitive mechanisms, future studies might develop parallel cognitive and affective ToM tasks to investigate each ToM aspect’s reliance on these cognitive processes more directly. Since the framework of Shamay-Tsoory et al. (2010) is well received in current ToM research and has been corroborated in different areas, it would be worthwhile to further disentangle the two concepts of cognitive and affective ToM.

6.3.3 Conceptual and methodical implications of performance matching

Several methodical but also conceptual concerns relate to the investigation of developmental differences between adolescents and young adults by use of fMRI. Since developmental cognitive neuroscience is a newly emerging field, these concerns are important to discuss. Fair, Brown, Petersen, and Schlaggar (2006) name as one of the most important concerns to assess and account for performance differences between children and adults. Regarding this concern, study III first of all assessed performance by use of a developmentally sensitive task. Moreover, not only assessing performance sensitively but also controlling performance is important. If performance is not controlled it is not sure whether the functional brain differences between groups are due to developmental differences or just due to the performance differences (Ernst & Mueller, 2008; Murphy & Garavan, 2004). This is essential because performance differences as measured in the scanner might be due to confounds such as inattentiveness or guessing (Church et al. 2010). The control of performance assures that both age groups performed successfully on the task. Thus performance serves as a control variable. Performance can be controlled with different methods. In the current study, the method of performance matching of both age groups was chosen. As expected, groups differed significantly with regard to performance. Similar performing adolescents were matched to adults leading to equal performance between age groups (Braet et al., 2009; Schlaggar et al., 2002).

This method is counterintuitive from a behavioral developmental perspective: in this research tradition, one goal is to detect that there are behavioral (performance) differences in different age groups (Salthouse, 1991). Indeed, this was one aim of the behavioral studies I and II of the current work. Therefore, it was already shown on the behavioral level that there
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is a performance difference in the respective task, the Faces test. This fact made the task and the underlying construct of affective ToM interesting to investigate on the functional brain level. In contrast to behavioral studies, the main goal of fMRI studies is not to investigate whether groups have a different behavioral performance but to sample the brain activation when both participant groups are successfully performing on the task. Here, the that (as related to the model of Salthouse, 1991) is a different brain activation of the task between age groups. Following theories of developmental cognitive neuroscience brain activation differences between groups might relate to different underlying neurocognitive strategies between groups (Johnson et al., 2011). This might be the underlying mechanism, how the different brain activation occurs referring to Salthouse’s model.

In contrast, when performance is not controlled and adolescents perform lower than adults two possible interpretations might follow from different brain activation between groups: (a) adolescents unsuccessfully implement a different neurocognitive strategy compared to adults (b) adolescents unsuccessfully implement the same neurocognitive strategy compared to adults. This has been termed the performance confound (Church et al., 2010; Durston & Casey, 2006). In contrast, the case of no behavioral performance difference but brain activation differences between groups represents a behavioral phenocopy (Schlaggar & McClandliss, 2007). Here, the interpretation space is narrowed to consideration of successful implementation of different neurocognitive strategies.

Brain activation differences with parallel behavioral differences between groups do not indicate developmental / maturational differences but behavioral / performance-related differences. Nevertheless, besides developmental differences, it might also be of interest to study performance differences between groups. Separately matched sub-groups could be built to disentangle performance and age-related differences: one performance matched group regarding underlying differences due to age, and another non-performance matched group regarding underlying differences due to performance (Brown et al., 2005; Schlaggar et al., 2002). However, for developmental cognitive neuroscience it might be particularly of interest to catch the underlying age differences in processing one task rather than performance differences.

Critical consideration of this method regards the selectivity of the sample. Only the “best” adolescents are selected (in other studies than the current study III probably also the best adults are selected). However, as was verified in the current data set, the neural differences are
usually also observable in the other subgroups (see also Brown et al., 2005; Schlaggar et al., 2002). Moreover, besides the performance match, groups are usually matched regarding other basic cognitive abilities. In the current study, groups were matched in terms of verbal and nonverbal ability. Additionally, groups were also matched regarding movement parameters and socio-demographic background. Another methodical disadvantage might be that both groups need to have overlapping performance. Thus, power is reduced by only choosing a part of the whole group. In the current case, 28 adolescents were successfully measured. Due to performance matching, 10 adolescents had to be excluded from further analysis to match the remaining 18 adolescents to 18 adults with similar performance.

Other methods to control performance exist such as including performance as a covariate of interest. However, this rather requires non-collinearity between age and performance (Fair et al., 2006). Another possibility is the adaptation of the task such that no performance differences are expected in the two groups. An interesting approach might be to assess not only in-scanner performance but also performance on similar tasks outside of the scanner and investigate related brain activation differences between groups (e.g. Cohen-Kadosh, Johnson, Dick, Cohen, & Blakemore, 2012). Future studies could more systematically point out the advantages and disadvantages of different methods controlling performance differences in developmental fMRI studies.

Most importantly, future studies and theoretical frameworks are needed to more thoroughly outline the conceptual meaning of developmental and performance differences in fMRI and therefore more closely integrate behavioral developmental psychology and developmental cognitive neuroscience.

6.3.4 The role of puberty on ToM

There are some open questions, which are closely related to this work. The first related topic, which has been targeted exploratory by study I is the role of puberty. Pubertal development, which is defined as the process of physical changes leading to sexual maturation, might be related to ToM in adolescence. Recently, several authors have pointed out this issue, which has mostly been neglected by previous studies on adolescent development (Blakemore, Burnett, & Dahl, 2010; Crone & Dahl, 2012b; Galvan et al., 2012). Importantly, few previous studies suggest a pubertal “dip”, that is lower performance in pubertal as opposed to pre- and postpubertal adolescents in face recognition or emotion perception tasks (Diamond et al. 1983; McGivern et al., 2002). This dip can be interpreted,
e.g., as related to underlying brain changes (McGivern et al., 2002). Therefore, an exploratory aim of study I was to test for a possible pubertal decline in accuracy. In contrast to previous studies, no dip in performance was found for either cognitive or affective ToM for pubertal in comparison to pre- and postpubertal adolescents. However, while previous studies mostly only estimated puberty by age (e.g., Thomas et al., 2007), study I used a self-report questionnaire and therefore measured puberty more directly. Taken together, study I is the first to show an increase of performance over puberty on both measures of cognitive and affective ToM. However, the open question still holds whether there is a specific pubertal influence on ToM in adolescence. Future studies are warranted to investigate systematically the relationship of puberty and ToM with larger sample sizes of pre- post- and mid-pubertal male and female adolescents and by using longitudinal studies. Moreover, as has been stated by Blakemore et al. (2010), to disentangle the effects of age and puberty, studies on adolescence should always measure pubertal status. Importantly, for study III, the group of female adolescents could therefore be classified as largely homogeneous in this regard, i.e. beyond pre-puberty; thus this factor could be controlled.

6.3.5 Predicting other’s economic behavior

The second open question is the role of ToM in the prediction of other’s economic behavior. This has been targeted by a study related to studies I and II (Leipold, Vetter, Dittrich, Lehmann-Waffenschmidt, & Kliegel, 2012). This prediction is a crucial aspect of ToM because it is also necessary to take other’s intentions into account in economic games. Here, a person’s own decisions interact with the decisions of other involved persons (Frith & Singer, 2008). This means ToM is measured online in economic games. In this related study each adolescent and adult separately played in an economic game the so-called Public Goods Game, together with an other (virtual) player (Leipold et al., 2012). This game required the participant to draw inferences about the other player’s intentions in order to predict his or her strategy and gain money (Frith & Singer, 2008). As is known from behavioral economics a player’s behavior depends on his or her social preference type (Fehr & Schmidt, 1999). There are two basic preference types: (1) the selfish type that is only concerned about his or her own monetary outcome and (2) the other-regarding type that is also concerned about others’ material payoffs motivated for example by fairness and reciprocity (Fehr & Fischbacher, 2002). One aim of the study was to measure age differences between adolescents and adults in estimation accuracy of the other player’s contribution in the Public Goods Game. Indeed, adults showed higher estimation accuracy than adolescents, i.e. cooperative adults estimated
the behavior of players of the same type better than cooperative adolescents. This can be interpreted as adults having more elaborate ToM to interpret cooperative signals than adolescents. Moreover, adolescents show lower cooperation levels and a slower adaption of behavior than adults indicating ongoing development of ToM in adolescence. Since first strategic (economic) decisions are important in this age span, further investigation of this topic is warranted.

6.3.6 Structural brain development

A third question, which is closely related to the functional brain development in adolescence, is the role of structural brain development. It has repeatedly been suggested that the observed functional activation differences of adolescents and adults might arise from underlying structural differences (Blakemore, 2008; 2012). The interpretation is as follows: Since grey matter of the adolescent brain undergoes synaptic pruning, possibly the excess synapses might lead to a low signal-to-noise ratio and therefore greater activation and less efficient processing in adolescents in comparison to adults. After pruning and thus “fine-tuning” has occurred, the signal-to-noise ratio might be higher because less synapses might process the task more efficiently (Blakemore, 2008, 2012). However, this speculation has rarely been tested yet. In some recent studies, grey and white matter was extracted by using voxel-based morphometry (VBM; Ashburner & Friston, 2000) and with a newer approach tested systematically in regions of functional differences between age groups (Cohen-Kadosh et al., 2012; Dumontheil, Houlton, Christoff, & Blakemore, 2010a; Dumontheil, Hassan, Gilbert, & Blakemore, 2010b). Indeed, these studies found, that age-related activation differences between adolescents and young adults could be partly explained by underlying grey and/or white matter differences. A follow-up project related to study III of this thesis seeks to investigate whether the observed functional activation differences in the vMPFC and DLPFC might be based on structural differences following the approach of Dumontheil et al. (2010a; 2010b). Overall, future work is warranted to focus on the parallel investigation of both functional and structural brain data and their relationship because the adolescent brain shows ongoing development on both levels. Relating both levels of data and possibly include behavioral data is a promising future endeavor. Most likely, the (neuro)cognitive development in adolescence is a complex interplay of factors such as gender, puberty, age and structural and functional brain development.
6.3.7 Applied perspective

From an applied perspective it is an important note that ToM seems to be relevant for social behavior. This can be seen for example in the disorders of the autism spectrum: although patients might be high-functioning and have a normal to above-average intelligence, these people suffer largely from limited ToM abilities, which lead to problems in everyday social encounters from private to work-related contexts. Also in children a positive relationship of ToM, peer acceptance and social skills has been found (Mostow, Izard, Fine, & Trentacosta, 2002; for a review see Hughes and Leekam, 2004). Specifically for affective ToM, the adequate evaluation of emotions relates to peer-nominated social status and social functioning at school in first graders (Miller et al., 2005). Moreover, a poor ToM in childhood might lead to becoming a victim of bullying in early adolescence as has been shown by a recent longitudinal study (Shakoor et al., 2012). However, there seems to be a bidirectional relationship of ToM and social interactions, i.e. being involved in social interactions might lead to a better ToM functioning and vice versa (Hughes & Leekam, 2004). Taken together, although this area is in need of further research, especially in the age span of adolescence, one can conclude that a well-functioning ToM is important for social functioning. Especially the developmental tasks in adolescence of forming stable peer relationships and exploring the possibilities and constraints of social interaction require efficient ToM (Crone & Dahl, 2012d). As has been shown by the current work, accuracy of ToM as well as the underlying (neuro)cognitive mechanisms are still developing in this age phase. Therefore, it is important to educate and share this finding with teachers, parents and also the adolescents themselves. At least since the time of Aristotle parents and teachers struggle with the specific adolescent behavior. Aristotle said youths “are hot-tempered, and quick-tempered, and apt to give way to their anger” Aristotle (350 B.C./1954). Previously in everyday knowledge hormones were thought to be the main trigger of such behavior. Taking recent findings of a developing social brain in adolescence into account, a new underlying mechanism might have been found. Moreover, the pure knowledge that adolescents still need to learn about others’ emotions and thoughts might make their behavior more plausible. To educate parents and teachers with these findings might induce more empathy and understanding for the specific behavior of adolescents. A practical example for an educational approach is the “parenting with the brain in mind” program (Wright, 2012). It delivers several “fact sheets” where state of the art neuroscience findings are translated to the language of everyday parenting. Educating parents might also include facts about social development related to ToM. Moreover, the current findings might relate to most recent practical concerns. For example, it has not only been
asked by Blakemore et al. (2010): are online social networks such as Facebook as useful to learn about others’ thoughts and emotions as real encounters with friends? The findings of the current and related works could also be introduced to adolescents themselves. It might surely be important to know what happens (in the brain) in this turbulent phase. Also it might be of interest which skills still need more time to unfold and also need social encounters to trigger expertise in these skills. Furthermore, since several psychopathological disorders arise in this sensitive age-phase (Paus et al., 2008), which are related with socio-emotional problems, the current work helps to describe the healthy and normative development. For making conclusions about pathological development, it might be essential to exactly know about the healthy development. The present thesis indicates that adolescence might be a rather sensitive phase of exploring emotions and thoughts of others, i.e. refining one’s ToM skills. The sensitive handling of this knowledge might be helpful not only for researchers but also for parents and teachers, and the adolescents themselves.

6.4 Summary

The aims of the current thesis were to investigate whether ToM continues to develop in adolescence until young adulthood and to detect possible underlying (neuro)cognitive mechanisms. With the present thesis important contributions were made to the conceptual debate in showing that there is indeed an ongoing development of both the cognitive and affective aspect of ToM. Moreover, the second benefit to the debate is to demonstrate how this change may occur. As important cognitive mechanisms basic cognitive and executive functioning mechanisms were revealed. Furthermore, neurocognitive mechanisms in the form of different neurocognitive strategies of adolescents in comparison to adults were shown.

ToM development in adolescence seems to be important for solving the wealth of socio-emotional developmental tasks that occur in this age span. This thesis shed light on the background of this development. Future research might further connect both that ToM development occurs and how it occurs to a developmental theory, i.e. why such developmental change occurs. The fruitful combination of both behavioral and functional brain imaging methods to a common result will not only help but will certainly be essential to achieve this goal.
References


References


References


References


Eidesstattliche Erklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als solche kenntlich gemacht. Die Arbeit wurde bisher weder im Inland noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt.

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Es haben keine früheren erfolglosen Promotionsverfahren stattgefunden.


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