Behavioral and neural development of cognitive control and riskydecision-making across adolescence

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Chapter 23: Behavioral and Neural Development of Cognitive Control and Risky Decision-Making across Adolescence

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General Introduction

Adolescence, which is defined as the transition phase between childhood and adulthood, roughly between 10 and 22 years of age, is marked by pronounced behavioral changes in cognitive control and decision-making (Crone & Dahl, 2012). For instance, adolescents show with advancing age an increased ability to control impulses and increases in goal-directed behavior (Hofmann, Schmeichel & Baddeley, 2012). At the same time, adolescence is often characterized by an increase in exploratory and risk-taking behavior, possibly related to the need to develop independence from parents and develop their identity (Steinberg, 2008). In addition to these behavioral changes, adolescence is marked by profound neural changes both in functional brain activity and connectivity, and in terms of structural brain changes and connections (Mills and Tamnes, 2014). In this chapter, we will discuss current literature on two aspects that develop in tandem across adolescence, cognitive control (part I) and risky decision-making (part II; for an overview of paradigms to measure these two aspects, see Table 1), as well as their neural developmental patterns (for an overview of brain regions and connections, see Figure 1). Part I covers the development of cognitive control and how structural brain development and sex steroids contribute to this development. Part II discusses which underlying behavioral and functional neural factors contribute to the development of risky decision-making. Finally, part III converges the two parts and considers avenues for future research.

Part I: Cognitive Control

Cognitive control has been described as the process by which goals or plans influence behavior. Hence, it is a form of goal-directed behavior and results from the selection of appropriate responses and ignoring or inhibiting inappropriate responses (see Chapter 20 & 21). Also referred to as executive control, cognitive control allows individuals to inhibit automatic or inappropriate responses and to keep information online in working memory. Cognitive control supports flexible, adaptive responses and complex goal-directed thought (Miller & Cohen, 2001; Diamond, 2013; Luna, Marek, Larsen, Tervo-Clemmens & Chahal 2015a; Crone & Steinbeis, 2017). Evidently, cognitive control is a multifaceted construct and relies on different functions, including working memory, behavioral inhibition, cognitive flexibility and monitoring of ongoing behavior (Diamond, 2013).

A large number of studies found that cognitive control skills rapidly improve from childhood into adolescence, reaching a plateau around late adolescence/early adulthood (for a review, see Diamond, 2013, see Chapter 20). Cognitive control is predictive for the development of academic achievement, for example, working memory and cognitive flexibility

are related to better reading and mathematic achievements two years later (Peters, Van der Meulen, Zanolie & Crone, 2017). In the famous marshmallow study by (Shoda, Mischel & Peake, 1990) it was found that self-control (i.e. delay of gratification) in preschool was predictive for adolescent achievement, socio-emotional development and brain structure development (Shoda et al., 1990; Casey et al., 2011; Mischel et al., 2011). These findings suggest that cognitive control is an important predictor for future development (see Chapter 20). It should be noted that a recent study could only partially replicate this effect (Watts, Duncan & Quan, 2018), as controlling for factors such as family background, early cognitive ability, and the home environment reduced the explained variance considerably of self-control predicting adolescent outcomes (Watts et al., 2018). In addition, cohort effects in self-control have recently been reported as well: the average ability to delay gratification in children has improved from 1960 to 2000, such that children from the 2000s could –on average– wait 2 minutes longer for a delayed reward compared to children from the 1960s (Carlson et al., 2018). These findings show that environmental influences can impact the development of cognitive control. Indeed, age differences in decision-making and cognitive control can be modulated by differential kinds of incentives, such as monetary incentives (i.e. reward/loss), or social incentives (i.e. acceptance or rejection by the peer group; Achterberg, van Duijvenvoorde, van der Meulen, Bakermans-Kranenburg, & Crone, 2018; Kray, Schmitt, Lorenz & Ferdinand 2018; Tan, Silk, Dahl, Kronhaus & Ladouceur, 2018).

Research has also reported a relation between *a lack* of cognitive control and detrimental developmental outcomes. For example, lack of (aberrant) cognitive control has been identified as a marker for susceptibility to develop impulse-related problems such as pathological gambling or addiction (van Timmeren, Daams , van Holst & Goudriaan, 2018). Furthermore, low levels of cognitive control have been associated with (neuro)psychiatric illnesses, such as schizophrenia (Matzke, Hughes, Badcock, Michie & Heathcote, 2017) and Attention Deficit Hyperactivity Disorder (ADHD) (Ma, van Duijvenvoorde & Scheres, 2016; Rubia, 2018). Recently, research has made significant progress in unraveling the neurocognitive processes that are associated with the development of cognitive control, leading to new insights in the mechanisms of cognitive control. In general, cognitive maturation closely follows the development of the prefrontal cortex (PFC) and its connections (Crone and Steinbeis, 2017), but different subparts of the PFC differentially relate to distinct aspects of cognitive control. Several examples of research linking behavioral development of self-control to brain development are described below.

1.1 Cortico-Subcortical Connections and the Development of Self-Control

Longitudinal studies into the brain anatomy of typically developing children and adolescents reveal largest gray matter volumes and cortical thickness during childhood followed by steady decline during adolescence (Raznahan et al., 2011; Tamnes et al., 2017). In addition, the increases in functional and structural connectivity contribute to local and distal integrative processes and gradually shift the balance in the cortico-subcortical circuits towards the cognitive-control-dedicated brain regions (Genc et al., 2018; Koenis et al., 2018). The marked changes in connectivity are further evidenced by findings showing an initial wave of synaptic overproduction during childhood, which is followed by selective synaptic elimination during adolescence (Huttenlocher & Dabholkar, 1997). Together with the increase in axonal myelination, the elimination of (non-functional) synaptic connections is presumed to be part of the brain's 'fine-tuning' mechanisms to maximize (metabolic) efficiency and functionality (Yakovlev, Lecours, Minkowski & Davis, 1967; Huttenlocher, 1979).

The observation that the maturational processes on the brain level occur during the pubertal stage of adolescence, which is characterized by major physical changes including the development of secondary sexual characteristics, possibly suggests an interrelation between hormonal development and brain development (Peper & Dahl, 2013; Herting & Sowell, 2017). Puberty, the initial phase of adolescents which is characterized by large changes in physical appearance of adolescents, involves a surge in the sex steroid hormones testosterone and estradiol, and hallmarks the biological transition from a non-reproductive into a reproductive state (Nussey & Whitehead, 2001). There is now a fair amount of evidence from both animal and human studies, showing that the activational and organizational processes involved in brain maturation are partly mediated by pubertal (and adolescent) sex steroids hormones (Peper et al., 2013; Herting, Gautam, Spielberg, Dahl & Sowell 2015; Wierenga et al., 2018). Research from our lab suggests that testosterone may play a substantial role in shaping white matter connectivity (Peper, de Reus, van den Heuvel & Schutter, 2015). Two-hundred fifty-eight healthy volunteers aged between 8 and 25 years underwent diffusion tensor imaging (DTI), a neuroimaging technique enabling the measurement of white matter connections *in vivo*. Tractographical analyses revealed associations between higher endogenous levels of testosterone, lower quality of structural fronto-temporo-subcortical connectivity and less behavioral inhibition in the form of aggressive personality (Peper, de Reus, van den Heuvel & Schutter, 2015). These findings possibly indicate that poorer cognitive control is related to less adequate inhibitory signal transfer from the cerebral cortex to the subcortical motivation circuits (Casey, Galvan & Somerville, 2016).

Support for this explanation comes from other DTI work that examined the relation between fronto-striatal fiber tracts and delayed discounting in 40 healthy adults (Peper, et al., 2013). Based on the previously mentioned Marshmallow task (Shoda et al., 1990), delay discounting evaluates cognitive control by examining the process of devaluation of a reward as a function of elapsed time. Volunteers who show a high rate of delay discounting typically discard an immediate small reward in favor of getting a significant larger reward after a prolonged period of time. Results revealed that lower integrity of the fronto-striatal tracts was correlated to lower rates of delayed discounting in both male and female participants. Furthermore, in the male participant group, endogenous testosterone levels were correlated to lower integrity of these fronto-striatal white-matter tracts (Peper et al., 2013).

In our longitudinal study evidence was found that the integrity of the fronto-striatal white matter tracts predicted the development of cognitive control over time (Achterberg, Peper, et al., 2016). Separated by a 2-year interval, 192 healthy volunteers between 8 and 26 years underwent DTI and performed the delay-discounting task twice. Results showed that delay-discounting rates decreased with age (i.e. increased self-control to wait for a delayed reward), reaching the lowest discounting rates during late adolescence/early adulthood. Analyses of the neuro-anatomical data showed that the fronto-striatal tracts developed relatively fast during childhood and early adulthood, and showed little change during mid-adolescence. Particularly the integrity of the frontal-striatal tracts during childhood and early adolescence predicted delay-discounting rates two years later. In sum, the presented results demonstrate the involvement of cortico-subcortical white matter tracts in cognitive control. Moreover, puberty-related sex steroids may be one of the underlying explanatory mechanisms for the relation between cortical-subcortical connectivity and delay discounting.

1.2 Social Self-Control

Another important form of behavioral control is social self-control. Social self-control includes for instance the inhibition of (unwanted) behavioral responses toward others such as social aggression (Twenge, Baumeister, Tice & Stucke, 2001). Negative social feedback (i.e. rejection) can trigger feelings of depression, frustration, or aggression (DeWall and Bushman, 2011). A relatively new field of research is concerned with studying the neural mechanisms underlying aggression after receiving negative social feedback (Achterberg, van Dujivenvoorde, et al., 2016).

Accordingly, in our lab, the Social Network Aggression Task (SNAT) paradigm was used during which young adult participants were evaluated by peers according to a profile

webpage they created at home (Achterberg, van Dujivenvoorde, et al., 2016). First, neural activity was measured after (positive and) negative feedback of the peers on their profile page. Second, the participant was offered the possibility to retaliate by –after each feedback- sending out a loud noise blast to the peer. A longer duration of the noise blast was considered a measure of aggression (Achterberg, van Dujivenvoord et al., 2016). It was found that noise blast duration was significantly longer after negative social feedback (disliking/rejection of their profiles), than after positive or neutral feedback. Moreover, greater brain activation in the dorsal lateral PFC (dlPFC) and also the amygdala, hippocampus and parietal cortices) was associated with shorter noise blast duration after negative social feedback compared to neutral and positive feedback. This finding was interpreted as participants showing relatively high dlPFC activation after negative social feedback also displayed relatively higher aggression regulation (i.e. behavioral control) after experiencing negative social feedback (Achterberg, van Dujivenvoord, et al., 2016). In another study using the SNAT paradigm which was carried out in middle childhood (7-10 years), similar brain-behavior interactions were found as in adults (Achterberg, an Duijvenvoorde, van der Meulen, Euser, Bakermans-Kranenburg, & Crone, 2017), rendering the SNAT a reliable tool to investigate social self-control in children and adults.

Taken together, social self-control is an important feature of studies into behavioral control, also from a developmental perspective, as the evaluation by others becomes especially salient during adolescence when teenagers are highly sensitive to acceptance and rejection by peers (Somerville, Heatherton &Kelley, 2006; Gunther Moor, van Leijenhorst, Rombouts , Crone & Van der Molen, 2010).

1.3 Intermediate Conclusion

Improvements in cognitive and social self-control throughout adolescence are associated with development of (subregions within) the frontal lobe and with marked increases in white matter integrity of cortico-subcortical and fiber bundles in the frontal lobe. These connections are associated with stronger delay of gratification and less direct aggression (self-report) and social aggression (e.g., social rejection-evoked aggression). Owing to their organization and activational effects on brain tissue, sex steroid hormones are implicated in shaping the white-matter architecture underlying cognitive control. It is proposed that even though adolescents can exert cognitive control, the continuing refinement of the white matter structure makes the young individual increasingly robust to effectively deal with a variety of more complex and cognitively demanding tasks and life situations.

Part II: Risky Decision-Making

In parallel with the development of cognitive control, individuals undergo a vast array of changes in risky decision-making across adolescence. For instance, adolescence has often been associated with heightened risk-taking behavior such as heightened substance (ab)use, reckless driving, and unsafe sex, relative to childhood and adulthood (Dahl, Allen, Wilbrecht & Suleiman 2018; Spear, 2018). Also in laboratory studies adolescent show elevated risky decision-making, especially under situations of immediate reward (Peper et al., 2013), uncertainty (Figner, Mackinlay, Wilkening & Weber, 2009), or social influence (Chein, Albert, O'Brien, Uckert & Steinberg, 2011). Like cognitive control, risk taking is a multifaceted construct (Harden et al., 2016; Mamerow, Frey & Mata, 2016; Frey, Pedroni, Mata, Rieskamp & Hertwig 2017; van Duijvenvoorde, Blankenstein, Crone & Figner, 2017) and different behavioral components of risk-taking mature along slightly different developmental non-linear curves (Peper, Braams, Blankenstein, Bos & Crone, 2018). In addition, pubertal hormones testosterone and estradiol contribute to the development of risk-taking, such that increases in testosterone and estradiol have been found to bolster risk-taking behavior and impulsive personality, and attenuated avoidance-like personality (Peper et al., 2018).

To better understand what drives this adolescent-specific maturation of risk-taking behavior, researchers made use of (economic) choice paradigms in which underlying sensitivities to different aspects of risk taking can be examined, such as sensitivity to rewards (e.g., winning versus losing) and risk (e.g., the probability of winning/losing). By investigating these separate sensitivities, it can be unraveled what aspects of risky choice behavior drive individuals' observed risk-taking behavior across adolescent development. Moreover, including neuroimaging measures (such as fMRI) has proven valuable in understanding the underlying mechanisms of these sensitivities (Glimcher & Rustichini, 2004; Van Duijvenvoorde & Crone, 2013). In the following sections, an overview is given of recent behavioral and neuroimaging studies specifically focused on examining these different sensitivities to adolescent risk taking. In particular, paradigms to measure these different aspects of risk taking are discussed, as well as their developmental trajectories, and neurobiological correlates.

2.1 Reward Sensitivity

It has been suggested that an important factor driving risk-taking behavior in adolescence is a heightened sensitivity to rewards (e.g., monetary gains). A way to examine this sensitivity to rewards is to study brain activation in response to rewards and losses during a simple gambling

game. For example, our lab (Braams, Peters, Peper, Guroglu & Crone, 2014; Braams, van Duijvenvoorde, Peper & Crone, 2015) studied changes in reward reactivity in the ventral striatum from childhood to young adulthood (8-25 years old; the 'Braintime' sample), using a simple heads-or-tails tossing game in the MRI scanner. Here participants could either win or lose money depending on whether they correctly guessed heads or tails (i.e., if participant matched the predetermined response of the computer they won money, and if they did not match this response they lost money). Using a two-wave longitudinal design, this study confirmed that ventral striatum activation in response to rewards versus losses is heightened in adolescence, as evidenced by a quadratic peak in ventral striatum reactivity in mid-adolescence (Braams et al., 2014; Braams et al., 2015). A number of studies have shown that adolescents' neural sensitivity to rewards is heightened relative to children and adults (Galvan, Hare, Voss, Glover & Casey, 2007; Van Leijenhorst, Moor, de Macks, Rombouts, Westenberg & Crone, 2010; van Duijvenvoorde, Peters, Braams & Crone, 2016; Schreuders, Braams, Blankenstein, Peper, Güroğlu & Crone 2018) and this adolescent peak in ventral striatum activity has been confirmed in a meta-analysis (Silverman, Jedd & Luciana, 2015).

An important question concerns the behavioral patterns that are associated with this rise and fall of ventral striatum activity in mid-adolescence. This question was addressed in a three-wave longitudinal study with the Braintime sample (8-29 years; Schreuders et al., 2018). Similar to previous research, this study confirmed an adolescent-specific peak in ventral striatum activity which was estimated around the age of 16 years. We further examined the contributions of individual differences in behavioral sensitivity to rewards. Specifically, we tested effects of state-like (the experienced enjoyment of winning versus losing money) and trait-like (the drive to obtain personal goals) behavioral reward sensitivity, on the increase in ventral striatum reactivity in early-to-mid adolescence (i.e., from 8-16 years old), followed by the decrease in mid-to-late adolescence and young adulthood (i.e., from 16-29 years old). It was found that the rise in this neural reactivity in early to mid-adolescence was related to the motivation to push boundaries to achieve goals that are personally relevant to the individual. In contrast, the subsequent decrease from mid-adolescence to early adulthood in ventral striatum activation was related to how those rewards are valued (Schreuders et al., 2018). Together, this study robustly documents that subcortical activation in response to rewards versus losses in heightened in mid-adolescence (see also Silverman et al., 2015, for a meta-analysis), and shows that the neural responses are related to the behavioral experiences of rewards. Furthermore, other research showed that neural activity to rewards was related to a tendency to task risks in daily life (Galvan et al., 2007) and to alcohol consumption (Braams, Peper, van der Heide,

Peters & Crone, 2016). Taken together, a heightened sensitivity to rewards is an important underlying factor driving risk-taking behavior in adolescence.

2.2 Risk Sensitivity

Although reward sensitivity in the ventral striatum has frequently been related to heightened risk-taking behavior in adolescence, risk taking is often influenced by both rewards and the associated risk, i.e., the variability in outcomes. That is, when choosing to take a risk, individuals make a tradeoff between the potential risks and the potential rewards (Figner & Weber, 2011). As such, reward sensitivity is often convoluted with risk sensitivity. An example of a risky choice paradigm in which effects of reward and risk were disentangled is the study by Van Duijvenvoorde et al. (2015), who administered the "hot" Columbia Card Task in the MRI scanner to a sample of children (8-11 years), adolescents (16-19 years), and adults (25-34). In this task, participants were presented with faced down playing cards, and were asked to turn over cards one at a time, resulting in either a gain or a loss. Each gain card was added to participants' earnings, while a loss card terminated the trial. Participants could decide to stop turning cards at any time, cashing their earnings from the moment they decided to stop playing. Van Duijvenvoorde et al. (2015) disentangled risky choice behavior during this task into a return component (i.e., expected value, or the product of the probability of a reward and the amount of that reward) and a risk component (outcome variability). Next, neural reactivity to changes in return (expected value) and risk (outcome variability) were compared across age groups. Neural reactivity in response to returns (expected value) increased linearly with age in a network of regions including the ventromedial PFC and the posterior cingulate cortex, also referred to as the "valuation network" of the brain. In contrast, neural reactivity in response to risk (outcome variability) peaked quadratically in adolescence, in the insula and dorsomedial PFC. Suggestively, adolescents may have a heightened emotional response to risks relative to children and adults, and in parallel engage more cognitive and regulatory processes when presented with risk (Van Duijvenvoorde et al., 2015). Together, these findings show that mid-to-late-adolescence may not only be a phase of heightened reward sensitivity (in subcortical regions such as the nucleus accumbens: Schreuders et al., 2018), but also of heightened risk sensitivity (in conflict and uncertainty-related regions: Van Duijvenvoorde et al., 2015).

2.2.1 Explicit risk and ambiguous risk

In the studies described above, even though the outcomes of decisions were uncertain (i.e., guessing heads or tails correctly; winning or losing after turning over another card), participants

did have explicit knowledge of the exact *probabilities* of these uncertain outcomes. For instance, the chance of guessing heads or tails correctly is 50% (Braams et al., 2015; Schreuders et al., 2018), and in the CCT, participants had knowledge of how many gain and loss cards were presented. However, risks in real life rarely present exact probabilities of different outcomes: there are often unknown, or *ambiguous* (Tversky & Kahneman, 1992). Classic behavior economic work with adults has shown that even though individuals are generally averse to risk (known probabilities), they are even more averse to ambiguity (unknown probabilities) than risk alone (Ellsberg, 1961; Von Gaudecker, Van Soest & Wengström, 2011). How adolescents deal with these two types of risk has started to receive greater attention in recent years, as it has been suggested that these different types of risk differentially influence overt risk-taking behavior (Tversky & Kahneman, 1992).

The first to study how adolescents deal with risk and ambiguity was Tymula et al. (Tymula et al., 2012) who developed a binary risky choice task in which participants (33 adolescents: 12-17 years; 31 adults: 30-50 years) could choose between a sure option (i.e., a 100% chance of winning a small amount of money), or a gamble, which could yield more money but could also yield nothing. Specifically, the gambling option varied in amount, probability, and ambiguity level (i.e., the portion of the stimulus that was concealed to the participant, so that probabilities were (partially) unknown). Using a model-based method, the authors estimated individuals' behavioral preferences towards risk (known probabilities) and ambiguity (unknown probabilities). This study showed that adolescents were relatively more tolerant towards ambiguity (i.e., less ambiguity averse) than adults. Moreover, ambiguity tolerance, but not risk tolerance, was related to real life risk-taking behavior such as smoking and underage drinking, suggesting that adolescent risk-taking is driven by a tolerance to ambiguity. These findings were replicated in a more recent study from our lab (Blankenstein, Crone, van den Bos, & van Duijvenvoorde, 2016) using a similar paradigm (i.e., a wheel of fortune task) and the same model-based approach, in a continuous adolescent age range (10-25 years old, N=157). Here, a linear decrease in ambiguity tolerance was observed across adolescence, and ambiguity tolerance was related to more real-life reckless behavior. Another recent behavioral study (van den Bos and Hertwig, 2017; 8-22 years old, N=105) also found pronounced age effects in ambiguity tolerance, i.e., an adolescent-specific peak in ambiguity tolerance, although in a loss domain, which also correlated with real-life risk-taking behavior. Together, these findings suggest that explicit risk (known probabilities) and ambiguous risk (unknown probabilities) differentially impact real-life risk taking in adolescence.

To understand the neural mechanisms underlying risk and ambiguity processing in adolescence, we presented an fMRI adaptation of the wheel of fortune task to adolescents (Blankenstein, Schreuders , Peper, Crone, & van Duijvenvoorde, 2018; N=198, 12-25 years old). Although there were no pronounced age differences in gambling behavior or neural processing (suggestively because no children (<12 years) were included), there were pronounced effects of individual differences in gambling behavior. That is, whereas individual differences in gambling under risk were related to activation in valuation regions of the brain (ventral striatum, parietal cortex), individual differences in gambling under ambiguity were related to regions associated with cognitive and affective processing (dMPFC, insula, DLPFC). These findings illustrate that different brain regions underlie risky and ambiguous gambling, which become particularly evident when including individual differences in task-based risk taking. In addition, this paradigm also included decision outcomes. After choosing to gamble, participants were presented with gain or no gain outcomes. This allowed to disentangle reward processing following risky gambles from reward processing following ambiguous gambles. Here it was shown that although the ventral striatum coded reward processing irrespective of risk or ambiguity (indicative of a general signal of reward value), the MFPC particularly differentiated between gain and no gain outcomes following ambiguity. This suggests that this region may function as an informative saliency signal of ambiguous decision outcomes in particular, which may be applied to subsequent decisions (van Noordt & Segalowitz, 2012; McCormick & Telzer, 2017a).

Furthermore, when including individual differences in indices of real-life risk taking (such as self-reported rebellious behavior and the drive to obtain personal goals), activation in the LPFC was observed. Specifically, those individuals who reported to take more risks in daily life showed less activation in this region during reward outcome processing, independent of risk or ambiguity. This finding is in line with the idea that self-control (reflected in the LPFC) in response to general rewards is lowered for those who take more risks (Gianotti et al., 2009).

Taken together, these studies on risk and ambiguity processing and their neural correlates show that 1) risk and ambiguity are different aspects of risk-taking behavior in adolescence; 2) behavioral preferences under risk and ambiguity follow different developmental trajectories; 3) risk and ambiguity are reflected in different brain systems. Finally, these studies highlight the importance of considering multiple aspects of risk-taking behavior (task-based and self-report measures) in the study of adolescent risk taking.

2.3 Intermediate Conclusions

The rise in risk-taking behavior during adolescence is characterized by changes in brain function and structure, pubertal hormones, and behavioral sensitivities to underlying components of risk taking, such as rewards, losses, and (explicit and ambiguous) risk. Moreover, different neural systems underlie these different components of risk taking, further demonstrating that risk taking is a multidimensional construct. By disentangling what underlying behavioral and neural components drive risk taking, it can ultimately be studied who takes risks and why, and in addition, how this contributes to our understanding of adolescents maturing into independent adults.

Part III. Conclusions and Future Directions

This chapter described the development of cognitive control and risky decision-making across adolescent development from a cognitive neuroscience perspective. Cognitive control development is often considered as the most important factor for resisting impulses and promoting future-oriented behavior, and it co-occurs in development with changes in how adolescents evaluate risks and rewards. The goal of this chapter was therefore to describe these changes in parallel and understand how these processes rely on partly similar and partly different neural structures.

We showed that cognitive control in terms of delay of gratification improves over the whole range of adolescence, peaking around late adolescence/early adulthood in both affective and social domains, and is partly mediated by stronger connectivity between prefrontal cortex and limbic brain regions. These connections are associated with stronger delay of gratification and less direct aggression (self-report) and social aggression (e.g., social rejection-evoked aggression). Together these patterns suggest that adolescence is a period of significant cognitive advancements with improving control and goal flexibility (Crone & Dahl, 2012; Luna, Marek, Larsen, Tervo-Clemmens & Chahal 2015b, see Chapter 21). Interestingly, risk-taking behavior shows a relative rise in adolescence, especially in the context of immediate rewards and social influences. These rises are associated with stronger activity in limbic brain regions when evaluating rewards. In search of mechanistic explanations for these changes, it was found that both these processes, i.e. increased prefrontal cortex-limbic connectivity and stronger reward-related activity in limbic brain areas, are associated with the rise of the hormone testosterone, suggesting that these hormones may have multiple influences on neural circuits in the adolescent brain. Finally, components of risk taking, such as risk and ambiguity processing, rely on partly overlapping and partly different circuits as cognitive control and reward

sensitivity. This may explain why these processes are sometimes interpreted in parallel (i.e., poor cognitive control explains some parts of risk taking behavior), but are not similar (i.e., additional brain circuits are involved in risk processing, such as the valuation network of the brain).

This multi-perspective view on adolescent development has received increased attention in recent years (e.g. dual-processing or circuit models, see Somerville & Casey, 2010 and Shulman et al., 2016) and shows the complexity of understanding the dynamic changes in behavioral and neural processes in adolescence. Inspection of data plots often shows that the elevated patterns of, for example, risk-taking in adolescence, are driven by subgroups of adolescents who engage in these behaviors (Willoughby, Good, Adachi , Hamza & Tavernier, 2014) and have been examined in different phases of adolescents development (van Duijvenvoorde et al., 2016). Current research remains inconclusive with respect of the specific age or pubertal phases in which these relative changes in cognitive control and decision-making occur, although several longitudinal cohort studies which combine behavioral and neural assessment are currently ongoing (Casey et al., 2018).

Recent views also demonstrate the context-specificity of adolescent cognitive control and risky decision-making behaviors. An intriguing question concerns whether adolescents who show the largest increases in risk taking in adolescence, are more sensitive to contextual influences on behavior in general. These adolescents may show more risk taking when risks result in higher incentives (Figner & Weber, 2011) or social acceptance (Chein et al., 2011), but may also show better cognitive control (Luna et al., 2015b) and prosocial behavior (Do, Guassi Moreira & Telzer, 2017) when these behaviors are rewarded. An important question for future research is thus to examine which adolescents show the strongest contextual reward sensitivity. Subsequently, a crucial questions concerns which adolescents are characterized by a risk profile (suggesting a stronger tendency to engage in health-detrimental risk-taking behavior) and which adolescents are characterized by a 'differential susceptibility' profile – i.e., in some contextual circumstances they may engage in dangerous risk behaviors, but in other circumstances they may engage in risk behaviors to help others (i.e., 'prosocial risk-takers', Schriber & Guyer, 2016; Do et al., 2017). For example, a higher tolerance to ambiguity has been associated with greater risk-taking behavior, but has also been associated with more trust and cooperation in adults (Vives & FeldmanHall, 2018).

Another important direction for future research is to understand the dynamics of change in terms of neural and hormonal influences. We showed several examples of how hormonal and neural development coincide, but it remains unclear whether these directly influence each other.

Indeed, evidence based on animal and adult studies provide evidence for this hypothesis, although this has not yet been explicitly tested in adolescence. Also, the majority of studies suggest hormonal effects on reward valuation and connections with reward circuitry. However, it remains to be determined how and when hormonal development influences cognitive control and decision-making among multiple contexts, and whether there are sensitive periods for hormonal influences on reward and cognitive control development. One approach to better understand these influences is by distinguishing between early and late pubertal adolescents and examine the developmental outcomes in terms of brain and behavior longitudinally (see Peper & Dahl, 2013).

Taken together, the current overview provided evidence for dynamic changes in multiple aspects of cognitive control and decision-making over the course of adolescent development, which are associated with dynamic neural changes in brain regions relevant for cognitive control and decision-making. There was consistent evidence for a role of prefrontal cortex-limbic activity and connectivity development in part explaining some of the behavioral improvements and changes observed during adolescence. New research approaches require better assessment of contextual influences and social-environmental influences on adolescent behavior and neural development. Such approaches will aid in understanding how these contextual influences predict long term outcomes in terms of risk for adverse outcomes and opportunity for positive outcomes, such as (social) explorative behaviors.

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Table 1. Overview of paradigms to measure cognitive control and risky decision-making across adolescence

Name	**Outcome measure**	**Example studies**
Paradigms to measure cognitive control		
Marshmallow task	Delay of gratification	Shoda et al., 1990; Watts et al., 2018
Delay Discounting study	Delay of gratification / area under curve	Peper et al., 2013; Achterberg et al., 2016
Social Network Aggression Task	Self-control in response to social evaluations	Achterberg et al., 2017; 2018
Paradigms to measure risky decision-making		
Heads-or-tails fMRI task	Neural sensitivity to rewards versus losses	Schreuders et al., 2018
Hot Columbia Card fMRI Task	Risk and return sensitivity	Van Duijvenvoorde et al., 2015
Risk and Ambiguity task	Risk and ambiguity attitude	Tymula et al., 2012; Blankenstein et al., 2016
Risk and Ambiguity fMRI task	Neural sensitivity to risk and ambiguity and outcome processing	Blankenstein et al., 2018

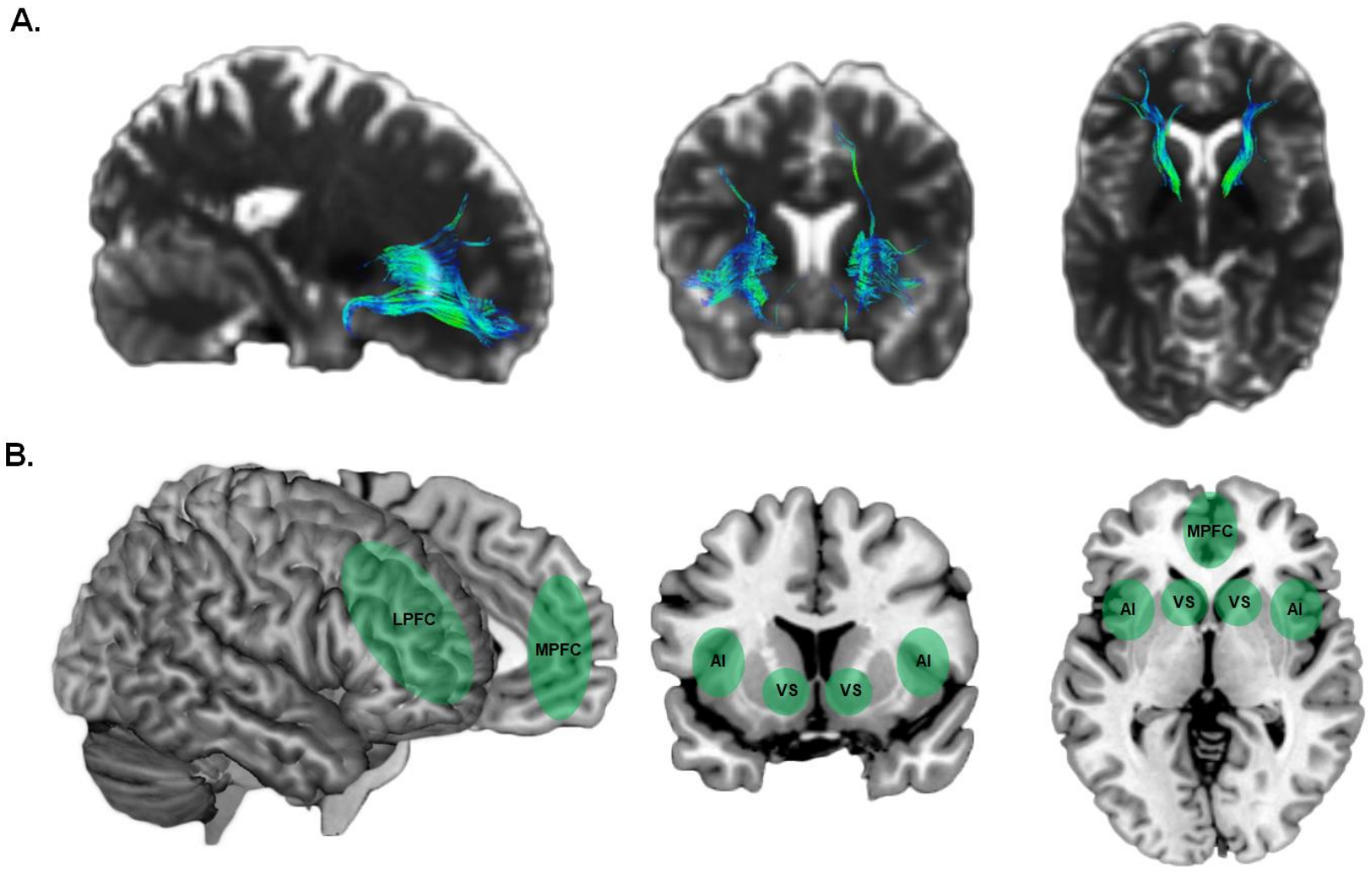

Figure 1. **A**. Sagittal (left), coronal (middle) and axial (right) views of frontostriatal white matter bundles of one random participant (from Peper et al (2013) Cerebral Cortex, with permission. **B.** Sagittal (left), coronal (middle) and axial (right) views of areas of activation involved in

cognitive control and risky decision-making. LPFC = lateral prefrontal cortex; VS = ventral striatum; MPFC = medial prefrontal cortex; AI = anterior insula.