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Risky business? Behavioral and neural mechanisms underlying risky decision-making in adolescents

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Chapter 7

Summary and General Discussion



Summary

The primary aim of this thesis was to unravel the behavioral and neural mechanisms underlying risky decision-making in adolescents. First, I decomposed risky choice behavior into their underlying components (risk and ambiguity attitudes), and investigated their neural mechanisms in adolescence. Second, I focused on how individual differences in real-life (risky) decision-making contribute to our understanding of adolescence as period of risks versus opportunities.

Risk and ambiguity attitudes in adolescence

In the first empirical chapter (chapter 2), I applied a behavioral wheel of fortune paradigm in a developmental sample of adolescents and young adults (N = 157, age range 10-25 years). Here, participants were presented with pairs of wheels and were asked to choose which wheel they preferred to (hypothetically) spin. One wheel was a consistent sure gain (i.e., a 100% chance of gaining a small amount of money). The other wheel reflected a gamble, which could result in more money but could also result in nothing. This gambling wheel thus varied in the gain amount and in the probability of gaining that amount. In addition, to manipulate the level of ambiguity associated with the gain probability, we varied the size of various 'lids' that could cover more or less of the gambling wheel. Using a model-based approach, I tested 1) the developmental trajectories of risk and ambiguity attitudes across adolescent development and 2) the extent to which risk and ambiguity attitudes were related to risk taking in real life. Given that risk taking in real life more often takes place within an ambiguous, rather than risky, choice context (i.e., real life risks rarely present known probabilities), it was expected that ambiguity attitude would show more prominent development change compared with risk attitude, and that real-life risk taking would be more prominently related to ambiguity attitude than to

risk attitude. A linear increase in ambiguity attitude, but not in risk attitude, was observed, such that ambiguity aversion slightly increased across adolescence. Given that ambiguity aversion is not yet present in childhood (8-9 years old; Li, Brannon, & Huettel, 2014), this finding suggests that ambiguity aversion may emerge in early adolescence. Moreover, real-life risk-taking behavior was related to attenuated ambiguity aversion, but not to risk aversion, further suggesting that ambiguity may be better reflective of risk taking in real life.

Additionally, in this study I explored whether social context influenced risk and ambiguity attitude. Specifically, I studied the effects of peers' choices as a source of information for individuals' own risky choices. To this end I added a social condition to the wheel of fortune task in which participants were shown the decisions of a high risk-taking peer before making their own choice. Tentatively, it was observed that individuals' risk attitudes, but not ambiguity attitudes, became more aligned (i.e., more risk seeking) with that of the observed choices, which appeared most pronounced for the youngest participants (10-12 years old). This finding suggests that risk taking may vary under conditions of social advice, and sets the stage for future studies on peer information in conditions varying in uncertainty.

In sum, these findings suggest that early adolescence (10-12 years) may be a starting point for emerging ambiguity aversion as is typically observed in adulthood, and that behavior under ambiguity may be a better naturalistic reflection of adolescent risk taking in daily life. Furthermore, first steps were taken to study effects of observed information from peers in a risky and ambiguous context. Most importantly, this chapter illustrates the potential of using a model-based method of disentangling risk and ambiguity attitude in a developmental sample, and investigating individual differences in these attitudes.

Risk and ambiguity attitudes in the adult brain

In chapter 3 I studied risk and ambiguity processing in 50 young adults (18-28 years), and charted their underlying neural mechanisms. The goal of this study was to examine to what extent these two types of risk are processed differentially within individuals. A way to examine the neural specificity of risk and ambiguity processing is to include individual differences in risk and ambiguity attitudes, which I estimated using the wheel of fortune task. Subsequently I related these risk and ambiguity attitudes to neural activation during a simplified fMRI version of the wheel of fortune task. This fMRI task resulted in a robust measure of neural activation of risky and ambiguous gambling in a general network typically associated with risky decision-making. Including risk and ambiguity attitudes revealed that relatively more risk-seeking attitudes were associated with greater activation in medial and

lateral orbital frontal cortex; while more ambiguity-seeking attitudes were reflected in greater medial temporal cortex activation. These findings suggest that different neural correlates underlie individual differences in risk and ambiguity attitude, and that risk and ambiguity impact overt risk-taking behavior in different ways.

Another question I addressed in this study was whether the neural coding of reward outcome processing differed following risky versus ambiguous gambling. The fMRI version of the wheel of fortune task therefore also included a reward outcome phase (i.e., gains and no gains, following risky and ambiguous gambles). Although ventral striatum activation reflected reward outcome processing irrespective of risk or ambiguity, greater dorsomedial prefrontal cortex activation was specifically observed during reward outcome processing following ambiguity. This activation pattern may function as a general signal of uncertainty coding, which may be particularly salient following ambiguous decision contexts. Together, this adult study set the stage for a developmental perspective on the neural coding of risk and ambiguity attitudes. In the next chapter I build on these findings and those described in chapter 2, in a study on the neural tracking of adolescents' subjective choice valuation under risk and ambiguity.

Subjective value tracking under risk and ambiguity in the adolescent brain

In chapter 4, I further tested how risk and ambiguity attitudes are coded in the brain, in a second adolescent sample spanning a broad age range (N = 188, 12-22 years). However, here I integrated participants' separately estimated risk and ambiguity attitudes, with the fMRI task during choice, on a trial-by-trial basis. That is, I inferred participants' *subjective value* of the choices presented in the fMRI task. As such, I studied which brain regions coded changes in subjective choice valuation under risk versus ambiguity, and possible overlap between these conditions. Parametric fMRI analyses showed that increasing subjective value under risk was coded by activation in ventral striatum and superior parietal cortex. In contrast, decreasing subjective value under ambiguity was coded by dorsolateral prefrontal cortex and superior temporal gyrus activation. Finally, dorsomedial prefrontal cortex activation reflected a general signal of decreasing subjective valuation, such that this region coded subjective value in both conditions. Interestingly, preliminary evidence suggested that these findings were less pronounced in a model testing for objective expected value (that is, the probability * amount, not weighted by individuals' risk and ambiguity attitudes). This suggests that making use of subjective - rather than objective - measures of valuation, is more meaningful when studying the neural underpinnings of adolescent choice valuation. Indeed, although limited age effects

were observed, there were pronounced individual differences in behavioral risk and ambiguity attitudes, which were reflected in participants' perceived riskiness of the risky and ambiguous wheels. Together, these findings indicate that distinct as well as similar patterns of brain activation underlie subjective value tracking under risk and ambiguity in adolescence, and illustrates the potential of combining model-based behavioral analyses with (parametric) fMRI in adolescents, which may ultimately explain who takes risks and why.

Individual differences in task-based and self-reported risk taking under risk and ambiguity in the adolescent brain

In chapter 5, I focused on the relation between neural risk and ambiguity processing and individual differences in risk-taking tendencies. Specifically, I focused on individual differences in task-related risk taking, as well as self-reported real-life risk taking, in relation to the neural correlates of risky and ambiguous choice and reward outcome processing (N = 198, 12-25 years, including the sample of chapter 4). Distinct neural correlates were observed when contrasting risky and ambiguous gambling, with risk more pronounced in parietal cortex and ambiguity more prominently with dorsolateral prefrontal cortex activation, as well as medial prefrontal cortex during reward outcome processing (as in chapter 2). When including individual differences in task-related risk taking (i.e., proportion gambling under risk and under ambiguity), a positive association was found in the ventral striatum activation in the choice phase, specifically for risk, and a negative association with insula and dorsomedial prefrontal cortex activation, specifically for ambiguity. Moreover, lateral prefrontal cortex activation during reward outcome processing seemed a prominent marker for individual differences in task-related risk taking under ambiguity, and indices of real-life risk taking (i.e., self-reported rebellious behavior and the drive to obtain rewards). Here, lower levels of risk taking were associated with greater dorsolateral prefrontal cortex activation. Together, these findings demonstrate the importance of including multiple risk-taking measures (lab-based and self-report measures), and multiple decision contexts (risk and ambiguity; choice and outcome), in understanding the neural mechanisms underlying adolescent risk taking. As such, this multidimensional perspective on risk taking contributes to our understanding of which individuals are most prone to display risk-taking behavior.

Predicting risk taking and prosociality from longitudinal behavioral and structural brain development

Finally, in chapter 6, I further studied adolescent susceptibility to risk taking. However, given that adolescence may also be an important phase for the development

of positive, other-oriented behavior, I also tested contributions to prosocial behavior, that is, behaviors intended to benefit someone else. To date, the relation between risk-taking behavior and prosocial behavior has been overlooked, while this is key to our understanding of how these two seemingly paradoxical behaviors develop in tandem in adolescence. This study addressed whether risk-taking behavior and prosocial behavior are related constructs in adolescence, and which processes predict these two disparate behaviors. To these ends I used longitudinal self-report and structural brain development data from the three-wave, biannual, Braintime study (N = 210 at the final wave, 8-29 years, including the sample of chapter 4 and 5). First, risk-taking behavior and prosocial behavior assessed at the final wave were positively correlated. Furthermore, it was found that higher levels of empathy, and perspective taking abilities (current levels and longitudinal change) uniquely predicted prosocial behavior, whereas higher levels of fun-seeking tendencies (current levels and longitudinal change) predicted *both* prosocial and risk-taking behaviors. Moreover, these changes were accompanied by reductions in nucleus accumbens and medial prefrontal cortex volume across development, regions previously implicated in both risk-taking and prosocial behavior. Preliminary evidence indicated that faster maturity of the medial prefrontal cortex was related to less rebellious behavior at the final wave, suggesting that structural brain maturity may be an informative predictor of behavior. This study points towards a ‘differential susceptibility’ marker (namely, fun seeking), as a predictor of diverse adolescent outcomes. Understanding the possible mechanisms that underlie these two seemingly disparate behaviors may help to identify pathways for reducing risks and promoting opportunities often inherent in adolescence, and point towards a more differentiated perspective on adolescent development.

General Discussion

The studies presented in this thesis converge to a number of main findings. First, I demonstrated that risk and ambiguity attitudes are distinguishable components of risky choice behavior in adolescence and (young) adulthood. That is, I showed that risk and ambiguity are reflected in distinct behavioral attitudes, processed by different underlying mechanisms, and separately inform – individual differences in – overt risk-taking behavior in adolescence. Second, the studies in this thesis suggest that adolescence may be a period of risks, but also of opportunities. For instance, by investigating risk-taking and prosocial behavior in relation to individual differences in their behavioral and neurobiological pathways, I provided evidence



that a single underlying trait may result in these diverse outcomes. In the following sections, I discuss this thesis' main findings in further detail within a neuroeconomic developmental framework, and provide recommendations for future research.

Risk and ambiguity: Distinguishable components underlying risk-taking behavior across adolescence

Across the first three empirical chapters, I showed that risk and ambiguity attitude can be behaviorally disentangled within individuals using a model-based approach. Across three separate samples (chapters 2, 3, and 4), risk and ambiguity attitude were not significantly correlated, suggesting they may reflect different aspects of risky choice behavior. In addition, I focused on the underlying neural mechanisms of risk and ambiguity (attitude) in an adult and adolescent sample (chapters 3; and chapters 4 and 5, respectively). Here I showed that risk and ambiguity are reflected in different brain systems, when considering individuals' risk and ambiguity attitudes. A number of key regions specifically tracked risk and ambiguity preferences. That is, in chapter 3 (adults) greater risk seeking attitudes positively scaled with activation in the medial and lateral orbital frontal cortex, regions part of the valuation network. Interestingly, in chapter 4 (adolescents) we observed that subjective value increases under risk (determined with individuals' risk attitudes), were coded by ventral striatum activation, a region also part of this network, and parietal cortex. Activation in this latter region was also heightened when contrasting risky versus ambiguous gambling in chapter 5. Furthermore, in chapter 3, greater ambiguity-seeking attitudes were related to greater temporal cortex activation, while in chapter 4 subjective value decreases under ambiguity were also coded in temporal cortex activation. Another ambiguity-specific region was the dorsolateral prefrontal cortex, which coded subjective value decreases under ambiguity (chapter 4), was heightened when contrasting ambiguous versus risky gambling (chapter 5), and showed greater reward activation for individuals who gambled less often under ambiguity (chapter 5). Finally, the (dorso)medial prefrontal cortex may reflect a common signal of uncertainty, since this region coded subjective value decreases under risk *and* ambiguity during choice (chapter 4). However, lower mean levels of gambling under ambiguity, but not risk, were related to greater activation in this region during choice (chapter 5). Moreover, during outcome this region particularly differentiated between gain and no gain outcomes following ambiguous gambles (chapters 2 and 5). This suggests the dorsomedial prefrontal cortex codes general uncertainty, but may be especially pronounced in ambiguous contexts. In sum, whereas valuation regions of the brain (e.g., ventral striatum, OFC, parietal cortex) primarily reflect explicit risk, conflict- and uncertainty-related regions (dorsolateral

PFC, temporal cortex, dorsomedial PFC) seem to primarily reflect ambiguous risk. The studies in this thesis thus point towards a neural distinction between risk and ambiguity in adolescence and (young) adulthood, which are particularly evidenced when including individual differences in behavior under risk and ambiguity.

Across studies, there were limited developmental effects, but prominent individual differences in behavior under risk and ambiguity. That is, although in chapter 2 we observed a linear increase in ambiguity aversion with age, we did not observe a similar effect in chapter 4 and 5. Similarly, risk attitude did not show consistent age effects across studies. The different age ranges across samples seem to suggest that a more narrow age range (starting at 12 years; chapters 4 and 5) results in less pronounced developmental differences than a broader age range (starting at 10 years; chapter 2). Furthermore, as described in chapters 4 and 5, there were no prominent age effects on neural activation under risk and ambiguity. Other studies did find more pronounced age differences in risk and ambiguity attitude, such as Tymula et al. (2012) who compared a group of adolescents (12-17 years) with a group of older adults (30-50 years). Here, adolescents were more tolerant towards ambiguity, and more averse to risk, than adults. Another, more recent, study on risk and ambiguity attitude in participants aged 8-22 years found pronounced age differences, but only in a loss frame (van den Bos & Hertwig, 2017). Specifically, a linear decrease in risk seeking with age was observed, and a quadratic peak in ambiguity tolerance in mid-adolescence (van den Bos & Hertwig, 2017). Together, these disparate findings across studies highlight the importance of 1) replication across different samples, 2) sample size, 3) the specific age ranges included, and 4) different choice contexts (i.e., gain versus loss), in determining the robustness of age effects.

Another explanation for the limited developmental differences across different studies is the relatively 'cold' nature of the wheel of fortune paradigm (e.g., see Defoe, Dubas, Figner, & van Aken, 2015; Rosenbaum, Venkatraman, Steinberg, & Chein, 2018). That is, a 'hot', affectively-laden task that includes reinforcing decision outcomes (such as the Balloon Analogue Risk-Taking task; e.g., Braams, van Duijvenvoorde, Peper, & Crone, 2015), or the presence of peers (such as the Stoplight driving game; e.g., Chein, Albert, O'Brien, Uckert, & Steinberg, 2011), is more likely to yield pronounced age differences than a 'cold', description-based task (e.g., the behavioral wheel of fortune paradigm in the current thesis) in which choice preferences are assessed in a relatively neutral context (Defoe et al., 2015). Future studies may test whether ambiguity, given its more naturalistic reflection of real life, heightens the affective nature of a relatively 'cold' task.

In addition to influencing affective processing, a recent review suggested that ambiguity (or less information) may lower the engagement of cognitive control and

therefore may result in less advantageous decision-making (Li, 2017). As such, the recruitment of cognitive control is flexible based on the available information.

Furthermore, this review suggests that this cognitive control recruitment interacts with age, such that children make poor decisions when information is lacking (such as in ambiguity), but also show the most improvement when information is present, also referred to as a ‘flexing dual-systems’ model (Li, 2017). The current thesis provides evidence that cognitive control regions like the lateral prefrontal cortex are involved in ambiguity processing (chapter 4, 5), but we did not observe pronounced age effects on neural risk and ambiguity processing. Although the current studies focused more on a neuroeconomic than imbalance perspective, an opportunity for future research is to integrate these two views, by including participants from childhood and early adolescence (8-10 years, an age range in which the most pronounced changes in ambiguity preferences may occur (chapter 2; Li et al., 2014).

Adolescence as a developmental phase of risks and opportunities

A second overarching goal of this thesis was to investigate how individual differences in risk-taking tendencies inform our understanding of adolescence as a period of risks and opportunities. In all studies, individual differences were examined across a variety of risk-taking domains, such as risk and ambiguity attitude (chapters 2, 3, and 4; discussed above), but also indices of real-life risk taking, trait-like reward sensitivity (chapters 2, 5, and 6), and social functioning (chapter 6). As shown across studies, these individual differences help us to better understand the underlying mechanisms of risk-taking behavior, yet also inform our understanding of adolescence as a period of risks and opportunities.

For instance, particularly in chapter 2 I showed that ambiguity attitude was related to real-life reckless behavior. On the neural level, it was showed that the lateral prefrontal cortex (a region particularly implicated in ambiguity processing, see above), was related to real-life risk taking, such that those participants who showed more real-life rebellious behavior and reward drive showed less activation in this region during reward outcome processing. Possibly, this concurs with the idea that those individuals who display higher levels of risk taking show lowered self-control in response to rewards. Finally, in chapter 6 I provided preliminary evidence that faster longitudinal maturity of the medial prefrontal cortex predicted less rebellious behavior. Together, these findings provide insights into the use of behavioral and neural measures in predicting which individuals will take excessive risks, and for whom adolescence is a developmental phase of risks.

However, as chapter 6 suggests, risk-taking behavior may not necessarily be maladaptive. That is, in chapter 6 it was demonstrated that prosocial and rebellious

behavior were positively correlated. This suggests that a subgroup of individuals display both high levels of prosocial, as well as high levels of risk-taking behavior, otherwise referred to as ‘prosocial risk takers’: individuals who may take risks in order to help others (Do, Guassi Moreira, & Telzer, 2017). As such, in some instances, high levels of risk-taking behavior such as rebellious behavior may be useful. Likewise, individual differences in fun-seeking tendencies predicted rebellious behavior, but also prosocial behavior. This underlying tendency of risk taking may function as a differential susceptibility marker, rather than solely predict potentially negative behaviors. Although future studies should confirm these findings in experimental studies in addition to self-report measures, these findings suggest that adolescence is a phase of opportunities, too, and that risk-taking behavior may give rise to these opportunities.

Outstanding questions

A number of future directions remain. For instance, this thesis had a strong focus on individual differences in adolescence, yet it was not explicitly tested whether adolescence is a time of heightened individual differences relative to adulthood. An opportunity for future research is to investigate whether adolescence is marked by *greater variability* between, and within, individuals, compared with adulthood, which may give rise to better predictions of positive versus negative life outcomes.

Another interesting question is whether risk taking fosters exploration and learning (Hartley & Somerville, 2015). Suggestively, a tolerance to ambiguity may be a factor that fosters these behaviors in adolescence (Tymula et al., 2012). A finding in support of testing this hypothesis is the heightened (dorso)medial prefrontal cortex activation that was observed during outcome processing specifically following ambiguity (chapter 2 and 5), potentially functioning as a saliency signal for future behavior. Future studies may formally address whether ambiguity tolerance is beneficial to learning, and the role of the (dorso)medial prefrontal cortex in this relation. Another adaptive purpose of ambiguity tolerance is prosocial behavior. For example, a recent study with adults showed that ambiguity tolerance predicted costly prosocial behaviors during cooperation and trust decisions (Vives & FeldmanHall, 2018). Future studies may test positive (e.g., learning, prosocial behavior) versus negative (e.g., health-detrimental risk taking) influences of ambiguity tolerance in adolescence.

Finally, an outstanding question for future studies is to what extent the current findings generalize to atypically developing individuals, such as those with extremely high levels of risk taking (such as those with externalizing disorders), or those with extremely low levels of risk taking (such as those with internalizing disorders). For

instance, a recent study showed that adults with antisocial personality disorder displayed blunted ambiguity aversion, but not risk aversion, compared to healthy controls (Buckholtz, Karmarkar, Ye, Brennan, & Baskin-Sommers, 2017). This blunted ambiguity aversion was evident for those characterized by impulsivity and aggression (but not for those characterized by psychopathy and rule-breaking), and predicted real-world arrest frequency (Buckholtz et al., 2017). In contrast, a study with adult patients suffering from obsessive-compulsive disorder (characterized by pathological indecisiveness and self-doubt) showed that they were considerably more ambiguity averse, but not more risk averse, than healthy controls (Pushkarskaya et al., 2015). Together, these studies suggest that ambiguity aversion is a prominent marker of aberrant decision-making. Whether similar or different findings can be established for adolescents diagnosed with such disorders remains an open question, and may provide insights for interventions within a decision-making domain. Relatedly, as the findings in chapter 5 illustrate, longitudinal studies are crucial if we want to track the development of precursors to positive (i.e., normative developmental) versus negative (i.e., atypical developmental) life outcomes. By using longitudinal studies, a central question that can be addressed is which developmental trajectories underlie such diverse adolescent outcomes (Crone & Dahl, 2012).

Conclusions

The title of this thesis (Risky business?) refers to two key questions. First, I addressed whether choices are perceived as ‘risky business’ *depending on the choice context*, specifically, when probabilities are known (explicit risk) or unknown (ambiguous risk), and *depending on the individual*. Using a model-based decomposition approach and by including neuroimaging, I demonstrated that these aspects of risks are differentially manifested in behavior and in their underlying neural mechanisms, and may differentially impact overt adolescent risk-taking behavior. In addition, I demonstrated that there are profound individual differences between adolescents in risk and ambiguity attitudes, self-report measures, and neural activation. These individual differences are very useful to better understand the underlying mechanisms of risk taking, but also strengthen the notion that not all adolescents are risk takers. Finally, a related question concerned whether adolescence can solely be conceived as a developmental period of ‘risky business’, or alternatively, of *risks and opportunities*. This thesis points towards the latter interpretation, since risk taking and its underlying components may fulfill adaptive purposes, and that underlying traits of risk taking may also be predictive of positive, other-oriented behavior.

The study of adolescent risk-taking behavior is complex and multifaceted. By adopting a multidisciplinary approach of behavioral economics, developmental psychology, and neuroscience, this thesis demonstrates that risk-taking behavior can be unraveled into separate constructs. This enables us to make predictions about who takes risks, what drives this behavior, and ultimately, which individuals are prone to positive versus negative life outcomes.

