Risky business? Behavioral and neural mechanisms underlying risky decision-making in adolescents
Blankenstein, N.E.

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Author: Blankenstein, N.E.
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General introduction

Scope

As human beings, we face many uncertainties in our decision-making. For example, when deciding to run a red light on our way to work, we do not know if this will result in a fine, cause a traffic accident, or save time. Or, when deciding to go out on the ice after the first frost of the season, it is difficult to anticipate whether we will fall through the ice or enjoy winter fun. Even a simple decision such as flipping a coin involves uncertainty: we do not know if the outcome is heads or tails. In these examples, a decision-maker is presented with a choice that involves risk, that is, outcomes may occur with a certain probability. Although a decision-maker may have some idea of the possible range of outcomes of their decisions (e.g., causing a traffic accident or not; falling through the ice or not; flipping heads or tails), he/she may lack information about the exact *probabilities* of these different outcomes. That is, in some of these examples, the exact probabilities of the different outcomes are known (for example, the chance of heads in a coin flip is 50%). In behavioral economics, this is referred to as explicit risk, or *risk* for short (Tversky & Kahneman, 1992). In other instances, these probabilities may not be known (for example, the chance of falling through the ice is unknown). This is referred to as ambiguous risk, or *ambiguity* (Tversky & Kahneman, 1992). Whether decisions involve risk (uncertain outcomes with a *known probability*) or ambiguity (uncertain outcomes with an *unknown probability*), influences our actual tendency to engage in taking risks to a great extent (Tversky & Kahneman, 1992; Tymula, Rosenberg Belmaker, Ruderman, Glimcher, & Levy, 2013). For instance, adults are generally averse to risk, and even more averse to ambiguity (Camerer & Weber, 1992). Although how we approach risks can be considered to be a stable trait, there may be developmental life periods in which our risk preferences change.

A developmental period possibly associated with greater risk-seeking preferences is adolescence, which is the transition phase between childhood and adulthood (Somerville, Jones, & Casey, 2010; Steinberg, 2008). In particular, adolescents display higher levels of risk taking in daily life, such as excessive substance use and reckless behavior in traffic, compared to children and adults (Eaton et al., 2008; Steinberg, 2008). Many experimental psychological studies on developmental changes in risk taking have used paradigms that involve explicit risks. However, real life predominantly presents ambiguous risks. In addition, defining how adolescents generally deal with (i.e., avoid or seek out) risk and ambiguity remains rarely done. Moreover, even though adolescence is described as a period of heightened risk taking on average, there are pronounced individual differences in observed risk-taking behavior (not all adolescents are risk takers), which remain largely overlooked (Bjork & Pardini, 2015). In addition, risk taking may not necessarily be negative, but may be useful such as when taking risks to explore the environment or to help others (Hartley & Somerville, 2015; Do, Guassi-Moreira, & Telzer, 2017). Finally, few studies have aimed to link experimental risky choice behavior to indices of risk taking in real life. Therefore, in this thesis I examine risk taking in adolescents as a multi-measure tendency that may be driven by behavioral preferences towards risk and ambiguity; and by assessing individual variation in these preferences and their relation to real-life risk taking. In addition to behavioral measures, I use a neuroscientific approach to study the underlying mechanisms of these different aspects of risk taking. Including measures of the function and structure of the brain enables to study whether distinguishable aspects of risk taking are driven by different neural systems and how these relate to developmental and individual differences in risk taking.

In sum, the main goals of this thesis are twofold. First, I study fundamental processes underlying risky decision-making. To this end, I make use of behavior modelling and functional neuroimaging to decompose the behavioral and neural mechanisms underlying risky choice behavior in adolescence, under conditions of risk (known probabilities) and ambiguity (unknown probabilities). Second, given the positive and negative aspects of risk taking, I study to what extent individual differences in risk-taking tendencies inform our understanding of adolescence as a period of risks and opportunities (Crone & Dahl, 2012). Here, I combine self-report measures with functional and structural neuroimaging. The current introduction starts out with an overview of risky decision-making and associated neural networks, followed by an overview of current models on adolescent development, and ends with an outline of the empirical chapters.

Risky business?

Decision-making under uncertainty: risk and ambiguity

Risky decisions always involve a level of uncertainty about what outcome will result from what choice (Platt & Huettel, 2008). To what extent this variability in outcome is known or unknown is referred to as explicit risk or ambiguous risk, respectively (Tversky & Kahneman, 1992). One of the first behavioral studies on how individuals deal with these two aspects of risky decision-making was Ellsberg (1961), who asked participants in a series of experiments to bet money on one of two vases filled with marbles. The first vase contained a known distribution of black and red marbles (50:50), whereas the second vase contained 100 black and red marbles in an unknown distribution. Participants preferred the first vase (with the known distribution) for drawing a black marble. Yet strikingly, when participants were asked to bet between vases for grabbing a red marble, participants again preferred the first vase. Because participants kept betting on the first vase with the known distribution of marbles, their prior beliefs about the distribution of the second vase (namely, that there are more red marbles in this vase) were contradicted. That is, one cannot simultaneously believe that there are both more and less black marbles in the second vase. These findings became known as the Ellsberg Paradox (Ellsberg, 1961) and illustrate individuals' aversion to unknown distributions. This research was extended by other classic behavioral economic work, showing that even though individuals are averse to both risk and ambiguity, most individuals show an even stronger aversion to ambiguity than risk alone (Camerer & Weber, 1992; Ellsberg, 1961; Von Gaudecker, Van Soest, & Wengström, 2011). However, even though in general, people are risk and ambiguity averse, risk and ambiguity preferences are correlated weakly at best, indicating they may differentially drive risk-taking behavior (Tversky & Kahneman, 1992). Furthermore, there are pronounced individual differences in risk and ambiguity preferences (Levy, Snell, Nelson, Rustichini, & Glimcher, 2010).

An elegant way to capture individuals' preference for risk and ambiguity is to present participants with an economic choice paradigm, in which specific task parameters (such as the gain probabilities, gain amounts, and ambiguity levels) are systematically varied, and individuals' choice behavior is analyzed (e.g., see Tymula et al., 2013). Specifically, by using a model-based approach, an individual's preferences towards risk and ambiguity can be estimated, otherwise known as *risk attitude* and *ambiguity attitude*. These measures are a reflection of an individual's behavioral tendency to shy away from, or seek out, risk and ambiguity, and therefore range from risk and ambiguity averse, to risk and ambiguity seeking tendencies (Levy et al., 2010). The advantage of this formal decomposition of risky choice behavior is

that it results in isolated measures of behavioral preferences under risk and under ambiguity. However, to understand whether risk and ambiguity are differentially processed within, and between, individuals, a fundamental understanding of the underlying mechanisms driving these processes is key.

A neuroeconomic perspective

With the rise of cognitive neuroscience studies (Poldrack, 2008), researchers have been more and more able to study the underlying mechanisms of risky decision-making. First, with structural magnetic resonance imaging (MRI), one can examine the relation between brain volume and individuals' choice preferences (e.g., see Levy, 2016). Second, functional MRI allows researchers to examine the function of the brain, for instance during a risky choice task, in relation to individuals' choice preferences. This 'neuroeconomic' approach, which combines insights from economics, psychology, and neuroscience, is a valuable addition to understanding the mechanisms underlying various aspects of the risky decision-making process (Glimcher & Rustichini, 2004). That is, whereas an economic and psychological approach is typically focused on modelling and understanding choice behavior, neuroscience provides a mechanistic account of the underlying, fundamental, processes. As such, the combination of behavioral and neural substrates of risky choice behavior (e.g., relating risk sensitivity to brain activation), ultimately provides much more explanatory power of what drives risk taking than either approach
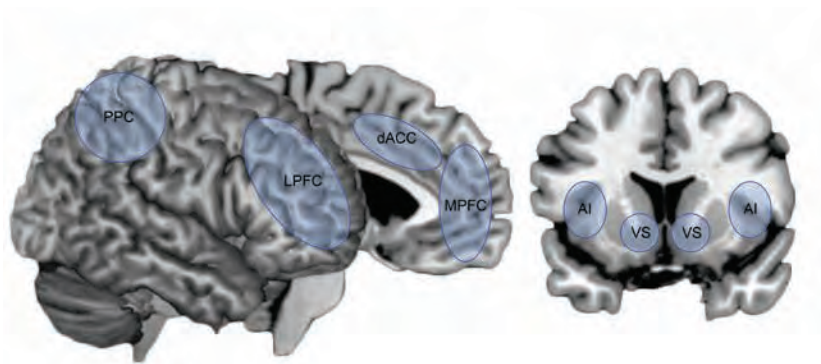

Figure 1. *Regions implicated in various aspects of risky choice behavior. PPC = posterior parietal cortex; LPFC = lateral prefrontal cortex; dACC = dorsal anterior cingulate cortex; MPFC = medial prefrontal cortex; AI = anterior insula; VS = ventral striatum. Figure based on the reviews by Knutson & Huettel, 2015; Mohr et al, 2010; Platt & Huettel, 2008.*

alone (Glimcher & Rustichini, 2004; Van Duijvenvoorde & Crone, 2013). Unraveling whether activation in the same, or in different, brain regions codes risk and ambiguity contributes to our understanding on whether these two aspects of risky decision-making differentially impact overt choice behavior.

Prior studies with adults have charted which brain regions are involved in risky decision-making *in general* (see Figure 1 below; for comprehensive reviews and meta-analyses, see Knutson & Huettel, 2015; Mohr, Biele, & Heekeren, 2010; Platt & Huettel, 2008). For instance, the ventral striatum (VS) and the (ventro)medial prefrontal cortex (PFC) have been associated with processing reward outcomes (Bartra, McGuire, & Kable, 2013; Delgado, 2007; Sescousse, Caldú, Segura, & Dreher, 2013) and reward learning (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001). In addition, the anterior insula, dorsal anterior cingulate cortex (dACC/dorsomedial PFC), and ventrolateral PFC, typically respond to increasing uncertainty (Levy, 2016; Mohr et al., 2010), while dorsolateral PFC and posterior parietal cortex (PPC) have been associated with making executive judgments about probability and value (Huettel, Song, & McCarthy, 2005). However, note that these brain systems are a *general* reflection of risky decision-making, and may not be specific to conditions of risk (known probabilities) or ambiguity (unknown probabilities). That is, the few studies on the neural coding of risk and/or ambiguity (preference) have yielded mixed findings within these brain systems (e.g., see Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Huettel, Stowe, Gordon, Warner, & Platt, 2006; Levy et al., 2010). Moreover, these studies have been conducted in relatively small samples of adults. Thus, there is a need to further investigate the neural mechanisms underlying risk and ambiguity attitude, in larger samples, and importantly, across adolescent development. That is, although some studies have started to focus on *behavioral* risk and ambiguity attitudes in adolescence (e.g., Tymula et al., 2012; van den Bos & Hertwig, 2017), it remains unstudied how their neural mechanisms are manifested in adolescence. This is not only a developmental phase characterized by ongoing neural changes, but also by heightened risk-taking behavior.

Prevailing models of risk-taking development in adolescence

Adolescence, or the developmental phase from childhood to adulthood, is associated with pronounced changes in brain development (Giedd, 2004; Giedd et al., 1999). Specifically, while some subcortical volumes (such as the amygdala) follow an inverted U-shaped trajectory, others (such as the nucleus accumbens of the striatum), follow a linear decrease across adolescence (Mills, Goddings, Clasen, Giedd, & Blakemore, 2014). Cortical gray matter follows a gradual inverted U-shaped trajectory, peaking between childhood and adolescence, and stabilizes across adolescence and early

adulthood (Mills et al., 2014; Mills et al., 2016). Importantly, the development of these brain regions do not all occur at the same rate. For instance, the development of parietal and prefrontal regions, involved in cognitive control, is relatively protracted (continuing well into the early twenties) compared to the development of subcortical regions (Lenroot & Giedd, 2006; Mills et al., 2014). These profound structural changes have inspired influential theoretical models on adolescent (brain) development. For instance, it has been proposed that the 'imbalance' between relatively fast-maturing subcortical, socio-affective brain regions and relatively slow-maturing cortical, cognitive control regions (and their interconnections), underlies heightened risk taking typically observed in adolescence, such that these affective regions are hyperactive compared to these cognitive control regions (Casey, Jones, & Hare, 2008; Casey, 2015; Somerville & Casey, 2010; Steinberg, 2008). Furthermore, this imbalance may be especially salient in 'hot', or affectively-laden, contexts, resulting in elevated levels of risk taking, such as when behaviorally reinforcing decision outcomes are provided (Figner, Mackinlay, Wilkening, & Weber, 2009), in a peer context (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011) and, suggestively, in other contexts that may be a more naturalistic reflection of risk taking in real life, such as ambiguity (Defoe, Dubas, Figner, & van Aken, 2015).

These 'imbalance' models thus describe changes in risky decision-making across adolescence and in various decision contexts, and are useful when making general assumptions about adolescents on a group level. However, one potential drawback of these models is that they may overlook prominent individual differences that are observed between adolescents. Extending these insights, recent literature highlights the importance of examining individual differences in behavioral and brain development, stressing that adolescence is not the same for each individual (e.g., see Foulkes & Blakemore, 2018). Prior developmental neuroimaging studies show that individual differences in various risk-taking tendencies relate to neural activation in the VS, (ventro)medial PFC, DMPFC, insula, and lateral PFC (for a comprehensive review, see Sherman, Steinberg, & Chein, 2017). These regions are in line with neural findings reported in adults (see Figure 1). However, like adult studies, these adolescent studies too have included relatively small samples, nor have they explicitly focused on conditions of risk versus ambiguity. Moreover, the relation with real-life risk taking is relatively understudied. In this thesis, I therefore decompose risky choice behavior into underlying risk and ambiguity attitude, assess individual variation in these attitudes, and examine how these measures relate to neural activation and to risk taking in real life.

Finally, recent related neurodevelopmental models have proposed that adolescence may not only be a developmental phase characterized by maladaptive

behaviors such as health-detrimental risk taking, but may be a flexible phase characterized by risks *and* opportunities (e.g., Crone & Dahl, 2012). For instance, risk-taking behavior may be adaptive, such as when taking risks to explore new environments (Hartley & Somerville, 2015; Romer, Reyna, & Satterthwaite, 2017) or to help others (i.e., prosocial risk taking; Do, Guassi Moreira, & Telzer, 2017). Moreover, adolescence is also a developmental phase during which positive, other-oriented behaviors emerge, such as prosociality and social perspective taking (Blakemore & Mills, 2014; Dumontheil, Apperly, & Blakemore, 2010; Güroğlu, van den Bos, & Crone, 2014). However, a formal investigation of this view of adolescence (i.e., of positive and negative developmental trajectories and their underlying neural pathways) is currently lacking. Therefore, in addition to a fundamental approach on adolescent risky choice behavior, I address this broader theme of adolescence as a developmental phase of risks and opportunities, by relating individual differences in real-life measures of (risky) decision-making to functional and structural neuroimaging measures.

Outline of the thesis

In sum, the goals of this thesis are twofold. First, I decompose risky choice behavior into their underlying components (risk and ambiguity attitudes), and investigate their neural mechanisms in adolescence. Second, I focus on how individual differences in real-life (risky) decision-making contribute to our understanding of adolescence as period of risks and opportunities. These two goals are further outlined in the following five empirical chapters.

In **chapter 2**, I administered a behavioral 'wheel of fortune' task in a large sample of adolescents, spanning a wide age range (N = 157, 10-25 years). In this task, participants were asked to choose between two wheels of fortune. One wheel represented a sure, but relatively small, gain, whereas the other wheel reflected a gamble with varied amount, probability, and ambiguity level. Using a model-based method, individuals' risk and ambiguity attitude were estimated. In this study I tested the age-related trajectories of risk and ambiguity aversion, and how individual differences in risk and ambiguity attitude are related to indices of real-life risk taking and reward sensitivity. Furthermore, given the saliency of the peer-context in adolescent risk taking (e.g., Steinberg, 2008), I also included a social condition in which participants were presented with choices from a high risk-taking peer before making their own choice, and tested whether adolescents' risk and ambiguity attitude became more aligned with the peers' choices. This study thus aimed to get

a thorough understanding of behavioral risk and ambiguity attitude in adolescence, by focusing on their age-related changes, relations to real life, and robustness in a social context.

In **chapter 3** I describe a functional neuroimaging study with 50 adult participants (18-28 years). Here I aimed to disentangle behavioral and neural measures of risk and ambiguity processing within individuals. That is, I aimed to get a fundamental understanding of risk and ambiguity attitudes and their neural correlates (during choice and choice outcome) in an adult sample. This allowed me to test whether these factors separately drive observed risky choice behavior, and whether these relied on distinct or overlapping neural substrates. To this end I used two versions of the wheel of fortune task. First, I administered the behavioral wheel of fortune task to estimate risk and ambiguity attitude. Second, I related these estimations to neural activation during a straightforward monetary gambling task: a simplified fMRI version of the wheel of fortune task which included a choice phase (choosing to gamble or not) and a reward outcome phase (gain and no gain), under conditions of risk and ambiguity. The resulting insights set the stage for further testing in an adolescent population.

Chapter 4 builds on the findings reported in chapters 2 and 3, and describes a study in which it was 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' individual *subjective value* of the choices presented in the fMRI task. While prior studies have investigated effects of objective expected value (i.e., the probability * amount of a risky option) in adolescence (e.g., Van Duijvenvoorde et al., 2015) , few studies have focused on *subjective* value coding, nor on whether this differs for risky and ambiguous decision contexts. Moreover, subjective, rather than objective, expected value tracking may be a more sensitive reflection of individual valuation processes. In this study I examined which brain regions positively and negatively scaled with subjective value under risk and under ambiguity in a large sample of adolescents.

Next, in **chapter 5** (N = 198, 12-25 years, including the sample of chapter 4), I focused on the relation between neural risk and ambiguity processing and individual differences in task-based (i.e., proportion gambling) and real-life (i.e., self-report measures) risk-taking tendencies. Although many prior studies have investigated brain-behavior associations of risk taking, few have included actual risk-taking behaviors inside and outside the laboratory in one comprehensive study (e.g., see Sherman et al., 2017). In addition, these brain-behavior associations have not been studied under conditions of risk versus ambiguity, both during choice (choosing to

gamble or not) and during outcome (processing rewards versus no rewards). Thus, to understand what drives risk taking in adolescence, multiple predictors of behavior on the individual level were included during gambling, as well as during reward-outcome processing.

Moving from this multidimensional perspective on adolescent risk taking, in **chapter 6** I further studied self-reported real-life risk-taking behavior and their underlying behavioral and neural predictors. Moreover, I also focused on prosocial behavior, that is, behaviors intended to benefit someone else. As such, the aim of this study was to understand which behavioral and neural underpinnings were predictive of these two seemingly paradoxical behaviors that emerge across adolescence in tandem; and whether adolescence can be conceived as a developmental phase of both risks and opportunities (Crone & Dahl, 2012). In this three-wave biannual longitudinal study (N = 210, 12-29 years at the final wave, including those participants of chapters 4 and 5), I predicted risk-taking and prosocial behavior from longitudinal behavioral data on approach tendencies and social functioning. In addition, I included longitudinal structural neuroimaging data (which follow the most consistent within-individual patterns of change), and focused on regions previously implicated in risk-taking as well as prosocial tendencies: the nucleus accumbens and the medial prefrontal cortex.

Finally, in **chapter 7** I summarize the empirical chapters, and provide a general discussion of the findings.