Development of Decision-Making Under Risk

by

David Jay Paulsen

Department of Psychology & Neuroscience
Duke University

Date:_______________________
Approved:

___________________________
Elizabeth M. Brannon, Supervisor

___________________________
Scott A. Huettel

___________________________
Michael L. Platt

___________________________
Philip R. Costanzo

Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology & Neuroscience in the Graduate School of Duke University

2012
ABSTRACT

Development of Decision-Making Under Risk

by

David Jay Paulsen

Department of Psychology & Neuroscience
Duke University

Date:_______________________
Approved:

___________________________
Elizabeth M. Brannon, Supervisor

___________________________
Scott A. Huettel

___________________________
Michael L. Platt

___________________________
Philip R. Costanzo

An abstract of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Psychology & Neuroscience in the Graduate School of Duke University

2012
Abstract

Decision-making under risk has been of interest to philosophers for centuries. In only in recent years through interdisciplinary approaches has knowledge concerning the descriptive nature of decision-making under risk increased. Although we know that risk-preference proceeds from a risk-seeking trend in childhood to risk-aversion in adulthood, little is known about the factors that contribute this development. The studies presented here take an interdisciplinary approach to identifying the factors that contribute to age-related changes in risk preference, where in the decision-making process these factors have influence, and changes in neural circuitry that could be responsible. The work presented herein finds that risk-preference is differentially modulated across development by risk level, the values of choice options, and the domain (gains or loss) in which options are presented. During valuation, many brain regions that have previously been associated with decision-making and risk were found to increase in activation with age, suggesting the maturation of a decision-making network. Activation in a few key areas were associated with greater risk-aversion in children, suggesting that maturation of the decision-making network leads to more adult-like behavior. The cognitive component of children’s greater risk-seeking was not found to be a deficiency in probabilistic reasoning, the ability to learn from negative feedback, or a general optimism for winning. Rather, children’s valuation of a gamble may be exaggerated by a disproportionate amount of attention given to the winning outcome of a gamble. It is further speculated that a lack of regret during outcome evaluation may also contribute to differences in children’s risk preference compared to adults.
Contents

Abstract .................................................................................................................................................. iv

List of Tables ......................................................................................................................................... ix

List of Figures ....................................................................................................................................... x

Chapter 1 - Introduction ...................................................................................................................... 1

   Introduction ....................................................................................................................................... 1

   Decision-making ............................................................................................................................... 4

   Valuation .......................................................................................................................................... 5

   Outcome evaluation & learning ......................................................................................................... 8

Neural systems and decision-making ................................................................................................. 9

Development of decision-making ....................................................................................................... 15

Development of neural systems related to decision-making ............................................................. 19

Summary and Dissertation Approach ................................................................................................. 27

Chapter 2 - Development of Risk Preference ..................................................................................... 30

   Methods .......................................................................................................................................... 33

   Participants ...................................................................................................................................... 34

   Design and stimuli ........................................................................................................................... 34

   Results ............................................................................................................................................ 36

   Safe-Safe trials ............................................................................................................................... 36

   Risk-Safe trials ............................................................................................................................... 36

   Risk-Risk trials ............................................................................................................................... 38
List of Tables

Table 1: Behavioral data: probability of selecting a gamble over a sure bet (RT in secs) ..... 61
Table 2: Whole-brain analysis linear effect of age group during decision-making .............. 64
Table 3: Uncorrected regions of activation from the quadratic contrast showing adolescent peaks .......................................................................................................................................................................................................................................................... 65
Table 4: Clusters of activation from group ANOVA and ROI analysis statistics during decision-making .................................................................................................................................................................................................................................................................................................................................................................................................................................................. 67
Table 5: Activation to winning outcomes by age group .................................................. 74
Table 6: Activation to losing outcomes by age group .................................................... 76
Table 7: Full Set of Predictors and Beta Weights for Exp. 1 Regression .......................... 95
Table 8: Predictors and Beta Weights for 0.5 Probability Trials .................................. 100
Table 9: Predictors and Beta Weights for Gain and Loss Domains .............................. 107
Table 10: Beta Weights for Age Group and CV ............................................................ 123
Table 11: Beta Weights for Age Group, CV, and Eye-Tracking Measures .................... 126
List of Figures

Figure 1: Experimental design. RT, response time. Trial types were pseudorandomized. Each trial consisted of a decision (blue frame), choice (salmon frame), confirmation (red frame), delay (no frame), and outcome (yellow frame) period. Safe-Safe trials offered the decision between two safe bet values, Risk-Safe trials offered the decision between a gamble and a safe bet, while Risk-Risk trials offered the decision between two gambles of different expected value and coefficient of variation.................................................. 33

Figure 2: Risk preferences vary with age, risk level, and expected value. Children show an increase in the proportion of gambles selected as risk level increases, while adults and adolescents tend to show a decrease in the proportion of gambles selected. Children also show greater preference for gambles when the expected value (EV) was large than when it was small. Note: EV of the sure bet option was always equal to the EV of the gamble option. .......................................................................................................................... 38

Figure 3: Preferences between two gambles vary with age, risk level, and expected value. EV, expected value; CV, coefficient of variation. (A) Preference for the higher risk/higher EV option was greater for EV 5 Medium risk than for EV 5 Low risk, and (B) declined as the EV 6 risk level increased. (C) Preference for the higher risk/higher EV option increased linearly and the difference in risk level between the EV 5 and EV 6 gamble options decreased. ........ 40

Figure 4: Age-related risk preferences are correlated across decision contexts. Preference for the higher risk/higher EV option in Risk-Risk trials is correlated with the probability of selecting the gamble option in Risk-Safe trials. These correlations were significant for children and adults, and marginally significant for adolescents. .................................................. 41

Figure 5: Experimental design. Each trial consisted of a decision (blue frame), choice (salmon frame), confirmation (red frame), delay (no frame), and outcome (yellow frame) period. Trial types were pseudorandomized and presented over three 8-minute runs. Variable timing for the delay and intertrial intervals were implemented to dissociate the temporal contingency between adjacent events. RT - response time.................................................. 54

Figure 6: Regions associated with decision-making and context show increased activation with age during the decision period. Several regions comprising a decision-making network showed increased activation with age during decision-making. This network consists of areas associated with processing risk - superior parietal cortex (sPAR) and insula (INS) – and regions associated with processing value - orbitofrontal cortex (OFC), ventromedial prefrontal cortex (vmPFC), and striatum (STR). Additionally, brain regions often associated with memory and context showed increased activation with age during the decision period. These regions include: anterior cingulate cortex (ACC), associated with fictive learning and conflict detection; frontal pole (FP), associated with goals and strategies; amygdala (AMY), associated with affective dimensions of previous outcomes and current stimuli; and hippocampus (HC), associated with contextual memory. Coordinates in MNI space........... 63
Figure 7: vmPFC showed age- and risk-related activation, while bilateral insula showed only age-related increases in activation during decision-making. Decision-related activation for the vmPFC ROI (b; yellow) was greater in adults and adolescents than it was in children (a), demonstrating that the age-related linear trend found here was due primarily to the difference between children and adults. Whole brain analysis revealed activation in children that correlated with risk aversion in ACC and vmPFC (b; green). The vmPFC cluster from this whole brain analysis overlapped with the vmPFC ROI (b; red). Regression slopes for each age group shown in (c) demonstrate the unique relationship between BOLD signal change in vmPFC and risk aversion scores found for children. Age-related linear trends of activation were also found in right and left insula ROIs (e). In contrast to vmPFC, these regions showed a more robust positive linear relationship to age (d, f). Coordinates in MNI space; circles – children; diamonds – adolescents; squares – adults; * - p < 0.05; * - p < 0.1. Note: Though some of the children’s data appear to be outliers, all of the children’s data points in Fig. 7 are less than 2.5 standard deviations from the group mean of the panel, and only two exceed 2 standard deviations. ................................. 69

Figure 8: Posterior insula shows age group by risk aversion interaction. An interaction between age group and risk aversion showed that while activation during decision making in adolescents and adults did not correlate in any way with risk aversion, in children, activation in posterior insula decreased with greater risk aversion. Coordinates in MNI space. .......................................................................................... 71

Figure 9: Whole brain analyses revealed that risk aversion was correlated with activation in caudate nucleus and OFC for children (shown here) but not for adults or adolescents, during decision-making. (a) activation maps and (b) scatterplots showing the relationship between BOLD signal and risk aversion. Coordinates in MNI space; Caud – caudate nucleus; OFC – orbitofrontal cortex .................................................................................................................. 72

Figure 10: Winning and losing outcomes elicit similar patterns of activation in children, adolescents, and adults. (a) Activations to winning outcomes in all age groups were found in superior temporal gyrus, insula, striatum, inferior frontal gyrus, and inferior parietal regions. Adults and adolescents showed additional activation in dIPFC, lateral OFC, and ACC. (b) Relative losses elicited activation for all age groups in superior temporal gyrus and insula, while adults and adolescents also showed activation in anterior cingulate. Coordinates in MNI space; z > 3.0. ........................................................................................................... 73

Figure 11: Reinforcement Learning and Risk Tasks (A) Reinforcement Learning (RL) task stimulus pairs were presented during training with instructions to “pick the animal that gives happy faces more often.” One animal out of each pair was more likely to return a happy face than a sad face; probability pairs were 80/20, 70/30, and 60/40. (B) After reaching a learning criterion or completing a maximum of 12 blocks, participants were tested with the three possible pairs of the higher reward probability images and the three pairs of the images associated with the lower reward probabilities. (C) Choices in the Risk Task were between a gamble and a sure bet. The gamble option had a mean equal to that of
the sure bet option. The probability of winning in the gamble option was 0.2, 0.3, 0.5, 0.7, or 0.8, and was indicated by an animal picture learned during the RL task, or with a grey square in the case of $P_{\text{WIN}} = 0.5$.

Figure 12: Reinforcement Learning and Gamble Task behavior (A) The number of blocks needed to reach criterion in the Reinforcement Learning task showed a quadratic trend ($p = 0.088$) that peaked during adolescence. (B) Accuracy for choosing the image associated with the better odds of winning the high payoff on the gamble increased with age for pairs of images associated with the high payoff (Pos FB; $p = 0.008$) and pairs of images associated with the lower payoff (Neg FB; $p = 0.032$). Overall accuracy tended to increase with age, and Pos FB accuracy showed a peak in accuracy during adolescence ($p = 0.04$). (C) The probability of choosing the gamble decreased with age. Note: Y-axis values were randomly jittered in A ($\pm 0.5$) & B ($\pm 0.02$) to better show overlapping data points.

Figure 13: Prediction plots generated from Risk Task regression coefficients (A) Shows predicted probabilities of choosing the gamble option at ages 7, 14, and 21 years, each with negative feedback accuracy (Neg FB) scores of 50% and 100%. Higher Neg FB scores decrease the predicted probability of choosing the gamble option for low and equal probability of winning trials, increases the predicted probability of choosing the gamble option when the probability of winning of high, and reduces the predicted effects of age. (B) The predicted probability of choosing the gamble option decreases over trials more quickly for older than for younger participants. (C) On trials containing gambles with an equal probability of winning, an increase in Neg FB of 25% predicts a decrease in the predicted probability of choosing the gamble option of 5-10% across ages. (D) On trials containing gambles with an equal probability of winning, younger participants are predicted to gamble more often with increasing coefficient of variation (CV) while older participants are predicted to gamble less often with increasing CV, with the inflection point at around 8.1 years of age.

Figure 14: Reinforcement Learning Task in Experiment 2 (A) the number of blocks to criterion as a function of age. (B) Positive and negative FB accuracy as a function of age. Patterns were similar to those in Exp. 1, but were non-significant (all $p > 0.18$). Figure 15: Gain and loss frame data and predictions (A) Probability of choosing a gamble over sure bet decreased with age for gains, and increased with age for losses. (B) Predicted probability of choosing a gamble over sure bet decreased over the session for gains, and increased over the session for losses. (C) Children younger than $\sim 10.3$ years showed increased probability of choosing a gamble as a function of increasing coefficient of variation (CV), while participants older $\sim 10.3$ years show decreased probability of choosing a gamble as a function of increasing CV. (D) The reflection effect (mean number of gambles for losses minus mean number of gambles for gains) increased with age, starting from a reverse reflection effect for the youngest participants.
Figure 16: Behavior during eye-tracking. Children showed risk-seeking behavior, while adults showed risk-averse behavior. ....................................................................................................................................... 123

Figure 17: Eye-tracking behavior during decision-making in Risk-Safe trials. (A) The first fixation objects (FFO) did not vary systematically between children and adults, and did not predict whether or not participants selected the gamble option. (B) Both children and adults tended to look at the Sure Bet object last before choosing the Safe Bet option, and at the Win last object before choosing the gamble option. (C) Prior to choosing Safe Bet options, children and adults looked longest at the Sure Bet object. (D) Prior to choosing the gamble option, children looked disproportionately longer at the Win object compared to adults, and less at the Sure Bet object. ....................................................................................................................................... 125

Figure 18: Eye-tracking behavior during outcome presentation in Risk-Safe trials. (A) After wins, children and adults look longest Win objects. (B) After losses, children looked longer at the Loss object and less at the Sure Bet object, than adults, suggesting less experienced regret. (C) After Sure Bets, children looked less often at the Win object compared to adults. ....................................................................................................................................... 127

Figure 19: Adults and children differ in pupil dilation after wins in Risk-Safe trials. The top two panels show relative pupil dilation for adults and children, respectively, during outcome presentation of safe bets, wins, and losses. The grey transparency blocks in these top panels indicate the time window during which significant main effects of outcome were found (0.747-1.344 sec). The lower three panels compare children to adults after safe bets, wins, and losses. The difference in pupil dilation between children and adults after wins is clear. The grey transparencies in these bottom panels indicate where interactions between age group and outcome were found (0.780-1.012 sec). ....................................................................................................................................... 129

Figure 20: Risk-Risk trial behavior. (A) Marginal interaction (p = 0.05) between age group and CV of the low risk-return choice shows adults tend to chose the higher risk-return option as low risk CV increases while children tend to do the opposite. (B) Participants chose higher risk-return option less often as it’s CV increases, and this effect was stronger in adults. (C) Adults tend to choose the lower risk-return option more often as the difference in CV between choice options increases....................................................................................................................................... 131

Figure 21: Looking behavior differs between children and adults after wins and losses. (A) After wins, both children and adults spend a large proportion of time viewing the Win object. (B) After losses, adults look at all objects of the chosen and unchosen options, while children tend to focus mostly on the Loss and Win objects of the chosen option, and relatively little time at all on the Win and Loss objects of the unchosen option, again suggesting less experienced regret ....................................................................................................................................... 132

Figure 22: Pupil dilation when viewing Risk-Risk outcomes shows a pattern similar to Risk-Safe outcomes. Children show similar pupillary responses after wins and losses, which are
also similar to adult pupillary response after losses. Adults differ in the relative pupillary constriction occurring after wins.
Chapter 1 - Introduction

Introduction

Research on the development of risky decision-making is important for both practical and theoretical reasons. Of practical import, it aims to identify the development of cognitive and neural mechanisms that promote excessive domain specific and domain general risk taking, which may allow early identification of individuals on track to become particularly risk prone. Thus research on the development of risky decision-making may provide opportunity for mitigating some of the harmful outcomes that can follow from excessive risk taking (Reyna & Farley, 2006; Wahlstrom, White, & Luciana, 2010). In addition to identifying individuals that would benefit most from intervention, a developmental approach could help to uncover the temporal and cognitive leverage points during which interventions may be the most to least effective.

Theoretically, a full understanding of the relationship between cognition and the mature human brain requires an understanding of how cognition and the brain mature. One way of characterizing the study of development is to frame it as a naturalistic approach to neural perturbation. This places development alongside lesion work as a valuable method of investigation. Concomitant changes in both a cognitive process and the neural systems hypothesized to support it provide evidence of their relationship. On the other hand, if a hypothesized cognitive construct develops asynchronously with its purported neural mechanisms, or perhaps more synchronously with other neural systems, then an adjustment to the theory may be called for.

Several gaps exist in the study of development and risky decision-making. First, there is the common disconnect between naturalistic risk-taking and the kinds of tasks used
in the laboratory to assess risk behavior. Part of this disconnect can be clarified by recognizing that risk can mean different things in different contexts. A major health concern is preventing anti-social behaviors such as drug use, alcohol abuse, reckless driving, and unprotected premarital sex. Adolescents have received the most attention in this research because they are known to exhibit these risky behaviors at higher rates than other age groups (Arnett, 1992) and are also more susceptible to addiction than adults. With respect to value-based decision-making (e.g. decisions to acquire food, water, or money), risk has a technical meaning that indicates uncertainty with known probabilities and values. Risk is often quantified with measures of probability, statistical moments like mean, variance, skew, and coefficient of variation, or combinations of these (Coombs & Bowen, 1971; Markowitz, 1952; Sharpe, 1964; Weber, Shafir, & Blais, 2004). This definition of risk stands in contrast to ambiguity, which is used to refer to the uncertainty of situations in which relevant information is incomplete (Knight, 1921). Thus, due to the nature of real-world uncertainty, behavioral risk is more closely aligned with ambiguity than value-based risk. Nevertheless, clear links between value-based risk, ambiguity, and behavioral risk – if, and where they exist – have not been established, despite the implied equivalence of these kinds of uncertainty in development of decision-making literature.

Two other gaps are also identifiable. First, if adolescents truly are the top behavioral risk takers, then what occurs during neural, cognitive, and/or social development that places them there? From an evolutionary perspective, risk seeking behavior during adolescence may be adaptive. Risk seeking behavior could promote exploration beyond one’s primary social group, allowing for a wider selection of potential mates. Successful emigration may have also depended on being neither too risky nor too safe. For example,
avoiding unfamiliar foods may ensure food safety, but it's adaptive for starving animals to take dietary risks (Spear, 2000a). Indeed, it has been noted that among chimpanzees, the younger members of a group are usually the more willing ones to try new foods (Kummer & Goodall, 1985; Nishida, Wrangham, Goodall, & Uehara, 1983). Additionally, risk seeking behavior in the form of sensation seeking could have led to physical displays of fitness that indicated desirability as a mate to prospective partners, thus preserving the risky phenotype (Spear, 2000a; Steinberg, 2008). While these perspectives focus on the evolutionary significance of adolescent risk-taking, a good deal of research is also being conducted on the proximal means, for example, changes in neural structure, cognitive, affective, and sexual maturation, and socialization (Chambers, Taylor, & Potenza, 2003; Chein, Albert, O'brien, Uckert, & Steinberg, 2010; Csikszentmihalyi, Larson, & Prescott, 1977; Galvan et al., 2006; Galvan, Hare, Voss, Glover, & Casey, 2007; Hare et al., 2008; Spear, 2000a, 2000b; Steinberg, 2005).

Finally, the extant literature does not yet provide a deep understanding of the maturation of mechanisms involved with value-based decision-making. Early work by Piaget and Inhelder (1975) suggested that young children (less than 11-13 years old) are incapable of probabilistic reasoning, a necessity for calculating risk, but subsequent work has shown that children are capable of making decisions based on probabilities and of decisions consistent with combining probabilistic and magnitude information (Acredolo, O'Connor, Banks, & Horobin, 1989; Scheres et al., 2006; Schlottmann & Anderson, 1994) Adult-like performance on probabilistic reasoning tasks, however, may not mature until early adolescence (Falk & Wilkening, 1998; Huizenga, Crone, & Jansen, 2007). The distinction between the ability to perform a task and the ability to provide reasons for
performance can lower the age range of what children are capable of (Brainerd, 1981; Garon & Moore, 2004). This is especially salient in the case of infants, who at less than one year of age show behaviors consistent with probabilistic expectations (Xu & Denison, 2009; Xu & Garcia, 2008). Thus, using performance, or in the case of decision-making, preference, rather than relying upon self-reports of strategy to indicate ability can help to identify what types of cognitive operations children are capable of and when.

With respect to decision-making under risk, several studies have shown that risk preference declines with age (Harbaugh, Krause, & Vesterlund, 2002; Levin, Hart, Weller, & Harshman, 2007; Rakow & Rahim, 2010; Reyna & Ellis, 1994; Weller, Levin, & Denburg, 2010). However, practically no studies have systematically examined the effects of manipulating decision-related variables, like the levels of risk, probability, and magnitude, on choice behavior across age, and if these might relate to the observation of a developmentally mediated decrease in risk preference. Studies on the neural bases of decision-making from early childhood to adulthood are virtually non-existent.

The remainder of this introductory chapter will proceed by discussing information related to the framework of value-based decision-making within which the current studies operate, followed by a discussion of the neural mechanisms associated with the components of this framework. Next will be a survey of developmental decision-making, followed by a discussion of the development of decision-related neural mechanisms. A final section will summarize and layout the dissertation approach.

**Decision-making**

Decision-making can be thought of as a cyclical process consisting of several stages. One breakdown of these stages begins with the (1) representation of decision variables,
including both internal and external states, followed by the (2) valuation of options, (3) selecting the appropriate action, (4) evaluating the outcome of that action, and finally a (5) learning stage that informs subsequent state representations, valuations, and actions (Rangel, Camerer, & Montague, 2008). Within this framework, the valuation process can be driven by one or more of three engines: Pavlovian conditioning, acquired habit, and goal-directed behaviors. Here I focus on goal-directed valuation, outcome evaluation, and learning.

**Valuation**

An important concept in the history of normative and prescriptive decision-making is expected value (EV). It is defined as the cumulative sum of the magnitude or value ($v$) of each outcome multiplied by it’s probability ($p$) of occurrence: $\text{EV} = \sum_{i=1}^{n} (p_i \ast v_i)$. In some decision-making scenarios the application of an EV rule provides a relatively simple indication of optimal choice, especially in circumstances that allow repeated sampling.

However, more than a few examples have been constructed to show that decisions based solely on EV seem irrational despite the apparent rationality of the model. An extreme case is found in Bernoulli’s St. Petersburg paradox (Bernoulli, 1954), in which Peter proposes to pay Paul one ducat if a coin toss lands heads on the first throw, two ducats for heads on the second throw, and so on until heads first appears. The expected value of this proposition, if we consider an infinite regression of probabilities for infinite coin tosses, is infinite. If Paul follows an EV rule, he should be willing to pay any amount of money for Peter’s proposition, but people do not behave this way. Bernoulli considers an emended version of the formula that attempts to identify values for Peter’s proposition that are more realistic and relative to Paul’s personal wealth. The introduction of relativity to the
problem of choice was an important step leading to expected utility (EU) theory, in which the values of a wager, proposition, or prospect, will have different utility to individuals of differing wealth.

The EU framework dominated models of rational choice for a long time until it was challenged by Kahneman & Tversky’s prospect theory in the late nineteen-seventies (1979). Prospect theory came about in response to several illustrations of effects in which EU did not align with human behavior. These phenomena were dubbed isolation, certainty, and reflection effects. Isolation effects describe the tendency for people to disregard similarities between choice options, which can lead to inconsistent choice behavior depending on how choice options, and their similarities, are described. For example, when two options differ in value and certainty, people tend to prefer certain over risky gains, but when both choice options are probable, people tend to focus on amount, preferring the larger value and discounting probability, provided the probabilities are not too different. However, if the choice between a certain and a risky option is contingent upon a prior probability, e.g. a 50% chance of having the opportunity to make the choice between the certain and risky option, people tend to ignore the fact that the proposed and often accepted ‘certain’ option is actually probabilistic, thus isolating the secondary choice as if the first stage in the decision-tree did not exist. The certainty effect illustrates the phenomenon of unequal probability weighting. In one example, the distribution of preferences between outcomes with a 1% difference in probability is markedly different when one of the probabilities is certain, compared to a 1% difference in the middle range, e.g. 10% vs. 11%. This observation led to the inclusion of a weighting parameter for probabilities, similar in function to the weighting parameter applied to value that determines individual utility, as
people tend to overweight the likelihood of low probability events and underweight high probability events. The reflection effect relates to a common observation that people are often risk averse in the domain of gains, but are risk seeking in the domain of losses (Kühberger, 1998).

Prospect theory proposes a value function with three essential characteristics: loss aversion, reference dependence, and diminishing sensitivity. The loss aversion aspect of prospect theory’s value function is that it is concave for gains and convex for losses, denoting the finding that “losses loom larger than gains.” However, the reference dependence component states that gains and losses are only such with respect to some reference point. For example, the choice between a gamble with outcomes of either $2 or $9 and a sure bet of $5 frames the gamble outcomes as -3 and 4, respectively. Diminishing sensitivity applies to both magnitudes and probabilities (Tversky & Kahneman, 1992). For magnitudes, in the domain of gains, for example, it states that an increase in value has less of an impact on prospects with larger potential outcomes than on prospects with smaller potential outcomes. For probabilities, it states that a change in probability has less of an impact as probability departs from certainty. For example, a change of 2% in the chance of winning or losing changes behavior more from 1-3% than it does from 50-53%.

Attention to particular outcomes affect prospect weighting. Addressing a few inadequacies of prospect theory, Kahneman and Tversky formulated a subsequent version that included a rank-dependent transformation of probabilities, or the cumulative functional, rather than weighting each probability individually (Tversky & Kahneman, 1992). This allows statements to be made that compare outcomes along a cumulative probability dimension, e.g. “I have 0.2 probability of winning at least $2.” The cumulative (or
decumulative) probability function can have different weighting patterns that reflect the importance of obtaining good outcomes and of avoiding bad outcomes, termed ‘potential-mindedness’ and ‘security-mindedness’, respectively (Lopes, 1995). These weighting patterns come about by the attention given to different outcomes. For example, if extra attention is given to best outcomes, these are weighted more and the bad outcomes weighted less, giving rise to a potential-minded weighting pattern. The reverse pattern of attention yields a security-minded weighting pattern. This makes intuitive sense as well; if no attention is given to the bad outcome, it should have zero weight in the decision process, thus giving greater weight to the good outcome than it should have objectively.

**Outcome evaluation & learning**

While prospect theory and EU theory generate models of valuation, they do not treat the evaluation of outcomes or learning as part of the decision making process. Because the primary interest here is in the changes that take place with age, i.e. we are interested in differences over years rather than days or trials, outcome evaluation and learning over the course of an experiment is not at first glance especially relevant. However, some have suggested that increased gambling rates, in particular among Parkinson’s disease patients on dopamine therapy, may be related from an impoverished ability to learn from negative feedback (Frank, Samanta, Moustafa, & Sherman, 2007; Maia & Frank, 2011). This idea makes sense intuitively, for if a person is unable to associate negative outcomes with a certain behavior, like placing and losing bad bets, then there is no reason to cease gambling. Combined with findings that learning to incorporate feedback into the decision-making process improves with age (Cauffman et al., 2010; Crone & van der Molen, 2004; Hooper, Luciana, Conklin, & Yarger, 2004), and that younger children tend to focus more on positive
than negative outcomes (Van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008), it is possible that the ability to learn from feedback, positive or negative, contributes to the age-related emergence of risk aversion.

Learning from negative feedback depends upon three things: the evaluation of a negative outcome as such, an association between the negative outcome including its evaluation and the preceding action, and finally on generalizing prior actions, outcomes, and evaluations, to new situations. Importantly, the evaluation of a negative outcome can take at least two forms that have the potential to differentially affect future behavior: regret and disappointment. The distinction between the two is that while disappointment is a negative association with the outcome, what happened compared to what could have happened, regret is a negative association with both the outcome and the action, what else could have been chosen (Bell, 1985; Loomes & Sugden, 1982; Mellers, Schwartz, Ho, & Ritov, 1997). This distinction is important to decision-making because while regret may suggest an alternative future course of action, disappointment on its own does not. In other words, regret entails a locus of control that includes the decision-maker.

**Neural systems and decision-making**

A number of brain regions, both cortical and subcortical, have been implicated in the decision-making process. Subcortically, midbrain dopamine (DA) neurons have received a lot of attention because of their characteristic response to reward and reward prediction, thus indicating something about value (Schultz, Dayan, & Montague, 1997). Unexpected rewards elicit phasic DA responses, but when paired with a cue, the DA response to rewards gradually shifts to the cue, thus imbuing the cue with the value of its expected reward. Rewards greater than or less than expected elicit DA responses that are
either greater or less than baseline, indicating what is now commonly referred to as the reward prediction error (RPE) signal. These RPE signals are modulated not just by the size of reward, but also by the probability of receiving the reward (Fiorillo, Tobler, & Schultz, 2003), and have been found to encode aversive stimuli as well (Matsumoto & Hikosaka, 2009). Thus, midbrain DA neurons tuned to predict reward can also be thought of as encoding expected value.

Research on the variety of midbrain DA neurons suggest that there are two types of DA neurons that take part in learning: value encoding and salience encoding (for review see Bromberg-Martin, Matsumoto, & Hikosaka, 2010). Value encoding neurons demonstrate standard RPE signals in terms of increased and decreased firing rates, while salience encoding neurons increase firing rate in response to stimuli that signal reward and punishments, as well as novelty, and stimuli that capture attention but have yet to acquire motivational value. According to the hypothesis of Bromberg-Martin, Matsumoto, and Hikosaka (2010), value encoding and salience encoding DA neurons project to some overlapping regions in prefrontal cortex, dorsal striatum, and ventral striatum, though divisions or gradients among the DA targets within these regions are suggested.

The discovery that DA neurons behaved in a fashion consistent with coding for RPE was important not just because it provided evidence for the neural instantiation of value, but also because there was already a lineage of computational models attempting to predict behavior based on the dynamics of expected value that could be now be tested against biology (Sutton & Barto, 1990). The success of these models at the level of single cells no doubt facilitated the testing of these models at higher levels of neural activity and activation, with expectations that brain regions responding to the basic components of the
RPE signal would be the downstream targets of reward-predicting DA neurons. Thus, areas of prefrontal cortex (PFC) and the striatum figure heavily into predictions concerning reward and punishment.

Ventromedial prefrontal cortex (vmPFC) activation is often associated with value. Several neuroimaging studies have found correlations vmPFC activation and different metrics of value, for example immediate rewards (McClure, Laibson, Loewenstein, & Cohen, 2004), estimated subjective value (Kable & Glimcher, 2007), the signed value of possible gamble outcomes (Tom, Fox, Trepel, & Poldrack, 2007), as well as the processing of outcomes themselves (B. Knutson, G. Fong, C. Adams, J. Varner, & D. Hommer, 2001).

Patients with ventromedial (vmPFC) lesions fare poorly in gambling tasks in which optimal solutions exist (Bechara, Damasio, Tranel, & Anderson, 1998; D. Bechara, A. R. Damasio, H. Damasio, & S. W. Anderson, 1994), and though cognizant of the odds involved with a gamble, these patients do not appear to regulate their bidding accordingly (L. Clark et al., 2008), thus failing to adjust for expected value. An integrative role for vmPFC has also been suggested, whereby vmPFC incorporates largely non-conscious affective information into the decision making process (Bechara, Damasio, Tranel, & Damasio, 1997; Dunn, Dalgleish, & Lawrence, 2006). However, this proposal is not inconsistent with an account of vmPFC that focuses on value.

Orbitofrontal cortex lies in close proximity to vmPFC, so it is not surprising that the function of OFC has also been related to value and the integration of value signals (Plassmann, O’Doherty, & Rangel, 2007; Wallis, 2007). Other’s have made the suggestion that while this region is involved with the integration of affective and sensory information (Kringelbach, 2005), OFC can be divided into the processing of rewards on the medial
aspect (mOFC) and punishments on the lateral (lOFC; Kringelbach & Rolls, 2004). However, there is evidence that mOFC encodes both appetitive reward and aversive values (Plassmann, O’Doherty, & Rangel, 2010). OFC activation during decision-making has also been found in relation to cumulative experience of loss, while dIPFC activation was predicted by the outcomes of immediately preceding trials leading to the suggestion of a nuanced role for medial OFC of “experiencing and anticipating the emotion of regret” (G. Coricelli et al., 2005). Under this view, OFC responds to and tracks rewards and losses, issuing signals during decision making that represent the cumulatively appraised level of risk with respect to gains and losses. These authors propose on the other hand that vmPFC signals the affective component of previous outcomes, and dIPFC activation contributes information concerning the immediately preceding outcomes (G. Coricelli, et al., 2005). In addition, OFC may be involved with overcoming some of the emotional contributions to decision-making, as OFC activation was found to be greater in participants who were less susceptible to the effects of gain vs. loss framing (De Martino, Kumaran, Seymour, & Dolan, 2006).

The influence of emotion in rational decision-making is increasingly becoming recognized (Bechara & Damasio, 2005; Slovic, Finucane, Peters, & MacGregor, 2004). One of the primary regions associated with emotion is the amygdala, which also appears to be a critical region involved in valuation and decision-making. (Gottfried, O’Doherty, & Dolan, 2003; Hampton, Adolphs, Tyszka, & O’Doherty, 2007; Talmi, Hurlemann, Patin, & Dolan, 2010). De Martino and colleagues (De Martino, et al., 2006) found greater amygdala activation when choosing the sure bet than when choosing a gamble in gain frames, and the reverse pattern in loss frames. This pattern of amygdala activation was interpreted as
reflecting the processing of negative emotional information during decision-making, steering choices away from losses, an interpretation consistent with subsequent work showing that damage to the amygdala reduces loss aversion in gambling contexts (De Martino, Camerer, & Adolphs, 2010).

The striatum has been identified as a primary neural substrate for processing reward and reward expectation (Bjork, Knutson, & Hommer, 2008; G. Coricelli, et al., 2005; D’Ardenne, McClure, Nystrom, & Cohen, 2008; M. R. Delgado, H. M. Locke, V. A. Stenger, & J. A. Fiez, 2003; M. Ernst et al., 2005; Hassani, Cromwell, & Schultz, 2001; B. Knutson, G. W. Fong, C. M. Adams, J. L. Varner, & D. Hommer, 2001; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; O’Doherty et al., 2004; Schultz, Apicella, Scarnati, & Ljungberg, 1992; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004). A functional distinction between dorsal and ventral aspects of the striatum is often made, noting the Pavlovian type of object-reward associations made by the ventral aspect (Berns, McClure, Pagnoni, & Montague, 2001; O’Doherty, et al., 2004) and the goal-oriented action-reward associations made by the dorsal aspect (Berns, et al., 2001; M. R. Delgado, et al., 2003; O’Doherty, et al., 2004). Activity in ventral striatum, or nucleus accumbens, has also been found to correlate with the magnitude of reward (Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; G. Coricelli, et al., 2005), and some studies have focused on the dorsal striatum’s greater sensitivity to magnitude in reward and punishment (M. R. Delgado, et al., 2003; B. Knutson, et al., 2001).

Finally, areas of posterior parietal cortex (PPC) are involved with processing risk, value, and numerical information (J. F. Cantlon, E. M. Brannon, E. J. Carter, & K. A. Pelphrey, 2006; G. Coricelli, et al., 2005; Dehaene, Piazza, Pinel, & Cohen, 2003; Fias, Lammertyn, Caessens, & Orban, 2007; Huettel, 2006; S. A. Huettel, C. J. Stowe, E. M. Gordon, B. T. Warner,
A large number of studies have identified the intraparietal sulci (IPS) of PPC in humans as one of the primary brain regions recruited for the processing of numerical information (J. F. Cantlon, et al., 2006; Dehaene, et al., 2003; Fias, et al., 2007; Piazza, et al., 2004; Pinel, et al., 2001; Pinel, et al., 2004) or magnitude information (e.g. size, luminance) more generally (Pinel, et al., 2004). PPC activation has also been found during risky decision making (Huettel, 2006; S. A. Huettel, et al., 2006), and has been found to be positively correlated with (a) the magnitude of difference between selected and unselected outcomes of a risky decision on a trial by trial basis (G. Coricelli, et al., 2005) and (b) increases in individual risk preference (S. A. Huettel, et al., 2006). In non-human primates, the homologue of this region has been found to contain neurons sensitive to number (Nieder & Miller, 2004; Roitman, et al., 2007) as well as neurons sensitive to the magnitude of reward values of stimuli (Sugrue, et al., 2004) and behavioral performance (M. L. Platt, 2002; M. L. Platt & P. W. Glimcher, 1999). It is possible that this region is involved with processing risk independent of magnitude, but because risk often involves magnitude, it is also possible that PPC performs the more general function of valuation; it is yet unclear how PPC activation is modulated by interactions between magnitude and risk information.

The neural systems supporting outcome evaluation include anterior cingulate cortex (ACC), OFC, insula (INS), midbrain DA neurons and the striatum. Midbrain DA neurons are sensitive to reward prediction error (Fiorillo, et al., 2003; Schultz, et al., 1997), but are also triggered by aversive and alerting events (Bromberg-Martin, et al., 2010;
Matsumoto & Hikosaka, 2009). These neurons project widely throughout PFC but have a dense projection to the striatum in particular, retaining some degree of anatomical division. Surprise, error, and attention, have long been associated with the ACC (Dehaene, Posner, & Tucker, 1994; Hayden, Heilbronner, Pearson, & Platt, 2011; Posner & Rothbart, 1998), while reward prediction error and information about probabilistic occurrences (risk prediction error) activate the striatum and insula, respectively (B Knutson, G Fong, et al., 2001; Preuschoff, Bossaerts, & Quartz, 2006; Preuschoff, Quartz, & Bossaerts, 2008). As previously mentioned, OFC is also sensitive to monetary reward (Breiter, et al., 2001; B Knutson, G Fong, et al., 2001).

Recently, outcome evaluation and learning of reward contingencies have been shown to involve the striatum and hippocampus (Sadeh, Shohamy, Levy, Reggev, & Maril, 2011). The degree to which each is involved with learning may differ depending on their temporal proximity between choice and feedback, with immediate feedback preferentially engaging the striatum and more delayed feedback engaging the hippocampus (Foerde & Shohamy, 2011). A further thought with respect to the striatum’s role in learning is that it acts as an information gate for value updating in OFC (see Frank & Claus, 2006 for a review).

**Development of decision-making**

Arnett (1992) uses the term ‘reckless behavior’ to distinguish problem behaviors like drug use, sexual and criminal activity, from behaviors like gambling and rock climbing which are also considered risky but may carry less enduring consequences or are more socially acceptable. I will use the term reckless behavior to be consistent with Arnett’s distinction, and naturalistic to refer to both of these kinds of behavioral risk taking. This
distinction is important because when talking about risky behavior, many people are referring to reckless behaviors. The common intuition that adolescents are risky is also in reference to reckless behavior. However, individual differences in risk-taking are usually domain-specific (Weber, Blais, & Betz, 2002). Thus, it would not be surprising to find that risk-taking in different domains follow different developmental trajectories. Our primary focus here is on decision-making under economic risk.

Although research on decision-making during development has involved a diversity of tasks and some conflicting findings, several general conclusions emerge. First, children usually show a preference for risky options, in the domain of gains that gradually declines into aversion (Crone & van der Molen, 2004; Harbaugh, et al., 2002; Levin & Hart, 2003; Levin, Hart, et al., 2007; Rakow & Rahim, 2010; Weller, et al., 2010). Some studies have found departures from this trend, however (Tymula, Rosenberg Belmaker, Manson, Levy, & Glimcher, 2011). Second, young children, and even infants, demonstrate behavior consistent with an understanding of probability, including the computation of EV (Schlottmann, 2001; Schlottmann & Anderson, 1994; Xu & Denison, 2009; Xu & Garcia, 2008). Third, as children mature, they become more capable of remembering and integrating multiple types of information, facilitating more adult-like behavior (Brainerd, 1981; Crone & van der Molen, 2004; Falk & Wilkening, 1998; Garon & Moore, 2004, 2007; Hooper, et al., 2004; Huizenga, et al., 2007). For example, when considering choices that involve learned probabilities of both gains and loss, children tend to focus first on the frequency and magnitude of gains, and with age are able to incorporate the magnitude and frequency of losses into decision-making (Huizenga, et al., 2007).
Other patterns in the development of decision-making are becoming apparent as data accumulates. For example, adolescents appear to be particularly sensitive to reward, while sensitivity to punishment appears to increase in a linear fashion (Burnett, Bault, Coricelli, & Blakemore, 2010; Cauffman, et al., 2010). Burnett and colleagues (2010) asked male participants aged 9-25 years to select one of two spinners that differed in expected value and probability of winning. In one version, participants only saw the outcome of the spinner that they had selected, while in the other version participants saw both this outcome and the counterfactual outcome. This was done to test the hypothesis that different age groups would be differentially sensitive to counterfactual information. Two of the highlighted findings were that adolescents selected the riskier (greater variance) options more often than children or adults, and that adolescents gave greater emotion ratings after seeing counterfactual outcomes. The choice data are one of the first to show a clear inverted U-shape trend for increased risky behavior in a laboratory task among children, adolescents, and adults. Post hoc analyses showed that the greater emotion ratings were largely due to greater feelings of ‘relief’ among adolescents when seeing counterfactual outcomes that were worse than their own. This finding was interpreted to be consistent with the idea that adolescents have a heightened sensitivity to reward. However, inconsistent with the idea that emotion modulates risk taking, emotion ratings did not predict risk preference.

Cauffman and colleagues (2010) implemented a modified version of the Iowa Gambling Task (IGT) with a sample of 10- to 30-year-olds. Rather than having participants choose a card from one of four decks, participant chose whether to accept or reject a card from one of the four decks chosen at random. This enabled separate analyses of selecting
from advantageous decks and avoiding disadvantageous decks. Sensitivity to the rewarding properties of a deck, as measured by the rate of learning to select from the advantageous decks, peaked among the adolescent age groups. In contrast, a linear trend was found when plotting the slope of learning to avoid the disadvantageous decks: as age increased, responsiveness to the punishing aspects of the disadvantageous decks increased, indicating faster learning.

Hooper and colleagues (2004) used the IGT with children and adolescents aged 9- to 17-years-old. They divided their sample into three age groups: 9-10, 11-13, and 14-17. Their data showed that the oldest age group learned to select from the advantageous decks most rapidly - by block 4 of 5. By block 5, both the middle and oldest age groups were selecting from the advantageous decks more often than the 9-10 year-old group. The take these findings to suggest that as children mature, they gradually become more sensitive to punishment, thus avoiding the disadvantageous decks and selecting from the advantageous decks earlier. Other explanations for these results could have been that impulse or low working memory prevented children from learning about the reward contingencies, but this was not likely as measures of response inhibition (go-no-go task) and working memory (forward digit span) were not predictive of gambling behavior. However, as in the original IGT, participants were only allowed to choose cards from one of the four decks, confounding sensitivity to reward with sensitivity to punishment.

Adolescents have also been suggested to be more risky when a decision making context involves an emotional component (Figner, Mackinlay, Wilkening, & Weber, 2009). Figner and colleagues (2009) tested the hypothesis that adolescents are riskier under emotional conditions compared to more calculating conditions. They presented younger
adolescents, older adolescents, and adults, with two versions of the Columbia Card Task (CCT): a Hot version and a Cold version. In both versions, participants accumulated points by successfully turning over happy face cards, and suffered a loss of points if they turned over a penalty card. In the Hot version, cards were turned over one at time with feedback after each choice. In the Cold version participants selected a number of cards that would be flipped over all at once. Although all three age groups chose a larger number of cards to flip over in the Hot condition compared to the Cold condition, the adolescent groups were riskier than the adults in the Hot condition, but did not differ from adults in the Cold condition. However, as Burnett and colleagues (2010) did not find a relationship between emotion ratings and risk taking behavior, more work on the ways in which emotion influences risk behavior is needed.

**Development of neural systems related to decision-making**

The characterized pattern of brain development is that prefrontal cortical regions develop more slowly than posterior regions. This is true for several aspects of neural architecture, including synaptic density, grey matter volume, and myelination. Post-mortem studies indicate that synaptic density takes longer to reach mature adult levels in prefrontal cortex (mid-adolescence) than it does in auditory or visual cortex (about 12 years of age) (Huttenlocher & Dabholkar, 1997). Synaptic density levels follow a curvilinear pattern, rising to a peak during middle childhood and declining thereafter, demonstrating the two stages of synaptic growth and synaptic pruning that takes place between childhood and adulthood (Huttenlocher & Dabholkar, 1997).

There are several methods of estimating myelination, including white matter (WM) volume, fractional anisotropy (FA), and mean diffusivity (MD) and these three measures
give slightly different pictures of the development of myelination in the PFC. WM volume can be estimated from structural magnetic resonance imaging (MRI), while FA and MD are measures acquired using diffusion tensor imaging (DTI). WM volume is often assumed to reflect the amount of axonal myelination, but as the ratio between myelination and axon caliber is generally constant, it’s also possible that measures of WM volume reflect axonal caliber (Paus, 2009). FA is a measure of the degree to which water molecules are constrained to travel in a specific direction and is sensitive structural properties like the degree of myelination, axonal size, and axonal density, while MD is a more general measure of the degree to which water molecules can diffuse and can be thought also as a measure of axonal density (Berns, Moore, & Capra, 2009; Tamnes et al., 2010).

WM volume generally increases in a linear fashion from 5 to 30 years of age, with changes between 5-10%, e.g. in medial OFC and cingulate cortex, and sometimes greater than 20%, e.g. in posterior parietal cortex, and dorsomedial PFC (Giedd et al., 1999; Tamnes, et al., 2010). In contrast to the linear pattern of increases in WM volume, Tamnes et al. (2010) report that FA and MD measures show curvilinear trends in development according to brain region. The greatest changes in FA tend to occur in lateral anterior PFC, posterior parietal cortex, and central-posterior cingulate cortex, indicating increases in fiber size and density in these regions. The age at which peak FA occurs also differs by region. Occipital and posterior parietal cortices peak between 10 and 20 years, and temporal and lateral PFC regions do not reach their peaks until after 23 years of age. Changes in MD follow a more clearly defined posterior to anterior development: occipital, posterior, and parietal regions show the least amount of change in MD and peak between 10 and 20 years, while temporal and prefrontal regions change most and peak after 20 years of age.
These findings parallel the maturation of grey matter (GM) volume in that GM also shows a posterior to anterior course of development, whereby prefrontal and temporal regions are the last to reach adult volumes (Gogtay, Giedd, Lusk, & Hayashi, 2004). Decreases in GM volume that are a part of maturation are generally thought to reflect the pruning of synapses during adolescence. Most cortical and subcortical regions demonstrate a reduction in GM with a few exceptions: the hippocampus, amygdala, and brainstem show curvilinear increases in GM volume that begin to taper off around age 20, and the thalamus shows a slow linear increase in GM volume between the ages of 10 and 30 (Østby et al., 2009). Shaw and colleagues (2008) report that the timeline of GM reduction varies according to its laminar structure type. Specifically, regions of isocortex that contain the typical 6-layer structure tend to mature in a cubic fashion: GM volume increases between approximately 5-10 years of age, decreases until the early twenties, and begins to level off thereafter. Posterior OFC and the insula, in contrast, have a slightly different laminar structure with fewer and more poorly defined layers. These regions tend to exhibit quadratic and linear trends of development with GM peaking during middle adolescents and declining thereafter. Thus, complexity in the pattern of cortical GM development tends to coincide with the complexity of cortical architecture (Shaw, et al., 2008).

The striatum has been identified as a primary neural substrate for processing reward and reward expectation, and is thus a natural starting point for theories of adolescent risky behavior predicated on changes in how rewards are processed (M. Delgado, H. Locke, V. Stenger, & J. Fiez, 2003; M Ernst et al., 2005; Schultz, et al., 1992). Although the striatum undergoes a prolonged linear decrease in volume between eight and thirty years of age (Østby, et al, 2009), one hypothesis of adolescent risky behavior suggests
that the striatum of adolescents is less responsive to reward than children's or adults', and thus the experience of rewards for adolescents is devalued in general (Bjork et al., 2004; Spear, 2000a). Because adolescents experience a less rewarding response to the same stimuli, they engage in greater risk seeking behavior than children or adults to make up for it. This is tantamount to suggesting that adolescents are a special developmental case for the dopamine deficiency hypothesis suggesting that individuals with a deficient amount of DA function increase activities that elicit DA response to achieve more normal levels of DA function (Blum, Cull, Braverman, & Comings, 1996). Bjork and colleagues (2004) partially tested this hypothesis with fMRI by testing adolescents (12- to 17-years-old) and young adults (22- to 28-years-old) in the monetary incentive delay (MID) task, which is designed to specifically target activation of the ventral striatum (Knutson, Adams, Fong, & Hommer, 2001). Supporting the dopamine deficiency hypothesis they found that adolescents exhibited less activation in the nucleus accumbens during gain trials compared to adults. However, data from younger children were not collected, so the full course of a U-shaped curve for reward responsivity could not be tested.

Alternatively, Galvan, and colleagues (2006) suggest that we should see an inverted U-shaped curve for striatal activation from childhood to adulthood that matches the trajectory of reckless behavior, while activation in prefrontal regions should show a linear pattern paralleling the development of executive function. They found this pattern of activity in a sample of individuals ranging in ages from 7- to 29-years-old while they performed a cued response task (Galvan, et al., 2006). The position of the cue on each trial indicated which hand to respond with, while the cue image indicated how much money a correct answer was worth. Activation in the nucleus accumbens was greater among
adolescents than it was among children and adults, while activation in lateral OFC was
greater in children than in adolescents and adults, showing the combination curvilinear and
linear predictions. Recently, Linda van Leijenhorst and colleagues (2010) found a similar
striatal response to rewards in a risky decision making task. They presented 8- to 26-year-
olds with the cake gambling task in which participants had to select between a low
probability large gain of differing amounts and a high probability small gain. Among their
findings was that the difference in caudate activation between winning outcomes and losing
outcomes showed an inverted U-shaped curve across age, with adolescents showing the
greatest activation to wins over losses. Thus, evidence is accumulating for this perspective
on the biological mechanisms of adolescent risk taking that many prominent developmental
researchers seem to be in favor of (Casey, Getz, & Galvan, 2008; Steinberg, 2009).

In contrast, Berns, Moore, and Capra (2009) have suggested that the development of
prefrontal cortical regions may actually promote risk taking behavior rather than reduce it.
They collected DTI measures of FA and MD, and measures of real world risk taking
behavior, e.g. skiing, smoking, drinking, and having unprotected sex, using Adolescent Risk
Questionnaire (ARQ). They found that measures of myelination and/or fiber density
(decreased transverse MD and increased FA) in frontal white matter tracts were positively
correlated with naturalistic risk taking behavior in their 14- to 18-year-old sample. Their
suggestion is that the development of prefrontal regions responsible for risky decision
making leads adolescents to make adult-like decisions at an age for which society deems
these behaviors risky. However, Berns and colleagues note that the questions on the ARQ
are more related to naturalistic risk seeking behavior than to executive functions like
inhibitory control. This opens the door for developmental models of risky behavior containing more than just striatal reward and prefrontal executive function factors.

In one proposal of such an expanded model, regions that contribute to goal-directed behavior have been divided into primary and secondary circuits (Chambers, et al., 2003). According to Chambers, Tayler, and Potenza (2003), primary motivation circuits have direct influence on motor output and include prefrontal cortical and striatal regions. Secondary motivation circuits include structures like the hippocampus, amygdala, and sensory-motor association areas that provide context and affect information. Secondary motivation circuits also include structures like hypothalamic and septal nuclei, which contribute information about basic functioning and instinctual behaviors like feeding, aggression, and reproductive behaviors. This model takes into account the relative increase in promotivational striatal activity on the part of dopamine (DA) compared to the relative decrease in input from inhibitory serotonergic (5-HT) afferents sourced in prefrontal regions. Thus, it is consistent with the ideas of Galvan and Casey concerning relative development of the striatum and orbitofrontal cortex (Casey, Getz, et al., 2008; Galvan, et al., 2006). In addition, secondary motivational circuits are thought to be modulated by the hormonal changes that take place during puberty (Chambers, et al., 2003). For example, a part of adolescence includes a gradual orienting towards social stimuli, such as a growing interest in sexual and peer relations. The signaling of these stimuli in the environment may be modulated by the effects of sex steroids in the hippocampus and thalamus, thus giving rise to actions on particular opportunities in a given context for novelty or reward. To adults, these actions may seem precocious given the age at which they occur, resonating with the sentiment of Berns and
colleagues (Berns, et al., 2009) that risky adolescent behavior may seem risky especially because it occurs during adolescence.

Wahlstrom and colleagues (Wahlstrom, Collins, White, & Luciana, 2009) propose that prefrontal and limbic/striatal development modulate adolescent behavior because of changes in DA function that take place during this time period. The role of DA in primary motivation circuits is a common if not implicit feature of models that include striatal and prefrontal development as factors of adolescent risky behavior. Increases in ‘go’ signals and decreases in ‘stop’ signals are thought to depend on the changes that take place during adolescence in the striatum and prefrontal cortex, leading to increases in the sense of reward and the inability to inhibit impulsive actions. The striatum and PFC are also targets of DA neurons projecting from the ventral tegmental area (VTA), making up the mesolimbic and mesocortical dopamine pathways, respectively. Two prefrontal targets of the mesocortical pathway are the orbitofrontal and dorsolateral prefrontal cortices, which are known to be key regions involved with decision making (Wahlstrom, et al., 2010; Wallis, 2007). Dopamine innervation to prefrontal cortex has been shown to peak during adolescence in rhesus macaques (Rosenberg & Lewis, 1994). Data on developmental DA innervation to the striatum is not clear, but does not appear to suggest an adolescence increase (Wahlstrom, et al., 2009). Coupled with the suggestion from research showing that DA signaling in PFC operates within a narrow window of efficacy - too much or too little impairs behavior - the proposal made by Wahlstrom et al. (Wahlstrom, et al., 2009) is that adolescent behavior is influenced by an altered DA function, which is itself modulated by the structural changes taking place in the adolescent brain, including myelination and synaptic pruning.
Chambers et al.’s (2003) and Wahlstrom et al.’s (2009) proposals are inconsistent with DA deficiency hypothesis, suggesting instead that striatal sensitivity to reward may be driven by changes in DA function in PFC rather than in the striatum itself. The discrepancy between imaging studies that have a relative decrease in adolescent striatal activity (Bjork, et al., 2004) and those that have found a relative increase in adolescent striatal activity (Galvan, et al., 2006; van Leijenhorst, Moor, et al., 2010) may be due to differences in cognitive processes as a result of task (Galvan, 2010); Bjork et al.’s (2004) study examined striatal activation during reward anticipation, while Galvan et al.’s (2006) and van Leijenhorst et al.’s (2010) imaging data showed striatal activation at the time of reward. Thus, with respect to reward processing, data are accumulating against the DA deficiency hypothesis to explain adolescent risk seeking behavior.

Adolescence is a time of growth in which maturing children acquire the physical, social, and cognitive skills that will be necessary for independent life as adults. There is an apparent stepping outside of the primary social unit during adolescence, across species, to engage in greater exploratory behavior and spend more time with peers. These behavioral changes are concomitant with neural changes that include the pruning of synapses, decreases in gray matter, and increases in myelination, all of which are consistent with the idea that the brain is settling into more efficient networks of connectivity, preparing itself with experience and through rehearsal for the physical and cognitive demands of adulthood.

One thing that is clear from the phylogenetic preservation of a pubertal developmental period is that adolescent changes in behavior are ubiquitous. This fact suggests that some of the cognitive changes occurring during adolescence may stem from
changes in evolutionarily primitive neural structures, like the basal ganglia. Maturational changes in 5-HT and DA innervation to the striatum may result in stronger “go” and reward signals with a reduction in “stop” signals, while hormonal changes may influence the type of stimuli that are found to be salient or rewarding, for example peer relations and members of the opposite sex. Novelty seeking also increases in adolescence (Laviola, Macrī, Morley-Fletcher, & Adriani, 2003), which may translate into greater exploratory behavior. In humans, exploratory behavior may have broadened from basic spatial exploration to the exploration of social and psychological conditions, for example experimentation with sex, drugs, and alcohol. To more experienced adults, this experimentation may seem precociously risky, although an adolescent’s rationale for engaging them may be no different than an adult’s. In this light, risky behavior may only appear risky in first person retrospect and to the outside observer.

**Summary and Dissertation Approach**

The process of decision-making can be broken down into several stages: (1) representation of decision variables, (2) valuation, (3) action selection, (4) outcome evaluation, and (5) learning. In many respects, young children and adults are similar in performance within these stages. For example, sensitivity to magnitude, a basic understanding of probability, the ability to compute expected value, and learning from the outcomes of choice, can be seen throughout the lifespan appropriate experimental designs are used. Differences have been found, however, between children and adults in their preference for risk and in their ability to integrate multiple pieces of information. It is likely that these and other differences observed in the development of decision-making under risk are due in large part to the prolonged maturation of the neural substrates supporting
decision-making. Although many studies have documented differences in risk preferences across age groups, little is known about why these preferences obtain. Where in the process of decision-making are these differences sourced, and what changes in neural circuitry could be responsible?

This dissertation addresses these questions with five experiments across four different studies. Chapter 2 focuses on the development of risk preference, sensitivity to risk, and the tradeoff between risk and return. Risk preference typically refers to either risk-seeking or risk-averse behavior when choosing between risky and non-risky options; the experimental findings in chapter 2 describe dynamic changes in risk preference as a function of risk level and age. Chapter 3 uses functional magnetic resonance imaging (fMRI) to identify age-related changes in neural activation. Several regions commonly found to be active during decision-making tasks are discussed in terms of a decision-making network that develops with age, with special attention paid to the insula, hippocampus, and amygdala, regions not often discussed in the developmental neuroimaging literature. Chapter 4 tests specific hypotheses concerning children’s estimates of probability compared to adults, learning from positive and negative feedback, and how these abilities related to risk preference. The two experiments in this study also examine more closely the changes in dynamic risk preference that are introduced in Chapter 2. Chapter 5 uses eye-tracking methodology to test hypotheses that emerged from Chapter 4 which suggest that children’s increased preference for risk may be explained by an attention-guided differential weighting of choice alternatives, as outlined in Cumulative Prospect Theory. This final experiment also breaks new ground in studying the development of outcome evaluation
through unmediated measures of gaze position and pupilometry. Chapter 6 concludes the dissertation with a synthesis of past and current findings, and future directions.
Chapter 2 – Development of Risk Preference

Adolescence is often considered an age of heightened risk-taking for many real-world behaviors: consumption of alcohol, drug use, unprotected sex, and driving while distracted (see for reviews Arnett, 1992; Steinberg, 2008). While it is becoming clear that contextual factors contribute to risk-taking behavior, it is unclear how risk parameters interact with the developmental trajectory of risk-taking behavior. Increases in risky behaviors in adolescence may reflect a heightened tendency towards risk seeking, or may instead be indicative of some other emerging changes, like openness to greater opportunities, changes in emotional context, or increases in exploratory behavior, rather than risk-seeking behavior per se (Casey, Duhoux, & Cohen, 2010).

Experimental studies of risk preference have generally found that children and adolescents are less risk-averse than adults (Burnett, et al., 2010; Harbaugh, et al., 2002; Levin & Hart, 2003; Levin, Hart, et al., 2007; Rakow & Rahim, 2010), but contextual differences sometimes elicit different age-related patterns (Figner, et al., 2009). For example, in choosing between a sure bet and a gamble of equal expected value (EV), young children tend to select risky options more often than adults (Harbaugh, et al., 2002; Levin & Hart, 2003). In the Columbia Card Task, in which successive card flips increase the probability of encountering a hazard card and threaten cumulative winnings, adolescents choose more risky options compared to adults (Figner, et al., 2009). Burnet et al. (2010) used a two-spinner task in which
both the probability and the payoff for winning were manipulated. They found that adolescents showed more willingness to make risky choices – defined as preference for the spinner with greater variance, distinct from EV – compared to pre-adolescent children (9-years-old and older) and young adults.

Yet, heightened preference for risky options amongst adolescents has not been demonstrated consistently across studies. When the Columbia Card task is modified so that participants preselect a number of cards to flip, adolescents made similar choices to adults (Figner, et al., 2009). In another study, van Leijenhorst and colleagues (2010) presented participants aged 8- to 26-years old with choices between a 66% chance of winning one Euro and a 33% chance of winning either 2, 4, 6, or 8 Euros. Risk preference decreased with age in the 2 Euro condition and did not vary with age in the other three conditions. Thus different studies have revealed either a developmental increase in risk aversion or a U-shaped trend in risk aversion. It is unclear which task parameters may be responsible for these two different age-related trends.

In the current study, we characterize the development of risk preference by systematically and independently manipulating risk and expected value. A key feature of our approach that differs from prior work on this topic is that we use a nonsymbolic task that was designed to avoid symbolic math knowledge and complex rule learning, which are both stumbling blocks for young children. This differs from most prior studies of adolescent choice, which typically use economic
tasks (Burnett, et al., 2010; Crone, Bullens, Van der Plas, Kijkuit, & Zelazo, 2008; Reyna & Ellis, 1994; van Leijenhorst, Crone, & Bunge, 2006; van Leijenhorst, Moor, et al., 2010). Yet, even across laboratory studies, there is a lack of consistency in definitions of risk: a choice may be risky if it is suboptimal for maximizing gains in the long run, or it may be risky if it has greater variability in outcomes compared to alternatives. Thus we operationally define risk as the coefficient of variation (CV) in the potential outcomes of risky choice, while keeping CV and EV orthogonal over the course of the experiment. The CV is a dimensionless representation of risk per unit of return, affording comparisons across tasks that use different units. CV has been shown to outperform more traditional economic measures of risk (e.g. variance) in explaining choice behavior in a range of species (Weber, et al., 2004). Finally, because of inconsistencies in the literature as to whether risk preference shows a decreasing trend over development or an inverted U-shaped trend (Weller, et al., 2010) we tested a wide age span with three age groups: young children (6- to 8-years-old), adolescents (15- to 16-years-old), and young adults (18- to 32-years-old).

Our task consisted of three different decision-making trial types, which are illustrated in Figure 1. Risk-Safe trials required a decision between a gamble and a sure bet where the two options had equal EV. Risk-Risk trials required a choice between two gambles. Finally, Safe-Safe trials offered a choice between two certain outcomes. Our results favor the idea that, at least for economic decisions,
adolescents are not especially risk taking as a group, but express a decision-making phenotype intermediate in character between children’s preference for risk and young adults’ risk aversion.

Figure 1: Experimental design. RT, response time. Trial types were pseudo-randomized. Each trial consisted of a decision (blue frame), choice (salmon frame), confirmation (red frame), delay (no frame), and outcome (yellow frame) period. Safe-Safe trials offered the decision between two safe bet values, Risk-Safe trials offered the decision between a gamble and a safe bet, while Risk-Risk trials offered the decision between two gambles of different expected value and coefficient of variation.

Methods
Participants
Twenty-one children (10 female; M = 7.1 years) and thirteen adolescents (6 female; M = 14.9 years) were recruited from the Raleigh-Durham-Chapel Hill area of North Carolina. Thirteen young adults (9 female; M = 21.6 years) were recruited from Duke University and the surrounding community. Duke IRB-approved informed consent was collected from adult participants and parents/legal guardians of minor participants, and written assent was obtained from minor participants.

Design and stimuli
Participants were informed that they would be playing a game in which the choices they made would yield different numbers of coins, and that the coins could be traded for a toy prize (children) or a gift card value up to $10 (adolescents and adults) at the end of the session. Figure 1 illustrates the three trial types: Risk-Safe, Risk-Risk, and Safe-Safe. Risk-Safe trials consisted of a choice between a safe option and a gamble option that consisted of two possible outcomes with equal probability. We define Risk level here as the coefficient of variation (CV) which is the standard deviation divided by the mean (Weber, et al., 2004). The expected value (EV) of the gamble option was always equivalent to the certain option (either 4 or 8 coins), while the CV for the gamble option was varied (0.35, 0.71, 1.06, or 1.41) across the two levels of EV creating 8 trial types. Risk-Risk trials consisted of a choice between two gamble options of differing EV and CV, but always such that the gamble option with the higher EV also had the higher CV. One gamble option with an EV of 5 coins was presented at two levels of CV (0.28, 0.57), while the other gamble option had an
EV of 6 coins at three levels of CV (0.94, 1.18, and 1.41), creating six trial types. CV and EV were confounded on Risk-Risk trials to examine the risk-return tradeoff, in which a larger expected payout generally requires assuming a higher level of risk. This condition was only slightly more complex than deciding between a sure bet and a risky option because it added a second risk dimension that was contrasted with EV, but did not manipulate probability. To our knowledge the risk-return tradeoff has not been examined developmentally. Crossing two levels of the lower risk EV 5 option with three levels of the higher risk EV 6 option provided a multileveled measurement of the risk-return tradeoff, while controlling for EV. Safe-Safe trials consisted simply of a choice between two certain outcomes, the values for which were derived from the values used in Risk-Safe trials. Each participant was given 16 Safe-Safe, 48 Risk-Safe, and 36 Risk-Risk trials.

As shown in Figure 1, the two choice stimuli were presented above and below a central fixation point. Choices remained visible for 4 seconds followed by a recording of a female voice that said “pick one” and right and left arrows which indicated which hand should be used to make a given response. Choices were made with a button press using the left or right hand. A second button press with the right thumb was required to confirm the choice, thus minimizing impulsive responses. After the choice was confirmed, the frame of the selected alternative turned red and was displayed for one second, followed by a variable 1-2 second blank-screen delay period. The outcome was then presented for 2-s accompanied by a playback of a
female voice saying “you get” and, if coins were received, a short (0.15 to 1.2 sec) playback of coin sounds, proportional in duration to the number of coins won. Trial types were pseudorandomly distributed and presented in four blocks. Gamble options for trial types were counterbalanced for location and response hand. Each block concluded with an image of toy prizes and the cumulative coin winnings.

The task was designed as a pilot study with timing that matched a future fMRI study, which resulted in making the analysis of response time measurements unreliable. In particular, choice options were displayed for four seconds before the choice-selection button presses could be initiated.

**Results**

**Safe-Safe trials**
All three age groups were highly accurate at choosing the larger value on Safe-Safe trials, with accuracy equal or greater than 98%, thus indicating that even the children understood the task and that all three age groups were highly motivated to maximize reward. There were no differences between age groups ($p > 0.42$).

**Risk-Safe trials**
We found significant differences in risk preference as a function of age on Risk-Safe trials, $F(2,44) = 12.69, p < 0.001, \eta^2 = 0.37$, indicating that children tended to gamble more often (70%) than both adolescents (56%; $t(32) = 1.83, p = 0.077$) and young adults (31%; $t(32) = 4.74, p < 0.001$), and adolescents gambled more often than young adults ($t(24) = 3.32, p < 0.01$). A group by risk level interaction was also found, $F(6,132) = 9.21, p < 0.001, \eta^2 = 0.30$, due to age related patterns of risky
choices as a function of risk level. As shown in Figure 2, children’s preference for the risky option increased as risk level (or CV) increased whereas adolescents and young adults showed the opposite pattern. These patterns were confirmed by significant linear trends of risk level (positive for children, negative for adolescents and young adults) for each group independently (all $p < 0.05$). Additionally, a significant quadratic trend was found for children, $F(1,20) = 6.09, p < 0.05, \eta^2 = 0.23$, showing that although risk preference was correlated with risk level, risk preference declined slightly at the highest level of risk. Following up on the group by risk level interaction, groups were also compared pair-wise at each risk level. No between groups differences were found at the lowest level of risk (all $p > 0.19$). Children’s risk preference was significantly greater than that of young adults and adolescents for the two highest levels of risk, and significantly greater than young adults at Med-Low risk. For Adolescents risk preference was greater than that of young adults for the Med-Low and Med-High levels of risk, and marginally greater than young adults at the highest level of risk ($p = 0.052$).
Figure 2: Risk preferences vary with age, risk level, and expected value. Children show an increase in the proportion of gambles selected as risk level increases, while adults and adolescents tend to show a decrease in the proportion of gambles selected. Children also show greater preference for gambles when the expected value (EV) was large than when it was small. Note: EV of the sure bet option was always equal to the EV of the gamble option.

Risk preference in children was also influenced by expected value independent of risk level, however this was not true for the adolescents or young adults as indicated in a significant interaction between EV and age group, $F(2,44) = 3.65, p < 0.05, \eta^2 = 0.14$. Children tended to select the gamble option more often for higher EV gambles (76%) than for lower EV gambles (65%), controlling for risk level, $F(1,20) = 11.20, p < 0.01, \eta^2 = 0.36$. There were no effects of Block on risk preference or interactions between Block and Group (both $p > 0.19$), suggesting that risk preference did not change over the course of the test session.

**Risk-Risk trials**
We define risk preference for Risk-Risk trials as the proportion of trials in which the option with the larger risk and return was selected. We first conducted an RM-ANOVA using two levels of risk for the EV 5 option, three levels of risk for the EV 6 option, and age group as a between-subjects factor. We found a significant main effect of age group on risk preference, $F(2,44) = 9.97, p < 0.001, \eta^2 = 0.31$. As in the Risk-Safe Trials, children showed a higher risk preference (77%) than both adolescents (51%; $t(32) = 3.42, p < 0.01$) and young adults (47%; $t(32) = 3.95, p < 0.001$). Adolescents and young adults did not differ from each other in their risk preference ($p > 0.65$). Main effects were also found for the risk levels EV 5 and EV 6: as risk level of EV 5 increased, risk preference increased (Fig. 3A), $F(1,44) = 20.834, p < 0.001, \eta^2 = 0.32$, but as the risk level of EV 6 increased, risk preference decreased (Fig. 3B), $F(2,88) = 18.33, p < 0.001, \eta^2 = 0.29$. Although these patterns in risk-return tradeoff were observed in the means for each age group, significant interactions between Group and EV 5 risk levels, as well as Group and EV 6 risk levels, were also found (both $p < 0.05$), suggesting that these effects were largest in the adult group.
Figure 3: Preferences between two gambles vary with age, risk level, and expected value. EV, expected value; CV, coefficient of variation. (A) Preference for the higher risk/higher EV option was greater for EV 5 Medium risk than for EV 5 Low risk, and (B) declined as the EV 6 risk level increased. (C) Preference for the higher risk/higher EV option increased linearly and the difference in risk level between the EV 5 and EV 6 gamble options decreased.

This pattern of main effects for EV 5 and EV 6 is consistent with a linear relation between risk preference and the difference between gamble option risk levels. Specifically, as the difference between the CVs of gamble options decreased, participants were more likely to choose the higher risk-return option. This was tested by regressing risk preference in Risk-Risk trials on the difference between the coefficients of variation (delta CV) for each group separately using mixed model regression. Significant regression coefficients were found for delta CV in the adult choices ($\beta = -0.74$), $t(64) = -5.31, p < 0.001$, and in the adolescent choices ($\beta = -0.41$), $t(64) = -3.28, p < 0.01$, confirming that as the difference in CV between gamble options decreased, preference for the larger risk-return option increased (Fig. 3C). Children showed a similar trend, although the coefficient for delta CV ($\beta = -0.15$) was only marginally significant ($p = 0.09$).
Relationship between risk preference on Risk-Safe and Risk-Risk trials
To assess the stability of risk preferences within individuals we examined the relationship between risk preference on Risk-Safe trials and Risk-Risk trials. Children’s risk preferences were highly correlated across the two conditions ($r = 0.88, p < 0.001$), and the correlation between adult’s risk preferences was marginally significant (Fig. 4; $r = 0.54, p = 0.056$). The correlation between adolescent’s preferences in the Risk-Safe and Risk-Risk conditions did not reach significance but showed the same positive trend ($r = 0.41, p > 0.16$).

![Relationship Between Risk Preference in Risk-Safe and Risk-Risk Trials](image)

**Figure 4**: Age-related risk preferences are correlated across decision contexts. Preference for the higher risk/higher EV option in Risk-Risk trials is correlated with the probability of selecting the gamble option in Risk-Safe trials. These correlations were significant for children and adults, and marginally significant for adolescents.

Discussion
Our results demonstrate clear developmental changes in decision-making, with aversion to risk strengthening from childhood to adulthood. Children showed a
heightened risk preference both when the choice was between a risky option and a sure-bet and when the choice was between two gambles. Children also showed a greater tendency to select the risky option at higher levels of EV. When a gamble was offered in conjunction with a sure bet adolescents showed risk preferences intermediate between children and young adults. Adolescents and young adults did not differ in their preferences between two gamble options that varied in risk level and EV. These findings are consistent with previous reports that risk preference declines between childhood and adulthood (Harbaugh, et al., 2002; Levin, Hart, et al., 2007; Levin, Weller, Pederson, & Harshman, 2007; Weller, et al., 2010), and partially consistent with those of Burnett et al. (2010) in which both children and adolescents displayed a greater preference for risky options with greater variance of outcomes than young adults. Our findings are also partially consistent with Levin, Weller, et al. (2007) who found that children’s risk preference increased with EV. However, we did not find a U-shaped pattern in this developmental progression.

Our second and more novel finding was that when faced with a gamble and a sure bet, risk level affected decision-making differently in children compared to both adolescents and young adults. Adolescents and young adults showed a strong tendency to avoid the risky option as risk level increased. In contrast, children showed increasing preference for the risky option as risk level increased. It is also important to note that in our study absolute levels of risk preference only varied as a function of age at the highest levels of risk. This finding stands in contrast to van
Leijenhorst et al. (2010) in which age-related declines in risk preference were apparent only at lower levels of risk, while at higher levels of risk individuals of all ages showed similar preferences for risk. Task differences between the two studies may be responsible for this discrepancy. Specifically, the EV of the high risk options was always greater than the low risk option in the van Leijenhorst et al. study (2010), whereas in our study EV was equated across Risky-Safe options.

When selecting between two gamble options, all three age groups displayed a similar pattern of behavior. We found a linear relationship between the change in CV and choice behavior; participants tended to select the higher risk-return option as the difference in risk level between the two options decreased. Thus given a pair of gamble options with constant but unequal EV, choice behavior favored the lower risk-return option when risk levels were disparate, but the higher risk and return as risk levels grew similar. Although children generally selected the higher risk-return option more often than older participants, variations in risk level effected all three age groups similarly suggesting that at least some of the mechanisms for processing the economic balance between risk and return are adult-like by the age of six or seven.

Developing a task that can be used across a wide age range is always a challenging endeavor. Our task was designed to avoid complex contingencies and symbolically mediated mathematics that might contribute to measurement error in younger children. The stimuli and task design were identical across age ranges.
However, to motivate participants across a wide age span we deemed it necessary to provide young adults and adolescents with gift cards and children with toys. While it is conceivable that this difference in reward structure led to differences in decision-making, we believe this unlikely. First, each age group showed clear changes in their patterns of risk taking as a function of risk level, suggesting that each increment in risk level was meaningful with respect to gains and therefore that gains were, as a whole, valuable. Second, the general pattern of decreasing risk preference with age is consistent with other studies that have used similar, dissimilar, or no economic incentives between groups (Harbaugh, et al., 2002; Levin & Hart, 2003; Rakow & Rahim, 2010)

Children’s preference for the risky option, across choice sets, could potentially be explained by either a myopic or a biased focus on the more numerous coin set in gamble options. If children are driven myopically to choose the option with the single highest value then they should in the extreme case choose the risky option 100% of the time, and at a minimum should increase risky option selection monotonically with CV. Children showed neither of these patterns. As shown in Figure 2, their choices in Risk-Safe trials varied as a function of CV at lower and intermediate levels of risk while reaching a plateau at the higher levels of risk. In Risk-Risk trials, children’s behavior showed a similar pattern to adolescents and adults, which was that risk preference decreased with increasing CV in the EV6
option, further indicating that children do not uniformly select the option with the greatest possible winnings.

However, our data do support an age-related shift in the bias with which risk outcomes are weighed. Given the choices that participants made, gamble options appear to have had greater value than sure bets for children, whereas the sure bets had greater value for adults. Because children as young as 5-years-old have been shown to be capable of computing EV (Schlottmann, 2001; Schlottmann & Tring, 2005), these age-related differences in the value of gamble options is likely to be subjective, as opposed to computational errors with objective values. Individual variability in the value of gamble options has been explained, in prospect theory for example, by individual differences in the subjective weight that is applied to the combination of objective probabilities and values (Kahneman & Tversky, 1979).

One possibility is that children weigh the winning probability-by-outcome value in a gamble more heavily than the losing probability-by-outcome value, while adults do the opposite. Thus, for children, as the value of the larger outcome increases, the subjective value of the risky option rises above that of the sure bet option, increasing the probability of its selection. In adults, as value of the smaller outcome decreases, the subjective value of the risky option dips below that of the sure bet option. A further prediction of this hypothesis is that children and adults should differ more dramatically in their risk preferences at high levels of risk where both the high and low payoff are more dramatically different from each other and...
from the sure bet or EV, and less so at lower levels of risk where the high and low payoffs are more similar. Our data support this hypothesis in that group differences in behavior were found at the higher levels of risk, but not at the lowest level of risk where all groups were roughly indifferent to the two options.

Notably, some nonhuman primates also show increasing preference for a risky option over a sure bet as reward CV increases (McCoy & Platt, 2005). This apparent risk-seeking behavior has been linked to saliency of the jackpot (Hayden & Platt, 2007) and preference for variability itself (Hayden, Heilbronner, Nair, & Platt, 2008). Similar processes may contribute to increasing preference for the risky option with increasing reward CV in children prior to the emergence of strong symbolic math skills.

**Conclusion**

We developed a child-friendly economic decision-making task that minimized the need for memory or symbolic math skills. Despite the relatively small sample size, similarities and robust differences in risk taking behavior were found across age groups, demonstrating the powerful effect of CV on choices in the presence of risk. Children showed stronger preferences for a risky gamble than either adolescents or young adults, and this age difference in risk preference was greatest at the highest risk levels. Our task revealed no evidence for an inverted U-shaped function in risk preference across age; instead adolescents were intermediate between children and young adults. Our findings endorse a view of development in which economic decision-making processes emerge gradually from
childhood to adulthood, in direct contrast with the conventional notion of heightened risk-seeking in adolescence. Resolving the apparent discrepancies between laboratory measures of economic decision-making under risk – such as in our non-symbolic token economy task – and real-world risk-taking will require further study.
Chapter 3: Neuroimaging the Development of Risk-Aversion

Behavioral data suggest both commonalities and differences in decision-making between adults and children. Across the few studies that have directly compared young children and adults in decision-making under risk, children tend to be less risk-averse than adults (Harbaugh, et al., 2002; Levin, Hart, et al., 2007; Paulsen, Platt, Huettel, & Brannon, 2011; Rakow & Rahim, 2010). These developmental changes could reflect heightened focus on reward or reduced sensitivity to prospective loss, each of which may have distinct neurobiological underpinnings.

A series of recent studies have identified brain systems that contribute to decision-making under risk in adults (reviewed in Platt & Huettel, 2008; Rushworth & Behrens, 2008). We use the term decision-making to refer to value- or goal-based decisions, in contrast to perceptual decision-making. Core regions for processing the basic components of a risky decision – expected reward values, the probability of outcomes, reward variance, and affective consequences – include orbitofrontal cortex (OFC), posterior parietal cortex (PPC), ventral striatum (vSTR), anterior insula, and amygdala (Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; S. Huettel, C. Stowe, E. Gordon, B. Warner, & M. Platt, 2006; Krawczyk, 2002; M. Platt & P. Glimcher, 1999; Wallis, 2007; Yang & Shadlen, 2007). The integration of this information into response plans appears to rely upon dorsolateral prefrontal cortex (dlPFC), posterior parietal cortex (PPC), and ventromedial prefrontal cortex (vmPFC) (Krawczyk, 2002; Wallis, 2007). In risk contexts, this integration requires that sensory information be decomposed into the basic components of a risky decision (e.g. value, probability, variance) and brought to bear on the comparison of alternatives (vmPFC).
followed by an action (dIPFC) that appropriates the selected alternative (see Rangel, et al., 2008 for a discussion of the components of decision-making). Structures known to contribute to memory encoding and memory retrieval, like the hippocampus (Maratos, Dolan, Morris, Henson, & Rugg, 2001), are also implicated in decision-making, as they provide organisms the ability to integrate their experiences with prior decision contexts, actions, and (M. Platt, 2002; Shohamy & Adcock, 2010), and are important in flexibly learning cue-outcome relationships (Shohamy, Myers, Hopkins, Sage, & Gluck, 2009).

Notably, regions of prefrontal cortex undergo marked structural changes from childhood to adulthood. For example, grey and white matter density in PFC do not reach adult levels until after adolescence (Giedd, et al., 1999). Hippocampus (HC) and amygdala (Amy) volume also increase with age, achieving approximate adult size between 12 and 15-years of age (Østby, et al., 2009). Thus, it is plausible that differences in decision-making between younger and older adults have roots in neural development.

Behavioral studies on the development of decision-making under risk have identified both linear and curvilinear trajectories in risk taking. Declines in risk taking between childhood and adulthood have often been found in tasks that present a choice between a sure bet and a gamble, in particular for gains (Harbaugh, et al., 2002; Levin & Hart, 2003; Levin, Hart, et al., 2007; Paulsen, et al., 2011; Weller, et al., 2010). Adolescents show a relative increase in risk taking compared to children and adults when tested in slightly more complicated gambling tasks with an emotional component (Burnett, et al., 2010; Figner, et al., 2009). Still, other studies have found age-related differences only under specific conditions. For example, Van Leijenhorst et al. (2010) did not find behavioral differences in choices between a gamble that had a 0.66 probability of returning 1 Euro and
gambles that had a 0.33 probability of returning 4, 5, or 8 Euros across a large age span of 8-26 years (see also van Leijenhorst, Westenberg, & Crone, 2008). In contrast, they found that young participants were more likely to choose a gamble with a 0.33 probability of winning only 2 Euros than a gamble with a 0.66 probability of winning 1 Euro. Although overall declines in risk-taking with age were found by Paulsen et al. (2010), there were no age-related differences in preference between sure bets and gambles with low coefficients of variation.

Two classes of hypothesis have been proffered to account for children's increased risk taking compared to adults. The first class speculates that young children may be less able to incorporate prior outcomes, in particular negative ones (Van Duijvenvoorde, et al., 2008), into choice evaluation, which could also be viewed as a reduced sensitivity to prospective loss. For example, young children typically perform poorly on the Iowa Gambling Task (IGT) (A. Bechara, A. Damasio, H. Damasio, & S. Anderson, 1994; Garon & Moore, 2004; Kerr & Zelazo, 2004), but do better on the IGT (Garon & Moore, 2007) and other gambling tasks (Brainerd, 1981) when the memory burden of the task is simplified or reminders of previous outcomes are provided. These observations suggest that in addition to general decision-making circuitry, the neural circuitry supporting the learning or integration of outcome history into current decision-making processes may mature with age.

A second class of hypotheses, drawn primarily from studies focusing on adolescents, centers on the idea that greater risk-taking may be driven by greater neural sensitivity to reward, coupled with an immature neural system supporting executive control 'stop' processes (Casey, Getz, et al., 2008; Galvan, et al., 2006). Although this idea is gaining
increased acceptance for explaining adolescents' tendency to exhibit greater real-world risky behaviors than younger children and adults, it may also be extended to the decline of risk-taking behavior in gambling tasks that occurs with age (Harbaugh, et al., 2002; Levin, Hart, et al., 2007; Paulsen, et al., 2011; Rakow & Rahim, 2010). Prior studies have indeed found curvilinear activations in the striatum that peaked in adolescents compared to children and adults during the anticipation and receipt of reward (Galvan, et al., 2006; van Leijenhorst, Moor, et al., 2010), though other studies have found both greater (M Ernst, et al., 2005) and lesser (Bjork, et al., 2004) striatal activation in adolescents than young adults during decision-making and reward anticipation. Results have also been mixed with respect to regions associated with cognitive control, finding decreases in OFC activation with age (Galvan, et al., 2006), increases in OFC activation with age (Eshel, Nelson, Blair, Pine, & Ernst, 2007), a peak in adolescence (van Leijenhorst, Moor, et al., 2010), or no significant change at all (van Leijenhorst, et al., 2006). The apparent inconsistencies of these findings have been notably attributed to differences in the age groups studied and the variety of tasks implemented, most of which have focused on reward processing rather than on the process of decision-making (Galvan, 2010). Here we focus on the decision-making process.

To address how the neural bases of decision-making under risk might change over development and whether individual differences in patterns of brain activity would predict risk preferences during decision-making, we used event-related functional magnetic resonance imaging (fMRI) in a risky decision-making task with 5-8 year-old children, 14-15-year-old adolescents, and young adults. An important aspect of our task was that it avoided the highly symbolic components of most gambling tasks used with adults and instead allowed children to rely on their approximate number system, which does not depend on
formal education (Barth, Beckmann, & Spelke, 2008). The age-appropriateness of this task was demonstrated in a previous study (Paulsen, et al., 2011). With regard to the first class of hypotheses, we would predict a monotonic increase in the activation of decision-making regions (OFC, dlPFC, vSTR, HC, Amy, PPC) with age during the decision-making phase of our task. The second class of hypotheses focuses on a subset of regions involved in decision-making and similarly predicts a monotonic increase in OFC activation with age during decision-making. However, in contrast, the second class of hypotheses would predict an overall decline in reward-related vSTR activation between childhood and adulthood, with a rise in vSTR activation during adolescence.

Our findings favor the first class of hypotheses, namely that age-related differences in risk-taking reflect the maturation of neural systems supporting decision-making and outcome evaluation. First, while some of the circuitry involved with risky decision-making was found to be online at an early age, several regions of prefrontal cortex were not fully engaged in children. Similarly, regions associated with contextual memory and the incorporation of aversive outcomes into the decision-making process showed less activation in children than in adults and adolescents. Second, we failed to find significant evidence of increased reward sensitivity in adolescents or children when compared to adults. In fact, children who showed adult-like risk aversion showed greater activation during the decision period for Risky Bets compared to Sure Bets in the vmPFC and striatum than children who were less risk-averse, consistent with the idea that the development of risk aversion co-occurs with the recruitment of regions supporting the integration of prior outcomes into current decision-making contexts.

Methods

Subjects and Task
Thirty-four children, 18 adolescents, and 17 adults, who were right-handed with normal or corrected to normal vision and no history of neurological disorders were recruited and scanned. Data from seventeen child participants were excluded for one of three reasons: ten for head motion exceeding a criterion of 2mm in any direction (see Imaging Data Analysis); four due to poor accuracy (choosing the larger value on Sure Bet trials less than 65%) or lack of response variation; and three for failing to complete the scanning session. Data from one adolescent was excluded for excessive head motion, and data from one adult was excluded for lack of response variation. The remaining 17 children (8 Female) ranged in age from 5.9 to 8.0 years ($M = 6.9$ years), 17 adolescents (8 Female) ranged in age from 14.2 to 15.9 years ($M = 14.8$ years), and 16 adults (6 Female) ranged in age from 18.5 to 35.5 years ($M = 23.7$ years). Duke IRB-approved consent forms and confidentiality agreements were obtained from adult participants, parents or legal guardians, and assent forms were collected from minor participants. Participants were given motion and task training in a mock scanner, after which children were allowed to investigate the selection of prizes they could choose from, prior to the actual task and scanning.

Participants were reminded that their goal was to collect as many coins as possible. Children were told that their coins could be traded for one of the toy prizes they had previously seen whereas adolescents and adults would exchange the coins earned for a gift card worth up to $25. On each trial, participants were presented with a choice between either two certain options (24 Sure Bet trials), or between a certain and a gamble option (48 Risk trials; Fig. 5).
Figure 5: Experimental design. Each trial consisted of a decision (blue frame), choice (salmon frame), confirmation (red frame), delay (no frame), and outcome (yellow frame) period. Trial types were pseudorandomized and presented over three 8-minute runs. Variable timing for the delay and intertrial intervals were implemented to dissociate the temporal contingency between adjacent events. RT - response time.

Participants were first introduced to the certain option through Sure Bet trials during training, with the explanation that ‘whichever big box you choose is the one you’re going to get’. Risk trials were then introduced with the explanation that if they choose the two smaller boxes, “you never know which one you’re going to get; it could be the box with more coins or it could be the box with less coins.” The gamble options consisted of two possible outcomes with equal probability and an expected value (EV) equivalent to the certain alternative. Two levels of EV (two and four coins) and two levels of risk were used. Risk was defined by the coefficient of variation (COV) of the gamble options (0.71 and 1.41). We chose to use coefficient of variation because this measure of risk is dimensionless, allowing comparison to other studies that may use different units of value, and because it has been shown to be a good predictor of decision-making behavior under risk across species (Shafir, 2000; Weber, et al., 2004). Thus, four types of gamble trials (12 each) were presented: small EV/low risk (1 or 3 vs 2), small EV/high risk (0 or 4 vs 2), large EV/low risk (2 or 6 vs 4), large EV/high risk (0 or 8 vs 4). The certain outcomes for the Sure Bet
trials were drawn from the sets of values used in each of the four gamble trial types (e.g., 1 vs 2, 1 vs 3, 2 vs 3, etc.). Risky Bet and Sure Bet trials were presented within blue frames for 4 seconds before the frames changed color, at which time right and left arrows appeared beside the choice alternatives indicating the associated response hand, and a recording of a female voice saying “pick one” was played. Choices were made with a button press with the left or right hand, after which the frame of the selected alternative turned red and was displayed for one second followed by a variable 1-8 second blank-screen delay period. After the variable delay period the outcome was presented for 2-s accompanied by a playback of a female voice saying “you get” and, if coins were received, a short (0.15 to 1.2 sec) playback of coin sounds. Intertrial intervals (ITI) ranged from one to eight seconds. The 12 trial types were pseudorandomly distributed and presented in an even distribution across three runs of 24 trials each. Each run concluded with an image of the toy prizes and the cumulative coin winnings.

Imaging

Imaging data were collected with a GE Excite 3T scanner equipped with a 40 mT/m gradient system and an 8-channel head coil. T2*-weighted functional images were acquired in 34 interleaved slices using the GE standard EPI sequence (TR = 2 s, TE = 30 ms, FOV = 25.6 cm, flip angle = 60°, voxel size = 4 mm^3). Functional data from the first three (child) participants were acquired using a SENSE spiral in/out sequence with the same parameters as the EPI sequence with the hope of increased sensitivity to activation in anterior regions near air/tissue interface (Law & Glover, 2009). EPI was used with all subsequent participants because we found the cost in signal-to-noise ratio by using a spiral in/out sequence to be too high in our child participants. Analyses run using only data from the 47
participants collected with EPI sequence confirmed only minor differences in activation compared to the n = 50 sample, e.g. slight shifts in peak voxel location and only a few regions that did not surpass cluster correction; notably these were regions unexpected to be affected by a spiral in/out sequence. Uncorrected patterns of activation remained the same. The differences between these analyses did not change our main conclusions. Each eight-minute run provided the acquisition for 240 functional volumes, including 4 discarded acquisitions at the beginning of each run. High-resolution T1-weighted anatomical images were also acquired using a fast spoiled gradient-recalled sequence (TR = 7.31 s, TE = 2.98 ms, FOV = 25.6 cm, flip angle = 25°, voxel size = 1 mm x 1 mm x 2 mm).

**Behavioral data analysis**
Response time (RT) and selection data were collected for every trial, but only data from runs that were included in the imaging analysis were analyzed for behavioral measures. Risk-aversion scores for each individual and trial type were calculated as the proportion of gamble trials for which the certain option was selected. Accuracy across participants on Sure Bet trials (choosing the larger amount) was greater than 93%. Risk-aversion scores and median RT from each trial type were submitted to repeated-measures ANOVA (RM-ANOVA) with two levels of Magnitude (Small, Large) and two levels of Risk (Low, High).

**Imaging data analysis**
Functional imaging data were preprocessed and analyzed using FSL 4.1.4 (http://www.fmrib.ox.ac.uk/fsl). Preprocessing steps included motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002), slice scan time correction, voxel intensity normalization, high-pass temporal filtering to remove low frequency artifacts, and trimming volumes beyond 6 seconds after the end of the final event for each run. Because
GE Signa EPI sequence automatically passes images through a Fermi filter with an effective spatial smoothing kernel of approximately 4.8 mm$^3$, EPI and SENSE images were smoothed using different Gaussian kernel full width half maximums of 8 mm and 9.4 mm smoothing kernels, respectively, during preprocessing to obtain an effective spatial smoothing of approximately 9.4 mm$^3$ for both acquisition sequences.

Data from runs with more than 5 volumes containing relative movement of greater than 2 mm in any direction were excluded from subject-level analyses. Because previous work has demonstrated that structural differences between children’s and adult’s brains are negligible following sufficient smoothing (Burgund et al., 2002; Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003), all images were normalized to the same template (Montreal Neurological Institute Template) as done in previous studies with children and adolescents (e.g., J. Cantlon, E. Brannon, E. Carter, & K. Pelphrey, 2006; Eshel, et al., 2007; Galvan, et al., 2006).

Whole-brain voxel-based statistical analyses were performed within the framework of the general linear model (GLM). Our model included regressors that were defined for the decision period of five trial types (Sure Bet trials and each of the four EV by risk level gamble types) and the outcome period (certain outcomes, gamble wins, gamble losses). Nuisance regressors were also included to account for physiological variance (time course of intensity for voxels situated in the right ventricle), motion-related variance (motion correction vectors), and variance due to motor response (right and left hand responses). With the exception of ventricle and motion-related regressors, each of the regressor events was convolved with a double-gamma hemodynamic response (HDR) function and included the temporal derivative to account for differences in the HDR between children. The
decision period was modeled with duration of four seconds and the outcome period was modeled with a duration of two seconds.

fMRI data from children have been shown to contain more variance than fMRI data from adults (Thomason, Burrows, Gabrieli, & Glover, 2005), as was the case with our data. Therefore, we used a mixed-effects approach that does not assume homogeneity of variance, but rather estimates and accounts for differences in within-group variance. FSL’s cluster correction for multiple comparisons (Gaussian-random field theory based) included a cluster threshold set to a height of $z > 2.3$ to identify a contiguous voxel cluster, and cluster probability set to $P < 0.05$ against which to compare the cluster’s estimated significance, whole-brain corrected (http://www.fmrib.ox.ac.uk/fsl). Additionally, risk aversion scores were mean adjusted by age group and used as a covariate in a parallel analysis.

We performed three primary analyses to examine age- and risk-related activations during decision-making. In all three, we restricted ourselves to activations in the Risk trial > Sure Bet trial. Although this contrast cannot dissociate certain aspects of the decision-making process, e.g. the computation of expected value or risk, it allows us to isolate activation involved with decision-making under risk by controlling for basic numerical processing and mental comparison. Our first whole-brain analysis looked for age-related increases or decreases in activation using linear contrast weighting by age group, and for searched peaks or troughs in activation using quadratic weighting by age group. A second whole-brain test examined relationship between behavior and brain activation by using our behavioral measure of risk-aversion as a covariate. This measure was mean corrected by
age group before submitting it to the GLM so that differences in activation due to risk-aversion would not be confounded by the general differences in risk-aversion due to age.

Region of interest (ROI) analyses were also performed. These analyses were less restrictive than the whole-brain analysis in that our ROIs were selected on the basis of significant activation in any one age group, pair of age groups, or all age groups together, rather than an a priori pattern of activation. However, we also restricted our ROIs by anatomical definitions. This process can be thought of as an omnibus test for activation with follow-up tests to identify the particular patterns of activation within an anatomically defined space (see below). Thus, the procedure that we used for ROI selection incorporated an anatomical constraint and used statistics that (a) were unbiased with respect to our hypotheses and (b) answered a more general question than the statistics that were used in the ROI analysis.

ROIs defined in the following manner. First, the Risky > Sure contrasts for each age group were submitted to an F-test within FSL to identify activations with parameter estimates significantly different from zero. This resulted in an ANOVA image of active regions due to significant activation in at least one age group. Possible approaches to proceeding from this point could have been to analyze the BOLD signal change of a peak voxel or a region surrounding a peak voxel in an area of activation, or the signal change in the whole of an activated region itself. However, these approaches have the potential to miss anatomical regions if only one peak is used in an activation that spans several regions, and may conflate different anatomical regions if the whole of a broad activation itself is used. Examination of the ANOVA results showed contiguous activation between a priori regions of interest with distinct anatomical boundaries, i.e. between insula and striatum and
between occipital and posterior parietal cortices. So to identify the location of potentially different peaks within these regions, we incrementally raised the z-statistic threshold of the cluster corrected image to the minimum at which the insula was separated from striatum ($z = 3.3$), allowing us to identify peaks in these regions. Over posterior sites, a large area of activation encompassing occipital, cuneus, and parietal cortices was decomposed at a slightly higher threshold ($z = 4$). The resulting peaks are listed in Table 3.

We next introduced anatomical constraints by masking each area of activation by the Harvard-Oxford anatomical region within which the ANOVA cluster peaks were located (Fig. 7B & 7E insets). For example, a cluster of activation with a peak voxel in the left insula could partially extend into OFC, but only the activation contained within the Harvard-Oxford atlas for left insula would remain as the left insula ROI. We ran two step-wise regressions with each ROI using mean percent signal change within the entire ROI, in each participant, in the Risky > Sure contrast: one to look for risk-related activations within and between groups (in order: group, risk aversion, group X risk aversion interaction), and one to identify age-related activation (in order: age, age$^2$) using an adjusted alpha of $p < 0.0017$ ($0.05/28$).

**Results**

**Decision-making behavior**

Children, adolescents, and adults made decisions about probabilistic and certain rewards, which were virtual tokens that could be traded for toys or gift card value at the end of the session (Fig. 5; Paulsen et al., 2010). On Sure Bet trials, participants chose between two certain options that differed in value, while on Risky Bet trials participants chose between certain and uncertain options with the same expected value (EV). On Risky Bet trials, the reward magnitude was either small ($EV = 2$) or large ($EV = 4$), and the risk
level, defined by the coefficient of variation (CV) in reward amount, was low (0.71) or high (1.41). Risk aversion was operationally defined as the proportion of Risky Bet trials in which a participant selected the certain option.

Overall, participants accurately selected the larger reward on greater than 97% of Sure Bet trials. A repeated-measures ANOVA on Risky Bet trials with reward magnitude and risk level as within-subject factors and age group as a between-subject factor revealed a significant main effect of reward magnitude ($F(1,47) = 21.8, p = 3e-5$) indicating that participants gambled more often with larger expected values ($M = 72\%$) than with smaller expected values ($M = 56\%$; Table 1). There was also a main effect of risk level ($F(1,47) = 21.9, p = 2e-10$) indicating that participants selected the gamble more often on low-risk ($M = 73\%$) than on high-risk ($M = 56\%$) trials. While there were no interactions between age group and reward magnitude ($p = 0.368$) or risk level ($p = 0.257$), risk aversion was different between groups ($F(2,47) = 8.35, p < 0.008$). Importantly, independent-sample $t$-tests between groups showed that children selected the gamble more often (79%) than both adolescents (57%; $p = 0.001$) and adults (56%; $p = 0.001$). Adolescents and adults did not differ in risk aversion, as defined here ($p > 0.80$).

**Table 1: Behavioral data: probability of selecting a gamble over a sure bet (RT in secs)**

<table>
<thead>
<tr>
<th>Group</th>
<th>Risk Level</th>
<th>Small EV</th>
<th>Large EV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Child</td>
<td>Low</td>
<td>0.76 (1.485)</td>
<td>0.90 (1.553)</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.66 (1.670)</td>
<td>0.83 (1.351)</td>
</tr>
<tr>
<td>Adolescent</td>
<td>Low</td>
<td>0.57 (0.776)</td>
<td>0.78 (0.890)</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.37 (0.794)</td>
<td>0.58 (0.841)</td>
</tr>
<tr>
<td>Adult</td>
<td>Low</td>
<td>0.63 (0.594)</td>
<td>0.71 (0.616)</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.40 (0.605)</td>
<td>0.51 (0.606)</td>
</tr>
</tbody>
</table>
Analysis of median RT data did not return any significant results (reward magnitude X risk X group: \( p = 0.232 \); all other \( p > 0.33 \)), although a marginal interaction between risk level and reward magnitude was found (\( p = 0.099 \)). This interaction suggests that participants took longer to respond to high risk than low risk on small magnitude trials, and longer to low risk than high risk on large magnitude trials (Table 1). However, it should be considered that all participants experienced a four-second delay between stimulus presentation and the opportunity to respond, confounding RT data as a measure of decision-making duration. A main effect of group was also found, showing the typical reduction in response time with age (\( p = 2\text{e}-8 \)).

**Changes in risk-related network activity with age**

To control for the contributions of numerical processing unrelated to risk, we examined within-participant contrasts between the Risky Bet trials and the Sure Bet trials (risky > sure) during the decision period (Fig. 5). Whole brain analyses included tests for two developmental trajectories in the activation of brain regions involved with risky decision-making, as well as an F-test for group activations that would later form the basis of our ROI approach. First, we report that the only regions showing significant cluster-corrected activation in all age groups was in posterior parietal and occipital cortex (see below for additional details). Our first test of development in decision-making used linear contrasts to identify regions of activation that increased or decreased from childhood to adulthood. This contrast revealed increasing activation with age during decision-making under risk in several areas of prefrontal and parietal cortex, as well as subcortical areas (Table 2), but did not show any regions decreasing in activation with age. Frontal regions that showed increasing activation with age included the anterior insula, ventromedial prefrontal cortex (vmPFC), anterior cingulate (ACC), frontal pole, orbitofrontal cortex
(OFC), amygdala (Amy), and hippocampus (HC); sub-cortical age-related increases in activations included the caudate, putamen, and thalamus (Fig. 6). Over posterior regions, linearly increasing activation was found in bilateral superior parietal cortex, occipital cortex, and precuneus during the decision period. We tested for robustness to group classification by regressing signal change at peak voxels for the regions identified in the linear contrast (Table 2) on age. With the exception of three foci in superior frontal gyrus, superior occipital gyrus, and dorsolateral prefrontal cortex (dLPFC), all regression coefficients were significant at \( p < 0.05 \). To be sure that these increases in activation were not a result of differences in the contrast condition, we checked for decreasing activation with age in the Sure Bet condition, which confirmed that there were no regions significantly more active in children than adults.

\[ \text{Figure 6: Regions associated with decision-making and context show increased activation with age during the decision period. Several regions comprising a decision-making network showed increased activation with age during decision-making. This network consists of areas associated with processing risk - superior parietal cortex (sPAR) and insula (INS) – and regions associated with processing value - orbitofrontal cortex (OFC), ventromedial prefrontal cortex (vmPFC), and striatum (STR). Additionally, brain regions often associated with memory and context showed increased activation with age during the decision period. These regions include: anterior cingulate cortex (ACC), associated with fictive learning and conflict detection; frontal pole (FP), associated with goals and strategies; amygdala (AMY), associated with affective dimensions of previous outcomes and current stimuli; and hippocampus (HC), associated with contextual memory. Coordinates in MNI space.} \]
Table 2: Whole-brain analysis linear effect of age group during decision-making

<table>
<thead>
<tr>
<th>number</th>
<th>region</th>
<th>size (vox)</th>
<th>z_val$^b$</th>
<th>x$^b$</th>
<th>y$^b$</th>
<th>z$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>R. precuneus</td>
<td>3014</td>
<td>4.92</td>
<td>6</td>
<td>-64</td>
<td>60</td>
</tr>
<tr>
<td>2</td>
<td>R. occipital</td>
<td>2144</td>
<td>4.53</td>
<td>8</td>
<td>-84</td>
<td>-4</td>
</tr>
<tr>
<td>3</td>
<td>R. insula</td>
<td>635</td>
<td>4.36</td>
<td>38</td>
<td>16</td>
<td>-10</td>
</tr>
<tr>
<td>4</td>
<td>L. Anterior Cingulate</td>
<td>598</td>
<td>3.94</td>
<td>-4</td>
<td>44</td>
<td>-2</td>
</tr>
<tr>
<td>5</td>
<td>L. Inferior Parietal</td>
<td>558</td>
<td>4.26</td>
<td>-40</td>
<td>-52</td>
<td>50</td>
</tr>
<tr>
<td>6</td>
<td>L. Insula</td>
<td>325</td>
<td>3.99</td>
<td>-30</td>
<td>20</td>
<td>-10</td>
</tr>
<tr>
<td>7</td>
<td>R. Caudate</td>
<td>203</td>
<td>3.9</td>
<td>18</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>8</td>
<td>R. Middle Frontal Gyrus</td>
<td>171</td>
<td>3.48</td>
<td>40</td>
<td>58</td>
<td>-6</td>
</tr>
<tr>
<td>9</td>
<td>R. HC</td>
<td>154</td>
<td>3.94</td>
<td>16</td>
<td>-38</td>
<td>2</td>
</tr>
<tr>
<td>10</td>
<td>L. Putamen</td>
<td>111</td>
<td>3.43</td>
<td>-20</td>
<td>8</td>
<td>-6</td>
</tr>
<tr>
<td>11</td>
<td>L. Hippocampus</td>
<td>98</td>
<td>3.47</td>
<td>-26</td>
<td>-38</td>
<td>-2</td>
</tr>
<tr>
<td>12</td>
<td>L. Caudate tail</td>
<td>90</td>
<td>3.41</td>
<td>-18</td>
<td>-22</td>
<td>18</td>
</tr>
<tr>
<td>13</td>
<td>R. Superior Frontal Gyrus, frontal pole</td>
<td>44</td>
<td>3.38</td>
<td>28</td>
<td>58</td>
<td>20</td>
</tr>
<tr>
<td>14</td>
<td>R. Superior Occipital Gyrus</td>
<td>36</td>
<td>3.45</td>
<td>36</td>
<td>-82</td>
<td>34</td>
</tr>
<tr>
<td>15</td>
<td>R. Thalamus</td>
<td>24</td>
<td>3.19</td>
<td>20</td>
<td>-18</td>
<td>8</td>
</tr>
<tr>
<td>16</td>
<td>L. Orbital Frontal Cortex</td>
<td>23</td>
<td>3.23</td>
<td>-26</td>
<td>10</td>
<td>-24</td>
</tr>
<tr>
<td>17</td>
<td>L. Caudate body</td>
<td>19</td>
<td>3.12</td>
<td>-16</td>
<td>-2</td>
<td>12</td>
</tr>
<tr>
<td>18</td>
<td>R. Middle Occipital Gyrus</td>
<td>17</td>
<td>3.15</td>
<td>44</td>
<td>-80</td>
<td>18</td>
</tr>
<tr>
<td>19</td>
<td>R. Orbital Frontal Cortex</td>
<td>14</td>
<td>3.17</td>
<td>34</td>
<td>40</td>
<td>-8</td>
</tr>
<tr>
<td>20</td>
<td>R. Orbital Frontal Cortex</td>
<td>11</td>
<td>3.09</td>
<td>44</td>
<td>52</td>
<td>-22</td>
</tr>
</tbody>
</table>

$^a$z-statistic values of thresholded (z > 2.95) cluster corrected image at x,y,z. $^b$Coordinates in MNI space.

We also tested for changes in the neural response to risk that were unique to adolescents using quadratic contrasts that would identify peaks or troughs of activation in the adolescent group for risky > sure, but did not find any regions showing such patterns of activation in the cluster corrected images. However, examination of the uncorrected images did reveal small clusters of activation peaking in adolescents in the caudate, hippocampus, and anterior cingulate gyrus, among several other regions (Table 3).
Table 3: Uncorrected regions of activation from the quadratic contrast showing adolescent peaks

<table>
<thead>
<tr>
<th>number</th>
<th>region</th>
<th>size (vox)</th>
<th>z_val(^a)</th>
<th>x(^b)</th>
<th>y(^b)</th>
<th>z(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>R. Middle Occipital Gyrus</td>
<td>200</td>
<td>3.7</td>
<td>38</td>
<td>-94</td>
<td>12</td>
</tr>
<tr>
<td>2</td>
<td>R. Superior Parietal Lobule</td>
<td>103</td>
<td>2.93</td>
<td>28</td>
<td>-50</td>
<td>58</td>
</tr>
<tr>
<td>3</td>
<td>Cerebellum</td>
<td>100</td>
<td>3.18</td>
<td>-16</td>
<td>-64</td>
<td>-14</td>
</tr>
<tr>
<td>4</td>
<td>R. Hippocampus</td>
<td>49</td>
<td>3.22</td>
<td>22</td>
<td>-38</td>
<td>2</td>
</tr>
<tr>
<td>5</td>
<td>L. Superior Parietal Lobule</td>
<td>28</td>
<td>2.84</td>
<td>-30</td>
<td>-48</td>
<td>58</td>
</tr>
<tr>
<td>6</td>
<td>Middle Occipital Gyrus</td>
<td>26</td>
<td>3.06</td>
<td>-34</td>
<td>-98</td>
<td>6</td>
</tr>
<tr>
<td>7</td>
<td>Middle Occipital Gyrus Medial Frontal Gyrus/Cingulate</td>
<td>23</td>
<td>2.73</td>
<td>38</td>
<td>-64</td>
<td>10</td>
</tr>
<tr>
<td>8</td>
<td>Gyrus</td>
<td>21</td>
<td>2.84</td>
<td>-6</td>
<td>28</td>
<td>42</td>
</tr>
<tr>
<td>9</td>
<td>Fusiform Gyrus</td>
<td>21</td>
<td>3.01</td>
<td>28</td>
<td>-38</td>
<td>-22</td>
</tr>
<tr>
<td>10</td>
<td>Cerebellum</td>
<td>21</td>
<td>2.83</td>
<td>-26</td>
<td>-42</td>
<td>-26</td>
</tr>
<tr>
<td>11</td>
<td>Temporal Fusiform Cortex</td>
<td>20</td>
<td>2.84</td>
<td>-36</td>
<td>-28</td>
<td>-30</td>
</tr>
<tr>
<td>12</td>
<td>Inferior Parietal Lobule</td>
<td>18</td>
<td>2.74</td>
<td>56</td>
<td>-26</td>
<td>48</td>
</tr>
<tr>
<td>13</td>
<td>Anterior Cingulate</td>
<td>16</td>
<td>2.79</td>
<td>-8</td>
<td>42</td>
<td>22</td>
</tr>
<tr>
<td>14</td>
<td>Middle Frontal Gyrus</td>
<td>15</td>
<td>2.8</td>
<td>-48</td>
<td>38</td>
<td>26</td>
</tr>
<tr>
<td>15</td>
<td>Postcentral Gyrus</td>
<td>14</td>
<td>2.73</td>
<td>-56</td>
<td>-28</td>
<td>50</td>
</tr>
<tr>
<td>16</td>
<td>Cerebellum</td>
<td>12</td>
<td>2.83</td>
<td>-36</td>
<td>-48</td>
<td>-28</td>
</tr>
<tr>
<td>17</td>
<td>Caudate</td>
<td>9</td>
<td>2.6</td>
<td>22</td>
<td>24</td>
<td>2</td>
</tr>
<tr>
<td>18</td>
<td>Precentral Gyrus</td>
<td>8</td>
<td>2.72</td>
<td>64</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>19</td>
<td>Postcentral Gyrus</td>
<td>7</td>
<td>2.73</td>
<td>26</td>
<td>-38</td>
<td>74</td>
</tr>
<tr>
<td>20</td>
<td>Lateral Occipital Cortex</td>
<td>6</td>
<td>2.59</td>
<td>50</td>
<td>-64</td>
<td>6</td>
</tr>
</tbody>
</table>

\(^a\)z-statistic values of thresholded (z > 2.5), uncorrected image at x,y,z. \(^b\)Coordinates in MNI space.
In order to confirm the previous results and to identify developmental effects in any regions of the brain involved with decision-making under risk that may have been missed by the whole-brain analysis, we also took a region of interest (ROI) approach. ROIs were identified using an F-test revealing cluster corrected activations that were significantly different during Risky Bet trials than Sure Bet trials on average across groups; significance could be due to a large change in one group or a small but consistent change across all groups. For each ROI, we ran two step-wise regressions to look for risk-related activations within and between groups (group, risk aversion, group X risk aversion interaction) and to look for age-related activation (age, age\(^2\); Table 4). As linear effects of age could be due to differences between the two younger groups and the oldest group, between the youngest group and the two older groups, or between each of the groups pairwise, we further performed post-hoc t-tests.

The F-test analysis yielded ROIs in portions of PFC, OFC, insula, cingulate, PPC, and striatum (Fig. 7B & 7E insets). These ROIs matched a subset of regions with overlapping activation between adolescents and adults that were found in anterior cingulate, dorsal striatum, insula, PPC, and occipital regions. Areas of activation in children overlapped with the areas activated in both adults and adolescents in PPC and occipital cortex, as mentioned above, with sub-threshold activations in anterior cingulate. These ROIs were similar to those identified in the linear contrast in whole-brain analysis using age group as a factor as described above.
Table 4: Clusters of activation from group ANOVA and ROI analysis statistics during decision-making

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Region</th>
<th>size (vox)</th>
<th>z_val&lt;sup&gt;a&lt;/sup&gt;</th>
<th>x&lt;sup&gt;b&lt;/sup&gt;</th>
<th>y&lt;sup&gt;b&lt;/sup&gt;</th>
<th>z&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Group F</th>
<th>Risk F-change</th>
<th>Risk*Group Intxn F-change</th>
<th>Age F</th>
<th>Age&lt;sup&gt;2&lt;/sup&gt; F-change</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>Inferior Parietal Lobule</td>
<td>1278</td>
<td>5.06</td>
<td>-58</td>
<td>-28</td>
<td>36</td>
<td>1.24</td>
<td>0.05</td>
<td>0.44</td>
<td>0.95</td>
<td>0.65</td>
</tr>
<tr>
<td>4</td>
<td>Cingulate Gyrus</td>
<td>1031</td>
<td>5.18</td>
<td>4</td>
<td>32</td>
<td>30</td>
<td>0.98</td>
<td>0.46</td>
<td>0.04</td>
<td>2.01</td>
<td>0.05</td>
</tr>
<tr>
<td>5</td>
<td>Inferior Parietal Lobule</td>
<td>985</td>
<td>4.85</td>
<td>-58</td>
<td>-32</td>
<td>28</td>
<td>4.99</td>
<td>0.25</td>
<td>0.78</td>
<td>5.07</td>
<td>1.81</td>
</tr>
<tr>
<td>6</td>
<td>Medial Frontal Gyrus</td>
<td>804</td>
<td>4.17</td>
<td>0</td>
<td>44</td>
<td>-18</td>
<td>14.72</td>
<td>6.79</td>
<td>4.77</td>
<td>15.43</td>
<td>6.46</td>
</tr>
<tr>
<td>7</td>
<td>Middle Frontal Gyrus</td>
<td>440</td>
<td>4.48</td>
<td>46</td>
<td>38</td>
<td>24</td>
<td>0.35</td>
<td>2.75</td>
<td>0.83</td>
<td>0.56</td>
<td>0.54</td>
</tr>
<tr>
<td>8</td>
<td>Posterior Cingulate Gyrus</td>
<td>332</td>
<td>4.42</td>
<td>-10</td>
<td>-56</td>
<td>12</td>
<td>7.08</td>
<td>0.04</td>
<td>0.22</td>
<td>10.9</td>
<td>2.63</td>
</tr>
<tr>
<td>9</td>
<td>Insula</td>
<td>300</td>
<td>4.9</td>
<td>36</td>
<td>16</td>
<td>-6</td>
<td>5.53</td>
<td>0.79</td>
<td>0</td>
<td>12.03</td>
<td>0.92</td>
</tr>
<tr>
<td>10</td>
<td>Caudate</td>
<td>243</td>
<td>4.32</td>
<td>16</td>
<td>6</td>
<td>10</td>
<td>3.44</td>
<td>0.23</td>
<td>0.48</td>
<td>6.27</td>
<td>1.02</td>
</tr>
<tr>
<td>11</td>
<td>Parahippocampal Cingulate Gyrus</td>
<td>156</td>
<td>4.43</td>
<td>22</td>
<td>-34</td>
<td>6</td>
<td>1.92</td>
<td>0.08</td>
<td>0.19</td>
<td>1.7</td>
<td>0.72</td>
</tr>
<tr>
<td>12</td>
<td>Middle Temporal Insula</td>
<td>152</td>
<td>4.08</td>
<td>12</td>
<td>-80</td>
<td>30</td>
<td>13.9</td>
<td>0.59</td>
<td>1.52</td>
<td>17.4</td>
<td>6.75</td>
</tr>
<tr>
<td>13</td>
<td>Medial Temporal Gyrus</td>
<td>144</td>
<td>3.97</td>
<td>-50</td>
<td>-70</td>
<td>28</td>
<td>0.14</td>
<td>0.88</td>
<td>1.6</td>
<td>0.46</td>
<td>0.04</td>
</tr>
<tr>
<td>14</td>
<td>Insula</td>
<td>130</td>
<td>4.13</td>
<td>-34</td>
<td>16</td>
<td>-10</td>
<td>5.44</td>
<td>1.16</td>
<td>0.3</td>
<td>11.2</td>
<td>0.92</td>
</tr>
<tr>
<td>15</td>
<td>Postcentral Gyrus</td>
<td>77</td>
<td>3.56</td>
<td>22</td>
<td>-32</td>
<td>62</td>
<td>2.09</td>
<td>0.27</td>
<td>0.84</td>
<td>2.86</td>
<td>0.98</td>
</tr>
<tr>
<td>16</td>
<td>Precentral Gyrus</td>
<td>75</td>
<td>3.97</td>
<td>48</td>
<td>-6</td>
<td>52</td>
<td>1.51</td>
<td>0.07</td>
<td>0.06</td>
<td>0.7</td>
<td>1.22</td>
</tr>
<tr>
<td>17</td>
<td>Insula</td>
<td>71</td>
<td>3.76</td>
<td>40</td>
<td>-12</td>
<td>2</td>
<td>6.73</td>
<td>3.26</td>
<td>2.38</td>
<td>10.35</td>
<td>2.08</td>
</tr>
<tr>
<td>18</td>
<td>Insula</td>
<td>63</td>
<td>3.75</td>
<td>-36</td>
<td>-14</td>
<td>2</td>
<td>6.27</td>
<td>6.53</td>
<td>8.74</td>
<td>8.76</td>
<td>1.92</td>
</tr>
<tr>
<td>19</td>
<td>Postcentral Gyrus</td>
<td>59</td>
<td>3.73</td>
<td>8</td>
<td>-48</td>
<td>76</td>
<td>0.22</td>
<td>1.59</td>
<td>0.65</td>
<td>0.4</td>
<td>0.18</td>
</tr>
<tr>
<td>20</td>
<td>Medial Frontal Gyrus</td>
<td>47</td>
<td>3.69</td>
<td>-10</td>
<td>-8</td>
<td>64</td>
<td>0.12</td>
<td>1.14</td>
<td>0.79</td>
<td>0.21</td>
<td>0.05</td>
</tr>
<tr>
<td>21</td>
<td>Precentral Gyrus</td>
<td>32</td>
<td>3.61</td>
<td>34</td>
<td>-16</td>
<td>46</td>
<td>1.82</td>
<td>0.03</td>
<td>1.04</td>
<td>2.21</td>
<td>0.88</td>
</tr>
<tr>
<td>22</td>
<td>Putamen</td>
<td>23</td>
<td>3.62</td>
<td>-22</td>
<td>10</td>
<td>-8</td>
<td>4.73</td>
<td>1.23</td>
<td>0.77</td>
<td>8.1</td>
<td>2.24</td>
</tr>
<tr>
<td>23</td>
<td>Orbital Frontal Cortex</td>
<td>15</td>
<td>3.59</td>
<td>32</td>
<td>44</td>
<td>-22</td>
<td>0.16</td>
<td>0.52</td>
<td>0.31</td>
<td>0.17</td>
<td>0.04</td>
</tr>
<tr>
<td>Cluster</td>
<td>Structure</td>
<td>x</td>
<td>y</td>
<td>z</td>
<td>F-statistic</td>
<td>p-values</td>
<td>Adjusted p</td>
<td>z-statistic</td>
<td>p-values</td>
<td></td>
<td></td>
</tr>
<tr>
<td>---------</td>
<td>-----------</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>-------------</td>
<td>----------</td>
<td>------------</td>
<td>-------------</td>
<td>----------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>post_01</td>
<td>Precuneus</td>
<td>3763</td>
<td>5.32</td>
<td>24</td>
<td>70</td>
<td>0.4</td>
<td>0.17</td>
<td>3.63</td>
<td>0.93</td>
<td></td>
<td></td>
</tr>
<tr>
<td>post_02</td>
<td>Middle Occipital</td>
<td>3070</td>
<td>5.36</td>
<td>34</td>
<td>-84</td>
<td>2</td>
<td>0.21</td>
<td>0.47</td>
<td>0.42</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>post_03</td>
<td>Inferior Occipital</td>
<td>2570</td>
<td>5.72</td>
<td>-30</td>
<td>-94</td>
<td>-2</td>
<td>1.88</td>
<td>1.04</td>
<td>0.26</td>
<td>2.29</td>
<td>0.45</td>
</tr>
<tr>
<td>post_04</td>
<td>Cingulate Gyrus</td>
<td>211</td>
<td>4.9</td>
<td>-12</td>
<td>-26</td>
<td>40</td>
<td>4.85</td>
<td>0</td>
<td>0.22</td>
<td>7.45</td>
<td>0.81</td>
</tr>
<tr>
<td>post_05</td>
<td>Cingulate Gyrus</td>
<td>141</td>
<td>4.79</td>
<td>14</td>
<td>-24</td>
<td>42</td>
<td>1.18</td>
<td>0.06</td>
<td>0.46</td>
<td>0.93</td>
<td>0.82</td>
</tr>
<tr>
<td>post_06</td>
<td>Postcentral Gyrus</td>
<td>25</td>
<td>4.25</td>
<td>-16</td>
<td>-32</td>
<td>64</td>
<td>0.41</td>
<td>0.41</td>
<td>0.47</td>
<td>0.19</td>
<td>0.49</td>
</tr>
</tbody>
</table>

Note: Clusters 1 and 2 (not shown) were subdivided into posterior clusters 1-6 by raising the z-statistic threshold of the cluster corrected image. z-statistic values of thresholded (z > 3.3 for clusters 3-24, z > 4 for posterior clusters 1-6), cluster corrected image at x,y,z. Coordinates in MNI space. F-statistic and p-values for parameters used in step-wise regressions as part of ROI analysis. Emboldened values indicate statistics that reached an adjusted p < 0.0017.
Figure 7: vmPFC showed age- and risk-related activation, while bilateral insula showed only age-related increases in activation during decision-making. Decision-related activation for the vmPFC ROI (b; yellow) was greater in adults and adolescents than it was in children (a), demonstrating that the age-related linear trend found here was due primarily to the difference between children and adults.

Whole brain analysis revealed activation in children that correlated with risk aversion in ACC and vmPFC (b; green). The vmPFC cluster from this whole brain analysis overlapped with the vmPFC ROI (b; red). Regression slopes for each age group shown in (c) demonstrate the unique relationship between BOLD signal change in vmPFC and risk aversion scores found for children. Age-related linear trends of activation were also found in right and left insula ROIs (e). In contrast to vmPFC, these regions showed a more robust positive linear relationship to age (d, f).

Coordinates in MNI space; circles – children; diamonds – adolescents; squares – adults; * - p < 0.05; ° - p < 0.1. Note: Though some of the children’s data appear to be outliers, all of the children’s data points in Fig. 7 are less than 2.5 standard deviations from the group mean of the panel, and only two exceed 2 standard deviations.

In tests of each ROI between age groups, our results fell into two classes: differences between children and adolescents/adults, and linear changes across age groups for risky > sure. We found no risk-related ROI that showed evidence of peak activation during adolescence. Significant linear trends were followed by t-tests, with correction in degrees of
freedom for unequal variance when appropriate, between each group showing group
differences in the vmPFC (Fig. 7a & 7b), cuneus, and middle temporal gyrus between
children and adults, and children and adolescents (all \( p < 0.001 \)), but not adults and
adolescents (all \( p > 0.45 \)). Thus, although a significant linear trend of age was found in
vmPFC in the whole-brain analysis, this effect appears to be largely due to the difference in
BOLD signal change between children and adolescents with little or no change from
adolescence to adulthood.

Linear effects of age were also found in right and left insula (Fig. 7d, 7e, & 7f). In the
right insula, t-tests revealed significant differences between children and adults \( (p = 0.009) \)
and between adolescents and adults \( (p = 0.023) \), while differences between children and
adolescents were marginal \( (p = 0.082) \). In the left insula, differences between children and
adults were also significant \( (p = 0.009) \), whereas differences between children and
adolescents \( (p = 0.057) \) and between adolescents and adults \( (p = 0.119) \) approached
significance demonstrating a trend similar to the right insula. A separate cluster within the
left posterior insula showed a significant interaction between risk aversion and age group:
activation in this ROI during the decision period for Risky Bet compared to Sure Bet trials
was negatively correlated with risk aversion in children (Fig. 8), but not in adolescents or
adults. Overall, we found strong evidence of child-specific risk-activation deficits in the
vmPFC, and linear developmental effects across age groups in the insula.
Figure 8: Posterior insula shows age group by risk aversion interaction. An interaction between age group and risk aversion showed that while activation during decision making in adolescents and adults did not correlate in any way with risk aversion, in children, activation in posterior insula decreased with greater risk aversion. Coordinates in MNI space.

More adult-like risk aversion in children correlates with greater vmPFC activation during risky decision-making

Developmental changes in the neural bases supporting risk and decision-related processing may or may not contribute to specific differences in behavior across age groups. To clarify the links between brain activations and risk aversive choices, we regressed our index of risk aversion against whole brain data within each age group. We found different networks of brain regions to be associated with risk preferences in each group. In children, risk aversion was correlated with activation in ACC, vmPFC (Fig. 7c), caudate and OFC during the decision period for Risky Bets compared to Sure Bets (Fig. 9), while in adolescents risk aversion was correlated with activation in medial frontal gyrus and central cingulate gyrus. In contrast to previous studies (Huettel, et al., 2006), we failed to find neural activation during the decision period in adults that was correlated with levels of risk aversion.
Figure 9: Whole brain analyses revealed that risk aversion was correlated with activation in caudate nucleus and OFC for children (shown here) but not for adults or adolescents, during decision-making. (a) activation maps and (b) scatterplots showing the relationship between BOLD signal and risk aversion. Coordinates in MNI space; Caud – caudate nucleus; OFC – orbitofrontal cortex.

Activation associated with outcome evaluation

The activation in response to winning, or positive outcomes (the greater of the possible gamble outcomes) and losing or negative outcomes (the lesser of the possible gamble outcomes) were analyzed with respect to the combined ISI and ITI baseline. Positive outcomes evoked a similar pattern of activation for adolescents and adults across a number of regions, including superior temporal gyrus (STG), ACC, dIPFC, lateral OFC, insula, striatum, inferior parietal cortex, inferior frontal gyrus (IFG), and fusiform gyrus (Fig. 10a; Table 5). In children, positive outcomes elicited activation overlapping with that of adolescents and adults in STG, insula, striatum, inferior parietal, and IFG. With age, increasing activation to positive outcomes was found in dIPFC, inferior parietal, and inferior occipital regions.

Overlapping activation to unfavorable or losing outcomes was also similar in adolescents and adults, and was found in insula, STG, and ACC (Fig. 10b; Table 6). Regions of activation that overlapped for all three age groups were restricted to STG and insula. Linear
trends of age in activation to losing outcomes were found in STG, occipital cortex, and precuneus.

Figure 10: Winning and losing outcomes elicit similar patterns of activation in children, adolescents, and adults. (a) Activations to winning outcomes in all age groups were found in superior temporal gyrus, insula, striatum, inferior frontal gyrus, and inferior parietal regions. Adults and adolescents showed additional activation in dIPFC, lateral OFC, and ACC. (b) Relative losses elicited activation for all age groups in superior temporal gyrus and insula, while adults and adolescents also showed activation in anterior cingulate. Coordinates in MNI space; z > 3.0.
<table>
<thead>
<tr>
<th>group</th>
<th>number</th>
<th>region</th>
<th>size (vox)</th>
<th>z_val&lt;sup&gt;a&lt;/sup&gt;</th>
<th>x&lt;sup&gt;b&lt;/sup&gt;</th>
<th>y&lt;sup&gt;b&lt;/sup&gt;</th>
<th>z&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Children</td>
<td>1</td>
<td>Temporal Lobe</td>
<td>911</td>
<td>4.31</td>
<td>50</td>
<td>-40</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Inferior Parietal Lobule</td>
<td>653</td>
<td>4.22</td>
<td>40</td>
<td>-48</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Insula</td>
<td>519</td>
<td>3.72</td>
<td>42</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Middle Frontal Gyrus</td>
<td>392</td>
<td>3.81</td>
<td>34</td>
<td>56</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Middle Temporal Gyrus</td>
<td>330</td>
<td>3.88</td>
<td>-64</td>
<td>-32</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Middle Frontal Gyrus</td>
<td>180</td>
<td>3.82</td>
<td>48</td>
<td>18</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>Superior Temporal Gyrus</td>
<td>71</td>
<td>3.46</td>
<td>62</td>
<td>10</td>
<td>-2</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Superior Temporal Gyrus</td>
<td>33</td>
<td>3.44</td>
<td>-66</td>
<td>-38</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>Superior Temporal Gyrus</td>
<td>26</td>
<td>3.62</td>
<td>-58</td>
<td>-44</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>Superior Frontal Gyrus</td>
<td>21</td>
<td>3.32</td>
<td>40</td>
<td>52</td>
<td>26</td>
</tr>
<tr>
<td>Adolescents</td>
<td>1</td>
<td>Inferior Parietal Lobule</td>
<td>1302</td>
<td>4.63</td>
<td>44</td>
<td>-36</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Middle Occipital Gyrus</td>
<td>1177</td>
<td>4.87</td>
<td>40</td>
<td>-74</td>
<td>-8</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Declive</td>
<td>980</td>
<td>4.6</td>
<td>-34</td>
<td>-66</td>
<td>-18</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Middle Temporal Gyrus</td>
<td>944</td>
<td>4.37</td>
<td>52</td>
<td>-30</td>
<td>-4</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Putamen</td>
<td>923</td>
<td>4.23</td>
<td>26</td>
<td>14</td>
<td>-2</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Putamen</td>
<td>426</td>
<td>4.28</td>
<td>-28</td>
<td>14</td>
<td>-8</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>Superior Frontal Gyrus</td>
<td>222</td>
<td>3.48</td>
<td>32</td>
<td>46</td>
<td>-4</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Cingulate Gyrus</td>
<td>204</td>
<td>4.19</td>
<td>4</td>
<td>28</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>Sub-Gyral</td>
<td>47</td>
<td>3.45</td>
<td>32</td>
<td>12</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>Inferior Frontal Gyrus</td>
<td>37</td>
<td>3.52</td>
<td>50</td>
<td>12</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>Middle Frontal Gyrus</td>
<td>31</td>
<td>3.22</td>
<td>44</td>
<td>44</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>Medial Frontal Gyrus</td>
<td>28</td>
<td>3.34</td>
<td>-10</td>
<td>40</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>Middle Frontal Gyrus</td>
<td>25</td>
<td>3.33</td>
<td>38</td>
<td>52</td>
<td>-20</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>Medial Frontal Gyrus</td>
<td>22</td>
<td>3.26</td>
<td>12</td>
<td>48</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>Cingulate Gyrus</td>
<td>20</td>
<td>3.21</td>
<td>10</td>
<td>-26</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>Sub-Gyral</td>
<td>19</td>
<td>3.24</td>
<td>28</td>
<td>-36</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>Inferior Frontal Gyrus</td>
<td>16</td>
<td>3.28</td>
<td>40</td>
<td>30</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>Superior Frontal Gyrus</td>
<td>10</td>
<td>3.1</td>
<td>-6</td>
<td>24</td>
<td>54</td>
</tr>
<tr>
<td>Adults</td>
<td>1</td>
<td>Superior Temporal Gyrus</td>
<td>8808</td>
<td>5.49</td>
<td>48</td>
<td>-32</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>---</td>
<td>------</td>
<td>-------</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Middle Frontal Gyrus</td>
<td>4169</td>
<td>5.19</td>
<td>42</td>
<td>36</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Inferior Parietal Lobule</td>
<td>2065</td>
<td>5.36</td>
<td>52</td>
<td>-42</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Cingulate Gyrus</td>
<td>1777</td>
<td>4.89</td>
<td>4</td>
<td>34</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Inferior Occipital Gyrus</td>
<td>1616</td>
<td>5.79</td>
<td>32</td>
<td>-84</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Inferior Occipital Gyrus</td>
<td>1593</td>
<td>5.13</td>
<td>-28</td>
<td>-90</td>
<td>-2</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Superior Temporal Gyrus</td>
<td>851</td>
<td>4.81</td>
<td>-66</td>
<td>-42</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Inferior Parietal Lobule</td>
<td>637</td>
<td>4.86</td>
<td>-42</td>
<td>-50</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Middle Frontal Gyrus</td>
<td>506</td>
<td>4.24</td>
<td>-42</td>
<td>14</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Precuneus</td>
<td>171</td>
<td>4.75</td>
<td>8</td>
<td>-66</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>Cingulate Gyrus</td>
<td>156</td>
<td>3.72</td>
<td>-4</td>
<td>-22</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Declive</td>
<td>135</td>
<td>3.76</td>
<td>0</td>
<td>-68</td>
<td>-12</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>Superior Temporal Gyrus</td>
<td>100</td>
<td>3.94</td>
<td>-54</td>
<td>-14</td>
<td>-2</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>Sub-Gyral (white matter)</td>
<td>83</td>
<td>3.83</td>
<td>-24</td>
<td>-38</td>
<td>38</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>Putamen</td>
<td>30</td>
<td>3.42</td>
<td>-26</td>
<td>-22</td>
<td>-2</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>Superior Frontal Gyrus</td>
<td>24</td>
<td>3.47</td>
<td>20</td>
<td>26</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>Inferior Temporal Gyrus</td>
<td>13</td>
<td>3.93</td>
<td>58</td>
<td>-56</td>
<td>-16</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>Sub-Gyral</td>
<td>10</td>
<td>3.27</td>
<td>-24</td>
<td>-22</td>
<td>30</td>
<td></td>
</tr>
</tbody>
</table>

*Z-statistic values of thresholded (z > 2.3), cluster corrected image at x,y,z. Coordinates in MNI space.*


<table>
<thead>
<tr>
<th>group</th>
<th>number</th>
<th>region</th>
<th>size (vox)</th>
<th>z_val</th>
<th>x</th>
<th>y</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Children</td>
<td>1</td>
<td>Superior Temporal Gyrus</td>
<td>1086</td>
<td>4.04</td>
<td>56</td>
<td>-40</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Middle Temporal Gyrus</td>
<td>627</td>
<td>3.81</td>
<td>-48</td>
<td>-30</td>
<td>-6</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Putamen</td>
<td>562</td>
<td>4.24</td>
<td>30</td>
<td>14</td>
<td>-8</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Inferior Parietal Lobule</td>
<td>244</td>
<td>3.96</td>
<td>42</td>
<td>-48</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Middle Temporal Gyrus</td>
<td>46</td>
<td>3.98</td>
<td>62</td>
<td>-48</td>
<td>-6</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Inferior Parietal Lobule</td>
<td>38</td>
<td>3.27</td>
<td>58</td>
<td>-42</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>Fusiform Gyrus</td>
<td>24</td>
<td>3.27</td>
<td>-38</td>
<td>-54</td>
<td>-16</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Insula</td>
<td>20</td>
<td>3.52</td>
<td>42</td>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>Inferior Frontal Gyrus</td>
<td>14</td>
<td>3.37</td>
<td>52</td>
<td>24</td>
<td>6</td>
</tr>
<tr>
<td>Adolescents</td>
<td>1</td>
<td>Insula</td>
<td>1500</td>
<td>4.76</td>
<td>42</td>
<td>26</td>
<td>-4</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Insula</td>
<td>1239</td>
<td>5.06</td>
<td>-40</td>
<td>18</td>
<td>-6</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Superior Temporal Gyrus</td>
<td>1023</td>
<td>4.57</td>
<td>48</td>
<td>-32</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Cingulate Gyrus</td>
<td>429</td>
<td>3.81</td>
<td>-4</td>
<td>34</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Medial Frontal Gyrus</td>
<td>108</td>
<td>3.39</td>
<td>0</td>
<td>58</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Middle Temporal Gyrus</td>
<td>106</td>
<td>4.1</td>
<td>46</td>
<td>4</td>
<td>-36</td>
</tr>
<tr>
<td>Adults</td>
<td>1</td>
<td>Insula</td>
<td>15915</td>
<td>5.92</td>
<td>32</td>
<td>12</td>
<td>-12</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Inferior Parietal Lobule</td>
<td>1274</td>
<td>5.13</td>
<td>44</td>
<td>-48</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Superior Temporal Gyrus</td>
<td>945</td>
<td>4.24</td>
<td>-56</td>
<td>-14</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Lingual Gyrus</td>
<td>644</td>
<td>4.36</td>
<td>32</td>
<td>-80</td>
<td>-8</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Cingulate Gyrus</td>
<td>530</td>
<td>4.78</td>
<td>2</td>
<td>-22</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Fusiform Gyrus</td>
<td>217</td>
<td>3.69</td>
<td>-42</td>
<td>-72</td>
<td>-16</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>Supramarginal Gyrus</td>
<td>181</td>
<td>4.43</td>
<td>-60</td>
<td>-52</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Superior Frontal Gyrus</td>
<td>122</td>
<td>3.87</td>
<td>12</td>
<td>30</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>Cuneus</td>
<td>72</td>
<td>3.65</td>
<td>4</td>
<td>-100</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>Sub-Gyral</td>
<td>62</td>
<td>3.58</td>
<td>-22</td>
<td>-40</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>Cuneus</td>
<td>48</td>
<td>3.53</td>
<td>-26</td>
<td>-20</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>Inferior Occipital Gyrus</td>
<td>33</td>
<td>3.21</td>
<td>-22</td>
<td>-98</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>Lingual Gyrus</td>
<td>24</td>
<td>3.83</td>
<td>-24</td>
<td>-92</td>
<td>-4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----</td>
<td>----</td>
<td>----</td>
<td>----</td>
<td>----</td>
<td>----</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>Middle Frontal Gyrus</td>
<td>13</td>
<td>3.34</td>
<td>-24</td>
<td>44</td>
<td>-18</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)z-statistic values of thresholded (z \(> 2.3\)), cluster corrected image at x,y,z. \(^b\)Coordinates in MNI space.
**Discussion**

Our data suggest that the development of risk aversion co-occurs with the recruitment of a network of brain regions that support decision-making under risk, including the integration of prior outcomes into current decisions. Within regions of the brain associated with decision-making under risk across age groups, we found that the insula showed robust linear patterns of activation with age. Furthermore, the vmPFC exhibited a unique relationship with risk aversion. While vmPFC activations were not perfectly overlapping, there was a region of vmPFC that was active in adolescents and adults that overlapped with the activation correlated with risk aversion in children, interpreted as vmPFC activation in children who made more adult-like risk-averse choices.

A novel finding was that young children engage structures involved with learning, affect, and memory (e.g. hippocampus, amygdala, and vmPFC) to a lesser extent than do both adults and adolescents when making decisions under risk. The hippocampus is known to be active during informed decision-making and is important for learning cue-target (Amso, Davidson, Johnson, Glover, & Casey, 2005; Ernst et al., 2002). Projections from HC to the midbrain signal the detection of new information, while midbrain dopamine neurons reciprocally modulate HC activity, thought to signal events of biological and motivational salience and giving weight to preserving important memories ((Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Lisman & Grace, 2005). Amygdala activation is often associated with the processing of emotional content but it is also involved with learning and representing stimulus value (Cardinal, Parkinson, Hall, & Everitt, 2002; Guitart-Masip, Talmi, & Dolan, 2010). In conjunction with hippocampus and amygdala, vmPFC activation signals the successful learning of abstract cue-outcome relations.
(Hampton, et al., 2007; Kumaran, Summerfield, Hassabis, & Maguire, 2009) as well as the subjective value of chosen options (Hare, Camerer, Knoepfle, & Rangel, 2010; Kable & Glimcher, 2007; Smith et al., 2010). Thus, our data could suggest that information from prior decisions and outcomes may not be as readily incorporated into children’s decision-making processes as they are in adults, with the caution that this suggestion relies on reverse inference (Poldrack, 2006). However, this hypothesis is supported by behavioral data that demonstrate an improvement in the slow learning rates of young children in gambling tasks by reducing memory load or by providing reminders of prior outcomes (Brainerd, 1981; Garon & Moore, 2004, 2007; Kerr & Zelazo, 2004).

We also found a robust correlation between age and insula activation during the decision period for Risky Bets compared to Sure Bets that can be interpreted in several ways. Prior studies have found anterior insula activation associated with classical conditioning of aversive stimuli and correlated with measures of harm avoidance (Büchel, Morris, Dolan, & Friston, 1998; Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003). Thus, one interpretation of these data is that increasing insula activation with age merely tracks the development of a region supporting loss aversion, if we assume that small gains are considered losses compared to the larger alternative outcomes (Tversky & Kahneman, 1991) and that losses are aversive. A recent meta-analysis has identified the anterior insula as particularly important for the representation of risk and the influence of emotion on risk processing (Mohr, Biele, & Heekeren, 2010). In this case, we might consider age-related activation of the insula to reflect a maturation in the processing or perception of risk, which in our case assumes a model adopting coefficient of variation as a risk index (Weber, et al., 2004). It has been suggested that the anatomical position of the insula is ideal for combining
affective and cognitive information during decision-making because of its connectivity to surrounding structures including the amygdala and nucleus accumbens (Preuschoff, et al., 2008). Thus, another more general interpretation of our data could be that the age-related increase in insula activation, as well as other regions, reflects the maturing connectivity of a decision-making network. These alternative interpretations are not necessarily exclusive. The importance of this region in risky decision-making and development is clearly an avenue for future research.

The association we have found between brain regions with age-related increases in activation and the development of risk aversion is supported by other lesion and fMRI studies. Amygdala and insula patients show an increased propensity to gamble, especially under gain conditions similar to the ones in our task (L Clark et al., 2008; Talmi, et al., 2010; Weller, Levin, Shiv, & Bechara, 2007). OFC and ACC activation during decision-making has been associated with greater risk aversion in adults compared to adolescents (Eshel, et al., 2007; Galvan, et al., 2006). Activation in these regions in our study was found to increase with age, as was risk aversion. Interestingly, bilateral amygdala damage has been shown to alter neural responses in the ACC, vmPFC, OFC, and insula (Hampton, et al., 2007), which adds further support to the notion that these regions develop as an interconnected network supporting decision-making.

In contrast to (Kuhnen & Knutson, 2005), we found that increased activation in decision value regions like the vmPFC and striatum in children was associated with a decrease in preference for the risky option rather than an increase, while activation in these same regions increased with age. Prior studies have found enhanced sensitivity of striatal reward processing regions in adolescents, who are as a group characterized by riskier real-
world behavior compared to adults or children (Casey, Jones, & Hare, 2008). Such findings offer the hypothesis that differences in striatal reward processing contribute to differences in risk preferences (Arnett, 1992; Casey, Getz, et al., 2008; Galvan, et al., 2006; van Leijenhorst, Moor, et al., 2010; van Leijenhorst, Zanolie, et al., 2010). We found little evidence to support this idea. Although an inverted U-shaped pattern of activation was identified in a small volume uncorrected cluster in the striatum, this region was more dorsal and lateral to the proposed reward sensitive region nucleus accumbens. Nevertheless, it is possible for a region to show fits to linear and curvilinear trends, but it will remain a subjective issue how to interpret data of this sort. We interpret the current data to suggest that there is greater evidence for a linear change in activation and maturity in decision-making regions between 5 years of age and early adulthood than there is for a purely quadratic one.

It is also important to note that reports of curvilinear activation in the striatum have been in response to rewards, rather than to reward cues or during decision-making (Galvan, et al., 2006; van Leijenhorst, Moor, et al., 2010). During decision-making in a gambling task, Eshel et al. (2007) report increasing activation with age in OFC and ACC, and similar to the current findings, also report a negative correlation between risk-taking and activation in OFC for adolescents. In a contrast between high risk and low risk trials during decision-making, however, decreasing activation with age was found in ACC, while an inverted U-shaped pattern was found in medial OFC (van Leijenhorst, Moor, et al., 2010). Using an interesting driving simulation paradigm, adolescents were found to show decreased activation in striatum and OFC compared to adults, those these decreases were particular to the condition in which peers were present and observing (Chein, et al., 2010). Similar to the
patterns of activation in the current study, Bjork and colleagues (Bjork, et al., 2004; Bjork, Smith, Chen, & Hommer, 2010) have found that adults exhibit greater activation in the striatum, insula, and amygdala, than do adolescents in response to reward cues.

There are at least three critical aspects of design that render direct comparisons between studies difficult: the part of the decision-making process being analyzed (e.g. decision-making, cue/anticipation, and outcome), the age groups included and excluded, and task contrasts and/or baselines being used (Galvan, 2010). Our study falls prey to each of these complications, perhaps most clearly when trying to compare our findings with a sample of children in the 5- to 8-year age range to findings from studies that sample children in the 7- to 11-year age range (M Ernst, et al., 2005; Galvan, et al., 2006; van Leijenhorst, et al., 2006; van Leijenhorst, Moor, et al., 2010). Adolescents in our study were not found to show enhanced striatal activation, but were not found to be especially risk-taking either. Our findings indicate that increased activation in reward processing regions during decision-making may not necessarily predict greater engagement in risky behavior, but may reflect partial maturation of decision-making circuitry.

Posterior parietal activation, which has been previously found to associate with risk preference, action selection, reward value, and probability of reward, was also found to increase linearly with age during the decision period for Risky Bets compared to Sure Bets (Boorman, Behrens, Woolrich, & Rushworth, 2009; S. Huettel, et al., 2006; M. Platt & P. Glimcher, 1999; Yang & Shadlen, 2007). This region is also well known for its role in numerical processing and attention (Boorman, et al., 2009; J. Cantlon, et al., 2006; S. Huettel, et al., 2006; Piazza, et al., 2004). Although we attempted to isolate the effects of risk processing from numerical computation, it is possible that at least some of the residual PPC
activation we observed was due to the addition of a third numerical value to be compared in Risky Bet trials compared to just the two involved with Sure Bet trials. Thus, it remains difficult to assess how much of the activation found in PPC was due to numerical processing and how much was due to risk.

Analysis of behavioral data showed relatively less risk-taking among older participants than among children. This difference raises questions regarding children's incentivization or their understanding of the task. Equating incentives across ages is often a problem in developmental research. However, our use of toys for children and monetary value for older participants as incentives returned results keeping with other studies that used similar, dissimilar, or no economic incentives between groups (Harbaugh, et al., 2002; Levin & Hart, 2003; Levin, Weller, et al., 2007; Paulsen, et al., 2011; Rakow & Rahim, 2010; Weller, et al., 2010). We also found that behavior across groups was modulated by risk level and EV. Together, this suggests that children both were properly incentivized and that they understood the task.

Unexpectedly, adolescent and adult participants on average selected gamble options on slightly more than 50% of trials, demonstrating risk-seeking behavior instead of the typical risk-averse behavior often associated with adult populations. It is possible that participants exhibited risk-seeking behavior because the outcomes associated with the gambles in our task were small, and therefore were not perceived as especially risky (Markowitz, 1952). However, the increase in risk taking for larger magnitude over smaller magnitude gambles is inconsistent with this suggestion. Other studies have found that risk-preference can be modulated by the probabilities and variance of outcomes (Paulsen, et al., 2011; Weber & Chapman, 2005). Thus, it is possible that the risk-seeking behavior we
observed in adolescents and adults was due to the particular parameters implemented in this version of the task.

There are limitations associated with the current task design. First, to dissociate decision-making and response selection, we presented choice options for four seconds before providing response cues. While this procedure was used to remove an important potential confound, it limited our ability to model the decision-making period as a function of response time, and may have increased the noise in our sample if there was a lot of variability in the time at which decisions were made. In this case, using a four second decision-making epoch in our model would be overestimating the expected duration of brain activation, reducing our ability to detect more rapidly occurring decision processes, or in identifying similarities in brain activation across age groups that have dissimilar time courses. Another potential limitation may have been our choice of a contrast condition. We chose to use the Sure Bet condition for our contrasts in order to control for the numerical comparison component of our economic decision-making task. While our Risk trials involved three numerical components, Sure Bet trials contained only two. Thus, we were unable to fully control for the effects of numerical comparison. Another potential limitation in our choice of the Sure Bet condition as a contrast is that effects other than numerical comparisons may also have been reduced. For example, the expectation of reward is clear with both a Sure Bet and choosing the safe option (Bjork, et al., 2004; Bjork, et al., 2010), and this expectation could potentially minimize differences in BOLD activation between Sure Bet and Risk conditions in the adult and adolescent groups, as they chose the Safe option more often in Risk trials than children. Finally, while the lower quantity gamble outcomes may have appeared as losses relative to the sure bet and larger gamble outcomes,
the value manipulations made it such that choosing a gamble would probabilistically be rewarded 75% of the time. This makes it difficult to directly compare the activation in response to outcomes in our task to studies in which losses are actually incurred.

In summary, we found that a shared network of brain regions was recruited when young children (5- to 8-years-old), adolescents (15- to 16-years-old), and adults (18- to 35-years-old) made decisions under risk. A number of brain regions previously shown to be involved with decision-making under risk showed increasing activation with age, including areas associated with contextual memory. In addition, regions of the brain associated with value determination such as the vmPFC were more active in adults and adolescents than children. Thus, our data provide more support for the hypothesis that the development of mature risk aversion occurs through the gradual development of the neural network that supports decision-making under risk, rather than an imbalance between reward-related and executive control-related regions. Further, children with a relatively more risk-averse profile and thus a more adult-like pattern of responding also showed an increased vmPFC response, suggesting that maturing risky decision making strategies may reflect relative maturation of decision value systems.
Chapter 4 – Reinforcement Learning, Probability, and Optimism

Normative adult risk aversion takes decades to mature. When presented with a choice between a gamble and a sure bet with the same expected value (EV), children are more likely to choose the gamble than the sure bet, with risk aversion emerging gradually between early childhood and adulthood (Crone & van der Molen, 2004; Harbaugh, et al., 2002; Levin, Hart, et al., 2007; Rakow & Rahim, 2010; Weller, et al., 2010). Previous work has shown that age differences in decision-making behavior depend on factors such as risk and magnitude (Paulsen, et al., 2011; van Leijenhorst, Moor, et al., 2010). However, little is known about the cognitive changes taking place between childhood and adulthood that may lead to such differences in behavior.

A handful of studies have examined the developmental time course of normative risk aversion (see for review Boyer, 2006). Harbaugh and colleagues (2002) manipulated probability and win magnitude to equate EV between gamble and sure bet options. They found that while children 9-13 years of age accepted gambles more often than would be expected by chance, participants 14-20 years of age did not. Weller and colleagues (2010) similarly presented participants with choices between sure bets and gambles and found that participants 18-22 years old exhibited similar rates of gambling to participants 25-44 years of age, while children 5-11 years of age were more likely to prefer gambles than older participants. Though there were no overall effects of age, van Leijenhorst et al. (2010; c.f. van Leijenhorst, et al., 2008) found that risk-seeking decreased with age for low monetary values. Finally, Paulsen et al. (2011) used a non-symbolic task and found that risk-taking declined with age, but that age differences were greatest for the highest risk gambles.
One mechanism hypothesized to be responsible for increased rates of gambling is the ability to learn from feedback, and in particular learning from negative feedback (Frank, et al., 2007; Maia & Frank, 2011). Intuitively this makes sense; if you don’t learn that choosing to gamble may result in the inferior outcome then it may appear that there is nothing to lose. Indirect support for this hypothesis comes from findings that Parkinson’s Disease (PD) patients receiving dopamine therapy fare poorly in tasks designed to assess learning from negative feedback (Bódi et al., 2009; Frank, et al., 2007; Frank, Seeberger, & O’Reilly, 2004), and that acquired pathological gambling has a prevalence rate of between 6-8% among PD patients who undergo dopamine therapy (Avanzi et al., 2006; Grosset et al., 2006), compared to approximately 1.6% of the normal adult population (Shaffer, Hall, & Vander Bilt, 1999). Additionally, computational modeling approaches suggest that the ability to learn from positive and negative reinforcement is an evolutionary basis for phenotypic risk aversion (Niv, Joel, Meilijson, & Ruppin, 2002).

Similar to risk aversion, feedback learning matures with age into adolescence and young adulthood. Performance on modified versions of the Iowa Gambling Task (IGT), which was designed to assess the incorporation of feedback into decision making (A. Bechara, et al., 1994), improves with age into young adulthood (Cauffman, et al., 2010; Crone & van der Molen, 2004; Hooper, et al., 2004). Children appear to be use the frequency and quantity of gains in their choice behavior before they begin to incorporate the frequency and quantity of losses (Huizenga, et al., 2007) suggesting an earlier developing ability to process positive feedback than negative feedback. For example, in a probabilistic rule identification task, 8-9 year-old children learned more from positive than negative feedback, performing disproportionately worse after negative feedback relative to positive
feedback compared to young adolescents (11-13 years) and young adults (Van Duijvenvoorde, et al., 2008).

An alternative hypothesis for why children are less risk-averse is that they may overestimate their chances of winning, or represent the probabilities of gamble outcomes differently than adults. Young children, and even infants, have shown behavior consistent with an understanding of probability (Acredolo, et al., 1989; Schlottmann, 2001; Schlottmann & Anderson, 1994; Xu & Denison, 2009; Xu & Garcia, 2008). In one decision-making study, probabilistic discounting was similar between 6 and 17 years of age (Scheres, et al., 2006). In another study, children adjusted their behavior in an adult-like fashion according to probabilistic outcomes (van Leijenhorst, et al., 2008). There is some evidence, however, that children’s subjective probabilities of success versus failure in gambles may differ from adults. When gambling for gains, it isn’t until about 20 years of age that subjective probabilities approximate the objective probabilities of a gamble, with younger participants underweighting low probabilities and overweighting high probabilities of winning (Harbaugh, et al., 2002). Similarly, Weller et al. (2010) found that sensitivity to combined probability and magnitude information, i.e. expected value (EV), increased from 5 years of age into adulthood.

Here we explore the relationship between reinforcement learning (RL) and risky decision making over development. In two experiments we use both a RL and a risky decision task with a cross-sectional developmental design. In Experiment 1, the training phase of the RL paradigm provided a criterion based learning experience for probability cues that were subsequently used in the risk task, and the testing phase provided measures of feedback learning. Subjects first learned to associate different animal pictures with
reward at different probabilities. Subjects then made choices between a sure bet and a gamble in the presence of the animal pictures. On one-fifth of trials, EV was equated between choice options, while the other four-fifths of trials were split evenly between trials where the gamble had a greater EV or a lesser EV compared to the safe bet. The coefficient of variation and magnitude of gamble options were orthogonally varied with the three EV conditions. Specifically we asked the following questions. Are there age differences in gambling behavior when the probability of success versus failure on gamble outcomes has to be learned from experience? In the absence of probability information, i.e. under conditions of relative ambiguity, do measures of learning about positive and/or negative feedback probabilities predict the rate of choosing a gamble over a sure bet? Finally, can we provide an estimate of the age at which risk-aversion emerges from risk-seeking behavior?

**Experiment 1**

**Method**

**Participants**

Forty-seven participants ranging in age from 5 years 1 month to 25 years 10 months (28 female) were included in the final sample. Data from 9 other participants were excluded from analyses: 5 failed to complete the RL task, three were disrupted during testing, and one failed to perform above a 20% accuracy criterion for positive negative FB learning. Duke IRB-approved informed consent was collected from adult participants and parents/legal guardians of minor participants; written assent was obtained from minor participants. All participants were compensated $10 per hour for their time and additionally given a performance based incentive of up to an additional $15 for participants
older than 10-years-old and either $15 or a toy with a price value of up to $10 for children younger than 10-years-old.

**Reinforcement Learning task**

The Reinforcement Learning task was modeled after Frank, et al., (2004). Animal pictures were used to indicate the probability of outcomes to help make the task more engaging for younger participants. Six animal pictures were randomly selected among nine images collected from the website “http://www.mod-tots.com/site/products/paintings/animals/”. The six animal images were randomly placed into 3 stimulus pairs, each with different probabilities of delivering positive (happy face) and negative (sad face) reinforcement (Fig. 11). For example, on gain trials the animal pairs were associated with the following probabilities of a successful outcome 80/20, 70/30 or 60/40. Thus when presented with a bear/monkey pair if the participant chose the bear there was an 80% probability of reward whereas when she chose the monkey there was a 20% probability of reward.
Figure 11: Reinforcement Learning and Risk Tasks (A) Reinforcement Learning (RL) task stimulus pairs were presented during training with instructions to “pick the animal that gives happy faces more often.” One animal out of each pair was more likely to return a happy face than a sad face; probability pairs were 80/20, 70/30, and 60/40. (B) After reaching a learning criterion or completing a maximum of 12 blocks, participants were tested with the three possible pairs of the higher reward probability images and the three pairs of the images associated with the lower reward probabilities. (C) Choices in the Risk Task were between a gamble and a sure bet. The gamble option had a mean equal to that of the sure bet option. The probability of winning in the gamble option was 0.2, 0.3, 0.5, 0.7, or 0.8, and was indicated by an animal picture learned during the RL task, or with a grey square in the case of $P_{\text{WIN}} = 0.5$.

Each stimulus pair was presented in the training phase a minimum of 20 times each and a maximum of 120 times each in blocks of 30 (3 pairs x 10 trials). Stimuli were presented randomly at right and left locations, and in pseudo-random order so that each pair was presented no more than twice in a row. Accuracy in selecting the animal that had the higher probability of delivering a happy face was checked at the end of each block for each
pair of stimuli separately. Criteria for passing the training phase was 70% accuracy for 80/20 pair, 70% accuracy for the 70/30 pair, and 60% accuracy for the 60/40 pair, or after 12 blocks, whichever came first. After training, participants were tested with pairs of the images that were more likely to give positive feedback. Thus the images associated with 80%, 70% and 60% were tested against each other to estimate each participant’s ability to learn about positive feedback (Pos FB). The images more likely to give negative feedback were similarly tested against one another to estimate each participant’s ability to learn about negative feedback (Neg FB).

**Risk task**

The risk task from Paulsen et al. (2010) was modified to include probabilistic outcomes. We presented 150 trials offering the choice between a safe option and a gamble option. The safe option in these Risk-Safe trials, if selected, returned a value of either 4 or 8 coins (different trials). On any given trial the safe option was always equal to the mean of the high payoff and low payoff values of the gamble option. There were three levels of risk for the gamble option as indexed by coefficient of variation for high and low payoffs (CV; Weber, et al., 2004): 0.71 (low risk), 1.06 (medium risk), and 1.41 (high risk). The probability of winning (P_{WIN}) the high payoff amount in Risk-Safe trials was also manipulated; four of the six animal pictures used in the Reinforcement Learning task representing 20%, 30%, 70%, and 80% happy face/winning probability appeared one per trial between the gamble values, with an even distribution of magnitude (mean value 4 or 8 coins) and CV (Fig. 11), for 120 trials. The remaining 30 Risk-Safe trials contained a blank square in place of the animal picture and on those trials there was a 50% chance of winning the high or low payoff value. The animal images that indicated probability of winning,
magnitude, and CV, were pseudorandomly ordered such that no more than two of any probability or CV could appear in succession. Three additional trials with a safe-safe choice between 2 or 6 coins, 1 or 7 coins, and 3 or 5 coins were presented as a check that each subject was motivated to obtain the largest number of coins and understood the task.

**Procedure**

Participants were seated in one of three testing rooms equipped with a computer monitor for stimulus presentation and a game control pad for behavioral response. Subjects were tested on the Reinforcement Learning (RL) task followed by the risky decision making task. In the RL task participants were informed that they would be presented with three pairs of animals, and that when chosen, each animal would either return a happy face or a sad face. They were told that on each trial their task was to choose the animal that gave the happy face more often, but that for some of the animals this would be difficult to figure out, and that they could only learn about the animals by choosing. Instructions were given verbally and presented in text on screen. Choices were made by selecting either the right or left animal picture using the right and left trigger buttons of a game control pad, and then by confirming the selection with a thumb-pressed button. After training criteria were met, or 12 blocks were completed, whichever came first, participants were informed that they would then see pairs of animals that had never been presented together, but that their task was the same: pick the animal that gives the happy face more often.

After completion of the RL task, participants were introduced to the Risk task with the instruction that their goal was to collect as many gold coins as possible, and that the number of gold coins they earned could be traded for up to an additional $15. Two Safe-Safe trials were presented first, in which participants were encouraged to select the larger of the
two values. Two Risk-Safe trials with 0.5 probability of winning were then presented, and participants were encouraged to select the gamble option so that they could see how gambles worked. As the outcomes were presented, a female voice stated “you win” followed by a sequence of slot machine sounds in one-to-one correspondence with the number of coins won. Finally, two more Risk-Safe trials were presented with a novel animal picture while informing subjects that the animals would ‘help the computer decide’ which outcome to deliver. Participants were not explicitly informed that the probabilities associated with each animal in the RL task would carry over into the risk task, nor were they told that the blank square trials had 50:50 odds.

Data Analysis

To examine the effect of Age² as a U-shaped pattern rather than an exponential one, Age was mean centered. RL task data were then analyzed for effects of Age, Age², and sex, on the number of blocks required to reach criterion, response time (RT), and accuracy scores for Pos FB and Neg FB.

To minimize effects of collinearity, Age, Neg FB, and Pos FB were normalized by subtracting the mean from individual scores and dividing by the standard deviation. First, a logistic mixed-effects regression model (Bates, Maechler, & Bolker, 2011) was used to predict the probability of choosing a gamble. Random intercepts and slopes for CV allowed for individual differences in risk preference and sensitivity to our risk manipulation, respectively. The predictors used in this regression are listed in Table 7. Second, we separately analyzed trials with a 0.5 probability of winning to examine the effects of Neg FB and Pos FB scores. All of the predictors included in the first regression analysis, except P\text{WIN} and its interactions, were entered as a first step in a backwards stepwise logistic mixed-
effects regression. Non-significant variables were removed one at a time, beginning with interactions, until Akaike information criterion (AIC) values stopped decreasing, indicating a transition between the improvement of model fit by removing predictors and the improved fit in keeping predictors, while accounting for the number of variables in the model.

**Table 7: Full Set of Predictors and Beta Weights for Exp. 1 Regression**

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\beta$</th>
<th>SE</th>
<th>z value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.135</td>
<td>0.381</td>
<td>-0.355</td>
<td>0.722</td>
</tr>
<tr>
<td>Age</td>
<td>0.168</td>
<td>0.318</td>
<td>0.527</td>
<td>0.598</td>
</tr>
<tr>
<td>Age$^2$</td>
<td>-0.327</td>
<td>0.250</td>
<td>-1.307</td>
<td>0.191</td>
</tr>
<tr>
<td>CV*</td>
<td>-0.749</td>
<td>0.315</td>
<td>-2.378</td>
<td>0.017</td>
</tr>
<tr>
<td>Magnitude***</td>
<td>0.317</td>
<td>0.076</td>
<td>4.175</td>
<td>2.97E-05</td>
</tr>
<tr>
<td>$P_{WIN}^{***}$</td>
<td>3.159</td>
<td>0.140</td>
<td>22.569</td>
<td>2.00E-16</td>
</tr>
<tr>
<td>Trial***</td>
<td>-0.009</td>
<td>0.001</td>
<td>-9.948</td>
<td>2.00E-16</td>
</tr>
<tr>
<td>Sex</td>
<td>0.024</td>
<td>0.291</td>
<td>0.082</td>
<td>0.935</td>
</tr>
<tr>
<td>Neg FB***</td>
<td>-0.938</td>
<td>0.179</td>
<td>-5.239</td>
<td>1.61E-07</td>
</tr>
<tr>
<td>Pos FB†</td>
<td>-0.301</td>
<td>0.181</td>
<td>-1.664</td>
<td>0.096</td>
</tr>
<tr>
<td>Age X Trial**</td>
<td>-0.003</td>
<td>0.001</td>
<td>-3.202</td>
<td>0.001</td>
</tr>
<tr>
<td>Age$^2$ X Trial***</td>
<td>0.002</td>
<td>0.001</td>
<td>3.343</td>
<td>0.001</td>
</tr>
<tr>
<td>Age X CV</td>
<td>-0.413</td>
<td>0.272</td>
<td>-1.521</td>
<td>0.128</td>
</tr>
<tr>
<td>Neg FB X Trial</td>
<td>-0.001</td>
<td>0.001</td>
<td>-1.436</td>
<td>0.151</td>
</tr>
<tr>
<td>Pos FB X Trial</td>
<td>0.001</td>
<td>0.001</td>
<td>0.779</td>
<td>0.436</td>
</tr>
<tr>
<td>Age$^2$ X CV</td>
<td>0.305</td>
<td>0.216</td>
<td>1.412</td>
<td>0.158</td>
</tr>
<tr>
<td>Age X Magnitude**</td>
<td>-0.201</td>
<td>0.068</td>
<td>-2.971</td>
<td>0.003</td>
</tr>
<tr>
<td>Age$^2$ X Magnitude**</td>
<td>0.153</td>
<td>0.053</td>
<td>2.878</td>
<td>0.004</td>
</tr>
<tr>
<td>Neg FB X $P_{WIN}^{***}$</td>
<td>1.660</td>
<td>0.150</td>
<td>11.076</td>
<td>2.00E-16</td>
</tr>
<tr>
<td>Pos FB X $P_{WIN}$</td>
<td>0.143</td>
<td>0.142</td>
<td>1.002</td>
<td>0.317</td>
</tr>
<tr>
<td>Age X Neg FB X $P_{WIN}^{*}$</td>
<td>0.327</td>
<td>0.148</td>
<td>2.218</td>
<td>0.027*</td>
</tr>
<tr>
<td>Age X Pos FB X $P_{WIN}$</td>
<td>-0.225</td>
<td>0.160</td>
<td>-1.408</td>
<td>0.159</td>
</tr>
</tbody>
</table>

Note: Number of blocks to criterion in RL task was also tested in this model, but was non-significant ($p > 0.62$) and increased model AIC by 1.8, and was therefore left out † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. 

95
Results

Reinforcement Learning

Both Neg FB accuracy ($p = 0.032$) and Pos FB accuracy ($p = 0.008$) on the novel test pairs significantly increased with age, and only Pos FB showed an effect of Age$^2$ ($p = 0.040$), indicating greater Pos FB accuracy among adolescents (Fig. 12B). A paired sample $t$-test indicated that across subjects Pos FB accuracy (64.6%) was marginally greater than Neg FB accuracy (58.4%), $t(46) = 1.694, p = 0.097$. The number of blocks needed to reach criterion was marginally larger among older participants (Age $p = 0.105$) and adolescents (Fig. 12A, Age$^2$ $p = 0.088$) compared with the youngest participants. To be sure that the curvilinear pattern in accuracy was not related to the curvilinear pattern in number of blocks to criterion, we regressed both Pos FB and Neg FB accuracy on number of blocks to criterion. Coefficients from both regressions were non-significant (both $p > 0.237$). Interestingly, although sex was not a significant predictor of accuracy or number of blocks to criterion (all $p > 0.34$), it did predict faster response times for males in Neg FB ($p = 0.002$) and Pos FB ($p = 0.048$) test pairs.

![Figure 12: Reinforcement Learning and Gamble Task behavior](image)

(A) The number of blocks needed to reach criterion in the Reinforcement Learning task showed a quadratic trend ($p = 0.088$) that peaked during adolescence. (B) Accuracy for choosing the image associated with the better odds of winning the high payoff on the gamble increased with age for pairs of images associated with the high payoff.
(Pos FB; $p = 0.008$) and pairs of images associated with the lower payoff (Neg FB; $p = 0.032$). Overall accuracy tended to increase with age, and Pos FB accuracy showed a peak in accuracy during adolescence ($p = 0.04$). (C) The probability of choosing the gamble decreased with age. Note: Y-axis values were randomly jittered in A ($\pm 0.5$) & B ($\pm 0.02$) to better show overlapping data points.

**Risk Task**

All participants successfully chose the larger of the two choice options on the three Safe-Safe performance check trials, indicating that they understood the task. Logistic mixed model regression on whether a gamble or sure bet was selected revealed a number of effects and interactions between age, magnitude, trial number, $P_{WIN}$, and Neg FB (Table 7). For all ages, the probability of selecting the gamble option increased significantly with the odds of winning. Although the hypothesis that selecting the gamble option would decrease with greater Neg FB scores was supported in general, interactions between Neg FB x $P_{WIN}$ ($p < 0.001$) and between Age x Neg FB x $P_{WIN}$ ($p = 0.036$) show a more nuanced relationship. We used the full set of regression coefficients to generate prediction plots based on select values for each of the different predictors (Fig. 13). Figure 13A shows that as Neg FB accuracy improved, age effects on gambling rates, especially in low and high $P_{WIN}$ trials, diminished and were more strongly modulated by $P_{WIN}$. Interestingly, while greater Neg FB scores predicted decreased gambling rates on low $P_{WIN}$ trials, Neg FB scores predicted increased gambling rates on high $P_{WIN}$ trials, especially among older participants. Similar to Neg FB, increased Pos FB scores ($p = 0.076$) also predicted a marginal decrease in gambling rates, although Pos FB did not interact with Age or $P_{WIN}$ predictors (all $p > 0.3$).
Figure 13: Prediction plots generated from Risk Task regression coefficients

(A) Shows predicted probabilities of choosing the gamble option at ages 7, 14, and 21 years, each with negative feedback accuracy (Neg FB) scores of 50% and 100%. Higher Neg FB scores decrease the predicted probability of choosing the gamble option for low and equal probability of winning trials, increases the predicted probability of choosing the gamble option when the probability of winning of high, and reduces the predicted effects of age. (B) The predicted probability of choosing the gamble option decreases over trials more quickly for older than for younger participants. (C) On trials containing gambles with an equal probability of winning, an increase in Neg FB of 25% predicts a decrease in the predicted probability of choosing the gamble option of 5-10% across ages. (D) On trials containing gambles with an equal probability of winning, younger participants are predicted to gamble more often with increasing coefficient of variation (CV) while older participants are predicted to gamble less often with increasing CV, with the inflection point at around 8.1 years of age.

Trial ($p < 0.001$) and Trial x Age ($p = 0.001$) interactions (Fig. 13B) show that while all participants decreased gambling rate across trials, this decline was greater for older participants. Because cumulative gambles and cumulative losses will also increase with cumulative number of trials, it’s possible that these factors could have led to decreased
rates of gambling over time. We compared effects of cumulative gambles and losses to cumulative trials by entering each into separate regression equations along with age and their interactions. Age remained a significant predictor in all three regressions \((p < 0.001)\), while trials \((p < 0.001)\) but not cumulative gambles \((p = 0.489)\), cumulative losses \((p = 0.897)\), or their interactions with age \((\text{both} \, p > 0.496)\) were significant.

Coefficient of variation modulated gambling rates in the expected direction; as CV increased, gambling rates decreased \((p = 0.017)\). The magnitude of choice options also modulated gambling rates; participants gambled more often for larger magnitude than smaller magnitude outcomes when CV was held constant. This effect interacted with Age and Age\(^2\) \((\text{both} \, p = 0.004)\) such that magnitude effects were found to be strongest for child and adult participants. However, the interaction between magnitude and Age\(^2\) was found to depend on our oldest participant, as removing this participant from the analysis returned an effect of magnitude and its interaction with Age but not Age\(^2\) \((p > 0.26)\) showing that magnitude effects declined among adolescent and adult participants. Removing this participant had negligible effects on the significance of other predictors.

We separately analyzed trials with a 0.5 probability winning using a backwards stepwise regression procedure. The resulting model included several of the predictors found to be significant in the previous analysis: Trial, CV, and Magnitude \((\text{Table 8})\). Interestingly, Neg FB was also moderately significant \((p = 0.066)\) in this model, predicting a 5-10% decrease in gambling rate for an improvement of 25% in Neg FB accuracy score \((\text{Fig. 13C})\). Interaction between Age and CV showed that while the youngest children increased gambling rate with increasing CV, older participants decreased gambling rate with
increasing CV with an inflection point at approximately 8.1 years of age, and that the effect of CV was strongest among the adolescent to early adult age groups (Fig. 13D).

| Table 8: Predictors and Beta Weights for 0.5 Probability Trials |
|---------------------|-------|-------|-------|
| (Intercept)**       | 1.770 | 0.594 | 2.981 | 0.003 |
| Age                 | -0.494| 0.542 | -0.912| 0.362 |
| Age²                | -0.387| 0.391 | -0.990| 0.322 |
| CV*                 | -1.446| 0.641 | -2.256| 0.024 |
| Magnitude***        | 0.486 | 0.142 | 3.434 | 0.001 |
| Trial*              | -0.007| 0.003 | -2.303| 0.021 |
| Neg FB†             | -0.400| 0.218 | -1.836| 0.066 |
| Age X CV            | -0.947| 0.596 | -1.588| 0.112 |
| Age X Trial         | 0.005 | 0.003 | 1.627 | 0.104 |
| Age² X CV*          | 0.781 | 0.356 | 2.192 | 0.028 |

Note: † p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001.

Discussion

Our first finding was that performance on ranking the novel test pairs of positive and negative animal images (e.g., 80%, 70% and 60%) increased with age, and this is consistent with prior studies (Cauffman, et al., 2010; Crone & van der Molen, 2004; Hämmerer, Li, Müller, & Lindenberger, 2011; Hooper, et al., 2004; Huizenga, et al., 2007). There was a trend for learning rate on the training pairs to decrease with age, as adolescents and young adults took slightly more trials to reach criterion than younger children. This stands in contrast to another study using a similar learning task that did not find age differences in learning rate (van den Bos, Güröglu, van den Bulk, Rombouts, & Crone, 2009). That study differed from ours in at least one important way; the probabilities 60:40 were not included, which could have leveled the means and reduced the variance in accuracy across ages. Even so, it may seem counter intuitive that the youngest children learned slightly faster than older participants. However, a similar curvature was found by
Weir (1964) in which younger children and young adults outperformed intermediate ages in choosing to pull the probabilistically rewarded lever in a three-armed bandit task. Weir suggested differences in strategy among the ages; whereas adolescents and adult participants were more likely to begin with complex hypotheses, adults abandon these hypotheses sooner than intermediately aged participants. Another way to describe this is that adult participants enter the experiment with ideas about the underlying probability structure of the rewards and then spend more time than young children trying to figure the structure out, and this may actually interfere with arriving at a particular strategy. Yet another way to describe this curvilinearity in blocks to criterion is to suggest that adolescents and peradolescents are more exploratory (Spear, 2000b). Interestingly, we did not find any relationship between Pos FB or Neg FB accuracy on the novel test pairs and number of blocks to criterion on the training pairs, suggesting that extra time spent exploring the probabilistic contingencies did not benefit the learner.

We set out to test the hypothesis that Neg FB accuracy would predict greater risk aversion. In fact our data support a slightly different conclusion. Neg FB accuracy was predictive of adaptive use of the animal images in the risk taking task. When presented with a choice between a safe bet and a gamble in the context of a positive animal picture (predicting a high probability of winning) subjects with higher Neg FB scores were more likely to choose the gamble. Conversely, when presented with a choice between a safe bet and a gamble in the context of a negative animal picture (predicting a low probability of winning) subjects with higher Neg FB scores were less likely to choose the gamble. On 50:50 trials where there was no animal image influencing the decision, higher Neg FB scores were also associated with risk aversion. For these 50:50 trials, the regression
coefficients indicate that an increase in Neg FB accuracy of 25% corresponds to a 5-10% decrease in gambling rate.

One of the stated hypotheses for the observed differences in children’s gambling behavior compared to adults was that children may overestimate their chances of winning, which we cannot yet rule out. Although children adjusted their behavior according to probability, consistent with previous studies on children’s probability assessments (Acredolo, et al., 1989; Scheres, et al., 2006; Schlottmann, 2001; Schlottmann & Anderson, 1994), they still tended to gamble on average more often than older participants.

In addition to interactions between age, Neg FB, and P_{win}, we found significant interactions between Age and Trial and between Age and Magnitude. Overall risk-taking declined over the course of the experiment, however it declined more rapidly and to a greater extent among adult and adolescent participants compared to children. The magnitude of gamble and sure bet options also influenced risk-taking behavior: participants accepted gambles more often for larger values, controlling for CV, although this effect was not as strong among adolescents and young adults as it was in children consistent with our prior findings (Paulsen, et al., 2011).

Also consistent with previous findings (Paulsen, et al., 2011), we found that CV modulated the probability of selecting a gamble on 50:50 trials. However, these data provide an estimate for the age at which risk-seeking for increasing CV crosses over to risk-aversion, which we found in this sample to occur around 8 years of age. This is an important piece of evidence in favor of sampling from young children in risky decision making tasks, as many studies tend to sample only from about this age onward when attempting to characterize developmental trajectories.
**Experiment 2**

Experiment 1 indicated that participants who learned the probabilities associated with negative feedback images in the RL task were more risk-averse in the 50:50 trials of the risky decision task, and that although children adjust their behavior according to probabilities, it is still possible that they overestimate their chances of winning. We followed up on these findings in Experiment 2. With respect to negative feedback learning, we kept the risk and RL tasks distinct by not presenting animal images on risk trials. With respect to subjective probability, we presented subjects with 0.5 probability risky choices to be made in both gain and loss domains. The rationale of this is that if children simply overestimate their chances of winning, or coming out ahead, then they should gamble equally as often across gain and loss domains.

**Method**

**Participants**

Thirty-two participants (21 female) ranging in age 7:4 to 25:5, mean age 14.5 years (SD = 5.2). Data from 5 additional participants were excluded from analysis: 1 had incomplete data due to computer error, 1 did not complete the RL task, and 3 had lower than 20% accuracy on the RL test trials. Informed consent was collected from adult participants and parents/legal guardians of minor participants; written assent was obtained from minor participants. All participants were compensated as in Experiment 1.

**Reinforcement Learning task**

The RL task in Exp. 2 was identical to that in Exp. 1.
Risk task

The risk task in Exp. 2 was presented in both a gain frame and a loss frame. The gain frame risk task was identical to the equal probability trials used in Exp. 1. Loss frame trials were identical to gain frame trials, except that participants were first endowed with 300 coins and participants' choices determined how many coins they would loose rather than gain. The borders of choice options were presented in distinct colors for gain and loss trials. When the outcomes were presented during loss trials, a recording of a male voice stated "you lose" followed by a sequence of sounds that corresponded to the number of coins lost. Three Safe-Safe trials were also presented in each of the gain and loss frames with the paired values 2 & 6, 1 & 7, and 3 & 5, as a check on performance.

Procedure

The order of presentation for the RL task, risk task for gains, and risk task for losses, was counterbalanced across subjects.

Results

Reinforcement Learning task

In contrast to Exp. 1, we did not find significant effects of Age ($p = 0.828$) or Age$^2$ ($p = 0.193$) on number of blocks to criterion (Fig. 14A). Nor did we find effects of Age or Age$^2$ on Pos FB ($p = 0.25$ and $p = 0.673$, respectively) or on Neg FB ($p = 0.182$ and $p = 0.393$, respectively; Fig. 14B). There was an effect of sex on Neg FB ($p = 0.034$) in whereby males (72.7%) scored higher than females (51.8%). Analysis of RT on Pos FB and Neg FB test trials showed that Age had a marginal effect on RT only for Pos FB ($p = 0.066$), with younger participants taking longer to respond than older participants; all other $p > 0.289$. 
Figure 14: Reinforcement Learning Task in Experiment 2 (A) the number of blocks to criterion as a function of age. (B) Positive and negative FB accuracy as a function of age. Patterns were similar to those in Exp. 1, but were non-significant (all \( p > 0.18 \)).

Risk task

All but one participant chose the larger option on all three Safe-Safe performance check trials in the gain frame; this single participant chose the larger on two out of the three trials. All participants chose the smaller of the two choice options on the loss frame performance check trials.

As can be seen in Fig. 15A, the probability of choosing a gamble in gain and loss domains was differentially predicted by age. The proportion of gambles selected decreased with age in the gain domain, but increased with age in the loss domain, indicating that a reflection effect (a preference shift between the domains of gains and losses as measured by loss domain risk taking minus gain domain risk taking) increased with age. This was confirmed by a correlation between the difference in gamble rates of loss and gain domains and age, \( r = 0.632, p < 0.001 \) (Fig 15B).
Figure 15: Gain and loss frame data and predictions (A) Probability of choosing a gamble over sure bet decreased with age for gains, and increased with age for losses. (B) Predicted probability of choosing a gamble over sure bet decreased over the session for gains, and increased over the session for losses. (C) Children younger than ~10.3 years showed increased probability of choosing a gamble as a function of increasing coefficient of variation (CV), while participants older ~10.3 years show decreased probability of choosing a gamble as a function of increasing CV. (D) The reflection effect (mean number of gambles for losses minus mean number of gambles for gains) increased with age, starting from a reverse reflection effect for the youngest participants.

We also implemented the same backwards stepwise regression procedure used in Exp. 1 using the same predictors: Trial, CV, and Magnitude. Recall that in Exp. 1 Neg FB predicted a 5-10% decrease in gambling rate for an improvement of 25% in Neg FB accuracy score. In Exp. 2 the same analysis for the gain and loss domains revealed no effects of Neg FB.

We did however find that trial was a significant predictor in both gain and loss domains, and similar to the effects of Age, the effects of trial in gain and loss domains were
in opposite directions (Fig. 15C). Gambling rate decreased over trials for gains but increased for losses. There was also a marginal trial by Pos FB interaction for gains ($p = 0.075$) showing that participants reduced gambling rate over the course of trials, but that those with greater Pos FB scores decreased their gambling rate more steeply.

**Crossover of effect of CV**

The final model of the backwards stepwise regression for the gain domain contained a similar pattern of effects for CV, and an age by CV interaction, as in Exp. 1 (Table 9; Fig. 15D), showing that younger children increase gamble rates with an increase in CV, while older participants decreased gamble rates with an increase in CV, with a crossover point at 10.3 years of age. This interaction also shows that age differences were strong for higher CV trials and relatively weak for lower CV trials.

**Table 9: Predictors and Beta Weights for Gain and Loss Domains**

<table>
<thead>
<tr>
<th></th>
<th>Gain Domain</th>
<th>Loss Domain</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Gain Domain</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)***</td>
<td>1.7117</td>
<td>† 0.4466</td>
</tr>
<tr>
<td>Age</td>
<td>0.5392</td>
<td>0.3869</td>
</tr>
<tr>
<td>CV†</td>
<td>0.8263</td>
<td>0.4290</td>
</tr>
<tr>
<td>Magnitude</td>
<td>0.1925</td>
<td>0.3251</td>
</tr>
<tr>
<td>Trial***</td>
<td>0.0341</td>
<td>0.0085</td>
</tr>
<tr>
<td>Pos FB</td>
<td>0.3251</td>
<td>0.3251</td>
</tr>
<tr>
<td>Age:CV*</td>
<td>1.0227</td>
<td>0.4876</td>
</tr>
<tr>
<td>trial:Pos FB†</td>
<td>0.0161</td>
<td>0.009</td>
</tr>
<tr>
<td>Age:Magnitude</td>
<td>0.2273</td>
<td>0.1537</td>
</tr>
<tr>
<td><strong>Loss Domain</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept†</td>
<td>0.4466</td>
<td>0.3696</td>
</tr>
<tr>
<td>Age*</td>
<td>0.3869</td>
<td>0.3869</td>
</tr>
</tbody>
</table>
To get a better estimate of when this crossover in risk preference occurs developmentally, we combined the data from the equal probability gain trials from both experiments and submitted them to a Markov chain Monte Carlo (MCMC) sampling routine to estimate the age at which the effect of CV on predicting a gamble is zero. We used a burn in of 5000 trials, 5000 iterations, 3 chains, non-informative priors (flat distributions), and a model that included the following parameters: age, age$^2$, CV, magnitude, trial, age*CV, age*trial, and age$^2$*CV. Gelman and Rubin diagnostics indicated convergence. This analysis revealed a 95% highest density interval for the age at which CV has no effect between 7.82 and 12.57 years of age, and that 95.3% of the estimates lay between 7.5 and 12.5 years. In other words, we can be 94% certain that risk-seeking behavior crosses over to risk-averse behavior in this type of gambling task between 7.5 and 12.5 years of age.

**Discussion**

The primary purpose of Exp. 2 was to determine whether the effect of Neg FB accuracy on gambling rate found in Exp. 1 would replicate when the risk taking task and feedback learning task were kept separate. A second goal was to determine whether children exhibit optimism in both gain and loss domains, indicating an overestimation of their probabilities of winning. We found, contrary to Exp. 1, that Neg FB accuracy did not predict risk taking in either the gain or loss domain, and that children did not uniformly exhibit risk seeking behavior across domains. In the gain domain, risk-taking decreased with age, while in the loss domain risk-taking increased with age. Taking the difference between risk-taking in gain and loss domains, we also showed a significant developmental
emergence of the reflection effect, beginning with a reverse reflection effect for younger participants, i.e. greater risk taking in the gain than loss domain.

This finding is consistent with Reyna & Ellis (1994) who showed reverse framing effects among 2nd graders and standard framing effects among 5th graders. However, it should be noted that the standard reflection effect has been found in younger children, and even non-human primates (Lakshminarayanan, Chen, & Santos, 2011). For example, both Levin & Hart (2003) and Schlottmann & Tring (2005) found standard reflection effects across all ages. In these studies, most gamble choices involved a chance of winning/losing prizes or jellybeans vs. a possible outcome of nothing at all. Further support for a ubiquitous effect of framing on decision under risk comes from a study that found that capuchin monkeys made more risky choices under loss than gain conditions (Lakshminarayanan, et al., 2011), suggesting that reflection effects in loss vs. gain choice behavior are evolutionary conserved.

Two other findings of Exp. 2 were found to be consistent with those of Exp. 1, namely a crossover in risk preference with age and a change in the rate of gambling over trials. In Exp. 1, the crossover point in the effect of CV occurred at around 8 years of age, and in Exp. 2 it occurred at around 10 years of age. MCMC sampling methods using data from both experiments provided a fairly high confidence for the age range during which this transition takes place between 8 and 12.5 years. Similar to Exp. 1, gambling rate decreased over gain frame trials. Conversely, gambling rate decreased over loss frame trials.

**General Discussion**

We conducted two experiments to examine which cognitive skills might predict increasing risk aversion over development. We tested two specific hypotheses. First that
negative feedback learning predicts risk aversion with faster learning from negative feedback being correlated with the more adult pattern of risk aversion. Second, that children's heightened risk taking may reflect higher subjective estimates of the probability of obtaining a favorable outcome on a gamble.

In Experiment 1 we found that increased negative feedback learning accuracy was associated with a decrease in gambling rate for gambles but only when there was an equal probability of winning or losing on the gamble or when a negative animal picture was presented with the gamble indicating a low probability of a favorable outcome on the gamble. In contrast negative feedback learning accuracy was correlated with an increase in gambling rate for gambles presented with a positive animal image, which indicated a high probability of winning. Additionally, high negative feedback accuracy was found to minimize the effects of age on gambling rate. In Exp. 2 negative feedback learning and risky decision-making were measured separately and in contrast to Exp. 1, Neg FB learning was not found to be a significant predictor of gambling rate in either gain or loss domains.

We found that across ages, the probability of winning significantly predicted gambling rate, suggesting that overall, children incorporate probability of winning into decision-making behavior. This is consistent with other studies that have examined children's understanding of described probabilities (Acredolo, et al., 1989; Scheres, et al., 2006; Schlottmann, 2001; Schlottmann & Anderson, 1994; Schlottmann & Tring, 2005).

The results from the gain and loss domains of Experiment 2 suggested that the simple prediction that children are always optimistic in their assessment of a gamble is false. Instead, children were more risk-prone compared to adults in gain frame gambles but more risk-averse compared to adults in loss frame gambles. One possibility is that
children's attention may be drawn disproportionately to the largest amounts. In gain frames this would lead children overweighing the probability of winning the larger amount, and in loss frames this would lead children to overweight the probability of losing the larger amount.

Similar to Reyna & Ellis (1994), we found that the reflection effect changed with development beginning with a reversed pattern in the youngest participants. However, in their study, typical reflection effects were found in 5th graders, and other studies have also found reflection effects at young ages (Levin & Hart, 2003; Schlottmann & Tring, 2005). In contrast, in our study it was not until around 12 years that the adult-like standard reflection effects were observed. A meta-analysis of framing effects found that they are reliable with a small-to-medium effect size, but also that framing gambles by domain and eliciting choice responses (as opposed to judgments) tend to yield greater effect sizes (Kühberger, 1998). But, as previously mentioned, our study differs in reward structure from other studies that have found standard reflection effects in younger children. Specifically, participants in our study gambled for coins in a computer game while previous studies used tangible all-or-nothing rewards of jelly beans and toys. The use of primary reinforcers may have made losing more salient to children in both gain and loss domains, thus aligning their behavior more closely to that of adults and generating stronger standard reflection effects.

The idea that salient losses and gains may drive the reflection effect is consistent with a study by De Martino and colleagues (De Martino, et al., 2006) who found greater amygdala activation when choosing the sure bet than when choosing a gamble in gain frames, and the reverse pattern in loss frames. This pattern of amygdala activation was thought to reflect the processing of negative emotional information during decision-making,
perhaps steering choices away from losses, an interpretation consistent with subsequent work showing that damage to the amygdala reduces loss aversion in gambling contexts (De Martino, et al., 2010). With respect to children, our prior work has shown that amygdala activation increases with age during decision-making in a task similar to the ones used in these experiments (Paulsen, Carter, Platt, & Huettel, 2012). Thus, our task may not have been as effective at engaging loss aversion circuitry in children as previous tasks.

Collectively data from Exps. 1 & 2 suggest that risk-seeking switches over to risk-aversion sometime between the ages of 7.5 and 12.5 years. In addition, the findings support our previous conclusion that differences between young children and adults in risk-taking behavior are more pronounced at higher levels of CV or risk (Paulsen, et al., 2011).

These results can be interpreted in at least two ways: they could indicate a shift in the balance of attention given to potential outcomes, or they could indicate a change in the differential sensitivity to reward and inhibitory control. A difference in the balance of attention to outcomes suggests that children may be relatively attentive to and driven more by potential gain whereas adults may be relatively more attentive to potential loss. Cognitively, this can be described by differential weighting functions between children and adults in their evaluation of the gamble option, (i.e., Tversky & Kahneman (1992).

Children’s weighting function could be described as ‘potential-minded’ or optimistic, while adults’ might be described as ‘security-minded’ or pessimistic (Lopes, 1995).

Alternatively, increases in risky behavior could result from an imbalance between brain regions involved with reward sensitivity and inhibitory control (Casey, Getz, et al., 2008; Galvan, et al., 2006). Neural signals promoting an approach response, driven by attention to potential gain, may compete with signals promoting an inhibition response,
driven by attention to potential loss. Mechanistically such behaviors could result from differences between developing dopaminergic and serotonergic signaling systems, which have been discussed as potential contributors to the balance between approach and inhibition behaviors (Boureau & Dayan, 2010; Cools, Nakamura, & Daw, 2010). However, this hypothesis need not be exclusive to the hypothesis regarding attention. Given equal attention to possible outcomes, differences in reward and inhibitory mechanisms could drive differences in behavior; given equally competent mechanisms, differences in attention could lead to an imbalance in their function.

While the probability of choosing a gamble decreased across trials for gains, it increased across trials for losses. In Exp. 1, the decrease in gambling rate across trials was not as large in young children as it was in older participants, and post-hoc analyses suggested that this decrease was due not to the number of trials gambled nor the number of losses accrued. Previous studies of children’s behavior in gambling paradigms have found that as children age, they become faster at learning to differentiate and select advantageous gambles over disadvantageous gambles (Crone, Bunge, Latenstein, & van der Molen, 2005; Huizenga, et al., 2007). Thus, differences in the rate of change in gambling behavior have been previously observed. However, while these and other studies have found changes in gambling rates when expected value is modulated (A. Bechara, et al., 1994; Lindman, 1971), we are not aware of any previous studies that have found decreases in gambling rate over trials for either gains or losses under conditions in which there are no optimal responses to be learned.
Conclusion

Two hypotheses regarding the decline in risk-taking behavior that occurs between early childhood and adulthood were tested. The first hypothesis was that children are more prone to take risks because of deficits in their ability to learn from negative feedback. The second hypothesis was that children are more prone to take risks due to overestimates in the subjective probability of coming out ahead. We found that neither hypothesis could account for developmental changes in preferences for gambles. We found a standard reflection effect in adults whereby decisions were more risk seeking in a loss frame compared to a gain frame. In contrast, we found a reverse reflection effect in children whereby decisions were more risk seeking in the gain frame compared to the loss frame. These results suggest that children and adults differentially weigh gamble outcomes in the valuation of the gamble prospect, and that this difference might be due to children paying more attention to the larger value in both gain and loss frames. Across all ages risky decisions decreased in frequency over the course of the session. Finally across the two experiments we found that children move from risk-seeking to risk-aversion between 7.5 and 12.5 years of age.
Chapter 5 – Valuation, Surprise, Disappointment, and Regret

Chapter 4 showed that children's developing understanding of probabilistic outcomes does not explain their preference for risky options. One long- and widely-held view of economic choice behavior is that between a set of differing alternatives, the option with the highest expected value (EV) should be chosen. Although this view has been challenged and found to be more prescriptive than descriptive (Kahneman & Tversky, 1979), it makes the more accepted assertion that probability is an important factor in decision-making. Given the influence of probability during decision-making under risk, a reasonable hypothesis for children's increased preference for risk is that children overestimate their probabilities of winning, either because they haven't quite developed probabilistic reasoning or because their subjective probability estimates of winning are inaccurate. However, prior research has shown that children can adjust their behavior according to EV and probability similar to adults (Acredolo, et al., 1989; Scheres, et al., 2006; Schlottmann, 2001; Schlottmann & Anderson, 1994; van Leijenhorst, et al., 2008).

Interestingly, although prior studies disagree on whether young children show standard or reverse reflection effects between gain and loss domains (Levin & Hart, 2003; Reyna & Ellis, 1994; Schlottmann & Tring, 2005), findings that their preferences do shift suggests that children are unlikely to simply overestimate their chances of winning gambles.

A point of distinction between children's and adult's preference for risk, is in their response to varying levels of risk. We have previously used the coefficient of variation (CV) as an index of risk level, not because it accords with the historical economic idea of variance as risk (Sharpe, 1964), but because dividing the mean by it's standard deviation cancels
units out, it a unitless measure of risk suitable for cross study comparison. It has been shown to be a better predictor of choice behavior than variance among humans and foraging animals (Weber, et al., 2004). In a previous study, we found that while children, adolescents, and adults, appear to be similarly indifferent in their preference to gambles over sure bets at low levels of risk (small CVs), children’s preferences for gamble options increase and adults preferences for gamble options decrease as CV grows larger (Paulsen, et al., 2011). The finding that CV modulates children’s preferences demonstrates that children do not uniformly select the choice option with largest value, just as adults do not uniformly avoid the choice option with the smallest value, but rather suggests that the magnitudes of gamble options influence choice behavior.

One prominent theory of decision-making in which the magnitude of gamble options could influence choice behavior is Cumulative Prospect Theory (CPT; Tversky & Kahneman, 1992). In this model, the value of a gamble, or prospect, depends in part on the subjective weights attached to possible outcomes, which themselves may be influenced by the amount of attention given to potential gains and losses (Lopes, 1995). At the extreme, the idea of attention to possible outcomes giving weight to the value of a gamble is intuitive and clear: if one attends only to what may be gained, then the value of gamble is positive, but if one attends only to what may be lost, then the value is negative. The difference in risk preference between children and adults could therefore be accounted for by differences in attention given to the possible outcomes of a gamble and choice alternatives. The different resulting weighting functions could be described as ‘potential-minded’ or optimistic for children, and ‘security-minded’ or pessimistic for adults (Lopes, 1995).
While many models of decision-making under risk, including CPT, tend to focus on the valuation of choice options to explain behavior, the evaluation of choice outcomes is another critical phase of the decision-making process (Rangel, et al., 2008). Outcome evaluation is one important route to learning about the contingencies between choices, actions, and outcomes. Feedback learning, a type of outcome evaluation, has figured into hypotheses concerning the basis of pathological gambling behavior (Maia & Frank, 2011). Decision affect theory suggests that the prospective evaluation of outcomes, or anticipated emotions, directs choice behavior (Bell, 1985; Loomes & Sugden, 1982). One distinction made within this framework is between disappointment and regret: disappointment is a negative emotion associated with what happened, while regret is a negative emotion associated with having taken a particular action compared to the counterfactual, or what could have happened otherwise. While anticipated emotions have been found to be predictive of choice behavior (Mellers, et al., 1997), individual differences in emotion ratings after outcomes have not (Burnett, et al., 2010). In addition to finding an adolescent peak in risk taking behavior, Burnett and colleagues (2010) also found that adolescents gave higher emotional ratings for relief after viewing counterfactual outcomes than children or adults. Another study examining regret and relief found that counterfactually mediated regret develops slowly between childhood and adulthood (Habib et al., 2012). Little is known about the development of regret and disappointment.

Eye-tracking methodology provides suitable measures for testing hypotheses concerning the relationship between attention and choice, and between expectancy and outcomes, during decision-making. Prior work has shown that the amount of time spent looking at particular choice option increases the likelihood that it will be selected (Krajbich,
Armel, & Rangel, 2010; Krajbich & Rangel, 2011). Consistent with the idea that differences in attention could lead to differences in risk preference, other work has shown that loss averse individuals pay greater relative attention to loss values than gain values (Janowski & Rangel, 2011). In addition to providing measures of eye-gaze position, many eye-tracking devices are also capable of monitoring pupil dilation. Recent work utilizing pupilometry has shown positive correlations between change in pupil diameter and surprise (Preuschoff, ’t Hart, & Einhäuser, 2011).

To answer questions about possible differences between children and adults in their allocation of attention during choice valuation, and in attention and surprise during outcome evaluation, the current study tested children and adults with a child-friendly decision-making paradigm (Paulsen, et al., 2011) while eye-tracking data, including gaze position and pupil size, were collected. Three types of trials were implemented: Safe-Safe trials presented the choice between two sure bets, Risk-Safe trials presented the choice between a gamble option and a sure bet option of equal EV, and Risk-Risk trials presented the choice between two gamble options that differed in both EV and CV, with the larger EV option always having a larger CV. We predicted that in Risk-Safe trials, compared to adults, children would select the risky option more often, and that they would spend a greater proportion of time looking at the largest value prior to choosing the risky option. During Risk-Risk trial valuation, we predicted that children would choose the riskier option more often, and that they would spend a disproportionate amount of time looking to the largest values of both gamble options, compared to adults. Consistent with the idea the regret develops slowly, we predicted that upon viewing a losing outcome after a gamble, children would spend proportionally less time looking at counterfactual choices than adults.
**Methods**

**Participants**

Data were collected from 17 children (4 female) with a mean age of 6.88 years, and 14 adults (8 female) with a mean age of 19.65 years. Adult participants were recruited from the Duke University undergraduate pool and awarded course credit for participating. Child participants were recruited from the Duke-Chapel Hill area and paid $10 per hour plus a toy prize. Signed IRB-approved consent forms were collected from all adult participants and the parents or guardians of child participants, and signed IRB-approved assent forms were collected from all child participants.

**Apparatus**

Participants were seated between approximately 50-70 cm away from a 24” TFT display containing the eye-tracking hardware (Tobii T60XL) mounted on an adjustable stand. Gaze-location and pupilometry data were collected at a rate of 60 Hz. Head motion was unrestricted. Freedom of movement for Tobii T60XL is estimated at 16 x 8 x 11”. Communication with the Tobii device was made possible with the use of the T2T package compiled for Mac OS X v10.6, Matlab R2010a, and a Mac Mini running Mac OS X v10.7.

**Task**

Participants were informed that they would be playing a game in which the choices they made would yield different numbers of coins, and that their goal was to collect as many coins as possible. We used three types of trials: Risk-Safe, Risk-Risk, and Safe-Safe. Risk-Safe trials consisted of a choice between a safe option and a gamble option with equiprobable outcomes. The expected value (EV) of the gamble option was always equivalent to the certain option (either 4 or 8 coins), while the coefficient of variation (CV)
for the gamble option was varied (0.35, 0.71, 1.06, or 1.41) to create 4 levels of risk (Weber, et al., 2004). **Risk-Risk trials** consisted of a choice between a higher EV (6 coins) but higher risk (CV: 0.94, 1.18, or 1.41) option and a lower EV (5 coins) but lower risk (CV: 0.28, 0.57) option, thus creating risk-return tradeoff scenarios. **Safe-Safe trials** consisted simply of a choice between two certain outcomes, the values for which were derived from the values used in Risk-Safe trials. Each participant was given 10 Safe-Safe, 48 Risk-Safe, and 35 Risk-Risk trials.

Before the practice and testing sessions, participants underwent a head position and six-point eye-position calibration routine to provide the Tobii system with accurate gaze information. Participants were first given 9 practice trials that included 2 Safe-Safe, 5 Risk-Safe, and 2 Risk-Risk trials, in that order.

Trials were initiated by fixating at the center of the screen for a duration of 80 milliseconds. Previously collected pilot data showed that when presenting all gamble and sure bet values simultaneously, both children and adults directed gaze to the largest value first. To avoid potential confounds in dwell time due to this behavior, we used a gaze-contingent stimulus presentation to present gamble and sure bet values. At the beginning of each trial, an empty color coded frame outlining each choice option was presented: red for gamble loss amount, green for gamble win amount, and blue for sure bet amount. The coin amount for each choice option was presented upon shifting gaze into its respective frame, and remained on-screen during the decision phase. Participants indicated that a decision had been reached by pressing a game controller button with their right thumb, initiation the choice phase in which all choice option values were removed and the color coded frames were replaced with salmon colored frames. Participants then selected their choice by
shifting gaze into any of the choice options and pressing the game controller button again. Feedback about the currently selected choice option was provided by a red square outlining the gamble or safe options. A variable delay between 1.5-2 seconds occurred between the choice and outcome phases during which a blank grey screen was presented. Outcome displays were then presented for two seconds. The outcome display was identical to the decision display except that the sure bet or gamble outcome, whichever was selected, was highlighted by a yellow frame, while all other options were given a transparency of 50%. Intertrial intervals varied between 1-2 seconds. Midway through the experiment, participants were shown a 'bank' display that indicated how many coins they had collected thus far.

**Analysis**

Data from 1 child participant was limited to 67 trials in total due to computer failure, and 1 other child participant was excluded for invariant behavior (did not choose safe bet). Missing eye-tracking data points with a duration of less than 180 ms (11 samples) were linearly interpolated separately for each eye. Trials containing more than 25% missing eye-tracking data points during the decision and outcome epochs were excluded from eye-tracking data analysis during decision and outcome phases, respectively. Trials in which participants did not view all choice options were also excluded from analysis of eye-tracking data from decision phase.

We excluded subjects who had fewer than 3 good trials per choice option from the analysis of decision phase eye-tracking data. We similarly excluded subjects who had fewer than 3 good trials per outcome (win, loss, and safe choice) from the analysis of outcome phase eye-tracking data. Subjects that had fewer than 6 trials contributing to winning and
losing outcome pupil dilations were excluded from the analysis of pupilometry data. Note that because of the difference in the type of analysis conducted, we did not exclude trials that went into subject pupilometry averages on the basis of missing data points, but rather increased the number of trials required of each subject that went into subject averages. The number of subjects that went into each analysis are reported in each section below. Due to a programming error, outcomes for Risk-Risk trials in which the lower EV/lower Risk option was selected were not displayed, and therefore eye-tracking data for these outcomes will not be analyzed.

**Results**

**Safe-Safe Trials**

All participants selected the larger amount of the two safe-safe options. Single sample t-tests on the proportion of dwell time spent on the larger amount were significant for both adult (62.4%; \( t(13) = 7.68, p < 0.001 \)) and child participants (61.3%; \( t(16) = 6.64, p < 0.001 \)). Independent sample t-tests showed that these proportions were not different between age groups (\( p > 0.65 \)).

**Risk-Safe Trials**

**Behavior**

As can be seen in Figure 16, children and adults diverged in risk preference as CV increased: children preferred greater risk while adults avoided it. We first analyzed choice behavior using mixed-effects logistic regression predicting the probability of choosing the gamble in risk-safe trials using CV, age group, and their interaction as predictors, allowing both slope of CV and the intercept to vary as subject specific random effects. Data from 16 children and 14 adults went into this analysis. Beta weights for all three predictors were
found to be significant (Table 10). We next ran this regression separately for each age group and found that the beta weight for CV for adults was significant ($p < 0.001$) and negative, while the beta weight for CV for children was trending towards significance ($p = 0.065$) and positive.

![Age Group by CV](image)

**Figure 16:** Behavior during eye-tracking. Children showed risk-seeking behavior, while adults showed risk-averse behavior.

<table>
<thead>
<tr>
<th></th>
<th>$\beta$</th>
<th>SE</th>
<th>$z$ value</th>
<th>$p$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept***</td>
<td>1.888</td>
<td>0.332</td>
<td>5.686</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Age Group*</td>
<td>-0.956</td>
<td>0.466</td>
<td>-2.051</td>
<td>0.040</td>
</tr>
<tr>
<td>CV**</td>
<td>-2.330</td>
<td>0.373</td>
<td>-6.248</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Age Group X CV***</td>
<td>2.933</td>
<td>0.526</td>
<td>5.573</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

**Adults**

<table>
<thead>
<tr>
<th></th>
<th>$\beta$</th>
<th>SE</th>
<th>$z$ value</th>
<th>$p$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept***</td>
<td>1.832</td>
<td>0.283</td>
<td>6.466</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>CV**</td>
<td>-2.261</td>
<td>0.330</td>
<td>-6.850</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

**Children**

<table>
<thead>
<tr>
<th></th>
<th>$\beta$</th>
<th>SE</th>
<th>$z$ value</th>
<th>$p$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept**</td>
<td>1.036</td>
<td>0.330</td>
<td>3.136</td>
<td>0.002</td>
</tr>
<tr>
<td>CV†</td>
<td>0.434</td>
<td>0.235</td>
<td>1.848</td>
<td>0.065</td>
</tr>
</tbody>
</table>

Note: † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.  

123
Eye-Tracking

After trial and participant exclusion, data from 8 children and 14 adults remained for the analysis of eye-tracking data from the decision phase. Figure 17A shows that participants looked to the Sure Bet object first on approximately 49%-68% of trials, while the Win and Loss objects were looked to first an approximately equal amount on the remaining trials, and that these proportions do no differ much between trials in which participants chose the Sure Bet or Gamble option. In contrast, Figure 17B shows that participants looked at the Sure Bet object last most often on trials in which the sure bet option was chosen, and at the Win object most often when the gamble option was chosen. Figure 17C shows that prior to choosing the safe option, both children and adults spent a greater proportion of the decision phase looking at the Sure Bet object than either the Win or Loss object, but that prior to choosing the gamble option (Fig. 17D), the greater proportion of dwell time was on the Win object.
Figure 17: Eye-tracking behavior during decision-making in Risk-Safe trials. (A) The first fixation objects (FFO) did not vary systematically between children and adults, and did not predict whether or not participants selected the gamble option. (B) Both children and adults tended to look at the Sure Bet object last before choosing the Safe Bet option, and at the Win last object before choosing the gamble option. (C) Prior to choosing Safe Bet options, children and adults looked longest at the Sure Bet object. (D) Prior to choosing the gamble option, children looked disproportionately longer at the Win object compared to adults, and less at the Sure Bet object.

To determine whether these patterns were significantly different between children and adults prior to choosing gambles and sure bets, or more specifically, whether differences in what children and adults attended to during the decision phase could predict their choosing either a sure bet or gamble, we used mixed-effects logistic regression to
predict the probability of choosing the gamble using CV, age group, the first fixation object (FFO), last fixation object (LFO), dwell time on gamble loss and sure bet objects, and the interactions between these regressors and age group. As before, CV and intercept were allowed to vary as random effects. The results from this analysis (Table 11) confirm that the FFO was not predictive of whether or not participants chose the gamble option, and that compared to the LFO being the Win object, looking at the Sure Bet object last was significantly predictive of choosing the safe option ($p < 0.001$). This analysis also confirmed that the as the proportion of time spent looking at the Sure Bet compared to the Win object grew larger, there was a greater likelihood of choosing the safe option.

<table>
<thead>
<tr>
<th></th>
<th>$\beta$</th>
<th>SE</th>
<th>z value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept***</td>
<td>4.072</td>
<td>0.965</td>
<td>4.219</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>FFO (Loss Object)</td>
<td>-0.118</td>
<td>0.342</td>
<td>-0.344</td>
<td>0.731</td>
</tr>
<tr>
<td>FFO (Sure Object)</td>
<td>0.468</td>
<td>0.313</td>
<td>1.493</td>
<td>0.135</td>
</tr>
<tr>
<td>LFO (Loss Object)</td>
<td>-0.168</td>
<td>0.397</td>
<td>-0.422</td>
<td>0.673</td>
</tr>
<tr>
<td>LFO (Sure Object)***</td>
<td>-2.828</td>
<td>0.305</td>
<td>-9.279</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Sure Object Dwell***</td>
<td>-4.298</td>
<td>1.418</td>
<td>-3.031</td>
<td>0.002</td>
</tr>
<tr>
<td>Loss Object Dwell</td>
<td>1.270</td>
<td>1.603</td>
<td>0.793</td>
<td>0.428</td>
</tr>
<tr>
<td>CV***</td>
<td>-2.095</td>
<td>0.475</td>
<td>-4.415</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Age Group</td>
<td>1.095</td>
<td>1.801</td>
<td>0.608</td>
<td>0.543</td>
</tr>
<tr>
<td>FFO (Loss Object) X Age Group</td>
<td>0.310</td>
<td>0.711</td>
<td>0.436</td>
<td>0.663</td>
</tr>
<tr>
<td>FFO (Sure Object) X Age Group</td>
<td>-0.705</td>
<td>0.589</td>
<td>-1.198</td>
<td>0.231</td>
</tr>
<tr>
<td>LFO (Loss Object) X Age Group</td>
<td>0.497</td>
<td>0.869</td>
<td>0.572</td>
<td>0.568</td>
</tr>
<tr>
<td>LFO (Sure Object) X Age Group</td>
<td>0.111</td>
<td>0.554</td>
<td>0.200</td>
<td>0.842</td>
</tr>
<tr>
<td>Sure Object Dwell X Age Group</td>
<td>-4.190</td>
<td>2.742</td>
<td>-1.528</td>
<td>0.127</td>
</tr>
<tr>
<td>Loss Object Dwell X Age Group</td>
<td>-4.935</td>
<td>3.388</td>
<td>-1.457</td>
<td>0.145</td>
</tr>
<tr>
<td>CV X Age Group***</td>
<td>2.899</td>
<td>0.828</td>
<td>3.500</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

Note: Age Group (children = 1, adult = 0), FFO – first fixation object, LFO – last fixation object, CV – coefficient of variation, *** $p < 0.001$. 

126
From the data shown in Figure 17D, it appears that compared to adults, children spent a greater proportion of time attending to the Win object than the Sure Bet object before choosing the gamble option, although this interaction was found to be only trending in the current data ($p = 0.127$). However, independent sample t-tests on the proportion of dwell time measures prior to sure bet and gamble choices, for each of the Win, Loss, and Sure Bet objects revealed significant group differences in dwell times prior to gambles on the Win ($p = 0.020$) and Sure Bet objects ($p = 0.003$); all other tests were $p > 0.312$.

Figure 18 shows that upon viewing winning outcomes, children (n = 10) and adults (n = 12) tended to look longer at the Win object than the Loss or Sure Bet objects. After losses, adults appeared to look equally often at each of the different gamble and sure bet objects, while children seemed to look longest at the Loss object, least at the Sure Bet object, and an intermediate amount at the Win object. After Sure Bet outcomes were presented, children and adults showed similar patterns of looking longest to the Sure Bet object, next longest to the Win object, and least of all to the Loss object.

Figure 18: Eye-tracking behavior during outcome presentation in Risk-Safe trials. (A) After wins, children and adults look longest Win objects. (B) After losses, children looked longer at the Loss object and less at the Sure Bet object, than adults, suggesting less experienced regret. (C) After Sure Bets, children looked less often at the Win object compared to adults.
To determine whether there were differences between children and adults in what they attended to after viewing the outcome of a gamble, we used independent sample t-tests on the proportion of dwell time measures after winning, losing, and sure bet outcomes, for each of the Win, Loss, and Sure Bet objects. The results demonstrate that children did not differ from adults in the proportion of time spent looking at each of the Win, Loss, and Sure Bet objects after wins (all $p > 0.508$). After sure bets, children spent less time looking at the Win object than adults ($p = 0.02$), but not significantly different at the Sure Bet or Loss objects ($p > 0.16$). After losses, children spent more time looking at the Loss object ($p < 0.001$) and less time at the Sure Bet object ($p < 0.001$) than adults, and a non-significantly different amount of time looking at the Win object ($p = 0.800$).

**Pupilometry**

We also analyzed pupilometry data for the four seconds following the presentation of gamble outcomes. The time-course of pupil dilations used a post-stimulus baseline of $\sim 200$ ms (12 samples). To identify the time-course of group differences in pupil dilations as a result of outcome, we used a 3x2, time-point by time-point repeated-measures ANOVA (RM-ANOVA) with outcome (Win, Loss, Safe Bet) and age group as factors. The resulting time-course of $F$-values were then smoothed using a kernel of 5 samples. Onsets and offsets were defined as the point at which $F$-values crossed the $p = 0.05$ level of significance for a duration of at least 10 continuous samples.

Figure 19 shows the general pattern of pupil dilation across trial outcomes that pupil diameter increased for approximately 0.5 seconds after the presentation of trial outcomes, but differences in this pattern were found depending upon condition and age group. In adults, pupils dilate quickly after losses until around 1 second, dilate slowly after
safe bets until about 1.5 seconds, but are delayed in dilating, if not constricting, after wins until approximately 750 ms. Children, in contrast, show steady pupil dilation after viewing loss and win outcomes until between 1-1.5 seconds, but after viewing the outcomes of safe bets, pupils constrict slowly after about 0.5 seconds.

Figure 19: Adults and children differ in pupil dilation after wins in Risk-Safe trials. The top two panels show relative pupil dilation for adults and children, respectively, during outcome presentation of safe bets, wins, and losses. The grey transparency blocks in these top panels indicate the time window during which significant main effects of outcome were found (0.747-1.344 sec). The lower three panels compare children to adults after safe bets, wins, and losses. The difference in pupil dilation between children and adults after wins is clear. The grey transparencies in these bottom panels indicate where interactions between age group and outcome were found (0.780-1.012 sec).
Analysis of the time-course of pupil returned a main effect of outcome condition from 0.747 sec to 1.344 sec as indicated by the shaded areas in the top two panels of Figure 19, confirming that for both children and adults, pupil diameter was larger for loss outcomes than safe bet outcomes. A group by outcome interaction was also found from 0.780 sec to 1.012 sec, indicated by the shaded areas in the bottom three panels of Figure 19 and confirming that pupil dilation to loss outcomes was different between groups.

**Risk-Risk Trials**

**Behavior**

A RM-ANOVA using Low Risk (2 levels) and High Risk (3 levels) as within group factors and age group as a between groups factor returned significant effect age group, $F(1,26) = 22.21, p < 0.001$, showing that in Risk-Risk trials, children chose the higher CV/higher EV gamble more often (79%) than adults (45%) of High Risk, $F(2,52) = 19.43, p < 0.001, \eta^2 = 0.31$. Figure 20B shows that participants were also influenced by High Risk CV, choosing the riskier option less often as it's CV increased, $F(2,52) = 19.43, p < 0.001, \eta^2 = 0.12$, while an interaction between High Risk and age group showed that the effect of High Risk CV was greater for adults than for children, $F(2,52) = 7.88, p = 0.001, \eta^2 = 0.05$. There was also a marginal Low Risk by age group interaction, $F(2,52) = 1.65, p = 0.054$, suggesting that adults chose the riskier option more often as the less risky CV level increased while children did the opposite (Fig. 20A).
Figure 20: Risk-Risk trial behavior. (A) Marginal interaction ($p = 0.05$) between age group and CV of the low risk-return choice shows adults tend to chose the higher risk-return option as low risk CV increases while children tend to do the opposite. (B) Participants chose higher risk-return option less often as it’s CV increases, and this effect was stronger in adults. (C) Adults tend to choose the lower risk-return option more often as the difference in CV between choice options increases.

As in a previous study (Paulsen, et al., 2011), we analyzed choice behavior in Risk-Risk trials as a function of the difference between CV levels (delta CV) of gamble options. Results from this mixed effects logistic regression showed a significant effect of delta CV ($p < 0.001$) and an interaction between delta CV and age group, $p < 0.001$. Running this regression on each age group separately showed the expected effect of delta CV for the adult group ($p < 0.001$) but not for children ($p > 0.67$).

**Eye-Tracking**

After trial and participant exclusion, only 6 children and 14 adults remained for the analysis of eye-tracking data during the decision phase of Risk-Risk trials. Five of these six children had fewer than 5 trials in which the lower EV/lower CV option was selected available for analysis. Thus, these data were underpowered with respect to predicting choice behavior from eye-tracking measures and were therefore not analyzed.
After trial and participant exclusion, 14 children and 9 adults remained for the analysis of eye-tracking data during the outcome phase of Risk-Risk trials. Recall that only trials in which the riskier option was selected were analyzed. After winning, children and adults showed similar patterns in what they attended to, looking most often at what they had won (Fig. 21A). After loses, children appeared to spend the greatest proportion of time looking at the High CV win object, next greatest at the High CV loss object, and less time at the Low CV win and loss objects (Fig. 21B). Adults on the other hand appeared to view each of the win and loss objects an approximately similar proportion of time, though slightly more time at the High CV win and loss objects than the Low CV win and loss objects.

**Figure 21:** Looking behavior differs between children and adults after wins and losses. (A) After wins, both children and adults spend a large proportion of time viewing the Win object. (B) After losses, adults look at all objects of the chosen and unchosen options, while children tend to focus mostly on the Loss and Win objects of the chosen option, and relatively little time at all on the Win and Loss objects of the unchosen option, again suggesting less experienced regret.

Independent sample t-tests between children and adults on proportion of dwell times after wins returned only a marginal difference for the Low CV loss object ($p = 0.089$), on which adults spent a slighter larger proportion of time (6.9%) than children (2.5%) did
(all other $p > 0.145$). After losses, however, adults and children differed in the proportion of dwell time spent on all but the High CV win object ($p = 0.488$), all other $p < 0.003$.

**Pupilometry**

The analysis of pupilometry data from Risk-Risk trials (16 children, 8 adults) followed the same procedure used in Risk-Safe trials, except that only 2 levels of outcome (Win, Loss) were used. The general pattern of pupil dilation after winning and losing outcomes for children and adults in Risk-Risk trials (Fig. 22) were similar to those observed in Risk-Safe trials (Fig. 19): pupil dilation increased until about 1 second after losses in both children and adults, and after wins in children. Adults showed a brief (~0.4 sec) period of dilation after wins, then ~0.2 sec constriction followed by another period of dilation. Also similar to Risk-Safe trials, a main effect of outcome was found from 0.59 sec to 1.21 sec, indicated by the shaded area in Fig. 22, showing that wins elicited greater dilation than losses in this time range. P-values for the interaction between age group and outcome were not significant for longer than 10 continuous samples.

**Figure 22:** Pupil dilation when viewing Risk-Risk outcomes shows a pattern similar to Risk-Safe outcomes. Children show similar pupillary responses after wins and losses, which are also similar to adult pupillary response after losses. Adults differ in the relative pupillary constriction occurring after wins.
Discussion

Our analyses of eye-tracking and pupilometry data revealed several noteworthy differences between children and adults during decision-making and outcome evaluation. First, children spent proportionately more time looking at winning values than adults before choosing to gamble. Second, children spent less time looking at alternative choice options after losing a gamble. And third, pupillary response was different between children and adults after wins, but not after losses or safe bets.

Although children and adults showed similar patterns of looking at the objects of choice options during decision-making, subtle differences suggest that children value gamble options more than adults. Both groups were more likely to look at the Sure Bet object most often and last before choosing a safe bet, and more likely to look at the Win object most often and last before choosing a gamble. These findings are consistent with previous work that has used drift diffusion modeling with eye-tracking and choice behavior (Krajbich, et al., 2010; Krajbich & Rangel, 2011). Differences between children and adults were found however in the amount of time they spent looking at the Win and Sure Bet objects prior to choosing a gamble. Children trended towards looking longer at the Win and less at the Sure Bet objects. In the framework of CPT, decision weights can be accorded differentially to relative gains and relative losses (Tversky & Kahneman, 1992), and in one formulation this has been translated as the amount of attention given to relative gains and losses (Lopes, 1995). Children’s patterns of looking behavior suggest that they assign relatively greater weight to the value of gamble options than adults do, and less weight to the value of safe bet options. Although we did not have the power to analyze looking
behavior as a function of risk level, these findings are consistent with the idea that children’s preference for increasing CV is related to increased attention to the larger winning value, but not decreased attention to the smaller losing value.

During outcome evaluation, adults displayed patterns of disappointment and regret, while children displayed patterns mostly of disappointment. Both disappointment and regret are negative emotions associated with undesirable outcomes, but regret differs in that it is also associated with unchosen actions (Bell, 1985; Loomes & Sugden, 1982). After losses, children spent more time looking at the losing outcome, less time looking at the unchosen sure bet object, and a similar proportion of time looking to the unobtained winning outcome, than adults. Because participants in our paradigm gain coins even for a loss, is reasonable to suggest that disappointment is enhanced by viewing what was not won. Depending on whether we consider the total proportion of time looking at the unobtained winning outcome or the ratio of looking time between the loss and winning outcome, children either display similar or less disappointment, respectively. Given the relative time that children and adults spent looking at the unchosen sure bet object, it is clear that the pattern of children’s looking behavior is consistent with displaying less regret. These patterns were found in the analysis of losses in Risk-Risk trials as well, where children spent relatively little time looking at the objects of the alternative choice. This interpretation is supported by recent studies showing that both anticipating and experiencing regret develop slowly between childhood and adulthood (Guttentag & Ferrell, 2008; Habib, et al., 2012).

Pupilometry measures suggest that children are equally surprised by both wins and losses, while adults show surprise only for losing. Previous research suggests that pupil
dilation is related to arousal (Bradley, Miccoli, Escrig, & Lang, 2008), surprise (Preuschoff, et al., 2011), and attention or sustained effort (Piquado, Isaacowitz, & Wingfield, 2010). Of these, the most related study is by Preuschoff et al. (2011). They used an auditory gambling task in which participants bet whether the first or second card flipped would have the largest value. Pupil diameter decreased with the level of uncertainty of winning after the first card flip, for example when the values of the first card were in the middle of the range of possible values. After the second card flip revealing outcome, pupil diameter increased with the level of surprise, defined as a change in sign between the expected and actual reward. Significant differences in this effect were found from 0.79 to 1.56 sec. This time frame is similar to the 0.75 to 1.34 sec time frame within which we found a significant main effect of outcome in our data, suggesting these pupillary responses could indicate level of surprise.

However, pupil dilation after viewing the certain outcome was found to be intermediate between wins and losses in the adult data, suggesting the need for an alternative interpretation of these data. The outcome of a sure bet is de facto unsurprising, so it would be strange to say that a sure bet outcome is more surprising for adults than a winning outcome. Previous studies have found increased pupillary diameter to arousing stimuli more than neutral stimuli (Bradley, et al., 2008), and to cues indicating win and loss more than neutral outcomes (Seymour, Daw, Dayan, Singer, & Dolan, 2007). Although in the Bradley et al. study (2008) both pleasant and unpleasant stimuli had the general effect of increasing pupil diameter, this effect was most pronounced for high arousal stimuli. For low arousal stimuli, pleasant stimuli elicited slightly smaller dilation than neutral stimuli (non-significant), while unpleasant stimuli elicited significantly larger dilation (Fig. 3 of Bradley,
et al., 2008). Thus, our pupilometry results could be interpreted as indicators of high arousal at outcome for children, and low arousal at outcome for adults. One issue remaining with this interpretation is the time frame within which arousal was found to affect pupil dilation; the effects of arousal were found after 2 sec, inconsistent with the earlier time frame of our effects.

Pupillary dilation has been associated with locus coeruleus (LC) activity and activation (Aston-Jones & Cohen, 2005; Critchley, Tang, Glaser, Butterworth, & Dolan, 2005; Gilzenrat, Cohen, Rajkowski, & Aston-Jones, 2003; Sterpenich et al., 2006). One of the proposed functions of LC is as a gating mechanism that facilitates processing of current stimuli, for example, when stimulus values need updating (Aston-Jones & Cohen, 2005; Sara, 2009). Projections to LC from anterior cingulate (Rajkowski, Lu, Zhu, Cohen, & Aston-Jones, 2000) and orbitofrontal cortex (Aston-Jones et al., 2002) are consistent with this proposed. On one hand, the relative pupillary constriction for adults in the win condition could indicate that wins do not signal a need to update the value of gamble prospects. Although we cannot know what participants were expecting upon choosing a gamble, we could speculate that when adults chose to gamble, they had a slightly higher expectation of winning than when they chose a sure bet. On the other hand, relative pupillary constriction for adults in the win condition could indicate that the value of gamble prospects were not updated upon winning, but that they were upon losing. This would predict that prospects lose value over time, with the consequence that gambling rate would decline until reaching equilibrium in both gambling rate and pupillary response to wins and losses.
**Conclusion**

Children and adults exhibit subtle differences in looking behavior and pupil dilation during decision-making and outcome evaluation. The disproportionate time children looked at winning values compared to adults before choosing to gamble suggests differential weighting in the valuation of gamble prospects. Second, the relatively little time that children looked to counterfactual choice options upon losing suggests that children experience less regret compared to adults. Finally, adults showed relative pupillary constriction after wins, but not losses, compared to children. This effect could suggest differences in the amount of surprise experienced by children and adults, or differences in either the signal to update the value of prospects or in actual updating.
Chapter 6 – Summary & Conclusions

Each of the studies presented in the previous chapters provide important details concerning the development of decision-making under risk. Most of these studies focused on choices between sure bets and gambles of equal expected value, where risk was defined as the coefficient of variation (CV), and task demands for working memory and symbolic numerical knowledge were kept to a minimum. Chapter 2 showed that economic risk-seeking behavior displays a linearly decreasing developmental trend. Chapter 3 found that neural systems supporting decision-making under risk increase activation with age during decision-making, with some areas in children showing increased activation with increased risk-aversion. The studies in chapter 4 found that children's general preference for gambles is not due to differences in probability estimates, their ability to learn from feedback, or to a general optimism for winning. Instead, it was suggested that children may simply value gambles more highly than their expected value. Evidence for this hypothesis was provided in chapter 5, in addition to evidence suggesting that children experience less regret during outcome evaluation than adults do, and that children and adults process winning in subtly different ways.

Risk-aversion has been defined by the concavity of the utility function in the expected utility framework, where a person is risk-averse if they prefer certain prospects over risky prospects of equal EV (Kahneman & Tversky, 1979). Weber and Milliman (1997) propose definitions of risk-seeking and risk-aversion as preferences for options that are perceived to have greater or lesser risk, respectively. This second definition better meets the needs of the data from chapter 2 in which terms are needed to describe the effect of CV on risk taking propensity. As the CV grows smaller, the values of the gamble option
approach their mean. It is safe to say, then, that in the limit, the values of a small CV are indistinguishable from a certain option of equal EV, and so should be indifferently preferred. Thus, both risk-averse and risk-seeking preferences should both start with indifference at the lowest levels of risk. Therefore, I will use the term risk-seeking to refer to a positive linear slope in the effect of CV, and risk-averse to refer to a negative linear slope, sticking to the domain of gains for simplicity.

**Chapter summaries**

One of the primary findings from the study in chapter 2 was that children showed risk-seeking behavior, adults showed risk-averse behavior, and adolescents were intermediate in their risk preference. Although this pattern of increasing risk-aversion with age has been reported from multiple labs and with different paradigms (Crone & van der Molen, 2004; Harbaugh, et al., 2002; Levin, Hart, et al., 2007; Rakow & Rahim, 2010; Weller, et al., 2010), it may seem surprising that adolescents were not the risky age group. Part of this surprise may be due to the emphasis recently of developmental researchers on importance of mitigating the negative outcomes of adolescent risky behavior (Casey, Jones, & Somerville, 2011; Galvan, et al., 2007; Steinberg, 2004, 2008). Thus, a strong contribution of the current findings to the developmental literature is that adolescents are not ipso facto risky, but that in at least one domain there is a clear, systematic shift from risk-seeking to risk-averse behavior that occurs over a relatively long time frame.

The imaging study from chapter 3 had three main findings. First, a network of decision-making related regions, including the striatum, anterior cingulate cortex, insula, orbitofrontal cortex, ventromedial prefrontal cortex, hippocampus, amygdala, and frontopolar cortex, increased in activation in age when deciding whether to choose a safe
bet or a gamble. This is an important finding for similar reasons to why the linear trend from risk-seeking to risk-averse behavior was important: a U-shaped pattern was not found. At least two studies have related inverted U-shaped activation in brain regions associated with decision-making to increased risk taking behavior among adolescents, though in both of these studies risk taking was not measured (Galvan, et al., 2006; Hare, et al., 2008). The second finding was that the insula, a region often associated with risk processing, showed a robust linear pattern of activation during decision-making from childhood to adulthood. This finding is important because it adds another region to the small list of executive function and reward processing regions often focused on with regard to risk taking in development. The third finding was that in children, OFC and striatum activation increased with increasing risk-aversion. This finding is important because it contrasts with studies that suggest increased reward sensitivity – evidenced by heightened striatal activation – could be one reason why adolescents are so risky (Chein, et al., 2010; Galvan, et al., 2006).

The main findings of the experiments in chapter 4 were that children, similar to adults, adjust their risk-taking behavior according to the probabilities of winning, and that children are not simply optimistic about their chances of winning, but that they shift risk preference depending on whether gambles are presented in the domain of gains or losses. Precision in the representation of probabilities was a significant predictor of gambling rate as a function of winning probability, which might be considered a droll result in a mature population, yet indicates that children capable of performing at adult like levels in the feedback learning task displayed risk preferences very similar to adults across different probabilities of winning. The finding that children were risk-seeking for gains and risk-averse for losses suggests that children are systematic in their preference for risk. The shift
in risk preference, in both children’s and adults’ behavior, can be explained by cumulative prospect theory (CPT; Kahneman & Tversky, 1979; Tversky & Kahneman, 1992). The explanation given by CPT is that children may differentially attend to the largest magnitude outcome possible in both gain and loss domains, which inflates and deflates the value of the gamble option in gain and loss domains, respectively.

A third finding of chapter 4 was that the effect of CV and its interaction with age shows a flip about the axis of indifference from risk-seeking to risk-averse between the ages of 8 and 12. This is roughly the age in Piagetian theory at which children are in the concrete-operational stage, capable of reasoning about physical objects, but unable to reason about hypotheticals and general cases. One possible link between these two observations may be the development of generalization skills. In chapter 3, it was found that activation in certain context-related regions, namely the amygdala and hippocampus, increased with age during decision-making. The interpretation of this pattern conjectured that children might not incorporate the outcomes of previous decisions into the current decision-making process. The application of experience to new situations requires the ability to generalize from one specific context to another.

Chapter 5 used an eye-tracking methodology to reveal differences between children and adults in the amount of attention given to the different elements of the sure bet and gamble propositions during decision-making, both prior to choice and at the time outcome presentation. Consistent with the hypothesis following from the results in chapter 4, children spent disproportionately more time attending to the largest possible outcome prior to choice, but this was true only on trials in which the gamble option was selected. Thus, at least in trials in which gambles were selected, children may have assigned a higher
value to the gambles. However, the direction of causality in the relationship between looking times and preference has not yet been established. Upon viewing outcomes, both adults and children look predominantly at the winning amount if they won, and at the sure bet amount if that is what was selected. After losses, adults attended to obtained outcomes, unobtained outcomes, as well as the unchosen sure bet and alternative gambles, while children looked primarily only to the obtained and unobtained outcomes of the selected gamble. These differences were interpreted to indicate that while adults experience both disappointment and regret after a losing outcome, children experience primarily disappointment. A primary distinction between the negative emotions of regret and disappointment is that while regret refers to a course of action that could have been taken, disappointment refers only to the course of action that was taken. Given this distinction, one could infer from the current data that children encode negative outcomes differently than adults do, and that the lack of regret could contribute to children’s increased preference for risk.

Children and adults showed differences in how wins were processed through pupil dilations after viewing outcomes. Two possible interpretations are that adults find losses, but not wins, surprising, while children find both losses and wins surprising. This could suggest that adults have different expectations when choosing a gamble than children do. Namely, adults may partly expect to win at the time of choosing a gamble. The other interpretation is related to the Adaptive Gain theory of LC-NE function (Aston-Jones & Cohen, 2005) in which pupil dilation indicates an information gating process that allows the value current stimuli to be updated. This would suggest that while children update the values of gambles after both wins and losses, adults only update the value of gambles after
losses. This account is consistent with the decreased rate of gambling over trials observed in chapter 4, especially the interaction between age and trials that found that the effect of trials was stronger among older participants. This is because if adults update the value of a gamble after losses, the value of the gamble options should decrease over. Although the specific tests for the effect of cumulative losses and cumulative gambles on gambling rate was not found to be significant, it’s possible that patterns of pupil dilation on an individual and/or trial-by-trial basis could predict subsequent choice behavior.

Across the studies presented, both similarities and differences were found during decision-making under risk in children and adults. First, participants of all ages adjusted risk taking behavior according to the probability of winning a gamble. Second, participants also demonstrated similar preferences when making risk-return tradeoffs, in particular preferring the smaller risk, smaller expected value option as the difference in risk level between risky options increased, though this pattern was stronger among older participants. Third, all participants tended to gamble less often across trials, though this pattern too was stronger among older participants. Children and adults similarly looked to the sure bet option longest, and last, before choosing the sure bet. They also tended to look longest at the obtained outcome after choosing the sure bet and winning a gamble. With respect to neural activation, all age groups exhibited activation in posterior parietal cortex when comparing their options, and all age groups showed activation in the striatum, insula, and inferior parietal cortex after winning, and in the insula and ACC after losing.

The primary behavioral difference found between adults and children was that children were increasingly risk-seeking with greater levels of risk, while adults were found to be increasingly risk-averse with greater levels of risk. Children and adults exhibited
opposite risk preferences in the domain of losses compared to the gain domain, switching from risk-seeking to risk-averse and risk-averse to risk-seeking, respectively. Prior to choosing gambles, children looked a little longer at the winning object than adults did, and upon losing a gamble, children did not look much at all to the unchosen options suggesting a lack in the experience of regret. Adults also differed from children in pupilometry measures after wins, indicating that adults may not have been surprised at winning while children were, or that adults did not update the value of gambles after winning while children did. Activation of a network of brain regions associated with decision-making was also found to increase linearly with age during decision-making, most robustly in bilateral insula.

Although risk preferences in adults and children differ prima facie, they can be viewed as similar within a Cumulative Prospect Theory (CPT) framework (Tversky & Kahneman, 1992). CPT suggests indirectly that the amount of attention given to different outcome possibilities contributes to the weighting of gamble prospects (Lopes, 1995). Although this theory was developed in part to account for the risk-averse behavior commonly observed in the normal adult population, the same model can account for the risk-seeking behavior observed in children across the different studies here. This is because if children preferentially attend to the largest magnitude outcome, it will inflate the value of, and increase preference for, the gamble option in the domain of gains, while deflating the value of, and decreasing preference for, the gamble option in the domain of losses. Support for this idea was found in the looking behaviors of children and adults prior to choosing gambles.
Discussion

How might the CPT explanation relate to brain activation? Prospect theory is essentially a theory of valuation. It requires the integration of multiple pieces of information, e.g. magnitude and probability. One region that has been discussed as performing this role is vmPFC (Krawczyk, 2002), which was found in chapter 3 to increase in activation across age in a linear fashion. Another aspect of CPT is that ‘losses loom larger than gains’, which suggests participation of amygdala during valuation (Trepel, Fox, & Poldrack, 2005). This anatomical region, too, was found to increase in activation with age in a linear fashion.

While some have found some support for the participation of vmPFC and amygdala during decision-making (De Martino, et al., 2010; De Martino, et al., 2006), other studies have not found amygdala participation, but have additionally found insula, striatum, ACC, and OFC (P. Mohr, et al., 2010; Mohr, Biele, Krugel, Li, & Heekeren, 2010; Tom, et al., 2007). Trepel and colleagues (2005) have proposed several of these regions to be involved with Prospect Theory’s model of valuation, and if children differ in the valuation of a gamble, then we would expect to see differential activation in these areas. However, it would difficult to say whether differences in valuation arise through computational differences, i.e. activation in areas supporting valuation, attentional differences, i.e. differences in input, or both.

Regions associated with counterfactual outcomes increase in activation with age. The experiments of chapter 5 indicated that children may experience the negative emotion of disappointment, but not regret, to the degree that adults do. One study focusing on the experience of regret and disappointment found the middle temporal gyrus (MTG),
precentral gyrus, subcallosal gyrus, and midbrain to be activated upon disappointment, while the main regions associate with regret were the amygdala, OFC, ACC, and hippocampus (G Coricelli et al., 2005). In that study, effects of cumulative regret, i.e. multiple losses, revealed activation in both OFC and amygdala during choice, and was predictive of choice behavior. These authors interpret their results to suggest that activation at time of outcome in OFC and amygdala are repeated during choice as anticipation of regret. It’s possible that the relatively decreased activation in these areas during choice in children relate to the both choice behavior and looking behavior across the different experiments reported here.

In addition to regret, results from the experiment of chapter 5 suggested that adults, but not children, selectively update the value of gambles after losses, but not wins. Two brain regions that have been associated with information gating are the locus coeruleus (LC; Aston-Jones & Cohen, 2005) and the striatum (Frank & Claus, 2006). Partial support for the LC Adaptive Gain theory comes from the fact that LC receives projections from ACC and OFC (Aston-Jones, et al., 2002; Rajkowski, et al., 2000), regions known to participate in the process of valuation. Differential activation between children and adults were not found in any of these regions in response to gains and losses. The inferior parietal lobule and superior temporal gyrus were both found to be activated in children after losses and gains in the experiments of chapter 3, but these areas were also found to be activated in adults after losses and gains. Thus, neural support for the interpretation of pupilometry findings as updating was not found in the imaging data, though it should be noted that the presentation of outcomes were different across the two studies.
The neural mechanisms involved with decision-making under risk contribute differentially between domains, and these mechanisms change independently with age. Although the slope of the transition from risk-seeking to risk-averse was emphasized, it is important to note that not all adults are risk-averse for losses and risk-seeking for gains (Schoemaker, 1990). Likewise, it is not the case that all children are risk-averse for losses and risk-seeking for gains. Moreover, individual levels of risk-aversion and risk-seeking between domains are not correlated. Future studies will do well to image risk behavior in multiple domains to track the neural sources involved with this developmental progress.

A major goal of research on the development of decision-making is to help avoid some of the harmful consequences of poor decision-making. Decision-researchers have classified several stages (Ernst & Paulus, 2005; Rangel, et al., 2008) and multiple domains, e.g. financial, health, recreational, ethical, and social domains, of decision-making (Weber, et al., 2002). The study of decisions leading to reckless behaviors like alcohol use, drug use, unsafe sex, stealing, etc., may be facilitated by using some of the definitions and insights gained from the study of neuroeconomics (Hasler, 2011). Ideally, a direct link would be made between domains. Whether or not these links are made, by breaking down the decision-making process into its components not only offers the identification of differences in valuation and motivation, but also how learning from outcomes and applying that learning to future contexts changes during development.

Another necessary approach is differentiating between risk-seeking, novelty-seeking, and exploratory behavior. Initial explorations are de facto both novel and uncertain, and because of this uncertainty there is an element of risk. It is not clear which, or how much, of adolescent risky behavior is better explained by novelty seeking or
exploration. The risky behaviors often cited to increase among adolescents tend to include alcohol use, smoking, drug use, premarital sex, unprotected sex, and reckless driving. From statistical reports citing increased incidence of these behaviors among adolescents, we can infer that the drive to engage in these behaviors declines with age. Coincident with this decline, it is reasonable to assume that these behaviors lose their novelty. Another interpretation could be that after adolescents have participated in these risky endeavors, their knowledge of the possible risks and rewards accompanying them informs their future risky decision making, and that this information, for most, suggests risk-averse courses of action. Thus, risky decision making in adolescence is potentially confounded by novelty seeking and information seeking.

In the literature on human development, exploratory behavior often refers to information seeking with respect to objects, events, and the surrounding environment (Gibson, 1988). The physical qualities of objects (textures, edges, and composition) can be explored manually and orally. The affordances of objects are learned by visual observation, or visual exploration. Young children can see how others handle objects, and conversely how these objects are handled. After an infant develops locomotion, they are able to explore their environment, acquiring not only information about the immediate spatial layout, but also information of long-term importance about the features of surfaces, gaps and openings, and object occlusion.

Exploratory behavior in rodents is also interpreted as an information seeking response to novelty (Belzung, 1999). Although situational contexts can be modified to predictably alter behavioral response to novelty, generally, rodents prefer novelty over familiarity. This investigative behavior has been demonstrated for novel spaces, objects, and
conspecifics (Belzung, 1999) [Holeboard, Y-maze spontaneous alternation]. Another method of assessing rodent exploratory behavior in rodents is through the use of an open field. The open-field test makes use of an open arena surrounded by a wall. Rodents are naturally agoraphobic, and therefore prefer to hug the walls of this open-field. Exploratory behavior can be measured by how far away from the walls a rodent will navigate. Given that food deprivation enhances this kind of exploratory behavior, it can be surmised that at least some exploratory behavior is motivated by the search for primary reward, i.e. food. In addition, the natural tendency to avoid open spaces, and light, is consistent with avoiding predation. Thus, behavior in the open-field test can also be interpreted as goal-directed behavior that trades off risk for reward.

Novelty, information, and rewards, share a common substrate. Midbrain dopamine neurons signal the unexpected receipt of reward, the conditioned anticipation of reward, and have also been found to respond to non-aversive novel stimuli (Kakade & Dayan, 2002; Schultz, et al., 1997). The ventral striatum – a known target of midbrain dopamine neurons – has also been shown to be activated by novel stimuli eliciting an orienting response (Berns, Cohen, & Mintun, 1997; Zink, Pagnoni, Martin, Dhamala, & Berns, 2003). In addition to novelty and reward prediction, midbrain dopamine neurons signal the receipt of reward-related information, which can be interpreted to suggest that information per se has inherent reward value (Bromberg-Martin & Hikosaka, 2009).

Exploratory behavior as information seeking can be extended to adolescents as well. The onset of puberty is met with hormonal changes, which in a sense opens up a new world to adolescents. Peers become an important part of life, as do members of the opposite sex,
and an uncharted social territory emerges in which social and environmental cues have yet to acquire meaning, motivating exploration of this new terrain.

**Conclusion**

The studies presented here aimed to identify three things: factors contributing to age-related changes in risk preference, where in the decision-making process these factors have influence, and changes in neural circuitry that could be responsible. During valuation, risk level, the values of choice options, and domain (gains or loss) in which options are presented, differentially modulate risk preferences across development. It is hypothesized that a lack of regret during outcome evaluation may also contribute to differences in children’s risk preference compared to adults, although this is not definitive. Although many brain regions become more active with age, suggesting that the development of a decision-making network leads to more adult-like behavior, greater activation of orbitofrontal cortex and the striatum were associated with greater risk-aversion, making these two regions stand out as particularly relevant to the development of risk-aversion from childhood to adult hood.
References


Bates, D., Maechler, M., & Bolker, B. (2011). lme4: Linear mixed-effects models using S4 classes (Version 0.999375-42).


Ernst, M., Bolla, K., Mouratidis, M., Contoreggi, C., Matochik, J., Kurian, V., et al. (2002). Decision-making in a risk-taking task: A PET study. *Neuropsychopharmacology, 26*(5), 682-691.


van den Bos, W., Güroğlu, B., van den Bulk, B., Rombouts, S., & Crone, E. (2009). Better than expected or as bad as you thought? The neurocognitive development of probabilistic feedback processing. *Frontiers in Human Neuroscience, 3*.


Biography

David Paulsen was born in Upland, California, on August 29, 1975. He attended Chemeketa Community College (1993-1995; 2000), and Mt. Hood Community College (2000), where he met the requirements for the Associate of Arts Oregon Transfer Degree completed in the Summer of 2000. David then attended University of Oregon (2001-2003) as an undergraduate, earning a Bachelor of Science degree, double majoring in Philosophy, with Honors, and Psychology, in the Spring of 2003. David was awarded a Graduate Teaching Fellowship at the University of Oregon in 2005 to complete his Master of Science degree in Psychology, Spring 2006. David matriculated into the Graduate School of Arts and Science through the Department of Psychology and Neuroscience at Duke University in the fall of 2007, and was awarded the Ruth L. Kirschtein pre-doctoral National Research Service Award from the National Institutes of Health, National Institute on Drug Abuse division, in 2010 to complete his doctoral education. In 2011, he was awarded with an honorarium by the Scientific Research Network on Decision Neuroscience & Aging.

Publications


