An experimental approach to examine behavior and brain activity during decision-making under risk as compared to ambiguity

Benjamin Albrecht[1], Johannes Hewig[1], Patrick Mussel[2], Isabell Welpe[3], Angela Stanton[4], and Wolfgang Miltner[5]

[1]Julius Maximilians University Würzburg
[2]Freie Universität Berlin
[3]Technische Universität München
[4]Affiliation not available
[5]Friedrich Schiller University Jena

October 30, 2023

Abstract

Neural correlates of decisions under risk and under ambiguity have been examined for several decades. In the current study, we focus on a neglected aspect that is a potential confounding of the average risk of alternatives in a trial, the average magnitude of the outcomes, and the difference in risk between the two alternatives. We present an experimental approach to solve this problem here and explicitly separate risk and ambiguity. In the present fMRI-study with 20 participants, we created different levels of risk and ambiguity to investigate their effects on behavior and brain activation. In a first experimental block, decisions with mixed-risk options (one high-risk option paired with one low-risk option) were compared to decisions with two high-risk or two low-risk options in terms of the effects on decision-making and neural activity. The second block consisted of the same risk levels crossed with high and low ambiguity by withholding information about the probabilities of the outcomes. During mixed-risk trials participants made cautious decision significantly more often. This effect was strongest during mixed trials with high ambiguity in the second block. In addition, risk behavior of subjects was correlated with the subjective importance of the amount of potential monetary losses or wins and the related probabilities. The fMRI results revealed activation of the dorsal anterior cingulate cortex (dACC), the insula, and the orbitofrontal cortex (OFC) during mixed risk trials without ambiguity. In contrast, activation of the amygdala was specifically present during mixed-risk trials with high ambiguity.

Introduction

Decision-making is influenced by the value of outcomes, the probability of outcomes, and the ambiguity or risk of outcomes (e.g. Kahneman et al., 1997; Kahneman & Tversky, 1979). According to a classic distinction between ambiguity and risk derived from Knight (e.g. Chen & Epstein, 2002; Huettel et al., 2006; Knight, 1921; Krain et al., 2006), a decision situation is defined risky when the actual outcome of the decision between options is unknown, but the probability distribution for different outcomes is known. In contrast, a decision is ambiguous when the actual outcome and the probability distribution of potential outcomes are both unknown (Ellsberg, 1961; Knight, 1921). In all these cases, preferences of decision options are defined according to the chance distributions of options, i.e., according to their expected value (EV). For risk, these chances are taken to be objective, whereas for uncertainty, they are subjective. Furthermore, the size of the risk of options can be described by the spread of outcomes (Rothschild & Stiglitz, 1970), and the size of ambiguity by the lack of information (Ellsberg, 1961; Knight, 1921). The size of risk and ambiguity reduce the utility of an option. Accordingly, the goal of the present study was to vary experimentally both risk and ambiguity in order to compare them on the behavioral and on the neural level. Usually, people are even

more averse to ambiguous options than to risky options supposedly also indicating a reduction in subjective utility.

During the past decades, many different studies investigated behavior of people under risk and ambiguity. Many different experimental approaches were used, which differed in paradigms and parameters, e. g. various kinds of gambles, known and risky options, or risky options only, gambles with possible gains and losses or only with gains, and special tasks like the Iowa Gambling Task (Bechara et al., 1997, 2005; Li et al., 2010), Blackjack (Hewig et al., 2010; Hewig et al., 2009; Hewig et al., 2007; Hewig et al., 2008) or the Balloon Analogue Risk Task (Lejuez et al., 2002; Mussel et al., 2015; Rao et al., 2008). Recent studies also used functional magnetic resonance imaging (fMRI) to identify blood oxygen level dependent (BOLD) responses to risky and ambiguous situations in order to reveal its neural underpinnings (e.g. Bach et al., 2009; Hsu et al., 2005; Smith et al., 2002; Tobler et al., 2007). Some of these studies found activations of brain areas associated with EV, like the ventral striatum (Breiter et al., 2001; Knutson et al., 2001; Knutson et al., 2005; Tobler et al., 2007; Yacubian et al., 2006) or the anterior cingulate cortex (Brown & Braver, 2005, 2007, 2008; Kuhnen & Knutson, 2005). Others compared ambiguous and risky decision-making and showed that ambiguous decision-making is related to increased neural activity in the dorsolateral prefrontal cortex (DLPFC), amygdala, posterior inferior frontal cortex, and posterior parietal cortex (e.g. Bach et al., 2009; Hsu et al., 2005), whereas risky decision-making is related to activity in OFC, ACC, and parietal cortex (e.g. Krain et al., 2006; Platt & Huettel, 2008; Tobler et al., 2007). These differences may indicate that ambiguity imposes not merely more intense uncertainty but might even represent a different kind of uncertainty, which is based on a different neural processing by different neural sources. To differentiate between risky and ambiguous decisions, the magnitude, the probability, and the EV of decision options have to be defined as independent experimental variables and the functional neural structures have to be described that account for their differential phenomenological cognitive and behavioral functions.

To master such challenges, Tom, Fox, Trepel, and Poldrack (2007) investigated risky gambles using a parametric experimental design to assess BOLD responses related to risk and loss aversion. The network functional relevant for gains included regions in dorsal and ventral striatum, ventromedial prefrontal cortex (VMPFC), ventrolateral prefrontal cortex (VLPFC), ACC, OFC, and other dopaminergic structures whereas structures relevant for losses included the striatum, the VMPFC, ventral ACC, and the medial OFC. In relation to loss aversion, they showed activity in bilateral ventral striatum, bilateral lateral and superior PFC (pre-supplementary motor area), and right inferior parietal cortex. The authors termed this pattern a neural system of loss aversion.

In a subsequent study also using parametric analyses, Canessa et al. (2013) replicated activations in regions in the left ventral striatum and in the posterior frontomedial cortex in response to gains and losses. In addition, they found an interesting differential pattern of activation between losses and gains of the right posterior insula and the parietal operculum. These areas showed greater activation to increasing losses than deactivation to gains. An opposite pattern was found in the left ventral striatum and the frontomedial cortex, which showed larger loss-related deactivation than gain-related activation. Furthermore, they identified a loss-related network involving the right amygdala, putamen, and portions of the right posterior insula, indicating that the neural system of loss aversion involves the amygdala, thalamus, striatum, and posterior insula.

Based on these studies using fMRI we expected risk-related activity in dorsal and ventral striatum, ventromedial prefrontal cortex (VMPFC), ventrolateral prefrontal cortex (VLPFC), dACC (mainly BA 32), OFC, parahippocampus, inferior frontal gyrus IFG (BA 47), SMA (BA 6), frontomedial cortex, and insular cortex in mixed-risk trials for the parameter “wins”. In contrast, for the parameter ”losses” we expected activity in insula, parietal operculum, amygdala, thalamus, striatum (in particular ventral), VMPFC, ventral ACC, the medial OFC, bilateral lateral and superior PFC (pre-supplementary motor area), and right inferior parietal cortex. We further expected ambiguity-related activity in dorsolateral prefrontal cortex (DLPFC), amygdala, posterior inferior frontal cortex, and posterior parietal cortex. Since our experimental design eliminated the confounding influence of average risk levels between our experimental conditions, the remaining regions are

considered to relate specifically to the risk difference in mixed gambles.

In the gambling paradigm used here, the probability of outcomes was known to the subjects to elicit decisions under risk in one part of the experiment, and in the other part of the experiment the probability of outcomes was unknown in order to induce decisions under ambiguity. We completely avoided fully known outcomes, because risk and ambiguity may appear to be more similar in their presence because they both entail some uncertainty as compared to known outcomes. Instead, we varied both risk and ambiguity systematically to contrast and compare them to each other. The degree of risk was varied experimentally by using three different combinations of high- and low-risk options in each trial of a two-choice decision-making task. High-risk gambles comprised two high-risk options, low-risk gambles comprised two low-risk options and mixed-risk gambles comprised a high- and a low-risk option. EV was always the same in each gamble. This enabled us to experimentally separate influences of the difference in risk from the overall level of risk or EV and from the overall level or magnitude of gains and losses. Previous studies used known outcomes versus risky gambles, or known outcomes versus ambiguous gambles. Thus, for each decision between two gambles the average risk level of both alternatives (high/low) is confounded with the risk difference between the two alternatives. For example, many studies use a known outcome option and a risky option. The risky option can vary in its variance of outcomes. Thus, the average risk of both alternatives and the average magnitude of the outcomes are confounded with the difference in risk between the two alternatives. A trial with a known option and a low-risk option has lower overall risk, lower difference in risk between the options, and lower outcome magnitudes. Whereas a trial with a known option and a high-risk option has higher overall risk, higher difference in risk, and higher outcome magnitudes. Accordingly, a difference in brain activation in the comparison of these two kinds of trials may be due to any of these three differences between trials. For this reason, we combined 2 kinds of options: high-risk options (larger variance in outcomes) and low-risk options (smaller variance in outcomes). Thus, we created a high-risk condition with two high-risk alternatives, a low-risk condition with two low-risk alternatives and a mixed risk condition with a low and a high-risk option. If we now compare brain activity between the mixed condition and the average of the two other conditions, we may disentangle risk level and risk difference.

We expected that minimizing the risk is primarily triggered by the difference of outcome variance between the two options, which should lead to the strongest risk aversive effects in mixed gambles. We further varied the degree of ambiguity experimentally in another block of trials by using one condition without any information about the probability (high ambiguity) as compared to another condition where we provided a range of probabilities for each outcome (low ambiguity). In a narrow sense of decision-making under risk, where all information is available, the latter trials with high ambiguity are not decision-making under risk. However, according to the definition of the degree of risk with the spread or variance of outcomes these trials can still be recognized in terms of higher or lower risk, since the magnitude of the difference between the potential wins and losses (variance of outcomes) is a function of risk level even in the absence of probability information. This allows a systematic comparison of decision-making under risk with decision-making under ambiguity across experimental blocks keeping all other aspects of the task comparable.

In the present study, we aimed to clarify and extend previous findings by using mixed-risk trials with and without ambiguity and compared them to high- and low-risk trials. Furthermore, we aimed to compare risk and ambiguity directly with each other. Thus, the target condition is as similar as possible to the control conditions. We focused on the moment of decision-making in our analyses. Following previous research (Canessa et al., 2013; Tom et al., 2007), we also used a parametric fMRI design to separate effects that are due to potential gains from those of potential losses. Importantly, previous research focused on the idea of neural loss aversion, which is related to the different degree of brain activity in response to gains and losses, and supposedly drives cautious decision-making under risk. In addition, Vorhold and colleagues (2007) showed that subjective ratings of risk are moderating decision-making. We therefore also assessed ratings of riskiness and reports about reasons of individual decision-making.

Methods

Participants

The study was approved by the local ethics committee. 20 right-handed volunteers participated in this study (10 females and 10 males; mean age: 24 years, SD = 3.1 years, range 19 – 32 years). They were paid 6 Euro per hour for participation and could earn an extra bonus depending on their success of gambling. Every participant gave written informed consent for participation after receiving verbal and written information about the purpose and course of the experiment and after examination by a physician whether any risk would not allow the MRI application. Following the MRI recording, participants completed several questionnaires (see below). For every participant, a log-file recorded during the time points when a trial started and the latency of choosing an option. Based on this information, the first-level analyses of imaging data were conducted, as described below. In addition, log-files of all three risk levels included information on the decisions of participants and their choice of riskier or less riskier options.

Procedure

In the MRI scanner, participants performed a two-choice decision-making task by deciding between two options (see Figure 1). Each option had a probability p (between 5% and 95%) for winning and a corresponding probability 1-p for losing. The EV of all options was kept constant at 0.10 Euro. Each option was either of high or low risk according to the variance of the monetary outcome per option (as compared to all options used in the study). A trial was defined as high-risk trial if both alternatives were high-risk options (both gambles with large variance in outcome). The range of wins was 15 to 100 Cents and that of losses between -15 to -100 Cents with a difference between winning and losing outcome of 100 and 200 Cents for high-risk options. A low-risk trial consisted of two low-risk options, which had a low variance in outcome. The range of wins here was 11 to 57 Cents and that for losses between -5 and -60 Cents and the difference between the winning and losing option ranged between 16 and 75 Cents. Finally, in mixed-risk trials one option of high risk was paired with one option of low risk.

The task included three scenario blocks of 99 trials each (see supplementary Table 4). In the scenario block with pure risk options every trial had one of the aforementioned risk levels (33 trials each). A second scenario block consisted of 99 trials with these three different risk levels transformed into trials with high or low ambiguity where the probabilities p and 1-p were either unknown (high ambiguity, 48 trials, see Figure 1 for an example) or given as a range of the probabilities (e.g. between 30% and 50%; low ambiguity, 51 trials, presented as "30-50%") in half of the trials, respectively. In the latter case, the range of outcomes was presented and indicated the level of risk to participants. And finally, in a third scenario block, risk and ambiguity trials were mixed (results for this block will be presented elsewhere). The order of the three scenario blocks was counterbalanced across participants.

Every trial started with an initial fixation cross that was presented on a monitor screen for 525 ms plus an individual period for each trial varying between 10 and 25 ms (timeline shown in Figure 1a). After this initial phase, the trial options to choose were presented on the screen for up to 3000 ms and participants were requested to decide for one of the options. If participants did not choose during this time period they lost the gamble. Then visual feedback with a colored frame around the chosen option was presented upon button press until 3000 ms elapsed since presentation of the options screen. Subsequently a screen informed whether they won or lost the gamble (for additional 1250 ms). Finally, a last screen showed the total amount of money they won so far (for 1250 ms).

fMRI Data Acquisition and Analysis

Brain activation of participants was measured using a 3 Tesla magnetic resonance scanner (Magnetom Trio A, Tim System, Siemens Medical Systems; Erlangen, Germany). For the functional analysis, 110 volumes of echo-planar-images were acquired using a T2*-weighted sequence (TE = 30 ms, flip angle = 90°, matrix = 64 x 64, FOV = 192 mm, TR = 2.7 s). Each volume comprised 40 axial slices with 3 mm thickness and an interslice space of one millimeter creating a voxel size of 3 x 3 x 3 mm. In addition, an anatomical scan with high resolution was acquired using a T1-weighted MPRAGE sequence with a voxel size of 1 x 1 x 1 mm. For data preprocessing, the first four volumes were discarded to secure steady-state tissue magnetization. Preprocessing and data analysis was performed using the software SPM8 (Wellcome

Trust Centre for Neuroimaging, University College London). Data were realigned to minimize effects of body movement. Realigned data then were normalized and transposed to the Talairach space (Talairach and Tournoux, 1988) using the anatomical image that was co-registered with a T1-template and the mean image of the realigned data. After normalization, the images were smoothed with a Gaussian kernel of 8 mm full width at half-minimum (FWHM). Preprocessed data were used for first level analysis where the onset and duration of the decision-screens were taken to assess the activation during the three different stimulus conditions (high, low, and mixed risk). In addition, we added two parameters in the parametric SPM model for every stimulus condition for the potential gain and the potential loss. These parameters were calculated as the sum of the potential wins the sum of potential losses of these two options. For the first-level analysis, contrasts of predictor estimates (beta-weights) were defined for each risk level (i.e.: high risk, mixed risk, and low risk). The expected blood oxygen level-dependent (BOLD) signal changes were modeled using a canonical hemodynamic response function. The resulting contrast images of each participant were used for second-level ANOVA calculations (group level). At the end we got group level predictor estimates (beta-weights) which we used for calculating contrasts for comparison between risk and ambiguity, mixed-risk trials in comparison to high- and low-risk trials with and without ambiguity and for the parametrical results of potential gains or losses. The analysis focused on the time of the decision-making. Results of the analysis within each Region of Interest (ROI) were regarded as statistically significant when t-values were < 0.001 uncorrected. ROIs were defined using the Talairach client software (Talairach Project, International Consortium for Brain Mapping). In order to prevent false positive activations, results are reported only for brain areas which showed z-value higher than 3.09 – i.e., $p < 0.001$, uncorrected – and a volume greater than 180 mm^3 - i.e., five voxels with a spatial resolution of 3 x 3 x 4 mm (here we opted for four millimeters, because the thickness of measured slices was three millimeter plus a distance between slices of one millimeter).

Questionnaires

Questionnaires presented after the fMRI experiment assessed the perceived risk of options and difficulty of decisions using a rating scale ranging from 1 (no difficulty) to 9 (very difficult). Participants were further asked to rate how much they decided between options as a function of the amount of potential gain or potential loss of the choice and how much they felt influenced while choosing by the probability of wins and losses of their decision options. For all of these rating questions, we presented examples taken from the real experiment, which represented each of the experimental conditions respectively (one sample trial for each condition to remind participant of the condition). We realized all levels of risk and ambiguity; the ratings were made separately for each experimental trial that represented each condition.

We also included several personality questionnaires (results will be presented elsewhere) to assess trait-like differences related to decision-making (Budner, 1962; Carver & White, 1994; McLain, 2009; Zuckerman, 1996).

Data Analyses

For the analyses of behavioral decision-making data, we used a general linear model. Risk (three levels: low, high, mixed risk) served as within-subject factor and gender as between-subjects factor for pure-risk trials. For ambiguous trials, the three levels of risk were fully crossed with either low ambiguity or high ambiguity. Accordingly, ambiguity served as a second within-subject factor with these two levels of ambiguity. In addition, an ANOVA comprising both trial types was used to examine differences between no ambiguity (pure-risk trials) and low and high ambiguity (ambiguous trials).

We used Huynh-Feldt corrections, when the assumption of sphericity was violated. Follow-up Helmert-contrasts and t-tests were conducted to identify the direction of the effects and tested one-tailed for evaluating directed hypotheses. Significance level was p=.05, and only significant p-values are reported.

Results

Behavioral results

For the pure-risk trials (low-risk, high-risk, mixed-risk) the ANOVA revealed a main effect of risk (F (2,36)

= 5.98, p = .007, eta^2 = .25, epsilon = .92) on the percentage of choices of the option with higher variance of the outcomes (higher risk). Follow-up Helmert contrasts showed the significantly most cautious decisions in the mixed-risk condition as expected compared to the other two conditions (p = .016; Mean of mixed (M) = .35, SD = .16 and Mhigh = .44 and Mlow = .41, see Figure 1b). In addition, the percentage of cautious decisions was not significantly different between the low-risk and high-risk condition. There were no further significant effects.

For ambiguous trials, the ANOVA revealed a main effect for risk (F(2,36) = 12.86, p < .001, eta^2 = .42, epsilon = .86). It is important to note here that the spread or variance of outcomes was the same as in block 1 and defined the factor risk. As for the pure-risk trials follow-up Helmert contrasts showed the significantly most cautious decisions in the mixed-risk condition (p = .001, M = .33, SD = .18). Again, the percentage of cautious decisions was not significantly different between high and low-risk conditions. All other main effects and interactions were not significant.

Taken together, for both, the risk and the ambiguity block, mixed-risk options led to the highest percentage of cautious decisions. A combined analysis of risk and ambiguity blocks revealed a significant main effect of risk (F(2,36) = 15.7, p < .001, eta^2 = .47, epsilon = .84) and an interaction of risk with ambiguity (F(2,36) = 3.03, p = .023, eta^2 = .14, epsilon = .99). Post-hoc Helmert-contrasts showed that the interaction was due to more cautious decisions under high ambiguity for the mixed-risk condition compared to high-risk and low-risk trials in the conditions of pure risk and low ambiguity (p=.008). The condition with mixed-risk and high ambiguity led to the most cautious decisions (M = .30, SD = .18). Accordingly, high ambiguity further increased the risk-minimizing behavior in the context of mixed risk. Further, participants were relatively less cautious in the high-risk condition as compared to the low-risk condition under low ambiguity as compared to pure risk (p=.036). No other effects were significant.

Correlations with ratings

Participants' ratings about how much the potential amount of loss or gain or the respective probabilities influenced their decisions were correlated with behavioral decision-making (i.e., the relative choice of high-risk alternative). Results showed that subjects decided riskier if their choice depended more on the amount (r = .55, p = .012) and on the probability of the gain (r = .47, p = .042) for pure risk decisions. In addition, participants acted more cautious if they their decision was more based on the variance of potential losses in an ambiguous situation (r = -.46, p = .040, all other tests not significant).

Imaging data results

Condition-based non-parametric analysis.

For the neuronal analyses we focused on mixed-risk trials with and without ambiguity in comparison to high- and low-risk trials. During mixed-risk trials as compared to high- and low-risk trials in the pure-risk block significant activation was observed in the left parahippocampal gyrus (Table 1, Figure 2). In the ambiguity block activations were present in the right inferior frontal gyrus IFG (BA 47) for mixed-risk trials with high ambiguity compared to high- and low-risk trials with high ambiguity (Table 2, Figure 3). For the same contrast with low ambiguity, activity in the left supplementary motor area (BA 6) and in the left posterior insula was significant (Table 2, Figure 4).

The contrast high versus low ambiguity showed a significant BOLD effect in the mixed-risk condition. High compared to low ambiguity was correlated with activations in the right inferior parietal cortex and the left DLPFC in BA 9 (Table 2, Figure 5). As noted above, mixed-risk trials under high ambiguity showed the highest amount of low-risk decisions on the behavioral level.

Parametric analysis.

The parametric design analysis, with all the magnitudes of possible gains and losses included as parameters for each trial, revealed three main results: First, when examining the influence of wins, the dorsal ACC was significantly more activated during mixed-risk trials than in high- or low-risk trials (Table 3, Figure 6).

Second, losses significantly activated the insular cortex (BA 13) and parts of the lateral OFC only during mixed-risk trials but not during high- or low-risk trials (Table 3, Figure 7). Third, for ambiguous trials, significant activation was found in the amygdala during mixed-risk trials with high ambiguity but not in response to mixed-risk trials with low ambiguity for the parameter magnitude of gains (Table 3, Figure 8). For ambiguous trials we found no significant activation with respect to the loss parameter.

Discussion

The present study on decision-making under risk and ambiguity investigated the decisions of participants under different levels of uncertainty. We aimed to contrast risk and ambiguity on the behavioral and the neural level by experimentally varying these two types of uncertainty. Subjects were exposed to three different levels of risk: i.e., low, high, and mixed-risk and two levels of ambiguity: i.e. high and low ambiguity. Probabilities and outcomes were composed such that the expected value for all decisions was the same. Further, we defined the different levels of risk based on a suggestions of Rothschild & Stiglitz (1970) as the spread of potential outcomes. On the behavioral level, data confirmed classical effects of risk and ambiguity (see Ellsberg, 1961; Kahneman et al., 1997; Kahneman & Tversky, 1979; Knight, 1921). Subjects behaved significantly more cautiously when they had to decide between one high-risk option and one low-risk option. In addition, we found an effect of ambiguity on decision-making. High ambiguity – i.e., during a condition where any probability information was absent – led to the highest percentage of cautious decisions.

On the neuronal level, we found increased activity in the parahippocampal region during mixed-risk trials compared to high- and low-risk trials in the risk block indicating an effect specific for the risk difference between options. This region is closely linked to the amygdala (e.g. Roy et al., 2009; Stein et al., 2007) and part of the network that became activated during loss aversion in previous research (e.g. Canessa et al., 2013) and we are thus able to replicate earlier findings.

In the ambiguity block we found activation of the supplementary motor area (SMA), which we showed for mixed-risk trials with low ambiguity in comparison to high- and low-risk trials with low ambiguity. SMA activation has been repeatedly related to reinforcement signals that may be used to guide decision-making and action planning under risk and uncertainty. Recently, Canessa and colleagues (2013) found greater activation in SMA for individuals with greater loss aversion. Our data also corroborated earlier findings that activity of the insular plays an important role in the emotional evaluation of ambiguous decision in conditions for which information about probabilities of options are missing.

Higher ambiguity activated the dorsolateral prefrontal cortex (DLPFC). Activation of this region was previously found to be related to ambiguity (Krain et al., 2006). This activation is likely related to rule-based action selection and likely indicates the conscious or cognitive evaluation and manipulation of the relevant information in working memory and the integration of negative evaluative emotional information from the amygdala under ambiguous choice conditions. In addition, the inferior parietal cortex (IPC) was during mixed trials with high ambiguity in comparison to mixed trials with low ambiguity as well. Accordingly, DLPFC and IPC accordingly seem to respond specifically to higher ambiguity independent of risk. This region may be directly linked to the DLPFC activity and was described as neural index of working memory functions (e.g. Friedman & Goldman Rakic, 1994) and mathematical operations (e.g. Arsalidou & Taylor, 2011). Further, we found significant inferior frontal gyrus activation under high ambiguity when participants where exposed to mixed risk blocks as compared to low- and high-risk blocks, which indicates a role in the interaction of risk and ambiguity. This also replicates previous research (e.g. Bach et al., 2009; Hsu et al., 2005).

We could also identify greater activity in the dACC for gain and in the insula and lateral OFC for loss in the mixed-risk condition as compared to the average activation during low- and high-risk levels. This ensured that our activations were independent from the overall level of risk and the overall level of outcomes or from EV. Activation of dACC was also observed during action selection under uncertain reward (Hampton & O'Doherty,(2007) and by Christopoulos et al. (2009) who characterized dACC activity as an objective metric of risk. Furthermore, Canessa et al. (2013) showed increased activation in clusters of the dACC for

the parameter representing the magnitude of gains and deactivation for the magnitude of losses. Our results replicate these findings and are particularly well in line with those of Christopoulos et al. (2009) who observed stronger activity in dACC and more cautious decisions during conditions of pure risk. It has further been suggested that dACC activity reflects conflict (Botvinick et al., 2001) or a decrease in reward expectation (Holroyd & Coles, 2002) when the choice condition is risky.

Further, activation of the OFC was found during decisions under risk (Bach et al., 2009; Bhatt & Camerer, 2005; Krain et al., 2006). Bhatt et al. (2005) associated the OFC activity to the probability of gains, which was positively correlated with the level of ambiguity, whereas Krain et al. (2006) described a bilateral OFC activation for decisions under risk. We found activations in the OFC in mixed-risk trials when the possible loss was integrated into the analysis. Our results are in compliance to Kringelbach & Rolls (2004) suggesting that activity in the lateral OFC "is related to the evaluation of punishers which may lead to a change in ongoing behavior". Therefore, we suggest that the present orbitofrontal activation relates to the coding of punishment contingencies and may be related to the emotional evaluation of losses in the decision alternatives. This is underlined by additional activation of the insular cortex, which is an important structure for the integration of emotions, subjective awareness, and experience, and the representation of internal states of affect and arousal (e.g. Craig, 2011; Duerden et al., 2013). In summary, the effects of losses seem to be primarily of emotional nature reflecting the representation of the value of losses and at the same time the effect of losses on subjective emotional awareness in conditions of mixed risk.

The fMRI analysis of integrated gain and loss parameters that compared the two ambiguous situations, identified significant activations for gains. Here, the amygdala was activated. This is in compliance with studies both on risk and ambiguity (Breiter et al., 2001 ; Hsu et al., 2005; Krain et al., 2006; Kuhnen & Knutson, 2005; Platt & Huettel, 2008). Since our experimental design controls for the overall level of risk, outcomes and EV, our result may suggest that increasingly high wins under ambiguity may act as a conditioned cue for excessive risk. This may bias subsequent processing towards a more negative evaluation of the risky gamble in total. This seems to be in line with the amygdala's prominent role in affective conditioning (e.g. LeDoux, 2003).

Further, we asked the participants why they chose an option. Correlational analyses indicated that focusing on the amount and the probability of the gain in pure-risk situations led to incautious decisions. This provides further evidence that risk-taking becomes modulated by the expected value of options. Thus, we observed higher risk-taking under decision-conditions where a gain is more likely (for related evidence see Fochmann et al., 2017; Vorhold et al., 2007). In contrast, when participants realize a greater likelihood of loss in ambiguous situations, the behavior is more cautious. One limitation of the present study is certainly sample size in particular, in relation to the correlational findings. Future research should aim to corroborate these findings in larger samples.

In summary, for a risky context dorsal anterior cingulate cortex (dACC), insula, and OFC were activated in mixed trials that led to the highest percentage of cautious decisions in risk trials. Accordingly, these regions might reflect risk aversion in decision-making under risk and support previous research (e.g. Krain et al., 2006; Platt & Huettel, 2008; Tobler et al., 2007). Because we integrated potential losses, our findings do not provide evidence for a clear differentiation of risk aversion and loss aversion. Recent evidence suggests that these two kinds of effects have the same neural basis. For example, Canessa et al. (2013) found a significant correlation of loss aversion with risk aversion and Rabin (2000) postulated that loss aversion explains risk aversion in gambles with wins and losses. In particular, our experimental design focuses on the evaluation of humans in decision situations with different amounts of uncertainty that may all drive cautious decisions The behavioral phenomenon of risk aversion may be motivationally driven by loss aversion. In line with this argument, we found activation in regions that were demonstrated being relevant for loss aversion by Canessa et al. (2013) and/or linked to these areas, i.e., activation of the amygdala and the posterior insula; the SMA, the parahippocampal region. In summary, our results corroborate and extend the findings of Canessa et al. (2013) and supports a link between loss aversion and risk aversion and highlights a neural network for it. For a more extensive analysis and interpretation of individual differences in our data, our sample was too small.

Concerning ambiguity, we found that activity of the amygdala and activation of the IFG was present in mixed trials with high ambiguity when participants made the most cautious decisions. Further, an increase in ambiguity from low to high was indicated by increased activity in DLPFC and parietal cortex. Again our findings corroborate previous results showing activity for dorsolateral prefrontal cortex (DLPFC), amygdala, inferior frontal cortex, and parietal cortex (e.g. Bach et al., 2009; Hsu et al., 2005; Krain et al., 2006) in the ambiguous context and not in the risky context for trials inducing cautious decisions.

Taken together, we replicated that both kinds of uncertainty – risk and ambiguity – induce more cautious decision-making. As argued by Rothschild & Stiglitz (1970), the risk of options can be described by the spread of outcomes and risk avoidance behavior is primarily driven by the difference of risk between options. Ambiguity amplifies behavioral risk avoidance in such situations entailing risk differences between options in a non-additive, interactive way. Although some of our evidence suggests that risk avoidance under both ambiguity and risk may be driven by neural systems related to loss aversion, the systematic differences in patterns of neural responses between conditions of risk and ambiguity suggest basic differences between risk and ambiguity (Ellsberg, 1961; Knight, 1921) and their underlying neural sources (e.g. Bach et al., 2009; Hsu et al., 2005; Krain et al., 2006). Our own findings particularly support a special role of working memory related structures in DLPFC and parietal cortex that showed significantly different activity between high and low ambiguity conditions. The latter structures might be involved in integrating information from affective structures like posterior insula and amygdala in order to compensate for the missing cognitive numerical information to assess uncertainty and potential losses.

Acknowledgements: This study was supported by a grant from VolkswagenStiftung to JH.

Table 1. Activations for mixed-risk trials compared to high and low risk in the risk block

Region		Talairach coordinates X	Talairach coordinates Y	Talairach coordinates Z	Max. T-value	N Voxel
Risk_mixed > Risk_high/low						
Parahippocampus	L	-36	-18	-18	4.24	14

R = right; L = left; TAL = Talairach coordinates (x, y, z) of activated clusters; Max T = T level at this cluster; N = number of activated voxels. Activation threshold: $p < 0.001$ for ROI, uncorrected, explorative clusters > 5 Voxels

Table 2. Activations for mixed risk level with high or low ambiguity

Region		Talairach coordinates X	Talairach coordinates Y	Talairach coordinate Z
Risk_mixed_amb_high> Risk_high/low_amb_high				
IFG (BA 47)	R	34	18	-6
Risk_mixed_amb_low> Risk_high/low_amb_low				
Supplementary motor area (SMA, BA6)	L	-16	-4	58
Posterior Insula (BA 13)	L	-42	8	-8
Risk_mixed_amb_high > Risk_mixed_amb_low				
Inferior parietal cortex	R	36	-20	30
DLPFC (BA 9)	L	-24	44	10

R = right; L = left; TAL = Talairach coordinates (x, y, z) of activated clusters; Max T = T level at this cluster; N = number of activated voxels; DLPFC = dorsolateral prefrontal cortex (BA 9, 46); IFG = inferior frontal gyrus (BA 47). Activation threshold: $p < 0.001$ for ROI, uncorrected, explorative clusters > 5 Voxels

Table 3. Activations for mixed-risk trials with potential win and loss regressors

Region		Talairach coordinates X	Talairach coordinates Y	Talairach coor Z
Risk_mixed_win > Risk_high/low_win				
dACC (BA 32)	L	-12	24	22
Risk_high/low_loss>Risk_mixed_loss				
Posterior Insula (BA 13)	R	26	20	-10
OFC (BA 11)	R	26	38	-14
Risk_mixed_amb_high_win > Risk_mixed_amb_low_win				
Amygdala	R	32	0	-20

R = right; L = left; Tailarach coordinates = coordinates (x, y, z) of activated clusters; Max T = T level at this cluster; N = number of activated voxels; dACC = dorsal anterior cingulate cortex (BA 32); OFC = orbitofrontal cortex. Activation threshold: $p < 0.001$ for ROI, uncorrected, explorative clusters > 5 voxels

Supplementary Table 4. All trials of an experimental block.

condition of risk	pwin1	win1	ploss1	loss1	pwin2	win2	ploss2	loss2
L	0,9	17	0,1	-50	0,65	23	0,35	-15
L	0,7	31	0,3	-40	0,45	41	0,55	-15
L	0,35	47	0,65	-10	0,95	12	0,05	-30
L	0,85	14	0,15	-15	0,9	13	0,1	-20
L	0,6	30	0,4	-20	0,95	12	0,05	-20
L	0,6	27	0,4	-15	0,75	25	0,25	-35
L	0,5	25	0,5	-5	0,55	30	0,45	-15
L	0,85	21	0,15	-50	0,3	45	0,7	-5
L	0,6	40	0,4	-35	0,7	19	0,3	-10
L	0,9	15	0,1	-35	0,55	26	0,45	-10
L	0,75	27	0,25	-40	0,65	34	0,35	-35
L	0,6	23	0,4	-10	0,95	13	0,05	-40
L	0,9	13	0,1	-15	0,85	13	0,15	-5
L	0,5	30	0,5	-10	0,6	20	0,4	-5
L	0,6	33	0,4	-25	0,8	18	0,2	-20
L	0,95	12	0,05	-25	0,95	11	0,05	-10
L	0,65	32	0,35	-30	0,8	25	0,2	-50
L	0,7	23	0,3	-20	0,3	57	0,7	-10
L	0,9	14	0,1	-25	0,85	16	0,15	-25
L	0,75	22	0,25	-25	0,75	18	0,25	-15
L	0,55	43	0,45	-30	0,8	15	0,2	-10
L	0,7	25	0,3	-25	0,55	39	0,45	-25
L	0,9	17	0,1	-55	0,75	15	0,25	-5
L	0,85	14	0,15	-10	0,95	12	0,05	-35
L	0,95	13	0,05	-55	0,95	11	0,05	-5
L	0,5	45	0,5	-25	0,65	26	0,35	-20
L	0,65	18	0,35	-5	0,8	14	0,2	-5
L	0,8	16	0,2	-15	0,4	55	0,6	-20
L	0,4	48	0,6	-15	0,95	11	0,05	-15
L	0,45	34	0,55	-10	0,75	17	0,25	-10
L	0,5	40	0,5	-20	0,8	19	0,2	-25
L	0,85	17	0,15	-30	0,55	22	0,45	-5
L	0,7	16	0,3	-5	0,35	38	0,65	-5

condition of risk	pwin1	win1	ploss1	loss1	pwin2	win2	ploss2	loss2
M	0,9	12	0,1	-10	0,55	71	0,45	-65
M	0,8	20	0,2	-30	0,6	53	0,4	-55
M	0,75	23	0,25	-30	0,75	38	0,25	-75
M	0,8	21	0,2	-35	0,15	95	0,85	-5
M	0,95	13	0,05	-45	0,6	83	0,4	-100
M	0,85	20	0,15	-45	0,85	29	0,15	-95
M	0,9	16	0,1	-45	0,65	53	0,35	-70
M	0,9	12	0,1	-5	0,95	16	0,05	-100
M	0,35	56	0,65	-15	0,8	35	0,2	-90
M	0,75	28	0,25	-45	0,65	67	0,35	-95
M	0,65	29	0,35	-25	0,65	69	0,35	-100
M	0,55	35	0,45	-20	0,85	25	0,15	-75
M	0,25	55	0,75	-5	0,2	90	0,8	-10
M	0,7	21	0,3	-15	0,45	77	0,55	-45
M	0,65	21	0,35	-10	0,7	40	0,3	-60
M	0,4	33	0,6	-5	0,5	95	0,5	-75
M	0,7	29	0,3	-35	0,8	30	0,2	-70
M	0,55	88	0,45	-85	0,85	19	0,15	-40
M	0,8	34	0,2	-85	0,7	27	0,3	-30
M	0,55	59	0,45	-50	0,9	16	0,1	-40
M	0,25	100	0,75	-20	0,95	13	0,05	-50
M	0,8	33	0,2	-80	0,95	14	0,05	-60
M	0,55	92	0,45	-90	0,45	47	0,55	-20
M	0,7	51	0,3	-85	0,8	24	0,2	-45
M	0,7	46	0,3	-75	0,6	37	0,4	-30
M	0,75	37	0,25	-70	0,75	20	0,25	-20
M	0,7	49	0,3	-80	0,4	40	0,6	-10
M	0,8	31	0,2	-75	0,5	35	0,5	-15
M	0,6	73	0,4	-85	0,45	28	0,55	-5
M	0,55	55	0,45	-45	0,9	14	0,1	-30
M	0,65	45	0,35	-55	0,85	15	0,15	-20
M	0,45	89	0,55	-55	0,85	18	0,15	-35
M	0,5	65	0,5	-45	0,8	23	0,2	-40
H	0,85	26	0,15	-80	0,4	85	0,6	-40
H	0,55	96	0,45	-95	0,5	90	0,5	-70
H	0,65	58	0,35	-80	0,55	63	0,45	-55
H	0,75	35	0,25	-65	0,6	57	0,4	-60
H	0,5	100	0,5	-80	0,25	85	0,75	-15
H	0,6	77	0,4	-90	0,65	50	0,35	-65
H	0,75	40	0,25	-80	0,65	56	0,35	-75
H	0,7	44	0,3	-70	0,9	21	0,1	-85
H	0,7	42	0,3	-65	0,6	63	0,4	-70
H	0,45	71	0,55	-40	0,75	47	0,25	-100
H	0,95	16	0,05	-95	0,75	45	0,25	-95
H	0,35	75	0,65	-25	0,55	100	0,45	-100
H	0,75	42	0,25	-85	0,45	96	0,55	-60
H	0,85	28	0,15	-90	0,65	48	0,35	-60
H	0,65	64	0,35	-90	0,65	61	0,35	-85
H	0,5	75	0,5	-55	0,7	57	0,3	-100
H	0,4	70	0,6	-30	0,55	75	0,45	-70

condition of risk	pwin1	win1	ploss1	loss1	pwin2	win2	ploss2	loss2
H	0,35	94	0,65	-35	0,7	53	0,3	-90
H	0,6	70	0,4	-80	0,75	43	0,25	-90
H	0,9	22	0,1	-95	0,6	60	0,4	-65
H	0,8	36	0,2	-95	0,55	67	0,45	-60
H	0,8	38	0,2	-100	0,4	100	0,6	-50
H	0,95	15	0,05	-90	0,9	22	0,1	-100
H	0,85	29	0,15	-100	0,7	55	0,3	-95
H	0,6	80	0,4	-95	0,5	85	0,5	-65
H	0,35	84	0,65	-30	0,55	84	0,45	-80
H	0,9	21	0,1	-90	0,85	27	0,15	-85
H	0,45	83	0,55	-50	0,5	60	0,5	-40
H	0,45	65	0,55	-35	0,5	80	0,5	-60
H	0,6	50	0,4	-50	0,4	78	0,6	-35
H	0,5	70	0,5	-50	0,4	93	0,6	-45
H	0,3	92	0,7	-25	0,6	67	0,4	-75
H	0,55	80	0,45	-75	0,3	80	0,7	-20

Conditions of risk: L = low, M = mixed, H = high; probabilities of the 2 alternative wins and losses in gamble options 1 and 2 of each trial: pwin1, ploss1, pwin2, ploss2; monetary outcome for wins and losses in the gambles 1 and 2: win1, loss1, win2, loss2.

FIGURE CAPTIONS (for files attached)

Figure 1a: Example trial with high ambiguity showing all events and their timing. The fixation cross (1^{st} frame) was followed by the option screen (2^{nd} frame). Upon button press green colour indicated the choice (3^{rd} frame) and subsequently feedback of the current trial was presented (4^{th} screen) followed by the sum of all trials (5^{th} screen) and the fixation cross of the next trial.

Figure 1b: Probability of choosing the higher risk option during the risk block (upper panel) and the ambiguity block (lower panel) for the three levels of risk.

Figure 2: Activation in parahippocampus during mixed-risk trials in comparison to high- and low-risk trials.

Figure 3: Activation of inferior frontal gyrus IFG (BA 47) during mixed-risk trials with high ambiguity versus averaged high- and low-risk trials with high ambiguity

Figure 4: Activation of SMA (BA 6) during mixed-risk trials with low ambiguity versus averaged high- and low-risk trials with low ambiguity

Figure 5: Activation of DLPFC (BA 9) during mixed-risk trials with high ambiguity versus mixed-risk trials with low ambiguity

Figure 6: Activation of dACC (BA 32) during mixed-risk trials for parameteric analysis of potential wins in comparison to high- and low-risk trials

Figure 7: Activation of the insular cortex and the OFC during mixed-risk trials for the parameteric analysis of potential losses in comparison to high- and low- risk trials

Figure 8: Activation of the amygdala during mixed-risk trials for trials with high ambiguity in the parameteric analysis of potential wins versus mixed-risk trials with low ambiguity.

References

Arsalidou, M., & Taylor, M. J. (2011, Feb 1). Is 2+2=4? Meta-analyses of brain areas needed for numbers and calculations. *Neuroimage, 54* (3), 2382-2393. https://doi.org/10.1016/j.neuroimage.2010.10.009

Bach, D. R., Seymour, B., & Dolan, R. J. (2009, Feb 11). Neural activity associated with the passive prediction of ambiguity and risk for aversive events. *Journal of Neuroscience, 29* (6), 1648-1656. https://doi.org/10.1523/JNEUROSCI.4578-08.2009

Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (1997). Deciding advantageously before knowing the advantageous strategy. *Science, 275* (5304), 1293-1295.

Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (2005). The Iowa Gambling Task and the somatic marker hypothesis: some questions and answers. *Trends in Cognitive Sciences, 9* (4), 159-162; discussion 162-154.

Bhatt, M., & Camerer, C. F. (2005, Aug). Self-referential thinking and equilibrium as states of mind in games: FMRI evidence [Print Electronic; Print]. *Games and Economic Behavior, 52* (2), 424-459.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001, Jul). Conflict monitoring and cognitive control. *Psychological Review, 108* (3), 624-652. <Go to ISI>://000170892100006

Breiter, H. C., Aharon, I., Kahneman, D., Dale, A., & Shizgal, P. (2001, May). Functional imaging of neural responses to expectancy and experience of monetary gains and losses.*Neuron, 30* (2), 619-639. https://doi.org/Doi 10.1016/S0896-6273(01)00303-8

Brown, J. W., & Braver, T. S. (2005, Feb 18). Learned predictions of error likelihood in the anterior cingulate cortex. *Science, 307* (5712), 1118-1121. https://doi.org/10.1126/science.1105783

Brown, J. W., & Braver, T. S. (2007, Dec). Risk prediction and aversion by anterior cingulate cortex.*Cognitive Affective & Behavioral Neuroscience, 7* (4), 266-277. https://doi.org/Doi 10.3758/Cabn.7.4.266

Brown, J. W., & Braver, T. S. (2008, Apr 2). A computational model of risk, conflict, and individual difference effects in the anterior cingulate cortex. *Brain Research, 1202* , 99-108. https://doi.org/10.1016/j.brainres.2007.06.080

Budner, N. Y. S. (1962). Intolerance of Ambiguity as a Personality Variable. *Journal of Personality, 30* (1), 29–50

Canessa, N., Crespi, C., Motterlini, M., Baud-Bovy, G., Chierchia, G., Pantaleo, G., Tettamanti, M., & Cappa, S. F. (2013, Sep 4). The functional and structural neural basis of individual differences in loss aversion [Research Support, Non-U.S. Gov't]. *The Journal of neuroscience : the official journal of the Society for Neuroscience, 33* (36), 14307-14317. https://doi.org/10.1523/JNEUROSCI.0497-13.2013

Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS scales.*Journal of Personality and Social Psychology, 67* , 319-333.

Chen, Z., & Epstein, L. (2002). Ambiguity, risk, and asset returns in continuous time.*Econometrica, 70* (4), 1403-1443.

Christopoulos, G. I., Tobler, P. N., Bossaerts, P., Dolan, R. J., & Schultz, W. (2009, Oct 7). Neural Correlates of Value, Risk, and Risk Aversion Contributing to Decision Making under Risk. *Journal of Neuroscience, 29* (40), 12574-12583. https://doi.org/10.1523/Jneurosci.2614-09.2009

Craig, A. D. (2011, Apr). Significance of the insula for the evolution of human awareness of feelings from the body [Review]. *Annals of the New York Academy of Sciences, 1225* , 72-82. https://doi.org/10.1111/j.1749-6632.2011.05990.x

Duerden, E. G., Arsalidou, M., Lee, M., & Taylor, M. J. (2013, Sep). Lateralization of affective processing in the insula [Research Support, Non-U.S. Gov't]. *Neuroimage, 78* , 159-175. https://doi.org/10.1016/j.neuroimage.2013.04.014

Ellsberg, D. (1961, November). Risk, ambiguity, and the Savage axioms. *Quarterly Journal of Economics, 75* , 643-669.

Fochmann, M., Hewig, J., Kiesewetter, D., & Schüßler, K. (2017). Affective reactions influence investment decisions: evidence from a laboratory experiment with taxation.*Journal of Business Economics, 87* (6), 779-808.

Friedman, H. R., & Goldman Rakic, P. S. (1994). Coactivation of prefrontal cortex and inferior parietal cortex in working memory tasks revealed by 2DG functional mapping in the rhesus monkey. *J-Neurosci, 14* (5 Pt 1), 2775-2788.

Hampton, A. N., & O'Doherty, J. P. (2007, Jan 23). Decoding the neural substrates of reward-related decision making with functional MRI. *Proceedings of the National Academy of Sciences of the United States of America, 104* (4), 1377-1382. https://doi.org/10.1073/pnas.0606297104

Hewig, J., Kretschmer, N., Trippe, R. H., Hecht, H., Coles, M. G., Holroyd, C. B., & Miltner, W. H. (2010, Apr 15). Hypersensitivity to reward in problem gamblers. *Biol Psychiatry, 67* (8), 781-783. https://doi.org/10.1016/j.biopsych.2009.11.009

Hewig, J., Straube, T., Trippe, R. H., Kretschmer, N., Hecht, H., Coles, M. G., & Miltner, W. H. (2009, Aug). Decision-making under risk: an fMRI study. *J Cogn Neurosci, 21* (8), 1642-1652. https://doi.org/10.1162/jocn.2009.21112

Hewig, J., Trippe, R., Hecht, H., Coles, M. G., Holroyd, C. B., & Miltner, W. H. (2007, Apr). Decision-making in Blackjack: an electrophysiological analysis.*Cereb Cortex, 17* (4), 865-877. https://doi.org/10.1093/cercor/bhk040

Hewig, J., Trippe, R. H., Hecht, H., Coles, M. G., Holroyd, C. B., & Miltner, W. H. (2008, Oct). An electrophysiological analysis of coaching in Blackjack. *Cortex, 44* (9), 1197-1205. https://doi.org/10.1016/j.cortex.2007.07.006

Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity.*Psychological Review, 109* (4), 679-709.

Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., & Camerer, C. F. (2005, Dec). Neural Systems Responding to Degrees of Uncertainty in Human Decision-Making [Empirical Study

Quantitative Study]. *Science, 310* (5754), 1680-1683. https://doi.org/10.1126/science.1115327

Huettel, S. A., Stowe, C. J., Gordon, E. M., Warner, B. T., & Platt, M. L. (2006). Neural signatures of economic preferences for risk and ambiguity. *Neuron, 49* (5), 765-775.

Kahneman, D., Schwartz, A., Thaler, R. H., & Tversky, A. (1997, Jul). The Effect of Myopia and Loss Aversion on Risk Taking: An Experimental Test. *Journal of Finance, 52* (3), 1237-1237. <Go to ISI>://000209883900062

Kahneman, D., & Tversky, A. (1979). Prospect Theory - Analysis of Decision under Risk. *Econometrica, 47* (2), 263-291. https://doi.org/Doi 10.2307/1914185

Knight, F. H. (1921). *Risk, Uncertainty, and Profit* . Hart, Schaffner & Marx; Houghton Mifflin. Library of Economics and Liberty.

Knutson, B., Adams, C. M., Fong, G. W., & Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *Journal of Neuroscience, 21* (16), NIL_1-NIL_5.

Knutson, B., Taylor, J., Kaufman, M., Peterson, R., & Glover, G. (2005, May 11). Distributed neural representation of expected value. *Journal of Neuroscience, 25* (19), 4806-4812. https://doi.org/10.1523/Jneurosci.0642-05.2005

Krain, A. L., Wilson, A. M., Arbuckle, R., Castellanos, F. X., & Milham, M. P. (2006, Aug 1). Distinct neural mechanisms of risk and ambiguity: a meta-analysis of decision-making. *Neuroimage, 32* (1), 477-484. https://doi.org/10.1016/j.neuroimage.2006.02.047

Kringelbach, M. L., & Rolls, E. T. (2004, Apr). The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in Neurobiology, 72* (5), 341-372. https://doi.org/10.1016/j.pneurobio.2004.03.006

Kuhnen, C. M., & Knutson, B. (2005). The neural basis of financial risk taking. *Neuron, 47* (5), 763-770.

LeDoux, J. (2003, Oct). The emotional brain, fear, and the amygdala [Review]. *Cellular and molecular neurobiology, 23* (4-5), 727-738. http://www.ncbi.nlm.nih.gov/pubmed/14514027

Lejuez, C. W., Read, J. P., Kahler, C. W., Richards, J. B., Ramsey, S. E., Stuart, G. L., Strong, D. R., & Brown, R. A. (2002, Jun). Evaluation of a behavioral measure of risk taking: The Balloon Analogue Risk Task (BART). *Journal of Experimental Psychology-Applied, 8* (2), 75-84. https://doi.org/10.1037//1076-898X.8.2.75

Li, X. R., Lu, Z. L., D'Argembeau, A., Ng, M., & Bechara, A. (2010, Mar). The Iowa Gambling Task in fMRI Images. *Human Brain Mapping, 31* (3), 410-423. https://doi.org/10.1002/hbm.20875

McLain, D. L. (2009, Dec). Evidence of the Properties of an Ambiguity Tolerance Measure: The Multiple Stimulus Types Ambiguity Tolerance Scale-Ii (Mstat-Ii).*Psychological Reports, 105* (3), 975-988. https://doi.org/10.2466/Pr0.105.3.975-988

Mussel, P., Reiter, A. M., Osinsky, R., & Hewig, J. (2015, Apr). State- and trait-greed, its impact on risky decision-making and underlying neural mechanisms. *Soc Neurosci, 10* (2), 126-134. https://doi.org/10.1080/17470919.2014.965340

Platt, M. L., & Huettel, S. A. (2008, Apr). Risky business: the neuroeconomics of decision making under uncertainty. *Nature Neuroscience, 11* (4), 398-403. https://doi.org/10.1038/nn2062

Rabin, M. (2000, September). Risk Aversion and Expected-Utility Theory: A Calibration Theorem.*Econometrica, 68 5* , 1281-1292. http://www.econometricsociety.org/tocs.asp

Rao, H., Korczykowski, M., Pluta, J., Hoang, A., & Detre, J. A. (2008, Aug 15). Neural correlates of voluntary and involuntary risk taking in the human brain: an fMRI Study of the Balloon Analog Risk Task (BART). *Neuroimage, 42* (2), 902-910. https://doi.org/10.1016/j.neuroimage.2008.05.046

Rothschild, M., & Stiglitz, J. E. (1970). Increasing Risk: I. A definition *Journal of Economic Theory, 2* (3), 225-243.

Roy, A. K., Shehzad, Z., Margulies, D. S., Kelly, A. M. C., Uddin, L. Q., Gotimer, K., Biswal, B. B., Castellanos, F. X., & Milham, M. P. (2009, Apr 1). Functional connectivity of the human amygdala using resting state fMRI.*Neuroimage, 45* (2), 614-626. https://doi.org/10.1016/j.neuroimage.2008.11.030

Smith, K., Dickhaut, J., McCabe, K., & Pardo, J. V. (2002, Jun). Neuronal substrates for choice under ambiguity, risk, gains, and losses [Empirical Study].*Management Science, 48* (6), 711-718. https://doi.org/10.1287/mnsc.48.6.711.194

Stein, J. L., Wiedholz, L. M., Bassett, D. S., Weinberger, D. R., Zink, C. F., Mattay, V. S., & Meyer-Lindenberg, A. (2007, Jul 1). A validated network of effective amygdalla connectivity. *Neuroimage, 36* (3), 736-745. https://doi.org/10.1016/j.neuroimage.2007.03.022

Tobler, P. N., O'Doherty, J. P., Dolan, R. J., & Schultz, W. (2007, Feb). Reward value coding distinct from risk attitude-related uncertainty coding in human reward systems.*Journal of Neurophysiology, 97* (2), 1621-1632. https://doi.org/10.1152/jn.00745.2006

Tom, S. M., Fox, C. R., Trepel, C., & Poldrack, R. A. (2007, Jan 26). The neural basis of loss aversion in decision-making under risk. *Science, 315* (5811), 515-518. https://doi.org/10.1126/science.1134239

Vorhold, V., Giessing, C., Wiedemann, P. M., Schutz, H., Gauggel, S., & Fink, G. R. (2007, Nov 5). The neural basis of risk ratings: evidence from a functional magnetic resonance imaging (fMRI) study. *Neuropsychologia, 45* (14), 3242-3250. https://doi.org/10.1016/j.neuropsychologia.2007.06.023

Yacubian, J., Glascher, J., Schroeder, K., Sommer, T., Braus, D. F., & Buchel, C. (2006, Sep 27). Dissociable systems for gain- and loss-related value predictions and errors of prediction in the human brain (vol 26, pg 9530, 2006).*Journal of Neuroscience, 26* (39). <Go to ISI>://000240825700027

Zuckerman, M. (1996, Apr). Item revisions in the sensation seeking scale form V (SSS-V).*Personality and Individual Differences, 20* (4), 515-515. https://doi.org/Doi 10.1016/0191-8869(95)00195-6