Neural foundations of risk–return trade-off in investment decisions

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Abstract

Many decisions people make can be described as decisions under risk. Understanding the mechanisms that drive these decisions is an important goal in decision neuroscience. Two competing classes of risky decision making models have been proposed to describe human behavior, namely utility-based models and risk–return models. Here we used a novel investment decision task that uses streams of (past) returns as stimuli to investigate how consistent the two classes of models are with the neurological processes underlying investment decisions (where outcomes usually follow continuous distributions). By showing (a) that risk–return models can explain choices behavioral and (b) that the components of risk–return models (value, risk, and risk attitude) are represented in the brain during choices, we provide evidence that risk–return models describe the neural processes underlying investment decisions well. Most importantly, the observed correlation between risk and brain activity in the anterior insula during choices supports risk–return models more than utility-based models because risk is an explicit component of risk–return models but not of the utility-based models.

Introduction

Many decisions people make—such as whether to try to catch a yellow light, choosing a journal for submission of an article, or choosing a financial investment—can be described as decisions under risk. Understanding the mechanisms that drive these decisions is an important goal in decision neuroscience. But while recent research has generated some progress in the understanding of value-based decision making, the underlying mechanisms of risky decision making are still debated.

Two main competing classes of models in risky choice have been proposed (d’Acremont and Bossaerts, 2008; Glöckner, 2008; Rangel et al., 2008; Mohr et al., in press). The first class of models, namely utility-based models, which includes Expected Utility Theory (EUT) and Prospect Theory (PT) (Kahneman and Tversky, 1979; von Neumann and Morgenstern, 1953) proposes that decision makers first determine the value and weight of each possible outcome and then calculate the overall value of a choice option as the weighted sum of possible outcome values. The second class of models, namely risk–return models, proposes that decision makers first determine the average return of the alternative and its associated risk, and then calculate the value of the alternative as the risk-corrected average return. In early economic models (e.g., Portfolio Theory) expected value and variance were used as measures for return and risk, respectively (Markowitz, 1952). Later, risk and return were generalized for subjective measures, such as perceived risk and subjective expected return (Sarin and Weber, 1993; Weber and Johnson, 2009a).

In the best case, the better model explains behavioral and neural data better than the other models. This might be untenable, however, if models can make near identical predictions on the behavioral level, as it is the case for utility-based and risk–return models (Bossaerts et al., 2009; d’Acremont and Bossaerts, 2008). In this case, fMRI data can serve as a tiebreaker, because they provided additional insight into the neurological processes that sub-serve the cognitive processes that ultimately lead to decisions. Hence, we suggest identifying the more appropriate class of models by comparing their ability to describe the process of valuation on which choices are based.

Recent research has found neural support for both classes of models. Some studies found representations of magnitudes and probabilities (supporting utility-based models) (e.g., Knutson et al., 2005) whereas others found representations of risk and return (supporting risk–return models) (e.g., Preuschoff et al., 2006). Hence, it remains to date unclear, which type of model provides a better description of the neural processes underlying economic decision making as both have proven biologically plausible.

One way to reconcile the apparent conflict is to associate both classes of models with certain types of decisions, environments, or decision contexts in which different strategies are appropriate. In this case, what is called for are experimental paradigms that provide data for further probing these two classes of models’ biological plausibility. One criterion by which different models can be assigned to different types of decisions is the amount of information processing required by...
Given the high computational demand of applying EUT or PT to decisions with (nearly) continuous outcome distributions, we expected individuals to use risk–return models rather than EUT or PT in these situations. To test this prediction, we conducted an fMRI study where participants made investment decisions in which the investments’ returns follow continuous distributions. By doing so we want to provide an additional empirical dimension (namely the amount of required information processing) for comparing utility-based models with risk–return models.

Risk is explicitly implicated only in risk–return models but not in EUT and PT. Thus, a representation of risk (together with a representation of value or return) would indicate that individuals use risk–return models when they make investment decisions. Even though some neuroimaging studies have identified neural representations of risk and return (value) simultaneously (e.g., Preuschoff et al., 2006), seldomly was the data collected before or during choice (but see, Tobler et al., 2009), and none of the previous studies have used gambles with continuous distributions or applied a risk–return model to relate these variables to actual choices. The goal of the present study is therefore to extend these results by testing whether risk and value as specified in risk–return models are represented in the brain simultaneously during investment decisions with the investments’ returns following continuous distributions.

To investigate the brain processes associated with investment decisions we used a novel investment decision task in an fMRI experiment (see Fig. 1). Based on prior research we hypothesized that value correlates with the blood oxygenation level dependent (BOLD) signal in the medial prefrontal cortex (MPFC) (Kable and Glimcher, 2007; Kennerley et al., 2009; Knutson et al., 2005) and that risk correlates with the BOLD signal in the anterior insula (aINS) (Critchley et al., 2001; Huettel et al., 2005; Paulus et al., 2003; Volz et al., 2003). Further, we hypothesized that inter-individual differences in risk attitudes (as determined by the trade-off factor in risk–return models) are related to inter-individual differences in decision-related brain activity.

Materials and methods

Experimental procedures

Nineteen young volunteers (age 18–35 years, 11 females) participated in this study. All participants were native German speakers, right-handed and had no history of neurological or psychiatric diseases. Three participants had to be excluded due to extensive head motion (>5 mm absolute head movement) and modeling problems (two participants always chose the risky alternative). All participants were paid for their participation and gave written informed consent. The study was approved by the local ethics committee of the Charité University Medicine, Berlin.

Each trial of the Risk Perception and Investment Decision (RPID) task consisted of two phases: the presentation of a return stream, followed by a decision or subjective judgment task (see Fig. 1). In investment situations investors are often confronted with past performance data of possible investments. To mimic this situation, in the first phase we sequentially presented a stream of 10 returns from an investment, each presented for 2 s without fixation-phases between the returns. These 10 returns provided information about the past performance of a given investment. In the experiment, each return stream was independent of the others and described a new investment option. We varied the mean and the standard deviation of the return streams parametrically with three means (6%, 9%, and 12%) and three standard deviations of 1%, 5%, and 9%. Each of the nine resulting return streams was used in three different return orders for each question.

Fig. 1. Risk Perception and Investment Decision (RPID) task: Subjects were presented with streams of 10 returns from an investment. They then either (a) judged the subjective expected return of the return stream, (b) judged the perceived risk of the return stream, or (c) chose between an investment with a fixed return of 5% and an investment with a variable return which was represented by the return stream the subjects saw before. We used a parametric design, in which the return streams had means of 6%, 9%, and 12% and standard deviations of 1%, 5%, and 9%. Each of the nine resulting return streams was used in three different return orders for each question.
deviations (1%, 5%, and 9%), resulting in nine different combinations of means and standard deviations.

In the second phase, subjects performed one of three possible tasks in each trial (each 7 s) without knowing in advance which one they would have to perform after the stream. We used three tasks to be able to investigate choices as well as perceived risk and subjective expected return, as specified in recent psychological risk–return models (Weber and Johnson, 2009a). In the decision task the subjects had to make a choice between an investment with 5% fixed return (safe investment) and the investment represented by the return stream they just saw (risky investment). In the other two tasks subjects reported their subjective expected return and perceived risk of the investment represented by the return stream. Subjects indicated subjective expected return on a scale ranging from -5% to +15% and perceived risk on a scale ranging from 0 (no risk) to 100 (maximum risk) (Klos et al., 2005). Subjects performed each task (decision, subjective expected return, perceived risk) 27 times (81 trials in total). Before the experiment subjects completed four training trials, knowing that the standard deviations in the experiment would be in the same range as in the training trials. But no explicit information regarding means or standard deviations was given to the participants.

Subjects received a flat payment of 10 Euro for their participation in the experiment and a virtual endowment of 100 Euros to invest. They were explicitly told that the returns they observe during the experiment are randomly drawn from Gaussian distributions. They were further instructed that after the experiment, 1 of their 27 choices will be randomly chosen to determine decision dependent payments. If the subject would choose the safe option in the respective trial, she would get 5 Euros (5% of 100 Euros) in addition to the 10 Euros. If a subject would choose the risky option in this trial, a random return was drawn from a Gaussian distribution with the same mean and standard deviation as the respective return stream. The resulting outcome (return times 100 Euro) was added to or subtracted from the flat payment.

Behavioral modeling

In financial economics it is usually assumed that individuals use the objective expected return and the variance of returns as basis for their choices (mean-variance approach/normative risk–return model) (Markowitz, 1952). While it is possible to infer these measures from past performance data, the actual return an individual expects (subjective expected return) and his/her perceived risk are unobservable during decision making. Importantly, behavioral research has shown that subjective expected return and perceived risk can vary significantly depending on the context of the decision, challenging the predictive power of the objective measures expected return and variance of returns (Weber and Milliman, 1997; Weber et al., 2005).

Therefore we applied all the following psychological risk–return model:

\[ V(x) = \mu(x) - \phi \sigma(x) \]

In this equation \( V(x) \) defines the value a subject assigns to an investment \( x \), \( \mu(x) \) represents the subjective expected return, \( \sigma(x) \) represents the perceived risk, and \( \phi \) is the individual risk weight.

To determine which model predicted subjective expected return and perceived risk judgments best, we used a “leaving one out at a time” cross-validation method (Browne, 2000), which ensures the predictive power especially in situations with few trials. First, we divided trials into 26 fitting trials and one test trial. Second, we estimated the parameters for every model that maximized the correlation between model predictions and stated subjective expected returns and perceived risks. For subjective expected return we compared five different models: (1) mean, (2) recency, (3) pri-
macy, (4) overweight< 0%, and (5) overweight< 5% (see behavioral results for a description of the models). All models are weighted average models that we modeled with memory (number of returns over which the model was computed) and weighting as free parameters. Regarding perceived risk we compared six different models: (1) standard deviation, (2) coefficient of variation, (3) probability< 0%, (4) probability< 5%, (5) range, and (6) coefficient of variation. Whereas the standard deviation and the range are measures of variation, the coefficients of variation and range are measures of variation divided by the mean. Probability<0% and probability<5% are models for the probability of a loss given a particular loss threshold. The only free parameter in all models was memory (number of returns over which the model was computed). Model predictions of risk models, generated by applying the models on the return streams, were regressed on the stated perceived risks to allow a transformation of the model predictions (which depend on the scale of the returns) into the dimensions of the scale used in the experiment (0–100).

Third, we applied all models to the return stream of the test trials, making predictions for subjective expected return and perceived risk. We then calculated the squared difference between model predictions and stated subjective expected returns/perceived risks in the test trial. We repeated this procedure for all 27 trials, that is, each trial once served as the test trial. The models with the least average squared difference between model predictions and stated subjective expected returns/perceived risks were identified as individual best models for subjective expected return and perceived risk. Finally, we used all 27 trials to estimate the parameters of these best models, which were later used to predict subjective expected return and perceived risk during choice trials.

We used these predictions to estimate the risk weight and test the risk–return models behaviorally. Risk weights were estimated by fitting a softmax function to the choice data. Best risk weights maximized the sum of loglikelihoods of all 27 choices.

Additionally, we tested how many of the actual choices could be explained by the fitted risk weight, if we assume a deterministic decision rule. The decision rule was defined as follows. If \( V(\text{safe}) > V(\text{risky}) \) the individual chooses the safe option and vice versa. The value of the safe option is always constant \( V(\text{safe}) = 5\% \) because there is no risk involved. This fitted risk weight was then used to make a prediction about the choice in all 27 trials. To compare the psychological risk–return model with the normative risk–return model we repeated the above described procedures for this model.

fMRI acquisition

Imaging was conducted on a 1.5 T Magnetom Sonata MRI system (Siemens, Erlangen, Germany) equipped with a standard head coil. We used a vacuum pad to minimize head motion. Functional images were acquired using a BOLD-sensitive T2*-weighted echo-planar imaging (EPI) sequence [TR, 2500 ms; echo time (TE), 40 ms; flip angle, 90°; field of view, 256 mm; matrix, 64 × 64 mm; 26 axial slices approximately parallel to the bicommissural plane; slice thickness, 4 mm]. Two functional runs were acquired (735 and 625 volumes). The first two scans of each run were discarded to allow longitudinal magnetization to reach equilibrium. After the functional runs, a high-resolution structural image was acquired to aid in normalization and co-registration.

fMRI data analysis

MRI data were analyzed using a mixed effects approach within the framework of the general linear model as implemented in the FMRI Expert Analysis Tool (FEAT; Smith et al., 2004), part of FSL 4.0 (FMRI’s Software Library, http://www.fmrib.ox.ac.uk/fsl/). Pre-
processing included slice-timing correction, motion correction, and spatial smoothing using an 8 mm Gaussian kernel. Additionally, pre-whitening was used and high-pass temporal filtering (50 s) was applied to the data. A double-gamma function was used to model the hemodynamic response.

Event-related fMRI data were analyzed using a GLM with task-related regressors. The goal of the present study was to test whether \textit{risk} and \textit{value} (as specified in risk–return models) are represented in the brain simultaneously during investment decisions with investments' returns following continuous. The \textit{value} of a choice option is, however, not independent of \textit{perceived risk} and \textit{subjective expected return}. Depending on the risk weight the \textit{value} might be highly correlated with \textit{subjective expected return} or \textit{perceived risk}. Therefore, it is impractical to include all three components of risk–return models—\textit{value}, \textit{risk}, and return—in the same analysis of the brain data. In our case, \textit{value} was on average highly correlated with \textit{subjective expected return}, \textit{value} of the chosen option, and \textit{value} derived from the normative risk–return model and \textit{objective expected return} (see Tables S1–S3). We therefore analyzed six different models.

In the first model we specified six different regressors to model different task phases and their parametric modulation. The first regressor (return stream regressor) modeled constant brain activity during the presentation of the returns (2 s each). Thus, in each return stream the regressor had 10 values, one for each return. Additionally, we modeled regressors for constant brain activity for each of the three tasks (expected return task regressor, risk task regressor, and decision task regressor). The last two regressors modeled parametric modulation of brain activity during the decision task with value derived from the psychological risk–return model (psychological value regressor) and perceived risk (PR regressor).

In the second and the third model we replaced the psychological value regressor with regressors modeling the parametric modulation with subjective expected return (SER regressor) and value of the chosen option (chosen value regressor). The fourth and the fifth model were specified with components of the normative risk–return model. We replaced in both models the PR regressor with a regressor for the objective standard deviation (SD regressor). Additionally, we replaced the psychological value regressor with a regressor for the value derived from the normative risk–return model (normative value) in the fourth model and with a regressor modeling the objective expected return (ER regressor) in the fifth model. The sixth model was designed to compare risky with safe choices. We replaced the decision task regressor by two regressors modeling constant brain activity during the decision task depending on the actual choice (risk decision regressor; safe decision regressor). Parametric regressors in all models were orthogonalized with respect to the constant regressors in the respective task phase.

Images of individual level regression parameters (contrast images) were normalized into a standard stereotaxic space (Montreal Neurological Institute (MNI), Montreal, Quebec, Canada) and included in a random-effects group analysis. Here we used the Bayesian modeling approach (Woolrich et al., 2004) implemented in FSL's FLAME (FMRI's local analysis of mixed effects) procedure to test whether regression parameters were significantly different from zero and whether individual differences in regression parameters might be explained by the individual risk weights from the risk–return models. For the a priori regions of interest we report those activations as significant that exceed an uncorrected threshold of z-score= 3.09 and a cluster size greater than 20 voxels. A priori regions of interest were regions that have been shown to be implicated in reward-based decision making tasks or uncertainty-related experiments (Hsu et al., 2005; Huettel et al., 2005; Knutson et al., 2005). These regions include the prefrontal cortex, the cingulate cortex, the striatum, the aNlS, and the amygdala.

\section*{Results}

\subsection*{Behavioral results}

The Risk Perception and Investment Decision (RPID) task was designed to identify mathematical models that describe how risk and return are perceived by individuals as well as to investigate how they make decisions between a safe and a risky investment (Fig. 1).

In the RPID task subjects first saw a stream of 10 past returns from an investment (each displayed for 2 s). Next, subjects either had to (1) state their \textit{perceived risk} of the investment, (2) their \textit{subjective expected return} from the investment, or (3) they had to make a choice between the investment described by the 10 returns and an investment with a fixed return of 5%. The subjects' statements for \textit{perceived risk} and \textit{subjective expected return} were used to identify which mathematical model best translates the 10 presented returns into predictions for \textit{perceived risk} and \textit{subjective expected return} on an individual level. Thus, one can use these models to predict \textit{perceived risk} and \textit{subjective expected return} during the choice between the risky and the safe investment, where they are otherwise unobservable.

We used a cross-validation procedure (see Materials and methods) to compare a range of models for \textit{subjective expected return} and \textit{perceived risk}. Five models calculated the \textit{subjective expected return} as a weighted average of the observed returns, whereby the models differed in the weights assigned to different returns. Only for four subjects (20%) was the \textit{expected return} model best able to predict \textit{subjective expected return}. Primacy, a model that gives greater weights to earlier returns in the return stream, was the best predictor for one subject (5%). Recency, a model where later returns are over-weighted, was the best model for four subjects (20%). Additionally, we tested two models that give greater weights to returns below a certain threshold, either 0% or 5%, reflecting the behaviorally observed phenomenon of loss aversion (Kahneman and Tversky, 1979). We found that overweight–0% was the best model for one subject (5%), whereas overweight–5% described the \textit{subjective expected return} statements of 10 subjects (50%). The correlation between model predictions from the best model for each individual and stated \textit{subjective expected returns} was on average $r=.73$ (Pearson's correlation coefficient, min = .41, max = .91), indicating a good predictive performance of the models. Thus, individual best models can be applied to predict \textit{subjective expected returns} of the risky investment in decision trials.

Based on the prior literature for risk measures (Klos et al., 2005), we tested six different \textit{perceived risk} models: (1) standard deviation, (2) coefficient of variation, (3) range, (4) coefficient of range, (5) probability $<0\%$, and (6) probability $<5\%$. Whereas the \textit{standard deviation} and the \textit{range} are measures of variation, the coefficients of variation and range are measures of variation divided by the mean. Probability $<0\%$ and probability $<5\%$ are models for the probability of a loss given a particular loss threshold.

\textit{Perceived risk} was best modeled by the \textit{standard deviation} in six subjects (30%), by \textit{coefficient of variation} in two subjects (10%), by \textit{probability}<5% and by \textit{range} in two subjects (10%). For six subjects (30%) \textit{coefficient of range} was the best model. The predictions from the best model for each individual correlated highly with stated \textit{perceived risks} ($r=.87$, min = .69, max = .94). This indicates that one can use these models to predict \textit{perceived risk} in the decision trials.

To make predictions regarding the \textit{value} individuals assign to the risky investment, we fitted the data with a psychological risk–return model. In contrast to the normative risk–return model, which uses the objective measures \textit{expected return} and \textit{standard deviation}, this model uses the subjective measures \textit{perceived risk} and \textit{subjective expected return} and thus allows to account for potential differences between normative and psychological evaluations of \textit{risk} and \textit{return}, leaving space for distorted perceptions of \textit{risk} and \textit{return} (e.g. caused by framing effects) as well as fundamentally.
different concepts of risk (e.g. related to potential losses). The normative risk–return model, however, remains as a special case of the psychological risk–return model. The value of a choice alternative in the psychological risk–return model is determined by the subjective expected return minus the perceived risk weighted with the risk weight (see Materials and methods).

All participants were risk averse, indicated by a positive risk weight (see Fig. 2 and Table S4). Additionally, we tested how well the fitted risk weights are able to explain choices if we assume a deterministic decision rule. On average 83% of the choices were correctly predicted by the model (see Table S5 for individual maximum likelihoods and percent correct model predictions).

Perceived risk and subjective expected return, however, still remain as unobservable variables in most economic decisions that can only be indirectly inferred from the subjective ratings, thus making it difficult to predict choices. Standard deviations and expected returns, however, are usually observable. Therefore we tested how well a risk–return model using these two observable metrics (which is in fact the normative risk–return model) can predict choices. We first compared the components of both models and found a mean correlation of $r = .93$ (min = 0.74; max = 1) between expected return and subjective expected return (as predicted by individual best models; see Tables S1–S3). Perceived risk and standard deviation were on average also highly correlated ($r = .86$; min = .26; max = 1), indicating that the objective measures (standard deviation and expected return, respectively) might be mostly good indicators for the subjective measures perceived risk and subjective expected return when these cannot be measured explicitly.

We fitted the risk–return model with expected return and standard deviation in the same way we fitted the psychological risk–return model and also tested how well the resulting risk weights could explain choices if we assume a deterministic decision rule. It was able to predict on average 85% of the choices (see Table S5). The difference in explanatory power between models (83% vs. 85% of the choices predicted correctly) was not significant ($t = .372, df = 36, p = .712$). Thus, in most situations objective measures should be as appropriate for predicting investment decisions as subjective measures, although behavioral research already pointed to situations in which this is not the case (Weber and Milliman, 1997; Weber et al., 2005). Reaction times did not correlate significantly with any of the components of the two tested risk–return models (see Tables S1–S3).

fMRI results

We conducted three separate analyses with components of the psychological risk–return model, including perceived risk and either value, subjective expected return, or value of the chosen option as parametric regressors. Because of the high correlation we expected similar activation patterns for value, subjective expected return, and value of the chosen option. Value as well as subjective expected return correlated significantly with the BOLD response in MPFC, bilateral DLPFC, and PCC during the decision phase of the task (see Fig. 3 and Tables S7–S9). Value of the chosen option correlated significantly with DLPFC and amygdala. The observed maximum z-scores as well as the cluster sizes were, however, greater in all clusters regarding value and subjective expected return compared to value of the chosen option (exception: amygdala), indicating that these clusters are more likely to represent value or subjective expected return. The crucial difference between risk–return models and EUT/PT is that risk is an explicit decision variable in risk–return models whereas it is only implicit, via the value and probability weighting function, in EUT and PT. The presence of a neural representation of risk during the decision process would therefore support the idea of a risk–return trade off. We found a significant correlation between perceived risk and the BOLD response during decisions in right aINS and right OFC (see Fig. 3 and Table S7).

Further, we investigated how (perceived) risk attitudes are represented in the brain. In the applied risk–return model the risk weight represents the risk attitude of an individual. There are basically two possible relationships between risk attitude and brain activity. Risk attitude could be either coded together with risk or independent of risk. In the first case the degree of the relationship between brain activity and risk in a certain brain region would depend on the risk attitude. In the second case risk attitudes would be reflected in inter-individual differences in constant (decision-related) brain activity. We did not find any differences in the relationship between perceived risk and the BOLD signal that was modulated by risk attitude. We did find, however, that decision-related constant brain activity in lateral orbitofrontal cortex (lOFC) and PCC was modulated by risk attitudes (see Fig. 3 and Table S7). This pattern was present for risky as well as safe choices.

We repeated the above-described analyses for the normative risk–return model with expected return and standard deviation and identified similar clusters showing a significant correlation with the tested variables (see Tables S10–S11). Maximum z-scores as well as cluster sizes were, however, greater in all clusters derived from components of the psychological risk–return model, indicating a better fit of the psychological risk–return model to the brain data (see Tables S7–S11).

Discussion

In our everyday life we often have to make important investment decisions, for instance in the context of retirement savings. Because individuals have to deal with limited processing capacity, different decision making strategies might be required in different situations. Two classes of risky decision making models have been proposed, one based on a transformation of outcomes and/or probabilities (EUT and PT) (Kahneman and Tversky, 1979; von Neumann and Morgenstern, 1953) and the other based on a risk–return trade-off (risk–return models) (Sarin and Weber, 1993; Weber and Johnson, 2009a).

To be superior to other models, a better model should, in the best case, explain behavioral and neural data better than the other models. As value- and choice predictions of both classes of models are usually highly consistent with each other (Bossaerts et al., 2009; d’Acremont and Bossaerts, 2008), we focused here on the question which class of models better describes the valuation process. In this case fMRI data can serve as a tiebreaker, because they provide additional insight into the neurobiological processes that sub-serve the cognitive processes, which ultimately lead to decisions. As previous research found neurobiological support for both classes of models we suggest to associate both classes of models with certain types of decisions, environments, or decision..
contexts in which different strategies are appropriate. One criterion by which different models can be assigned to different types of decisions is the amount of information processing required by each. In investment decisions, where investment returns often follow continuous distributions, both classes of models differ significantly regarding this criterion. By comparing both classes of models on the neurobiological level during investment decisions, we provide an additional empirical dimension for comparing these models.

Risk is an explicit component of risk-return models but not of EUT and PT. By showing that risk (as well as value) is represented in the brain during a choice between different investments and by identifying a representation of risk attitude, our data support the hypothesis that risk-return models describe the mechanism underlying investment decisions.

Using the RPID task, which mimics real-life investment decisions by providing subjects with past returns of investments, we found that value and return covaried with brain activity in bilateral DLPFC, PCC, VLPFC, and MPFC. Activation in these regions has usually been observed in the context of value and reward. Changes in the BOLD signal in these regions correlate with the magnitude of experienced and anticipated rewards as well as with the subjective value of (delayed) rewards and the willingness to pay for consumer goods (Amiez et al., 2006; Kable and Glimcher, 2007; Kennerley et al., 2009; Knutson et al., 2005; Kuhnen and Knutson, 2005; Markowitz, 1952; Plassmann et al., 2007; Tom et al., 2007). Our results especially support the findings of a recent study investigating simple decisions with discrete distributions (Tobler et al., 2009). The authors of this study identified lateral prefrontal areas as key brain regions coding for

Fig. 3. Brain regions showing a significant correlation with value, perceived risk, and risk attitude. (A) Value correlated significantly with activity in MPFC ($x = -8, y = 26, z = 34$ mm, $z$-score $= 3.86$), bilateral DLPFC ($x = -42, y = 16, z = 42$ mm, $z$-score $= 4.31$; $x = 38, y = 18, z = 44$ mm, $z$-score $= 3.80$), and VLPFC ($x = -56, y = 16, z = -4$ mm, $z$-score $= 3.88$). (B) Perceived risk correlated significantly with activity in the aINS ($x = 44, y = 22, z = -2$ mm, $z$-score $= 3.90$). (C) Inter-individual differences in brain activity in the IOFC ($x = 18, y = 68, z = -12$ mm, $z$-score $= 5.00$) during a choice between a risky and a safe investment correlated with individual risk attitudes as measured by the risk weight.
the value of choice alternatives. Crucially, brain activity in these areas changed depending on the risk attitude of the subject if risk was present (higher in risk seeking subjects and lower in risk averse subjects), demonstrating the effect of risk on value.

Previous studies have also highlighted the role of the VMPC and the VST in reward processing (Delgado et al., 2000; Elliott et al., 2003; Knutson et al., 2001; O'Doherty et al., 2004; O'Doherty et al., 2001; Preuschoff et al., 2006; Xue et al., 2008). In the VMPC we observed a small cluster of nine voxels when applying a more liberal threshold (z-score> 2.6), but we did not find any significant voxels in the VST even for a very liberal threshold (z-score> 2.0). This lack of striatal activation cannot be explained by the lack of an immediate outcome in the RD task. Recently, a study investigating loss aversion reported reward-related striatal brain activity even when an immediate outcome was missing (Tom et al., 2007). Note however, that ventral striatal activity is most closely associated with the prediction error, when people learn to obtain a reward or learn about reward (Hare et al., 2008). During the return streams of the RD task participants processed prediction errors, probably leading to a highly activated striatum at the beginning of the decision phase. In this case signal changes are difficult to detect and our experimental design likely did not have enough power to do so.

We found that perceived risk correlated significantly with the BOLD signal in the aINS. Risk-related brain activity in the aINS was observed in a variety of studies (Critchley et al., 2001; Grinband et al., 2006; Huettel et al., 2005; Paulus et al., 2003; Preuschoff et al., 2006; Preuschoff et al., 2008; Rolls et al., 2008). None of these studies did, however, use lotteries with continuous distributions. Thus, our finding supports the results from previous studies and extends them by showing that risk is represented in the aINS in situations where subjects have to make a choice between two independent alternatives where one alternative is described by a continuous distribution of possible outcomes. Most importantly, the existence of a neural representation of risk during choices offers neural support for risk–return models because in the case of EUT and PT one would not expect a neural representation of risk whereas risk is explicitly specified in risk–return models.

The finding that inter-individual differences in decision-related brain activity in IOFC and PCC covaried with inter-individual differences in risk attitudes derived from the psychological risk–return model provides additional support for this model. The more risk averse a participant was, the greater was her decision-related brain activity in IOFC and PCC (independent of current risk and value). As stated above, there are basically two possible relationships between risk attitudes and brain activity. Risk attitudes could be either coded together with risk or independent of risk. A recent study found correlations between risk attitude and risk-related brain activity in lateral OFC for risk averse individuals and in medial OFC for risk seeking individuals, supporting the latter view (Tobler et al., 2007). Whereas our results support the general finding that IOFC codes for risk attitudes in risk averse individuals (all participants in our study were risk averse) it points into the direction that risk attitudes are also coded independent of risk.

Together, our results provide neural support for a risk–return trade-off in investment decisions. Previous neuroimaging studies, however, have also shown that specific characteristics of PT are reflected in neural data when simple gambles are used to describe an investment. De Martino et al. (2006) found that the framing of gambles as gains or losses influences choice behavior as well as neural representations of values. Tom et al. (2007) found neural support for the idea of loss aversion that is implemented in PT. De Martino et al. (2009) presented data that support the hypothesis of a reference dependency of value computation. These studies reflect the facts that people are usually more sensitive to losses than to gains and compute value in relation to a certain reference point that can be different across individuals and situations. A closer look at our behavioral results of subjective expected return shows that this phenomenon is also present in our data and can be explained by the psychological risk–return model that we applied. For 11 out of 20 subjects a model where returns below a certain threshold (either 5% or 0%) are over-weighted accounted best for subjective expected return. For these subjects losses regarding a certain reference point influence the value of a choice alternative more strongly than gains. Thus, our behavioral data indicate that the psychological risk–return model results in similar value and choice predictions as PT. As these data entered our fMRI analysis, they also indicate that the brain can compute a PT-like value signal by trading off (perceived) risk and (subjective) expected return.

Finally, we have to emphasize that although our data support risk–return models they do not generally speak against utility-based models in risky decision making and do not challenge the predictive power of these models for behavioral data (see Birnbaum, 2008). Moreover, there are several studies supporting these models in situations with simple gambles and given outcomes and probabilities (e.g., Knutson et al., 2005). In contrast, our data support the view that the brain is able to compute value either on the basis of utility-based models or on the basis of risk–return models (d’Acremont and Bossaerts, 2008). One criterion to choose among these mechanisms could be the amount of required information processing. In the case of decisions between alternatives with continuous outcome distributions, where less information has to be processed using risk–return models compared to utility-based models, our data support the former class of models.

In sum, we found support for the hypothesis of a risk–return trade-off in investment decisions. We extended existing evidence regarding the neurobiological basis of risky decision making (a) by predicting both behavioral data and neuroimaging data with the same choice model (risk–return model), (b) by showing that (perceived) risk and risk attitude not only influence the value signal but are represented independently in the aINS (perceived risk) and the IOFC (risk attitude), and (c) by showing that risk and value are not only represented in the brain during choices between simple gambles with discrete outcome distributions but especially during choices where outcomes follow continuous distributions (like stocks usually do). While not the focus of the present study future research should investigate in more detail how subjective expected return and perceived risk are formed and learned during the presentation of a return stream.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.10.060.

References


