NEURAL CORRELATES OF VALUE, RISK AND RISK AVERSION CONTRIBUTING TO DECISION MAKING UNDER RISK

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Abstract

Decision-making under risk is central to human behavior. Economic decision theory suggests that value, risk and risk aversion influence choice behavior. Although previous studies identified neural correlates of decision parameters, the contribution of these correlates to actual choices is unknown. In two different experiments, participants chose between risky and safe options. We identified discrete blood-oxygen-level-dependent (BOLD) correlates of value and risk in the ventral striatum and anterior cingulate, respectively. Notably, increasing inferior frontal gyrus activity to low risk and safe options correlated with higher risk aversion. Importantly, the combination of these BOLD responses effectively decoded the behavioral choice. Striatal value and cingulate risk responses increased the probability of a risky choice, whereas inferior frontal gyrus responses showed the inverse relationship. These findings suggest that the BOLD correlates of decision factors are appropriate for an ideal observer to detect behavioral choices. More generally, these biological data contribute to the validity of the theoretical decision parameters for actual decisions under risk.

Keywords

Risk; uncertainty; fmri; decision-making; neuroeconomics; inferior frontal gyrus; ACC

INTRODUCTION

Consider somebody selling you a lottery ticket offering £40 or £60, depending on the flip of a coin. You decide to pay up to £50 to buy this ticket. Conversely, your friend might consider this ticket as risky and pay a maximum of £45. Although both of you face exactly the same average payoff, your reactions are different and vary between risk neutrality (you) and risk avoidance (your friend). Such decisions involving risky options characterize a wide spectrum of human and animal behaviour.

Faced with such situations, the agent should accumulate information about the characteristics of the different options and synthesize them to select an alternative. Typically, options with higher expected value (i.e. the sum of each possible outcome

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weighted by its probability) are preferred, all other things being equal. However, the introduction of risk influences the subjective value (or utility) attached to a risky option (or gamble). The influence of risk depends on individual attitudes towards risk, with increasing risk aversion reducing the utility of the gamble.

Therefore, decision making is a function of the statistical properties of the options offered (value and risk), with the influence of risk being modulated by the subjective evaluation of the riskiness of the gamble (risk aversion). Risk averse agents need to trade-off between value and risk, suggesting that these two parameters are two competing dimensions.

Previous research has begun to identify BOLD responses related to expected value, risk and risk aversion. Neuroimaging experiments in humans suggest that ventral striatum (VSt) activity increases with EV or its components (magnitude and probability) (Abler et al. 2006; Yacubian et al., 2006; Tobler et al., 2007; Knutson et al., 2005; Knutson et al., 2001; Rolls et al. 2008; Breiter et al. 2001). Conversely, activity of the anterior cingulate (ACC) has been associated with the volatility of reward environment (Behrens et al., 2007) and the variability of expected outcomes (Brown and Braver, 2005; 2008; Critchley et al. 2001; Kuhnen and Knutson, 2005). Dorsal ACC (dACC) has been related to directing action selection for uncertain rewards (Hampton and O'Doherty, 2007). Although neural correlates of EV and risk have been extensively studied, the neural basis of attitudes towards risk in a choice situation is less well described (Tobler et al., 2007). Yet, right dorsolateral prefrontal cortex (DLPFC) has been implicated in the modification of risk attitudes (Fecteau et al., 2007; Knoch et al., 2006).

However, it is less well known whether these parameter-related BOLD signals merely reflect the characteristics of the choice situation or actually carry information that combines to contribute to the choice process. We hypothesized that BOLD signals in different brain structures reflecting key decision parameters can combine in a way that allows an ideal observer to detect the nature (risky or safe) of the behavioral choice during risky decision making. To investigate this hypothesis, in two different experimental paradigms we identified BOLD responses preferentially encoding value (magnitude (first experiment) and/ or expected value (second experiment)) risk and risk aversion. Subsequently, we used these parameter-specific responses to test the extent to which they could detect the choice behavior and decode their contribution to the probability of a risky or a safe choice.

MATERIALS AND METHODS

Definitions

Objective risk—Under certain conditions, risk can be objectively defined. Rothschild and Stiglitz (1970) provide a formal, minimal definition of risk and characterize it as the spread of outcomes, with the condition that the EV of options is preserved. For example, a gamble equiprobably (p=.5) offering 10 or 90 points (10/90) is riskier than a gamble equiprobably offering 40/60. Probabilities and EV are the same, but risk is different. In this study we follow the Rothschild-Stiglitz definition of risk as a mean-preserving increase in the spread of outcomes. This definition is analogous to risk measures such as standard deviation and variance in skewness free distributions with the other moments kept constant (e.g. expected value / mean). Notice that the gambles used in this study also coincide with other definitions of risk (coefficient of variation, Weber et al., 2004; McCoy and Platt, 2005).

Subjective risk (risk aversion)—On the other hand, risk aversion is subjective. The degree of risk aversion can be behaviorally demonstrated within a psychophysical framework by identifying the safe amount for which the agent is indifferent in choices against a risky outcome (Luce, 2000; fig.1A). This indifference amount, or certainty

equivalent (CE), precisely reflects the value attached to the risky option and allows for comparisons between different options and their expressions across individuals. For instance, a risk neutral agent will attach the same CE to both 40/60 and 10/90 gambles. On the contrary, a risk averse decision maker will be affected by the increase of risk from the 40/60 to the 10/90 gamble and will lower her CE for the riskier option. Hence, the difference between the certainty equivalents of each gamble reflects the degree of risk aversion of the agent.

Participants

All participants were right-handed, had normal or corrected-to-normal vision and were screened to exclude those with a prior history of neurological or psychiatric disease. All gave informed written consent. The Local Research Ethics Committee (National Hospital for Neurology and Neurosurgery and the Institute of Neurology Joint Research Ethics Committee) approved the study. In the first experiment, three risk seeking participants were excluded. One more participant was excluded (and not scanned) because s/he violated monotonicity. These participants were not scanned. Restriction to risk averse agents was done to ensur homogeneity of data and straightforward evaluation of results. In the second experiment there were no risk-attitude related exclusion criteria; still all participants more or less exhibited risk aversion (see results), which is in accordance with numerous studies suggesting that persons predominantly exhibit risk averse preferences (Binswanger, 1980; Holt and Laury 2002; Dohmen et al., 2008).

Experimental tasks and behavior

First experiment—All participants made repeated choices between a risky ("gamble") and a safe alternative, offering a single amount with certainty. In the first experiment (n=13, mean age 24.5 years, 5 females) two gambles were offered, one resulting in either 40 or 60 points (low risk gamble), and one, riskier, resulting in either 10 or 90 points (high risk gamble), where each outcome had an equal probability (p=0.5) of occurrence (fig. 1C). Participants were paid according to the cumulative total amount of points (converted to real money) they acquired during the experiment.

For the first experiment, we adjusted the value of the safe options according to the risk preferences of each participant. We did this in order to ensure that within each choice set the alternatives had the same utility (it should be underlined that the concept of utility as used here refers to decision utility, i.e. an ordering representing preference, and not to experienced utility, which refers to the pleasure derived from the consumption of an outcome (Kahneman et al., 1997)). To achieve this we approximated, before scanning, the CEs for both gambles for each participant, using a staircase method (fig. 1B; Parameter Estimation by Sequential Testing (PEST), Luce, 2000; see supplemental material). During scanning (fig. 1B; trials after the vertical lines), the safe alternatives were initially set to the corresponding, previously determined, approximated CE; consequently, their value was updated to accommodate temporal variations in risk aversion. This method ensured an approximately equal number of risky and safe choices (by X^2 test all comparisons non significant (n.s.)), which reflected indifference between the values of the safe alternative and the risky gamble. In addition, choices between risky and safe options were independent of the previous choices and did not constitute simple alternations (p>0.1). Therefore, by the overt behavioral preferences shown ('revealed preferences'), for each participant the utilities of a gamble and its safe alternative were the same, as both were equally preferred.

Choice trials were randomly interspersed with no-choice trials. In each choice trial, participants were presented, on a computer monitor, with two alternatives (fig. 1d – see also supplemental material), randomly positioned to the left and right of an ocular fixation cross

(evaluation phase). Participants had always to choose between a risky and a safe option. Two risky options with equiprobable outcomes were used (40/60 and 10/90). After 5.5 seconds, the fixation cross was circled ('go' signal), signalling that the participant should press a button to indicate her choice. If the participant failed to respond within 600 ms, an error message appeared. In correct trials, the circled cross remained on the screen until 1000 ms had elapsed; subsequently, the choice was framed for a random period with an average of 4 seconds (2 secs fixed + 2 secs variable according to a exponential distribution truncated at 15 seconds), allowing temporal decorrelation (via jittering, Dale, 1999) between choice and outcome phase. Subsequently, the outcome of the choice was shown for 1 sec. A cross, to which participants had to fixate, appeared for the same random period, indicating the onset of a new trial. Fixation was added to allow temporal decorrelation of the outcome phase with the presentation of options in the next trial. No-choice trials had exactly the same sequence of screens as choice trials, with the exception that during the presentation of options, a small arrow placed next to the fixation cross indicated what the choice should be (left or right); the participant had to press the corresponding button, otherwise an error screen was shown.

Structure of experiment: The actual experiment started with an 'estimation session', during the acquisition of structural images. During the estimation session, we approximated the CE of each participant, for both gambles. This was followed by three sessions of the task ('main sessions'), during which functional scans were acquired.

Main (scanned) sessions: After the estimation session, each participant played three 'main' sessions, during which functional images were acquired. During each session, the participant faced 20×2 (choice/no-choice) $\times 2$ (high/low risk) = 80 trials minus the errors (average errors per participant = 4.7).

In order to ensure an approximately equal number of safe and risky choices, denoting that the risky and safe alternatives have the same utility, the safe alternative was updated according to a PEST-like algorithm that took into account previous choices (see supplemental material).

The payment method limited wealth effects and diversification strategies (see supplemental material).

Estimating certainty equivalent (CE): Because of the updating algorithm, the values of the safe alternative during scanning reflected indifference with the risky option, adjusted for temporal variations in risk aversion. For each participant and gamble, the median of these values was set to be the corresponding CE.

Second experiment—In experiment 2, a separate group of 14 participants had again to choose between a risky and a safe option. The main changes were: a) the outcome of each choice was not shown, ensuring that decision-related responses were not influenced by outcome-related responses, and choices were not influenced by the history of previous outcomes; b) only one choice obtained at the end of the experiment (i.e. participants did not accumulate points after each choice; they were told that they will make a series of decisions but only one, randomly selected choice will determine their reimbursement) to remove any wealth effects c) the safe alternatives were not set to indifference level, which allowed testing that the responses were independent of the value of the safe alternative, d)no-choice trials were not used (increasing power), e) gambles represented real money rather than points (increasing participant involvement), and f) risky gambles were studied at two different levels of mean gain, allowing further testing of value processing.

Four even chance gambles were offered (£15/£45, £10/£50, £40/£80, £30/£90). The first two had expected value of £30, with the first one offering £15 or £45 and the second gamble offering £10 or £50. The other pair of gambles had an expected value of £60, with the first one offering £40 or £80 and the second one offering £30 or £90. Therefore, within each pair, one gamble was riskier than the other. The trial structure was exactly the same as in the first experiment, with the exception that no outcome was shown. The second experiment comprised of two sessions. Each session consisted of 20 trials per gamble.

Estimating certainty equivalent (CE): The CE was estimated as the frequency-weighted average of the values of the safe alternative for which participants at some point during the experiment chose both the risky and safe option (see supplemental material).

Data analysis for both experiments

Measuring risk aversion: certainty equivalents (CE)—We identified the risk aversion of each participant using the CEs. The difference between the CEs of two gambles with the same EV ($CE_{LOW\ RISK\ GAMBLE} - CE_{HIGH\ RISK\ GAMBLE}$) reflects risk aversion. Less risk averse participants (with low difference between the CEs of the two gambles – fig. 1E (left side); see supplemental material for results of the second experiment) perceive the increase in risk as less important in comparison to more risk averse participants (fig. 1E right side), who perceive the risk manipulation as a significant escalation of risk. As a result, risk averse participants had lower safe alternatives for the high risk gamble (fig. 1C). A larger difference between the two CEs indicates higher risk aversion.

Data analysis: Imaging

Statistical analysis of images: Image acquisition and preprocessing parameters are described in the supplemental material. For each participant, all instances of a particular event type were modeled through convolution with a canonical hemodynamic response function (and its temporal and dispersion derivatives). For the first experiment (analyzed with SPM2; see supplemental material), in the first-level analysis, two main events were included in the same model: presentation of gambles and presentation of outcome. Both events had eight different conditions, forming a $2 \times 2 \times 2$ design: 2 (choice or no-choice) $\times$ 2 (high or low risk gamble condition) $\times$ 2 (safe or risky choice). As a result, sixteen regressors were entered for each participant. For the second experiment (analyzed with SPM5), one main event was included (presentation of options); the event had 4 (four gambles) $\times$ 2 (risky or safe choice) = 8 conditions. Errors were modeled as a different regressor. Movement parameters and errors were modeled as covariates of no interest.

We tested for different temporal profiles of BOLD response (phasic and sustained [with duration equal to the time till the 'go' signal appeared (5.5 seconds)]). For each participant, two different models were constructed to evaluate phasic (event-related design) and sustained response (5.5 seconds epoch-based design) to the onset of options. We used a participant-specific, fixed-effects model for each event type. Parameters estimates for each regressor were calculated for each voxel (Friston et al. 1994). Contrast images were constructed, demonstrating the size of the certain effect at each voxel. Subsequently, these data were entered into a second-order, random-effects analysis (Friston et al., 1999). At that level, contrast images were entered into one-sample t-tests, simple regressions or ANOVAs. Non-sphericity correction (as implemented in SPM2 and SPM5 and described at Glaser and Friston, 2003) was used at ANOVA analyses'.

Throughout, we used whole brain or small volume correction for multiple comparisons controlled at p<0.05 (family-wise error). We used small volume correction with family-wise error controlled at p<0.05 for the analysis for value and risk. Since previous studies

(described in the introduction) have implicated VSt and cingulate cortex for EV and risk encoding, they were employed as a priori anatomical regions of interest (ROI). Despite that many studies (e.g., Kuhnen and Knutson, 2005; Huettel et al., 2006; De Martino et al., 2006; Paulus et al., 2003), have examined the BOLD responses of risk averse choices, none of them had incorporated in their analysis a model-free subjective estimation of the riskiness of the gamble. Therefore, selecting an ROI (such as insula) would have been unjustifiable; as a result we used whole brain correction for the related analysis. Therefore, rDLPFC activity was corrected for the whole brain. Ventral striatum ROI was hand-drawn in MRIcro (Rorden et al., 2000) according to the anatomical description by Martinez et al. (2003), as used elsewhere (Murray et al., 2007), adjusted to the anatomical specificities of our sample. The cingulate ROI included anterior and posterior cingulate and was constructed using the Pickatlas Toolbox (Maldjian et al., 2003). Reported voxels conform to MNI (Montreal Neurological Institute) coordinate space, with the right hand side of the image corresponding to the right side of the brain. The most significant voxel (peak voxel) within the cluster of activation is reported.

RESULTS

Behavior: risk aversion

The mean CEs for the first experiment were 48.9 points (low risk gamble) and 35.3 points (high risk gamble). For the second experiment the mean CEs were £25.7 (gamble offering £15/£45), £23 (gamble £10/£50), £53.8 (gamble £40/£80) and £48.1 (gamble £30/£90). The difference between the CEs of the low and high risk gamble was used to measure risk aversion. For the first experiment, risk aversion coefficients ranged from 2.5 to 31 (mean = 13.57), with higher values implying higher risk aversion. For the second experiment with a comparable risk assessment, risk aversion coefficients ranged between −£0.87 and £8 (mean = £2.66) for the low EV gambles (£15/£45 and £10/£50) and between −1.5 and 12.08 (mean = 5.69) for the high EV gambles (£40/£80 and £30/£90). For both the first and second experiment the values of the CEs of the low and high risk gambles were statistically different from each other (first experiment $p < .001$ (paired t-test), second experiment $p < .001$ (high mean gambles) and $p < .005$ (low mean gambles).

Brain imaging

Neuronal correlates of decision parameters—We tested the blood-oxygenation-level-dependent (BOLD) responses to the onset of the stimuli (presentation of the risky and safe alternative).

Magnitude / expected value coding

First experiment: We identified value coding in the brain. In our paradigms, the expected value changes while keeping the probabilities constant, according to the Rothschild-Stiglitz definition of risk. In the first experiment, the difference between the monetary values of the two safe alternatives varies across participants (fig. 1F). Therefore, an area encoding magnitude should be sensitive to this variability. We measured the differential BOLD response preceding the choice of the safe alternatives [comparison B, (fig. 1D): $\text{Activity}_{\text{Low risk safe}} - \text{Activity}_{\text{High risk safe}}$] and correlated it with the value difference between the two CEs. The difference between the values of the CE positively correlated with increasing differential response of VSt (fig. 2.A; 2.B1, solid line; peak at −14/6/−2; $R^2 = 0.68$, $p < 0.01$, small volume correction (Worsley et al., 1996), suggesting that this area is sensitive to magnitude. A similar result was found in the no-choice trials (fig.2.B2 solid line;−20/8/−8; $R^2 = 0.70$, $p < 0.01$, svc).

We also performed a paired t-test comparing BOLD responses to the safe alternatives. When all participants are included, the striatal response does not survive correction. Yet, this apparently negative result could be misleading: It is most likely owed to the fact that for participants that are close to risk neutrality, the difference in the values of the safe alternatives between the two conditions of interest is very small (i.e. <=3 units); consequently, the associated small difference in BOLD response may add primarily noise to the t-test (but not to the correlation). In other words, given that the difference in value for almost risk neutral agents is small, it should be also expected that the difference between the BOLD responses corresponding to these safe alternatives should also be small.

In agreement with this reasoning, if we exclude the two almost-risk-neutral participants, then a significant striatal response differentiating between the values of the safe alternatives appears also in the t-test, even though the sample is smaller (p<.05; svc; 4/12/−8 and −12/20/−4). This response is bilateral.

Note that the two excluded participants are not handpicked. They are the participants that have a very low difference between the safe alternatives they face; indeed, for these two participants, the difference between safe alternatives was over one standard deviation away from (i.e. smaller than) the mean difference of the safe alternatives of the group.

Interestingly, exactly the same happens in the no-choice trials: including all participants the striatal response seems to be unable to differentiate between the different magnitudes. Again, excluding exactly the same participants, the striatal response significantly differentiates between the two conditions (p<.05; svc; 4/10/2).

Taken together, these results suggest that the striatum codes value both in choice and no-choice situations, as long as differences in value are clearly present in the behavior.

Control for utility encoding—The experimental design also allowed controlling for utility encoding: the striatal response could actually be interpreted as representing utility (or pure preferences), as larger differences between the values of the safe alternatives represent larger differences in utility as well. We controlled for this confound by using the comparison between the two risky options ([comparison A: $Activity_{High\ risk\ gamble}$ − $Activity_{Low\ risk\ gamble}$]). Note that gambles have the same utility with their corresponding safe alternatives. If striatum encodes utility, then the differential activity between the two risky options should also correlate with the differences between the two safe alternatives. We found that striatal activity did not change with respect to utility differences (fig. 2.B1; 2.B2 dotted lines ; R^2=0.0, n.s.) between the low and the high risk gamble. An analysis of the interaction effects, comparing the slopes of the two regression lines was significant for both the choice and no-choice trials (p<.05).

<u>Second experiment:</u> We used the data from the second experiment and compared the activity between the high and low mean gambles in order to test whether striatum activity changes with EV. We first compared the 'safe' conditions (where the subsequent choice was a safe alternative) with different magnitudes (high vs. low values of safe choice); the comparison confirmed striatal sensitivity to magnitude (fig.2B3; peak at −12/12/−8; p<.05, svc). In addition, we also compared the BOLD responses preceding a choice of a high vs. a low EV gamble (i.e. including only the occasion where the choice is risky) and we found a sustained response to the gambles with higher EV, again in striatum (fig.2B4; peak at 12/6/−8; p<.05, svc).

Risk coding

First experiment: In order to test risk coding, we compared the BOLD response preceding choices of the high risk gamble to the response preceding low risk gamble choices. Dorsal anterior cingulate (dACC) (fig.2C; peak at 8/30/34; p<.05), showed higher BOLD response when the subsequent choice was the high risk gamble compared to when the choice was the low risk gamble). Interestingly, such an activity differentiating between high and low risk trials was not found in no-choice trials, potentially signifying that the dACC response is mainly choice-specific (interaction analysis p<.05).

Control for magnitude or utility coding—We also tested whether the dACC signal is independent from magnitude or utility variations. To control for these we compared the dACC response to the safe alternatives of each gamble [$Activity_{Low\ risk\ safe}$ − $Activity_{High\ risk\ safe}$]. On average, the value of the low risk safe alternative (mean=48.92) is higher than the value of the high risk safe alternative (mean=35.34). If the ACC signal was in fact encoding either EV or utility, then it should differentiate between the two safe alternatives. We observed a significant interaction showing that whereas dACC differentiates between the two risky options, it shows no differential activity between the corresponding safe alternatives (p<.05, whole brain correction). Moreover, dACC activity does not covary with risk aversion (R^2=0.05, n.s.). This potentially suggests that dACC encodes risk in an objective manner, irrespective of magnitude, utility or the subjective evaluation of the riskiness of the gambles (risk aversion).

Second experiment

Risk coding with control for fictive / regret signals: In the first experiment, because of the indifference level setting, the safe alternative of the high risk is lower in comparison to the alternative of the low risk gamble. The difference in the BOLD response between high and low risk gambles might therefore be owed to the fact that their safe alternatives differ in magnitude (Loomes and Sugden, 1982; Lohrenz et al., 2007). Accordingly, this difference could actually reflect an inverse coding of the foregone safe amount. On the contrary, in the second experiment, the safe alternatives are approximately the same across gambles with the same EV, as they were not adjusted to indifference levels; therefore the comparison between high and low risk gambles does not suffer from the possibility that the safe alternatives are also different (as it is the case in the first experiment). In order to control for this possibility, we used data from the second experimental paradigm, where the offered safe alternatives are not set to indifference level and are approximately the same across participants and gambles with the same EV. Again, the risk encoding function of dACC was found when we compared the gambles offering £40/£80 and £30/£90, in the same way as in the first experiment. Dorsal ACC was sensitive to higher risk (fig. 2D.2; peak at 16/22/28; p<.05, svc). As in the first experiment, this difference weakly and insignificantly correlated with risk attitudes, expressed as the difference between the CEs (R^2=.16, n.s.).

Differential response to risky options according to risk aversion

First experiment: The fact that participants attached different CEs to each gamble suggests that the increase in risk (from the low risk to the high risk gamble) was perceived differently by each individual. This subjective evaluation of risk is reflected in the difference between the CEs. In both experiments, participants demonstrated sufficient variability of risk attitudes enabling us to study the corresponding differences in bold response (Friston et al., 1999). To determine whether these individual differences in behavioral responses to risk are reflected in brain activity, we correlated the difference in the brain response to the two gambles [comparison A, (fig. 1D): $Activity_{low\ risk\ gamble}$ − $Activity_{high\ risk\ gamble}$] with risk aversion (defined as the difference between the values of the two CEs [$CE_{low\ risk\ gamble}$-

$CE_{\text{high risk gamble}}$]). A strong correlation ($R^2=0.89$, $p<.01$, whole brain corrected, fig.3A) was evident in the inferior frontal gyrus (IFG) (48/32/14; fig.3A): increasing risk aversion provoked better differentiation between the BOLD responses of the two gambles, reflecting the behavioral difference in the CEs. This result is based on the increased IFG activity preceding a choice of the low risk gamble in correlation with risk aversion (fig.3B); on the contrary, activity for the high risk gamble remains unchanged (again with respect to risk aversion). A similar, yet less strong, result was also found in the no-choice trials (peak at 48/26/14; $R^2=0.77$, $p<.05$, svc). IFG activity differentiated between high and low risk according to risk aversion, in a similar way to choice trials.

There were no other areas surviving whole brain correction. Nevertheless, given that insula has been implicated in risk averse choices, we tested whether the BOLD response of this area correlates with risk aversion, using an ROI analysis. In the first experiment there is a non-significant trend of anterior insula correlating with risk attitudes. However, this activation does not survive at all in the second experiment. We are therefore forced to reject the hypothesis that insula BOLD responses correlate with risk attitudes.

Second experiment: In the second experiment, we correlated the differences in the BOLD response of gambles £30/£90 and £40/£80 with risk aversion. Again, right IFG BOLD response (peak at 52/14/22; $p<.05$, fdr, svc) correlated with risk aversion, in a similar fashion as in the first experiment (positive correlation in parallel with increasing risk aversion; see supplem. material). Hence, these results suggest that IFG BOLD response increases with lower risk gambles, and this increase is more pronounced in risk averse agents.

Decoding the behavioral choice by BOLD response—We next sought to identify whether neuronal signals solely reflect decision-making parameters, or are, in addition, relevant to actual choice behavior. Our analysis so far identified three different structures preferentially processing basic decision parameters: ventral striatum (VSt), dorsal anterior cingulate (dACC) and inferior frontal gyrus (IFG) reflecting magnitude, risk and risk aversion respectively.

Using a similar methodology with previous studies (Knutson et al., 2007; Kuhnen and Knutson, 2005) we employed binary logistic regression (Hosmer and Lemeshow, 1989) to determine whether the combination of BOLD responses correlates with a risky or safe choice and also to elucidate the potential contribution of each structure to decision-making. We used three variables (trial-by-trial activity of VSt, dACC and IFG) and the actual choice made on each trial (risky or safe) as the dependent variable.

Overall coefficients of the logistic model related to activity of each structure were significant (Table 1), suggesting that all three structures contributed to the choice. Importantly, the overall logistic regression coefficients allowed us to clarify the exact role of each structure. Logistic regression coefficients were positive for VSt and dACC activity ($B_{VSt}=1.161$, $B_{dACC}=0.966$, $p<.05$), whereas IFG had a negative coefficient ($B_{IFG}=-0.326$, $p<.05$). A similar result was obtained in the second experiment (see supplemental material). This indicates that increasing activity of VSt and ACC increases the probability of a risky choice, whereas the IFG activity pattern does the opposite (fig. 4C). To further investigate the contribution of IFG activity to choice behavior, we identified how the model-based probabilities of a risky choice change with different levels of IFG activity, in relation to the activity of VSt and dACC. Increasing IFG activity moves the psychophysical function towards the right (fig.4D). Thus, the overall logistic regression model suggests that given an increase in IFG activity, increased VSt and ACC activity is required in order to obtain the same probability of a risky choice.

Above, we presented the logistic regression results from a fixed effects analysis in order to evaluate the overall contribution of the three structures, independent of variability in between-subjects task characteristics (which is the case for the first experiment), as it was done in previous studies (Kuhnen and Knutson, 2005). Adopting a stricter random-effects approach we next calculated the subject-specific coefficients of the logistic regression and then evaluated these parameters in second-level random-effects tests.

For the first experiment, striatal and dACC responses were significant (p<.001), whereas IFG approached significance (p=.10). Yet, it should be remembered that the BOLD response of the IFG is more relevant as risk aversion increases. Therefore, if we only include participants which are at least slightly risk averse (i.e. the difference between the CEs is >=3 monetary units, which is one standard deviation away from the average value of the sample) then the IFG response indeed becomes significant at p =.05. This implies that the IFG BOLD response plays a role in the forthcoming choice primarily when the participant is risk averse.

To test this notion further, we performed a similar random effects analysis also in the second experiment. In agreement with the findings from the first experiment, the significance of the IFG BOLD response for the logistic regression model increases when we exclude risk neutral participants (responses of the three structures are all significant at p = .05). These data further reinforce the notion that dACC, IFG and striatal BOLD responses contribute to decisions in risky situations, with IFG response being more relevant to the decisions of risk averse agents.

Using the coefficients we determined the model-based computed probability of a risky choice, given the activity of VSt, dACC and IFG on each trial. We then calculated the receiver operating characteristic (ROC) curve comparing these model-based probabilities of a risky choice to the actual choice. The ROC analysis describes how effectively an ideal observer would detect a signal (a risky choice, in our case) in the presence of noise. The ROC has been effectively used (Chandrasekaran et al., 2007; Britten et al., 1996; Thielscher and Pessoa, 2007) to elucidate the relation between neuronal responses and perceptual choices.

For the choice trials of the first experiment, the model detected the behavioral choice significantly well above chance (ROC=.77, p<.01; fig. 4A). We used exactly the same method in the second experiment and again found a similar ROC value (ROC=.74 p<.01; fig. 4A). In addition, the ROC values derived from models using each structure separately were lower (fig.4A). In the no-choice trials, the ROC value was also lower (ROC=. 72).

Stricter validation analyses confirmed the generalizability of the detective power of the model. Specifically, leave-one-out cross-validation produced a similar, statistically significant ROC value (ROC=0.65), which was slightly lower due to the smaller sample size inherent in the procedure.

DISCUSSION

From both a behavioral and theoretical perspective, the value and risk of an option along with the agent's risk aversion are the basic factors implicated in the choice behavior. Our approach in studying choice behavior was to first identify the components of the system (magnitude, risk and risk aversion) and then to piece them together to produce a function relating them to a behavioral outcome (i.e. the choice). To achieve this, we first located the neuronal responses that are more relevant to decision factors. In the final step we tested whether these responses can indeed describe the function of the system (i.e. detect the behavioral choice).

Previous studies have uncovered the neural correlates of independent decision factors as well. Our design disentangled decision parameters from utility encoding, took into account the behaviorally demonstrated risk attitudes of each participant and minimized any learning elements. The present findings suggest that the computational and theoretical deconstruction of the decision procedure into specific parameters meets with distinct BOLD responses, which could contribute crucial inputs for actual choices.

In two different experiments, where important behavioral parameters were differentiated, we found distinct neuronal responses towards different decision factors. The striatum was particularly responsive to changes in magnitude, dorsal anterior cingulate (dACC) was involved in –mainly objective- risk coding, and inferior frontal gyrus (IFG) signaled risk aversion. Importantly, by combining the information from these different brain regions, these BOLD responses were informative enough to allow an ideal observer to detect the overt choice: a risky choice was more probable when striatal and cingulate activity was higher, whereas increased BOLD signals from IFG correlated with increased probability of a safe choice.

High correlations between BOLD responses and personality traits have been recently criticized (Vul et al., 2009). While the critique is highly controversial and disputable (see Lieberman et al., 2009), our study nevertheless escapes the criticism as we use two separate sets of data (and experimental designs) to evaluate our hypotheses; in both experiments, the brain regions BOLD response correlated with the behavioral measurement. In addition, the principal measurement (risk aversion) is not approached as a personality trait but rather as a behavioral measurement. Finally, the regions reflecting individual differences in risk processing were identified independently from those coding risk.

Value, objective and subjective risk

Our results show that VSt activation increases with increasing value. Importantly, our analysis suggests that striatal activity encoded value, independent from utility. Due to our design, the term 'value' refers to either 'magnitude' (first experiment) or 'expected value' (second experiment). We need to underline that our experiments do not clarify to which of these two parameters the VSt is responsive to, as such a study would require a design that includes different levels of probabilities. This should be addressed in future studies, though similar issues have been tested by previous reports; our results are in line with their results linking striatal activity to computing value (or processing its components)(Knutson et al., 2005; Abler et al. 2006; Yacubian et al., 2006; Tobler et al., 2007).

According to the present results, dACC activity increases when the forthcoming choice has higher risk. The magnitude of this increase does not covary with individual differences in the estimation of risk (risk aversion). Therefore, dACC activity seems to preferentially mirror an objective metric of risk. In addition, we found no differences in dACC activity with respect to the utility of the subsequent choice. Previous studies have implicated dACC activity with the volatility of the reward environment (Behrens et al. 2007), whereas Critchley et al. (2001) relate the increased BOLD response of ACC in anticipation of risky outcomes to autonomic arousal. We also control for conflict of choice (Carter et al., 1998), which is a common function ascribed to ACC, as both alternatives are equally preferred – therefore conflict in every trial of the first experiment is maximal. A possible caveat of our study is that both experiments have a relatively small number of participants; this might significantly lower the power to find correlations. Although that the size of our sample was sufficient to detect correlations in IFG, the fact that we did not find a correlation of dACC BOLD response to risk does not necessarily preclude the possibility that this area might also be sensitive in subject-wise differences in risk assessments.

Yet, it should be emphasized that the brain responses attributed to specific decision parameters are not exclusive but mainly preferential. Our study adopted a formal definition of risk, which is independent of changes in probabilities; this is a crucially different aspect of risk (Rushworth and Behrens 2008). The control of probability might be a contributing factor for not finding risk signals in brain structures such as insula (Critchley et al., 2001; Preuschoff et al., 2008) and areas of prefrontal cortex (Rogers et al., 1999; Elliott et al., 1999). Yet, a thorough examination of risk-related choice behavior necessitates the detailed, separate identification of the different facets of risk. Given that variance is the first moment of a distribution, it is evident that it is one of the primary aspects of risk.

IFG BOLD responses found in this study reflected risk aversion. The currently observed BOLD response of IFG is located within right dorsolateral prefrontal cortex whose stimulation accordingly modulates risk aversion (Fecteau et al. 2007; Knoch et al. 2006). Our results demonstrate that this area does not influence the objective evaluation of risk but rather the subjective perception of the riskiness of the option. Further analysis suggests that this IFG BOLD response functions as a 'safety' signal, as it shows higher response to safer options, especially for more risk averse participants.

Combined BOLD signals contributing to decision making

To use an analogy, in perceptual decisions, the choice can be decoded by comparing neuronal activity between areas that are selectively tuned to the basic characteristics of each option (for instance areas sensitive to either faces or houses, Heekeren et al., 2004). Lee et al. (2007) suggest that, in order to make a choice, the brain should collect information on different decision parameters and then combine this information in an effective way to produce the choice. In economic choices, specific values are assigned to the individual options; these values are modulated, among others, by the risk of the options. The conjecture that risk has an influence on value constitutes the key characteristic of one of the prominent theories in economic decision making, namely the mean variance approach (Levy and Markowitz 1979, Preuschoff et al., 2006; Rangel et al., 2008). Essentially, the underlying hypothesis is that the overt choice is the output of internal processes combining the neuronal information pertaining to each choice parameter. Our experiment followed this rationale of combined decision parameters.

We indeed found a group of areas that are sensitive to specific decision parameters. Logistic regression analysis of signals from different regions revealed relationships not obvious from single-structure analysis. The relationship between activity and choice can be approximated by a competing activity between striatum and dACC on one hand, correlating with riskier choices, and IFG, on the other hand, holding an inhibitory, risk averse role.

Our analysis brings forward the possibility of evaluating the effect of 'virtual' lesions in the implicated areas. Striatal and cingulate lesions would potentially be associated with less risk averse (and more risk neutral) choices. A striatal lesion could reduce the ability to evaluate magnitude, an effect which is also implied by negative motivational changes in patients with globus pallidus lesions (Vijayaraghavan et al., 2008). Nevertheless, such a lesion could be compensated by functions in other areas, namely ventromedial prefrontal cortex. In addition, our prediction is that lateral prefrontal cortex lesions will lead to riskier choices, which as said before is in accordance with neuromodulatory studies (Fecteau et al. 2007; Knoch et al. 2006). A recent study (Gianotti et al., 2009) also suggested that participants with higher baseline cortical activity in the right prefrontal cortex are more risk averse. In addition, patients with predominantly right-sided prefrontal lesions demonstrate a riskier behavior (Clark et al., 2003).

It should be noted that individual brain regions, and especially striatum, independently have high ROC values. The latter suggests that encoding of isolated decision parameters already contains information able to decode the choice. Yet, the incorporation and appropriate combination of information stemming from aptly selected regions improves the overall representation of the choice behavior.

Cognitive functions such as decision making might necessitate the combination of signals from different brain areas instead of contributions from a single structure. Such distributed neuronal contributions to cognitive functions have also been found in other paradigms, such as emotional perceptual decisions (Pessoa and Padmala, 2007) and a probabilistic-reversal learning task (Hampton and O'Doherty, 2007). Our study demonstrates that neural combinations of information can be beneficial on economic decisions under risk, as well.

It has been suggested (MacDonald et al. 2000; Fleck et al. 2006) that dACC engagement indexes conflict and the need for cognitive control (Barch et al. 2001, whereas DLPFC assumes a more evaluative role, including cognitive control and response selection. Importantly, Rushworth et al. (2004) suggest that the main function of ACC is to perform a cost-benefit analysis in order to guide action. The present results fit in that framework. Dorsal ACC evaluates the riskiness of the situation (which which may correspond to an evaluation of costs and benefits), indexing the need to engage cognitive control over the competing choice between a risky and a safe alternative. Higher risk requires higher cognitive control in comparison to low risk trials. Therefore, dorsal ACC activity signals whether and to what extent cognitive control is needed according to the riskiness of the situation, whereas IFG / DLPFC activity idiosyncratically guides the choice according to risk attitudes.

In conclusion, our analysis sheds light to the mechanisms employed in decision-making under risk. Behavioral evidence suggests that the output of the choice process heavily depends on the statistical properties of the options. This implies that the brain not only encodes these properties but also combines them to produce the overt choice. An analogous mechanism is suggested by our data. From a more general point of view, the generation and combination of neuronal signals representing lower-level properties of the stimulus might be a general decision making mechanism across different modalities (Heekeren et al., 2008).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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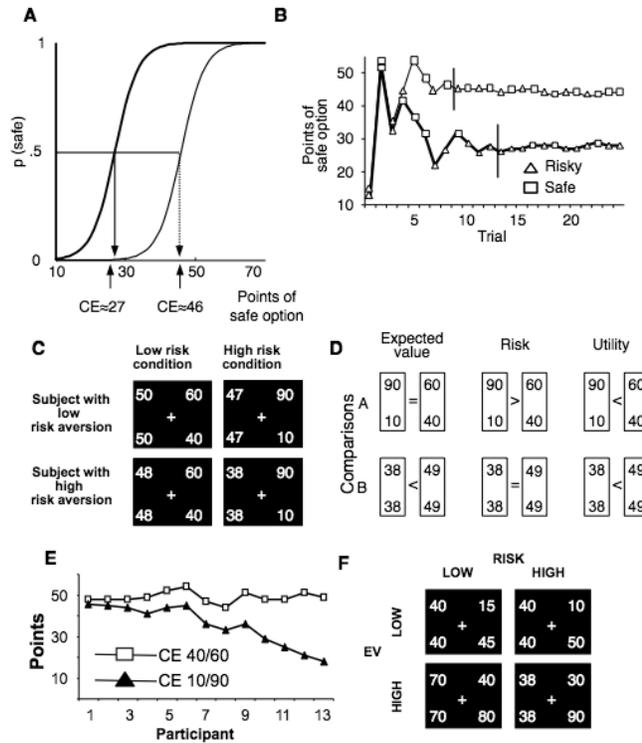
Fig.1. Task and behavioural results

A. Psychophysical definition of certainty equivalent. The certainty equivalent (CE) of a gamble is the amount for which an agent is indifferent between receiving it for sure and opting for the gamble. This definition implies that the probability of choosing the CE instead of the gamble is p=0.5. Examples show probability distributions of safe choices as function of safe amounts for two participants with different degrees of risk aversion (thick line for stronger risk aversion with lower CE).

B. Iterative determination of Certainty Equivalent (CE). In each trial, participants chose between a safe and a risky option. The staircase method (Parameter Estimation by Sequential Testing procedure) iteratively adjusted the safe option in consecutive trials to approximate choice indifference between the two options. Lines show data from two participants with different CEs (thicker line represents higher risk aversion). The shape of each dot illustrates safe and risky choices. Vertical lines indicate good approximation of indifference values and mark onset of scanning.

C. Choice options as presented to participants (first experiment). Participants chose between either a safe option or one of two gambles with two equiprobable outcomes (40/60 and 10/90, respectively). Each screen shows a safe (left) and a risky option, the safe value being set to choice indifference. The first row represents the choice set a less risk averse participant faced, whereas the second row the choice set of a very risk averse participant. The first column represents the low risk condition (choices involving the low risk gamble), whereas the second column the high risk condition (choices involving the high risk gamble).

D. Differential assessment of key decision parameters: expected value (EV), risk (as increase in spread) and utility. Each comparison serves to identify differences in two of these parameters. Comparison A tests differences in risk and utility but not EV; comparison B tests EV and utility, controlling for risk.

E. Certainty Equivalents (CE) of participants. CEs of individual participants for the two gambles (40/60 & 10/90) are displayed according to increasing risk aversion. Lower CEs, and larger differences between CEs for the two gambles, indicate increasing risk aversion. **F. Choice options as presented to participants (second experiment)**. Participants again chose between a safe and an even chance gamble. This time, four gambles were used: the first two (offering £10 or £50 and £15 or £45, respectively) had expected value of £30 whereas the other two (offering £40 or £80 and £30 or £90, respectively) had an expected value of £60. For gambles with the same expected value, one was riskier than the other. Importantly, safe alternatives were not set to indifference level, but took semi-random values.
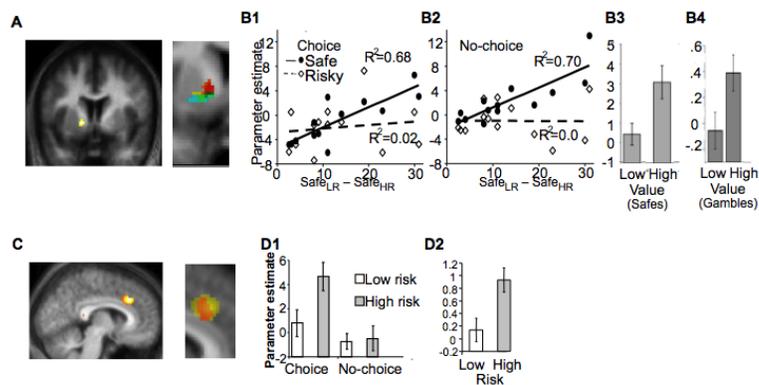
Fig. 2. Brain activity related to value and risk

All BOLD responses presented were modelled on presentation of the stimuli (options) and are estimated by the related regression slope parameter estimates (beta).

A. Value coding by ventral striatum (VSt). Response location in VSt sensitive to magnitude / EV differences ($p < 0.05$, small volume correction, displayed at $p = .01$). Red: First experiment, comparing safe alternatives, choice situation; Yellow: First experiment, same in no-choice situation; Green: Second experiment, comparing safe choices having different magnitude; Blue: Second experiment, comparing risky choices having different EV. Darkest voxels reflect common activation areas.

B. Quantitative value coding by ventral striatum.

B1. Increasing difference in the magnitude of the safe alternatives of each gamble (x axis) correlates with the differential VSt response to the choice of these alternatives (y axis) (solid line; $R^2=0.68$, $p=.0005$). This signal does not change when we compare high and low risk gambles (comparison A in fig.1, signaling either risk or utility) (dotted line).

B2. The same area shows a similar activation pattern in no-choice trials.

B3,B4. In addition, a neighboring voxel (peak at $-22/6/8$) distinguishes between high and low expected value in the second experiment. Figure B4 is essentially the same as fig.B1, with the exception that we now compare the two risky options with different expected values, whereas in the first experiment we compared safe options with different magnitudes.

C. Risk coding by dorsal anterior cingulate cortex (dACC). Comparing activity emerging from a choice of the high risk option to activity related to a choice of the low risk one, risk-sensitive areas were identified. This comparison reached significance in dACC ($p < 0.05$, displayed at $p = .01$). This signal also does not covary with risk attitudes or the utility of each option. Red: First experiment, comparing high and low risk gambles, choice condition; Yellow: Second experiment, comparing high and low risk gambles.

D. Quantitative coding of risk by dorsal anterior cingulate cortex (dACC). dACC shows higher response for the high risk gamble than to the low risk option.

D1. An interaction effects analysis suggested that this sensitivity of dACC to the high risk occurs only in choice trials and not in no-choice trials ($p<.05$). Error bars represent standard error of the mean.

D2. The same area showed increasing response to high risk in comparison with low risk in the second experiment, where the safe alternatives are not set to indifference level. This suggests that the dACC response to higher risk is not attributable to the lower value of the alternative offer (which is the case in the first experiment).
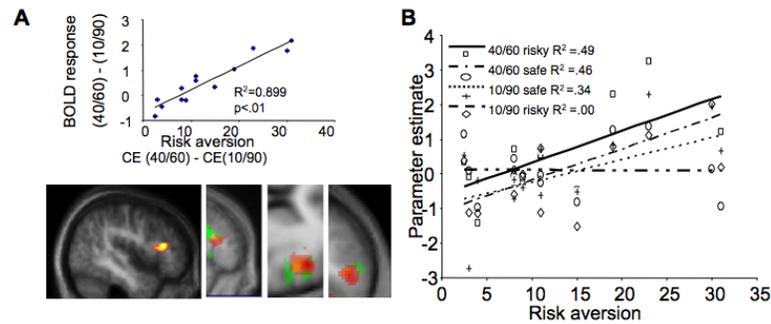
Fig.3. Modulation of inferior frontal gyrus (IFG) activity by risk aversion

A. Increased differential IFG activity with risk aversion. Y-axis represents the difference of the IFG parameter estimate of the BOLD response preceding a choice of the low risk gamble minus the corresponding IFG parameter preceding a choice of the high risk gamble. X-axis represents risk aversion of each participant, as measured by the monetary difference between the certainty equivalents (CE) of the two gambles ($CE_{Low\ risk\ gamble}$ - $CE_{High\ risk\ gamble}$). The more risk averse the participant the larger the difference in BOLD response in IFG ($p<.05$, whole brain correction). The first image is from the first experiment. The next three images depict sagittal, axial and coronal planes showing the common rDLPFC activated voxels for the risk-attitude related contrast. Red: First experiment, choice condition; Yellow: First experiment, no-choice condition; Green: Second experiment.

B. Correlation of BOLD response in inferior frontal gyrus (IFG) to safe and low risk gambles with individual risk aversion. The IFG response slope increases with gambles of decreasing risk, thus providing better discrimination of lower risks in risk averse participants. This selective coding of a 'safety signal' for more risk averse participants is verified by the similar (increasing) activity of the same voxel as a response to safe choices. By contrast, activity related to a choice of the high risk option does not correlate with individual risk aversion. The R^2 for each regression line are: low risk gamble: .49; low risk safe: .46; high risk safe: .34; high risk gamble: .00.
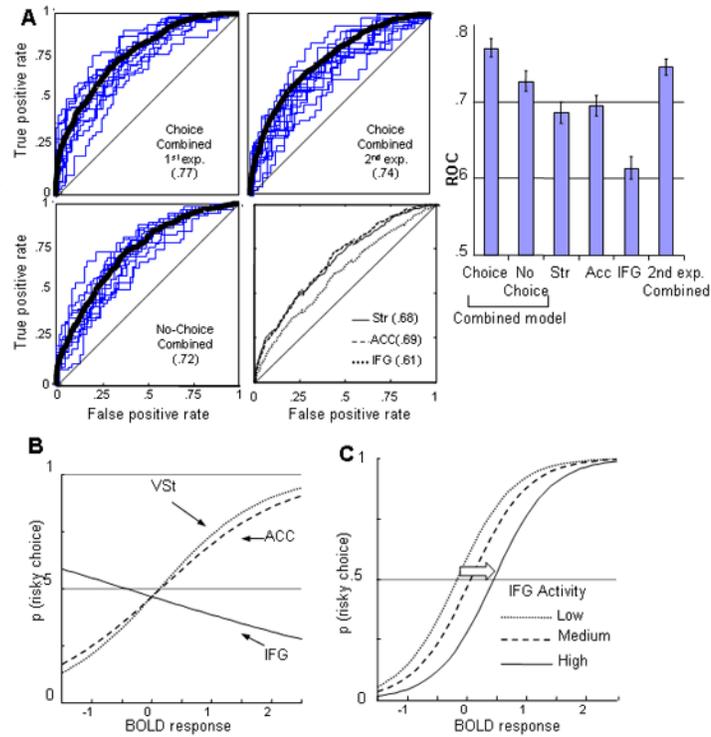
Fig. 4. Detection of risky choices by combined brain signals of decision parameters
A. Evaluation of detection. By applying binary logistic regression, we tested whether a model combining signals of VSt, dACC and IFG (corresponding to EV, risk and risk aversion) could detect the choice on a trial-by-trial basis. Receiver operating characteristic (ROC) values depicted here indicate the model-based probability of correctly detecting a risky choice. The ROC values for the combined model, (using activity from all structures) are .77 (first experiment; top left panel) and .74 (second experiment; top right). Both are significantly different from chance performance (ROC = 0.5; straight diagonal lines; see also panel on the right) and models using the BOLD response from one structure only (bottom right).
B. Contribution of brain structures to probability of risky choice. X axis represents level of BOLD responses (of VSt, dACC or IFG), whereas y axis the probability of a risky choice, as computed by the regression equations. Increasing activity of VSt and dACC increases the probability of a risky choice. On the contrary, increasing activity of IFG increases the probability of a safe choice.
C. Effect of IFG activity. X axis represents the activity of both VSt and dACC. Dotted line (left) depicts the probability of a risky choice (as computed by the regression equation), with respect to VSt and dACC activity, when IFG activity is low. When the activity of IFG is high (solid line) then higher compensatory activity of VSt and dACC is required to elicit the same probability of a risky choice.

Table 1

Logistic Regression parameters detecting decisions from ventral striatum, dorsal anterior cingulate (dACC) and inferior frontal gyrus (IFG) BOLD response.

Variables	Coefficients (betas)	Standard Error	Wald Statistic	p	Odds ratio (Exp(B))
VSt	1.161	.152	58.131	.000	3.195
dACC	.966	.136	50.528	.000	2.626
IFG	−.326	.158	4.276	.039	.722
Constant	−.141	.055	6.549	.010	.869