NeuroImage 103 (2014) 355–363

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Neural mechanisms underlying context-dependent shifts in risk preferences

Annabel B. Losecaat Vermeer [a,b,*], Maarten A.S. Boksem [b,c], Alan G. Sanfey [a,b,d]

[a] Behavioural Science Institute, Radboud University Nijmegen, PO Box 9104, 6500 HE Nijmegen, The Netherlands
[b] Donders Institute for Brain, Cognition and Behaviour, Radboud University, PO Box 9101, 6500 HB, Nijmegen, The Netherlands
[c] Rotterdam School of Management, Erasmus University, PO Box 1738, 3000 DR, Rotterdam, The Netherlands
[d] Department of Psychology, University of Arizona, Tucson, AZ 85721, USA

ARTICLE INFO

Article history:
Accepted 23 September 2014
Available online 2 October 2014

Keywords:
Decision-making
Gains
Losses
Risk preferences
Ventromedial prefrontal cortex

ABSTRACT

Studies of risky decision-making have demonstrated that humans typically prefer risky options after incurring a financial loss, while generally preferring safer options after a monetary gain. Here, we examined the neural processes underlying these inconsistent risk preferences by investigating the evaluation of gains and losses, and demonstrating how these responses can impact subsequent preference for either risky or safe choice options. Participants performed a task while undergoing fMRI in which they experienced both gains and losses. Immediately following a gain or loss, participants decided to either play or pass on a "double-or-quits" gamble. The outcome of the gamble could either double or eliminate their initial gain (from the time-estimation task) or redeem or double their initial loss. If they chose not to play this gamble, they retained the initial gain or loss. We demonstrate a shift in risk-taking preferences for identical sets of gambles as a function of previous gains or losses, with participants showing a greater preference towards riskier decisions in the context of a prior loss. An interaction between evaluating gain/loss contexts and subsequent behavioral risk pattern revealed an increased BOLD response in the ventromedial prefrontal cortex (vmPFC), with stronger responses for both gambling in a loss context and safety in a gain context. This suggests that the vmPFC is responsible for integrating these contextual effects, with these processes impacting on subsequent risky choice.

Introduction

In daily life, people are typically faced with numerous risky decisions, for instance choosing whether or not to buy insurance on an expensive smartphone, or whether to invest money in stocks or save it for retirement. When deciding what to choose in a risky, uncertain environment, people generally exhibit risk averse tendencies, that is, they generally shy away from options with increased risk, even when the so-called expected value of the choice options is equal (Tversky and Kahneman, 1981, 1992). That is, if given a choice between €10 for sure and a gamble with a 50% chance of €20 and a 50% chance of €0, people overwhelmingly favor the certain €10, and in fact the 'winning' outcome of the gamble usually needs to be considerably higher to induce players to choose the risky option. Classical models of economic decision-making (e.g. utility theory and its variants) also assume that these individual choice preferences should be consistent over situations in which the same choice set is offered. For example, the decision to purchase a €5 lottery ticket should not be affected if you had previously either just found €5 on the street, or if alternately you had unfortunately just lost €5 from your wallet — the choice to spend the money to buy the lottery ticket should in theory be independent of these two events. However, several decades of behavioral work (e.g. Kahneman and Tversky, 1979) have convincingly demonstrated that outcomes unrelated to the decision at hand (e.g., recent financial gains or losses) do in fact play an important role in determining our choices. For example, Xue et al. (2011) had participants play a task where they decided to play or pass on a gamble consisting of one cup with a large gain and multiple cups with small losses, varying in expected value. They showed that participants decided to play the gamble more often after they lost the gamble on the previous trial, whereas when they won the gamble on the previous trial they were more reluctant to play the gamble.

In fact, when deciding between relatively risky and a relatively safe options, individuals typically have higher preferences for riskier options when the choice is made immediately after experiencing a financial loss (which we term here a *loss context*), while they generally prefer safer options when the choice takes place after experiencing a financial gain (i.e. *gain context*) (Tversky and Kahneman, 1992). This phenomenon can occur even when faced with a choice set presented as either gains or losses (Tversky and Kahneman, 1981; De Martino et al., 2006; Porcelli and Delgado, 2009).

* Corresponding author at: Behavioural Science Institute, Radboud University Nijmegen, PO Box 9104, 6500 HE Nijmegen, The Netherlands. Fax: +31 24 3610989.
E-mail address: a.losecaatvermeer@donders.ru.nl (A.B. Losecaat Vermeer).

http://dx.doi.org/10.1016/j.neuroimage.2014.09.054
1053-8119/

In the current study, we are interested in exploring the neural processes underlying these inconsistent risk preferences following gains and losses respectively. Specifically, we aim to gain greater insight into the mechanisms underlying risk assessment and preference, by investigating the neural substrate during the evaluation of gains and losses prior to a risky decision situation and demonstrating how these responses can predict and influence subsequent preference for either risky or safe choice options.

Vitally important for decision-making is an adequate evaluation of gains and losses, as these outcomes usefully inform us whether or not to continue a particular behavioral strategy (Barto and Sutton, 1997). Brain areas associated with the evaluation of gains/losses and with value-guided decision-making are, among others, ventromedial prefrontal cortex (vmPFC), striatum, and insula (Breiter et al., 2001; Delgado et al., 2003; Tom et al., 2007; Rangel and Hare, 2010; Basten et al., 2010; Boorman et al., 2013). For instance, Tom et al. (2007) observed that when participants were presented with a mixed gamble offering an equal chance of a monetary gain or loss, BOLD responses in striatum and mPFC increased with the size of the monetary gain; in contrast, BOLD responses in the insula increased with gambles containing greater losses. Similar effects were found when gain and loss outcomes were anticipated (Breiter et al., 2001; Knutson et al., 2001; Kuhnen and Knutson, 2005), or when the gain and loss were not monetary but instead delivered in the form of primary incentives, such as tasty versus nontasty liquids (see also Bartra et al., 2013). Different decision parameters (e.g. outcome evaluation, choice riskiness, magnitude) are believed to be integrated via a common network in the assessment of choice preference and guiding subsequent behavior. Interestingly, this network, in particular the vmPFC may play an important role in integrating the gain/loss outcomes and in light of choice options to assess their subsequent preference.

Moreover, studies have shown that the vmPFC is also involved in the prediction of choice. Studies found that while viewing different goods the vmPFC response correlated with the actual preference for those goods, even in the absence of choice, suggesting that the vmPFC also reflects a choice preference signal prior to making a choice (Lebreton et al., 2009; Levy et al., 2011). Specifically with regard to value-based decision-making, the medial orbitofrontal cortex (mOFC) and vmPFC, including striatum and insula, exhibit a significant increase in signal for options yielding higher expected value, and a significantly reduced signal for options yielding lower or negative expected value (e.g. loss) (Platt and Huettel, 2008; Rangel et al., 2008; Rangel and Hare, 2010; Tom et al., 2007). Options that have ultimately been chosen, with respect to those that have not been chosen, also correlate with the value response of the vmPFC (Boorman et al., 2009).

In particular, the vmPFC has been suggested as a general "hub" for value-guided decisions. This area has strong connections with other reward- and control-related areas (Grabenhorst and Rolls, 2011). It has been suggested that vmPFC guides the valuation process (Plassmann et al., 2010; Rangel et al., 2008), taking into account the decision-makers goals and the current context, by integrating information signals related to the valuation of rewarding and aversive outcomes, choice signals, and signals from regions involved in cognitive control (e.g. IFG, lateral PFC; Hare et al., 2009; Weller et al., 2007; Rosenbloom et al., 2012). The aforementioned studies imply that the vmPFC may be a key region that operates in shaping preference for which choice option to pursue. However, a relevant question is how different values related to each phase of the decision are integrated and updated, and subsequently impact the decision process. More specifically, it is important to understand how appraisals of the context (i.e. gain and loss) of choice guide subsequent decision-making.

We hypothesize here that in the light of different gain and loss contexts prior to making a risky choice, engagement of the vmPFC may mediate risk preferences in line with the behavior described by previous studies, that is, a stronger involvement for risk avoidance in the gain context and for risk seeking in the loss context.

To investigate this, in the present study we varied the delivery of monetary gains and losses preceding a risky choice. We expected that this contextual change would in turn alter risk preferences, even though the actual choice facing the participant was the same in each event. We expected that the engagement of the vmPFC reflected a combined value of the appraisal of the current gain or loss by the subsequent anticipated choice and outcome, and that this relative engagement would be potentially predictive of the degree of riskiness of subsequent decisions in the context of gains or losses.

Materials and methods

Participants

Thirty undergraduate students participated in the study. All provided written informed consent and were financially compensated via a flat fee (25 Euro) for completion of the task. In addition, they also had the opportunity to win a bonus on top of this participation fee, a maximum amount of 10 Euro. Exclusion criteria were self-reported claustrophobia, neurological or cardiovascular diseases, psychiatric disorders, regular use of marijuana, use of psychotropic drugs, or metal parts in the body. Four participants were excluded due to technical problems during scanning. Data is therefore reported from twenty-six participants (14 men and 12 women, $M = 22$ years, $SD = 2.68$, range = 19 to 27 years, all right-handed). The study was approved by the local ethics committee.

Task design and procedure

We developed a novel paradigm in order to study risk-taking behavior in the context of prior gains and losses. Each trial began with a simple time-estimation task in which participants either won or lost money depending on their performance (Boksem et al., 2011). The purpose of this task was to induce either a gain or a loss context. Directly after the gain or loss feedback from the time-estimation task, participants received a mixed (50/50 chance, gain/loss) gamble (see Fig. 1), which they could decide to either pass or play. If they decided to pass on the gamble they would simply retain their gain or loss from the preceding time-estimation trial, which would then be added to the total balance of the money won so far. However, if they decided to play the gamble, the gamble was resolved for them and the corresponding win or loss amount was added to their total experimental balance. The mixed gamble contained either a positive expected value ('+ EV'), a negative expected value ('− EV'), or an equal expected value ('0 EV') by varying the gain or loss outcome from €1.00, €1.20, to €1.40 as compared to the 'pass' option (i.e. choosing to keep the €1.20 gain or loss) (Table 1). We created these three different gamble types to assess whether participants were attending and sensitive to the expected value of the gamble.

This study differs in important ways from previous efforts to assess contextual influences on risky decision-making (such as the 'framing effect'; Kahneman and Tversky, 1979; Tversky and Kahneman, 1981; De Martino et al., 2006). The current task design allowed us to disentangle the context from the decision itself. In other words, the current task design enables us to test how a gain/loss context influences risk preferences for identical choice sets. Other tasks (Porcelli and Delgado, 2009) have not been able to purely disentangle the choice from the context, as the gambles were not of comparable value, but contained either only losses or only gains. Other studies (De Martino et al., 2006) have manipulated the decision options by phrasing them either as a gain or a loss, even though the outcome of the options always had a positive expected value (i.e. contained an expected gain). To avoid this confound, we implemented a task design where we can always compare the decision play or pass on a gamble using the same gambles across both gain and loss contexts. Other studies (Xue et al., 2010, 2011) have used mixed gambles too, however not by separating them from the respective

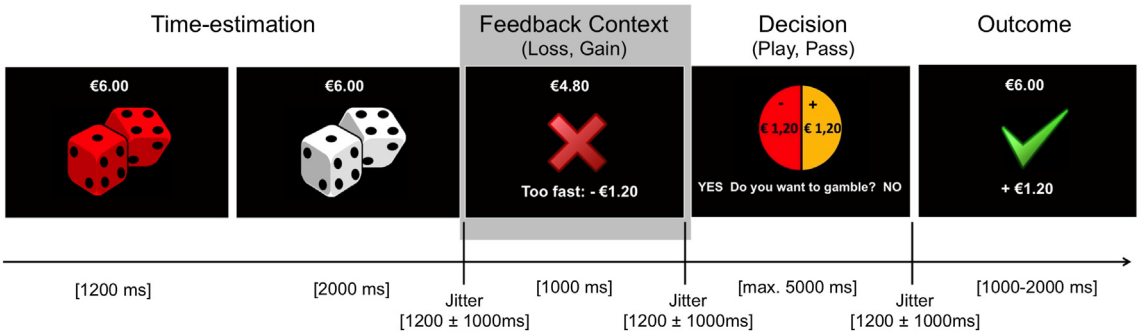

Fig. 1. Task design. The structure of a single trial is presented. Each picture represents a screen in the experiment. The trial started with a time-estimation task, where participants were required to press a button exactly 1 s after the dice color changed to white. Feedback on performance was shown as a monetary gain of €1.20 if correct, or a loss of €1.20 if incorrect. Following this feedback, participants had the opportunity to choose a mixed gamble with a 50/50 chance to either gain or lose money. If participants decided to gamble, the gamble was played and the outcome then presented. Average duration of a trial is 9–13 s, jittered between time-estimation response and feedback context and decision screen. fMRI analysis was time-locked to the feedback onset prior to the gamble (gray shaded area).

context, as these studies only looked at previous outcomes of these gambles on subsequent behavior for other mixed gambles. As shown by these studies, the presentation of a choice can substantially affect how people perceive risk, and subsequently how much risk they decide to take. The current design therefore provided a more precise measure of the effect of gain/loss context on subsequent risky decision-making. The gain/loss context in our design is unrelated, in the sense that it is an outcome related to a different, independent, task.

Procedure

Participants first performed two practice sessions of 5 min each while lying in the MRI scanner. In the first session participants practiced the time-estimation trial. Here, participants were required to estimate a one-second time duration. After a cue on the screen changed color, they were instructed to wait exactly 1 s and then press a response button, with their precise response times recorded. We used the minimum and maximum response times to determine an initial allowable response time-window in the experiment, which in turn was used to give feedback on whether the time-estimation was correct or incorrect.

The second session gave participants the opportunity to practice the gambling task. This session was run concurrently with the collection of an anatomical scan. After these practice sessions, the experiment lasted for one continuous run of approximately 60 min, while collecting fMRI data.

Before beginning the task, participants were instructed that their goal was to win as much money as they could, and that their final balance would be paid out as a bonus (with a maximum amount of €10) in addition to their participation fee (a flat fee of €25) for completion of the task. Hence, participants' total payment at the end of the experiment would range between a minimum of €25 and a maximum of €35. At the start of each trial, participants saw a red visual cue that changed in color to white after 1200 ms (Fig. 1). Participants were then required to press the response button exactly 1 s after this color change. Responses to this time-estimation task were considered correct when they were within an allowable time-interval. For correct responses, participants gained €1.20. Participants lost €1.20 if their response was not within this time-interval, i.e. either too fast or too slow.

The allowable response-interval was initially calculated based on their performance in the practice run and then covertly adjusted throughout the task as a function of the variance in response time of the participant, in order to ensure an equal number of gains and losses on this task. Therefore, if participants responded within the allowable response-interval, this interval was shortened by 5 ms; if they responded either too quickly or too slowly, the interval was lengthened by 5 ms. Importantly, although the number of gains and losses was manipulated, the feedback was contingent upon participants' performance. What differed between participants was the time-interval within which responses were considered correct (see Boksem et al., 2011).

In the gambling section of the task, participants were given the opportunity to play a gamble on 75% of trials. They were forewarned on each trial about this by the presence of a specific visual cue, namely a pair of dice. On these trials, after receiving the feedback from the time estimation task (gain or loss), participants could choose to either play or pass on a mixed (50/50 chance, gain/loss) gamble. Playing the gamble led to two possible outcomes: 1) A win outcome which added €1.00, €1.20 or €1.40 to their overall experimental balance, or 2) a loss outcome which subtracted €1.00, €1.20 or €1.40 from this balance, dependent on the type of gamble offered (see Table 1). Alternatively, the participant could decide to pass on the gamble, thereby keeping the earlier gain or loss (i.e. +/−€1.20) from the time-estimation task. The gamble outcomes were independent from the performance on the time-estimation task.

All gamble outcomes (both gains and losses) immediately updated the total running balance for each participant. This balance was displayed on the screen at all times. Participants were informed that they would be paid this balance (if positive) as a bonus at the end of the experiment.

In the remaining 25% of trials, participants were not presented with a gamble after receiving feedback on the time-estimation trial. These "no-gamble" trials, indicated in advance by a specific visual cue (cubes instead of dice), were employed to potentially prevent participants using a fixed strategy, e.g. always or never gambling, and to enhance engagement in the gamble trials, as well as to allow for more rapid transitions through the sets of experimental balances. Time-estimation performance on these trials did however affect the experimental balance.

During the task we manipulated the experimental balance to create phases of "neutral" (total balance range of €-5 to €5), "negative" (range €-5 to €-17), and "positive" experimental balances (range €5 to €17) (for specific details about the phase transitions, see Boksem et al., 2012). The order of these three phases of experimental balance was counterbalanced. By adding these different phases we could also examine if this overall balance would affect individual risk preferences,

Table 1
Mixed gambles by expected value (EV) and EV type.[a]

50|50 mixed gamble	Expected value (EV)	Gamble type
−€1.40|+€1.20	−0.10	− EV
−€1.20|+€1.00	−0.10	− EV
−€1.20|+€1.20	0	0 EV
−€1.00|+€1.20	0.10	+ EV
−€1.20|+€1.40	0.10	+ EV

[a] All gambles contained a 50–50 probability to lose–win money.

in addition to the effect of immediate gains and losses incurred on that particular trial.

Each trial varied between 9–13 s, jittered (1200 ms ± 1000 ms) between time-estimation response and the feedback context and the gamble presentation. The interstimulus-intervals are relatively short in comparison to other studies looking at brain responses reflecting subsequent behavior. The rationale for using these short time-intervals was to ensure that the gain/loss feedback was as close in time as possible to the gamble decision, to ensure maximal framing impact. Moreover, by using multiple short random jitters, we reduce correlation between the different task phases and therefore improve the ability to tease these apart. In total, participants played on average 240 experimental trials (approximately 60 "no-gamble" trials (range = 42 trials, SD = 7.77) and 180 "gamble" trials (range = 24 trials, SD = 7.19)). The design contained a nested structure including on average a total of 90 gain and 90 loss trials; these gain/loss outcomes were presented contingently on the participants' behavior. Within each set of these 90 trials, we had 30 negative EV, 30 neutral EV, and 30 positive EV gambles randomly presented. Within the 180 total trials 60 occurred with a positive running balance, 60 with a neutral running balance, and 60 with a negative running balance, counterbalanced across participant. The large amount of trials was employed to ensure adequate power to examine both play and pass decisions, since we cannot control participants' choice behavior. The task was presented in Presentation® software (Version 14, www.neurobs.com). After scanning, the participants were debriefed.

Behavioral analysis

In order to assess the degree of risk-taking following gains and losses respectively, we used the percentage of gambles played as the dependent measure. We then performed a within-subject repeated measures ANOVA with 'feedback context' (loss, gain), and 'running balance' (positive, neutral, negative) and the 'gamble type' (+ EV, 0 EV, − EV) as independent variables. All behavioral analyses were performed in SPSS (IBM Corp. Released 2010. Version 19.0. Armonk, NY.).

fMRI data acquisition and analysis

Imaging was performed at the Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands, using a 3-Tesla head-dedicated MRI system (Magnetom TrioTim; Siemens Medical Systems). Functional MRI (fMRI) images were acquired using a 32-channel head coil, with a standard multi-echo imaging pulse T2*-weighted sequence [field of view (FOV), 224 mm; 64 × 64 matrix; repetition time (TR), 2390 ms; echo times (TE), 9.4 ms, 21.2 ms, 33 ms, 45 ms, 56 ms; flip angle, 90°, 0.5 mm slice gap]. Using a multi-echo sequence provides a better signal-to-noise ratio for brain areas susceptible to dropout, while allowing for scanning of the whole brain (Poser et al., 2006). Thirty-one ascending slices were acquired (thickness of 3.0 mm; voxel size 3.5 × 3.5 × 3.0 mm) from the whole brain. High-resolution anatomical T1-weighted image (MPRAGE; 192 slices; TR 2300 ms, voxel size 1 × 1 × 1 mm) was acquired for anatomical localization. Participants' heads were lightly restrained with tape loosely placed on their head and the coil within the scanner in order to limit movement during image acquisition. The task consisted of a single run of 60 min; a standard high-pass filter (cut-off 128 s) was used during the GLM analysis to account for possible slow-frequency drifts.

fMRI data analysis was performed using SPM8 (Statistical Parametric Mapping; Wellcome Department, London, UK). Prior to preprocessing we combined and realigned the five read-outs acquired via the multi-echo sequence by using standard procedures described by Poser et al. (2006). Preprocessing consisted of realignment, slice-timing to the middle slice, co-registration of the functional images to the anatomical images, segmentation of the functional and anatomical image, and normalization to the Montreal Neurological Institute (MNI) template using the segmentation parameters. Functional images were then smoothed with a Gaussian kernel of 8 mm full-width at half maximum (FWHM). The first 30 volumes, acquired prior to task initiation, were used to estimate the weighted echo time per voxel for optimal echo combination (Poser et al., 2006) including allowing T1 equilibration effects, and discarded from the analysis. Motion parameters were stored and used as nuisance variables, including the quadratic effect and second derivatives, in the generalized linear model (GLM) analysis.

For the statistical analyses of the brain data, we performed a GLM for each participant consisting of four regressors of interest (1. $Gain_{Play}$, 2. $Gain_{Pass}$, 3. $Loss_{Play}$, 4. $Loss_{Pass}$) that were time-locked to the feedback of the time-estimation task (see Fig. 1), with 'gain' and 'loss' referring to the time-estimation outcomes and 'play' and 'pass' to the participants' choice in the risk task. The GLM also included the regressors' temporal derivatives, and the eighteen motion regressors of non-interest. We also performed a GLM containing a breakdown of running balance (Positive, Neutral, Negative), feedback context (Gain, Loss) and decision (Play, Pass), resulting in 12 regressors. This GLM did not yield significant voxels nor cluster of voxels by adding the running balance. Moreover, with this analysis procedure six out of the 26 participants contained missing data points for the 12 regressors, resulting in a substantial loss of power. Additionally, the experimental running balance did not show a significant effect on behavior, and all of the three gamble type conditions demonstrated similar behavioral effects on risk-taking. Therefore, and to maximize sensitivity in subsequent brain analysis, we collapsed across three running balance conditions and gamble type conditions for fMRI analysis. We performed a full factorial 2 × 2 analysis at the group-level, with *Feedback context* (loss, gain) as the first factor, and *Decision* (play or pass on gamble) as the second factor. All reported coordinates are presented in MNI space.

Results

Behavioral data

Gambling behavior following gains and losses

A significant main effect of feedback context ($F(1,25) = 6.95$, $p = 0.01$, $\eta^2 = 0.22$) was observed (Fig. 2), that is, participants played the gamble significantly more after a prior loss ($M = 46.2\%$, $SE = 4.7$, 95% confidence intervals (CIs) [36.6, 55.8]) than after a prior gain ($M = 36.6\%$, $SE = 4.3$, 95% CIs [27.8, 45.5]). Participants were also sensitive to the expected values of the gambles, where

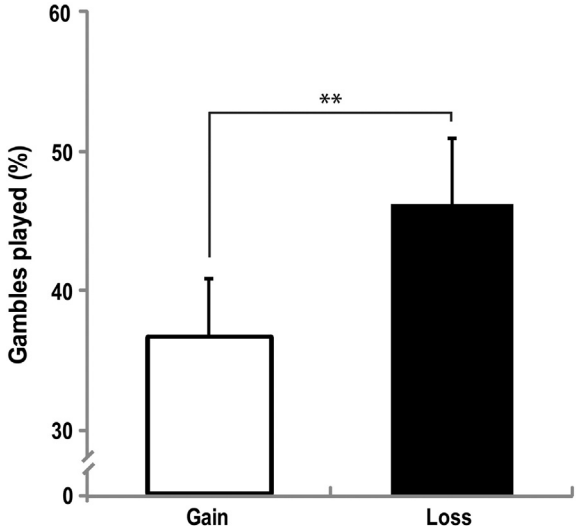

Fig. 2. Behavioral results. Mean percentage (estimated marginal mean) of trials in which participants chose to play a gamble after a loss (black bar, $M = 46.2\%$, 95% CIs [36.6, 55.8]) and after a gain (white bar, $M = 36.6\%$, 95% CIs [27.8, 45.5]), error bars represent + SE, $^{**}p = .01$.

participants decided to play the positive EV gamble the most and the negative EV gamble the least ($M_{+\ EV} = 62\%$; $M_{0\ EV} = 41\%$; $M_{-\ EV} = 21\%$; $F\,(1,24) = 23.73$, $p < .001$, $\eta^2 = 0.49$). The expected value of the gamble did not affect risk preferences differently following gains and losses (Feedback context × EV gamble: $F\,(2,24) = 2.44$, $p = 0.10$, $\eta^2 = 0.09$). The different phases of experimental running balance did not significantly affect behavior ($M_{positive} = 40\%$, $M_{neutral} = 40\%$, $M_{negative} = 44\%$; $F\,(1,24) = 0.88$, $p = 0.40$, $\eta^2 = 0.03$), nor did it interact with the feedback context ($F\,(2,24) = 3.27$, $p = 0.05$, $\eta^2 = 0.17$). In line with the assumption that people evaluate risky choices with respect to small changes to their asset position (i.e. an immediate gain or loss), rather than their absolute total wealth (i.e. cumulative gains and losses; mental accounting: Kahneman and Tversky, 1979) we find that immediate gains or losses shift risk preferences.

Reaction times of decision to play or pass on a gamble following gains and losses

We tested whether type of decision and feedback context affected reaction times for decision to play or pass on a gamble, which could imply a difference in difficulty in processing the decision depending on the context. A main effect of type of decision on reaction times was found, $F\,(1,25) = 5.49$, $p = 0.027$, $\eta^2 = 0.18$, that is, participants who decided to play the gamble took significantly longer in confirming their choice than when deciding to pass on the gamble ($M_{Play} = 1219$ ms, $SD = 332$ ms; $M_{Pass} = 1129$ ms, $SD = 306$ ms). However, and importantly, there is no effect of the gain/loss feedback context on the decision time, $F\,(1,25) = 0.03$, $p = 0.87$, $\eta^2 = .001$, nor is there an interaction between feedback context and decision on reaction time, $F\,(1,25) = 0.68$, $p = 0.42$, $\eta^2 = 0.03$. Hence, the gain/loss feedback did not affect how long participants took to make a decision to play or pass the gamble.

fMRI data

Feedback context (Gain and Loss) and Decision (Play or Pass)

We found expected brain response patterns for feedback to gains. Brain regions exhibiting increased activity for Gain as opposed to Loss feedback (Gain > Loss) were the bilateral dorsal striatum (putamen and caudate), PCC (posterior cingulate cortex), superior frontal gyrus (SFG) and activity in the mPFC, areas typically associated with reward processing. No suprathreshold voxels were found for Loss > Gain (see Fig. 3a and Table 2 for details of areas). These analyses were corrected for multiple comparisons ($p_{FWE} < 0.05$, cluster voxels > 10).

Comparing the decision to take risk with the decision to avoid risk (the main effect of decision, time locked to the feedback of the time-estimation task), we found increased activation of IFG extending into AI, and also in dmPFC extending into ACC, the striatum, midbrain, thalamus, and visual cortex. When participants chose to avoid risk, lateral parietal lobule extending into superior temporal gyrus (STG) (Brodmann area 39) showed increased activation (both at $p_{FWE} < 0.05$, cluster voxels > 10) (see Fig. 3b, Table 3 for details of areas).

Context-dependent risky decision-making

To test how the observed preference shift towards risky choices in loss as compared to gain contexts is instantiated in the brain, we tested for an interaction between Feedback context

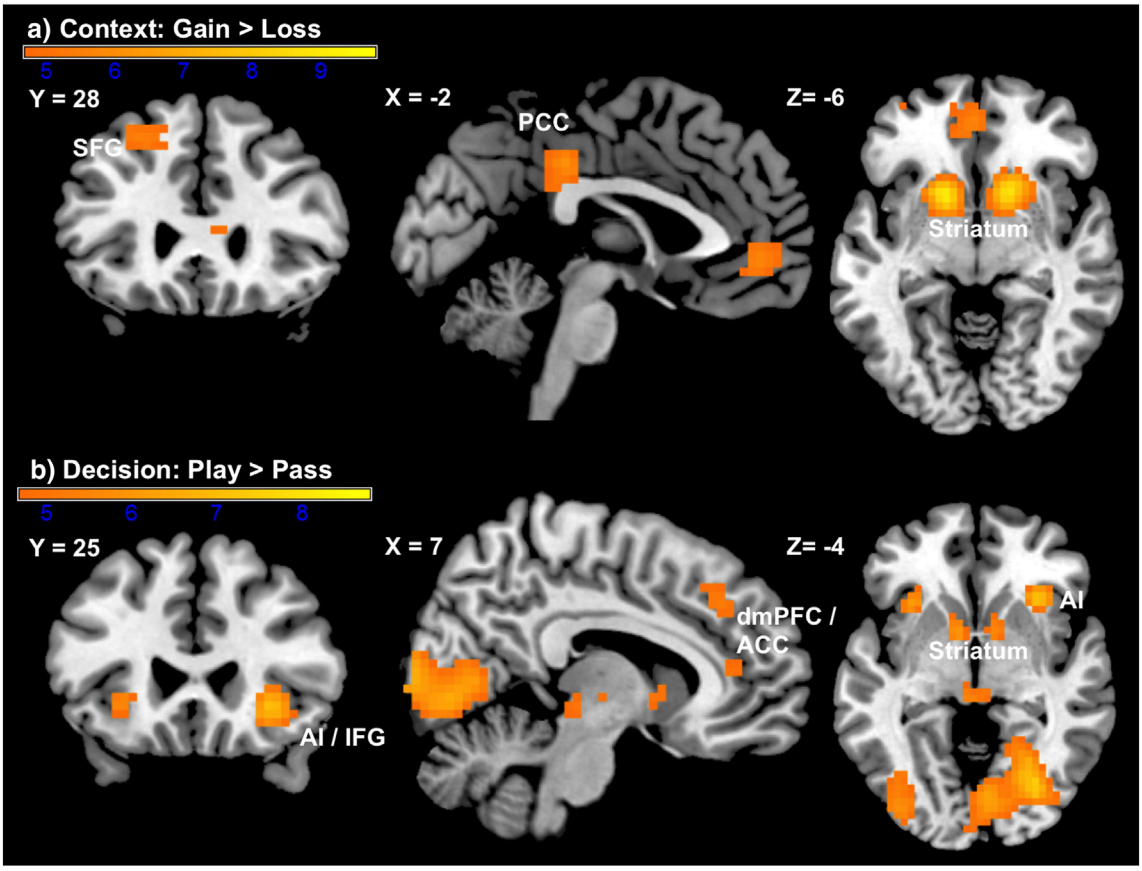

Fig. 3. fMRI activation to Context and Decision. a) Gain feedback > Loss feedback revealed stronger activity in the mPFC (−1,49,−5), PCC (−1,−32,38), MFG extending into SFG (−22,32,48), and bilateral striatum (−15,11,−8; 13,11,−8), see Table 1 for more details not shown here. There were no significant voxels for the context Loss > Gain. b) fMRI activation to Decision: Decision to play the gamble > decision to pass on the gamble showed increased dmPFC (6,35,38), ACC (10,39,10), AI overlapping IFG (31,25,−5; −33,21,−5), bilateral striatum (−8,7,−1; 10,11,−1), midbrain (−5,−28,−5) and visual cortex (27,−70,−8) to be increased. When participants decided to take the pass option (i.e. avoid risk) over the decision to play the gamble, an area consisting of the lateral parietal lobule/STG (45,−67,27) was increased (not shown here, for more details see Table 3). Thresholds are at $p_{FWE} < 0.05$ with extended threshold of >10 voxels.

Table 2
Brain activations for Context (Gain, Loss).

Anatomy	Hemisphere	MNI			Cluster size	Z
	L/R	*x*	*y*	*z*	[voxels]	
Gain > Loss						
Putamen	L	−15	11	−8	149	Inf
Putamen	R	13	11	−8	166	Inf
PCC	L	−1	−32	38	53	5.68
Medial frontal gyrus	L	−1	49	−5	90	5.27
Middle frontal gyrus	L	−22	32	48	53	5.18
IPL/precuneus	L	−47	−60	41	81	5.09
Loss > Gain						
No suprathreshold voxels						

Note: Regions listed exceeded threshold of $p < 0.05$, family-wise corrected, with at least 10 contiguous voxels. Z-values for each peak are given. Abbreviations: L, left; R, right; Inf, Infinite; PCC, posterior cingulate cortex; IPL, inferior parietal lobule.

(Gain, Loss) × Decision (Play, Pass): [(contrast $Gain_{Pass}$ + $Loss_{Play}$) − (contrast $Gain_{Play}$ + $Loss_{Pass}$)]. The interaction revealed increased activity specifically in the ventral parts of the mPFC (cluster corrected on whole-brain for multiple comparisons, $p_{FWE} < 0.05$, with prior threshold of $Z > 3.21$, see Fig. 4a and Table 4).

This area is particularly active when individuals receive a gain and subsequently decide to choose the option to pass, as well as when they decide to play the gamble after receipt of a loss. We did not find any significant voxels that reflect to gain and loss feedback preceding the opposite behavioral performance: ($Gain_{Play}$ + $Loss_{Pass}$) − ($Gain_{Pass}$ + $Loss_{Play}$).

Beta values for each individual participant, extracted from the vmPFC cluster for each main regressor (Feedback context by Decision), showed an opposing response of the vmPFC for risk-taking following gains and losses respectively: relatively high vmPFC responses following gains were associated with subsequent safe choices (i.e. pass on the gamble), while relatively high vmPFC responses following losses were associated with subsequent risk-taking (see Fig. 4b). Within the gain context, vmPFC activity significantly differed for Decision, with higher values for pass as compared to play ($t\,(25) = 3.34$, $p = .003$). For the loss context this pattern was reversed, showing higher values for play as compared to pass ($t\,(25) = 2.54$, $p = 0.018$). Activity for the decision to pass was significantly higher in the gain context than in the loss context ($t\,(25) = 5.43$, $p < .001$), with no significant differences in vmPFC response for the decision to play between the gain and loss contexts ($t\,(25) = 0.71$, $p = 0.487$) (see Fig. 4b). To test whether observed differences in vmPFC activation truly resulted from differential processing of gain/loss information, without contamination from activity related to the subsequent choice, we performed a time-course analysis. Fig. 4c illustrates the mean time course of the vmPFC cluster extracted from the interaction contrast for the four main regressors. For each participant, we ran a single finite impulse response (FIR) time course model on the vmPFC for a length of 24 s, creating 10 time bins each with a length of one TR (2.39 s). This analysis showed that vmPFC responses following gains and losses differed between decisions to play or pass already within one TR after the feedback onset (Between Play–Pass: $t_{bin2}\,(25) = -4.429$, $p < .001$ following the gains, and $t_{bin2}\,(25) = 2.046$, $p = 0.051$ following losses, between Gain–Loss for decision to Pass: $t_{bin2}\,(25) = 3.525$, $p = .002$, and for decision to Play: $t_{bin2}\,(25) = -0.243$, $p = 0.810$), indicating that it is the differential processing of gains and losses that drives subsequent choices (also see Fig. 4c and Table 5).[1]

Table 3
Brain activations for subsequent Decision (Play, Pass).

Anatomy	Hemisphere	MNI			Cluster size	Z
	L/R	*x*	*y*	*z*	[voxels]	
Play > Pass						
Fusiform gyrus	R	27	−70	−8	1244	7.53
IFG/anterior insula	R	31	25	−5	52	6.35
IFG/anterior insula	L	−33	21	−5	27	5.67
Globus pallidus	L	−8	7	−1	34	5.61
Caudate	R	10	11	−1	29	5.38
Midbrain/thalamus	L	−5	−28	−5	35	5.11
IFG/dlPFC	L	−40	7	24	13	5.04
Superior parietal lobule	L	−29	−53	48	12	4.98
dmPFC/ACC	R	6	35	38	15	4.9
ACC	R	10	39	10	10	4.83
Pass > Play						
Lateral parietal lobe/STG	R	45	−67	27	44	5.58
Lateral occipital cortex	L	−43	−77	31	10	5.11

Note: Regions listed exceeded threshold of $p < 0.05$, family-wise corrected, with at least 10 contiguous voxels. Z-values for each peak are given. Abbreviations: L, left; R, right; ACC, anterior cingulate cortex; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; STG, superior temporal gyrus.

The processing of gains and losses could of course potentially be affected by the outcome of the gamble. To investigate this, we ran a separate GLM to analyze the BOLD response to feedback processing based on the outcome of the gamble. This GLM contained the regressors for Feedback context (gain, loss) by Gamble outcome (won, lost) time-locked to the feedback context onset. This GLM also included a regressor for the Gamble outcome (won gamble, lost gamble, no gamble) time-locked to the gamble onset, and 18 realignment parameters of non-interest. This analysis showed no significant differences in gain and loss processing related to the outcome of the gamble. Furthermore, we also investigated whether the BOLD response of the vmPFC observed for the interaction contrast (feedback context by decision) could reflect the signal of the event preceding the receipt of the gain and loss outcome (i.e. white dice cue). We ran an additional GLM analyzing the BOLD response to the onset of the white dice cue based on interaction contrast feedback context by decision. The interaction did not reveal any significant voxels or cluster of voxels at the onset of the white dice cue. Hence, the results show that the vmPFC is associated with context-dependent risky decision-making, broadly following the observed behavioral choices.

Discussion

The current study identified brain mechanisms that are engaged in the evaluation of monetary gains and losses, showing that these areas are associated with patterns of risk preference, even though these choice patterns are inconsistent with classical economic models of decision-making. Exploring the brain mechanisms that underlie how gain/loss contexts can lead to a switch between risky or safe choices when presented with the same gamble can provide useful insights into how valuation processes can exert a strong effect on our evaluation of risk, and in turn on the likelihood of players to select risky or safe choice options.

Here, we showed that participants' risk attitudes for identical mixed (50–50, gain–loss) gambles were significantly affected by the receipt of either a small monetary gain or a loss immediately prior to the risky decision itself. Interestingly, and importantly for theories of economic preference, this effect was evident even within subjects, with our participants displaying inconsistent risk patterns, for the identical sets of gambles, across the entire span of the experiment. As expected, and in line with previous literature on preference shifts for risk

[1] The FIR model estimates an average effect of the vmPFC seed region, at the time of the onset of the feedback onset. The model assumes that overlapping hemodynamic response functions linearly add up. Therefore, the current time course can contain some activity related to the onset of the decision event, because of the short interstimulus-interval. However, in addition there is a trial-by-trial short, however randomly jittered interval in between the feedback context and decision event, the time-course would mostly reflect the pattern of the vmPFC response towards the onset of the feedback outcome.

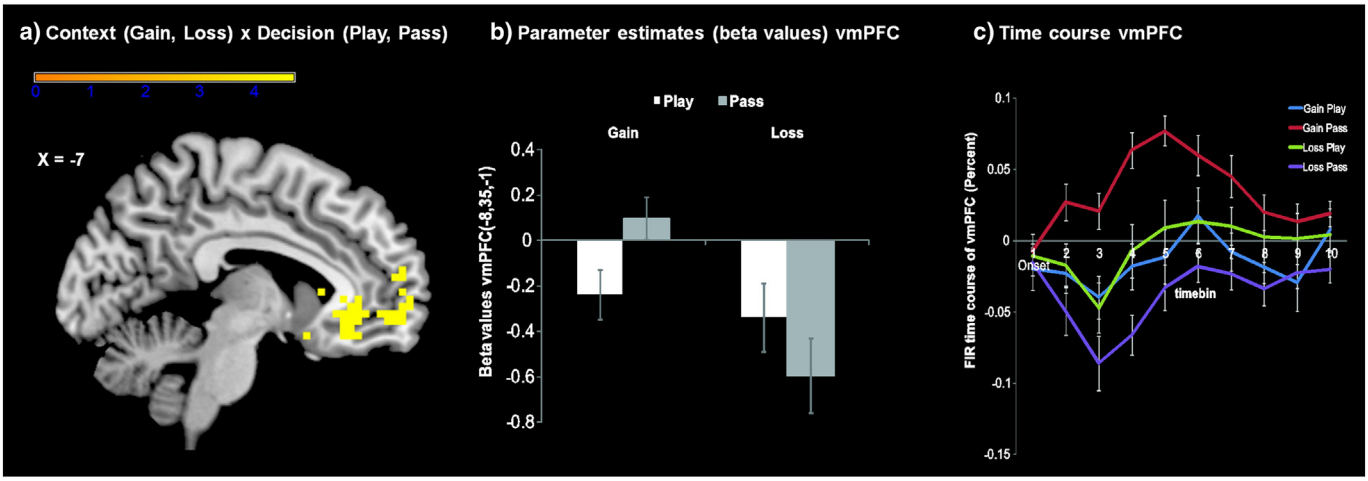

Fig. 4. a) fMRI activation maps of the interaction contrast Context × Decision [($Loss_{Play}$ + $Gain_{Pass}$) − ($Loss_{Pass}$ + $Gain_{Play}$)]. The activation patterns show a cluster of vmPFC (sgACC extending into mPFC (−8,35,−1)) activity correlating to subjects' behavioral tendency to choose to play the gamble after they have experienced a small loss, and to pass on the gamble when they have experienced a small gain. Cluster-level $p_{FWE} < 0.05$ on whole-brain, with extended threshold >100 voxels at Z > 3.21. b) Parameter estimates (beta values) of vmPFC for context (Gain, Loss) by decision (Play, Pass). c) Time series of the vmPFC of each regressor from the interaction contrast. The time courses were estimated with the finite impulse response model from the onset of the delivery of the gain/loss feedback, for a length of 24 s. A significant difference between gain and loss feedback and the decision to play and pass on the gamble is shown from time bin 2 (~2.4 s after feedback onset). See Table 5 for detailed statistics. Error bars show ±SE.

(Kahneman and Tversky, 1979; Tversky and Kahneman, 1981, 1992; De Martino et al., 2006; Tom et al., 2007; Xue et al., 2011), participants who had experienced a gain typically decided to subsequently choose the safer option (i.e. passing on the gamble), thereby showing an aversion to risk. In contrast, when participants had just experienced a loss they showed a shift in preference towards the risky gamble, now exhibiting increased risk-seeking tendencies as compared to when gains preceded the choice. Additionally, these effects were observed using real, consequential choices, where decisions were paid out at the conclusion of the experiment, in contrast to other studies that have used either hypothetical rewards (Gonzalez et al., 2005) or chosen one trial at random for payment (Venkatraman et al., 2009; Porcelli and Delgado, 2009; Christopoulos et al., 2009 (exp. 2); Sokol-Hessner et al., 2012a (selecting 10 random trials)). In the current study the context induced by the time-estimation feedback is a monetary gain or loss and always associated with either successful or unsuccessful performance on the task.

In terms of brain activation, we found significant reward-related activity for gains as compared to losses in the bilateral dorsal striatum, mPFC, SFG, and precuneus. These areas are consistent with those previously found for reward-related activity (Breiter et al., 2001; Delgado et al., 2003; Elliott et al., 2003; Tom et al., 2007). We did not find any significant differences in BOLD response for losses as compared to gains at this time point. Previous studies have reported increased activity in areas such as AI, amygdala, ACC, and lOFC while evaluating losses, implicated as a function of negative stimulus aversion, error detection, or loss aversion (Breiter et al., 2001; Paulus et al., 2003), though these activations are not always observed (Seymour et al., 2007) and have even shown to overlap to some extent with the receipt of rewards as well as of punishments (Bartra et al., 2013).

Also in accordance with previous work, a significant main effect in the BOLD response for the choice to play as opposed to pass on the gamble was observed in the dmPFC/ACC, AI overlapping IFG, IPS, caudate, and thalamus. A large number of studies have reported activity in these areas correlating with risk-taking behavior (e.g. Paulus et al., 2003; see Mohr et al., 2010 for overview). Conversely, when participants chose to pass on the gamble, hence avoiding subsequent risk, increased activity of the lateral parietal lobule and STG (BA 39) was observed. These areas have been previously associated with promoting safe behavior over risk-taking, and have been reported when selecting a safe over a risky option (Matthews et al., 2004).

The primary goal of the study was to determine how the evaluation of prior gains and losses may affect preferences for risk, as has been shown behaviorally, by studying the underlying neural mechanisms associated with the evaluation and integration of gain and loss information which in turn can potentially predict risk preferences. We hypothesized that when experiencing gains and losses we engage in value-computation and integration of these appraisals, and when a subsequent gamble is offered these processes have a differential impact on preferences for risk.

Supporting this hypothesis, we found a strongly significant interaction between the monetary outcome of the previous – unrelated – time-estimation task (i.e. gain or loss) and the subsequent decision to play or pass on the gamble in the risky decision task. This interaction was associated with enhanced activation in the ventral part of mPFC. This vmPFC region responded more strongly when individuals experienced a €1.20 gain prior to selecting a safe option (i.e. passing on the gamble and accepting the current state) as compared to selecting a risky option (i.e. playing a mixed "double-or-quits" gamble). Conversely, the same area responded more strongly at the time individuals experienced a €1.20 loss, though only when they then decided to select the risky option as compared to selecting the safe option. Importantly, this interaction was found within-subjects for identical sets of choices, that is, when the gambles comprised of the same probabilities and outcomes, and was in line with the observed decision behavior; choosing the safe option to retain the gain, and choosing to play the gamble to compensate for the loss. These results therefore suggest that the same area that has previously been shown to be important for encoding value, regulation, and control of affect and guidance of subsequent choice behavior (Urry et al., 2006; Koenigs and Tranel, 2007; Hare et al., 2009; Rushworth et al., 2011; Sokol-Hessner et al., 2012a; Rosenbloom et al., 2012) is also associated with preference for either taking or avoiding risk depending on the current context.

Table 4
Brain activations for the interaction Feedback Context (Gain, Loss) × Decision (Play, Pass).

Anatomy	Hemisphere	MNI			Cluster size
	L/R	x	y	z	[voxels]
vmPFC/sgACC	L	−8	35	−1	226

Note: Regions listed exceeded threshold of $p < 0.05$, family-wise corrected on cluster-correction of whole-brain, with at least 100 contiguous voxels. Abbreviations: L, left; sgACC, subgenual anterior cingulate cortex; vmPFC, ventromedial prefrontal cortex.

Table 5
Statistics of paired t-tests of the vmPFC time course.

Contrasts	Gain Play–Gain Pass		Loss Play–Loss Pass		Gain Pass–Loss Pass		Gain Play–Loss Play	
Time bin (TR)	*t (25)*	*p-Value*	*t (25)*	*p-Value*	*t (25)*	*p-Value*	*t (25)*	*p-Value*
1	−0.840	0.409	0.469	0.643	0.500	0.621	−0.550	0.587
2	−4.429	<0.001	2.046	0.051	3.525	0.002	−0.243	0.810
3	−3.559	0.002	2.205	0.037	5.505	<0.001	0.326	0.747
4	−4.080	<0.001	3.036	0.006	7.821	<0.001	−0.431	0.670
5	−4.429	<0.001	1.838	0.078	6.824	<0.001	−0.744	0.464
6	−1.973	0.060	1.481	0.151	5.160	<0.001	0.155	0.878
7	−2.706	0.012	1.830	0.079	3.694	0.001	−0.770	0.449
8	−2.158	0.041	1.732	0.096	2.615	0.015	−0.975	0.339
9	−1.694	0.103	1.148	0.262	2.134	0.043	−1.023	0.316
10	−0.551	0.587	1.619	0.118	2.595	0.016	0.197	0.846

Note: The onset (time bin 1) is time-locked at the feedback delivery of the time-estimation over a time period of 24 s (10 TR time bins). Results obtained from a repeated measures ANOVA testing the interaction contrast for each time bin separately and adjusted for multiple comparisons using a Bonferroni adjustment resulted in the same results as presented in the above table conducted with t-tests.

A plausible explanation for these findings is that the vmPFC functions in a regulatory capacity, providing a mechanism to allow for adaptive decision-making behavior as a function of the current (monetary) context, that is, one of gain or loss. Greater contribution of the vmPFC when experiencing a gain stimulated safer subsequent behavior, suggesting an inhibition of the temptation to gamble, hence 'locking-in' the current gain. When experiencing a loss, the contribution of the same area switches, and now greater activation stimulates riskier behavior, potentially as a means to attempt to recover from the prior loss and break-even on the trial. The vmPFC seems thus to respond differently as a function of whether the current context is one of the immediate gains or losses, consistent with its role in value encoding. In other words, these results suggest that vmPFC may not be solely tracking and evaluating how desirable a current outcome and subsequent risky choice is, but rather that it may be executing a more complex function: assessing the specific choice response (play or pass behavior) that seems most adaptive given the particular situation. By "adaptive" here we refer to the ability of individuals to flexibly adapt their preferences in order to obtain a particular outcome that is most valued at the given time, and which is reflected in their decision behavior itself.

An alternative explanation for the current findings is that when vmPFC responds more strongly towards the gain or loss, in a positive and negative way respectively, then safer rather than risky behavior is more valued. When the vmPFC response for the same gain or loss is relatively weak, risky behavior follows. This explanation would suggest that the vmPFC may engage control or regulatory strategies that inhibit risk-taking, and when this control is absent then there is the temptation to gamble. However, brain activity observed at the cue preceding the feedback does not seem to support this explanation, as these results did not reveal overlapping significant voxels with the observed clusters for the feedback processing, nor did it reveal significant voxels of regions associated with affective nor cognitive control. Previous research has implicated the dlPFC in reflecting flexibly adaptive behavior, via a strong indirect coupling with the vmPFC (Hare et al., 2009; Christopoulos et al., 2009). The dlPFC, implicated in self-control and impulsivity, indirectly modulates the vmPFC value signal to guide goal-directed behavior (Hare et al., 2009). The relatively weak valuation signal of the vmPFC prior to the decision to play the gamble may be a result of a lack of self-control and therefore modulation by the dlPFC on the value signal of the vmPFC, resulting in choosing to play the gamble. It would be interesting to examine how self-control may interact with gain/loss contexts for risky choice sets in guiding risky choice.

The current results extend our knowledge of vmPFC functioning in decision-making, supporting previous work suggesting that this area is involved in several processes in addition to pure value computation. For example, this area has been shown to be active during emotion regulation and extinction to aversive stimuli (Phelps et al., 2004; Urry et al., 2006). Other studies have also reported a role of the ventral parts of the forebrain in behavioral and affective control (O'Doherty et al., 2003; Di Pellegrino et al., 2007; Etkin et al., 2006, 2011; Roy et al., 2012). Additionally, lesion studies have shown that patients with vmPFC damage were unable to evaluate and integrate so-called 'somatic markers', hypothesized to be an affective response to aversive stimuli, when attempting to choose from advantageous and disadvantageous options when playing the Iowa gambling task (Bechara et al., 1994). In other studies, vmPFC patients showed increased risk-taking following losses, a behavior which they were unable to inhibit (Sanfey et al., 2003; Shiv et al., 2005), and an insensitivity to differences in expected value between choices of gains and losses (Weller et al., 2007; Clark et al., 2008). The above studies support an important role of the vmPFC in integrating contextual appraisals (gain or loss) and linking this to specific patterns of behavior and autonomic responses (Rosenbloom et al., 2012; Sokol-Hessner et al., 2012b).

In short, we show here that risk-taking behavior is strongly modulated by the gain or loss context of the decision. This modulation has its neural basis in the vmPFC, which appears to integrate and represent the contextual value of a stimulus in light of subsequent choice in order to adaptively guide the decision-making process for risky prospects. That is, vmPFC activation supported safe behavior after a monetary gain, and risky behavior following a monetary loss. How the integration of decision context (i.e. gain and loss) by the vmPFC may vary by different expected values of gambles is still an interesting open question for understanding the adaptive role of the vmPFC in combining the different values in guiding risk behavior. The current design does not allow us to disentangle whether the behavioral effects are driven more by the receipt of monetary gains/losses or by performance-based success/failure independent of monetary reward. For future studies, it would be interesting to test whether the behavioral effects are specific for performance feedback or for the receipt of monetary reward.

In conclusion, our study extends the existing literature by examining the specific brain networks involved in risky decision-making involving gains and losses. At the same time it emphasizes the importance of disentangling the different phases of the decision-making process. Finally, our study demonstrates that choice cannot be studied in isolation, but that the broader context the choice is placed in has an important role to play.

Conflict of interest

None declared.

References

Barto, A.G., Sutton, R.S., 1997. Ch. 19 Reinforcement learning in artificial intelligence. Adv. Psychol. 121, 358–386. http://dx.doi.org/10.1016/S0166-4115(97)80105-7.
Bartra, O., McGuire, J.T., Kable, J.W., 2013. The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of

subjective value. Neuroimage 76, 412–427. http://dx.doi.org/10.1016/j.neuroimage.2013.02.063.
Basten, U., Biele, G., Heekeren, H.R., Fiebach, C.J., 2010. How the brain integrates costs and benefits during decision making. Proc. Natl. Acad. Sci. U. S. A. 107, 21767–21772. http://dx.doi.org/10.1073/pnas.0908104107.
Bechara, A., Damasio, A.R., Damasio, H., Anderson, S.W., 1994. Insensitivity to future consequences following damage to human prefrontal cortex. Cognition 50, 7–15. http://dx.doi.org/10.1016/0010-0277(94)90018-3.
Boksem, M.A.S., Kostermans, E., De Cremer, D., 2011. Failing where others have succeeded: medial frontal negativity tracks failure in a social context. Psychophysiology 48, 973–979. http://dx.doi.org/10.1111/j.1469-8986.2010.01163.x.
Boksem, M.A.S., Kostermans, E., Milivojevic, B., De Cremer, D., 2012. Social status determines how we monitor and evaluate our performance. Soc. Cogn. Affect. Neurosci. 7, 304–313. http://dx.doi.org/10.1093/scan/nsr010.
Boorman, E.D., Behrens, T.E.J., Woolrich, M.W., Rushworth, M.F.S., 2009. How green is the grass on the other side? Frontopolar cortex and the evidence in favor of alternative courses of action. Neuron 62, 733–743. http://dx.doi.org/10.1016/j.neuron.2009.05.014.
Boorman, E.D., Rushworth, M.F.S., Behrens, T.E.J., 2013. Ventromedial prefrontal and anterior cingulate cortex adopt choice and default reference frames during sequential multi-alternative choice. J. Neurosci. 33, 2242–2253. http://dx.doi.org/10.1523/JNEUROSCI.3022-12.2013.
Breiter, H.C., Aharon, I., Kahneman, D., Dale, A., Shizgal, P., 2001. Functional imaging of neural responses to expectancy and experience of monetary gains and losses. Neuron 30, 619–639. http://dx.doi.org/10.1016/S0896-6273(01)00303-8.
Christopoulos, G.I., Tobler, P.N., Bossaerts, P., Dolan, R.J., Schultz, W., 2009. Neural correlates of value, risk, and risk aversion contributing to decision making under risk. J. Neurosci. 29, 12574–12583. http://dx.doi.org/10.1523/JNEUROSCI.2614-09.2009.
Clark, L., Bechara, A., Damasio, H., Aitken, M.R.F., Sahakian, B.J., Robbins, T.W., 2008. Differential effects of insular and ventromedial prefrontal cortex lesions on risky decision-making. Brain 131, 1311–1322. http://dx.doi.org/10.1093/brain/awn066.
De Martino, B., Kumaran, D., Seymour, B., Dolan, R.J., 2006. Frames, biases, and rational decision-making in the human brain. Science 313, 684–687. http://dx.doi.org/10.1126/science.1128356.
Delgado, M.R., Locke, H.M., Stenger, V.A., Fiez, J.A., 2003. Dorsal striatum responses to reward and punishment: effects of valence and magnitude manipulations. Cogn. Affect. Behav. Neurosci. 3, 27–38. http://dx.doi.org/10.3758/CABN.3.1.27.
Di Pellegrino, G., Ciaramelli, E., Làdavas, E., 2007. The regulation of cognitive control following rostral anterior cingulate cortex lesion in humans. J. Cogn. Neurosci. 19, 275–286. http://dx.doi.org/10.1162/jocn.2007.19.2.275.
Elliott, R., Newman, J.L., Longe, O.A., Deakin, J.F.W., 2003. Differential response patterns in the striatum and orbitofrontal cortex to financial reward in humans: a parametric functional magnetic resonance imaging study. J. Neurosci. 23, 303–307 (doi:10.1.1.411.355).
Etkin, A., Egner, T., Peraza, D.M., Kandel, E.R., Hirsch, J., 2006. Resolving emotional conflict: a role for the rostral anterior cingulate cortex in modulating activity in the amygdala. Neuron 51, 871–882. http://dx.doi.org/10.1016/j.neuron.2006.07.029.
Etkin, A., Egner, T., Kalisch, R., 2011. Emotional processing in anterior cingulate and medial prefrontal cortex. Trends Cogn. Sci. 15, 85–93. http://dx.doi.org/10.1016/j.tics.2010.11.004.
Gonzalez, C., Dana, J., Koshino, H., Just, M., 2005. The framing effect and risky decisions: examining cognitive functions with fMRI. J. Econ. Psychol. 26, 1–20. http://dx.doi.org/10.1016/j.joep.2004.08.004.
Grabenhorst, F., Rolls, E.T., 2011. Value, pleasure and choice in the ventral prefrontal cortex. Trends Cogn. Sci. 15, 56–67. http://dx.doi.org/10.1016/j.tics.2010.12.004.
Hare, T.A., Camerer, C.F., Rangel, A., 2009. Self-control in decision-making involves modulation of the vmPFC valuation system. Science 324, 646–648. http://dx.doi.org/10.1126/science.1168450.
Kahneman, D., Tversky, A., 1979. Prospect theory: an analysis of decision under risk. Econometrica 47, 263–292. http://dx.doi.org/10.2307/1914185.
Knutson, B., Adams, C.M., Fong, G.W., Hommer, D., 2001. Anticipation of increasing monetary reward selectively recruits nucleus accumbens. J. Neurosci. 21, RC159.
Koenigs, M., Tranel, D., 2007. Irrational economic decision-making after ventromedial prefrontal damage: evidence from the Ultimatum Game. J. Neurosci. 27, 951–956. http://dx.doi.org/10.1523/JNEUROSCI.4606-06.2007.
Kuhnen, C.M., Knutson, B., 2005. The neural basis of financial risk taking. Neuron 47, 763–770. http://dx.doi.org/10.1016/j.neuron.2005.08.008.
Lebreton, M., Jorge, S., Michel, V., Thirion, B., Pessiglione, M., 2009. An automatic valuation system in the human brain: evidence from functional neuroimaging. Neuron 64, 431–439. http://dx.doi.org/10.1016/j.neuron.2009. 09.040.
Levy, I., Lazzaro, S.C., Rutledge, R.B., Glimcher, P.W., 2011. Choice from non-choice: predicting consumer preferences from blood oxygenation level-dependent signals obtained during passive viewing. J. Neurosci. 31, 118–125. http://dx.doi.org/10.1523/JNEUROSCI.3214-10.2011.
Matthews, S.C., Simmons, C.A.A.N., Lane, S.D., Paulus, M.P., 2004. Selective Activation of the Nucleus Accumbens During Risk-taking Decision Making 15, pp. 3–7. http://dx.doi.org/10.1097/00001756-200409150-00025.
Mohr, P.N.C., Biele, G., Heekeren, H.R., 2010. Neural processing of risk. J. Neurosci. 30, 6613–6619. http://dx.doi.org/10.1523/JNEUROSCI.0003-10.2010.
O'Doherty, J.P., Dayan, P., Friston, K., Critchley, H., Dolan, R.J., 2003. Temporal difference models and reward-related learning in the human brain. Neuron 38, 329–337. http://dx.doi.org/10.1016/S0896-6273(03)00169-7.
Paulus, M.P., Rogalsky, C., Simmons, A., Feinstein, J.S., Stein, M.B., 2003. Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. Neuroimage 19, 1439–1448. http://dx.doi.org/10.1016/S1053-8119(03)00251-9.
Phelps, E.A., Delgado, M.R., Nearing, K.I., LeDoux, J.E., 2004. Extinction learning in humans: role of the amygdala and vmPFC. Neuron 43, 897–905. http://dx.doi.org/10.1016/j.neuron.2004.08.042.
Plassmann, H., O'Doherty, J.P., Rangel, A., 2010. Appetitive and aversive goal values are encoded in the medial orbitofrontal cortex at the time of decision making. J. Neurosci. 30, 10799–10808. http://dx.doi.org/10.1523/JNEUROSCI.0788-10.2010.
Platt, M.L., Huettel, S.A., 2008. Risky business: the neuroeconomics of decision making under uncertainty. Nat. Neurosci. 11, 398–403. http://dx.doi.org/10.1038/nn2062.
Porcelli, A.J., Delgado, M.R., 2009. Acute stress modulates risk taking in financial decision making. Psychol. Sci. 20, 278–283. http://dx.doi.org/10.1111/j.1467-9280.2009.02288.x.
Poser, B.A., Versluis, M.J., Hoogduin, J.M., Norris, D.G., 2006. BOLD contrast sensitivity enhancement and artifact reduction with multiecho EPI: parallel-acquired inhomogeneity-desensitized fMRI. Magn. Reson. Med. 55, 1227–1235. http://dx.doi.org/10.1002/mrm.20900.
Rangel, A., Hare, T.A., 2010. Neural computations associated with goal-directed choice. Curr. Opin. Neurobiol. 20, 262–270. http://dx.doi.org/10.1016/j.conb.2010.03.001.
Rangel, A., Camerer, C., Montague, P.R., 2008. A framework for studying the neurobiology of value-based decision making. Nat. Rev. Neurosci. 9, 545–556. http://dx.doi.org/10.1038/nrn2357.
Rosenbloom, M.H., Schmahmann, J.D., Price, B.H., 2012. The functional neuroanatomy of decision-making. J. Neuropsychiatry Clin. Neurosci. 24, 266–277. http://dx.doi.org/10.1016/j.brainres.2011.05.053.
Roy, M., Shohamy, D., Wager, T.D., 2012. Ventromedial prefrontal–subcortical systems and the generation of affective meaning. Trends Cogn. Sci. 16, 147–156. http://dx.doi.org/10.1016/j.tics.2012.01.005.
Rushworth, M.F.S., Noonan, M.P., Boorman, E.D., Walton, M.E., Behrens, T.E.J., 2011. Frontal cortex and reward-guided learning and decision-making. Neuron 70, 1054–1069. http://dx.doi.org/10.1016/j.neuron.2011.05.014.
Sanfey, A.G., Hastie, R., Colvin, M.K., Grafman, J., 2003. Phineas gauged: decision-making and the human prefrontal cortex. Neuropsychologia 41, 1218–1229. http://dx.doi.org/10.1016/S0028-3932(03)00039-3.
Seymour, B., Daw, N., Dayan, P., Singer, T., Dolan, R., 2007. Differential encoding of losses and gains in the human striatum. J. Neurosci. 27, 4826–4831. http://dx.doi.org/10.1523/JNEUROSCI.0400-07.2007.
Shiv, B., Loewenstein, G., Bechara, A., Damasio, H., Damasio, A.R., 2005. Investment behavior and the negative side of emotion. Psychol. Sci. 16, 435–439. http://dx.doi.org/10.1111/j.0956-7976.2005.01553.x.
Sokol-Hessner, P., Camerer, C.F., Phelps, E.A., 2012a. Emotion regulation reduces loss aversion and decreases amygdala responses to losses. Soc. Cogn. Affect. Neurosci. 10. http://dx.doi.org/10.1093/scan/nss002.
Sokol-Hessner, P., Hutcherson, C., Hare, T.A., Rangel, A., 2012b. Decision value computation in DLPFC and VMPFC adjusts to the available decision time. Eur. J. Neurosci. 35, 1065–1074. http://dx.doi.org/10.1111/j.1460-9568.2012.08076.x.
Tom, S.M., Fox, C.R., Trepel, C., Poldrack, R.A., 2007. The neural basis of loss aversion in decision-making under risk. Science 315, 515–518. http://dx.doi.org/10.1126/science.1134239.
Tversky, A., Kahneman, D., 1981. The framing of decisions and the psychology of choice. Science 211, 453–458. http://dx.doi.org/10.1126/science.7455683.
Tversky, A., Kahneman, D., 1992. Advances in Prospect Theory: Cumulative Representation of Uncertainty 323, pp. 297–323. http://dx.doi.org/10.1007/BF00122574.
Urry, H.L., van Reekum, C.M., Johnstone, T., Kalin, N.H., Thurow, M.E., Schaefer, H.S., Jackson, C.A., Frye, C.J., Greischar, L.L., Alexander, A.L., Davidson, R.J., 2006. Amygdala and ventromedial prefrontal cortex are inversely coupled during regulation of negative affect and predict the diurnal pattern of cortisol secretion among older adults. J. Neurosci. 26, 4415–4425. http://dx.doi.org/10.1523/JNEUROSCI.3215-05.2006.
Venkatraman, V., Payne, J.W., Bettman, J.R., Luce, M.F., Huettel, S.A., 2009. Separate Neural Mechanisms Underlie Choices and Strategic Preferences in Risky Decision Making. Neuron 593–602. http://dx.doi.org/10.1016/j.neuron.2009.04.007.
Weller, J.A., Levin, I.P., Shiv, B., Bechara, A., 2007. Neural correlates of adaptive decision making for risky gains and losses. Psychol. Sci. 18, 958–964. http://dx.doi.org/10.1111/j.1467-9280.2007.02009.x.
Xue, G., Lu, Z., Levin, I.P., Bechara, A., 2010. The impact of prior risk experiences on subsequent risky decision-making: the role of the insula. Neuroimage 50, 709–716. http://dx.doi.org/10.1016/j.neuroimage.2009.12.097.
Xue, G., Lu, Z., Levin, I.P., Bechara, A., 2011. An fMRI study of risk-taking following wins and losses: implications for the gambler's fallacy? Hum. Brain Mapp. 32, 271–281. http://dx.doi.org/10.1002/hbm.21015.