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Brain correlates of risky decision-making

David Polezzi [a,b,*], Giuseppe Sartori [b], Rino Rumiati [c], Giulio Vidotto [b], Irene Daum [a]

[a] Institute of Cognitive Neuroscience, Department of Neuropsychology, Ruhr-University of Bochum, Universitätsstraβe 150, D-44780 Bochum, Germany
[b] Department of General Psychology, University of Padova, via Venezia 8, 35131 Padova, Italy
[c] Department of Developmental Psychology and Socialization, University of Padova, via Venezia 8, 35131 Padova, Italy

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ABSTRACT

Understanding the neurocognitive basis of risk-taking behavior is an important issue, especially in economic decision-making. Classical behavioral studies have shown that risk-attitude changes across different contexts, but little is so far known about the brain correlates of processing of outcomes across such context shifts. In this study, EEG was recorded while subjects performed a gambling task. Participants could choose between a risky and a safer option, within two different contexts: one in which options yielded gains and losses of the same magnitude (Zero Expected Value context) and another in which gains were larger than losses (Positive Expected Value context). Based on their risk-attitude, two groups were compared: subjects who are risk-seekers in the zero Expected Value context (Zero-Oriented group) and subjects who are risk-seekers in the positive Expected Value condition (Positive-Oriented group). The Feedback Related Negativity (FRN) reflects this distinction, with each group being insensitive to magnitude of outcomes in the condition in which they were risk-prone. P300 amplitude mirrored the behavioral results, with larger amplitudes in the condition in which each group showed a higher risk-tendency. Source analyses highlighted the involvement of posterior cingulate cortex in risky decision-making. Taken together, the findings make a contribution to the clarification of the neurocognitive substrates of risky decision-making.

Introduction

In many daily decisions, we are faced with some degree of risk. In the financial field, savings could be invested in stocks or the safer treasury bills; for mortgages there is a choice between floating or fixed rates. Understanding the conditions in which people are more likely to accept risk is important to predict their decisions. In order to further elucidate the neurocognitive mechanisms underlying risky decision-making and the factors influencing changes in risk-taking behavior, the current study focused on the electrophysiological correlates of choice behavior during the performance of a gambling task. ERPs, with their high temporal resolution, are the preferred method to investigate changes occurring with ongoing decision processes.

Classical theoretical models of decision-making under risk focus on a strictly logical approach, relying on the net assets of the outcomes (von Neumann and Morgenstern, 1944; Machina, 1982; McElroy and Seta, 2004). For instance, in deciding between two or more options, the expected value (EV) should be assessed, weighting each possible outcome by its probability. The sum of each probability-weighted outcome is the EV of an option and, as a result, the option with the highest EV should be chosen in a rational decision (Markowitz, 1952; Machina, 1982). An important limitation of classical models is the assumption that people are risk-neutral (Trepel et al., 2005) while a person might prefer a certain gain over a risky condition of equal or higher EV (*Risk averse*) or a risky condition to a certain gain of equal or higher EV (*Risk-seeker*). By contrast, the most influential view in this field, prospect theory, focuses on changes from status quo and is sensitive to relative differences in gains and losses (Kahneman and Tversky, 1979; McElroy and Seta, 2004). In addition, it has been shown that depending on the context, people can be prone or averse to risk (Kahneman and Tversky, 1979) and that individual differences play an important role in risk-taking (Lee, 2005).

In recent neurocognitive studies of economic decision-making (Trepel et al., 2005), animal models yielded evidence for a bias towards certain food options in bumblebees (Real, 1999) and a bias towards risky options in monkey (McCoy and Platt, 2005). The preference of monkeys for risky decision-making, even when it led to unfavorable outcomes, was associated with posterior cingulate activations.

Risk-taking associated with reward processing has been comprehensively studied in human subjects (Paulus et al., 2003; Kuhnen and Knutson, 2005; Knoch et al., 2006; Tom et al., 2007). Taken together, these studies indicate that frontolimbic circuits involving ventromedial prefrontal cortex (vmPFC), amygdala and insula, and structures linked to reward and conflict processing, i.e. the ventral striatum and anterior and posterior cingulate cortex, are implicated in risk-taking

* Corresponding author. Department of General Psychology, University of Padova, via Venezia 8, 35131 Padova, Italy. Fax: +39 049 8276511.
E-mail address: david.polezzi@unipd.it (D. Polezzi).

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behavior (Li et al., 2009). EEG studies of decision-making in human subjects have mainly focused on the feedback-related negativity (FRN) which reflects the activity of medial frontal/anterior cingulate activity (Miltner et al., 1997) and its amplitude codes the ongoing evaluation of events and prediction of future events in terms of favorable or unfavorable outcomes (Holroyd and Coles, 2002). However, FRN amplitude does not seem to vary depending on outcome magnitude; it mainly reflects the distinction between gains and losses (Miltner et al., 1997; Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Nieuwenhuis et al., 2005; Yeung and Sanfey, 2004; Hajcak et al., 2006), although a recent study reported a direct link between FRN and magnitude of the prediction error in outcome processing (Bellebaum and Daum, 2008). FRN amplitude has been reported to be modulated by outcome expectation (Hajcak et al., 2005; Cohen et al., 2007) and was also found to correlate with risk-taking behavior (Gehring and Willoughby, 2002; Yeung and Sanfey, 2004).

The P300 has also been reported to reflect decision-making (Yeung and Sanfey, 2004; Ma et al., 2008). According to Nieuwenhuis and colleagues (2005), the P300 is linked to the noradrenergic system and locus coeruleus activity, and its amplitude is thought to reflect the outcome of stimulus evaluation and decision-making. The P300 amplitude varies with variables such as event probability, motivational significance of stimuli and magnitude of feedback outcome, regardless of whether the outcome is a gain or a loss (Yeung and Sanfey, 2004). In economic decision-making, FRN and P300 seem to reflect different aspects of reward processing, valence and magnitude, respectively (Yeung and Sanfey, 2004). A third component potentially linked to risky decision making is the N500 (Yang et al., 2007; Polezzi et al., 2008b). The N500 is generally larger for unpredictable outcomes (Polezzi et al., 2008a,b) and it is thought to be generated by posterior cingulate cortex and visual association cortex (Carretié et al., 2006).

As outlined above, risk-taking behavior is modulated by context. Kahneman and Tversky (1979) have shown that moving toward gains domains, people tend to be risk-averse while the majority of people are risk-seekers shifting toward losses domain. Recent EEG studies, which investigated outcome processing, have focused on choices between options with zero EV (Gehring and Willoughby, 2002; Hajcak et al., 2006), or positive EV (Polezzi et al., 2008a,b) or different EV (Yeung and Sanfey, 2004), but, to our knowledge, there are as yet no EEG studies which directly compare changes in decision-making across the different contexts. In the current study, people are required to make decisions in a context in which options have positive EV and in another context in which they have zero EV. The first aim of the current study was to assess changes in risk-taking behavior across different EV contexts and its neuronal correlates. The previous studies on outcome processing have outlined that the cognitive processes reflected by FRN and P300 are related to risk-taking, but they did not address the issue why the same person could prefer a safer option in one context and a riskier option in another. The direct comparison of the electrophysiological correlates of changes in decision-making across context should help to understand the neurocognitive mechanisms underlying such context-dependent shifts. In addition, given the considerable interindividual variability in risk-taking behavior (Gehring and Willoughby, 2002; Yeung and Sanfey, 2004) and differences in subjective perception of options depending on attitudes to risk (Lee, 2005), individual differences in risk-taking (i.e. risk-prone vs. risk-averse) were also considered.

Materials and methods

Participants

Twenty-four undergraduate students from the University of Bochum (17 females and 7 males with age ranged 19 to 41 years, mean = 23.5) participated in this study. All subjects were healthy and had normal or corrected-to-normal vision. They were recruited by advertisements, signed an informed consent form and were debriefed at the end of the experiment, after they received the money they earned during the gambling task.

Task

We employed a gambling task, which involved choices between *Risky* and *Safer* options. To ensure ecological validity of the task and to enhance motivation, subjects were informed that they would receive a remuneration corresponding to what they won in the game. Instructions were given in written. Participants were told that on each trial they had to choose between two options, yielding different outcomes, and they should try to earn as much money as possible. They were specifically told that they would be paid out the sum total of their gains at the end of the experiment. Participants were also told that the gambling task was divided in two parts. Subjects did not know *a priori* either the outcomes or their probabilities, but they had to make the relevant inferences during the task. On each trial, two colored circles, one blue and one yellow, appeared on a black computer screen. The circles were located to the left and the right of the centre of the screen; positions changed across trials in random order and were counterbalanced within the task. Blue represented the *Risky* option and yellow the *Safer* option in half of the subjects, for the other half the opposite pattern applied. Participants were instructed to press a left-sided ("A") or a right-sided ("L") key, depending upon the option they chose for this particular trial. Both options had zero EV but led to different outcomes and, in accordance with the task employed by Gehring and Willoughby (2002), the option with the larger outcomes is termed *Risky* and the other option is termed *Safer*.

In this study, we refer to the procedure as "decisions under risk", because previous studies adopted this term (Yeung and Sanfey, 2004; McCoy and Platt, 2005). It is important to note that formally the decisions should be referred to as "decisions under uncertainty," given that they involve conditions which are characterized by knowledge about the outcomes, but not about their precise probabilities (Knight, 1921). In everyday life, the precise probability associated with different outcomes is generally not known. Hence, decisions under uncertainty situations represent an ecologically valid situation.

The *Safer* option yielded a gain of 5 cents or a loss of 5 cents while the *Risky* option yielded a larger gain of 25 cents or a larger loss of 25 cents. The probability of each outcome was 50 %. This part of the task comprised 120 trials and it is referred to as *Zero EV* condition. The maximum possible gain in this part was 18€ (gains only), while the maximum possible loss was 18€ (losses only). Since gains and losses are each associated with a 50 % probability, the overall outcome would be approximately 0€.

In a second part, termed *Positive EV* condition, both options had a positive EV of 2.5 cents but they led to different outcomes: The *Safer* option yielded a gain of 10 cents or a loss of 5 cents while the *Risky* option yielded a larger gain of 25 cents or a larger loss of 20 cents. The probability of each outcome was 50%, and there were 120 trials. Half of the subjects performed the *Zero EV* condition first, followed by the *Positive EV* condition, the remainder performed the tasks in the reverse order. The maximum possible gain in this part was 21€ (gains only), while the maximum possible loss was 15€ (losses only). With both gains and losses being associated with a probability of 50%, the overall outcome would be approximately 6€.

The average earning was 6€ if based on a random choice. In addition to a 5€ reimbursement for participation, the subjects won between 2.55€ and 9.10€.

Ideally, a full experimental design which would also include a *Negative Value* condition would be desirable. This condition might, however, require subjects to pay money after completion of the task and is thus not feasible for ethical reasons. This limitation might have been addressed by disclosing the aim of the study after completion of

the task. It is, however, doubtful that subjects would have really believed that they would have to pay (rather than earn) money for participating in a study and this condition would thus not have been comparable to other conditions. Therefore, while the Zero and Positive Value are real conditions, the Negative Value would be only a dummy condition.

On individual trials, the corresponding outcome was displayed in the centre of the screen after the choice had been made. A single trial entailed the following sequence: Initially, a fixation cross appeared in the screen centre for 1000 ms, then the two circles (yellow and blue) appeared until the participant had made his/her choice (with a time limit of 2000 ms). Then the screen went blank for 500 ms; followed by presentation of the outcome in the screen centre for 2000 ms (see Fig. 1). After an interval of 3000 ms, the next trial started. Presentation software was used for stimuli presentation, markers and response recording.

The instructions were presented in written form, and subjects completed an informed consent form. EEG electrodes were then applied, using an electrocap (see below). The experimental session lasted about 45 min.

ERP recording

Scalp voltages were recorded using 32 Ag/AgCl electrodes in a cap according to the 10-20 international system: F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8. Mastoids served as reference and electrode impedance was kept under 10 KΩ for all recordings. Vertical and horizontal ocular movements were also recorded. The EEG was recorded continuously, digitized at a sampling rate of 500 Hz, and stored on hard disk for off-line analyses. Electrical signals were amplified with Synamps amplifier. The signal was off-line filtered using a 0.5–30 Hz *band pass filter*. Ocular movements' artifacts were corrected using the algorithm provided by Brain Vision Analyzer 2004. The EEG was segmented for 1000 ms in *epochs* starting 100 ms before presentation of the offer. The epochs were aligned to the 100 ms baseline before onset of the offer stimuli. Trials affected by ocular or movements artifacts were excluded from averaging. Analyses focused on the ERP components known to reflect cognitive processes linked to decision making (FRN, P300 and N500).

Source analysis

ERP amplitudes from all 32 electrodes entered source analysis with LORETA (Low Resolution Brain electromagnetic tomography) (Pascual-Marqui et al., 1994; Pascual-Marqui, 1999). LORETA is an inverse solution technique that estimates the distribution of the electrical neuronal activity in three-dimensional space. LORETA-images represent brain activity through 2394 voxels, which include gray matter as well as hippocampus, amygdala, and cingulate gyrus (Congedo et al., 2004).

For source analysis, we followed the procedure suggested by Bellebaum and Daum (2006). For all subjects, LORETA-images were generated for contrast of interest relating to risk attitude (see below results section). The images were converted (http://www.ihb.spb.ru/~pet_lab/L2S/L2Smain.htm) and further analyzed using SPM99 (http://www.fil.ion.ucl.ac.uk/spm/). A PET/SPECT design with multi-subjects, conditions and covariates was performed with the following parameters: Global Normalization with a proportional scaling to a mean of 50, no absolute threshold masking and global calculation of mean voxel value (within per image). The level of significance was set to $p = 0.001$, uncorrected for multiple comparison. The coordinates of the foci of significant differences between conditions were transformed into Talaraich coordinates (Talairach and Tournoux, 1988) with the algorithm suggested by Brett (http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml). The Talaraich Daemon was then used to identify the brain structures involved (Lancaster et al., 2000).

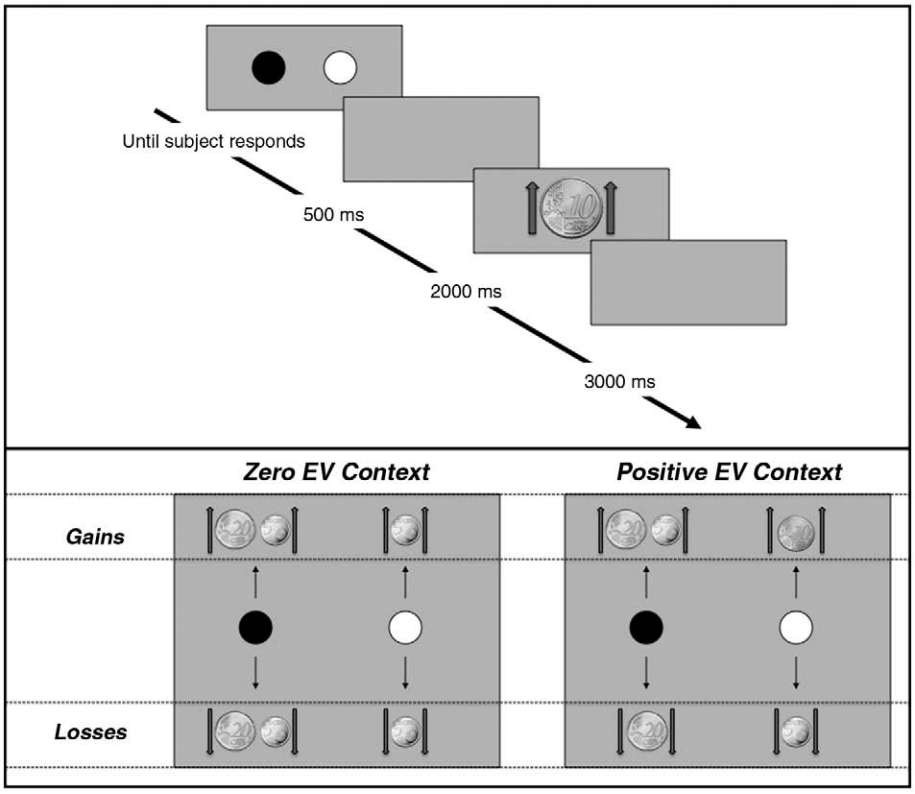

Fig. 1. Participants choose between one of the two circles yielding different outcomes. After the decision, the outcome was displayed. In the lower part, the two contexts and their relative outcomes are shown.

Results

Behavioral results

In order to assess whether there was a shift in risk-taking behavior between the *Zero EV* and the *Positive EV* condition, the percentage of risky choices was determined for the two conditions. Two groups of subjects were identified on the basis of the pattern of behavioral change across the two conditions: *Zero-Oriented* and *Positive-Oriented*. *Zero-Oriented* participants ($N=11$) made more risky choices in the Zero EV condition and fewer in the Positive EV condition. *Positive-oriented* participants ($N=13$) showed the opposite pattern (see Fig. 2d and f. It is important to note that participants belonging to the *Positive-oriented* group were not necessarily risk-prone in the positive EV context and risk-averse in the zero EV context, but they simply choose the risky option more frequently in the positive EV context compared to the zero EV one. The same rationale applies to the *Zero-oriented* group. We also assessed whether changes in risk tendency occurred within the same condition, as subjects became more familiar with the task by including a Block factor (first (trials 1–40), second (trials 41–80) and third (trials 81–120) parts). Repeated measures ANOVA with Group (*Zero-Oriented* vs. *Positive-Oriented*), Order (*Zero-Positive* vs. *Positive-Zero*), EV (*Zero* vs. *Positive*) and Blocks (1–40 vs. 41–80 vs. 81–120) was performed. The two groups did not differ significantly on overall percent risky choices ($F(1,20)=0.01$, $p=0.95$ $\eta^2_{\text{partial}}=0.00$), and the other main effects did not yield significant results either (Order ($F(1,20)=0.01$, $p=0.93$ $\eta^2_{\text{partial}}=0.00$); EV ($F(1,20)=0.31$, $p=0.58$ $\eta^2_{\text{partial}}=0.02$); Blocks ($F(1,20)=1.83$, $p=0.17$ $\eta^2_{\text{partial}}=0.08$)). Analysis yielded however a significant Group × EV interaction ($F(1,20)=22.39$, $p<0.001$ $\eta^2_{\text{partial}}=0.53$), indicating higher rate of risky choice of the *Positive-Oriented* group in the Positive EV condition ($t(10)=-5.10$, $p<0.001$) and of the *Zero-Oriented* group in the Zero EV condition ($t(12)=4.17$, $p<0.01$), confirming the subdivision of the two groups based on their behavioral results. No other significant effects emerged ($p>0.1$).

Moreover, we performed an additional two-step cluster analysis in order to support the division of the sample. We calculated the difference in percentage of risky choices between the zero EV and positive EV conditions in the first (trials 1–40), second (trials 41–80) and third (trials 81–120) part, aiming for sample division. We considered the three different parts of the task, to assess whether switching behavior is consistent or just present in same part. The analysis confirmed that 13 participants belonged to a group, which we termed Positive-oriented, and that this group choose the risky options more frequently in the positive compared to the zero condition in the first (Mean = +12.3%, Dev. St. = 23.6%), in the second (Mean = +11.7%, Dev. St. = 14.1%) as well as in the third (Mean = +11.7%, Dev. St. = 12.7%) part of the task. The remaining 11 participants belonged to another group, which we termed Zero-Oriented, and choose less frequently the risky options in the positive compared to the zero condition in the first (Mean = −19.8%, Dev. St. = 15.0%), in the second (Mean = −7.3%, Dev. St. = 8.8%) as well as in the third (Mean = −8.2%, Dev. St. = 16.2%) part of the task.

In addition, the risky choices of the Positive-Oriented group did not differ from chance in the Zero EV condition (50.3%, $t(12)=0.09$ $p=0.93$), while these subjects were clearly risk prone in the Positive

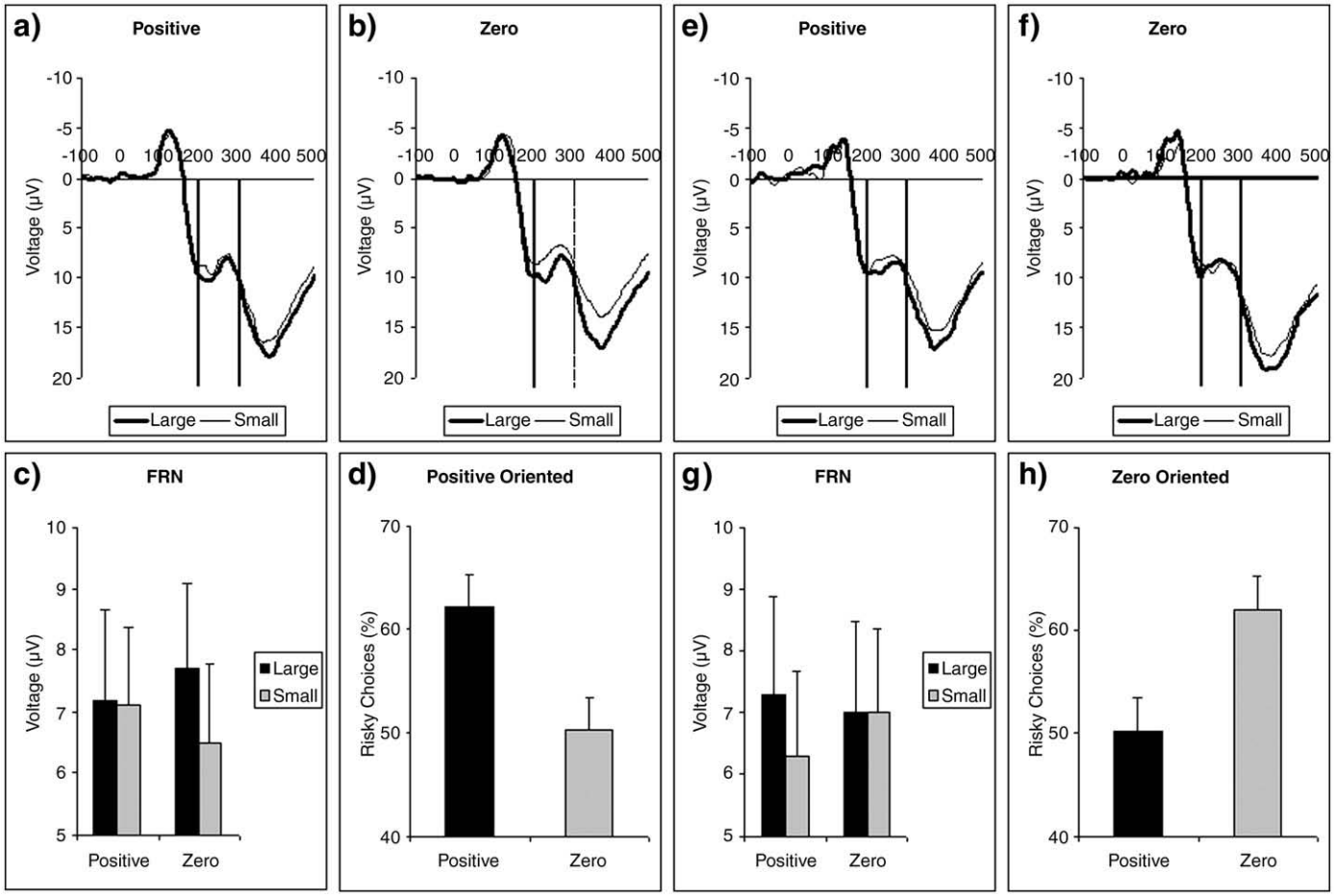

Fig. 2. Positive Oriented Group was sensitive to magnitude of outcomes in the Zero EV condition (b) but not in the Positive EV condition (a) [see also section c], where this group is risk-prone (d). By contrast, Zero Oriented Group, showed different FRN amplitude in the Positive EV condition (e) and not in the Zero EV condition (f) [see also section g], where the group showed risk seeking behaviour (h).

EV condition (62.2%, $t(12)=4.78$ $p<0.001$). By contrast, the Zero-Oriented group was risk-seeking in the Zero EV condition (61.9%, $t(10)=3.17$ $p<0.05$) and showed random choice behavior in the Positive EV condition (50.1%, $t(10)=0.04$ $p=0.970$) (see Fig. 2).

In order to assess whether making risky choices might be affected by the outcome of the previous trial, we calculated the frequency of risky choices after participants experienced a loss or a gain. The frequencies of the safer option after losses and gains were also obtained. Wilcoxon tests showed that the frequencies of risky choices after a loss or a gain were not significantly different ($Z=-0.29$, $p=0.77$) nor did analysis of the safer option yield a significant difference ($Z=-1.08$, $p=0.28$).

Event related potentials

As outlined above, processing of outcomes of decisions are mainly reflected in the FRN, P300 and N500 (Gehring and Willoughby, 2002; Yeung and Sanfey, 2004; Hajcak et al., 2006; Yang et al., 2007). All following analyses refer to brain activity evoked by presentation of outcomes. FRN amplitude was assessed as the mean amplitude in the 200–300 time window, P300 amplitude as the mean amplitude within the 300–500 ms time window and N500 amplitude as the mean amplitude within 500–700 ms time window, relative to the baseline preceding presentation of the outcomes.

ANOVA were performed with Group (*Zero-Oriented* vs. *Positive-Oriented*), EV (*Zero vs. Positive*), Valence (*Gains vs. Losses*) and Magnitude (*Small vs. Large*) as factors and the respective ERP amplitudes as dependent measures.

FRN

Given that the maximum FRN amplitudes are observed at frontal sites (e.g. Gehring and Willoughby, 2002; Hajcak et al., 2006; Holroyd and Coles, 2002), data from electrode sites F3, Fz and F4 were pooled.

The main EV effect was not significant ($F(1,22)=0.10$, $p=0.75$ $\eta^2_{partial}=0.01$). FRN amplitude was significantly modulated by Valence ($F(1,22)=7.51$, $p<0.05$ $\eta^2_{partial}=0.26$), with larger FRN for losses than for gains. Magnitude effects did not reach significance ($F(1,22)=3.52$, $p=0.08$ $\eta^2_{partial}=0.14$). The significant Group×EV×Magnitude interaction ($F(1,22)=8.55$ $p<0.01$ $\eta^2_{partial}=0.28$) indicated that Magnitude affected the behavior of the Zero-Oriented subjects in the Positive EV condition ($t(10)=2.01$, $p=0.07$) but not in the Zero EV condition ($t(10)=0.02$, $p=0.98$). The Positive-Oriented group, on the other hand, showed a tendency towards behavioral differences depending upon Magnitude in the Zero EV condition ($t(12)=2.05$, $p=0.06$), but not in the Positive EV condition ($t(12)=0.20$, $p=0.84$). The highest order interaction (Group×EV×Valence×Magnitude) was also significant ($F(1,22)=11.63$, $p<0.01$ $\eta^2_{partial}=0.35$), showing that the behavior of the zero-oriented group is sensitive to magnitude of gains in the Positive EV context ($t(10)=3.20$, $p<0.01$) but not in the Zero EV context ($t(10)=-1.04$, $p=0.33$). In the positive-oriented group the opposite pattern emerged ($t(12)=-0.63$, $p=.54$; $t(12)=2.70$, $p<0.05$). No other effect reached or approached significance ($p>0.1$).

P300

The P300 is observed at parietal and frontal sites (Nieuwenhuis et al., 2005); findings are therefore reported for pooled frontal (F3, Fz and F4) and parietal electrodes (CP3, CPz and CP4).

Frontal sites

The main EV effect was not significant ($F(1,22)=0.57$, $p=0.46$ $\eta^2_{partial}=0.02$). The significant Group×EV interaction ($F(1,22)=14.09$, $p<0.01$ $\eta^2_{partial}=0.39$) reflected a larger P300 amplitude in the *Zero-Oriented* group P300 in the Zero compared to the Positive EV conditions ($t(10)=-2.81$, $p<0.05$), whereas the *Positive-Oriented* group showed the opposite pattern ($t(12)=2.41$, $p<0.05$) (see Fig. 3). The main Valence effect was significant ($F(1,22)=35.59$, $p<0.001$ $\eta^2_{partial}=0.62$), reflecting a larger P300 amplitude for gains compared to losses. The significant Group×Valence interaction ($F(1,22)=5.00$, $p<0.05$ $\eta^2_{partial}=0.19$) mirrored a larger P300 amplitude difference between gains and losses in the Zero-Oriented compared to the Positive-oriented group. The P300 amplitude was affected by Magnitude ($F(1,22)=14.34$, $p<0.01$ $\eta^2_{partial}=0.40$), with higher amplitudes for large compared to the smaller magnitude. The interaction of EV with Valence, Magnitude and Group approached significance ($F(1,22)=3.77$, $p=0.07$ $\eta^2_{partial}=0.15$). No other effects reached or approached significance ($p>0.1$).

Parietal sites

The main EV effect was not significant ($F(1,22)=0.30$, $p=0.59$ $\eta^2_{partial}=0.01$). The significant Group×EV interaction ($F(1,22)=10.75$, $p<0.01$ $\eta^2_{partial}=0.33$), reflected larger P300 amplitudes in the Zero EV compared to the Positive EV condition in the Zero-Oriented Group ($t(10)=-1.98$, $p=0.08$), while the Positive-Oriented group showed the opposite pattern ($t(12)=3.20$, $p<0.01$). The main Valence effect was significant ($F(1,22)=29.05$, $p<0.001$ $\eta^2_{partial}=0.57$), with higher amplitudes for gains compared to losses. The Group×Valence interaction approached significance ($F(1,22)=3.34$, $p=0.08$ $\eta^2_{partial}=0.14$). P300 amplitude was significantly affected by Magnitude ($F(1,22)=8.03$, $p<0.05$ $\eta^2_{partial}=0.27$), with higher P300 amplitudes for larger than for smaller magnitude. The highest order interaction (Group×EV×Valence×Magnitude) approached significance ($F(1,22)=346$, $p=0.08$ $\eta^2_{partial}=0.14$). No other factor or interaction reached or approached significance ($p>0.1$).

N500

In accordance with Yang et al. (2007), N500 was analyzed over frontal sites (pooled across F3, Fz and F4).

The main EV effect did not reach significance ($F(1,22)=3.27$, $p=0.08$ $\eta^2_{partial}=0.13$). The significant Group×EV interaction ($F(1,22)=11.22$, $p<0.01$ $\eta^2_{partial}=0.34$), showed that while N500 amplitudes were higher for Positive EV rather than for Zero EV in the Zero-Oriented group ($t(10)=-2.94$, $p<0.05$), there were no significant differences in the *Positive-Oriented* ($t(12)=1.42$, $p=0.18$). N500 amplitude was modulated by Valence ($F(1,22)=15.69$, $p<0.01$ $\eta^2_{partial}=0.42$), with higher amplitudes for losses than for gains. The main Magnitude effect was significant ($F(1,22)=14.56$, $p<0.01$ $\eta^2_{partial}=0.40$). The Group×EV×Valence interaction ($F(1,22)=4.01$ $p=0.06$ $\eta^2_{partial}=0.15$) and the Group×EV×Magnitude interaction ($F(1,22)=3.59$ $p=.08$ $\eta^2_{partial}=0.14$) approached significance, as did the main Group effect ($F(1,22)=4.31$, $p=0.05$ $\eta^2_{partial}=0.16$). No other effects reached or approached significance ($p>0.1$).

Source analysis

In order to further investigate the brain correlates of the observed effects, source analyses were performed for each main effect and for each interaction, which reached significance in ERP analyses. The reported coordinates follow the Montreal Neurological Institute system.

FRN

For the FRN, voxels survived the significance level only for the Valence factor (Gains vs. Losses contrast), the critical area being the anterior cingulate cortex (see Fig. 4, section a) ($F(1,161)=16.77$, $p<0.001$, [−3 31 −5]. This result is consistent with the frequently

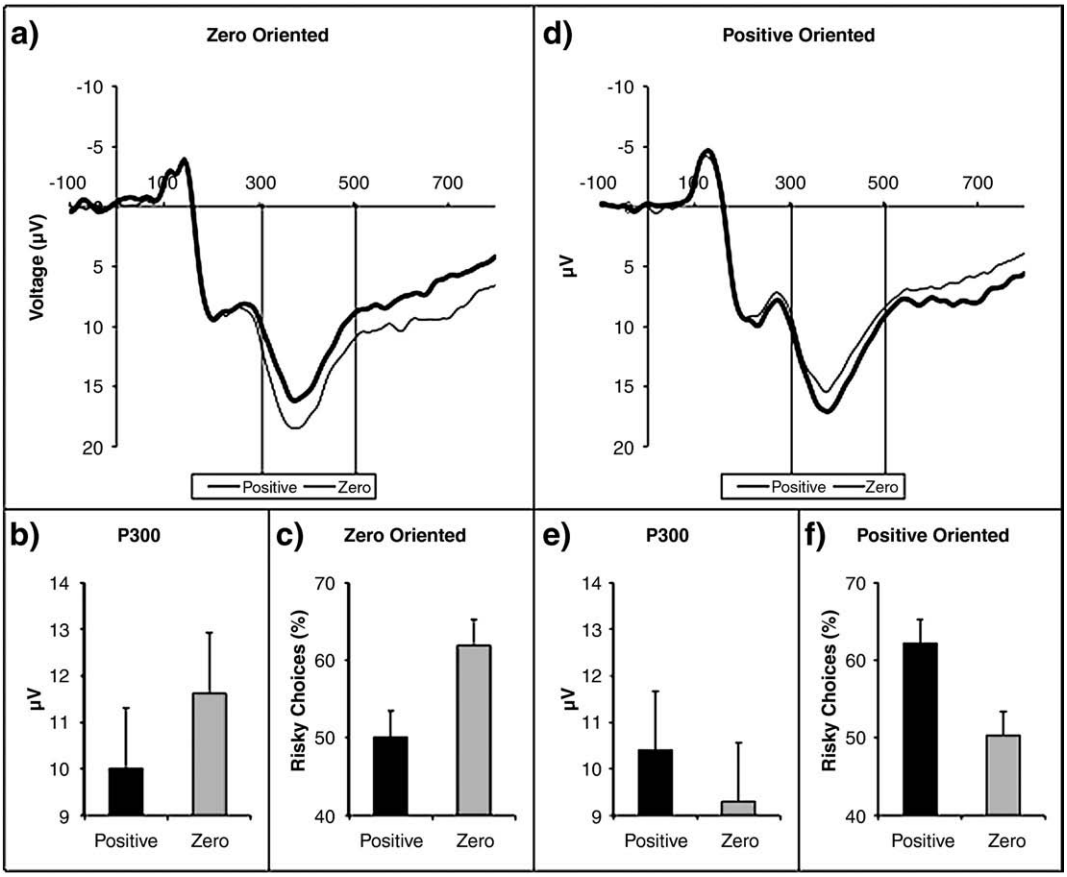

Fig. 3. Zero-Oriented group was more likely to risk in the Zero EV condition (c) in association with larger P300 (b). By contrast, Positive-Oriented group showed the opposite pattern (f) mirrored by a reverse pattern in P300 (e).

reported FRN sources (Gehring and Willoughby, 2002). No other contrasts yielded significant activation differences.

P300

No voxels survived the level of significance.

N500

For the N500, LORETA revealed different activation patterns for different EV levels (Positive vs. Zero contrast), implicating the posterior cingulate gyrus (see Fig. 4, section b) ($F(1,161) = 14.41$, $p < 0.001$, [−3 −18 36]), which showed higher activation for the Zero

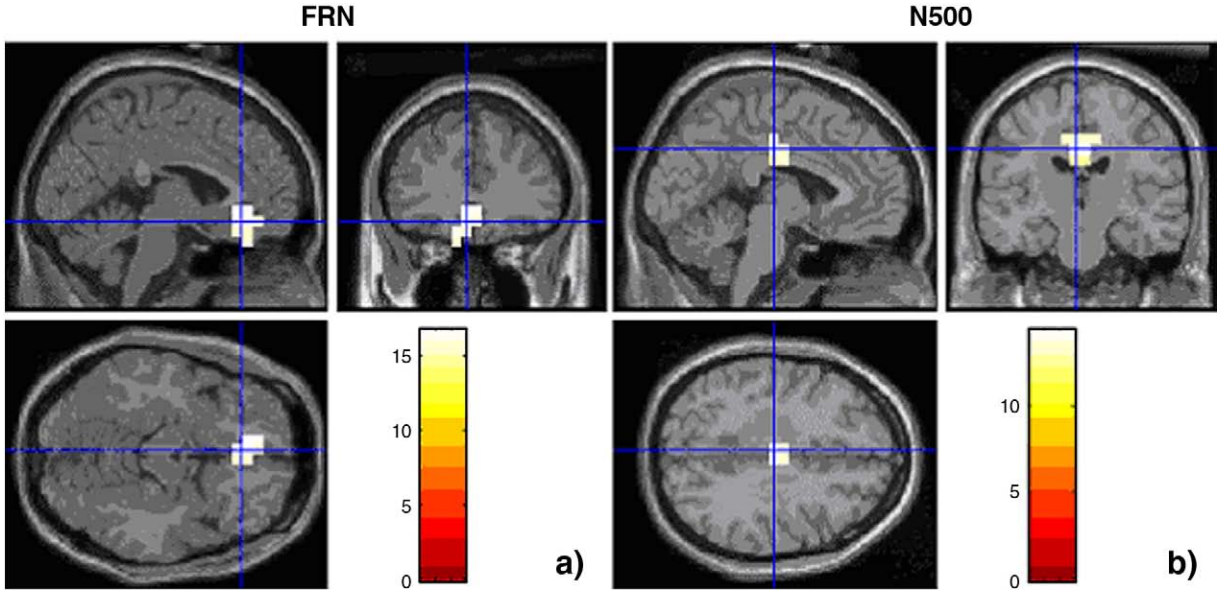

Fig. 4. FRN is generated by Anterior Cingulate Cortex (a), while N500 is generated by Posterior Cingulate Cortex (b).

than for the Positive EV condition ($t(161)=3.80$, $p<0.001$). In addition, the Positive-Oriented group showed differences in the posterior cingulate gyrus activation patterns ($F(1,84)=14.89$, $p<0.001$, [−3 −11 29]), with higher activation in the Zero compared to the Positive EV condition ($t(84)=3.86$, $p<0.001$). No other contrasts yielded significant results.

Discussion

The neural mechanisms underlying risky decision-making have been the subject of rising research interest in recent years. Risk-taking behavior was found to be modulated by the decision context as well as by interindividual differences. Previous EEG studies have investigated risky decision making in zero EV (Gehring and Willoughby, 2002) or positive EV contexts (Polezzi et al., 2008a,b), but to our knowledge this study is the first which directly compares decision making across different contexts and associated changes in the neurocognitive correlates of decision making. The direct comparison across contexts allows the assessment of changes in the processing of behavioral outcomes with changes in context. A further aim addressed interindividual differences in risk taking behavior, by comparing subjects with differential decision strategies across two contexts: Zero EV and Positive EV.

In one of the most influential articles in the economic decision making field, Kahneman and Tversky (1979) showed that people tend to be risk-averse in the gains domain and risk-prone in the losses domain, suggesting that decisions can be greatly affected by the context. In the present study, subjects showed a shift in risky choices with change of context, regardless of the order in which the different contexts were introduced. In the present experiment, subjects showed a shift in risky choices with change of context, regardless of the order in which the different contexts were introduced. Analysis of individual decision patterns yielded two different subgroups: subjects who risked more in the Positive EV condition (termed *Positive-Oriented* group) and subjects who showed more risk-taking behavior in the zero-EV condition (termed *Zero-Oriented* group). Thus both groups are risk-seekers in one context and choose randomly in the other. As outlined in the introduction, when two options have the same EV, rational behavior would imply random choices. Risk-seeking behavior represents an interesting deviation from rationality, as outlined by Kuhnen and Knutson (2005). This behavior is constant with the ongoing of the task, as shown by cluster analyses. In addition, it needs to be noted that the outcome probabilities were not known, but had to be inferred, which differs from classical studies such as those by Kahneman and Tversky (1979) in which probabilities were known *a priori*. Recent studies reported a difference in experienced risk if outcomes and probabilities are unknown but can be identified with experience, and descriptive risk, when outcomes and probabilities are known at the time of choice, on behavioral level as well as on neural level. Camerer and Weber (1992) reported that many people are more willing to bet on risky outcomes when probabilities are known and later, Hsu and colleagues (2005) showed that the level of uncertainty in probabilities is linked to amygdala and orbitofrontal cortex activity.

As outlined above, we investigated brain activity evoked by the presentation of outcomes, with the three ERPs reflecting different stages of outcome processing. The FRN amplitudes were modulated by the well-known distinction between gains and losses (Gehring and Willoughby, 2002; Hajcak et al., 2006), and by early processing differences between the two groups. FRN amplitudes in the Positive-Oriented group were modulated by outcome magnitude in the zero EV condition, where risky choices did not exceed the chance level, whereas there were no magnitude effects in the positive EV condition, where the subjects adopted a risk-seeking strategy. By contrast, FRN amplitudes of Zero-Oriented subjects were affected by outcome magnitude in the positive EV condition, where their decision-making behavior was random, but not in the Zero condition, where they showed risk-prone behavior. These findings are consistent with the idea that risk-taking behavior partly relies on a very early evaluation (within 300 ms) of the outcomes (Gehring and Willoughby, 2002; Yeung and Sanfey, 2004). In addition, the evaluation of response options also is not only related to payoffs, but changes in risk-taking are also affected by interindividual differences in decision-making strategy. As a note of caution, it has to be pointed out that even in case of significant interactions, the comparisons yielded only trends towards significance. Source analysis relating to FRN yielded the expected findings, with FRN being linked to anterior cingulate cortex activity.

P300 amplitudes were generally higher for gains compared to losses, which is in line with previous findings (Yeung and Sanfey, 2004). P300 amplitudes also reflected the distinction between large and small outcomes, regardless of their valence. Taken together, these data further support the idea of the independent coding of outcome magnitude and valence in FRN and P300, respectively, as previously reported by Yeung and Sanfey (2004). Interestingly, P300 amplitude also mirrored changes in risk-taking behavior across contexts in both subgroups of subjects, the P300 being larger in the context in which participants were more likely to show risk-prone decision behavior. The Zero-Oriented group was more risk-prone in the Zero EV condition in which P300 amplitudes were increased, while reduced P300 amplitudes were observed in the Positive EV condition in which they showed random choice behavior. The Positive-Oriented group, on the other hand, was risk-prone in the Positive EV condition in which they also showed larger P300 amplitude, while reduced P300 amplitudes and low risk-seeking behavior characterized the Zero EV condition. A possible interpretation of these effects is that P300 amplitudes reflect high motivation. First, P300 amplitudes are higher for target stimuli (i.e. gains), which generally have a higher motivational significance than non-target stimuli (Duncan-Johnson and Donchin, 1977). Second, P300 amplitudes are higher for larger compared to smaller outcomes, as previously reported by Yeung and Sanfey (2004), who also suggested that P300 amplitude varies with outcomes magnitude because of the increased motivational significance of larger reward and penalties (Yeung and Sanfey, 2004). Third, emotionally significant stimuli are associated with higher P300 amplitudes than emotionally neutral stimuli (Johnston et al., 1986; Keil et al., 2002). The current findings are consistent with the idea that subjects tend to risk more and show higher P300 amplitudes if their motivation is enhanced. By contrast, with lower motivational status, their decisions were random and the P300 was reduced. This pattern is consistent with the hypothesis that the P300 reflects the activity of a neuromodulatory and motivational system as suggested by Nieuwenhuis and colleagues (2005). Despite significant differences in P300 amplitude, source analyses failed to reveal generators linked to these effects. In a comprehensive review of the P300 literature, Nieuwenius and colleagues (2005) concluded that multiple generators may underlie the P300. The authors suggested that P300 activity reflects the effect of locus coeruleus and norepinephrine in different brain areas which may not lend themselves to source analyses.

The third component related to outcome processing is the N500, which has been linked to the subjective pleasantness of stimuli (Carretié et al., 2006; De Pascalis et al., 1999; Mack et al., 2005) and to decision-making processes (Polezzi et al., 2008a,b). The N500 is thought to be generated by the posterior cingulate cortex and visual association cortex (Carretié et al., 2006). Consistently with previously reported data, the N500 amplitude was higher for losses than for gains. In addition, in the Zero-Oriented group, the N500 was higher for the Positive EV context, in which they risked less compared to the Zero EV context in which they showed more risk-seeking behavior. Interestingly, source analyses yielded an involvement of posterior cingulate cortex in the generation of the N500.

Activity in this region was found to correlate with risky decisions in monkeys (McCoy and Platt, 2005) and the authors interpreted these data as evidence for coding of risk in the posterior cingulate cortex. However, Lee (2005), commenting on McCoy and Platt's (2005) experiment, pointed out that it is as yet unclear whether the posterior cingulate cortex represents EV or risk, given that these two factors are not separated in the experiment. Our data findings would support this interpretation, since in the Zero-Oriented group, the posterior cingulate cortex showed higher activation during the Zero EV context compared to the Positive EV context. The Zero EV context is, however, also the condition in which these subjects are more likely to make risky decision, therefore the relative contributions of risk and EV cannot be clearly separated. Also a recent fMRI study has linked posterior cingulate cortex activation to changes in risk-taking (Li et al., 2009). In sum, the present ERP findings provide converging evidence of an involvement of the posterior cingulated cortex in risky decision-making, consistent with the previous findings in monkeys (McCoy and Platt, 2005) and fMRI data in human subjects (Li et al., 2009), even if strong conclusions about the role of the posterior cingulate cortex cannot yet be drawn. Risky decisions have also been related to dorsolateral prefrontal cortex (DLPFC) (Knoch and colleagues, 2006). Kuhnen and Knutson (2005) have pointed out that the adoption of risk in preference to rational behavior, is linked to the involvement of the nucleus accumbens which anticipates possible gains, while, risk avoidance is correlated with insula activation and the anticipation of possible losses. ERP studies, on the other hand, have consistently related the ACC to risky behavior (Gehring and Willoughby, 2002; Yeung and Sanfey, 2004), and the functional implications of the involvement of the posterior cingulate cortex, which emerged in the current study needs to be clarified by further studies.

In conclusion, the current study highlights the idea that economic decision-making is not exclusively determined by payoffs but strongly affected by context. ERP data suggest that risk-taking behavior may depend (i) on sensitivity to outcome magnitude, as indicated by FRN data, (ii) on motivation, as indicated by P300 data with people being more likely to take risks when motivation is high. Moreover, most studies which investigated economic decisions highlighted the role of dopamine, at genetic (Kreek et al., 2005), electrophysiological (Holroyd and Coles, 2002) and behavioral levels (Driver-Dunckley et al., 2003). The present study addresses the importance of the FRN which is thought to reflect dopamine activity in the decision-making process, but, at the same time, suggests a crucial role of P300. This is consistent with the hypothesis of Nieuwenius and colleagues (2005) who suggested that in decision processes norepinephrine plays a pivotal role. Thus, further studies might elucidate the role of norepinephrine, an issue which has so far been neglected. In addition, source analyses provided evidence for an important involvement of the posterior cingulate cortex in risk taking behavior. Economic decisions are known to depend upon reward contingences (McClure et al., 2004) and social context (Sanfey et al., 2003; Moretti et al., 2009; Polezzi et al., 2008a). Cognitive neuroscience can offer important insights into the neurocognitive mechanisms, which may help to reduce the gap between formal theories and real choice behavior.

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