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Size and probability of rewards modulate the feedback error-related negativity associated with wins but not losses in a monetarily rewarded gambling task

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ABSTRACT

Feedback error-related negativity (fERN) has been referred to as a negative deflection in the event related potential (ERP), which distinguishes between wins and losses in terms of expected and unexpected outcomes. Some studies refer to the "expected outcome" as the probability to win vs. to lose, and others as expected size of rewards. We still do not know much about whether these alternative interpretations of "expected outcome" affect the fERN in a different manner, nor do we know the effect of their interaction in an expected value fashion. We set a gambling task with four game categories; two had the same expected value, while the other two categories were equivalent to the first ones, but alternatively in the size or probability of the offered rewards. Results show that fERN preceded by a P200, and followed by a Pe-like wave differentiates between losing in the category with a higher expected value and the rest of the experimental conditions. fERN differentiates between wins and losses, but changes in the size and probability of rewards impact the fERN amplitude only in win conditions. Results also show greater positivity following win feedback when the size and/or probability of the outcome rewards were higher, so that the higher the expected value the greater the positivity following win feedback. Our findings support the notion that both the probability and size of the offered rewards modulate the motivational value for the win feedback, this being also true for their interaction in an expected value fashion.

Introduction

A basic capacity implicated in what we call "intelligence" has to do with the ability to assess the outcome of our actions and use that evaluation for the sake of optimizing goal-directed behaviors. Recently, the field of neuroeconomics (reviewed in Clithero et al., 2008; Schultz, 2008) has been interested in these matters, noting that these processes are less obvious than it would seem. For example, losing a lottery game is a bad outcome, but is its degree of "badness" defined only by the cost of the ticket? Is it affected by the size of the non-earned prize? Is it affected by how likely it seemed to win? Winning a poker pot is a good result, but what is its degree of "goodness"? Is it defined only by the amount of money earned? Does it have to do with having avoided the scenario of losing when having a good hand? In this respect, cognitive neuroscience of decision-making is shedding light on the subject in terms of the evaluation of results in economic contexts reflecting the action of general behavioral monitoring mechanisms. These findings are helping to solve questions regarding expectations and outcome evaluations.

An important finding toward understanding the neurocognitive mechanisms underlying behavioral monitoring in humans is the discovery of an event-related potential (ERP) differentiating between successes and errors in reaction time tasks, the so-called error-related negativity (ERN; Falkenstein et al., 1990; Gehring et al., 1993). Successive studies showed that the ERN could also be elicited by the subject's results feedback (Gentsch et al., 2009; Mars et al., 2004; Miltner et al., 1997; for reviews, see Holroyd et al., 2004b; Nieuwenhuis et al., 2004a). The resulting ERP distinguishes between positive and negative feedbacks, showing a more pronounced negativity for the negative ones reaching a peak around 250 ms after the feedback (Holroyd and Coles, 2002). Given the evidence in favor of this second type of ERN, literature generally distinguishes between a response-locked ERN and a feedback-locked ERN, or feedback ERN (fERN).

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According to an extended theory called the "reinforcement learning theory of ERN," both forms of ERN reflect the function of a generic, high-level error-processing system in humans (Holroyd and Coles, 2002). An important corpus of evidence (Holroyd et al., 2002, 2003, 2005), shows that ERN indicates when outcomes are worse than expected.

A key factor for understanding ERN amplitude modulation would be the difference between the actual and the expected outcome of the actions, that is to say the difference between the subject's expectations and the outcomes of their behavior. In the case of the fERN, this difference would define the motivational meaning of the received feedback (Nieuwenhuis et al., 2004a; Potts et al., 2006; Yeung et al., 2005).

While some research refers to expected outcome in terms of the expected size of rewards and/or punishments (Gehring and Willoughby, 2002; Holroyd et al., 2004a, 2006; Nieuwenhuis et al., 2004b), others refer to the probability of winning vs. losing (Cohen et al., 2007; Hajcak et al., 2005; Hewig et al., 2007; Holroyd et al., 2009; Potts et al., 2006). In the former, the fERN amplitude reflects the difference between the size of the expected and actual outcomes. In the latter, the fERN amplitude reflects the improbability of an actual negative outcome. To date, little is known with respect to whether these alternative interpretations of expected outcome affect the fERN in a different manner, and when comparisons between studies are performed, this distinction appears to vanish. For this reason, a primary goal of our study was to clarify the fERN modulating effects of sizes and probabilities.

It would be useful to review some examples of both alternative interpretations of expected outcome. With respect to the first, Gehring and Willoughby (2002) present a game sequence where participants are to choose between two boxes, one showing the number 5 and other showing the number 25 (referring to U.S. cents). One second after a choice has been made, each box turns either red or green. If the chosen box turned green, the participant wins an amount equal to the number in the box. If it turned red, the amount is lost and therefore subtracted from current earnings. Results show not only a greater amplitude of the fERN for loss feedback in comparison to win feedback, but also for losses of a bigger size (−25¢), compared to those of a smaller size (−5¢). Gehring and Willoughby (2002) referred to this component as medial-frontal negativity (MFN), nevertheless a later study (Nieuwenhuis et al., 2004b) showed an equivalence between MFN and fERN. Another study (Holroyd et al., 2004a) showed fERN reflecting loss size in relative terms, rather than according to its absolute value. For instance, winning nothing (0¢) when the other possible outcomes were winning 2.5¢ or 5¢, would generate greater negativities than winning nothing (0¢) when the other possible outcomes were losing 2.5¢ or 5¢. Authors of these studies pointed out that their designs assign equal probabilities to different outcomes, so that the observed differences could only be explained by differences in reward and punishment sizes.

A more recent study focused on the effect of outcome probabilities. Hewig et al. (2007) conducted an electrophysiological analysis using a version of the Blackjack gambling task. Cards, holding the values from 2 to 11, are given in a random sequence and the player must choose at each time whether to ask for a new card or to stop and keep the current score. After the subject stops, a computer-simulated opponent takes a turn, and the player with the best score wins the game (as close as possible to 21 points, inclusive, without exceeding it). Results showed that the fERN amplitude correlated with the expected outcome (win or lose), in terms of the most probable outcome. For example, losing by exceeding 21 points is less likely when one has 11 points and asks for a new card compared to when one has 18 points and asks for a new card. The fERN amplitude was larger in the first case when compared to the latter.

As per the classical theory of rational decision-making under risk situations, drawn from the pioneering work of Pascal and Fermat on S. XVII (reviewed in Trepel et al., 2005), the interaction precisely between the size and the probability of possible outcomes ultimately configure the expectations of rational agents. This postulate formalized the normative idea of expected outcome as expected value (EV):

$$\mathrm{EV} = x_1 p_1 + x_2 p_2 + \ldots + x_n p_n = \sum_{i=1}^{n} x_i p_i .$$

In the formula above, x_i is the value associated to the i-th outcome, while p_i is the probability of observing that outcome. Therefore, a game paying 40¢ (x_1) with a probability of 25% ($p_1 = 0.25$) and −10¢ (x_2) with a probability of 75% ($p_2 = 0.75$), has the same expected value as another game paying 15¢ (x_3) with a probability of 50% ($p_3 = 0.5$) and −10¢ (x_4) with the remaining 50% ($p_4 = 0.5$), since in both cases the formula yields the same expected value: $x_1p_1 + x_2p_2 = x_3p_3 + x_4p_4 = 2.5$¢. Given that both games have the same expected value, both games should generate the same expectations.

A second goal of our study was to determine the possibility that the EV regulates the interaction between probability and size when modulating the fERN amplitude.

On the one side, if it is true that the fERN amplitude accounts for the difference between expectations and actual outcomes, and on the other side those expectations correspond to the expected value, then the expected value should predict the fERN amplitude in situations where information regarding the sizes and probabilities of rewards is available to subjects. Now, a recent theory argues that differences between wins and losses could be better explained by a positivity associated with better than expected outcomes, rather than a negativity associated with worse than expected ones (Holroyd et al., 2008). Then, the EV could modulate the amplitude of fERN after winning and not after losing.

In order to assess these issues, we designed a four category gambling task, each corresponding to a particular configuration of reward size and probability. Two of these categories have an equivalent EV, while another category has a bigger EV and the final category is associated with a smaller one. The amount of the possible losses remains constant among categories, so any difference in the fERN associated with losses is derived from different expectations resulting from different configurations of the size and probability of the offered reward. Also, the existence of two pairs of game categories with offered rewards of equivalent size and two pairs with an equal reward probability, allowed us to analyze feedback-locked ERPs and their modulation by size and probability.

Materials and methods

Participants

A total of 22 right-handed participants that were students enrolled in university, took part in the experiment (12 men and 10 women; aged M = 20.68 years, SD = 1.12, in a range of 19 to 23 years; without gender age differences [t = −0.30, p = 0.76]). Participants did not present visual deficits; nor did they show any history of psychiatric or neurological disorders. All participants were rewarded with the amount earned in the gambling task. All participants signed a voluntary consent form in accordance with the Declaration of Helsinki, in addition to the approval granted by the ethical committee of the institution. Four participants were excluded from the ERP analysis due to excessive ocular movements and artifacts during the recordings.

Paradigm design

We designed a game that emulates a gambling roulette. The game presented four game categories, each one showing a green card representing a possible gain (40¢ or 15¢) and either one or three red cards bearing a possible loss (−10¢). As explained in the procedure section, the software implementation pseudo-randomly selected one of the two or four presented cards as the actual trial outcome. The probability of winning is defined by the proportion of green cards (always one) to red cards; and the gain or loss sizes are shown on the cards themselves. As a result, two levels arose in terms of winning probability (50% or 25%) and the other two in terms of positive reward sizes (40¢ or 15¢). Two of these categories, LOW-size-HIGH-probability of reward (LsHp) and HIGH-size-LOW-probability of reward (HsLp), have equivalent expected values, despite the different relationships between size and probability of positive rewards (see Fig. 1).

To measure the differential effect of reward size and probability, the other two categories were defined: HIGH-size-HIGH-probability of reward (HsHp) and LOW-size-LOW-probability of reward (LsLp). Each of these categories is equivalent in size or probability with one of the two previously mentioned categories (equivalences by size: Hs [HsHp and HsLp]; Ls [LsLp and LsHp]; equivalence by probability: Hp [HsHp and LsHp]; Lp [LsLp and HsLp]). Due to these equivalences, we could assess the effects of high vs. low size, by comparing the result of collapsing HsHp with HsLp with the result of collapsing LsHp with LsLp. Likewise, we were able to assess the effects of high vs. low probability by comparing the results of collapsing HsHp with LsHp with the results to collapsing HsLp with LsLp (Fig. 1 shows the relationships among the four designed game categories).

Procedure

Before the experiment, every participant was informed of its purpose: investigating brain reactions within a chance and ability game. After verbally receiving the instructions of the game, participants were offered retribution equal to the amount accumulated at the end of the game. The subjects were told that on average, participants accumulate a final profit of $18, but that this profit would depend on their decisions and their luck. The instructions given to participants was “after the presentation of a game, that is, when a screen appears with two or four cards exposing different amounts of money, you must select one of two buttons that trigger a random system and selects one of the shown cards. That card will be the outcome of that game. If a green card is chosen, you win the presented amount (40¢ or 15¢, depending on the kind of game) for your final earnings. If a red card is selected, 10¢ will be subtracted from your accumulated earnings. Each button activates a different random system, such that the result of the selected button might be different from the selection of the other. Finally, if you do not chose a button before the end of 2500 ms, you will be penalized by setting −10¢ as the trial outcome.” After 15 practice trials on the computer, participants gave their written consent for participating in the study. Importantly, since both buttons activate a random selection, actually using the same random distribution, neither is better than the other in any trial. In strict sense choices are irrelevant for the results.

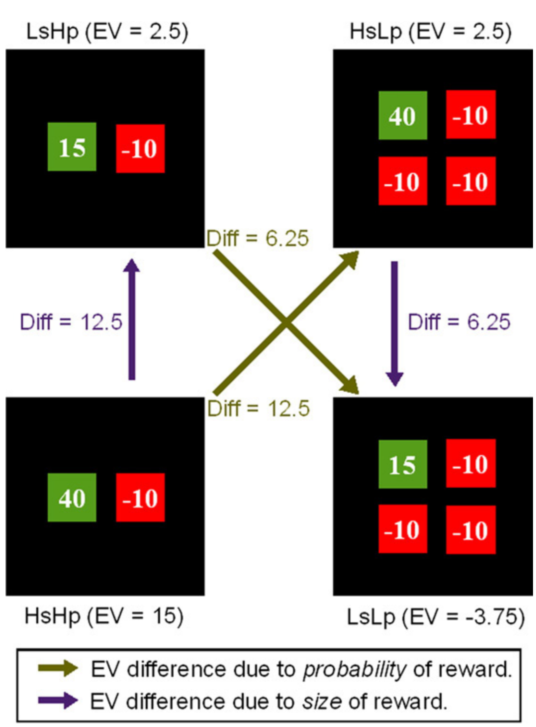

Fig. 1. Expected values associated with each category of the game and numerical relationships among them. In categories sharing equal size in potential rewards, we observed differences due to distinct probabilities of winning (1/2 or 1/4). Among the categories sharing the same probability of reward, we observe differences due to the size of the potential rewards (40¢ or 15¢).

Every trial started with the presentation of a white visual fixation cross for 1000 ms, centered on the screen with a black background. The cross was followed by the presentation of cards for one of the game categories (HsLp, HsHp, LsHp and LsLp) for a total of 2500 ms, which entailed the simultaneous screen-centered presentation of 2 or 4 boxes, a green box showing a potential win (40¢ or 15¢), the remaining one or three red boxes showing a potential loss (−10¢). Following the appearance of the cards, and before expiration of the 2500-ms time limit, participants had to decide between the two buttons. The chosen button randomly selects one of the boxes presented in the game. After a second fixation cross, the selected box was shown as the trial outcome for 600 ms. We used the onset time of this feedback for the extraction of event-related potentials. Every trial finished with a stimulus onset asynchrony (SOA) in the range of 800 ± 200 ms. Fig. 2 shows, for example, the timeline for a win trial in an HsHp and a loss trial in an LsLp game.

Since the color by itself does not produce any effect in fERN modulation (Gehring and Willoughby, 2002), we used different colors in order to facilitate the identification of positive and negative amounts. Green boxes were used for the former and red ones for the latter. Furthermore, in order to facilitate the differentiation between game conditions and outcomes, the boxes corresponding to the outcomes were presented within a yellow frame. Finally, in order to ease the differentiation between a −10¢ normal outcome and −10¢ penalty outcome, the latter was presented in an orange box.

Participants played a total of 40 blocks of 10 trials each. Every 10 blocks, participants were presented the accumulated amount of money earned up to that moment. Within each block, the four conditions were presented pseudo-randomly. According to their outcomes in the game, participants received a mean reward of $18.22 (SD = 310.2¢) corresponding to the amount accumulated through the trials.

Once the task concluded with the EEG recording, participants were asked to answer a Likert questionnaire, using a 1–5 scale to assess their frustration–satisfaction in every possible outcome at each of the four categories of the game. In this scale, 1 corresponded to the greatest dislike or frustration, and 5 to the greatest satisfaction.

In order to validate stimuli and the experimental procedure, a previous study was conducted (see Supplementary data), evidencing that: 1) participants understood both the instructions and procedures of the game; 2) the four game categories were attractive and motivating, and we could observe predictable differences given different size-probability configurations of the reward; 3) participants adequately perceived the game categories prior to choosing an answer button; and 4) participants were sufficiently implicated in the proposed game task, searching among the options aiming at maximizing their rewards. Regarding the last point, despite the actual irrelevance of choices for results, the designed paradigm generates a sense or illusion of control, making the feedback relevant for choices.

Electrophysiological recordings

Participants were individually placed in a Faraday cage. Signals were recorded online using a GES300, 129-channel system with

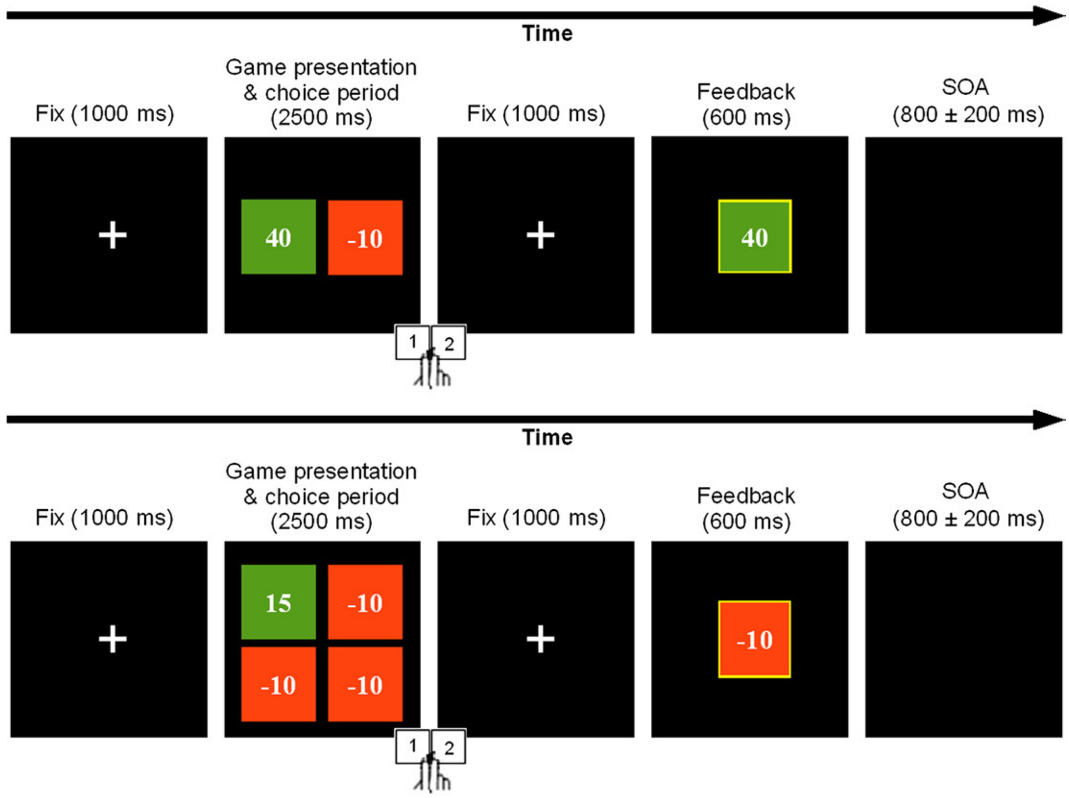

Fig. 2. Sequence of events during a win trial of an HsHp game (above) and a loss trail of an LsLp game (below). The task for participants is to decide, on the second screen, between two buttons activating the random selection of one of the boxes presented in the game. The selected box became the outcome of that particular trial.

HydroCel Sensors from Electrical Geodesic Inc. with a DC coupled Amplifier, a 24-bit A/D converter, with 200 MΩ input impedance, 0.7 µV RMS/1.4 µV pp noise, and NetStation™ software. Analog filters were set between 0.1 and 100 Hz (−12 dB/octave roll-off). A digital band pass filter between 0.5 and 30 Hz was later applied off-line to remove unwanted frequency components. Signals were sampled at 500 Hz. The reference was set by default to vertex but was then re-referenced off-line to average reference. Two bipolar derivations were designed to monitor vertical and horizontal ocular movements (EOG). A bipolar horizontal EOG was recorded from the epicanthus of each eye, and a bipolar vertical EOG was recorded from supra- and infraorbital positions of the left eye.

Feedback-locked epochs were selected from the continuous data, beginning 200 ms prior to feedback onset. All epochs with eye movement contamination were removed from further analysis, using an automatic (Gratton et al., 1983) method for removing eye-blink artifacts and visual procedures. Artifact-free segments were averaged separately to obtain the ERPs for each of the 18 participants in each of the eight experimental conditions (HsLpwin, HsLploss, LsLpwin, LsLploss, HsHpwin, HsHploss, LsHpwin and LsHploss). Then ERP waveforms were averaged for each experimental condition. The EEGLAB Matlab toolbox (Delorme and Makeig, 2004) and the T-BESP software (http://www.neuro.udp.cl/software) were used for EEG off-line processing and analysis.

Data analysis

Behavioral measures

Reaction times were calculated for each subject based on the reaction times obtained from the responses to each of the four game categories. A repeated measures ANOVA with probability (High vs. Low) and size (High vs. Low) of the reward were considered. Results of the Likert questionnaire, answered after the EEG recordings, were analyzed using the same 2×2 model. After that, a 2×2×2 design was considered, adding valence (Win vs. Loss) as a third factor. Finally, the participant's tendency to persevere (stay) vs. change their button choice (leave) after winning or losing in every category was measured. A four-way ANOVA was then performed, considering probability, size, valence and choice behavior (leave vs. stay).

To determine the statistical significance of the effects ($p = 0.05$), the averages and contrasts were calculated using the Tukey's post-hoc test.

ERPs

After a valence and electrode position analysis (see Supplementary data), two main fERN-associated sites with larger amplitudes and loss-minus-win differences were evaluated to represent and analyze the ERP components in a manner that was consistent with previous reports (Fz and FCz: electrodes E11 from the front midline site and electrode E6 at the center–frontal position; Holroyd et al., 2003; Miltner et al., 1997; Yeung and Sanfey, 2004). For the sake of the statistical analysis of each component, the average was chosen from the 180–230 ms time frame for P200, from 240–310 ms for fERN and 365–440 ms for the Pe-like wave.

After an average data remotion of 6% due to artifact, 56 trails on average per subject were used for the HsHpwin waveform, 55 for HsHploss, 57 for LsHpwin, 55 for LsHploss, 20 for LsLpwin, 56 for LsLploss, 19 for HsLpwin and 55 for HsLploss. Recognizing a potential limitation of our study due to an effect of the different frequency of categories, we performed an additional analysis (see Supplementary data). This analysis suggested that frequency does not add useful information when probability has been considered, but probability does add useful information, even when frequency has been considered. However, future research is needed to obtain an empirical answer to this concern.

For each component, a repeated measures ANOVA with probability (High vs. Low) and size (High vs. Low) of the reward were considered. A 2×2×2 design was then considered: probability (High vs. Low), size (High vs. Low) and valence (Win vs. Loss). Analysis of the difference waveforms was utilized when necessary. The results were corrected using Greenhouse–Geisser and Bonferroni's methods to adjust the unvaried output of the repeated measures ANOVA for violations of the compound symmetry assumption. Tukey's HSD method was used in the calculation of post-hoc contrasts.

Results

Behavioral results: gambling task

Reaction times (RTs)

By collapsing the conditions according to their probability distributions and the size of the offered rewards, it was possible to assess the effect of the mentioned variables over the RTs. A two-way repeated measures ANOVA on feedback probability (Hp vs. Lp) and size (Hs vs. Ls) revealed a main effect of probability $F(1, 21) = 21.079$, $p < 0.001$. Low reward probability categories (Lp) were associated with significantly longer RTs ($M = 612.93$ ms, $SD = 45.60$) than categories with high reward probability [Hp: ($M = 581.45$ ms, $SD = 44.75$)]. Size was not associated with significant differences, $F(1, 21) = 0.43$, $p = 0.51$, and no interaction between the two factors was found.

Choice behavior

Following each trial, subjects had two alternatives: stay (to choose the same button as in the last trial), or leave (to try the alternative button). Consistent with the reinforcement learning theory of ERN, it has been observed that participants tend to change their behavior after losing and to repeat it after winning (Gehring and Willoughby, 2002; Hewig et al., 2007). We calculated each subject's tendency to stay vs. leave after a win or a loss trial as a proportion of stay and leave choices with respect to all the win and loss trials they play.

A four-way repeated measures ANOVA on feedback probability (Hp vs. Lp), size (Hs vs. Ls), valence (Win vs. Loss) and choice behavior (leave vs. stay) revealed an interaction effect between the four factors, $F(1, 21) = 4.97$, $p < 0.05$, and between valence and choice, $F(1, 21) = 11.80$, $p < .005$. In our sample, 57.8% of loss trials and 48% of win trials were followed by trying the alternative button (leave) ($SD = 2.51\%$), whereas they left after 48.5% of win trials ($SD = 3.4$ %). A Tukey's HSD post-hoc test ($Ms = 648.13$, $df = 21$) only found differences between stay ($M = 42.22\%$, $SD = 2.51\%$) and leave ($M = 57.78\%$, $SD = 2.51\%$) after the loss condition ($p < 0.005$).

The results suggest what is referred to as a loss avoidance tendency, namely the tendency to use the feedback more to avoid repeating losses rather than repeating wins. To explore this issue, we performed a two-way repeated measures ANOVA on feedback probability (Hp vs. Lp) and size (Hs vs. Ls). The inputs for that analysis were the differences between the proportion of loss feedback-associated leave choices and win feedback-associated stay choices observed in each participant (loss and leave minus win and stay). Results showed that the difference was bigger in Hp ($M = 9.55$, $SD = 2.91$) than in Lp ($M = 2.92$, $SD = 5.68$), $F(1, 21) = 8.2726$, $p < 0.001$, with no differences between Hs ($M = 6.24$, $SD = 5.53$) and Ls ($M = 6.23$, $SD = 5.25$), $F(1, 21) = 0.00007$, $p = 0.99$. No interaction between probability and size was found.

The difference between the efficacy of loss feedbacks promoting leave decisions and win feedbacks promoting stay decisions was maximal on Hp categories (see Discussion).

The analysis of choice behavior led us to conclude the existence of a loss avoidance tendency related to the use of feedback that was 1) not influenced by the size of the rewards at stake, 2) was maximized after Hp categories, and 3) minimized after Lp categories.

Behavioral results: questionnaire (off-line task)

A three-way repeated measures ANOVA on feedback probability (Hp vs. Lp) size (Hs vs. Ls) and valence (Win vs. Loss), showed that outcome valence was associated with significant differences in satisfaction reports, $F(1, 21) = 405.11$, $p < 0.001$, with a larger reported satisfaction for the win conditions [Win ($M = 4.54$, $SD = 0.06$); Loss ($M = 1.86$, $SD = 0.09$)]. The only significant effect was found in the interaction between valence and size, $F(1, 21) = 29.938$, $p < 0.001$. A Tukey's HSD post-hoc ($Ms = 0.35$, $df = 21$) test showed differences between all combinations of valence × size, where the bigger the size of the possible reward, the bigger the satisfaction upon winning and the smaller the satisfaction when losing [Hswin ($M = 4.77$, $SD = 0.06$); Lswin ($M = 4.32$, $SD = 0.08$); Lsloss ($M = 2.09$, $SD = 0.12$); Hsloss ($M = 1.64$, $SD = 0.11$)]. For all post-hoc contrasts, $p < 0.001$, with the exception of Hswin > Lswin ($p < 0.05$).

Event related potentials

P200

Given that the visual differences between the waveforms of wins and losses are observed earlier than in the fERN time window (see Fig. 3), and, given that this component has been associated with salience and attention capture modulation (Kenemans et al., 1993; Potts et al., 1996, 2006; Potts, 2004), we decided to include statistical analysis of an early window (P200).

A two-way repeated measures ANOVA on the feedback probability (Hp, Lp) and size (Hs, Ls), showed that the Hp category ($M = 5.72$ µV, $SD = 0.70$) was associated with a greater P200 amplitude than the Lp ($M = 4.59$ µV, $SD = 0.84$), $F(1, 17) = 8.73$, $p < 0.01$. A similar relationship was true for Hs categories ($M = 5.45$ µV, $SD = 0.82$), which were greater than Ls ($M = 4.86$ µV, $SD = 0.67$), $F(1, 17) = 9.55$, $p < 0.01$ (see Fig. 4). No interaction between probability and size was found. Then the valence factor was included in a probability (2) × size (2) × valence (2) ANOVA design. In addition to the above reported results of probability and size effects, a strong valence effect was found ($F(1, 17) = 43.69$, $p < 0.001$). Win conditions (6.24 µV, $SD = 0.80$) seem to elicit more positive P200 compared to loss conditions (4.05 µV, $SD = 0.63$). No interactions between any of the three factors were found. Given the possible superposition of P200 with respect to the fERN amplitude, a peak to peak analysis for those components was performed (P200 to fERN, see Supplementary data). Results from the analysis suggest the presence of an early modulation by valence and by probability × valence interaction. The overall results suggest an early discrimination of probability, size and valence, without any interaction between those factors. Valence factor was the strongest effect which affects the P200 amplitude.

fERN

By collapsing the conditions according to their probability distributions and the size of the offered rewards, it was possible to assess the effect of mentioned variables over the fERN amplitude (see Fig. 4). A two-way repeated measures ANOVA on feedback probability (Hp, Lp) and size (Hs, Ls), revealed a significant effect of probability (Lp [$M = 2.98$ µV, $SD = 0.43$] > Hp [$M = 3.86$ µV, $SD = 0.52$]), $F(1, 17) = 12.03$, $p < 0.005$, and size (Ls [$M = 2.99$ µV, $SD = 0.37$] > Hs [$M = 3.85$ µV, $SD = 0.40$]), $F(1, 17) = 26.33$, $p < 0.001$. This shows that the fERN amplitude distinguishes the high and low reward probability categories, as well as size of offered rewards, in a manner that is independent from the valence of the result. The interaction between size and probability showed a tendency towards significance, $F(1, 17) = 4.00$, $p = 0.061$.

In order to assess the valence effects, a probability (2) × size (2) × valence (2) ANOVA design was introduced. In addition to the already reported effects of probability and size, a valence effect was found ($F(1, 17) = 79.75$, $p < 0.001$); win categories (5.52 µV, $SD = 0.44$) elicit a less negative fERN compared to loss categories (1.31 µV, $SD = 0.48$). The interaction between probability, size and valence yield significant differences too ($F(1, 17) = 4.86$, $p = 0.04$). A Tukey HSD post-hoc test ($Ms = 2.02$, $df = 17$) performed over this last interaction showed that HsHpwin generates the greatest positivity ($M = 7.08$ µV, $SD = 0.53$), and,

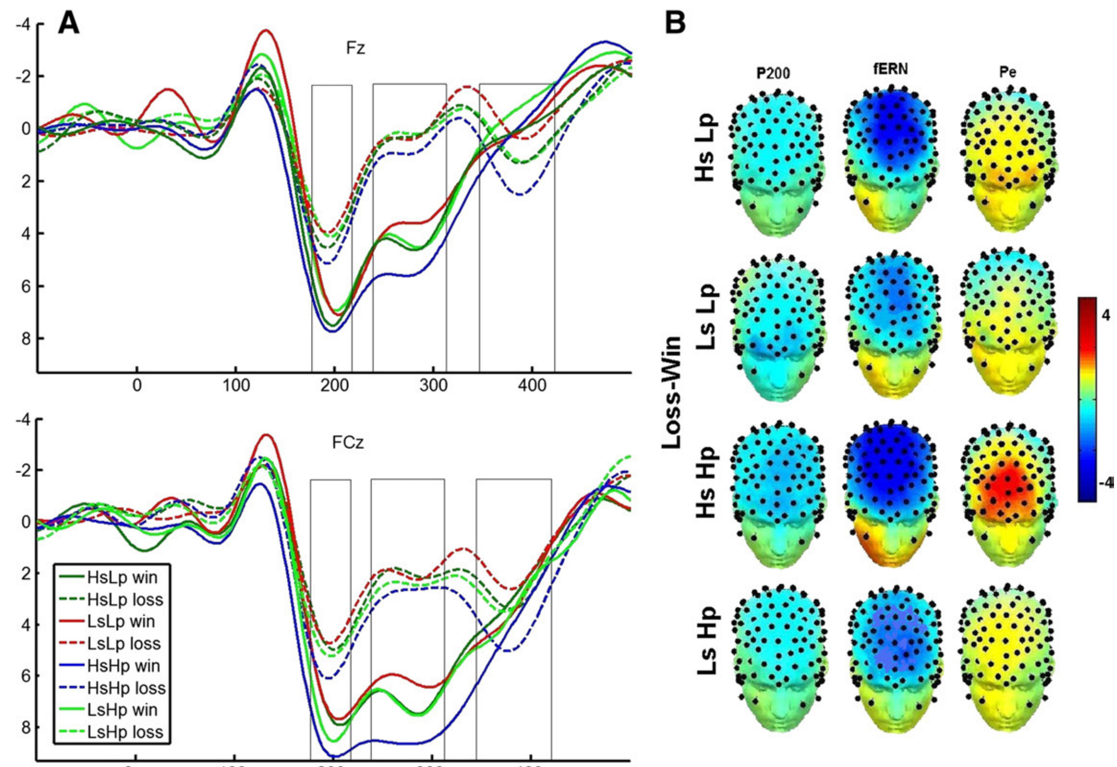

Fig. 3. Overall effects. (A) ERPs from Fz and FCz showing the P200, fERN and Pe-like effects. Boxes within the ERP figures are indicative of the time windows for P200, fERN and Pe-like. (B) Voltage map of loss-minus-win subtractions. Rows present the four categories (LsHp, HsHp, LsLp and HsLp) and columns the temporal windows for P200, fERN and Pe-like.

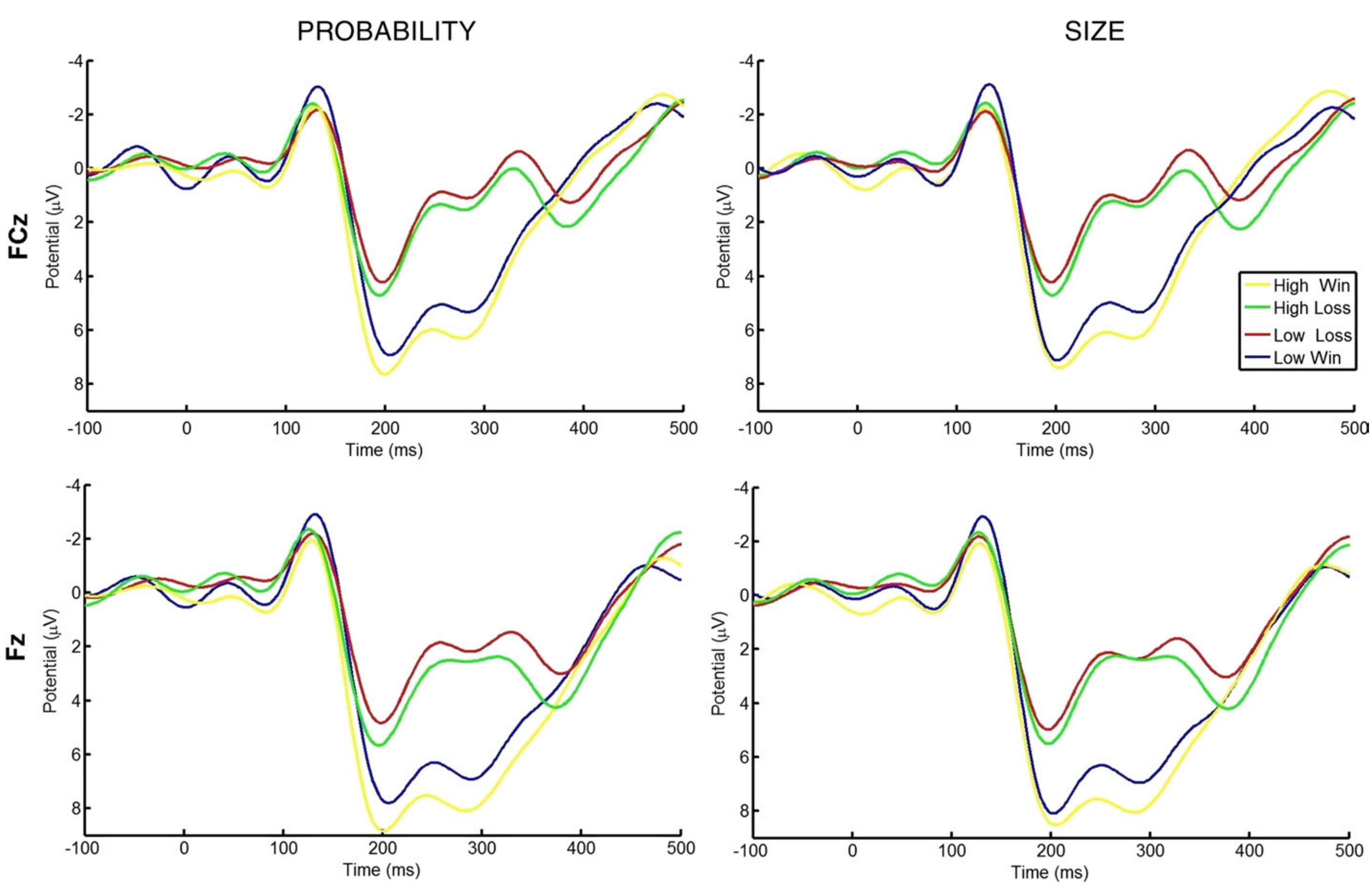

Fig. 4. Probability, size and valence effects. (1) Left: ERPs from Fz and FCz showing the P200, fERN and Pe-like effects elicited by probability (high vs. low) and valence (Win vs. Loss). (2) Right: ERPs from Fz and FCz showing the P200, fERN and Pe-like effects elicited by size (high vs. low) and valence (Win vs. Loss).

it was significantly different from HsLpwin ($M=5.37\ \mu V$, $SD=0.49$, $p<0.05$), from LsHpwin ($M=5.42\ \mu V$, $SD=0.63$ $p<0.05$) and LsLpwin ($M=4.23\ \mu V$, $SD=0.64$ $p<0.001$). This last category (LsLpwin) was significantly less positive with respect to the rest of the win conditions ($p=0.01$ for all comparisons). Interestingly, the two categories bearing equal expected values, namely HsLp and LsHp, did not yield fERN amplitude differences between them when associated with win feedback, $p=0.99$. No differences appeared between the loss conditions.

These results suggest that, in our experiment, only feedback-associated ERPs discriminated according to the probability and size of the reward independent of the valence. Moreover, we could observe that the bigger the expected value, the greater the positivity (smaller the negativity) only in the win feedback-associated fERN. When participants lose, these effects are not found.

Error positivity (Pe-like). A third peak was visually observed around the 300–400 ms time window, especially in the loss conditions (see Fig. 3). Given its scalp distribution, along with reaching its maximum in the case of the most salient loss (HsHploss), this component appears to be Pe-like, as it is modulated like the Pe and P300 (Boksem et al., 2008; Endrass et al., 2007; Nieuwenhuis et al., 2001; O'Connell et al., 2007; Shalgi et al., 2009) with a different scalp position associated with the response-locked ERN.

By collapsing the conditions according their probability distributions and the size of the offered rewards, it was possible to assess the effect of these variables over the Pe amplitude. A two-way repeated measures ANOVA on probability (Hp, Lp) and size of rewards (Hs, Ls) revealed a significant effect of probability, $F(1, 17)=8.24$, $p<0.05$, and size, $F(1, 17)=8.76$, $p<0.01$. Interactions between size and probability, $F(1, 17)=10.00$, $p<0.01$, resulted in a significant difference. Post hoc comparison over this interaction (HSD test, $MS=0.45$, $df=17$) showed differences between the most salient category HsHp ($M=2.82\ \mu V$, $SD=0.69$) when compared to LsLp ($M=1.06\ \mu V$, $SD=0.73$; $p<0.001$), HsLp ($M=1.56\ \mu V$, $SD=0.71$; $p<0.001$), and LsHp ($M=1.32\ \mu V$, $SD=0.85$; $p<0.001$).

In order to assess the valence effects over the Pe-like component, a probability $(2)\times$size $(2)\times$valence (2) ANOVA design was introduced. In addition to the above 2×2 design effects reported, valence effect was not significant ($F(1, 17)=2.48$, $p=0.13$). Nevertheless, interactions between valence and size, $F(1, 17)=8.83$, $p<0.005$, and between valence and probability, $F(1, 17)=7.28$, $p<0.05$, resulted in a significant difference. A Tukey HSD test ($Ms=2.92$, $df=17$) for the interaction between valence and size showed that Hsloss ($M=2.86\ \mu V$, $SD=0.69$) was associated with a greater positivity than Lsloss ($M=1.25\ \mu V$, $SD=0.70$; $p<0.005$), Hswin ($M=1.29\ \mu V$, $SD=0.91$; $p<0.005$) and Lswin ($M=1.37\ \mu V$, $SD=0.87$, $p<0.01$). These results suggest that losing in the context of bigger potential earnings generates greater Pe-like amplitude than winning, regardless of the size of potential earnings, and losing in the context of smaller potential earnings. Results also suggest greater amplitude of the Pe-like for losing compared with winning, regardless of the reward size. As for an interaction between valence and probability a Tukey HSD test ($Ms=2.36$, $df=17$) showed Hploss ($M=2.90\ \mu V$, $SD=0.66$) was associated with greater amplitudes than Lploss ($M=1.21\ \mu V$, $SD=0.80$), $p<0.005$, Hpwin ($M=1.48\ \mu V$, $SD=0.78$), $p<0.01$, and Lpwin ($M=1.18\ \mu V$, $SD=0.88$), $p<0.005$. This analysis suggests that losing, in the context of a high probability of winning, generates larger Pe amplitudes than in the context of a low probability; that remains true when compared to winning in both levels of probability (see Fig. 4). Analysis performed with difference waveforms yielded similar results (see Supplementary data).

Discussion

Fig. 5 outlines the main behavioral results, both in terms of online measures (choice behavior and reaction times) and the off-line task (satisfaction questionnaire). As expected, (1) win feedback generates greater satisfaction reports than loss feedback; (2) winning highly rewarded games (40¢ or "Hs") generates greater satisfaction reports than wins in the lower rewarded ones (15¢ or "Ls"); and (3) losing games with the greatest offered rewards generates smaller satisfaction reports. Probability did not show statistically significant effects, such that the levels of satisfaction seem to depend on the size and valence of outcomes. Reaction times and choice behaviors were affected by probability. Reaction times are significantly greater for Lp categories. Regarding choice behaviors, loss feedback are followed by a tendency not to repeat the button choice. The difference between the efficacy of loss feedbacks promoting leave decisions, and win feedbacks promoting stay decisions, was maximal on Hp categories.

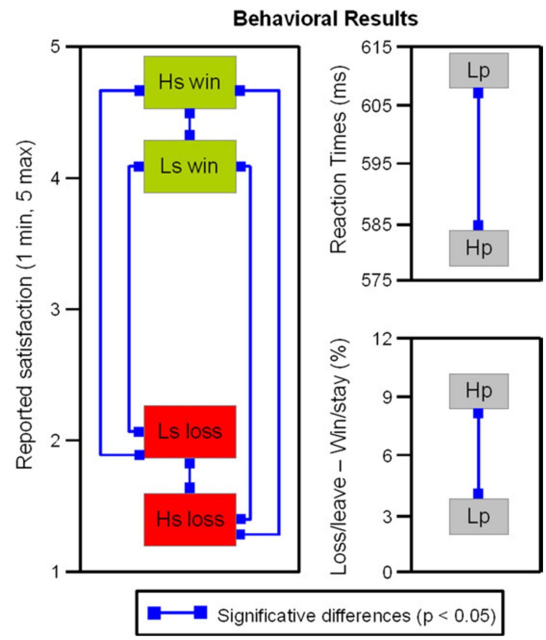

Fig. 5. Main behavioral results. Satisfaction reports are affected by the interaction between the size of the rewards at stake and the outcome valence (Win vs. Loss). Reaction times and loss avoidance tendency (loss and leave minus win and stay) seem to be affected by the probability to win on each game category.

Within the ERP results, a first finding is a frontal–central P200. Even though this deflection could be assumed to be the beginning of fERN (Holroyd et al., 2008; Nieuwenhuis et al., 2004b; Yeung, and Sanfey, 2004), we analyzed it as a distinct phenomenon given the fact that it was associated with different effects from those typically observed in the fERN. In our study, the P200 showed that it was modulated by each trial outcome, in terms of win and loss. Also, P200 was differentially modulated by a high probability and high size of the offered rewards (see Fig. 6).

The modulation of the observed P200 could suggest an early effect of the salience of stimuli, in the sense that a greater amount of attention was given to the win feedback, and to feedbacks following high probability or high size of the offered rewards. In fact, the P200 has been reported to be consistently associated with greater arousal levels (Carretié et al., 2001; Schutter et al., 2004) and attention capturing by target stimuli (Potts et al., 1996, 2006; Potts, 2004), supporting the idea of modulation by attention facilitation. This P200 has also been referred to as frontal selection positivity (FSP) (Kenemans et al., 1993) because of the function to which it associates. The lack of interactions between valence and probabilities, or between valence and sizes of reward, suggests that in the stage of P200 processing these factors are not yet integrated. P200 would be accounting for an early attention modulation, rather than an early feedback evaluation regarding game conditions.

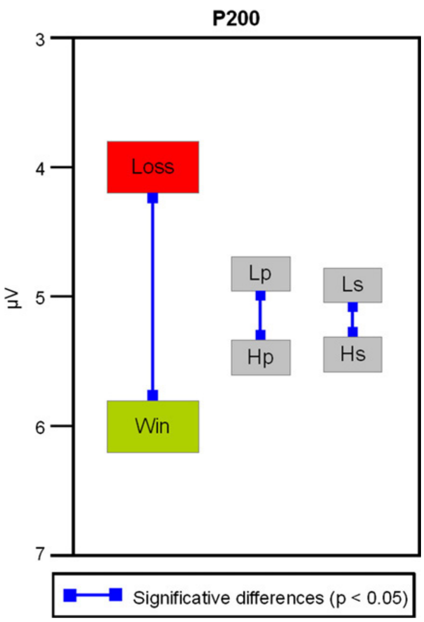

Fig. 6. Main results in the 180–230 ms time window (P200). The win feedbacks are associated with greater positivities than those presented in loss feedback. Independently of its valence, feedback following the Hp and Hs categories, are associated with greater positivities than those following categories Lp and Ls.

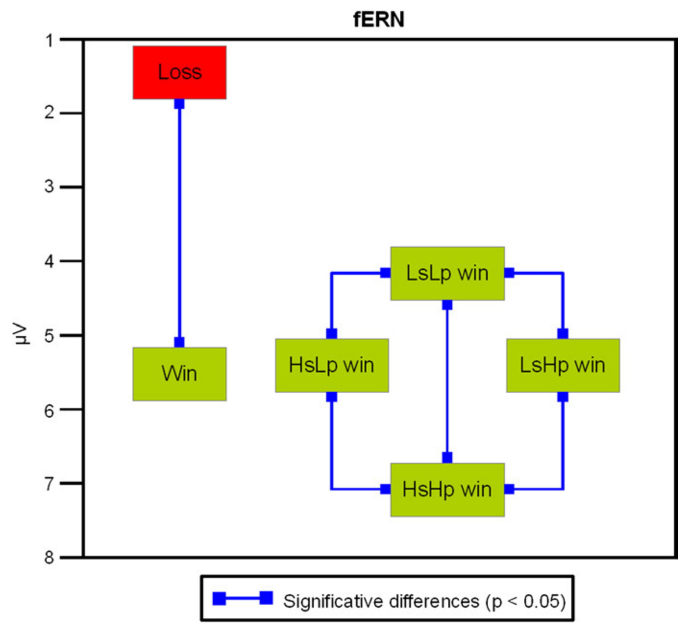

Fig. 7. Main results in the 240–310 ms time window (fERN). Win feedback were associated with greater positivities than loss feedback. Differences were not observed within the loss conditions. Within win conditions, winning in the category holding the highest expected value (HsHp) is associated with the greatest positivities, while winning in the category holding the smallest expected value (LsLp) is associated with the smallest positivities. Meanwhile, winning in categories with equivalent expected values (HsLp and LsHp) does not generate differences in the fERN amplitude.

Results show a clear difference between wins and losses in fERN temporal window, with a less positive fERN associated with loss feedback. However, changes in size and probability impacted the fERN amplitude only when it was associated with win feedback. The greater the size and probability of earned rewards, the greater the positive waveform amplitude (see Fig. 7).

Our results contribute to a growing body of empirical evidence showing a greater modulation of the fERN for win feedback in comparison to loss feedback (Cohen et al., 2007; Eppinger et al., 2008; Hajcak et al., 2005; Hewig et al., 2008; Holroyd et al., 2008; Potts et al., 2006).

The existence of fERN modulation in wins but not in the loss trials is a recent finding (Cohen et al., 2007; Holroyd et al., 2008), and distinctive patterns have not been observed in experimental designs helping to explain these outcomes. Recent studies propose that the neural mechanisms of feedback processing may differ between wins and losses (Cohen et al., 2007), resulting in the notion of feedback correct-related positivity (fCRP), which argues that the difference between wins and losses could be better explained by a positivity associated with better than expected outcomes, rather than negativity associated with worse than expected scenarios (Holroyd et al., 2008).

The reinforcement learning theory of the error-related negativity (Holroyd and Coles, 2002), applied to correct trials (Holroyd, 2004), states that positive dopamine reward prediction error signals, indicating that events are better than expected, reduce the amplitude of the fERN (or amplify the amplitude of fCRP) by indirectly inhibiting the apical dendrites of motor neurons in the ACC. This hypothesis could help to enlighten our understanding regarding the existence of modulation associated with wins, rather than losses. Accordingly, rather than evoking an ERP component specific for error trials, loss feedback simply elicits a more common phenomenon, namely the N200, which is elicited by task-relevant events in general (Towey et al., 1980). The positivity associated with win trials reflects either the inhibition of the process producing the N200 or the superposition of a frontal–central, positive-going deflection (Holroyd et al., 2008). To the best of our knowledge, there have been no previously reported studies regarding which of these possibilities is the most plausible one.

Now, the fCRP hypothesis does not seem sufficient for explaining the observed direction of ERP modulation in our study. We should observe greater positivity associated with a higher reward (Hs), and we should observe greater positivity associated with less probable rewards (Lp). The latter not only does not occur, the opposite occurs (see Fig. 7).

We consider the behavioral patterns in choice behavior as closely related to our fERN results. As we report, loss feedbacks are followed by a tendency not to repeat the choice of button. This finding suggests, despite the fact that it was impossible for subjects to learn an optimal behavior for our gambling task, that subjects do consider the loss feedback for the sake of avoiding new losses. We have called this a loss avoidance tendency, meaning a tendency to consider more loss feedback for avoiding losses, than win feedback for repeating wins. In this regard, subjects show themselves as negative learners (Frank et al., 2005, 2007), learning more from the negative than from the positive outcomes of their decisions. This loss avoidance tendency, in accordance with behavioral results from Hewing et al. (2007), seems to be larger in Hp categories than in Lp ones (see Fig. 5). The same loss is more aversive in categories where winning seems to be more likely, with a greater frequency of behavioral change.

The behavioral results of this study can be interpreted according to the distinction between utilitarian and performance information allegedly embedded in feedback (Li et al., 2009; Nieuwenhuis et al., 2004b). The utilitarian information refers to the profit earned from each trial, whereas the performance information refers to the extent to which the choice, producing the present outcome, was correct or incorrect. For instance, a feedback indicating a gain of 5¢ would have a positive utilitarian value (winning 5¢) (Gehring and Willoughby, 2002), but a negative utilitarian value if it is revealed that an alternative decision could have yielded 25¢ (Nieuwenhuis et al., 2004b).

In our study, according to satisfaction reports, it appears that the size of the offered rewards defines the utilitarian information conveyed by feedback. On the other hand, reward probabilities appear to define the performance information of feedback. The RTs suggest that subjects do recognize the fact that gaining a reward in the Hp trials is more probable than winning in the Lp trials (see Fig. 5). As expected, a decision resulting in a loss in the easiest categories (Hp) would be assessed as worse than a decision yielding the same result in the hardest categories

(Lp), with a larger tendency not to repeat choices that lead to losses in Hp. When valence is added to the feedback, the distribution of probabilities among the possible outcomes appears to be the evaluation parameter for the subjects when it comes to assessing how correct/incorrect their choices were.

From the perspective of utilitarian information, it would be most important to win in the Hs categories, but from the perspective of performance information, the most important action would be to avoid losing in the Hp categories. Then, the win feedback comporting the more positive motivational value, as suggested by the fERN results, would be signaling a win after the HsHp category. Win feedback after HsLp and LsHp, which are categories with equivalent expected values, would have indistinguishable motivation values, and would be followed by indistinguishable positive waveform amplitudes. Finally, within the win games, winning in the LsLp condition would have a smaller motivational value given a smaller positivity in the fERN time window.

According to our study, we suggest that both the size and probability of offered rewards modulate the motivational value of win feedback, with the former regulating the utilitarian value of earned rewards and the latter defining the performance value of received feedback. Expected value, which is a function of the size and probabilities of the possible outcomes, appears as a good candidate for accounting the interaction between utilitarian and performance information.

The amplitude of positivity following win feedback accounts for its motivational value, but not regardless of the motivational value of losing. The goodness of winning has to do with the badness of avoided loses, and the badness of avoided loses has to do with the expected value for the situation. This interpretation cannot be fully substantiated without further ERP studies dealing specifically with the loss avoidance value of the win feedback. Studies have investigated the functional role of the ACC in avoidance learning (Botvinick, 2007; Magno et al., 2006), suggesting that this structure is linked to the medial orbitofrontal cortex in regulating avoidance learning in humans (Coricelli et al., 2005; Kim et al., 2006). These studies clearly illustrate that avoidance learning is an important and interesting issue for further broadening fERN/fCRP research.

It may seem that in our study modulation in wins but not in losses could be explained by the existence of two degrees of win feedback and only one for loss feedback. Nonetheless, this interpretation goes against the evidence that fERN is modulated by feedback value in the context of other possible results, and not for its absolute value (Holroyd et al., 2004a). Furthermore, this interpretation does not explain why probability only modulates the win fERN, given that reward probabilities affect the occurrences of both losses and gains. In any case, future studies could explore the plausibility of this interpretation, for instance by inverting the paradigm and keeping the amount of gains constant while showing two possible amounts for losses.

The ERP results showed a late positivity that distinguishes losing in the most salient categories, Hs and Hp (see Fig. 8). The observed positivity presents a frontal–central scalp distribution and is distinguished according to the valence. This clearly differentiates it from the P300 that is normally associated with the fERN, which is rather posterior (Donchin and Coles, 1988; Holroyd, 2004; Yeung and Sanfey, 2004) and is modulated by the feedback magnitude rather than the valence (Hajcak et al., 2005; Nieuwenhuis et al., 2004a; Yeung and Sanfey, 2004). Its modulation and scalp distribution is coherent with fMRI evidence that refers to the role of the rostral ACC in loss-related responses to errors (Taylor et al., 2006).

Since late positivities, such as P300, LPC or LPP, showed different scalp positions independent of the task, instruction and stimuli (i.e., Cornejo et al., 2009; Hurtado et al., 2009; Ibáñez et al., 2009, 2010; Olofsson et al., 2008; Polich, 2007), this component appears to be Pe-like, as it is modulated like the Pe and P300 but has a different scalp position. In reaction time paradigms, the Pe is shown as an index of error awareness (Nieuwenhuis et al., 2001; Endrass et al., 2007; O'Connell et al., 2007). Our results show that within the fERN time window, only broad discrimination of losses exists (see below), so this Pe-like wave could be acting as an index of a late evaluation process regarding the motivational significance of losses, a process in which Hsloss and Hploss would stand out as the worst class of losses. However, future studies are needed to assess the neural generators of this Pe-like wave as well as the functional properties of this component and its similarities or discrepancies with Pe and P300.

To our knowledge, this is the first report concerning expected value effects on fERN, not only—or separately—regarding the size or probability of reward effects. In summary, our results led us to conclude that win feedback and feedback following game conditions with the greatest reward sizes and probabilities are differentially captured by attention at a pre-fERN stage (P200). In a post-fERN stage (Pe-like) a

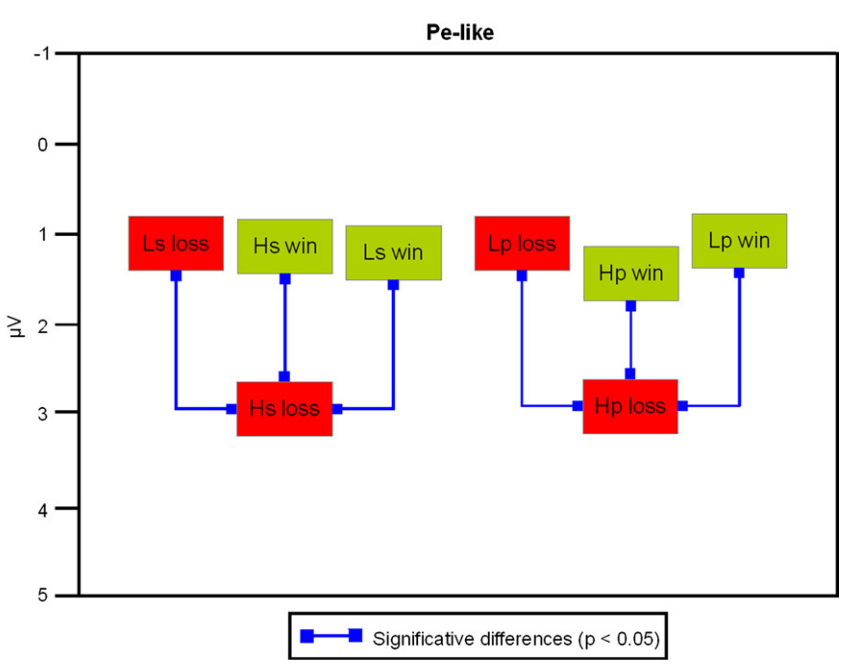

Fig. 8. Main results in the 365–440 ms time window (Pe-like). The observed waveform distinguishes losing in the most salient categories (Hs and Hp).

later frontal positivity appears, distinguishing the worst losses, while in the fERN temporal window there is only a broad discrimination of losses. According to the fERN results, as an interaction of size and probability of reward, the expected value modulates the motivational value of the win feedback. This result is closely related to the distinction between performance and utilitarian information. In our study, probability appears to be a predictor to discriminate the performance value of the feedback, and size appears to be a predictor to discriminate its utilitarian value. The observed direction of the modulation of fERN is consistent with a behavioral loss avoidance tendency, which appears to assign a greater performance value to avoid losses under conditions that are more likely to be rewarded. The bigger the expected value, therefore, the more rewarded the loss avoidance is, and the fERN is less negative following the win feedback.

Our results suggest that fERN could be an index of the neurocognitive processing of performance and utilitarian information, which can be studied by manipulating the expected value of gambling. These results also suggest that the relationship between fERN/fCRP and avoidance learning is an interesting issue for further research, especially to understand the modulation of fERN associated with wins but not losses in gambling tasks.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2010.03.031.

References

Boksem, M., Tops, M., Kostermans, E., De Cremer, D., 2008. Sensitivity to punishment and reward omission: evidence from error-related ERP components. Biol. Psychol. 79, 185–192.
Botvinick, M.M., 2007. Conflict monitoring and decision making: reconciling two perspectives on anterior cingulate function. Cogn. Affect. Behav. Neurosci. 7, 356–366.
Carretié, L., Mercado, F., Tapia, M., Hinojosa, J., 2001. Emotion, attention, and the 'negativity bias', studied through event-related potentials. Int. J. Psychophysiol. 41, 75–85.
Clithero, J.A., Tankersley, D., Huettel, S.A., 2008. Foundations of neuroeconomics: from philosophy to practice. PLoS Biol. 6, e298 (Electronic publication).
Cohen, M., Elger, C., Ranganath, C., 2007. Reward expectation modulates feedback—related negativity and EEG spectra. NeuroImage 35, 968–997.
Coricelli, G., Critchley, H.D., Joffily, M., O'Doherty, J.P., Sirigu, A., Dolan, R.J., 2005. Regret and its avoidance: a neuroimaging study of choice behavior. Nat. Neurosci. 8, 1255–1262.
Cornejo, C., Simonetti, F., Ibañez, A., Aldunate, N., Lopez, V., Ceric, F., Nuñez, R., 2009. Gesture and metaphor comprehension: electrophysiological evidence of cross-modal coordination by audiovisual stimulation. Brain Cogn. 70.
Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134, 9–21.
Donchin, E., Coles, M.G.H., 1988. Is the P300 component a manifestation of context updating? Behav. Brain Sci. 11, 355–372.
Endrass, T., Reuter, B., Kathmann, N., 2007. ERP correlates of conscious error recognition: aware and unaware errors in an antisaccade task. Eur. J. Neurosci. 26, 1714–1720.
Eppinger, B., Kray, J., Mock, B., Mecklinger, A., 2008. Better or worse than expected? Aging, learning and the ERN. Neuropsychologia 46, 521–539.
Falkenstein, M., Hohnsbein, J., Hoormann, J., Blanke, L., 1990. Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In: Brunia, C., Gaillard, A., Kok, A. (Eds.), Psychophysiological Brain Research. Tilburg University Press, Tilburg, The Netherlands, pp. 192–195.
Frank, M., Woroch, B., Curran, T., 2005. Error-related negativity predicts reinforcement learning and conflict biases. Neuron 47, 495–501.
Frank, M., D'Lauro, C., Curran, T., 2007. Cross-task individual differences in error processing: Neural, electrophysiological and genetic components. Cogn. Affect. Behav. Neurosci. 7, 297–308.
Gehring, W., Willoughby, A., 2002. The medial frontal cortex and the rapid processing of monetary gains and losses. Science 295, 2279–2282.
Gehring, W., Goss, B., Coles, M., Meyer, D., Donchin, E., 1993. A neural system for error detection and compensation. Psychol. Sci. 4, 385–389.
Gentsch, A., Ullsperger, P., Ullsperger, M., 2009. Dissociable medial frontal negativities from a common monitoring system for self-and externally caused failure of goal achievement. NeuroImage 47, 2023–2030.
Gratton, G., Coles, M.G.H., Donchin, E., 1983. A new method for off-line removal of ocular artifact. Electroencephalogr. Clin. Neurophysiol. 55, 468–484.
Hajcak, G., Holroyd, C.B., Moser, J., Simons, R., 2005. Brain potentials associated with expected and unexpected good and bad outcomes. Psychophysiology 42, 161–170.
Hewig, J., Trippe, R., Hecht, H., Coles, M.G.H., Holroyd, C.B., Miltner, W.H.R., 2007. Decision-making in blackjack: an electrophysiological analysis. Cereb. Cortex 17, 865–877.
Hewig, J., Trippe, R.H., Hecht, H., Coles, M.G.H., Holroyd, C.B., Miltner, W.H.R., 2008. An electrophysiological analysis of coaching in blackjack. Cortex 44, 1197–1205.
Holroyd, C.B., 2004. A note on the Oddball N200 and the feedback ERN. In: Ullsperger, M., Falkenstein, M. (Eds.), Errors, Conflicts, and the Brain. Current Opinions on Performance Monitoring. MPI of Cognitive Neuroscience, Leipzig, pp. 211–218.
Holroyd, C.B., Coles, M.G.H., 2002. The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. Psychol. Rev. 109, 679–709.
Holroyd, C.B., Coles, M.G.H., Nieuwenhuis, S., 2002. Medial prefrontal cortex and error potentials. Science 296, 1610–1611.
Holroyd, C.B., Nieuwenhuis, S., Yeung, N., Cohen, J.D., 2003. Errors in reward prediction are reflected in the event-related brain potential. Neuroreport 14, 2481–2484.
Holroyd, C.B., Larsen, J., Cohen, J.D., 2004a. Context dependence of the event-related brain potential associated with reward and punishment. Psychophysiology 41, 245–253.
Holroyd, C.B., Nieuwenhuis, S., Mars, R., Coles, M.G.H., 2004b. Anterior cingulate cortex, selection for action, and error processing. In: Posner, M. (Ed.), Cognitive Neuroscience of Attention. Guilford Publishing, Inc., New York, pp. 219–231.
Holroyd, C.B., Yeung, N., Coles, M.G.H., Cohen, J.D., 2005. A mechanism for error detection in speeded response time tasks. J. Exper. Psychol. 134, 163–191.
Holroyd, C.B., Hajcak, G., Larsen, J., 2006. The good, the bad and the neutral: electrophysiological responses to feedback stimuli. Cogn. Brain Res. 1105, 93–101.
Holroyd, C.B., Pakzad-Vaezi, K.L., Krigolson, O.E., 2008. The feedback correct-related positivity: sensitivity of the event-related brain potential to unexpected positive feedback. Psychophysiology 45, 688–697.
Holroyd, C.B., Krigolson, O.E., Baker, R., Lee, S., Gibson, J., 2009. When is an error not a prediction error? An electrophysiological investigation. Cogn. Affect. Behav. Neurosci. 9, 59–70.
Hurtado, E., Gonzalez, R., Haye, A., Manes, F., Ibanez, A., 2009. Contextual blending of ingroup/outgroup face stimuli and word valence: LPP modulation and convergence of measures. BMC Neurosci. 26 (10), 69.
Ibáñez, A., Haye, A., González, R., Hurtado, E., Henríquez, R., 2009. Multi-level analysis of cultural phenomena: the role of ERP approach to prejudice. J. Theory Soc. Behav. 39, 81–110.
Ibáñez, A., Manes, F., Escobar, J., Trujillo, N., Andreucci, P., Hurtado, E., 2010. Gesture influences the processing of figurative language in non-native speakers. Neurosci. Lett. 471, 48–52.
Kenemans, J.L., Kok, A., Smulders, F.T., 1993. Event-related potentials to conjunctions of spatial frequency and orientation as a function of stimulus parameters and response requirements. Electroencephalogr. Clin. Neurophysiol. 88, 51–63.
Kim, H., Shimojo, S., O'Doherty, J.P., 2006. Is avoiding an aversive outcome rewarding? The neural substrates of avoidance learning in the human brain. Plos Biol. 4, e233 (Electronic publication).
Li, P., Yuan, J., Jia, S., Feng, T., Chen, A., Li, H., 2009. Feedback-related negativity effects vanished with false or monetary loss choice. Neuroreport 20, 788–792.
Magno, E., Foxe, J.J., Molholm, S., Robertson, I.H., Garavan, H., 2006. The anterior cingulate and error avoidance. J. Neurosci. 26, 4769–4773.
Mars, R., De Bruijn, E., Hulstijn, W., Miltner, W.H.R., Coles, M.G.H., 2004. What if I told you: 'you were wrong'? Brain potentials and behavioral adjustments elicited by feedback in a time-estimation task. In: Ullsperger, M., Falkenstein, M. (Eds.), Errors, Conflicts, and the Brain. Current Opinions on Performance Monitoring. MPI of Cognitive Neuroscience, Leipzig, pp. 129–134.
Miltner, W.H.R., Braun, C.H., Coles, M.G.H., 1997. Event-related brain potentials following incorrect feedback in a time-estimation task: evidence for a "generic" neural system for error detection. J. Cogn. Neurosci. 9, 788–798.
Nieuwenhuis, S., Ridderinkhof, K., Blom, J., Band, G., Kok, A., 2001. Error-related brain potentials are differentially related to awareness of response errors: evidence from an antisaccade task. Psychophysiology 38, 752–760.
Nieuwenhuis, S., Holroyd, C.B., Mol, N., Coles, M.G.H., 2004a. Reinforcement-related brain potentials from medial frontal cortex: origins and functional significance. Neurosci. Biobehav. Rev. 28, 441–448.
Nieuwenhuis, S., Yeung, N., Holroyd, C., Schurger, A., Cohen, J.D., 2004b. Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. Cereb. Cortex 14, 741–747.
O'Connell, R., Dockree, P., Bellgrove, M., Kelly, S., Hester, R., Garavan, H., Robertson, I., Foxe, J., 2007. The role of cingulate cortex in the detection of errors with and without awareness: a high-density electrical mapping study. Eur. J. Neurosci. 25, 2571–2579.
Olofsson, J., Nordin, S., Sequeira, H., Polich, J., 2008. Affective picture processing: an integrative review of ERP findings. Biol. Psychol. 77, 247–265.
Polich, J., 2007. Updating P300: an integrative theory of P3a and P3b. Clin. Neurophysiol. 118, 2128–2148.

Potts, G.F., 2004. An ERP index of task relevance evaluation of visual stimuli. Brain Cogn. 56, 5–13.
Potts, G.F., Liotti, M., Tucker, D.M., Posner, M.I., 1996. Frontal and inferior temporal cortical activity in visual target detection: evidence from high spatially sampled event-related potentials. Brain Topogr. 9, 3–14.
Potts, G.F., Martin, L.M., Burton, P., Montague, P.R., 2006. When things are better or worse than expected: the medial frontal cortex and allocation of processing resources. J. Cogn. Neurosci. 18, 1112–1119.
Schultz, W., 2008. Introduction. Neuroeconomics: the promise and the profit. Philos. Trans. R. Soc. B: Biol. Sci. 363, 3767–3769.
Schutter, D., De Haan, E., Van Honk, J., 2004. Functionally dissociated aspects in anterior and posterior electrocortical processing of facial threat. Int. J. Psychophysiol. 53, 29–36.
Shalgi, S., Barkan, I., Deouell, L.Y., 2009. On the positive side of error processing: error-awareness positivity revisited. Eur. J. Neurosci. 29, 1522–1532.
Taylor, S., Martis, B., Fitzgerald, K., Welsh, R., Abelson, J., Liberzon, I., Himle, J., Gehring, W., 2006. Medial frontal cortex activity and loss-related responses to errors. J. Neurosci. 26, 4063–4070.
Towey, J., Rist, F., Hakerem, G., Ruchkin, D.S., Sutton, S., 1980. N250 latency and decision time. Bull. Psychon. Soc. 15, 365–368.
Trepel, C., Fox, C., Poldrack, R., 2005. Prospect theory on the brain? Toward a cognitive neuroscience of decision under risk. Cogn. Brain Res. 23, 34–50.
Yeung, N., Sanfey, A.G., 2004. Independent coding of reward magnitude and valence in the human brain. J. Neurosci. 24, 6258–6264.
Yeung, N., Holroyd, C.B., Cohen, J.D., 2005. ERP correlates of feedback and reward processing in the presence and absence of response choice. Cereb. Cortex 15, 535–544.