RESEARCH ARTICLE

CrossMark

Correlation of cue-locked FRN and feedback-locked FRN in the auditory monetary incentive delay task

Elena Krugliakova[1] · Vasily Klucharev[1] · Tommaso Fedele[2] · Alexey Gorin[1] · Aleksandra Kuznetsova[1] · Anna Shestakova[1]

Abstract
Reflecting the discrepancy between received and predicted outcomes, the reward prediction error (RPE) plays an important role in learning in a dynamic environment. A number of studies suggested that the feedback-related negativity (FRN) component of an event-related potential, known to be associated with unexpected outcomes, encodes RPEs. While FRN was clearly shown to be sensitive to the probability of outcomes, the effect of outcome magnitude on FRN remains to be further clarified. In studies on the neural underpinnings of reward anticipation and outcome evaluation, a monetary incentive delay (MID) task proved to be particularly useful. We investigated whether feedback-locked FRN and cue-locked dN200 responses recorded during an auditory MID task were sensitive to the probability and magnitude of outcomes. The cue-locked dN200 is associated with the update of information about the magnitude of prospective outcomes. Overall, we showed that feedback-locked FRN was modulated by both the magnitude and the probability of outcomes during an auditory version of MID task, whereas no such effect was found for cue-locked dN200. Furthermore, the cue-locked dN200, which is associated with the update of information about the magnitude of prospective outcomes, correlated with the standard feedback-locked FRN, which is associated with a negative RPE. These results further expand our knowledge on the interplay between the processing of predictive cues that forecast future outcomes and the subsequent revision of these predictions during outcome delivery.

Introduction

Tightly interwoven with reinforcement learning (RL) theory (Bush and Mosteller 1951), decision theory assumes that individuals' choices are driven by the values attached to prospective outcomes (Steele and Stefansson 2015). The magnitude and probability of outcomes are integrated to form the expected value (Bandura 1977; Von Neumann and Morgenstern 1944). For example, the temporal difference model of RL (Rescorla and Wagner 1972) indicates that an individual assigns high values to states that predict future rewards when encountered unexpectedly. Therefore, the reward prediction error (RPE) reflects the discrepancy between obtained and expected outcomes: unexpected unfavorable outcomes (i.e., monetary loss) produce negative RPEs, whereas unexpected favorable outcomes (i.e., monetary gain) result in positive RPEs. Subsequently, with the seminal work of Wolfram Schultz (1997), RL theory has come to play an important bridging role between economics (e.g., Camerer and Ho 1999; Erev and Roth 1998), psychology (Rescorla

✉ Elena Krugliakova
krugliakova.es@gmail.com

Vasily Klucharev
vklucharev@hse.ru

Tommaso Fedele
Tommaso.Fedele@usz.ch

Alexey Gorin
gorinspbu@gmail.com

Aleksandra Kuznetsova
aakuznetsova_2@edu.hse.ru

Anna Shestakova
a.shestakova@hse.ru

[1] Centre for Cognition and Decision Making, National Research University Higher School of Economics, 3a Krivokolenniy sidewalk, Moscow 101000, Russian Federation

[2] Neurosurgery Department, University Hospital Zürich, Frauenklinikstrasse 10, 8091 Zurich, Switzerland

Springer

and Wagner 1972), and neuroscience (Schultz 1997). The dopaminergic system has been proposed to broadcast a "prediction error" signal of precisely the form needed in reinforcement algorithms to drive convergence toward a standard dynamic programming value function (Barto and Sutton 1982). Since then, the dopaminergic RPE hypothesis has been tested with the use of a variety of neuroimaging techniques, including electroencephalography (EEG) (Düzel et al. 2009; Holroyd and Coles 2002; Knutson et al. 2005; O'Doherty et al. 2001; Pessiglione et al. 2006; Talmi et al. 2012). Using EEG-evoked responses to the obtained and expected outcomes, Holroyd and Coles (2002) suggested that a feedback-related negativity (FRN) component of event-related potentials (ERPs) can code an RPE learning signal that modifies performance on the task.

FRN is a relatively negative deflection in the ERP following losses or error feedback compared with wins or positive feedback. Two main interpretations have been proposed to explain the nature of this negative difference wave, FRN, which occurs approximately 250–350 ms after feedback onset. FRN can represent a negative ERP component, elicited by an unfavorable outcome (Ullsperger et al. 2014). Alternatively, this negative deflection can be explained by a positive ERP component, elicited by a favorable outcome, which is the reward positivity (RewP) (Proudfit 2015). Interestingly, Holroyd et al. (2008) hypothesized that the negative deflection observed between 250 and 350 ms after feedback onset reflects the same ERP component as a stimulus-locked N200: the difference in processing favorable and unfavorable outcomes results from the summation of the "default" negative N200 and the reward-related positive RewP. Consequently, FRN/RewP should be stronger modulated by the expectations of positive outcomes. While the interpretation of FRN/RewP is still under debate, a general agreement exists on its involvement in context-sensitive feedback evaluation underlying RPEs. In addition, electro- and magnetoencephalographic (E/MEG) and functional magnetic resonance imaging (fMRI) studies suggested the causal role of dopaminergic activity in the cingulate cortex and the surrounding medial prefrontal cortex in FRN generation (Agam et al. 2011; Emeric et al. 2008; Miltner et al. 1997; Walsh and Anderson 2012; Warren et al. 2015).

The sensitivity of FRN to the valence of the outcome constitutes the main proof of the hypothesis that FRN might be an encoder of RPE's sign (Holroyd and Coles 2002; Luu et al. 2000). A number of recent studies reported that FRN responds to the contextually most salient information and thus reflects an unsigned prediction error (Hauser et al. 2014; Oliveira et al. 2007; Talmi et al. 2012, 2013). A recent meta-analysis (Sambrook and Goslin 2015) refuted this hypothesis and clearly demonstrated the main effect of valence and the interaction of RPE size and valence. Thus, FRN is sensitive to the size of the RPE, which can be

manipulated by changing two components of expected value, namely, magnitude and probability. While the majority of neuroimaging studies suggest that FRN is more sensitive to the probability of outcomes than to their magnitude (Walsh and Anderson 2012), evidence also shows that the outcome magnitude exerts a modulatory effect on FRN (Sambrook and Goslin 2015).

Importantly, the brain constantly modifies expectations of prospective outcomes. According to RL theory, not only discrete outcomes but also the upcoming predictive stimuli can elicit RPEs. Predictive cues signaling the valence of future outcomes have been hypothesized to elicit an FRN-like signal. ERPs to cues predicting future unfavorable outcomes show a more pronounced negative deflection in the time window corresponding to FRN than do ERPs to cues predicting future rewards (Baker and Holroyd 2009; Dunning and Hajcak 2007). In other studies in which cues indicated the probability of obtaining outcomes, ERPs were more negative after the cues that predicted probable negative outcomes than after those that predicted probable future positive outcomes (Holroyd et al. 2011; Liao et al. 2011; Walsh and Anderson 2011). This cue-locked FRN-like response (difference N200, dN200) also shapes the feedback-locked FRN: in the case of predicted outcomes, the RPE and the amplitude of the feedback-locked FRN were smaller, and in the case of unpredicted outcomes, the RPE and the amplitude of the feedback-locked FRN were larger (for a review, see Walsh and Anderson 2012).

One of the paradigms that can be utilized to study the association between cue-locked (FRN-like) dN200 and standard FRN is a monetary incentive delay task (MID). The MID task is an elegant tool to study the different stages of RL from reward anticipation to its delivery (Knutson et al. 2000, 2005). It can be used to delineate the neural mechanisms of performance monitoring during behavioral acts with different expected values and RPEs. Initially, the MID task was used in fMRI studies on the neural processing of gains and losses (Knutson et al. 2000). Subsequent EEG and MEG studies utilized the MID task to examine the neural dynamics of reward processing with a temporal resolution in the millisecond range (Broyd et al. 2012; Doñamayor et al. 2012; Thomas et al. 2013). The MID task introduces incentive cues that signal both the magnitude and the probability of prospective outcomes. It enables the investigation of the effects of these two components of expected value on neural activity associated with the processing of incentive cues and feedback (Knutson et al. 2005). To our knowledge, no previous studies have investigated the simultaneous effects of the magnitude and probability of outcomes on incentive cue-locked dN200 and feedback-locked FRN. In the classic MID task, visual stimuli, such as circles, squares, and triangles, are utilized as incentive cues that code the probabilities and magnitudes of outcomes. We developed an auditory version

of an MID task that relied on the sounds of different physical characteristics as incentive cues. This auditory version of the MID task was validated in this study and was further used in the examination of auditory perceptual learning.

The main purpose of this study is to investigate the influence of the expected probability and magnitude of the outcome on (FRN-like) dN200 evoked by incentive cues at the beginning of each trial, as well as on FRN registered during feedback delivery at the end of each trial. We also examined the association between the amplitude of cue dN200 and FRN.

Methods

Participants

Twenty-seven subjects (17 women, 23 ± 3 years old) participated in an EEG experiment, in which both behavioral and electrophysiological data were collected. Data from 18 additional subjects were excluded because of the insufficient number of trials in one of the conditions for the averaging procedure (less than 20 in at least one of the conditions, according to Marco-Pallares et al. 2011) or because of excessive EEG artifacts. All subjects were right-handed, with normal or corrected-to-normal vision. They did not report any history of psychiatric or neurological problems, and they all reported to be right-handed. The study was approved by the local ethics committee. All participants gave their written informed consent prior to their participation.

Auditory stimuli

Acoustic cues signaled a high or low prospective reward probability (0.80 and 0.20, respectively) and a high or low prospective reward magnitude (4 and 20 rubles, the equivalent of 0.07 USD or 0.4 USD, respectively). The participants were given the cumulative reward they had earned, and this was, on average, equal to the cost of a dinner. A set of four sounds (cues) consisted of two levels of frequency (fundamental frequencies of 562 and 487 Hz) and two levels of intensity (55 and 80 dB) to encode the prospective reward probability and magnitude. All tones had a duration of 200 ms (including 5 ms of rising and falling times). Stimuli were generated with PRAAT software (Boersma 2001). The probability and magnitude of reward were encoded differently in the two experimental groups. In group 1 ($n = 14$), the outcome magnitude was encoded by the intensity of the acoustic cue, whereas the gain probability was encoded by the frequency of the acoustic cue. In group 2 ($n = 13$), the encoding of the gain magnitude and gain probability was reversed. To decrease the effects of the physical parameters

of stimuli on ERP processing, we polled the data of two experimental groups.

Study design

The main goal of this study was to investigate the effect of the valence, magnitude, and probability of gains on FRN and dN200. Because this study is a part of a larger research project, the experiment consisted of two MID task sessions performed on 2 consecutive days. Each MID task session involved 152 trials. The total duration of the experiment, including the technical preparation, was proximately 90 min.

Day 1 At the beginning of each experiment, the ability of the participants to identify auditory stimuli was tested during a recognition test. Prior to the MID task, the trial structure and the meaning of each acoustic cue were explained to the participants. Next, the participants performed the first session of the MID task.

Day 2 At approximately the same time of the day, the participants performed the second session of the MID task.

Recognition test

The recognition test was designed to ensure that the participants were able to discriminate acoustic cues coding expected values. The participants were instructed to press a button corresponding to the delivered sound. The sound descriptions and target buttons were displayed on the screen (i.e., high, loud sound, button 1, etc.) during the task. The participants received positive and negative visual feedback to facilitate learning. The EEG session started when a subject successfully identified 8 out of 10 consecutive sounds. On an average, the participants made more mistakes in frequency identification (4.19 ± 0.86; $S \pm$ SEM) than in intensity identification (1.85 ± 0.41), and in simultaneous frequency and intensity identification (1.33 ± 0.43).

Auditory MID task

During the auditory MID task (Fig. 1), the participants were exposed to acoustic cues encoding the prospective gain magnitude (4 or 20 rubles) and probability of a win (0.80 or 0.20). After a variable anticipatory delay period (2000–2500 ms), the participants responded with a single button press immediately after the presentation of a visual target (white square) (Fig. 1). 800 ms after the button press, the subsequent (2000 ms long) feedback notified the participants about both current and cumulative outcomes. The 800-ms delay of the feedback aimed to eliminate the possible confound of the visual target duration on feedback-locked ERPs. The overall duration of a single trial was 8 s. The probability of a win was manipulated by altering the average target duration through an adaptive timing algorithm that

Fig. 1 Structure of the auditory version of the monetary incentive delay (MID) task
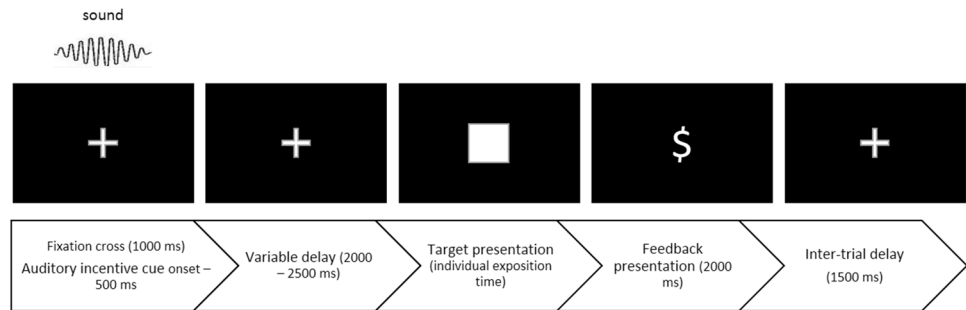
followed the subjects' performance, such that they would succeed in ~ 80% of the high-probability trials and in ~ 20% of the low-probability trials (Knutson et al. 2005). Thus, in high-probability trials, the participants had more time to give a response than in low-probability trials. The outcomes were positive (a gain of 4 or 20 rubles) or negative (omission of gain—participants did not gain 4 or 20 rubles).

At the beginning of the task, the initial duration of the target was based on the reaction times (RTs) collected during the training session. Prior to the MID task, the participants were instructed on which acoustic cues corresponded to which probabilities and magnitudes of outcomes.

On average, the duration of the visual target was set to 272 ± 28 ms for trials with a high-gain probability and 189 ± 26 ms for trials with a low-gain probability. The reward feedback was presented in an average of 58 ± 6 trials out of 76 in the case of 80% gain probability, and an average of 14 ± 3 trials out of 76 for the 20% gain probability.

Analysis of behavioral results

The RT in each trial type was averaged for each participant, grand averaged, and subjected to two-way repeated measures ANOVA, with *Magnitude* (small vs. large magnitude) and *Probability* (low vs. high probability) as the within-subject variables.

EEG data acquisition

EEG data were recorded with the following 28 active electrodes (Brain Products GmbH) according to the extended version of the 10–20 system: Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, Fz, Cz, Pz, Oz, FC1, FC2, CP1, CP2, FC5, FC6, CP5, and CP6. Active channels were referenced against the mean of two mastoid electrodes to display the maximal FRN response at the frontal electrode sites. The electrooculogram was recorded with electrodes placed at the outer canthi and below the right eye. Data were acquired with a BrainVision actiCHamp amplifier (Brain Products GmbH) and sampled at 500 Hz. Impedance was confirmed to be less than 5 kΩ in all electrodes prior to recording.

Auditory MID task EEG data analysis

EEG signals were pre-processed with BrainVision Analyzer 2.1 (Brain Products GmbH). The EEG was filtered offline (passband 1–30 Hz, notch filter 50 Hz), and then ICA-based ocular artifact correction was performed. After manual inspection of the raw data for remaining artifacts, the data were segmented into epochs of 600 ms, including a 100-ms pre-stimulus. Each trial was baseline corrected to an average activity between − 100 and 0 ms before stimulus onset. Epochs including voltage changes exceeding 75 mV at any channel were omitted from the averaging. Epochs were separately averaged for different trial types. ERPs obtained during the first and second sessions were pooled together. This procedure also helped increase the number of trials averaged for each type of feedback because of a small number of trials for unexpected outcomes. Averaged ERP waveforms were computed within each subject and condition with a minimum number of 20 trials per condition. Furthermore, we separately processed auditory ERPs evoked by the presentation of incentive cues and visual ERPs evoked by feedback presentation. Statistical analyses were performed for the Fz electrode, a standard electrode location for FRN analysis (e.g., Gehring and Willoughby 2002; topographic maps Figs. 2, 3). Peak amplitudes were quantified as the average amplitude (± 20 ms) around the local minimum occurring within the timeframe of interest (250–350 ms) post-stimulus onset. A time window chosen for the statistical analysis of N200 and FRN was based on visual inspection of the grand-average waveforms and the results of previous studies. The timeframes of interest were the same for all ERP waveforms. All statistical analyses were performed with Matlab 2015a and SPSS software package (22.0).

We averaged the auditory cue-locked ERPs according to the combination of reward magnitude or reward probability that they signaled: small magnitude × low probability (75 ± 4 trials), small magnitude × high probability (76 ± 4 trials), large magnitude × low probability (73 ± 4 trials), and large magnitude × high probability (73 ± 3 trial). As a result, we obtained four types of the cue-locked waveforms. Two-way repeated measures ANOVA, with *Probability* (unlikely vs. likely) and *Magnitude* (small vs. large) as the

Fig. 2 Grand-averaged auditory ERP waveforms (Fz) superimposed for two types of cues, signaling the probabilities (low and high) and the magnitudes (big or and small) of gains (upper row). Difference waveforms were calculated separately for the probability (low − high) and the magnitude (small − big) of the gains. The width of the blue bars corresponds to the 250–350-ms time window within which the differences between corresponding ERPs were measured and plotted in the form of difference waveforms (upper row) and voltage topographical distributions (bottom row)
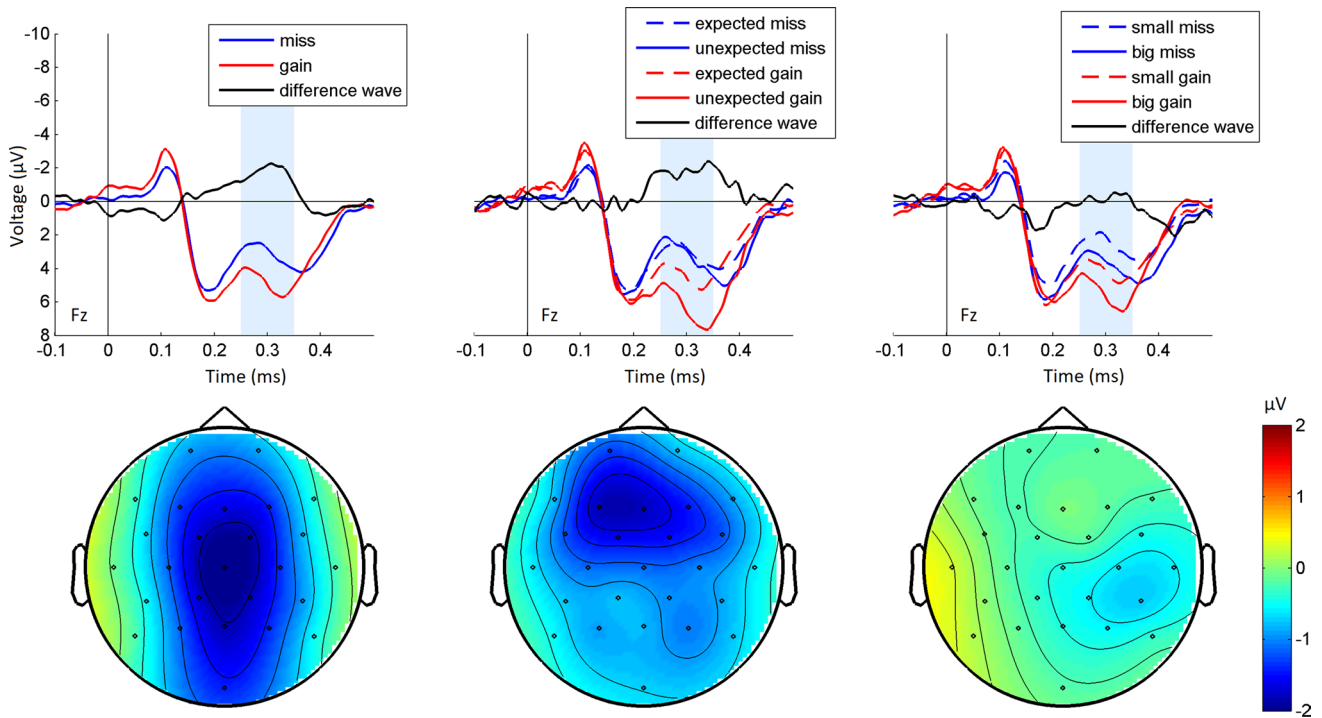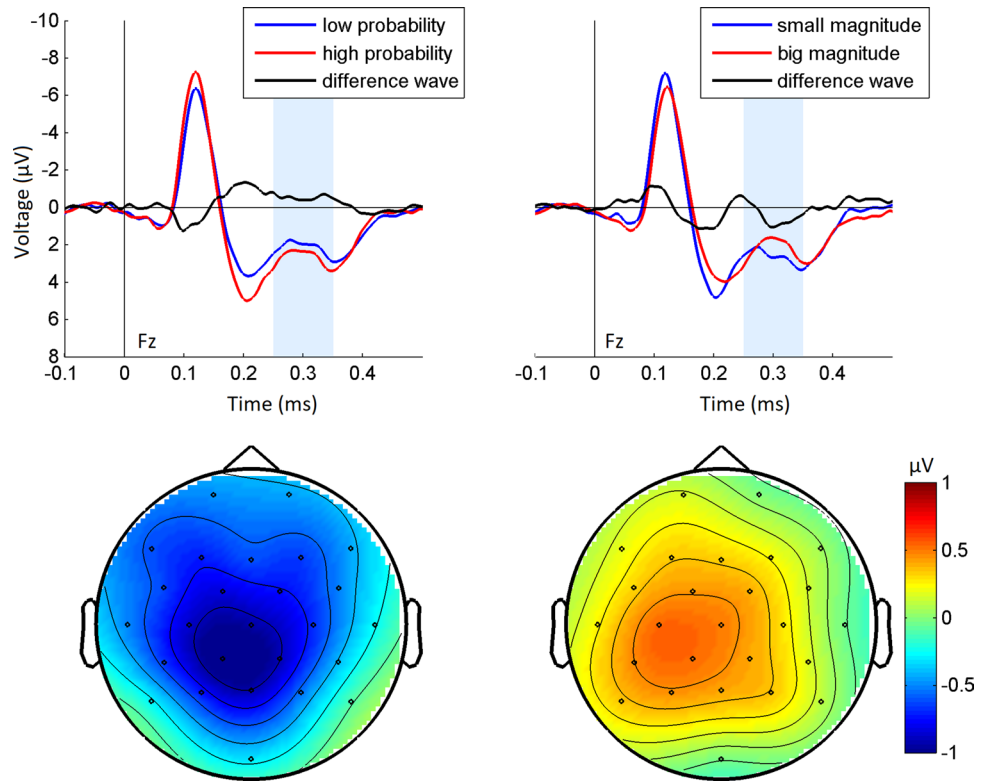
Fig. 3 Grand-averaged visual ERP waveforms (Fz) superimposed for different types of feedback (upper row). Difference waveforms were calculated separately for valence (misses − gains), probability ((unexpected misses − unexpected gains) − (expected misses − expected gains)), and magnitude ((big misses − big gains) − (small misses − small gains)) of the outcomes. The width of the blue bars corresponds to the 250–350-ms time window within which the differences between corresponding ERPs were measured and plotted in the form of difference waveforms (upper row) and voltage topographical distributions (bottom row)

within-subject variables, was conducted for the N200 amplitudes for the cues signaling different gain probabilities and gain magnitudes. Then, we processed feedback-locked visual ERP in two different ways: by pooling the ERPs for expected (highly likely) and unexpected (highly unlikely) outcomes, irrespective of magnitude, and by pooling the ERPs for the large (20 rub) and small (4 rub) magnitudes, irrespective of probability. Taking into account the valence of the outcome (gain or omission of gain), we obtained 4×2 different types of waveforms. For probability-pooled ERPs, we calculated the ERPs (29 ± 3 trials) to unlikely positive outcomes (gain, $p = 0.20$), the ERPs (112 ± 7 trials) to likely positive outcomes (gain, $p = 0.80$), the ERPs (29 ± 5 trials) to unlikely negative outcomes (miss, $p = 0.80$), and the ERPs (112 ± 11 trials) to likely negative outcomes (miss, $p = 0.20$). For magnitude-pooled ERPs, we calculated the ERPs (67 ± 5 trials) to small positive outcomes (4 rub), the ERPs (84 ± 10 trials) to large positive outcomes (20 rub), the ERPs (71 ± 8 trials) to small negative outcomes (misses of 4 rub), and the ERPs (68 ± 7 trials) to large negative outcomes (misses of 20 rub). The ERPs obtained during the first and second sessions were pooled together. Two-way repeated measures ANOVA, with *Valence* (gain vs. miss) and *Probability* (unlikely vs. likely) as the within-subject variables, was conducted for the FRN amplitudes derived from the probability-pooled ERPs. Two-way repeated measures ANOVA, with *Valence* (gain vs. miss) and *Magnitude* (small vs. large) as the within-subject variables, was conducted for the FRN amplitudes derived from the magnitude-pooled ERPs.

In all repeated measures ANOVAs, significant interactions were further decomposed with simple effect tests (Howell and Lacroix 2012; Stevens 1991). The level of significance was set to $p < 0.05$. The *p* values reported for the ANOVAs were adjusted with Greenhouse–Geisser correction.

For correlation analyses, we calculated two sets of data. The first set comprised two types of cue-locked dN200. For this, following the logic of FRN computation, we obtained two difference waveforms for the cue-locked ERPs: (1) we subtracted ERPs evoked by the cues indicating a high probability of a win from ERPs for cues indicating a low probability of a win (*probability*-dN200); (2) we subtracted ERPs for the cues predicting large potential gains from ERPs for the cues predicting small potential gains (*magnitude*-dN200). Additionally, we calculated three different types of dFRNs (defined as the most negative value of the difference waveform). The standard FRN (we use the term *standard* dFRN hereafter) identified for the difference waveform was obtained by subtracting all positive outcomes (gains) from ERPs for all negative outcomes (omission of gain). *Probability*-dFRN and *magnitude*-dFRN were calculated similar to RPE-FRN, as introduced by Sambrook and Goslin (2015). By subtracting the waveforms for gains and misses

with the same size of RPE, we obtained difference waveforms reflecting differences in processing feedback valence in the case of small and large RPEs. Then, we subtracted the obtained difference waveforms for the small RPE from waveforms for the large RPE. Thus, the overall scheme of *probability*-dFRN calculation was as follows: ((unexpected misses − unexpected gains) − (expected misses − expected gains)), irrespective of their magnitude of outcome. For the *magnitude*-dFRN, the calculation scheme was similar ((large misses − large gains) − (small misses − small gains)).

Furthermore, we estimated whether the cue-locked dN200 can vary as a function of the feedback-locked dFRN with the use of Spearman correlation. For this purpose, we first calculated the correlation for two types of dN200 and *standard* dFRN. Then, we correlated *probability*-dN200 with *probability*-dFRN, and *magnitude*-dN200 with *magnitude*-dFRN. Cook's distance was used to identify outliers. Cases with a Cook's distance greater than $4/n$ were excluded from further analysis (Bollen and Jackman 1985).

Results

Behavioral results

We calculated the RTs for all trial types in both MID sessions. The probability and magnitude of the expected outcome significantly modulated RTs (factors *Probability* [$F_{(1, 26)} = 73.937$, $p < 0.001$, $\eta_p^2 = 0.733$] and *Magnitude* [$F_{(1, 26)} = 17.598$, $p < 0.001$, $\eta_p^2 = 0.395$]). On average, the participants were faster in trials with a low probability of positive outcomes (212 ± 5 ms) than in trials with a high probability (230 ± 4 ms). The RT was faster in trials with larger expected gains (218 ± 4 ms) than in those with smaller expected gains (224 ± 5 ms). No significant interactions between factors were observed.

Electrophysiological results

We first analyzed cue-locked ERPs with a 250–350-ms time window, which is typical for the standard FRN. Figure 2 (left) suggests that N200 was relatively more negative for cues signaling a low probability of gain than for those signaling a high probability of gain. However, the omnibus ANOVA showed no significant effect of the factor *Probability* [$F(1, 26) = 1.520$, $p = 0.229$, $\eta_p^2 = 0.055$] or *Magnitude* [$t(1, 26) = 2.009$, $p = 0.168$] on N200 amplitudes in the interval 250–350 ms post-cue onset. The interaction *Probability × Magnitude* was also not significant [$F(1, 26) = 0.287$, $p = 0.596$, $\eta_p^2 = 0.011$].

Figure 3 illustrates different types of feedback-locked visual ERPs and the scalp distributions of the dFRNs (250–350 ms post feedback). In all conditions, feedback was followed by FRN as a negative deflection with a maximum around 300 ms. The modulation of FRN by the probability and magnitude of gains was investigated in two separate ANOVA analyses. We evaluated the effect of *Valence* and *Probability* on FRN amplitude in ERPs pooled for different probabilities (Fig. 3, middle). The significant main effect of *Valence* [$F_{(1, 26)} = 15.196$, $p = 0.001$, $\eta_p^2 = 0.369$] resulted from more negative amplitudes of FRN for misses (1.017 ± 0.501 μV) than for gains (2.550 ± 0.594 μV). The main effect of *Probability* was not significant [$F_{(1, 26)} = 0.001$, $p = 0.978$, $\eta_p^2 = 0$]. Instead, we found a significant interaction of *Valence* × *Probability* [$F_{(1, 26)} = 8.379$, $p = 0.008$, $\eta_p^2 = 0.244$]: the effect of *Probability* for misses was not significant [$F_{(1, 26)} = 2.326$, $p = 0.139$, $\eta_p^2 = 0.082$], but that for gains was significant [$F_{(1, 26)} = 9.301$, $p = 0.005$, $\eta_p^2 = 0.263$].

We further tested the effects of *Valence* and *Magnitude* on FRN amplitude in ERPs pooled for different magnitudes of outcome (Fig. 3, right). The significant main effect of *Valence* [$F_{(1, 26)} = 6.519$, $p = 0.017$, $\eta_p^2 = 0.200$] resulted from the more negative amplitude of FRN to misses (1.445 ± 0.474 μV) than to gains (2.800 ± 0.565 μV).

The analysis also revealed a significant main effect of *Magnitude* [$F_{(1, 26)} = 19.094$, $p < 0.001$, $\eta_p^2 = 0.423$], indicating a smaller FRN for large gains (2.724 ± 0.545 μV) than for small gains (1.521 ± 0.463 μV). The interaction *Valence* × *Magnitude* was not significant [$F_{(1, 26)} = 0.123$, $p = 0.730$, $\eta_p^2 = 0.005$].

Correlation analyses showed a significant positive correlation between *standard* dFRN and *magnitude*-dN200 (Fig. 4) forecasting different magnitudes of prospective outcomes (Spearman $r = 00.540$, $p = 0.005$). The significant correlations between *magnitude*-dN200 and *standard* dFRN was positive, indicating that the larger N200 to the cues forecasting larger gains predicts the larger dFRN to the negative feedback. None of the other correlation analyses yielded a significant result (ps > 0.10).

Discussion

The main purpose of this study is to investigate whether the feedback-locked FRN and cue-locked FRN-like activity (dN200) recorded during an auditory MID task are sensitive to the probability and magnitude of outcomes and whether the amplitudes of these two components are correlated. We

observed a significant interplay between *magnitude*-dN200 and *standard* dFRN. Moreover, we show that the feedback-locked FRN component is sensitive to both the magnitude and the probability of outcomes, whereas the analysis of N200 did not reveal any significant effects.

We were particularly interested in the interplay between the FRN and RPE functions. Consistent with previous studies, the amplitude of negative deflection between 250 and 350 ms after feedback onset was modulated by outcome valence, which is believed to reflect the neural correlate of RPE (Hajcak et al. 2006; Holroyd and Coles 2002; Miltner et al. 1997; Nieuwenhuis et al. 2004; Yeung and Sanfey 2004). FRN amplitude was also affected by RPE magnitude, which was varied by manipulating the magnitude and probability of outcomes. For the probability-pooled ERPs, FRN was modulated by outcome probability only for positive outcomes, whereas for the magnitude-pooled ERPs, FRN was modulated by the magnitude of both positive and negative outcomes.

Previous studies demonstrated gain/loss asymmetry of the effect of probability on FRN: the likelihood of outcomes affects FRN for gains (positive RPE) more strongly than FRN for losses or omissions of gains (negative RPE) (for a review, see Walsh and Anderson 2012). In our study, outcome probability was manipulated using different durations of the visual target, which could potentially affect the feedback processing by making the outcome probability more salient than the outcome magnitude. We observed a preferential sensitivity of probability-pooled FRN to the degree of only positive RPEs. It can be attributed to the different neural mechanisms underlying feedback processing for positive and negative outcomes (Cohen et al. 2007), and it is consistent with the hypothesis on the greater range of dopaminergic responses to positive outcomes than to negative outcomes because of the low baseline firing rate of dopamine neurons (Walsh and Anderson 2012). The norepinephrine system has also been suggested to play a role in the processing of infrequent motivationally salient events by modulating the ongoing activity in the anterior cingulate cortex (ACC). Therefore, the ACC represents a crucial hub integrating the activity of both norepinephrine and dopamine neuromodulatory systems and thus providing high sensitivity to both the expectedness and the valence of task-relevant events (Warren and Holroyd 2012).

We observed a modulation of FRN by the magnitude of outcome for both positive and negative outcomes. However, evidence of FRN modulation by the magnitude of the expected outcome has been controversial. Some studies suggest that FRN is not influenced by reward magnitude (Cui et al. 2013; Hajcak et al. 2003, 2006; Holroyd et al. 2006; Marco-Pallares et al. 2008; Nieuwenhuis et al. 2004; De Pascalis et al. 2010; Yeung and Sanfey 2004). However, increasing evidence also shows that FRN encodes
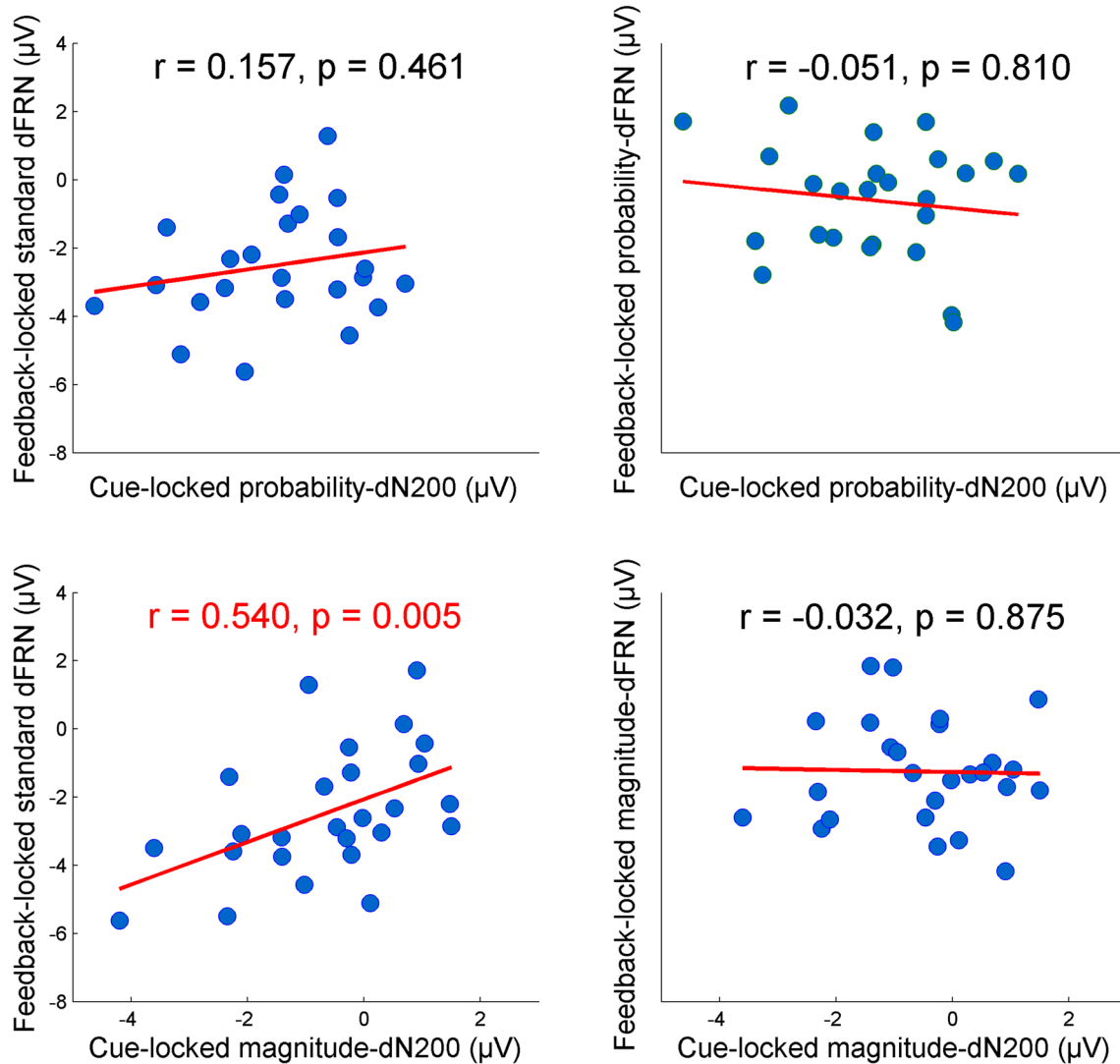
Fig. 4 Cue-locked dN200 amplitudes (Fz) as a function of feedback-locked dFRN (Fz) amplitudes

magnitude in addition to probability and valence (Bellebaum et al. 2010; Kreussel et al. 2012; Toyomaki and Murohashi 2005). One previous study reported that FRN modulation by the magnitude of outcome was stronger for positive feedback than for negative feedback (Kreussel et al. 2012). In our opinion, the apparent discrepancy between the results of previous studies could be attributed to differences in study designs and data analyses. For example, Kreussel et al. (2012) instructed subjects to choose between two stimuli (cues) signaling potential monitory wins (vs. no wins) or monitory losses (vs. losses), whereas the participants in our MID task did not select cues and faced only monitory wins (vs. no wins). Taken together, these discrepancies in experimental designs must be considered in the direct comparison of results across studies, which in turn call for the further

investigation of the effect of the reward magnitude on FRN.

According to the RL theory of FRN, the size of the cue-locked RPE should vary with the amount of information that the cue carries about the future outcome (i.e., probability or magnitude of gain). More specifically, the cue-locked FRN should increase with the amount of information that the cue is carrying, and this should modulate the neural response to feedback presentation: if the outcome is in line with the expectation formed by the cue, the prediction error and the feedback-locked FRN will be relatively small. In the opposite condition, if the outcome violates the expectation formed by the cue, it will result in a larger prediction error and feedback-locked FRN (Walsh and Anderson 2012). In the majority of studies that investigated cue-feedback RPE processing, cues provided complete information about

upcoming outcomes (Dunning and Hajcak 2007; Baker and Holroyd 2009). In some studies in which cues provided probabilistic information about outcomes, the cues signaling highly probable negative outcomes evoked larger cue-locked FRN than those signaling highly probable positive outcomes (Holroyd et al. 2011; Liao et al. 2011; Walsh and Anderson 2011).

Although in our study, we observed a larger amplitude of the N200 response to cues signaling a low probability of gains than to those signaling a high probability of gains (*probability*-dN200), which is similar to that in Walsh and Anderson (2010), the effect was not significant. We also did not find any correlation between *probability*-dN200 and *standard* dFRN or *probability*-dFRN. In previous studies (Holroyd et al. 2011; Liao et al. 2011; Walsh and Anderson 2011) in which cues provided probabilistic information about outcomes, the probability of success was determined automatically and independently from the subjects' performance. However, in our MID task, the probability of success was determined by the time window for the response. This difference in paradigms might explain the lack of modulation of cue-locked dN200 by outcome probability. We did not also observe any significant modulation of the cue-locked dN200 by the magnitude of the expected outcome at the group level. The lack of sensitivity of cue-locked dN200 to the components of expected value (probability and magnitude) observed at the group level could also be explained by the sensory modality of the incentive cues in our study: the processing of auditory cues could differ from the processing of visual cues (horizontal and vertical lines, such as those in Knutson et al. 2005). Despite the possible difficulties in auditory cue recognition, the cueing was successful in providing information about the magnitude and probability of the expected outcome, as revealed by the modulation of the participants' RT (similarly to studies with visual cues: Helfinstein et al. 2013; Knutson et al. 2003, 2005; Rademacher et al. 2014).

Nevertheless, across all participants, we observed a positive correlation between *magnitude*-dN200 and *standard* dFRN. Thus, a larger *magnitude*-dN200 is associated with a more pronounced *standard* dFRN. Importantly, dN200 is derived by contrasting neural responses to auditory cues that forecast small gains with cues that forecast large gains. One possible interpretation of our finding is that the neural activity generating cue-locked dN200 provides complementary information for the processing of favorable and unfavorable outcomes underlying FRN. This interpretation is consistent with the RL theory of FRN. Interestingly, according to (Walsh and Anderson 2012), when participants know the magnitude of the forthcoming feedback (as indicated by a cue at the beginning of each trial) but not its valence, no effect of magnitude on FRN is observed. This meta-scale finding may indicate that the relations between cue-locked

dN200 and feedback-locked dFRN can be different in the case of cues signaling the valence of future outcomes and cues signaling magnitude. Further studies are needed to clarify the sensitivity of feedback-locked FRN to the cueing of probability and magnitude and how this information is processed in the brain.

Conclusion

Overall, we showed that feedback-locked FRN was modulated by both the magnitude and the probability of outcomes during an auditory version of the MID task. Furthermore, the cue-locked dN200, which is associated with the update of information about the magnitude of prospective outcomes, correlated with the standard feedback-locked dFRN, which is associated with the processing of favorable and unfavorable outcomes (RPE). The results further expand our knowledge of the interplay between the processing of the evaluation of ongoing predictive events and future outcomes and the following revision of these predictions during outcome delivery.

References

Agam Y, Hämäläinen MS, Lee AKC, Dyckman KA, Friedman JS, Isom M et al (2011) Multimodal neuroimaging dissociates hemodynamic and electrophysiological correlates of error processing. Proc Natl Acad Sci USA 108:17556–17561. https://doi.org/10.1073/pnas.1103475108

Baker TE, Holroyd CB (2009) Which way do I go? Neural activation in response to feedback and spatial processing in a virtual T-maze. Cereb Cortex 19:1708–1722. https://doi.org/10.1093/cercor/bhn223

Bandura A (1977) Self-efficacy: toward a unifying theory of behavioral change. Psychol Rev 84:191–215

Barto AG, Sutton RS (1982) Simulation of anticipatory responses in classical conditioning by a neuron-like adaptive element. Behav Brain Res 4:221–235. https://doi.org/10.1016/0166-4328(82)90001-8

Bellebaum C, Polezzi D, Daum I (2010) It is less than you expected: the feedback-related negativity reflects violations of reward magnitude expectations. Neuropsychologia 48:3343–3350. https://doi.org/10.1016/j.neuropsychologia.2010.07.023

Boersma P (2001) PRAAT, a system for doing phonetics by computer. Glot Int 5:341–345. https://doi.org/10.1097/AUD.0b013e31821473f7

Bollen KA, Jackman RW (1985) Regression diagnostics: an expository treatment of outliers and influential cases. Sociol Methods Res 13:510–542. https://doi.org/10.1177/0049124185013004004

Broyd SJ, Richards HJ, Helps SK, Chronaki G, Bamford S, Sonuga-Barke EJS (2012) An electrophysiological monetary incentive delay (e-MID) task: a way to decompose the different components of neural response to positive and negative

monetary reinforcement. J Neurosci Methods 209:40–49. https://doi.org/10.1016/j.jneumeth.2012.05.015

Bush RR, Mosteller F (1951) A model for stimulus generalization and discrimination. Psychol Rev 58:413–423. https://doi.org/10.1037/h0054576

Camerer C, Ho T-H (1999) Experience-weighted attraction learning in normal form games. Econometrica 67:827–874. https://doi.org/10.1111/1468-0262.00054

Cohen MX, Elger CE, Ranganath C (2007) Reward expectation modulates feedback-related negativity and EEG spectra. Neuroimage 35:968–978. https://doi.org/10.1016/j.neuroimage.2006.11.056

Cui J-F, Chen Y-H, Wang Y, Shum DHK, Chan RCK (2013) Neural correlates of uncertain decision making: ERP evidence from the Iowa Gambling Task. Front Hum Neurosci 7:776. https://doi.org/10.3389/fnhum.2013.00776

De Pascalis V, Varriale V, D'Antuono L (2010) Event-related components of the punishment and reward sensitivity. Clin Neurophysiol 121:60–76. https://doi.org/10.1016/j.clinph.2009.10.004

Doñamayor N, Schoenfeld MA, Münte TF (2012) Magneto- and electroencephalographic manifestations of reward anticipation and delivery. Neuroimage 62:17–29. https://doi.org/10.1016/j.neuroimage.2012.04.038

Dunning JP, Hajcak G (2007) Error-related negativities elicited by monetary loss and cues that predict loss. NeuroReport 18:1875–1878. https://doi.org/10.1097/WNR.0b013e3282f0d50b

Düzel E, Bunzeck N, Guitart-Masip M, Wittmann B, Schott BH, Tobler PN (2009) Functional imaging of the human dopaminergic midbrain. Trends Neurosci 32:321–328. https://doi.org/10.1016/j.tins.2009.02.005

Emeric EE, Brown JW, Leslie M, Pouget P, Stuphorn V, Schall JD (2008) Performance monitoring local field potentials in the medial frontal cortex of primates: anterior cingulate cortex. J Neurophysiol 99:759–772. https://doi.org/10.1152/jn.00896.2006

Erev I, Roth AE (1998) Predicting how people play games: reinforcement learning in experimental games with unique, mixed strategy equilibria. Am Econ Rev 88:848–881. https://doi.org/10.1086/250095

Gehring WJ, Willoughby AR (2002) The medial frontal cortex and the rapid processing of monetary gains and losses. Science 295:2279–2282. https://doi.org/10.1126/science.1066893

Hajcak G, McDonald N, Simons RF (2003) To err is autonomic: error-related brain potentials, ANS activity, and post-error compensatory behavior. Psychophysiology. 40(6):895–903. https://doi.org/10.1111/1469-8986.00107

Hajcak G, Moser JS, Holroyd CB, Simons RF (2006) The feedback-related negativity reflects the binary evaluation of good versus bad outcomes. Biol Psychol 71:148–154. https://doi.org/10.1016/j.biopsycho.2005.04.001

Hauser TU, Iannaccone R, Stampfli P, Drechsler R, Brandeis D, Walitza S et al (2014) The feedback-related negativity (FRN) revisited: new insights into the localization, meaning and network organization. Neuroimage 84:159–168. https://doi.org/10.1016/j.neuroimage.2013.08.028

Helfinstein SM, Kirwan ML, Benson BE, Hardin MG, Pine DS, Ernst M et al (2013) Validation of a child-friendly version of the monetary incentive delay task. Soc Cogn Affect Neurosci 8:720–726. https://doi.org/10.1093/scan/nss057

Holroyd CB, Coles MGH (2002) The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. Psychol Rev 109:679–709. https://doi.org/10.1037//0033-295X.109.4.679

Holroyd CB, Hajcak G, Larsen JT (2006) The good, the bad and the neutral: electrophysiological responses to feedback stimuli. Brain Res 1105:93–101. https://doi.org/10.1016/j.brainres.2005.12.015

Holroyd CB, Pakzad-Vaezi KL, Krigolson OE (2008) The feedback correct-related positivity: sensitivity of the event-related brain potential to unexpected positive feedback. Psychophysiology 45:688–697. https://doi.org/10.1111/j.1469-8986.2008.00668.x

Holroyd CB, Krigolson OE, Lee S (2011) Reward positivity elicited by predictive cues. NeuroReport 22:249–252. https://doi.org/10.1097/WNR.0b013e328345441d

Howell GT, Lacroix GL (2012) Decomposing interactions using GLM in combination with the COMPARE, LMATRIX and MMATRIX subcommands in SPSS. Tutor Quant Methods Psychol 8:1–22

Knutson B, Westdorp A, Kaiser E, Hommer D (2000) FMRI visualization of brain activity during a monetary incentive delay task. Neuroimage 12:20–27. https://doi.org/10.1006/nimg.2000.0593

Knutson B, Fong GW, Bennett SM, Adams CM, Hommer D (2003) A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: characterization with rapid event-related fMRI. Neuroimage 18:263–272. https://doi.org/10.1016/S1053-8119(02)00057-5

Knutson B, Taylor J, Kaufman M, Peterson R, Glover G (2005) Distributed neural representation of expected value. J Neurosci 25:4806–4812. https://doi.org/10.1523/JNEUROSCI.0642-05.2005

Kreussel L, Hewig J, Kretschmer N, Hecht H, Coles MGH, Miltner WHR (2012) The influence of the magnitude, probability, and valence of potential wins and losses on the amplitude of the feedback negativity. Psychophysiology 49:207–219. https://doi.org/10.1111/j.1469-8986.2011.01291.x

Liao Y, Gramann K, Feng W, Deák GO, Li H (2011) This ought to be good: brain activity accompanying positive and negative expectations and outcomes. Psychophysiology 48:1412–1419. https://doi.org/10.1111/j.1469-8986.2011.01205.x

Luu P, Collins P, Tucker DM (2000) Mood, personality, and self-monitoring: negative affect and emotionality in relation to frontal lobe mechanisms of error monitoring. J Exp Psychol Gen 129:43–60. https://doi.org/10.1037/0096-3445.129.1.43

Marco-Pallares J, Cucurell D, Cunillera T, García R, Andrés-Pueyo A, Münte TF et al (2008) Human oscillatory activity associated to reward processing in a gambling task. Neuropsychologia 46:241–248. https://doi.org/10.1016/j.neuropsychologia.2007.07.016

Marco-Pallares J, Cucurell D, Münte TF, Strien N, Rodriguez-Fornells A (2011) On the number of trials needed for a stable feedback-related negativity. Psychophysiology 48:852–860. https://doi.org/10.1111/j.1469-8986.2010.01152.x

Miltner WHR, Braun CH, Coles MGH (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. https://doi.org/10.1162/jocn.1997.9.6.788

Nieuwenhuis S, Yeung N, Holroyd CB, Schurger A, Cohen JD (2004) Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. Cereb Cortex 14:741–747. https://doi.org/10.1093/cercor/bhh034

O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C (2001) Abstract reward and punishment representations in the human orbitofrontal cortex. Nat Neurosci 4:95–102. https://doi.org/10.1038/82959

Oliveira FTP, McDonald JJ, Goodman D (2007) Performance monitoring in the anterior cingulate is not all error related: expectancy deviation and the representation of action-outcome associations. J Cogn Neurosci 19:1994–2004. https://doi.org/10.1162/jocn.2007.19.12.1994

Pessiglione M, Seymour B, Flandin G, Dolan RJ, Frith CD (2006) Dopamine-dependent prediction errors underpin reward-seeking behaviour in humans. Nature 442:1042–1045. https://doi.org/10.1038/nature05051

Proudfit GH (2015) The reward positivity: from basic research on reward to a biomarker for depression. Psychophysiology 52:449–459. https://doi.org/10.1111/psyp.12370

Rademacher L, Salama A, Gründer G, Spreckelmeyer KN (2014) Differential patterns of nucleus accumbens activation during anticipation of monetary and social reward in young and older adults.

Soc Cogn Affect Neurosci 9:825–831. https://doi.org/10.1093/scan/nst047

Rescorla RA, Wagner AR (1972) A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and nonreinforcement. Class Cond II Curr Res Theory 21:64–99. https://doi.org/10.1101/gr.110528.110

Sambrook TD, Goslin J (2015) A neural reward prediction error revealed by a meta-analysis of ERPs using great grand averages. Psychol Bull 141:213–235. https://doi.org/10.1037/bul0000006

Schultz W (1997) A neural substrate of prediction and reward. Science (80-.) 275:1593–1599. https://doi.org/10.1126/science.275.5306.1593

Steele K, Stefansson HO (2015) Decision theory. Stanf Encycl Philos. https://doi.org/10.1111/1467-9973.00225

Stevens JP (1991) Intermediate statistics: a modern approach. Detecting outliers. PsycCRITIQUES. https://doi.org/10.1037/031331

Talmi D, Fuentemilla L, Litvak V, Duzel E, Dolan RJ (2012) An MEG signature corresponding to an axiomatic model of reward prediction error. Neuroimage 59:635–645. https://doi.org/10.1016/j.neuroimage.2011.06.051

Talmi D, Atkinson R, El-Deredy W (2013) The feedback-related negativity signals salience prediction errors, not reward prediction errors. J Neurosci 33:8264–8269. https://doi.org/10.1523/JNEUROSCI.5695-12.2013

Thomas J, Vanni-Mercier G, Dreher J-C (2013) Neural dynamics of reward probability coding: a magnetoencephalographic study in humans. Front Neurosci 7:214. https://doi.org/10.3389/fnins.2013.00214

Toyomaki A, Murohashi H (2005) Discrepancy between feedback negativity and subjective evaluation in gambling. NeuroReport 16:1865–1868. https://doi.org/10.1016/j.clinph.2012.03.005

Ullsperger M, Fischer AG, Nigbur R, Endrass T (2014) Neural mechanisms and temporal dynamics of performance monitoring. Trends Cogn Sci 18:259–267. https://doi.org/10.1016/j.tics.2014.02.009

Von Neumann J, Morgenstern O (1944) Theory of games and economic behavior, vol 625. Princeton University Press, Princeton. https://doi.org/10.1177/1468795X06065810

Walsh MM, Anderson JR (2010) Neural correlates of temporal credit assignment. In: 10th International conference on cognitive modeling, ICCM 2010, pp 265–270. http://www.scopus.com/inward/record.url?eid=2-s2.0-84877757970&partnerID=40&md5=f6112d2887e8eb943b50b3e8554a8831

Walsh MM, Anderson JR (2011) Learning from delayed feedback: neural responses in temporal credit assignment. Cogn Affect Behav Neurosci 11:131–143. https://doi.org/10.3758/s13415-011-0027-0

Walsh MM, Anderson JR (2012) Learning from experience: event-related potential correlates of reward processing, neural adaptation, and behavioral choice. Neurosci Biobehav Rev 36:1870–1884. https://doi.org/10.1016/j.neubiorev.2012.05.008

Warren CM, Holroyd CB (2012) The impact of deliberative strategy dissociates ERP components related to conflict processing vs reinforcement learning. Front Neurosci. https://doi.org/10.3389/fnins.2012.00043

Warren CM, Hyman JM, Seamans JK, Holroyd CB (2015) Feedback-related negativity observed in rodent anterior cingulate cortex. J Physiol Paris 109:87–94. https://doi.org/10.1016/j.jphysparis.2014.08.008

Yeung N, Sanfey AG (2004) Independent coding of reward magnitude and valence in the human brain. J Neurosci 24:6258–6264. https://doi.org/10.1523/JNEUROSCI.4537-03.2004