This ought to be good: Brain activity accompanying positive and negative expectations and outcomes

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Abstract

The current study employed a modified gambling task, in which probabilistic cues were provided to elicit positive or negative expectations. Event-related potentials (ERPs) to "final outcome" and "probabilistic cues" were analyzed. Difference waves between the negative condition and the corresponding positive condition were examined. The results confirm that feedback related negativity (FRN) amplitude is modulated by the interaction of outcome valence and expectancy by showing larger FRN difference waves for unexpected than expected outcomes. More interestingly, the difference wave between ERPs elicited by positive and negative expectations showed a negative deflection, with a frontal midline source density around 280 ms after onset of the predictive cue. Negative expectations were associated with larger FRN amplitudes than positive expectations. This suggests that FRN is elicited by probabilistic cues to pending outcomes.

Descriptors: ERN, Error signals, Feedback, FRN, Reward expectancy, Reinforcement learning

Our brains continuously predict future outcomes and compare these predictions with subsequent outcomes. The discrepancy between an outcome and a prior prediction is often called *prediction error*. Prediction errors are critical for learning and decision making because they constitute feedback that can modify future decisions and increase accuracy in similar events or situations (Rescorla & Wagner, 1972; Sutton & Barto, 1998). Thus, prediction error feedback is necessary to improve decision making and performance.

Reinforcement learning-ERN theory (RL-ERN theory) proposes that an event-related potential (ERP) component known as feedback-related negativity (FRN, also called feedback error-related negativity or fERN) is a *reward prediction error* signal (Holroyd & Coles, 2002). FRN is a frontocentral negative-going ERP that originates in the anterior cingulate cortex (ACC; Amiez, Joseph, & Procyk, 2005; Brown & Braver, 2005; Niki & Watanabe, 1979; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Shidara & Richmond, 2002). It peaks around 200 to 300 ms following feedback and differs for unfavorable versus favorable outcomes (Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Miltner, Braun, & Coles, 1997; Nieuwenhuis, Holroyd, Mol, & Coles, 2004). According to RL-ERN theory, an evaluative system monitors ongoing events to predict whether these events will end well or poorly. When the system revises its predictions, such that circumstances are either better than

expected or worse than expected, a respective positive or negative prediction error signal is issued by the midbrain dopamine system to ACC, where that activity manifests at the scalp as an amplitude modulation of the FRN (Holroyd & Coles, 2002). Larger FRN amplitudes are usually observed to be associated with outcomes that are worse than expected (e.g., Holroyd & Krigolson, 2007; Miltner et al., 1997; Ruchsow, Grothe, Spitzer, & Kiefer, 2002; see Nieuwenhuis et al., 2004, for a review). However, because the FRN is analyzed by using a difference waves approach, the difference between negative feedback trials and positive feedback trials might also be caused by a larger positive-going deflection in the time range of the fERN elicited by positive feedback (Holroyd, Pakzad-Vaezi, & Krigolson, 2008).

Consistent with the RL-ERN theory, previous studies have shown that the amplitude of the FRN is modulated by an interaction of feedback valence and expectancy: Specifically, larger FRNs are elicited by unexpected negative feedback (Holroyd & Coles, 2002; Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003; Nieuwenhuis, Nielen, Mol, Hajcak, & Veltman, 2005). Moreover, the modulation of the interaction between outcome valence and expectancy on FRN amplitude has a larger effect when the prediction–outcome association is stronger. Larger FRNs are elicited for outcomes that are at odds with relatively more salient subjective outcome predictions (Hajcak, Moser, Holroyd, & Simons, 2007; Moser & Simons, 2009) or if the outcome was less predictable (Sailer, Fischmeister, & Bauer, 2010). In other words, reward prediction error seems to depend not only on valence, but also on the degree of the prediction–outcome discrepancy.

As the brain constantly updates outcome predictions based on past experiences and current stimuli, prediction errors can be

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elicited not only by a discrete outcome, but also by cues that update or modify a prediction. Dunning and Hajcak (2007) reported that the error-related negativity (ERN)[1] was elicited by cues that predicted with certainty an impending loss, but not by cues that predicted with certainty an impending win. Krigolson and Holroyd (2007) also demonstrated that external predictive visual information – predictive error comparison between an internal motor command and related behavior elicits an ERN-like waveform. Baker and Holroyd (2009) reported that the FRN is modulated by predictive cues indicating the absence versus the presence of a reward in a "virtual T-maze" environment. These results suggest that FRN/ERN can be elicited not only by discrepant outcomes, but also by cues that signify a future outcome.

However, prediction cues in these earlier studies perfectly predicted all of the outcomes, and it remains to be determined whether external cues that *probabilistically* predict an outcome will also elicit a FRN. Cues to a future outcome can lead us to modify our predictions, but these cues are almost never perfectly predictive. In many situations we predict outcomes in a probabilistic and incremental fashion, based on an accrual of imperfect cues and information. Even when we are confident about a prediction, it is still possible that an outcome will violate the prediction; that is, outcome cues seldom are absolutely perfect. Thus, it is important to test whether RL-ERN theory can predict people's responses to *probabilistic* outcome cues. This will indicate to what extent RL-ERN theory can account for brain activity associated with everyday prediction.

To investigate whether FRN is associated with cues that indicate probabilistic pending outcome, the current study employed a modified gambling task in which predictive cues with probabilistic outcomes were presented after participants made selections but prior to the final outcomes. ERPs time-locked to cue stimuli were examined, as well as ERPs time-locked to final outcomes. According to RL-ERN theory, FRN should be elicited by predictive cues, and larger FRN amplitude should be elicited by cues indicating negative outcomes than cues indicating positive outcomes.

Method

Participants

Nineteen undergraduate students volunteered to participate. Four subjects had to be removed from the study because of excessive artifacts in the electroencephalogram (EEG) recordings. The remaining subjects (8 women, 7 males), aged 20 to 25 years (mean = 22.1, $SD = 1.2$) had normal or corrected-to-normal vision, were right-handed, and had no self-reported diagnosed neurological or psychological disorders. The University's Ethics Committee approved the study. Participants received RMB ¥23–¥26 (about $3.80–$4.30) for their participation, with exact payment dependent on performance (see below).

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1. ERN is a negative-going, midfrontally distributed potential that is elicited by errors on speeded response tasks. It has also been used for an entire class of error related negativity ERP components (i.e., response ERN, FRN, etc.). The ERN here indicts an ERP component that shared a similar latency and morphology with the traditional FRN.

Experimental Design and Procedure

Participants were seated comfortably ~1 m in front of a computer screen in an electromagnetically shielded room. Before the initial training phase, participants were told that they would play a gambling game and that there was a triangle or a square on the back side of two "cards" (i.e., squares on a computer monitor). Participants received 20 training trials to make sure that they understood the task. On each trial one of the shapes was designated the winner. Participants were asked to guess which of the two cards had the winning shape on the other side. Participants were told they would receive 100 points for every winning trial, and their final payment would be based on their total points at the end of the experiment. They were encouraged to maximize their winnings.

Additionally, participants were told that in each block some complicated rule would dictate which shape would win. They were told that in most trials (80%, although participants were not told the exact percentage) the card with the triangle was on the left and the square was on the right; however, the two cards would occasionally switch positions. Participants were advised to assume that the left card would have the triangle and the right card would have the square in order to maximize their chances to win. When participants finished the task, they were interviewed about whether, and how, they had tried to figure out the rule throughout the task.

As shown in Figure 1, each trial had two stages. Participants' outcome predictions were induced in the first stage: *expectancy generation*. In this stage, two cards were displayed face down, and participants could choose a card by pressing "1" for the left card and "2" for the right, using the index and middle fingers of their right hand. After participants selected a card, a prediction cue—the *winning shape*—was presented in the center of the monitor. This indicated which shape was the winner in a given trial. The winning shape on every trial was selected randomly (with a cumulative proportion of .50 per shape). Because participants knew which card (i.e., left or right) was most likely to have each shape (i.e., triangle or square), they could predict whether their choice would be right or wrong, that is, whether the outcome would be positive or negative. This prediction was the *generated expectancy*. Their expectation was positive if the winning shape was usually at the chosen location and negative if it was usually at the nonchosen location. To check that expectancy generation worked as intended, during the first five practice trials, after the winning shape was shown, participants were asked, "Do you think you will win or lose in this trial?" All of their answers indicated that they had learned the probabilistic rule that would generate expectancies.

In the second stage of each trial, participants received a *final outcome*. In 80% of trials this was congruent with participants' expectancies; in 20% it was not. In half of the congruent trials (40% of all trials), participants expected to be correct, and indeed positive feedback was displayed ("ΥΥΥΥ"). In the other half (40%), participants expected to be incorrect and indeed saw negative feedback ("0000"). In half of the incongruent (unexpected) trials (10% of all trials) negative feedback ("0000") was displayed after a positive expectancy. In the other half of incongruent trials (10%) positive feedback ("ΥΥΥΥ") was displayed after negative expectancy. Unexpected trials were separated by at least three expected trials.

This design produced four conditions when the final outcome was presented: (i) expected positive outcomes, (ii) expected
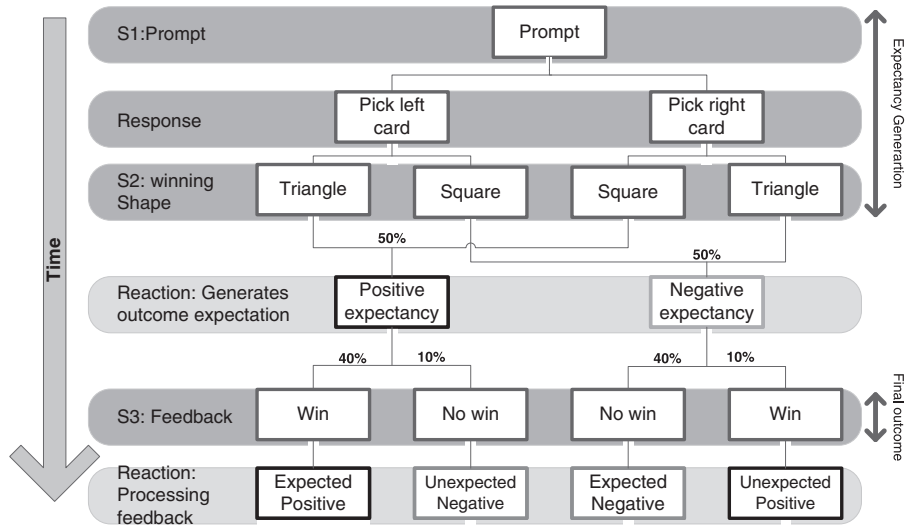
Figure 1. Flowchart of the events in the task, with expectancy generation and outcome feedback noted.

negative outcomes, (iii) unexpected positive outcomes, and (iv) unexpected negative outcomes.

The time course of a trial is shown in Figure 2. Each trial started with a fixation cross lasting for 500 ms, followed by the two cards facing down. The prompt picture was displayed until participants selected one of the cards, which then was highlighted. Then a fixation cross was displayed for 500 ms, followed by the winning shape for 1000 ms. Then a blank screen was shown for a random period of 1000 to 1500 ms, followed by the fixation cross for 500 ms and then the final outcome for 1000 ms. The intertrial interval was 500 ms. Participants were informed of their cumulative winnings at the end of each block of 100 trials. There were 800 trials divided into eight blocks.

EEG Methods

The EEG was recorded continuously at 500 Hz from 64 Ag/AgCl electrodes placed according to the 10-10 system (American Electroencephalographic Society, 1994). Electrodes were mounted on an elastic cap (Easy Cap, Munich, Germany). Vertical and horizontal eye movements were monitored by electrodes placed on the outer canthi of the eyes and the superior and inferior orbits of the left eye. Electrophysiological signals were amplified using BrainAmps (BrainProducts, Munich) with a 0.01 to 100 Hz bandpass filter. The data was low-pass filtered off-line

(40 Hz, 24 dB). All electrodes were referenced to the right mastoid during recording and re-referenced off-line to the average of both mastoids. Subsequently, eye movements were corrected by independent component analyses (ICA) of the continuous data, using Brain Vision Analyzer software (Brain Products, Munich). ERPs were averaged off-line for 800-ms epochs relative to a 200-ms prestimulus baseline. Epochs with artifacts, including excessive peak-to-peak deflections (>100 mV), bursts of electromyographic activity (exceeding maximal voltage step/sampling points of 50 mV), and activity lower than 0.5 mV within intervals of 100 ms, were excluded from averaging on an individual-channel basis.

EEG Measures

Separate epochs were extracted for the onset of the winning shape (positive vs. negative expectancy) and for the final outcome display (expected positive, expected negative, unexpected positive, unexpected negative). These were time–locked to the onset of the stimulus display.

To minimize variance associated with FRN that could have arisen from other overlapping ERP components, difference waves were created. These were calculated by subtracting each type of positive-outcome ERP from its corresponding negative-outcome ERP (Hajcak, Holroyd, Moser, & Simons, 2005;
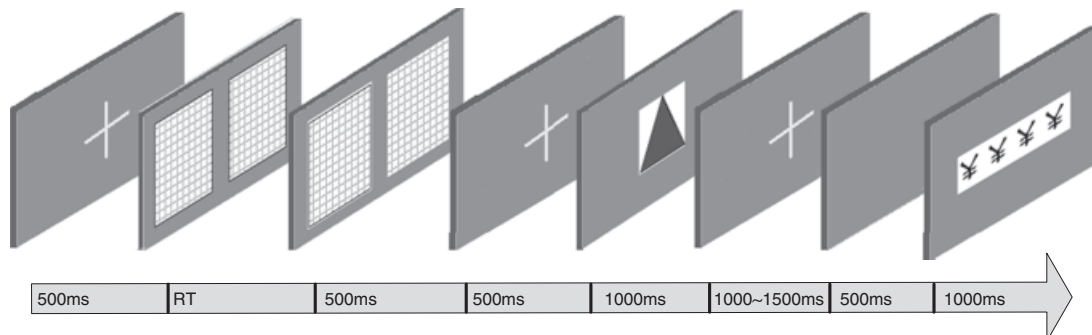

Figure 2. Sequence and durations of stimuli and events in each trial.

Holroyd & Krigolson, 2007). Specifically, for each participant and channel, we created three FRN difference waves by (1) subtracting the positive expectancy ERP from the negative expectancy, creating a "expectancy" difference wave; (2) subtracting the positive outcome related ERP in the expected condition from the negative outcome related ERP in expected condition, creating an "expected-outcome" difference wave; and (3) subtracting the positive outcome related ERP in the unexpected condition from the negative outcome related ERP in the unexpected condition, creating an "unexpected-outcome" difference wave. We first detected the peaks of FRNs as the most negative deflection within 150 to 500 ms following the winning shape or the feedback stimulus onset for each individual. Maximum FRN amplitudes were aggregated with neighboring amplitude values (peak maximum ± 10 ms) and analyzed for midline channels Fz, Cz, and Pz. The FRN was statistically evaluated using SPSS (version 15.0) software. For all analyses of variance (ANOVAs), the degrees of freedom were Greenhouse–Geisser corrected when appropriate. Current source density was computed using spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989, 1990). The spline number was set to be 4 and the maximal degree of Legendre polynomials was 10. The default lambda was set to 1E-5.

Results

Behavioral Results

To ensure the validity of the data, we analyzed whether participants were, in fact, trying to figure out the winning rule. This would indicate that they remembered the instructions and were motivated to succeed. To rule out any simplistic strategy such as a side bias, we examined the data for nonrandom patterns of answers that were not tied to the cues or reward contingencies. To this end, we calculated the percentage of trials on which each participant selected the left card ($P[l]$) and the right card ($P[r]$). We then examined how often participants selected the left card just after selecting the left card ($P[l/l]$) or right card ($P[l/r]$), and how often they selected the right card just after choosing the left card ($P[r/l]$) or the right card ($P[r/r]$). We assumed that if participants followed the task demand to figure out the rule that determined the winning shape, they would not randomly select the cards but would attempt to infer some kind of rule, which would be evident in nonrandom sequences of responses. Thus, if participants have a side bias, their overall choice of left versus right cards should be nonrandom; by contrast, if they are choosing strategically, their current response should not be independent of the previous choice.

Overall, participants selected left cards as often as right cards. No difference was found between $P(l)$ (mean = .52; SD = .05) and $P(r)$ (mean = .48; SD = .05). Thus, participants had no side bias. However, $P(l/l)$ was significantly higher than $P(r/l)$, $t(14) = 4.39$, $p < .01$, and $P(r/r)$ was significantly higher than P(l/r), $t(14) = 2.51$, $p < .05$, indicating that card selection was partly dependent on the previous trial. The result suggests that participants believed that they could learn the rule and therefore continuously tried to update their expectancies. Participants' exit interviews also confirmed this: All participants reported that they tried to figure out the rules that dictated the winning shape. Thus, the behavioral data showed that participants were motivated and followed the task instructions.

ERPs Time-Locked to the Predictive Cue

Negative-expectancy trials were associated with a frontal negative-going deflection that peaked approximately 280 ms after onset of the predictive cue (the winning shape; Figure 3). Figure 3 also presents the difference waves for the three midline electrodes (Fz, Cz, and Pz) obtained by subtracting positive expectancy from negative expectancy. Table 1 presents the average FRN amplitudes at each recording site. The FRN amplitude was maximal at channel Fz and declined toward more posterior sites. A repeated measures ANOVA revealed significant differences for channel location (frontal, central and parietal), $F(2,28) = 9.44$, $p < .01$, $\eta^2 = .403$. A post hoc LSD test showed FRN amplitude to be significantly larger at Fz as compared to Cz ($p < .05$ or, at Pz, $p < .01$), and FRN amplitude to be larger at Cz as compared to Pz ($p < .05$). Figure 3 also shows the scalp current density of the difference wave at 288 ms as well as the topographic distribution of the component. Both of these features revealed a prominent frontal midline distribution.

FRN Time-Locked to the Final Outcome

We obtained average ERPs for positive and negative feedback for expected and unexpected outcomes at Fz, Cz, and Pz (see Figure 4). Consistent with previous studies, negative outcome was associated with a frontally maximal negative deflection that peaked approximately 290 ms following the final outcome. Figure 5 presents the difference wave obtained by subtracting positive from negative feedback for both levels of expectancy (expected negative minus expected positive and unexpected negative minus unexpected positive) as well as the associated source densities. Table 1 presents the average FRN amplitudes at each recording site. A 2×3 repeated measures ANOVA on difference wave amplitudes with the factors expectancy (expected vs. unexpected) and location (Fz, Cz, and Pz) revealed significantly larger FRN amplitudes for unexpected than expected outcomes, $F(1,14) = 21.16$, $p < .001$; $\eta^2 = .602$. That is, when the feedback was unexpected, it had a greater impact on FRN amplitudes. In addition, there was a main effect of location, $F(2,28) = 6.98$, $p < .01$; $\eta^2 = .332$. Consistent with the fronto-central maximum reported in previous studies, post hoc tests indicated that the FRN was larger at Fz and Cz as compared to Pz ($p < .01$ and $p < .01$, respectively) but that FRN amplitude was not significantly different at Fz and Cz ($p = .903$). The interaction of expectancy and location did not reach significance.

Comparison between Cue-Related and Outcome-Related FRN

A 3×3 repeated measures ANOVA for difference wave amplitudes with the factors location (Fz, Cz, and Pz) and FRN class (cue-related FRN, expected outcome-related FRN vs. unexpected outcome-related FRN) revealed significant differences in FRN amplitudes at different electrode locations, $F(2,28) = 11.29$, $p < .01$, $\eta^2 = .446$. Post hoc tests indicated that FRN amplitudes were larger at Fz and Cz as compared to Pz (all $ps < .01$) but showed no difference between Fz and Cz ($p = .618$). In addition, the main effect of FRN class reached significance, $F(2,28) = 13.91$, $p < .01$, $\eta^2 = .50$. Post hoc tests revealed that predictive cues elicited smaller FRN amplitudes as compared to unexpected outcomes ($p < .01$), but predictive cues elicited marginally significant larger FRN amplitudes than expected
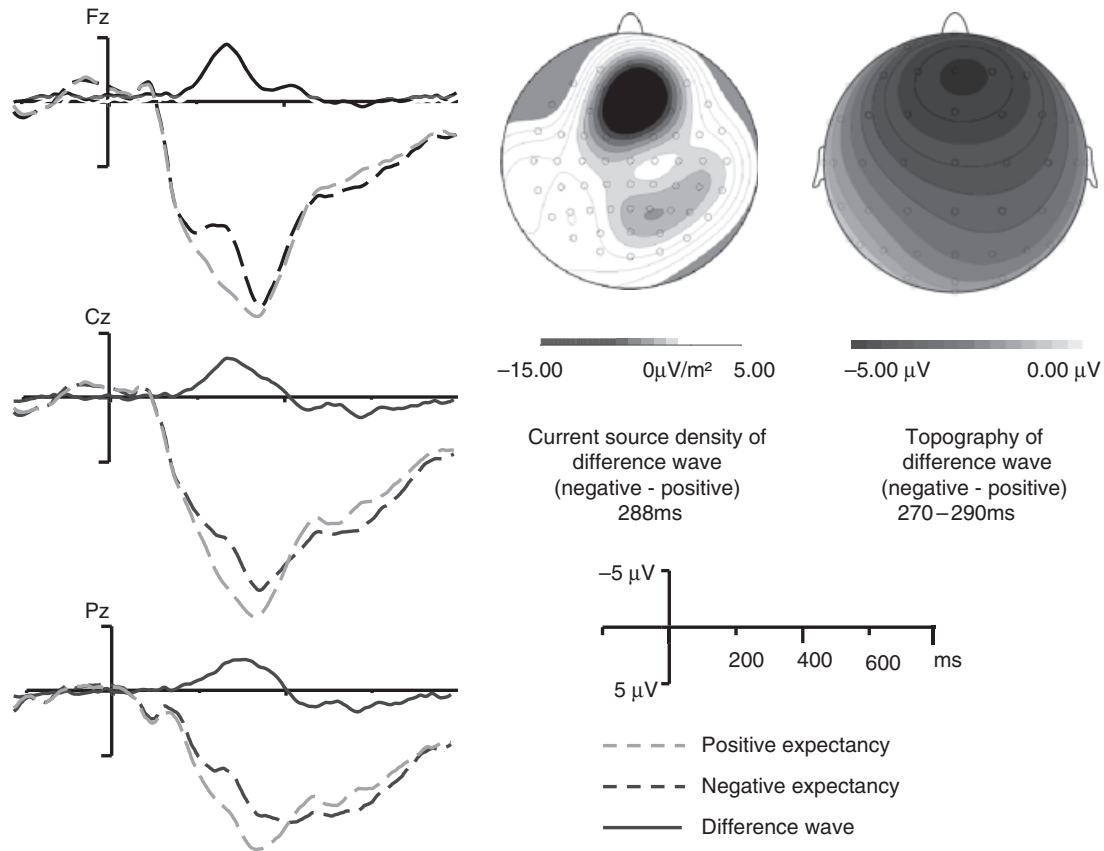
Figure 3. Grand-average ERPs at Fz (top), Cz (middle), and Pz (bottom) time-locked to the winning shape stimulus. The gray dashed line represents positive expectations, the black dashed line represents negative expectations, and the black line represents the difference wave between negative and positive expectations. The inset shows the scalp current density of the difference wave at 288 ms and the topography during 270 to 290 ms. A middle frontal distribution is apparent.

outcomes ($p = .072$). The interaction did not reach significance, $F(4,56) = 1.285$, $p = .293$.

Discussion

The current study examined whether the FRN is elicited by cues that only probabilistically predict impending outcomes. Unlike previous studies, in our modified gambling task, predictive cues (the winning shape) were presented after participants made a selection but prior to the final outcome. The winning shape did not carry any direct information about the value of the final outcome. That is, neither shape was differentially associated with wins or losses. The resulting prediction of a final win or loss required participants to interpret the cue relative to their own

Table 1. *Mean (M) and Standard Deviation (SD) for FRN Magnitudes (in Microvolts)*

			Outcome-locked			
	Cue-locked		Expected		Unexpected	
Electrode	M	SD	M	SD	M	SD
Fz	− 5.53	3.35	− 4.22	3.21	− 9.03	3.81
Cz	− 4.27	2.43	− 4.16	3.06	− 9.01	4.62
Pz	− 3.70	2.07	− 3.64	2.39	− 7.46	3.49

choice and relative to the probable location of the winning shape. Thus, participants' expectations were probabilistic. Consistent with the typical features of FRN, the component we examined (i.e., difference wave between the negative and positive expectancy trials) showed a negative deflection peaking approximately 290 ms after the winning shape onset. The current source density and topographic maps of this component indicated a maximum over the frontal midline. In addition, statistical comparisons of cue- and outcome-related FRN amplitudes indicate a functional equivalence of both components in the sense that there were no differences in topographic distribution and no difference in the topography of the FRN regardless of its association with probabilistic cues or deterministic outcomes. Instead, outcome-related FRN amplitudes were smaller for expected outcomes as compared to FRNs associated with cue onset, but larger for unexpected outcomes as compared to cue-related FRN amplitudes. These results indicate functional equivalence for cue- and outcome-related FRNs, with additional modulation of FRN amplitude based on the final outcomes. Based on these results, we conclude that FRN is also associated with probabilistic outcome prediction.

Several studies showed that FRN/ERN was associated with predictive cues; however, the cues were definite predictors and not probabilistic (Baker & Holroyd, 2009; Dunning & Hajcak, 2007; Krigolson & Holroyd, 2007). Dunning and Hajcak asked participants to select one out of two doors (on a computer screen) to get a reward. Prior to participants' selection, a white "0," "1," or "2" cue was presented to inform participants about how many
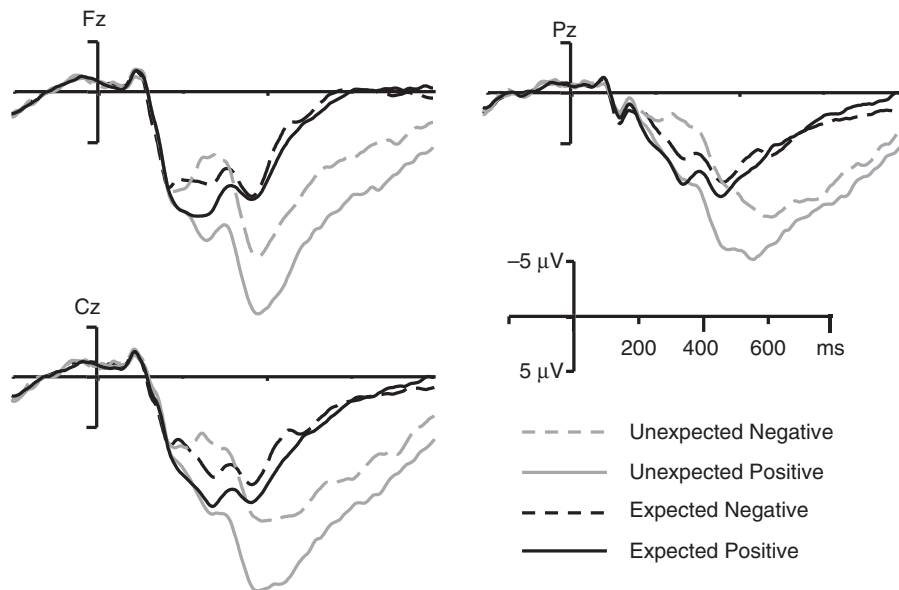
Figure 4. Grand-average ERPs at Fz (left top), Cz (left bottom), and Pz (right top) locked with onset of the final outcome stimulus as a function of expectancy and valence: won-as-expected (expected-positive), lost-as-expected (expected-negative), won unexpectedly (unexpected-positive), lost unexpectedly (unexpected-negative). Dashed lines represent average waveforms for all negative (lost) trials; solid lines represent positive (won) trials. Darker lines represent expected trials; lighter lines represent unexpected trials.
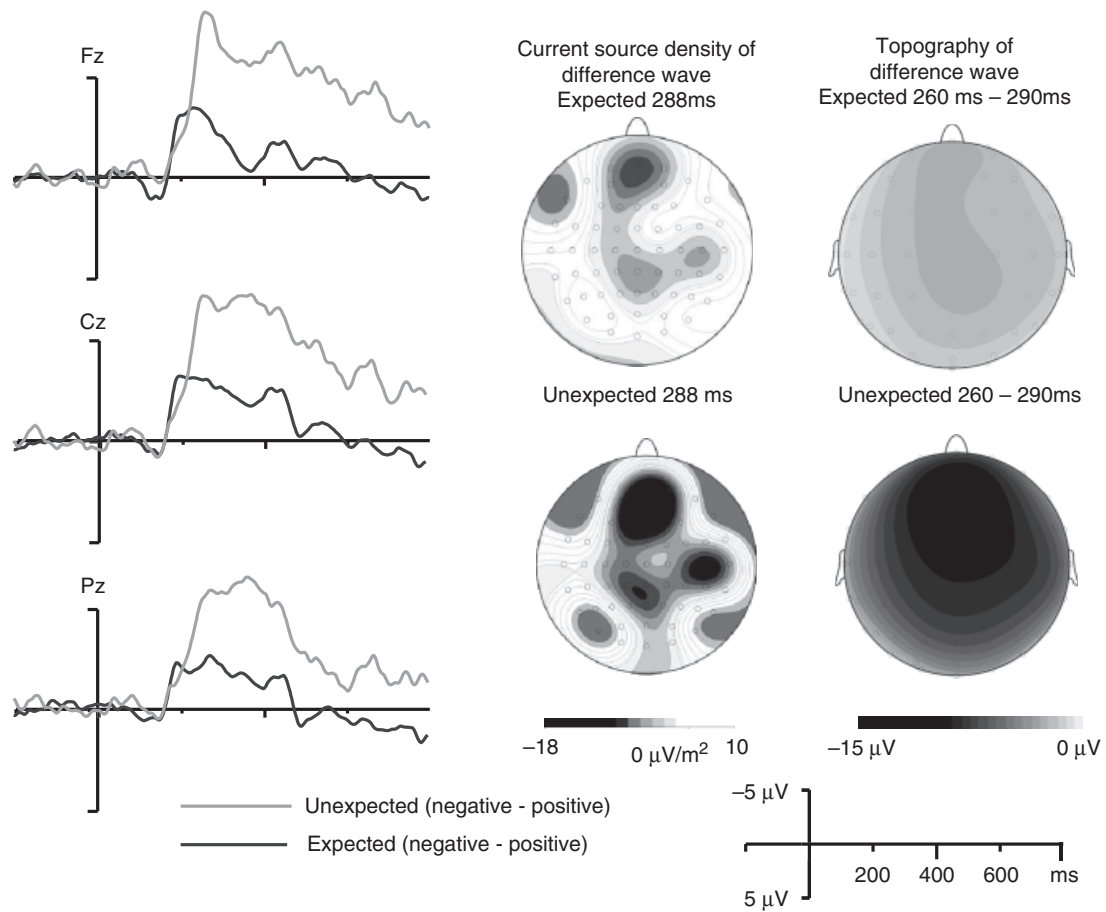

Figure 5. Grand average difference waves (negative–positive) time-locked to expected and unexpected outcomes at Fz (top), Cz (middle), and Pz (bottom). The gray lines represent the unexpected-outcome difference waves; the black lines represent the expected-outcome difference waves. The inset shows the associated scalp current density and topography for each difference wave.

of the doors would contain a prize on that trial. They found that a "0" cue that predicted an upcoming loss elicited an ERN. In Krigolson and Holroyd's (2007) study, participants used a joystick to perform a computer-based continuous tracking task in which some tracking errors were inevitable. Half of these errors were preceded by a predictive cue. They reported that an ERN-like waveform was elicited by tracking errors. More recently, Baker and Holroyd reported that when participants were asked to find a reward in a "virtual T-maze" environment, predictive cues indicating the absence versus presence of a reward differentially modulated FRN amplitudes.

In all of these studies, the cues were definite predictors of a win or loss. In such studies the "cue" essentially serves as perfect error feedback. By contrast, the current study proved that FRNs are elicited by probabilistic expectancy-generating cues and that the amplitude is greater when the outcome is expected to be negative. Thus, the FRN is sensitive to positive/negative evaluation of one's performance relative to probable outcomes, even if those outcomes are uncertain.

Also, ERPs locked to the feedback given at the end of the trial confirm the interaction between outcome valence and expectancy in FRN amplitude (Holroyd & Coles, 2002; Holroyd & Krigolson, 2007; Holroyd et al., 2003; Nieuwenhuis et al., 2005). Difference waves between positive and negative trials show a larger FRN difference following unexpected outcomes, but a relatively small FRN difference following expected outcomes. According to Holroyd et al. (2008), negative difference waves are not due to a negative potential elicited by negative feedback, but are, in fact, due to a positive-going deflection elicited by the positive feedback in the time range of the FRN. In the authors' view, the FRN is essentially another form of the N200 that is elicited by negative feedback and is modulated by the superposition of a positive-going deflection on correct trials, which they call the feedback-correct-related positivity (fCRP). Unexpected positive feedback elicits a larger fCRP than expected positive feedback. Consistent with this view, our results demonstrate more positive-going ERP deflections when the final outcome was unexpected and positive as compared to expected and positive. This might contribute to the main effect of larger ERP difference waves when the final outcomes were unexpected than when they were expected.

The fCRP, however, does not seem to account for the cue-related data because there does not seem to be an obvious difference in positivity between the two waveforms. Compared to FRNs that are associated with final outcomes, the present results revealed smaller cue-related FRN amplitudes than unexpected *outcome*-related FRN, but slightly larger cue-related amplitudes than *expected* outcome-related FRN (marginally significant). The results are consistent with the prediction of RL-ERN theory that FRN amplitude is positively related to the size of the outcome prediction error (Holroyd & Coles, 2002; Holroyd, Krigolson, Baker, Lee, & Gibson, 2009). In the current study, unexpected outcomes generated a large prediction error whereas expected outcomes generated a small prediction error. This is because the discrepancy between participants' expectation and outcome is large when outcome is unexpected and this discrep-

ancy (if any) is small when outcome is expected. A prediction error also occurred when the predictive cue indicated a negative outcome. This is due to the discrepancy between participants' initial expectation of the outcome when they selected a card and their updated expectations when the predictive cue was presented. Given that participants' initial expectations would not be so strong because they had limited information (i.e., their prior probabilities) and that predictive cue is only probabilistic, the size of the prediction error generated by the predictive *cue* was not as big as the one generated by unexpected outcomes, but larger than the one generated by expected outcomes. That is, it was of intermediate magnitude. The variance in FRN difference-wave amplitudes thus seem to be related to the magnitude of the prediction error in each condition.

In sum, ERPs time-locked to outcome feedback replicate previous findings that the FRN amplitude is modulated by an interaction of outcome valence and outcome prediction. In addition, the current study is the first to demonstrate that FRN could be elicited by cues that probabilistically predict impending outcome. The FRN elicited by predictive cues peaked around 280 ms after stimuli onset and revealed a maximum over the frontal midline. This was similar to FRN elicited by unexpected outcomes. It is also consistent with previous reports on FRN. Thus, the results are consistent with RL-ERN theory. According to RL-ERN theory, FRN is a reward prediction error signal. When ongoing events are worse than expected, phasic decreases in the midbrain dopamine system are issued to anterior cingulate cortex, such that a large FRN is produced (Holroyd & Coles, 2002). The theory holds that any reward prediction error will modulate FRN amplitude. The results also are consistent with single-neuron recordings from dopamine-efferent cells in non-human animals. Single-neuron recordings from DA neurons in rats or primates have shown that when an animal is presented with a conditioned cue that predicts a future reward, phasic responses are induced that encode an expectation of the time of reward as well as a prediction error if the outcome does not occur (Roesch, Calu, & Schoenbaum, 2007; Schultz, 2006). One of the main projection regions of midbrain dopaminergic nuclei, the striatum, encodes the expected value of possible actions as well as the difference between the expected and obtained values of the results of actions (Samejima, Ueda, Doya, & Kimura, 2005). Similar parallels have been found in ACC, which is the likely source of the FRN, and is another prominent target of DA projections (Williams & Goldman-Rakic, 1998). ACC neurons in nonhuman primates encode a reward prediction that includes information about reward magnitude and reward probability (Amiez, Joseph, & Procyk, 2006; Matsumoto, Suzuki, & Tanaka, 2003). Furthermore, ACC neurons encode a quantitative reward prediction error of the outcome (Amiez et al., 2005; Matsumoto, Matsumoto, Abe, & Tanaka, 2007; Seo & Lee, 2007). The current results support the view that FRN is a reward prediction error signal in humans. They suggest that FRN is sensitive to reward prediction errors that are signaled by discrepant outcomes as well as reward prediction errors that are based strictly on probabilistic predictive cues.

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