

Research Report

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or MFN (i.e., medial-frontal negativity), which is a negative deflection at frontocentral recording sites that reaches maximum between 250 and 300 ms post-onset of feedback stimulus (Gehring and Willoughby, 2002; Heldmann et al., 2008; Holroyd and Coles, 2002; Holroyd, 2004; Nieuwenhuis et al., 2004; Miltner et al., 1997; Yu and Zhou, 2006a, 2006b). The FRN is more pronounced for negative feedback associated with unfavorable outcomes, such as incorrect responses or monetary losses, than for positive feedback. Another component is the P300, which is the most positive peak in the 200–600 ms period post-onset of feedback and which typically increases in magnitude from frontal to parietal sites.

It has been claimed that the FRN and the P300 encode different aspects of outcome evaluation (Yeung and Sanfey, 2004). While the FRN is sensitive to feedback valence, the P300 is sensitive to the magnitude of reward, with a more positive response to a larger (whether positive or negative) than to a smaller reward (Sato et al., 2005; Yeung and Sanfey, 2004). In contrast, feedback valence has no impact upon the P300 (Sato et al., 2005; Yeung and Sanfey, 2004). Yeung and Sanfey (2004), for example, asked the participant to choose between cards that were unpredictably associated with monetary gains or losses of various magnitudes. After selection, a positive or a negative number appeared on the chosen card to indicate how much money the participant won or lost on that trial. After an additional interval, the participant was shown what he would have won or lost had he selected the alternative card. It was found that the P300 was insensitive to the valence of the actual outcome but was sensitive to the valence of the alternative outcome, with a larger P300 associated with a positive outcome. The authors concluded that the valence effect on the P300 is observed when valence is defined in terms of high-level motivational/affective evaluations, such as regret or disappointment, but not when valence is defined in terms of the straightforward reward value. However, other studies found that the P300 is sensitive to reward valence as well as to reward magnitude in monetary gambling tasks, with more positive amplitudes for positive feedback than for negative outcomes (e.g., Hajcak et al., 2005, 2007; Holroyd et al., 2006; Yeung et al., 2005).

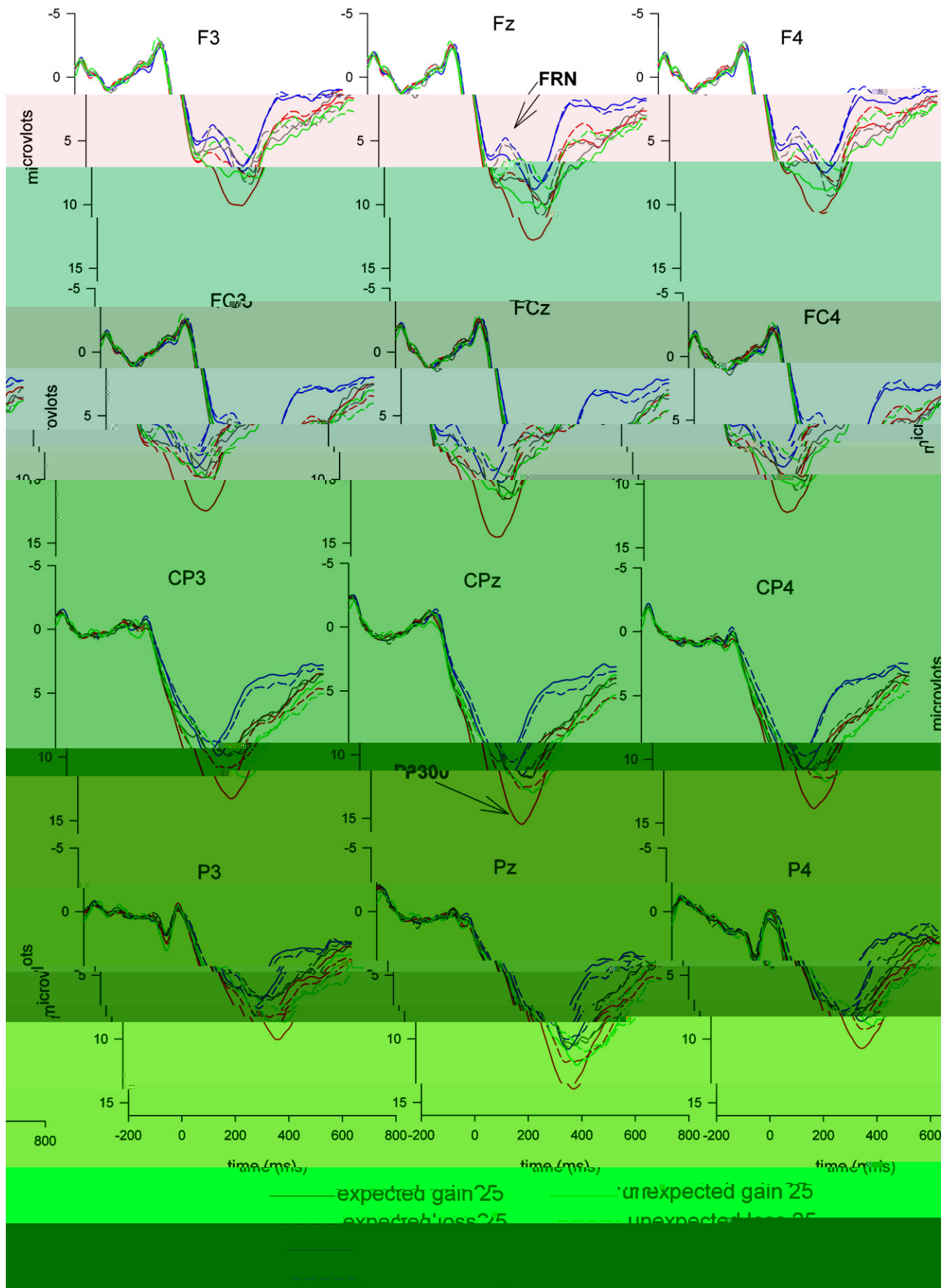
Another aspect of the significance of feedback is the probability of the positive or negative outcome experienced by the participant. This probability, manipulated either on a trial-by-trial basis (Hajcak et al., 2005, 2007) or in a blocked manner (Cohen et al., 2007; Hajcak et al., 2005; Holroyd et al., 2003; Holroyd and Krigolson, 2007), would allow the participant to form expectancy towards a particular outcome and hence could affect brain responses to the upcoming feedback. Although these studies reported inconsistent results regarding whether the FRN effect is affected by this probability manipulation, they provided evidence that the P300 is modulated by the probability, with more positive amplitudes to unexpected feedback than to expected feedback (Hajcak et al., 2005, 2007). This pattern of the P300 effect is consistent with earlier studies employing the classic oddball paradigm and manipulating the probability of the appearance of a particular stimulus (Courchesne et al., 1977; Duncan-Johnson and Donchin, 1977; Johnson and Donchin, 1980).

The main purpose of this study is to provide further evidence for the impacts of reward valence, reward magni-

tude, and a previously unexamined form of expectancy, magnitude expectancy, upon the P300 in outcome evaluation. Importantly, we investigate to what extent these aspects of feedback would interact to determine the pattern of the P300 effect (and also the pattern of the FRN effect). To achieve this aim, we used a cued gambling task in which a cue about the amount of monetary reward in the current trial (e.g., the number “25”, standing for 2.5 Chinese yuan) was first presented, followed by the participant’s selection of a choice card. Finally, a feedback stimulus (e.g., “+25” or “+5”) was presented, which encoded information concerning the valence of reward (gain or loss), the magnitude of reward (a small or a larger amount of money), and magnitude expectancy (whether the amount of reward was consistent or inconsistent with expectation built upon the magnitude of the cue number). Note that, most previous studies manipulated reward expectancy by presenting a particular, valenced outcome with a specific probability in a testing block or in the whole experiment. Here the magnitude expectancy was built upon whether the magnitude of reward (the gain or loss outcome) was consistent with the magnitude of the cue presented at the beginning of a trial. Although this cue was valid in 80% of the trials (i.e., the cue “25” was followed by the reward “25” or the cue “5” was followed by the reward “5”), the valence of feedback was still unpredictable (i.e., gain or loss in 50% of the trials). By measuring ERP responses to the feedback stimuli, we would be able to examine the main effects of reward valence, magnitude and expectancy, as well as interactions between them on the P300.

We hypothesized that outcome evaluation can be roughly divided into two related processes: an early evaluation of the cognitive or motivational significance of the feedback stimuli, followed by more elaborative evaluation, in which factors that affect the allocation of attentional resources, such as intentionality or expectancy, come into play in a top-down controlled manner (Goyer et al., 2008; Leng and Zhou, in revision). On this view, reward valence, reward magnitude, and magnitude expectancy may modulate the amplitude of the P300, which represents the controlled process in outcome evaluation. It is not clear, however, whether these factors would interact in modulating the amplitude of the P300. Previous studies found that the impacts of reward valence and reward expectancy on the P300 are generally non-interactive (e.g., Hajcak et al., 2005, 2007). On the other hand, it is not clear either whether reward magnitude or magnitude expectancy would affect the early process represented by the FRN given that evidence concerning this issue is either contradictory or lacking. While some studies found that the FRN is insensitive to the reward magnitude (Hajcak et al., 2006; Holroyd et al., 2006; Sato et al., 2005; Polezzi et al., 2008; Toyomaki and Murohashi, 2005; Yeung and Sanfey, 2004), other studies obtained a magnitude effect on the FRN (Goyer et al., 2008; Marco-Pallares et al., 2008). The inconsistency may partly be caused by different parameterization of the FRN in those studies.

There are essentially three ways to measure the FRN or the FRN effect. The first way is to measure the base-to-peak or peak-to-peak difference, defining the FRN as the difference between the most positive point (P2) and the most negative point (N2) in the 150–350 ms time window post-onset of



feedback (Holroyd et al., 2003; Holroyd, 2004; Holroyd et al., 2006; Hajcak et al., 2006; Nittono et al., 2008; Sato et al., 2005). If there is no negative deflection in the 150–350 ms time window, as in many cases of positive feedback, the FRN is scored as zero. A problem with this measurement is that the positive feedback itself elicits a positive response and by setting its FRN as zero, the FRN effect (i.e., the differential ERP responses to negative and positive feedback) would be underestimated (Holroyd et al., 2008; Potts et al., 2006). The second way of measurement is to compute the mean amplitude in a time window (say, 200–300 ms) post-onset of feedback for gain and loss trials respectively and to enter mean amplitudes into statistical analyses (Gehring and Willoughby, 2002; Marco-Pallares et al., 2008; Yeung et al., 2005; Yeung and Sanfey, 2004). The third way of measurement, essentially the same as the second, is to compute the loss-minus-gain difference and use either the mean amplitude or the peak value of the difference wave in a time window as the FRN effect (Cohen and Ranganath, 2007; Hajcak et al., 2005, 2007). A problem with the second and the third methods is that the computation of mean amplitudes or the loss-minus-gain differences may be affected by the following P300, which could respond differentially to experimental conditions. One way to minimize this confound is to remove slow wave ERP responses, with which the P300 is associated, through bandpass filtering (Donkers et al., 2005; Heldmann et al., 2008; Luu et al., 2003). In this study we analyzed the FRN effects by using the mean amplitudes of ERP responses to different trials after bandpass filtering.

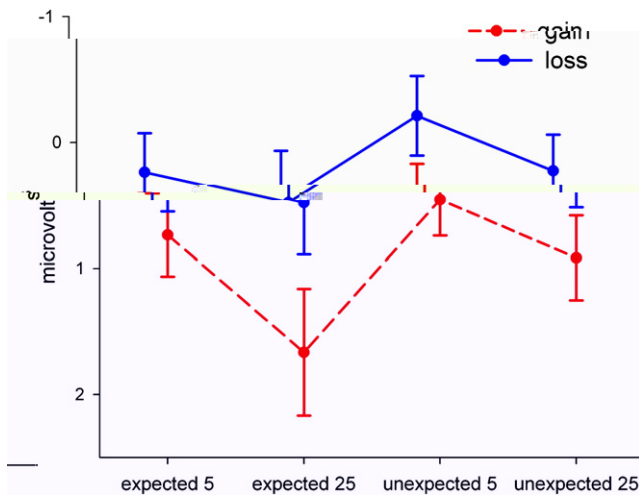


Fig. 2. ERP amplitude (microvolts) for gain and loss conditions across four expectation levels: expected 5, expected 25, unexpected 5, and unexpected 25. Error bars represent standard error.

(1, 15)=8.85, $p < 0.01$, with the FRN effect being larger in the midline than on the left or right hemisphere and being larger at the Fz row than at the FCz row. There was a three-way interaction between magnitude expectancy, reward magnitude and valence, $F(1, 15)=6.72$, $p < 0.05$, but no two-way interactions between these variables. This three-way interaction was mainly caused by the surprisingly more positive ERP responses to the expected large gain (see Fig. 2). Separate analyses of ERP responses to loss feedback found a significant main effect of magnitude expectancy, $F(1, 15)=10.45$, $p < 0.01$, and a main effect of reward magnitude, $F(1, 15)=5.37$, $p < 0.05$. Importantly, the interaction between magnitude expectancy and reward magnitude was not significant, $F(1, 15) < 1$, indicating that the three-way interaction in the overall analysis was not caused by the variation of ERP responses in loss trials. Analyses of ERP responses to positive feedback obtained also a significant main effect of magnitude expectancy, $F(1, 15)=6.44$, $p < 0.05$, and a main effect of reward magnitude, $F(1, 15)=13.29$, $p < 0.005$. But unlike the loss trials, the interaction between magnitude expectancy and reward magnitude approached significance, $F(1, 15)=4.35$, $p=0.055$. It is clear from Fig. 2 that this interaction was caused by the more positive ERP responses to the expected large gain. Detailed analyses confirmed this observation. While the difference between the expected and the unexpected small gains was not significant, $F(1, 15)=2.07$, $p > 0.1$, the difference between the expected and the unexpected large gains was significant, $F(1, 15)=8.05$, $p < 0.05$. Analyses of the FRN effects on Fz, on which the amplitudes and effects were the maximal, obtained the same pattern of effects as the above electrode group analyses.

3. D

The ERP patterns of both the P300 and the FRN effects are very clear. The P300 peak amplitude was sensitive to both reward

valence and reward magnitude. Moreover, this sensitivity was modulated by expectancy towards the reward magnitude, with the reward magnitude effect and the valence effect being either eliminated or reduced when the amount of reward was inconsistent with expectation built upon a preceding cue. The FRN amplitude, after bandpass filtering to reduce the influence of the P300, was modulated not only by reward valence, but also by reward magnitude and magnitude expectancy. In the following paragraphs, we discuss the functional significances of the P300 and the FRN in outcome evaluation, respectively.

3.1. The role of P300 in differentiating good from bad outcomes

The finding of a magnitude effect on the P300 replicated previous studies (e.g. Sato et al., 2005; Yeung and Sanfey, 2004). Importantly, we found a valence effect on the P300, with more positive amplitudes for positive outcomes than for negative outcomes. This finding is inconsistent with some of the previous studies (e.g. Sato et al., 2005; Yeung and Sanfey, 2004), but consistent with several other studies (Holroyd, 2004; Hajcak et al., 2005, 2007). It is possible that the failure of Yeung and Sanfey (2004) in observing the valence effect on the P300 was due to their use of a particular paradigm, in which the participant was first presented with the outcome of his choice and then the alternative outcome of the unselected action. They obtained a valence effect on the P300 for the latter, not for the former. In this design the participant could not judge whether he had made the best decision on the presentation of the choice outcome since the alternative outcome could even be better. For the present paradigm, the outcome was deterministic and there could be no comparison between this outcome and an alternative one. Although Sato et al. (2005) did provide the deterministic information concerning gain or loss in the feedback stage in their monetary gambling task, they did not provide information concerning the amount of gain or loss directly. The information of reward magnitude, which was provided as a cue at the beginning of the trial, had to be retrieved from working memory. It is possible that, in this case, the gain or loss information was encoded efficiently by the FRN and the attentional resources, represented by the P300, were devoted to retrieve and encode information of the amount of reward, rather than the valence of reward. In the present experiment, the valence and the magnitude information was provided simultaneously by the feedback stimulus. It is thus easy for the P300 to encode this information in an integrated manner, showing both the magnitude and the valence effects.

The P300 effect has been reported in some previous studies for the processing of affective pictures, with a more positive P300 for affective stimuli than for neutral stimuli over the parietal sites (Briggs and Martin, 2009; Dolcos and Cabeza, 2002; Ito et al., 1998; Junghöfer et al., 2001; see Olofsson and Nordin, 2008 for a review). One may be inclined to relate the role of P300 in reward processing to that in affective information processing, since both types of stimuli are of affective significance. However, the P300 amplitude in outcome evaluation is stronger for positive than for negative feedback while the P300 is often reported to be stronger for

both negative and positive than for neutral information in affective picture processing (Briggs and Martin, 2009; Olofsson and Nordin, 2008), with little difference between the valenced information even after the arousal level of stimuli is controlled (Briggs and Martin, 2009; but see Conroy and Polich, 2007 for a slightly different pattern of the P300 effect). Moreover, studies on decision making have shown that losses loom larger than gains (Tversky and Kahneman, 1981), indicating that the arousal for a loss of a certain magnitude should be greater than the arousal for a gain of the same magnitude. If the P300 responds simply to the arousal level elicited by feedback stimuli in a monetary gambling task, we should have observed stronger P300 responses to negative outcomes than to positive outcomes.

Earlier studies using the oddball paradigm (Courchesne et al., 1977; Duncan-Johnson and Donchin, 1977; Johnson and Donchin, 1980) have consistently found that unexpected stimuli elicit stronger P300 responses. Studies employing gambling tasks also found that unexpected outcomes elicit stronger P300 responses than expected outcomes (e.g. Hajcak et al., 2005, 2007). However, in the present study, we failed to observe this sensitivity to the manipulation of expectancy towards reward magnitude even though the unexpected feedback was infrequently presented (20% of the total trials). There could be two reasons for this absence of probability effect on the P300. First, information concerning expectancy violation has already been coded by the preceding FRN (see below) and hence the neural system does not need to code it again on the P300. Second, the expectancy here was manipulated by inducing expectation towards the amount of reward, rather than towards the valence of reward. It is possible that the P300 encodes only the most significant properties of feedback when these properties are at different levels of relevance to one's self-interest.

Although expectancy towards the reward magnitude did not elicit a P300 effect, it did modulate the valence and the magnitude effects, with the absence of these effects when the magnitude of reward was inconsistent with expectation built upon a cue. This may indicate that the inconsistency captures attention such that the attentional resources allocated to other aspects of feedback, i.e., the valence and the magnitude, are reduced in this situation, resulting in the non-significant effect of valence or magnitude on the P300.

These findings suggest a role of the P300 in coding the motivational significance of reward (Nieuwenhuis et al., 2005). This coding enables the system to differentiate good from bad outcomes of decision making and to potentiate and optimize further actions. Our behavioral results showed that the participants were more likely to stay on the previous choice following positive as compared to negative feedback (see also Gehring and Willoughby, 2002; Yeung and Sanfey, 2004). However, the present study failed to find a statistical relation between the participants' P300 response to the current trial and the choice behavior in the next trial (the analysis of data was not reported here). The failure of finding this relationship was perhaps due to the totally random presentation of feedback, whose valence, magnitude, and the congruency with the cue were predetermined by the experimenter and

were performance-independent. It is interesting to investigate in the future the relationship between the P300 amplitude and the subsequent choice behavior by employing intelligent programming, such as the reinforcement learning algorithm (e.g., Cohen and Ranganath, 2007).

3.2. The FRN codes violation of expectancy

The FRN results obtained in this study are generally consistent with those observed in previous studies on outcome evaluation. We found that feedback concerning monetary loss elicited a negative deflection at the frontocentral regions compared with feedback concerning monetary gain (Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Holroyd, 2004; Nieuwenhuis et al., 2004; Miltner et al., 1997; Yu and Zhou, 2006a, 2006b), irrespective of magnitude expectancy or reward magnitude. We found that the FRN effect (i.e., the difference between ERP responses to loss and gain trials in the 250–350 ms time window) was in general not modulated by reward magnitude (see also Sato et al., 2005; Yeung and Sanfey, 2004), nor by expectancy towards the magnitude of reward, although there was a three-way interaction between reward valence, magnitude expectancy and reward magnitude due to the surprisingly more positive ERP responses to the expected large gain (see Fig. 2).

Interestingly, however, we found that violation of expectancy towards the magnitude of reward elicited an FRN effect. This novel finding extended the reinforcement learning theory of the FRN (Hajcak et al., 2007; Holroyd and Coles, 2002), which is built upon work done by Schultz et al. (1997) and which suggests that the FRN reflects the coding of prediction error. According to this theory, the FRN reflects

would reduce the size of the FRN effect for the correctness of guessing.

Previous studies using the base-to-peak measurement of the FRN suggest that the FRN is insensitive to reward magnitude (Hajcak et al., 2006; Holroyd et al., 2006; Sato et al., 2005; Toyomaki and Murohashi, 2005; Yeung and Sanfey, 2004). However, another study using the loss-minus-gain difference parameterization of the FRN found that the FRN effect is greater for monetary outcomes with large magnitude than for outcomes with small magnitude (Goyer et al., 2008). Using the mean amplitude of ERP responses in a time window together with the 2–20 Hz bandpass filtering, the present study also observed an effect of reward magnitude on the FRN. It is possible that different measurements have different sensitivities to the magnitude effect in the FRN. It is also possible that the manipulation of expectancy towards reward magnitude in this study highlighted the magnitude dimension, making it easier being encoded into the FRN.

An unresolved issue is why we observed a three-way interaction between reward valence, magnitude expectancy and reward magnitude. As can be seen in Fig. 2, this interaction was caused mainly by the most positive ERP responses to the expected large gain. Clearly, the finding of more positive responses to the expected large gain than to the unexpected large gain is inconsistent with the reinforcement learning theory of FRN, which would predict otherwise. Further studies are needed to replicate this finding and to manipulate expectancy based on properties other than the valence of reward.

4. C

Overall, this study provides further insights into the role of the P300 in outcome evaluation and reward processing. In particular, the P300 is sensitive to both feedback valence and reward magnitude. Moreover, this sensitivity can be modulated by expectancy towards reward magnitude, with the magnitude effect and the valence effect being either eliminated or reduced when the amount of reward is inconsistent with expectation. Furthermore, the FRN effect can be observed for the valence of reward, expectancy towards the magnitude of reward, and the magnitude of reward, suggesting that the FRN may function as a general mechanism that evaluates whether the outcome is consistent or inconsistent with expectancy, irrespective of on what attribute the expectancy is built.

5. E t

5.1. Participants

Nineteen graduate students (6 females, aged between 22 and 26 years) at the Southeast University in China participated in the experiment. All the participants were right-handed and had no history of neurological or psychiatric orders. Each person received a basic pay of 30 yuan (about \$4.5) for his/her participation, plus a bonus of about 10 yuan based on his/her performance in the task. Data from 3 participants were

excluded due to excessive artifacts in EEG recording. The study was approved by the local research ethics committee.

5.2. Design and procedure

The experiment used a 2 (valence) × 2 (reward magnitude) × 2 (expectancy towards reward magnitude) factorial design, with the outcome being either positive (i.e., winning money) or negative (i.e., losing money), either a large amount of money (i.e., 2.5 yuan) or a small amount of money (0.5 yuan), either expected (i.e., reward being consistent with the cue) or unexpected (inconsistent with the cue). The expected trials were 80% of the total 1000 trials while the unexpected trials were 20%. Half of the trials had positive feedback, half negative; and half of the trials had the large reward feedback (i.e., 2.5 yuan), half the small reward feedback (i.e., 0.5 yuan).

Each trial began with the presentation of a cue (“25” or “5”), representing, in most cases, the amount of the money involved in the current round of gamble. Then two cards were presented for 800 ms at the center of the screen, side by side. The participant was informed that one card represented “winning” and the another “losing”, and his/her task was to chose the winning card using whatever strategies he/she could appeal to. The participant was instructed to press the left or the right key of a joystick with his/her left or right index finger to indicate the card he/she selected, which would then flash for 500 ms, by thickening the frames of the card, to confirm the selection. Finally, a feedback stimulus appeared at the center of the screen for 1000 ms that informed the participant of the outcome of the current gamble. This stimulus could be either “+25” or “+5”, indicating “winning”, or “-25” or “-5”, indicating “losing”. The participant was told that he/she would be rewarded or penalized the amount of money indicated by the feedback.

Unknown to the participant, different types of trials were pseudo-randomized in the sequence and the feedback were predetermined, with the restrictions that no more than 4 consecutive trials were winning or losing and no more than 4 consecutive trials were from the same experimental condition. The total 1000 trials were divided into 10 blocks. Different orders of the blocks were created with a Latin square design and each participant received one particular order. The presentation of stimuli and recording of the participant's responses were controlled by Presentation software (Neurobehavioral Systems, Inc.).

5.3. EEG recording

EEGs were recorded from 64 scalp sites using tin electrodes mounted in an elastic cap (NeuroScan Inc. Herndon, Virginia, USA) according to the International 10/20 system. Eye blinks were recorded from left supraorbital and infraorbital electrodes. The horizontal electro-oculogram (EOG) was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. The linked bilateral mastoids served as the reference point and the GND electrode on the cap served as ground. During recording, all activities were referenced to the averaged mastoids. Electrode impedance was kept below 5 kΩ. The biosignals were amplified with a bandpass from 0.05 Hz to 70 Hz and digitized at 500 Hz for offline analysis. Ocular

artifacts were corrected with an eye-movement correction algorithm. Separate EEG epochs of 800 ms (together with 200 ms pre-stimulus baseline) were extracted offline, time-locked to the onset of feedback. Epochs were baseline-corrected by subtracting from each sample the average activity of that channel during the baseline period. All trials in which EEG voltages exceeded a threshold of $\pm 60 \mu\text{V}$ during recording were excluded from further analysis. The EEG data were low-pass filtered below 30 Hz.

5.4. ERP analysis

The P300 was defined as the most positive peak in the 250–600 ms time window following the feedback onset. To minimize overlap between the FRN and other ERP components, we offline filtered the EEG data through a zero phase shift with 2–20 Hz bandpass. The FRN was then defined as the mean amplitude in the 250–350 ms time window post-onset of feedback. The P300 and the FRN were statistically evaluated, with reward valence, magnitude expectancy, and reward magnitude as three critical factors and electrodes as topographic factors. For the P300, the electrodes CP3, P3, CPz, Pz, CP4, and P4 were included. For the FRN, the electrodes of F3, FC3, Fz, FCz, F4, and FC4 were included. Data were analyzed with repeated-measures analysis of variance (ANOVA). The Greenhouse–Geisser adjustment for non-sphericity was used where appropriate. Bonferroni correction was used for multiple comparisons.

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REFERENCES

- Briggs, K.B., Martin, F.H., 2009. Affective picture processing and motivational relevance: arousal and valence effects on ERPs in an oddball task. *Int. J. Psychophysiol.* 72, 299–306.
- Conroy, M.A., Polich, J., 2007. Affective valence and P300 when stimulus arousal level is controlled. *Cogn. Emo.* 21, 891–901.
- Cohen, M.X., Ranganath, C., 2007. Reinforcement learning signals predict future decisions. *J. Neurosci.* 27, 371–378.
- Cohen, M.X., Elger, C.E., Ranganath, C., 2007. Reward expectation modulates feedback-related negativity and EEG spectra. *NeuroImage* 35, 968–978.
- Courchesne, E., Hillyard, S.A., Courchesne, R.Y., 1977. P3 waves to the discrimination of targets in homogeneous and heterogeneous stimulus sequences. *Psychophysiology* 14, 590–597.
- Dolcos, F., Cabeza, R., 2002. Event-related potentials of emotional memory: encoding pleasant, unpleasant, and neutral pictures. *Cogn. Affect. Behav. Neurosci.* 2, 252–263.
- Donkers, F.C.L., Nieuwenhuis, S., van Boxtel, G.J.M., 2005. Mediofrontal negativities in the absence of responding. *Cogn. Brain Res.* 25, 777–787.
- Duncan-Johnson, C.C., Donchin, E., 1977. On quantifying surprise: the variation of event-related potentials with subjective probability. *Psychophysiology* 14, 456–467.
- Gehring, W.J., Willoughby, A.R., 2002. The medial frontal cortex and the rapid processing of monetary gains and losses. *Science* 295, 2279–2282.
- Goyer, J.P., Woldorff, M.G., Huettel, S.A., 2008. Rapid electrophysiological brain responses are influenced valence and magnitude of monetary rewards. *J. Cogn. Neurosci.* 20, 2058–2069.
- Hajcak, G., Holroyd, C.B., Moser, J.S., Simons, R.F., 2005. Brain potentials associated with expected and unexpected good and bad outcomes. *Psychophysiology* 42, 161–170.
- Hajcak, G., Moser, J.S., Holroyd, C.B., Simons, R.F., 2006. The feedback-related negativity reflects the binary evaluation of good versus bad outcomes. *Biol. Psychol.* 71, 148–154.
- Hajcak, G., Moser, J.S., Holroyd, C.B., Simons, R.F., 2007. It's worse than you thought: The feedback negativity and violations of reward prediction in gambling tasks. *Psychophysiology* 44, 905–912.
- Heldmann, M., Rüsseler, J., Münte, T.F., 2008. Internal and external information in error processing. *BMC Neurosci.* 9, 33.
- Holroyd, C.B., 2004. A note on the oddball N200 and feedback ERN. In: Ullsberger, M., Falkenstein, M. (Eds.), *Errors, Conflicts, and the Brain: Current Opinions on Response Monitoring*. Leipzig: MPI of Cognitive Neuroscience, 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., Krigolson, O.E., 2007. Reward prediction error signals associated with a modified time estimation task. *Psychophysiology* 44, 913–917.
- 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., Hajcak, G., Larsen, J.T., 2006. The good, the bad and the neutral: electrophysiological responses to feedback stimuli. *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.
- Ito, T.A., Larsen, J.T., Smith, N.K., Cacioppo, J.T., 1998. Negative information weighs more heavily on the brain: the negativity bias in evaluative categorizations. *J. Pers. Soc. Psychol.* 75, 887–900.
- Jia, S., Li, H., Luo, Y., Chen, A., Wang, B., Zhou, X., 2007. Detecting perceptual conflict by the feedback-related negativity in brain potentials. *NeuroReport* 18, 1385–1388.
- Johnson Jr., R., Donchin, E., 1980. P300 and stimulus categorization: two plus one is not so different from one plus one. *Psychophysiology* 17, 167–178.
- Junghöfer, M., Bradley, M.M., Elbert, T.R., Lang, P.J., 2001. Fleeting images: a new look at early emotion discrimination. *Psychophysiology* 38, 175–178.
- Leng, Y., Zhou, X.L., in revision. Modulation of the brain activity in outcome evaluation by interpersonal relationship: An ERP study.
- Luu, P., Tucker, D.M., Derryberry, D., Reed, M., Poulsen, C., 2003. Electrophysiological responses to errors and feedback in the process of action regulation. *Psychol. Sci.* 14, 47–53.
- Luu, P., Shane, M., Pratt, N.L., Tucker, D.M., 2009. Corticolimbic mechanisms in the control of trial and error learning. *Brain Res.* 1247, 100–113.
- Marco-Pallares, J., Cucurell, D., Cunillera, T., García, R., Andrés-Pueyo, A., Thomas, F., Münte, T.F., Rodríguez-Fornells, A., 2008. Human oscillatory activity associated to reward processing in a gambling task. *Neuropsychology* 46, 241–248.
- 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, 787–796.
- Nieuwenhuis, S., Holroyd, C.B., Mol, N., Coles, M.G.H., 2004. Reinforcement-related brain potentials from medial frontal

- cortex: origins and functional significance. *Neurosci. Biobehav. Rev.* 28, 441–448.
- Nieuwenhuis, S., Aston-Jones, G., Cohen, J.D., 2005. Decision making, the P3, and the locus coeruleus-norepinephrine system. *Psychol. Bull.* 131, 510–532.
- Nittono, H., Otsuka, Y., Ullsperger, P., 2008. Asymmetrical effects of frequent gains and frequent losses in a gambling task. *NeuroReport* 19, 1345–1349.
- Olofsson, J.K., Nordin, S., 2008. Affective picture processing: an integrative review of ERP findings. *Biol. Psychol.* 77, 247–265.
- Polezzi, D., Lotto, L., Daum, I., Sartori, G., Rumiati, R., 2008. Predicting outcomes of decisions in the brain. *Beh. Brain Res.* 187, 116–122.
- Polich, J., 2007. Updating P300: an integrative theory of P3a and P3b. *Clin. Neurophysiol.* 118, 2128–2148.
- Polich, J., Kok, A., 1995. Cognitive and biological determinants of P300: an integrative review. *Biol. Psychol.* 41, 103–146.
- Potts, G.F., Martin, L.E., Burton, P., Montague, P.R., 2006. When things are better or worse than expected: the medial frontal cortex and the allocation of processing resources. *J. Cogn. Neurosci.* 18, 1112–1119.
- Sato, A., Yasuda, A., Ohira, H., Miyawaki, K., Nishikawa, M., Kumano, H., Kuboki, T., 2005. Effects of value and reward magnitude on feedback negativity and P300. *NeuroReport* 4, 407–411.
- Schultz, W., Dayan, P., Montague, P.R., 1997. A neural substrate of prediction and reward. *Science* 275, 1593–1599.
- Squires, N.K., Squires, K.C., Hillyard, S.A., 1975. Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalogr. Clin. Neurophysiol.* 38, 387–401.
- Sutton, S., Braren, M., Zubin, J., John, E.R., 1965. Evoked-potential correlates of stimulus uncertainty. *Science* 150, 1187–1188.
- Toyomaki, A., Murohashi, H., 2005. The ERPs to feedback indicating monetary loss and gain on the game of modified “rock–paper–scissors”. *Int. Congr. Ser.* 1278, 381–384.
- Tversky, A., Kahneman, D., 1981. The framing of decisions and the psychology of choice. *Science* 211, 453–458.
- 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.
- Yu, R., Zhou, X.L., 2006a. Brain potentials associated with outcome expectation and outcome evaluation. *NeuroReport* 17, 1649–1653.
- Yu, R., Zhou, X.L., 2006b. Brain responses to outcomes of one’s own and other’s performance in a gambling task. *NeuroReport* 17, 1747–1751.
- Yu, R., Luo, Y., Ye, Z., Zhou, X.L., 2007. Does the FRN in brain potentials reflect motivational/affective consequence of outcome evaluation? *Prog. Nat. Sci.* 17, 136–143.