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Research article

The neural basis of feedback-guided behavioral adjustment

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ABSTRACT

Given feedback on the outcomes of our choices, humans can then make adjustments to future decisions. This is how we learn. However, how knowing the outcome of one's decisions influences behavioral changes, and especially the neural basis of those behavioral changes, still remains unclear. To investigate these questions, we employed a simple gambling task, in which participants chose between two alternative cards and received trial-by-trial feedback of their choices. In different sessions, we emphasized either utility (win or loss) or performance (whether the choice was correct [better than the alternative] or incorrect), making one of the two aspects more salient to participants. We found that trial-by-trial feedback and the saliency of the feedback modulated behavioral adjustments and subjective evaluations of the outcomes. With simultaneous electroencephalogram (EEG) recording, we found that the feedback-related negativity (FRN), P300, and late positive potential (LPP) served as the neural substrates for behavioral decision switching. Together, our findings reveal the neural basis of behavioral adjustment based on outcome evaluation and highlight the key role of feedback evaluation in future action selection and flexible adaptation.

1. Introduction

To optimize behavior, people need to evaluate outcomes of their actions and use these evaluations to guide future decisions [1]. Humans have a dedicated neural system to learn from negative feedback and switch to a different strategy when outcomes do not turn out to be as good as expected (e.g., loss in gambling) [2–5]. In particular, neuroimaging studies have revealed that the striatum plays a critical role in value computation, reward-based learning, and reward prediction error [6–9], and in turn it guides people to make corresponding behavioral adjustments [7,10–12]. On the other hand, electroencephalogram (EEG) studies have identified several components that are sensitive to outcome evaluations: the feedback-related negativity (FRN), P300, and the late positive potential (LPP).

The FRN is a frontocentral negative deflection after the delivery of a probabilistic reward and it has long been associated with outcome evaluation [2,13,14] as well as adaptive decision making based on reward prediction errors [3,15,16]. Another ERP component of interest is the P300. The P300 peaks around 300–600 ms after feedback, has the most positive deflection at posterior electrode locations, and often accompanies the FRN [5,17–20]. Using a prediction task in the perceptual domain, it has been shown that the P3b (a subcomponent of P300) not only systematically relates to prior events but also predicts future behavior [21]. Furthermore, the LPP has the maximal signal over the anterior frontal or frontocentral sites in economic outcome evaluation, and it plays an attentional and motivational role in decision-making [22–24]. Lastly, in addition to ERPs, oscillatory activities are involved in coding outcomes during reward processing. Enhanced midline-frontal theta oscillations are associated with outcome-related negativity during loss conditions [25,26], and compared to wins, losses are associated with enhanced power and phase coherence in the theta frequency band [27].

Although the above studies have consistently indicated a role of the FRN, P300, LPP and neural oscillations in outcome evaluation and behavioral adjustments, it remains unclear how these neural signals lead to behavioral adjustment following outcome evaluation. To investigate the neural bases of saliency-based decision making and behavioral adjustment, we employed a simple gambling task, where participants chose between two alternative cards and then received trial-by-trial feedback. Importantly, in different sessions, we emphasized either utility (win or loss) or performance (whether the choice was correct [better than the alternative] or incorrect), making one of the two aspects more salient to participants. We found that trial-by-trial feedback and the saliency of feedback modulated behavioral adjustments and subjective evaluation of outcomes. Neurophysiological responses to feedback, indexed by the FRN, P300, and LPP amplitudes,

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and theta-band oscillations, corroborated the behavioral adjustment.

2. Materials and methods

2.1. Participants

Eighteen healthy, right-handed participants (7 male; mean age ± SD: 21.0 ± 1.41 years) participated in the EEG experiment. Another 13 participants participated in the control experiment. All participants had normal or corrected-to-normal vision and no self-reported history of neurological or psychiatric disorders. All participants provided written informed consent according to protocols approved by the South China Normal University Institutional Review Board.

2.2. Stimuli and procedure

Participants were seated comfortably about 1.1 m in front of a computer screen in a dimly lit and electromagnetically shielded room. Experiments were administered on a 19-inch (37.7 × 30.1 cm) IBM LCD display (1280 × 1024 screen resolution). We used E-prime (Psychology Software Tools, Inc. Pittsburgh, PA, USA, www.pstnet.com/e-prime) for stimulus presentation and response recording. At the beginning of each trial, participants viewed two gambling cards (shown as gray rectangles with white frames in Fig. 1A, **B**; rectangle size = 204 × 230 pixels) and were required to choose one card within 1.5 s by using the keyboard to press either “F” (to select the card on the left) or “J” (to select the card on the right) using their left or right index finger, respectively (Fig. 1A, **B**). The trial was discarded if participants did not make a response within 1.5 s. The chosen card was highlighted by a yellow frame surrounding the card immediately after button press for the rest of the 1.5 s. Subsequently, the outcome associated with both the chosen card and unchosen card was shown for 1.5 s, followed by an inter-trial-interval (ITI) of 0.5 s.

There were four types of outcomes: win-correct (WC), win-incorrect (WI), loss-correct (LC), and loss-incorrect (LI). ‘Win’ and ‘loss’ mean that the chosen card yields a reward and penalty, respectively. ‘Correct’ and ‘incorrect’ mean that the chosen card yields a better (a larger reward or a smaller penalty) and worse (a smaller reward or a larger penalty) outcome compared to the unchosen card, respectively. Four corresponding examples were given and explicitly explained to each participant (see Fig. 1**A** for examples). Unbeknownst to participants, all outcomes were predetermined (the same for all participants) and pseudo-randomized across conditions. Each pair of chosen and unchosen cards was presented randomly within each condition.

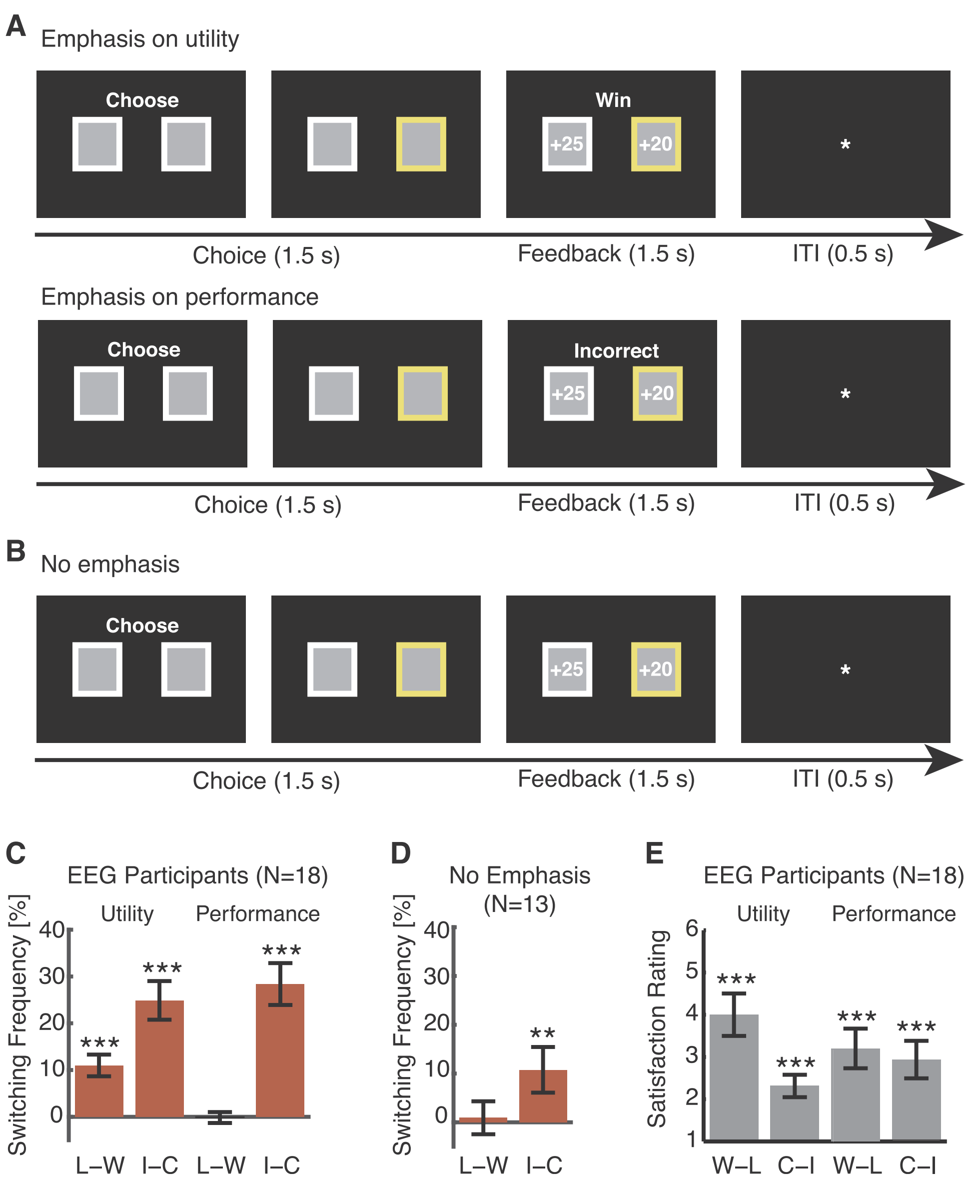

Fig. 1. Task and behavior. **(A)** Task with saliency emphasis. At the beginning of each trial, two gambling cards were presented and participants were required to choose one card within 1.5 s. The chosen card was highlighted in yellow. Then both outcomes associated with the chosen card and the alternative card were shown, followed by an inter-trial interval. To emphasize utility (win or loss) or performance (correct or incorrect), a highlight message (‘Win’, ‘Loss’, ‘Correct’, ‘Incorrect’) about the chosen outcome was displayed. **(B)** Task without saliency emphasis. **(C)** Switching frequency for the task with saliency emphasis. **(D)** Switching frequency for the task without saliency emphasis. **(E)** Satisfaction rating for the task with saliency emphasis. Error bars denote one SEM across participants. Asterisk indicates a significant difference using two-tailed one-sample *t*-test: **: $p < 0.01$ and ***: $p < 0.001$. L − W: difference in switching frequency following loss vs. win trials. I − C: difference in switching frequency following incorrect vs. correct trials.

Specifically, the value of the chosen card was randomly decided (in integers) from a uniform distribution ranging from −¥40 to +¥40 (about \$6.2), whereas the value of the unchosen card was also determined randomly from a uniform distribution, but with the constraint that the difference between the chosen and unchosen outcomes was less than ¥20 (but not less than ¥2). The values of the chosen and unchosen cards were independent of card positions. Participants were told that their goal was to earn as much money as possible, and they were free to employ any strategies to achieve that goal.

Before the experiment, participants were informed that one trial would be selected randomly from the experiment, and the value of the chosen outcome would be added to (or subtracted from) their base payment (¥60 (about \$10)). Ten practice trials were given before the experiment, allowing participants to familiarize themselves with our procedure. No reward was given for practice trials.

Each participant underwent two sessions. Each session consisted of two blocks of 80 trials each, and there was a short break between the two blocks. In the main experiment, each session had a different saliency manipulation (emphasizing one of the task aspects). To emphasize utility (win/loss) or performance (correct/incorrect), a highlighted message was displayed above the outcomes (Fig. 1A). The two sessions were counterbalanced across participants. It is worth noting that one of the task aspects (loss − win or incorrect − correct) became congruent with the emphasized dimension (utility or performance) and thus became salient after emphasis. Specifically, the difference in switching frequency following loss vs. win (L − W) trials was congruent with the emphasis on utility and was thus salient when utility was emphasized. Similarly, the difference in switching frequency following incorrect vs. correct (I − C) trials was congruent with the emphasis on performance and was thus salient when performance was emphasized. The control experiment did not have any saliency emphasis, i.e., no words were displayed above the outcomes (Fig. 1B).

2.3. Subjective rating

After the EEG experiment, participants were debriefed and required to indicate how satisfied and surprised they felt for the 8 examples of outcomes (WL, WI, LC, and LI for each session) using an 11-point analogue Likert scale (0 = not at all, 10 = very intensely).

2.4. Data analysis

To compare switching frequency between conditions in behavior, we performed a three-way repeated-measures ANOVA of Saliency (emphasis on utility vs. performance) x Utility (win vs. loss) x Performance (correct vs. incorrect). In addition, we used a two-way repeated-measures ANOVA of Strategy (switch vs. stay) x Outcome (L − W vs. I − C) to characterize the neural response to feedback and subsequent behavioral adjustment, separately for each saliency emphasis.

2.5. Electroencephalogram (EEG)

Methods regarding EEG data recording, preprocessing, event-related potential (ERP) analysis, and time-frequency analysis are shown in **Supplementary Methods**.

3. Results

3.1. Behavioral adjustment after feedback

To investigate the impact of feedback and saliency on participants' decision-making strategies, we analyzed the frequency of switching cards, i.e., choosing an alternative card in the next trial (Fig. 1**C, D**). Switching frequency can index adjustment of behavior (see Fig. S**1** for absolute switching frequencies). Previous studies using reinforcement learning have consistently indicated a behavioral tendency of choosing alternative choices following loss or less optimal decisions [16,28,29].

We found that participants switched more frequently following loss trials (mean ± SD: 45.86 % ± 13.43 %) than win trials (34.88 % ± 13.56 %) when utility was emphasized (Fig. 1**C**; paired t-test, $t(17) = -4.73$, $p = 1.91 \times 10^{-4}$, Cohen's $d = -1.15$), but not when performance was emphasized ($t(17) = 0.13$, $p = 0.90$, $d = 0.03$; interaction of Saliency x Utility: $F(1,17) = 18.40$, $p = 4.96 \times 10^{-4}$, $\eta_p^2 = 0.52$), suggesting that feedback on utility (i.e., win or loss) could influence decision strategy only when it was salient. On the other hand, participants switched more frequently following incorrect trials than correct trials when either utility (Fig. 1**C**; $t(17) = -6.02$, $p = 1.4 \times 10^{-5}$, $d = -1.46$) or performance ($t(17) = -6.34$, $p = 7 \times 10^{-6}$, $d = -1.54$) was emphasized, suggesting that feedback on performance (i.e., correct or incorrect) could always influence individuals' subsequent decisions (main effect of Performance: $F(1,17) = 46.69$, $p = 3 \times 10^{-6}$, $\eta_p^2 = 0.73$).

We further confirmed our results by a control experiment without emphasis (Fig. 1B), which showed a similar pattern of behavioral strategy as emphasis on performance (Fig. 1C), but a smaller difference between conditions (I − C) (Fig. 1**D**; mean ± SD: 10.76 % ± 16.87 %) compared to emphasis on performance (Fig. 1**C**; 28.39% ± 18.98%; two-tailed two-sample t-test, $t(29) = 2.67$, $p = 0.012$, $d = 0.50$), indicating that the saliency of performance could further modulate behavior.

Furthermore, we analyzed response times (RT) for behavioral adjustment. No significant difference in RT was found when participants made either stay or switch choices, indicating an equal response effort that was not influenced by saliency or outcome.

Lastly, subjective pleasantness and surprise ratings showed that behavioral adjustments were based on subjective values or motivation, but not on anticipation (**Supplementary Results**; Fig. 1E).

Together, participants were more likely to switch their choices when the chosen outcome was inferior to the unchosen alternative, but only tended to switch after loss when such outcome was salient, indicating different strategies in behavioral adjustment.

3.2. The FRN, P300 and LPP served as the neural substrates for behavioral adjustment

To investigate the neural substrates of the above saliency-modulated behavioral adjustment, we grouped trials into "switch" trials and "stay" trials (whether switch or stay in the immediately subsequent trial) and examined three ERP components: the FRN, P300, and LPP, which have been indicated in feedback processing and outcome evaluation (see Introduction for details). As expected, we observed clear FRN, LPP, and P300 components after feedback onset (Fig. 2 and Fig. 3). Importantly, these ERP components were sensitive to different outcomes and subsequent choices (Figs. 2 and 3). Note that to have a sufficient number of trials for each condition, we combined WC and WI into "win", LC and LI into "loss", WC and LC into "correct", and WI and LI into "incorrect".

We characterized the neural response to feedback and subsequent behavioral adjustment, separately for each saliency emphasis. These ERP components showed main effect of Strategy or interaction of Strategy x Outcome as a function of saliency emphasis (see Table S**1** for a summary of all statistics). Specifically, we found a significant main effect of Strategy for the P300, a significant main effect of Outcome for the P300, and a significant interaction of Strategy x Outcome for the FRN when utility (win/loss) was emphasized, and we found significant main effects of Outcome for the FRN, Fz LPP, and P300 when performance (correct/incorrect) was emphasized.

First, when utility was emphasized, the FRN was enhanced for L − W when it was associated with "stay" than "switch" (Fig. 2A**, E**; two-tailed paired t-test: $t(17) = 2.49$, $p = 0.024$, $d = 0.60$), indicating that the FRN encoded utility information that in turn drove behavioral adjustment (Fig. 1C). Second, we observed a significant main effect of

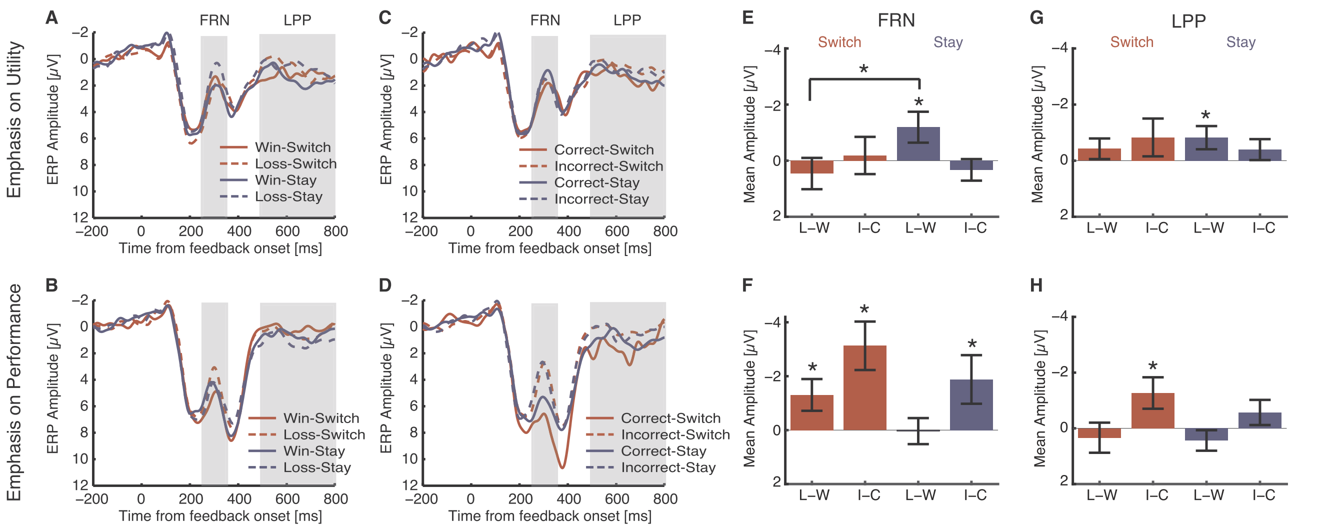

Fig. 2. ERP at electrode Fz. **(A, C, E, G)** Emphasis on utility (win/loss). **(B, D, F, H)** Emphasis on performance (correct/incorrect). **(A-D)** The FRN and LPP as a function of behavioral "switch" or "stay" in the next trial. Gray shaded areas denote the FRN (250-350) and LPP (500-800) interval. **(E-F)** Mean FRN amplitude (as indicated in A & B gray shaded area) at electrode Fz. **(G-H)** Mean LPP amplitude (as indicated in C & D gray shaded area) at electrode Fz. Error bars denote one SEM across participants. Asterisk indicates a significant difference using two-tailed one-sample t-test: +: $p < 0.1$ and *: $p < 0.05$. Red: switch in the next trial. Blue: stay in the next trial. Note that values shown in **(E, F, G, H)** are differences between conditions. L − W: difference in ERP amplitude between loss vs. win trials. I − C: difference in ERP amplitude between incorrect vs. correct trials.

Saliency for the P300 ($F(1,17) = 12.42$, $p = 0.003$, $\eta_p^2 = 0.42$; Fig. 3), where its amplitude was significantly greater when performance was emphasized (two-tailed paired t-test: $t(17) = 3.52$, $p = 0.003$, $d = 0.85$). We also observed a significant interaction between Saliency and Outcome ($F(1,17) = 5.79$, $P = 0.028$, $\eta_p^2 = 0.25$). Specifically, the P300 was enhanced for I − C when performance was emphasized compared to when utility was emphasized ($t(17) = 3.35$, $p = 0.004$, $d = 0.81$), but showed no difference for L − W when either utility or performance was emphasized ($t(17) = -0.44$, $P = 0.663$, $d = -0.16$). These results suggest that the P300 was sensitive to performance when it was emphasized. Third, the P300 (Fig. 3**A, E**; $t(17) = 2.38$, $p = 0.029$, $d = 0.58$) and Pz LPP (Fig. 3A, **G**; $t(17) = 2.12$, $p = 0.049$, $d = 0.51$) showed a greater response to L − W for "stay" compared to "switch" when utility was emphasized. We next investigated whether there was a direct relationship between behavior and neural activity.

3.3. Trial-by-trial coupling between behavior and neural activities

Is there a direct coupling between behavior and neural activity? To answer this question, we constructed a generalized linear mixed model using single-trial ERPs or oscillations to predict subsequent behavioral switching. One model was built to test the effects of ERPs (i.e., the FRN, P300, and LPP at Fz) and a separate model was built to test the effects of neural oscillations (i.e., theta-band power).

For ERPs, a full model was built using the category of saliency emphasis, single-trial FRN, P300, and LPP mean amplitude (the same time windows as in Fig. 2), and their interactions as fixed effects; each participant as random effects; and behavioral switching (stay or switch)

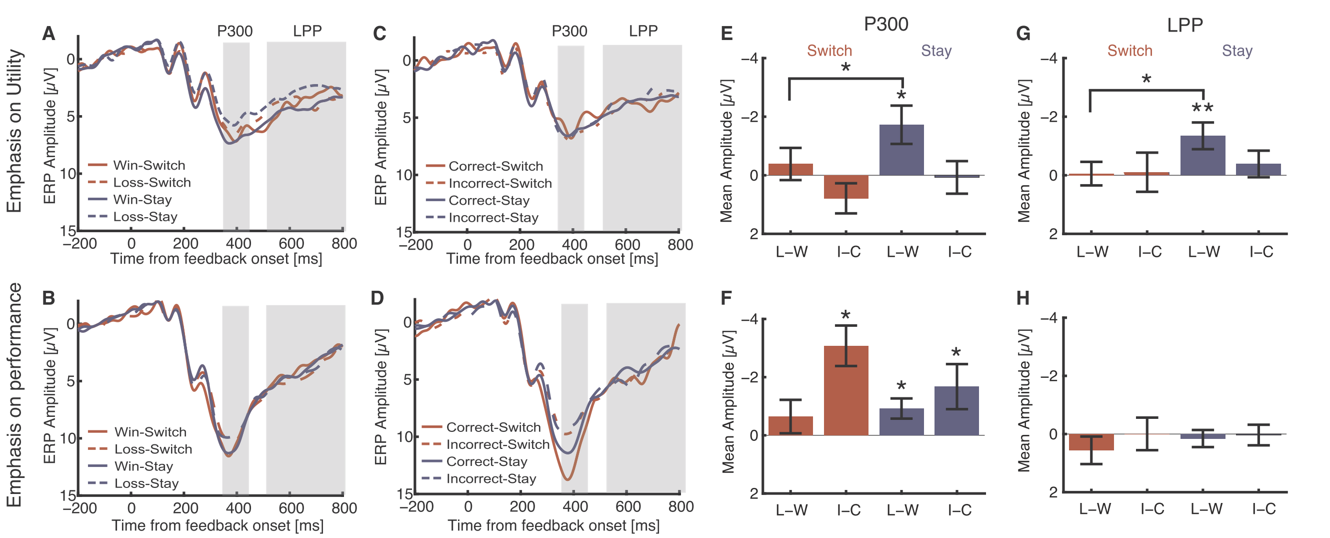

Fig. 3. ERP at electrode Pz. **(A, C, E, G)** Emphasis on utility (win/loss). **(B, D, F, H)** Emphasis on performance (correct/incorrect). **(A-D)** The P300 and LPP as a function of behavioral "switch" or "stay" in the next trial. Gray shaded areas denote the P300 (350-450) and LPP (500-800) intervals. **(E-F)** Mean P300 amplitude (as indicated in A & B gray shaded area) at electrode Pz. **(G-H)** Mean LPP amplitude (as indicated in C & D gray shaded area) at electrode Pz. Error bars denote one SEM across participants. Asterisk indicates a significant difference using two-tailed one-sample t-test: *: $p < 0.05$ and **: $p < 0.01$. Red: switch in the next trial. Blue: stay in the next trial. Note that values shown in **(E, F, G, H)** are differences between conditions. L − W: difference in ERP amplitude between loss vs. win trials. I − C: difference in ERP amplitude between incorrect vs. correct trials.

as a binomial response variable. In the full model, we found a significant interaction between FRN, LPP, P300 and Saliency (slope; $\beta = -0.00012$, $p = 0.002$), as well as a significant interaction between FRN and LPP (slope; $\beta = -0.005$, $p = 0.001$), and intercept ($\beta = 0.49$, $p < 0.001$). Statistics were performed by likelihood ratio tests to test the significance of the full model with the fixed effects of the FRN, LPP, and P300 against a reduced model lacking one individual fixed effect. We found that the full model with all fixed effects significantly outperformed the reduced model lacking the FRN ($\chi^2(17) = 15.54$, $p = 0.04$) and the reduced model lacking the LPP ($\chi^2(17) = 17.72$, $p = 0.02$), but not the reduced model lacking the P300 ($\chi^2(17) = 6.36$, $p = 0.61$), suggesting that the FRN and LPP contributed significantly to predict single-trial behavioral switching. It is worth noting that behavioral switching was not predicted by each ERP component individually (slope; all *P*s > 0.05), supporting the result that these ERP components encoded behavioral adjustment (Figs. 2 and 3).

Although the P300 did not contribute significantly to predict single-trial behavioral switching, we found that only the P300, but not the FRN or LPP, contributed to predict the absolute value of outcomes (against a reduced model without the P300: $\chi^2(18) = 15.54$, $p = 0.04$). Moreover, both the FRN and P300 contributed to predict the relative value between outcomes (FRN: $\chi^2(18) = 19.73$, $p = 0.01$; P300: $\chi^2(18) = 14.92$, $p = 0.06$). Therefore, these ERP components were involved in representing rewards and outcomes. We also found that the LPP mediated the saliency-guided behavioral adjustment (Fig. S2).

For neural oscillations, a similar analysis was performed using single-trial mean theta-band power (250 − 500 ms after feedback onset) from Fz and Pz as fixed effects. We found that the full model with the fixed effect of theta power at Fz significantly outperformed the reduced model lacking the theta power at Fz ($\chi^2(5) = 7.24$, $p = 0.027$), but not the reduced model lacking the theta power at Pz ($\chi^2(5) = 2.16$, $p = 0.34$), suggesting a crucial role of the frontal theta power in predicting behavioral switching.

Together, our results show that the FRN and LPP as well as frontal theta-band power play an important role in predicting trial-by-trial behavioral switching.

4. Discussion

In this study, we employed a simple gambling task with two alternative choices and found that trial-by-trial feedback of choice outcome could influence subsequent choices, which was in turn modulated by the saliency of the outcome. Neurophysiological responses to feedback, indexed by the FRN, P300, and LPP amplitudes and theta-band oscillations, served as the neural substrates for behavioral adjustment.

In this study, we found that participants switched ∼25 % more frequently following incorrect trials than correct trials when either utility (win/loss) or performance (correct/incorrect) was emphasized whereas participants only switched more frequently following loss trials than win trials when utility was emphasized. This is likely because participants may relate the performance feedback but not the utility feedback to their preceding act of choosing. Consistent with our findings, it has been shown that events that have to be predicted (thereby to be compared to the act of prediction) evoke larger P300s than those that are independent of participants' responses [30]. Together with the neural substrates identified in this study, our results may suggest that response to feedback may involve multiple psychological and neural processes that may be in turn modulated by saliency differentially.

The FRN is a negative deflection at the frontocentral recording sites that reaches its maximum between 250 and 350 ms after feedback [5,27,31,32]. It originates from the medial prefrontal cortex and is involved in reward processing [2,3,15,16,33–35], especially outcome evaluation [2,13,14]. In this study, the FRN might encode prediction errors that in turn guide behavioral adjustments. Indeed, evidence from aversive reward processing suggests that the FRN is sensitive to positive prediction errors (i.e., loss omission) rather than merely negative prediction errors, depending on which aspect (or context) is more salient [36,37]. Furthermore, saliency (shown by visibility of cues) interacts with reward and influences subsequent decisions, and the FRN indexes the prediction error in this process [38]. However, compared to [38], where saliency is manipulated by learned reward probability of the stimuli that is task relevant, our present study employed a random reward probability and thus participants could not learn the distribution of outcomes from feedback, resulting in a more spontaneous behavioral adjustment based on the feedback from the most immediate trial. Our study has also extended previous findings by showing that saliency of the outcome, although redundant, could modulate subsequent decisions.

Similar to the FRN, another relatively early ERP component, the P300, also encoded outcomes and behavioral adjustment. The P300 is suggested to be related to attention allocation as well as motivational and affective evaluation [39]. In our present study, the FRN might evaluate expectations or prediction errors, whereas the P300 might exert top-down control of outcome evaluation [39,40]. Notably, consistent with our findings, it has been shown that the P300 encodes the interaction between signal sequence and participants' predictions and it also relates to future behavior [21]. On the other hand, the LPP, a relatively late positive-polarity ERP component, not only encoded behavioral adjustment but also played a mediator role between saliency-based outcome evaluation and behavioral adjustment. The relatively longer latency of the LPP is consistent with its role in evidence accumulation [41], monitoring decision ambiguity and strength [42,43], and spontaneous behavioral correction or adjustment based on confidence evaluation [44,45]. Furthermore, we found that frontal theta power played an important role in predicting trial-by-trial behavioral switching. It has been shown that an enhanced theta-band power over frontocentral electrodes can predict individual performance or learning in the next trial [28,38]. In addition, theta oscillations are sensitive to saliency manipulation [27,46–48] and we found that theta-band differentiated emphasized vs. non-emphasized dimensions. Future studies will be needed to further distinguish the roles of these ERP components.

In conclusion, we have identified the neural basis of behavioral adjustment based on outcome evaluation. Successful goal-directed behavior requires not only action correction and mental planning, but also flexible adaptation after learning and outcome evaluation [1]. Our findings have highlighted the important role of feedback evaluation that guides action selection and recruits adaptive mechanisms to compensate errors and optimize goal achievement.

Author contributions

S.S. designed and performed research. S.S. and S.W. analyzed data. S.S. and S.W. wrote the paper.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.neulet.2020.135243.

References

[1] M. Ullsperger, C. Danielmeier, G. Jocham, Neurophysiology of performance monitoring and adaptive behavior, Physiol. Rev. 94 (1) (2014) 35–79.
[2] W.J. Gehring, A.R. Willoughby, The medial frontal cortex and the rapid processing of monetary gains and losses, Science 295 (5563) (2002) 2279–2282.
[3] S. Nieuwenhuis, et al., Reinforcement-related brain potentials from medial frontal cortex: origins and functional significance, Neurosci. Biobehav. Rev. 28 (4) (2004) 441–448.
[4] M.J. Frank, B.S. Woroch, T. Curran, Error-related negativity predicts reinforcement learning and conflict biases, Neuron 47 (4) (2005) 495–501.
[5] R. San Martín, Event-related potential studies of outcome processing and feedback-guided learning, Front. Hum. Neurosci. (2012) 6.
[6] M. Delgado, et al., Dorsal striatum responses to reward and punishment: effects of valence and magnitude manipulations, Cogn. Affect. Behav. Neurosci. 3 (1) (2003) 27–38.
[7] J.P. O'Doherty, Reward representations and reward-related learning in the human brain: insights from neuroimaging, Curr. Opin. Neurobiol. 14 (6) (2004) 769–776.
[8] P. Rodriguez, A. Aron, R. Poldrack, Ventral–striatal/nucleus–accumbens sensitivity to prediction errors during classification learning, Hum. Brain Mapp. 27 (4) (2006) 306–313.
[9] K. Oyama, et al., Discrete coding of stimulus value, reward expectation, and reward prediction error in the dorsal striatum, J. Neurophysiol. 114 (5) (2015) 2600–2615.
[10] J.P. O'Doherty, et al., Temporal difference models and reward-related learning in the human brain, Neuron 38 (2) (2003) 329–337.
[11] M.R. Delgado, Reward-related responses in the human striatum, Ann. N. Y. Acad. Sci. 1104 (1) (2007) 70–88.
[12] M. Guitart-Masip, et al., Action versus valence in decision making, Trends Cogn. Sci. (Regul. Ed.) 18 (4) (2014) 194–202.
[13] W.H.R. Miltner, C.H. Braun, M.G.H. Coles, 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 (6) (1997) 788–798.
[14] S. Nieuwenhuis, et al., Activity in human reward-sensitive brain areas is strongly context dependent, NeuroImage 25 (4) (2005) 1302–1309.
[15] C.B. Holroyd, M.G.H. Coles, The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity, Psychol. Rev. 109 (4) (2002) 679–709.
[16] M.X. Cohen, C. Ranganath, Reinforcement learning signals predict future decisions, J. Neurosci. 27 (2) (2007) 371–378.
[17] N. Yeung, A.G. Sanfey, Independent coding of reward magnitude and valence in the human brain, J. Neurosci. 24 (28) (2004) 6258–6264.
[18] C. Bellebaum, I. Daum, Learning-related changes in reward expectancy are reflected in the feedback-related negativity, Eur. J. Neurosci. 27 (7) (2008) 1823–1835.
[19] C. Bellebaum, D. Polezzi, I. Daum, It is less than you expected: the feedback-related negativity reflects violations of reward magnitude expectations, Neuropsychologia 48 (11) (2010) 3343–3350.
[20] Z. Zhou, R. Yu, X. Zhou, To do or not to do? Action enlarges the FRN and P300 effects in outcome evaluation, Neuropsychologia 48 (12) (2010) 3606–3613.
[21] R. Munson, et al., The relation of P3b to prior events and future behavior, Biol. Psychol. 19 (1) (1984) 1–29.
[22] Y. Wu, et al., Brain potentials in outcome evaluation: when social comparison takes effect, Int. J. Psychophysiol. 85 (2) (2012) 145–152.
[23] Y. Wu, et al., Social comparison affects brain responses to fairness in asset division: an ERP study with the ultimatum game, Front. Hum. Neurosci. (2011).
[24] Y. Zhang, et al., Brain responses in evaluating feedback stimuli with a social dimension, Front. Hum. Neurosci. 6 (2012) 82–100.
[25] W.J. Gehring, A.R. Willoughby, Are all medial frontal negativities created equal? Toward a richer empirical basis for theories of action monitoring. Errors, conflicts, and the brain, . Current opinions on performance monitoring (2004) 14–20.
[26] J. Marco-Pallares, et al., Human oscillatory activity associated to reward processing in a gambling task, Neuropsychologia 46 (1) (2008) 241–248.
[27] M.X. Cohen, C.E. Elger, C. Ranganath, Reward expectation modulates feedback-related negativity and EEG spectra, Neuroimage 35 (2) (2007) 968–978.
[28] J.F. Cavanagh, et al., Frontal theta links prediction errors to behavioral adaptation in reinforcement learning, NeuroImage 49 (4) (2010) 3198–3209.
[29] H.W. Chase, et al., Feedback-related negativity codes prediction error but not behavioral adjustment during probabilistic reversal learning, J. Cogn. Neurosci. 23 (4) (2010) 936–946.
[30] R. Verleger, et al., On Why Targets Evoke P3 Components in Prediction Tasks: Drawing an Analogy between Prediction and Matching Tasks, Front. Hum. Neurosci. 11 (2017).
[31] C.B. Holroyd, et al., Errors in reward prediction are reflected in the event-related brain potential, NeuroReport 14 (18) (2003) 2481–2484.
[32] G. Hajcak, et al., Brain potentials associated with expected and unexpected good and bad outcomes, Psychophysiology 42 (2) (2005) 161–170.
[33] W.J. Gehring, R.T. Knight, Prefrontal–cingulate interactions in action monitoring, Nat. Neurosci. 3 (5) (2000) 516–520.
[34] S. Nieuwenhuis, et al., Knowing good from bad: differential activation of human cortical areas by positive and negative outcomes, Eur. J. Neurosci. 21 (11) (2005) 3161–3168.
[35] H.W. Chase, et al., Feedback-related negativity codes prediction error but not behavioral adjustment during probabilistic reversal learning, J. Cogn. Neurosci. 23 (4) (2011) 936–946.
[36] D. Talmi, R. Atkinson, W. El-Deredy, The feedback-related negativity signals salience prediction errors, not reward prediction errors, J. Neurosci. 33 (19) (2013) 8264–8269.
[37] Y. Huang, R. Yu, The feedback-related negativity reflects "more or less" prediction error in appetitive and aversive conditions, Front. Neurosci. 8 (2014) 108.
[38] B. Lou, W.-Y. Hsu, P. Sajda, Perceptual salience and reward both influence feedback-related neural activity arising from choice, J. Neurosci. 35 (38) (2015) 13064–13075.
[39] J.K. Olofsson, et al., Affective picture processing: an integrative review of ERP findings, Biol. Psychol. 77 (3) (2008) 247–265.
[40] Y. Wu, X. Zhou, The P300 and reward valence, magnitude, and expectancy in outcome evaluation, Brain Res. 1286 (2009) 114–122.
[41] R.G. O'Connell, P.M. Dockree, S.P. Kelly, A supramodal accumulation-to-bound signal that determines perceptual decisions in humans, Nat. Neurosci. 15 (12) (2012) 1729–1735.
[42] S. Sun, R. Yu, S. Wang, A neural signature encoding decisions under perceptual ambiguity, eneuro 4 (6) (2017) 1–14.
[43] S. Sun, et al., Decision ambiguity is mediated by a late positive potential originating from cingulate cortex, NeuroImage 157 (2017) 400–414.
[44] P.R. Murphy, et al., Neural evidence accumulation persists after choice to inform metacognitive judgments, Elife 4 (2015) e11946.
[45] S.M. Fleming, Changing our minds about changes of mind, Elife 5 (2016) e14790.
[46] C. Başar-Eroglu, et al., P300-response: possible psychophysiological correlates in delta and theta frequency channels. A review, Int. J. Psychophysiol. 13 (2) (1992) 161–179.
[47] R. Ishii, et al., Medial prefrontal cortex generates frontal midline theta rhythm, Neuroreport 10 (4) (1999) 675–679.
[48] K.M. Spencer, J. Polich, Poststimulus EEG spectral analysis and P300: attention, task, and probability, Psychophysiology 36 (02) (1999) 220–232.