NeuroImage: Clinical 31 (2021) 102751

Contents lists available at ScienceDirect

NeuroImage: Clinical

journal homepage: www.elsevier.com/locate/ynicl

Impaired probabilistic reversal learning in anxiety: Evidence from behavioral and ERP findings

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ARTICLE INFO

Keywords:
Decision-making
Reversal learning
Trait anxiety
Event-related potential
Feedback-related negativity
P3

ABSTRACT

Background: Reversal learning reflects an individual's capacity to adapt to a dynamic environment with changing stimulus–reward contingencies. This study focuses on the potential influence of anxiety on reversal learning skills.

Methods: We asked 40 participants with a high level of trait anxiety (HTA) and 40 counterparts with a low anxiety level (LTA) to finish a probabilistic reversal learning task with event-related potential (ERP) recording, during which stimulus–reward contingencies are reversed after players have learned the optimal choice.

Results: We found that compared to their LTA counterparts, the HTA participants showed worse learning performance and were less likely to make lose-shift choices. The FRN amplitude might help interpret these behavioral results, which is suggested to be associated with punishment sensitivity and was positively correlated with the number of lose-shift in this study. Seeing that anxiety level predicted the FRN amplitude for lose-shift, we explain that anxious individuals' inflexible behavioral responses to losses are due to their impaired sensitivity to negative feedback.

Conclusions: A higher level of anxiety is associated with weaker reversal learning performance, possibly because of abnormal sensitivity to negative outcomes. These findings have implications for the understanding of behavioral symptoms in anxiety.

1. Introduction

Anxiety, an unpleasant emotional state that directs an organism's response to potentially threat-related stimuli, plays an important role in our everyday life (Clark, 1999). Although anxiety is evolutionarily adaptive, inappropriate anxiety reactions to the environment may damage daily functioning and life quality (Gulpers et al., 2016; Mathews & MacLeod, 2005). Depending on its duration and intensity, the negative impacts of anxiety extend beyond aversive feelings and involve disruptions in cognitive functions and goal-directed behaviors (Hartley & Phelps, 2012; Paulus & Yu, 2012). It is well established that a heightened level of anxiety is associated with aberrant cognitive task performance, including an attentional bias toward irrelevant stimulus and limited working memory capacity (for reviews, see Bishop, 2009; Bishop et al., 2004). Recently, a series of studies have revealed that anxious individuals show abnormalities in feedback learning (e.g., Blair et al., 2016; Hein et al., 2021; Hunt et al., 2019; Reilly et al., 2020). For instance, Jiang et al. (2018) reported that compared to their non-anxious counterparts, anxious participants made more pessimistic outcome expectation and allocated fewer attentional resources to negative outcomes, indicated by event-related potentials (ERPs) (see also Andreatta et al., 2017). Seeing that feedback learning allows individuals to predict future outcomes and therefore helps optimize gains and minimize losses (Cohen et al., 2011), investigating anxious people's feedback learning performance should be meaningful to understand cognitive behavioral symptoms associated with anxiety.

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https://doi.org/10.1016/j.nicl.2021.102751
Received 11 December 2020; Received in revised form 19 June 2021; Accepted 28 June 2021
Available online 3 July 2021

Environmental contingencies are usually not static but vary over time, requiring information updating and corresponding behavioral adjustment to attain desirable outcomes (Blair & Cipolotti, 2000; Donaldson et al., 2016). Thus, the present study focuses on reversal learning skills, which are critical for survival and adaptation to a changing circumstance (Gorrindo et al., 2005). According to the literature, a typical reversal learning paradigm: (1) needs participants to acquire stimulus-outcome associations through trial-and-error feedback learning; (2) these associations would be reversed without explicit warning after participants reach a learning criterion for accuracy (Cools et al., 2002; Hampton & O'Doherty J, 2007; Izquierdo & Jentsch, 2012). Difficulties with reversal learning is associated with behavioral problems including impulsiveness, disinhibition, and reactive aggression (Fellows & Farah, 2003; Greening et al., 2011; Hornak et al., 2004). Experimental studies commonly model this process with either deterministic (i.e., fully predictive) or probabilistic reversal learning (PRL) tasks. For example, in a two-armed bandit PRL task, rewards are stochastically related to two stimuli A and B. At the beginning of the task, choosing A may lead to a reward more often than choosing B (e.g., 80% vs. 20%). Nonetheless, after participants have learned the rule and consistently select A, the stimulus-outcome mapping would be reversed such that B becomes the more frequently rewarded option; finally, the same thing may happen again after participants consistently select B (Bartolo & Averbeck, 2020). The learned association between stimuli and outcomes needs to be inhibited when facing unexpected changes in reward contingency (Bari & Robbins, 2013). Reversal learning tasks have been frequently used to study behavioral flexibility (Bartolo & Averbeck, 2020; Rudebeck et al., 2013).

A potential relationship between anxiety and reversal learning has been implicated in the literature. From a behavioral perspective, many studies have confirmed that anxious individuals are impaired at shifting from a previously effective strategy to a currently valid strategy (Ansari et al., 2008; Eysenck et al., 2007; George et al., 2015). For example, Browning et al. (2015) found that participants with a higher anxiety level are less capable of adjusting outcome expectancies between stable and volatile environments (see also Huang et al., 2017). From a neuroscientific perspective, a wide range of brain structures are involved in reversal learning, including the prefrontal cortex, anterior cingulate cortex (ACC), parietal regions, amygdala, and striatum (Bartolo & Averbeck, 2020; Cools et al., 2002; Fellows & Farah, 2003; Mitchell et al., 2008; Robinson et al., 2010; Rudebeck et al., 2013; Xue et al., 2008); the activities of these brain areas are sensitive to both clinical and non-clinical anxiety (Domschke & Dannlowski, 2010; Grupe & Nitschke, 2013). However, a behavioral study by Dickstein et al. (2010) recruited thirty pediatric patients (aged 7–17 years) suffering from generalized anxiety disorder, separation anxiety disorder, or social phobia, but failed to detect any difference in reversal learning compared to healthy controls. To explain the null results, Dickstein et al. (2010) suggested that employing more homogeneous samples would help determine whether and how anxiety is associated with reversal learning deficits. Thus, this study only considered young adults who showed subthreshold anxiety symptoms.

In short, the relationship between anxiety and reversal learning abnormalities has been indicated in the literature. Taking a step further, the current study aims to understand the cognitive mechanisms of anxious individuals' reversal learning biases with the help of neuroscience techniques. As pointed out by Bari and Robbins (2013), the understanding of reversal learning deficits are often masked by the relatively simplicity of PRL tasks. Actually, reversal learning involves multiple cognitive factors that monitor ongoing actions, stimulus–outcome relationships, and future actions based on outcome history (Greening et al., 2011; Park & Moghaddam, 2017). Here, the first major factor is reward/punishment sensitivity (Bari & Robbins, 2013). After a reversal, as the previously rewarded stimuli could no longer maximize gains, individuals with a higher level of reward/punishment sensitivity might be more capable to notice changes in the reinforcement value of different stimuli (Greening et al., 2011). Interestingly, anxiety interferes with behavioral and neural responses to punishment (e.g., Gu et al., 2010a, 2010b; Jiang et al., 2018; Takács et al., 2015; Xu et al., 2013; Zhang & Gu, 2018). For instance, the association between anxiety and impoverished adaptation of learning rate could be observed in the loss condition but not in the gain condition (Bishop & Gagne, 2018). Therefore, it is reasonable to predict that punishment sensitivity during reversal learning would be modulated by anxiety.

The second pertains to the capacity of updating reinforcement values associated with different responses to stimuli (Xue et al., 2008). As pointed out by Izquierdo and Jentsch (2012), reversal learning requires individuals to efficiently update the representation of reinforcement contingencies. In a volatile task environment, people build beliefs about choice-outcome mappings for estimating the incentive value of different choices; these beliefs should be adjusted according to environmental changes, so as to ensure that behavioral adaptation is timely and successful (Bartolo & Averbeck, 2020; Hein et al., 2021). Damage to brain regions that contribute to information updating, such as the orbital prefrontal cortex, negatively affects reversal learning performance (Fellows & Farah, 2003; Hornak et al., 2004). A relationship between anxiety and information updating deficit has been implicated in recent studies (Browning et al., 2015; Jiang et al., 2018). For instance, Hein et al. (2021) discovered that anxious individuals' beliefs about reward contingencies are more resistant to new information, leading to impairments in reward-based learning. Consequently, the factor of information updating is also taken into account in this study.

To dissociate different cognitive processes that may overlap in the time domain, the ERP technique was engaged in this study regarding its exquisite temporal resolution (Amodio et al., 2014). Specifically, the feedback-related negativity (FRN) and P3 component were chosen for data analysis, both of which have been successfully applied to investigate reversal learning (Donaldson et al., 2016; Peterson et al., 2011; von Borries et al., 2013). The FRN is a frontal-midline distributed, negative-going wave that reaches its maximum approximately from 250 to 400 ms following feedback presentation (Chase et al., 2011; Gehring & Willoughby, 2002); this ERP component has been considered as one of the most important ERP indexes of outcome evaluation (Nieuwenhuis et al., 2004; Walsh & Anderson, 2012). While its cognitive function is still debated (Ferdinand et al., 2012; Heydari & Holroyd, 2016; Proudfit, 2015; Talmi et al., 2013), the most consistent feature of the FRN is that its amplitude becomes more negative-going for negative feedback (e.g., performance errors and monetary losses) compared to positive feedback across studies (Sambrook & Goslin, 2015; San Martín, 2012). For this reason, the FRN has been closely associated with the sensitivity of outcome feedback, especially punishment (Balconi & Crivelli, 2010; Ferdinand et al., 2016; He et al., 2017; Lange et al., 2012; Marco-Pallares et al., 2008). Santesso et al. (2011) discovered that self-reported scores of punishment sensitivity were positively correlated with FRN amplitude. Further, Cohen and Ranganath (2007) reported that a larger FRN elicited by negative feedback predicted subsequent behavioral adjustment (i.e., more lose-shift choices) in a reinforcement learning task.

Following the FRN, the P3 is a centro-parietal distributed, positive-going wave that peaks between 400 and 600 ms after feedback presentation (San Martín et al., 2013; Wu & Zhou, 2009). This component has been associated with various cognitive functions depending on experimental design (Polich, 2007; Polich & Criado, 2006). In the field of decision-making, the feedback P3 has been suggested to reflect information updating of salient outcomes (for reviews, see Glazer et al., 2018; San Martín, 2012). That is, outcome-related information (e.g., probability and magnitude) derived from the ongoing feedback are integrated into human memory systems to guide future decision for the goal of reward maximization (San Martín et al., 2013; Wu & Zhou, 2009; Zhang et al., 2013). We consider the P3 as an ERP index of information updating process during reversal learning, an idea that has been supported by the literature (Donaldson et al., 2016; von Borries et al.,

2013). In some of our previous studies, the FRN (but not P3) amplitude was sensitive to individual level of trait anxiety (Gu et al., 2010a, 2010b). Nevertheless, it should be pointed out that these studies applied a simple gambling task in which the winning probability was set at chance level regardless of participants' choices, therefore the reversal learning process was not involved.

Here, we measured personal level of trait anxiety and divided the participants into two groups according to their self-reported scores. Both the high-trait anxiety (HTA) and low-trait anxiety (LTA) groups finished a two-armed bandit PRL task. We made between-group comparison of behavioral data and predicted that the reversal learning rate would be lower among HTA participants. Additionally, electroencephalographic (EEG) signals were recorded and analyzed to unravel the underlying mechanisms of the relationship between anxiety and reversal learning. Specifically, the FRN and P3 elicited by feedback presentation were used to investigate two cognitive factors of reversal learning, that is, outcome sensitivity and information updating. Our ERP analyses were aimed to explore whether anxiety influences reversal learning by modulating either or both of these factors. Seeing that anxiety is associated with abnormalities in punishment sensitivity and information updating (see above), we suggest that the amplitudes of both the FRN and P3 would be sensitive to individual level of trait anxiety.

2. Methods

2.1. Participants

In 2016, all the freshman students ($n = 6903$) in Shenzhen University were asked to complete the Chinese version of the Trait form of Spielberger's State–Trait Anxiety Inventory (STAI-T: Shek, 1993; Spielberger et al., 1983), which was one part of an annual mass screening for mental disorder using multiple self-report psychometric questionnaires including the Symptom Checklist-90-revised (Derogatis, 1977), University Personality Inventory (Hirayama, 2011), and Minnesota multiphasic personality inventory (Hathaway & McKinley, 1940). 788 of the STAI-T questionnaires were unfinished or not returned. As a result, the total effective sample was 6115 (effective rate = 88.6%). In this sample, individuals with STAI-T scores in the upper and lower 25% of the distribution were considered as HTA and LTA participants, respectively (see also Gu et al., 2010a; Luo et al., 2014; Xia et al., 2017, 2020 for similar grouping methods). The Chinese version of the Beck Depression Inventory Second Edition (BDI-II: Beck et al., 1996; Wang et al., 2011) was used to assess self-reported symptoms of depression. In view of the fact that anxiety and depression are highly comorbid (Brown et al., 2001; Garber et al., 2016) and that depressive individuals also have deficits in PRL tasks (Murphy et al., 2003; Pizzagalli et al., 2008), we only recruited nondepressed participants with high vs. low trait anxiety in this study. Specifically, only the participants with BDI-II scores < 13 (indicating minimal depression: see Beck et al., 1996) were considered for the formal study. From those who met these criteria, we randomly recruited 80 students as paid participants (40 in the HTA group and 40 in the LTA group). The trait anxiety levels of the two groups were generally consistent with the standardized norm of Chinese college students (high anxiety: 52.51; low anxiety: 34.11) proposed by Li and Qian (1995). Participants in the HTA group reported a higher STAI-T score than those in the LTA group, while there was no significant difference between the two groups with respect to age, handedness, and BDI-II scores (see Table 1). The STAI-T and BDI scores were not significantly correlated ($r = 0.124$, $p = 0.275$).

Exclusion criteria for both groups were: (1) any Axis I and II disorders according to the Diagnostic and Statistical Manual (DSM-V: American Psychiatric Association, 2013); (2) seizure disorder; (3) history of head injury with possible neurological sequelae; and (4) substance abuse or dependence in the past six months. Here, the first criterion was assessed during the mass screening mentioned above. The other criteria were assessed according to participants' self-reports before the experiment. The study was approved by the Ethics Committee of Shenzhen University.

Table 1
Demographic data of high- (HTA) and low-trait anxiety (LTA) participants.

Characteristics	LTA (n = 40)	HTA (n = 40)	Statistics
Mean age (year)	19.05 ± 0.64	19.23 ± 0.70	$t(78) = -1.17$, $p = 0.245$
Sex (male/female)	20/20	20/20	
Handedness (right/left)	40/0	40/0	
STAI-T	29.68 ± 5.77	56.05 ± 7.42	$t(78) = -17.749$, $p < 0.001$
BDI	5.00 ± 1.85	5.48 ± 1.92	$t(78) = -1.125$, $p = 0.264$

STAI-T, Trait form of Spielberger's State-Trait Anxiety Inventory; BDI, Beck Depression Inventory (second edition). Descriptive data are presented as mean ± standard deviation.

2.2. Procedures

The PRL task (see Fig. 1) was adopted from Hampton et al. (2007). At the beginning of each trial, participants chose one of two Hebrew letters "א" (aleph) and "ש" (shin) in dark color as two alternative options on the left and right-hand sides of a fixation cross. The locations of these options were counterbalanced across trials. Participants had up to 1500 ms to finish the decision, then the chosen option increased in brightness for 1000 ms. After a jitter screen (300 to 500 ms) on which only the fixation cross was left, participants received the outcome ("+0.5"/"−0.5") of their choice for 1000 ms, that is, winning or losing 0.5 Chinese RMB (approximately 8 US cent). If the participants did not make a decision within 1500 ms, then the outcome of this trial would be "−1," indicating minus one RMB. Finally, the fixation cross appeared again as an inter-trial interval for 500 ms. The formal task consisted of two blocks (100 trials per block) and participants had a short break between them.

At the beginning of the task, one option was randomly set as the optimal choice, of which the winning probability was 70%. Meanwhile, the winning probability of the other option was set as 40%. However, after the participants chose the optimal option in four consecutive trials (which was defined as an index of successfully learning the winning rule), the winning probability of the optimal option would decrease for 25% when it was selected again, while that of the other option would increase for 25% (Hampton et al., 2007). In that case, the other option would become the new optimal choice (65% vs. 45%). After that, the reversal process would occur again if the new optimal option was also chosen for four consecutive times. No information was given about the winning probabilities or the potential reversals.

Prior to the task, the participants were instructed to choose the option that they expected to get rewarded from, so as to maximize their final incomes. They also performed a training session (20 trials) to familiarize with the task. During this training, no reversal occurred. After the whole task, the participants were paid according to their task performance (range: 40 ~ 80 RMB) and were debriefed.

2.3. EEG recording and analysis

Brain electrical activity was recorded referentially against left mastoid and off-line re-referenced to the average of the left and right mastoids, by a 64-channel amplifier with a sampling frequency of 250 Hz (Brain Products, Gilching, Germany). EEG data were collected with electrode impedances kept below 5 kΩ. Ocular artifacts were removed from EEGs using a regression procedure implemented in NeuroScan software (Scan 4.3, NeuroScan Inc., Herndon, VA).

The recorded EEG data were filtered (0.01–30 Hz; slope 12 dB/oct; zero phase) and segmented beginning 200 ms prior to the onset of

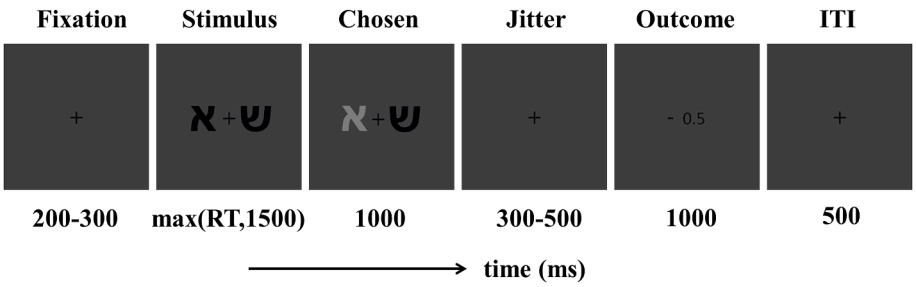

Fig. 1. Illustration of an exemplar trial of the probabilistic reversal learning task, in which a player chooses the left stimulus and loses 0.5 Chinese RMB.

outcome and lasted for 1200 ms. All epochs were baseline-corrected with respect to the mean voltage over the 200 ms preceding the onset of outcome, followed by averaging separately for each participant and each condition (win-stay, win-shift, lose-stay, and lose-shift). Trials contaminated with large artifacts (peak-to-peak deflection exceeded ± 100 μV) and behavioral responses longer than 1500 ms (overall 16 trials across all participants; 0.2 ± 0.54 trials on average) were excluded from further analyses. As a result, 2.96 ± 2.11 trials, 1.16 ± 2.79 trials, 1.58 ± 2.33 trials, and 1.98 ± 2.33 trials were rejected for each participant in the win-stay, win-shift, lose-stay, lose-shift conditions, respectively. The rejected trials were <10% of the total trials (see also Xia et al., 2017, 2020; Yang et al., 2015). The remaining trial numbers after artifact rejection did not show significant difference between the four conditions.

We analyzed the mean amplitudes of the frontal-midline FRN and centro-parietal P3. These measures were averaged based on different sets of electrodes according to grand-mean ERP topographies and relevant literatures (Huang et al., 2009; Kim et al., 2007; Righi et al., 2009). Specifically, the mean amplitude of the FRN was measured using the average data across the electrode sites Fz, F1, F2, FC1, FC2, FCz, C1, C2, and Cz, within a time window of 280–350 ms (see also Holroyd & Krigolson, 2007). Meanwhile, the mean amplitude of the P3 was measured using the average data across the electrode sites Pz, P1, P2, P3, P4, CPz, CP1, CP2, CP3 and CP4, within a time window of 370–440 ms (see also Wu et al., 2016). The time windows were selected according to visual detection on grand-mean ERP waveforms.

2.4. ERP source localization

The standardized low resolution brain electromagnetic tomography (sLORETA, the version updated on December 22th, 2015), downloaded from the official website (http://www.uzh.ch/keyinst/loreta.htm), was employed to determine the possible neuronal generators of the ERP components (Pascual-Marqui, 1999, 2002; Pascual-Marqui et al., 1994).

2.5. Statistics

Statistical analysis was performed using SPSS Statistics 21.0 (IBM, Somers, NY). Descriptive data were presented as mean ± standard deviation. The significance level was set at 0.05. Significant interactions were analyzed using simple effects model. Partial eta-squared (η_p^2) was reported to demonstrate the effect size in ANOVA tests.

Regarding the mean number of choices, accuracy, response time (RT), and the mean amplitude of the FRN and P3, three-way repeated-measures ANOVAs were performed, with *outcome valence* (win vs. loss) and *subsequent choice* (stay vs. shift) as the within-subject factors, and *group* (HTA vs. LTA) as the between-subject factor. We also calculated two behavioral indexes associated with rule reversals, that is, "the total number of rule reversals throughout the task" and "the number of trials that each participant needed to shift to the other option after rule reversals" (see also Hampton et al., 2007a, 2007b); we analyzed independent sample *t* test (rather than ANOVAs) on these two indexes, seeing that rule reversal could only happen after wins but not losses. Further, two-tailed Pearson's *r* correlation and linear regression were performed between the two self-reported measures (STAI-T and BDI-II) and behavioral/ERP indexes. Correction for multiple comparisons was based on Bonferroni's method.

3. Results

3.1. Behavioral indexes

3.1.1. Mean number of choices

The main effect of group was not significant ($F(1, 78) < 1$; $p = 0.930$, $\eta_p^2 < 0.001$). The main effect of outcome valence was significant ($F(1, 78) = 77.779$, $p < 0.001$, $\eta_p^2 = 0.499$), indicating that the participants won for more times (56.18 ± 33.98) than lost (43.22 ± 19.67). The main effect of subsequent choice was significant ($F(1, 78) = 56.467$, $p < 0.001$, $\eta_p^2 = 0.420$), indicating that the participants were more willing to keep choosing the same option in adjacent trials (58.85 ± 31.63) rather than shift to the other option (40.55 ± 21.38).

The two-way interaction of outcome valence by subsequent choice was significant ($F(1, 78) = 81.415$, $p < 0.001$, $\eta_p^2 = 0.511$): simple effect analysis indicated that the participants were more willing to keep choosing the same option (81.23 ± 25.67 times) rather than shift to the other option (31.14 ± 19.88 times) after wins ($F(1, 78) = 104.07$, $p < 0.001$, $\eta_p^2 = 0.568$), but the reverse was true after losses (36.48 ± 18.48 times vs. 49.96 ± 18.58 times; $F(1, 78) = 13.04$, $p = 0.001$, $\eta_p^2 = 0.142$).

The three-way interaction of outcome valence by subsequent choice by group was significant ($F(1, 78) = 4.221$, $p = 0.043$, $\eta_p^2 = 0.051$; Fig. 2): simple-simple effect analysis indicated that lose-shift happened

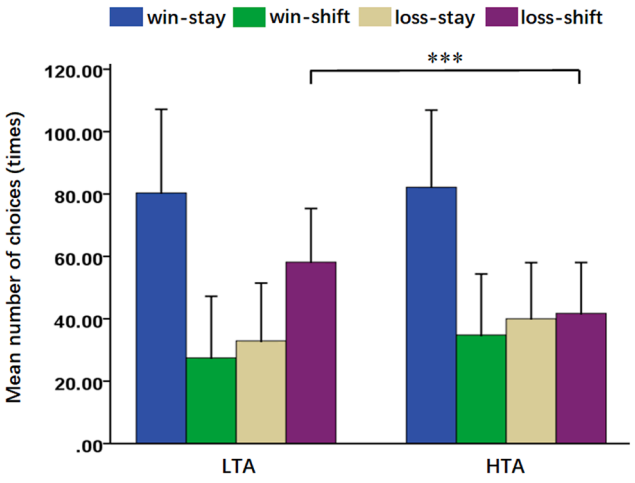

Fig. 2. Mean number of different kinds of choices. Error bars indicate one standard deviation. LTA: the low-trait anxiety group; HTA: the high-trait anxiety group. ***: $p < 0.001$.

less frequently in the HTA group (41.75 ± 16.29 times) than in the LTA group (58.18 ± 17.18 times; $F(1, 78) = 19.25$, $p < 0.001$, $\eta_p^2 = 0.197$); however, this group difference did not achieve the significance level for win-stay ($F(1, 78) < 1$, $p = 0.749$, $\eta_p^2 = 0.001$; HTA = 82.15 ± 24.74 times, LTA = 80.30 ± 26.85 times), win-shift ($F(1, 78) = 2.78$, $p = 0.100$, $\eta_p^2 = 0.034$; HTA = 34.80 ± 19.59 times, LTA = 27.48 ± 19.73 times), or lose-stay ($F(1, 78) = 2.98$, $p = 0.088$, $\eta_p^2 = 0.037$; HTA = 40.00 ± 18.00 times, LTA = 32.95 ± 18.50 times).

Concerning that the number of win vs. loss trials might differ due to randomness in the task, we also calculated the proportion of lose-shift trials out of all loss trials, as well as the proportion of win-shift trials out of all win trials, for each participant. A two-way repeated-measures ANOVA which takes *outcome valence* and *group* into account reveals that the main effect of group was not significant ($F(1, 78) = 3.936$; $p = 0.051$, $\eta_p^2 = 0.048$). The main effect of outcome valence was significant ($F(1, 78) = 68.728$, $p < 0.001$, $\eta_p^2 = 0.468$). Most importantly, the two-way interaction of *outcome valence* by *group* was significant ($F(1, 78) = 5.613$, $p = 0.02$, $\eta_p^2 = 0.067$): the proportion of lose-shift was lower in the HTA group (51.45 ± 19.10%) than the LTA group (64.49 ± 15.64%; $p = 0.001$, $\eta_p^2 = 0.125$), but the group difference did not achieve the significance level for win-shift (HTA = 30.50 ± 18.90%, LTA = 26.77 ± 21.81%; $p = 0.416$, $\eta_p^2 = 0.008$).

3.1.2. Accuracy

The main effect of group was significant ($F(1, 78) = 6.760$, $p = 0.011$, $\eta_p^2 = 0.080$; Fig. 3): the HTA group (55.88 ± 7.53%) showed a lower accuracy than the LTA group did (60.39 ± 7.98%). The main effect of outcome valence was significant ($F(1, 78) = 21.263$, $p < 0.001$, $\eta_p^2 = 0.214$): the accuracy following wins (61.91 ± 21.35%) were higher than that following losses (54.36 ± 16.48%). The main effect of subsequent choice was significant ($F(1, 78) = 38.043$, $p < 0.001$, $\eta_p^2 = 0.328$): the decision of staying on the same option (63.17 ± 18.87%) showed a higher accuracy than shifting to the other option (53.10 ± 18.69%).

Neither the interaction of outcome valence by group nor that of subsequent choice by group was significant (*ps* > 0.05). The two-way interaction of outcome valence by subsequent choice was significant ($F(1, 78) = 112.562$, $p < 0.001$, $\eta_p^2 = 0.591$): simple effect analysis indicated that staying on the same option after wins (76.67 ± 13.23%) showed a higher accuracy than shifting between options (47.15 ± 17.37%; $F(1, 78) = 157.32$, $p < 0.001$, $\eta_p^2 = 0.666$), but the reverse was true after losses (49.67 ± 13.13% vs. 59.05 ± 18.16%; $F(1, 78) = 12.73$, $p = 0.001$, $\eta_p^2 = 0.139$).

The three-way interaction of outcome valence by subsequent choice by group was significant ($F(1, 78) = 4.410$, $p = 0.039$, $\eta_p^2 = 0.054$; Fig. 3): simple-simple effect analysis indicated that the accuracy for lose-shift was lower in the HTA group (51.91 ± 17.05%) than in the LTA group (66.20 ± 16.52%; $F(1, 78) = 14.51$, $p < 0.001$, $\eta_p^2 = 0.157$); however, this group difference did not achieve the significance level for win-stay ($F(1, 78) < 1$, $p = 0.415$, $\eta_p^2 = 0.009$; HTA = 75.46 ± 13.22%, LTA = 77.89 ± 13.29%), win-shift ($F(1, 78) < 1$, $p = 0.974$, $\eta_p^2 < 0.001$; HTA = 47.08 ± 17.14%, LTA = 47.21 ± 17.82%), or lose-stay ($F(1, 78) < 1$, $p = 0.687$, $\eta_p^2 = 0.002$; HTA = 49.07 ± 13.15%, LTA = 50.27 ± 13.25%).

3.1.3. Number of rule reversals

The number of rule reversals in the HTA group (4.80 ± 2.47 times) was smaller than that in the LTA group (6.15 ± 3.25 times; $t(78) = 2.089$, $p = 0.040$, $d = 0.467$).

3.1.4. Number of trials of shifting to the other option after rule reversals

The number of trials after rule reversals for participants to shift choice in the HTA group (3.52 ± 2.73 times) was larger than that in the LTA group (2.50 ± 1.31 times; $t(78) = -2.118$, $p = 0.037$, $d = 0.474$).

3.1.5. RT

The main effect of group was significant ($F(1, 78) = 4.787$, $p = 0.032$, $\eta_p^2 = 0.058$; Fig. 4): the HTA group (654.56 ± 127.40 ms) responded faster than the LTA group did (712.66 ± 109.44 ms). The main effect of outcome valence was significant ($F(1, 78) = 26.286$, $p < 0.001$, $\eta_p^2 = 0.252$): the RT following wins (636.03 ± 165.64 ms) was faster than that following losses (731.19 ± 184.72 ms). The main effect of subsequent choice was significant ($F(1, 78) = 10.571$, $p = 0.002$, $\eta_p^2 = 0.119$): the RT of the decision to stay (663.92 ± 174.70 ms) was faster than that of the decision to shift (703.29 ± 178.65 ms).

Neither the interaction of subsequent choice by group, nor that of outcome valence by subsequent choice, nor that of outcome valence by subsequent choice by group was significant (*ps* > 0.05). The interaction of outcome valence by group was significant ($F(1, 78) = 4.409$, $p =$

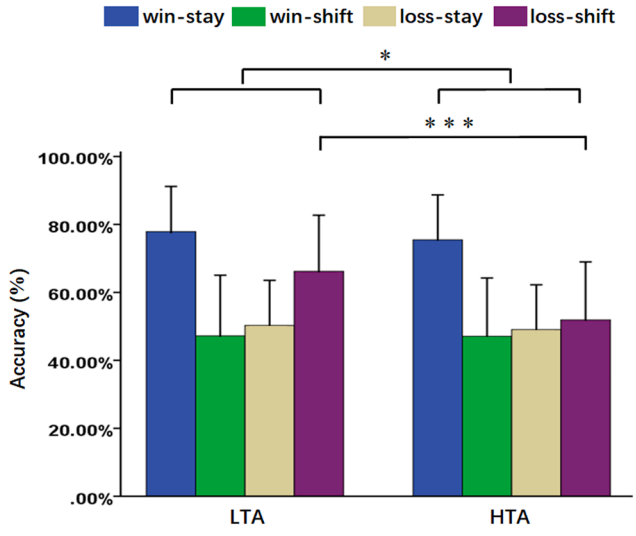

Fig. 3. Accuracy of different kinds of choices. Error bars indicate one standard deviation. LTA: the low-trait anxiety group; HTA: the high-trait anxiety group. *: $p < 0.05$; ***: $p < 0.001$.

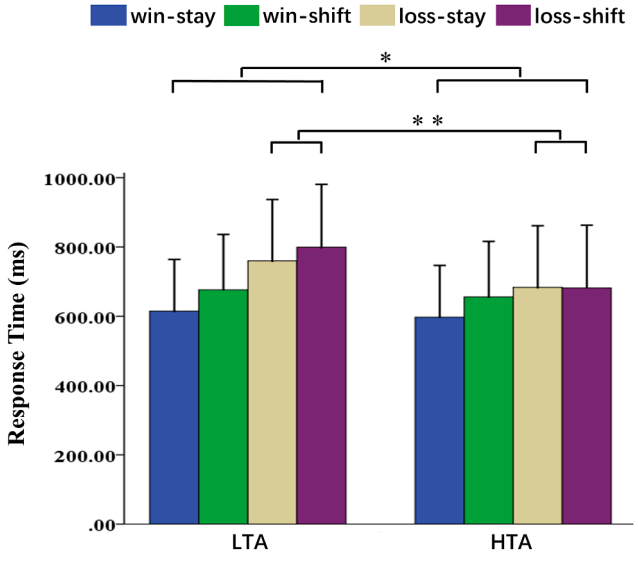

Fig. 4. Response time of different kinds of choices. Error bars indicate one standard deviation. LTA: the low-trait anxiety group; HTA: the high-trait anxiety group. *: $p < 0.05$; **: $p < 0.01$.

0.039, $\eta_p^2 = 0.054$; Fig. 4): simple effect analysis indicated that the RT following losses was faster in the HTA group (682.65 ± 178.40 ms) than in the LTA group (779.72 ± 179.11 ms; $F(1, 78) = 9.009$, $p = 0.004$, $\eta_p^2 = 0.103$); however, this group difference did not achieve the significance level following wins ($F(1, 78) < 1$, $p = 0.557$, $\eta_p^2 = 0.004$; HTA = 626.46 ± 156.83 ms, LTA = 645.59 ± 156.86 ms).

3.2. ERP indexes

3.2.1. FRN

The main effect of group was significant ($F(1, 78) = 14.226$, $p < 0.001$, $\eta_p^2 = 0.154$): the HTA group (8.23 ± 2.85 μV) showed a smaller (i.e., less negative-going) FRN than the LTA group did (6.92 ± 2.59 μV). The main effect of outcome valence was significant ($F(1, 78) = 46.40$, $p < 0.001$, $\eta_p^2 = 0.373$): a larger FRN was evoked by losses (6.39 ± 2.64 μV) compared to wins (8.76 ± 2.43 μV). The main effect of subsequent choice was significant ($F(1, 78) = 44.146$, $p < 0.001$, $\eta_p^2 = 0.361$): a smaller FRN was associated with shift choices (7.17 ± 2.98 μV) compared to stay choices (7.98 ± 2.55 μV).

The interaction effect of outcome valence by group was significant ($F(1, 78) = 4.328$, $p = 0.041$, $\eta_p^2 = 0.053$): simple effect analysis indicated that the FRN in the loss condition was smaller in the HTA group (7.41 ± 2.50 μV) compared to the LTA group (5.38 ± 2.38 μV; $F(1, 78) = 18.533$, $p < 0.001$, $\eta_p^2 = 0.192$); however, this group difference did not achieve the significance level in the win condition ($F(1, 78) = 1.309$, $p = 0.256$, $\eta_p^2 = 0.017$; HTA = 9.05 ± 2.42 μV, LTA = 8.47 ± 2.43 μV).

The interaction effect of subsequent choice by group was significant ($F(1, 78) = 18.438$, $p < 0.001$, $\eta_p^2 = 0.191$): simple effect analysis indicated that the FRN associated with shift choices (6.25 ± 3.04 μV) was larger than stay choices (7.59 ± 2.50 μV) in the LTA group ($F(1, 78) = 59.822$, $p < 0.001$, $\eta_p^2 = 0.434$); however, this difference did not achieve the significance level between shift choices (8.08 ± 2.63 μV) and stay choices (8.37 ± 2.56 μV) in the HTA group ($F(1, 78) = 2.762$, $p = 0.101$, $\eta_p^2 = 0.034$).

The interaction effect of outcome valence by subsequent choice was significant ($F(1, 78) = 12.380$, $p = 0.001$, $\eta_p^2 = 0.137$): simple effect analysis indicated that the FRN associated with shift choices (5.71 ± 2.58 μV) was larger than stay choices (7.07 ± 2.53 μV) in the loss condition ($F(1, 78) = 46.439$, $p < 0.001$, $\eta_p^2 = 0.373$); however, this difference did not achieve the significance level between the FRN associated with shift choices (8.62 ± 2.62 μV) and stay choices (8.89 ± 2.24 μV) in the win condition ($F(1, 78) = 1.916$, $p = 0.170$, $\eta_p^2 = 0.024$).

The three-way interaction of outcome valence by subsequent choice by group was significant ($F(1, 78) = 15.598$, $p < 0.001$, $\eta_p^2 = 0.167$; Fig. 5): simple-simple effect analysis indicated that the FRN for lose-shift was smaller in the HTA group (7.30 ± 2.46 μV) than in the LTA group (4.13 ± 1.53 μV; $F(1, 78) = 47.72$, $p < 0.001$, $\eta_p^2 = 0.379$); however, this group difference did not achieve the significance level for win-stay ($F(1, 78) = 1.78$, $p = 0.186$, $\eta_p^2 = 0.022$; HTA = 9.23 ± 2.26 μV, LTA = 8.56 ± 2.20 μV), win-shift ($F(1, 78) = 0.72$, $p = 0.399$, $\eta_p^2 = 0.009$; HTA = 8.87 ± 2.59 μV, LTA = 8.37 ± 2.66 μV), or lose-stay ($F(1, 78) = 2.53$, $p = 0.116$, $\eta_p^2 = 0.031$; HTA = 7.52 ± 2.57 μV, LTA = 6.63 ± 2.43 μV).

3.2.2. P3

The main effect of group was marginally significant ($F(1, 78) = 2.884$, $p = 0.093$, $\eta_p^2 = 0.036$). The main effect of outcome valence was significant ($F(1, 78) = 73.890$, $p < 0.001$, $\eta_p^2 = 0.486$): a larger (i.e., more positive-going) P3 was evoked by losses (8.91 ± 2.69 μV) compared to wins (6.56 ± 2.58 μV). The main effect of subsequent choice was significant ($F(1, 78) = 19.874$, $p < 0.001$, $\eta_p^2 = 0.203$): a larger P3 was associated with shift choices (8.24 ± 3.06 μV) compared to stay choices (7.23 ± 2.61 μV).

The interaction effect of outcome valence by group was significant ($F(1, 78) = 14.023$, $p < 0.001$, $\eta_p^2 = 0.152$): simple effect analysis indicated that the P3 associated with losses was smaller in the HTA group (8.10 ± 2.76 μV) compared to the LTA group (9.72 ± 2.38 μV; $F(1, 78) = 12.485$, $p = 0.001$, $\eta_p^2 = 0.138$); however, this group difference did not achieve the significance level for wins (HTA = 6.77 ± 2.62 μV, LTA = 6.36 ± 2.54 μV; $F(1, 78) = 0.930$, $p = 0.338$, $\eta_p^2 = 0.012$). Neither the interaction of subsequent choice by group, nor that of outcome valence by subsequent choice, was significant (*ps* > 0.05).

The three-way interaction of outcome valence by subsequent choice by group was significant ($F(1, 78) = 6.368$, $p = 0.014$, $\eta_p^2 = 0.075$;

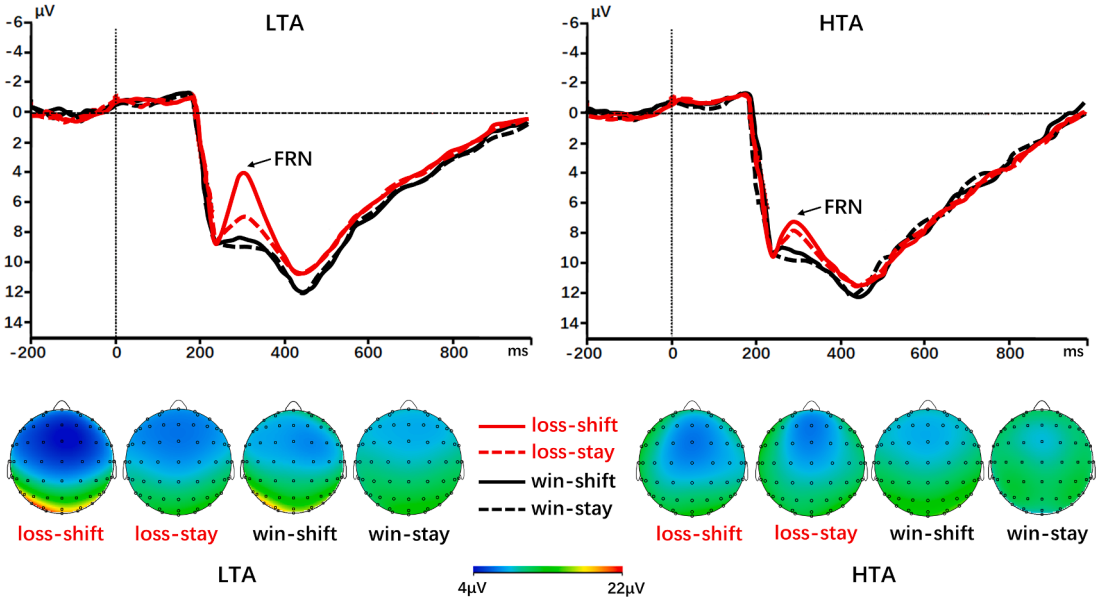

Fig. 5. Grand-mean waveforms (time-locked to the onset of outcome) averaged across the electrode sites of Fz, F1, F2, FCz, FC1, FC2, Cz, C1, and C2, where the feedback-related negativity (FRN) was analyzed. The scalp topographies of the difference wave between losses and wins are presented beneath. LTA: the low-trait anxiety group; HTA: the high-trait anxiety group.

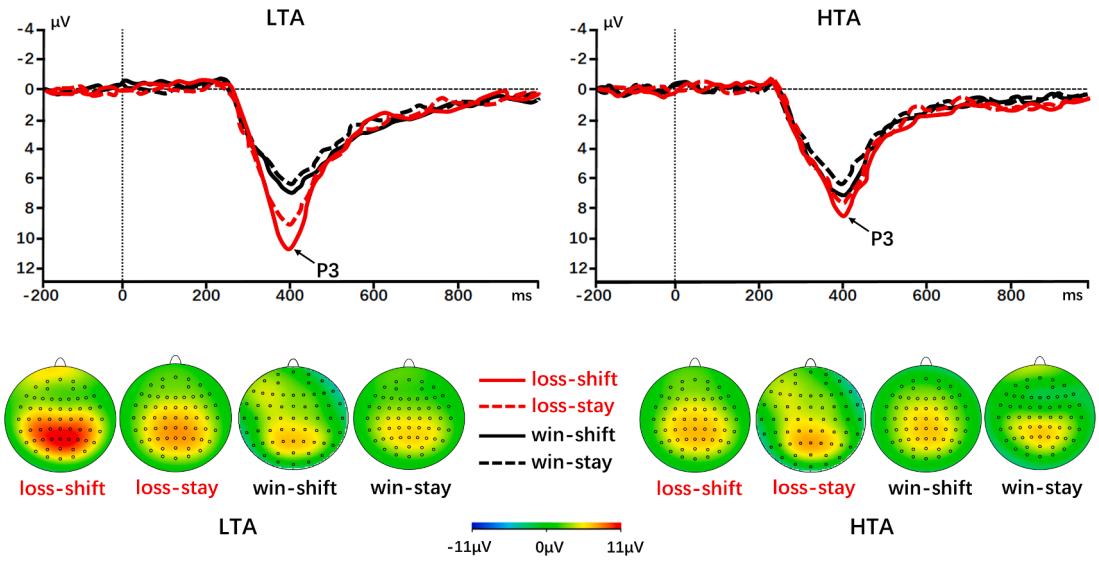

Fig. 6. Grand-mean waveforms (time-locked to the onset of outcome) averaged across the electrode sites of Pz, P1, P2, P3, P4, CPz, CP1, CP2, CP3, and CP4, where the P3 component was analyzed. The scalp topographies for wins and losses are presented beneath. LTA: the low-trait anxiety group; HTA: the high-trait anxiety group.

Fig. 6): simple-simple effect analysis indicated that the P3 for lose-shift was smaller in the HTA group (8.30 ± 3.07 μV) than in the LTA group (10.79 ± 2.32 μV; $F(1, 78) = 16.88$, $p < 0.001$, $\eta_p^2 = 0.178$); however, this group difference did not achieve the significance level for win-stay ($F(1, 78) < 1$, $p = 0.990$, $\eta_p^2 < 0.001$; HTA = 6.19 ± 2.35 μV, LTA = 6.20 ± 2.79 μV), win-shift ($F(1, 78) = 2.20$, $p = 0.142$, $\eta_p^2 = 0.027$; HTA = 7.36 ± 2.77 μV, LTA = 6.51 ± 2.30 μV), or lose-stay ($F(1, 78) = 2.31$, $p = 0.133$, $\eta_p^2 = 0.029$; HTA = 7.90 ± 2.45 μV, LTA = 8.64 ± 1.93 μV).

3.2.3. Source localization

After combining all conditions in the whole sample, we found that the FRN and the P3 component may have been generated from the ACC (Brodmann area 10, Montreal Neurological Institute [MNI] coordinates = [−3, 52, 1]) and the parietal cortex (Brodmann area 40, MNI coordinates = [67, −25, 29]), respectively (Fig. 7).

3.3. Relationship between anxiety and behavioral/ERP indexes

We further conducted simple linear regression analyses in the whole sample, using the two self-reported scores (STAI-T and BDI) as independent variables simultaneously, and the seven behavioral/ERP indexes which were sensitive to the grouping factor as dependent variables (i.e., the mean number of lose-shift, the accuracy associated with lose-shift, the RT following losses, the number of rule reversals, the number of trials to shift to the other option after rule reversals, as well as FRN and P3 amplitudes associated with lose-shift). Results showed that the STAI-T (but not BDI) score was a significant predictor of: (1) the number of lose-shift choices, (2) the accuracy of lose-shift choices, (3) the RT following losses, (4) the FRN amplitude associated with lose-shift, and (5) the P3 amplitude associated with lose-shift (see Table 2 for details).

We also conducted two-tailed Pearson correlation analyses between RT and accuracy associated with win-stay, win-shift, lose-stay, and lose-shift, so as to examine whether the behavioral differences between

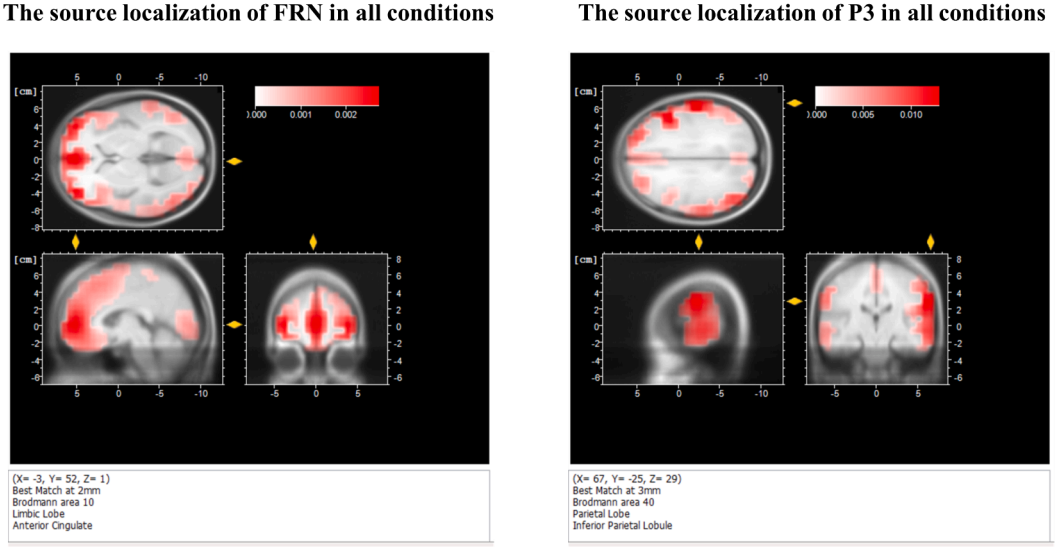

Fig. 7. sLORETA images of the standardized current density maximum associated with the FRN (left panel) and P3 (right panel) in the whole sample (combining all conditions). The results at the peak latency of the FRN (312 ms) and P3 (396 ms) are illustrated.

Table 2
The results of simple linear regression analyses in the whole sample.

dependent variables	*F*	R^2	*STAI-T: beta value*	*STAI-T: p value*	*BDI: beta value*	*BDI: p value*
lose-shift	21.005***	0.336	−0.565	< 0.001	−0.128	0.169
accuracy	6.475**	0.122	−0.360	0.001	−0.774	0.441
RT in loss	3.904*	0.068	−0.294	0.009	−0.048	0.660
NRR	2.653	0.040	−0.246	0.029	−0.038	0.736
NRR-shift	2.046	0.026	0.214	0.059	0.046	0.683
FRN	44.243***	0.523	0.718	< 0.001	0.075	0.342
P3	7.410**	0.140	−0.403	< 0.001	0.008	0.939

STAI-T, the Trait form of Spielberger's State-Trait Anxiety Inventory; BDI, Beck Depression Inventory (second edition). Lose-shift, the number of lose-shift choices; accuracy, the accuracy associated with lose-shift choices; RT, the reaction time following losses; NRR, the number of rule reversals; NRR-shift, the number of trials after rule reversals for participants to shift choice. FRN, the FRN amplitude associated with lose-shift; P3, the P3 amplitude associated with lose-shift. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

groups could be explained by a speed-accuracy tradeoff. In total, we performed eight (4 × 2) correlations in the HTA and LTA groups (Table 3). Results showed one significant correlation before correction for multiple comparisons, that is, RT and accuracy associated with lose-shift was positively correlated with one another in the LTA group ($r = 0.389$, $p = 0.013$).

3.4. Relationship between behavioral and ERP indexes

We finally examined the relationship between the above behavioral indexes and ERP indexes with two-tailed Pearson correlation analyses. In total, we performed 10 (5 × 2) correlations (Table 4). These analyses are exploratory. Results showed only one significant correlation after correction for multiple comparisons. Specifically, the number of lose-shift ($r = -0.318$, $p = 0.004$, corrected $p = 0.04$) was correlated with the FRN amplitude elicited by lose-shift. The FRN is a negative-going component, therefore this negative correlation indicates that a larger FRN was associated with a higher frequency to shift choice after losses.

4. Discussion

Reversal learning is critical for individuals to overcome old habitual behaviors and take adaptive goal-directed actions in dynamic environments (Xue et al., 2008). The current study compared HTA and LTA participants' ability to track changes of stimulus-reward contingencies in a PRL task. We found that both behavioral strategies and electrophysiological activity were sensitive to STAI-T scores, indicating that a higher level of trait anxiety is associated with impaired reversal learning performance. More specifically, participants with a high trait anxiety level were less capable of finding out the optimal strategy, thus they encountered fewer reversals throughout the task compared to their low-anxiety counterparts. This phenomenon might be resulted from diminished sensitivity to negative outcomes, seeing that a higher level of trait anxiety was related to fewer lose-shift choices and weaker ERP responses to lose-shift.

In the whole sample, participants won more frequently than lost during the PRL task, indicating that they have learned the winning rule to some extent. In addition, participants were more likely to keep choosing the same option rather than shift to the other option after wins, but the reverse was true after losses, indicating the application of the "win-stay/lose-shift" strategy. In fact, behavioral results showed that using this strategy in our task was more effective than "win-shift/lose-stay" (see also Starcke & Brand, 2016). Regarding anxiety, we found that the HTA group had a lower task accuracy (as well as a shorter RT) compared to the LTA group. To explain this phenomenon, we further discovered that HTA participants made fewer lose-shift decisions than LTA participants, while the accuracy of these decisions was also lower in the HTA group. According to Bari and Robbins (2013), the frequency of lose-shift is associated with punishment sensitivity in PRL paradigms. Further, HTA participants require more trials to shift to the other option after a rule reversal happens, indicating a lower learning rate of discovering the new optimal choice after rule reversals. Meanwhile, the RT following losses (but not wins) was faster in the HTA group than in the LTA group. Finally, the LTA group might have used a speed-accuracy tradeoff strategy when making lose-shift choices (that is, sacrificing RT for a higher accuracy), but the same was not true for the HTA group. Overall, the behavioral data strongly suggest that anxious people's reversal learning deficits are mainly due to their processing of negative outcomes, that is, they not only show weaker sensitivity to negative outcomes, but also are less efficient in adjusting their decision strategy according to these outcomes (see Huys et al., 2013; Starcke & Brand, 2016, for explanation).

The above opinion is supported by our ERP results. Consistent with the classic literature (Gehring & Willoughby, 2002; Miltner et al., 1997), the FRN was larger (i.e., more negative-going) for losses than wins. Most critically, the HTA group showed a smaller FRN than the LTA group did (see also Gu et al., 2010a, 2010b; Jiang et al., 2018; Takács et al., 2015), and this between-group difference was significant for lose-shift but not for other conditions. Further, the FRN amplitude was correlated with the number of lose-shift, such that the participants who showed a smaller FRN were less likely to make lose-shift choices; this result highlights the FRN as a learning signal that guides behavioral adjustment (Cohen & Ranganath, 2007; Frank et al., 2005; Luu et al., 2003). Finally,

Table 3
The correlation matrix between RT and accuracy in four experimental conditions (win-stay, win-shift, lose-stay, and lose-shift) in the LTA and HTA group, respectively.

		RT in win-stay	RT in win-shift	RT in loss-stay	RT in loss-shift
LTA	ACC in win-stay	$r = 0.092$ ($p = 0.572$)			
	ACC in win-shift		$r = -0.103$ ($p = 0.526$)		
	ACC in loss-stay			$r = -0.152$ ($p = 0.350$)	
	ACC in loss-shift				$r = 0.389$ ($p = 0.013$)
HTA	ACC in win-stay	$r = 0.242$ ($p = 0.132$)			
	ACC in win-shift		$r = -0.034$ ($p = 0.836$)		
	ACC in loss-stay			$r = -0.023$ ($p = 0.888$)	
	ACC in loss-shift				$r = -0.005$ ($p = 0.974$)

LTA, the low-trait anxiety group; HTA, the high-trait anxiety group.

Table 4
The correlation matrix (before correction for multiple comparisons) between five behavioral and two ERP indexes, all of which were sensitive to the grouping factor.

	Loss-shift	Accuracy	RT	NRR	NRR-shift
FRN	$r = -0.323$ ($p = 0.003$)	$r = -0.266$ ($p = 0.017$)	$r = -0.259$ ($p = 0.021$)	$r = -0.100$ ($p = 0.378$)	$r = 0.108$ ($p = 0.341$)
P3	$r = 0.189$ ($p = 0.092$)	$r = 0.056$ ($p = 0.621$)	$r = 0.065$ ($p = 0.566$)	$r = 0.150$ ($p = 0.185$)	$r = -0.240$ ($p = 0.032$)

FRN, the FRN amplitude associated with lose-shift; P3, the P3 amplitude associated with lose-shift. Lose-shift, the number of lose-shift choices; accuracy, the accuracy associated with lose-shift choices; RT, the reaction time following losses; NRR, the number of rule reversals; NRR-shift, the number of trials after rule reversals for participants to shift choice.

individual trait anxiety level predicted not only the number of lose-shift choices, but also the FRN amplitude associated with lose-shift. Taken together, we suggest that anxiety modulates punishment sensitivity (indexed by the FRN) during reversal learning, to the extent that anxious people's ability of adjusting strategies according to negative outcomes is significantly weakened.

Seeing that anxiety is characterized as stronger reactions to potentially threat-related information (Bishop et al., 2004; Etkin et al., 2004; Mogg & Bradley, 2018), one might question why anxious participants' sensitivity to negative outcomes would decrease during reversal learning. To clarify this issue, it should be noted that anxiety evolves from defense mechanisms that enhance our chances for survival, thus anxiety is essentially associated with threatening stimuli rather than economically disadvantageous outcomes (Grillon, 2002b; LeDoux, 1998). As pointed out by Schonberg et al. (2011), the cognitive and neural mechanisms involved in naturalistic risk-taking are dissociated from those involved in economic risk-taking. We therefore suggest that the relationship between anxiety and diminished sensitivity to monetary losses should not be surprising (see also Giorgetta et al., 2012 for similar results).

Numerous studies have demonstrated that anxiety consistently leads to a pessimistic outcome expectation, such as in economic games (Eisenberg et al., 1998; Lauriola & Levin, 2001; Shepperd et al., 2005; Stöber, 1997). In other words, anxious people are more prone to predict that they would get unfavorable outcomes in the future (Butler & Mathews, 1987; MacLeod et al., 1991; Mitte, 2007; Wray & Stone, 2005). In our opinion, this phenomenon may help understand why anxiety reduces punishment sensitivity. That is, negative outcomes are more likely to meet anxious individuals' prior expectation and thus are unable to attract sufficient attention. Consequently, the diminished punishment sensitivity associated with pessimistic expectation hinders anxious individuals from detecting changes in stimulus-reward contingencies. Many ERP studies have provided support for the above explanation (Gu et al., 2010a, 2010b; Jiang et al., 2018).

Meanwhile, the P3 amplitude associated with lose-shift (but not other conditions) was smaller in the HTA group compared with the LTA group. In the whole sample, individual trait anxiety level predicted the P3 amplitude in this condition. These results suggest that anxiety also affects information updating targeting on negative outcomes, which are consistent with our experimental hypothesis. Unlike the FRN, we found that the P3 amplitude showed no relationship with behavioral indexes. Accordingly, we believe that anxious participants' impaired reversal learning performance could not be attributed to their abnormalities in information updating, but this idea should be treated with caution since it is based on null results. A study by Donaldson et al. (2016) found that the P3 amplitude predicted behavioral adjustment during reversal learning. Regarding these heterogeneous findings, we notice that Donaldson et al. (2016) used visually complex picture (human faces and landscape scenes) as options to learn, while we used alphabetic symbols. It is possible that visual complexity of experimental stimuli interferes with the learning process, manifesting as different patterns of electrophysiological activity (see also Luyckx et al., 2019).

According to the results of our ERP source analysis, the FRN and the P3 were originated from the ACC and the parietal cortex, respectively. These results are supported by many previous studies including those using simultaneous ERP-functional magnetic resonance imaging recording (Gehring & Willoughby, 2002; Hauser et al., 2014; Linden, 2005). Further, these results indicate that compared to other key nodes within the neural networks of reversal learning (Budhani et al., 2007; Hampton et al., 2007; Hampton & O'Doherty J, 2007), the ACC and the parietal cortex are particularly susceptible to emotional influence, which might be of clinical significance. Indeed, these two regions have been considered to play important roles in the etiology of anxiety disorders (Grupe & Nitschke, 2013; Tovote et al., 2015) as well as in the relationship between anxiety and decision-making behavior (Amemori & Graybiel, 2012; Aupperle & Paulus, 2010; Krain et al., 2008). Follow-up brain-imaging studies should test our findings to account for the limited accuracy of ERP source localization (Zhukov et al., 2000).

Recently, Aylward et al. (2019) reported that anxious individuals under stress showed a better learning rate in response to negative outcomes, which is inconsistent with our findings. The reason for this discrepancy is unclear to us, but we note some methodological difference between the two studies. First, in the learning task designed by Aylward et al. (2019), reward contingencies fluctuated over time automatically, not depending on participants' performance. This difference in probabilistic structure may have modulated the effect of anxiety. Second, Aylward et al. (2019) applied stress manipulation before the learning task, while this study focuses on trait anxiety. Another possibility lies in the fact that the two studies were conducted under different cultural backgrounds (United Kingdom vs China). In our opinion, the relationship between anxiety and feedback learning might be sensitive to culture-emotion interaction – that is, emotional influence on behavior manifest in different ways for people from different cultures (Boiger & Mesquita, 2012; Kitayama & Park, 2007). This possibility could be examined with a cross-cultural experimental design in the future.

In our opinion, a main strength of our study is that we have controlled the potential influence of depression. It is well known to clinical researchers that anxiety and depression have a high comorbidity rate (Brady & Kendall, 1992; Dobson, 1985; Stavrakaki & Vargo, 1986). Thus, we only recruited participants with a low BDI-II scores to ensure that our findings were not modulated by depression (see also Beuke et al., 2003). Meanwhile, a few limitations should be pointed out for future research to consider. First, this study selectively investigates trait anxiety, therefore the impact of transient anxiety state remains undetermined (but see Aylward et al., 2019). Second, we recruited our participants from extreme groups, which is a common practice in many studies but may have resulted in a bimodal distribution of anxiety scores across groups; alternative grouping methods (e.g., median split) could be considered in future research. Moreover, our task did not manipulate reward magnitude; modulating this factor would help examine anxious individuals' learning performance under varied motivational levels. Likewise, it would be interesting to explore the effect of task difficulty (e.g., by changing the number of available options) on the relationship between anxiety and reversal learning.

In short, the present study enriches the knowledge about the impact of anxiety on feedback learning. Considering the association between abnormal learning ability and behavioral symptoms in anxiety (Britton et al., 2011; Grillon, 2002a), our findings may provide insights into the nature of anxiety with the perspective of targeted interventions. Also, our findings may help understanding reversal learning deficits associated with other types of emotional symptoms; this transdiagnostic perspective is supported by recent studies indicating common abnormalities in reward processing across traditional diagnostic boundaries (Husain & Roiser, 2018; Nusslock & Alloy, 2017; Treadway & Zald, 2013). In this study, participants in the HTA group were not formally diagnosed with anxiety. Some recent studies have indicated that anxiety disorders are related to increased punishment learning rates, but their tasks did not involve a reversal process (Laufer et al., 2016; Morris & Rottenberg, 2015). We suggest that follow-up research should directly compare clinical and nonclinical samples with the same behavioral paradigm, so as to determine the robustness of our findings in clinical populations. Moreover, as pointed out by Izquierdo and Jentsch (2012), the neurobiological basis of reversal learning is complicated, including "a circumscribed neural circuitry" and "an orchestrated balance of neurotransmitters" (see also Chudasama & Robbins, 2003). Regarding that, investigating the treatment effects of non-invasive brain stimulation (e.g., Sturm et al., 2003) and neurotransmitter modulation (e.g., Nuss, 2015) on anxious individuals' reversal learning performance would be fruitful.

CRediT authorship contribution statement

Lisheng Xia: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing. **Pengfei Xu:** Methodology, Writing - review & editing. **Ziyan Yang:** Writing - review & editing. **Ruolei Gu:** Conceptualization, Writing - original draft, Writing - review & editing. **Dandan Zhang:** Supervision, Project administration, Funding acquisition.

Acknowledgments

This study was funded by the PhD research startup foundation of Guizhou Normal University (GZNUD[2018]35), the National Natural Science Foundation of China (32071083, 32020103008), Shenzhen-Hong Kong Institute of Brain Science (2021SHIBS0003), the Major Program of the Chinese National Social Science Foundation (17ZDA324), and Youth Innovation Promotion Association CAS (2019088). The authors thank Yongling Lin for her help with manuscript revision.

Declaration of ethics

All procedures performed in this study were in accordance with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Declaration of Competing Interest

The authors have declared that there is no conflict of interest in relation to the subject of this study.

Data availability statement

The data and code of this study would be available upon request and with approvals of School of Psychology, Guizhou Normal University. More information on making this request can be obtained from the first author, Dr. Lisheng Xia (xials@szu.edu.cn).

References

Amemori, K.-I., Graybiel, A.M., 2012. Localized microstimulation of primate pregenual cingulate cortex induces negative decision-making. Nat. Neurosci. 15 (5), 776–785. https://doi.org/10.1038/nn.3088.

American Psychiatric Association, 2013. Diagnostic and statistical manual of mental disorders (DSM-5®). American Psychiatric Publishing.

Amodio, D.M., Bartholow, B.D., Ito, T.A., 2014. Tracking the dynamics of the social brain: ERP approaches for social cognitive and affective neuroscience. Soc. Cogn. Affect. Neurosci. 9 (3), 385–393. https://doi.org/10.1093/scan/nst177.

Andreatta, M., Michelmann, S., Pauli, P., Hewig, J., 2017. Learning processes underlying avoidance of negative outcomes. Psychophysiology 54 (4), 578–590. https://doi.org/10.1111/psyp.12822.

Aupperle, R.L., Paulus, M.P., 2010. Neural systems underlying approach and avoidance in anxiety disorders. Dialogues Clin. Neurosci. 12 (4), 517–531. http://www.ncbi.nlm.nih.gov/pubmed/21319496.

Aylward, J., Valton, V., Ahn, W.Y., Bond, R.L., Dayan, P., Roiser, J.P., Robinson, O.J., 2019. Altered learning under uncertainty in unmedicated mood and anxiety disorders. Nat. Hum. Behav. 3 (10), 1116–1123. https://doi.org/10.1038/s41562-019-0628-0.

Balconi, M., Crivelli, D., 2010. FRN and P300 ERP effect modulation in response to feedback sensitivity: the contribution of punishment-reward system (BIS/BAS) and Behaviour Identification of action. Neurosci. Res. 66 (2), 162–172. https://doi.org/10.1016/j.neures.2009.10.011.

Bari, A., Robbins, T.W., 2013. Inhibition and impulsivity: behavioral and neural basis of response control. Prog. Neurobiol. 108, 44–79. https://doi.org/10.1016/j.pneurobio.2013.06.005.

Bartolo, R., Averbeck, B.B., 2020. Prefrontal cortex predicts state switches during reversal learning. Neuron 106 (6), 1044–1054 e1044. https://doi.org/10.1016/j.neuron.2020.03.024.

Beck, A. T., Steer, R. A., & Brown, G. K., 1996. Beck Depression Inventory—Second Edition. The Psychological Corporation.

Beuke, C.J., Fischer, R., McDowall, J., 2003. Anxiety and depression: why and how to measure their separate effects. Clin. Psychol. Rev. 23 (6), 831–848. https://doi.org/10.1016/S0272-7358(03)00074-6.

Bishop, S.J., 2009. Trait anxiety and impoverished prefrontal control of attention. Nat. Neurosci. 12 (1), 92–98. https://doi.org/10.1038/Nn.2242.

Bishop, S., Duncan, J., Brett, M., Lawrence, A.D., 2004. Prefrontal cortical function and anxiety: controlling attention to threat-related stimuli. Nat. Neurosci. 7 (2), 184–188. https://doi.org/10.1038/nn1173.

Bishop, S.J., Gagne, C., 2018. Anxiety, depression, and decision making: a computational perspective. Annu. Rev. Neurosci. 41 (1), 371–388. https://doi.org/10.1146/annurev-neuro-080317-062007.

Blair, R.J., Cipolotti, L., 2000. Impaired social response reversal: a case of 'acquired sociopathy'. Brain 123 (Pt 6), 1122–1141. https://doi.org/10.1093/brain/123.6.1122.

Blair, K.S., Otero, M., Teng, C., Geraci, M., Lewis, E., Hollon, N., Blair, R.J., Ernst, M., Grillon, C., Pine, D.S., 2016. Learning from other people's fear: amygdala-based social reference learning in social anxiety disorder. Psychol. Med. 46 (14), 2943–2953. https://doi.org/10.1017/S0033291716001537.

Boiger, M., Mesquita, B., 2012. The construction of emotion in interactions, relationships, and cultures. Emotion Rev. 4 (3), 221–229. https://doi.org/10.1177/1754073912439765.

Brady, E.U., Kendall, P.C., 1992. Comorbidity of anxiety and depression in children and adolescents. Psychol. Bull. 111 (2), 244–255. http://www.ncbi.nlm.nih.gov/pubmed/1557475.

Britton, J.C., Lissek, S., Grillon, C., Norcross, M.A., Pine, D.S., 2011. Development of anxiety: the role of threat appraisal and fear learning. Depression Anxiety 28 (1), 5–17. https://doi.org/10.1002/da.v28.110.1002/da.20733.

Brown, T.A., Campbell, L.A., Lehman, C.L., Grisham, J.R., Mancill, R.B., 2001. Current and lifetime comorbidity of the DSM-IV anxiety and mood disorders in a large clinical sample. J. Abnormal Psychol. 110 (4), 585–599. https://doi.org/10.1037//0021-843x.110.4.585.

Browning, M., Behrens, T.E., Jocham, G., O'Reilly, J.X., Bishop, S.J., 2015. Anxious individuals have difficulty learning the causal statistics of aversive environments. Nat. Neurosci. 18 (4), 590–596. https://doi.org/10.1038/nn.3961.

Budhani, S., Marsh, A.A., Pine, D.S., Blair, R.J., 2007. Neural correlates of response reversal: considering acquisition. Neuroimage 34 (4), 1754–1765. https://doi.org/10.1016/j.neuroimage.2006.08.060.

Butler, G., Mathews, A., 1987. Anticipatory anxiety and risk perception. Cognit. Ther. Res. 11 (5), 551–565.

Chase, H.W., Swainson, R., Durham, L., Benham, L., Cools, R., 2011. Feedback-related negativity codes prediction error but not behavioral adjustment during probabilistic reversal learning. J. Cognit. Neurosci. 23 (4), 936–946. https://doi.org/10.1162/jocn.2010.21456.

Chudasama, Y., Robbins, T.W., 2003. Dissociable contributions of the orbitofrontal and infralimbic cortex to pavlovian autoshaping and discrimination reversal learning: further evidence for the functional heterogeneity of the rodent frontal cortex. J. Neurosci. 23 (25), 8771–8780. https://www.ncbi.nlm.nih.gov/pubmed/14507977.

Clark, D.M., 1999. Anxiety disorders: Why they persist and how to treat them. Behav. Res. Ther. 37, S5–S27. https://doi.org/10.1016/S0005-7967(99)00048-0.

Cohen, M.X., Ranganath, C., 2007. Reinforcement learning signals predict future decisions. J. Neurosci. 27 (2), 371–378. https://doi.org/10.1523/JNEUROSCI.4421-06.2007.

Cohen, M.X., Wilmes, K., van de Vijver, I., 2011. Cortical electrophysiological network dynamics of feedback learning. Trends Cognit. Sci. 15 (12), 558–566. https://doi.org/10.1016/j.tics.2011.10.004.

Cools, R., Clark, L., Owen, A. M., & Robbins, T. W., 2002. Defining the neural mechanisms of probabilistic reversal learning using event-related functional magnetic resonance imaging. Journal of Neuroscience, 22(11), 4563-4567. https://doi.org/20026435.

Derogatis, L.R., 1977. SCL-90-R: Administration, scoring, and procedures manual. Clinical Psychometric Research, Baltimore.

Dickstein, D.P., Finger, E.C., Brotman, M.A., Rich, B.A., Pine, D.S., Blair, J.R., Leibenluft, E., 2010. Impaired probabilistic reversal learning in youths with mood and anxiety disorders. Psychol. Med. 40 (7), 1089–1100. https://doi.org/10.1017/S0033291709991462.

Dobson, K.S., 1985. The relationship between anxiety and depression. Clinical Psychol. Rev. 5 (4), 307–324. https://doi.org/10.1016/0272-7358(85)90010-8.

Domschke, K., Dannlowski, U., 2010. Imaging genetics of anxiety disorders. Neuroimage 53 (3), 822–831. https://doi.org/10.1016/j.neuroimage.2009.11.042.

Donaldson, K.R., Ait Oumeziane, B., Helie, S., Foti, D., 2016. The temporal dynamics of reversal learning: P3 amplitude predicts valence-specific behavioral adjustment. Physiol. Behav. 161, 24–32. https://doi.org/10.1016/j.physbeh.2016.03.034.

Eisenberg, A. E., Baron, J., & Seligman, M. E. P., 1998. Individual difference in risk aversion and anxiety [working paper]. https://www.sas.upenn.edu/~baron/papers.htm/amyold.html.

Etkin, A., Klemenhagen, K.C., Dudman, J.T., Rogan, M.T., Hen, R., Kandel, E.R., Hirsch, J., 2004. Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. Neuron 44 (6), 1043–1055. https://doi.org/10.1016/j.neuron.2004.12.006.

Fellows, L.K., Farah, M.J., 2003. Ventromedial frontal cortex mediates affective shifting in humans: evidence from a reversal learning paradigm. Brain 126 (Pt 8), 1830–1837. https://doi.org/10.1093/brain/awg180.

Ferdinand, N.K., Mecklinger, A., Kray, J., Gehring, W.J., 2012. The processing of unexpected positive response outcomes in the mediofrontal cortex. J. Neurosci. 32 (35), 12087–12092. https://doi.org/10.1523/JNEUROSCI.1410-12.2012.

Ferdinand, N.K., Becker, A.M.W., Kray, J., Gehring, W.J., 2016. Feedback processing in children and adolescents: is there a sensitivity for processing rewarding feedback?

Neuropsychologia 82, 31–38. https://doi.org/10.1016/j.neuropsychologia.2016.01.007.
Frank, M.J., Woroch, B.S., Curran, T., 2005. Error-related negativity predicts reinforcement learning and conflict biases. Neuron 47 (4), 495–501. https://doi.org/10.1016/j.neuron.2005.06.020.
Garber, J., Brunwasser, S.M., Zerr, A.A., Schwartz, K.T., Sova, K., Weersing, V.R., 2016. Treatment and prevention of depression and anxiety in youth: test of cross-over effects. Depression Anxiety 33 (10), 939–959. https://doi.org/10.1002/da.22519.
Gehring, W.J., Willoughby, A.R., 2002. The medial frontal cortex and the rapid processing of monetary gains and losses. Science 295 (5563), 2279–2282. https://doi.org/10.1126/science.1066893.
Giorgetta, C., Grecucci, A., Zuanon, S., Perini, L., Balestrieri, M., Bonini, N., Sanfey, A.G., Brambilla, P., 2012. Reduced risk-taking behavior as a trait feature of anxiety. Emotion 12 (6), 1373–1383. https://doi.org/10.1037/a0029119.
Glazer, J.E., Kelley, N.J., Pornpattananangkul, N., Mittal, V.A., Nusslock, R., 2018. Beyond the FRN: broadening the time-course of EEG and ERP components implicated in reward processing. Int. J. Psychophysiol. 132 (Pt B), 184–202. https://doi.org/10.1016/j.ijpsycho.2018.02.002.
Gorrindo, T., Blair, R.J., Budhani, S., Dickstein, D.P., Pine, D.S., Leibenluft, E., 2005. Deficits on a probabilistic response-reversal task in patients with pediatric bipolar disorder. Am. J. Psychiatry 162 (10), 1975–1977. https://doi.org/10.1176/appi.ajp.162.10.1975.
Greening, S.G., Finger, E.C., Mitchell, D.G., 2011. Parsing decision making processes in prefrontal cortex: response inhibition, overcoming learned avoidance, and reversal learning. Neuroimage 54 (2), 1432–1441. https://doi.org/10.1016/j.neuroimage.2010.09.017.
Grillon, C., 2002a. Associative learning deficits increase symptoms of anxiety in humans. Biol. Psychiatry 51 (11), 851–858. https://doi.org/10.1016/s0006-3223(01)01370-1.
Grillon, C., 2002b. Startle reactivity and anxiety disorders: aversive conditioning, context, and neurobiology. Biol. Psychiatry 52 (10), 958–975. https://doi.org/10.1016/s0006-3223(02)01665-7.
Grupe, D.W., Nitschke, J.B., 2013. Uncertainty and anticipation in anxiety: an integrated neurobiological and psychological perspective. Nat. Rev. Neurosci. 14 (7), 488–501. https://doi.org/10.1038/nrn3524.
Gu, R., Ge, Y., Jiang, Y., Luo, Y.J., 2010a. Anxiety and outcome evaluation: the good, the bad and the ambiguous. Biol. Psychol. 85 (2), 200–206. https://doi.org/10.1016/j.biopsycho.2010.07.001.
Gu, R., Huang, Y.X., Luo, Y.J., 2010b. Anxiety and feedback negativity. Psychophysiology 47 (5), 961–967. https://doi.org/10.1111/j.1469-8986.2010.00997.x.
Gulpers, B., Ramakers, I., Hamel, R., Köhler, S., Voshaar, R.O., Verhey, F., 2016. Anxiety as a predictor for cognitive decline and dementia: a systematic review and meta-analysis. Am. J. Geriatric Psychiatry 24 (10), 823–842. https://doi.org/10.1016/j.jagp.2016.05.015.
Hampton, A.N., Adolphs, R., Tyszka, M.J., O'Doherty, J.P., 2007a. Contributions of the amygdala to reward expectancy and choice signals in human prefrontal cortex. Neuron 55 (4), 545–555. https://doi.org/10.1016/j.neuron.2007.07.022.
Hampton, A.N., O'Doherty, J.P., 2007b. Decoding the neural substrates of reward-related decision making with functional MRI. Proc. Natl. Acad. Sci. U.S.A. 104 (4), 1377–1382. https://doi.org/10.1073/pnas.0606297104.
Hartley, C.A., Phelps, E.A., 2012. Anxiety and decision-making. Biol. Psychiatry 72 (2), 113–118. https://doi.org/10.1016/j.biopsych.2011.12.027.
Hathaway, S.R., Mckinley, J.C., 1940. A multiphasic personality schedule (Minnesota): I. Construction of the schedule. J. Psychol. 10 (2), 249–254. https://doi.org/10.1080/00223980.1940.9917000.
Hauser, T.U., Iannaccone, R., Stämpfli, P., Drechsler, R., Brandeis, D., Walitza, S., Brem, S., 2014. The feedback-related negativity (FRN) revisited: new insights into the localization, meaning and network organization. Neuroimage 84, 159–168. https://doi.org/10.1016/j.neuroimage.2013.08.028.
He, W., Qi, A., Wang, Q., Wu, H., Zhang, Z., Gu, R., Luo, W., 2017. Abnormal reward and punishment sensitivity associated with Internet addicts. Comput. Hum. Behav. 75, 678–683. https://doi.org/10.1016/j.chb.2017.06.017.
Hein, Thomas P., de Fockert, Jan, Ruiz, Maria Herrojo, 2021. State anxiety biases estimates of uncertainty and impairs reward learning in volatile environments. Neuroimage 224, 117424. https://doi.org/10.1016/j.neuroimage.2020.117424.
Heydari, Sepideh, Holroyd, Clay B., 2016. Reward positivity: Reward prediction error or salience prediction error? Psychophysiology 53 (8), 1185–1192. https://doi.org/10.1111/psyp.2016.53.issue-810.1111/psyp.12673.
Hirayama, K., 2011. Japanese Association for College Mental Health: User guide for the University Personality Inventory. In. Tokyo: Sozo-shuppan.
Holroyd, Clay B., Krigolson, Olave E., 2007. Reward prediction error signals associated with a modified time estimation task. Psychophysiology 44 (6), 913–917. https://doi.org/10.1111/j.1469-8986.2007.00561.x.
Hornak, J., O'Doherty, J., Bramham, J., Rolls, E.T., Morris, R.G., Bullock, P.R., Polkey, C.E., 2004. Reward-related reversal learning after surgical excisions in orbito-frontal or dorsolateral prefrontal cortex in humans. J. Cognit. Neurosci. 16 (3), 463–478. https://doi.org/10.1162/089892904322926791.
Huang, Y.X., Bai, L., Ai, H., Li, W., Yu, C., Liu, J., Luo, Y.J., 2009. Influence of trait-anxiety on inhibition function: Evidence from ERPs study. Neurosci. Lett. 456 (1), 1–5. https://doi.org/10.1016/j.neulet.2009.03.072.
Huang, H., Thompson, W., Paulus, M.P., 2017. Computational dysfunctions in anxiety: Failure to differentiate signal from Noise. Biol. Psychiatry 82 (6), 440–446. https://doi.org/10.1016/j.biopsych.2017.07.007.
Hunt, C., Cooper, S.E., Hartnell, M.P., Lissek, S., 2019. Anxiety sensitivity and intolerance of uncertainty facilitate associations between generalized Pavlovian fear and maladaptive avoidance decisions. J. Abnorm. Psychol. 128 (4), 315–326. https://doi.org/10.1037/abn0000422.
Husain, M., Roiser, J.P., 2018. Neuroscience of apathy and anhedonia: a transdiagnostic approach. Nat. Rev. Neurosci. 19 (8), 470–484. https://doi.org/10.1038/s41583-018-0029-9.
Huys, Q.J., Pizzagalli, D.A., Bogdan, R., Dayan, P., 2013. Mapping anhedonia onto reinforcement learning: a behavioural meta-analysis. Biol. Mood Anxiety Disorders 3 (1), 1–16. https://doi.org/10.1186/2045-5380-3-12.
Izquierdo, A., Jentsch, J.D., 2012. Reversal learning as a measure of impulsive and compulsive behavior in addictions. Psychopharmacology 219 (2), 607–620. https://doi.org/10.1007/s00213-011-2579-7.
Jiang, D., Zhang, D., Chen, Y., He, Z., Gao, Q., Gu, R., Xu, P., 2018. Trait anxiety and probabilistic learning: Behavioral and electrophysiological findings. Biol. Psychol. 132, 17–26. https://doi.org/10.1016/j.biopsycho.2017.10.010.
Kim, Myung-Sun, Kim, Young Youn, Yoo, So Young, Kwon, Jun Soo, 2007. Electrophysiological correlates of behavioral response inhibition in patients with obsessive-compulsive disorder. Depression Anxiety 24 (1), 22–31. https://doi.org/10.1002/da.20195.
Kitayama, S., Park, H., 2007. Cultural shaping of self, emotion, and well-being: How does it work? Soc. Pers. Psychol. Compass 1 (1), 202–222. https://doi.org/10.1111/j.1751-9004.2007.00016.x.
Krain, A.L., Gotimer, K., Hefton, S., Ernst, M., Castellanos, F.X., Pine, D.S., Milham, M.P., 2008. A functional magnetic resonance imaging investigation of uncertainty in adolescents with anxiety disorders. Biol. Psychiatry 63 (6), 563–568. https://doi.org/10.1016/j.biopsych.2007.06.011.
Lange, S., Leue, A., Beauducel, A., 2012. Behavioral approach and reward processing: results on feedback-related negativity and P3 component. Biol. Psychol. 89 (2), 416–425. https://doi.org/10.1016/j.biopsycho.2011.12.004.
Laufer, O., Israeli, D., Paz, R., 2016. Behavioral and neural mechanisms of overgeneralization in anxiety. Curr. Biol. 26 (6), 713–722. https://doi.org/10.1016/j.cub.2016.01.023.
Lauriola, M., Levin, I.P., 2001. Personality traits and risky decision-making in a controlled experimental task: an exploratory study. Personality Individ. Differ. 31 (2), 215–226. https://doi.org/10.1016/S0191-8869(00)00130-6.
LeDoux, J., 1998. Fear and the brain: where have we been, and where are we going? Biol. Psychiatry 44 (12), 1229–1238. https://doi.org/10.1016/S0006-3223(98)00282-0.
Li, W., Qian, M., 1995. Revised norm of State-Trait Anxiety Inventory in Chinese college students. Acta Scientiarum Naturalium Universitatis Pekinensis 31 (1), 108–112.
Linden, D.E., 2005. The P300: where in the brain is it produced and what does it tell us? Neuroscientist 11 (6), 563–576. https://doi.org/10.1177/1073858405280524.
Luo, Yi, Wu, Tingting, Broster, Lucas S., Feng, Chunliang, Zhang, Dandan, Gu, Ruolei, Luo, Yue-Jia, 2014. The temporal course of the influence of anxiety on fairness considerations. Psychophysiology 51 (9), 834–842. https://doi.org/10.1111/psyp.12235.
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 (1), 47–53. https://doi.org/10.1111/1467-9280.01417.
Luyckx, F., Nili, H., Spitzer, B., & Summerfield, C., 2019. Neural structure mapping in human probabilistic reward learning. Elife, 8. DOI:10.7554/eLife.42816.
MacLeod, A.K., Williams, J.M.G., Bekerian, D.A., 1991. Worry is reasonable: the role of explanations in pessimism about future personal events. J. Abnorm. Psychol. 100 (4), 478–486. https://doi.org/10.1037/0021-843X.100.4.478.
Marco-Pallares, J., Cucurell, D., Cunillera, T., Garcia, R., Andres-Pueyo, A., Munte, T.F., Rodriguez-Fornells, A., 2008. Human oscillatory activity associated to reward processing in a gambling task. Neuropsychologia 46 (1), 241–248. https://doi.org/10.1016/j.neuropsychologia.2007.07.016.
Mathews, Andrew, MacLeod, Colin, 2005. Cognitive vulnerability to emotional disorders. Annu. Rev. Clin. Psychol. 1 (1), 167–195. https://doi.org/10.1146/annurev.clinpsy.1.102803.143916.
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. Cognit. Neurosci. 9 (6), 788–798. https://doi.org/10.1162/jocn.1997.9.6.788.
Mitchell, D.G., Rhodes, R.A., Pine, D.S., Blair, R.J., 2008. The contribution of ventrolateral and dorsolateral prefrontal cortex to response reversal. Behav. Brain Res. 187 (1), 80–87. https://doi.org/10.1016/j.bbr.2007.08.034.
Mitte, K., 2007. Anxiety and risk decision-making: the role of subjective probability and subjective cost of negative events. Personal. Individual Differences 43 (2), 243–253. https://doi.org/10.1016/j.paid.2006.11.028.
Mogg, K., Bradley, B.P., 2018. Anxiety and threat-related attention: cognitive-motivational framework and treatment. Trends Cognit. Sci. 22 (3), 225–240. https://doi.org/10.1016/j.tics.2018.01.001.
Morris, B.H., Rottenberg, J., 2015. Heightened reward learning under stress in generalized anxiety disorder: a predictor of depression resistance? J. Abnorm. Psychol. 124 (1), 115–127. https://doi.org/10.1037/a0036934.
Murphy, F.C., Michael, A., Robbins, T.W., Sahakian, B.J., 2003. Neuropsychological impairment in patients with major depressive disorder: the effects of feedback on task performance. Psychol. Med. 33 (3), 455–467. https://doi.org/10.1017/s0033291702007018.
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 (4), 441–448. https://doi.org/10.1016/j.neubiorev.2004.05.003.
Nuss, P., 2015. Anxiety disorders and GABA neurotransmission: a disturbance of modulation. Neuropsychiatr. Dis. Treat. 11, 165–175. https://doi.org/10.2147/NDT.S58841.

Nusslock, R., Alloy, L.B., 2017. Reward processing and mood-related symptoms: An RDoC and translational neuroscience perspective. J. Affect. Disorder 216, 3–16. https://doi.org/10.1016/j.jad.2017.02.001.
Park, J., Moghaddam, B., 2017. Impact of anxiety on prefrontal cortex encoding of cognitive flexibility. Neuroscience 345, 193–202. https://doi.org/10.1016/j.neuroscience.2016.06.013.
Pascual-Marqui, R.D., 1999. Review of methods for solving the EEG inverse problem. Int. J. Bioelectromagnetism 1 (1), 75–86.
Pascual-Marqui, R.D., 2002. Standardized low-resolution brain electromagnetic tomography (sLORETA): Technical details. Methods Find. Exp. Clin. Pharmacol. 24D, 5–12.
Pascual-Marqui, R.D., Michel, C.M., Lehmann, D., 1994. Low resolution electromagnetic tomography: a new method for localizing electrical activity in the brain. Int. J. Psychophysiol. 18 (1), 49–65. https://doi.org/10.1016/0167-8760(84)90014-X.
Paulus, M.P., Yu, A.J., 2012. Emotion and decision-making: affect-driven belief systems in anxiety and depression. Trends Cognit. Sci. 16 (9), 476–483. https://doi.org/10.1016/j.tics.2012.07.009.
Peterson, D.A., Lotz, D.T., Halgren, E., Sejnowski, T.J., Poizner, H., 2011. Choice modulates the neural dynamics of prediction error processing during rewarded learning. Neuroimage 54 (2), 1385–1394. https://doi.org/10.1016/j.neuroimage.2010.09.051.
Pizzagalli, D.A., Iosifescu, D., Hallett, L.A., Ratner, K.G., Fava, M., 2008. Reduced hedonic capacity in major depressive disorder: evidence from a probabilistic reward task. J. Psychiatr. Res. 43 (1), 76–87. https://doi.org/10.1016/j.jpsychires.2008.03.001.
Polich, J., 2007. Updating P300: An integrative theory of P3a and P3b. Clin. Neurophysiol. 118 (10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019.
Polich, J., Criado, J.R., 2006. Neuropsychology and neuropharmacology of P3a and P3b. Int. J. Psychophysiol. 60 (2), 172–185. https://doi.org/10.1016/j.ijpsycho.2005.12.012.
Proudfit, G.H., 2015. The reward positivity: from basic research on reward to a biomarker for depression. Psychophysiology 52 (4), 449–459. https://doi.org/10.1111/psyp.12370.
Reilly, Erin E., Whitton, Alexis E., Pizzagalli, Diego A., Rutherford, Ashleigh V., Stein, Murray B., Paulus, Martin P., Taylor, Charles T., 2020. Diagnostic and dimensional evaluation of implicit reward learning in social anxiety disorder and major depression. Depression Anxiety, published online. 37 (12), 1221–1230. https://doi.org/10.1002/da.v37.1210.1002/da.23081.
Righi, S., Mecacci, L., & Viggiano, M. P., 2009. Anxiety, cognitive self-evaluation and performance: ERP correlates. Journal of Anxiety Disorders, 23(8), 1132-1138. DOI: 10.1016/j.janxdis.2009.07.018.
Robinson, O.J., Frank, M.J., Sahakian, B.J., Cools, R., 2010. Dissociable responses to punishment in distinct striatal regions during reversal learning. Neuroimage 51 (4), 1459–1467. https://doi.org/10.1016/j.neuroimage.2010.03.036.
Rudebeck, P.H., Saunders, R.C., Prescott, A.T., Chau, L.S., Murray, E.A., 2013. Prefrontal mechanisms of behavioral flexibility, emotion regulation and value updating. Nat. Neurosci. 16 (8), 1140–1145. https://doi.org/10.1038/nn.3440.
Sambrook, T.D., Goslin, J., 2015. A neural reward prediction error revealed by a meta-analysis of ERPs using great grand averages. Psychol. Bull. 141 (1), 213–235. https://doi.org/10.1037/bul0000006.
San Martín, R., 2012. Event-related potential studies of outcome processing and feedback-guided learning. Front. Hum. Neurosci. 6, 304. https://doi.org/10.3389/fnhum.2012.00304.
San Martín, R., Appelbaum, L.G., Pearson, J.M., Huettel, S.A., Woldorff, M.G., 2013. Rapid brain responses independently predict gain maximization and loss minimization during economic decision-making. J. Neurosci. 33 (16), 7011–7019. https://doi.org/10.1523/JNEUROSCI.4242-12.2013.
Santesso, D.L., Dzyundzyak, A., Segalowitz, S.J., 2011. Age, sex and individual differences in punishment sensitivity: factors influencing the feedback-related negativity. Psychophysiology 48 (11), 1481–1489. https://doi.org/10.1111/j.1469-8986.2011.01229.x.
Schonberg, T., Fox, C.R., Poldrack, R.A., 2011. Mind the gap: Bridging economic and naturalistic risk-taking with cognitive neuroscience. Trends Cognit. Sci. 15 (1), 11–19. https://doi.org/10.1016/j.tics.2010.10.002.
Shek, D.T., 1993. The Chinese version of the State-Trait Anxiety Inventory: its relationship to different measures of psychological well-being. J. Clin. Psychol. 49 (3), 349–358. https://doi.org/10.1002/1097-4679.
Shepperd, J.A., Grace, J., Cole, L.J., Klein, C., 2005. Anxiety and outcome predictions. Pers. Soc. Psychol. Bull. 31 (2), 267–275. https://doi.org/10.1177/0146167204271322.
Spielberger, C.D., Gorsuch, R.L., Lushene, R., Vagg, P.R., Jacobs, G.A., 1983. Manual for the state-trait anxiety inventory. Consulting Psychologist Press, Palo Alto, CA.
Starcke, K., Brand, M., 2016. Effects of stress on decisions under uncertainty: a meta-analysis. Psychol. Bull. 142 (9), 909–933. https://doi.org/10.1037/bul0000060.
Stavrakaki, Chrissoula, Vargo, Beverley, 1986. The relationship of anxiety and depression: a review of the literature. Br. J. Psychiatry 149 (1), 7–16. https://doi.org/10.1192/bjp.149.1.7.
Stöber, J., 1997. Trait anxiety and pessimistic appraisal of risk and chance. Personality Individ. Differ. 22 (4), 465–476. https://doi.org/10.1016/S0191-8869(96)00232-2.
Sturm, V., Lenartz, D., Koulousakis, A., Treuer, H., Herholz, K., Klein, J.C., Klosterkotter, J., 2003. The nucleus accumbens: a target for deep brain stimulation in obsessive-compulsive- and anxiety-disorders. J Chem Neuroanat 26 (4), 293–299. https://doi.org/10.1016/j.jchemneu.2003.09.003.
Takács, Á., Kóbor, A., Janacsek, K., Honbolygó, F., Csépe, V., Németh, D., 2015. High trait anxiety is associated with attenuated feedback-related negativity in risky decision making. Neurosci. Lett. 600, 188–192. https://doi.org/10.1016/j.neulet.2015.06.022.
Talmi, D., Atkinson, R., El-Deredy, W., 2013. The feedback-related negativity signals salience prediction errors, not reward prediction errors. J. Neurosci. 33 (19), 8264–8269. https://doi.org/10.1523/JNEUROSCI.5695-12.2013.
Tovote, P., Fadok, J.P., Luthi, A., 2015. Neuronal circuits for fear and anxiety. Nat. Rev. Neurosci. 16 (6), 317–331. https://doi.org/10.1038/nrn3945.
Treadway, M.T., Zald, D.H., 2013. Parsing Anhedonia: translational models of reward-processing deficits in psychopathology. Curr. Direct. Psychol. Sci. 22 (3), 244–249. https://doi.org/10.1177/0963721412474460.
von Borries, A.K., Verkes, R.J., Bulten, B.H., Cools, R., de Bruijn, E.R., 2013. Feedback-related negativity codes outcome valence, but not outcome expectancy, during reversal learning. Cognit., Affect. Behav. Neurosci. 13 (4), 737–746. https://doi.org/10.3758/s13415-013-0150-1.
Walsh, M.M., Anderson, J.R., 2012. Learning from experience: event-related potential correlates of reward processing, neural adaptation, and behavioral choice. Neurosci. Biobehav. Rev. 36 (8), 1870–1884. https://doi.org/10.1016/j.neubiorev.2012.05.008.
Wang, Z., Yuan, C.M., Huang, J., Li, Z.Z., Chen, J., Zhang, H., Fang, Y.R., XIao, Z.P., 2011. Reliability and validity of the Chinese version of Beck Depression Inventory-II among depression patients. Chinese Mental Health J. 25 (6), 476–480. https://doi.org/10.3969/j.issn.1000-6729.2011.06.014.
Wray, Laura D., Stone, Eric R., 2005. The role of self-esteem and anxiety in decision making for self versus others in relationships. J. Behav. Decision Making 18 (2), 125–144. https://doi.org/10.1002/bdm.v18:210.1002/bdm.490.
Wu, H., Gui, D., Lin, W., Gu, R., Zhu, X., Liu, X., 2016. The procrastinators want it now: behavioral and event-related potential evidence of the procrastination of intertemporal choices. Brain Cognit. 107, 16–23. https://doi.org/10.1016/j.bandc.2016.06.005.
Wu, Y., Zhou, X.L., 2009. The P300 and reward valence, magnitude, and expectancy in outcome evaluation. Brain Res. 1286, 114–122. https://doi.org/10.1016/j.brainres.2009.06.032.
Xia, L., Gu, R., Zhang, D., Luo, Y.J., 2017. Anxious individuals are impulsive decision-makers in the delay discounting task: an ERP study. Front. Behav. Neurosci. 11, 5. https://doi.org/10.3389/fnbeh.2017.00005.
Xia, L., Mo, L., Wang, J., Zhang, W., Zhang, D., 2020. Trait anxiety attenuates response inhibition: evidence from an ERP study using the Go/Nogo task. Front. Behav. Neurosci. 14, 28. https://doi.org/10.3389/fnbeh.2020.00028.
Xu, P., Gu, R., Broster, L.S., Wu, R., Van Dam, N.T., Jiang, Y., Fan, J., Luo, Y.J., 2013. Neural basis of emotional decision making in trait anxiety. J. Neurosci. 33 (47), 18641–18653. https://doi.org/10.1523/JNEUROSCI.1253-13.2013.
Xue, G., Ghahremani, D.G., Poldrack, R.A., 2008. Neural substrates for reversing stimulus-outcome and stimulus-response associations. J. Neurosci. 28 (44), 11196–11204. https://doi.org/10.1523/JNEUROSCI.4001-08.2008.
Yang, Q., Tang, P., Gu, R., Luo, W., Luo, Y.J., 2015. Implicit emotion regulation affects outcome evaluation. Soc. Cogn. Affect. Neurosci. 10 (6), 824–831. https://doi.org/10.1093/scan/nsu124.
Zhang, D., Gu, R., Wu, T., Broster, L.S., Luo, Y., Jiang, Y., Luo, Y.J., 2013. An electrophysiological index of changes in risk decision-making strategies. Neuropsychologia 51 (8), 1397–1407. https://doi.org/10.1016/j.neuropsychologia.2013.04.014.
Zhang, Dandan, Gu, Ruolei, 2018. Behavioral preference in sequential decision-making and its association with anxiety. Human Brain Mapping 39 (6), 2482–2499. https://doi.org/10.1002/hbm.v39.610.1002/hbm.24016.
Zhukov, L., Weinstein, D., Johnson, C., 2000. Independent component analysis for EEG source localization. IEEE Eng. Med. Biol. Mag. 19 (3), 87–96. https://doi.org/10.1109/51.844386.