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# Evidence for specificity of the impact of punishment on error-related brain activity in high versus low trait anxious individuals

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## ABSTRACT

A previous study suggests that when participants were punished with a loud noise after committing errors, the error-related negativity (ERN) was enhanced in high trait anxious individuals. The current study sought to extend these findings by examining the ERN in conditions when punishment was related and unrelated to error commission as a function of individual differences in trait anxiety symptoms; further, the current study utilized an electric shock as an aversive unconditioned stimulus. Results confirmed that the ERN was increased when errors were punished among high trait anxious individuals compared to low anxious individuals; this effect was not observed when punishment was unrelated to errors. Findings suggest that the threat-value of errors may underlie the association between certain anxious traits and punishment-related increases in the ERN.

## 1. Introduction

Detecting errors is fundamental for learning and survival (Hajcak, 2012; Holroyd and Coles, 2002). Indeed, errors increase distress (Spunt et al., 2012) and initiate a cascade of physiological responses that suggest preparation for defensive action, including: skin conductance response and heart rate deceleration (Hajcak et al., 2003), potentiated startle reflex (Hajcak and Foti, 2008; Riesel et al., 2013), pupil dilation (Critchley et al., 2005), and corrugator (i.e. frowning) muscle contraction (Lindström et al., 2013). The detection of errors is also associated with distinct neural activity evident in the event-related potential (ERP) (Falkenstein et al., 1991; Gehring et al., 1993). Specifically, the error-related negativity (ERN) is a response-locked, negative-going, sharp deflection with fronto-central scalp distribution, occurring approximately 50 ms after an incorrect response (Falkenstein et al., 1991; Gehring et al., 1993; Hajcak, 2012).

Many theories regarding the function of the ERN have focused on cognitive processes (Bernstein et al., 1995; Botvinick et al., 2001; Carter et al., 1998; Falkenstein et al., 1991; Holroyd and Coles, 2002), and predict that variation in the ERN should relate to task performance and subsequent behavioral adjustments. However, there are many instances in which variation in the ERN occurs in the absence of behavioral differences (for a review, see: Weinberg et al., 2012). Recent work has sought to address additional sources of variance in the ERN related to affect and motivation. Indeed, source localization analyses, as well as fMRI data suggest that the ERN is generated in the anterior cingulate cortex (ACC) (Agam et al., 2011; Carter et al., 1998; Kiehl et al., 2000; Mathalon et al., 2003), a region of the brain thought to integrate information about negative affect, pain, threat, and punishment is integrated to modulate fear and anxiety-related behaviors, as well as signal the need for control (Cavanagh and Shackman, 2015; Shackman et al., 2011).

Consistent with these theories of ACC function, a growing body of literature suggests that the amplitude of the ERN can be modulated by experimental manipulations that alter error significance. For example, an increased ERN has been observed when instructions emphasize performance accuracy over response speed (Gehring et al., 1993), when participant performance is explicitly evaluated (Hajcak et al., 2005; Kim et al., 2005), by introducing monetary incentives for correct responses (Chiu and Deldin, 2007; Endrass et al., 2010; Hajcak et al., 2005) and when errors are associated with punishment (Riesel et al., 2012). In these cases, the experimental manipulations modulate affect or motivation integral to error commission. However, affective modulations that are incidental to error commission, such as the presence of a spider while a spider phobic completes a flanker task, do not seem to impact the ERN (Moser et al., 2005).

Based on these data, we have argued that the ERN may reflect the relative threat value or significance of errors—and that variation in the amplitude of the ERN reflects individual differences linked to certain anxious phenotypes (Proudfit et al., 2013). For example, the amplitude of the ERN is enhanced in patients with general anxiety disorder (Weinberg et al., 2010; Xiao et al., 2011) and obsessive-compulsive

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disorder (Gehring et al., 2000; Hajcak et al., 2008; Riesel et al., 2011). Additionally, two recent meta-analyses have confirmed the association between the ERN and trait anxiety (Cavanagh and Shackman, 2015; Moser et al., 2013).

Overall then, there are both trait- and state-like effects on the ERN: it is increased among trait anxious individuals and in experimental conditions in which errors are more aversive or valuable. Indeed, these effects may be related: Riesel et al. (2012) found that modulation of the ERN by punishment varied by individual differences in anxiety. In this study, participants were sometimes punished after errors with a loud, unpleasant sound. The ERN was enhanced in blocks where errors could be punished, and this effect was most evident in individuals with higher levels of trait anxiety. These results suggest that punishing errors may potentiate the ERN differentially, as a function of certain traits and dispositions. However, the Riesel et al. study did not include a condition in which punishment was unrelated to performance errors, leaving it unclear whether the "punishment-related" modulation of the ERN was due to a general increase in anxiety induced by the threat of punishment, or was specifically due to punishment following errors.

To further investigate this possibility, in the current study, participants were punished after error commission with an electrical shock in one condition; however, participants were punished *randomly* (i.e., unrelated to error commission) in another condition; in a final control condition, no punishment was administered. By introducing a block with random punishment, the current study aimed to investigate whether the relationship between anxiety and punishment-related increases in the ERN is related specifically to the threat-value of errors, or to anxiety elicited by potential punishment more generally. Rather than employing a loud sound, the current study used electrical shock as the aversive punishment to be more consistent with the fear conditioning literature (Lissek et al., 2005). Based on previous findings, we hypothesized that the ERN would be increased only in blocks in which errors were followed by punishment, and that this effect would be larger among individuals characterized by high trait anxiety.

## 2. Methods

### 2.1. Participants

Fifty-seven undergraduate students (30 female) participated in this study. Data from six subjects were excluded from analysis due to excessive electroencephalogram (EEG) artifacts. Three of the participants committed fewer than six errors in at least one condition (Olvet and Hajcak, 2009b) and were therefore excluded from further analysis. Two of the participants did not complete the STAI due to experimenter error. The final sample consisted of 46 participants (27 female). The mean age was 20.08 (*SD* = 4.68) and 37% of the sample reported being Caucasian, 4.3% Hispanic, 6.5% African-American, 47.8% Asian, and 4.3% as "other". All participants were given verbal and written information about the procedure of the study, and written consent was obtained. Participants received course credit for participation in the study.

### 2.2. Measures

Individual differences in trait anxiety were measured with the trait version of the State-Trait Anxiety Inventory (STAI) (Speilberger et al., 1983). The STAI scores of the participants ranged from 28 to 54 (*M* = 41.44, *SD* = 6.55); higher scores indicate more anxiety.

### 2.3. Stimuli

An arrowhead version of the flanker task (Eriksen and Eriksen, 1974) was used with Presentation software (Neurobehavioral Systems, Inc., Albany, CA). During each trial, five horizontally aligned arrowheads (white font on a black background) were presented for 200 ms and participants were told to respond with the left or right mouse button according to what direction the center arrow was pointing. The inter-stimulus interval varied between 2500 and 3000 ms on trials that participants did not receive a shock, and between 3000 and 5500 ms on trials in which participants received a shock. Half of the trials were compatible ("$>>>>>$" or "$<<<<<$") and half were incompatible ("$<<><<$" or "$>><>>$"); the order of trials was randomly determined. Each set of arrowheads occupied approximately 0.9° of visual angle vertically and 7.5° horizontally. Throughout the experiment, participants were encouraged to be both fast and accurate: performance-based feedback was presented at the end of each block. If performance accuracy was below 75%, the message "Please try to be more accurate" was displayed; if performance was above 90%, the message "Please try to respond faster" was displayed; otherwise the message "You're doing a great job" was displayed.

### 2.4. Procedure

Electrical shocks were administered to the participants' left triceps using an electrical stimulator and PSYLAB hardware and software (Contact Precision Instruments), producing 60 Hz constant AC stimulation between 0 and 5 mA for 500 ms. Shock intensity was determined on an individual basis. Participants initially received a mild shock, which was increased incrementally until participants reported they were at a level of shock that was uncomfortable but manageable. After participants' shock level was individually determined, it was kept constant throughout the rest of the task.

The flanker task consisted of three conditions (4 blocks of each), administered quasi-randomly block-wise, such that no block was repeated sequentially (e.g., ACBABACBCACB). Each block consisted of 64 trials (768 total in the entire task). In the *punishment after errors condition*, participants were instructed they could only be shocked after committing an error; at the beginning of these blocks, a screen was presented that read, "In the next block, shocks will only follow some of your errors". In this condition, participants were randomly shocked after 50% of their errors, 600 ms after response commission. In the *random punishment condition*, participants were instructed they would be randomly shocked throughout the block, regardless of error commission; prior to these blocks, a screen was presented that read, "In the next block, shocks will be completely random". In the random punishment condition, participants were shocked 600 ms after response commission on exactly 4 of the 64 trials, randomly determined and independent of trial accuracy. Finally, in the *no punishment condition*, participants were instructed they would never be shocked; these blocks were preceded with the following screen: "In the next block, there will be NO shocks".

After completing the flanker task, participants completed the STAI and a self-report rating of discomfort/anxiety (on a 1–7 scale) for each condition (i.e., punishment after errors, random punishment, and no punishment). The questions were phrased in the following way: "How uncomfortable or anxious did you feel during the blocks in the experiment where you were shocked randomly (1 = not anxious, 7 = extremely anxious)?", "How uncomfortable or anxious did you feel during the blocks in the experiment where you did not receive any shocks (1 = not anxious, 7 = extremely anxious)?", "How uncomfortable or anxious did you feel during the blocks in the experiment where you were sometimes shocked for making errors (1 = not anxious, 7 = extremely anxious)?".

### 2.5. Psychophysiological recording, data reduction, and analysis

The continuous EEG was recorded using an elastic cap and the ActiveTwo BioSemi system (BioSemi, Amsterdam, The Netherlands). Thirty-four electrode sites were used, as well as two electrodes on the right and left mastoids. The electrooculogram (EOG) was recorded using four additional facial electrodes: two electrodes placed approximately 1 cm outside of the right and left eyes and two electrodes placed

**Table 1**
Behavioral and ERP variables during the three experimental conditions, presented based on high and low trait anxiety groups based on a median-split of STAI scores.

| | Punishment after errors | | No punishment | | Random punishment | |
|---|---|---|---|---|---|---|
| | High Anxiety | Low Anxiety | High Anxiety | Low Anxiety | High Anxiety | Low Anxiety |
| Number of Errors | 21.32 (2.23) | 21.95 (11.46) | 26.59 (13.85) | 30.25 (15.56) | 24.50 (13.43) | 25.33 (13.93) |
| Correct RT (ms) | 410 (59) | 408 (46) | 402 (67) | 399 (50) | 415 (73) | 403(44) |
| Error RT (ms) | 341 (81) | 360 (83) | 328 (73) | 331 (73) | 371 (120) | 359(64) |
| Post-correct RT (ms) | 433 (110) | 414 (48) | 458 (127) | 430 (84) | 468 (152) | 424 (82) |
| Post-error RT (ms) | 527 (295) | 469 (148) | 509 (294) | 461 (195) | 474 (243) | 437 (114) |
| Post-error slowing (ms) | 94 (234) | 55 (121) | 51 (201) | 31 (128) | 5 (151) | 13 (73) |
| ERN at FCz (μV) | − 2.64 (5.38)* | 3.02 (4.75)* | − 0.67 (7.35) | 0.87 (5.81) | − 0.47 (7.55) | − 0.59 (5.96) |
| CRN at FCz (μV) | 8.47 (5.22) | 10.18 (6.85) | 7.93 (6.31) | 8.57 (6.55) | 8.03 (7.21) | 7.83 (5.76) |
| ΔERN at FCz (μV) | − 11.11 (4.32)* | − 7.16 (6.38)* | − 8.60 (6.94) | − 7.70 (6.92) | − 8.51 (8.74) | − 8.42 (7.79) |

* $p < 0.05$ for differences between high/low anxiety groups.

approximately 1 cm above and below the right eye. The EEG signal was preamplified at the electrode with a gain of 1 × by the BioSemi ActiveTwo system. The EEG was digitized with a sampling rate of 1024 Hz using a low-pass fifth order sinc filter with a half-power cutoff of 204.8 Hz. A common mode sense (CMS) active electrode producing a monopolar (nondifferential) channel was used as a recording reference. Offline, the data was referenced to the average of the left and right mastoids, and bandpass filtered from 0.1 to 30 Hz. To detect and reject artifacts, we used a semiautomatic procedure for all segmented data, with a criteria of a voltage step of > 50.0 μV within any 100 ms interval, and a voltage difference of 300.0 μV within a trial. Afterwards, the data were visually inspected to detect and reject any remaining artifacts. Eye movement artifacts were corrected per Gratton et al. (1983).

The EEG was segmented beginning 500 ms before the response and continuing for 1000 ms after the response; a 200 ms window from − 400 to − 200 before the response served as the baseline. Correct and error trials were averaged separately. For each subject, the ERN was scored as the mean activity between 0 and 50 ms after error responses at FCz, where error-related brain activity was maximal; the CRN was scored in the same way, on correct trials. The ΔERN was defined as the ERN minus the CRN. Behavioral measures included the number of error trials for each subject per condition. Average reaction times (RTs) on error and correct trials for each condition were calculated separately, as were RTs on correct trials that followed correct and error trials to evaluate post-error RT slowing. All analyses included both compatible and incompatible trials.

Statistical analyses were conducted using SPSS (Version 18.0). General Linear Model software, with Greenhouse-Geisser correction was applied to $p$ values associated with multiple-df. Repeated-measures ANOVAs were completed to examine behavioral and ERP data by condition. Consistent with Riesel et al. (2012) a median-split was conducted on the STAI to create high and low anxiety groups. A 3 (Condition: shock after errors, random shock, no shock) × 2(STAI groups: low anxiety, high anxiety, entered as a between subjects factor) was conducted to examine the impact of trait anxiety on the ERN between the three conditions. Follow-up $t$-tests were conducted to examine during which condition the ERN varied by group. Additionally, correlational analyses (Pearson's $r$) were conducted between continuous anxiety symptoms (STAI) and the ERN in each condition. Following this, the analyses were then repeated in relation to the CRN and ΔERN (error minus correct). Since sex (Larson et al., 2011) and behavioral differences between conditions (Gehring et al., 1993) may influence the ERN, additional analyses were conducted with sex, reaction time, and error rate introduced as covariates.

## 3. Results

### 3.1. Self-reports

Results from a repeated-measures ANOVA suggested that participants reported a significant difference in discomfort/anxiety between experimental conditions, $F(2, 90) = 78.32$, $p < 0.001$, $\eta_p^2 = 0.64$, such that discomfort/anxiety was rated higher in the punishment after errors condition ($M = 3.65$, $SD = 1.65$) and random punishment condition ($M = 3.28$, $SD = 1.33$) compared to the no punishment condition ($M = 1.48$, $SD = 0.84$; $t(45) = 10.75$, $p < .001$and $t(45) = 10.49$, $p < 0.001$, respectively); differences between the punishment after errors and random punishment condition also trended towards significance, $t(45) = -2.03$, $p = 0.05$. Ratings did not correlate with STAI scores, behavioral results, or error-related brain activity (all $ps > 0.08$).

### 3.2. Behavioral data

Behavioral results for all three conditions and by anxiety group are presented in Table 1. Results from a repeated-measures ANOVA suggested that error rates differed significantly between the three conditions, $F(2, 90) = 17.35$, $p < 0.001$, $\eta_p^2 = 0.28$. Post hoc tests indicated that subjects committed fewer errors in the punishment after errors condition compared to both the no punishment, $t(45) = 5.19$, $p < 0.001$ and the random punishment conditions, $t(45) = 3.14$, $p = 0.003$. Additionally, participants made fewer errors in the random punishment condition compared to the no punishment condition, $t(45) = 3.23$, $p = 0.002$. Error rates in the three conditions did not correlate with trait anxiety (all $ps > 0.08$).

Consistent with previous studies, reaction times were faster on error trials compared to correct trials, $F(1, 45) = 49.34$, $p < 0.001$, $\eta_p^2 = 0.50$. Reaction times also varied by condition, $F(2, 90) = 5.52$, $p = 0.007$, $\eta_p^2 = 0.11$; participants were slower during both the punishment after errors and random punishment conditions compared to the no punishment condition, $t(45) = 2.38$, $p = 0.02$, and $t(45) = 2.83$, $p = 0.007$, respectively. Reaction times during the punishment after errors and random punishment conditions did not differ from one another, $t(45) = 1.25$, $p = 0.22$. The interaction of response type and condition did not reach significance, $F(2, 90) = 2.70$, $p = 0.07$. Additionally, trait anxiety did not correlate with reaction times in any condition (all $ps > 0.08$).

Post-error slowing was analyzed by comparing the post-error and post-correct reaction times. Results from a repeated-measures ANOVA suggested that participants were slower to respond after committing errors, $F(1,4 5) = 5.42$, $p = 0.02$, $\eta_p^2 = 0.11$, and this was qualified by an interaction with condition that trended towards significant, $F(2, 90) = 3.06$, $p = 0.06$. Post hoc tests indicated that post-error slowing was increased during the punishment after errors condition compared to the random shock condition, $t(45) = 2.75$, $p = 0.009$. The degree of post-error slowing did not differ between the no punishment and random punishment conditions, $t(45) = 1.12$, $p = 0.27$, or between the no punishment and punishment after errors conditions, $t(45) = 1.26$, $p = 0.21$. Additionally, trait anxiety was not correlated with post-error slowing (all $ps > 0.08$).

### 3.3. Error-related brain activity and anxiety

Consistent with previous studies, a fronto-central negative deflection in the waveform (i.e., an ERN) was observed shortly after error commission. A 3 (condition) × 2 (high vs. low trait anxiety) repeated-measures ANOVA focusing on the ERN indicated that the overall ERN magnitude did not vary as a function of experimental condition, $F(2, 88) = 0.24$ $p = 0.78$. However, the impact of experimental condition was qualified by a significant interaction with trait anxiety, $F(2, 88) = 3.40$, $p = 0.04$, $\eta_p^2 = 0.07$. Follow-up analyses suggested that the magnitude of the ERN did not differ between the high vs. low trait anxiety groups during the no shock or random shock conditions, $t(44) = 0.79$, $p = 0.44$, and $t(44) = 0.06$, $p = 0.96$, respectively. However, during the shock after errors condition, individuals in the high trait anxiety group were characterized by a larger ERN, $M = -2.64$, $SD = 5.37$, compared to individuals in the low anxiety group, $M = 3.02$, $SD = 4.75$, $t(44) = 3.77$, $p < 0.001$ (see Figs. 1 and 2).

Additionally, trait anxiety was significantly correlated with ERN during the shock after errors condition only, $r(44) = -0.36$, $p = 0.01$, and did not relate to ERN during the random shock or no shock conditions, $r(44) = -0.12$, $p = 0.41$ and $r(44) = -0.17$, $p = 0.26$, respectively (see Fig. 3). These results suggest that higher trait anxiety was associated with a larger ERN, but only when errors were punished. Moreover, when we created a difference score (ERN during shock minus ERN during no shock), the difference was significantly increased in the anxious group, $F(1, 45) = 4.09$, $p < 0.05$.

To examine specificity, we also completed analyses including the CRN. A 3 (condition) × 2(ERN vs. CRN) × 2 (high vs. low trait anxiety) ANOVA showed that the 3-way interaction between condition, response, and anxiety groups did not reach significance, $F(2, 88) = 1.71$, $p = 0.19$. Additionally, the magnitude of the CRN did not differ between groups during the no shock, random shock, or shock after errors condition, $t(44) = 0.34$, $p = 0.74$, $t(44) = 0.11$, $p = 0.92$, and $t(44) = 0.96$, $p = 0.34$, respectively. When examining the ΔERN (error minus correct), neither the no shock nor random shock conditions differed between the anxiety groups, $t(44) = 0.44$, $p = 0.66$, and $t(44) = 0.04$, $p = 0.97$, respectively. However, the ΔERN during the shock after errors condition did differ between the anxiety groups, $t(44) = 2.48$, $p = 0.02$, such that among anxious individuals the ΔERN was increased, $M = -11.11$, $SD = 4.31$, compared to the low anxiety group, $M = -7.16$, $SD = 6.38$. Additionally, trait anxiety did not significantly correlate with the CRN nor ΔERN during any condition, all $ps > 0.10$.

Follow-up analyses were completed, focusing on the ERN, to examine whether differences between groups may be due to gender or behavioral differences. When gender was entered as a covariate in a 3 (condition) × 2 (high vs. low trait anxiety) repeated-measures ANOVA focusing on the ERN, results suggested that the interaction between trait anxiety and condition remained significant, $F(2, 86) = 4.01$, $p = 0.03$. Furthermore, when reaction times during all three conditions were added as covariates, the interaction between trait anxiety and condition remained significant, $F(2, 82) = 3.34$, $p = 0.04$. Additionally, when error rates in all three conditions were added as covariates, the interaction between trait anxiety and condition remained significant, at a trend level, $F(2, 82) = 2.50$, $p = 0.09$. Results remained significant when the number of shocks in the punishment after errors and random punishment condition were included as covariates in the model, $F(2, 86) = 3.29$, $p = 0.04$. Taken together, these analyses suggest that neither sex nor behavioral differences between the conditions fully accounted for the observed interaction between condition and anxiety group.[1]

## 4. Discussion

Consistent with previous findings (Riesel et al., 2012), results from the current study suggest that among individuals characterized by increased trait anxiety, the amplitude of the ERN was significantly larger when errors were punished using electric shock as an aversive unconditioned stimulus compared to those low in trait anxiety. Results from the current study extend previous findings by demonstrating that this effect between high and low anxiety groups was not observed when punishment was unrelated to errors, suggesting that the *threat-value of errors*, specifically, may underlie the association between anxiety and punishment-related increases in ERN.

These results are consistent with previous work suggesting that the impact of experimental manipulations on the ERN may be moderated by individual differences in traits and psychopathology (Amodio et al., 2008; Bush et al., 2000; Dikman and Allen, 2000; Endrass et al., 2010; Olvet and Hajcak, 2012; Pailing and Segalowitz, 2004; Riesel et al., 2012). That is, trait-related individual differences interact with experimental manipulations to impact the amplitude of the ERN. Although an increased ERN has consistently been associated with anxiety (Endrass et al., 2008; Gehring et al., 2000; Hajcak et al., 2008; Weinberg et al., 2012; Xiao et al., 2011), in both the current study and in Riesel et al. (2012), there was no overall relationship between anxiety and the ERN during the no punishment condition. It is possible that by introducing a punishment condition, the relationship between error monitoring and anxiety may be altered. In fact, previous work has found that relatively small modulations in task parameters, like providing performance feedback, can alter the relationship between the ERN and anxiety (Olvet and Hajcak, 2009a). It is possible that for trait anxious individuals, conditions in which they are not being punished for errors during the course of an experiment wherein they are sometimes punished for errors, are perceived as "safe" conditions and therefore the relationship between anxiety and the ERN may diminish. Further work is needed to explore this possibility.

Moreover, in the current study, we did not observe an overall effect of punishing errors on ERN magnitude – these results contrast with Riesel et al. (2012). There were several experimental design differences between the two studies. It is possible that the introduction of the random punishment condition reduced the impact of punishing errors on the ERN. For example, punishment may have become less meaningful or aversive over the course of the experiment because it was sometimes administered randomly. Alternatively, it is possible that using a loud sound as a punishment (as in Riesel et al.) is more aversive than using an electric shock. Because anxiety ratings for the conditions were not collected in the first study, we cannot compare them. However, in the current study, the average anxiety rating during the punishment condition was relatively low (i.e., 3.7 on a 7 point scale). Alternatively, using shocks versus loud sounds as aversive stimuli may be associated with unintentional social evaluative differences. Specifically, while participants were completing the task in the Riesel et al. (2012) study, the experimenter could hear the loud sound (indicating that the participant had made a mistake). When participants received a shock as a punishment in the current study, there was no similar social evaluative component. Given previous work suggesting that the ERN is sensitive to social evaluation (Hajcak et al., 2005; Kim et al., 2005), this may account for the differences we observed between the two studies. Finally, in the Riesel et al. (2012) study, participants had to learn which

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[1] It should be noted that participants received a total of 16 shocks during the random punishment condition (4 per block) and a variable number of shocks depending on their accuracy during the punishment after errors condition (randomly shocked after 50% of their errors; on average, 11 shocks during this condition). However, anxiety ratings between the two conditions did not differ and the magnitude of the ERN in the punishment after errors condition was not related to the number of errors committed.

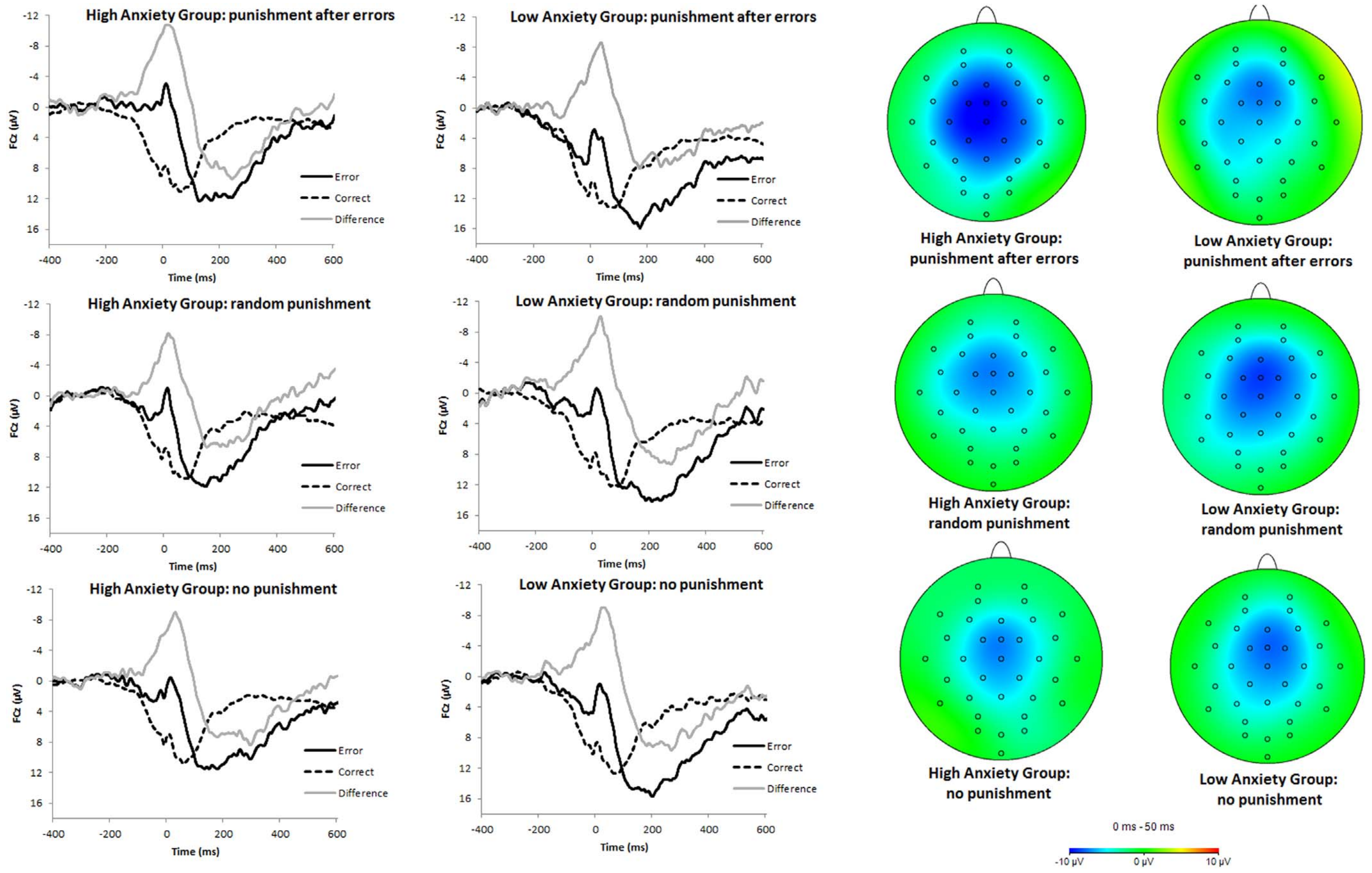

**Fig. 1.** On the left, response-locked ERP waveforms at FCz during the punishment after errors, random punishment, and no punishment conditions are presented for high (left) and low (right) STAI groups, based on a median-split. On the right, topographical headmaps are presented depicting the activity during 0–50 ms after response commission for error minus correct trials, presented for high and low STAI groups, based on a median split.

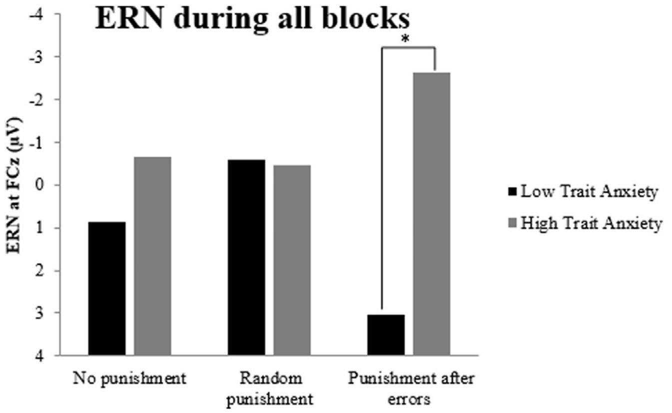

**Fig. 2.** Bar graphs depicting the magnitude of the ERN during the no punishment, random punishment, and punishment after errors condition. Results are presented for low and high anxiety groups, based on a median-split of STAI scores.

color arrow (blue or yellow) was associated with the punishment condition, adding an element of uncertainty to the task. In the current study, participants were instructed at the beginning of each block regarding the shock contingency.

Overall, participants committed fewer errors and were slower to respond in the punishment after errors and random punishment conditions. These behavioral data suggest increased attention and vigilance during punishment conditions. It is also possible that these behavioral differences were due to the increase in the inter-stimulus interval on punishment trials (Jentzsch and Dudschig, 2009). Moreover, Riesel et al. (2011) found that post-error slowing was increased in the punishment after errors condition compared to the no punishment condition. We found a similar pattern in the current study: post-error slowing was increased in the punishment after errors condition compared to the random punishment condition, suggesting that punishment following errors may have led to a more cautious response strategy—yet, these results too may reflect increased inter-stimulus interval. Although punishment did seem to impact behavior, follow-up analyses indicated that behavioral differences did not account for the interaction between condition and anxiety on the ERN.

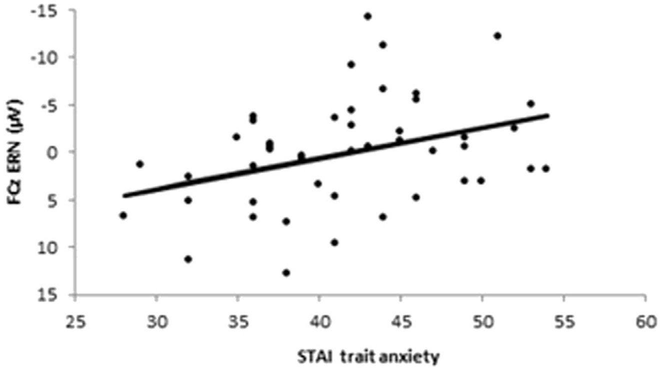

**Fig. 3.** Scatter plot depicting the relationship between STAI symptoms and ERN magnitude during the punishment after errors condition.

The present results are consistent with previous evidence suggesting that variation in the ERN may reflect differences in the motivational significance of errors modulated via individual differences in affective distress or threat sensitivity (Cavanagh and Shackman, 2015; Proudfit et al., 2013; Weinberg et al., 2015). Specifically, anxious individuals may be particularly sensitive to punishment experiences surrounding their errors. Alternatively, Moser et al. (2013) proposed that the increased ERN observed in trait anxious individuals reflects a temporary increase in cognitive control to combat a decrease in active goal maintenance processes due to increased verbal processing (i.e., worrying). In the current investigation, it is possible, although it seems unlikely, that worrying increased among high STAI participants only during the punishment after errors condition.

It should be noted that visual inspection of the ERP waveforms suggested that group differences during the punishment condition may have emerged before response onset. Indeed, follow-up analyses did suggest that group differences emerged around 50 ms before response onset and localized at FCz. Additionally, we analyzed the stimulus-locked P300 and found that high and low anxious groups did not differ in P300 amplitude during the punishment condition. Taken together, these results support the notion that it is error-related (and not stimulus related) neural activity that differentiates these two groups in the punishment condition. Future work should investigate whether error-related neural activity occurring prior to response onset may be useful in differentiating anxious from healthy individuals.

One limitation of the current study includes the fact that participants rated how anxious each condition made them feel after the task was completed. Future studies should have participants complete anxiety ratings after each block. Additionally, the number of shocks received during the random punishment and punishment after errors condition differed. Ideally, the number of shocks administered during the random punishment condition would match the number of shocks administered during the punishment after errors condition. Another issue to consider is the fact that error rates differed across conditions. While the interaction between condition and anxiety was significant at a trend level after controlling for error rates across conditions, we cannot fully exclude the possibility that the differences in the ERN among highly anxious individuals were due, in part, to error rate.

Another limitation to the current investigation is that the baselines do appear to differ between conditions. Although we conducted analyses to investigate potential stimulus driven effects, we cannot be certain that these baseline differences are not confounding group effects. Additionally, the current investigation focused analyses on the ERN and the CRN separately. When both the ERN and CRN were entered in the model, there was not a significant interaction between condition, response, and anxiety group. While this may be due to lack of power, this is a limitation to the current study.

Insofar as punishing errors potentiated the ERN among individuals high in trait anxiety relative to those low in trait anxiety, these data suggest that sensitivity to errors may reflect the interplay between certain traits and aversive experiences related to errors. These results have implications for understanding how individual differences in the ERN relate to real-world learning-related feedback and experiences surrounding error commission. We have hypothesized that one real-world analog of the current experimental paradigm is the early childhood learning environment – especially a harsh or critical parenting style. Indeed, we have recently found that a hostile or punitive parenting style prospectively predicted an increased ERN in young children (Meyer et al., 2015). Furthermore, ERN magnitude mediated the relationship between hostile parenting and child anxiety disorder status, suggesting that harsh or critical parenting may potentiate children's error processing, and thereby, risk for anxiety (Meyer et al., 2015). The relationship between harsh parenting and children's ERN has been replicated in a group of preschool aged children (Brooker and Buss, 2014); moreover, Brooker and Buss (2014) found that the relationship between harsh parenting and an increased ERN was stronger among fearful children. This is consistent with the current findings insofar as individuals with increased anxiety may be especially prone to punishment-related changes in error monitoring. As the current study was completed in college-aged participants, future work should investigate whether there are developmental periods in which error monitoring may be particularly prone to modulation by punishment – both in the lab and via harsh parenting – and whether this relates to increased risk for clinical anxiety. And, as the ERN clearly has a heritable component (Anokhin et al., 2008), but is also sensitive to learning experiences (e.g., punishment and parenting) – and the current study suggests there may be trait by experience interactions - future work should explore whether certain children may be particularly sensitive to harsh parenting.

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