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Felicia Jackson, Brady D. Nelson, and Greg Hajcak Proudfit

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BRIEF REPORT

In an Uncertain World, Errors Are More Aversive: Evidence From the Error-Related Negativity

Felicia Jackson, Brady D. Nelson, and Greg Hajcak Proudfit
Stony Brook University

Unpredictability increases amygdala activity and vigilance toward threat. The error-related negativity (ERN) is an electrophysiological response to errors and is posited to reflect sensitivity to potential threat. The present study examined whether the ERN was modulated by predictable or unpredictable task-irrelevant auditory stimuli. Twenty-three participants completed a speeded response task designed to elicit the ERN, and were simultaneously exposed to predictable and unpredictable tone sequences. Participants retrospectively rated their anxiety to the predictable and unpredictable tone sequences and indicated which tone sequence they disliked the most. Unpredictable tones were rated as slightly more anxiety-provoking compared to predictable tones, but participants were evenly split regarding which sequence they disliked the most. Fewer errors were committed during unpredictable relative to predictable tones. Finally, the ERN—but not the correct response negativity (CRN)—was increased during unpredictable relative to predictable tones. The present study demonstrated that an unpredictable *context* can increase vigilance and potentiate neural processing of errors. These data suggest that an unpredictable environmental context may increase error value. Implications for understanding anxiety disorders are discussed.

Keywords: anxiety, ERN, ERP, threat, unpredictability

The ability to detect internal and external threat is an adaptive process that is important for survival. Predictability is an important feature that can impact emotional responding to threat (Grillon, Baas, Lissek, Smith, & Milstein, 2004). For instance, people prefer predictable over unpredictable threat (Grillon, Baas, Cornwell, & Johnson, 2006; Lejuez, Eifert, Zvolensky, & Richards, 2000), as threat predictability allows for better preparation (Grupe & Nitschke, 2013). Moreover, a heightened sensitivity to unpredictable threat has been implicated as a potential unique characteristic of anxiety disorders (Nelson et al., 2013; Shankman et al., 2013). Importantly, past studies have primarily administered discrete punishments (e.g., electric shock) to investigate the effect of unpredictability on psychophysiological and behavioral responses.

However, Herry and colleagues (2007) recently examined whether unpredictability alone (i.e., independent of concurrent external threat) demonstrated anxiogenic properties. Specifically, participants were exposed to repetitive auditory tone sequences that occurred at completely predictable or unpredictable intervals. Importantly, the mean interval between tones was the same in both conditions. Compared with predictable tones, unpredictable tones elicited greater amygdala activation and increased behavioral measures of attentional bias toward threat. Overall, these results suggest that an unpredictable context can bias individuals toward greater sensitivity to potential threat (Whalen, 2007).

Errors are endogenous events that have the potential to place an individual in danger (Hajcak, 2012; Hajcak & Foti, 2008). Consider an individual cutting a piece of wood on an electric saw: an error in movement could lead to injury. In this way, and from an affective science perspective, errors are motivationally salient endogenous events, which are similar to external threats (e.g., shock), that activate defensive motivational systems (Hajcak, 2012). Consistent with this view, errors have been shown to initiate physiological responses associated with defensive mobilization, such as increased startle reflex (Hajcak & Foti, 2008; Riesel, Weinberg, Moran & Hajcak, 2013), heart rate deceleration (Hajcak, McDonald, & Simons, 2003), skin conductance (Hajcak, McDonald, & Simons, 2004), and amygdala activation (Pourtois et al., 2010). Moreover, errors have been shown to elicit activation of neural circuits that are commonly associated with the experience of negative affect and punishment (Shackman et al., 2011). Together, these findings suggest that errors are motivationally salient and threatening endogenous events that induce preparation for action (Weinberg, Riesel, & Hajcak, 2012; Hajcak, 2012).

The electrophysiological index of errors is the error-related negativity (ERN), a negative deflection in the event-related potential (ERP) that occurs after the commission of an error (Hajcak, 2012). The ERN is increased when errors are motivationally salient, such as

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Felicia Jackson, Brady D. Nelson, and Greg Hajcak Proudfit, Department of Psychology, Stony Brook University.

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Correspondence concerning this article should be addressed to Felicia Jackson, Department of Psychology, Stony Brook University, Stony Brook, NY 11794. E-mail: felicia.jackson@stonybrook.edu

when punished by monetary loss (Hajcak, Moser, Yeung & Simons, 2005) or electric shock (Riesel, Weinberg, Endrass, Kathmann & Hajcak, 2012). Furthermore, the ERN is enhanced in individuals with a heightened sensitivity to errors, including those with generalized anxiety disorder (GAD; Weinberg, Olvet & Hajcak, 2010) and obsessive–compulsive disorder (OCD; Gehring, Himle & Nisenson, 2000; Hajcak, Franklin, Foa & Simons, 2008). Thus, variation in the amplitude of the ERN reflects the relative threat value of errors, such that a larger ERN is elicited when errors are more salient and aversive.

If unpredictability potentiates the processing of potential threat, then this contextual manipulation might similarly increase the ERN. To test this possibility, participants in the present study completed a speeded response flanker task while exposed to either predictable or unpredictable tone sequences. Based on the work by Herry and colleagues (2007), we hypothesized that, relative to predictable tones, unpredictable tones would *increase* sensitivity to potential threat—and thus potentiate the ERN.

Method

Participants

Twenty-nine undergraduates from Stony Brook University participated for course credit. Six participants were excluded from analyses for committing less than 6 errors during the Flanker task in either of the two conditions ($n = 2$; Olvet & Hajcak, 2009) and excessive EEG artifacts ($n = 4$). The final sample consisted of 23 participants (11 females), with a mean age of 18.83 years ($SD = 1.30$), and an ethnic/racial distribution that was 47.8% Caucasian, 30.4% Asian, 13.0% Black, and 8.7% ‘Other.’

Flanker Task

On each trial of the flanker task (Hajcak & Foti, 2008), five horizontally aligned white arrowheads were presented for 200 ms. Participants were instructed to indicate the direction of the central arrowhead using the left or right mouse button. Half the trials were compatible (e.g., <<<<< or >>>>>) and half were incompatible (e.g., <<><< or >><>>); trial type was randomly determined. A variable intertrial interval of 600 to 1000 ms followed the response. The arrows filled 2° of visual angle vertically and 10° horizontally, and were presented at a viewing distance of approximately 65 cm.

Stimuli were presented using Presentation software (Neurobehavioral Systems Inc., Albany, CA). Participants initially completed a practice block containing 20 trials. The actual task consisted of 8 blocks of 64 trials (512 total trials). During a block, either the predictable (P) or unpredictable (U) tones (described below) were played. Block order was either UPUPUPUP or PUPUPUPU, counterbalanced across participants.

Tones

Predictable and unpredictable tones were identical to those used in Herry et al. (2007). Briefly, the carrier frequency was 1 kHz with pulse duration of 40 ms and mean pulse spacing of 200 ms (5 Hz pulse repetition rate). The randomized (i.e., unpredictable) tones were generated from the predictable sequence by random temporal shift of each single tone. Thus, predictable and unpredictable sequences contained an identical number of tones and equivalent mean tone spacing (i.e., 200 ms). The sequences were played at 85 dB through external computer speakers positioned approximately 50 cm in front of the participant.

At the end of the task, participants rated their anxiety during the predictable and unpredictable blocks on a 7-point Likert scale from 1 (*Not anxious*) to 7 (*Extremely anxious*). Participants were also asked to indicate which tone sequence they disliked the most (predictable or unpredictable). Tones were presented again at the end of the session to confirm that participants correctly labeled the tones during subjective ratings.

EEG Recording and Processing

Continuous EEG was recorded using an elastic cap with 34 electrode sites placed according to the 10/20 system and two electrodes on the left and right mastoid. Electrooculogram was recorded from electrodes placed above and below the right eye and two placed on the outer canthus of both eyes. All electrodes were sintered Ag/AgCl electrodes. Data were recorded using ActiveTwo BioSemi system (BioSemi, Amsterdam, The Netherlands). The EEG was digitized with a sampling rate of 512 Hz using a low-pass fifth order sinc filter with a half-power cutoff of 102.4 Hz. A common mode sense active electrode producing a monopolar (nondifferential) channel was used as recording reference.

EEG data were analyzed using Brain Vision Analyzer (Brain Products, Gilching, Germany). Data were referenced offline to averaged mastoids, band-pass filtered with low and high cutoffs (0.1 and 30 Hz, respectively), and corrected for eye movement artifacts (Gratton, Coles, & Donchin, 1983). Response-locked epochs with duration of 1500 ms, including a 500-ms preresponse interval, were extracted. Epochs containing a voltage greater than 50 μV between sample points, a voltage difference of 300 μV within a segment, or a maximum voltage difference of less than 0.50 μV within 100-ms intervals were rejected. Additional artifacts were identified and removed based on visual inspection. The 500–300 ms pre-response interval was used as the baseline (Weinberg et al., 2010). Trials with response times below 200 ms and above 700 ms were excluded from averaging.

A negative deflection is observable after both error (i.e., the error-related negativity, ERN) and correct trials (i.e., correct response negativity, CRN). The ERN and CRN were quantified as the mean amplitude between 0 and 100 ms after responses at electrode FCz, where the ERN was maximal.

Results

Self-Report Ratings and Behavior

Table 1 displays descriptive and inferential statistics for self-report ratings and behavior. Unpredictable tones were rated as slightly more anxiety-provoking compared with the predictable tones (i.e., unpredictable tones were rated as moderately anxiety-provoking). Tones were comparable in terms of which sequence participants disliked the most. Fewer errors were made during the unpredictable relative to predictable tones, but there were no differences in reaction time (RT) on correct or error trials.

ERN

Grand average ERPs are shown in Figure 1; descriptive and inferential statistics for ERN, CRN, and ΔERN (i.e., ERN minus

Table 1
Mean Self-Report Ratings, Behavior, and ERPs for Predictable and Unpredictable Tone Sequence Trials

Variable	Tone sequence: Predictable	Tone sequence: Unpredictable	t or χ^2	Cohen's d	p
Self-report ratings					
Anxiety (au)	3.04 (1.58)	3.78 (1.48)	$t = -2.10$	−.48	$< .05$
Disliked most (%)	43.5%	56.5%	$\chi^2 = 0.39$	—	.53
Behavior					
Number of errors	35.13 (17.16)	28.96 (13.77)	$t = 2.49$	.40	$< .05$
Error RT (ms)	323.06 (41.49)	325.07 (35.77)	$t = -0.37$	−.05	.71
Correct RT (ms)	394.62 (49.77)	401.16 (44.25)	$t = -1.59$	−.14	.13
ERPs (μV)					
Errors	−.57 (4.24)	−2.01 (4.08)	$t = 2.22$	.35	$< .05$
Correct	5.06 (3.45)	5.73 (3.76)	$t = -1.25$	−.19	.22
ΔERN	−5.62 (4.52)	−7.74 (4.65)	$t = 2.28$	.46	$< .05$

Note. ΔERN was calculated by subtracting the CRN from the ERN. Standard deviations are presented in parentheses. au = arbitrary units; ERPs = event-related potentials; ms = milliseconds; RT = reaction time.

CRN) are given in Table 1. The ERP data were examined using a Response (Correct vs. Error) × Condition (Predictable Tones vs. Unpredictable Tones) repeated measures analysis of variance (ANOVA). Results indicated a main effect of Response, $F(1, 22) = 63.68$, $p < .001$, $\eta_p^2 = .74$, that was qualified by a Response × Condition interaction, $F(1, 22) = 5.22$, $p < .05$, $\eta_p^2 = .19$. Follow-up analyses indicated that the ERN was *enhanced* during the unpredictable relative to predictable tones condition, $F(1, 22) = 4.92$, $p < .05$, $\eta_p^2 = .18$, whereas there were no differences between the tones conditions for the CRN, $F(1, 22) = 1.57$, *ns*.

In follow-up ANCOVAs, the Response × Condition interaction remained significant after controlling for number of errors in the predictable and unpredictable tones conditions, $F(1, 20) = 5.61$, $p < .05$, $\eta_p^2 = .22$. The interaction also remained significant after controlling for subjective anxiety ratings during predictable and

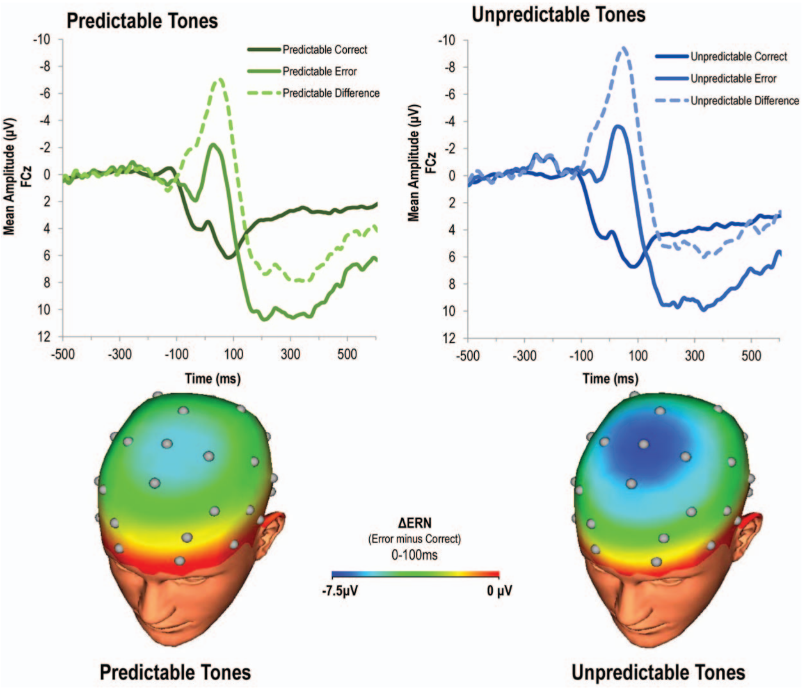

Figure 1. ERP waveforms (top) show the average electrocortical response to error (ERN) and correct trials (CRN), and their difference (ERN minus CRN: ΔERN) while participants were exposed to predictable (left) versus unpredictable (right) tone sequences. ERN was scored between 0 and 100 ms post response. Headmaps (bottom) show the scalp topography of the ΔERN as a function of predictable (left) and unpredictable (right) tone sequences. See the online article for the color version of this figure.

unpredictable tones, $F(1, 20) = 4.94$, $p < .05$, $\eta_p^2 = .20$. These analyses suggest that neither the number of errors nor the subjective anxiety ratings accounted for the observed effect of unpredictable tones on the ERN.

Discussion

In the present study, the ERN was measured while participants were exposed to predictable and unpredictable auditory tone sequences. As hypothesized, the ERN was enhanced during unpredictable relative to predictable tones. In contrast, there was no impact of unpredictable tone sequences on the CRN. These results remained significant even after controlling for condition-related differences in accuracy and subjective anxiety ratings, suggesting that behavioral differences did not account for the observed effect on the ERN.

These findings demonstrate for the first time an enhanced ERN to a contextual manipulation of unpredictability. Similar to Herry et al. (2007), in which unpredictability potentiated amygdala activation and behavioral bias toward threat, the current study found that unpredictability increased neural response to errors. The present findings, paired with the results from Herry and colleagues, demonstrate that an unpredictable environment alone is sufficient to potentiate defensive reactivity (i.e., increased amygdala activation, vigilance, and attention to threat)—and the processing of endogenous threat. These data support the notion that variation in the ERN is related to sensitivity to potential threat (Hajcak, 2012; Hajcak & Foti, 2008; Proudfit, Inzlicht, & Mennin, 2013), which can be altered by environmental contingencies.

Predictable and unpredictable tones also had several effects on behavior and self-report ratings. Participants committed fewer errors during the unpredictable relative to predictable blocks. Improved accuracy during unpredictable tones may reflect increased task vigilance in an unpredictable context. In terms of self-report data, participants were evenly split regarding which sequence they disliked the most—replicating prior self-report data (Herry et al., 2007). Although unpredictable tones were rated as slightly more anxiety-provoking compared with predictable tones, the mean anxiety ratings were below the midpoint of the rating scale—suggesting that unpredictable tones were not particularly anxiogenic. Importantly, neither improved accuracy nor increased anxiety ratings accounted for the impact of unpredictable tones on the ERN.

Being in an unpredictable environment is associated with greater uncertainty—and in this context, errors may be more aversive or associated with more dangerous consequences. Indeed, previous work has demonstrated that the amplitude of the ERN can be modulated by contextual factors that impact the threat value of errors: both punishing errors (Riesel et al., 2012) and harsh parenting (Meyer et al., in press) have been associated with an increased ERN. The current study further suggests that contextual manipulations that render potential threats more salient may similarly increase the ERN. Of course, increased vigilance and enhanced processing of errors in unpredictable contexts may be adaptive. However, *hypersensitivity* to unpredictability is posited to be an important characteristic unique to anxiety disorders (Nelson et al., 2013; Shankman et al., 2013). Future studies might therefore examine the degree to which the modulation of the ERN by unpredictable contexts relates to individual differences in anxiety and real-world indicators of environmental instability (e.g., adversity).

We have previously suggested that an increased ERN may reflect individual differences in certain forms of anxiety (Hajcak, 2012; Proudfit et al., 2013). In this context, the present findings suggest that unpredictability in the environment may increase an individual's neural response to errors—an effect that may mediate increases in anxiety and sensitivity to threat. Future studies might investigate the degree to which individual differences in trait anxiety, threat sensitivity, and emotion regulation interact with manipulations of unpredictability to potentiate the ERN, and how these individual differences interact in the development of anxiety disorders.

The current study is not without limitations. Given the relatively small sample size ($n = 23$), statistical power of the current study is limited. Further research, with a larger sample size, is necessary to explore how the environmental manipulations of uncertainty may interact with trait features, such as individual differences in intolerance of uncertainty (Dugas, Buhr, & Ladouceur, 2004). Moreover, participants in the current study did not complete the flanker task in the absence of tones. Therefore, it is unclear whether predictability impacts the ERN. Future studies might include a no-tones condition to better understand the impact of predictability on the ERN. Another important direction for future research is to examine whether potentiation of the ERN to unpredictability is associated with increased amygdala activation or behavioral measures of threat bias observed in unpredictable contexts (Herry et al., 2007).

In summary, the present study demonstrated that unpredictable environmental stimuli can increase task accuracy and potentiate the ERN. These findings suggest that environmental uncertainty biases individuals toward potential threat and potentiates the neural processing of errors. Furthermore, these data support the notion that variation in the amplitude of the ERN can be modulated by environmental contingencies that alter sensitivity to potential threat. These findings lay important groundwork for understanding the role of unpredictability in threat sensitivity, error processing, and the development and maintenance of anxiety disorders.

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