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Alterations in error-related brain activity and post-error behavior over time

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ABSTRACT

This study examines the relation between the error-related negativity (ERN) and post-error behavior over time in healthy young adults (N = 61). Event-related brain potentials were collected during two sessions of an identical flanker task. Results indicated changes in ERN and post-error accuracy were related across task sessions, with more negative ERN associated with greater improvements in post-error accuracy. This relationship was independent of any cross-sectional relationships between overall task performance, individual difference factors, including personality and self-efficacy, and indices of self-regulatory action monitoring. These results indicate that the relation between ERN and post-error accuracy remains intact and consistent regardless of variation in this set of individual difference factors previously associated with both of these indices of self-regulatory action monitoring, providing support for the strength, robustness, and persistence of this relationship in the process of adaptively controlling behavior to enhance task performance.

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1. Introduction

Action monitoring refers to the online self-regulatory monitoring of one's behavioral interactions with the environment and is vital for learning and goal-directed behavior (Holroyd & Coles, 2002, 2008). Research suggests that action monitoring processes are not only related to the identification of behavioral errors or conflict, but also the subsequent adjustments and adaptations of behavior to correct those problems and improve performance in accord with internal intentions (Gehring, Goss, Coles, Meyer, & Donchin, 1993; Holroyd & Coles, 2002; Kerns et al., 2004; Yeung, Botvinick, & Cohen, 2004).

Examinations of action monitoring were initially confined to behavioral measures of error-related processes (e.g., error corrections, post-error slowing; Laming, 1968; Rabbitt, 1966, 1967; Rabbitt, Cumming, & Vyas, 1978). However, recent investigations have identified neural indices of action monitoring processes. Most notable among these is the error-related negativity (ERN). The ERN is a negative-going deflection of the response-locked event-related brain potential (ERP), typically occurring approximately 50 ms following an erroneous response (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring et al., 1993). The ERN has been identified as either a reinforcement learning index of error detection (Holroyd & Coles, 2002) or an early indicator of response conflict in association with erroneous task performance (Yeung et al., 2004). Electrophysiological source localization studies suggest that the ERN is generated in the anterior cingulate cortex (ACC; Dehaene, Posner, & Tucker, 1994; Herrmann, Römmler, Ehlis, Heidrich, & Fallgatter, 2004; van Veen & Carter, 2002) and recent studies have shown the ERN to be a reliable (Olvet & Hajcak, 2009a) and stable (Olvet & Hajcak, 2009b; Pontifex et al., 2010) neural index of action monitoring.

The reinforcement learning theory of the ERN (Holroyd & Coles, 2002) proposes that the ERN reflects a learning signal carried by the mesencephalic dopamine system that is evidenced on error trials. In turn, this error signal trains the ACC to select the appropriate motor controllers to successfully complete the task based upon this input. Alternatively, the conflict monitoring theory (Botyinick, Braver, Barch, Carter, & Cohen, 2001: Yeung et al., 2004) suggests the ERN reflects ACC activity that detects (or monitors) levels of response conflict. The ACC then transmits that information to processing control centers and triggers adjustments in relative influences on processing among the control centers to improve performance (Botvinick et al., 2001). Importantly, both theories suggest that the ERN should be related with error-correcting activity. To date, this functional characterization of the ERN has been evident in studies showing a linkage between the ERN and behavioral indices of post-error correction (but see also Hajcak, McDonald, & Simons, 2003). For example, increased ERN magnitude has been shown to predict changes in behavior that suggest increased recruitment and implementation of cognitive control on subsequent trials, including response slowing and increased accuracy





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following error commission (Botvinick et al., 2001; Gehring et al., 1993; Themanson, Hillman, & Curtin, 2006; Themanson, Hillman, et al., 2008; Themanson, Pontifex, & Hillman, 2008; Themanson, Pontifex, Hillman, & McAuley, 2011; Yeung et al., 2004). Moreover, ACC activation during errors and task conditions that elicit response conflict predicted the recruitment of additional prefrontal (PFC) neural structures believed to be crucial for the implementation of control on subsequent trials (Garavan, Ross, Murphy, Roche, & Stein, 2002; Kerns et al., 2004). More specifically, ACC activity on error and high-conflict trials has been directly related to behavioral adjustments on subsequent task trials. These behavioral adjustments have been directly associated with enhanced PFC activation on those post-error or post-conflict trials, which, in turn, has been directly related back to ACC activation on the previous error- or conflict-related task trial (Kerns et al., 2004). Multiple studies have found different regions of PFC activation associated with post-conflict or post-error trial behavioral adjustments, including the right middle frontal gyrus (Kerns et al., 2004), left inferior gyrus (Garavan et al., 2002), and left middle frontal gyrus (MacDonald, Cohen, Stenger, & Carter, 2000). It is believed that these different regions of the PFC are associated with separate control processes engaged by the varied tasks and task conditions used across the aforementioned studies (Garavan et al., 2002; Kerns et al., 2004) and behavioral control is largely accomplished through an interplay among these PFC structures and the ACC.

In addition to the functional attributes of the ERN, research has shown an array of variables that are related with ERN amplitude. Those variables associated with larger ERN amplitudes include enhanced task performance (Holroyd & Coles, 2002), psychological factors such as obsessive-compulsive disorder (Gehring, Himle, & Nisenson, 2000), worry (Hajcak et al., 2003), neuroticism (Boksem, Topps, Wester, Meijman, & Lorist, 2006; Pailing & Segalowitz, 2004), negative affect (Hajcak, McDonald, & Simons, 2004; Luu, Collins, & Tucker, 2000), and self-efficacy (SE; Themanson, Hillman, et al., 2008; Themanson, Pontifex, et al., 2008). More specifically, SE is theorized to positively influence effort expenditure and perseverance under failure and aversive stimuli (Bandura, 1986) and has been detailed as a self-regulatory agent for the improvement of goal directed behavior (Bandura, 2001). In relation to action monitoring, greater SE has been associated with larger ERN amplitudes and enhanced post-error accuracy, with ERN mediating the relationship between SE and post-error behavior (Themanson et al., 2011).

In addition to psychological factors, task instructions stressing accuracy over speed (Gehring et al., 1993) have been associated with enhanced ERN amplitudes, suggesting motivational factors associated with an increased salience of errors under accuracy instructions (Gehring et al., 1993; Hajcak, Moser, Yeung, & Simons, 2005) or an increase in attentional focus on the target stimulus leading to a more rapid upsurge in post-error activation of the correct response (Yeung et al., 2004) may influence this component. Conversely, lifestyle factors including levels of physical activity (Themanson et al., 2006) or cardiorespiratory fitness (Themanson & Hillman, 2006) have been associated with decreased ERN amplitude in conjunction with improved task performance, suggesting an enhanced efficiency of the action monitoring system. However, when combined with accuracy instructions, cardiorespiratory fitness has been associated with enhanced ERN amplitudes, suggesting enhanced cognitive flexibility in higher fit individuals to match situational demands on task performance (Themanson, Pontifex, et al., 2008).

Although the ERN has been found sensitive to psychological and performance variables and has been linked with corrective behavioral actions, no study to date has examined whether changes in the ERN across task experiences are associated with similar changes in post-error behavior. Given the functional characterization of the ERN suggest as part of a larger action monitoring system utilized to improve performance (Holroyd & Coles, 2002; Yeung et al., 2004), alterations in ERN amplitude should be associated with commensurate changes in post-error behavior. These common variations between the measures should not only be present within a task session, but also across task sessions, showing persistence in the functional relation over time. Further, although psychological traits or characteristics (e.g., SE, personality) may be related with levels of ERN activation, the functional connections within the action monitoring system between the ERN and control centers adjusting posterror behavior should be generally insensitive to those differences, suggesting influences on the detection sensitivity of the action monitoring system are different than functional adjustments within the action monitoring system. Therefore, we set forth to examine the relation between alterations in ERN and post-error behavior across two testing sessions of an identical cognitive task.

It was predicted that the modulation of the ERN across task sessions would relate to similar alterations in post-error behavioral indices, with larger (more negative) changes in ERN amplitudes associated with greater post-error response accuracy and slowing on subsequent trials. Further, it was predicted that this relationship would be independent of any cross-sectional relations between indices of self-regulatory action monitoring (ERN, posterror behavior) and factors previously associated with action monitoring (SE, task performance, personality). This pattern of findings would show that the functional association between ERN and posterror behavior is robust and resilient to trait differences in SE and personality constructs. Finally, it was predicted that a cross-sectional examination of variables related to the ERN would replicate previous findings, with indices of overall task performance (response accuracy, response time), SE, and personality traits (specifically conscientiousness and emotional stability/neuroticism) showing significant relationships with enhanced ERN amplitudes. Combined, these findings would show that although factors previously associated with the ERN may be related with cross-sectional indices of the error-detection or conflict monitoring response, they do not significantly impact the activity of the ongoing dynamic self-regulatory monitoring system aimed at improving subsequent behavioral outcomes.

2. Materials and methods

2.1. Participants

Eighty-one healthy adults (18–25 years) were recruited from the undergraduate population at Illinois Wesleyan University. Participants fulfilled a psychology course requirement in exchange for their participation, which took place over two testing sessions that occurred on separate days. Twenty participants were excluded due to either excessive artifact in their neuroelectric data (n = 3), not performing the cognitive task at or above 50% accuracy in each task condition (n = 3), incomplete participation (n = 4) or an insufficient number of commission errors in either task session (# of errors < 6; n = 10) to obtain a stable ERN (Olvet & Hajcak, 2009a; Pontifex et al., 2010), leaving data from 61 participants eligible for statistical analyses. The study was approved by the Institutional Review Board at Illinois Wesleyan University.

2.2. Cognitive task

Participants completed a modified version of the Eriksen flanker task (Eriksen & Eriksen, 1974) utilizing symbols that were either congruent (<<<<< or >>>>>), or incongruent (>><>> or <<><) to the central target stimulus. The central target symbol pointing to the right (">") required a right-handed response and the central

target symbol pointing to the left ("<") required a left-handed response. Participants viewed a series of white stimuli on a black background presented focally on a computer monitor at a distance of 1 m and each array of five arrows subtended 13.5° of the horizontal visual angle and 3.4° of the vertical visual angle when presented on the computer monitor. Stimuli were 4 cm in height and were presented for 80 ms with an inter-trial interval (ITI) varying between either 1000, 1200, or 1400 ms for each trial. For each session, the symbols were grouped into two task blocks, with a brief rest period between each block. Each block contained 300 trials. Congruent and incongruent trials were equiprobable and randomly ordered within each task block. The two blocks were counterbalanced across participants and task sessions and participants were asked to respond as quickly and as accurately as possible.

2.3. Behavioral assessment

Behavioral data were collected on response time (i.e., time in ms from the presentation of the stimulus) and response accuracy (i.e., number of correct and error responses) for all trials across task blocks. Multiple average response latencies were calculated for each participant (Themanson, Hillman, et al., 2008; Themanson, Pontifex, et al., 20008; Themanson et al., 2011). Specifically, these latencies were calculated for (1) error trials, (2) matched-correct trials (the subset of correct trials matched to specific error trials based on RT), (3) correct trials following an error trial (post-error RT), and (4) correct trials following a matched-correct trial (postmatched-correct RT). Each participant's post-error RT was compared to his or her post-matched-correct RT due to the consistent finding that average error RT is faster than average correct RT (Mathewson, Dywan, & Segalowitz, 2005; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Yeung et al., 2004) and thus accounts for any effects of RT slowing that are present simply because error RT generally tends to be faster than correct RT (Themanson & Hillman, 2006; Themanson, Hillman, et al., 2008).

2.4. Neural assessment

The electroencephalogram (EEG) was recorded from 64 sintered Ag-AgCl electrodes embedded in a lycra cap arranged in an extended montage based on the International 10-10 system (Chatrain, Lettich, & Nelson, 1985) with a ground electrode (Afz) on the forehead. The sites were referenced online to a midline electrode placed at the midpoint between Cz and CPz. Vertical and horizontal bipolar electrooculographic activity (EOG) was recorded to monitor eye movements using sintered Ag-AgCl electrodes placed above and below the right orbit and near the outer canthus of each eye. Impedances were kept below $10 \text{ k}\Omega$ for all electrodes. A Neuroscan Synamps2 bioamplifier (Neuro Inc., El Paso, TX), with a 24 bit A/D converter and ±200 millivolt (mV) input range, was used to continuously digitize (500 Hz sampling rate), amplify (gain of 10), and filter (70 Hz low-pass filter, including a 60 Hz notch filter) the raw EEG signal in DC mode (763 μ V/bit resolution). EEG activity was recorded using Neuroscan Scan software (v 4.3.1). Stimulus presentation, timing, and measurement of behavioral response time and accuracy were controlled by Neuroscan Stim (v 2.0) software.

Offline neural processing of the response-locked components included eye blink correction using a spatial filter (Compumedics Neuroscan, 2003), re-referencing to average mastoids, creation of response-locked epochs (-400 to 1000 ms relative to behavioral response), baseline removal (100 ms time window that runs from -100 ms to 0 ms prior to the response; Yeung et al., 2004), bandpass filtering (1-15 Hz; 24 dB/octave), and artifact rejection (epochs with signal that exceeded $\pm 75 \,\mu$ V were rejected). Average

ERP waveforms for correct trials were matched to error trial waveforms on response time and number of trials to protect against differential artifacts from any stimulus-related activity (Coles, Scheffers, & Holroyd, 2001). This procedure removes any differences that may exist in the timing of processing due to differences in response latency for correct and error trials (Falkenstein, Hoormann, & Hohnsbein, 2001; Mathewson et al., 2005; Yeung et al., 2004) and results in an equal number of matched-correct trials and error trials for each individual to compare differences across accuracy conditions (Themanson & Hillman, 2006; Themanson, Hillman, et al., 2008; Themanson et al., 2011). ERN was quantified as the average amplitude between 0 and 100 ms post-response in each of these two average waveforms (error and matched-correct) at FCz.

2.5. Procedure

The procedure for this study was divided into two testing sessions. In the first session (T1), after providing informed consent, participants completed a brief demographics questionnaire, the Edinburgh handedness inventory (Oldfield, 1971), and a personality inventory developed from the International Personality Item Pool scale (IPIP; Goldberg, 1999; Goldberg et al., 2006). The IPIP inventory was a 100-item measure used to obtain scores for each participant on five personality factors (Extraversion, Agreeableness; Conscientiousness; Emotional Stability (Neuroticism, and Intellect) as previous research has shown associations between personality and action monitoring (Pailing & Segalowitz, 2004). Participants were then seated in a comfortable chair 1 m in front of a computer screen and prepared for neural measurement in accordance with the guidelines of the Society for Psychophysiological Research (Picton et al., 2000). After acceptable EEG signals were observed, the participant was briefed on the flanker task. The lights were dimmed and the participants were administered 20 practice trials. Following the practice trials, participants completed a measure of self-efficacy (SE; McAuley, Morris, & Doerksen, 2005) that followed the format recommended by Bandura (1977) and has been used in previous research (Themanson, Hillman, et al., 2008; Themanson et al., 2011). The participants were then given two blocks of 300 trials each, with a brief rest provided in between the task blocks. This session lasted approximately 90 min.

For the second session (T2), participants returned to have their behavioral and neural measures collected during the flanker task. This session was scheduled to take place two days after the initial testing session (M = 2.3 days, SD = .81; range = 1–4 days). The participants were once again prepared for EEG measurement and completed 20 practice trials of the flanker task. After finishing the practice trials, the participants completed two blocks of the flanker task. Following the completion of the last task block, the participants were briefed on the purpose of the experiment. This session lasted approximately 60 min.

2.6. Statistical analyses

For the primary analyses, change scores (T2–T1) were created for ERN (Δ ERN) and post-error behavior (Δ post-error accuracy, Δ post-error RT), with the measures from the first testing session (T1) subtracted from the second testing session (T2). Then, Bivariate Pearson Product Moment correlations were calculated to determine the relationships between the change scores, SE, personality, and change scores in overall task performance (Δ response accuracy, Δ RT). Separate hierarchical regression analyses were conducted regressing change scores in post-error behavior (Δ posterror accuracy, Δ post-error RT) on Δ ERN, with any correlated individual difference factors or change scores for overall performance entered in the first step of the analyses (Miller & Chapman, 2001) and Δ ERN entered in the second step of the regressions to ensure the hypothesized relationships between Δ post-error behavior and Δ ERN were not just artifacts of larger relations between ERN and overall behavior. Goodness-of-fit of the models was considered in terms of variance explained by the variables in the equation, expressed as R^2 . The increase in variance explained by the models was tested for significance after each step to establish whether the independent factors accounted for a significant proportion of the variance in the dependent measure. The alpha level was set at $p \leq .05$ for each individual analysis and all analyses included every participant in the final sample (n = 61). Additional hierarchical regression analyses were conducted on measures collected from the first testing session to corroborate previous findings on the relations between SE, personality, task performance, and indices of self-regulatory action monitoring (ERN, post-error behavior). In the case of no significant correlations between individual difference factors and the dependent measures, regression analyses were conducted as described above with post-error behavior regressed on overall task performance measures in the first step of the analysis and ERN entered in the second step of the analysis.

3. Results

3.1. Alterations in ERN and post-error behavior across task sessions

Behavioral and ERN data from Sessions 1 and 2 are presented in Table 1. Correlations between individual difference factors (SE, five-factor personality) with task performance and action monitoring indices during the first session and change scores (T2-T1) in overall task performance and action monitoring indices across sessions are provided in Table 2. Omnibus analyses revealed significant session effects on ERN, F(1,60) = 5.2, p = .03, $\eta^2 = .08$, posterror accuracy, F(1,60) = 20.0, p < .001, $\eta^2 = .25$, post-error RT, F(1,60) = 38.6, p < .001, $\eta^2 = .39$, overall task accuracy, F(1,60) = 44.8, p < .001, $\eta^2 = .43$, and overall RT, F(1,60) = 37.4, p < .001, $\eta^2 = .38$. Specifically, participants' ERNs were larger (more negative) and their performance was both more accurate and faster overall and following errors in the second session compared to the first session (see Table 1), suggesting the influence of practice on the improvement of task performance over time.

Fig. 1 provides grand-averaged response-locked waveforms by response accuracy (error, correct) and testing session (T1, T2). Correlations between change scores (T2-T1) in overall task performance and action monitoring indices are provided in Table 3a. Correlations revealed that larger (more negative) changes in ERN (Δ ERN) across sessions were associated with greater (more positive) changes in post-error response accuracy (Δ post-error accuracy) across sessions, but not with changes in post-error RT (Δ post-error RT). Furthermore, Δ ERN was significantly correlated with SE and intellect, with more positive changes in ERN associated with greater reported levels of SE and intellect at the beginning of the study (see Table 2). However, when accounting for ERN

Table 1

Means (SD) for overall task performance (RT, % correct), ERN, and post-error behavioral indices (post-error RT, post-error-accuracy) by testing session.

Variable	Testing session 1	Testing session 2
Overall RT	407 (51)	387 (42)
Overall PC	88.7 (6.3)	93.3 (6.1)
ERN	-4.1(4.1)	-4.8(4.0)
P-E RT	427 (57)	397 (47)
P-E PC	87.7 (9.8)	93.2 (6.1)

Note: RT = response time in ms; PC = percentage correct (response accuracy); P-E = post-error.

Table 2

Correlations of individual difference variables (self-efficacy, five-factor personality)				
with overall behavior, ERN, and post-error behavior during the first testing session				
and changes in behavior, ERN, and post-error behavior across testing sessions.				

-		-			-	
Variable	SE	Ι	II	III	IV	V
1. PC	.45**	.06	16	03	07	.08
2. RT	34**	06	.03	10	.04	27^{*}
3. ERN	26^{*}	10	24	01	26*	14
4. P-E PC	.37**	03	08	.16	06	.20
5. P-E RT	39**	04	.06	12	.05	34^{**}
6. Δ PC	30*	05	11	.07	.01	05
7. Δ RT	.16	.14	06	.09	.16	.34**
8. Δ ERN	.26*	03	08	.04	.14	.27*
9. Δ P-E PC	27^{*}	.04	13	13	01	21
10. ∆ P-E RT	.23	.04	.07	.09	.16	.20

Note: SE = self-efficacy; I = extraversion; II = agreeableness; III = conscientiousness; IV = emotional stability; V = intellect; PC = percentage correct (response accuracy); RT = response time; ERN = error-related negativity; P-E = post-error. Δ = change across task sessions (T2-T1).

^{*} p < .05.

p < .01.

amplitude measured during the first task session, the relationships SE and intellect have with Δ ERN are no longer significant, suggesting these relationships do not have unique influences on Δ ERN.

In addition to being correlated with Δ ERN, Δ post-error accuracy were also negatively correlated with greater changes in overall response accuracy and SE, but not with any other variables or factors (see Tables 2 and 3a). Given the significant relationships mentioned above, a hierarchical regression analysis was performed regressing Δ post-error accuracy on SE, changes in overall response accuracy, and Δ ERN, with Δ ERN entered separately in the second step of the analysis. The overall regression model was significant $(R^2 = .30, F(3, 57) = 8.4, p < .001)$, with no significant effect for SE, but both significant effects for changes in overall accuracy in the first step and ERN in the second step, $\Delta R^2 = .06$, F(1,57) = 4.8, p = .03. These findings suggest that the relationship between Δ ERN and Δ post-error accuracy is independent of the relationship Δ post-error accuracy has with changes in overall response accuracy. Table 4 provides a summary of this regression analysis and Fig. 2 presents a scatter plot of the statistically independent relation between Δ ERN and Δ post-error accuracy. Because no significant relationships were present between Δ ERN and Δ post-error RT across sessions, there were no regression analyses conducted between the two variables.¹

3.2. Cross-sectional findings (session 1)

Correlations between individual difference factors (SE, personality) with task performance and action monitoring indices during the first session are provided in Table 2 while correlations between measures of overall task performance and action monitoring indices during the first testing session are provided in Table 3b. Correlations revealed the expected relationships between larger (more negative) ERN with greater SE, greater emotional stability (neuroticism), better overall response accuracy, faster overall RT, greater post-error response accuracy, and slower post-error RT. These relationships largely corroborate previous cross-sectional action monitoring research (Botvinick et al., 2001; Gehring et al., 1993; Holroyd & Coles, 2002; Pailing & Segalowitz, 2004; Themanson,

¹ These analyses were also conducted by forming residuals for the second session measures of the ERN and post-error behavior indices (post-error accuracy, post-error RT) based upon first session measures. The residual findings replicate the difference score findings, with a significant relationship present between the residuals of the ERN and post-error accuracy, while no significant relationship was present between the residuals of the ERN and post-error RT.

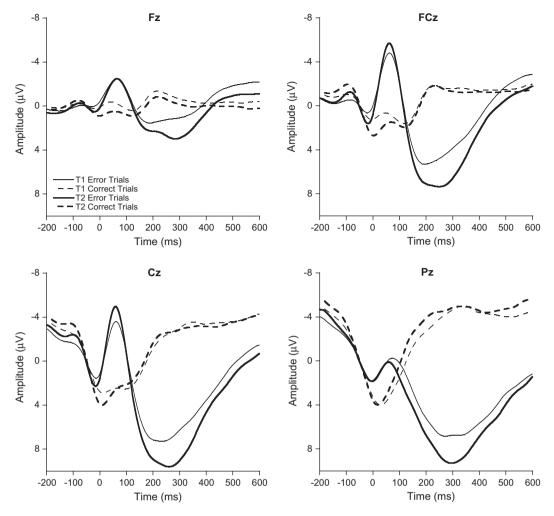


Fig. 1. Grand-averaged response-locked waveforms by testing session (T1, T2) on error and correct trials at the Fz, FCz, Cz, and Pz electrode sites.

Table 3

Correlations among (a) measures of changes in overall behavior, ERN, and post-error behavior across testing sessions, among (b) measures of overall behavior, ERN, and post-error behavior during the first testing session, and among (c) measures of overall behavior, ERN, and post-error behavior during the second testing session.

				0	
Variable	1	2	3	4	5
(3a)					
1. Δ PC	-				
2. Δ RT	16	-			
3. Δ ERN	10	08	-		
4. Δ P-E PC	.48**	05	33**	-	
5. Δ P-E RT	25	.64**	01	11	-
(3b)					
1. PC	_				
2. RT	27*	_			
3. ERN	29*	.27*	-		
4. P-E PC	.64**	41**	42**	-	
5. P-E RT	28*	.90**	.26*	38**	-
(3c)					
1. PC	_				
2. RT	03	-			
3. ERN	.15	02	-		
4. P-E PC	.62**	12	14	-	
5. P-E RT	11	.84**	09	27^{*}	-

Note: Δ = change across task sessions (T2–T1); PC = percentage correct (response accuracy); RT = response time; ERN = error-related negativity; P-E = post-error. Note: PC = percentage correct (response accuracy); RT = response time; ERN = errorrelated negativity; P-E = post-error.

p < .01.

Table 4

Summary of the regression analysis for variables predicting changes in post-error accuracy across the two testing sessions.

Variables	В	SE B	β
Step 1 Δ Overall PC SE	.78 –.09	.21 .07	.44** 14
Step 2 Δ Overall PC SE Δ ERN	.76 –.03 –1.12	.21 .07 .51	.42** 05 25*

Note: Δ = change across task sessions (T2–T1); PC = percentage correct (response accuracy); SE = self-efficacy; ERN = error-related negativity.

Hillman, et al., 2008; Themanson et al., 2011; Yeung et al., 2004) detailing the individual difference and performance factors associated with neural and behavioral indices of self-regulatory action monitoring. However, no significant relationship was evidenced between ERN and conscientiousness, which has been shown in previous research (Pailing & Segalowitz, 2004).

To further examine the relations between ERN and the significant individual difference and performance factors, a linear regression analysis with ERN regressed on overall response accuracy, overall RT, SE, and emotional stability. The analysis showed that

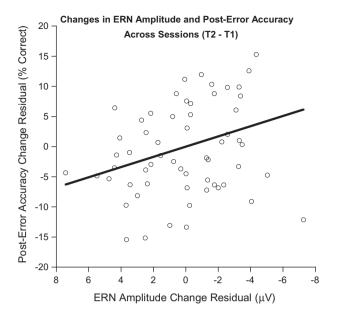


Fig. 2. Scatter plot for the relationship between residuals for changes in ERN and post-error accuracy across testing sessions (T2–T1) after controlling for the influence of SE and changes in overall response accuracy across testing sessions.

Table 5

Summary of regression analyses for (a) variables predicting ERN, (b) variables predicting post-error accuracy, and (c) variables predicting post-error RT during the first testing session.

$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Variables	В	SE B	β
Overall PC 12 $.11$ 12 Overall RT $.02$ $.01$ $.13$ Emot. Stab. 08 $.04$ 22 SE 08 $.05$ 14 (5b) Post-error accuracyStep 1 $.02$ $.07$ Overall PC $.87$ $.17$ $.56^{\bullet \bullet \bullet}$ Overall RT 05 $.02$ $25^{\bullet \bullet}$ SE $.02$ $.07$ $.04$ Step 2 $.07$ $.04$ Overall RT 04 $.02$ $22^{\bullet \bullet}$ Overall RT 04 $.02$ $22^{\bullet \bullet}$ SE 01 $.07$ $22^{\bullet \bullet}$ Overall RT 04 $.02$ $22^{\bullet \bullet}$ Step 1 $$	(5a) ERN amplitude			
Overall RT.02.01.13Emot. Stab. 08 .04 22 SE 08 .05 14 (5b) Post-error accuracyStep 1 0 Overall PC.87.17.56***.02.725**SE.02.07.04.02 $25**$ SE.02.07.04.02 $22**$ SE.02.07.04.02 $22**$ SE.01.07.02.22**SE.01.07.02.22**SE.01.07.02ERN 44 .19 $24*$ (5c) Post-error RTStep 1.07.08.09SE.31.23.09SE.31.23.09Step 2.07.02.07.02.07.03.07.04.02.05.07.06.38.09.38.09.38.09.17.02.09Step 2.07.02.07.02.14.05.00.04.02.05.23.00.10	Step 1			
Emot. Stab08.0422SE08.0514(5b) Post-error accuracyStep 1Overall PC.87.17.56***Overall RT05.0225**SE.02.07.04Step 2.02.07.04Overall PC.82.16.52**Overall PC.82.16.52**Overall RT04.0222*SE01.0702ERN44.1924*(5c) Post-error RT	Overall PC	12	.11	12
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Overall RT	.02	.01	.13
(5b) Post-error accuracy .17 .56*** Overall PC .87 .17 .56*** Overall RT 05 .02 25** SE .02 .07 .04 Step 2 .02 .07 .04 Overall PC .82 .16 .52*** Overall PC .82 .16 .52*** Overall RT 04 .02 22** SE .01 .07 .02 ERN 44 .19 24* (5c) Post-error RT	Emot. Stab.	08	.04	22
Step 1Overall PC.87.17.56***Overall RT 05 .02 $25**$ SE.02.07.04Step 2.02.07.04Overall PC.82.16.52**Overall RT 04 .02 $22**$ SE 01 .07 02 ERN 44 .19 $24*$ (5c) Post-error RT	SE	08	.05	14
Overall PC.87.17.56**Overall RT 05 .02 25^* SE.02.07.04Step 2.02.07.04Overall PC.82.16.52**Overall RT 04 .02 22^* SE 01 .07 02 ERN 44 .19 24^* (5c) Post-error RT	(5b) Post-error accuracy			
Overall RT 05 $.02$ 25^{**} SE $.02$ $.07$ $.04$ Step 2 $.02$ $.07$ $.04$ Overall PC $.82$ $.16$ $.52^{***}$ Overall RT 04 $.02$ 22^{*} SE 01 $.07$ 02 ERN 44 $.19$ 24^{*} (5c) Post-error RTStep 1 $.07$ $.85^{***}$ Overall RT $.95$ $.07$ $.85^{***}$ Overall PC 07 $.57$ 01 Intellect 60 $.38$ 09 Step 2 $.07$ $.85^{***}$ Overall PC 14 $.57$ 02 Intellect 67 $.38$ 10 SE 36 $.23$ 10	Step 1			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Overall PC	.87	.17	
Step 2	Overall RT	05	.02	25**
Overall PC .82 .16 .52*** Overall RT 04 .02 22* SE 01 .07 02 ERN 44 .19 24* (5c) Post-error RT	SE	.02	.07	.04
Overall RT 04 $.02$ 22^* SE 01 $.07$ 02 ERN 44 $.19$ 24^* (5c) Post-error RTStep 1 07 $.57$ 01 Overall RT $.95$ $.07$ $.85^{***}$ Overall PC 07 $.57$ 01 Intellect 60 $.38$ 09 SE 31 $.23$ 09 Step 2 14 $.57$ 02 Intellect 67 $.38$ 10 SE 36 $.23$ 10	Step 2			
SE 01 .07 02 ERN 44 .19 24* (5c) Post-error RT	Overall PC	.82	.16	.52***
ERN 44 .19 24* (5c) Post-error RT 5 .07 .85*** Overall RT .95 .07 .85*** Overall PC 07 .57 01 Intellect .60 .38 09 SE 31 .23 09 Step 2 0 .07 .85*** Overall PC 14 .57 02 Intellect 67 .38 10 SE 36 .23 10	Overall RT	04	.02	22**
(5c) Post-error RT	SE	01	.07	
Step 1 .95 .07 .85*** Overall RT .95 .07 .85*** Overall PC 07 .57 01 Intellect 60 .38 09 SE 31 .23 09 Step 2	ERN	44	.19	24^{*}
Overall RT .95 .07 .85*** Overall PC 07 .57 01 Intellect 60 .38 09 SE 31 .23 09 Step 2	(5c) Post-error RT			
Overall PC 07 .57 01 Intellect 60 .38 09 SE 31 .23 09 Step 2 - - 07 .57 01 Overall RT .96 .07 .85*** 02 Intellect 67 .38 10 SE 36 .23 10	Step 1			
Intellect 60 .38 09 SE 31 .23 09 Step 2 - - - Overall RT .96 .07 .85*** Overall PC 14 .57 02 Intellect 67 .38 10 SE 36 .23 10	Overall RT	.95	.07	.85***
SE 31 .23 09 Step 2	Overall PC	07	.57	01
Step 2	Intellect	60	.38	09
Overall RT .96 .07 .85*** Overall PC 14 .57 02 Intellect 67 .38 10 SE 36 .23 10	SE	31	.23	09
Overall PC 14 .57 02 Intellect 67 .38 10 SE 36 .23 10	Step 2			
Intellect 67 .38 10 SE 36 .23 10	Overall RT	.96	.07	.85***
SE36 .2310	Overall PC	14	.57	02
	Intellect		.38	10
ERN –.67 .65 –.06				
	ERN	67	.65	06

Note: PC = percentage correct (response accuracy); Emot. Stab. = emotional stability; SE = self-efficacy.

* *p* = .02.

** p < .05.

**** p < .01.

the overall regression model was significant ($R^2 = .20$, F(4,56) = 3.4, p = .02), with no significant effects for any of the individual factors in the analysis, suggesting no personality or performance factors had a significant relation with ERN independent of the other

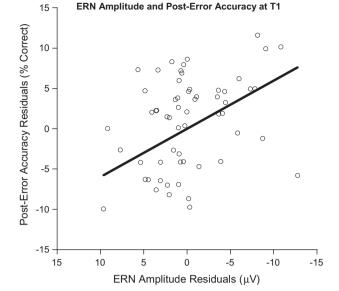


Fig. 3. Scatter plot for the relationship between residuals for ERN amplitude and post-error response accuracy after controlling for the influences of overall behavior (response accuracy, RT) and SE during the first testing session.

personality or performance factors. Table 5a provides a summary of this regression analysis.

In addition to the cross-sectional relationship with ERN, posterror accuracy was correlated with overall response accuracy, overall RT, and SE, but not with any other individual difference factors. Accordingly, a hierarchical regression analysis was performed regressing post-error accuracy on overall accuracy, overall RT, SE, and ERN, with ERN entered separately in the second step of the analysis. The overall regression model was significant ($R^2 = .52$, F(4,56) = 15.3, p < .001), with no significant effect for SE, but signifiicant effects for both overall accuracy and overall RT in the first step and a significant ERN influence in the second step, $\Delta R^2 = .05$, F(1,56) = 5.6, p = .02. These findings suggest that larger ERN was associated with greater post-error accuracy independent of the relationship between overall performance (accuracy, RT) and post-error accuracy. Table 5b provides a summary of this regression analysis and Fig. 3 presents a scatter plot of the statistically independent relation between ERN and post-error accuracy.

Aside from the association with ERN, post-error RT was correlated with overall RT, overall response accuracy, SE, and intellect (see Tables 2 and 3b). A hierarchical regression analysis was performed entering all variables aside from ERN in the first step and adding ERN to the second step of the analysis. The analysis showed a significant overall regression model ($R^2 = .84$, F(5,55) = 58.1, p < .001), with a significant effect of overall RT in the first step, but no effects for overall accuracy, SE, or intellect in the first step and no significant ERN influence in the second step, $\Delta R^2 = .01$, F(1,55) = 1.0 p = .31, suggesting that larger ERN was not independently associated with slower post-error RT. Importantly, overall RT showed a very strong positive correlation with post-error RT (r = .90; see Table 3b). Though very high, the nature of the strong positive relationship between these two measures is expected as the post-error metric includes variance from the overall RT metric. Table 5c presents a summary of the regression analysis.

3.3. Cross-sectional findings (session 2)

Finally, correlations were obtained among measures of task performance (overall accuracy, RT) and action monitoring indices (ERN, post-error behavior) to investigate whether the pattern of interrelations among the measures obtained in the first session and across sessions remained consistent when obtained in the second session (see Table 3c). Importantly, the ERN was not associated with either post-error accuracy or post-error RT in the second session. This finding suggests that the association shown between changes in the ERN and post-error accuracy across sessions is not simply a reflection of a static cross-sectional relation evident in multiple testing sessions.

4. Discussion

The present study analyzed both neural and behavioral indices of action monitoring across two sessions of a flanker task to examine the relation between changes in the ERN and post-error behavior over time. Overall, changes in ERN across sessions were associated with changes in post-error accuracy across sessions, independent of any relations these self-regulatory action monitoring indices may have with SE, personality, or more general performance factors. Collectively, these data suggest that the wellestablished functional relation between ERN and post-error behavioral adjustments is linked over time and task experiences and is not dependent upon this set of personality and performance variables that have been previously associated with indices of action monitoring in cross-sectional research.

Although different in describing how the ERN is generated, current accounts of the ERN and its relation with the control of behavior posit that the neural activation leading to the ERN should be associated with subsequent improvements in behavior. Both the reinforcement learning model (Holroyd & Coles, 2002) and conflict monitoring theory (Botvinick et al., 2001; Yeung et al., 2004) propose that the ERN is part of a process that leads to the selection of, or adjustment in, the appropriate motor controllers and processing control centers to improve performance. The current study suggests that this functional relationship is both robust and consistent over time. Regardless of (a) trait differences in SE and five-factor personality. (b) the direction of change in ERN over time, or (c) changes in overall task performance across time and separate task experiences, alterations in post-error accuracy mimicked those of ERN, with larger (more negative) ERN changes associated with greater improvements in post-error accuracy above and beyond the influence of overall changes in behavior.

This finding provides evidence for current theoretical and computational models detailing the functional significance of the ERN to include the relation between the ERN and post-error alterations in behavior (Holroyd & Coles, 2002; Yeung et al., 2004). Additionally, this finding supports research showing that larger (more negative) ERN amplitudes are associated with a greater implementation of post-error cognitive control resulting in greater changes in post-error behavior (Gehring et al., 1993; Kerns et al., 2004; Themanson et al., 2006). Findings from a number of studies call this relationship into question as research has shown that certain clinical or psychopathological samples have evidenced larger ERN amplitudes, but worse post-error response accuracy, when compared to healthy samples (Holmes & Pizzagalli, 2008; Pizzagalli, Peccoralo, Davidson, & Cohen, 2006). However, explanations of these effects have found grounding in the psychopathological nature of the participant groups, with enhanced sensitivity to mistakes and negative events (Olvet & Hajcak, 2008; Steffens, Wagner, Levy, Horn, & Krishnan, 2001) or hyperactivity of selfmonitoring processes (Ursu, Stenger, Shear, Jones, & Carter, 2003), suggesting "abnormalities of the ERN" (Olvet & Hajcak, 2008, p. 1349). The inefficiency, miscalibration, or misuse of the action monitoring system associated with the "hyperactive or hypoactive error-processing" (Olvet & Hajcak, 2008, p. 1349) that is present in clinical or psychopathological populations can be viewed as an indicator of the larger unhealthy and maladaptive state of the individual (Olvet & Hajcak, 2008). Further, research evidence suggests that psychopathology may be associated with "disrupted connectivity" (Holmes & Pizzagalli, 2008, p. 186) between the ACC and dorsolateral PFC regions utilized to implement the cognitive control processes necessary for effective post-error behavioral adaptations. In sum, these studies suggest that in a healthy adult population, with cognitive control and action monitoring systems intact and properly calibrated, ERN amplitude is a predictor of adaptive post-error behavioral adjustments aimed at improving task execution. Conversely, in clinical samples, the association between the ERN and post-error behavioral adaptations is less consistent due to the increased variability in the action monitoring system associated with psychopathology. Accordingly, the nature of the psychopathology (e.g., internalizing versus externalizing disorders: Olvet & Haicak, 2008) needs to be considered to better understand this association in clinical or sub-clinical participant samples.

It is also important to note the overall neural and behavioral differences between the two sessions. Participants were both more accurate and faster in their overall responses as well as their post-error responses in the second session; suggesting comprehensive improvements in performance, rather than any speed-accuracy trade-off, from the first session to the second session. This may very well be due to practice effects and the short amount of time between testing sessions, allowing participants to build upon their initial exposure and familiarity with the task. In the current study, these practice effects were considered in the analyses by accounting for the overall changes in response accuracy across task sessions, suggesting that the observed relation between alterations in the ERN and post-error behavior are not simply artifacts of practice or learning. Additionally, ERN was larger in the second session, consistent with other research examining ERN amplitudes over time (Olvet & Hajcak, 2009a). This difference may be related to the aforementioned behavioral improvements. Current ERN theory predicts that improved performance should be associated with larger ERNs (Holroyd & Coles, 2002; Yeung et al., 2004) and the present study has provided empirical evidence for that relationship as well.

The current findings further corroborate research on action monitoring and cognitive control showing that the ERN is associated with alterations in behavior following error commission (improved post-error accuracy, slower post-error RT) aimed at improving subsequent task performance (Botvinick et al., 2001; Gehring et al., 1993; Themanson, Hillman, et al., 2008; Themanson, Pontifex, et al., 2008). Moreover, given the substantial evidence suggesting that the ERN is generated in the ACC (Dehaene et al., 1994; Herrmann et al., 2004; van Veen & Carter, 2002), the present study supports fMRI research showing greater levels of ACC activation predicting the greater adjustments in behavior (Kerns et al., 2004). In comparison with other research, however, the present investigation is novel by extending the examination that relates indices of action monitoring and cognitive control across separate task sessions. Further, the present investigation reveals that the functional relationship between changes in the ERN and post-error behavior over time is not sensitive to SE, personality, or changes in overall task behavior. However, one factor that may explain this functional relationship is the degree of connectivity between the ACC and PFC. In their study on patients with major depressive disorder (MDD), Holmes and Pizzagalli (2008) showed that MDD patients with the greatest dorsolateral PFC activation showed enhanced post-error behavior (both higher accuracy and greater RT slowing) when compared to MDD patients who recruited less PFC activation, even though the severity of depression symptoms was nearly identical across the MDD groups. This suggests that the greater recruitment of the PFC resulting from the stronger

connectivity between the ACC and PFC regions is associated with the successful adaptation of post-error behavior and may account for variation in the functional relationship between changes in the ERN and post-error behavior. Additionally, other psychological factors known to influence both the ERN and post-error behavior, including differences in motivation (Gehring & Willoughby, 2002; Hajcak et al., 2005; Pailing & Segalowitz, 2004) or negative affect (Hajcak et al., 2004; Luu et al., 2000; Wiswede, Münte, Goschke, & Rüsseler, 2009) may be helpful in explaining variation in the functional relationship between changes in ERN with changes in post-error behavior.

Further, the current findings are largely consistent with previous cross-sectional studies examining influences on the ERN. Similar to the current study, this research has shown ERN amplitude to be sensitive to task performance (Holroyd & Coles, 2002), emotional stability (neuroticism: Boksem, Topps, Wester, Meijman, & Lorist, 2006; Pailing & Segalowitz, 2004), and SE (Themanson, Hillman, et al., 2008; Themanson et al., 2011). However, there are some discrepancies between the current findings and past research regarding personality, SE, and the ERN. For example, previous studies have found evidence for ERN relationships with conscientiousness (Pailing & Segalowitz, 2004) and extraversion (Boksem et al., 2006), but neither of those relationships were present in the current study. One explanation for the absence of these findings may lie in the inconsistent nature of these relationships across other studies. Importantly, Pailing and Segalowitz (2004) did not find a relationship between ERN and extraversion while Boksem et al. (2006) did not find an association between ERN and conscientiousness. Thus, these relationships appear to be equivocal across the existing literature, unlike the relationship ERN has with emotional stability/neuroticism, which was evidenced in the present findings as well as both of the aforementioned studies (Boksem et al., 2006; Pailing & Segalowitz, 2004). Additionally, while SE exhibited a significant zero-order relationship with ERN and post-error behavior in the current study, corroborating previous findings (Themanson, Hillman, et al., 2008; Themanson et al., 2011), these relationships were not evident when accounting for the influence of overall task performance. This finding may be due to a difference in task instructions in the current study. Previous research on the SE only found relationships with the ERN under accuracy instructions, not speed instructions. However, the current study asked participants to respond as quickly and as accurately as possible, which may have weakened the relationships SE has with the ERN and post-error behavior. Further, it may be that the influence of SE on action monitoring indices is better predicted by overall indices of performance as SE has been shown to exert an influence on overall task performance (Berry & West, 1993; Bouffard-Bouchard, 1990; Lachman & Jelalian, 1984), not just post-error behavior.

4.1. Limitations

Although we report on the relationships among neural and behavioral indices of action monitoring, there are a number of limitations to the present study. Only one relatively simple cognitive task was utilized in the current investigation. Future research should implement an array of cognitive measures with greater levels of complexity to more completely assess the relationships between neural and behavioral indices of action monitoring and the potential development of action monitoring processes across task experiences. Additionally, this study utilized a correlational design and did not assess other psychological factors (i.e., motivation, negative affect, psychopathology) that have been associated with the ERN. Future research would be well-served to employ an experimental design aimed at manipulating motivation (Hajcak et al., 2005; Pailing & Segalowitz, 2004) in an attempt to alter the ERN or induce changes in negative affect to modulate the ERN (Wiswede et al., 2009) and determine the effects on subsequent action monitoring processes.

4.2. Conclusions

Overall, our findings provide evidence for the persistence of the relationship between the ERN and post-error behavioral adjustments across time, with larger changes in ERN associated with greater improvements in post-error response accuracy. Additionally, no other variables were independently associated with alterations in post-error accuracy across testing sessions. This suggests that the functional relationship between ERN and post-error adjustments in behavior is not sensitive to the cross-sectional relations these indices of action monitoring have with measures of overall performance or some individual difference factors, including SE and personality. This study and previous cross-section research have shown a relationship between ERN and post-error behavior, with larger ERN was associated with increased post-error behavioral adjustments (i.e., greater response slowing, enhanced post-error response accuracy), providing evidence for the functional role of the ERN in the self-regulatory action monitoring system designed to improve subsequent actions (Holroyd & Coles, 2002; Yeung et al., 2004). However, this study provides additional support for the strength and persistence of the direct and independent functional relationship between the initial detection signal (indexed by the ERN) and the subsequent adaptive control of behavior following erroneous action, which leads to greater success immediately following error commission (i.e., greater post-error accuracy) and is intended to enhance all subsequent performance during task execution.

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