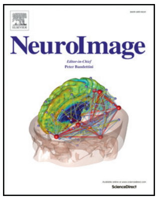
NeuroImage 128 (2016) 158–166

Contents lists available at ScienceDirect

NeuroImage

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



Electrophysiological correlates of error initiation and response correction

Paul D. Kieffaber [a,*], Jamie Hershaw [b], Jonathan Sredl [a], Robert West [c]

[a] Department of Psychology College of William and Mary I.S.C., Room 1137 540 Landrum Drive Williamsburg, VA 23185, USA
[b] Department of Medical and Clinical Psychology, Uniformed Services University of the Health Sciences, 4301 Jones Bridge Road, Bethesda, MD 20814, USA
[c] Department of Psychology, DePauw University, 7 E. Larabee Street Harrison Hall, Greencastle, IN 46135, USA

ARTICLE INFO

Article history:
Received 15 October 2014
Accepted 25 December 2015
Available online 31 December 2015

ABSTRACT

Adaptive, goal-directed behavior requires the ability to monitor the perception-action cycle, detect errors, and make adjustments to restore volitional action. One limiting factor in gaining a clearer understanding of the functional significance of the neural correlates of error detection has been the predominant use of discrete responses (e.g., a button press) as measures of behavior that do not easily afford an assessment of online error correction. This limitation was addressed in the current study by examining the neural correlates of error initiation and correction with respect to dynamic cursor movements that permitted measurement of the initiation and correction of errant responses within individual trials. Results indicate that the ERN may reflect a general error alarm following the initiation of an error but that the Pe component may be more closely related to the initiation of corrective action. The data also reveal that the amplitude and latency of frontal midline Theta oscillations may be more closely related to corrective action, suggesting that error detection and corrective action are mediated by an overlapping neural network.

Introduction

Adaptive, goal-directed behavior requires the ability to monitor the perception-action cycle, detect errors, and make adjustments to restore volitional action (Fuster, 2008). Considerable efforts have been invested over the last two decades toward understanding the neural correlates of error detection. Two event-related brain potentials (ERPs) that have received considerable attention are the error-related negativity (ERN) and the error positivity (Pe) (Gehring et al., 1993; Scheffers et al., 1996; Yeung et al., 2004). The functional significance of the ERN/Pe components with respect to the detection and/or correction of erroneous behavioral responses continues to be a topic of debate. Here we propose that one limiting factor in gaining a clear understanding of the functional significance of the ERN/Pe has been the use of discrete responses (e.g., a button press) as measures of behavior that do not easily afford an assessment of online error correction (Ullsperger and von Cramon, 2006). This limitation was addressed in the current study by examining the neural correlates of error detection and correction with respect to dynamic cursor movements that permitted measurement of the initiation and correction of errant responses within individual trials.

The ERN is a negative going deflection of the ERP that peaks shortly (i.e., 50–100 ms) after the commission of errors in many choice response tasks (Falkenstein et al., 1991; Gehring et al., 1993). The ERN has a fronto-central distribution which, through source localization (Herrmann et al., 2004; Van Veen and Carter, 2002a, 2002b) and convergent imaging data (Mathalon et al., 2003; Van Veen and Carter, 2002a), has been attributed to the activity of a neural generator in the anterior cingulate cortex (ACC).

The Pe follows the ERN and may represent two subcomponents. The early Pe has a fronto-central distribution and peaks between 150 to 300 ms after a response, and the late Pe has a more posterior distribution and peaks between 400 and 600 ms after a response (Arbel and Donchin, 2009; Endrass et al., 2007; Van Veen and Carter, 2002b). Compared with ERN, there is much less agreement in the literature regarding the neuroanatomical source of the Pe with some investigators reporting a generator in the posterior ACC (Vocat et al., 2008) and others reporting a generator in the rostral ACC (Herrmann et al., 2004; O'Connell et al., 2007). Part of the uncertainty regarding the location of the neural generator of the Pe may stem from the failure to consider the early and late subcomponents separately in some cases.

Partial phase-locking of Theta oscillations is thought to represent a dominant contribution to both the ERN and Pe (Cavanagh et al., 2009; Luu et al., 2004; Selimbeyoglu et al., 2012; Yordanova et al., 2004). Frontal midline Theta band oscillations have consistently been reported to increase in power just prior to and following the commission of errors. A study by Cavanagh et al. (2009) found that mid-frontal Theta power increases as the degree of Theta synchrony between medial and lateral PFC increases, and that both mid-frontal power and synchrony predict post-error slowing of response time. This finding has been interpreted as evidence for a relationship between limbic theta-band oscillations, error monitoring and learning.

Despite being the subject of intense investigation, the functional significance of the ERN remains a topic of debate. Some postulate that the

---

* Corresponding author.
E-mail address: pdkieffaber@wm.edu (P.D. Kieffaber).

http://dx.doi.org/10.1016/j.neuroimage.2015.12.046
1053-8119/

ERN reflects the activity of an error alarm system that signals a mismatch between intended and executed responses (Coles et al., 2001; Falkenstein et al., 1991, 2000; Ito et al., 2003). Others suggest that the ERN reflects the activity of a more general conflict-detection network (Botvinick et al., 2001). According to conflict monitoring theory, the conflict detected between activation of the incorrect response set and the correct response set results in increased ACC activity and generation of the ERN (Bartholow et al., 2005; Botvinick et al., 2004; Danielmeier et al., 2009; Gehring and Fencsik, 2001; Hughes and Yeung, 2011).

The Pe is often associated with conscious awareness of error commission. In studies wherein participants were instructed to indicate whether a response was correct or incorrect, the Pe is larger in amplitude on those trials that participants later report having made an error than for trials where errors go undetected (Endrass et al., 2007; Nieuwenhuis et al., 2001; Wessel et al., 2011). Despite the association between error awareness and the Pe, there is uncertainty as to whether the Pe is a reflection of a process that precedes and contributes to error awareness (Endrass et al., 2012, 2007; Murphy et al., 2012) or is a product of error awareness (Endrass et al., 2005; Nieuwenhuis et al., 2001). Emerging evidence favors the hypothesis that Pe precedes error awareness, and specifically that it is an index of the accumulation of evidence that an error has been made (Steinhauser and Yeung, 2010, 2012). For example, Steinhauser and Yeung (2010) varied reward schedules to manipulate the criteria participants used to determine whether an error had been made. The authors asserted that more evidence was needed to reach the decision that an error had been committed on high-criterion trials and reported that Pe amplitude was greater when subjects indicated that an error had occurred in the high-criterion condition compared to the low-criterion condition. Thus, these researchers concluded that Pe amplitude is a reflection of the accumulation of evidence required to determine an error has been made and bring it into conscious awareness.

It is widely accepted that the ERN/Pe are products of an error monitoring system related to the execution and correction of goal-directed behavior (Burle et al., 2008; Gehring and Fencsik, 2001; Van Veen and Carter, 2002b). However, just how they are related to corrective behavior remains an open question. Some suggest that the ERN acts as a non-specific alarm system (e.g., signaling that something is amiss), and the Pe acts as a specific alarm system (e.g., collection of evidence that the problem is the commission of an error) (Dhar et al., 2011; Nieuwenhuis et al., 2001). However, like the Pe, the ERN has also been shown to be modulated by subjective awareness of errors in some cases (Endrass et al., 2007; Hughes and Yeung, 2011; Wessel et al., 2011). For instance, a study by Wessel et al. (2011) showed that larger ERN amplitude was related to an increased likelihood of error awareness, suggesting that larger ERNs connote higher certainty of error commission. However, Nieuwenhuis et al. (2001) used an antisaccade task to show that participants were faster to correct subjectively unaware errors and that these rapidly-corrected, implicit errors elicited similar ERN (but reduced Pe) amplitudes relative to aware errors. One interpretation of these findings is that when error certainty is high (reflected in larger ERN amplitude), there is less need for additional evidence accumulation processes (reflected in larger Pe amplitude).

Although a great deal of progress has been made in understanding the functional significance of the ERN/Pe, there has been very little research investigating the functional relationships between ERN/Pe and the corrective behaviors they are thought to support. One significant limitation of the extant literature is that the predominant use of discrete responses (e.g., button presses), which limits measurement of online error correction (Murphy et al., 2012). One way that this limitation has been addressed is by examining “partial errors” – trials on which participants appear to initiate an incorrect response but ultimately make a correct response. Partial errors have been measured using electromyography (EMG) and the lateralized readiness potential (LRP; Coles et al., 1995). Using these techniques, trials can be identified on which EMG or LRP measures indicate “activation” of the incorrect effector. On partial error trials, the ERN can be observed roughly 100 ms after onset of the EMG or LRP related to "activation" of the incorrect effector, despite the fact that a correct response is ultimately executed (Burle et al., 2008). Although ERN/Pe are typically observed following the commission of an error, observations of ERN following covert “partial errors” and overt corrected errors in the antisaccade tasks (Nieuwenhuis et al., 2001) supports the notion that the ERN reflects an alarm signal of error initiation as opposed to error commission. Although “partial errors” yield a potential signal of implicit error initiation, this approach does not provide a means by which to measure the dynamics of response correction. This limitation is less obvious in research using eye-tracking (e.g., saccadic eye movements); however, the short time between stimulus onset, response initiation, and saccadic corrections makes it difficult to examine the neural correlates of error correction without contamination of the ERPs elicited by neighboring events.

Given the very limited number of studies measuring dynamic error correction, there is relatively little known about the relationships between error detection and correction. There is evidence from neuroimaging research that the detection and correction of errors are associated with common neuroanatomical substrates in the ACC (Fiehler et al., 2004). In one study using ERPs, Fiehler et al. (2005) observed that corrected errors were associated with an ERN-like correction-related negativity (CoRN) that occurred at about 200-240 ms following an erroneous response that was incidentally corrected. However, because the CoRN was measured with respect to error commission, it is difficult to know whether and how this brain potential may be related to the execution of corrective action.

Motivated by the open questions identified in the previous paragraphs, the present study was designed to determine whether the ERN and Pe are related to the initiation and/or correction of overt erroneous responses in a task requiring dynamic, rather than discrete, responses. In the task, participants responded by moving a cursor from a starting location to a target location, an action that required several hundred milliseconds to complete. This protracted response permitted measurement of the initiation and completion of the action for correct and errant responses. This task also permitted us to distinguish $\text{Error}_{\text{Committed}}$ trials, wherein erroneous responses were initiated (cursor moves toward incorrect response) and completed, from $\text{Error}_{\text{Corrected}}$ trials wherein erroneous responses were initiated (indicated by cursor movement toward the incorrect response) but were corrected online (i.e., the response ended at the correct location). Because these dynamic responses were tracked during response execution, this procedure also permits a unique view of the neural correlates of error correction. The neural correlates of corrective action were measured by time-locking the recorded data to the point at which the trajectory of a response changed from the direction of an incorrect response toward the correct response.

The following predictions were examined in the analyses: (1) If the ERN reflects a general alarm system that is related to error detection, then it should be elicited following the *initiation* of an erroneous response and should be similar in amplitude following committed ($\text{Error}_{\text{Committed}}$) and corrected ($\text{Error}_{\text{Corrected}}$) responses. (2) If this general alarm (i.e., ERN) is related to error certainty, then the timing of response correction should be modulated by ERN amplitude, with its amplitude being largest for rapidly corrected errors (e.g., Wessel et al., 2011). (3) If the Pe reflects the accumulation of evidence that an error has been made, then this component should be larger on $\text{Error}_{\text{Corrected}}$ trials than $\text{Error}_{\text{Committed}}$ trials and be largest for slow error corrections wherein there is more time for the accumulation of evidence that an error has occurred (Steinhauser and Yeung, 2010, 2012). (4) If the Pe component reflects error awareness, then (to the extent that the correction of an overt response can be interpreted as awareness that an error has been made) the latency and/or amplitude of the Pe component should be related to the timing of the error correction. With the exception of the CoRN that is time-locked to error commission, this is the first study to our knowledge to investigate the neural correlates of online corrective action. To this end, we examined