

The Error-Related Negativity

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Abstract

We look back on the events surrounding the genesis of our 1993 article on the error-related negativity (ERN), a component of the event-related brain potential that accompanies errors in the performance of speeded-response tasks. Our reminiscences focus on the personal friendships, intellectual influences, and chance occurrences that shaped the article. To put our work in historical context, we consider subsequent trends in neuroimaging, computational modeling, and psychiatry that gave the ERN high visibility and contributed to the longevity of its scientific interest.

Keywords

cognition, neuroscience

We are delighted to bring our group together again to reminisce about our first article on the error-related negativity (Gehring, Goss, Coles, Meyer, & Donchin, 1993). The substance of the article was based on the first author's doctoral dissertation and the second author's first-year graduate project, which grew from a collaboration between the Cognitive Psychophysiology Laboratory (CPL) at the University of Illinois and David Meyer's lab at the University of Michigan. It pleases us that the article continues to influence psychological science, psychophysiology, cognitive neuroscience, and psychiatry. Indeed, this retrospective issue provides a welcome opportunity to put our work in historical context and to consider what has happened since then (for a review, see Gehring, Liu, Orr, & Carp, 2012).

Our article concerned properties of the error-related negativity (ERN, or Ne), a component of the event-related brain potential (ERP) that accompanies error responses during performance of choice reaction-time (RT) tasks. The ERN is a relatively large deflection in the ERP waveform that peaks within 100 ms of an erroneous response. As reported in our article, we found that the ERN was larger under task instructions that emphasize accuracy than under those that emphasize speed. The analysis of our data held the RT constant in comparing speed and accuracy conditions, eliminating a confound between slow responses in accuracy conditions and fast responses in the speed conditions.

Using a single-trial measure of ERN amplitude, we also showed that greater ERN activity was associated with corrective actions: a greater proportion of corrected errors, less forceful (inhibited) error responses, and slower responses on trials immediately following errors. In essence, observed properties of the ERN pointed to the existence of a brain system for detecting errors and engaging in corrective behavior, complementing Rabbitt's classic behavioral evidence that such processes exist (e.g., Rabbitt, 1966).

Antecedents of the Article

Our work on the ERN began with a serendipitous finding. In the mid-1980s, Mike Coles, Manny Donchin, and Gabriele Gratton at Illinois, as well as David Meyer at Michigan, were interested in how information is transmitted within the set of processes that happen between the perception of a stimulus and the execution of a motor response. The approaches taken by both labs were consistent with the long tradition of mental chronometry within psychological science and psychophysiology. The Illinois group focused on the Eriksen flanker

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task (Eriksen & Eriksen, 1974) and in particular on incongruent-stimulus trials, which induce conflict between the incorrect and correct responses. Their work revealed motor-cortex activity (reflected in the lateralized readiness potential, or LRP) that showed subjects covertly starting to make an error before overcoming this tendency to produce the overt, correct response. These findings suggested that response slowing and errors occur because of *partial-information transmission*—that is, preliminary, incorrect activation of the motor system before stimulus evaluation is complete (for review, see Coles, 1989). Concurrently, Meyer and his students (David Irwin, John Kounios, Allen Osman, and Steven Yantis) were investigating similar issues by using an advanced analytic-experimental technique known as *speed-accuracy decomposition* (reviewed in Meyer, Osman, Irwin, & Yantis, 1988).

Around the time of these studies, Bill Gehring joined the CPL, Coles and Meyer met at a National Institute of Mental Health (NIMH) study-section meeting, and Allen Osman became a CPL postdoc. Several fruitful collaborations and friendships emerged from this fortuitous combination. In 1987, Bill and Allen traveled to the International Conference on Cognitive Neuroscience (ICON) in the village of Dourdan, France, near Paris. There, they met David for a stroll around Montmartre and began to discuss their mutual interest in mental chronometry. A short time later, Bill and David designed a new experiment. Their experiment relied on a sentence-verification task, in which subjects respond “true” or “false” to such statements as “All robins are birds.” Previously, in his doctoral dissertation, David had found that subjects responded slowly when the subject and predicate were related but the sentence was false (e.g., “All birds are robins”; Meyer, 1970). Bill and David thought that the response slowing occurred because partial information activated the incorrect, “true” response, even when the overt response was “false” and therefore correct.

A combination of subsequent ideas led us to our observation of the ERN. We wanted to look for partial-information effects manifested by the LRP and the N400 (an ERP component reflecting semantic relatedness that peaks at around 400 ms after stimulus presentation). However, our analysis of stimulus-locked ERPs elicited in the sentence-verification task failed to show the anticipated effects on the LRP and N400. Two suggestions then led us to analyze response-locked ERPs, which emphasize brain activity temporally related to the response. David suggested that response locking the ERP waveforms would help to uncover LRP signatures of partial-information transmission. In addition, at around the same time, Marta Kutas visited the CPL and, over coffee with Bill, suggested that response

locking could show relationships between relatedness effects on the N400 and RT. Thus, the ERN emerged when we compared response-locked ERPs on correct and error trials.

Our first observation of the ERN remains, for Bill, a vivid visual memory (also recounted in Luck, 2014): One hot July day in 1989, as he was valiantly battling Fortran programs to analyze his ERP data, Bill finally managed to carry out the response-locking procedure suggested by Marta and David. In that era, CPL’s Harris computer (which occupied an entire room) had a CRT display that plotted the waveforms as bright green traces moving from left to right on a black background, much like an oscilloscope does. As the plots traced across the screen, an unexpected finding emerged when the error-response waveform suddenly grew into a large spike at about the time of the response. In fact, the ERN was so large that Bill worried about it being an artifact, either physiological or from his error-prone Fortran programming. So Bill spent most of the rest of his graduate training reanalyzing other data sets to confirm the presence of the ERN. During this time, Brian Goss joined the CPL and conducted a study to examine the effects of speed-accuracy manipulations on the LRP and ERN. That study became our 1993 *Psychological Science* article. The other analyses, including the first comparison suggested by Marta and David, appeared in a later book chapter (Gehring, Coles, Meyer, & Donchin, 1995).

Our initial ERN data were reported at the 1990 conference of the Society for Psychophysiological Research (Gehring, Coles, Meyer, & Donchin, 1990). Soon afterward, we received a very kind note from Michael Falkenstein, a researcher at the Institut für Arbeitsphysiologie an der Universität Dortmund (IfADo) in Germany, informing us that his group had already observed this error-related activity, naming it the “Ne,” and had presented the discovery at the Evoked Potentials International Conference in the Netherlands (May 23–June 3, 1989; see Falkenstein, Hohnsbein, & Hoormann, 1990; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1989). Our 1993 article cited their earlier work. Although we are sometimes credited as codiscoverers of the ERN/Ne, Michael Falkenstein most certainly observed and reported it first.

Why Our Article Has Been Highly Cited

If the history recounted thus far constituted our entire ERN story, we would probably not be writing this retrospective article.

However, further developments in cognitive neuroscience pushed the ERN into much wider visibility. Perhaps most important is the link that we hypothesized between the ERN and the anterior cingulate cortex

(ACC). Mike Gabriel, a colleague at Illinois, said that the ERN reminded him of error-related activity that Vernon Brooks had identified previously in the ACCs of monkeys (Gemba, Sasaki, & Brooks, 1986). We mentioned this link in our article, and shortly thereafter, Dehaene, Posner, and Tucker (1994) reported evidence supporting a plausible source of the ERN in the ACC.

A key complementary development was that the neuroimaging literature began to consider the ERN in trying to explain why the ACC is active in a wide variety of cognitive tasks. Jonathan Cohen and Cameron Carter's group hypothesized that the primary computational role of ACC activity is conflict detection (Carter et al., 1998), contrasting their theory with our proposal that the ERN reflects ACC activity involved in error detection. The conflict-monitoring hypothesis thus became a leading theory about both ACC function and the ERN. Furthermore, Matt Botvinick and Nick Yeung, from the Cohen-Carter group, developed computational models explaining the appearance and peculiarly fast timing of the ERN on error trials (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Yeung, Botvinick, & Cohen, 2004).

Another theory of ACC function and the ERN emerged concomitantly from the Illinois group, when one of its doctoral students, Clay Holroyd, saw similarities between the activity of the ERN and the role of dopamine in reinforcement learning. Clay's seminal work led to a large number of studies on the feedback-related negativity (FRN), an ERN-like deflection following perceptually salient external feedback about errors and losses of reward (Holroyd & Coles, 2002; Miltner, Braun, & Coles, 1997).

A final source of frequent citations is the burgeoning literature on the role of the ERN and ACC in psychopathology, particularly anxiety. For example, Luu, Collins, and Tucker (2000) showed evidence of a link between the ERN and negative affect. In addition, in another *Psychological Science* article, Gehring, Himle, and Nisenson (2000) showed that a group of individuals with obsessive-compulsive disorder (OCD) had exaggerated ERN activity compared with matched controls. Although by today's standards the sample size of the OCD study was small, the enhanced ERN in OCD has been replicated numerous times, and the laboratory of Bill Gehring and Greg Hanna is one of several further clarifying the link between the ERN and psychopathology (e.g., Hanna et al., 2016).

Likewise adding to its prominence, the ERN is listed in three domains of the Research Domain Criteria (RDoC) that form the basis of NIMH efforts to understand psychopathology. From this literature, new theories about functional significance of the ERN continue to emerge. One states that the ERN reflects perceptions of *endogenous sustained threat*—the degree to which

errors are seen as threatening (Weinberg et al., 2016). Another claims that the ERN in OCD manifests compensatory activity undertaken to deal with the cognitive demands of worrying (Moser, Moran, Schroder, Donnellan, & Yeung, 2013).

Many articles cite our original article because it appeared in a prominent journal—*Psychological Science*—and so became an obligatory reference for ERN research. Most investigators who cite our article also correctly cite the earlier reports by Falkenstein et al. (1990, 1991). Nevertheless, with this reflection on the attention our article has received, it is important that we emphasize the initial observation and pioneering research by Michael Falkenstein and his colleagues.

The Test of Time

Although these developments have been impressive (beyond all our expectations in 1993), support for some specific claims in our original article has been mixed. The most consistent finding is the effect of speed-accuracy instructions: When accuracy is stressed over speed, ERNs are typically larger than when speed is emphasized over accuracy. Increasing the motivational salience of errors in other ways also increases the ERN (Hajcak, Moser, Yeung, & Simons, 2005). We originally suggested that the effect reflected the importance of errors to the subject, which inspired our later research on OCD.

Less well supported are our initial findings that corrective behaviors were associated with greater ERN activity. Indeed, we uncovered some such contradictory evidence ourselves (Gehring & Fencsik, 2001; Scheffers, Coles, Bernstein, Gehring, & Donchin, 1996). To date, there is still no clear causal link between the ERN, corrective behaviors, and the performance adjustments that occur when errors are detected. Finding such a link will probably require investigating the ERN by focusing on behaviors more like those for which the brain evolved, such as reaching and grasping. As Gehring et al. (2012) pointed out, the brain did not evolve to press E-prime button boxes.

Apart from these latter findings, a few puzzles suggested by our original article remain almost 25 years later. First, after reading an early draft, Neal Cohen commented that the ERN in Figure 2 of our article appeared to be one within a series of peaks. Similar observations have led to a growing literature exploring the relationship between the ERN and oscillatory theta-frequency (4–8 Hz) activity (e.g., Cavanagh & Frank, 2014). Unfortunately, extant methods cannot conclusively determine whether the ERN is a single peak or part of an ongoing series of oscillations (Luck, 2014). Second, numerous studies have measured posterror slowing and have attempted to relate this to the ERN,

following from the idea that such slowing is a strategic attempt to avoid additional errors. Yet this slowing might instead reflect the persistence of problems that caused the error or the disruptive effects of the error, perhaps because the error captures attention (Gehring et al., 1993; Notebaert et al., 2009). A third puzzle, described in a footnote of our 1993 article, is the ERN-like activity that occurs on correct trials, which has come to be known as the correct response negativity (CRN). There is still no consensus about why the CRN occurs in some tasks and not others or about whether the CRN and ERN indeed reflect the same underlying neural process (see Coles, Scheffers, & Holroyd, 2001; Vidal, Burle, Bonnet, Grapperon, & Hasbroucq, 2003). Finally, a foundational puzzle regarding the ERN concerns how cognitive theories derived from computational models (such as conflict monitoring and reinforcement learning) can be reconciled with the robust literature on the ERN and anxiety.

At the root of all the mysteries is the ERN itself. New theories, new methods, and new questions continue to emerge, making the situation both exciting and complicated. Although a consensus view of the ERN is still elusive after 25 years, we often return to a pleasant thought: We might not know what psychological science (or science in general) will look like in a thousand years, but we do know that people will still have ERNs when they make mistakes. That's replicability!

Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

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