Errors can elicit an error positivity in the absence of an error negativity: Evidence for independent systems of human error monitoring

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ABSTRACT

Errors in human behavior elicit a cascade of brain activity related to performance monitoring and error detection. Whereas the early error-related negativity (Ne/ERN) has been assumed to reflect a fast mismatch or prediction error signal in the medial frontal cortex, the later error positivity (Pe) is viewed as a correlate of conscious error processing. A still open question is whether these components represent two independent systems of error monitoring that rely on different types of information to detect an error. Here, we investigated the prediction that the Ne/ERN but not the Pe requires a representation of the correct response to emerge. To this end, we created a condition in which no information about the correct response was available while error detection was still possible. We hypothesized that a Pe, but no Ne/ERN should be obtained in this case. Participants had to classify targets but ignore flankers that were always associated with an incorrect response. Targets but not flankers were masked with varying target-masking intervals. Crucially, on some trials no target at all was presented, thus preventing the representation of a correct response and the emergence of an Ne/ERN. However, because flankers were easily visible and responses to the flankers were always incorrect, detection of these flanker errors was still possible. In line with predictions of a multiple-systems account, we observed a robust Pe in the absence of an Ne/ERN for these errors. Moreover, this Pe relied on the same neural activity as that on trials with a visible target, as revealed by multivariate pattern analysis. These findings demonstrate that the mechanisms reflected by the two components use different types of information to detect errors, providing evidence for independent systems of human error monitoring.

Introduction

Error monitoring is crucial for achieving optimal goal-directed performance. Scalp EEG methods provide important evidence about the neural mechanisms underlying this ability. The error negativity (Ne; Falkenstein et al., 1990) or error-related negativity (ERN; Gehring et al., 1993) is a negative deflection over frontocentral electrodes, which peaks around 50 ms after an erroneous response, and is generated in the medial-frontal cortex (MFC; Ullsperger and von Cramon, 2001; Debener et al., 2005; Iannaccone et al., 2014). Whereas early theories suggested the Ne/ERN to reflect a mismatch between correct and actual responses (Scheffers and Coles, 2000), it has later been proposed to represent a post-response conflict (Yeung et al., 2004) or a prediction error (Holroyd and Coles, 2002). All these accounts have in common that the Ne/ERN is based on the detection of a discrepancy between the expected correct response and the actual response at an early stage of error processing. The Ne/ERN is followed by the error positivity (Pe), which is a parietal

positivity occurring at about 200–500 ms after an error (Falkenstein et al., 1991; Overbeek et al., 2005). In tasks in which participants had to signal whether their response was correct or incorrect, the Pe was larger (e.g. Nieuwenhuis et al., 2001; Endrass et al., 2007) or appeared only (Murphy et al., 2012) when participants were aware of their errors. Therefore, the Pe is believed to be a correlate of error awareness (Steinhauser and Yeung, 2010; Ullsperger et al., 2014) or confidence about response correctness (Boldt and Yeung, 2015) representing a later stage of error processing.

Despite extensive research on the functional significance of the Ne/ERN and Pe, fundamental questions on their relationship remain. In particular, there has been little research investigating whether both components are causally related. One possibility is that the earlier Ne/ERN provides the basis for the later emergence of the Pe and error awareness (Scheffers and Coles, 2000; Yeung et al., 2004; Ullsperger et al., 2014), which implies a stage-like architecture of error monitoring. The other possibility is that Pe and error awareness can emerge

independently of the Ne/ERN, which implies that different error detection mechanisms exist and may proceed independently of each other (Charles et al., 2013; Falkenstein et al., 2000; Maier et al., 2015). So far, little attempt has been made to directly test between these two accounts. Several studies investigated the relationship between Ne/ERN and error awareness (for a review, see Wessel, 2012), but these studies yielded mixed results. Some found that Ne/ERN amplitudes were positively correlated with error awareness (Scheffers and Coles, 2000; Wessel et al., 2011), while others reported no relationship (Endrass et al., 2007; Hughes and Yeung, 2011; Nieuwenhuis et al., 2001) or even a negative correlation (Di Gregorio et al., 2016; Maier et al., 2008). These inconclusive results might reflect that correlations between Ne/ERN and Pe can be moderated or even mediated by third variables which affect both components, such as stimulus perceptibility, attention or response conflict (for a discussion, see Di Gregorio et al., 2016).

The goal of the present study was to directly test the idea that Ne/ERN and Pe reflect independent mechanisms of error monitoring by asking whether the two mechanisms rely on different types of information to detect an error. More specifically, we hypothesized that only the mechanism underlying the Ne/ERN but not the mechanism related to the Pe requires a representation of the correct response to detect an error. This prediction can be derived from current theoretical accounts of both components. The Ne/ERN is assumed to result from the detection of a mismatch or post-response conflict between correct and actual response (Scheffers and Coles, 2000; Yeung et al., 2004) and thus necessarily requires a representation of the correct response. In contrast, error detection reflected by the Pe might be based on an evidence accumulation process (Steinhauser and Yeung, 2010; Ullsperger et al., 2010) which receives input from various sources, such as cognitive, autonomous, and sensory processing (Wessel et al., 2012; Wessel et al., 2011), and hence, does not necessarily require a representation of the correct response. Our approach was to construct a paradigm in which error detection was possible even if information about the correct response was fully omitted. In such a condition, we would expect that a Pe is still observed (because the error is detectable) while an Ne/ERN is absent (because no representation of the correct response is available). While such a pattern would demonstrate that the mechanisms underlying the Ne/ERN and Pe operate on different types of information, it would also provide direct evidence for the independence of the Ne/ERN and Pe. If the two components were causally related, no Pe should be observable in a condition in which no Ne/ERN was generated.

In the present experiment, participants performed a flanker task (Eriksen and Eriksen, 1974), in which they had to respond to the central target while ignoring the lateral flankers. The target but not the flankers was masked with varying stimulus-masking intervals. Crucially, on some trials, a zero interval was used and no target appeared at all. Because the Ne/ERN is assumed to require a representation of the correct response, we predicted the Ne/ERN to be absent on these trials. However, because we used a three-choice task and flankers were always associated with a different response than the target, participants knew that responses associated with the unmasked flankers must have been errors, thus making the detection of these errors easily possible. This allowed us to directly study whether a Pe can emerge in the absence of an Ne/ERN, and thus, whether Ne/ERN and Pe are based on dissociable and independent processes.

Materials and methods

Participants

Twenty-four right-handed participants (20 female) between 19 and 32 years of age (mean 20.8) with normal or corrected-to-normal vision participated in the study. One participant was excluded from the analysis because less than three errors were available in one condition after artifact rejection. Three participants were excluded during application of the artifact correction algorithm (see below). Participants were recruited at the Catholic University of Eichstätt-Ingolstadt and received course credit or 8 Euro per hour. The study was approved by the ethical committee of the Catholic University of Eichstätt-Ingolstadt, and informed consent was obtained from all participants.

Task and stimuli

A PC running Presentation software (Neurobehavioral Systems, Albany, CA) controlled stimulus presentation and response registration. Stimuli were presented on a 21-inch color monitor at a viewing distance of 70 cm. Stimuli were strings of seven white letters in Arial font. The central letter in each string was designated as the target and the remaining letters were designated as the flankers. Possible target letters were P, W, M, V, X, or K. Participants were asked to execute a response by pressing the 'S', 'D' or 'F' keys of a standard computer keyboard with the left ring finger, the left middle finger, or the left index finger. Two target letters were assigned to each response and this target-response mapping was counterbalanced across participants. For each target, the flankers were six identical copies of a letter associated with a different response than the target. This resulted in 24 possible incongruent target-flanker combinations as each target could be combined with four flanker letters. Each letter comprised a height of 5 mm and a width of 3 mm. Six different feature masks of the same size as a letter were created by randomly rearranging features of the original letter stimuli.

Participants were instructed to respond to the target and to ignore the flankers (Eriksen and Eriksen, 1974). Each trial (Fig. 1) started with the presentation of a fixation cross for 350 ms, then the stimulus was presented. After a variable stimulus-masking interval (SMI), a randomly drawn mask was presented at the position of the target. SMIs of 240 ms, 128 ms, and 0 ms were used. Whereas the target stimulus was replaced by a mask in the 240-SMI and 128-SMI conditions, no target at all was presented in the 0-SMI condition. The flankers and the mask remained on the screen until a response was given. Then, a black screen appeared for 1200 ms followed by the start of the next trial. No trial-wise feedback about the correctness or latency of the response was provided.

In each block, each possible stimulus was presented with 240-SMI, 128-SMI and 0-SMI resulting in a block length of 72 trials. These trials were presented in random order. The experiment was carried out over a two-day period. On the first day (practice session), participants had to perform eight blocks to learn the stimulus-response mapping. Prior to the beginning of each block, participants were instructed to respond more quickly whenever the average error rate in the previous block was below 15%. This speed instruction was maintained throughout the whole experiment to obtain a sufficient number of error trials for the analyses. Furthermore, participants were instructed to guess if they felt it was not possible to recognize the target (but they were not told that no target at all was presented on some trials). Additionally, they were instructed that a response to the flankers would have been always an error. On the second day (test session), two practice blocks of 48 randomly drawn trials were initially administered followed by twelve blocks of 72 trials. The EEG was recorded only on the second day, and only the data from the twelve test blocks on the second day were analyzed. The test session lasted for approximately 1 h, and participants could take short breaks between successive blocks.

Data acquisition

The electroencephalogram (EEG) was recorded during the test sessions using a BIOSEMI Active-Two system (BioSemi, Amsterdam, The Netherlands) with 64 Ag-AgCl electrodes from channels Fp1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2 as well as the left and right mastoid. The CMS (Common Mode Sense) and DRL (Driven Right Leg) electrodes were used as reference and ground electrodes.