Error-Related Scalp Potentials Elicited by Hand and Foot Movements: Evidence for an Output-Independent Error-Processing System in Humans

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Abstract

The Error-related Negativity (ERN) is a fronto-centrally distributed component of the event-related brain potential (ERP) that occurs when human subjects make errors in a variety of experimental tasks. In the present study, we recorded ERPs from 128 scalp electrodes while subjects performed a choice reaction time task using either their hands or feet. We applied the Brain Electric Source Analysis technique to compare ERNs elicited by hand and foot errors. The scalp distributions of these error potentials suggest that they share the same neural generator and, therefore, that the ERN process is outputindependent. Together with other findings, the results are consistent with the hypothesis that the ERN is generated within the anterior cingulate cortex and is elicited by the activation of a generic error-processing system.

Keywords: Error-related Negativity, error processing, source localization, anterior cingulate, executive control

Human beings enjoy the capacity to make and follow plans, as well as to monitor and correct their behavior for errors in execution. According to cognitive theories of executive control, such abilities comprise a specific cognitive system dedicated to the orchestration of complex behaviors [9], a position which is supported by neuropsychological evidence (e.g. [13]). Although relatively few neurophysiological studies have investigated the neural substrate of executive control, a newly discovered component of the eventrelated brain potential (ERP) has provided evidence for the existence of a neural system that implements error-processing [5,6]. This "Error-related Negativity" (ERN) is sensitive to the accuracy of motor events, both as human subjects make errors in speeded reaction time (RT) tasks, where the ERN peaks about 100 ms following error response onset [6], as well as in response to feedback informing the subject that a previous response was incorrect [10]. We have argued that this fronto-centrally distributed component is a manifestation of a control system engaged either in error detection itself, or in the utilization of error information for long term motor adjustments (see [1] for review). Previous electroencephalographic [2,10] and magnetoencephalographic [11] dipole source localization studies have indicated that the ERN is generated frontally, perhaps within the anterior cingulate cortex.

The present study applies the Brain Electric Source Analysis (BESA) technique [12] to ERNs associated with errors committed with the hands and with the feet, and compares the locations of the fitted dipoles across output modality. The aims of the study are two-fold: first, to the extent that the ERNs elicited by hand and foot errors are describable by dipoles located in the same region, one can infer that the neural system that generates the ERN does so independently of output modality. Previous findings have demonstrated that the locus of the source of the ERN is insensitive to input modality (auditory, somatosensory, and visual in a feedback task [10]), and to specific task characteristics [1]. In this context, an insensitivity of the ERN to output modality would support the contention that the computation underlying ERN generation is part of a generic error processing system that is indifferent to the specific nature of the error. Second, the resulting dipole locations can help to elucidate the nature of a prefrontal contribution to response monitoring indicated by neuropsychological evidence [7], as well as suggest further avenues for exploration.

Six male and nine female undergraduate students, ages 18 to 23, with normal or corrected-to-normal vision, served as subjects and were paid for their participation. The experiment consisted of two sessions, one for practice and

one for recording, during which subjects sat on the floor in a dark, shielded room. Each session contained two conditions, one in which subjects responded with their hands and the other in which they responded with their feet, with order of presentation of the two conditions counterbalanced across subjects. During the hand condition, subjects responded by squeezing two zerodisplacement dynamometers. For the foot condition, subjects sat with their backs to the wall with their legs outstretched; they were instructed to keep their legs straight, to minimize upper body movement, and to respond by pressing their feet against the dynamometers using simple ankle rotations. Analog output from the dynamometers was sampled at 250 Hz and collected continuously with the INSTEP data collection system. The electroencephalogram (EEG) was recorded with a 128 channel Geodesic Sensor Net applied to each subject. Stimulus presentation and EEG data acquisition were driven by a Macintosh computer running the Electrophysiological Graphical Interface System (EGIS). Stimuli (50 ms duration) were delivered with a 1420 ms ISI to a CRT placed on a low table 45-55 cm in front of the subject. The EEG was sampled during each trial at 250 Hz for 1024 ms beginning 200 ms before stimulus presentation. A closed circuit TV allowed for the monitoring of subjects for movement artifact.

Subjects performed the Eriksen Flankers task [4], chosen because of its demonstrated success at eliciting ERNs (e.g., [6]). For this task, subjects were presented with four stimulus arrays ("HHHHH", "HHSHH", "SSHSS", "SSSSS") in random order with equal probabilities. The subjects were directed to focus their attention on the central letter of each array and to respond with the limb on one side if the letter was an "H" and with the contralateral limb if the letter was an "S"; stimulus/response-side mappings were counterbalanced across subjects, but maintained within subjects across output modalities. To achieve an error rate of 10-20%, verbal feedback was provided to each subject after each block of trials indicating whether he or she should respond faster or slower. During the practice session, each condition consisted of 2-4 blocks of 100 trials each, whereas during the recording session, each condition consisted of a 100 trial practice block followed by 4 blocks of 300 trials each. A response was defined as dynamometer output in excess of 25% of a subject's maximum force output, determined for each subject prior to each condition.

For data analysis, a computer program calculated response onset from the dynamometer data for each of the two limbs by searching within a 120 to 824 ms window following stimulus onset for the data point corresponding to the maximum force; if this value did not exceed a criterion of 12.5% maximum

force, the trial was discarded. For those trials that were retained, the algorithm then searched backward from this point for the point at which the trace crossed the 12.5% threshold; if the sample was not contained within a 120 to 600 ms window following stimulus onset, the trial was discarded. Otherwise, the algorithm continued searching in the same direction for the point at which the force signal deviated from the baseline. The point of deviation was defined as the sample where the value of ratio of the slopes of the four points preceding and following the sample achieved a maximum, excluding those samples in which the leading slope had a value of less than 1. This point defined response onset. Response accuracy was determined by comparing the side of response to the identity of the target stimulus. If two responses occurred, accuracy was defined in terms of the response that had the earlier onset.

The data from three of the 15 subjects were discarded due to excessive noise in the EEG, leaving the data from the remaining 12 for analysis. Ocular artifact was removed from the EEG data with the algorithm described by Gratton et al. [8]. For every subject, the data for each trial from the pool of incorrect responses were randomly matched by RT (+/- 4 ms) with the data for a corresponding trial from the pool of correct responses before averaging by condition; this procedure ensures against a differential contribution of stimulus-related activity to the ERP, as errors are typically faster than correct responses. The matching procedure yielded for analysis 96% of the total number of errors and 12% of the total number of correct responses, with an average 118.5 trials per subject per response modality per response type (correct vs. incorrect). The waveforms were baseline-corrected by subtracting the average signal activity across the 200 ms prior to stimulus presentation, and response synchronized averages were derived for each subject, response modality, and response type. Difference waveforms were obtained by subtracting average waveforms for correct trials from the corresponding averages for incorrect trials. Grand averages were obtained by averaging the difference waveforms across subjects for each response modality separately. For waveform display the maps were mathematically referred to linked mastoids.

The BESA procedure [12] was applied to the difference waveforms for both the hand and foot grand-averages. Data were filtered from below 2 Hz and above 10 Hz. The difference waveforms were fitted at the instant of maximal ERN activity using single and multiple dipole solutions. The appropriateness of these solutions was tested with the techniques outlined by Scherg and Berg [12]. These include, for example, ensuring the consistency of the results by reiterating the procedure with randomly seeded initial dipole configurations; by comparing the solution with plausible alternatives (e.g., bilaterally symmetric dipoles); and by probing the stability of the solution by including additional dipoles. These tests suggested that a single dipole solution was appropriate [cf. 2].

When subjects made incorrect responses while engaged in the Eriksen Flankers Task, a negative deflection is evident in the ERP regardless of whether the errors were committed with the hands or with the feet (Fig. 1). The scalp distribution, latency, and polarity of this deflection are all consistent with its identification as an ERN [e.g. 5, 6]. Equivalent dipole solutions for both the hand- and foot- generated difference waveforms converge to nearly the same location (Fig. 2a,b and Table 1), indicating that the two distributions share a very similar scalp topography. This observation was confirmed by application of a spatial principal components analysis [3] to the data set (ten factors extracted, accounting for 98.2 percent of the total variance). For each factor, the factor scores were averaged across subjects and plotted by time. For only one factor did the factor scores show the same time course as the ERNs and, for this factor, the scores for hands and feet were of equivalent amplitude. Furthermore, for this factor, the factor loadings associated with each electrode position corresponded to the distribution of the ERN. For all these reasons, we

infer that the computation underlying ERN generation appears to be indifferent to the output modality with which errors are committed. Moreover, the locations of the ERN-dipoles coincide with those found in previous studies, both for those associated with negative feedback presented in any of three input modalities (auditory, visual, somatosensory) [10], as well for those associated with errors in reaction time tasks [2] (Fig. 2c). Taken together, these results suggest that the ERN is elicited by a generic error processing system, one which can be made sensitive to different sources of error information.

Although dipole studies alone cannot resolve questions of source localization (because of the "inverse problem"; see references in [12]), these results provide evidence against the possibility that activity in hand and foot areas in primary motor cortex contributes to the ERN. Rather the results are consistent with the hypothesis that the ERN is generated by activity in anterior cingulate cortex [2, 10], perhaps as a consequence of the modulatory effects of the mesencephalic dopaminergic system.

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[13] Stuss, D.T. and Benson, D.F., The Frontal Lobes, Raven Press, New York, 1986, pp. 303. Figure 1. Event-related potentials for correct and incorrect hand- and footgenerated responses. The potentials are averaged with respect to motor onset indicated by the vertical arrow (0 ms). The potentials were recorded at channel 7 of the EGI electrode net, just rostral and left of channel Cz in the 10-20 system.

Figure 2. Source localization of the error-related negativity. Circles represent locations of sources determined for hand and foot responses: (a) coronal view; (b) sagittal view; (c) for comparison, source locations of the ERN determined in previous studies are depicted along with the locations of the ERN obtained in the present study. Squares represent locations of sources found for ERNs elicited by visual, auditory, and somatosensory feedback [10]. Crossed symbols represent locations of sources found for ERNs elicited by errors in two reaction time experiments [2].

Table 1.

	X	Y	Z	THhor	PHhor	RV
Hands	-0.081	0.278	0.319	1.85	-5.66	7.14 %
Feet	0.003	0.216	0.427	10.12	54.13	10.7 %

"X","Y","Z": dipole co-ordinates, expressed in percent radius (8.5 cm);

"THhor", "PHhor": dipole orientations (see [12]). "RV": Residual Variance.







