Source localization of error negativity: additional source for corrected errors

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Error processing in corrected and uncorrected errors was studied while participants responded to a target surrounded by flankers. Error-related negativity (ERN/NE) was stronger and appeared earlier in corrected errors than in uncorrected errors. ERN neural sources for each error type were analyzed using low-resolution electromagnetic tomography method of source localization. For corrected errors, the ERN source was located at the anterior cingulate (BA 24) and the medial and superior frontal regions (presupplementary motor area, BA 6), whereas it was located at the anterior cingulate (BA 24) for uncorrected errors. It is suggested that the anterior cingulate is the main source of the ERN with the presupplementary motor area contributing to ERN initiation only if the correct response tendency is sufficiently active to allow for full execution of a correction response. *NeuroReport* 20:1144–1148 © 2009 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

Immediately after the production of an incorrect response, a negative event-related potential (ERP) is observed [1,2]. This error-related negativity (ERN/NE), peaks about 80 ms after the erroneous response, and has a frontocentral scalp distribution [3,4]. Attempts to localize the source of this response have revealed somewhat different solutions; most studies suggest the anterior cingulate cortex to be the main generator of the ERN [4–8]. However, some results from modeling techniques such as brain electrical source analysis (BESA) and low-resolution electromagnetic tomography method (LORETA) suggest the supplementary motor area and the presupplementary motor area as possible additional or sole generators of the ERN/NE, see Refs [4,9,10]. In addition, intracranial ERP recordings suggest that sources at the medial frontal cortex, other than the anterior cingulate, may contribute to ERN/NE generation including the presupplementary motor area [11]. In a study that used transcranial magnetic stimulation (TMS), it was found that medial frontal stimulation of the presupplementary motor area led to an attenuation of the ERN/NE [12].

Erroneous responses in speeded reaction time (RT) tasks are usually faster than correct responses [13,14]. According to the response conflict model of the ERN, these premature errors occur because a response is executed before the stimulus is fully processed. Nevertheless, continuous processing of the stimulus after the response may lead to the concurrent activation of the correct response tendency, which gives rise to the ERN. If the correct response tendency is sufficiently active, it will lead to a correction response [15]. Although the anterior cingulate is considered to be related to conflict detection [16], it was recently suggested that the presupplementary motor area has a role in conflict resolution through the exertion of inhibitory mechanisms [17].

As mentioned above, most ERN studies suggest the anterior cingulate as the main generator of the ERN. Nevertheless, in the majority of ERN studies, responses are made bimanually with each response option represented by the contralateral finger. Under these conditions, once the correct response tendency is sufficiently active to result in its execution, a correction response can be made almost independently of the contralateral incorrect response. In this case, the exertion of inhibitory mechanisms by the presupplementary motor area may not play a significant role in the activation of conflict resolution mechanisms, regardless of whether the error is corrected or not. In contrast, when the same finger is used to produce both responses (for example, the use of a joystick involves moving the thumb of one hand from one key to another), the execution of the correction response requires a complete stop of the incorrect response. This may call for strong activation of the presupplementary motor area once the correct response tendency exceeds

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the execution threshold, but not if the correct response tendency fails to reach the execution threshold. In this latter case, source localization of the ERN for 'uncorrected' errors should reveal local maxima only at the anterior cingulate, signifying the activation of postresponse conflict mechanisms, whereas in the former case, source localization of the ERN for 'corrected' errors should reveal local maxima at both the anterior cingulate and the presupplementary motor area signifying the activation of both postresponse conflict and conflict resolution/inhibition mechanisms.

An argument against this hypothesis can be based on the imaging study by Fiehler *et al.* [18], who showed that both the anterior cingulate and the presupplementary motor area are active on erroneous trials, irrespective of whether the error was corrected or not. However, because of the poor temporal resolution of the functional MRI, the relationship between the time point of this activation and the time point of the ERN cannot be determined.

The source localization analysis in this study was made using the LORETA [19]. Participants performed a two-choice flanker task using the thumb of their right hand.

Methods

Participants

ERP data were gathered from 12 right-handed undergraduate students (seven males, mean age 23.3 ± 2.1 years) of University of Haifa. All were healthy young adults, in good standing in their studies with no known medical conditions involving the central nervous system.

Materials and methods

The task that was used to assess error monitoring is based on the original flanker task [20] that is often used in the error detection literature. The stimuli were black equilateral triangles, each side measuring 0.75° of visual angle. Two types of triangles were used: 'down' pointing triangles had a flat edge on top, with a point at the bottom. 'Up' triangles were flipped so that the pointed end faced upwards. Triangles were presented on a gray background. Each trial began with a fixation cross presented alone for 100 ms. Immediately afterwards, two distractor triangles appeared, one 1.5° above and the other 1.5° below the center of fixation. The distractors remained alone for 100 ms and then, the target triangle appeared between these two at fixation location, for 50 ms. All three triangles disappeared at the same time. The next trial began 1000 ms after the first response to the target. Second responses (corrections) could be made until the beginning of the next trial. Half of the targets were pointing up and half were pointing down. The flanking stimuli were compatible, pointing in the same direction as the target, or incompatible, pointing in the opposite direction. The two flanking stimuli always pointed in the same direction as each other. Half of the trials were compatible and half incompatible. Participants were instructed to respond to the central triangle. The experimental session consisted of 1200 trials.

General procedure

The participants were seated with their head leaning against a back rest that held their eyes 57 cm from the screen. Before each task, the participants performed a practice set of 80 trials, during which feedback was given about the correctness of the response (happy or sad face at the fixation). No feedback was given during the experimental trials. The participants were asked to respond as quickly and as accurately as possible, using the thumb of the right hand. Instructions were to hold the thumb up between responses. Responses were made using a joystick. Participants were encouraged to spontaneously correct themselves if they thought they had made an error.

To keep the subjective significance of avoiding errors as high as possible despite the option to compensate for errors (by the production of a correction response), a bonus system was administered giving full credit for correct responses and half a credit for each successful correction response. No credit was given for false corrections (a correct response is replaced by incorrect response).

Psychophysiological recording

We recorded the electroencephalogram (EEG) from 32 scalp locations using tin electrodes (standard 10–20 system) referenced to the chin. The impedance of all electrodes did not exceed 5 kΩ. The vertical eye movements were recorded from electrodes placed below the left eye. EEG and electrooculogram data were accumulated using a low-pass filter of 70 Hz and analog-to-digital converted with 22-bit resolution. Sampling rate was 256 Hz. Eye movement correction procedure for each EEG trial was based on a linear regression method [21]. Response-locked ERPs were computed from artifact-free trials for each participant according to the different types of responses: incorrect-uncorrected responses, and incorrect-corrected responses, starting 100 ms before the response and continuing 600 ms postresponse. The baseline used for response-locked averages was from −100 to 0 ms. ERN/NE amplitude was defined as the largest negative pick in the −50 to 100 ms interval after the onset of response. ERN/NE latency was defined as the time interval between the onset of response and maximal amplitude. ERN was measured at Cz.

Source localization

The LORETA was used to determine the brain electrical sources of the ERN after the execution of corrected and uncorrected errors at the time point of the individual peak over Cz.

Statistical analysis

Differences for correct, corrected, and uncorrected responses in the LORETA analysis were analyzed according to the statistical nonparametric mapping method offered by Holmes *et al.* [22]. Only incongruent trials were analyzed because the congruent trials did not yield enough erroneous trials to allow for statistical analysis. Localization differences between conditions were computed by using voxel-by-voxel *t*-tests for dependent measures of the average LORETA images over the time frame, based on the subject-wise normalized and the log-transformed power of the estimated electric current density. The LORETA analysis is based on a bootstrap method with 5000 randomized samples (LORETA-key-01 Free BrainWare) [23]. The use of this method enables calculating the exact significance thresholds regardless of non-normality, and is corrected for multiple comparisons. The Talairach coordinates of local maxima for the statistical comparisons of corrected and uncorrected errors are listed in Table 1. Note that these localizations do not represent the complete listing of all significantly different cortical areas, but a listing of the local maxima of these differences.

Results

Reaction time and accuracy analysis

The distribution of response types was as follows: correct responses, frequency = 82%, SD = 4.47, RT = 523 ms, SD = 53.5; uncorrected errors, frequency = 7.8%, SD = 3.67, RT = 512 ms, SD = 62.8; corrected errors, frequency = 9.5%, SD = 4.32, RT = 431 ms, SD = 52.7. Errors were shorter than correct responses [$F(1,11) = 11.2$, $P < 0.001$].

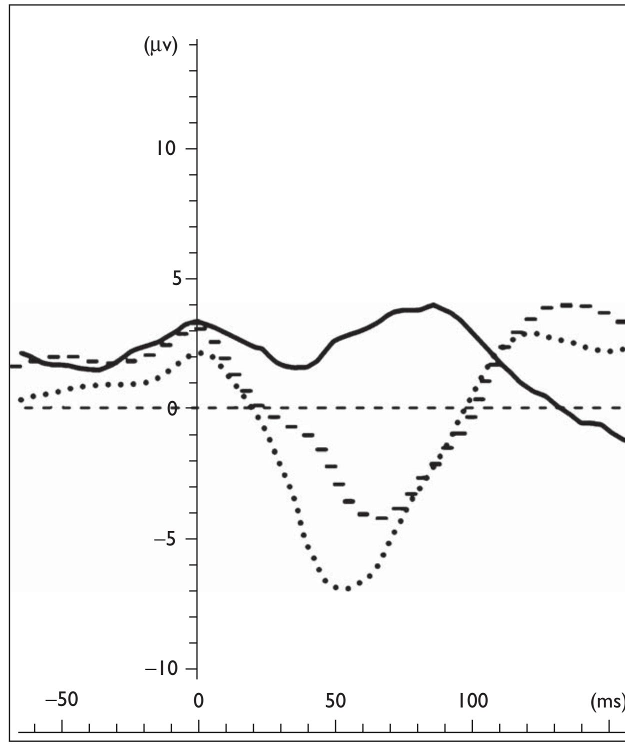
Event-related potential data

A clear ERN was observed in the response-locked averages for both corrected and uncorrected errors in all tasks (Fig. 1). Both corrected and uncorrected errors showed an increased negativity compared with correct responses [corrected errors, $F(1,11) = 9.81$, $P < 0.001$; uncorrected errors, $F(1,11) = 18.2$, $P < 0.001$]. A comparison between response types revealed significantly stronger ERN amplitude and shorter ERN latency for corrected errors than for uncorrected errors [amplitude, $F(1,11) = 6.03$, $P < 0.05$; latency, $F(1,11) = 37.3$, $P < 0.05$]. These findings accord with previous studies showing the same ERN differences between corrected and uncorrected errors (in amplitude: [2,24,25]; in latency: [24]).

Source localization

The localization of the ERN after corrected errors was compared with the localization of the ERN after uncorrected errors. Each of the error types was compared against correct responses. The results revealed differences between the anatomical origins of the two error types (Table 1). ERN source for corrected errors was mainly located in the anterior cingulate (BA 24) and the medial and superior frontal regions (BA 6), whereas it was located in the anterior cingulate (BA 24) for uncorrected errors, only. A graphical representation of the LORETA *t*-statistics is depicted in Fig. 2.

Fig. 1



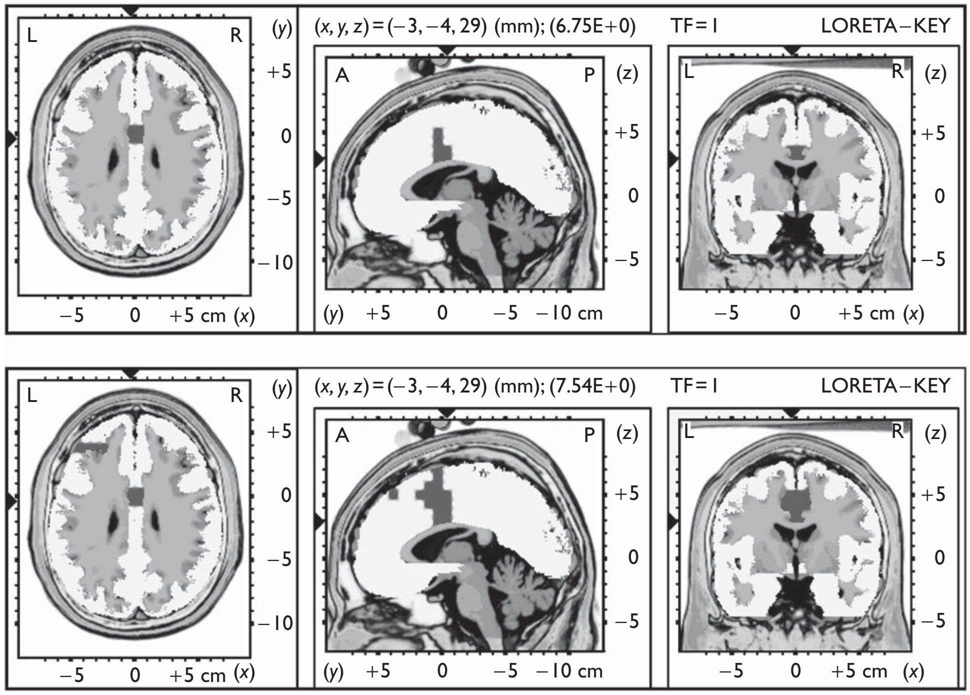
Grand average of response-locked event-related potentials (Cz) for corrected errors (dotted line), uncorrected errors (dashed line), correct responses (solid line).

Table 1 Areas of statistical stronger activation for uncorrected and corrected errors, as compared with correct responses at the time point of the ERN

	BA	*x*	*y*	*z*	*t*-value
Uncorrected					
CG	24	−3	−4	29	6.75
CG	24	−3	0	33	6.75
CG	24	0	−4	33	6.75
CG	24	3	2	29	6.75
CG	24	2	−3	29	6.75
Corrected					
CG	24	−3	−4	29	7.54
CG	24	−3	0	39	7.54
CG	24	5	−4	45	7.54
CG	24	2	−4	43	6.97
SFG	6	−3	7	54	6.97
MFG	6	−3	8	51	6.97
MFG	6	6	10	49	6.97

x, y, z coordinates in Talairach space in mm; *x* corresponds to the left-right and *y* to the anterior-posterior dimension; *z* corresponds to the cranial-caudal.
BA, Brodmann area; CG, cingulate gyrus; ERN, error-related negativity; MFG, medial frontal gyrus; SFG, superior frontal gyrus; *t*-value, value of the statistical comparison with $P < 0.05$.

Fig. 2



Graphical representation of the low-resolution electromagnetic tomography method (LORETA) *t*-statistics comparing the event-related potentials for uncorrected (upper panel) and corrected (lower panel) errors against correct responses at the time point of the individual peak over Cz for the error-related negativity. Colored regions indicate local maxima of increased electrical activity in axial, sagital, and coronar slice through the reference brain. This image shows significant results only.

Discussion

The goal of this study was to localize the ERN for corrected and uncorrected errors using an electrophysiological source localization method (LORETA). We predicted that both error types would share local maxima at conflict monitoring related to brain areas, with only corrected errors showing local maxima at brain areas related to postconflict inhibition. The experimental question was addressed by calculating the three-dimensional localization of the electrical sources contributing to the electrical scalp field for each participant and condition at the time point of the individual peak of the ERN over Cz. The results confirmed our hypothesis as different local maxima were found for each error type. In corrected errors, local maxima were found at the anterior cingulate (BA 24), the medial frontal cortex (BA 6), and the superior frontal cortex (BA 6). In uncorrected errors, a local maxima was found only at the anterior cingulate (BA 24).

All of the areas found active after erroneous behavior in this study have been suggested as potential generators of the ERN in earlier studies. The anterior cingulate is considered by many studies to be the main source of the ERN [4–6]. BA 6, which includes the premotor/supplemental motor area, was suggested as an additional source by some [4,10], or as a main source by others [9].

The results of this study suggest that both the anterior cingulate and the presupplementary motor area are involved in ERN generation. The fact that the anterior cingulate was found active in both corrected and uncorrected errors suggests the anterior cingulate as the main source of the ERN, with the presupplementary motor area contributing to ERN initiation only when the correct response tendency exceeds its execution threshold. It is possible that the role of the presupplementary motor area is inhibiting the incorrect response tendency to allow for swift execution of the correction response.

Conclusion

The results of this study suggest that the anterior cingulate is the main source of the ERN. It is also suggested that the presupplementary motor area contributes to the generation of the ERN when the correct response tendency is sufficiently active to allow for error correction.

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