Technical Commentary

LOCALIZATION OF A NEURAL SYSTEM FOR ERROR DETECTION AND COMPENSATION

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Gehring, Goss, Coles, Meyer, and Donchin (1993) have reported electrophysiological evidence for a brain mechanism dedicated to monitoring performance and compensating for errors (see also Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990). They have described a component of the human event-related potential, called the error-related negativity (ERN), which is characterized by a negative peak about 100 ms following the onset of electromyographic (EMG) activity when the subject is in error on that trial. The amplitude of the ERN is larger when the subject strives for response accuracy than when the subject concentrates on speed. It is also correlated with several error-compensation variables. The larger the ERN, the smaller the force with which the erroneous key is pressed, the higher the probability of correcting the error by immediately depressing the other key, and the slower the reaction time on the next trial. These correlations suggest that the neural system whose activity is reflected by the ERN is involved in the active inhibition and correction of an error as soon as it is detected.

Gehring et al. (1993) noted that the data from their study did not allow for the localization of this neural system in the brain. They recorded from five electrode sites and observed only that the ERN was largest over the front and middle of the scalp. They did, however, offer some speculation, based on animal evidence, pointing toward "a system involving the anterior cingulate cortex and supplementary motor areas" (p. 389). Our own data allow for a direct confirmation of this localization in humans.

We recorded high-density event-related potentials using a 64-channel geodesic electrode net (Tucker, 1993), with an interelectrode spacing of about 4 cm. This methodology enabled us to fully characterize the scalp topography of the ERN in two different experiments. In the first experiment (Dehaene, 1994), 12 subjects were presented on each trial with a single Arabic or spelled-out numeral. They had to press one key with one hand if the target was larger than 5 and another key with the other hand if it was smaller than 5. In the second experiment (Dehaene, unpublished data), 12 other subjects were presented with lists of words, which they had to classify as belonging or not to a target semantic category (e.g., animals) using bimanual response keys. In both experiments, subjects gave their informed consent. Event-related potentials were digitized at 250 Hz over a 1-s epoch, initially referenced to the right mastoid and ultimately transformed into reference-free estimates using the average-reference transform. Trials with artifacts were automatically rejected by computer before stimulus-locked or response-locked averaging.

In both experiments, a sharp ERN was observed following erroneous responses, but not following correct responses. The ERN was sharper on response-locked averages than on stimulus-locked averages, suggesting that it occurred at a relatively constant delay following an incorrect response. The latency between an incorrect key press and the peak of the ERN was 64 ms in Experiment 1 and 72 ms in Experiment 2. However, the first significant difference between correct and incorrect trials occurred earlier, around the time of the key press. We concur with Gehring et al. (1993) in concluding that the ERN onset is too short for sensory or proprioceptive feedback and must reflect an internal monitoring of behavior.

The topography of the grand-averaged ERN recorded in our second experiment appears in Figure 1. The negativity was extremely focal to the medial prefrontal region, and was accompanied by a broad and widespread positivity. The peak of the negativity was concentrated to only one electrode site (FzS) located on the midline, halfway between Cz and the nasion. Analysis of this topography with the spherical spline Laplacian measure of scalp current density (Perrin, Pernier, Bertrand, & Echallier, 1989) showed a focal negativity at the same medial prefrontal site. A source/sink gradient also appeared over the left frontal pole in voltage maps (Fig. 1) and current density maps from the second experiment. However, this effect was small, was found at only one electrode site, and was not replicated in the first experiment. Thus, the bulk of the error effect was concentrated on the midline of the prefrontal region.

We used a forward-search dipole localization algorithm, Brain Electric Source Analysis (BESA; Scherg & Berg, 1990), to model the neural generators that could have generated this electrical field. First, we attempted to model the voltage surface observed during error trials only. A single-dipole solution was sufficient to account for 89.7% of the variance in Experiment 1. The equivalent dipole was located by the BESA program along the midline of the brain, within the anterior cingulate cortex,

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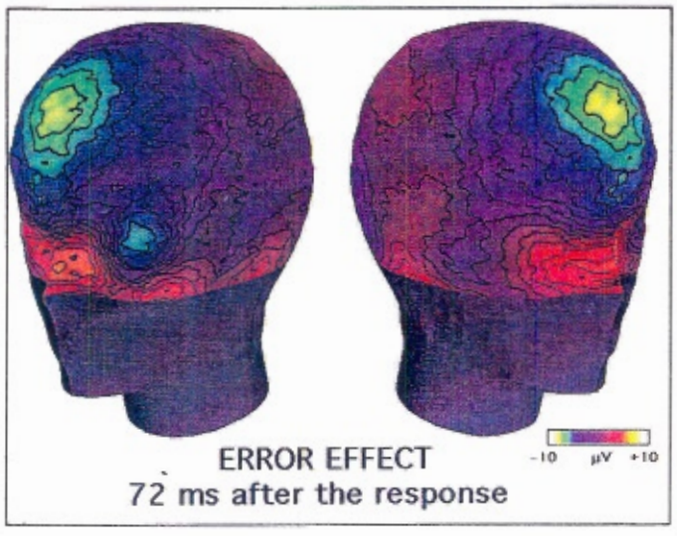

Fig. 1. Topography of the error-related negativity (ERN), as observed on erroneous trials in Experiment 2. Colors code for levels of scalp-recorded voltages, interpolated between measurement points to the entire surface of the scalp. Front left and front right views are shown.

oriented downward at a moderate angle toward the center of the head. For Experiment 2, however, only 71.0% of the variance in the voltage topography could be accounted for by a single-dipole model, and the best-fitting dipole was more anterior than in Experiment 1. When the dipole was forced to remain at exactly the same location as in Experiment 1, only 56.5% of the variance could be accounted for. No satisfactory and stable multiple-dipole solution was found.

We reasoned that this difference in the ERN observed in Experiments 1 and 2 could be due to the concomitant activation of other task-specific brain areas that would partially mask or distort the electrical signature of the error-processing system. For instance, the large positivity in the region of the eyes and nose in Experiment 2 (Fig. 1), which was largely responsible for the poor fit of single-dipole models, was not seen in Experiment 1 and therefore seemed related to some aspect of the semantic categorization task. In order to isolate the electrical contribution of the error-processing system only, we computed, for each experiment, the difference between voltages recorded on error trials and on correct trials. This subtraction technique was quite successful in revealing a task-independent error effect. The topography of this difference was essentially identical for both experiments and was quasi-dipolar (Fig. 2). A single dipole, oriented downward and located on the midline of the inferior anterior cingulate cortex, accounted for 94.3% of the variance in Experiment 1 and for 88.5% of the variance in Experiment 2. Multiple-dipole models did not improve these scores significantly.

In both experiments, the equivalent dipole was so close to the midline that we could not tell with any confidence whether it indicated a left, right, or bilateral activation. Furthermore, when the data from left-hand and right-hand responses were examined separately, the topography of the ERN did not seem to be affected by the side of response. The ERN was always maximal on the midline and not on the side contralateral to the response. This finding suggests that the error-processing system operates at an abstract level, relatively independently of the exact motor contingencies.

In both experiments, the BESA program always converged very rapidly toward the same anterior cingulate solution, regardless of the initial conditions. Nevertheless, such a dipole solution is necessarily approximate and makes unrealistic assumptions concerning the sphericity of the head and its conductance. The actual generator is more likely to be a sheet of dipoles rather than a single dipole, and as such it is probably more superficial than the single-dipole solution. The observed scalp negativity is so tightly localized, however, as to support the idea that the generator is located relatively closely underneath electrode FzS, within either the supplementary motor area (SMA) or the anterior cingulate cortex.

Cognitive theorists distinguish two types of errors: *slips*, incorrect executions of appropriate motor programs, and *mistakes*, selection of inappropriate intentions, based, for instance, on faulty knowledge (Reason, 1990). In our two experiments, the cognitive task was so simple that most errors were probably slips due to speed pressure. Data from a third experiment suggested that the ERN is observed only after slips, and not after mistakes. In that experiment (Tucker, Liotti, Potts, Russell, & Posner, in press), subjects learned to classify some screen locations as good and others as bad, and could take as much as 2 s to respond. Given the absence of speed pressure, errors were probably due to mistakes in retrieving the attributes of locations from memory. No ERN was observed either immediately following an incorrect key press or later when negative feedback informed the subjects of their errors. Instead of an ERN, negative feedback elicited a broad frontal positivity (P300) congruent with the fact that the subjects were surprised to find that their previous responses were incorrect. Thus, neither making an error nor realizing that an error was made seemed sufficient for the ERN to occur. We conclude that the observed anterior cingulate-SMA activity reflects the activation of a system for the on-line monitoring of performance, and this system comes into play only when an error is detected in time for a correction to be attempted. This conclusion meshes well with the postulated role of the anterior cingulate in "attention for action" (Posner, Petersen, Fox, & Raichle, 1988).

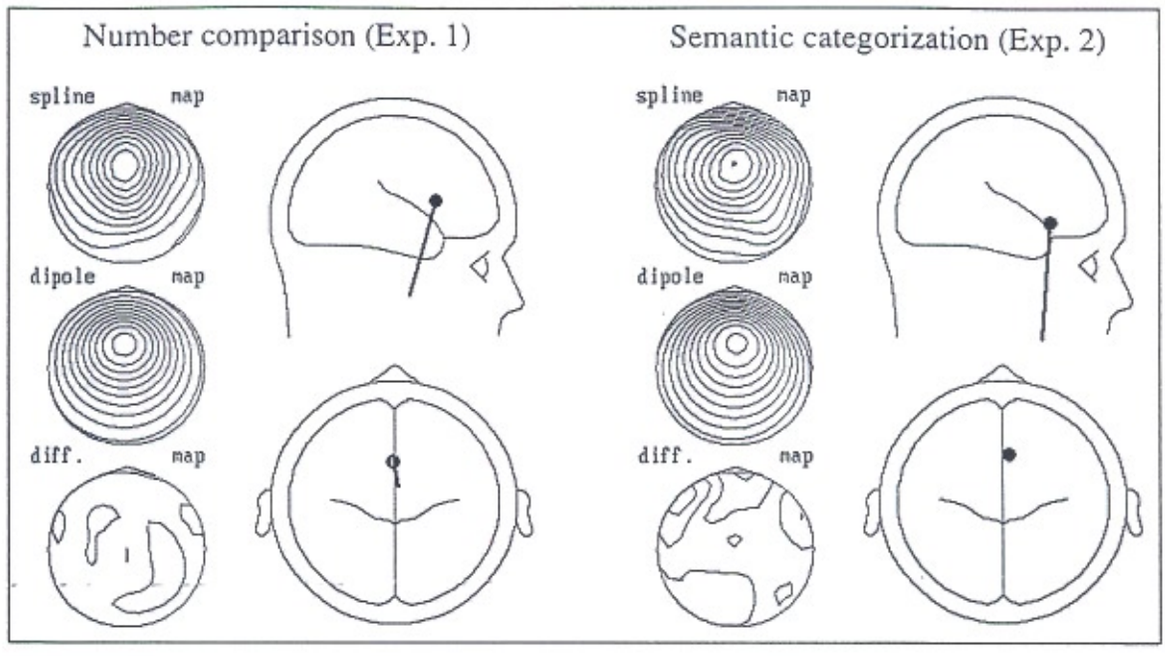

Fig. 2. Single-dipole models of the voltage difference between erroneous and correct trials. For each experiment, the spline map shows the topography of the measured difference (the front of the head is on top), the dipole map shows the best-fitting electrical field, and the difference map (diff. map) shows the residual voltage unaccounted for by the single-dipole model. The localization (circle) and orientation of the best-fitting dipole are shown on right and top views of the head.

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