

Event-Related Brain Potentials Following Incorrect Feedback in a Time-Estimation Task: Evidence for a “Generic” Neural System for Error Detection

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Abstract

■ We examined scalp-recorded event-related potentials following feedback stimuli in a time-estimation task. Six hundred msec after indicating the end of a 1 sec interval, subjects received a visual, auditory, or somatosensory stimulus that indicated whether the interval they had produced was correct. Following feedback indicating incorrect performance, a negative deflection occurred, whose characteristics corresponded closely to those of the component (the error-related negativity) that accompanies errors in choice reaction time tasks. Further-

more, equivalent dipole analysis suggested that, for all three modalities, the distribution of the scalp potential was consistent with a local source in the anterior cingulate cortex or a more distributed source in the supplementary motor areas. These loci correspond closely to those described previously for the error-related negativity. We conclude that the error-related negativity is the manifestation of the activity of a “generic” neural system involved in error detection. ■

INTRODUCTION

Human beings have the ability to monitor their own actions. This ability is evident in a number of settings, including speech production and the control of action, where the role of error detection and error correction has received considerable attention (e.g., Levelt, 1989; Rabbitt, 1966). Research using measures of the human event-related brain potential (ERP) has provided evidence for the existence of a neural system that may implement these kinds of error-related processes (e.g., Dehaene, Posner, & Tucker, 1994; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993). When subjects make errors in choice reaction time (RT) tasks, a negative potential is observed at the scalp. This potential, labeled the NE or error-related negativity (ERN), begins to develop at around the time of the erroneous response and peaks about 100 msec later. It is smaller or absent on trials where the subject makes the correct response.

Implicit in the concept of error detection is the idea that the monitoring system can make some kind of

comparison, and recent data suggest that this comparison can involve representations of the current action and the correct action (Bernstein, Scheffers, & Coles, 1995). Such a comparison results in a mismatch if the current action is not correct. In turn, the mismatch signal can be used as input to an error-correction or error-compensation system, whose function is to inhibit the error, correct the error, or reduce the likelihood of future errors. Indeed, Gehring et al. (1993) showed that the neural process manifested at the scalp by the ERN is related to these kinds of error-correction and error-compensation activities. In a choice RT task, large ERNs were found to be associated with less forceful errors, with more attempts to correct an error, and with a reduction in response speed on future trials (see Rabbitt, 1966). Furthermore, the size of the ERN is related to the degree to which experimental instructions and payoffs emphasize fast or accurate performance. An error made when a subject is instructed to respond accurately elicits a larger ERN than one made under speed instructions (Falkenstein et al., 1990; Gehring et al., 1993). These kinds of data provide support for the claim that the ERN

is indeed a manifestation of either error-detection or error-compensation processes.

Recent data collected by Scheffers, Coles, Bernstein, Gehring, and Donchin (1996; see also Falkenstein, Hohnsbein, & Hoormann, 1995) suggest that the ERN is more closely associated with error detection than with error correction. These investigators used a hybrid choice/Go-NoGo task and found that an ERN was present for both errors of choice (using the wrong hand to respond on Go trials) and for errors of action (responding on NoGo trials). Since errors of action cannot be corrected by the execution of a second motor response, Scheffers et al. reasoned that the presence of the ERN for these kinds of errors implied that the ERN was not directly associated with error correction.

These psychophysiological investigations of error monitoring have all utilized tasks in which errors can almost certainly be attributed to impulsive behavior rather than to some kind of data limitation (see Gehring, Coles, Meyer, & Donchin, 1995; Falkenstein et al., 1990). In some cases, the task stimuli are easily discriminable letters or tones, and subjects are quite able to determine the stimulus that was presented and, therefore, to select the appropriate response. In these cases, erroneous behavior appears to occur when subjects activate responses without processing the stimuli—that is, they guess. In other cases, we have used visual stimuli that could mislead the subjects about the appropriate response (Gehring et al., 1993; Scheffers et al., 1996). For example, a target letter, requiring one response, may be surrounded by noise letters requiring the other response. In this case, errors can occur if subjects respond on the basis of the noise letters before they have determined the identity of the target letter. These errors appear to occur because of partial or incomplete processing of the stimuli, and they can also be regarded as instances of impulsive behavior. Given time, subjects are able to establish the identity of the target letter and to select the appropriate response. These observations are important because they imply that, in these tasks, there is always the possibility for the subject to determine the appropriate response on the basis of complete processing of the task stimulus. This means that, in principle, errors can always be detected on the basis of a comparison between the actual response and the appropriate response (i.e., the response that is mapped to the task stimulus).

The present experiment was designed to investigate the error detection process in a situation where detection cannot be performed on the basis of a representation of the correct response that is derived from processing the task stimulus. In particular, we required subjects to perform a time interval production task and provided them with a feedback stimulus after each interval. Each trial of the task began with a cue, and the subject had to respond by pressing a button 1 sec later. The feedback stimulus, presented 600 msec after the

response, informed the subject about the accuracy of the previous interval and, therefore, provided the critical information that would enable error detection to occur. The criterion for determining whether the feedback on any trial would be correct or incorrect was varied continuously on the basis of the subject's performance. As the subject's performance improved, the criterion became more strict; as it deteriorated, the criterion became more relaxed. As a result, the global probability of correct and incorrect feedback was 0.5. In different conditions of a single session, feedback was either auditory (1000- and 1400-Hz tones), visual (the letters X and O), or somatosensory (nonpainful electrical stimulation of the middle and ring fingers of the nondominant hand). Within each modality condition, the meaning of the two stimuli (either correct or incorrect) was randomly varied between subjects. ERPs were recorded from 36 scalp electrodes and were evaluated for an epoch beginning 100 msec before the feedback and extending for 1000 msec thereafter.

The critical question concerned the ERP following the feedback stimulus, when the stimulus indicated that the performance was incorrect. Would we find a negative component like the ERN we had observed previously in choice RT tasks? If so, this would provide evidence for a generic error-detection system that compares representations of correct and actual responses. By *generic*, we mean a system whose activity does not depend on the specific nature of the response representations and which can be engaged by task-events other than the erroneous response itself.

This question was addressed using both traditional measures of component amplitude at different electrode sites as well as equivalent dipole analysis. Dehaene et al. (1994) have recently used this kind of analysis to claim that the source of the ERN lies in the anterior cingulate cortex or supplementary motor area, in accordance with speculations made by Gehring et al. (1993) on the basis of theories of the functions of these structures. Furthermore, comparison among the ERPs and the dipole solutions for the three different feedback modalities allowed us to evaluate the modality independence of any neural activity related to the processing of incorrect feedback. Modality independence would constitute additional evidence for the generic nature of the error-detection system.

RESULTS AND DISCUSSION

Performance Data

In all conditions, subjects consistently overestimated the 1 sec interval (auditory, 1.075 sec; somatosensory, 1.066 sec; visual, 1.044 sec). The average window widths, on the basis of which correct or incorrect feedback was given, were ± 132 msec, ± 138 msec, and ± 124 msec, respectively. Although not significant, this difference be-

tween conditions was consistent with the self-report of subjects that the somatosensory condition was the most difficult because of the relatively low discriminability of the two feedback stimuli in this condition.

To determine whether subjects used the feedback to guide their estimations, we measured the degree to which the estimate changed from one trial to the next by computing the absolute difference in the duration of the estimates between trial n and $n + 1$. Then we examined the effect of feedback (correct vs. incorrect) on this difference. Subjects changed their estimates more after negative (198.5 msec) than after positive feedback (132.7 msec), $F(1, 17) = 135.7, p < 0.001$. The main effect of modality and the interaction between modality and feedback were not significant although the average change in the estimate in the somatosensory condition was smaller than in the other two conditions. These data indicate that the subjects were indeed using the feedback to guide their behavior.

The ERP in Response to Feedback: Traditional Analysis

Figures 1, 2, and 3 show the ERPs elicited by the feedback stimulus. Separate waveforms are shown for feedback indicating correct and incorrect performance, and for the three modalities in which the feedback information was delivered. For each of the three feedback modalities, there is a series of early deflections that are always observed following the occurrence of these kinds of sensory events. These deflections (exogenous components) are identical for correct and incorrect feedback but differ for the different modalities, reflecting the fact that different sensory systems are involved. At about 250 msec, the traces for correct and incorrect feedback diverge, and this divergence is apparent for all three feedback modalities. The waveforms following incorrect feedback include a negative peak, or a negative displace-

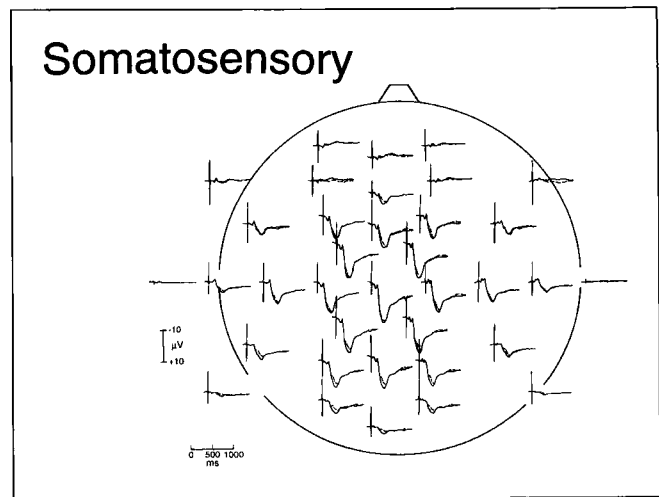


Figure 2. Grand average ERP waveforms for correct and incorrect feedback stimuli for the somatosensory condition. Note the spike at 0 msec, corresponding to an electrical stimulus artifact.

ment, that is not evident in the waveform following correct feedback. Almost coincident with this negative shift in the incorrect feedback waveform, there is a positive peak in the correct feedback waveform. This positivity has the parietal-maximal distribution of the classic P300 or P3b. This positivity is evident later in the waveform for the incorrect feedback stimulus.

To isolate the difference between correct and incorrect feedback trials, we followed the same strategy as Dehaene et al. (1994). We subtracted the correct waveform from the incorrect waveform, and the results of this subtraction are shown in Figure 4 (for anterior-posterior electrodes). This subtraction procedure should remove contributions of any components that are elicited in response to both kinds of feedback (e.g., the exogenous components), leaving only those components that are specifically related to differences in the processing of

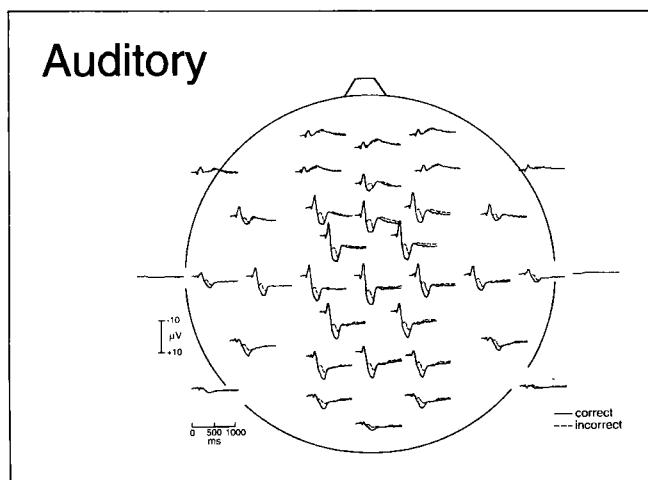


Figure 1. Grand average ERP waveforms for correct and incorrect feedback stimuli for the auditory condition.

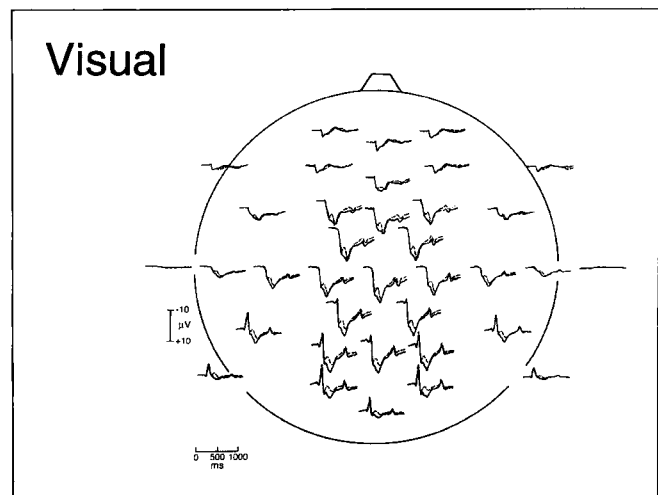


Figure 3. Grand average ERP waveforms for correct and incorrect feedback stimuli for the visual condition.

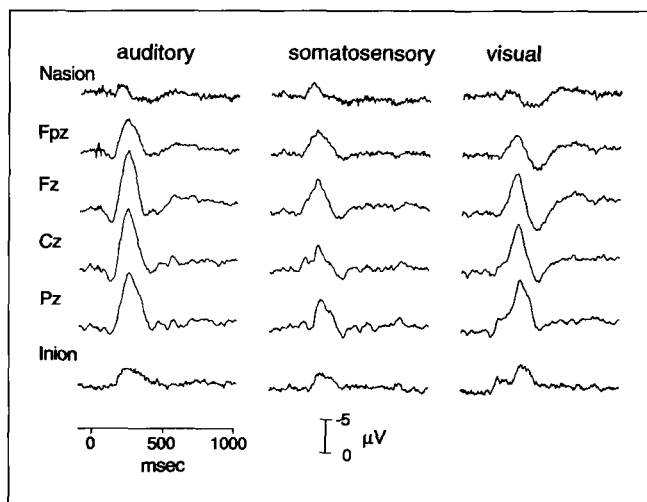


Figure 4. Difference waveforms derived by subtracting the grand average waveform for correct feedback condition from the corresponding waveform for the incorrect feedback condition. Waveforms for the anterior-posterior electrodes for each modality are shown.

correct and incorrect feedback. Scrutiny of Figures 1, 2, and 3 indicates that there are no differences in the early components, and they will therefore have no contribution to the difference waveforms. For the auditory and visual feedback conditions, the difference between correct and incorrect feedback appears to involve both a negative deflection and a difference in the latency of a later positivity. In the case of the somatosensory feedback condition, the difference in the latency of the positivity seems to describe the entire difference between feedback conditions, at least at the more frontal electrode sites. The componential structure of these difference waveforms will be discussed later in the paper when we apply equivalent dipole analytic procedures. For present purposes, it is sufficient to note the similarity in the form and scalp distribution of the difference wave across modalities that is shown in Figure 4. For all modality conditions, the difference waves reveal a deflection that has an onset latency of about 140 msec and an offset latency of about 400 msec, with the peak of the deflection being earlier at frontal than posterior sites.

To analyze the deflection further, we derived an amplitude measure by identifying the latency of the peak of the difference wave at the Cz electrode (for each subject and each modality separately) and then measuring the amplitude of the difference trace at this latency for all electrodes.¹ The latency of the peak varied as a function of modality, $F(2, 34) = 9.724$, $\epsilonpsilon = 0.663$, $p < 0.01$. The conditions were ordered as follows (from shortest to longest latency): somatosensory, auditory, visual. Subsequent post hoc analyses revealed that all between condition differences were significant except between auditory and somatosensory modalities for which $p = 0.06$. The amplitude at this latency was then used as the dependent variable in an analysis of variance that in-

cluded modality, lateral (left hemisphere, midline, and right hemisphere) and anterior-posterior (frontal, central, and parietal) as factors. The analysis used data from nine electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4). For the lateral factor, the three levels were defined as left (F3, C3, P3), midline (Fz, Cz, Pz), and right (F4, C4, P4). For the anterior-posterior factor, the three levels were defined as frontal (F3, Fz, F4), central (C3, Cz, C4), and parietal (P3, Pz, P4).

Analysis of the distribution of the amplitude of the peak-difference measure revealed that it was larger at central than lateral sites, $F(2, 34) = 13.125$, $\epsilonpsilon = 0.674$, $p < 0.01$. Subsequent post hoc tests revealed that the amplitudes at the lateral sites did not differ from each other ($p = 0.82$) but that both were significantly smaller than the amplitude at the central site ($p = 0.001$ in both cases). There was no significant effect of the anterior-posterior factor, $F(2, 34) = 1.269$, suggesting that the amplitude of the peak-difference measure did not vary across anterior-to-posterior recording sites.

The sensitivity of the measure to the modality of the feedback was assessed by evaluating the main effect of modality and interactions between modality, lateral, and anterior-posterior factors. As Figure 4 suggests, the amplitude of the peak-difference measure was smaller in the somatosensory condition than in the other two conditions, $F(2, 34) = 6.502$, $\epsilonpsilon = 0.785$, $p < 0.01$. Furthermore, a significant interaction between modality and anterior-posterior factors revealed that the modalities also differed in terms of scalp distribution, $F(4, 68) = 5.076$, $\epsilonpsilon = 0.584$, $p < 0.01$.² In this case, the distribution for visual modality showed a frontal maximum/parietal minimum function, while the distribution for the other two modalities was "flat" across anterior-posterior sites.

These modality effects challenge the view that the same neural process is engaged in the different modality conditions. The amplitude effect may be a simple consequence of the fact that the discriminability of the two somatosensory stimuli (stimulation of the middle and ring fingers) was more difficult (by subjects' report) than the discriminability of the stimuli in the other two modalities. Any processing differences between correct and incorrect feedback stimuli would, of course, depend on the degree to which the stimuli were discriminable. The distributional data are more problematic, however. First, the overall distribution of the amplitude difference measure was flat across anterior-posterior sites. This contrasts with the findings of Gehring et al. (1993) and other studies reviewed earlier in which the ERN had a frontal distribution. Second, the difference in scalp distribution between the visual condition and the other two conditions suggests that the intracranial sources of the scalp potentials are different (e.g., see Rugg & Coles, 1995). However, interpretation of distributional data is complicated by the fact that the observed distribution at the scalp may be the result of the activities of more than one

neural source. In the present case, the difference waveform used as a basis for the amplitude measure could be made up of more than one component waveform. As we noted above, the "raw" waveforms appeared to contain at least two components, an early negativity (the ERN?) and a later positivity (the P300?). Furthermore, the difference between modality conditions might be due to the differential overlap between the components rather than to a real difference in the componential structure in the different conditions. We will return to this issue later when we review the results of application of the BESA procedure to these data.

Gehring et al. (1993; see also Scheffers et al., 1996) showed that the magnitude of the ERN on trial n was related to performance on trial $n + 1$ with a large ERN predicting more conservative future behavior in the form of slower responses. In the present situation, where the subject had to produce intervals of particular durations, measurement of response speed is clearly an inappropriate measure. So instead, we evaluated the relationship between the ERN and future behavior using two alternative measures. These included the accuracy of the estimate following an error and the absolute change in the estimate from trial n to trial $n + 1$. There were no significant differences in the amplitude of the ERN as a function of either accuracy or absolute change measures.

Equivalent Dipole Analysis

Dehaene et al. (1994) have recently shown that the ERN (as measured in two different choice RT tasks) can be explained quite well by a single equivalent dipole located in the anterior cingulate cortex. If, indeed, the deflection we have identified in the present time-estimation experiment is related to the ERN observed in choice RT tasks, the locus of the equivalent dipole corresponding to the component should be similar to that described for the ERN by Dehaene et al. Furthermore, if the component is modality independent, the locus should be the same regardless of the modality of the eliciting stimulus.

To address these issues, we applied the BESA procedure (Scherg & Berg, 1990) to the difference waveforms (incorrect minus correct) using the data for all 36 channels (cf. Dehaene et al., 1994). This was done separately on the grand-average difference waveforms for each feedback modality. A time window of 145- to 395-msec postfeedback stimulus was chosen on the basis of the difference waveforms shown in Figure 4. This window covers the period of significant ERP activity for all three modalities. Initially, we tried a single-dipole solution as Dehaene et al. had done. However, the residual variances, across the time window, were quite high for the solutions for each modality (Auditory: 14.4%; Somatosensory: 40.8%; Visual: 17.4%), suggesting that these single-dipole solutions were inadequate. Furthermore, as we men-

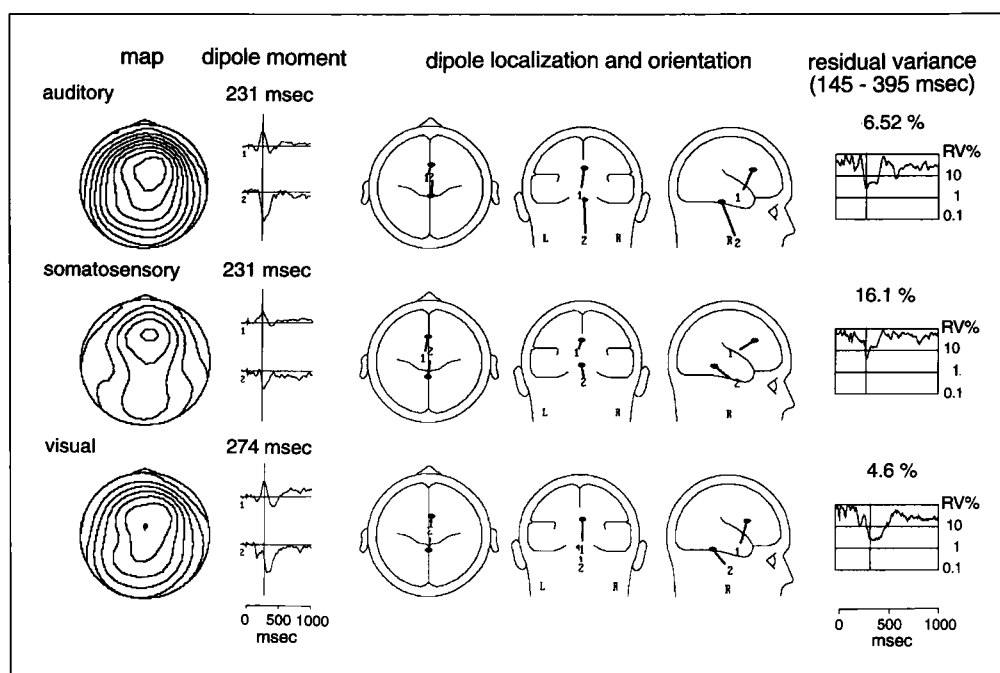
tioned earlier, it seems likely that two components are active during the time window: the negative component and a P300 component. Thus, we next tried a two-dipole solution using the same time window. Following the principles of the spatial-temporal approach, the dipole solutions were constrained according to the following criteria: (1) the dipole moments should have a phasiclike appearance, with clearly defined onsets and offsets, and a limited duration, (2) the interaction of the two dipoles should be minimized using an iterative procedure, and (3) the residual variance should also be minimized.

The results of the two-dipole solutions are shown in Figure 5. Several aspects of these data are notable. First, in two of the three cases, the residual variance (for the interval from 145 to 395 msec) in each case is quite low (Auditory: 6.5%; Somatosensory: 16.1%; Visual: 4.6%). The larger residual variance in the somatosensory condition is probably due to the smaller amplitude (and, therefore, lower signal-to-noise ratio) in this condition (see above). Second, across the three modalities, the loci of the two equivalent dipoles are remarkably consistent. In each case, one dipole is located in the frontal region and the other, at the base of the brain.

There are no standard procedures for estimating the error of these kinds of dipole solutions. Possible sources of variability include measurement error, "noise" associated with background activity of the brain, and intersubject differences in brain structure and function. Rather than approaching the issue from the perspective of these sources of variability, the procedures used here focus on the stability of the estimates of the parameters of the dipole (location and orientation). In particular, we estimated (1) the degree to which the solutions are independent of the starting positions of the dipoles and (2) the steepness of the error surface surrounding the local minima.

A reasonable starting position for estimating the dipole parameters is the center of the head with the orientation pointing at the vertex, and the estimates described above were based on these starting parameters. To explore the effect of varying starting parameters, we used 14 different conditions (7 for each dipole). In a coordinate system where (0, 0, 0) is the center of the head, with the x axis pointing to the right ear, the y axis to the nasion, the z axis to the vertex, and the radius of the head set to 100, the starting locations were (0, 50, 0), (0, 0, 50), (0, -50, 0), and (0, 0, -50). For orientation, where theta is the angle (in degrees) between the orientation and the z axis, and phi is the angle (in degrees) between the projection of the orientation vector onto the xy plane and the x axis, the starting parameters (theta, phi) were (0, 0) and (90, 90). For dipoles 1 and 2, the range of estimates based on these different starting parameters (x , y , z , theta, phi) were (8.4, 3.7, 2.0, 3.2, 16.4) and (0.2, 2.7, 5.3, 0.2, 9.8), respectively. These values reveal that the solutions are relatively independent of starting position.

Figure 5. Results of equivalent dipole analysis using the BESA procedure with two sources. Each of the three rows contains data relevant to a modality. See text for further information.



To examine the steepness of the error surface, we began by identifying the latency of the peak of the dipole activity for each of the two dipoles separately (for each modality). Then, the residual variances were estimated at these two latencies, rather than over an epoch. Then, we derived the value of these residual variances plus 10%. Next, for each of the three dipole location (x , y , and z) and the two orientation (theta, phi) parameters separately, we determined the range of values for that parameter for which the residual variance was less than or equal to the residual variance plus 10%. This range value indicates by how much each parameter can be changed before the residual variance increases by more than 10%. These values are given in Table 1, while those for location are also shown diagrammatically in Figure 6. Note that the frontal dipoles (Equivalent Dipole 1) for the three modalities are in almost identical locations and that they fall within overlapping ranges. For Equivalent Dipole 2, the loci are less consistent.

Figure 6 also shows the dipole locations for the ERNs elicited in the two experiments described by Dehaene et al. (1994), and Table 1 provides the values for the location parameters of their dipoles.³ Note that the loci of the frontal dipoles based on our feedback data are very similar to those observed by Dehaene et al. for the ERNs elicited in their choice RT tasks. This similarity provides a basis for inferring that the same process is elicited in both feedback and choice RT tasks and, specifically, that the ERN process can be elicited by feedback stimuli.⁴ If the source corresponding to this equivalent dipole is focused, its locus is consistent with a focused generator in the anterior cingulate cortex. On the other hand, if the source is more widely distributed,

the locus of the equivalent dipole is consistent with a more superficial and more extended generator in the supplementary motor area (cf. Dehaene et al., 1994).

It is harder to interpret the second equivalent dipole (labeled 2 in Figure 5) because generators of scalp activity are very unlikely to be located so deep in the brain. Deep brain structures do not have the kind of parallel architecture, or the level of activity, needed to produce the large-scale voltage changes that are observed at the scalp (Braun, Lutzenberger, Miltner, & Elbert, 1990). Rather these deep equivalent dipoles can be more plausibly interpreted in terms of a widely distributed sheet of generators that extends more superficially across substantial areas of the cortex. In the present case, the locus and orientation of the equivalent dipole suggest that it may be associated with a sheet of generators in extended areas of the posterior cortex. While the source of the P300 component is still the subject of considerable debate, a distributed cortical source of this kind is certainly consistent with the extant data (Lutzenberger, Elbert, & Rockstroh, 1987).

Finally, we should note that the BESA analyses confirm our speculations about the influence of an overlapping positive component on the scalp-recorded negativity. The residual variances were much lower for the two-dipole than for the single-dipole solution, suggesting that a two-component structure is more plausible. Furthermore, the peak latencies of the dipole moments (see Table 1) suggested that the pattern of overlap between the two components varied as a function of modality. In particular, the values for the visual modality are quite different from those for the other two modalities. This difference may explain why the traditional amplitude

Table 1. Latency, Variance, and Parameter Information for the Two Equivalent Dipoles

	Equivalent Dipole 1			Equivalent Dipole 2				
	Auditory	Somato-sensory	Visual	Exp. 1 ^a	Exp. 2 ^a	Auditory	Somato-sensory	Visual
Latency (msec)	231	231	274			266	257	326
Residual Variance (%)	2.33	5.57	2.40	3.70	10.50	4.42	7.99	2.36
Residual Variance +10%	2.56	6.13	2.64			4.86	8.79	2.60
X value (mm) (range)	+1.6 (-6 to +17)	-1.3 (-10 to +7)	+4.2 (+1 to +24)	+0.9	+7.1	+1.5 (-13 to +13)	-1.2 (-13 to +10)	-0.4 (-11 to +5)
Y value (mm) (range)	+31.4 (+23 to +41)	+34.3 (+27 to +42)	+26.0 (+19 to +33)	+18.9	+21.2	-11.6 (-21 to +2)	-20.7 (-28 to -10)	-21.3 (-26 to -13)
Z value (mm) (range)	+26.4 (+16 to +34)	+29.6 (+25 to +41)	+22.2 (+11 to +27)	+22.3	+5.6	-18.5 (-31 to -9)	-6.1 (-15 to -5)	-17.1 (-23 to -10)
Theta (degrees) (range)	26.0 (13 to 75)	59.4 (49 to 68)	15.0 (9 to 33)			21.2 (15 to 29)	52.7 (41 to 59)	39.0 (29 to 43)
Phi (degrees) (range)	74.8 (40 to 93)	78.5 (74 to 87)	92.5 (70 to 103)			265.4 (255 to 276)	262.3 (259 to 274)	262.3 (259 to 270)

^a Parameters for Exps. 1 and 2 refer to the "ERN" equivalent dipoles described by Dehaene et al. (1994).

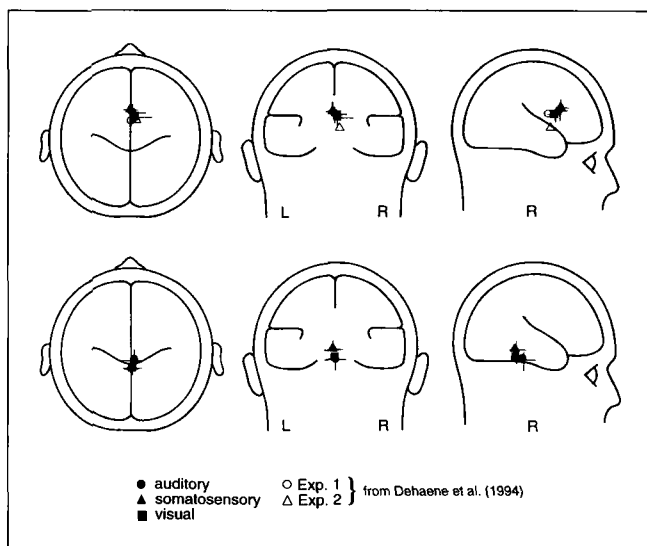


Figure 6. Equivalent dipole locations for the two-dipole solution for the three modality conditions of the present experiment. Top and bottom rows show loci for Equivalent Dipoles 1 and 2, respectively. In the upper row, open symbols designate loci for the single dipole solutions for the two experiments described by Dehaene et al. (1994). "Bars" reflecting range values are also shown. See text for elaboration.

analysis indicated that the scalp distribution for the visual modality was different from that for the other two modalities.

CONCLUSIONS

When subjects receive feedback indicating incorrect performance in a time-production task, a negative deflection or shift is observed in the ERP. The negativity peaks between 230 and 330 msec following incorrect feedback, has a duration of about 260 msec, and is larger at midline than at lateral electrode sites. While the amplitude of the negativity depends on the modality of the feedback stimulus, this effect appears to be secondary to an effect of stimulus discriminability. The characteristics of this negativity correspond in many respects to those of the negative component (the ERN), described by Dehaene, Falkenstein, Gehring, and their respective colleagues (e.g., Dehaene et al., 1994; Falkenstein et al., 1990; Gehring, et al., 1993) in the context of choice RT tasks. Because of the indeterminacy of dipole analysis, we cannot use our dipole data alone to make inferences about the neural source of the component. However, the dipole analysis does allow us to look for consistencies both within our own dataset (across modalities) and within other sources of information. In this respect, the analysis reveals that an almost identical dipolar source can account for the scalp-recorded activity associated both with the ERN (as described by Dehaene et al., 1994) and with the present feedback-related negativity for all three feedback modalities. Furthermore, the struc-

ture(s) implicated by the dipole analysis are consistent with neuropsychological and neurophysiological data (as reviewed by Gehring et al., 1993). For all these reasons, it appears that the same neural process, involving the anterior cingulate cortex or the supplementary motor area, is associated with incorrect response execution in an RT task and with error feedback in a time-estimation task.

This suggests that the ERN component may reflect the activity of a generic error-detection mechanism, whose operation is not limited to the identification of particular kinds of errors in particular kinds of tasks. Rather, it appears that the mechanism can be specifically invoked to deal with errors of choice (as in choice RT tasks), errors of action (as in Go-NoGo tasks), and time-estimation errors (as in the current time-production task). The error-detection system, then, can be set up to compare those representations that are relevant to correct task performance as defined by the goals of the task. Furthermore, the representations to be compared can be derived from both internal (e.g., collateral) and external (e.g., feedback) sources. One important difference between the present and preceding studies is that, in the present case, the deflection was observed several hundred milliseconds after the erroneous response, when the opportunity to inhibit or correct the error has passed. This observation strengthens earlier claims (Bernstein et al., 1995; Scheffers et al., 1996) that the ERN is more likely to reflect the activity of a detection mechanism than a mechanism involved in immediate error correction.

Two observations complicate the identification of the negative deflection observed here with the ERN. First, unlike the ERN, the present deflection was not related to measures of performance change that followed negative feedback. Neither the accuracy of the post-error estimate nor the degree to which the estimate changed following an error were related to the amplitude of the negative deflection. This failure to find a relationship may be because the feedback stimulus did not inform the subject of the nature of the error—that is, whether the production interval was longer or shorter than the criterion. Under these conditions, the negative feedback might be used to initiate a change in behavior, but that change would not necessarily lead to an improvement in performance. Furthermore, because the criterion for correct behavior was always changing, subjects could not use the feedback to determine how much to change their estimate after an error. For these reasons, a simple relationship between the response to the feedback and subsequent behavior could not have been expected.

A second problem with the claim that the feedback-related negativity is an ERN involves its scalp distribution. The negativity described here does not have the same scalp distribution as the ERN. This difference appears to be due to the presence of other, overlapping components that contribute both to the incorrect wave-

forms and to the difference wave we obtained by subtracting correct from incorrect waveforms. Indeed, the equivalent dipole analyses revealed that the difference waveform can be accounted for by two equivalent dipoles: an "ERN" dipole and a dipole that may be related to the P300.

Thus, it appears reasonable to claim that the ERN, a manifestation of a neural process involved in error detection, contributes to the difference between correct and incorrect feedback conditions and, therefore, that the same mechanism is involved in the detection of errors in quite different situations. The precise specification of the computations performed by the error-detection mechanism awaits further research. However, knowledge of the neural structures that may be involved, and of the conditions under which the mechanism operates, will be invaluable in guiding that research.

METHODS

Subjects

Eighteen right-handed student volunteers (8 females) aged 20 to 26 served as subjects. They were healthy at the time of experiment and free of any medication. They were paid 15 DM per hour for their participation.

Task and Stimuli

The subjects' task was to estimate the duration of 1 sec by pressing a button as soon as they thought 1 sec had elapsed following presentation of an auditory cue (800 Hz, 65 dB, 50 msec long). In three successive conditions of the experiment, subjects received feedback about the accuracy of their time estimations in the form of either an auditory, visual, or somatosensory stimulus presented 600 msec after the button press response. For each modality, there was one stimulus that indicated that the estimate was correct and another that the estimate was incorrect.

In the auditory feedback condition, the two feedback stimuli were low and high tones of 1000 and 1400 Hz, 50 msec long and 65 dB (SPL). Assignment of the tones as signifying correct or incorrect estimates was random across subjects. Thus, for half the subjects, the high tone meant correct and the low tone meant incorrect, and the converse was the case for the other subjects.

In the visual feedback condition, the letters X and O served as feedback stimuli. They were presented for 1 sec on a video monitor with a vertical and horizontal size of approximately 5°. Again assignment of the meaning of the two stimuli was random across subjects, with half the subjects receiving the X for correct and the O for incorrect estimations, and the other subjects receiving the converse assignment.

In the somatosensory feedback condition, the stimuli were bipolar-electrical-square pulses 10 msec long, ap-

plied intracutaneously. Stimuli were applied either to the middle finger or the ring finger of the left hand. Again, the assignment of meaning to each stimulus was random across subjects.

Because it is difficult to produce an exact estimate of 1 sec, the kind of feedback provided to the subject (correct or incorrect) was a function of whether the duration of the estimate fell within a time window. The width of this window was adjusted automatically from trial to trial (by ± 10 msec) on the basis of the subjects' performance on the preceding trial (cf. Johnson & Donchin, 1978). As performance improved, the window became narrower; as performance deteriorated, the window became wider. The result of this procedure was that the global probability of correct and incorrect feedback stimuli was 50%. The initial window width was ± 100 msec.

Recording

Brain electrical activity was recorded with an AC amplifier from 36 electrodes, 20 of which were arranged according to the international 10/20 system (including the two earlobes), with the remaining 16 electrodes being systematically interspersed within the square array of electrodes from Fz to Pz and from T3 to T4. The Cz electrode was used as the common reference for all other electrodes. Additionally, horizontal and vertical EOG were recorded using a montage suggested by Elbert, Lutzenberger, Rockstroh, and Birbaumer (1985).

All electrode sites were first cleaned with alcohol and Omniprep skin prepping paste. For EEG recordings, In-vivoMetrics Ag/AgCl electrodes were affixed to the scalp by Grass paste, and the impedance was less than 3 k Ω at all electrodes. Beckman Ag/AgCl electrodes, Beckman electrode jelly, and adhesive collars were used for EOG recordings. All signals were amplified using a Nihon-Koden system with a time constant of 10 sec and a low-pass filter of 70 Hz. The signals were digitized with a sample rate of 256 Hz for an epoch of 1100 msec starting 100 msec prior to the presentation of the feedback stimulus.

Prior to analysis, the original Cz-referenced waveforms were transformed offline to produce a new set of waveforms based on an equivalent linked-ears reference. The formula we used to derive the value for the linked ears reference waveform was $[u(a1) + u(a2)] / 2$, where $u(a1)$ and $u(a2)$ are the values for each of the left and right ear-lobe electrodes referenced to Cz. This value for the linked-ears reference waveform was then subtracted from each of the Cz-referenced waveforms. Note that this procedure also produces a waveform for Cz.

Procedure

The experiment was conducted in a single session of approximately 2½ h. After subjects reported for the

experiment, they were informed about the purpose of the experiment and signed a consent form in accordance with the Helsinki Accords. After electrodes were attached, subjects were given instructions about the task and were given 20 practice trials of the task with one pair of feedback stimuli. To ensure that the somatosensory stimuli were easy to perceive but not painful, subjective perception and pain thresholds were assessed and the intensity was adjusted for each subject. Care was taken to assure that the perceived intensity of the stimulation was the same for the two fingers.

All subjects performed the task under each of the three feedback-modality conditions, with the order of conditions being randomized across subjects. For each condition, 200 time-estimation trials were given. Each trial began with the auditory cue (800 Hz, 65 dB, 50 msec long). Subjects then pressed a button with the index finger of their right hand to indicate that 1 sec had elapsed. Then, after a further 600 msec, the feedback stimulus was given. The interval between the feedback stimulus and the next cue was 2.5 sec (± 100 msec). After each condition, there was a pause of about 10 min before the next condition began.

Data Analysis

After all EEG data were corrected for EOG artifacts according to a procedure described by Gratton, Coles, and Donchin (1983), the data for each electrode site were averaged separately according to the feedback modality and the accuracy of the time estimation (correct/incorrect).

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Notes

1. We also used a measure of average amplitude by taking the mean of the three amplitude values before and after the peak (approximately ± 10 msec around the peak). Since the results

of the analyses using this measure were very similar to those using the measure of peak amplitude, we will not discuss them further.

2. The interaction was also significant when the amplitude were normalized using the procedure recommended by McCarthy and Wood (1985).

3. We are grateful to Stan Dehaene, Mike Posner, and Don Tucker for providing their data and permitting us to use them. We also thank Joe Dien for assistance with the application of BESA to these data.

4. The values for the dipole location parameters for their Experiment 1 data are within the corresponding ranges for our data. The values for their Experiment 2 data are deviant with respect to the z parameter. However, the residual variance for these data is relatively high, indicating a poorer fit for their Experiment 2 dipole.

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