Slamming on the Brakes: An Electrophysiological Study of Error Response Inhibition

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Introduction

The human cognitive system can rapidly detect errors, correct them, and adjust behavior to prevent future errors. This basic executive control function is critical for survival, yet little is known about how the brain processes errors. In this study, we use electrophysiological measures to address two fundamental questions concerning the neurocognitive substrates of error processing.

In reaction time and typing tasks, error responses are less forceful than correct responses (e.g., Rabbitt, 1978) Why this is so remains unclear: the error response may be weak (i.e., pre-programmed to be smaller), correct responses or error corrections may compete with the error, or inhibitory processes may suppress the error once it is detected.

In unidirectional, single joint movements, a burst of **antagonist muscle activity** accompanies the activity in the agonist muscle. A number of studies suggest that the antagonist activity may be involved in **braking the movement** (Gordon & Ghez, 1987; Karst and Hasan, 1987). One can argue that the agonist muscle propels the response and the antagonist brakes it. Observing increases in antagonist muscle activity on error trials would provide direct evidence for error inhibition. Thus, our first question is:

Question 1: Do inhibitory processes reduce the force of error responses?

The Error-Related Negativity (ERN) is an event-related brain potential component that may shed light on the mechanisms by which the brain monitors behavior and corrects errors. The onset of the ERN is roughly concurrent with the start of an error response in speeded reaction time tasks (see Falkenstein et al., 1991; Gehring et al., 1993). Dipole modeling studies in humans and field potential recordings in monkeys both suggest that a **medial frontal structure**, possibly the **anterior cingulate cortex**, gives rise to the ERN (Dehaene et al., 1994; Gemba et al., 1986).

The functional significance of the ERN (and the neural tissue that generates it) is a matter of controversy:

- The ERN may manifest processes involved in **detecting and recovering from errors**. In some tasks more ERN activity is observed when corrective action occurs (Gehring et al., 1993).
- Studies have argued that the ERN may reflect **error detection processes only**, based on evidence that the ERN can be dissociated from corrective action (Miltner et al., 1997; Scheffers et al., 1996).
- Carter et al. (1998) proposed that the anterior cingulate (and any cingulate activity reflected by the ERN) **detects conflict between responses**, rather than errors per se. In this scenario, the cingulate detects when errors are likely to occur.
- Other, largely unexplored possibilities exist: the ERN could reflect **affective or motivational processes** resulting from error or conflict detection.

Question 2: What is the function of the medial frontal activity reflected by the ERN?

Method

12 participants performed a choice reaction time task in which they responded according to the identity of a central letter of a visual letter string (HHHHH, SSHSS, SSSSS, HHSHH; see Eriksen & Eriksen, 1974). Participants responded with one arm if the letter was "H" and with the other arm if the letter was "S." Responses consisted of fast, isometric elbow extensions. Participants gripped a joystick and responded by pressing downward against a zero-displacement dynamometer, with 2 lbs. set as the threshold at which a response was recorded.

Errors consisted of trials where participants responded with the incorrect arm. Participants were asked to **correct the errors**, by making the correct response following each error.

Measures:

- Response force.
- Integrated agonist (triceps) EMG activity.
- Integrated antagonist (biceps) EMG activity.
- Event-related brain potentials (38 scalp electrodes), recorded from .01 to 100 Hz using tin electrodes in a nylon mesh cap.

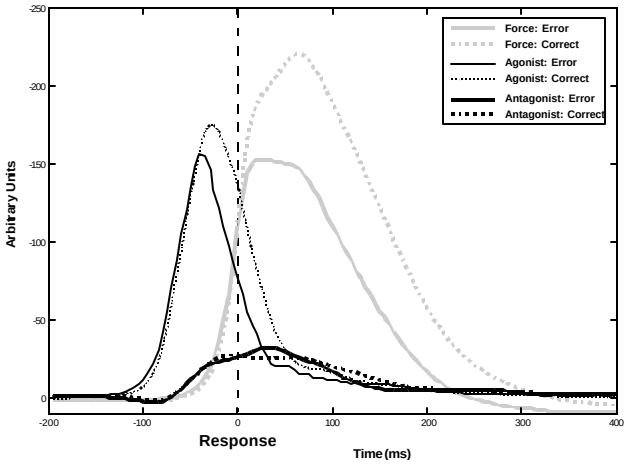
Results

All differences reported here were established with within-subjects ANOVAs, $p<.05$.

Behavioral data:

- Mean correct reaction time: 361 ms.
- Mean error reaction time: 328 ms.
- Mean proportion correct: .94.

Figure 1. Errors are less forceful than correct responses.

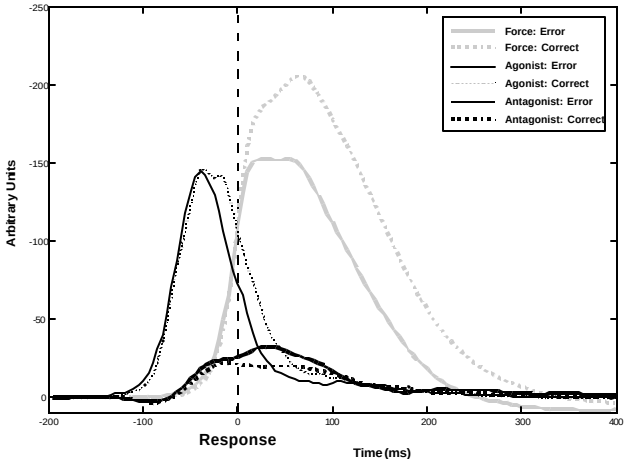


This figure compares correct and error trials in response force, agonist EMG, and antagonist EMG.

- Error responses are less forceful than correct responses.
- The antagonist activity is larger on error trials than on correct trials.
- Agonist activity is smaller on error trials than on correct trials.

These data are consistent with the occurrence of error inhibition. The effect on the antagonist muscle activity is fairly small, however. Because antagonist activity can include pre-programmed braking as well as on-line compensatory adjustments (see Gordon & Ghez, 1987), we present other analyses in the following figures that better isolate compensatory braking activity.

Figure 2. Error vs. correct responses matched on agonist muscle activity: Isolating the role of the antagonist in braking the response.

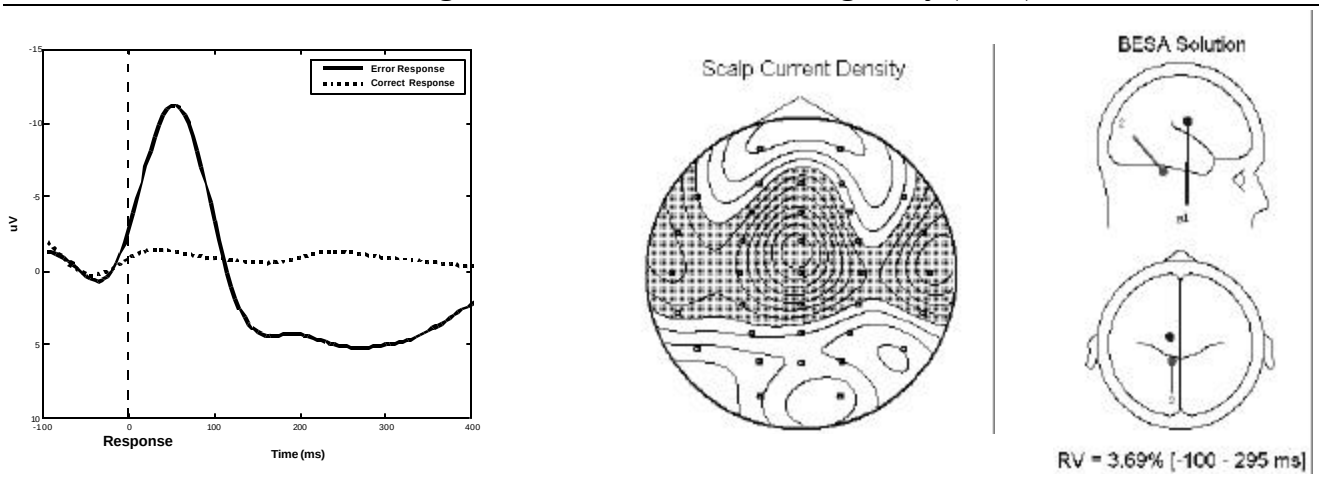


To isolate the role of the antagonist muscle in compensatory braking, we matched trials on the amount of agonist activity (peak amplitude). This presumably holds constant any contribution of pre-programmed braking activity. If antagonist activity is involved in braking error responses, then this comparison should still show (1) a difference in error and correct antagonist EMG and (2) that error response force is smaller than correct response force.

This figure compares correct and error trials in response force, agonist EMG, and antagonist EMG. The data suggest that the **antagonist muscle activity does indeed contribute to braking the movement on error trials.**

- **Error responses are less forceful than correct responses**, even when the initial agonist burst is the same size. This suggests that errors are not simply programmed to be less forceful but that inhibitory processes cause the force reduction to occur after the initial agonist burst.
- The **antagonist activity is larger on error trials** than on correct trials.
- The **agonist activity on error and correct trials diverges soon after the peak**. This suggests that the error response is being suppressed before the onset of the overt response.

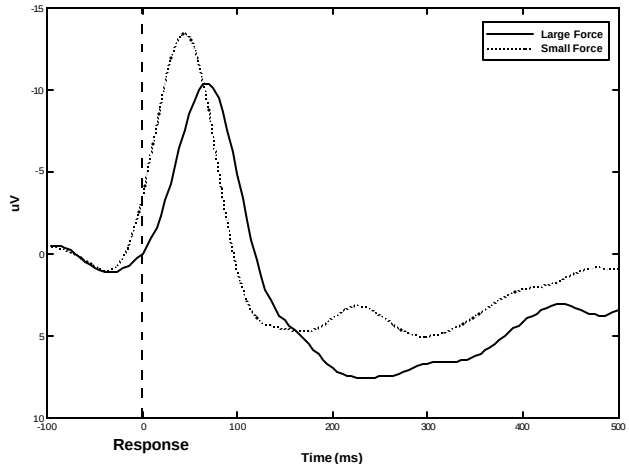
Figure 3. The Error Related Negativity (ERN).



Left Panel: The ERN was evident on error trials, consistent with previous studies using tasks similar to the one here. This is the waveform from the FCz electrode. The middle panel shows a map of scalp current density (Perrin et al., 1989), with the shaded areas representing regions where current flowed into the head. Contour line spacing is .055 uV/cm^2. The ERN is evident as a focal current sink at the FCz electrode.

Right panel: Using Brain Electrical Source Analysis (BESA: Scherg, 1990), we found that a **two dipole solution** accounted well for the scalp topography of the ERN. The dipole corresponding to the ERN shows a localization consistent with a **medial frontal source**, possibly in the **anterior cingulate cortex**. This result is similar to the dipole solutions in several previous studies (e.g., Dehaene et al., 1994; Miltner et al., 1997).

Figure 4. The ERN occurs earlier when error responses are less forceful.

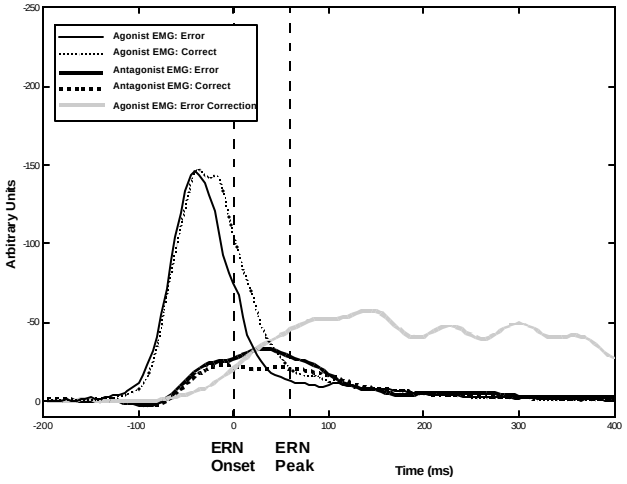


We examined the ERN at the FCz electrode as a function of the force of the error, dividing the error trials into large-force and small-force averages (median split).

- The ERN occurred earlier when responses were less forceful.
- The amplitude difference was marginally significant, with the ERN tending to be larger when errors were less forceful.

These data could be consistent with the ERN being involved in detecting or inhibiting the error. In particular, the latency difference would be consistent with the view that effective response inhibition is more likely when the error is detected quickly.

Figure 5. Does the ERN occur too late to reflect error detection?

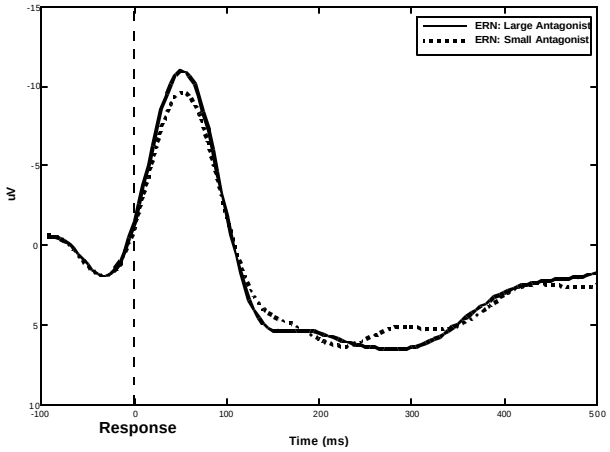


The analyses presented in Figure 2 suggest that error detection happens well before the response. The agonist EMG on error trials is reduced immediately following the peak. Error detection must occur before this reduction. This figure shows the time of the onset of the ERN and its peak, relative to EMG measures of corrective behavior.

- The ERN begins after the agonist muscle shows the effects of error suppression.
- The peak of the ERN occurs after the enhancement in antagonist muscle activity on error trials.
- The ERN peak occurs after the onset of agonist EMG activity associated with the error correction (i.e., in the arm opposite to the error).

These data are difficult to reconcile with the theory that the ERN manifests error detection activity. The timecourse data suggest that **the ERN must occur after error detection.**

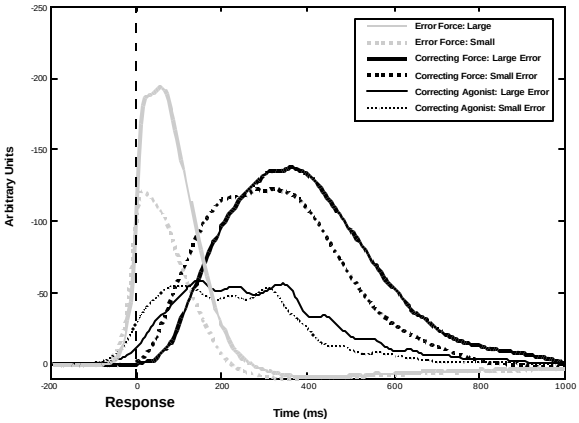
Figure 6. The ERN is not related to antagonist braking activity.



To determine whether there is a relationship between ERN activity and the antagonist EMG enhancement on error trials, we compared ERPs from trials with relatively large antagonist EMG activity to another group of trials with smaller antagonist activity. To do this, we matched each error trial to another error trial in error response force. We then identified the response with more antagonist EMG activity in each pair. We averaged ERPs from the large-antagonist trials to the ERPs from the small-antagonist trials. Presumably, more inhibitory activity was present on trials with large antagonist EMG.

- There is no relationship between the ERN and the antagonist muscle activity involved in braking the movement. Its relationship to response force must result from some other process that correlates with response force.

Figure 7. Error force is modulated by response conflict.



In addition to braking mechanisms, response conflict may contribute to the reduction in force on error trials: on most error trials, error corrections quickly followed the error response. Conflict (response competition) between the correction and the error response could reduce the force of the error. This figure shows the EMG and force activity for the limb that corrected the error, plotted with the error force from small and large force trials.

- Small-force error responses were associated with earlier error corrections (more response conflict) than large-force errors.

The results suggest that one factor contributing to the reduction in force on error trials is competition from the correction response.

The ERN data raise the intriguing possibility that the ERN is earlier on small-force error trials because error corrections are earlier on those trials.

Summary and Conclusions

1. **Error inhibition via the antagonist muscle.** The enhancement of antagonist activity on error trials points to the existence of **inhibitory processes** that reduce the size of the error even before the error response is evident. The **antagonist muscle** appears to play a critical role in inhibiting the error response, although we were not able to identify ERP activity associated with that inhibitory process. Another factor contributing to the reduction in response force appears to be **response competition** from the correction response.

2. **Medial Frontal Error Processing Activity.** There are several interpretations of the ERN that accommodate the observations that the **ERN occurs after error detection**, that **it is unrelated to antagonist braking activity**, and that **its latency parallels the latency of error corrections**.

    a. The process reflected by the ERN **may monitor or detect the conflict between the error response and the error correction**. This is consistent with the formulation of Carter et al. (1998), except that the conflict occurs between the error and the correction to that error, not (as in Carter et al.'s theory) between production of the error and production of the normal correct response.

    b. The process reflected by the ERN **may be involved in initiating compensatory activity**. This would be consistent with theories linking the cingulate and other medial frontal structures with the initiation of action (Picard & Strick, 1996).

    c. Finally, the lateness of the ERN would be consistent with it being involved in **some process that evaluates the motivational significance of the error**, after it is detected. It is possible that error corrections are initiated in response to this evaluative activity. Such an interpretation would be consistent with the role of the anterior cingulate and associated structures in affective processing (Devinsky et al., 1995).

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