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# Toward a More Sophisticated Response Representation in Theories of Medial Frontal Performance Monitoring: The Effects of Motor Similarity and Motor Asymmetries

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**Cognitive control in the posterior medial frontal cortex (pMFC) is formulated in models that emphasize adaptive behavior driven by a computation evaluating the degree of difference between 2 conflicting responses. These functions are manifested by an event-related brain potential component coined the error-related negativity (ERN). We hypothesized that the ERN represents a regulative rather than evaluative pMFC process, exerted over the error motor representation, expediting the execution of a corrective response. We manipulated the motor representations of the error and the correct response to varying degrees. The ERN was greater when 1) the error response was more potent than when the correct response was more potent, 2) more errors were committed, 3) fewer and slower corrections were observed, and 4) the error response shared fewer motor features with the correct response. In their current forms, several prominent models of the pMFC cannot be reconciled with these findings. We suggest that a prepotent, unintended error is prone to reach the manual motor processor responsible for response execution before a nonpotent, intended correct response. In this case, the correct response is a correction and its execution must wait until the error is aborted. The ERN may reflect pMFC activity that aimed to suppress the error.**

**Keywords:** anterior cingulate, error correction, error-related negativity, inhibition, motor representation

## Introduction

It is commonly believed that activity in the posterior medial frontal cortex (pMFC) reflects a monitoring function in which the outcome of a motor plan is evaluated by a computation that operates upon representations of the appropriate/expected and inappropriate/unexpected response alternatives. For example, several models of pMFC function postulate the computations that are sensitive to the similarity between the 2 representations, ranging from a direct comparison of the correct and error-response representations (comparator model, Bernstein et al. 1995; Falkenstein et al. 1996), to a comparison of the reward outcome associated with one stimulus-response pair with that associated with another (reinforcement learning-error-related negativity [RL-ERN] model, Holroyd and Coles 2002; Holroyd et al. 2005; error-likelihood model, Brown and Braver 2005), to a comparison of the discrepancy between the predicted and actual outcomes of a response (predicted response-outcome model [PRO], Alexander and Brown 2010, 2011). Another prominent model, the conflict monitoring model (Carter et al. 1998; Yeung et al. 2004) postulates computation sensitive to the conflict between the 2 responses. The model does not include a comparator process per se, but the computation at the heart of the model depends on the extent to which the error and correct responses are congruent or compatible. Hence, the model implicitly assumes that 2 responses can be mutually compatible or congruent to greater or lesser degrees, and the amount of mutual inhibition when 2 responses are active will depend on this type of similarity. (This property of the model is less obvious than the others, because the modeling work has not been extended to tasks where the compatibility or congruence can vary.)

One line of research testing these models uses measures of the ERN, an event-related brain potential associated with the execution of errors in choice reaction time (RT) tasks (Falkenstein et al. 1990; Gehring et al. 1993; see Gehring et al. 2012 for a review). The ERN is often assumed to originate in the dorsal anterior cingulate cortex (dACC), a division of the pMFC (Dehaene et al. 1994; Herrmann et al. 2004; Hochman et al. 2009). Although a great deal of progress has been made in testing these models (see Gehring et al. 2012, for a review), the field would benefit from some new theoretical directions and empirical approaches. For example, despite the importance of motor representations in these models, there has been very little progress in specifying the details of the representations, such as how representational elements map onto movement features such as side, direction, or extent. Yet it is clear that such detail is needed: A large literature exists showing that response representations can vary in the amount of information they represent and that computations involving those representations will differ depending on that information (Buys et al. 1986; Humphrey 1986; Schieber 1990, 2001; Huntley and Jones 1991; Sanes et al. 1995; Schieber et al. 2005).

A newer model illustrates a promising approach for integrating the motor representations into a theory of the ERN. The parallel task set model (PTS, Seymour and Scumacher 2009, an elaboration of the executive process interactive control model of Meyer and Kieras 1997) describes a process that resolves post error conflict in speeded-choice tasks. In this model, a manual motor processor handles requests to prepare specific responses. Conflict occurs when a request to prepare a motor response arrives at the manual motor processor and that request differs from a request that is already being processed. Conflicts of this type will occur between prepotent (e.g., the stronger response channel) unplanned errors and preplanned nonpotent correct responses. The model suggests that conflict resolution involves suppressing the erroneous motor representation and that the resolution process depends on the prepotency of the error response: The more prepotent is the erroneous tendency, the more difficult is the processing needed to suppress the error, and thus, the more likely it is that the error will reach the manual motor processor before the preplanned correct response, resulting in an overt error. In this case, the preplanned correct response is a correction and its execution must wait until the error is suppressed. The PTS model suggests that the difficulty of conflict resolution will differ depending on the relationship between the representation of the prepotent error response and that of the more deliberative correct response.

The PTS model offers an attractive framework for understanding the ERN. In particular, if the ERN reflects an error-aborting process, the timing of the process is consistent with the findings of Burle et al. (2008), which showed that the ERN appeared in the interval between the error and the error correction, that its peak was larger when error corrections were later, and that the duration of the ERN depended on the time needed to correct the error. These findings were interpreted to contradict the conflict model's prediction that the ERN will be smaller when error corrections are later and suggested that the ERN reflects a process aimed to expedite error correction.

The PTS model suggests that the difficulty of conflict resolution will differ depending on the relationship between the representation of the prepotent error response and that of the more deliberative correct response. In the current study, we tested 4 predictions drawn from the idea that the ERN reflects the error-aborting process described by the PTS model. In some cases, these predictions run counter to claims of extant models of the pMFC.

1) The difficulty in aborting an error will depend on how prepotent the error response is relative to the error correction. Therefore, the greater ERN is expected when the error is prepotent/correct is nonpotent than when the error is nonpotent/correct is prepotent. This form of asymmetry is not addressed in studies designed to test the error-correct dissimilarity assumptions of the comparator model. In those studies, dissimilarity is symmetrical (e.g., the amount of dissimilarity from the portion of the error not shared with the correct response is equal to the amount of dissimilarity from the portion of the correct response not shared with the error, Bernstein et al. 1995; Gehring and Fencsik 2001; Arbel and Donchin 2011). Error-correct asymmetries would suggest a need for revision of the comparator models, because if one response is more important than the other in the dissimilarity computation, there is more to this computation than simple mismatch detection.
2) An increase in error prepotency relative to the correct response will cause an increase in the number of overt errors. If the ERN reflects the error-aborting process, then an increase in ERN amplitudes should accompany the increase in the number of overt errors. This prediction contradicts the prediction of error probability models (such as RL-ERN, PRO, and the error-likelihood models), which hold that the ERN amplitude reflects the degree to which the error is unexpected.
3) An increase in error prepotency relative to that of the correct response will also result in slower and fewer corrections. In contrast, both the comparator (Falkenstein et al. 1991; Gehring et al. 1993; Coles et al. 2001) and the conflict detection models conceive of the ERN as a signal of error detection in which more error detection activity makes error corrections more likely.
4) Correcting the error response requires aborting only those movement features that are not shared with the correct movement (Meyer and Kieras 1997). Hence, more error-aborting activity, evident as greater ERN amplitudes, will be required when the error and the correct response are dissimilar, sharing fewer motor features. This prediction is derived from the PTS model indirectly, by considering how movements are represented as movement features (Meyer and Kieras 1997). A correct response can take over the manual motor processor more quickly—making a correct response more likely—when the 2 responses are similar, sharing a greater number of movement features. Hence, it should be more difficult to abort the error when the error and the correct response are dissimilar, being more independent of each other. This is in contrast with the assumption that the ERN should grow larger with error-correct motor similarity, attributed to the conflict detection model by Gehring and Fencsik (2001).

To investigate predictions (1) to (3), we tested extreme right-handed participants in 2-choice tasks that required choosing between the right and the left index fingers or the right index and middle finger. Evidence suggests that the right hand is dominant over the left hand (see Hammond 2002 for a review) and the index finger is dominant over the middle finger (Hager-Ross and Schieber 2000; Keen and Fuglevand 2004; Schieber et al. 2005; Coxon et al. 2007). In right-handed individuals, this makes the right index more potent than the left index and the index finger more potent than the middle finger response. The more potent effector should correspond to the more prepotent dominant response tendency (Wiersema et al. 2005), and should thus generate greater ERN, more errors, and fewer and slower corrections.

Greater ERN and fewer and slower corrections when the error is prepotent than when it is nonpotent would suggest that the error and the correct response are not equally weighted in the computation that results in the ERN effect. Nevertheless, it would not be informative as to which response is driving the asymmetry effect. The ERN could be greater due to the prepotent error or due to the nonpotent correct response. We examined whether it is the error that is most critical to the ERN effect in a further comparison of a 2-choice response pairing in which both responses are prepotent with a 2-choice response pairing in which both responses are nonpotent. We compared blocks pairing 2 movements of the right index finger (index finger moved between one key and the immediately adjacent key) with blocks pairing 2 movements of the left index finger. If the ERN is greater and error corrections are fewer and slower in the task pairing 2 prepotent responses than in the task pairing 2 nonpotent responses, then the prepotent error response must be responsible for the asymmetry in a task pairing a prepotent and nonpotent response.

We examined the hypothesis (4) by comparing the errors of hand (right vs. left index) with the errors of finger (right index vs. right middle finger) to the errors of movement (2 movements of the right index finger). The right and left index responses share fewer motor features than right index and right middle finger responses (Fetz and Cheney 1980; Bremner et al. 1991; Matsumaura et al. 1996; Schieber 2001), which in turn share fewer features than 2 movements of the right index finger. Therefore, greater ERN, more errors, and fewer and slower corrections should be observed in hand errors than in finger errors and in finger errors than in movement errors.

In addition to these analyses focusing on the ERN, we also report post hoc analyses of the early Pe, a positive-polarity component that often follows the ERN, because of the wide interest in that component. The late fronto-parietal Pe and the early fronto-central Pe are 2 error-related positive components that may reflect different processes (Arbel and Donchin 2009). The question of whether the ERN and early Pe can be dissociated is a timely issue in the literature on these components (see Arbel and Donchin 2009; Gehring et al. 2012).

## Materials and Methods

### *Analytic Approach and Design*

We designed 2 complementary studies to determine whether the ERN and error correction are preferentially sensitive to the error responses and to the degree that the error motor program is independent from the correct motor program. We recruited only strongly right-handed participants (all ranked within the 10th right decile of the Edinburgh inventory, Oldfield 1971), because participants who are less strongly right-hand dominant may be less likely to show right-left asymmetries. In study 1, participants rotated between blocks of right index and left index finger responses (Fig. 1, upper panel), to blocks in which they moved the right index between keys (Fig. 1, upper panel), and blocks where they moved the left index between keys (Fig. 1, upper panel). We refer to the 3 conditions as the "hand pair," "right movement pair," and "left movement pair" conditions, respectively. The purpose of study 1 was 2-fold. First, we tested hypothesis (1) to (4) by comparing right index finger errors (left index correct) with left index finger errors (right index finger correct). Secondly, we examined which response, error or correct, is the most important for the computation that generates the ERN by comparing blocks pairing 2 movements of the right index finger with blocks in which both movements were left index finger movements.

In study 2, participants rotated between blocks in which they had to choose between the index and the middle finger of the right hand (Fig. 1, middle panel) and blocks in which they moved the right index finger between 2 keys (Fig. 1, middle panel). We refer to the 2 conditions as the "finger pair" and "movement pair," respectively. The purpose of study 2 was 2-fold. We first aimed to replicate the error-correct asymmetry within a hand, adopting the logic used in study 1, by comparing right index finger errors (right middle finger correct) with right middle finger errors (right index finger correct). Thus, as in the right–left hand comparison in study 1, if the ERN and error correction are more sensitive to either the error or the correct response, an asymmetric pattern should be observed showing greater ERN and fewer and slower corrections in one pair over the other. Secondly, we tested hypothesis (4), namely, the assumption that greater ERN and fewer corrections would be observed when the error motor program is more independent from the correct motor program. We compared index finger errors from the finger pair with similar index finger errors from the movement pair. If the ERN and error corrections are sensitive to motor features that the error does not share with the correct response, greater ERN and fewer corrections are expected in finger pair than in movement pair errors.

Also, our design allowed us to test whether the ERN would react to an inaccurate scaling of the movement. Although this was not the primary test of interest, the test can show whether the ERN is sensitive to features of the motor representation other than those that distinguish between the correct and erroneous effector. In the movement pair, the resting position is the key pressed for the immediately preceding response. Thus, a response could consist of either a downward movement (key needed for the current response is the same as the previous trial; Fig. 1, lower panel) or a sideward movement (the key needed is the opposite key; Fig. 1, lower panel). "Downward errors" (the index incorrectly tapped the key it already lay upon) are shorter and involve fewer submovements than "sideward errors" (the index incorrectly moved up, across, and then tapped the adjacent key). If the ERN is only sensitive to the gross level of detail specified in the response representation (e.g., effector), no difference is expected between downward and sideward errors because both are produced by the same effector. However, if the ERN

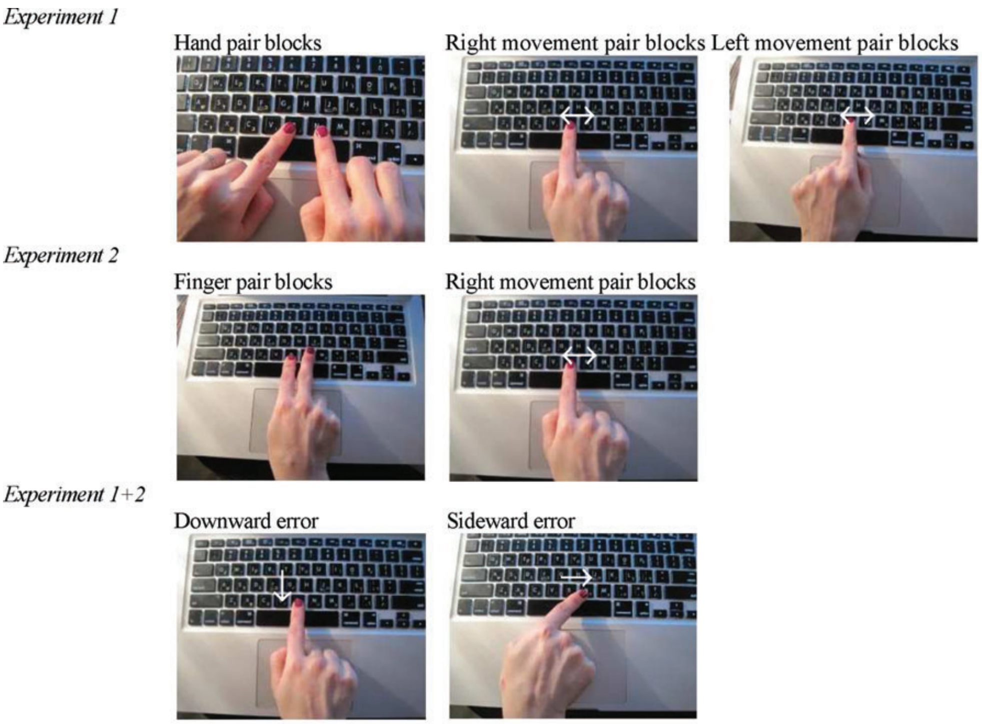

**Figure 1.** Studies 1 and 2. The experimental conditions.

is also sensitive to the fine level of detail specified in the accurate scaling of the movement, it should react to the more detailed representation of sideward errors.

### *Participants*

Twenty-three undergraduate students at the University of Michigan participated in study 1 (13 females, mean age 19.1 years, standard deviation [SD] = 3.22) and 19 participated in study 2 (12 females; mean age 19.3 years, SD = 3.34). All participants were in good health (no self-report of any neurological or psychiatric disorders, learning disabilities, major head trauma, or recent regular use of psychoactive drugs). All were extreme right handed (all ranked within the 10th right decile of the Edinburgh inventory, Oldfield 1971) with normal or corrected-to-normal vision.

### *Flanker Task*

Participants performed an arrowhead version of the Eriksen flanker task with congruent (i.e., > > > > > or < < < < <) or incongruent (i.e., > > < > > or < < > < <) trials (Eriksen and Eriksen 1974). On each trial, a central fixation cross was presented for 500 ms followed by 1 of the 4 stimulus arrays appearing for 75 ms. The probability of appearance of each of the stimulus arrays was 0.25. Participants responded on the "B" and "N" keys (adjacent keys) of a low profile key keyboard (Apple, Inc., Cupertino, CA, United States of America) to the central arrow, which appeared in the same location as the fixation cross. Subsequent to the presentation of stimulus array, participants were given 1000 ms to respond, after which a fixation cross appeared, indicating the beginning of the next trial. In study 1, participants underwent 3 types of blocks differentiated by responding effectors. On one-third of the blocks (hand pair blocks) responses were made with the left or the right index finger. On the other two-thirds (right and left movement pair blocks), responses were made with the right or the left index finger (in separate blocks) moved between 2 adjacent keys. In study 2, on half of the blocks responses were made with the right index finger or with the right middle finger (finger pair blocks). On the other half, responses were made with the right index finger moved between the 2 keys (movement pair blocks). Blocks were pseudorandomly ordered in both studies. The various conditions were divided between the studies in this fashion to allow for the key contrasts to be performed as within-subject or between-subject contrasts, while minimizing confusion on the part of the subjects by presenting each subject with only 2 conditions. This also had the advantage of allowing us to maximize the number of trials in the critical right finger and movement pair conditions.

### *Procedure*

Participants were seated 57 cm from the computer screen. Participants were instructed to respond as quickly and as accurately as possible. Instructed corrections are usually slower than noninstructed corrections and thus may be activated by a different mechanism (Fiehler et al. 2005). To increase the proportion of rapid, "automatic" corrections, participants were not instructed to correct their errors. In study 2, in the movement pair (single-finger) blocks, participants were instructed to keep the responding finger on top of the last key pressed (following stimulus presentation or following a correction response) to allow for a comparison of downward and sideward errors. In both studies 1 and 2, during a practice block, the experimenter verified by visual inspection that responding effectors are positioned according to the experimental instructions. Participants received 12 blocks of 200 trials with each block initiated by the participants. At the end of each block, subjects were informed of the proportion and average RT of correct responses to encourage fast and accurate responding.

### ***Electrophysiological Recording and Analysis***

The electroencephalography was recorded at 512 Hz using an ActiveTwo Biosemi system (Amsterdam, The Netherlands) from 64 Ag/AgCl electrodes relative to a common mode sense (CMS) active electrode and to a driven right leg (DRL) passive electrode. The data were recorded from direct current to 104 Hz (−3 dB down at one-fifth the sampling rate). The CMS–DRL electrodes form a feedback loop, which drives the average potential close to the amplifier zero, as per BioSemi's standard design (http://www.biosemi.com/faq/cms&drl.htm). Electrooculogram was recorded from electrodes placed above and below the left eye and on the outer canthi of both eyes.

Data were analyzed offline using EEGLAB (Delorme and Makeig 2004). The data were downsampled to 256 Hz following application of a finite impulse-response antialiasing filter and referenced offline to the 2 mastoid electrodes. Epochs were time-locked to correct and erroneous responses and consisted of a window of 500 ms prior to 1500 ms following the response. Epochs were excluded if they contained amplitudes greater than ±500 µV or had power in the 0–2- or 20–40-Hz frequency ranges that were greater than ±50 dB. (The amplitude range used for rejection was fairly large so that trials with correctable eye movements were not eliminated.) The remaining epochs were inspected visually for movement artifact, drift, or any other impurities. Oculomotor movements were corrected using the procedure described by Gratton et al. (1983). All error-related components of interest were measured in average response-locked waveforms with the ERN as the most negative peak between −20 and 80 ms, the early Pe as the most positive peak between 80 and 180 ms, and the late Pe as the most positive peak between 300 and 400 ms (Arbel and Donchin 2009), following the response, relative to a preresponse baseline period of −150 to −50 ms. This measure was calculated for both error and correct trials, separately for each experimental condition. The statistical analyses were performed on data from electrode sites yielding the largest ERN amplitudes: Fz, FCz, and Cz.

## Results

In study 1, we tested for an effect of response asymmetry in error processing by comparing, in the hand pair, right index with left index errors. A repeated-measures analysis of variance (ANOVA) with error potency (right vs. left) as the within-subject variable was performed on the behavioral indices and on the amplitude of the electrophysiological components of interest. We further tested which response is driving the asymmetry effect by comparing, in the movement pair, right index with left index errors (collapsed across downward and sideward errors). A repeated-measures ANOVA with response potency (right vs. left) as the within-subject variable was performed on the behavioral indices and on the amplitude of the electrophysiological components of interest. We also tested the effect of the independence of the error and correct motor representations (based on shared movement features) by comparing hand pair errors (collapsed across right and left) with movement pair errors (downward errors, collapsed across right and left). Repeated-measures ANOVAs with an error-correct overlap (hand pair vs. movement pair) as the within-subject variable were performed on the behavioral indices and on the amplitude of the electrophysiological components of interest.

In study 2, we tested the effect of response asymmetry in error processing by comparing, in the finger pair, index with middle finger errors. Repeated-measures ANOVA with error potency (index vs. middle) as the within-subject variable was performed on the behavioral indices and on the amplitude of the electrophysiological components of interest. We tested the effect of the error motor independence by comparing index finger errors from the hand pair with downward errors from the movement pair. Repeated-measures ANOVA with an error-correct overlap (finger pair vs. movement pair) as the within-subject variable was performed on the behavioral indices and on the amplitude of the electrophysiological components of interest. Between studies 1 and 2, we tested the same effect by comparing right index errors from the hand pair (study 1) with right index errors from the finger pair (study 2).

### *Behavioral Data*

Because of an insufficient number of errors on congruent flanker trials, only incongruent flanker trials were analyzed.

#### *Initial Responses*

The error rates were quantified as the proportion of errors for each member within a pair. Error rate results are summarized in the upper panel of Figure 2. The first set of analyses examined asymmetric patterns within each pair of responses. Within a pair, the more potent/dominant effector should correspond to the more prepotent/dominant response tendency (Wiersema et al. 2005) and should thus generate more errors. In study 1, within the hand pair, participants made more errors with the right index finger than with the left index finger ($F_{1,22} = 16.57$, $P < 0.001$). Within the movement pair, the difference between the right index and the left index was not significant ($F < 1$). In study 2, within the finger pair, participants made more errors with the index finger than with the middle finger ($F_{1,18} = 7.13$, $P < 0.02$). Similar analysis on error RTs revealed no significant differences ($F < 1$, Fig. 3).

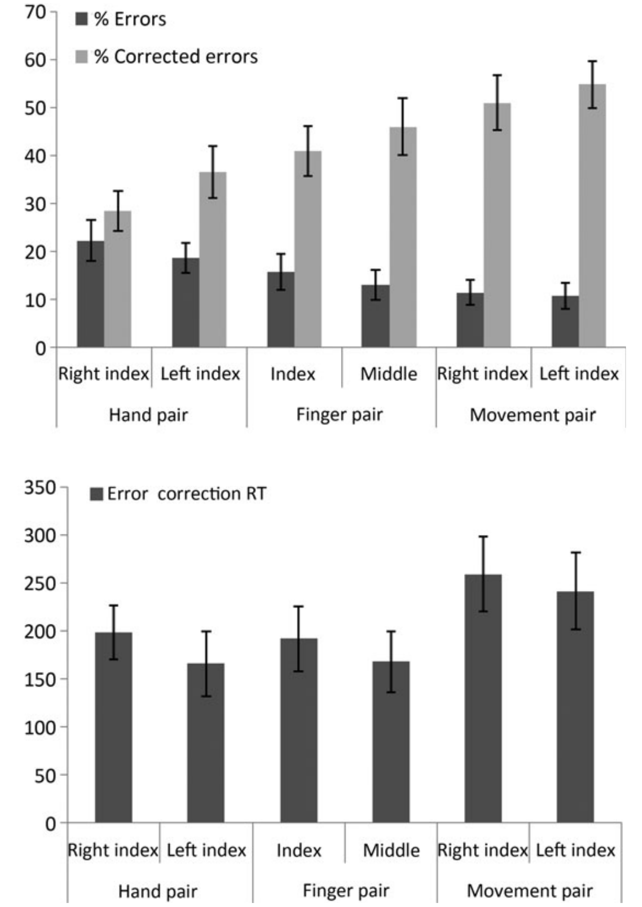

**Figure 2.** Studies 1 and 2. (Upper panel) Proportion of errors and corrected errors. (Lower panel) error-correction RT by erring effector. The greater the error representation the more the errors and the fewer and slower are the corrective responses. Error bars represent standard deviation.

The second set of analyses examined the effect of the motor independence of the error. As the upper panel of Figure 2 suggests, the less the amount of overlap between an error and its correction, the greater was the error rate. In study 1, the error rate was greater in the hand pair than in the movement pairs ($F_{1,22} = 164.46$, $P < 0.000$). In study 2, the error rate was greater in the finger pair than in the movement pair ($F_{1,18} = 27.7$, $P < 0.000$). Comparison between studies revealed a higher error rate for right index errors when they were part of a hand pair than when they were part of a finger pair ($F_{1,40} = 27.2$, $P < 0.000$). Similar analysis on error RTs revealed no significant differences ($F < 1$, Fig. 3).

#### *Error Correction*

Error corrections were defined as a correct key press that follows an incorrect key press within a trial. The error-correction rates were quantified as the proportion of corrected errors out of all errors within a condition. The error-correction rates are summarized in the upper panel of Figure 2. In general, high error-correction rates accompanied low rates of error commission. With respect to our hypothesis, first, we tested for asymmetric patterns in the error-correction rate. We hypothesized that increasing the potency of the error response relative to that of the correction reduces the error-correction rate. In study 1, within the hand pair, left hand errors were corrected significantly more often than right-hand errors ($F_{1,22} = 24.3$, $P < 0.000$). In study 2, within the finger pair, middle finger errors were corrected significantly more often than index finger errors ($F_{1,18} = 5.8$, $P < 0.03$).

The relative disadvantage in correcting the prepotent error (nonpotent correct) could result either from the prepotency of the error or from the nonpotency of the correct response. Critically, in study 1, left movement pair errors (both the error and the correct response are nonpotent) were corrected significantly more than right movement pair errors (both the error and the correct response are prepotent; $F_{1,22} = 4.5$, $P < 0.04$), suggesting that error correction is more frequent when the error and correct representations are nonpotent. Thus, the advantage in correcting the nonpotent error (with the prepotent correct response) resulted from the nonpotency of the error rather than from the potency of the correct response.

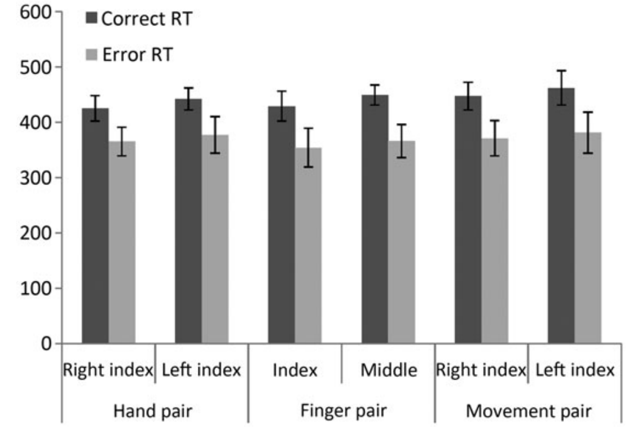

**Figure 3.** Studies 1 and 2. Error and correct response RTs. Error bars represent standard deviation.

Secondly, contrasts were carried out to test the hypothesis that error correction is facilitated when the error and correct response are more dependent, that is, consist of more overlapping movement features. Consistent with this, in study 1, the correction rate was greater in the movement pair than in the hand pair condition ($F_{1,22} = 863.7$, $P < 0.000$). In study 2, the correction rate was greater in the movement pair than in the finger pair condition ($F_{1,18} = 23.6$, $P < 0.000$). Comparison between studies revealed a greater correction rate for right index errors in the finger pair than in the hand pair condition ($F_{1,40} = 73.04$, $P < 0.000$).

As seen on the lower panel of Figure 2, in general, error-correction RTs (measured as the time from the incorrect key press to the corrective key press) revealed the same asymmetric pattern as the error-correction rate. Within the hand pair, left hand errors were corrected significantly faster than right-hand errors ($F_{1,22} = 7.6$, $P < 0.01$). A comparison between left movement pair errors and right movement pair errors aimed to elucidate the response driving the asymmetry effect; the comparison revealed a nonsignificant trend of faster corrections on left movement pair errors than on right movement pair errors ($F_{1,22} = 4.1$, $P < 0.06$). In study 2, within the finger pair, middle finger errors were corrected significantly faster than index finger errors ($F_{1,18} = 6.3$, $P < 0.02$).

Analysis of the effect of the error-correct motor overlap on error-correction RTs was only conducted between hand pair errors in study 1 and finger pair errors in study 2, because movement pair errors always involve a sideward corrective movement that is longer than the downward corrective response in the other conditions. The effect was not significant ($F < 1$).

### *Flanker Effect*

Theories that model the response conflict have thus far not included detailed response representations, making them silent as to whether a greater overlap in conflicting responses will result in greater response conflict. We examined the flanker effect (RT on correct incongruent trials minus RT on correct congruent trials) as an index of response conflict. The results consistently showed that the greater overlap resulted in greater response conflict. In study 1, the flanker effect was greater in the movement pair than in the hand pair condition (movement pair, $M = 102.4$, hand pair, $M = 51.2$ ms, $F_{1,22} = 12.44$, $P < 0.002$). In study 2, the flanker effect was greater in the movement pair ($M = 100.8$ ms) than in the finger pair condition ($M = 77.4$ ms, $F_{1,18} = 12.86$, $P < 0.002$). In a comparison between studies, a greater flanker effect was evident in the finger pair than in the hand pair condition ($F_{1,40} = 10.64$, $P < 0.002$).

### *Post Error Slowing*

Suppression of an error may make it more difficult to produce the same response on subsequent trials. Post error slowing (the difference between correct-trial RT following correct trials and correct-trial RT following errors) was statistically significant only in study 1, in the hand pair condition (post correct, $M = 428$ ms, post error, $M = 474$ ms, $F_{1,22} = 20.26$, $P < 0.001$), with no difference between the left and the right hand. Within the hand pair condition, we compared RTs of 2 types of post error-correct trials: Those in which the error and the correct response on the following trial involved the same effector, and those in which the 2 responses involved different effectors. A significant difference was observed (same, $M = 491$ ms; different, $M = 457$ ms; $F_{1,22} = 12.5$, $P < 0.002$). The same comparison for correct following the correct trials was not statistically significant.

### *Error-Related Negativity*

The analyses of the ERN focused on testing whether the ERN was sensitive to the differences within a condition in the potency of either the error or the correct response (asymmetry analysis) and whether the ERN was sensitive to the degree of motor independence of the 2 responses. Because of an insufficient number of errors on congruent flanker trials, only incongruent flanker trials were analyzed. The ERN was most pronounced at the frontocentral electrode site, FCz. Little or no ERN was observed on correct trials (a component known as the "correct-related negativity," see Ford 1999), so our analysis focused on the error-trial ERN alone.

When the response condition paired 2 different effectors, asymmetries were evident, with the ERN being greater for the prepotent error response. In study 1, as seen in the upper panel of Figure 4, the greater ERN was observed for right-hand errors than for left hand errors in the hand pair ($F_{1,22} = 9.35$, $P < 0.006$). Asymmetries were not evident when the condition paired 2 movements of the same effector: No significant difference was observed between the 2 index finger responses in the movement pairs ($F < 1$, collapsed across the right and left movement pairs). Thus, the asymmetries were isolated to those cases where the 2 responses corresponded to 2 different effectors.

Critically, a greater ERN amplitude was observed for the right movement pair than for the left movement pair (collapsed across downward and sideward movements; $F_{1,22} = 9.23$, $P < 0.006$), indicating that the error response is driving the ERN asymmetry.

Study 2 results were consistent with the asymmetric pattern observed in study 1. In study 2, within the finger pair, the ERN revealed the asymmetric pattern being greater for index finger errors than for middle finger errors ($F_{1,18} = 4.81$, $P < 0.041$; Fig. 4, lower panel). As in study 1, such an asymmetry was not seen within the movement pair: No significant difference was observed between the 2 index finger responses (sideward vs. downward, $F < 1$, Fig. 5).

The size of the ERN associated with a specific error movement depended on the degree of motor independence from the movement that would correct the error. In general, greater ERNs were observed when the error response overlapped less with the correcting movement. As seen in Figure 6, the greater ERN amplitude was observed in study 1 for hand pair errors than for movement pair errors (downward, collapsed across left and right pairs; $F_{1,22} = 14.43$, $P < 0.001$). In study 2, the greater ERN amplitude was observed for index finger errors in the finger pair than for equivalent movements of the same index finger (downward errors) in the movement pair ($F_{1,18} = 5.56$, $P < 0.049$). A comparison between studies revealed the greater ERN for right index finger errors in the hand pair than for right index finger errors in the finger pair ($F_{1,40} = 10.18$, $P < 0.003$, Fig. 6). Thus, the ERN grew bigger with the dissimilarity of the error and correction.

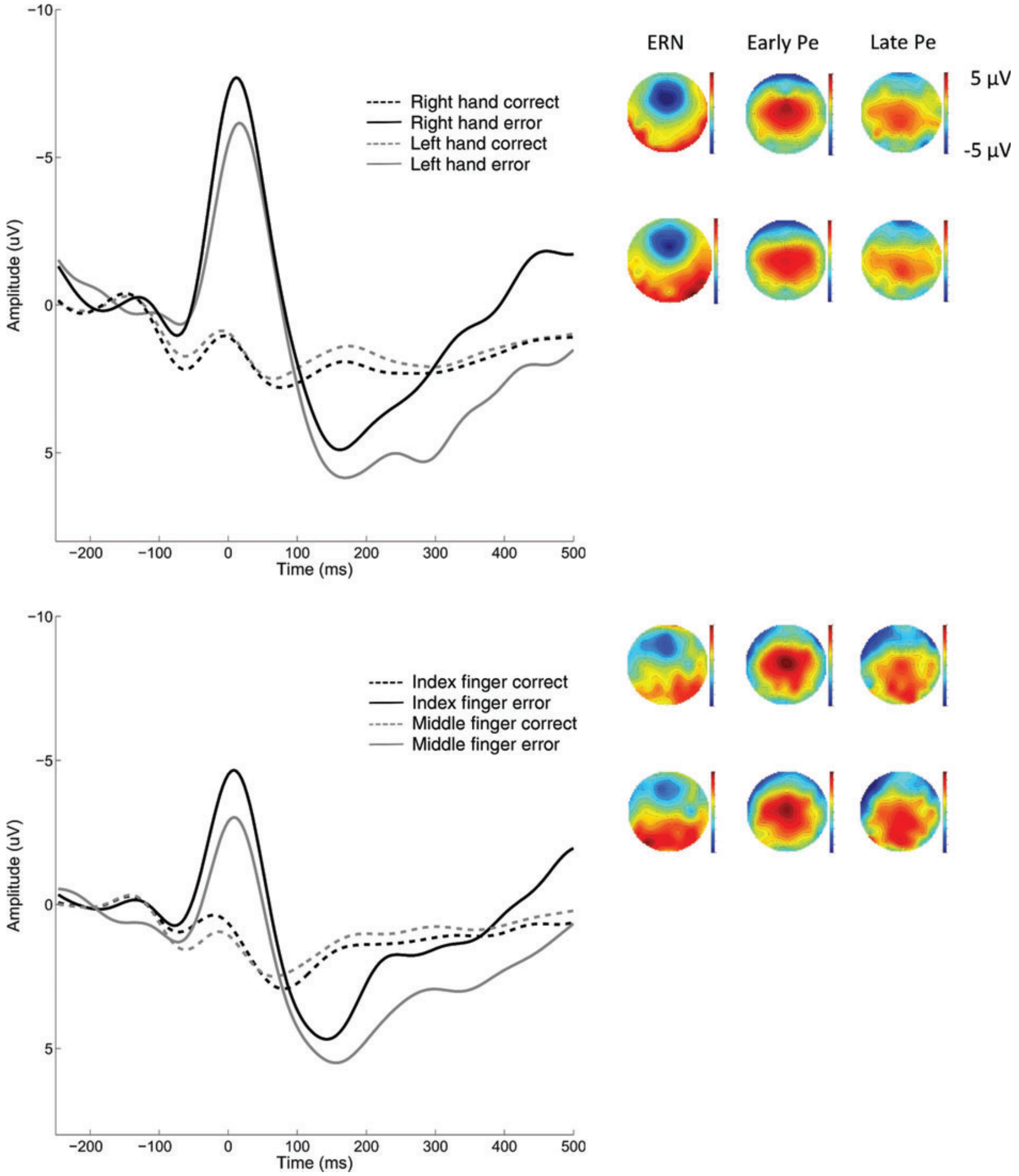

**Figure 4.** Studies 1 and 2. Within-pair comparisons. Grand average response-locked waveforms at FCz (negative polarity is plotted upward). Asymmetric patterns, with the ERN being greater for the error-response representation associated with greater information. To the right are topographic maps of error ERPs (dominant effector on top). ERN maps show the mean amplitude between −20 and 80 ms, early Pe maps show the mean amplitude between 80 and 180 ms, and late Pe maps show the mean amplitude between 300 and 400 ms.

### *The Pe*

The late Pe was hardly apparent in most of the conditions and thus was not analyzed. The early Pe, in study 1 (most prominent at Cz), did not react to error potency; however, the greater early Pe (measured at Cz) amplitude was observed for hand pair errors than for movement pair errors (downward, collapsed across left and right pairs; $F_{1,22} = 5.76$, $P < 0.03$). In the movement pair, the greater early Pe amplitude was observed for sideward errors than for downward errors (collapsed across left and right pairs, $F_{1,22} = 13.45$, $P < 0.001$). To rule out the possibility that these effects were caused by response repetition (in most of the downward movements, the error response was a repetition of the previous correct response), we compared the early Pe on downward errors that were preceded by similar (same key) downward correct responses with downward errors that were preceded by sideward correct responses. No significant differences were found ($F < 1$). In study 2, again the early Pe did not react to error potency. However, the greater early Pe amplitude was observed for finger pair errors than for movement pair errors (downward errors; $F_{1,22} = 5.96$, $P < 0.02$). In the movement pair, the greater early Pe amplitude was observed for sideward errors than for downward errors ($F_{1,18} = 9.50$, $P < 0.006$, Fig. 5). A comparison between studies revealed no significant difference between right index finger errors in the hand pair and right index finger errors in the finger pair ($F < 1$). Thus, the early Pe was not sensitive to the potency or the motor independence of the error. It was sensitive to the number of

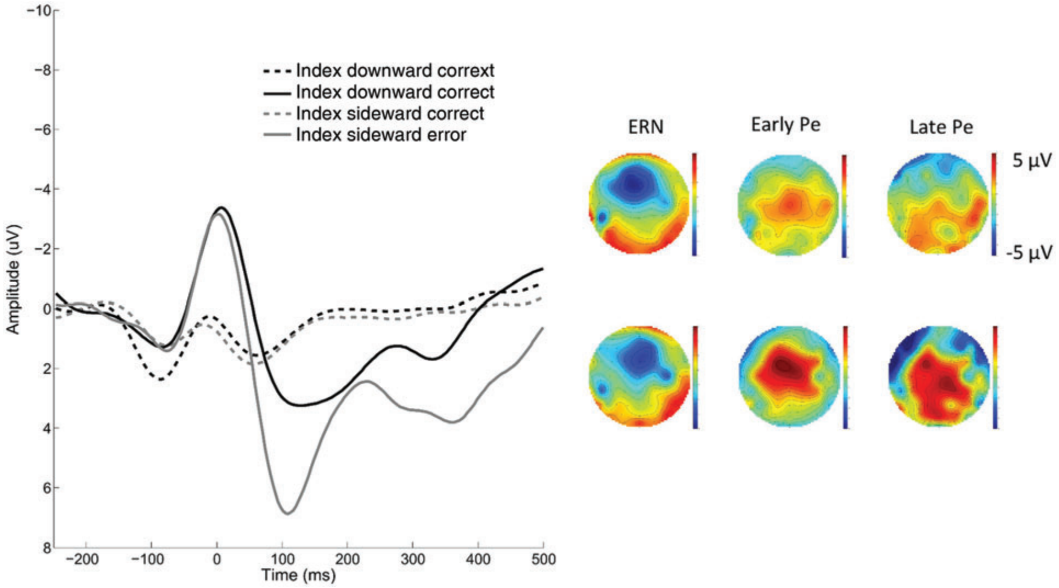

**Figure 5.** Study 2. Movement pair. Downward versus sideward errors. Grand average response-locked waveforms at FCz (negative polarity is plotted upward). The early Pe but not the ERN was greater on sideward than on downward errors. To the right are topographic maps of error ERPs (downward errors on top). ERN maps show the mean amplitude between −20 and 80 ms, early Pe maps show the mean amplitude between 80 and 180 ms, and late Pe maps show the mean amplitude between 300 and 400 ms.

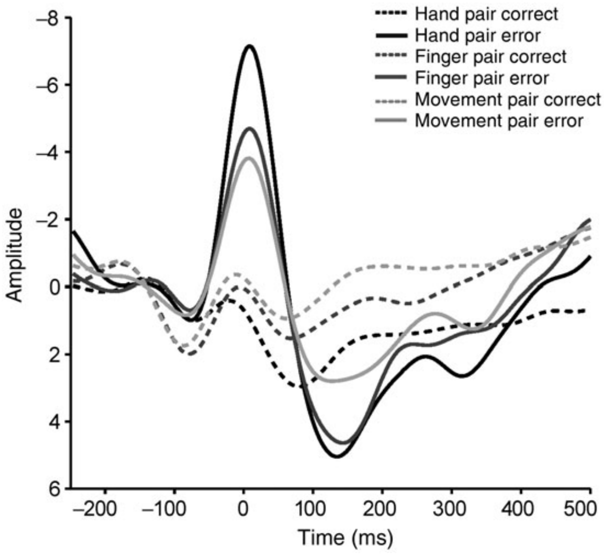

**Figure 6.** Studies 1 and 2. Between pairs comparisons. Grand averages at FCz for response-locked waveform (negative polarity is plotted upward). Waveforms represent right index downward errors. The more dissimilar the error and its correction the greater the ERN.

submovements involved and the accurate scaling of the incorrect movement (sideward errors involve more submovements and are longer than downward errors).

## Discussion

Most models of medial frontal performance monitoring postulate computations that require response representations, yet extant models have not been adequately detailed in the response representations they assume. The PTS model (Seymour and Scumacher 2009), a newer model of response conflict resolution that has not yet been applied to the ERN, describes a mechanism that speeds up the execution of delayed correct responses by aborting already-active prepotent, erroneous response tendencies. The model predicts a direct relationship between the potency of the erroneous response tendency and the probability of an overt error and the RT of error corrections. Here, we suggest that the ERN reflects the difficulty of the processing needed to abort the error. Our results confirm 4 predictions drawn from this account of the ERN: The ERN was greater 1) when the error response was prepotent, 2) when more errors were committed, 3) when fewer and slower corrections were observed, and 4) when the error response shared fewer motor features with the correct response.

Each of these findings is inconsistent with one or more existing models of the ERN, suggesting that the models need to be modified. The RL-ERN model (Holroyd et al. 2005) and other models, predicting that the ERN reflects the low likelihood of the error event (Brown and Braver 2005; Oliveira et al. 2007; Alexander and Brown 2010, 2011), hold that stimulus–response conjunctions that yield fewer errors are associated with a large negative reinforcement value or a large violation of outcome expectancy. For example, according to the RL-ERN model, errors on those trials tend to result in a large change in value from very good to very bad, resulting in the greater ERN. However, in the current study, the ERN was always smaller in the conditions that yielded fewer errors (Maier et al. 2012). A more recent account of the RL-ERN model suggests that the ERN reacts to the degree to which the outcome deviates from participants' intention or goal, in addition to or instead of reacting to the degree of reward expectation (Holroyd et al. 2006; Hewig et al. 2007). This explanation may account for our data by arguing that errors resulting from prepotent response tendencies represent a larger deviation from goal than attention errors resulting from flanker processing. This explanation is plausible. However, this new account of the RL-ERN model does not specify what constitutes a task goal nor what is considered a larger deviation from task goal. According to a most recent interpretation of the model (Maier et al. 2012), goals are set by task instructions. Therefore, flanker/attention errors represent larger deviations than "confusion" errors, because unlike confusion errors—which violate a goal to respond to the target—flanker/attention errors violate both a goal to respond to the target and a goal to ignore the flanker. Moreover, flanker/attention errors are corrected less than confusion errors, because less attention is directed toward the target (Maier et al. 2008). In the current study, unintended, prepotent errors may be the equivalent of confusion errors, should thus represent a smaller violation of task goals with more attention directed toward the target than intended errors resulting from flanker processing, and should thus result in smaller ERNs and more corrections.

The comparator model (Falkenstein et al. 1991; Gehring et al. 1993; Bernstein et al. 1995) assumes that the ERN responds to the degree of the error-correct mismatch. Our between pairs results confirm this assumption, showing that the ERN grows larger with error-correct dissimilarity. However, in studies designed to test the dissimilarity assumption, the dissimilarity was always symmetrical (Bernstein et al. 1995; Gehring and Fencsik 2001; Arbel and Donchin 2011). Critically, our results show asymmetrical effects in which the ERN grew larger with the prepotency of the error with little or no effect of the correct response. Therefore, there is more to the computation that drives the ERN than a simple detection of error-correct mismatch. Moreover, the comparator model assumes that the ERN reflects the degree of error-correct dissimilarity and predicts that greater ERNs will be accompanied by faster and more corrections (Falkenstein et al. 1991; Gehring et al. 1993; Coles et al. 2001). In the current study, an asymmetric manipulation of the error-correct dissimilarity violated these predictions, revealing greater ERNs accompanied by slower and fewer corrections. These results further indicate that an asymmetrical view of the dissimilarity computation would require amendments to the comparator models of the ERN.

The conflict detection theory (Carter et al. 1998; Yeung et al. 2004) holds that the ERN represents post-error conflict intensity, determined by the amount of simultaneous activation of the error and correct responses. Therefore, the conflict model could account for our asymmetry results by arguing either for greater error-correct temporal overlap or for greater correct response activation when the error response is more prepotent than the correct one. However, both accounts would also require faster error corrections in those conditions of greater conflict, whereas error corrections were in fact slower, ruling out this explanation. Moreover, according to one interpretation of the conflict model, the ERN should grow larger with the portion of the motor program shared between responses (Gehring and Fencsik 2001). In contrast, our data show that the ERN grew larger with the portion of motor program not shared between responses.

A role for the ERN in aborting the erroneous response would suggest that activity at the pMFC is regulative rather than evaluative in nature. However, our data cannot rule out the possibility that whereas the pMFC subregion that produces the ERN (e.g., dACC) plays a regulative function, outcome evaluation activity occurs elsewhere in the pMFC (e.g., Nee et al. 2011).

The idea that the potent effector should correspond to the more prepotent dominant response tendency requires that errors of the potent effector will be faster than errors of the nonpotent effector. In the current study, although this was the general pattern (Fig. 3), the differences were not significant. However, the interpretation of the ERN as a reflection of processing needed to abort the error can explain such findings simply by arguing that prepotent errors involve greater inhibition, which in turn would slow down those errors.

In contrast to the findings of the current study, Gehring et al. (1993) showed that greater ERN amplitudes were associated with greater likelihood of error corrections. However, this analysis included correct trials in which the correct response electromyography (EMG) was followed by an error EMG. In line with our error-aborting account, greater ERN on those trials may have been elicited by the second, erroneous response which was not corrected. Gehring et al. (1993) also showed that emphasizing speed over accuracy reduces the size of the ERN (Falkenstein et al. 1990; Gehring et al. 1993; Falkenstein et al. 1995; Hajcak et al. 2003; Ullsperger and Szymanowski 2004; Ganushchak and Schiller 2008). Also in line with the error-aborting account, emphasizing speed may reduce the need for aborting the fast error, resulting in smaller ERNs.

It has been argued that the ERN is too late to be related to the suppression of the erroneous response (Rodríguez-Fornells et al. 2002). This argument overlooks the fact that programming a correction will require removing erroneous response features from the manual motor processor even after the error response has occurred. Alternatively, selective error inhibition reflected by the ERN may follow the immediate nonspecific attempt to suppress all motor activity: As soon as both responses are slowed down, the selective inhibitory process begins. This suggestion arises from the response-inhibition literature. According to the models of response inhibition, an immediate attempt to stop an ongoing response has global affects over the motor system (Coxon et al. 2007; Aron and Verbruggen 2008; Badry et al. 2009). Thus, any immediate attempt to stop an error would hinder both the error and the corrective response. Subsequent to global inhibition, a selective process begins within which motor features associated with the unwanted response are kept suppressed, whereas motor features associated with the desired response are enhanced (Coxon et al. 2007, 2009). Consistent with such an account, the present study demonstrated that the ERN is proportional to the size of the motor program associated exclusively with the error response, suggesting that the process reflected by the ERN allows the overt activation of the corrective response. Thus, pMFC activity reflected by the ERN may represent selective error inhibition. Interestingly, in accordance with our notion that selective error inhibition is more difficult when the error response is prepotent, Coxon et al. (2007) showed that it is harder to selectively prevent movements of the index than of the middle finger. Moreover, Coxon et al. (2007) showed that the finger that was stopped selectively on a stop trial is slower on the subsequent go trial. In the current study, within the hand pair, post error RTs were longer if the same finger was used on both trials than if a different finger was used on each trial, consistent with an effect of selective inhibition. Coxon et al. (2009) suggested that the neural basis of stopping and going at the same time occurs at the pMFC, upstream from the primary motor cortex, perhaps at the *presupplementary motor area (pre-SMA)*. The pre-SMA is suggested as an additional or perhaps even the sole source of the ERN (Herrmann et al. 2004; Hochman et al. 2009; Gehring et al. 2012).

At first glance, connecting pMFC activity with the immediate attempt to selectively stop an ongoing response does not accord with pMFC activity observed after response completion in feedback paradigms. Such activity in the form of the feedback-related negativity (FRN) is often used to demonstrate effects predicted by error prediction models (e.g., Holroyd and Coles 2002). Although there are good reasons to doubt that the FRN and ERN reflect exactly the same activity (Gehring et al. 2012), it is also possible that immediate error processing may be a specific case engaging a more general pMFC mechanism for the allocation of control that acts whenever there is a need for suppression of one set of representations in favor of another. Facing the unexpected feedback, the pMFC suppresses the expected response outcome set in favor of activating the unexpected one. It is for future studies to test between the error potency and error probability accounts of the FRN.

Recent studies of the temporal relationship between the ERN and error correction are consistent with the selective error suppression account. LRP activity associated with the preparation of the corrective response occurs slightly before or in parallel with the ERN (Rodríguez-Fornells et al. 2002). Moreover, Burle et al. (2008) showed that the ERN appeared in the interval between the error and the error correction, and its peak was higher (and later) when corrections were later. Finally, several studies have suggested that successful error corrections are associated with earlier ERNs than trials on which errors are not corrected (Falkenstein et al. 1996; Fiehler et al. 2005). Thus, the ERN may serve a process aimed to clear out only those incorrect motor features that may interfere with the execution of the correction response. Lesion studies demonstrating impaired ERN and corrective behavior after lesions to the MFC (Swick and Turken 2002; Modirrousta and Fellows 2008) were interpreted to reflect an impaired conflict detection or error prediction. In our view, these impairments may reflect the impaired error-aborting process.

The opposing index finger errors within each movement pair did not differ in rate or RT, suggesting that none was more prepotent than the other. Consequently, as predicted by the error-aborting account, neither the ERN nor the correction rate difference was observed between the 2 responses. Note, however, that within a movement pair, downward errors (the index incorrectly tapped the key it already lay upon) were shorter and involved fewer submovements than sideward errors (the index incorrectly moved up, across, and then tapped the adjacent key). Surprisingly, in contrast to the ERN, the early Pe (FCz, 150 ms post error) was greater for sideward errors than for downward errors. Thus, our results suggest that whereas the process reflected by the ERN is not sensitive to the accurate scaling of movement parameters (i.e., parameters that are not associated with response selection; see also, Krigolson and Holroyd 2007, for a similar idea), the early Pe reacts to fine-grained movement features. The bulk of Pe literature addresses the late Pe which is said to reflect further processing of the error, such as error awareness (Overbeek et al. 2005). However, most recently, Arbel and Donchin (2009) argued that the late centroparietal error positivity is the attention-related, stimulus-locked P300 (P3b). The early frontocentral error positivity on the other hand is more likely to be a distinct ERP component uniquely associated with error processing. This distinction is supported by a recent study, showing an effect of error awareness on late Pe but not on early Pe (Endrass et al. 2007).

In sum, extant models of performance monitoring in the pMFC assume that the error and correct response representations are critical to the computations performed by that structure, but thus far, models have not described those representations. Here, we made an attempt at defining the response representation by its neural infrastructure, namely, the neural representation of the responding effectors. Our design allowed us for the first time to isolate the effect of the error motor representation from that of the correct response. Our data shows that the presumed electrophysiological index of outcome evaluation in the pMFC, the ERN, and subsequent corrective behavior is affected by the representation of the error response rather than by error-correct dissimilarity, error probability or conflict. Although some of our findings can probably be accommodated by extending the existing models of the ERN, it is clear that the space of possible ERN theories remains relatively unexplored. The PTS model points to a new account of the ERN in which it serves automatic error correction by inhibiting that portion of the erroneous motor program that stands in the way of correcting the error.

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## Notes

*Conflict of Interest*: None declared.

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