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Errors are foreshadowed in brain potentials associated with action monitoring in cingulate cortex in humans

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Abstract

Previous studies have reported electrophysiological brain activity that is modulated when subjects commit errors in speeded reaction time tasks. This activity is thought to index an action monitoring system in anterior cingulate cortex that signals the need for performance adjustments to minimize the risk of future errors. Consistent with this view, we report here that performance errors are foreshadowed in a modulation of this brain activity on the immediately preceding trial. We propose that this modulation reflects fluctuations in the efficiency of the action monitoring system, which may occasionally compromise subsequent performance and thus comprise a prelude to performance errors.

Keywords: Anterior cingulate cortex; Action monitoring; Performance errors; Performance adjustment; Monitor lapses; Event-related potential; Error-related negativity; Error-preceding positivity

Adequate adaptive performance in cognitive tasks requires continuous monitoring for the need to adjust performance strategies and executive control [1,12]. Neuroimaging studies and event-related brain potential research have identified the anterior cingulate cortex (ACC) as a critical component of the neural control circuit that implements this action monitoring system [2,7,9]. The ACC is thought to detect preconsciously the activation of erroneous or conflicting responses [8,10,13] and to signal the need to activate adaptive control processes, serving to instigate performance adjustments that minimize the risk of subsequent errors [1,13]. Theoretical positions, although differing somewhat in their emphasis on error detection [3,8] versus conflict detection [1,2], agree on the central role of this mediofrontal action monitoring circuit in the dynamic control of behavior. Here we examine variability in performance monitoring and consequent failures in performance adjustments.

The action monitoring system described above is indexed by electrophysiological brain activity, the error-related negativity (ERN) [6] or error negativity (Ne) [4], which occurs immediately following the response. This negative-polarity event-related brain potential component is substantially larger following errors than following correct trials and is thought to originate in the ACC [2,8,9]. While typically associated with errors, small negative-going brain-potential deflections resembling the ERN are sometimes also present after correct responses [5,7,9,15]. These deflections in the post-response segment of the event-related potential have been taken to signify, within well-defined methodological constraints [3], that the action monitor detects not only response activations associated with overt errors, but also subthreshold incorrect or conflicting response tendencies that do not result in full errors but nonetheless call for fine-grained adjustments in performance [7,9].

We tested the hypothesis that fluctuations in the amplitude of the event-related potential in the ERN time window following correct responses are reflected in subsequent performance. We hypothesized that such trial-

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to-trial fluctuations reflect variations in the efficiency of action monitoring, and hence may be associated with failures to modify the level of executive control required for adequate cognitive processing. These failures may incidentally yield suboptimal task performance and, eventually, errors. To test our hypothesis, we compared the event-related brain potential associated with correct trials preceding response errors with that associated with correct trials preceding correct responses. We predicted that erroneous responses should be preceded, on average, by a distinct pattern of electrophysiological brain activity in the time window typically associated with the ERN.

Seven right-handed males, aged 18–25, served as volunteer subjects and completed a version of the arrow flanker task. They viewed a series of horizontal arrow arrays presented just above a central fixation cross. All stimuli were presented in white against a black background on a computer screen. Congruent arrow arrays were composed of five arrows pointing in the same direction (e.g. → → → → →). In incongruent arrays flankers pointed in the direction opposite to that designated by the central target arrow (e.g. ← ← → ← ←). Each arrow covered 1.0 degrees of visual angle; arrow arrays subtended 6.5 degrees horizontally. The four possible arrow arrays occurred equally often. Subjects were instructed to ignore the arrows on the flanks and to indicate their choice by pressing a button beneath their left index finger in response to a target pointing to the right and vice versa. This incompatible stimulus-response mapping was chosen to ensure that the frequency of error commission for each subject was sufficiently high for the present purposes. The fixation cross was displayed continuously during a block of 100 trials. The arrow arrays were visible for 100 ms. The interval between presentations of the arrays varied randomly between 1500 and 2500 ms. Subjects completed five blocks of trials. Performance feedback was provided by the experimenter at the end of each block. Informed consent was obtained from all subjects prior to the experiment, after the nature and possible consequences of the study were explained to them. The experiment was performed in compliance with relevant laws and institutional guidelines, and was approved by the ethical committee of the Department of Psychology of the University of Amsterdam.

The behavioral data replicated the typical pattern reported for variations in flanker congruity in this task: RTs were longer on incongruent compared to congruent trials ($M = 420$ and 380 ms, $t(6) = 6.26$, $P < 0.001$). Incongruent trials also elicited more errors than congruent trials ($M = 15.6$ and 5.9%, $t(6) = 11.62$, $P < 0.001$). This pattern of performance argues against an interpretation in terms of a speed–accuracy trade-off.

The flanker task was chosen because of its demonstrated success at eliciting ERNs [10,11,13]. Because conflicting response tendencies and errors are elicited more commonly by incongruent than congruent arrays [8,14], our EEG analyses focus on responses to incongruent stimuli. We compared event-related potential waveforms associated with correct response trials that preceded an error trial (*error-preceding* trials) and waveforms associated with correct response trials that preceded a correct trial (*correct-preceding* trials). Consistent with typical findings [12], on incongruent trials, errors were generally faster than correct responses ($M = 365$ and 420 ms, $t(6) = 4.86$, $P < 0.002$) and error-preceding trials were faster than correct-preceding trials ($M = 407$ and 422 ms, $t(6) = 4.45$, $P < 0.002$). To control for the influence of these confounding factors on the waveforms [3], we selected a subset of correct-preceding trials (i) that was equal in number to the set of error-preceding trials, and (ii) whose RTs were matched as closely as possible on a trial-by-trial basis to the RTs of error-preceding trials (incidental deviations of no more than 2 ms were accepted). Mean RTs for the resulting sets of error- and correct-preceding trials were 407 ms (SD 24 ms; each set consisted of 21 trials on average). The RT-matching procedure also minimized the possibility that the two groups of trials differed in terms of response conflict or subthreshold erroneous response activation (trials that elicit more conflict/subliminal error will be associated with slower responses than other trials; matching for RT will thus tend to correct for differences in conflict or subliminal error). In addition, for each subject this procedure yielded numbers of response repetitions and condition repetitions that were approximately equal between error- and correct-preceding trials, thus excluding sequential patterns as a potential factor in explaining differences between event-related potentials associated with error- and correct-preceding trials.

EEG activity was recorded from six electrode sites (Fz/Cz/Pz/Oz/C3′/C4′), referenced to an electrode on the left earlobe. Standard psychophysiological procedures were applied to correct for eye movement artifact, exclude trials containing other types of movement artifact, filter EEG activity (digital low-pass, 15.625 Hz cut-off), and compute response-locked averaged time-series (for details see previously published work [10,13,14]).

Apparent in the waveforms associated with incorrect responses was a distinct ERN that, consistent with typical findings, was largest in amplitude at frontocentral scalp sites proximal to ACC and attained its maximum amplitude shortly after the button press (Fig. 1A). Subsequent analyses focused on the pattern of activity in the event-related potential associated with *correct* responses to incongruent stimuli obtained from the same electrode sites during the same time period following the response as the ERN. The amplitude of these post-response deflections was defined operationally as the mean value (aligned to a baseline from 150 to 50 ms preceding the response) of the segment 0–100 ms following the response at electrode Fz, where these deflections were most pronounced (as was the case for ERN).

Visual examination of the resulting waveforms (Fig. 1B) reveals, in accord with our hypothesis, a pattern of activity in the time period after the response that differs not only

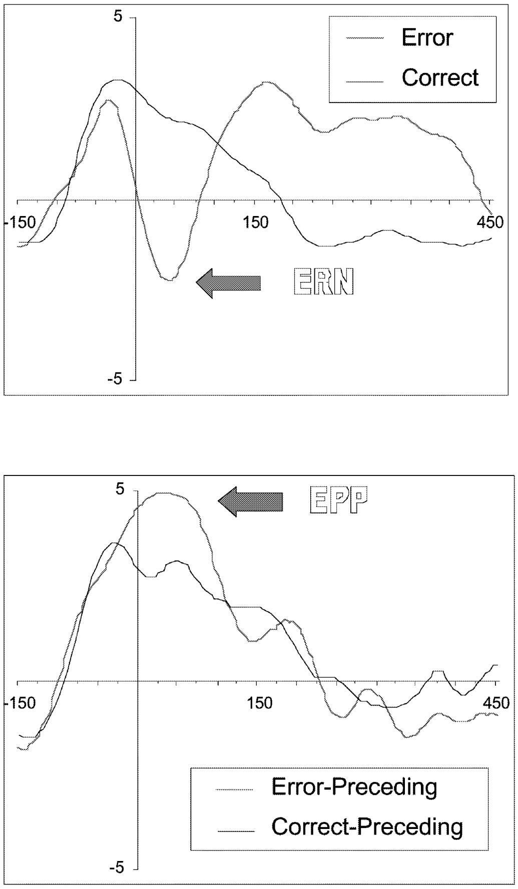

Fig. 1. Response-locked event-related potentials recorded from Fz. (A) Correct responses (thin black line) versus errors (thick gray line). The abscissa reflects the time axis (marked in steps of 50 ms). The ordinate (indicated by the black vertical lines) reflects amplitude (from $+5$ μV on the top to -5 μV on the bottom). The vertical lines are horizontally positioned to indicate the time of the response. Relative to correct responses, erroneous responses are characterized by a negative component identified as the ERN (indicated by the arrow). The ERN is followed by a subsequent positive deflection, typically identified as the error positivity or Pe [10]. (B) Correct-preceding responses (thin black line) versus error-preceding responses (thick gray line). Relative to correct-preceding responses, error-preceding responses are characterized by a positive component identified as the EPP (indicated by the arrow).

from the pattern seen when an error was produced, but also between error-preceding and correct-preceding trials. In contrast to the *negative* deflection evident in the waveform after erroneous responses (Fig. 1A), the waveform observed after correct responses was characterized by a *positive* deflection. Moreover, the mean amplitude of this positive deflection varied with response accuracy on the next trial (Fig. 1B). It was significantly larger when it preceded an erroneous as compared to a correct response (4.62 versus 2.75 μV), as confirmed by a statistical pair-wise comparison ($t(6) = 3.46$, $P = 0.007$, one-tailed). Since these deflections are response-locked, the procedure of matching the error-preceding and correct-preceding trials on RT (on an individual-trial basis) renders it unlikely that the presently observed effect could result from differences in latency jitter. For convenience, we will tentatively use the term *error-preceding positivity* (EPP) to refer to the pattern of activity expressed in the event-related brain potential associated with error-preceding correct responses. EPP appeared to show a frontocentral scalp distribution (the difference between error-preceding and correct-preceding event-related potentials amounted to 1.87, 1.79, and 1.41 μV at Fz, Cz, and Pz, respectively), but this difference failed to obtain statistical significance ($F(2, 6) = 0.27$).

To establish the robustness of this pattern of electrocortical activity, we examined whether (a) EPP is specific to the difference in amplitude of post-response waveform segments between error- and correct-preceding trials (i.e. would not be produced by a comparison between just any two samples of matched responses), and (b) EPP is obtained regardless of whether or not the selection of correct-preceding trials differs in response speed from the total population of correct-preceding trials. This was established by comparing the present subset of correct-preceding trials to (a) two other, independent subsets of RT-matched correct-preceding responses, and (b) the total set of correct-preceding trials. All four selections yielded essentially identical amplitudes of the post-response segments; none of the comparisons approached statistical significance (all $t(6) < 0.8$). Preliminary support for the robustness of our finding is derived from a recent independent replication in an analysis of data collected from 40 subjects in a Stroop-type task (Greg Hajcak, 2003, pers. commun.).

To summarize, errors were observed to be presaged by a distinct pattern of electrophysiological brain activity on the trial preceding the error. The timing, phasic nature, and frontocentral scalp distribution of this brain activity were reminiscent of those of the ERN, an electrophysiological component that is elicited following response errors, and that is thought to index action monitoring by ACC. An interpretation consistent with available evidence is that EPP reflects occasional failures of the action monitoring system to detect subthreshold incorrect or conflicting response tendencies, elicited by ambiguous stimuli, that do not result in full errors but nonetheless call for fine-grained adjustments in performance [7,9]. Failure to implement these performance adjustments may result, eventually, in error. This interpretation suggests that EPP reflects activity originating from ACC during action monitoring; more specifically, we propose that the EPP provides a psychophysiological expression of transient deficiencies in the functioning of the monitor system prior to actual execution of an error.

ACC putatively serves to indicate the need to engage executive control processes (such as response inhibition) to minimize the risk of errors [1]. Our observation of EPP provides suggestive support for the hypothesis that the net result of processing in the action monitoring system is subject to trial-by-trial fluctuations, and that transient deficits in monitoring may be associated with occasional failures to activate adaptive control processes sufficiently to reduce the likelihood of future errors. Importantly, beyond a descriptive account of trial-by-trial behavioral modifications, the notion of monitor lapses depicts the contours of a neural mechanism for dynamic performance adjustment.

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